LEABHARLANN CHOLÁISTE NA TRÍONÓIDE, BAILE ÁTHA CLIATH | TRINITY COLLEGE LIBRARY DUBLIN
Ollscoil Átha Cliath | The University of Dublin

Terms and Conditions of Use of Digitised Theses from Trinity College Library Dublin

Copyright statement

All material supplied by Trinity College Library is protected by copyright (under the Copyright and Related Rights Act, 2000 as amended) and other relevant Intellectual Property Rights. By accessing and using a Digitised Thesis from Trinity College Library you acknowledge that all Intellectual Property Rights in any Works supplied are the sole and exclusive property of the copyright and/or other IPR holder. Specific copyright holders may not be explicitly identified. Use of materials from other sources within a thesis should not be construed as a claim over them.

A non-exclusive, non-transferable licence is hereby granted to those using or reproducing, in whole or in part, the material for valid purposes, providing the copyright owners are acknowledged using the normal conventions. Where specific permission to use material is required, this is identified and such permission must be sought from the copyright holder or agency cited.

Liability statement

By using a Digitised Thesis, I accept that Trinity College Dublin bears no legal responsibility for the accuracy, legality or comprehensiveness of materials contained within the thesis, and that Trinity College Dublin accepts no liability for indirect, consequential, or incidental, damages or losses arising from use of the thesis for whatever reason. Information located in a thesis may be subject to specific use constraints, details of which may not be explicitly described. It is the responsibility of potential and actual users to be aware of such constraints and to abide by them. By making use of material from a digitised thesis, you accept these copyright and disclaimer provisions. Where it is brought to the attention of Trinity College Library that there may be a breach of copyright or other restraint, it is the policy to withdraw or take down access to a thesis while the issue is being resolved.

Access Agreement

By using a Digitised Thesis from Trinity College Library you are bound by the following Terms & Conditions. Please read them carefully.

I have read and I understand the following statement: All material supplied via a Digitised Thesis from Trinity College Library is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of a thesis is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form providing the copyright owners are acknowledged using the normal conventions. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone. This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

Epiphyte diversity in Irish conifer plantations

Linda Coote

TRINITY COLLEGE
LIBRARY DUBLIN

Thesis submitted to the University of Dublin, Trinity College for the degree of Doctor of Philosophy

2007

TRINITY COLLEGE
05 JUL 2007
LIBRARY DUBLIN
THESIS
8081

Declaration

This thesis has not been submitted as an exercise for a degree at this or any other University. This thesis is entirely the candidate's own work. Data collection was undertaken, in part, jointly with others and this is duly acknowledged in the text. The library may lend or copy this thesis upon request.

Linda Coote

.....

Acknowledgements

Many people have helped, supported an encouraged me during the course of my PhD studies. My supervisors Daniel Kelly and Paul Dowding have given me invaluable advice and support throughout. I would particularly like to thank George Smith for his enthusiastic assistance with fieldwork and for all the other valuable help and advice he gave me. For their assistance with fieldwork I would also like to thank Saoirse O'Donoghue, Siobhan McNamee, Deirdre Ninaber, Bastian Egeter and Erika Buscardo. The information on the ground flora at a number of sites was provided by Laura French and collected by Laura, Saoirse O'Donoghue and Anne-Marie McKee and for this I would like to thank them. I would also like to thank the BIOFOREST project manager Susan Iremonger and all the other members of the BIOFOREST research group.

All fieldwork was carried out in Coillte Teoranta plantations and for this I would like to thank them. Many other Coillte staff members have provided me with information and assistance and they are: Bernard Burke Jnr, Ned Dore, Joseph Finn, Larry Kelly, Nicholas Kirwan, Tim O'Regan, Dr David Thompson and Tom Quinn.

I am grateful to Mr. T.H. Blackstock, Dr B. Coppins, Dr H. Fox, Dr D.T. Holyoak, Mr. G.P. Rothero and Mr. R. Porley for assistance with identification of difficult specimens.

I am indebted to the Environmental Protection Agency (EPA) and the National Council for Forest Research and Development (COFORD) who were the funding bodies for this PhD. Finally, I would like to thank my friends and in particular my family for their constant encouragement and support.

Summary

Government policy aims to increase the area under forestry in Ireland from its current 10% to 17% by 2030. Baseline information on the biodiversity of these forestry plantations is required if they are to be effectively managed, particularly in the light of Ireland's commitment to Sustainable Forest Management (SFM). Epiphytes are an important but little studied component of forest biodiversity in Ireland. No previous studies have been undertaken on epiphytes in Irish forestry plantations. This study is therefore innovative and attempts to address this major information gap.

Epiphyte communities (bryophytes, lichens and vascular plants) were studied on mature Sitka spruce (*Picea sitchensis*) and Japanese larch (*Larix kaempferi*) trees in the interior of 28 stands in two geographic clusters centred on counties Wicklow and Cork. The trunk and branches were studied, with the higher parts of the tree being reached by climbing. The contribution made by epiphytes to the total flora of plantations was assessed at five sites. The effects of open spaces on the epiphyte flora of Sitka spruce were also examined by studying trees at the edge of open spaces and in the forest interior at twelve sites. In order to account for differences in the epiphyte diversity of different stands, a large amount of environmental and structural information was collected for each site and each tree. A preliminary investigation of the physical and chemical properties of the bark of Sitka spruce and Japanese larch was also made.

Trees were found to support a reasonably diverse range of bryophytes and lichens, including two relatively rare bryophyte species. More species were recorded in this study than have been reported in British conifer plantations. Nonetheless, Irish plantations were found to be species-poor relative to semi-natural woodland, missing, in particular, cyanolichen and fern species. Two silviculturally over-mature larch stands were found to support elements of the epiphytic flora of pine recorded in native Scottish pinewoods. No differences in diversity were found between Sitka spruce and Japanese larch trees, although larch trees supported more lichen species. Geographic location was found to be important for epiphyte diversity, with trees in the Cork cluster having higher epiphyte diversity than those in the Wicklow cluster. Clear patterns in vertical distribution were identified, with bryophyte richness decreasing and lichen richness increasing from the tree base to the upper zones on the trunks of trees. Larch trees also displayed differences with aspect, with greater lichen richness and cover on the south side of trunks and greater bryophyte cover on the north side at the tree base. Epiphytes, particularly lichen species, were found to contribute a substantial proportion to the total flora of plantations, with bryophyte species also making an important contribution in dense stands with high humidity. Open spaces did not appear to affect overall epiphyte diversity on spruce, with no significant differences in any of the diversity measures between edge and interior trees. Climatic factors appeared to have the most important influence on epiphyte diversity overall, with a positive relationship with total rainfall received and an apparently unimodal relationship

with total incident radiation. However, forest management practices in the form of levels of thinning were also found to be important, with denser stands supporting more bryophytes. However, very dense stands virtually excluded bryophytes.

Contents

Chapter 1 Research context 17

1.1 History of forestry in Ireland 19

1.2 Biodiversity 21

1.3 The BIOFOREST project 22

1.4 Importance of epiphytes 22

1.5 Studying epiphytes 23

1.6 Previous research 26

1.7 Aims and objectives of the study 28

Chapter 2 Research Design 29

2.1 Species selection 31

2.1.1 Sitka spruce 31

2.1.2 Larch 31

2.2 Site selection 33

2.3 Data collection 37

2.3.1 Epiphyte sampling 37

2.3.2 Environmental and structural data sampling 42

2.3.3 Additional data 44

2.4 Species identification 46

2.4.1 Classification of species 47

2.5 Independent and joint research 47

2.6 Additional analyses 48

2.6.1 Comparison of the age, environmental and structural characteristics 48

2.6.2 Stand structural characteristics of the open space sites 52

2.7 Diversity 53

2.7.1 Species richness 53

2.7.2 Equitability indices 53

2.7.3 Diversity indices 55

2.7.4 Beta diversity 56

2.7.5 Choosing diversity measures 56

Chapter 3 Epiphyte diversity of Sitka spruce and Japanese larch 59

3.1 Introduction 61

3.1.1 Diversity of Irish forestry plantations 61

3.1.2 Epiphytes in European forestry plantations 62

3.1.3 Epiphytes of Sitka spruce and Japanese larch in their native ranges 63

3.1.4 Differences in epiphytic vegetation between tree species 64

3.1.5 Vertical distribution of epiphytes 67
3.1.6 Contribution of epiphytes to overall plant diversity 68
3.2 METHODS 70
3.2.1 Measuring diversity and cover 70
3.2.2 Statistical analyses 71
3.2.3 Non-metric multidimensional scaling (NMS) 71
3.2.4 Bark analyses 72
3.3 RESULTS 73
3.3.1 Overall diversity 73
3.3.2 Epiphyte diversity of the forest interior trees 74
3.3.3 Effects of tree species on the epiphyte flora 100
3.3.4 Vertical distribution of epiphytes 117
3.3.5 Distribution of epiphytes on branches 159
3.3.6 Effects of aspect on epiphytes 173
3.3.7 Bark physical and chemical properties 179
3.3.8 Contribution of epiphytes to the overall flora of plantation forests 186
3.4 DISCUSSION 192
3.4.1 Epiphyte diversity 192
3.4.2 Epiphyte composition 196
3.4.3 Vertical distribution 201
3.4.4 Epiphyte plot composition 204
3.4.5 Distribution on branches 208
3.4.6 The effects of aspect 209
3.4.7 Contribution to the overall flora 210
3.4.8 Comparison to other studies 211
3.5 CHAPTER SUMMARY 213
3.5.1 Epiphyte diversity 213
3.5.2 Epiphyte composition 213
3.5.3 Environmental factors 214

Chapter 4 Effects of open spaces on the epiphytes of Sitka spruce 217
4.1 INTRODUCTION 219
4.1.1 Open spaces in forestry plantations 219
4.1.2 Open spaces and epiphytes 220
4.1.3 Microclimate of the forest edge and interior 220
4.2 METHODS 223
4.2.1 Measuring diversity, statistical analysis and ordination 223
4.3 RESULTS 223
4.3.1 Tree Diversity 223

4.3.2 Trunk diversity 226
4.3.3 Branch diversity 236
4.3.4 Comparison of the open space edge and forest interior trees 244
4.3.5 Vertical distribution of epiphytes 249
4.3.6 The effects of aspect on epiphytes 264
4.4 DISCUSSION 274
4.4.1 Epiphyte diversity 274
4.4.2 Epiphyte composition 279
4.4.3 Factors affecting epiphyte diversity and composition 282
4.4.4 Vertical distribution and the effect of open spaces 283
4.4.5 Aspect and the effect of open spaces 284
4.5 CHAPTER SUMMARY 285
4.5.1 Epiphyte diversity 285
4.5.2 Epiphyte composition 286
4.5.3 Environmental factors 286

Chapter 5 Conclusions 289
5.1 INTRODUCTION 291
5.2 AIMS OF THE STUDY 291
5.3 OBJECTIVES OF THE STUDY 292
5.4 PLANTATION MANAGEMENT 294
5.5 CONSTRAINTS ON THE PRESENT STUDY 295
5.6 OPPORTUNITIES FOR FURTHER STUDY 297

REFERENCES 299
APPENDICES 317

Tables

Chapter 2 Research Design

2.1 Study site codes and locations 35
2.2 Summary of the sites, stands and trees studied 36
2.3 Type of open space studied at each site 37
2.4 Independent and joint research 48
2.5 Comparison of age and environmental variables of the stands 49
2.6 Thirty-year climate averages for Dublin and Cork airport 50
2.7 Comparison of the stand structural variables of the stands 52
2.8 Comparison of the stand structural variables of the edge and interior trees 52

Chapter 3 Epiphyte diversity of Sitka spruce and Japanese larch

3.1 New vice-county record species recorded in the study 74
3.2 Total number of epiphyte species recorded on spruce and larch 75
3.3 Total low, intermediate and high affinity epiphyte species richness 75
3.4 Mean epiphyte richness (SR_C) in the Wicklow and Cork clusters 79
3.5 Mean low, intermediate and high affinity epiphyte richness (SR_C) in the Wicklow and Cork clusters 79
3.6 Mean epiphyte diversity ($1/D_M$) in the Wicklow and Cork clusters 79
3.7 Total number of epiphyte species recorded on trunks 82
3.8 Epiphyte species recorded only on the trunks of either spruce or larch 82
3.9 Mean epiphyte beta (β_w) diversity in the Wicklow and Cork clusters 84
3.10 Mean epiphyte richness (SR_{MT}) on trunks in the Wicklow and Cork clusters 84
3.11 Mean epiphyte diversity ($1/D_{MT}$) on trunks in the Wicklow and Cork clusters 87
3.12 Mean epiphyte cover ($Cover_{MT}$) on trunks in the Wicklow and Cork clusters 88
3.13 Total number of epiphyte species recorded on branches 91
3.14 Epiphyte species recorded only on the branches of either spruce or larch 91
3.15 Number of plots studied on living, moribund and dead branches 93
3.16 Mean epiphyte diversity ($1/D_{MB}$) on branches in the Wicklow and Cork clusters 95
3.17 Mean epiphyte cover ($Cover_{MB}$) on branches in the Wicklow and Cork clusters 95
3.18 Epiphyte species recorded only on either Sitka spruce or Japanese larch 105
3.19 Significant indicator species for Sitka spruce and Japanese larch 106
3.20 Correlations between axes of the NMS ordination of trees and certain variables 113
3.21 Diversity and environmental information for the tree cluster analysis groups 114
3.22 Indicator species for the tree cluster analysis groups 115
3.23 Overall epiphyte composition of the trees 122
3.24 Epiphyte species restricted to a single height zone on spruce or larch trunks 126
3.25 Epiphyte species occurring in all height zones on spruce or larch trunks 127

3.26 Epiphyte species occurring in over ten percent of trunk plots on spruce or larch 135
3.27 Correlations between axes of the NMS ordination of trunk plots and certain variables 149
3.28 Indicator species for the trunk plot cluster analysis groups 154
3.29 Diversity and environmental information for trunk plot cluster analysis groups 155
3.30 Epiphyte communities of the trunk plots 158
3.31 Epiphyte species occurring in over ten percent of branch plots on spruce or larch 159
3.32 Percentage of inner, mid and outer branch plots containing epiphytes 161
3.33 Indicator species for the branch plot cluster analysis groups 169
3.34 Diversity and environmental information for branch plot cluster analysis groups 170
3.35 Epiphyte communities of the branch plots 173

Chapter 4 Effects of open spaces on the epiphytes of Sitka spruce

4.1 Total number of epiphyte species recorded on edge and interior trees 223
4.2 Total number of epiphyte species recorded on trunks of edge and interior trees 226
4.3 Total number of epiphyte species recorded on branches of edge and interior trees 236
4.4 Number of plots studied on living, moribund and dead branches 236
4.5 Epiphyte species recorded only on either edge or interior trees 244
4.6 Epiphyte species occurring in over ten percent of trunk plots on edge or interior trees 246
4.7 Correlations between axes of NMS ordination of all trees and certain variables 250
4.8 Correlations between axes of NMS ordination of edge trees and certain variables 255
4.9 Correlations between axes of NMS ordination of trunk plots and certain variables 263

Appendices

1 Epiphyte species recorded in this study 319
2 Trunk plots occurring in the ten cluster analysis groups 323
3 Branch plots occurring in the eight cluster analysis groups 324
4 Environmental variables of the stands studied 319
5 Stand structural variables of the stands studied 320

Figures

Chapter 1 Research context

1.1 Forest cover in the Republic of Ireland 1900-present 20
1.2 Two sampling strategies employed in the study of epiphytes 25

Chapter 2 Research Design

2.1 Tree species composition in Coillte owned plantations in Ireland 32
2.2 Location of the stands where trees were studied 34
2.3 Plot sampling design used to study epiphytes 40
2.4 Procedures followed for determining the proximity to and area of old woodland 45
2.5 Pre-afforestation land use and thinning status of the stands 51
2.6 Concept of species richness and evenness 54

Chapter 3 Epiphyte diversity of Sitka spruce and Japanese larch

3.1 Total epiphyte species accumulation curves for spruce and larch 76
3.2 Epiphyte species richness (SR_C) of all trees studied 77
3.3 Mean epiphyte species richness (SR_C) of spruce and larch 78
3.4 Mean low, intermediate and high affinity epiphyte species richness (SR_C) 78
3.5 Epiphyte diversity ($1/D_M$) of all trees studied 80
3.6 Mean epiphyte diversity ($1/D_M$) of spruce and larch 81
3.7 Relationship between epiphyte diversity ($1/D_M$) and epiphyte richness (SR_C) 81
3.8 Beta (βw) diversity of all trees studied 83
3.9 Mean beta (βw) diversity of spruce and larch 85
3.10 Mean epiphyte species richness (SR_{MT}) on trunks of spruce and larch 85
3.11 Epiphyte species richness (SR_{MT}) on trunks of all trees studied 86
3.12 Epiphyte diversity ($1/D_{MT}$) on trunks of all trees studied 88
3.13 Mean epiphyte diversity ($1/D_{MT}$) on trunks of spruce and larch 89
3.14 Mean epiphyte cover ($Cover_{MT}$) on trunks of spruce and larch 89
3.15 Epiphyte cover ($Cover_{MT}$) on trunks of all trees studied 90
3.16 Relationship between epiphyte diversity ($1/D_{MT}$) and epiphyte richness (SR_{MT}) on trunks 92
3.17 Relationship between beta (βw) diversity and epiphyte richness (SR_{MT}) on trunks 92
3.18 Epiphyte diversity ($1/D_{MB}$) on branches of all trees studied 94
3.19 Mean epiphyte diversity ($1/D_{MB}$) on branches of spruce and larch 96
3.20 Mean epiphyte cover ($Cover_{MB}$) on branches of spruce and larch 96
3.21 Epiphyte cover ($Cover_{MB}$) on branches of all trees studied 97
3.22 Mean diversity of all plots on living and dead or moribund branches 98
3.23 Mean cover of all plots on living and dead or moribund branches 99

3.24 Mean diversity of plots on living and dead or moribund middle branches 101
3.25 Mean cover of plots on living and dead or moribund middle branches 102
3.26 Mean diversity of plots on living and dead or moribund upper branches 103
3.27 Mean cover of plots on living and dead or moribund upper branches 104
3.28 NMS ordination of the spruce and larch trees 107
3.29 Cluster dendrogram of the spruce and larch trees 108
3.30 Graphs used to assess the appropriate number of tree cluster analysis groupings 109
3.31 Relationship between estimated rainfall and epiphyte species richness (SR_C) 111
3.32 Relationship between elevation and bryophyte richness (SR_C) 112
3.33 Relationship between elevation and lichen richness for Cork cluster spruce trees 112
3.34 Total number of species recorded in the four height zones on spruce and larch 123
3.35 Proportions of the four bryophyte growth forms in the four height zones 124
3.36 Proportions of the four lichen growth forms in the four height zones 125
3.37 Mean epiphyte richness in trunk plots in the four height zones 128
3.38 Mean epiphyte richness of the four bryophyte growth forms in the four height zones 129
3.39 Mean epiphyte richness of the four lichen growth forms in the four height zones 130
3.40 Mean low, intermediate and high affinity epiphyte species richness in the four height zones 132
3.41 Mean diversity in trunk plots in the four height zones 133
3.42 Mean cover in the trunk plots in the four height zones 134
3.43 Mean cover of the four bryophyte growth forms in the four height zones 136
3.44 Mean cover of the four lichen growth forms in the four height zones 137
3.45 Mean cover and frequency of *Hypnum jutlandicum* in the four height zones 138
3.46 Mean cover and frequency of *Metzgeria temperata* in the four height zones 140
3.47 Mean cover and frequency of *Dimerella lutea* in the four height zones 141
3.48 Mean cover and frequency of *Microlejeunea ulicina* in the four height zones 142
3.49 Mean cover and frequency of *Lepraria incana* in the four height zones 143
3.50 Mean cover and frequency of *Lophocolea bidentata* in the four height zones 144
3.51 Mean cover and frequency of *Hypotrachyna revoluta* in the four height zones 146
3.52 NMS ordination of the trunk plots with height zones indicated 147
3.53 NMS ordination of the trunk plots with tree cluster analysis groups indicated 148
3.54 Relationship between plot height and epiphyte richness in the trunk plots 150
3.55 Graphs used to assess the appropriate number of trunk plot cluster analysis groups 151
3.56 Cluster dendrogram of the trunk plots 152
3.57 NMS ordination of the trunk plots with trunk plot cluster analysis groups indicated 153
3.58 Mean diversity in the plots on the middle and upper branches 160
3.59 Mean cover in the plots on the middle and upper branches 162
3.60 Mean diversity in the inner, mid and outer branch plots on the middle branches 163

3.61 Mean diversity in the inner, mid and outer branch plots on the upper branches 164
3.62 Mean cover of epiphytes in the inner, mid and outer branch plots 166
3.63 Cluster dendrogram of the branch plots 167
3.65 Mean epiphyte richness on the north and south side of the trunk 174
3.66 Mean epiphyte diversity on the north and south side of the trunk 175
3.67 Mean epiphyte cover on the north and south side of the trunk 176
3.68 Mean epiphyte richness on the north and south side of the trunk in the four height zones . 177
3.69 Mean epiphyte diversity on the north and south side of the trunk of spruce in the four height zones 178
3.70 Mean epiphyte diversity on the north and south side of the trunk of larch in the four height zones 180
3.71 Mean cover on the north and south side of the trunk in the four height zones 181
3.72 Mean diversity in the branch plots on the north and south sides of the trees 183
3.73 Mean cover in the branch plots on the north and south sides of the trees 183
3.74 Mean diversity on middle and upper branches on the north and south sides of the trees 184
3.75 Mean cover on middle and upper branches on the north and south sides of trees 185
3.76 Median bark pH of spruce and larch 187
3.77 Median bark pH of the pairs of spruce and larch trees 187
3.78 Median bark pH of spruce and larch in the four height zones 188
3.79 Relationship between bark pH and epiphyte species richness 189
3.80 Mean water absorption capacity of spruce and larch 190
3.81 Mean water absorption capacity of the pairs of spruce and larch trees 190
3.82 Mean water absorption capacity of spruce and larch in the four height zones 191
3.83 Contribution of epiphytes to the total flora 193

Chapter 4 Effects of open spaces on the epiphytes of Sitka spruce

4.1 Cumulative species curve for the trees studied 224
4.2 Epiphyte richness (SR_C) of all trees studied 224
4.3 Mean epiphyte richness (SR_C) of edge and interior trees 227
4.4 Mean low, intermediate and high affinity epiphyte species richness on edge and interior trees 227
4.5 Epiphyte diversity ($1/D_M$) of all trees studied 228
4.6 Mean epiphyte diversity ($1/D_M$) of edge and interior trees 228
4.7 Relationship between epiphyte diversity ($1/D_M$) and epiphyte richness (SR_C) 229
4.8 Beta (β_w) diversity of all trees studied 231
4.9 Mean beta (β_w) diversity of edge and interior trees 231
4.10 Epiphyte richness (SR_{MT}) on trunks of all trees studied 232
4.11 Mean epiphyte richness (SR_{MT}) on trunks of edge and interior trees 232

4.12 Epiphyte diversity ($1/D_{MT}$) on trunks of all trees studied 233
4.13 Mean epiphyte diversity ($1/D_{MT}$) on trunks of edge and interior trees 233
4.14 Epiphyte cover ($Cover_{MT}$) on trunks of all trees studied 234
4.15 Mean epiphyte cover ($Cover_{MT}$) on trunks of edge and interior trees 234
4.16 Relationship between epiphyte cover ($Cover_{MT}$) and epiphyte richness (SR_{MT}) on trunks . 237
4.17 Diversity ($1/D_{MB}$) on branches of all trees studied 239
4.18 Mean epiphyte diversity ($1/D_{MB}$) on branches of edge and interior trees 239
4.19 Epiphyte cover ($Cover_{MB}$) on branches of all trees studied 240
4.20 Mean epiphyte cover ($Cover_{MB}$) on branches of edge and interior trees 240
4.21 Mean diversity in plots on living and dead or moribund branches 241
4.22 Mean cover in plots on living and dead or moribund branches 242
4.23 Mean diversity of plots on living and dead or moribund middle branches 243
4.24 Mean cover of plots on living and dead or moribund middle branches 245
4.25 NMS ordination of the edge and interior trees 247
4.26 Relationship between tree density and epiphyte richness (SR_C) 250
4.27 Relationship between total incident radiation and epiphyte richness (SR_C) 251
4.28 NMS ordination of the edge trees 252
4.29 Relationship between (a) canopy openness and (b) total radiation transmitted and epiphyte cover ($Cover_{MT}$) in trunk plots 253
4.30 Total number of species recorded in the four height zones 254
4.31 Proportions of the four bryophyte growth forms in the four height zones 256
4.32 Proportions of the four lichen growth forms in the four height zones 257
4.33 Mean epiphyte richness in trunk plots in the four height zones 258
4.34 Mean epiphyte diversity in trunk plots in the four height zones 260
4.35 Mean epiphyte cover in trunk plots in the four height zones 261
4.36 NMS ordination of the trunk plots 262
4.37 Mean epiphyte richness on north and south sides of trunks 265
4.38 Mean epiphyte diversity on north and south sides of trunks 266
4.39 Mean epiphyte cover on north and south sides of trunks 268
4.40 Mean epiphyte richness on north and south sides of trunks in the four height zones 269
4.41 Mean epiphyte diversity on north and south sides of trunks of the edge trees in the four height zones 270
4.42 Mean epiphyte diversity on north and south sides of trunks of the interior trees in the four height zones 271
4.43 Mean epiphyte cover on north and south sides of trunk in the four height zones 272
4.44 Mean diversity on the branches on north and south sides of the trees 273
4.45 Mean cover on the branches on north and south sides of the trees 275
4.46 Mean diversity on the middle and upper branches on north and south sides of trees 276

4.47 Mean cover on middle and upper branches on north and south sides of trees 277

Photographs

Chapter 2 Research Design

2.1 Ballinastoe (STOE), Co. Wicklow (GR O180 084) 38
2.2 Tree climbing method used 41

Chapter 3 Epiphyte diversity of Sitka spruce and Japanese larch

3.1 Ballinagappoge (GAPP), Co. Wicklow (GR T081 843) 118
3.2 Trunk plots from Fuhiry (FURY), Co. Cork (GR W144 734) 119
3.3 Barnamuinga (MUIN), Co. Wicklow (GR S962 696) 120
3.4 Athdown (ATHN), Co. Wicklow (GR O076 158) 120
3.5 Curtlestown (CURT), Co. Wicklow (GR O181 172) 121

Chapter 4 Effects of open spaces on the epiphytes of Sitka spruce

4.1 Glade at Athdown (ATHN), Co. Wicklow (GR O076 158) 225
4.2 Road at Mucklagh One (MUCK), Co, Wicklow (GR T083 864) 235

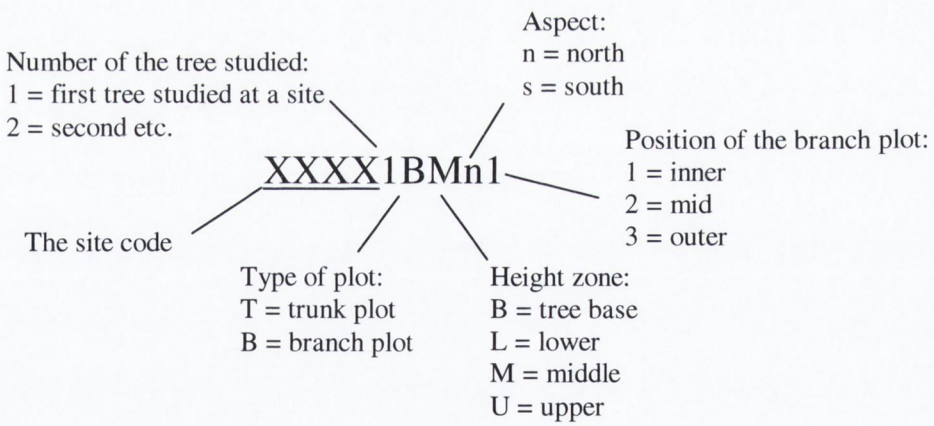
Where not otherwise indicated, photographs were taken by the author.

Abbreviations

In **Chapter 3** and **Chapter 4** the following abbreviations are used when analysing the diversity and cover of the epiphyte flora:

SR_C	The overall species richness derived from the data from all plots on a tree.
SR_{MT}	The mean species richness of all eight trunk plots on an individual tree.
$1/D_M$	The mean Simpson's reciprocal diversity of all trunk and branch plots on an individual tree.
$1/D_{MT}$	The mean Simpson's reciprocal diversity of all eight trunk plots on an individual tree.
$1/D_{MB}$	The mean Simpson's reciprocal diversity of the six to twelve branch plots on an individual tree.
$Cover_{MT}$	The mean percentage cover of all eight trunk plots on an individual tree.
$Cover_{MB}$	The mean percentage cover of the six to twelve branch plots on an individual tree calculated using the percentage cover of epiphytes converted to a percentage of the cover of branches within each plot.

Each plot studied is identified by a unique alphanumeric code as follows:



Chapter 1 Research context

1.1 HISTORY OF FORESTRY IN IRELAND

Ireland is one of the least wooded countries in Europe (EPA, 2004) despite the fact that broadleaved woodland would be the prevailing natural vegetation (Cross, 1998). Around 8000 B.P. mixed deciduous woodland covered approximately 80% of the land surface (Mitchell, 1995). The midlands were dominated by elm (*Ulmus*) and hazel (*Corylus*), the more acid soils of the south and northeast by oak (*Quercus*), and the more exposed acid soils of the west by pine (*Pinus*). This situation continued until the clearance of woodland for agriculture began with the arrival of the first farmers in the Neolithic (6000 B.P.). This marked the beginning of the decline in woodland cover (O'Connell, 1990) and a reduction in woodland species diversity (Bradshaw & Hannon, 1988). Around 5100 B.P. pollen records indicate a dramatic decline in elm, possibly as the result of a pathogenic agent (Mitchell & Ryan, 1997). Neolithic farmers continued to arrive and clear woodland, leading to its replacement with grassland and heathland. Around 100AD Ireland's main conifer, Scots pine (*Pinus sylvestris*), is believed to have died out. This may have been as a result of woodland clearance or of the change to a cooler wetter climate which favoured the development of blanket bogs (Mitchell & Ryan, 1997). By the Middle Ages very little original woodland remained in Ireland (Cross, 1987). Forest cover continued to fall steadily, covering no more than 3% of the country by 1650 (Rackham, 2005). By the beginning of the twentieth century, forest cover had dropped to 1% (EPA, 2004), although some sources put this figure as low as 0.5% (Fitzpatrick, 1966). Only an estimated 0.1% of the land surface is believed to have been covered by ancient woodland (sites with continuous woodland cover since 1600 (Peterken, 1981)) (McEvoy, 1944).

Forest cover in the Republic of Ireland now stands at 10% of the land area (Forest Service, 2003) (**Figure 1.1**). However, the country remains one of the least forested in the EU. The recent increase in forest cover began with the birth of state forestry in 1904 (O Carroll, 2004), but it was not until the 1920s that any substantial increase in forest cover was seen. A target of 400,000ha of afforestation was set in 1948 due to timber shortages during the World Wars, but this target was not achieved until 1991 (O Carroll, 2004). Government policy now aims to increase forest cover in the Republic of Ireland to 17% of the land area by 2030 with an annual afforestation target of 20,000ha per year (Forest Service, 1996). Forest policy has favoured the planting of fast growing conifers, often in monocultures, so that currently 79% of Irish forests consist of coniferous species, with over 50% being Sitka spruce (*Picea sitchensis*) plantations (EPA, 2004). These new plantations bear little resemblance to the native woodlands of 8000B.P. The introduction of a grant in 1997 for the planting of 20% diverse species and the compulsory 10% broadleaf planting requirement has essentially ended the practice of monoculture (DAFRD, 2000), however, conifers will still be predominant in plantation forests for the foreseeable future (Forest Service, 1996).

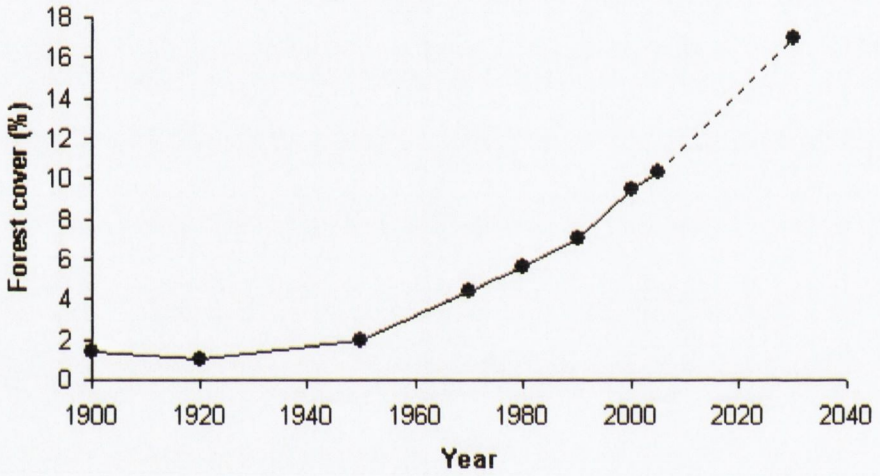


Figure 1.1 Forest cover in the Republic of Ireland 1900-present (Forest Service, 2003), including the target 17% afforestation (dashed line).

1.2 BIODIVERSITY

At the 1992 Earth Summit in Rio de Janeiro, the Convention on Biological Diversity (CBD) was adopted. Three main goals were established:

1. Conservation of biodiversity
2. Sustainable use of its components
3. Fair and equitable sharing of the benefits from genetic resources

The CBD defines biodiversity as - "The variability among living organisms from all sources...and the ecological complexes of which they are a part, this includes diversity within species, between species and of ecosystems" (UNEP, 1992). This considers biodiversity at three levels: genetic, species and ecosystem. Biodiversity assessments usually focus on only one of these levels.

Following on from the Earth Summit, the concept of Sustainable Forest Management (SFM) was developed. The aim of SFM is to ensure that forests are managed in accordance with best forest practices under relevant legislation and regulations. It can be defined as: "The stewardship and use of forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now and in the future, relevant ecological, economic and social functions, at local, national and global levels, and that does not cause damage to other ecosystems" (Anon., 1995). Thirty-nine countries, including the EU member states, have signed up to the principles of SFM. Ireland has implemented SFM through the production of guidelines and regulations from the Forest Service of the Department of Communications, Marine and Natural Resources, including the *Irish National Forest Standard* (Forest Service, 2000c), *Code of Best Forest Practice* (Forest Service, 2000a) and the series of *Forestry Guidelines* (Forest Service, 2000b). Certification was also introduced in the early 1990s as a method of verifying that SFM is being practiced, and Coillte's forests were formally certified in 2001 (Coillte Teoranta, 2002).

Biodiversity is important to us because of the values we derive from it. These values are often divided into direct- and indirect-use values. Direct-use values include such things as food, medicine, biological control, industrial materials, recreational harvesting (hunting, fishing, plant and animal collecting etc.) and ecotourism (Gaston & Spicer, 1998). We also depend on biodiversity for a range of indirect-use values or 'ecosystem services' (Hale & Edwards, 2002). These services include atmospheric, climatic and hydrological regulation, nutrient cycling, pest control, pollination and soil formation and maintenance. In addition to these direct- and indirect-use values associated with biodiversity other authors also consider associated 'non-use' values. These include eudaemonic values, i.e. values related to the "well-being of human soul" (e.g. aesthetic, emotional and religious values) and moral values, related to man's moral obligation to other beings (Wiegleb, 2002).

The question of the potential value of biodiversity for the sustainability of intensively managed forests is an important one in the current climate of SFM. The importance of biodiversity for ecosystem functioning is also a well-recognised and important issue in ecology (Gaston & Spicer, 1998). It is known that a certain composition of organisms is required to sustain ecosystem function and that this composition will vary with changes in environmental conditions (Folke *et al.*, 1996). A decrease in biodiversity may eliminate certain ecosystem interactions and affect the ecosystem processes which support the stability of the system i.e. its ability to resist or recover from perturbations (Moore & Allen, 1999). The typical uniform forest structure of plantation forests may support fewer species than natural forests and so decrease their stability. Some studies have also suggested that ecosystem productivity increases with increased diversity (Naeem *et al.*, 1994; Tilman *et al.*, 1996) and enhancing productivity of the crop species is the main objective of intensive timber management (Moore & Allen, 1999). However, Cameron (2002) suggests that this hypothesis has not been accurately tested.

1.3 THE BIOFOREST PROJECT

In Ireland, before 2001, there were virtually no existing data on forest plantation biodiversity. This information is vital for the implementation of SFM, particularly in the light of the plan to plant 20,000ha of forest every year up to 2030 (Forest Service, 1996). For this reason the BIOFOREST project was established. BIOFOREST is a large-scale project running from 2001 to 2006 with the aim of addressing some of the gaps that existed in the information on biodiversity in Irish plantation forests. The project was funded from the National Development Plan funds through the Environmental Protection Agency (EPA) and the National Council for Forest Research and Development (COFORD). The project was structured as three smaller projects, each addressing a separate aspect of forest biodiversity. These are:

- Project 3.1.1 Biodiversity assessment of afforestation sites
- Project 3.1.2 Assessment of biodiversity at different stages of the forest cycle
- Project 3.1.3 Investigation of experimental methods to enhance biodiversity in plantation forests.

This research on epiphytes was a component part of the BIOFOREST project and of project 3.1.3 in particular.

1.4 IMPORTANCE OF EPIPHYTES

An epiphyte is an organism living on a plant, or in the dead outer tissues of a plant, without drawing water or food from its living tissues (Barkman, 1958). Epiphytes can be found in every major group of the plant kingdom, but in Ireland the main types of epiphytes are mosses, liverworts and lichens. The sensitivity of epiphytes to environmental conditions makes them important indicators of changes in climate, forest structure and ecosystem health (Gradstein *et al.*, 1996).

Their complete dependence on woody plants makes them particularly sensitive to forest management practices. The value of epiphytes as biological indicators of pollution is also well known (Richardson, 1987). Lichens are particularly sensitive to sulphur dioxide pollution and also accumulate metals (Richardson, 1987). Epiphytes also play an important hydrological role by trapping water (Jarvis, 1999), part of which is retained, part re-evaporates and part slowly drops or flows to the ground (Pócs, 1982). Epiphytes are also important in nutrient cycling since they have access to nutrient sources which originate outside the ecosystem and transfer nutrients to other members of the forest (Nadkarni, 1994). They provide food shelter and nest material for forest invertebrates and vertebrates (Gerson & Seaward, 1977; Richardson & Young, 1977) and are particularly important for birds (Nadkarni & Matelson, 1989). Petterson *et al.* (1995) found that the number and biomass of invertebrates was related to the abundance of lichens, with particular implications for foraging birds. Epiphytes, particularly lichens, have also been used for centuries by man as dyes, perfumes and medicines and have been recognised as containing many pharmaceutically relevant metabolites (Muller, 2001).

Epiphytes have been found to form a major component of the diversity of tropical forests (Gentry & Dodson, 1987) and of the total botanical diversity of semi-natural woodland in Ireland (Kelly, 2000). Epiphytes, particularly non-vascular epiphytes (e.g. bryophytes and lichens) are known to be decreasing because of habitat destruction, forest operations and air pollution (Mitchell *et al.*, 2002). However, non-vascular epiphytes have been the focus of comparatively little research (Rhoades, 1995). Most work on canopy epiphytes has been carried out in tropical forests (Burns & Dawson, 2005) and comparatively less is known about temperate forests. In the tropics, proportionally more biodiversity work is being done, while in temperate regions the main focus of canopy research is on canopy atmosphere fluxes (Barker & Pinard, 2001).

1.5 STUDYING EPIPHYTES

The main reason for the lack of research on epiphytes is the difficulty faced by those who wish to study them. The two main problems are: 1) the difficulty of gaining access to the tree canopy and 2) the difficulty of sampling the structurally diverse environments found there (Rhoades, 1995). The difficulty of access has meant that many studies have been limited to trunk surfaces below 2m, or have depended on analysis of litterfall. For those studies that do sample the higher parts of the tree, the most common methods of access used currently are ground-based and rope techniques or a combination of the two. Towers/walkways, ladders, cranes and scaffolding are also commonly used (Barker & Pinard, 2001). Some researchers have used climbing spurs (e.g. Rhoades, 1981), but the damage they cause to trees is a major disadvantage (Houle *et al.*, 2004). Other researchers have taken advantage of treefalls (Eversman *et al.*, 1987; Hale, 1952; Kelly *et al.*, 2004) or have felled trees for study (Fox *et al.*, 2001; Hale, 1965; Liu *et al.*, 2000; McCune, 1993; Pentecost, 1998).

One of the problems acknowledged by researchers is the difficulty of obtaining a sufficient number of replicates when a fixed sampling point is used. However, the rope access method has been reported to have only some or no effect on obtaining adequate replication (Barker & Pinard, 2001). Independent sampling can be increased by climbing a number of trees and, in this case, achieving replication is only limited by the researcher's time and energy (Barker & Pinard, 2001). The main determinant of the method of access used, however, is usually cost. Rope access is a relatively inexpensive technique, while more high-tech methods, although less time demanding, have higher costs and also tend to be less versatile (Barker & Pinard, 2001).

In a forest, each phorophyte and each part of the canopy can support a different set of epiphytes (Rhoades, 1995). In selecting which trees to study, most researchers admit to some degree of bias, since trees must either be of a suitable size and architecture to climb safely or occur next to a walkway, below a crane etc. (Mitchell *et al.*, 2002). Complete inventories of epiphyte diversity on large numbers of trees are generally not logistically possible (Burns & Dawson, 2005). Instead, a series of plots can be investigated (Gradstein *et al.*, 1996). Some studies have employed a sampling strategy which divides the tree into different vertical zones in which plots are then sampled (**Figure 1.2a & b**). The subdivisions of Johansson (1974) (**Figure 1.2a**), or modified versions of this method, are applicable to many broadleaved trees, but are not suited to the study of many coniferous species which are structurally different. Lyons *et al.* (2000), when studying western hemlock (*Tsuga heterophylla*), divided the crown into three equal 'crown zones' from which branches were sampled (**Figure 1.2b**). The tree base and branch free lower bole were not studied however.

As previously mentioned, many studies of epiphytes have been limited to trunk surfaces below 2m (Rhoades, 1995). This trunk-based sampling is particularly amenable to the use of standard plots. Bates (1982) suggests a size of 15cm x 15cm for epiphytic bryophytes but a range of plot sizes from 10cm x 10cm (e.g. Franks & Bergstrom, 2000; Trynoski & Glime, 1982) to 20cm x 50cm (e.g. Kuusinen, 1996a) have been used. This standard plot method is particularly appropriate if different aspects are being recorded separately (Bates, 1982). A cylindrat method, involving wrapping a tape around the trunk at a certain height or heights and recording the presence of epiphytes at marked intervals on the tape, is also suggested (Bates, 1982). This method has been used to monitor epiphytes for the Irish Ecological Monitoring Network (Little *et al.*, 2001). Another method used is random sampling with a pin quadrat (Harris, 1971; Kershaw, 1964). This is particularly useful when the upper zones of the tree are being examined, as the basic size of quadrat used for sampling is often too large (Kershaw, 1964). Branches pose particular problems in sampling and, for practical reasons, few studies of epiphytes have quantitatively sampled branch communities (McCune, 1990). The two main problems associated with sampling branches are: 1)

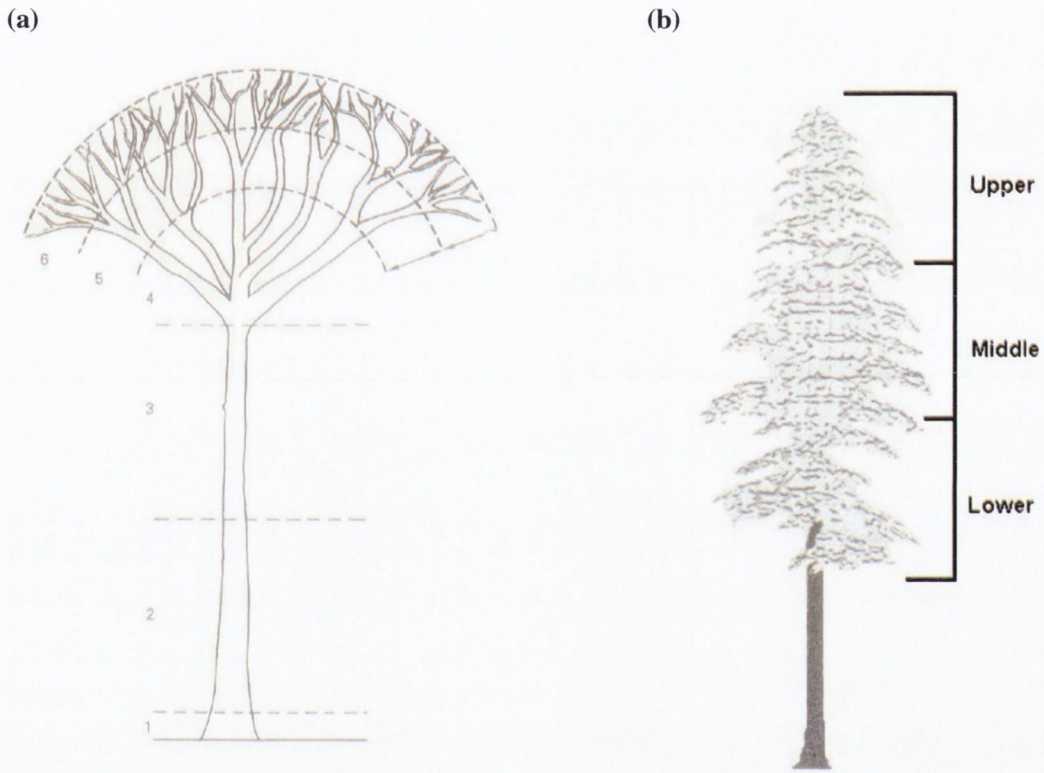


Figure 1.2 Two sampling strategies employed in the study of epiphytes. (a) Subdivision of the tree into six vertical zones after Johansson (1974) (Cornelissen & ter Steege, 1989) and (b) division of the crown into three equal crown zones from which branches are sampled (Lyons *et al.*, 2000).

the selection of branches to be a representative sample of the canopy and 2) the evaluation of the abundance of epiphytes on those branches. A rectangular plot shape can be used to sample small branches (Gradstein *et al.*, 1996). Kelly *et al.* (2004) used a standard plot length (25cm for non-vascular epiphytes) and varied the width of the plot up to a maximum value of 25cm where the diameter of the branch permitted. McCune *et al.* (1997) used a standard quadrat size, holding the frame vertically and looking through it like a window. This 'window' method, however, can underestimate the cover of lichens which grow close to the branch due to their being obscured by foliage (Lyons *et al.*, 2000). Lyons *et al.* (2000) also used a standard quadrat size but placed a quadrat frame horizontally on top of branches. Relative percent cover was calculated based on the percent of foliage and twigs in the quadrat and the percent cover of epiphytes. Ellyson & Sillett (2003) used a combination of methods when studying Sitka spruce branches. A spiral transect, with a tape marked at π-cm intervals wrapped five times around 0.5m segments was used on branch axes (>5cm diameter), while a standard 50 x 50cm quadrat was used for branchlets (<5cm diameter). An additional problem posed when studying branches is the fact that the outer portions of the canopy cannot always be reached by climbing. In this case, branches can be studied by cutting and lowering them to the ground with ropes (Cornelissen & ter Steege, 1989; Wolf, 1993). This allows all parts of the branch to be studied. Lyons *et al.* (2000) divided branches into inner, middle and outer zones and studied a plot in each zone.

1.6 PREVIOUS RESEARCH

As mentioned above, canopy cryptogams have been the focus of little research (Rhoades, 1995) and most work has been carried out in tropical forests (Burns & Dawson, 2005). Comprehensive studies of tropical forest cryptogams over the entire height of trees have been carried out by Pentecost (1998) in Uganda, Gradstein *et al.* (2001) and Holz *et al.* (2002) in Costa Rica, Gradstein (1995) in the Andes (Peru, Colombia and the Guianas), Wolf (1993) in Colombia, Kelly *et al.* (2004) in Venezuela, Cornelissen & ter Steege (1989) in Guyana and Aceby *et al.* (2003) in Bolivia. The majority of comprehensive studies outside the tropics have been carried out in the United States, particularly in Washington and Oregon (e.g. Lyons *et al.*, 2000; McCune, 1993; McCune *et al.*, 1997; McCune *et al.*, 2000; Pike *et al.*, 1977; Rhoades, 1981; Sillett, 1995; 2000). Trees in California (Ellyson & Sillett, 2003), Wyoming (Eversman *et al.*, 1987), Wisconsin (Hale, 1952), Connecticut (Hale, 1965) and New Hampshire (Lang *et al.*, 1980) have also been studied. In Europe, an overview of cryptogamic epiphyte communities has been presented by Barkman (1958) but a limited number of whole tree studies have been carried out, namely in Finland (Liu *et al.*, 2000), Great Britain (Harris, 1971; Kershaw, 1964) and on a single felled oak in Ireland (Fox *et al.*, 2001).

There is little published work on epiphytes in Ireland. A large proportion of the Irish publications relate to the study of lichens as indicators of pollution (cf. Richardson, 1987). Of the existing studies, the majority concentrate on the tree bases and lower trunk only or on a particular epiphyte group. Richards (1938) described the bryophyte communities of Derrycunihy oakwood in Killarney on seven habitats including tree bases, tree trunks and tree branches. Inspired by Richards' work, Phillips (1959) described the bryophyte communities at breast height (4.5ft, 1.37m) on 91 trees of various species in 15 woods in the south of the country. Mitchell (1964) listed the lichens found on *Arbutus unedo* around Killarney and Dickinson & Thorp (1968) examined the lichens of an open scrub hazel community and a sheltered hazel woodland in the Burren. Folan & Mitchell (1970) listed the lichens and lichen parasites of Derryclare Wood, Co. Galway and Kelly (1975) studied epiphytes in the Killarney oak and yew woods between 0.5m and 14m height on tree trunks. McCarthy (1980) studied the lichens in a dense alder carr near Cork and Kirby & O'Connell (1982) listed the epiphytes occurring up to 2m in Shannawoneen wood, Co. Galway. McCarthy *et al.* (1986) studied the lichens of *Calluna vulgaris* at 23 locations in the east, midlands and west of Ireland. Fox *et al.* (2001) studied the epiphytes at 1.2m on 21 oak trees in Brackloon wood, Co. Mayo, as well as the lichens of the entire surface of a felled oak tree in the same wood. However, all these studies relate to semi-natural woodland and scrub which is, compared to forestry plantations, a minority habitat in Ireland.

There is currently no published information on epiphytes in Irish forestry plantations, with the exception of a description of pendulous *Hypnum jutlandicum* growing on lodgepole pine (*Pinus contorta*) in a plantation in the west of Ireland (Doyle, 1987). Any study of forest plant diversity which excludes epiphytes runs the risk of overlooking what could be a significant component of the flora, particularly considering the often poor diversity of the ground flora in closed canopy plantations (French, 2005; Smith *et al.*, 2005). There has also been little published work on the epiphytes of forestry plantations in the United Kingdom, or in the rest of Europe. Watson (1936) listed the bryophytes and lichens of British woods, including coniferous woods. Martin (1938) studied the epiphytic moss flora of 18 coniferous trees in Argyll, although the species of these trees are not given. Bates *et al.* (1997) studied epiphytic bryophytes in a transect across southern Britain, which included areas of coniferous plantations. Bates *et al.* (1996) recorded the abundance of three lichens on young conifers, including Sitka spruce, growing under different SO_2 and O_3 regimes in south-eastern England. More recently, in their comparison of the diversity of spruce and pine plantations with semi-natural pine and oak woods in Britain, Humphrey *et al.* (2002) recorded the bryophytes and lichens occurring on mature trees up to 2m. Vanderpoorten *et al.* (2004) examined the diversity of obligate epiphytic bryophytes in the Semois river basin (Belgium and France), which contains large areas of Norway spruce (*Picea abies)* plantations. The largest volume of research in Europe comes from the managed forests of mainly native species in Norway, Sweden and Finland (e.g. Dettki & Esseen, 1998; Esseen *et al.*, 1996; Halonen *et al.*, 1991; Hazell *et al.*,

1998; Hilmo, 2002; Hyvarinen *et al.*, 1992; Uliczka & Angelstam, 1999) which differ from the even aged intensively managed plantations of non-native species in Britain and Ireland.

1.7 AIMS AND OBJECTIVES OF THE STUDY

Since there is no known previous work on the epiphytes of Irish forestry plantations, the main aim of this work was to characterise, quantitatively and qualitatively, the diversity of the epiphytic flora of these plantations and to determine whether these plantations provide an alternative habitat for native woodland epiphyte species. The following objectives will also be addressed:

- To examine differences in the epiphyte diversity of stands of different tree species.
- To assess the contribution made by epiphytes to overall plant diversity in these plantations.
- To assess the effect of open spaces within forestry plantations on epiphyte diversity.

Chapter 2 Research Design

2.1 SPECIES SELECTION

In order for the research to be most useful and informative it was important that the tree species selected for study were representative of current and future trends in planting. As previously stated, Sitka spruce makes up over 50% of the forest estate (EPA, 2004) and 66% of Coillte owned forests (Coillte Teoranta, 2005) (**Figure 2.1**). It is likely that plantations of this species will still account for at least 60% of the forest cover in Ireland up to 2030 (Forest Service, 1996). For this reason Sitka spruce was selected as the main species for study.

In order to offer a comparison with Sitka spruce a second tree species was selected for study. Comparison with a broadleaved species was judged to be of limited value because of the multiplicity of differences in growth form and habit, and the limited area of established broadleaved plantations. As a deciduous conifer, larch (*Larix* spp.) provides an interesting contrast to its evergreen counterparts. Larch is also one of the more frequently planted tree species in Ireland today. Planting of larch peaked in 2002 when it reached 15% of annual afforestation (D. Thompson, pers. comm.)

2.1.1 Sitka spruce

Sitka spruce (*Picea sitchensis*) is a native of northwestern North America, growing in a narrow strip along the north Pacific coast from south central Alaska to northern California (Harris, 1990). The first record of Sitka spruce being planted in Ireland is from the 1830s when specimen trees were planted on estates (Joyce & O Carroll, 2002). From the beginning of publicly funded afforestation in 1904 it has been the favoured species on many sites and since the 1960s has held a pre-eminent position in Irish forestry (Joyce & O Carroll, 2002). It is now the most widely planted and successful exotic tree species grown in Ireland (Horgan *et al.*, 2004). The main reasons for its popularity are its rapid growth rate and its versatility, with its wood being suited to a wide range of end uses (Joyce & O Carroll, 2002). It also grows well over a wide range of site conditions (Horgan *et al.*, 2004) and is tolerant of exposure (Anon., 2005b).

2.1.2 Larch

Larch is the only deciduous conifer commonly planted in Ireland and, for that reason, it is often included in plantations for its variety of colour throughout the seasons (Anon., 2005a). Three kinds of larch have been used in forestry plantations in Ireland: European larch (*Larix decidua*), Japanese larch (*L. kaempferi*) and a hybrid between the two (*L. x marschlinsii*). European larch is native to central Europe and was popular from the period of early plantings in the 18th century until the 1940s and 1950s when it was replaced by Japanese larch (Anon., 2005a). Japanese larch is native to the island of Honshu in Japan. It is favoured over European larch because of its higher productivity, resistance to larch canker disease, greater tolerance of exposure and wet conditions,

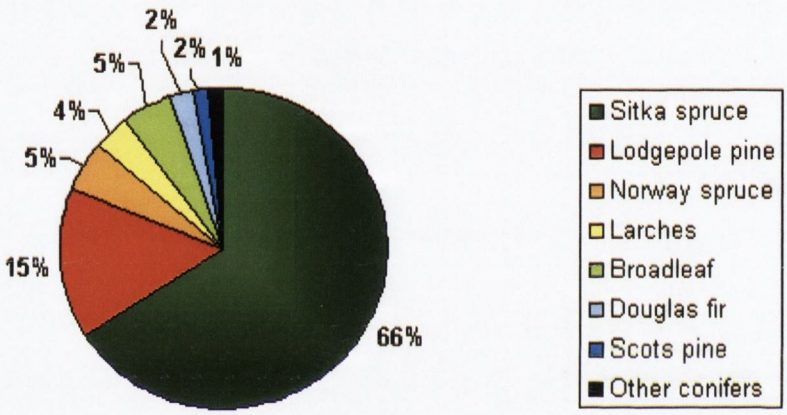


Figure 2.1 Tree species composition in Coillte owned plantations in Ireland (Coillte Teoranta, 2005).

and later flushing, meaning it is less susceptible to frost damage (Anon., 2005a; Horgan *et al.*, 2004). More recently hybrid larch has been favoured as being superior to both its parents in terms of its vigour, form and resistance to disease. The majority of the areas of larch managed by Coillte are of Japanese larch (Anon., 2005a).

2.2 SITE SELECTION

This study can be divided into three main parts:

Part A A study of the epiphytes of mature Sitka spruce and Japanese larch trees in the forest interior.

Part B A study of the epiphytes of mature Sitka spruce and Japanese larch stands, in which the ground flora had previously been studied, in order to assess the contribution of epiphytes to overall plant diversity.

Part C A study of the effects of open spaces on the epiphytes of mature Sitka spruce trees.

Parts A, and B will all be covered in **Chapter 3** of this thesis. Part C will be covered in a separate chapter: **Chapter 4**.

Sites were selected for each of these three parts of the study based on the characteristics of certain stands within each site. A stand is a group of trees and their associated vegetation of similar structure, growing under similar site conditions and sufficiently uniform to be considered a homogeneous ecological unit (Roberts & Gilliam, 1995). A plantation is usually made up of more than one stand. The plantation, in turn, is located in the landscape, which is a heterogeneous land area composed of different, interacting ecosystems (Roberts & Gilliam, 1995). Forest management in Ireland usually operates at the stand level. In some cases, the sites selected contained more than one stand of interest. All of the sites selected were managed by Coillte Teoranta. The research group was given access to Coillte's GIS database, which contains detailed forest management information. Sites were selected from this database based on certain criteria, which are detailed below.

In order to reduce the effects of large-scale environmental variation, sites were located in two geographic clusters: the Wicklow/Dublin Mountains (Wicklow cluster) and Cork and neighbouring parts of Kerry and Limerick (Cork cluster) (**Figure 2.2**). Each study site was identified by a unique four letter alphabetic code, based on the site name as it appeared in the Coillte database. Site codes will be used in the figures, tables and text and are shown in **Table 2.1**. These site codes may be followed by a number, which identifies each tree at a site – 1 for the first tree studied at the site, 2 for the second etc. The site code and tree number combined are referred to as the tree code. Trees were studied in 28 stands at 24 sites in total.

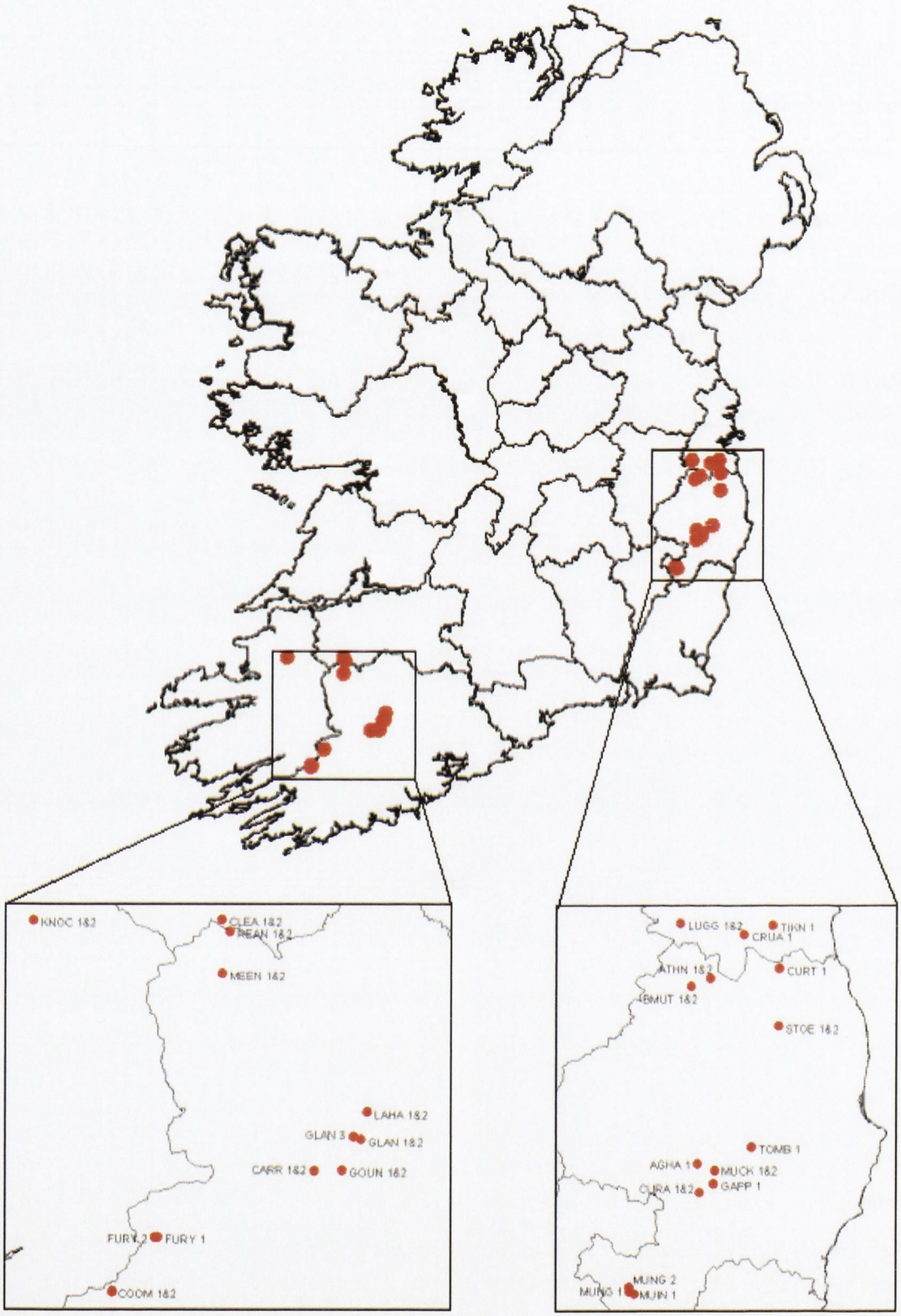


Figure 2.2 Location of the 28 stands where trees were studied. Labels refer to the site and tree codes (cf. Table 2.1).

Table 2.1 Study site codes and locations

Site Code	Site Name	County	Grid Ref.
AGHA	Aghavannagh	Wicklow	T057 874
ATHN	Athdown	Wicklow	O076 158
BMUT	Ballysmuttan	Wicklow	O047 145
CARR	Carrigagulla	Cork	W384 835
CLEA	Cleanglass	Limerick	R244 218
COOM	Coomroe	Cork	W079 651
CRUA	Cruagh	Dublin	O127 225
CURA	Ballycurragh	Wicklow	T061 831
CURT	Curtlestown	Wicklow	O181 172
FURY	Fuhiry	Cork	W146 734
GAPP	Ballinagappoge	Wicklow	T081 843
GLAN	Glannaharee West	Cork	W444 887
GOUN	Knocknagoun	Cork	W427 836
KNOC	Knocknagoum	Kerry	Q958 217
LAHA	Laharane	Cork	W464 924
LUGG	Lugg	Dublin	O031 242
MEEN	Meentinny	Cork	R245 135
MUCK	Mucklagh One	Wicklow	T083 864
MUIN	Barnamuinga	Wicklow	S962 696
MUNG	Mungacullin	Wicklow	S954 683
REAN	Toureenmacauliffe	Cork	R256 200
STOE	Ballinastoe	Wicklow	O180 084
TIKN	Tiknock	Dublin	O171 239
TOMB	Ballintombay	Wicklow	T140 900

All stands selected were approaching, at or beyond commercial maturity (**Table 2.2**) so that the trees had reached a sufficient size to be safe to climb and had also had time to develop their epiphytic flora. Stands were chosen to have at least 80% of their net productive area in the species in question (Sitka spruce or Japanese larch). In fact only four stands contained less than 100% of the species in question: KNOC, which contained 95% Sitka spruce and 5% alder (*Alnus glutinosa*) as edge planting; CLEA, which contained 80% Sitka spruce and 20% lodgepole pine (*Pinus contorta*) as an intimate mixture; TOMB, which contained 80% Japanese larch and 20% Corsican pine (*Pinus nigra)* as an intimate mixture; and MUNG which contained 80% Japanese larch and 20% Sitka spruce as a non-intimate mixture.

Stands were also chosen so that the tree studied was in a forest area of at least 3ha, and preferably greater than 5ha. An area of 5ha is the frequently-cited minimum for a functioning woodland patch which provides interior conditions free of edge effects (Purdy & Ferris, 1999). Only one stand, CURT, had an area less than 5ha.

Seventeen Sitka spruce stands were selected for Part A of the study; nine in the Wicklow cluster and eight in the Cork cluster (**Table 2.2**). One tree was studied in the forest interior in each stand. Eleven Japanese larch stands were also selected for Part A of the study; six in the Wicklow cluster and five in the Cork cluster. These stands were located as close as possible to the Sitka spruce stands selected. In two of the Sitka spruce stands and three of the larch stands studied in Part A, the ground flora had previously been studied by members of the BIOFOREST botanical team. This

information was used for Part B of the study to assess the contribution made by epiphytes to total plant diversity in these stands. At twelve of the 17 Sitka spruce stands studied in Part A - six in the Wicklow cluster and six in the Cork cluster - the forest interior tree studied was one of a pair of trees studied in relation to open spaces within the forestry plantations for Part C of the study. One open space was studied at each of the twelve sites (**Table 2.3**). At nine sites the open space studied was a glade. Glades are non-linear areas of retained habitat within the forestry plantation and include sub-compartments that have been designated as unplantable or set aside as deer glades. At the other three sites; KNOC, MUCK and REAN; glades were not present, or not suitable for study. In these cases an east-west running linear open space was studied. This consisted of one ride and two roads respectively (**Table 2.3**). Rides are unpaved linear open spaces and roads are gravelled linear open spaces, not muddy tracks or tarmac. All epiphyte surveying took place on the north side (i.e. south-facing side) of each open space, as this side will receive more light than the south side (Carter & Anderson, 1987; Ferris & Carter, 2000).

Table 2.2 Summary of the 24 sites, 28 stands and 40 trees studied.

Tree Codes	Cluster	Part	Species	Age* (years)	Elevation (m)	Aspect†	Slope (°)
ATHN1&2	Wicklow	A,C	Sitka spruce	28	510	0.74	13
BMUT1&2	Wicklow	A,C	Sitka spruce	38	325	1.99	7
CURA1&2	Wicklow	A,C	Sitka spruce	42	445	1.45	21
LUGG1&2	Wicklow	A,C	Sitka spruce	31	290	1.57	3
MUCK1&2	Wicklow	A,C	Sitka spruce	42	420	1.33	22
MUIN1	Wicklow	A	Sitka spruce	53	260	1.05	6
MUNG2	Wicklow	A,B	Sitka spruce	42	280	1.99	14
STOE1&2	Wicklow	A,C	Sitka spruce	29	540	0.01	14
TIKN1	Wicklow	A	Sitka spruce	53	330	0.91	10
CARR1&2	Cork	A,C	Sitka spruce	43	220	1.33	2
CLEA1&2	Cork	A,C	Sitka spruce	31	310	0.14	2
COOM2	Cork	A	Sitka spruce	64	180	1.56	3
FURY2	Cork	A,B	Sitka spruce	41	290	1.56	8
GLAN1&2	Cork	A,C	Sitka spruce	38	320	1.26	9
KNOC1&2	Cork	A,C	Sitka spruce	32	180	1.56	6
MEEN1&2	Cork	A,C	Sitka spruce	32	320	1.66	10
REAN1&2	Cork	A,C	Sitka spruce	39	380	1.68	5
AGHA1	Wicklow	A	Japanese larch	32	280	0.02	7
CRUA1	Wicklow	A,B	Japanese larch	65	360	1.48	13
CURT1	Wicklow	A,B	Japanese larch	68	350	0.34	8
GAPP1	Wicklow	A	Japanese larch	38	340	0.66	11
MUNG1	Wicklow	A	Japanese larch	34	285	1.84	16
TOMB1	Wicklow	A,B	Japanese larch	42	290	0.03	8
COOM1	Cork	A	Japanese larch	63	180	0.36	25
FURY1	Cork	A	Japanese larch	41	270	1.69	17
GLAN3	Cork	A	Japanese larch	40	280	1.50	5
GOUN1	Cork	A	Japanese larch	42	230	1.72	7
LAHA1	Cork	A	Japanese larch	43	255	1.94	17

Note. * years after planting at time of study. Trees ca. 2-4 years old at time of planting. † Aspect expressed on a linear scale. See Section 2.3.2 for details.

Table 2.3 Type of open space studied at each site

Site code	Open space type
ATHN	Glade
BMUT	Glade
CURA	Glade
LUGG	Glade
MUCK	Road
STOE	Glade
CARR	Glade
CLEA	Glade
GLAN	Glade
KNOC	Ride
MEEN	Glade
REAN	Road

2.3 DATA COLLECTION

2.3.1 Epiphyte sampling

Fieldwork for the majority of the Sitka spruce stands in Part A and all stands in Part C of the study was carried out between July and November 2003. Fieldwork for the remainder the spruce stands and all of the Japanese larch stands in Part A and all stands in Part B was carried out during April and May, and October and November 2004.

Trees were selected based on their representativity, structure and suitability for safe climbing. Trees with a forked or contorted main trunk or a noticeable lean were excluded, as were unhealthy or damaged trees. Trees were also required to be of a sufficient size to be safe to climb. In many cases, the structure and safety considerations limited the selection based on representativity. The forest interior trees studied were located at a distance from the edge of the stand greater than or equal to the height of the edge trees at that point (**Photograph 2.1**). In three stands it was not possible to locate the tree a full tree height from all edges. The width of the stands at MUCK, between the road studied and another road; CLEA, between the glade and an area of thinning; and CURT, between a road and an adjacent Scots pine (*Pinus sylvestris*) stand, were not sufficient. However, despite this, the trees were judged to be subject to forest interior conditions. The trees studied for Part B of the study were located as close as possible to the 10 x 10m plots previously studied for ground flora. The forest edge trees studied in Part C directly adjoined the open space (**Photograph 2.1**), with the exception of KNOC1 where alder had been planted between the tree studied and the open ride. The trees studied were not adjacent to rows that had been entirely removed during thinning with the exception of BMUT2.

Photograph 2.1 An aerial photograph of the glade studied at Ballinastoe (STOE), Co. Wicklow (GR O180 084); a 29-year-old Sitka spruce stand. The approximate location of the two trees studied at this site are indicated.

Epiphytes were studied in plots located on the trunk and branches in four different height zones in the tree: tree base (B), lower (L), middle (M) and upper (U) (**Figure 2.3**). The tree base zone began at the point where the trunk emerged from the soil or needle litter and reached to 0.5m above this point. In a number of cases this point was at a different level on the two sides of the trunk, meaning tree base plots were not always at the same level. All subsequent measurements were taken from the uphill side of the tree. The lower zone was centred on breast height (1.3m), and the middle and upper zones were centred on one-third and two-thirds of the height of the tree respectively. Tree-climbing techniques were used to study the middle and upper zones. This involved the use of a rope and harness and climbing spurs (**Photograph 2.2**). Branches were removed with a pruning saw where necessary to facilitate upward movement in the tree. Trunk plots were positioned on opposite sides of the trunk. For the twelve pairs of trees studied with respect to an open space (Part C), the side of the trunk facing the open space and the opposite side were studied (referred to as south and north sides). For all other trees, the plots were centred on magnetic north and south respectively. Plots were 50cm high and the width varied from a maximum of 25cm to that required to sample a half cylinder of the trunk. In the middle and upper zones the trunk plots were centred vertically on a branch whorl where possible. A branch from the north side and a branch from the south side of the whorl were removed for study on the ground. Where a whorl with both north and south facing branches was not present, the plots were centred on either the north or south facing branch, whichever present, and the closest branch on the opposite side to the first became the second branch to be studied. In some cases, where there was no nearby branch, only a single branch was studied (or in the case of COOM1 in the middle height zone, no branches). Three plots, 25cm long by 50cm wide, were studied on each branch (**Figure 2.3**). These plots ran perpendicular to the main axis and included the main axis and that side of the branch with the most cover of side branches. The upper half cylinder of branches was studied. The first plot was placed at the base of the branch, the third plot was placed near the tip of the branch, but did not include the last two years growth on the main axis, and the second plot was centred half way between the previous two plots. A certain proportion of each plot was therefore occupied by empty space (**Figure 2.3**). The percentage of the plot taken up by branches and by needles was estimated.

In both trunk and branch plots a list of epiphyte species was made with percentage cover estimated to the nearest 5%. Below 5% two different cover-abundance units were distinguished: 3% (indicating cover of 1-5%), and 0.5% (indicating cover <1%). Total percentage cover of bryophytes, lichens, others (algae, fungi), needle litter, and total percentage bare bark were also recorded. Overlap of species meant that recorded cover occasionally exceeded 100%. If epiphytes proved to be scarce in branch plots, a list of epiphyte species occurring outside the plots was made. Their location on the branch (inner, mid or outer) was noted.

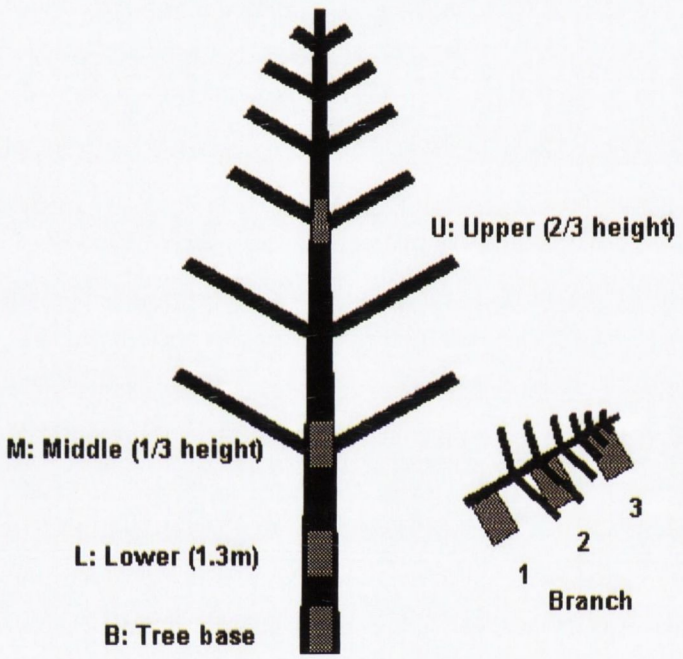


Figure 2.3 Plot sampling design used to study epiphytes. All plots are 25cm x 50cm in dimension.

Photograph 2.2 The method used to gain access to the middle and upper height zones. The trees were ascended using a combination of ropes and climbing spurs. The climber was secured to the tree at all times by an arborist's climbing rope and harness. (Photograph: George Smith).

2.3.1.1 Plot codes

Each epiphyte plot was identified by a unique alphanumeric code. The first four letters were the site code (cf. **Table 2.1**), followed by a number identifying the individual tree (1 for the first tree studied at each site, the edge tree in the case of sites with open spaces; 2 for the second etc.). Individual plots were identified with either a T for trunk plots or B for branch plots, followed by a B, L, M or U indicating the zone (tree base, lower, middle or upper) followed by an n or s for the north or south side of the tree. For branch plots, the individual plots were identified by a number progressing from inner to outer branch (1 to 3) (**Figure 2.3**). For example, in the (hypothetical) Ballygolightly site the tree base trunk plot on the north side of the first tree studied would be BALL1TBn. For the mid (second) branch plot in the middle zone of the south side of the same tree the code would be BALL1BMs2.

2.3.2 Environmental and structural data sampling

In each stand the slope and aspect were recorded. Slope was measured with a clinometer. Stand aspect data were recorded in degrees. To aid comparison, aspect was transformed to a linear scale, using the equation (Beers *et al.*, 1966):

$$A' = \cos(45 - A) + 1 \qquad \textbf{Equation 2.1}$$

where A is the aspect in degrees and A' is the transformed aspect. Using this transformation, southwest, the driest, sunniest aspect in the northern hemisphere, receives a value of zero and northeast, the shadiest, has a value of two. The intermediate aspects of southeast and northwest are both transformed to one.

The thinning status of each stand was recorded as thinned or unthinned. Thinning can be in the form of line thinning – removal of lines of trees, usually following the original planting rows; or selection thinning – removal of dead, suppressed and poorly formed trees (Forest Service, 2000a). First thinning usually takes place a few years after canopy closure and thinning can take place a number of times over the life of a plantation. For Sitka spruce the first thinning usually takes place when the trees are 10-12m tall, and for Japanese larch when trees are 8m tall (Horgan *et al.*, 2004). First thinning for Sitka spruce usually involves the removal of one line in seven and subsequent thinnings involve selection thinning only on a cycle of three to six years. First thinning for Japanese larch is particularly heavy because it is a light demanding species, followed by thinning at three to five year intervals (Horgan *et al.*, 2004).

In stands where trees were studied in relation to an open space, the orientation of the edge at which trees were studied was recorded. The area of glades was recorded using aerial photographs and the

width of rides and roads and glades was measured from tree trunk to tree trunk. The light environment of each open space was measured using hemispherical photography. Hemispherical photographs were taken in the centre of each open space. Photographs were taken using a tripod-mounted Canon AE-1 35mm camera with a Canon 7.5mm f/5.6 fisheye lens. The lens uses simple polar projection to represent a hemispherical distribution of points onto a circular image (Herbert, 1987). Ilford FP4 Plus black-and-white film was used. The camera was erected at 1.3m above ground, levelled and oriented towards magnetic north. At least four combinations of shutter speed (1/60 and 1/125) and aperture (5.6 and 8) were used at each point. Developed negatives were scanned using a Microtek ScanMaker X12 flatbed scanner. Negatives were converted to positive grey-scale images at 1200ppi resolution and saved in JPEG format. Scanned images were then analysed using Gap Light Analyser 2.0 software (Frazer *et al.*, 1999). In addition to percentage canopy cover, above-canopy and transmitted direct and diffuse solar radiation were estimated with Gap Light Analyser 2.0 using data collected in the field for latitude, longitude, elevation, slope and aspect. Direct radiation is that fraction of total solar radiation that emanates directly from the sun and is not absorbed or reflected by the atmosphere. Diffuse radiation is the fraction that is scattered by the atmosphere towards the earth from all portions of the sky. Transmitted direct radiation is the portion of direct radiation that is transmitted through gaps in the forest canopy into the open space below. Transmitted diffuse radiation includes diffuse radiation that passes directly through canopy gaps and direct radiation that has been scattered by the forest canopy. Above-canopy solar radiation parameters were estimated using the ratio of mean daily hours of sunshine to day length on a monthly basis in conjunction with the equation developed by McEntee (1980) and equations in the Gap Light Analyser 2.0 software manual (Frazer *et al.*, 1999). Sunshine data were based on thirty year averages obtained from the Met Éireann website (Met Éireann, 2006); for Wicklow stands, sunshine data from Dublin Airport were used and Cork Airport data were used for Cork stands. The clear-sky transmission coefficient was set at 0.8, following Garvey (1998).

Tree density and DBH (at 1.3m) were recorded from plots located within the forest. For stands where trees were studied in relation to an open space (Part C), two 10m x 10m plots were set up. The first had its outer edge centred on the edge tree studied for epiphytes and ran perpendicular to this edge. The second was centred on the interior tree studied for epiphytes and its outer edge was parallel to the forest edge. For stands where only forest interior trees were studied a single 10m x 10m plot was recorded, centred on the studied tree and with the mid point of each side at magnetic north, south, east and west. Stand basal area was later calculated from the data.

For each tree studied, the DBH (at 1.3m), tree height, heights to first live branch and base of live crown were recorded. The base of live crown was defined as that height at which branches on all aspects of the trunk were living. For trees studied in relation to an open space, the distance of the tree from the open space edge was also recorded (zero for the edge trees). The height above

ground, tree girth and inclination at the centre of each trunk plot were recorded. The distance from the trunk and the diameter of the main axis at the centre of each branch plot were recorded. The vitality of branches was also recorded as living, moribund or dead.

2.3.3 Additional data

Additional site information was collected from a number of sources including Ordnance Survey (O.S.) maps, the Coillte database, Met Éireann website (Met Éireann, 2006), field notes and correspondence with forest managers.

2.3.3.1 Elevation

Elevation data were taken from the 1995 1:50,000 Discovery Series O.S. maps using ArcView GIS 3.2. The position of each individual tree was located on the map and the elevation recorded to the nearest 10m.

2.3.3.2 Pre-afforestation habitat

The pre-afforestation habitat was defined according to the four site fertility classification codes given in the Coillte database (Horgan *et al.*, 2004):

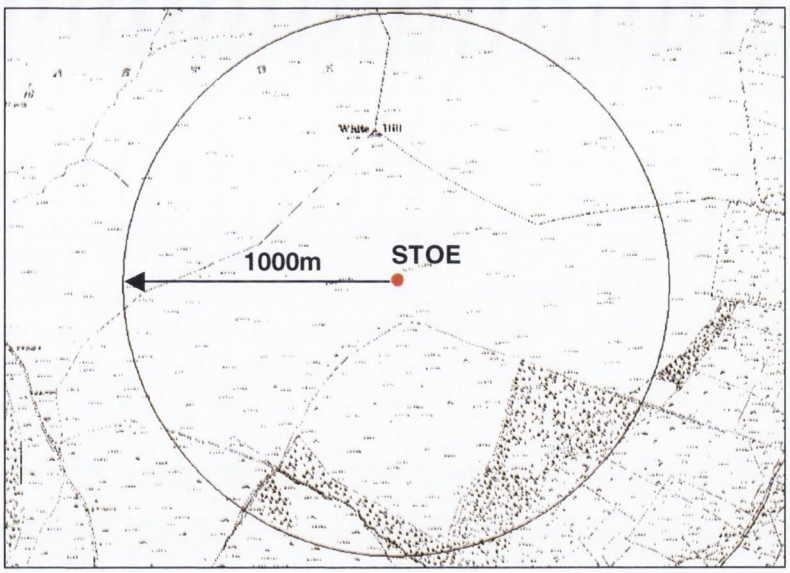
1. Fields and ornamental grounds – areas that have been in intensive agricultural use up to recent times.
2. Furze or bracken – areas that were once enclosed and therefore previously used for agriculture, but the presence of furze or bracken indicates they had not been intensively managed for a long time.
3. Rough pasture (with or without outcropping rock) – areas never brought under intensive agricultural use. They typically have unimproved peatland or heathland vegetation.
4. Old woodland – areas under woodland prior to planting.

Information was also collected from forest managers and field observations.

2.3.3.3 Proximity to old woodland

The proximity of each tree to areas marked as deciduous, coniferous or mixed woodland or scrub within 1km was determined using the 3rd edition six-inch to a mile Ordnance Survey maps printed between 1900 and 1915. The methods used are outlined in **Figure 2.4**. Where no woodland or scrub occurred within 1km the distance was recorded as 1001m. A distance of zero indicates that the site was formerly scrub or woodland on the six-inch to a mile Ordnance Survey maps. The area of old woodland or scrub within 1km was also measured.

(a)



(b)

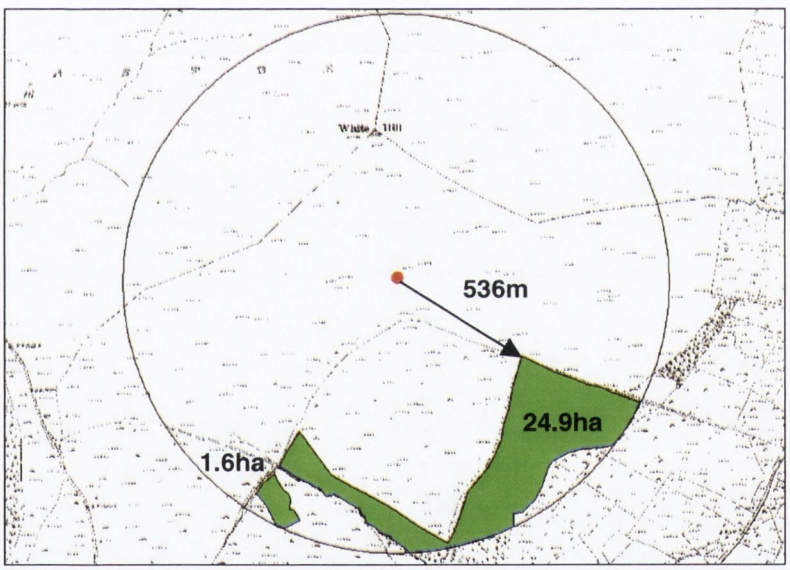


Figure 2.4 Procedures followed using ArcView GIS 3.2 for determining the proximity of the studied trees to old woodland and for determining the area of old woodland within a 1km radius. (a) The position of each tree (or average position of the pair of trees in the case of open space (Part C) sites) was located on the 3rd edition six-inch to a mile O.S. maps and a radius of 1km was then traced around this position. (b) Polygons were created for all woodland (including broadleaf, conifer and mixed) and scrub on the six-inch to a mile O.S. maps located within this 1km radius, and their total area (in ha) was calculated. The shortest distance between the studied tree and woodland/scrub within the 1km radius was calculated in order to represent the proximity of the tree to old woodland. Where the distance from old woodland was greater than 1km, distance was recorded as 1001m. In the example presented STOE is located 536m from old woodland and there are 26.5ha of old woodland within the 1km radius.

2.3.3.4 Proximity to built-up areas

A similar method was employed to determine the proximity of each tree to areas marked as 'buildings grouped' within 3km on the 1995 1:50,000 Discovery Series O.S. maps. Where no buildings grouped occurred within this range, the distance was recorded as 3001m. The area of buildings grouped within 3km was also recorded.

2.3.3.5 Climate

Climate data, such as rainfall, temperature and humidity, were not recorded in the field because of the problems posed by varying weather conditions when visiting different sites. It was not considered worthwhile to acquire more detailed climate data from local weather stations, as these are generally located in lowland areas while many of the sites were in mountainous terrain where elevation and topographic effects are significant. However, the 30-year averages were obtained from the Met Éireann website (Met Éireann, 2006) for Dublin Airport and Cork Airport in order to offer an indication of the climatological differences between the two clusters. The estimated rainfall for each site was also extrapolated from the 30-year rainfall average contour map (Met Éireann, 2006). These data are presented in rainfall ranges so the midpoint of each range was used in calculations.

2.4 SPECIES IDENTIFICATION

Some of the epiphyte species encountered could be identified in the field, while others needed to be confirmed by microscopy. A number of species were sent to experts for confirmation. The plant species nomenclature used in this thesis follows Stace (1997) for vascular plants, Smith (2004) for mosses, Paton (1999) for liverworts and Coppins (2002) for lichens. The two *Ulota* species - *U. crispa* and *U. bruchii* - were not separated and are referred to as *Ulota crispa s.l.*. Non-lichenised fungi and free-living algae were not recorded.

Most epiphytes were identifiable to species level. However, a few were only identifiable to generic level due to lack of fruiting bodies or poor development. Those species identified only to generic level were treated in such a way that their inclusion did not cause an overestimation of species richness. If no other species belonging to the genus of the unidentified species was present in the unit under consideration, the specimen was included and identified to generic level only. If other species of the same genus were present, the data were amalgamated and the cover of the most abundant species for the genus was increased accordingly. Some sterile crustose lichens were not identifiable to genus level and were excluded from analyses. Voucher specimens are deposited in the herbarium of the Department of Botany, Trinity College Dublin (TCD).

2.4.1 Classification of species

Epiphytic bryophytes, lichens and vascular plants were examined separately in order to examine the differing effects on them as a result of their differing ecological requirements. Bryophytes were also divided further into mosses and liverworts. These four groups were referred to as 'epiphyte groups'. The different bryophyte and lichen growth forms were also considered. Bryophyte were divided into turfs, wefts, mats and cushions after Gimingham & Birse (1957). Lichens were divided into leprose, crustose, foliose and fruticose lichens after Dobson (2005).

In order to assess the importance of Sitka spruce and Japanese larch stands as habitats for species which are typically epiphytic, the epiphyte species were classified according to their affinity for an epiphytic lifestyle. Species classified as having a low affinity for epiphytism are primarily found in other non-epiphytic habitats, those classified as having an intermediate affinity are found both in epiphytic an non-epiphytic habitats, while those classified as having a high affinity are primarily found in epiphytic habitats. This classification is similar to the occasional, facultative and typical epiphytes of Oliver (1930) and Benzing (1990) (cf. **Section 3.1.6**). However, those classifications take into account the usual substrate preference of a species within a given study area and this information was not available. Classification was instead determined using the information contained in various texts. For bryophytes, the following moss and liverwort texts were consulted: Hill (1991), Hill (1992), Hill (1994), Smith (1990), Watson (1981), Paton (1999) and Phillips (1980). For lichens, Dobson (2005), Purvis *et al.* (1992) and Phillips (1980) were consulted.

2.5 INDEPENDENT AND JOINT RESEARCH

This research was carried out as a component study of project 3.1.3 of the BIOFOREST project (cf. **Section 1.3**). For this reason, certain areas of research were carried out in conjunction with other members of the BIOFOREST research team, while other areas were carried out independently. The areas of research carried out independently and those carried out in conjunction are clarified in **Table 2.4**. Site selection for the open space (Part C) sites was carried out by the BIOFOREST research team but the selection of the open spaces to be studied within the sites was carried out by the author. All additional site selection was carried out by the author. All trees to be sampled were selected by the author and all but one were climbed and the trunk plots sampled by the author. Sampling of branches was carried out jointly by the author and a member of the research team. Environmental and management information were collected jointly by the author and members of the research team. Identification of species unidentified in the field was carried out by the author, with the assistance of experts being sought where necessary. The collection and analysis of bark samples was carried out independently by the author. The hemispherical photographs were taken jointly by the author and other members of the team and analysis of the hemispherical photographs

was carried out by a member of the research team. All data analyses presented in this thesis were carried out by the author.

Table 2.4 Research carried out by the author (LC) independently and in conjunction with other members of the BIOFOREST research team

	LC	BIOFOREST
Site selection	X	X
Tree selection	X	
Plot sampling	X	X
Environmental and management information	X	X
Sample identification	X	
Hemispherical photograph capture and analysis	X	X
Bark analysis	X	
Data analysis	X	

2.6 ADDITIONAL ANALYSES

In order to allow better interpretation of the results of the study it was important to be aware of any confounding factors. For this reason the selected stands were compared in order to reveal any significant differences between them for a number of factors. This information will be used when interpreting results and will be referred to in subsequent chapters. Analyses were carried out using independent and paired samples t-tests, as appropriate, where variables conformed to the assumptions of parametric statistics. Where they did not, the non-parametric Mann-Whitney U test and Wilcoxon signed ranks test were used as appropriate.

2.6.1 Comparison of the age, environmental and structural characteristics

To facilitate comparison of the epiphytes of Sitka spruce and Japanese larch trees in the forest interior (Part A) it was important that the stands were comparable in their age, environment and structure. The similarity of these factors was also important when considering any geographical differences in the epiphyte flora. For this reason, stands were considered in two groups in terms of various environmental and structural variables. The groups considered were as follows:

- Sitka spruce and Japanese larch stands
- Wicklow and Cork cluster stands

2.6.1.1 Differences in age and environmental variables

No significant differences were found in the mean ages of the Sitka spruce and Japanese larch stands (Mann-Whitney U test: $p = 0.211$) or between the Wicklow and Cork cluster stands (Mann-Whitney U test: $p = 0.973$) (**Table 2.5**). Older stands were less well represented overall (cf. **Table 2.2**), reflecting the scarcity of plantations of this age from which to select suitable stands. There was also no significant difference in the elevation of the spruce and larch stands (Mann-Whitney U test: $p = 0.220$), although there were no particularly high elevation larch stands studied (cf. **Table**

2.2). The Wicklow stands did have a significantly greater elevation than the Cork stands however (independent samples t-test: p = 0.005). There was no significant difference in the transformed aspect between either of the two groups of stands (Mann-Whitney U test: p = 0.737 and p = 0.621 respectively) (**Table 2.5**), however the larch stands tended to be at either ends of the aspect range and few had an intermediate aspect (cf. **Table 2.2**). The slope was higher in the larch stands than the spruce stands but this difference was not statistically significant (Mann-Whitney U test: p = 0.171). Also, despite the higher mean slope in the Wicklow stands, the difference was again not statistically significant (independent samples t-test: p = 0.243).

Table 2.5 Mean (+/- standard error) age, elevation, aspect, slope, estimated rainfall, old woodland area within 1km and distance to old woodland within 1km of the two groups of stands. Pairs having the same letter indicates no significant difference between them.

Factor	Spruce (n=17)	Larch (n=11)	Wicklow (n=15)	Cork (n=13)
Age (years)	39.9[a] (± 2.4)	46.0[a] (± 3.9)	42.5[a] (± 3.2)	42.1[a] (± 2.9)
Elevation (m)	329.4[a] (± 24.9)	283.6[a] (± 16.0)	353.7[a] (± 22.2)	263.5[b] (± 17.8)
Aspect	1.28[a] (± 0.14)	1.05[a] (± 0.23)	1.03[a] (± 0.18)	1.38[a] (± 0.15)
Slope (°)	9.1[a] (± 1.5)	12.2[a] (± 1.8)	11.5[a] (± 1.4)	8.8[a] (± 1.9)
Estimated rainfall ($mmyr^{-1}$)	1400.0[a] (± 86.2)	1500.0[a] (± 105.0)	1306.7[a] (± 62.1)	1592.3[a] (± 111.2)
Old woodland area (ha)	7.2[a] (± 5.6)	4.3[a] (± 2.0)	11.1[a] (± 6.2)	0.3[b] (± 0.2)
Distance to old woodland (m)	832.5[a] (± 76.4)	720.8[a] (± 104.0)	674.5[a] (± 92.6)	920.4[b] (± 63.9)

There was no significant difference in the estimated rainfall of the Sitka spruce and Japanese larch stands (Mann-Whitney U test: p = 0.374) (**Table 2.5**), although few larch stands received less than $1300mmyr^{-1}$ while a number of spruce stands received less rain (cf. **Appendix 1**). The higher rainfall in the Cork cluster than the Wicklow cluster stands was close to significance however (Mann-Whitney U test: p = 0.056). The 30-year averages obtained from the Met Éireann website (Met Éireann, 2006) also offer an indication of the climatological differences between the two clusters. At Dublin airport the mean temperature was higher, but the relative humidity, rainfall, number of days with fog and number of days with no sun were lower than at Cork airport (**Table 2.6**).

There was no difference in the area of old woodland within 1km of the Sitka spruce and Japanese larch stands (Mann-Whitney U test: p = 0.493), however there was a significantly greater area of old woodland within 1km of the Wicklow cluster than the Cork cluster stands (Mann-Whitney U test: p = 0.010) (**Table 2.5**). Only two of the Cork cluster stands were within 1km of areas of old woodland compared to nine of the Wicklow cluster stands (cf. **Table 2.2**). The Wicklow cluster stands were therefore also significantly closer to old woodland than the Cork cluster stands (Mann

Whitney U test: p = 0.017) but there was no significant difference in distance to old woodland between the spruce and larch stands (Mann-Whitney U test: p = 0.493). Only three Wicklow cluster sites; LUGG, TIKN and CRUA; were within 3km of built up areas (**Appendix 1**).

Table 2.6. The 30-year averages for mean temperature, relative humidity, monthly rainfall, number of days with more than 5mm rain, number of days with fog and number of days with no sun at the Dublin airport (1961-1990) and Cork airport (1962-1991) synoptic stations (Met Éireann, 2006)

	Dublin airport	Cork airport
Mean temperature (°C)	9.6	9.4
Mean relative humidity* (%)	72	77
Mean monthly rainfall (mm)	732.7	1194.4
Mean no. days >5mm rain	48	75
Mean no. days with fog	50.5	99.5
Mean no. days with no sun	61	69

* at 1500 UTC

The pre-afforestation habitat of all stands, with the exception of LUGG, was either rough pasture, or furze or bracken (**Figure 2.5a**) (see **Section 2.3.3.2** for details of classification). LUGG was a reforested site and was therefore classified as old woodland. None of the stands was planted on improved grassland. The majority of Wicklow cluster stands were planted on sites classified as furze or bracken, while the majority of Cork cluster stands were planted on sites classified as rough pasture; the less intensively managed of the aforementioned habitats and typically with peatland or heathland vegetation (**Figure 2.5a**). This is a crude classification however and, in reality, the vast majority of the Cork cluster Sitka spruce stands were on poorly drained sites and planted on blanket peat while the majority of the Wicklow cluster Sitka spruce stands were planted on well-drained upland sites on mineral soils. The larch stands were planted mainly on dry to mesic sites.

2.6.1.2 Differences in stand structure

The higher tree density in larch stands compared to spruce stands was close to significance (Mann-Whitney U test: p = 0.059) (**Table 2.7**). All of the larch stands had been thinned, while a number of spruce stands were unthinned (**Figure 2.5b**). Despite the higher density in the Cork cluster than Wicklow cluster stands (cf. **Appendix 2**), there was no significant difference between them (Mann-Whitney U test: p = 0.136) (**Table 2.7**). The proportion of unthinned stands in the Wicklow and Cork clusters were similar (**Figure 2.5b**). There was also no significant difference in mean DBH between either of the two groups of stands (independent samples t-test: p= 0.615 and p = 0.163 respectively). There was, however, a significantly higher basal area in the spruce than larch stands (independent samples t-test: p = 0.006) but no difference between the Wicklow and Cork cluster stands (independent samples t-test: p = 0.997) (**Table 2.7**). There was also no significant difference in the mean height (independent samples t-test: p = 0.244 and p = 0.774 respectively) or mean DBH (independent samples t-test: p = 0.826 and Mann-Whitney U test p = 0.110 respectively) of the studied trees in either of the two groups (**Table 2.7**), although no very small larch trees were studied (cf. **Appendix 2**).

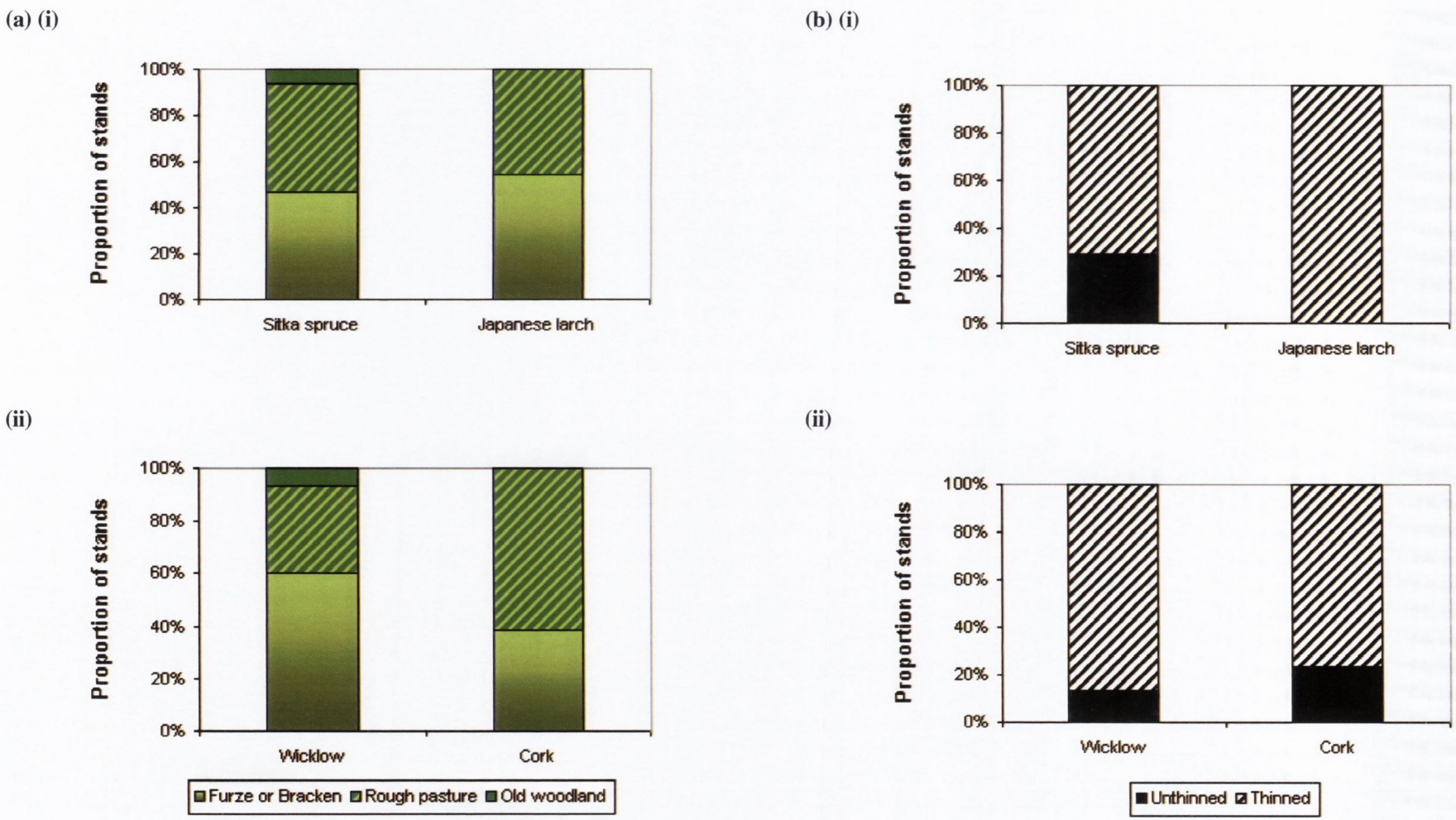


Figure 2.5 (a) Pre-afforestation land use and (b) thinning status of the (i) Sitka spruce and Japanese larch and (ii) Wicklow and Cork cluster stands (cf. Sections 2.3.2 & 2.3.3).

Table 2.7 The mean (± standard error) tree density, mean DBH, and basal area from the 10x10m plots for the forest interior trees and the tree height and DBH of the forest interior trees studied. Pairs having the same letter indicates no significant difference between them.

Factor	Spruce (n=17)	Larch (n=11)	Wicklow (n=15)	Cork (n=13)
Tree density (no. $100m^{-2}$)	10.7^a (± 1.8)	6.4^a (± 0.8)	7.1^a (± 1.1)	11.2^a (± 2.1)
Mean DBH (cm)	27.9^a (± 2.5)	29.1^a (± 2.3)	30.3^a (± 2.4)	25.4^a (± 2.4)
Basal area (m^2100m^{-2})	0.52^a (± 0.04)	0.34^b (± 0.04)	0.45^a (± 0.05)	0.45^a (± 0.04)
Studied tree height (m)	20.2^a (± 1.4)	22.5^a (± 1.0)	20.8^a (± 1.2)	21.4^a (± 1.5)
Studied tree DBH (cm)	33.0^a (± 2.5)	33.8^a (± 2.3)	34.5^a (± 1.9)	31.9^a (± 3.1)

2.6.2 Stand structural characteristics of the open space sites

In the stands where trees were studied in relation to open spaces (Part C), it was the comparison between the open space edge and forest interior trees that was of interest. The similarity of edge and interior trees for certain structural factors was considered.

2.6.2.1 Differences in stand structure

For comparisons of stand structural variables, edge and interior trees were compared. The higher tree density in the edge than the interior plots approached significance (paired samples t-test: $p = 0.108$) and the mean DBH and basal area of the edge plots were significantly greater than in the interior plots (Wilcoxon signed ranks test: $p = 0.016$ and paired samples t-test $p < 0.001$ respectively) (**Table 2.8**). No significant difference was found in the height of the edge and interior trees studied (paired samples t-test: $p = 0.388$) but the edge trees had significantly greater DBH (paired samples t-test: $p < 0.001$) (**Table 2.8**).

Table 2.8 The mean (± standard error) tree density, mean DBH and basal area from the 10x10m plots and the tree height and DBH of the trees studied in relation to open spaces for Part C. Pairs having the same letter indicates no significant difference between them (i.e. p>0.05).

Factor	Edge (n=12)	Interior (n=12)
Tree density ($no.m^{-2}$)	15.2^a (+/-2.2)	13.4^a (+/-2.1)
Mean DBH (cm)	26.3^a (+/-2.34)	23.9^b (+/-1.9)
Basal area (m^2100m^{-2})	0.75^a (+/-0.04)	0.51^b (+/-0.04)
Studied tree height (m)	18.4^a (+/-1.5)	17.7^a (+/-1.0)
Studied tree DBH (cm)	39.3^a (+/-2.5)	28.5^b (+/-1.4)

2.7 DIVERSITY

The assessment of epiphyte diversity is an important component of this research. However, although diversity is a central theme in ecology, there is no generally accepted definition (Peet, 1974). Hurlbert (1971) even went so far as to describe diversity as a 'non-concept'. However, species diversity is still a widely used measure in ecological studies. Several models and indices exist for measuring diversity, but there is no consensus on which is the best (Hill, 1973). Therefore some consideration needed to be given to how best to assess diversity.

One of the reasons that diversity is so difficult to define is that it consists of two components (Magurran, 1998). These components are species richness - the number or variety of species - and evenness - the relative abundance of the species (Begon *et al.*, 1990; Gaston & Spicer, 1998).

2.7.1 Species richness

Species richness is the oldest and most fundamental concept of diversity (Peet, 1974) and has been referred to as the 'common currency' of diversity measurement (Gaston & Spicer, 1998). Many ecological studies still restrict their investigations of diversity to species richness i.e. a simple count of the number of individuals present (Magurran, 1998). In botanical studies, species density is favoured and is the number of species per specified collection area (Magurran, 2003). However, species richness is highly dependent on area, with more species being found the larger the area sampled (Gaston & Spicer, 1998; Magurran, 1998). Therefore, the sample size must be the same for sites or studies to be meaningfully compared.

In no community are all species equally common. Instead there are a few very abundant species, some species with medium abundance, while most species are represented by few individuals (Magurran, 2003). A community where abundance is distributed more evenly among species is considered more diverse than a community where few species are very abundant and the remainder sparse (Magurran, 1998) (**Figure 2.6**). Measures of species richness give us no information on the relative abundance of species. Therefore measures of evenness are often also considered

2.7.2 Equitability indices

Equitability indices measure evenness, the second component of diversity. May (1975) has concluded that one of the most satisfactory equitability indices available is the Berger-Parker index.

The Berger-Parker index (d) is defined as (Berger & Parker, 1970):

$$d = N_{max} / N \qquad \textbf{Equation 2.2}$$

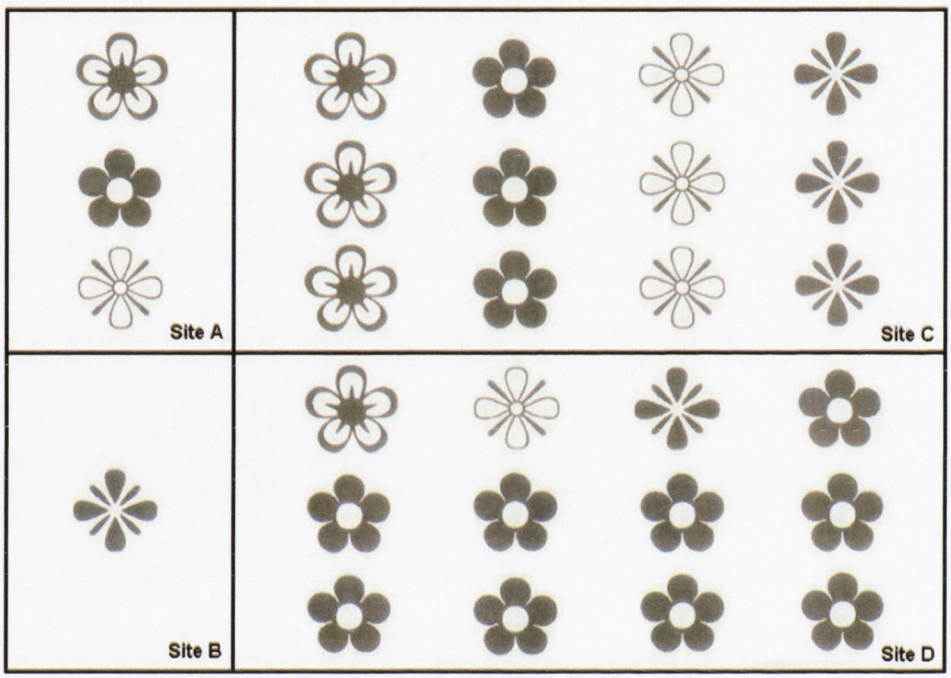


Figure 2.6 Concept of species richness and evenness (French, 2005) after (Magurran, 1998). In a comparison of Site A and Site B, Site A is more diverse than site B because it has three species of plant whereas site B only has one. When sites C and D are compared there is no difference in species richness, with both sites containing four species. However, while site C has three individuals of each of the four species, site D has nine individuals of one species and only one individual of each of the remaining three species. So site C would be considered more diverse because it has greater evenness.

where N_{max} is the number of individuals in the most abundant species and N is the total number of individuals.

The index is simple and easy to calculate and expresses the proportional importance of the most abundant species (Magurran, 1998). The reciprocal of d is often used so that the value increases with increasing evenness. The index is independent of species richness but it is affected by sample size (Magurran, 1998).

2.7.3 Diversity indices

Diversity indices attempt to combine both species richness and evenness into a single figure. The most commonly used indices are the Shannon index and Simpson's index (Nagendra, 2002).

The Shannon index (H) is defined as (Shannon & Weaver, 1949):

$$H = -\sum_{i}^{s} p_i \log p_i \qquad \textbf{Equation 2.3}$$

where s is species richness and p_i is the relative abundance of species i in the samples.

The Shannon index ranges theoretically from zero to infinity and estimates the average uncertainty in predicting which species a randomly selected individual will belong to (Nagendra, 2002). Therefore, as diversity increases, so will the uncertainty and therefore H. However, the index is strongly biased towards species richness and is sensitive to changes in the importance of rare species (Magurran, 1998; Peet, 1974). The antilog of H (Exp$H$) is sometimes used to simplify interpretation. It is a measure of the number of equally common species which would produce the same value of H as the sample (Peet, 1974).

The Simpson's index (D) is defined as (Simpson, 1949):

$$D = \sum_{i}^{s} p_i^2 \qquad \textbf{Equation 2.4}$$

where s is the species richness and p_i is the relative abundance of species i in the sample.

Simpson's index ranges from zero to one (Begon *et al.*, 1990) and is the probability that any two individuals selected at random from a sample will belong to different species (Magurran, 1998). Therefore, as diversity decreases, the value of D increases. For this reason the index is often expressed as 1-D or 1/D, giving an increase in the value with increased diversity. Simpson's reciprocal (1/D), unlike 1-D, can be expressed on a uniform scale (Hill, 1973) and can be defined as the number of equally common species required to produce the same heterogeneity as the sample. However, Rosenzweig (1995) has noted that Simpson's reciprocal can have severe

variance problems and recommends using $-\ln(D)$. French (2005) also found Simpson's reciprocal to generate ambiguous results when measuring the diversity of the ground flora of forestry plantations. However, Magurran (2003) has described it as one of the most meaningful and robust diversity measures available. The index is biased towards the most abundant species and is less sensitive to species richness (Magurran, 1998).

2.7.4 Beta diversity

The indices discussed up to now all measure what is know as alpha (α) diversity, the diversity of a defined sampling unit or habitat. But if we look at differences in diversity between sampling units then we are looking at beta (β) diversity. Beta diversity essentially measures how different a range of habitats or samples are in terms of the variety of species found in them (Magurran, 1998). For example, if a trees' epiphyte flora (Tree A) is studied using four plots and there is no overlap in species identity between the plots, then Tree A has high beta diversity. In contrast, if the plots on Tree B are equally as species-rich as those on Tree A, but many of the same species are found in all four plots, then Tree B has a lower beta diversity than Tree A.

Whittaker's measure of β diversity is one of the simplest and most effective measures. It is defined as (Whittaker, 1972):

$$\beta_w = \frac{Sc}{S} \qquad \textbf{Equation 2.5}$$

where Sc is the number of species in the composite sample and S is the average species richness of the sample units.

Whittaker's measure has been compared to other β diversity measures and found to fulfil most of the criteria of a good ecological measure (Wilson & Schmida, 1984). A good index will reflect the range of community composition within an area, is additive, has independence from alpha diversity and is independent of sample size (Wilson & Schmida, 1984).

2.7.5 Choosing diversity measures

As previously stated, there is no consensus on the best way to measure diversity. Species richness is the most widely used measure (Magurran, 1998) and, as the 'common currency' of diversity measurement (Gaston & Spicer, 1998), it is important that it is examined. Magurran (1998) advocates the combination of a measure of species richness with a measure of dominance or evenness. Of the measures that combine species richness and evenness, the Shannon index is the most widely used (Magurran, 1998), although given its sensitivity to sample size there may be few

reasons for choosing it over species richness (Magurran, 2003). Simpson's index, and in particular its reciprocal, is a widely used alternative to the Shannon index (Magurran, 2003). A combination of the results for species richness and Simpson's reciprocal should therefore be informative. Whittaker's measure will be used to assess beta diversity. It is important to remember, however, that these indices do not distinguish between species and therefore cannot identify sites which contain regionally or nationally rare species. These sites may have low species richness but a higher conservation value compared with sites with a high species richness of common species.

Chapter 3 Epiphyte diversity of Sitka spruce and Japanese larch

3.1 INTRODUCTION

Epiphytes are known to be decreasing worldwide because of habitat destruction, forest operations and air pollution (Mitchell *et al.*, 2002). In Ireland, the dramatic reduction in the area of woodland over the last few thousand years is likely to have severely affected the extent and abundance of epiphytic communities (Humphrey *et al.*, 2002). Although there has been a recent increase in forest cover, this has been mainly as the result of plantations of exotic species, with Sitka spruce the predominant species (cf. **Section 1.1**). As there have been no studies of epiphytes in Irish plantation forests, the potential of these plantations to provide habitats for epiphytes in unknown. There is also little known about how these plantations might be managed to improve the habitat quality for epiphytes.

3.1.1 Diversity of Irish forestry plantations

The potential of plantations to provide habitats for woodland plant species in general was little studied prior to the commencement of the BIOFOREST project in 2001 (cf. **Section 1.3**). Doyle & Moore (1982) studied vascular plant and bryophyte communities in young (four- to twelve-year-old) Sitka spruce and lodgepole pine (*Pinus contorta*) plantations on blanket peat in Co. Mayo, tracking the changes in vegetation as the plantations matured. This mainly highlighted the reduction in typical bog vegetation and invasion of generalist species, with only the initial stages of woodland species colonisation recorded. Fahy & Gormally (1998) compared the vascular plant and bryophyte ground flora communities in a 34-year-old Sitka spruce plantation with a nearby 200-year-old semi-natural oakwood and a clearfelled conifer plantation. They found that plant species richness was greatest in the oakwood and lowest in the plantation. Magurran (1998) compared the ground vegetation in a maturing Sitka spruce plantation with a relic oakwood in Banagher, Northern Ireland. Again the oakwood was found to be more diverse than the plantation. More recently, Coroi *et al.* (2004) investigated the ground flora and bryophytes in streamside forests, which included semi-natural broadleaved woods, conifer plantations and mixed stands in counties Cork and Waterford. Sitka spruce was the dominant species in the conifer plantations, but hybrid larch (*Larix x. marschlinsii*) was also present. The authors found double the number of plant species in the semi-natural broadleaved stands compared to the conifer plantations.

These comparative studies have all found the ground vegetation of plantations, particularly Sitka spruce plantations, to be the least diverse of the habitats studied. However, these studies are site specific and provide little basis for generalisation. The BIOFOREST growth cycle project (Project 3.1.2, cf. **Section 1.3**) (French, 2005; Smith *et al.*, 2005) gave a comprehensive overview of the ground flora diversity of Sitka spruce, ash (*Fraxinus excelsior*) and larch (*Larix* spp.) plantations in a range of locations and over a range of forest ages. The investigators found that Sitka spruce plantations, particularly in the closed canopy stage, can have a negative impact on ground flora

diversity. However, they also found Sitka spruce forests to be important habitats for bryophyte diversity, with the structurally mature stands supporting the richest communities. Mature larch was found to support a less species-rich woodland flora than mature Sitka spruce (French, 2005). However, larch had a less impoverished vascular plant flora at the closed maturing stage and had higher ground flora cover, particularly of graminoids and bryophytes. Ash stands supported higher numbers of vascular species.

This information on ground flora communities in forestry plantations is important for the sustainable management of these forests. However, this information may not necessarily be useful in predicting epiphyte diversity, as epiphytes 'read' the environment differently to vascular plants (McCune & Antos, 1982). McCune & Antos (1981) found that, while the composition of one forest layer (tree, shrub, herb, bryoid or epiphyte) could be roughly predicted from another, the different strata did not change composition across environmental gradients at the same rate or in the same pattern. Forest management methods which enhance the diversity of the ground flora may not affect epiphytes in the same way. For this reason separate studies of epiphytes in plantation forests are needed.

3.1.2 Epiphytes in European forestry plantations

As previously stated, there have been no studies of epiphytes in Irish forestry plantations. There has also been little study of the epiphytes in intensively managed plantations of non-native species in Britain or the rest of Europe. In Britain, Humphrey *et al.*'s (2002) study of lichens and bryophytes in Sitka spruce and pine (*Pinus sylvestris*) plantations and semi-natural pine and oak (*Quercus* spp.) woodlands included the study of epiphytes on trees up to two metres, as well as species on rocks and deadwood. They found that plantations had a less species-rich lichen flora than semi-natural stands but bryophyte species richness was similar in both. However, they reported only a handful of species on substrates other than deadwood in Sitka spruce plantations. Bates *et al.* (1997) studied epiphytic bryophytes in a transect across southern Britain, which included areas of coniferous plantations. Conifer species (Norway spruce (*Picea abies*) and pine (*Pinus* spp.)), despite being quite commonly encountered, were found to support epiphytic bryophytes only infrequently. Vanderpoorten *et al.* (2004), in their study of obligate epiphytes in the Semois river basin (Belgium and France), which contains large areas of Norway spruce (*Picea abies*) plantations, found that spruce plantations had a negative impact on species diversity and abundance.

The main body of work in Europe comes from the managed forests of mainly native species in Norway, Sweden and Finland. Moe & Botnen (2000) studied the epiphytes on pollarded trunks of *Fraxinus excelsior* in four habitats in western Norway: a Norway spruce (*Picea abies*) plantation, deciduous wood, wooded hay meadow and open meadow. They found the plantation to be the

shadiest habitat, with very sparse epiphytic vegetation. Dettki & Esseen (2003) studied epiphytic lichen litter in an area of commercial forestry, in stands of various ages managed mainly by clearcutting, in northern Sweden. The stands were mainly composed of Scots pine (*Pinus sylvestris*), but also contained Norway spruce and deciduous trees. The combined biomass of all pendulous lichens was found to increase with forest age. Uliczka & Angelstam (1999) studied the epiphytic macrolichens of Scots pine, Norway spruce, birch (*Betula* spp.) and aspen (*Populus tremula*) in managed forests in south-central Sweden. As with Dettki & Esseen's (2003) results, they found that the number and abundance of lichen species increased with tree age. A number of other studies have compared managed and natural stands in terms of their epiphytes. In northern Sweden, Dettki & Esseen (1998) compared epiphytic macrolichens in stands managed by clearcutting with those in natural forests. Stands were composed of Norway spruce, Scots pine and deciduous trees, with Scots pine dominating in managed stands and Norway spruce in natural stands. Species richness was higher in the natural forests at the stand level. Esseen *et al.* (1996) compared epiphytic lichens of Norway spruce branches in stands managed by selective logging and natural regeneration with old-growth forests, also in northern Sweden. Old growth stands had six times higher lichen mass per spruce branch than mature managed stands. Halonen *et al.* (1991) studied epiphytic lichens on the trunks of Scots pine and Norway spruce in open commercial forests and dense natural or semi-natural forests in middle boreal Finland. They found a difference in species abundance between the two tree species with most lichens having lower cover on spruce. Certain species also favoured dense forests over more open forests and vice versa. Hyvärinen *et al.* (1992) studied epiphytic lichens in open, thinned and denser, near-natural stands dominated by either Scots pine or Norway spruce in central Finland. The distribution and abundance of lichens was dependent on the age of the stand with a slight increase in total cover of epiphytic lichens with age. The young stands in the 'managed' and 'near-natural' classes did not separate out in the ordination, indicating a similar species composition.

3.1.3 Epiphytes of Sitka spruce and Japanese larch in their native ranges

As well as the lack of information on epiphytes of forestry plantations (and of Sitka spruce and Japanese larch plantations in particular) in Ireland and other parts of Europe, there is also little published information on the epiphytes of Sitka spruce, and no known published information on the epiphytes of Japanese larch, in their native ranges. Peck *et al.* (1995) studied epiphytic bryophytes up to 5m on Sitka spruce, western red-cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) growing at Thermal Meadow, Queen Charlotte Islands, Canada. They found more species per tree on Sitka spruce and greatest cover on branches for Sitka spruce and western red-cedar but on the trunk from 3-5m for western hemlock. Glime & Hong (2002) studied the trunk epiphytes up to 3m on Sitka spruce, Alaska yellow-cedar (*Chamaecyparis nootkatensis*) and western hemlock on Graham Island, Queen Charlotte Islands. They found that tree species was of

little importance in determining epiphyte cover or presence of epiphyte taxa. Total and mean species richness was highest on western hemlock followed by Alaska yellow-cedar and Sitka spruce. Price & Hochachka (2001) compared lichen litterfall in stands with either Sitka spruce, western red-cedar or amabilis fir (*Abies amabilis*) - all growing in mixes with western hemlock - in western Vancouver Island, British Colombia. Sitka spruce mixes had the greatest lichen litterfall and amabilis fir mixes had more cyanolichens than western red-cedar or Sitka spruce mixes. Sillett and Bailey (2003) used rope techniques to study vascular epiphytes, and *Polypodium scouleri* in particular, in the crowns of Sitka spruce and redwood (*Sequoia sempervirens*) trees in an old-growth redwood forest in California. They found that, although redwoods supported larger fern mats than spruce, mainly as a result of larger branch diameters, the composition of these mats was almost identical. Ellyson & Sillett (2003) studied branch epiphytes over the entire height of the same Sitka spruce trees. They found that bryophytes dominated the epiphyte communities.

3.1.4 Differences in epiphytic vegetation between tree species

The question of whether different tree species differ in terms of their epiphytes has been the subject of much interest to researchers. Most of this research, however, has been on native species growing in natural or semi-natural situations (e.g. Bates, 1992; Bates & Brown, 1981; Cornelissen & ter Steege, 1989; Ellyson & Sillett, 2003; Eversman *et al.*, 1987; Glime & Hong, 2002; Halonen *et al.*, 1991; Hong & Glime, 1997; Hyvarinen *et al.*, 1992; Martin, 1938; Peck *et al.*, 1995; Trynoski & Glime, 1982; Uliczka & Angelstam, 1999). One exception is Bates *et al.*'s (1996) comparison of eight-year-old Sitka spruce, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) stands, growing under different SO_2 and O_3 regimes. However, this was limited to a study of the lichens *Evernia prunastri*, *Hypogymnia physodes* and *Lecanora conizaeoides* and was primarily concerned with the effects of pollution.

It is known that some tree species support more epiphytes than others (Barkman, 1958). Watson (1936) noted that, in Britain, birches and conifer species in general have the fewest epiphytes. Hale (1952), in a study of ten trees of five broadleaved and two coniferous species in the upland forests of southern Wisconsin, found that the conifers supported the smallest number of species of cryptogams per tree. Conversely, Esseen (1981), when studying the epiphytic macrolichens of four broadleaved and two coniferous species in spruce forests in Sweden, has found the largest numbers of species in total on Norway spruce. Of particular interest to researchers is whether epiphyte species exhibit host specificity. Host specificity can refer to the absolute restriction of an epiphytic species to a host species or it may refer to the ecological success of an epiphytic species, measured as cover, fertility, vitality or frequency (Studlar, 1982a). Hale (1952), in his study in Wisconsin, found that nearly every cryptogam had a preference for a certain tree or tree group and avoided other trees. Bates (1981), studying the epiphytes of oak and ash in native woods in Scotland,

recorded several epiphyte taxa on only one tree species. Some epiphyte species, however, appear to be indifferent to their host species (Hale, 1952). Hong & Glime (1997) found that some of the bryophyte and lichen taxa they recorded occurred on all of the single broadleaved and two coniferous species they studied on Ramsay Island. Studlar (1982a) found that only three of the more frequent species were restricted to one of five broadleaved and one coniferous tree species studied in a cove forest in Virginia. Similarly, Trynoski and Glime (1982) found that, of the bryophytes occurring on four broadleaved species studied, none was frequent on one species and absent on another. However, even where a particular species occurs on a range of host species, it may have greater vitality or occur more frequently on one host species. This means that some species of tree will differ in the relative abundances of different epiphytic species rather than in their overall epiphytic floras (Halonen *et al.*, 1991). Bates & Brown (1992), studying free-standing oak and ash trees in southwest England, found that, while only ten species were restricted to one or other tree species, many species which occurred on both trees had significantly higher cover values on one tree species. Cornelissen and ter Steege (1989), in a comparison between the epiphytic floras of two congeneric trees in a Guyanese rain forest, observed that, while only eight bryophytes and seven macrolichens were restricted to one species, 26 species of bryophytes were more common on *Eperua grandiflora* than *E. falcata* and eight species more common on *E. falcata*. Individual epiphytes may be common to many host species but occur in different combinations on different species (Barkman, 1958). Some authors have suggested that, rather than supporting different epiphyte species, different host species support different epiphyte communities (Jesberger & Sheard, 1973; Palmer, 1986; Schmitt & Slack, 1990). Jesberger & Sheard (1973) have suggested that variation between these communities is essentially discontinuous and discrete community groups can be recognised. Schmitt & Slack (1990), studying four broadleaved and one coniferous species in New York and North Carolina, found that lichen and bryophyte communities, and both combined, were specific to particular species. However Bates (1981) and Bates & Brown (1992) found that ordination either failed to separate or only partially separated the epiphytes of ash and oak, suggesting a more or less continuous pattern of floristic variation between these species.

It is clear that differences in epiphyte species or communities do exist among some host tree species. The exact causes of this are less clear. Differences in the structure of different trees can be important (Esseen, 1981). Trees with centrifugal crowns, which are strongly water absorbing, can be particularly poor in epiphytes (Barkman, 1958). The organisation of the branching system, and hence the number of different attachment points provided, can also influence the richness of the epiphytic vegetation (Esseen, 1981). The branches can also influence the microclimate of trunks by holding back showers and producing shade (Halonen *et al.*, 1991). This sheltering can have a positive effect by protecting epiphytes from fast desiccation, direct sunlight and wind (Eversman *et al.*, 1987). The physical structure of the bark is also an important factor. Trees with scaling bark tend to be poor in epiphytes (Barkman, 1958). Uliczka and Anglestam (1999) suggested that the

flaking bark of pine (*Pinus*) species was one of the reasons they had fewer fruticose and more foliose lichens than spruce (*Picea*). Kuusinen (1996a) also gave peeling bark as a factor explaining the low species richness and diversity on pine. Jesberger and Sheard (1973) suggested that the different species composition of four broadleaved and four coniferous species they studied in Saskatchewan was a response, at least partly, to differences in the scaliness of the bark. Rough-barked trees should also support more species and have a greater range of microhabitats than smooth-barked trees (Studlar, 1982a). McGee & Kimmerer (2002) found the greatest cover of bryophytes on broadleaved trees with thick, coarse, textured bark. Cornelissen & ter Steege (1989) concluded that the fissured bark of *Eperua grandiflora* was one of the main reasons for its greater bryophyte cover and the pronounced host preference of many bryophytes compared to the smooth-barked *E. falcata*. However, bark texture can change with age and with height in the tree (Cornelissen & ter Steege, 1989; Studlar, 1982b). The water capacity of the bark is also important (Barkman, 1958). This was one of the factors Hale (1952) found could be correlated with host specificity on trees in Wisconsin. Studlar (1982a) also found that epiphyte communities could be ordered according to water absorption capacity to some extent.

Bark chemical factors have been focussed on by many authors as one of the main causes of the difference in epiphytes among host species (e.g. Bates, 1992; Bates & Brown, 1981; Kuusinen, 1996a). Bates *et al.* (1996) suggested the more acidic bark pH of Scots pine as a reason for its lower abundance of *Hypogymnia physodes* and *Lecanora conizaeoides* compared with Sitka spruce or Norway spruce. Studlar (1982a) found that epiphyte communities on five broadleaved and one coniferous species in Virginia could be ordered according to increasing bark acidity. However, Culberson (1955) found no apparent relationship between pH and the species richness of four coniferous and five broadleaved species studied in northern Wisconsin. It is important to remember that bark pH is not a measure of all the organic chemicals present in bark and too strong reliance on pH values can lead to other, possibly more important factors being overlooked (Hale, 1955). Barkman (1958) has stressed the importance of total electrolyte concentration and the buffer capacity of bark in determining the distribution of epiphytes. The pH among trees of a single species can also vary, leading to an overlap in pH values between tree species (Bates, 1992). Kuusinen (1996a) was able to divide the six broadleaved and coniferous species he studied in Finland into three groups according to their bark pH. It has been suggested that, rather than responding to the biological species of the host or any phorophyte dependent nutritional factors, epiphytes respond to the intensities of bark chemical variables, such as pH, Mg, K and Ca concentrations (Bates, 1992; Bates & Brown, 1981). The same gradients of bark characteristics may exist in two geographically separated sites even if the phorophyte species are not shared (Palmer, 1986).

Other factors which may confound the effect of host-specific factors must also be taken into consideration when studying differences in host preference among epiphytes. For example, Hyvarinen *et al.* (1992) found that stand age was more important than host tree in determining the species composition on spruce (*Picea*) and pine (*Pinus*) in Finland. Stand structure also has an influence on epiphytic vegetation, with variation between open and dense woods (Barkman, 1958). Culberson (1955) concluded that, while substrate factors are the most important factors governing the composition of bark vegetation in a closed forest in a region of relatively homogeneous vegetation, the influence of climatic gradients should not be ignored. A favourable climate can make up for an unfavourable substrate; for instance, bark with a low water capacity can be compensated for by high humidity levels (Barkman, 1958). Hale (1955) found that, while bark factors such as pH and moisture capacity seemed to be important in determining host specificity, these factors were superseded by the environment of widely separated stands, with the same tree species supporting different epiphytes species under differing moisture regimes. Trynoski (1982) also pointed out that host preference might not be the only factor involved in the distribution of epiphytes, since competitive pressures may exclude less competitive species from favourable host species. This suggests that epiphytes can have optimum or compromise habitats (Barkman, 1958). However, most researchers feel that both physical and chemical factors of the host bark play a large part in determining epiphyte-phorophyte associations within a forest, with environmental factors interacting (Trynoski & Glime, 1982).

3.1.5 Vertical distribution of epiphytes

When ecologists try to understand the variation resulting from the structural complexity of a forest, the vertical gradient attracts a great deal of interest (McCune *et al.*, 2000). The attraction of studies of vertical distribution lies in the fact that a range of ecological conditions are compressed into the vertical height of a tree and development of epiphytic species along this gradient can be accurately measured (Hale, 1965). No single environmental factor will control the spatial distribution and abundance of an epiphyte (Kershaw, 1964), but a mechanistic separation of the various environmental factors influencing epiphytes is not possible without detailed measurements (Sillett, 1995). However, it is known that both light intensity and evaporation increase with height in forests and that water capacity and rate of absorption of the bark decrease (Barkman, 1958). This combination of factors is often reflected in vertical zonation of species (Barkman, 1958), which is often exhibited as a change in abundance from one zone to another, rather than a change of presence to absence (Harris, 1971). Cornelissen & ter Steege (1989) suggest that the lowest occurrence of a canopy species is determined by illumination and the uppermost occurrence of a trunk species by humidity. However, this zonation may also reflect the responses of particular species to the other factors (Studlar, 1982b). Bark age and chemistry are considered to be important factors (Pentecost, 1998). The upper trunk will be younger than the lower trunk and some authors

have used vertical distribution to infer successional trends (Studlar, 1982b). Bark pH and levels of tannins and resins in the bark can vary with height and this can also affect epiphytes (Studlar, 1982b). Life strategies in terms of interspecific competition, avoidance of competition and rapid colonisation are also major factors (Cornelissen & ter Steege, 1989). Sillett (1995) suggests that the preferences for different crown positions are probably a result of the interplay between desiccation tolerances and competitive abilities.

What most studies have in common is that they have observed that epiphyte composition changes with height in the canopy (McCune *et al.*, 2000). However, distance from the ground has little meaning on its own and is only a rough substitute for other factors that have more ecological importance (Parker & Brown, 2000). Other habitat variation is present besides the variation with height (McCune *et al.*, 2000) and the fact that environmental factors are thoroughly confounded with structure and succession (McCune, 1993) makes it even more difficult to explain the distribution of epiphytic lichens. McCune (1993) has put forward the similar gradient hypothesis. This proposes that epiphyte species are ordered similarly on three distinct spatial and temporal gradients: 1) vertical differences in species composition within a given stand, 2) species compositional differences among stands differing in moisture regime but of the same age, and 3) changes in species composition through time in a given stand. However, in tall forests in moist environments, epiphytes are strongly stratified with height. (McCune *et al.*, 2000).

The distribution of species around a phorophyte is also not homogeneous (Franks & Bergstrom, 2000). This is as a result of variation in microclimatic factors among aspects. There is variation in illumination, prevailing wind direction and direction of rain bearing winds (Barkman, 1958). The difference between north and south sides of the tree is mainly attributed to the declination of the sun which affects temperature, evaporation rates and light intensity (Trynoski & Glime, 1982). The highest annual light sum is on the south side of the tree in the northern hemisphere, therefore this side has the maximum temperature and evaporation (Barkman, 1958). There is least variation with aspect on vertical trunks in dense forests and deep shaded ravines (Barkman, 1958). Some factors such as available moisture will change with both height and direction of exposure, so, for example, floras of higher levels on moist aspects will resemble those of lower levels on dry aspects (Franks & Bergstrom, 2000).

3.1.6 Contribution of epiphytes to overall plant diversity

The importance of epiphytes has previously been discussed (cf. **Section 1.4**), however it is necessary also to put epiphyte diversity into the context of overall plant diversity. It is estimated that vascular epiphytes account for 10% of the total vascular plant diversity (Nadkarni *et al.*, 2001). The percentage of epiphytic plants would increase if non-vascular species were also included (Wolf

& Flamenco-S, 2003). In general bryophytes account for 9-10% of total plant diversity. Smith (1982) has estimated that, in Britain, of the 781 bryophyte species, there are 33 obligate epiphytes and about 44 facultative epiphytes. However, no one has calculated the number of non-vascular plants occurring as epiphytes worldwide as the idea of an obligate epiphyte is a "slippery concept" (Nadkarni *et al.*, 2001).

When considering the contribution of epiphytes to overall diversity, it is important to clarify which forms of epiphyte are being considered. Barkman (1958) uses the term holoepiphyte for forms that pass their whole life on the host plant. Hemiepiphytes, on the other hand, have an 'umbilical' connection to the ground at some point in their lives (Nadkarni *et al.*, 2001). Different degrees of epiphytism have also been described. An obligate epiphyte is a plant that always grows epiphytically (Nadkarni *et al.*, 2001). However, the idea of an obligate epiphyte is a subjective concept. Oliver (1930) refers instead to typical epiphytes, which are species that are habitually epiphytic, but not necessarily exclusively so, though some may not have been recorded on other substrates. Benzing (1990) uses the term facultative epiphyte, to refer to species growing regularly to maturity both at ground level and as epiphytes. The term occasional epiphyte is used for species that are usually terrestrial within a study area (or occur on rocks i.e. saxicolous), but which occasionally occur as epiphytes (Benzing, 1990; Oliver, 1930). Ephemeral or accidental epiphytes are species whose juvenile stages can occur as epiphytes but which cannot usually mature in their epiphytic position (Benzing, 1990; Oliver, 1930).

Several researchers have attempted to quantify the contribution of epiphytes to the overall plant diversity of an area. Nieder (2001) refers to holoepiphytism degrees, which he defines as the percentage of epiphyte species in the total flora of a country or region. The epiphyte quotient of Hosokawa (1950), which represents the percentage of typical epiphytes (or epiphyta typica) out of all the vascular plants in a forest flora or vegetation sampling unit, works at a smaller scale. This index puts epiphyte diversity into the context of overall plant diversity in a given study area (Nieder *et al.*, 2001). When climatic conditions, especially precipitation and air moisture, differ between sites, the values of their epiphyte quotient will also differ (Hosokawa, 1950). Nieder (2001) estimated the epiphyte quotient of a montane rain forest in western Venezuela to be 45%. Kelly *et al.* (2004) gave a figure of 52% for a forest in the same region. Gentry (1987) gave a figure of 22% for a lowland wet tropical forest in western Ecuador and Nieder (2001) a figure of 28% for an upland Ecuadorian stand. When comparing studies it is important to remember that epiphytes will contribute more in smaller plots, because their accumulation curves per ground surface area are steeper than those of forest trees (Wolf & Flamenco-S, 2003). The epiphyte quotient can also be prejudiced by edge effects if the epiphytes in the crown boundary outside a plot are included. Transect studies are particularly subject to this source of error (Wolf & Flamenco-S, 2003).

All of the studies mentioned above, and all of the published work on epiphyte quotients, come from the tropics and refer only to vascular epiphytes. Clearly there is a major gap in our knowledge of the contribution of epiphytes to overall plant diversity in temperate regions. In Ireland, while less than 10% of European flowering plants occur, about 51% of European liverworts and an almost equally rich moss flora is found (Holyoak, 2003). The proportion of European lichens occurring in Ireland is more difficult to ascertain, as an overall European lichen checklist does not exist. However, of the 2272 lichens and lichenicolous fungi occurring in Great Britain and Ireland (British Lichen Society, 2007), 1161 (51%) are found in Ireland (LichenIreland, 2007). This compares with 2202 species in Germany, 3053 species in mainland Spain and 2054 species in Norway (Universität Hamburg, 2007). This means that the native woods have a relative poverty of vascular plant flora and non-vascular species are the main epiphytic groups (Kelly, 2000). The richness of Ireland's non-vascular flora is related to its climate. At the European scale, the whole of Ireland has an Oceanic climate (Hill & Preston, 1998), although there is a strong east-west gradient in rainfall and humidity across the island, as there is in Britain. However, the presence of the coastal mountain belt means that many areas of the east still have a wet climate (Ratcliffe, 1968). The result is one of the richest bryophyte floras in Europe, particularly of Atlantic bryophytes, that is shared only with western Scotland (Holyoak, 2003). This means that the contribution of non-vascular epiphytes to overall plant diversity is of particular interest.

3.2 METHODS

3.2.1 Measuring diversity and cover

Species richness, diversity (cf. **Section 2.7**) and cover were assessed at a number of different levels. The species richness, diversity and cover of the total epiphyte flora (referred to as 'total epiphyte richness', 'total epiphyte diversity' and 'total epiphyte cover') were assessed, as well as the diversity and cover of the bryophyte, lichen and vascular plant flora and in some cases also the eight bryophyte and lichen growth-forms (cf. **Section 2.4.1**). Species richness, diversity and cover were assessed for individual 25x50cm plots. Each individual tree was considered as a whole, and the trunk (T) and branch system (B) were also considered separately. The species richness (SR_C) of each individual tree was assessed using the combined data derived from all 25x50cm plots studied on each tree to give an absolute species count. The diversity of each tree was assessed, using Simpson's reciprocal, by taking the mean diversity of all 25x50cm trunk and branch plots ($1/D_M$) on each tree. Beta diversity was assessed using Whittaker's index (β_w) (cf. **Section 2.7.4**) to examine the compositional variation of the eight trunk plots studied on each individual tree. The mean species richness (SR_{MT}), diversity ($1/D_{MT}$) and cover ($Cover_{MT}$) of all eight trunk plots on each tree were also considered. The mean species richness in branch plots was not calculated since the area available for epiphyte colonisation differed among plots (cf. **Figure 2.3**). However, the mean diversity ($1/D_{MB}$) and cover ($Cover_{MB}$) of epiphytes in the six to twelve branch plots on each

tree was calculated; in the case of cover, the cover of epiphytes was converted to a percentage of the total cover of branches within each plot.

3.2.2 Statistical analyses

Independent samples t-tests, or the non-parametric equivalent Mann-Whitney U tests, were used to identify differences in the diversity and cover of epiphytes between the two tree species and the two geographic regions and in considering other independent factors. For comparisons of the north and south sides of trees, paired samples t-tests or the non-parametric equivalent Wilcoxon signed ranks tests were used. One-way ANOVA, or the non-parametric equivalent, Kruskal-Wallis test, with Tukey's HSD or Tamhane's test for unequal variances as the post-hoc multiple comparison test, were used to compare species richness, diversity and cover among the different height zones on the trees and among inner, mid and outer branch plots. The Levene statistic was used to test for equality of group variances.

To assess the relationship between species diversity and environmental variables, linear regressions were used. Bonferroni corrections were not used due to the fact that, when there are a relatively low number of regressions carried out, these corrections may cause the significance of real relationships to be lost. Therefore, where significant relationships were found, the form of the relationship was investigated in more detail and these relationships were viewed with caution where they did not appear to be ecologically meaningful. Prior to any parametric statistical testing, the Kolmogorov-Smirnov procedure was used to confirm normality. Statistical analyses were carried out using SPSS version 11.0.1 (SPSS, 2001).

3.2.3 Non-metric multidimensional scaling (NMS)

Ordination attempts to express many-dimensional relationships in a small number of dimensions by the ordering of objects along axes according to their resemblances (McCune & Mefford, 1999). Non-metric multidimensional scaling (NMS) is an indirect gradient analysis ordination technique. In indirect gradient analysis, sample units are positioned according to covariation and association among the species. Correlations between environmental variables and the ordination axes are subsequently calculated. NMS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k-dimensional configuration (McCune & Mefford, 1999). This technique is well suited to data that are non-normal or are on arbitrary, discontinuous, or otherwise questionable scales (McCune & Mefford, 1999).

When examining between-tree variation, the sum of the cover data in all plots on each tree was used. For between-trunk plot variation the cover values for each 25x50cm plot were used. Sørensen (Bray-Curtis) distance measures were used. A random starting configuration was applied and 20

runs with real data were performed. Ten iterations were undertaken to evaluate the stability of the final solution or a maximum of 250 iterations if the pre-defined criterion of stability was not met. A final stability of less than 0.0005 was selected and the stability of the final solution was assessed by examining the final stress versus iteration plot. Monte Carlo testing (with 50 randomised runs) was used to evaluate whether the NMS ordination extracted stronger axes than expected by chance. The proportion of variance represented by each axis (r^2), and the correlation coefficients between the ordination axes and selected diversity and environmental variables, were calculated to aid interpretation of the NMS ordination diagram. The NMS ordination diagram was rotated so that the relationship between total epiphyte richness and axis 1 was maximised, in order to assist with the identification of factors which may be important in determining epiphyte diversity.

Groups of trees and trunk and branch plots with similar epiphyte assemblages were identified using flexible-beta hierarchical cluster analysis on Sørensen distance measures with the parameter β set to -0.25. This setting of β produces a solution intermediate between single-linkage and complete-linkage agglomerative clustering (Legendre & Legendre, 1998). Indicator species analysis was used to identify the appropriate level of clustering. Good indicator species should be found mostly in a single cluster and should be present on most of the trees belonging to that cluster. The indicator value is 100% when a species is observed on all trees belonging to a single cluster and on no trees in the other clusters (Legendre & Legendre, 1998). Species with indicator values of more than 25% are considered to be the best indicators (Dufrene & Legendre, 1997). Dufrene and Legendre (1997) found that indicator values peak at some intermediate level of clustering, and that this peak will vary. Monte Carlo testing was used to assess the significance of the indicator values. Average significance (p-value) of the species indicators plotted against the number of clusters, and a plot of the number of significant species indicators against the number of clusters, were used to identify the most suitable number of cluster groupings. Indicator species analysis was also used to identify species characteristic of the different tree species. NMS, cluster and indicator species analysis were carried out using PC-ORD for Windows version 4.01 (McCune & Mefford, 1997).

3.2.4 Bark analyses

The bark of Sitka spruce and Japanese larch trees was studied in order to make a comparison between the two species. Pairs of trees, one spruce and one larch, were studied at three sites: MUNG, FURY and COOM. Notes were taken on the bark texture of the studied trees. Pieces of bark were removed with a knife from each trunk plot (cf. **Figure 2.3**), making a total of eight samples from each tree. Each piece of bark was stored in a separate plastic bag until it was returned to the laboratory.

3.2.4.1 Water absorption capacity

Water absorption capacity was determined following the method of Studlar (1982a) for 8g to 36g samples. The bark samples were air-dried for twelve hours and all epiphytes were removed where possible using a stiff brush. The cut surfaces were coated with candle wax and the samples were weighed. The samples were then immersed in water for 15 minutes before being removed, blotted dry for ten seconds, and reweighed. Water absorption capacity was expressed as a percentage of the dry weight of the bark.

3.2.4.2 Bark pH

Bark pH was determined following a combination of the methodology of Farmer *et al.* (1990) and Gustafsson & Eriksson (1995). Two small pieces of bark with a total surface area of approximately $1cm^2$ were taken from each of the eight samples. All epiphytes were removed where possible. The cut surfaces were coated with candle wax and each piece was placed in a small beaker containing 10ml of 25mM KCl solution for ten minutes. The bark pieces were then removed and the pH of the solution measured using a pH meter with a glass electrode. Although pH values obtained using KCl are not directly comparable to values obtained using ground bark and deionised water, the former method is more likely to record the bark pH of the actual environment experienced by the epiphytes (Farmer *et al.*, 1990).

3.3 RESULTS

3.3.1 Overall diversity

A total of 767 plots were studied on 40 trees; 320 trunk plots and 447 branch plots. A total of 83 plots contained no epiphyte species. Ninety epiphyte species were recorded in the plots in total. The 33 bryophytes consisted of 21 moss and twelve liverwort species and of five turf, five weft, 20 mat and three cushion species. The 54 lichens consisted of 26 crustose, one leprose, 18 foliose and nine fruticose species (**Appendix 3**). Three vascular plant species were also recorded, one of which was a juvenile pteridophyte species not identifiable to genus level. A total of 40 of the species recorded were classified as having a high affinity for epiphytism (cf. **Section 2.4.1**): two cushion and six mat bryophytes, and 18 crustose, six foliose and eight fruticose lichens. Five additional lichen species were also encountered on the studied branches outside the plots. These consisted of two crustose, and three foliose lichens; three of these were classified as having a high affinity for epiphytism.

3.3.1.1 Rare species

There are currently no red data books for bryophytes and lichens in existence for Ireland, although all-Ireland bryophyte and lichen red data books are in the process of being compiled. One of the species recorded on Sitka spruce, *Daltonia splachnoides*, is listed as 'Vulnerable' in the *Red Data*

Book of British Mosses and Liverworts (Church *et al.*, 2001). It is also likely to appear on the Irish red list, although a number of recent records mean it may be classified as 'Near Threatened' (D. Holyoak, pers. comm.). Another species recorded on spruce in this study, *Plagiothecium laetum*, is also likely to appear on the Irish red list (D. Holyoak, pers. comm.) and its two records in this study constitute only the 3rd and 4th records of this species in Ireland. None of the lichen species appears in the *British Red Data Book for Lichens* (Church, 1996), although two of the species recorded on spruce, *Byssoloma subdiscordans* and *Usnea esperantiana*, are listed as 'Near Threatened' in the *Conservation Evaluation of British Lichens* (Woods & Coppins, 2003). A total of six species encountered in the course of the study were new vice-county records (Holyoak, 2003; Seaward, 1994) (**Table 3.1**).

Table 3.1 New vice-county record species recorded in the study

	Vice-county number	Vice-county
Colura calyptrifolia	H20	Wicklow
Daltonia splachnoides	H4	Mid Cork
Plagiothecium laetum	H20	Wicklow
Gyalideopsis anastomosans	H3, H4	West Cork, Mid Cork
Lecanora pulicaris	H21	Dublin
Usnea esperantiana	H2	North Kerry

A number of indices have been developed which use the presence of certain species of lichens as indicators of the ecological continuity of deciduous woodlands (Coppins & Coppins, 2002). Two of these indices are applicable to Ireland. Two species listed on the New Index of Ecological Continuity (NIEC) (Coppins & Coppins, 2002) were encountered in the course of this study. *Anisomeridium ranunculosporum* was recorded on Japanese larch in one stand (COOM) and *Dimerella lutea* was recorded on both spruce and larch in a number of stands. *Anisomeridium ranunculosporum* is not included in the Western Scotland Index of Ecological Continuity as it is not a good indicator in the west; COOM is one of the most westerly sites studied. *Dimerella lutea* also appears in the Western Ireland Index of Ecological Continuity which is applicable to sites in the southwest and extreme west of Ireland.

The remainder of this chapter will deal with the results for the forest interior trees only. Results for the open space edge trees will be covered in **Chapter 4**.

3.3.2 Epiphyte diversity of the forest interior trees

3.3.2.1 Tree diversity

A total of 28 forest interior trees were studied: 17 Sitka spruce and eleven Japanese larch trees. A total of 82 species of epiphytes were recorded on these trees (**Table 3.2, Appendix 3**). More species were recorded in total on Sitka spruce than on Japanese larch due to the greater number of bryophyte species recorded on spruce than on larch (**Table 3.2**). A total of 36 species with a high

affinity for epiphytism were recorded (**Table 3.3**). Slightly more species with a high affinity for epiphytism were recorded on spruce. The species accumulation curves for both spruce and larch (**Figure 3.1**) do not plateau, indicating that the number of trees sampled will have strongly affected the total number of species recorded and that an accurate estimate of the number of epiphyte species occurring on each tree species is not possible.

Table 3.2 The total number of epiphyte species and the number of bryophyte, lichen and vascular plant species recorded on all trees and all Sitka spruce and Japanese larch trees

	n	Total	Bryophyte	Lichen	Vascular
All trees	28	82	29	50	3
Spruce	17	63	26	36	1
Larch	11	59	21	36	2

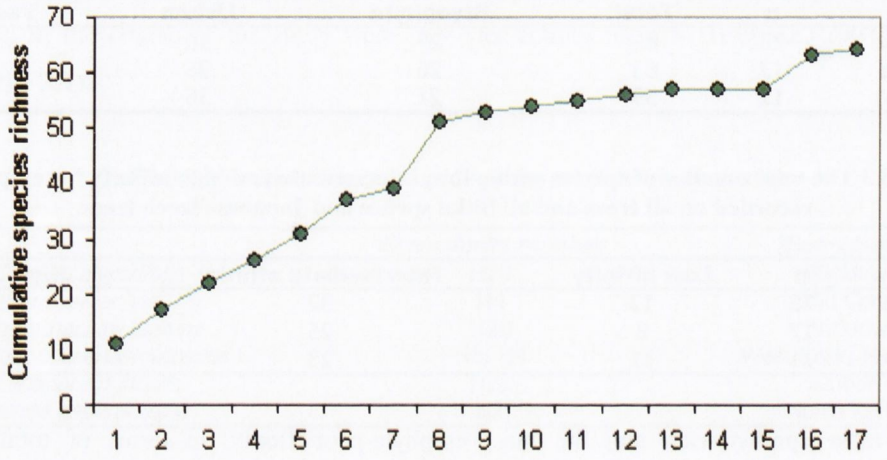
Table 3.3 The total number of species with a low, intermediate and high affinity for epiphytism recorded on all trees and all Sitka spruce and Japanese larch trees.

	n	Low affinity	Intermediate affinity	High affinity
All trees	28	13	32	36
Spruce	17	8	25	29
Larch	11	11	23	25

Both the most epiphyte-rich and the most epiphyte-poor floras, in terms of total epiphyte, bryophyte and lichen richness, were recorded on Sitka spruce trees. The most epiphyte-rich tree was KNOC2, a spruce tree from the Cork cluster, with an SR_C of 26 (**Figure 3.2**). This tree was also the most lichen-rich, with a lichen SR_C of 16. The most bryophyte-rich tree was FURY2, also a spruce tree from the Cork cluster, with a bryophyte SR_C of 15. The most epiphyte-poor tree was TIKN1, a spruce tree from the Wicklow cluster, with an SR_C of two. This tree was especially species-poor compared to the other trees studied (**Figure 3.2**). The next most species-poor tree was a Wicklow cluster larch tree, MUNG1, with an SR_C of ten.

The mean total epiphyte richness (SR_C) was higher on larch trees than on spruce trees (**Figure 3.3**). This was due to a significantly higher lichen SR_C on larch (independent samples t-test: $p = 0.026$). There were no significant differences in the number of species with either low (Mann-Whitney U test: $p = 0.133$) intermediate (independent samples t-test: $p = 0.230$) or high (Mann-Whitney U test: $p = 0.460$) affinities for epiphytism between Sitka spruce and Japanese larch (**Figure 3.4**). The total epiphyte SR_C was significantly higher for the Cork cluster trees than the Wicklow cluster trees (independent samples t-test: $p < 0.001$), as was the bryophyte richness (Mann-Whitney U test: $p < 0.001$) (**Table 3.4**). There was also a significantly greater number of species in all categories of epiphyte affinity on the trees in the Cork cluster compared to those in the Wicklow cluster (Mann-Whitney U test, low $p = 0.028$; independent samples t-test, intermediate $p = 0.001$; Mann-Whitney U test, high $p = 0.001$) (**Table 3.5**).

(a)



(b)

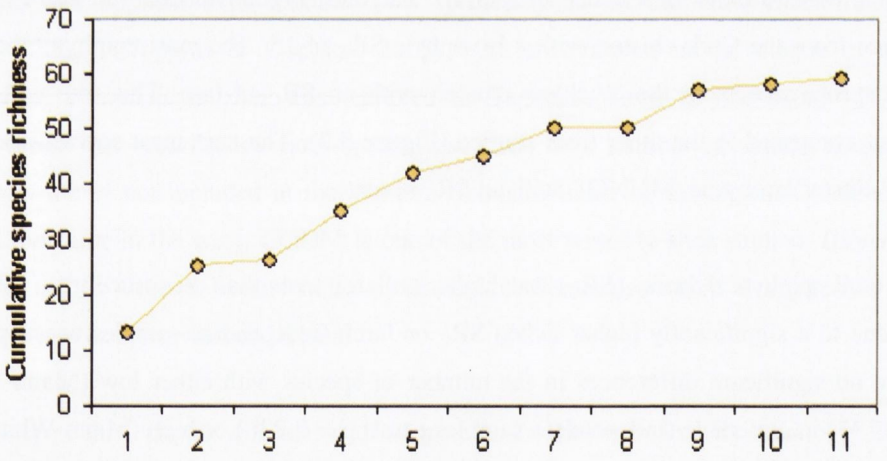
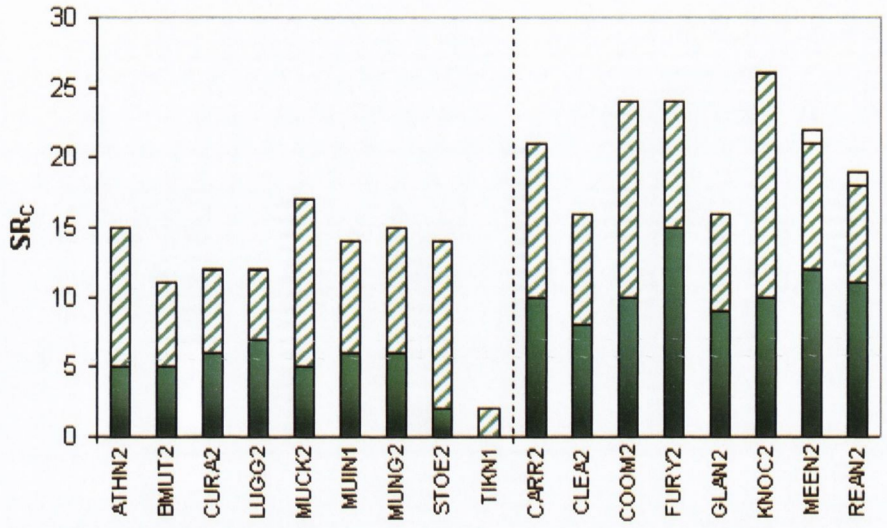


Figure 3.1 Total epiphyte species accumulation curves for (a) Sitka spruce and (b) Japanese larch.

(a)



(b)

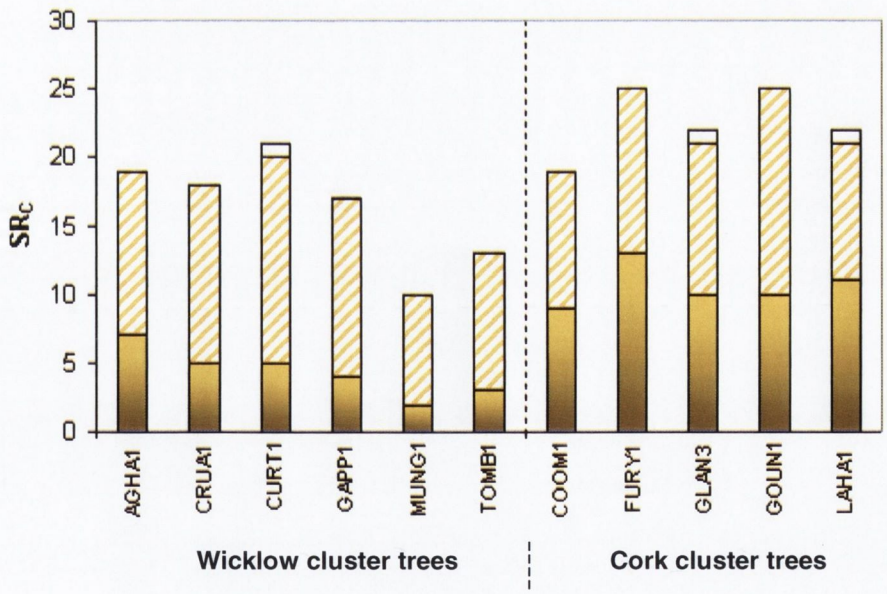


Figure 3.2 Epiphyte species richness (SR_C) of the (a) Sitka spruce and (b) Japanese larch trees. The total epiphyte richness is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant (unshaded) species are indicated.

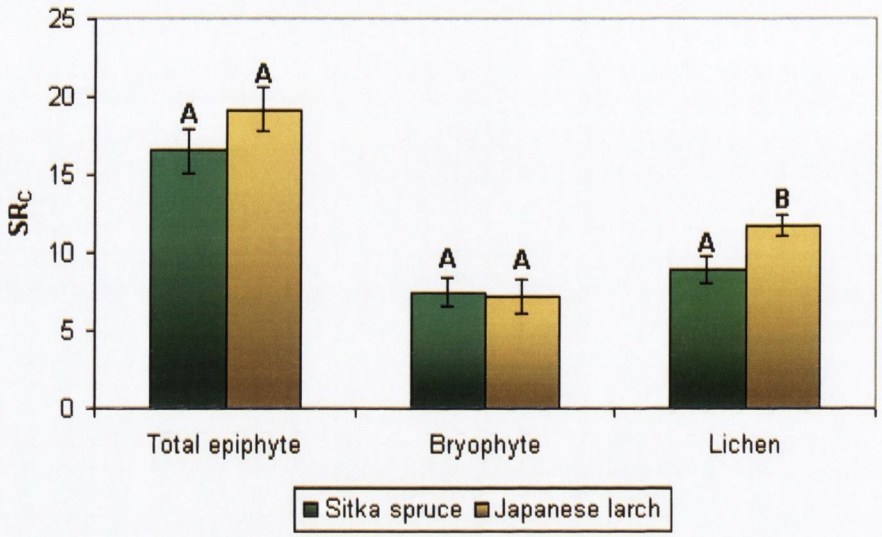


Figure 3.3 Mean epiphyte species richness (SR_C) of Sitka spruce (n = 17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in species richness between the two tree species if indicated by the same letter.

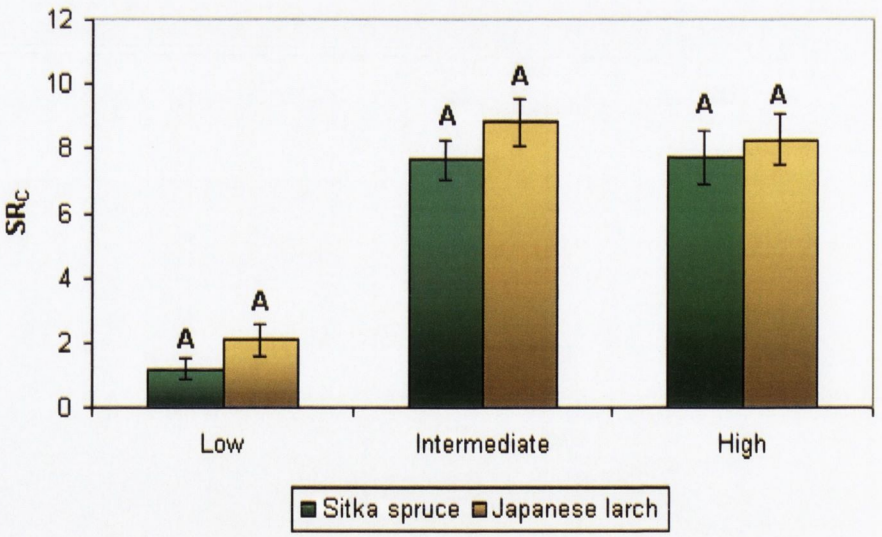


Figure 3.4 Mean epiphyte species richness (SR_C) of species with a low, intermediate and high affinity for epiphytism on Sitka spruce (n = 17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in species richness between the two tree species if indicated by the same letter.

The mean diversity of all plots (trunk and branch) studied on each tree was examined. The tree with the highest mean total epiphyte diversity of all plots ($1/D_M$) was FURY1, a larch tree from the Cork cluster, with a $1/D_M$ of 4.4 (**Figure 3.5**). This was also the most lichen diverse tree on average witha lichen $1/D_M$ of 3.2. The most bryophyte-diverse tree on average was KNOC2, a spruce tree from the Cork cluster with a bryophyte $1/D_M$ of 2.4. There was a close to significantly higher total epiphyte $1/D_M$ on larch (independent samples t-test: $p = 0.068$) and lichen diversity was significantly higher on larch (independent samples t-test: $p < 0.001$) compared with spruce (**Figure 3.6**). Total epiphyte $1/D_M$ and bryophyte $1/D_M$ were significantly higher on the trees in the Cork cluster (independent samples t-test: total epiphyte, $p = 0.025$; bryophyte, $p < 0.001$) (**Table 3.6**).

Table 3.4. Mean (± standard error) total epiphyte, bryophyte and lichen richness (SR_C) for all trees in the Wicklow and Cork clusters. There are no significant differences in species richness between the geographic clusters if indicated by the same letter.

	n	Total epiphyte SR_C	Bryophyte SR_C	Lichen SR_C
Wicklow	15	14.1 (± 1.2)^a	4.5 (± 0.5)^a	9.5 (± 0.9)^a
Cork	13	21.7 (± 0.9)^b	10.6 (± 0.5)^b	10.7 (± 0.8)^a

Table 3.5 Mean (± standard error) epiphyte species richness (SR_C) of species with a low, intermediate and high affinity for epiphytism for all trees in the Wicklow and Cork clusters. There are no significant differences in species richness between the geographic clusters if indicated by the same letter.

	n	Low affinity SR_C	Intermediate affinity SR_C	High affinity SR_C
Wicklow	15	0.9 (± 0.3)^a	6.8 (± 0.6)^a	6.3 (± 0.6)^a
Cork	13	2.2 (± 0.4)^b	9.6 (± 0.5)^b	9.8 (± 0.8)^b

Table 3.6 Mean (± standard error) of the mean total epiphyte, bryophyte and lichen diversity ($1/D_M$) of all plots on each tree, according to Simpson's reciprocal, for all trees in the Wicklow and Cork clusters. There are no significant differences in diversity between the geographic clusters if indicated by the same letter.

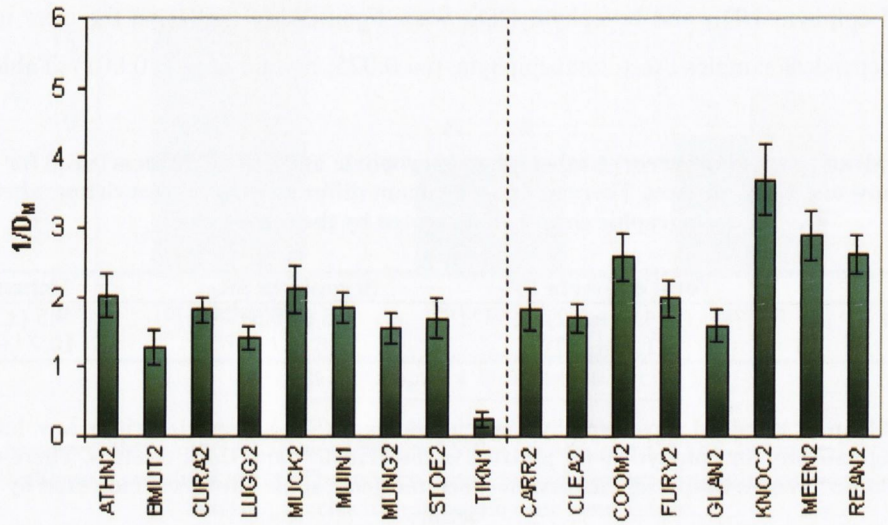
	n	Total epiphyte $1/D_M$	Bryophyte $1/D_M$	Lichen $1/D_M$
Wicklow	15	1.8 (± 0.2)^a	0.5 (± 0.1)^a	1.6 (± 0.2)^a
Cork	13	2.5 (± 0.2)^b	1.5 (± 0.1)^b	1.5 (± 0.2)^a

There was a significant positive relationship between the total epiphyte richness and the mean total epiphyte diversity of both the Sitka spruce ($r^2 = 0.750$, $p < 0.001$) and Japanese larch trees ($r^2 = 0.537$, $p = 0.010$) (**Figure 3.7**). This suggests that the more species-rich floras overall are more even at the plot level (i.e. no one species dominates in the plots).

3.3.2.2 Trunk diversity

A total of 64 species were recorded on the trunks of the trees (**Table 3.7**). The 27 bryophyte species recorded consisted of 17 moss and ten liverwort species and of three turfs, five wefts, 17 mats and two cushions. The 34 lichen species consisted of 16 crustose, one leprose, ten foliose and seven fruticose species. There were more epiphyte species recorded in total on the trunks of Japanese

(a)



(b)

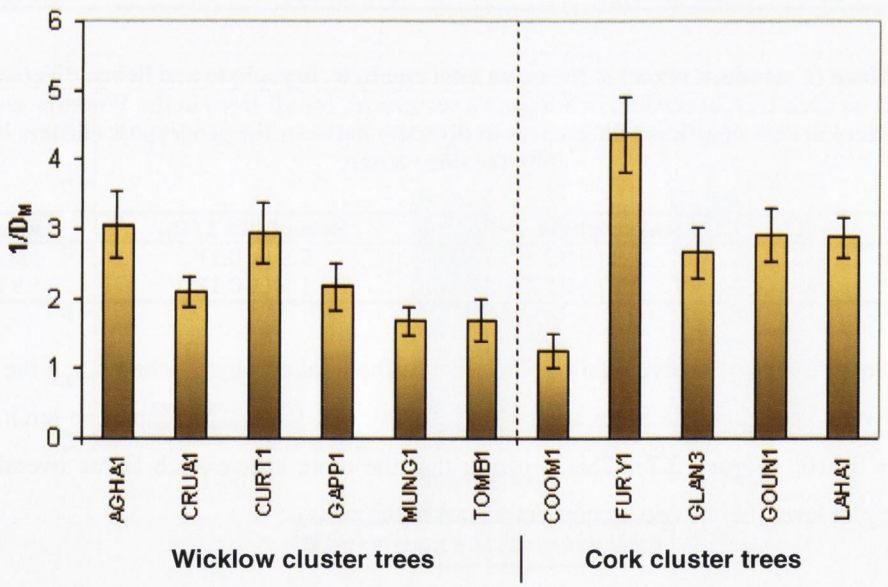


Figure 3.5 Mean Simpson's reciprocal diversity ($1/D_M$) of all plots studied on the (a) Sitka spruce (n = 17-20) and (b) Japanese larch trees (n = 14-20). Error bars indicate ± standard error.

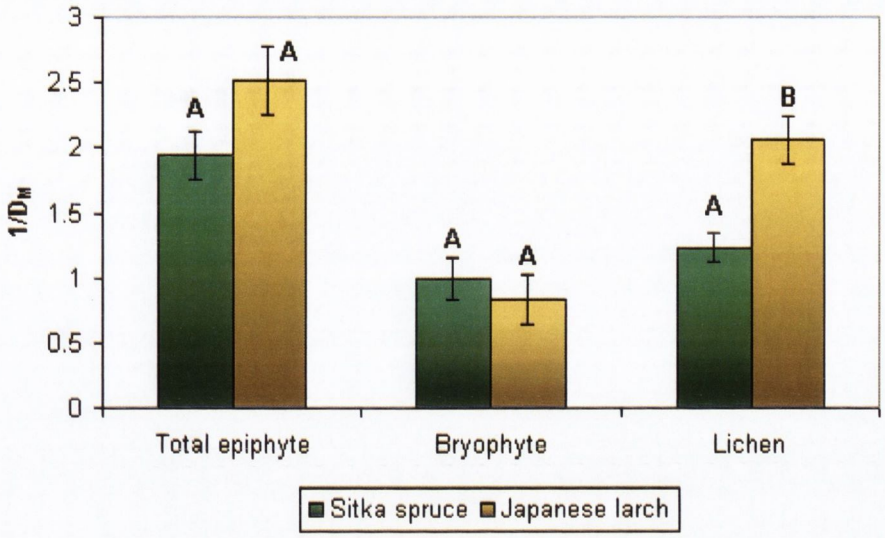


Figure 3.6 Mean of the mean Simpson's reciprocal diversity of all plots studied ($1/D_M$) on Sitka spruce (n = 17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in diversity between the two tree species if indicated by the same letter.

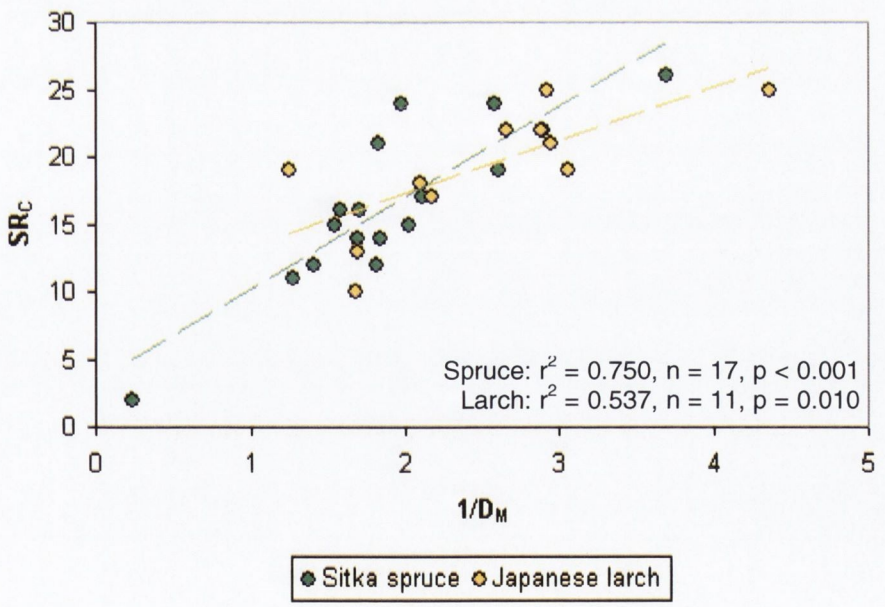


Figure 3.7 Relationship between the mean Simpson's reciprocal diversity ($1/D_M$) and the total epiphyte richness (SR_C) for Sitka spruce (n = 17) and Japanese larch (n = 11).

larch than of Sitka spruce (**Table 3.7**). Again the difference was mainly due to the greater number of lichen species recorded on larch. A total of 13 species were recorded only in trunk plots and not in branch plots on Sitka spruce: eleven bryophyte, one lichen and one vascular plant species. On Japanese larch, 22 species were recorded only in trunk plots: twelve bryophyte, eight lichen and two vascular plant species. However, only a total of 19 of the species recorded only in trunk plots occurred in more than one trunk plot (**Table 3.8**). The majority of species only occurring on trunks were mosses, liverworts, vascular plants and *Cladonia* species, and only one of the species had a high affinity for epiphytism. Two moss species recorded only on larch trunks were recorded on both trunks and branches on spruce (**Table 3.8**).

Table 3.7 The total number of epiphyte species and the total number of bryophyte, lichen and vascular plant species recorded on the trunks of all trees and all Sitka spruce and Japanese larch trees.

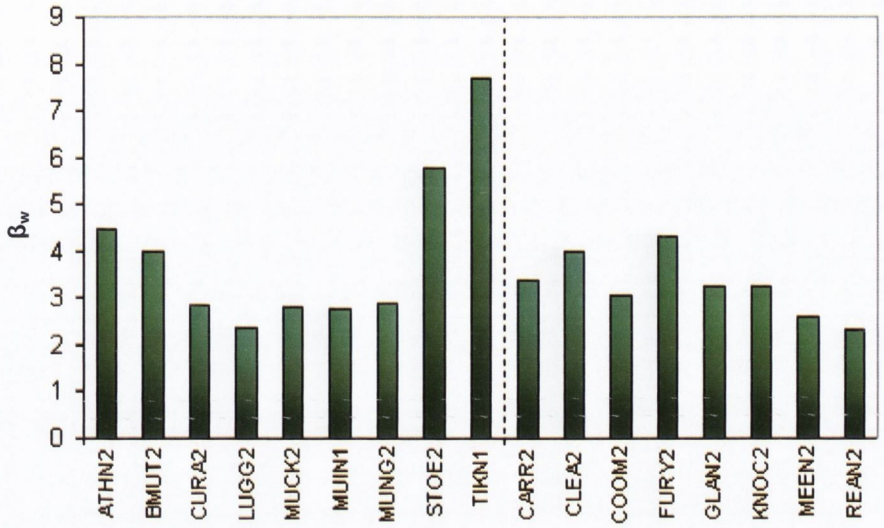
	n	Total epiphyte	Bryophyte	Lichen	Vascular
All trees	28	64	27	34	3
Spruce	17	41	24	16	1
Larch	11	54	20	32	2

Table 3.8 Species recorded only in trunk plots on either Sitka spruce or Japanese larch and occurring in more than one plot. The epiphyte group and growth form of each species and their affinity for epiphytism are indicated. √ indicates the epiphyte species occurred only in trunk plots on that tree species, X indicates the species occurred in both trunk and branch plots on that tree species and – indicates the species did not occur on that tree species.

Species	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Thuidium tamariscinum	Mo	We	Low	√	√
Hypnum resupinatum	Mo	Ma	Int	√	√
Rhytidiadelphus loreus	Mo	We	Low	√	√
Hypnum resupinatum	Mo	Ma	Int	√	√
Pseudotaxiphyllum elegans	Mo	Ma	Low	√	√
Plagiothecium undulatum	Mo	Ma	Low	√	√
Cladonia chlorophaea	Li	Fo	Low	√	√
Isothecium myosuroides	Mo	We	Int	√	X
Plagiothecium laetum	Mo	Ma	Int	√	-
Calypogeia muelleriana	Lv	Ma	Low	√	-
Juvenile pteridophyte	Va	-	-	√	-
Kindbergia praelonga	Mo	Ma	Int	X	√
Hypnum andoi	Mo	Ma	Int	X	√
Campylopus flexuosus	Mo	Tu	Low	-	√
Dicranum scoparium	Mo	Tu	Int	-	√
Cladonia macilenta	Li	Fo	Int	-	√
Cladonia coniocraea	Li	Fo	Int	-	√
Thelotrema lepadinum	Li	Cr	High	-	√
Oxalis acetosella	Va	-	Low	-	√

Beta (β_w) diversity was calculated for each tree based on the trunk plot data (**Table 3.9**), since the area of branch plots available for epiphyte colonisation and the number of branch plots studied on each tree varied. Values of the index could range from a minimum of one to a maximum of eight. The tree with the highest β_w diversity was TIKN1 with a value of 7.7 (**Figure 3.8**); however, this tree had only a single species on its trunk in a single trunk plot. The next highest value was for STOE2 at 5.8. STOE2 also had the highest bryophyte β_w diversity with the maximum value of 8.0.

(a)



(b)

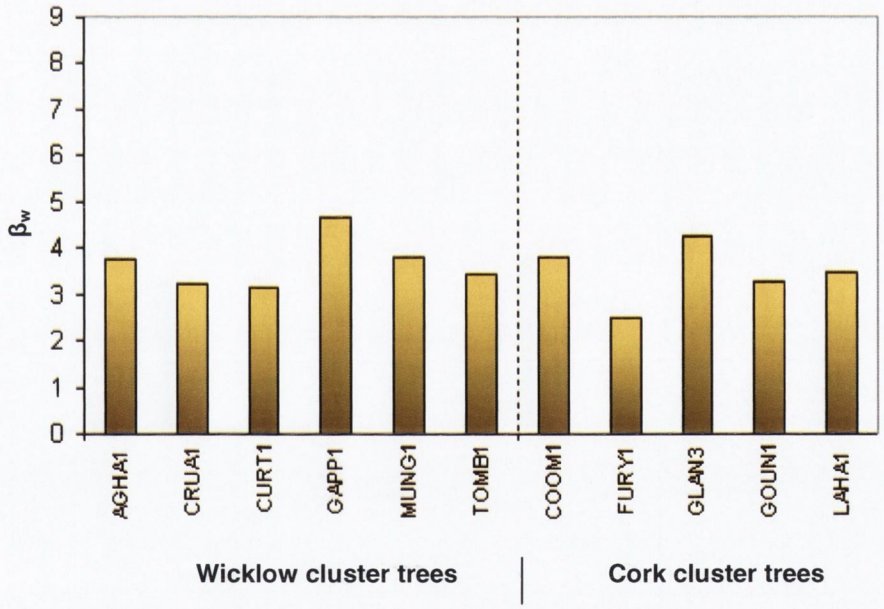


Figure 3.8 Total epiphyte beta (βw) diversity, according to Whittaker's index, on the trunks of the (a) Sitka spruce and (b) Japanese larch trees.

FURY2 had the maximum lichen β_w diversity value of 8.0. There were no significant differences in β_w diversity between Sitka spruce and Japanese larch (**Figure 3.9**). There was, however, a significantly higher bryophyte β_w diversity on the trees in the Wicklow cluster compared with those in the Cork cluster (independent samples t-test: $p = 0.004$) (**Table 3.9**).

Table 3.9. Mean (± standard error) total epiphyte, bryophyte and lichen beta (β_w) diversity on the trunks of all trees in the Wicklow and Cork clusters. There are no significant differences in β_w diversity between the geographic clusters if indicated by the same letter.

	n	Total epiphyte βw	Bryophyte βw	Lichen βw
Wicklow	15	3.6 (±0.3)[a]	4.6 (± 0.5)[a]	3.3 (± 0.4)[a]
Cork	13	3.3 (± 0.2)[a]	2.9 (± 0.2)[b]	4.8 (± 0.5)[a]

Eight trunk plots were studied on each tree making a total of 224 trunk plots studied in total: 136 on Sitka spruce and 88 on Japanese larch. The most species-rich trunk plot was an upper plot from GOUN1 (TUs) (cf. **Section 2.3.1.1** for plot codes), a larch tree in the Cork cluster, which had a total epiphyte richness of twelve. This was also the most lichen-rich trunk plot with a lichen richness of nine. The most bryophyte-rich trunk plot was a tree base plot from FURY1 (TBn), also a larch tree in the Cork cluster, which had a bryophyte richness of eight. A total of 14 trunk plots contained no epiphytes, seven of these from TIKN1. There was a significantly higher mean total epiphyte richness in the eight trunk plots (SR_{MT}) (independent samples t-test: $p = 0.028$) on larch trunks compared to spruce (**Figure 3.10**). Lichen SR_{MT} was also significantly higher on larch (independent samples t-test: $p < 0.001$) while bryophyte SR_{MT} was higher on spruce, although not significantly so (independent samples t-test: $p = 0.590$). There was also a significantly higher total epiphyte SR_{MT} (independent samples t-test: $p = 0.003$) and bryophyte SR_{MT} (independent samples t-test: $p < 0.001$) on the Cork cluster trees compared to the Wicklow cluster trees (**Table 3.10**). The highest total epiphyte SR_{MT} and the highest bryophyte SR_{MT} was on FURY1 at 7.6 and 5.1 respectively (**Figure 3.11**). The highest lichen SR_{MT} was on CURT1, a Japanese larch tree from the Wicklow cluster, at 5.5 (**Figure 3.11**).

Table 3.10. Mean (± standard error) of the mean total epiphyte, bryophyte and lichen richness (SR_{MT}) in the eight trunk plots on the trees in the Wicklow and Cork clusters. There are no significant differences in species richness between the geographic clusters if indicated by the same letter.

	n	Total epiphyte SR_{MT}	Bryophyte SR_{MT}	Lichen SR_{MT}
Wicklow	15	3.3 (± 0.4)[a]	1.2 (± 0.2)[a]	2.1 (± 0.4)[a]
Cork	13	4.8 (± 0.3)[b]	3.3 (± 0.2)[b]	1.5 (± 0.3)[a]

The most species-rich trunk plot, the upper plot from GOUN1 (TUs), was also the most diverse trunk plot according to Simpson's reciprocal (1/D) with a value of 5.9. The most bryophyte-diverse plot was a tree base plot from MEEN2 (TBn), a spruce tree from the Cork cluster with a 1/D of 4.0. The most lichen-diverse plots were a middle plot from TOMB1 (TMn), a larch tree from the Wicklow cluster, and an upper plot from ATHN2 (TUn), a spruce tree from the Wicklow cluster,

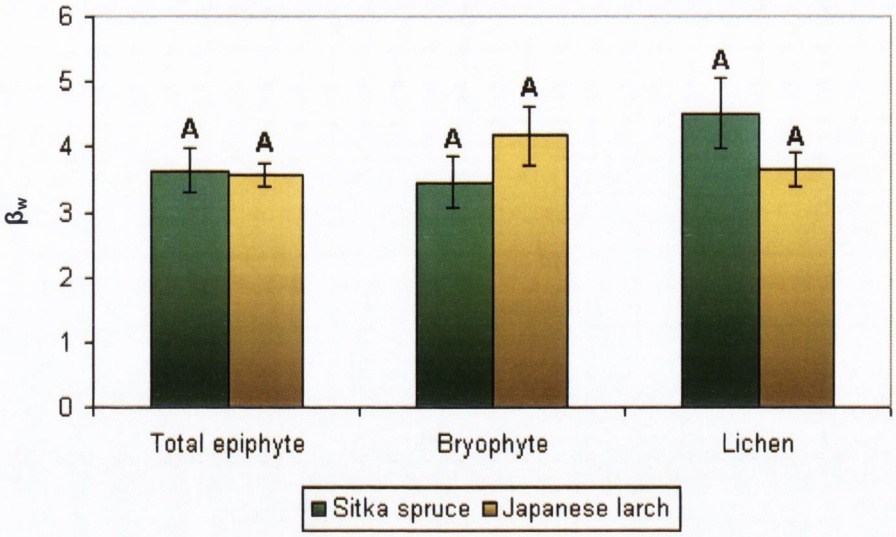


Figure 3.9 Mean beta (β_w) diversity on the trunks of Sitka spruce (n=17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in beta diversity between the two tree species if indicated by the same letter.

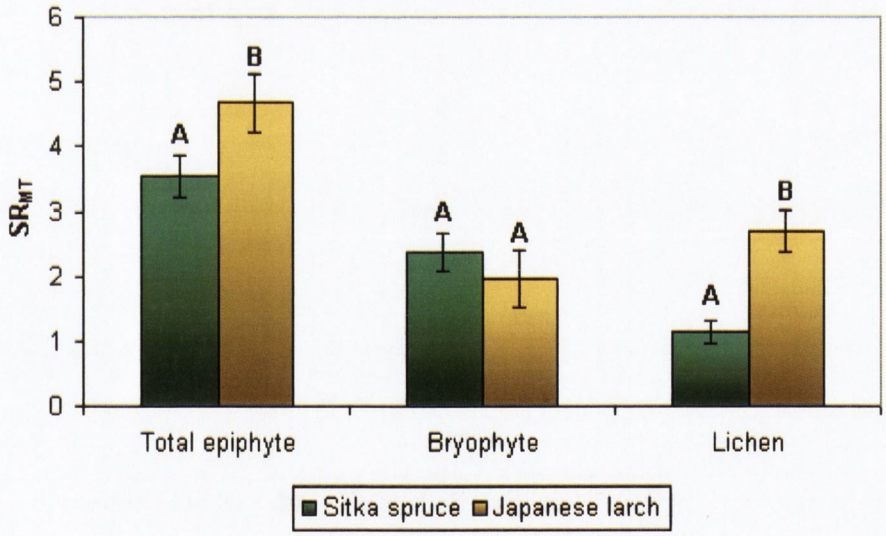
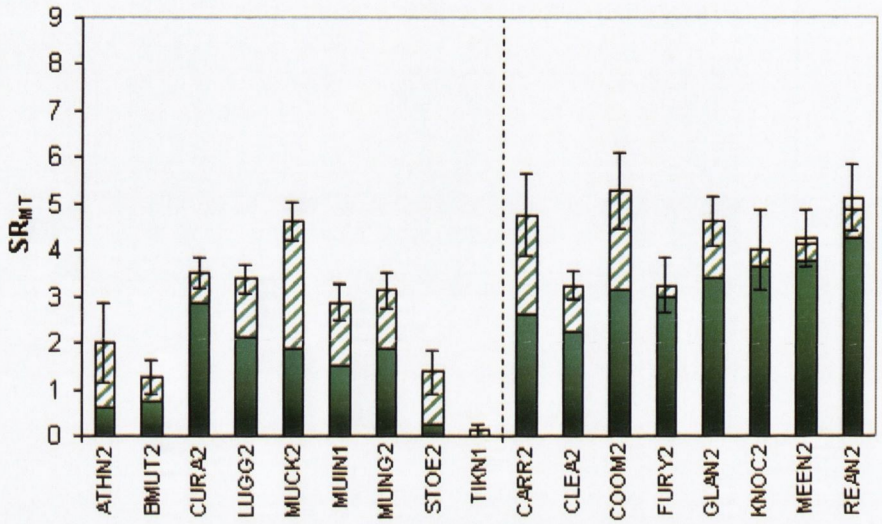


Figure 3.10 Mean of the mean epiphyte species richness (SR_{MT}) of the eight trunk plots on Sitka spruce (n = 17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in species richness between the two tree species if indicated by the same letter.

(a)



(b)

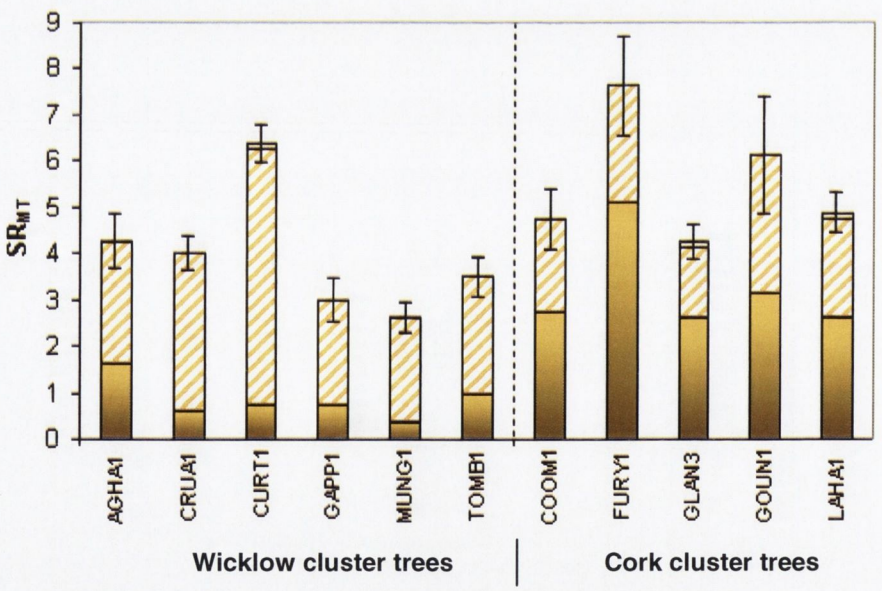


Figure 3.11 Mean epiphyte species richness (SR_{MT}) of the trunk plots (n = 8) on the (a) Sitka spruce and (b) Japanese larch trees. The mean total epiphyte richness is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant species (unshaded) are indicated. Error bars indicate ± standard error.

both with a 1/D of 5.0. The highest mean total epiphyte diversity in the eight trunk plots ($1/D_{MT}$) was on LAHA1, a larch tree from the Cork cluster, at 2.8 (**Figure 3.12**). The highest bryophyte $1/D_{MT}$ was on KNOC2, a spruce tree from the Cork cluster, at 2.2. MUCK2, a spruce tree from the Wicklow cluster, had the highest lichen $1/D_{MT}$ at 2.4. Total epiphyte $1/D_{MT}$ was significantly higher on larch trunks compared to spruce (Mann-Whitney U test: $p = 0.001$), as was lichen $1/D_{MT}$ (Mann-Whitney U test: $p < 0.001$) (**Figure 3.13**). There was also a significantly higher bryophyte $1/D_{MT}$ on the trunks of the trees in Cork than in Wicklow (Mann-Whitney U test: $p < 0.001$) (**Table 3.11**).

Table 3.11 Mean (± standard error) of the mean total epiphyte, bryophyte and lichen diversity ($1/D_{MT}$) in the eight plots on the trunks of all trees in the Wicklow and Cork clusters. There are no significant differences in diversity between the geographic clusters if indicated by the same letter.

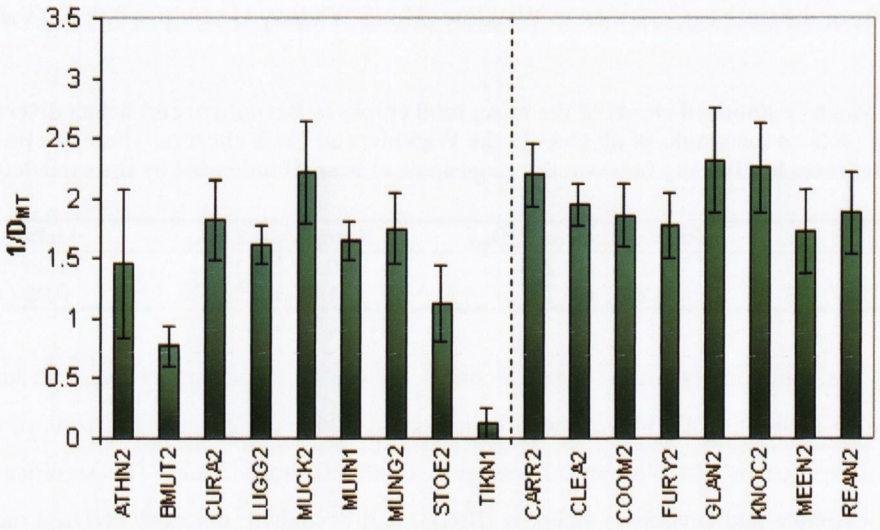
	n	Total epiphyte $1/D_{MT}$	Bryophyte $1/D_{MT}$	Lichen $1/D_{MT}$
Wicklow	15	1.8 (± 0.2)^a	0.8 (± 0.1)^a	1.34 (± 0.2)^a
Cork	13	2.1 (± 0.1)^a	1.8 (± 0.1)^b	0.98 (± 0.1)^a

As well as the significantly higher lichen richness (SR_{MT}) and diversity ($1/D_{MT}$) on larch trunks, there was also a significantly higher mean lichen cover ($Cover_{MT}$) in the eight trunk plots on larch compared to spruce (Mann-Whitney U test: $p < 0.001$) (**Figure 3.14**). The significantly higher mean total epiphyte and bryophyte richness (SR_{MT}) and bryophyte diversity ($1/D_{MT}$) on the trunks of the trees in the Cork cluster was also accompanied by a significantly higher mean total epiphyte cover ($Cover_{MT}$) (independent samples t-test: $p = 0.003$) and bryophyte $Cover_{MT}$ (independent samples t-test: $p < 0.001$) (**Table 3.12**). The highest total epiphyte $Cover_{MT}$ was recorded on REAN2, a spruce tree from the Cork cluster, at 71.9% (**Figure 3.15**). The vast majority of this cover was made up by bryophytes, also giving REAN2 the highest bryophyte $Cover_{MT}$. This tree, along with three other spruce trees, CURA2 from the Wicklow cluster and MEEN2 and COOM2 from the Cork cluster, stood out from the other trees in having more than 50% bryophyte $Cover_{MT}$ and virtually no lichen cover (**Figure 3.15**). The highest lichen $Cover_{MT}$ was on CURT1, a larch tree from the Wicklow cluster, which also had the highest lichen SR_{MT}, at 50.6%. This tree, along with two other larch trees, CRUA1 from the Wicklow cluster and COOM1 from the Cork cluster, stood out from all the other trees in having more than 40% mean lichen $Cover_{MT}$ (**Figure 3.15**). MUIN1, and to some extent MUNG2, two spruce trees from the Wicklow cluster, also stood out from the other spruce trees in terms of their lichen cover (**Figure 3.15**). The majority of the lichen cover on both of these spruce trees consisted of two crustose species, *Dimerella lutea* and *D. pineti*.

Table 3.12. Mean (± standard error) of the mean cover ($Cover_{MT}$) of the total epiphyte, bryophyte and lichen species in the trunk plots for all trees in the Wicklow and Cork clusters. There are no significant differences in cover between the geographic clusters if indicated by the same letter.

	n	Total epiphyte $Cover_{MT}$ (%)	Bryophyte $Cover_{MT}$ (%)	Lichen $Cover_{MT}$ (%)
Wicklow	15	24.1 (± 4.7)^a	11.8 (± 3.6)^a	12.3 (± 4.1)^a
Cork	13	40.6 (± 5.3)^b	34.8 (± 5.3)^b	5.9 (± 3.1)^a

(a)



(b)

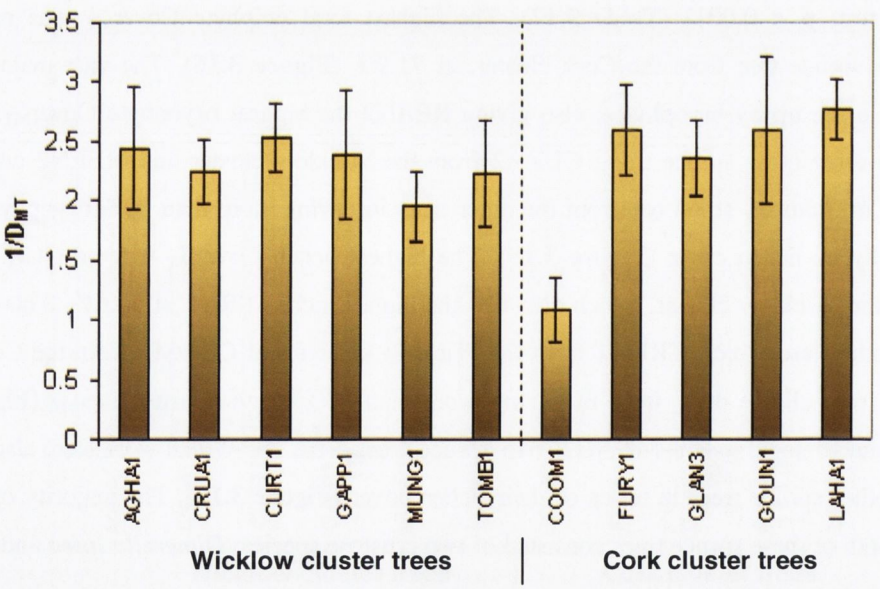


Figure 3.12 Mean Simpson's reciprocal diversity ($1/D_{MT}$) of the total epiphyte flora in the trunk plots (n = 8) of the (a) Sitka spruce and (b) Japanese larch trees. Error bars indicate ± standard error.

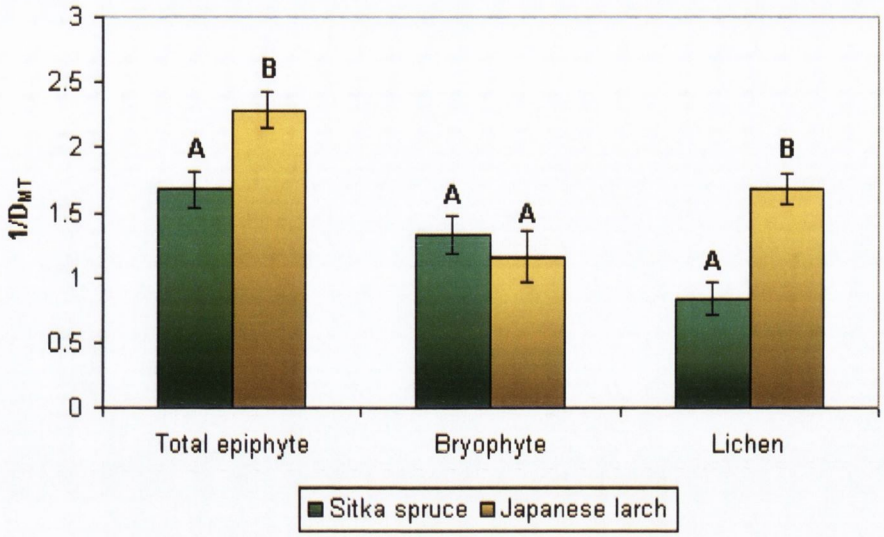


Figure 3.13 Mean of the mean Simpson's reciprocal diversity ($1/D_{MT}$) of the eight trunk plots on Sitka spruce (n=17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in diversity between the two tree species if indicated by the same letter.

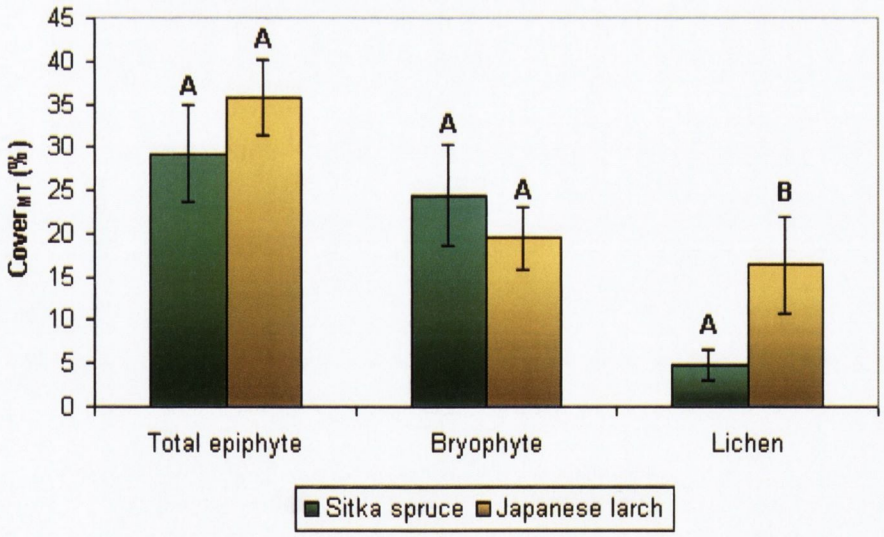
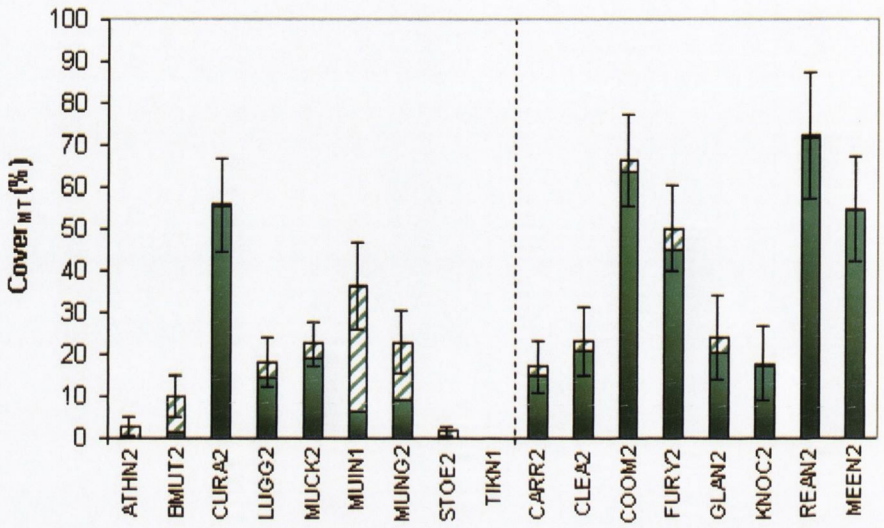


Figure 3.14 Mean of the mean cover ($Cover_{MT}$) in the eight trunk plot on Sitka spruce (n=17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in cover between the two tree species if indicated by the same letter.

(a)



(b)

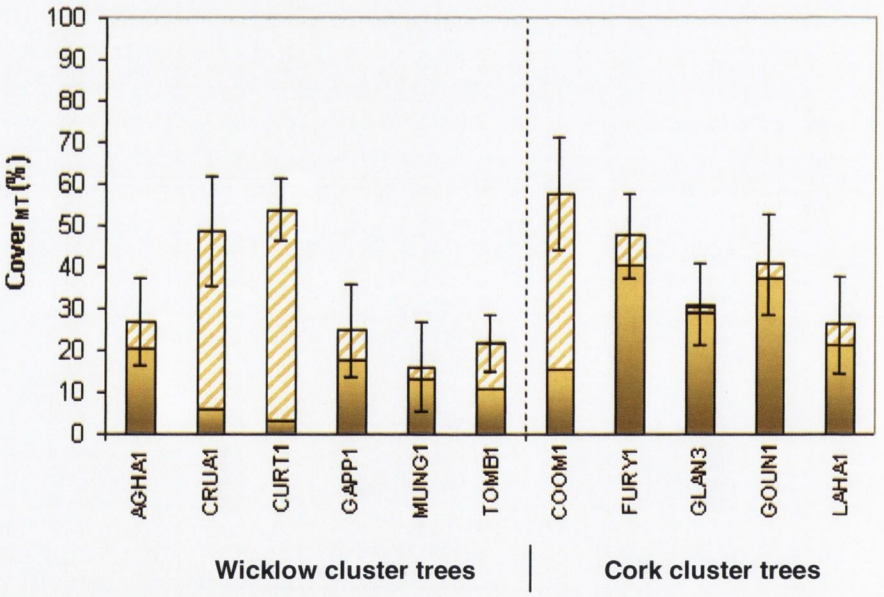


Figure 3.15 Mean epiphyte cover ($Cover_{MT}$) in the trunk plots (n = 8) of the (a) Sitka spruce and (b) Japanese larch trees. The mean total epiphyte cover is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant cover (unshaded) are indicated. Error bars indicate ± standard error.

Analysis of the relationship between mean diversity ($1/D_{MT}$) and mean species richness (SR_{MT}) in the trunk plots revealed a significant positive relationship between these factors for spruce (r^2 = 0.782, $p < 0.001$) but not for larch (r^2 = 0.110, p = 0.319) (**Figure 3.16**). This suggests that the more species-rich trunk plots on spruce are also more even (i.e. no one species dominates) and that this is not the case for larch. In contrast, there was a significant negative relationship between total epiphyte beta (β_w) diversity and mean total epiphyte richness (SR_{MT}) for spruce (r^2 = 0.630, $p < 0.001$), and larch (r^2 = 0.576, p = 0.07) (**Figure 3.17**). High β_w diversity was only found when epiphyte richness was particularly low.

3.3.2.3 Branch diversity

A total of 57 species were recorded on the branches of the trees (**Table 3.13**). The 16 bryophyte species recorded consisted of five moss and eleven liverwort species and of 14 mats, one weft and one cushion. The 41 lichen species consisted of 23 crustose, one leprose, twelve foliose and five fruticose species. A total of 20 species were only recorded in branch plots and not in trunk plots on either Sitka spruce or Japanese larch. However, only eight of these species in total occurred in more than two branch plots: six lichen and one liverwort species on spruce, and two lichen and one liverwort species on larch (**Table 3.14**). All species had either an intermediate or high affinity for epiphytism.

Table 3.13 The total number of epiphyte species and the total number of bryophyte, lichen and vascular plant species recorded on the branches of all trees and all Sitka spruce and Japanese larch trees.

	n	Total epiphyte	Bryophyte	Lichen	Vascular
All trees	28	57	16	41	0
Spruce	17	49	15	34	0
Larch	11	36	10	26	0

Table 3.14 Those species occurring only in branch plots on either Sitka spruce or Japanese larch and occurring in more than one branch plot. The epiphyte group and growth form of each species and their affinity for epiphytism is indicated. √ indicates the epiphyte species occurred only in branch plots on that tree species, X indicates the species occurred in both trunk and branch plots on that tree species and – indicates the species did not occur on that tree species.

Species	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Physcia tenella	Li	Fo	High	√	√
Usnea filipendula	Li	Fr	High	√	√
Graphina ruiziana	Li	Cr	High	√	X
Fellhanera bouteillei	Li	Cr	Int	√	-
Parmotrema chinense	Li	Fo	Int	√	-
Frullania teneriffae	Lv	Ma	Int	√	-
Pyrrhospora quernea	Li	Cr	High	√	-
Frullania dilatata	Lv	Ma	High	X	√

In contrast to the situation on trunks, there were more species recorded in total on the branches of Sitka spruce compared to Japanese larch (**Table 3.13**). With a maximum of twelve and a minimum of six

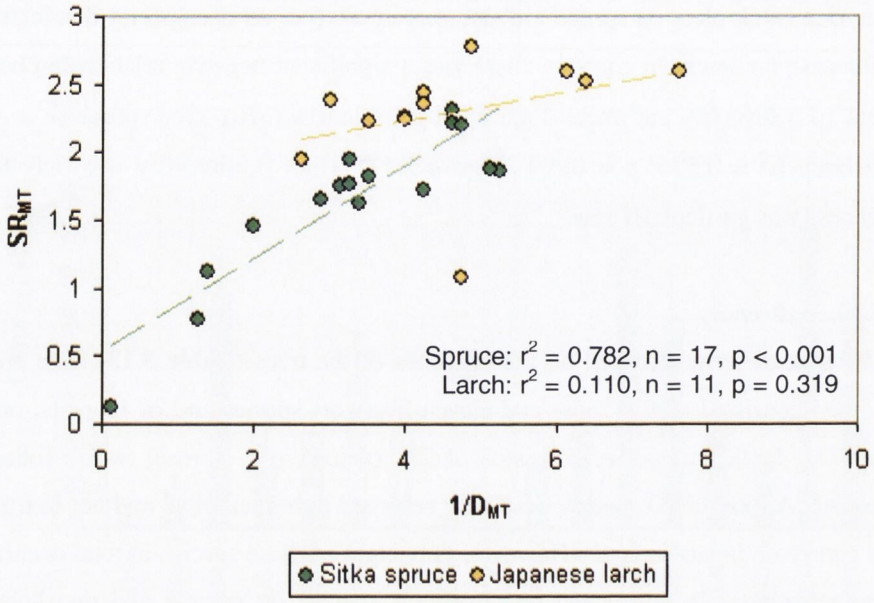


Figure 3.16 Relationship between mean total epiphyte diversity ($1/D_{MT}$) and mean total epiphyte richness (SR_{MT}) in the eight trunk plots on Sitka spruce (n = 17) and Japanese larch (n = 11).

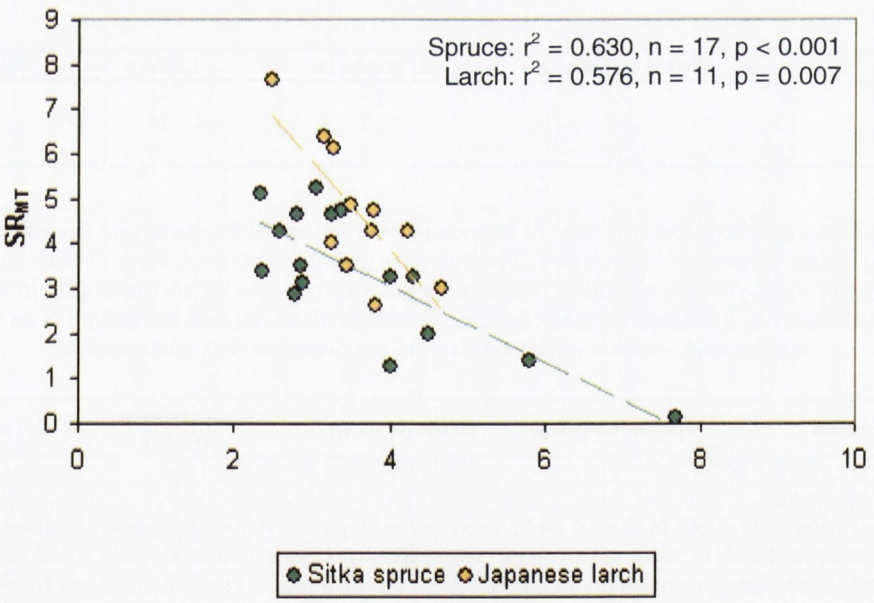


Figure 3.17 Relationship between (βw) diversity and mean total epiphyte richness (SR_{MT}) in the eight trunk plots on Sitka spruce (n = 17) and Japanese larch (n = 11).

branch plots studied on each tree, a total of 303 branch plots were studied overall. Almost twice as many plots were studied on spruce as on larch: 198 on spruce and 105 on larch. Plots were studied on living, moribund and dead branches. Just over half the branch plots studied on both spruce and larch were on living branches (**Table 3.15**). The majority of middle branch plots on both spruce and larch were on dead branches, while the majority of upper branch plots were on living branches. The dead branches varied in their stages of decay. All branches retained their bark, although in some the bark had begun to loosen and was easily dislodged. Dead needles were rarely retained.

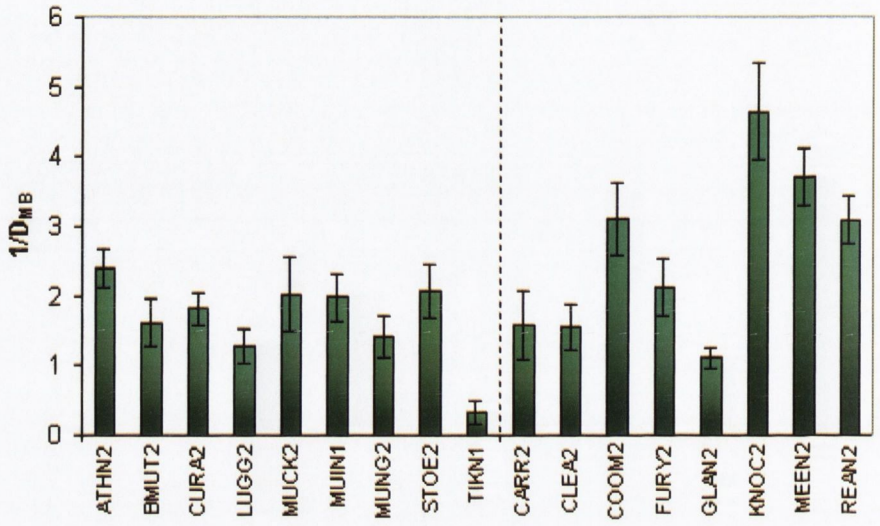
Table 3.15 The number (and percentage) of branch plots from the middle and upper branches, and the total number of branch plots studied on living, moribund and dead branches on both Sitka spruce and Japanese larch

	n	Living	Moribund	Dead
Spruce:				
Middle	96	6 (6.3%)	9 (9.34%)	81 (84.4%)
Upper	102	96 (94.1%)	3 (2.9%)	3 (2.9%)
Total	198	102 (51.5%)	12 (6.1%)	84 (42.4%)
Larch:				
Middle	40	3 (7.5%)	0	37 (92.5%)
Upper	65	51(78.5%)	0	14 (21.5%)
Total	105	54 (51.4%)	0	51 (48.6%)

The area available for epiphyte colonisation differed among branch plots (cf. **Figure 2.3**) so the mean epiphyte richness is not presented for branches. With this inequality in mind, the most species-rich branch plots were all recorded on Japanese larch trees. The most species-rich branch plot was on a middle branch from FURY1 (BMs1), a larch tree from the Cork cluster, with an epiphyte richness of eleven, and the most bryophyte-rich branch plot on the middle branch from the opposite side of the same tree (BMn1) with a bryophyte richness of six. These branch plots were both on dead branches. The most lichen-rich branch plots were on an upper branch from GOUN1 (BUn2) in the Cork cluster and a middle branch from CURT1 (BMs2) in the Wicklow cluster, both with a lichen richness of eight. These branch plots were both on living branches. A total of eight trees - four spruce and four larch trees from the Wicklow cluster - had no bryophyte species in their branch plots. A total of 34 branch plots contained no epiphyte species; 26 of these were outer plots from the upper branches.

The most diverse (1/D) branch plots were also all on larch trees. The most bryophyte-rich branch plot from FURY1 (BMn1) was also the plot with the highest total epiphyte and bryophyte diversity, with a total epiphyte 1/D of 10.0 and a bryophyte 1/D of 6.0. The most lichen-rich branch plot from CURT1 (BMs2) was also the most lichen-diverse with a 1/D of 8.0. The highest mean total epiphyte and lichen diversity ($1/D_{MB}$) on branches was on FURY1 at 5.5 (**Figure 3.18**) and 4.5 respectively. The highest bryophyte $1/D_{MB}$ was on KNOC2 at 2.5. There was a higher total epiphyte $1/D_{MB}$ on the branches of larch than spruce, although this difference was not significant

(a)



(b)

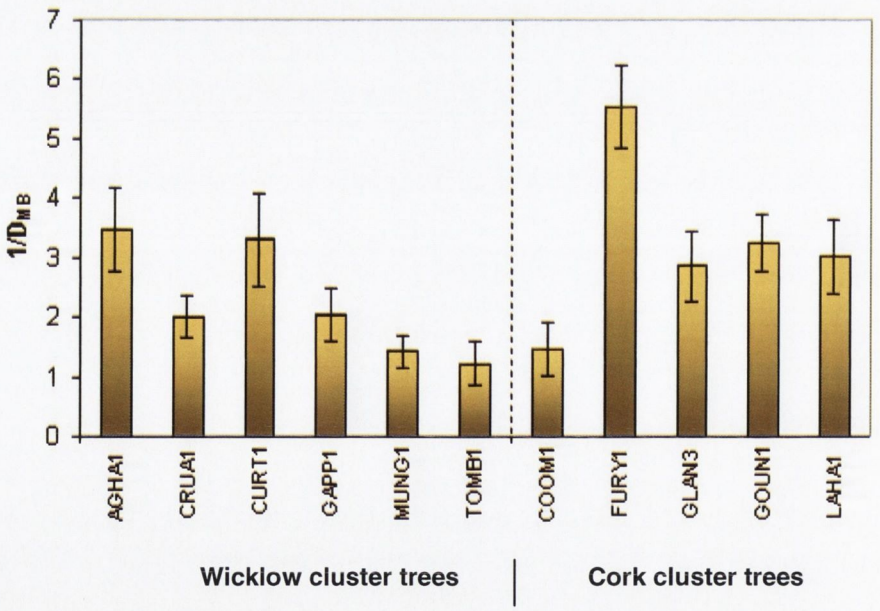


Figure 3.18 Mean total epiphyte diversity ($1/D_{MB}$) of all branch plots studied on the (a) Sitka spruce (n = 10-12) and (b) Japanese larch trees (n = 6-12). Error bars indicate ± standard error.

(Mann-Whitney U test: p = 0.290) (**Figure 3.19**). There was a significantly higher lichen $1/D_{MB}$ on larch, however (independent samples t-test: p = 0.009). Total epiphyte and bryophyte $1/D_{MB}$ were both significantly higher in the Cork cluster (independent samples t-test: total epiphyte $1/D_{MB}$, p = 0.024; Mann-Whitney U test: bryophyte, p < 0.001) (**Table 3.16**).

Table 3.16 Mean (± standard error) of the mean diversity ($1/D_{MB}$) of the total epiphyte, bryophyte and lichen species in the branch plots for all trees in the Wicklow and Cork clusters. There are no significant differences in diversity between the geographic clusters if indicated by the same letter.

	n	Total epiphyte $1/D_{MB}$	Bryophyte $1/D_{MB}$	Lichen $1/D_{MB}$
Wicklow	15	1.9 (± 0.2)^a	0.2 (± 0.1)^a	1.8 (± 0.2)^a
Cork	13	2.9 (± 0.4)^b	1.2 (± 0.2)^b	1.9 (± 0.3)^a

Epiphyte cover in branch plots was converted to a percentage of the total cover of branches within each plot. There was a significantly higher mean lichen cover ($Cover_{MB}$) on larch branches compared to spruce (independent samples t-test: p = 0.002) (**Figure 3.20**). Bryophyte $Cover_{MB}$ was higher on spruce but this difference was not statistically significant (Mann-Whitney U test: p = 0.120). There was, however, a significantly higher bryophyte $Cover_{MB}$ on the trees in the Cork cluster compared to those in the Wicklow cluster (Mann-Whitney U test: p = 0.001) (**Table 3.17**). The highest total epiphyte $Cover_{MB}$ and the highest lichen $Cover_{MB}$ was on FURY1, at 75.0% and 57.2% respectively, and the highest bryophyte $Cover_{MB}$ was on CURA2 at 51.3% (**Figure 3.21**).

Table 3.17 Mean (± standard error) of the mean cover ($Cover_{MB}$) of the total epiphyte, bryophyte and lichen species in the branch plots of all trees in the Wicklow and Cork clusters. Cover is expressed as a percentage of the cover of branches within each plot. There are no significant differences in cover between the geographic clusters if indicated by the same letter.

	n	Total epiphyte $Cover_{MB}$ (%)	Bryophyte $Cover_{MB}$ (%)	Lichen $Cover_{MB}$ (%)
Wicklow	15	27.9 (± 4.4)^a	5.2 (± 3.4)^a	23.9 (± 3.7)^a
Cork	13	36.8 (± 5.4)^b	16.8 (± 4.1)^b	25.3 (± 4.5)^a

The epiphyte diversity (1/D) and cover of the plots on living branches was compared with those on dead or moribund branches. Bryophyte diversity (1/D) was significantly higher on dead or moribund branches on spruce (Mann-Whitney U test: p < 0.001) and the higher total epiphyte diversity on spruce was close to significance (Mann-Whitney U test: p = 0.063) (**Figure 3.22a**). On larch, total epiphyte, bryophyte and lichen diversity were all significantly higher on dead or moribund branches (Mann-Whitney U test: total epiphyte, p < 0.001; bryophyte, p = 0.001; lichen, p < 0.001) (**Figure 3.22b**). Total epiphyte, bryophyte and lichen cover were all significantly higher on dead or moribund branches on both spruce and larch (Mann-Whitney U test: total epiphyte cover, spruce, p < 0.001; larch, p = 0.001; bryophyte cover, spruce, p < 0.001; larch, p = 0.001; lichen cover, spruce, p = 0.002; larch, p = 0.028) (**Figure 3.23**).

Since the majority of plots on dead or moribund branches were from the middle height zone and the majority of plots on living branches were from the upper height zone (cf. **Table 3.15**), the plots

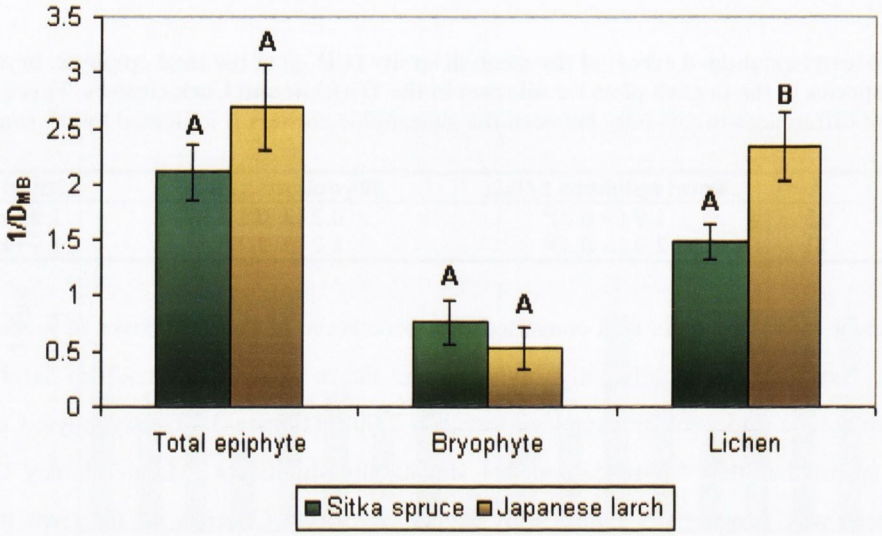


Figure 3.19 Mean of the mean epiphyte diversity ($1/D_{MB}$) of all plots studied on the branches of Sitka spruce (n = 17) and Japanese larch (n = 11). Error bars indicate ± standard error. There is no significant difference in diversity between the two tree species if indicated by the same letter.

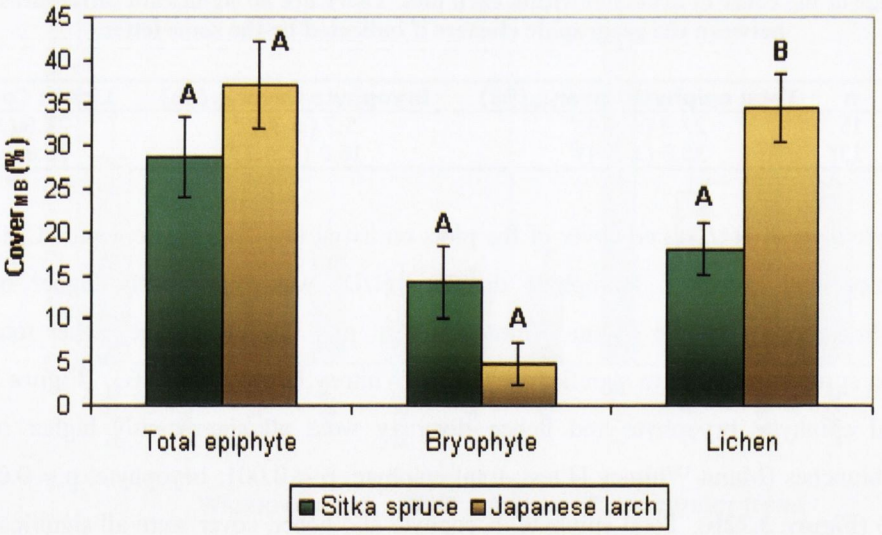
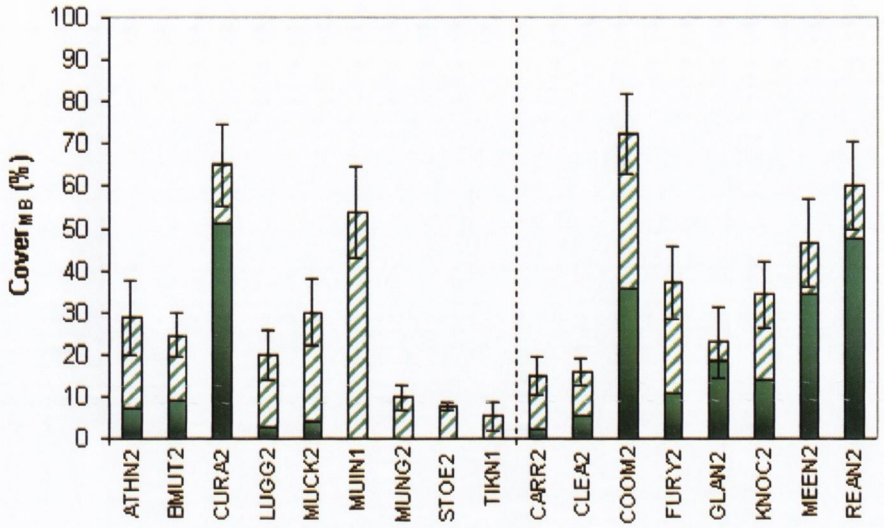


Figure 3.20 Mean of the mean epiphyte cover ($Cover_{MB}$) of all plots studied on the branches of Sitka spruce (n = 17) and Japanese larch (n = 11). Cover is expressed as a percentage of the cover of branches within each plot. Error bars indicate ± standard error. There is no significant difference in cover between the two tree species if indicated by the same letter.

(a)



(b)

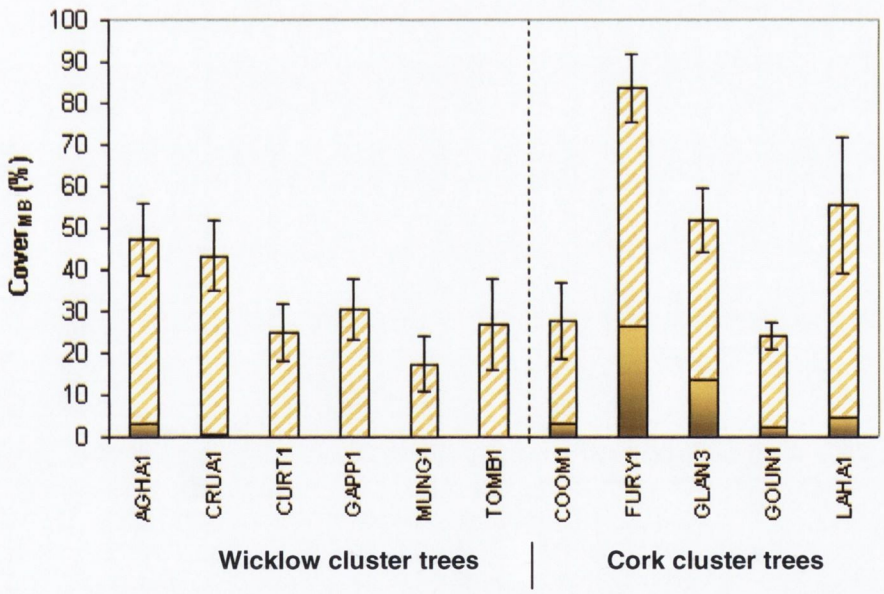
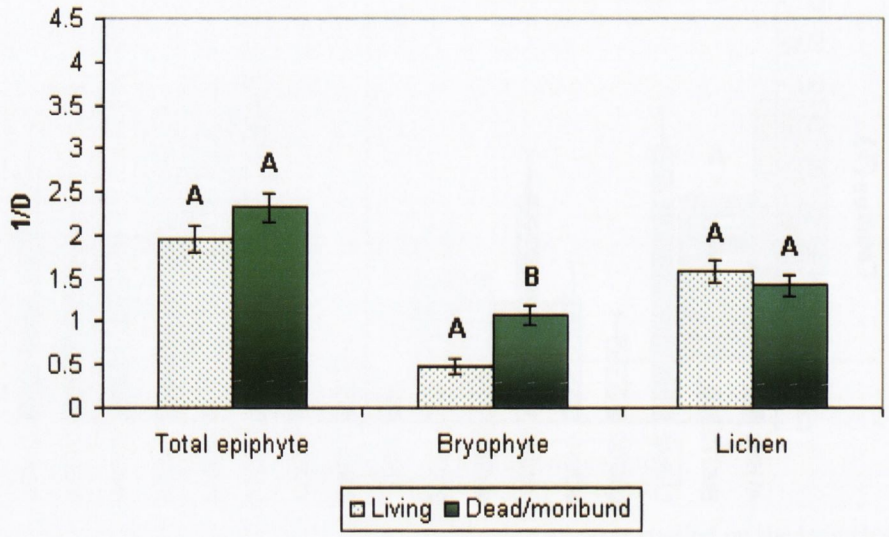


Figure 3.21 Mean epiphyte cover ($Cover_{MB}$) of all branch plots studied on the (a) Sitka spruce (n = 10-12) and (b) Japanese larch trees (n = 6-12) . Cover is expressed as a percentage of the cover of branches within each plot. The mean epiphyte cover is shown and the relative proportions of bryophyte (solid shading) and lichen cover (hatched shading) are indicated. Error bars indicate ± standard error.

(a)



(b)

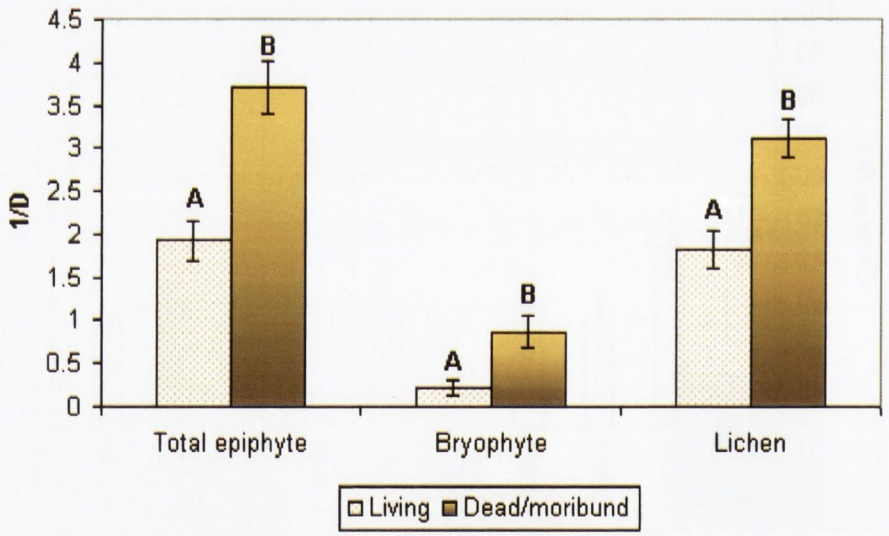
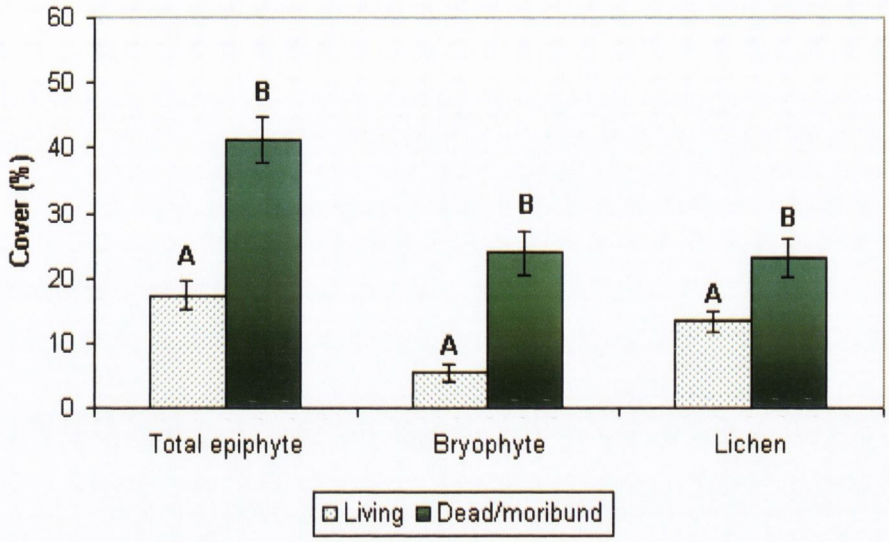


Figure 3.22 Mean Simpson's reciprocal diversity (1/D) of all plots on living and dead or moribund branches on (a) Sitka spruce (living: n = 102, dead/moribund: n = 96) and (b) Japanese larch (living: n = 54, dead/moribund: n = 51). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

(a)



(b)

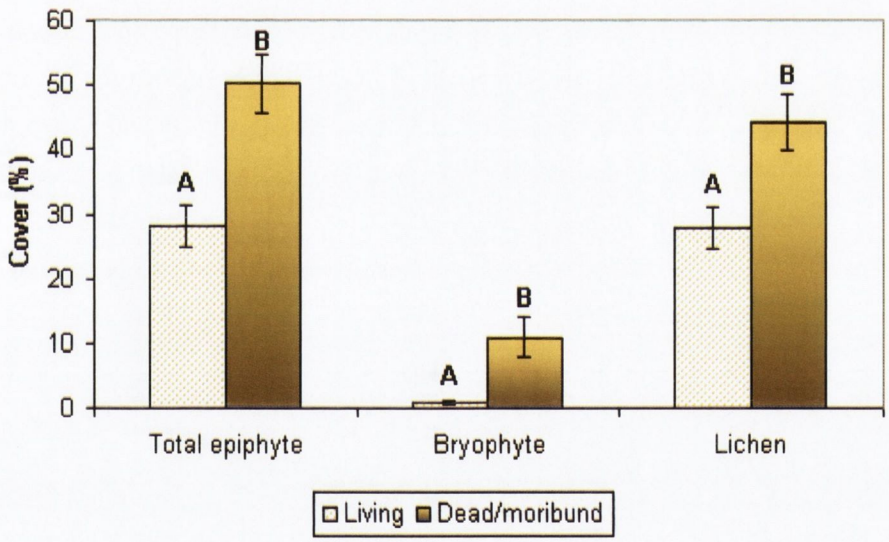


Figure 3.23 Mean cover in all plots on living and dead or moribund branches on (a) Sitka spruce (living: n = 102, dead/moribund: n = 96) and (b) Japanese larch (living: n = 54, dead/moribund: n = 51). Error bars indicate ±standard error. There is no significant difference in cover between bars if indicated by the same letter.

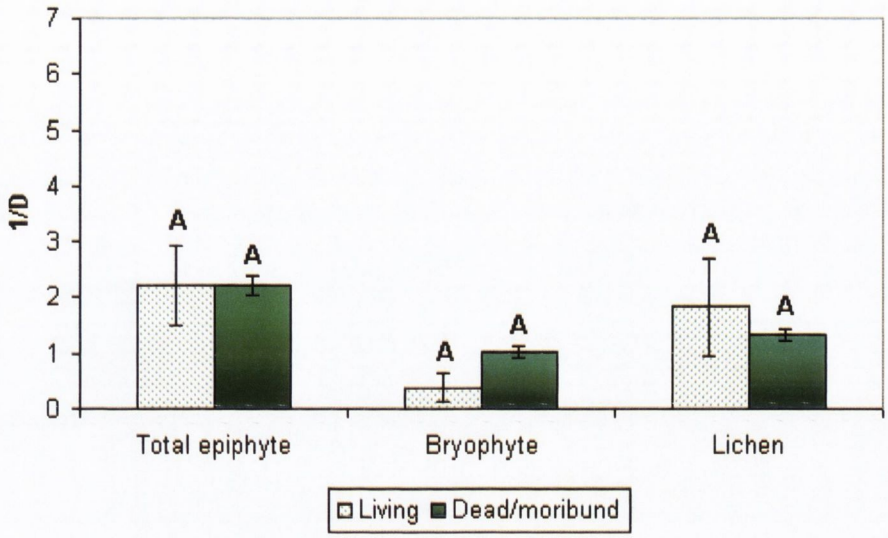
from these two height zones were examined separately. While bryophyte diversity was higher on dead or moribund branches and lichen diversity was higher on living branches in the middle height zone on both species, these differences were not statistically significant (Mann-Whitney U test: spruce, bryophyte 1/D, p = 0.178; lichen 1/D, p = 1.000; larch, bryophyte 1/D, p = 0.256; lichen 1/D, p = 0.443) (**Figure 3.24**). Cover was higher on dead or moribund middle branches, but again this difference was not statistically significant for either species (Mann-Whitney U test: spruce, bryophyte cover, p = 0.264; lichen cover, p = 0.083; larch, bryophyte cover, p = 0.144; lichen cover, p = 0.937) (**Figure 3.25**). In the upper height zone there was significantly higher total epiphyte, bryophyte and lichen diversity (1/D) on dead or moribund branches on spruce (Mann-Whitney U test: total epiphyte 1/D, p = 0.002; bryophyte 1/D, p = 0.002; lichen 1/D, p = 0.016) and significantly higher total epiphyte and lichen 1/D on larch (independent samples t-test: total epiphyte 1/D, p = 0.007; Mann-Whitney U test: lichen 1/D, p = 0.007) (**Figure 3.26**). As with diversity, there was significantly higher total epiphyte, bryophyte and lichen cover on dead or moribund branches on spruce (Mann-Whitney U test: total epiphyte cover, p = 0.001; bryophyte cover, p = 0.001; lichen cover, p = 0.003) and a significantly higher total epiphyte and lichen cover on dead or moribund branches on larch (Mann-Whitney U test: total epiphyte cover, p = 0.002; lichen cover, p = 0.002) (**Figure 3.27**).

A total of seven of the species that occurred only on branches, all lichen species, were recorded only on dead or moribund branches. However only two of these species occurred in more than one plot in total: *Pyrrhospora quernea*, which was only recorded on spruce, and *Usnea filipendula*, which was recorded on both tree species. *Pyrrhospora quernea* is reported to be found on nutrient-rich bark in well-lit situations (Dobson, 2005), however it occurs on substrates with no evident enrichment in the Scottish highlands (B. Coppins, pers. comm.). *Usnea filipendula* is common on conifers in upland woods (Dobson, 2005).

3.3.3 Effects of tree species on the epiphyte flora

Epiphyte species were examined in relation to their occurrence on Sitka spruce and Japanese larch. A total of 44 species were restricted to one or other tree species, with 24 species being recorded only on Sitka spruce - eight bryophyte, 15 lichen and one vascular plant species – and 20 species being recorded only on larch: four bryophyte, 14 lichen and two vascular plant species (cf. **Appendix 3**). However, of these 44 species, 28 were recorded on only one of the trees studied: 18 on spruce and eleven on larch. Of the remaining 16, only six were recorded on more than two trees (**Table 3.18**). The species restricted to spruce consisted of four liverwort mat species, one crustose and one foliose lichen and a juvenile pteridophyte species. All these species, with the exception of the crustose lichen, *Fellhanera bouteillei*, were also recorded only in the Cork cluster. The most common species recorded only on spruce, *Lejeunea cavifolia*, is characteristic of damp shaded

(a)



(b)

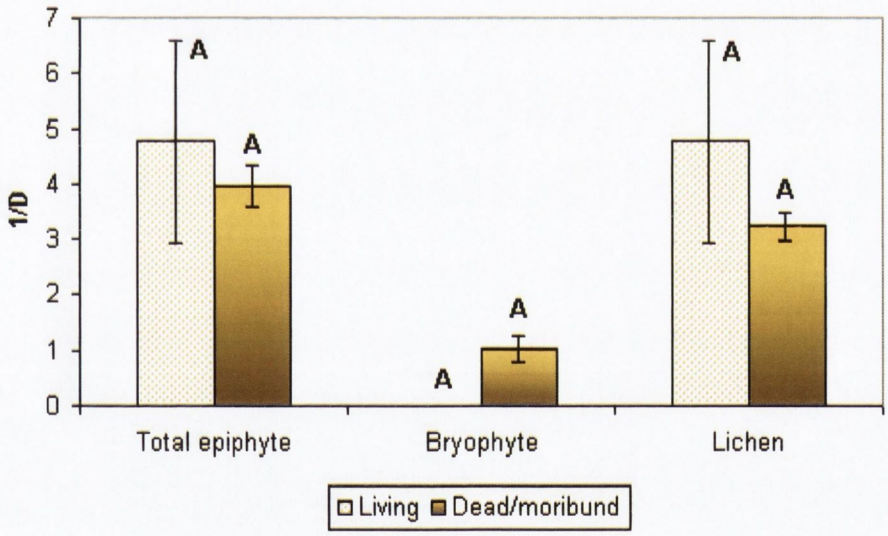
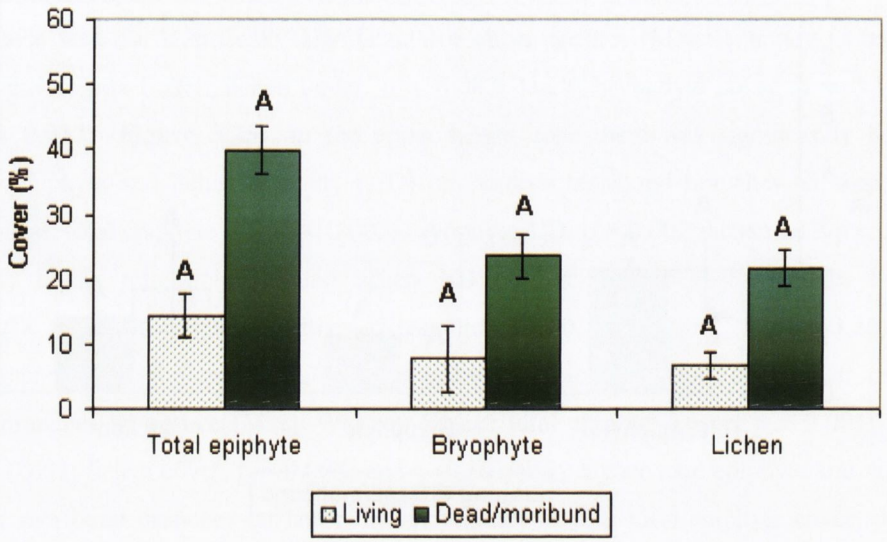


Figure 3.24 Mean Simpson's reciprocal diversity (1/D) in all plots on living and dead or moribund branches from the middle height zone on (a) Sitka spruce (living: n = 6, dead/moribund: n = 90) and (b) Japanese larch (living: n = 3, dead/moribund: n = 37). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

(a)



(b)

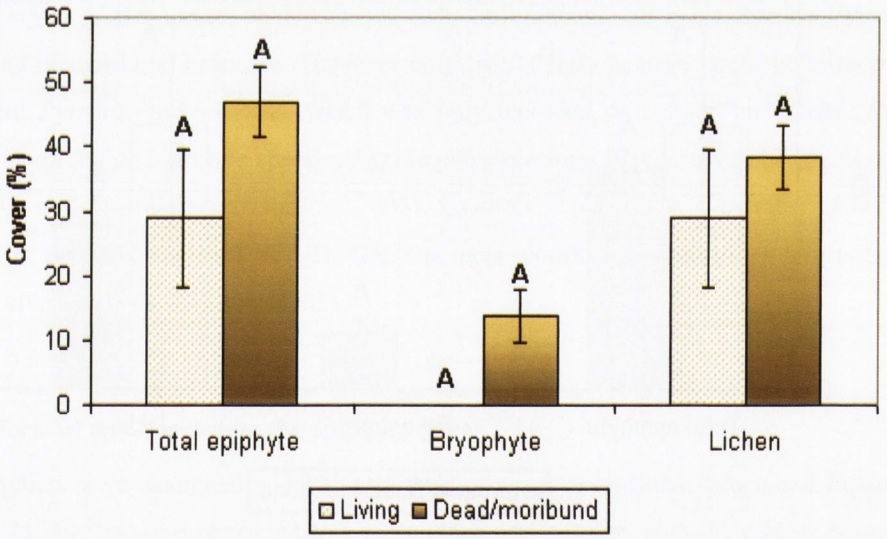
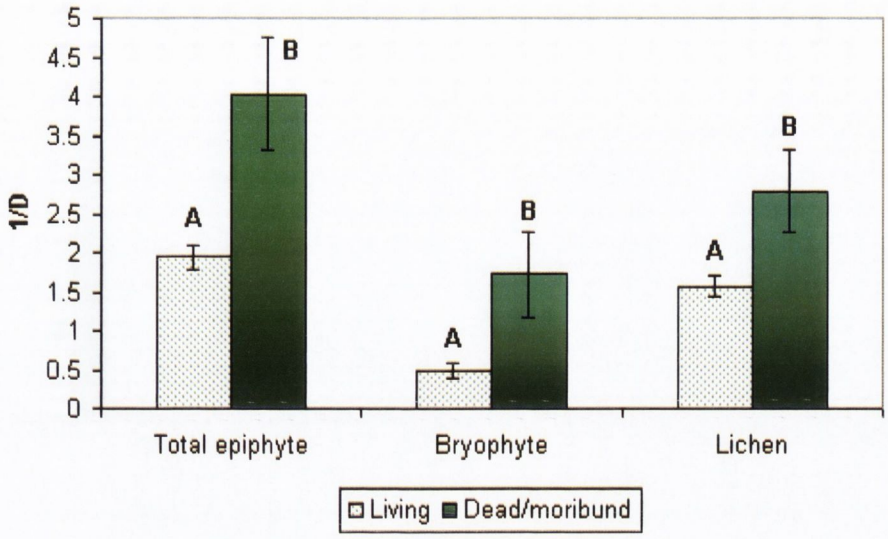


Figure 3.25 Mean cover in all plots on living and dead or moribund branches from the middle height zone on (a) Sitka spruce (living: n = 6, dead/moribund: n = 90) and (b) Japanese larch (living: n = 3, dead/moribund: n = 37). Error bar indicate ±standard error. There is no significant difference in cover between bars if indicated by the same letter.

(a)



(b)

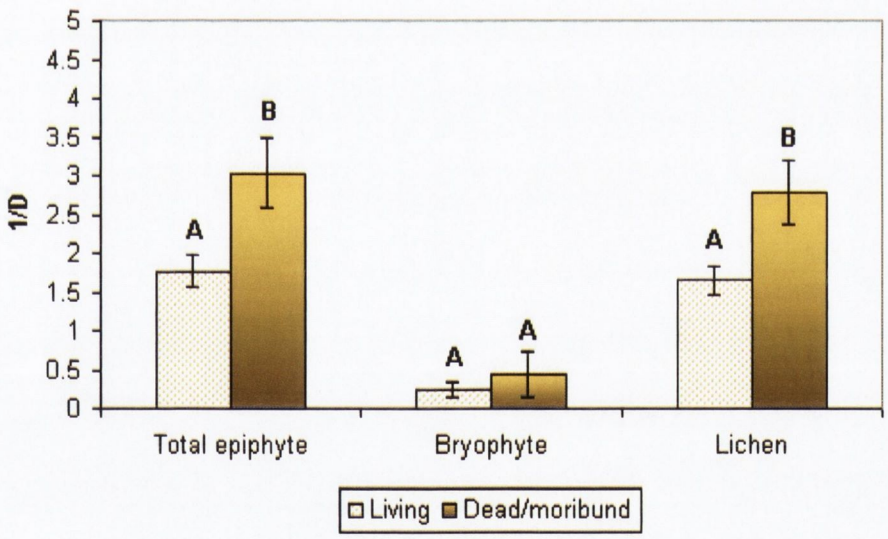
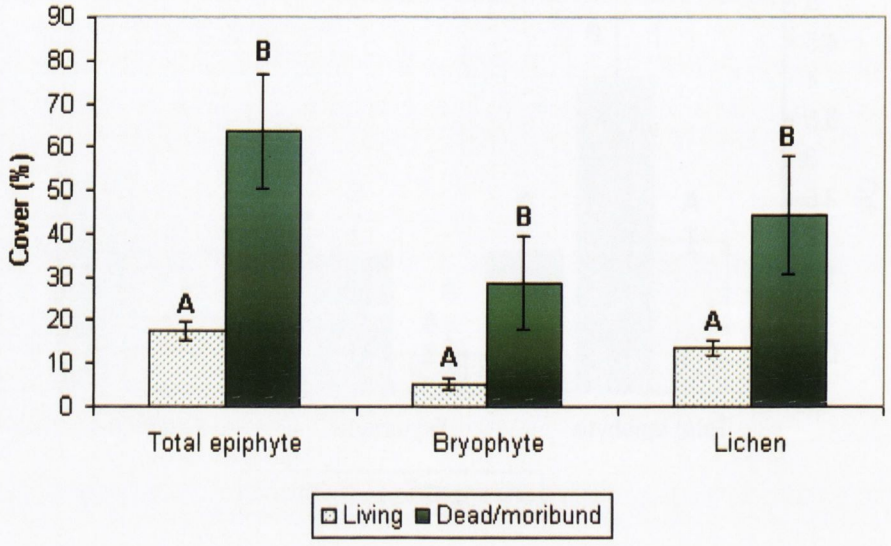


Figure 3.26 Mean diversity (1/D) in all plots on living and dead or moribund branches from the upper height zone on (a) Sitka spruce (living: n = 96, dead/moribund: n = 6) and (b) Japanese larch (living: n = 51, dead/moribund: n = 14). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

(a)



(b)

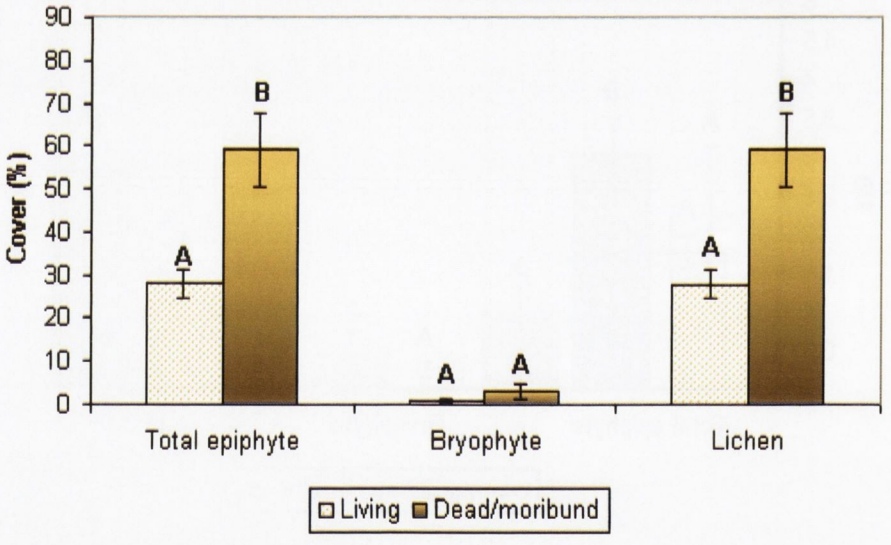


Figure 3.27 Mean cover in all plots on living and dead or moribund branches from the upper height zone on (a) Sitka spruce (living: n = 96, dead/moribund: n = 6) and (b) Japanese larch (living: n = 51, dead/moribund: n = 14). Error bars indicate ± standard error. There is no significant difference in cover between bars if indicated by the same letter.

habitats or dry surfaces where the humidity is fairly high (Paton, 1999). The other three liverwort species, *Calypogeia muelleriana*, *Frullania teneriffae* and *Metzgeria fruticulosa*, are also characteristic of moist situations (Paton, 1999; Smith, 1990). In contrast, the two lichen species are both characteristic of well-lit situations (Dobson, 2005; Purvis *et al.*, 1992). *Fellhanera bouteillei*, *Frullania teneriffae*, *Metzgeria fruticulosa* and *Parmotrema chinense* are all particularly pollution sensitive (Dobson, 2005; Paton, 1999). The species restricted to Japanese larch consisted of one moss turf, one vascular plant species and five foliose and two fruticose lichens (**Table 3.18**). None of these species is characteristic of moist situations. The five foliose lichens and *Usnea subfloridana* were only recorded in the Wicklow cluster. The moss species, *Dicranum scoparium*, has a wide ecological range and is common in open or shaded situations (Hill *et al.*, 1992). *Hypogymnia physodes*, *Cladonia coniocraea*, *Platismatia glauca* and *Pseudevernia furfuracea* are all particularly common on acid substrates and *Cladonia coniocraea*, *C. macilenta*, *Platismatia glauca*, and *Usnea subfloridana* are all tolerant of pollution (Dobson, 2005; Purvis *et al.*, 1992).

Table 3.18. A list of the epiphyte species recorded only on either Sitka spruce or Japanese larch and recorded on more than one tree. The epiphyte group, degree of affinity for epiphytism and the number of trees each species was recorded on are indicated.

	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Lejeunea cavifolia	Lv	Ma	Int	**5**	0
Fellhanera bouteillei	Li	Cr	Int	**4**	0
Calypogeia muelleriana	Lv	Ma	Low	**3**	0
Frullania teneriffae	Lv	Ma	Int	**2**	0
Metzgeria fruticulosa	Lv	Ma	High	**2**	0
Parmotrema chinense	Li	Fo	Int	**2**	0
Juvenile pteridophyte	Va	-	-	**2**	0
Dicranum scoparium	Mo	Tu	Int	0	**4**
Hypogymnia physodes	Li	Fo	Int	0	**4**
Usnea cornuta	Li	Fr	High	0	**4**
Oxalis acetosella	Va	-	Low	0	**2**
Cladonia coniocraea	Li	Fo	Int	0	**2**
Cladonia macilenta	Li	Fo	Int	0	**2**
Platismatia glauca	Li	Fo	Int	0	**2**
Pseudevernia furfuracea	Li	Fo	Int	0	**2**
Usnea subfloridana	Li	Fr	High	0	**2**

As well as species which were restricted to one or other tree species, there were also certain species which, while not completely absent from one tree species, were more common on the other species. Indicator species analysis (cf. **Section 3.2.3**) identified twelve species with significant indicator values for Sitka spruce or Japanese larch: two for spruce and ten for larch (**Table 3.19**). The two significant indicators for spruce were a crustose lichen and a liverwort mat species and both species had high indicator values. The crustose lichen, *Dimerella lutea*, is common in damp or humid, shaded situations and is often found in areas of old woodland (Dobson, 2005; Purvis *et al.*, 1992). *Metzgeria temperata* is also characteristic of damp shaded habitats and is intolerant of prolonged desiccation (Hill *et al.*, 1991; Paton, 1999; Smith, 1990). The significant indicators for larch were four crustose, one leprose, two foliose and one fruticose lichen species and a moss weft and moss

turf species. Three of these species were also species that only occurred only on larch (cf. **Table 3.18**). The species with the highest indicator value (88%), the crustose lichen *Fuscidea lightfootii*, is typically epiphytic and is described as being characteristic of damp areas, usually near boggy sites (Dobson, 2005; Purvis *et al.*, 1992). The next highest indicator value (80%) is for *Lepraria incana*, which is common on acid, shaded bark and is pollution tolerant. *Trapeliopsis flexuosa* is also reported to normally occur on bark mainly in polluted areas (Dobson, 2005), although it is common on bark in unpolluted areas of the Scottish Uplands and Highlands (B. Coppins, pers. comm.). *Lecanora pulicaris*, *Graphis scripta* and *Parmelia sulcata* are all widespread and common on trees, with *P. sulcata* also common on rocks (Dobson, 2005; Purvis *et al.*, 1992). *Thuidium tamariscinum* is characteristic of a wide range of moist habitats (Hill *et al.*, 1994).

Table 3.19. The significant indicators for Sitka spruce and Japanese larch according to indicator species analysis. The epiphyte group, degree of affinity for epiphytism and the indicator value (%) for each species are shown and the highest indicator value is highlighted in bold.

	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Dimerella lutea	Li	Cr	Int	**85**	2
Metzgeria temperata	Lv	Ma	High	**72**	3
Fuscidea lightfootii	Li	Cr	High	11	**88**
Lepraria incana	Li	Lp	Int	1	**80**
Thuidium tamariscinum	Mo	We	Low	4	**54**
Lecanora pulicaris	Li	Cr	High	1	**51**
Trapeliopsis flexuosa	Li	Cr	Int	1	**44**
Graphis elegans	Li	Cr	High	1	**43**
Parmelia sulcata	Li	Fo	Int	1	**43**
Dicranum scoparium	Mo	Tu	Int	0	**36**
Hypogymnia physodes	Li	Fo	Int	0	**36**
Usnea cornuta	Li	Fr	High	0	**36**

3.3.3.1 NMS ordination of the Sitka spruce and Japanese larch trees

The NMS ordination (**Figure 3.28**) was based on the sum of the cover of the epiphyte species in all trunk and branch plots on each tree. Cluster and indicator species analysis were used to divide the trees into cluster groups (**Figure 3.29 & Figure 3.30**). The plots of the number of cluster groups versus the average significance of the indicator species and the total number of significant indicator species (**Figure 3.30a & b**) suggest that the optimum number of clusters is five or six. The average significance of the indicator species is lowest for the six cluster option ($p = 0.31$), while the number of significant indicators ($n = 15$) is highest for five clusters. Examination of the NMS ordination plot suggested that, while choosing the six cluster option would produce a second group containing only two trees (Cluster E), this option was the most sensible choice, as clusters D and E, which would have been grouped together in the five cluster option, would not have formed a homogeneous cluster. The six cluster groups are indicated on the NMS ordination plot (**Figure 3.28**).

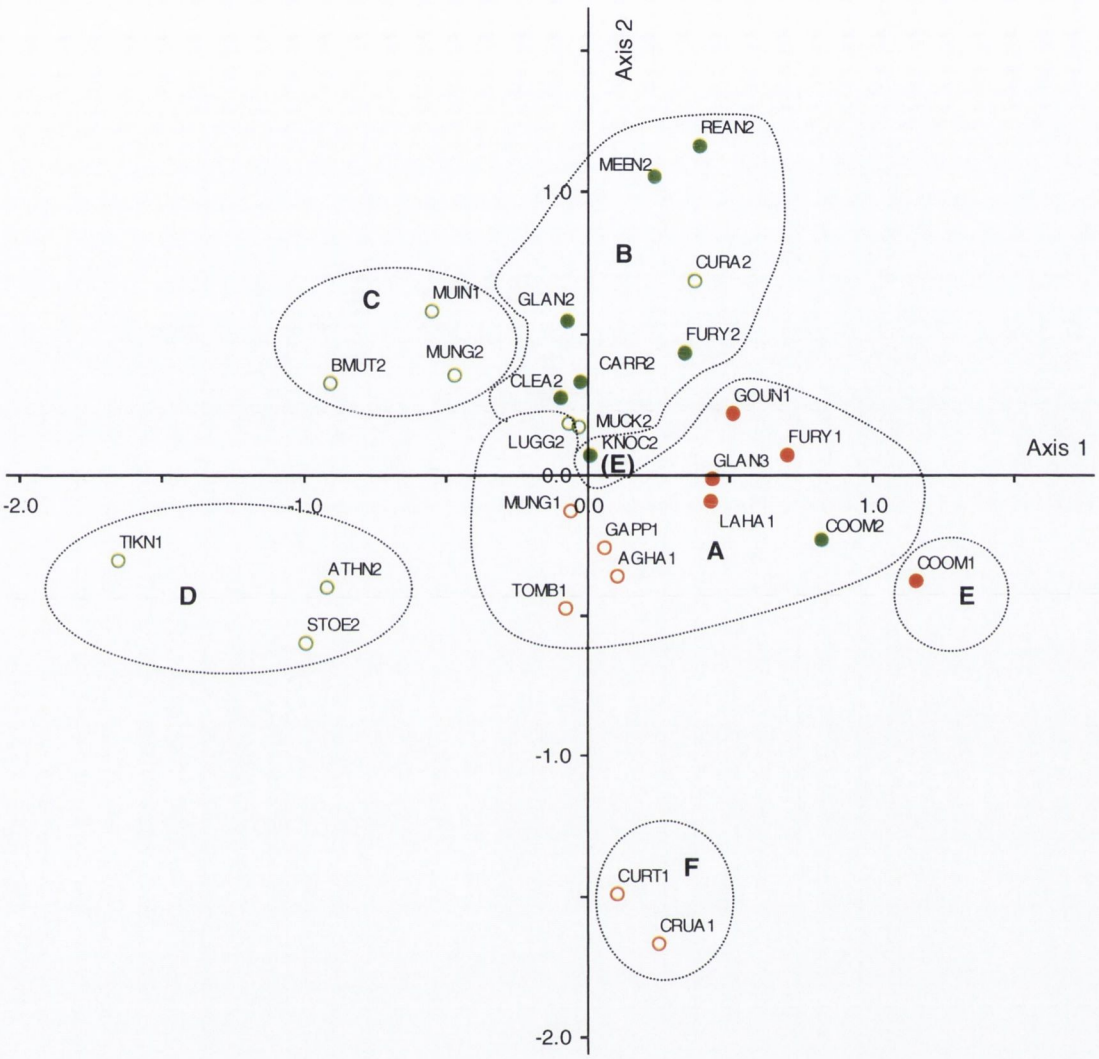


Figure 3.28 NMS ordination of the Sitka spruce and Japanese larch trees according to the sum of the epiphyte plot cover data for each tree. The letters A-F indicate groups of trees with similar species composition according to cluster and indicator species analysis. The outlier from group E is indicated in brackets. Sitka spruce (green) and Japanese larch (red) and Wicklow (unshaded) and Cork cluster trees (shaded) are indicated. Final stress for 3-dimensional solution = 10.69, final instability = 0.00043, axis 1 r^2 = 0.253, axis 2 r^2 = 0.297.

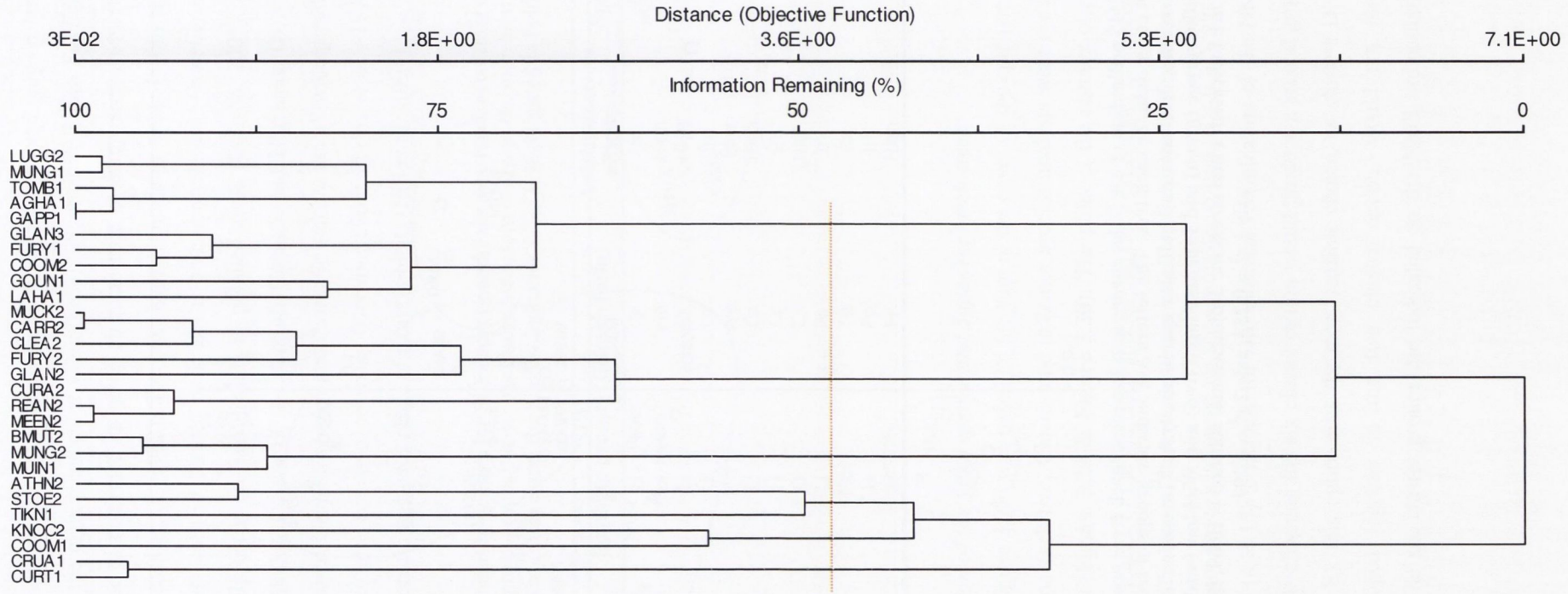
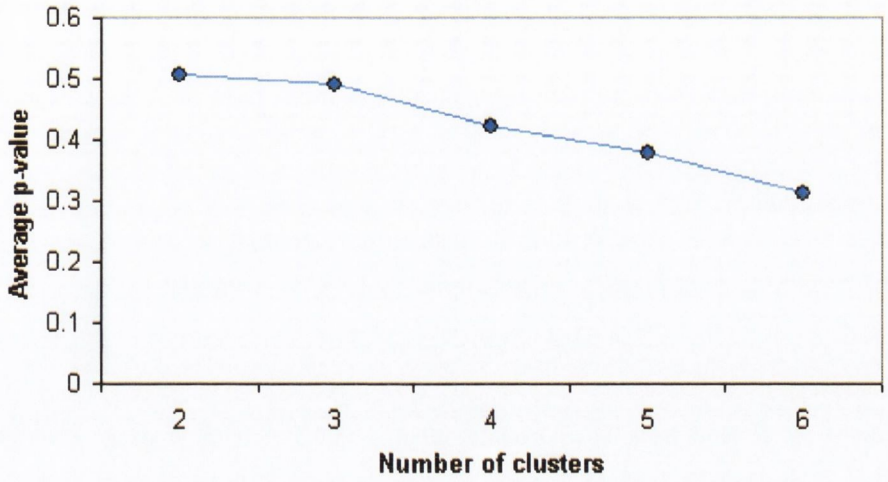


Figure 3.29 Cluster dendrogram of the Sitka spruce and Japanese larch trees, according to their overall epiphyte composition, scaled by Wishart's objective function and percent of information remaining. The position of the cut leading to the six resulting clusters indicated in Figure 3.28 is shown.

(a)



(b)

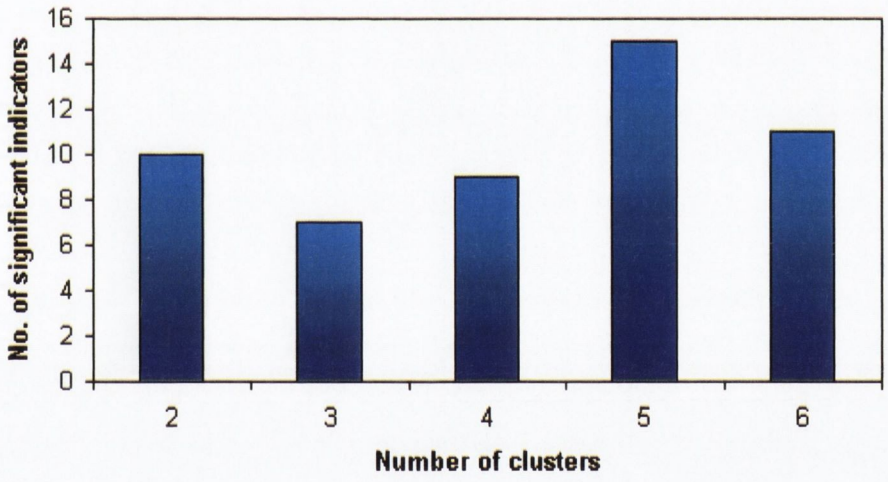


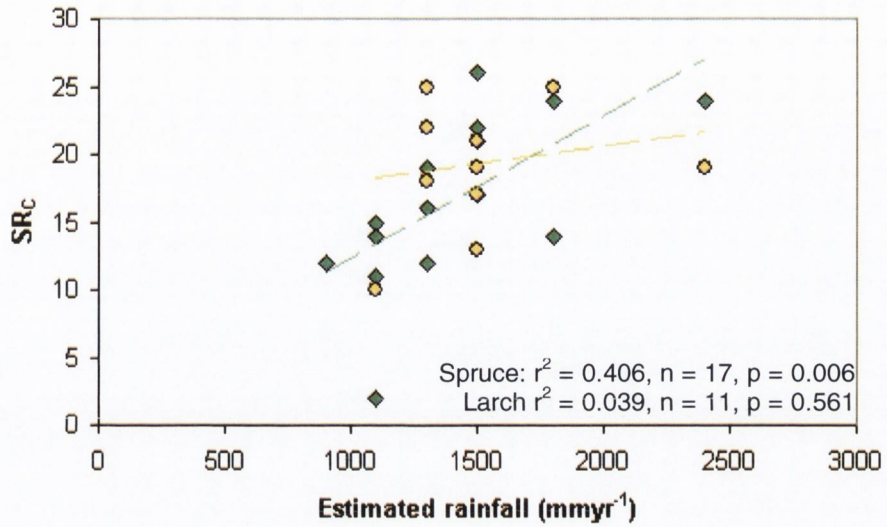
Figure 3.30 Graphs used to assess the appropriate number of cluster analysis groupings. Number of clusters is plotted against (a) average significance of the indicator species and (b) number of significant indicators. *Note*. Species indicators could not be derived for more than six clusters because further division caused at least one cluster to contain only one tree.

The NMS ordination highlights the differences in the overall composition of the epiphytic flora between Sitka spruce and Japanese larch trees and also between trees in the Wicklow and Cork clusters. Clusters B, C and D contained only spruce trees and the majority of larch trees were grouped together in clusters A and F. The Wicklow cluster trees were positioned towards the left hand end of axis one and clusters C, D and F contained only trees from this cluster. The relationship of total epiphyte richness with axis 1 of the ordination had been maximised (cf. **Section 3.2.3**) and this axis mainly separated species-poor Wicklow cluster spruce trees in relatively low rainfall areas from more species-rich Wicklow and Cork cluster spruce and larch trees with high epiphyte cover (**Table 3.20**). Stands with high basal area were also positioned towards the left hand end of axis 1; however, the cause of this high basal area was in some cases owing to a lack of thinning in stands, resulting in a large number of small trees, and in other cases to heavy thinning, resulting in few large trees. The height to the base of the live crown was also correlated with axis 1, as the older trees and larch trees towards the right hand end of axis 1 tended to have their live crowns higher. The correlation of the area of buildings grouped with axis 1 was strongly affected by TIKN1, which was one of only three trees located within 3km of 'buildings grouped' and had the largest area of buildings within 3km. Axis 2 separated dense spruce stands with high bryophyte cover from lichen-rich larch stands. Stands towards the top of axis 2 also tended to have more shady aspects. Older larch trees were positioned towards the bottom of axis 2.

The relationship between the environmental variables with significant correlations with axis 1 of the NMS ordination (**Table 3.20**) and species richness was examined further. Regression analyses revealed a significant positive relationship between estimated rainfall (cf. **Section 2.3.3.4**, **Appendix 1**) and total epiphyte richness (SR_C) for spruce ($r^2 = 0.406$, $p = 0.006$) although there was no significant relationship for larch ($r^2 = 0.039$, $p = 0.561$) (**Figure 3.31a**). Bryophyte and lichen richness were examined separately and, while there was no significant relationship between rainfall and bryophyte richness for either species, there was a significant positive relationship with lichen richness for spruce ($r^2 = 0.468$, $p = 0.002$) but again not for larch ($r^2 = 0.003$, $p = 0.879$) (**Figure 3.31b**).

There was a significant negative relationship between bryophyte richness (SR_C) and elevation for spruce ($r^2 = 0.237$, $p = 0.047$) and the relationship for larch was also close to significance ($r^2 = 0.305$, $p = 0.078$) (**Figure 3.32**). Since the elevation in the Wicklow cluster stands was significantly greater than in the Cork cluster stands (cf. **Section 2.6.1.1**) and total epiphyte and bryophyte SR_C were significantly higher in the Cork cluster, the trees from the Cork and Wicklow clusters were examined separately. No significant within-cluster relationships were found between bryophyte SR_C and elevation. However a strong negative relationship was found between lichen SR_C and elevation for the Cork cluster spruce trees ($r^2 = 0.854$, $p = 0.001$) (**Figure 3.33**). None of the other environmental variables had a significant relationship with species richness.

(a)



(b)

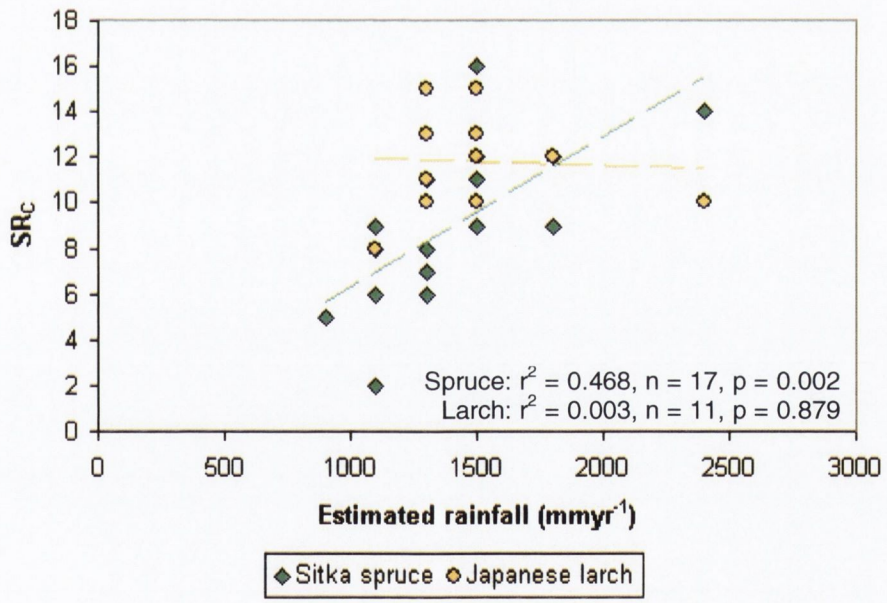


Figure 3.31 Relationship between estimated rainfall and (a) total epiphyte and (b) lichen richness (SR_C) for Sitka spruce (n = 17) and Japanese larch (n = 11).

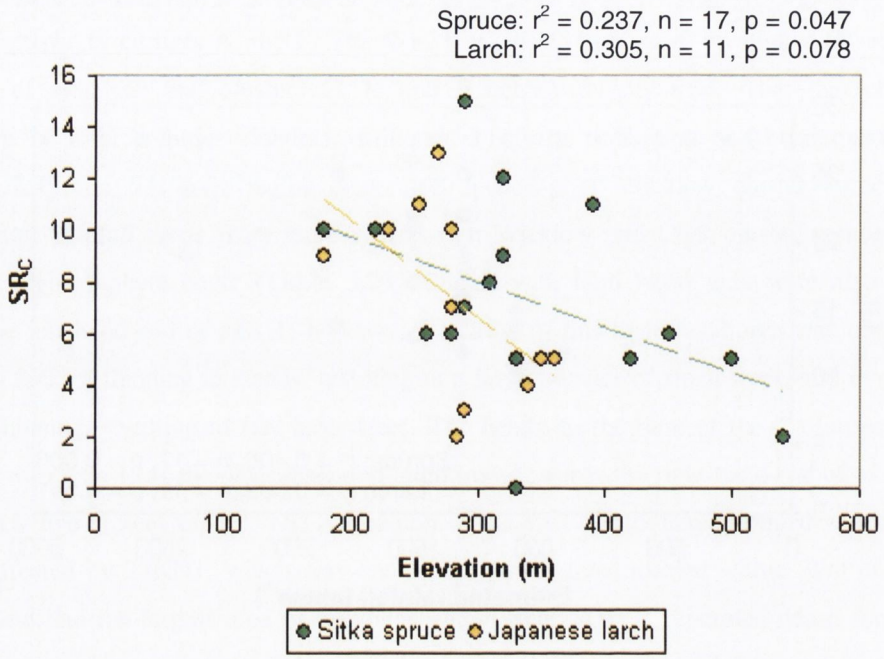


Figure 3.32 Relationship between elevation and bryophyte richness (SR_C) for Sitka spruce (n = 17) and Japanese larch (n = 11).

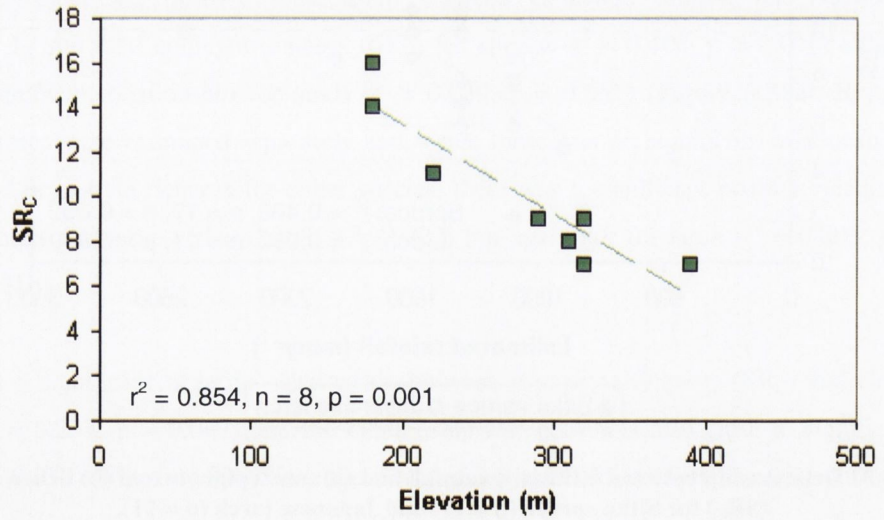


Figure 3.33 Relationship between elevation and lichen richness (SR_C) for the Cork cluster Sitka spruce trees (n = 8).

Table 3.20. Pearson's correlations (r) between the axes from the NMS ordination (Figure 3.28) and selected diversity, cover, tree, stand and site variables.

Correlation variable	Axis 1	Axis 2
Diversity:		
Total epiphyte SR_C	0.713**	0.038
Bryophyte SR_C	0.674**	0.459*
Lichen SR_C	0.422*	-0.452*
High epiphytism affinity SR_C	0.490**	-0.134
Total epiphyte $1/D_M$	0.545**	0.001
Total epiphyte β_w diversity	-0.612**	-0.313
Cover:		
Trunk total epiphyte $Cover_{MT}$	0.783**	0.134
Trunk bryophyte $Cover_{MT}$	0.633**	0.558**
Trunk lichen $Cover_{MT}$	0.222	-0.624**
Branch total epiphyte $Cover_{MB}$	0.561**	0.121
Branch bryophyte $Cover_{MB}$	0.391*	0.541**
Branch lichen $Cover_{MB}$	0.412*	-0.283
Tree:		
Age	0.282	-0.485**
DBH	0.128	-0.361
Height	0.364	-0.214
Height to 1st live branch	0.378*	0.136
Height to base of crown	0.478**	-0.143
Stand:		
Tree density	-0.088	0.434*
Average DBH	-0.009	-0.380*
Basal area	-0.432*	0.140
Site:		
Elevation	-0.477**	-0.096
Aspect	0.185	0.455*
Slope	0.137	-0.142
Estimated rainfall	0.537**	-0.195
Area of old woodland	-0.091	-0.160
Distance to old woodland	0.141	0.380*
Area of 'buildings grouped'	-0.530**	-0.096

Note. * indicates the correlation coefficient is significant at the $p < 0.05$ level and ** indicates significance at the $p < 0.01$ level.

The six cluster groups were compared in terms of certain diversity and environmental variables (**Table 3.21**). Cluster A was composed of the majority of the larch trees studied (**Photograph 3.1**), four from the Wicklow cluster and four from the Cork cluster, as well as two spruce trees, one from each geographic cluster. The single significant indicator species for this cluster was *Hypnum jutlandicum* (Table 3.22). This species can be found in dry to damp, exposed to deeply shaded situations (Hill *et al.*, 1994; Smith, 2004) and was commonly encountered in this study; it occurred on all but two of the trees studied. However, it occurred with particularly high cover on the trees in this cluster. Bryophyte cover in general, particularly cover of mosses, was high on the trunks of the trees (**Table 3.21**). The lichen *Graphis elegans* was also a commonly recorded species on the trees in this cluster. It is characteristic of moderately shaded smooth bark (Purvis *et al.*, 1992). *Lecanora pulicaris*, which is widely distributed on trees (Purvis *et al.*, 1992), was common on the trees in theWicklow cluster and *Colura calyptrifolia*, which is found on well drained surfaces in humid habitats (Paton, 1999), was common on the trees in the Cork cluster. This cluster was relatively species-rich (SR_C) on average with relatively high lichen SR_C, and the number of species with a

Table 3.21. The mean (± standard error) of selected variables for the cluster analysis groups shown in (Figure 3.28). There is no significant difference between clusters for any variable if indicated by the same letter.

Variable	Cluster A (n = 10)	Cluster B (n = 8)	Cluster C (n = 3)	Cluster D (n = 3)	Cluster E (n = 2)	Cluster F (n = 2)
Diversity:						
Total epiphyte SR_C	18.9 (± 1.8)^a	18.4 (± 1.4)^a	13.3 (± 1.2)^a	10.7 (± 4.4)^a	22.5 (± 3.5)^a	19.5 (± 1.5)^a
Bryophyte SR_C	7.7 (± 1.2)^a	9.5 (± 1.2)^a	5.7 (± 0.3)^a	2.3 (± 1.5)^a	9.5 (± 0.5)^a	5.0 (± 0.0)^a
Lichen SR_C	11.0 (± 0.9)^a	8.6 (± 0.7)^a	7.7 (± 0.9)^a	8.3 (± 3.2)^a	13.0 (± 3.0)^a	14.0 (± 1.0)^a
High epiphytism affinity SR_C	8.9 (± 1.0)^a	7.4 (± 0.7)^a	7.0 (± 1.0)^a	5.0 (± 2.0)^a	12.5 (± 3.5)^a	6.5 (± 0.5)^a
Total epiphyte $1/D_M$	2.5 (± 0.3)^a	2.1 (± 0.2)^a	1.6 (± 0.2)^a	1.3 (± 0.6)^a	2.5 (± 1.2)^a	2.5 (± 0.4)^a
Cover:						
Trunk total epiphyte $Cover_{MT}$ (%)	31.5 (± 5.0)^a	40.3 (± 7.5)^a	23.0 (± 7.6)^a	1.5 (± 0.8)^a	37.3 (± 19.6)^a	52.4 (± 1.4)^a
Trunk bryophyte $Cover_{MT}$ (%)	26.8 (± 6.0)^a	37.8 (± 7.6)^a	5.6 (± 2.2)^b	0.1 (± 0.1)^{ab}	16.2 (± 0.9)^{ab}	4.4 (± 1.3)^b
Trunk lichen $Cover_{MT}$ (%)	5.0 (± 0.9)^a	2.2 (± 0.7)^b	17.4 (± 6.4)^c	1.4 (± 0.7)^{bc}	21.5 (± 20.8)^{abc}	46.8 (± 3.9)^c
Branch total epiphyte $Cover_{MB}$ (%)	39.6 (± 6.4)^a	31.5 (± 5.7)^a	30.1 (± 15.7)^a	13.0 (± 6.5)^a	26.0 (± 0.4)^a	33.9 (± 9.1)^a
Branch bryophyte $Cover_{MB}$ (%)	8.8 (± 4.0)^a	21.7 (± 7.1)^a	3.0 (± 3.0)^a	2.4 (± 2.4)^a	8.6 (± 5.5)^a	0.1 (± 0.1)^a
Branch lichen $Cover_{MB}$ (%)	34.1 (± 4.4)^a	14.9 (± 2.7)^b	26.5 (± 13.9)^{ab}	11.9 (± 5.1)^{ab}	22.4 (± 2.3)^{ab}	33.9 (± 9.1)^{ab}
Tree:						
Age (years after planting)	40.5 (± 2.9)^a	38.5 (± 1.6)^a	44.3 (± 4.5)^a	36.7 (± 8.2)^a	47.5 (± 15.5)^a	66.5 (± 1.5)^a
DBH (cm)	33.5 (± 3.4)^a	28.0 (± 1.5)^a	40.6 (± 4.3)^a	31.6 (± 3.9)^a	34.9 (± 11.6)^a	43.4 (± 0.8)^a
Height (m)	22.1 (± 1.6)^a	18.9 (± 0.9)^a	25.4 (± 2.1)^a	15.3 (± 2.8)^a	22.4 (± 6.9)^a	25.5 (± 0.3)^a
Stand:						
Tree density (no.$100m^{-2}$)	5.9 (± 1.0)^a	14.6 (± 2.6)^b	5.0 (± 1.0)^a	11.0 (± 3.1)^{ab}	10.5 (± 6.5)^{ab}	3.5 (± 0.5)^a
Average DBH (cm)	28.6 (± 2.6)^{ab}	21.8 (± 1.8)^a	37.5 (± 6.5)^{ab}	26.4 (± 4.7)^{ab}	24.3 (± 6.7)^{ab}	41.4 (± 3.5)^b
Basal Area (m^2100m^{-2})	0.35 (± 0.04)^a	0.51 (± 0.04)^{ab}	0.56 (± 0.13)^{ab}	0.67 (± 0.08)^b	0.35 (± 0.09)^{ab}	0.44 (± 0.21)^{ab}
Site:						
Elevation (m)	270.0 (± 13.4)^a	340.0 (± 26.6)^{ab}	290.0 (± 20.8)^{abc}	456.7 (± 64.4)^{abc}	180.0 (± 0.0)^c	355.0 (± 5.0)^{bc}
Aspect	1.25 (± 0.23)^a	1.30 (± 0.17)^a	1.68 (± 0.31)^a	0.55 (± 0.28)^a	0.96 (± 0.60)^a	0.91 (± 0.57)^a
Slope (°)	9.2 (± 1.7)^a	9.9 (± 2.8)^a	9.0 (± 2.5)^a	12.3 (± 1.2)^a	15.5 (± 9.5)^a	10.3 (± 2.8)^a
Estimated rainfall ($mmyr^{-1}$)	1460.0 (± 130.1)^a	1437.5 (± 62.5)^a	1100.0 (± 0.0)^a	1400.0 (± 208.2)^a	1950.0 (± 450.0)^a	1400.0 (± 100.0)^a
Area of old woodland (ha)	11.1 (± 9.2)^a	0.1 (± 0.1)^a	0.6 (± 0.6)^a	9.0 (± 8.7)^a	0^a	14.6 (± 4.7)^a
Distance to old woodland (m)	718.9 (± 123.7)^a	963.8 (± 28.79)^a	715.0 (± 286.0)^a	765.3 (± 134.3)^a	1001.0 (± 0.0)^a	370.0 (± 206.0)^a
Area 'buildings grouped' (ha)	11.0 (± 11.0)^a	0^a	0^a	126.2 (± 126.2)^a	0^a	6.7 (± 6.7)^a

high affinity for epiphytism was also high. The mean total epiphyte diversity ($1/D_M$) was highest in this group and lichen cover ($Cover_{MB}$) was particularly high on the branches (**Table 3.21**). The stands containing the two spruce trees, LUGG2 and COOM2, were very heavily thinned and had the lowest tree density and basal area of all spruce stands studied (cf. **Appendix 2**). LUGG is a second rotation plantation and COOM is silviculturally over-mature.

Table 3.22. The significant indicators for the cluster analysis groups indicated in Figure 3.28. The indicator value (%) for each species in each of the six groups is shown and the highest indicator value is highlighted in bold.

Species	A	B	C	D	E	F
Hypnum jutlandicum	**54**	28	15	0	1	1
Metzgeria temperata	3	**95**	1	0	0	0
Dimerella lutea	3	2	**91**	2	0	0
Cladonia macilenta	0	0	0	0	0	**100**
Hypogymnia physodes	0	0	0	0	0	**100**
Platismatia glauca	0	0	0	0	0	**100**
Pseudevernia furfuracea	0	0	0	0	0	**100**
Usnea subfloridana	0	0	0	0	0	**100**
Lepraria incana	1	0	0	0	0	**98**
Parmelia sulcata	1	0	0	0	1	**93**
Thuidium tamariscinum	10	0	0	0	0	**79**

Cluster B was composed of the majority of the Cork cluster spruce trees studied, as well as two spruce trees from the Wicklow cluster (**Photograph 3.2**). The liverwort *Metzgeria temperata* was a significant indicator for this group (**Table 3.22**). This species is found in shaded or damp situations and is intolerant of prolonged desiccation (Hill *et al.*, 1991; Paton, 1999; Smith, 1990). It occurred with high cover on the trees in this cluster. The moss, *Hypnum jutlandicum*, also had an indicator value of greater than 25%, making it a good indicator for this group (Dufrene & Legendre, 1997), as well as for cluster A. The moss, *Kindbergia praelonga*, was also common on the trees in this cluster. Both the aforementioned moss species have broad habitat ranges (Hill *et al.*, 1994). *Lejeunea cavifolia*, which is found in damp humid habitats (Paton, 1999) and *Plagiothecium undulatum*, which favours shaded situations (Hill *et al.*, 1994; Smith, 2004) were also recorded on a number of trees. The juvenile pteridophyte species, the only vascular epiphyte recorded on spruce, was recorded on trees in this cluster. This cluster was particularly bryophyte-rich (SR_C) on average and had very high bryophyte cover, especially of liverworts, and of *Metzgeria temperata* in particular. The bryophyte cover was high on both trunks ($Cover_{MT}$) and branches ($Cover_{MB}$) (**Table 3.21**). The trees were relatively small and the stands in which the trees were located were dense and had very low DBH on average. The Cork cluster stands were all planted on peat, while the two Wicklow cluster spruce trees, MUCK2 and CURA2, were from high-elevation stands on steep slopes with N to NW aspects.

Cluster C was composed of three spruce trees from the Wicklow cluster (**Photograph 3.3**). The single significant indicator for this group was *Dimerella lutea* (**Table 3.22**), which is characteristic of damp or humid shaded situations, often in old woodland (Dobson, 2005; Purvis *et al.*, 1992). It

was also a significant indicator for Sitka spruce (cf. **Table 3.19**). *Dimerella pineti*, which is common on shaded acid bark (Purvis *et al.*, 1992), also had high cover on the trees in this cluster. *Hypnum jutlandicum* had some cover at the tree base and *Metzgeria furcata* occurred with low cover on some trees. *Physcia tenella*, which is common in well-lit situations (Purvis *et al.*, 1992), also occurred on branches. This cluster was poor on average in bryophyte and lichen richness (SR_C) and diversity ($1/D_M$) (**Table 3.21**). Bryophyte cover was also low on trunks ($Cover_{MT}$) and branches ($Cover_{MB}$). Lichen cover ($Cover_{MT}$ and $Cover_{MB}$) was moderate, but was high compared to the other spruce trees studied and mostly consisted of cover of *Dimerella* species. The trees in this cluster were large, both in height and DBH, and the stands in which the trees were located had low tree density as a result of heavy thinning. The stands at MUNG an MUIN were silviculturally over-mature. The stands were also low elevation and with little slope and this cluster had the lowest estimated rainfall and shadiest aspect of all the cluster groups.

Cluster D also was composed of three spruce trees from the Wicklow cluster (**Photograph 3.4**). There were no significant indicators for this group (**Table 3.22**). This cluster was species-poor (SR_C) on average, particularly in bryophytes, and had the lowest mean total epiphyte diversity ($1/D_M$) (**Table 3.21**). Bryophyte cover was low on both trunks ($Cover_{MT}$) and branches ($Cover_{MB}$) but extremely low on trunks. This cluster had the youngest and smallest trees on average, however TIKN1 was significantly older and taller than the other two trees in the cluster. This tree was located close to suburban Dublin and was the most species-poor tree studied. Tree density and basal area were high in this cluster and ATHN2 and STOE2 were in unthinned stands. The stands were also high-elevation on average.

Cluster E was composed of one spruce tree, KNOC2, and one larch tree, COOM1; both from the Cork cluster. KNOC2 was separated from COOM1 in the ordination diagram (**Figure 3.28**) and was located between clusters A and B, suggesting it is intermediate between the majority of spruce and larch trees. The two trees in this cluster were quite dissimilar in their diversity and environmental variables, as can be seen by the large standard errors of some variables (**Table 3.21**). Again there were no significant indicators for this cluster (**Table 3.22**). This is not surprising considering the two trees had few species in common. It was an extremely species-rich (SR_C) cluster in both bryophytes and lichens (**Table 3.21**). Individually each tree supported a number of species not recorded on any other trees. The number of species with a high affinity for epiphytism (SR_C) was also high. The mean total epiphyte diversity ($1/D_M$) was relatively high and lichen β_w diversity was high on trunks. Cover was relatively high on trunks ($Cover_{MT}$) and branches ($Cover_{MB}$), particularly for lichens, although lichen cover was very low on the trunk of KNOC2. The trees were relatively old and tall on average and the stands were relatively dense and with low basal area; COOM1 was almost twice as old and tall as KNOC2 and had very low density and basal

area. COOM1 was in a very high rainfall area while the estimated rainfall received at KNOC2 was moderate. The stands were both at low elevation and had no old woodland within 1km.

Cluster F was composed of two larch trees (CRUA1 and CURT1) from the Wicklow cluster (**Photograph 3.5**). There were eight significant indicators for this group: seven lichens and one moss species (**Table 3.22**). *Cladonia macilenta, Hypogymnia physodes, Platismatia glauca, Pseudevernia furfuracea* and *Usnea subfloridana* all had the perfect indicator value of 100%. *Hypogymnia physodes*, *Platismatia glauca* and *Pseudevernia furfuracea* are all particularly common on acid substrates and *Cladonia macilenta*, *Platismatia glauca*, *Usnea subfloridana* and *Lepraria incana* are all particularly tolerant of pollution (Dobson, 2005; Purvis *et al.*, 1992). *Cladonia coniocraea*, *Lecanora pulicaris* and *Oxalis acetosella* also commonly occurred on these trees. This cluster was particularly lichen-rich (SR_C) but had low bryophyte richness (SR_C) (**Table 3.21**). Liverworts were absent from the trees. The number of species with a high affinity for epiphytism (SR_C) was also low. This group had high mean total epiphyte diversity ($1/D_M$) according to Simpson's reciprocal and bryophyte β_w diversity was high on trunks. Lichen cover was also high on trunks and branches. The trees in this cluster were the oldest and largest on average, both in terms of height and DBH. Tree density in the stands was low and both stands were silviculturally over-mature. These stands had the greatest area of old woodland within 1km and shortest distance to old woodland.

Overall epiphyte composition described

The results of the NMS and cluster analysis have highlighted the different overall species composition of the trees studied. This information was tabulated, with each distinct composition informally named and described, and the indicators and stand types with which each composition was associated being given (**Table 3.23**). The overall epiphyte composition of the trees from cluster A was named 'moss-dominated', with that of the trees in cluster B named 'liverwort-dominated'. The overall epiphyte composition of the trees from cluster C was named '*Dimerella lutea*-dominated'. Because of the heterogeneity of cluster D, TIKN1 was excluded from the description. The overall composition of the epiphyte flora of the remaining pair of trees was named 'bryophyte-poor'. As the two members of cluster E, COOM1 and KNOC2, had few similarities in their epiphyte floras, this pair of trees were not considered to have a distinct epiphyte composition. The overall epiphyte composition of the pair of trees from cluster F was named 'lichen-dominated'.

3.3.4 Vertical distribution of epiphytes

The overall epiphyte composition of the trees has been discussed, but the distribution of epiphytes within the tree is also of interest. The species richness, diversity and cover in the four height zones on the trunk were examined. The overall number of species recorded on the trunk at each of the

Photograph 3.1 Tree studied at Ballinagappoge (GAPP), Co. Wicklow (GR T081 843); a 38-year-old Japanese larch stand. Note the relatively open canopy and graminoid dominated ground flora. *Hypnum jutlandicum* is covering the base of the tree.

Photograph 3.2 Two trunk plots from FURY2; a Sitka spruce tree from a 41-year-old stand at Fuhiry, Co. Cork (GR W144 734). The low light levels in the stand are evident. (a) A tree base trunk plot (TBs) containing *Hypnum jutlandicum*, *Kindbergia praelonga, Plagiothecium undulatum* and *H. andoi* and (b) a middle trunk plot (TMn) at 7m above the ground containing the liverworts *Metzgeria temperata* and *Microlejeunea ulicina*.

Photograph 3.3 Barnamuinga (MUIN), Co. Wicklow (GR S962 696); a 52-year-old Sitka spruce stand. Note the low tree density and the poor ground flora. The buttressed bases of the trees have some cover of the moss *Hypnum jutlandicum*. The cover of the crustose lichen *Dimerella lutea* was extremely high in this stand. (Photograph: George Smith)

Photograph 3.4 Athdown (ATHN), Co. Wicklow (GR O076 158); a 28-year-old unthinned Sitka spruce stand. A branch that has been removed from the tree is being studied in a more open area of the stand. Note the density of the stand, the low light levels, the absence of bryophytes at the base of the trees and the absence of ground flora. (Photograph: George Smith).

Photograph 3.5 Curtlestown (CURT), Co. Wicklow (GR O181 172); a 68-year-old Japanese larch stand. The lichens *Hypogymnia physodes, Platismatia glauca* and *Usnea* spp. were particularly abundant on the trunks of the trees.

height zones on the trees was greatest in the upper zone on Sitka spruce and in the middle zone on Japanese larch, as was the total number of lichen species (**Figure 3.34**). The most bryophyte species were recorded at the tree base for both species. Vascular species were only recorded in the tree base zone on larch while they were also found in the lower and middle zones on spruce. When the bryophyte and lichen species were further split into their different growth-forms (cf. **Section 2.4.1, Appendix 3**), the overall number of bryophyte mat species recorded decreased from the tree base to upper zones on both species (**Figure 3.35**). Wefts were only recorded in the tree base and lower zones, with the most species being recorded at the tree base, and cushions were only recorded in the middle and upper zones on both species. Turfs were only recorded in the tree base and lower zone on larch but occurred in the tree base and middle zones on spruce (**Figure 3.35**). In contrast to the situation on larch, there were no fruticose lichens recorded in the tree base and lower zones on spruce (**Figure 3.36**).

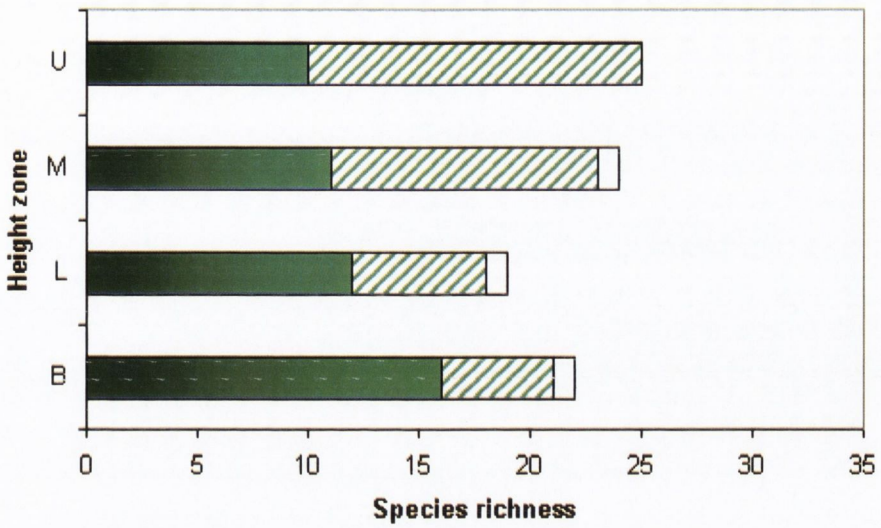
Table 3.23 The overall epiphyte composition of the trees surveyed for the present study. The cluster group on which each composition described is based is given, the epiphyte composition is described and the indicators and stand types with which each epiphyte composition is associated are presented.

Cluster	Epiphyte composition	Indicators	Stand types
A	'Moss-dominated' - with crustose and foliose lichens	High cover of *Hypnum jutlandicum*; *Graphis elegans*; High moss cover	Larch stands; heavily thinned spruce stands (but not in dry sites)
B	'Liverwort-dominated' - with mosses and crustose lichens	High cover of *Metzgeria temperata*; *Hypnum jutlandicum*; High liverwort cover	Dense spruce stands on peat; High-elevation stands with shaded aspects
C	'*Dimerella lutea*-dominated' - with low bryophyte cover	High cover of *Dimerella lutea*; *D. pineti*; *Hypnum jutlandicum*	Heavily thinned spruce stands (mainly silviculturally over-mature) in dry sites with shaded aspects
D*	'Bryophyte-poor' – with crustose lichens	Very low bryophyte cover	Young (< 30 years), unthinned spruce stands at high elevations
F	'Lichen-dominated' – with low moss cover. Liverworts absent.	*Cladonia macilenta*; *Hypogymnia physodes*; *Platismatia glauca*; *Pseudevernia furfuracea*; *Usnea subfloridana*; *Lepraria incana*; *Parmelia sulcata*; *Thuidium tamariscinum*	Heavily thinned, silviculturally over-mature larch stands close to old woodland.

Note. * Cluster D excluding TIKN1

A total of 18 species were restricted to a single height zone on the trunks of Sitka spruce: five to the tree base, three to the lower, one to the middle and nine to the upper zones. All five species restricted to the tree base were bryophytes and all but three of the species restricted to the upper zone were lichens. Only nine of the species restricted to one height zone occurred in more than one plot (**Table 3.24**). On larch, 20 species were restricted to a single zone: ten to the tree base, one to the lower, six to the middle and three to the upper zone. The species restricted to the tree base were seven bryophyte species, two vascular plant species and the lichen *Cladonia chlorophaea*. Unlike on spruce, all species restricted to the middle and upper zones were lichens. Only seven of the

(a)



(b)

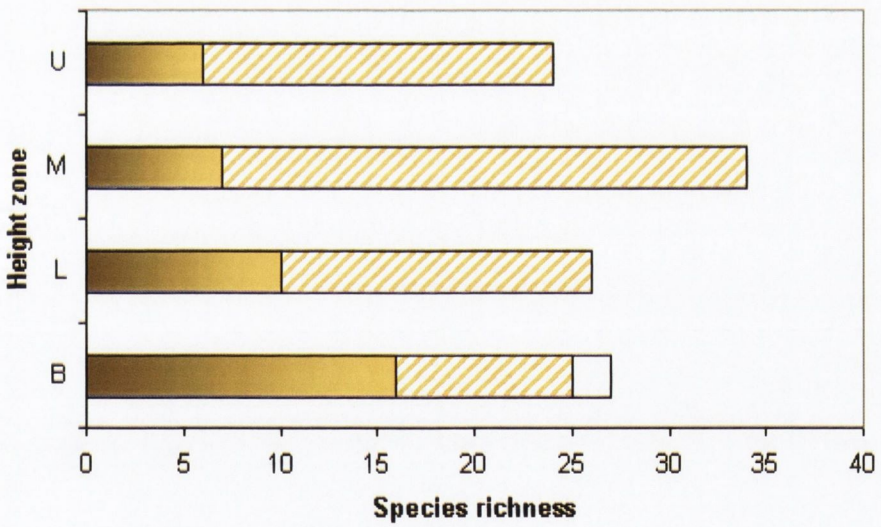
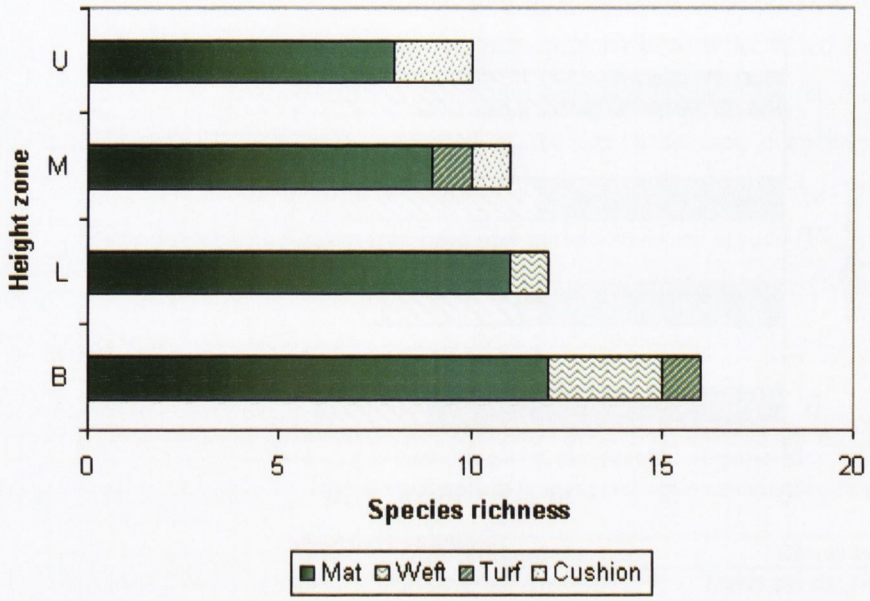


Figure 3.34 Overall number of species recorded in the four height zones (B = tree base, L= lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species (unshaded) are indicated.

(a)



(b)

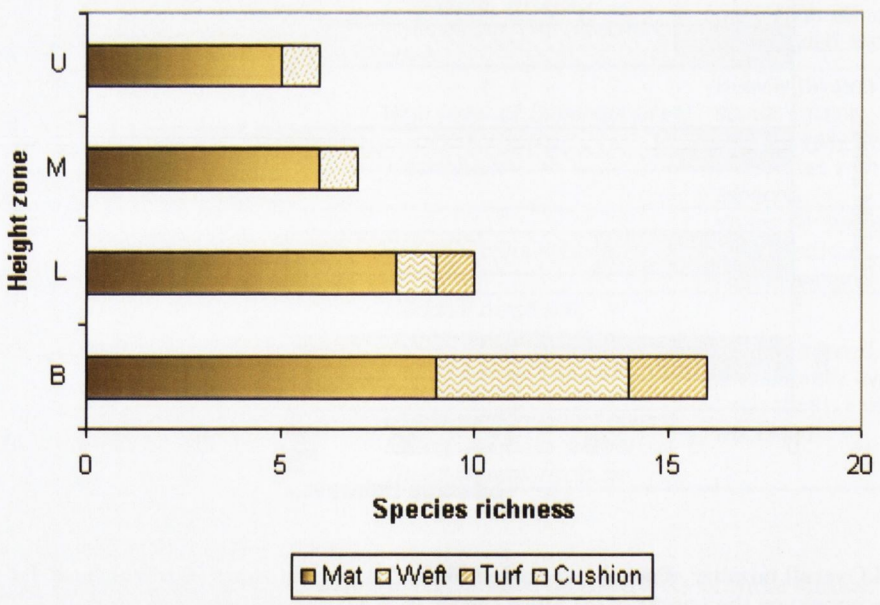
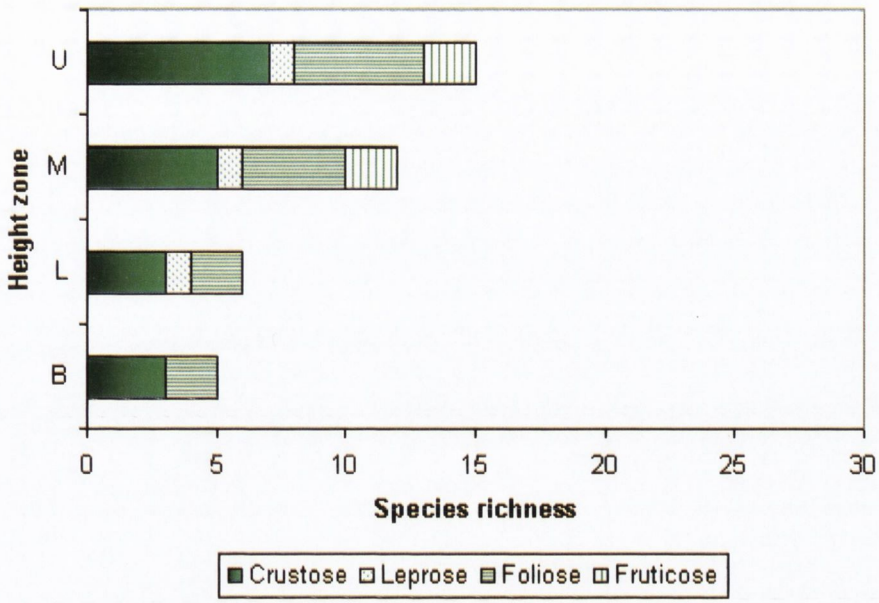


Figure 3.35 Relative proportions of the four bryophyte growth forms making up the overall bryophyte species richness in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22).

(a)



(b)

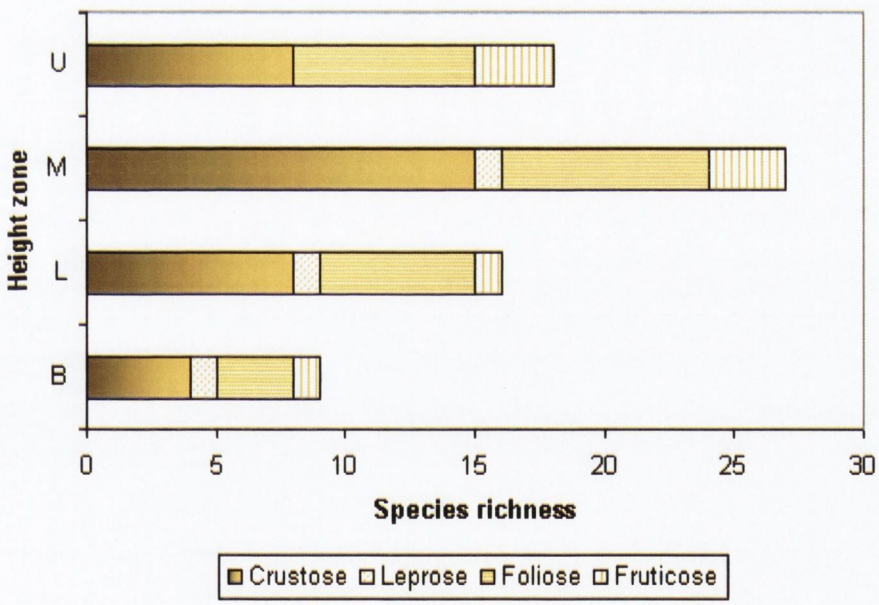


Figure 3.36 Relative proportions of the four lichen growth forms making up the overall lichen species richness in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22).

species restricted to a single zone occurred in more than one plot; all species were restricted to the tree base (**Table 3.24**). All species restricted to either the tree base or lower zones had a low or intermediate affinity for epiphytism, while those restricted to either the middle or upper zones had an intermediate or high affinity for epiphytism. A number of moss species restricted to the tree base on larch occurred in a number of zones on spruce, while some species restricted to the upper zone on spruce occurred in a number of zones on larch (**Table 3.24**).

Table 3.24 Epiphyte species restricted to a single height zone on either Sitka spruce or Japanese larch and occurring in more than one plot. The epiphyte group, growth form and degree of affinity for epiphytism of each species is indicated, as well as the height zones (B = tree base, L = lower, M= middle, U = upper) in which they occurred. – indicates the epiphyte species did not occur on that tree species.

	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Calypogeia muelleriana	Mo	Ma	Low	**B**	-
Isothecium myosuroides	Mo	We	Int	**B**	BL
Rhytidiadelphus loreus	Mo	We	Low	**B**	**B**
Kindbergia praelonga	Mo	Ma	Int	BL	**B**
Thuidium tamariscinum	Mo	We	Low	BL	**B**
Plagiothecium undulatum	Mo	Ma	Low	BLM	**B**
Campylopus flexuosus	Mo	Tu	Low	-	**B**
Cladonia coniocraea	Li	Fo	Int	-	**B**
Oxalis acetosella	Va	-	Low	-	**B**
Frullania tamarisci	Lv	Ma	Int	**L**	BLM
Frullania dilatata	Lv	Ma	High	**U**	-
Colura calyptrifolia	Lv	Ma	Int	**U**	MU
Lecanora pulicaris	Li	Cr	High	**U**	MU
Hypogymnia tubulosa	Li	Fo	Int	**U**	MU
Fuscidea lightfootii	Li	Cr	High	**U**	BMU

A total of ten species were recorded in only two height zones on spruce, all of these in either the tree base and lower or middle and upper zones. The species restricted to the tree base and lower zones were all bryophytes. Six species were recorded in three of the zones; two lichen species not recorded in the tree base zone and three bryophyte and one vascular plant species not recorded in the upper zone. Six species were recorded in all four zones on spruce; all bryophyte mats or crustose lichens (**Table 3.25**). A total of 18 species were recorded in only two zones on larch but, in contrast to spruce, the two zones that species were restricted to consisted of all possible combinations with the exception of the tree base and upper zones combined. All but one species restricted to the tree base and lower zones were bryophytes; the exception being the foliose lichen *Cladonia macilenta*. Eleven species occurred in three zones: six lichens not recorded at the tree base, a liverwort and three lichens not recorded in the upper zones and *Fuscidea lightfootii* which was absent from the lower zone. Five species were recorded in all four height zones on larch (**Table 3.25**).

The pattern for mean total epiphyte richness in the plots from each height zone (**Figure 3.37**) reflected that of the overall number of epiphyte species recorded in each height zone (cf. **Figure 3.34**). Comparison of the species richness among the four height zones revealed no significant

differences in total epiphyte richness among them for either spruce (H = 0.89, df = 3, p = 0.890) or larch (H = 6.00, df = 3, p = 0.112). There were, however, significant differences among the four zones for bryophyte and lichen richness on both spruce (bryophyte, H = 17.99, df = 3, p < 0.001; lichen, H = 35.29, df = 3, p < 0.001) and larch (bryophyte, H = 16.85, df = 3, p = 0.001; lichen, H = 32.66, df = 3, p < 0.001) (**Figure 3.37**). On both tree species, bryophyte richness decreased with height and lichen richness increased. Lichen richness was significantly greater on larch compared to spruce in all height zones (Mann-Whitney U test: B, p = 0.006; L, p < 0.001: M, p < 0.001; U, p = 0.001).

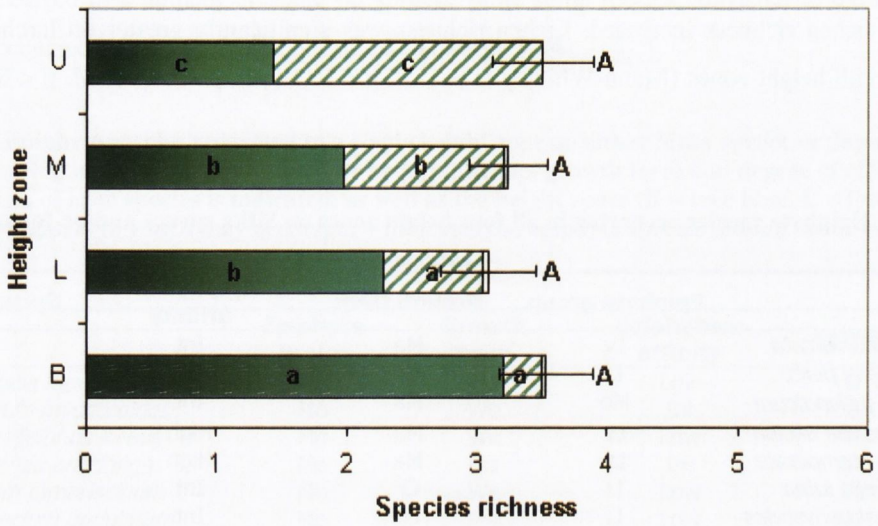
Table 3.25. Epiphyte species occurring in all four height zones on Sitka spruce and/or Japanese larch.

	Epiphyte group	Growth form	Epiphytism affinity	Spruce	Larch
Metzgeria furcata	Lv	Ma	Int	√	
Dimerella pineti	Li	Cr	High	√	
Hypnum jutlandicum	Mo	Ma	Int	√	√
Microlejeunea ulicina	Lv	Ma	High	√	√
Metzgeria temperata	Lv	Ma	High	√	√
Dimerella lutea	Li	Cr	Int	√	√
Hypogymnia physodes	Li	Fo	Int		√

Analysis of the distribution of the different bryophyte and lichen growth forms revealed significant differences in epiphyte species richness among the four height zones for bryophyte turfs on larch only (spruce: H = 2.02, df = 3, p = 0.569; larch: H = 9.92, df = 3, p = 0.019) and for bryophyte wefts (spruce: H = 14.88, df = 3, p = 0.002; larch: H = 43.13, df = 3, p < 0.001), mats (spruce: H = 21.98, df = 3, p < 0.001; larch: H = 8.21, df = 3, p = 0.042), and cushions (spruce: H = 22.54, df = 3, p < 0.001; larch: H = 7.83, df = 3, p = 0.019) (**Figure 3.38**), and leprose (spruce: H = 20.02, df = 3, p < 0.001; larch: H = 16.60, df = 3, p < 0.001), crustose (spruce: H = 31.13, df = 3, p < 0.001; larch: H = 38.45, df = 3, p < 0.001), foliose (spruce H = 14.53, df = 3, p = 0.002; larch H = 15.19, df = 3, p = 0.002) and fruticose lichens (spruce H = 12.47, df = 3, p = 0.006; larch H = 10.38, df = 3, p = 0.016) on both species (**Figure 3.39**). The mean species richness of bryophyte turf, weft and mat species was greatest in the tree base zone, while the species richness of cushions was greatest in the upper zone on both species (**Figure 3.38**). The mean species richness of crustose, foliose and fruticose lichens increased from the tree base to the upper zone on both tree species, while leprose lichen richness was greatest in the middle zone on spruce and the lower zone on larch (**Figure 3.39**).

Analysis of the distribution of species with low, intermediate and high affinities for epiphytism (cf. **Section 2.4.1**) in the four height zones revealed a significant difference in species richness among zones for species with low (H = 25.88, df = 3, p < 0.001) and high (H = 15.95, df = 3, p = 0.001) affinities for epiphytism on spruce and for all three groups on larch (low, H = 38.83, df = 3, p < 0.001; intermediate, H = 9.29, df = 3, p = 0.026; high, H = 42.81, df = 3, p < 0.001). Species with a

(a)



(b)

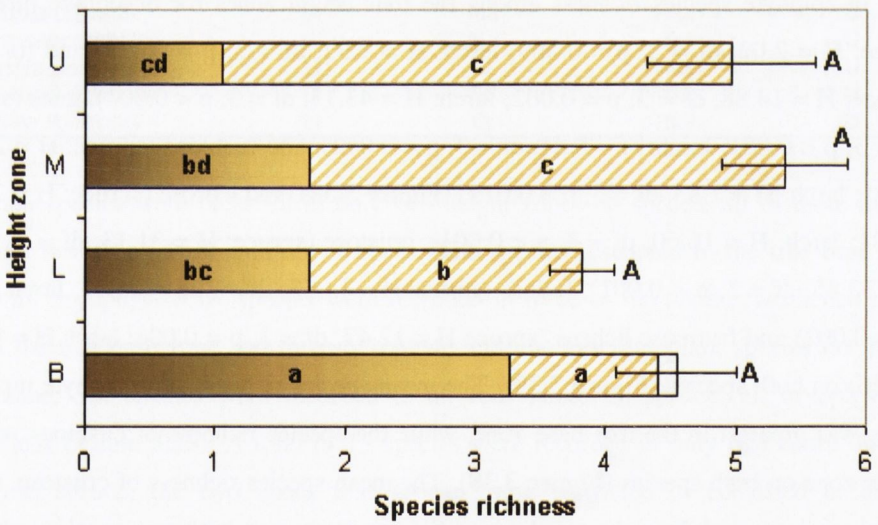


Figure 3.37 Mean epiphyte species richness in the trunk plots in the four height zones (B = tree base, L = lower, M = middle, U = upper) on (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species (unshaded) are indicated. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) richness between two height zones if indicated by the same letter.

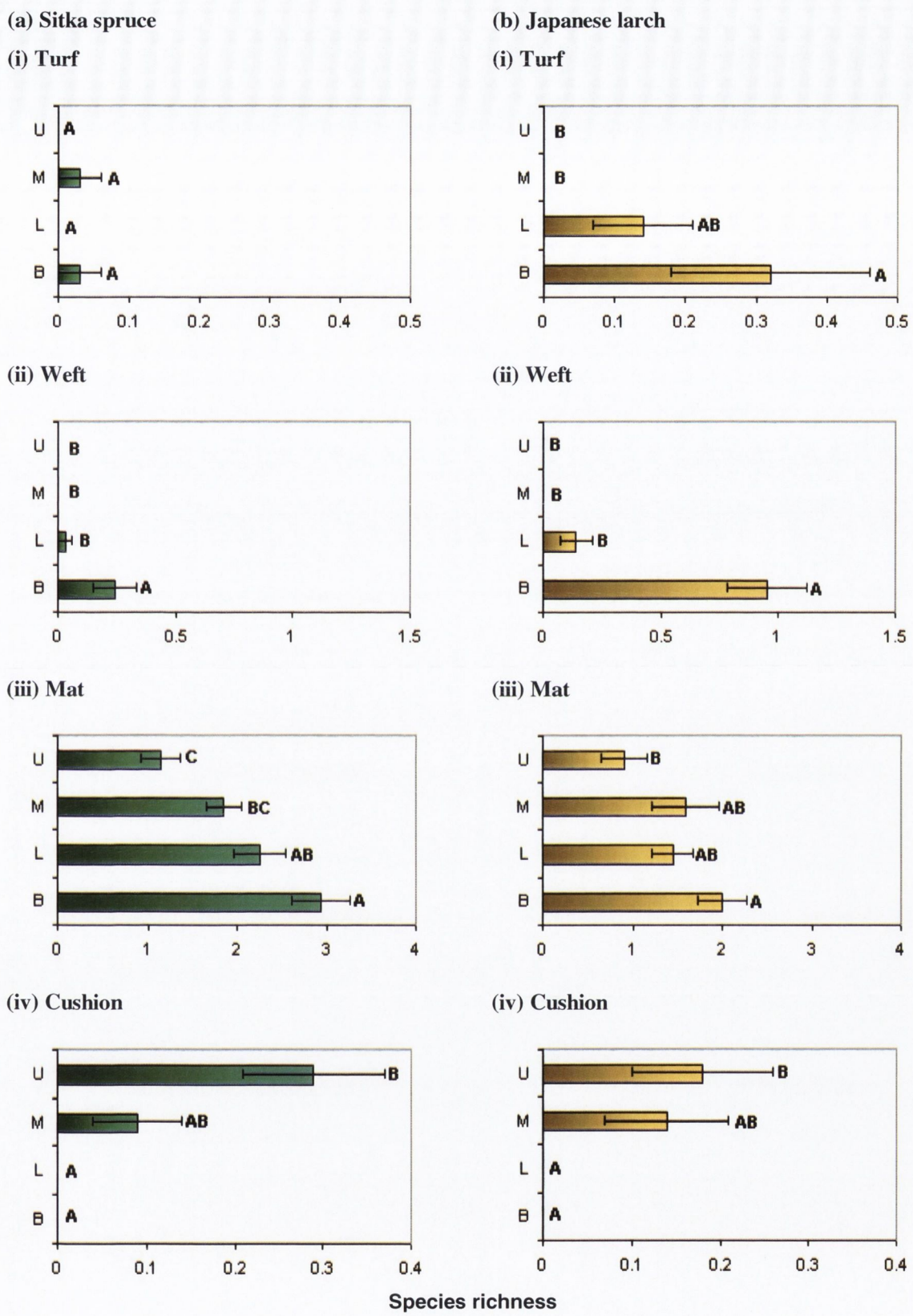


Figure 3.38 Mean species richness of the (i) turf, (ii) weft, (iii) mat and (iv) cushion bryophyte growth forms in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in species richness between two height zones if indicated by the same letter. *N.B.* Horizontal scales vary among plots.

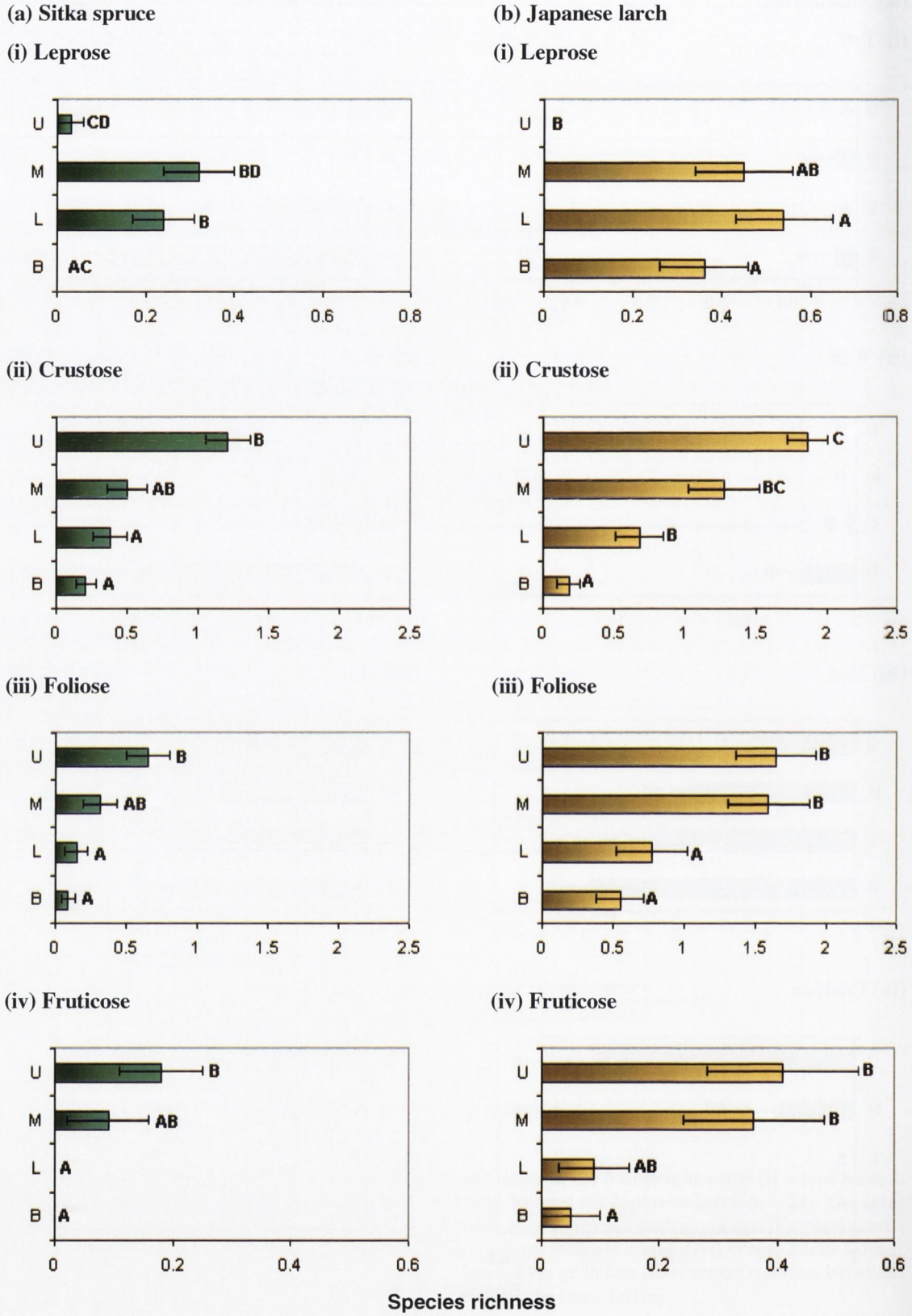


Figure 3.39 Mean species richness of the (i) leprose, (ii) crustose, (iii) foliose and (iv) fruticose lichen growth forms recorded in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in species richness between two height zones if indicated by the same letter. *N.B.* Horizontal scales vary among plots.

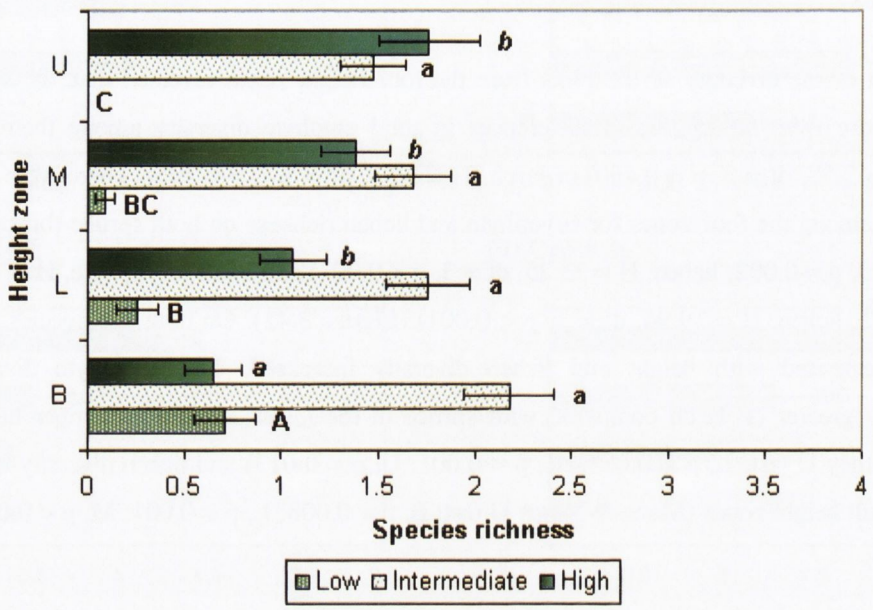
low affinity for epiphytism had a significantly higher species richness in the tree base zone than all other zones and were absent from the upper zone on both tree species (**Figure 3.40**). In contrast, species with a high affinity for epiphytism had a significantly lower species richness in the tree base zone than in all other zones and species richness was highest in the upper zone on both tree species.

Comparison of the diversity of the plots from the four height zones revealed that, as with species richness, there were no significant differences in total epiphyte diversity among them for either spruce ($H = 2.58$, $df = 3$, $p = 0.460$) or larch ($H = 3.71$, $df = 3$, $p = 0.295$). There were significant differences among the four zones for bryophyte and lichen richness on both spruce (bryophyte, $H = 15.12$, $df = 3$, $p = 0.002$; lichen, $H = 33.25$, $df = 3$, $p < 0.001$) and larch (bryophyte, $H = 14.65$, $df = 3$, $p = 0.002$; lichen, $H = 19.94$, $df = 3$, $p < 0.001$) (**Figure 3.41**). On both tree species, bryophyte diversity decreased with height and lichen diversity increased. Total epiphyte diversity was significantly greater on larch compared with spruce in the lower, middle and upper height zones (Mann-Whitney U test: L, $p = 0.034$; M, $p < 0.001$; U, $p = 0.013$) and lichen diversity was greater on larch in all height zones (Mann-Whitney U test: B, $p = 0.008$; L, $p = 0.001$; M, $p < 0.001$; U, $p = 0.002$).

There were no significant differences in total epiphyte cover among the height zones on spruce ($H = 4.83$, $df = 3$, $p = 0.185$) although there were significant differences present on larch ($H = 30.59$, $df = 3$, $p < 0.001$) (**Figure 3.42**). There were significant differences in bryophyte and lichen cover among the zones on both spruce (bryophyte $H = 18.52$, $df = 3$, $p < 0.001$; lichen $H = 45.12$, $df = 3$, $p < 0.001$) and larch (bryophyte $H = 40.68$, $df = 3$, $p < 0.001$; lichen $H = 12.00$, $df = 3$, $p = 0.007$). Total epiphyte cover was significantly higher in the tree base zone than in all other zones on larch, as was bryophyte cover (**Figure 3.42**). On spruce, the upper zone had significantly lower bryophyte cover and significantly higher lichen cover than all other zones. Total epiphyte cover was significantly higher at the tree base on larch than on spruce (Mann-Whitney U test: $p = 0.002$) and the difference in bryophyte cover was close to significance (Mann-Whitney U test: $p = 0.082$). Lichen cover was significantly higher on larch compared to spruce in all height zones with the exception of the upper zone, although the difference there was close to significance (Mann-Whitney U test: B, $p = 0.002$; L, $p < 0.001$; M, $p = 0.001$; U, $p = 0.061$).

Analysis of the distribution of the cover of the different bryophyte and lichen growth forms revealed that, as with species richness, there were significant differences in cover among the four height zones for the bryophyte turfs on larch only (spruce: $H = 2.02$, $df = 3$, $p = 0.569$; larch: $H = 9.97$, $df = 3$, $p = 0.019$) and for bryophyte wefts (spruce: $H = 14.97$, $df = 3$, $p = 0.002$; larch: $H = 41.77$, $df = 3$, $p < 0.001$), mats (spruce: $H = 18.74$, $df = 3$, $p < 0.001$; larch: $H = 28.18$, $df = 3$, $p < 0.001$) and cushions (spruce: $H = 22.72$, $df = 3$, $p < 0.001$; larch: $H = 7.86$, $df = 3$, $p = 0.049$)

(a)



(b)

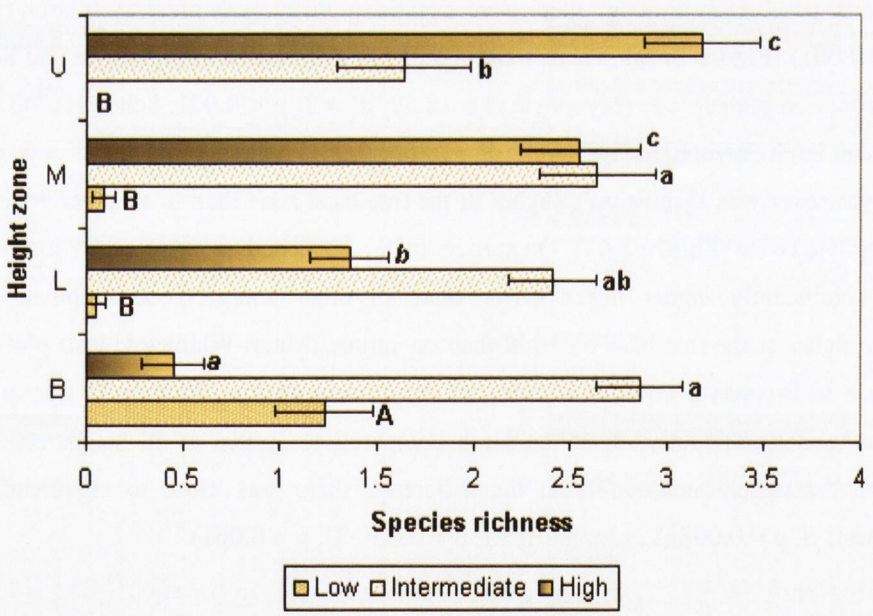
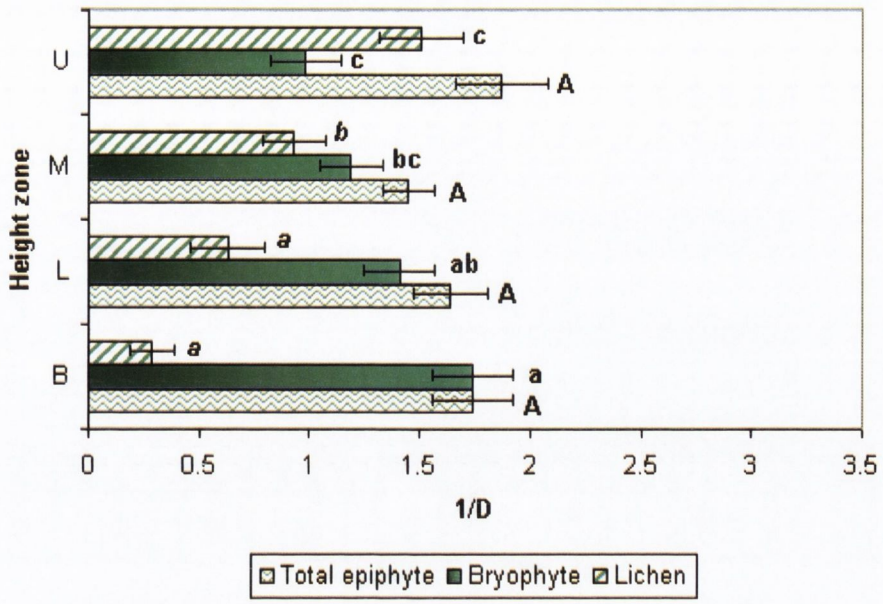


Figure 3.40 Species richness of species with low, intermediate and high affinities for epiphytism in the trunk plots at the four height zones (B = tree base, L = lower, M = middle, U = upper) on (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in species richness between two height zones if indicated by the same letter. (Uppercase letters compare low affinity bars, lowercase compare intermediate affinity bars and lowercase italics compare high affinity bars).

(a)



(b)

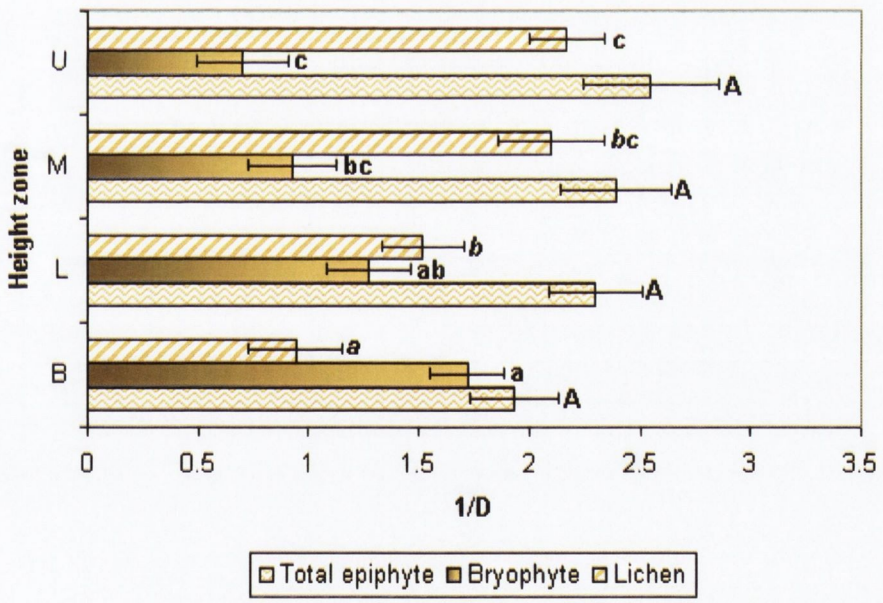
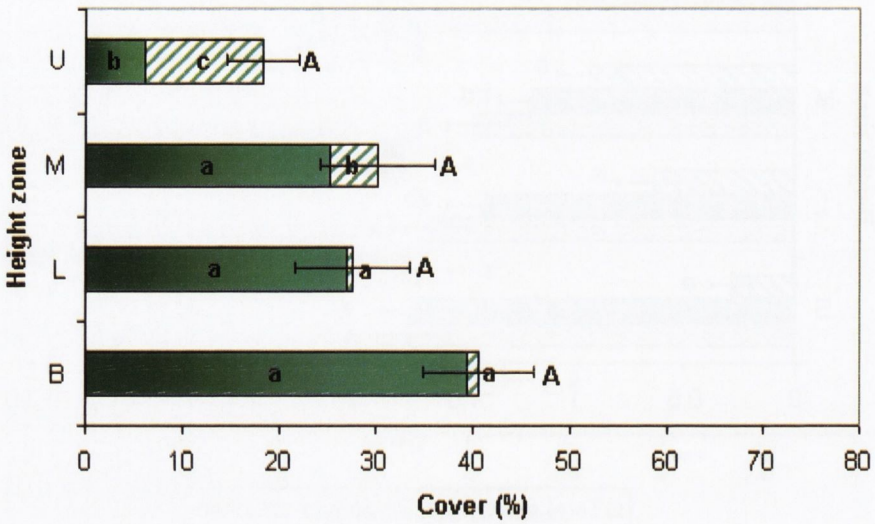


Figure 3.41 Mean epiphyte diversity (1/D) in the trunk plots in the four height zones (B = tree base, L = lower, M = middle, U = upper) on (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen (lowercase italic) diversity between two height zones if indicated by the same letter.

(a)



(b)

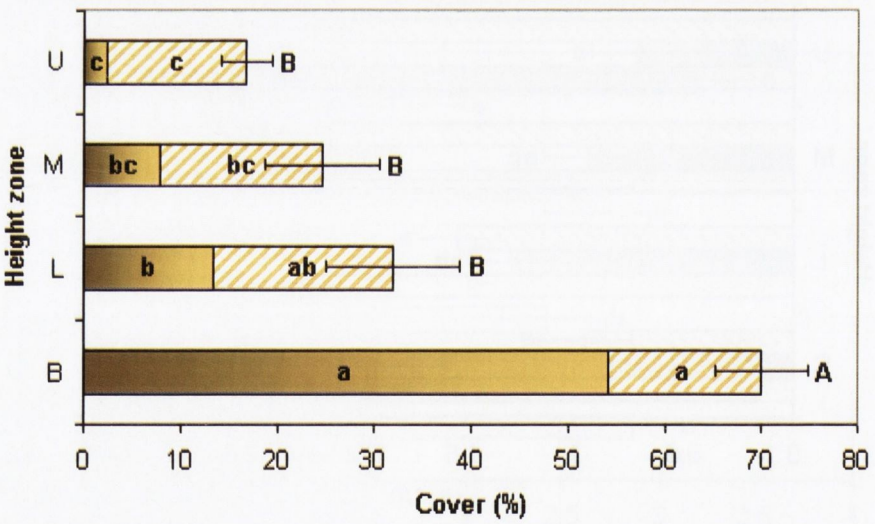


Figure 3.42 Mean epiphyte cover in the trunk plots in the four height zones (B = tree base, L = lower, M = middle, U = upper) on (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). The total epiphyte cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) cover between two height zones if indicated by the same letter.

(**Figure 3.43**) and leprose (spruce: H = 20.02, df = 3, p < 0.001; larch: H = 15.83, df = 3, p =0.001), crustose (spruce: H = 28.86, df = 3, p < 0.001; larch: H = 17.25, df = 3, p = 0.001), foliose (spruce H = 15.04, df = 3, p = 0.002; larch H = 9.86, df = 3, p = 0.020) and fruticose lichens (spruce H = 12.47, df = 3, p = 0.006; larch H = 10.41, df = 3, p = 0.015) on both species (**Figure 3.44**). As with species richness, the cover of turfs, wefts and mats was greatest at the tree base, while cushions had greatest cover in the upper zone (**Figure 3.43**). Cover of crustose foliose and fruticose lichens was greatest in the upper zone on spruce, while cover on larch was quite variable (**Figure 3.44**).

A total of seven species - four bryophyte and three lichen species - had more than ten percent frequency in the trunk plots on both Sitka spruce and Japanese larch (i.e. occurred in more than 13 trunk plots on spruce and more than eight trunk plots on larch) (**Table 3.26**). An additional four species had more than ten percent frequency on spruce only and an additional six on larch only. The seven species with greater than ten percent frequency on both species were examined in relation to their cover and percent frequency in the four height zones.

Table 3.26. A list of the epiphyte species occurring in more than ten percent of trunk plots on Sitka spruce and/or Japanese larch with the percent frequency indicated. The epiphyte group, growth form and degree of affinity for epiphytism of each species are indicated.

Species	Epiphyte group	Growth form	Epiphytism affinity	Spruce (n = 136)	Larch (n = 88)
Hypnum jutlandicum	Mo	Ma	Int	**52.2**	**50.0**
Metzgeria temperata	Lv	Ma	High	**41.9**	**18.2**
Dimerella lutea	Li	Cr	Int	**25.0**	**11.4**
Microlejeunea ulicina	Lv	Ma	High	**22.1**	**33.0**
Lepraria incana	Li	Lp	Int	**14.7**	**34.1**
Lophocolea bidentata	Lv	Ma	Int	**13.2**	**13.6**
Hypotrachyna revoluta	Li	Fo	High	**11.0**	**24.4**
Kindbergia praelonga	Mo	Ma	Int	**15.4**	2.3
Metzgeria furcata	Lv	Ma	Int	**13.2**	3.4
Plagiothecium undulatum	Mo	Ma	Low	**11.8**	6.8
Dimerella pineti	Li	Cr	High	**11.0**	3.4
Fuscidea lightfootii	Li	Cr	High	7.4	**20.5**
Hypogymnia physodes	Li	Fo	Int	0	**19.3**
Lecanora pulicaris	Li	Cr	High	2.9	**15.9**
Thuidium tamariscinum	Mo	We	Low	3.7	**12.5**
Graphis elegans	Li	Cr	High	0.7	**12.5**
Parmelia sulcata	Li	Fo	Int	2.2	**10.2**

The mean cover of the moss *Hypnum jutlandicum* decreased from the tree base to the upper height zone on both spruce and larch (**Figure 3.45**). This is similar to the distribution pattern shown by bryophyte mat species in general (cf. **Figure 3.43**). The tree base zone had significantly higher cover and the upper zone significantly lower cover of *Hypnum* than all other zones (**Figure 3.45**). The cover in the tree base zone on larch was significantly greater than in that on spruce (Mann-Whitney U test: p = 0.022). The percent frequency of *Hypnum* followed the same pattern as cover in larch, while on spruce there was greater frequency in the middle than lower zone, this was not reflected in a greater cover in this height zone (**Figure 3.45**).

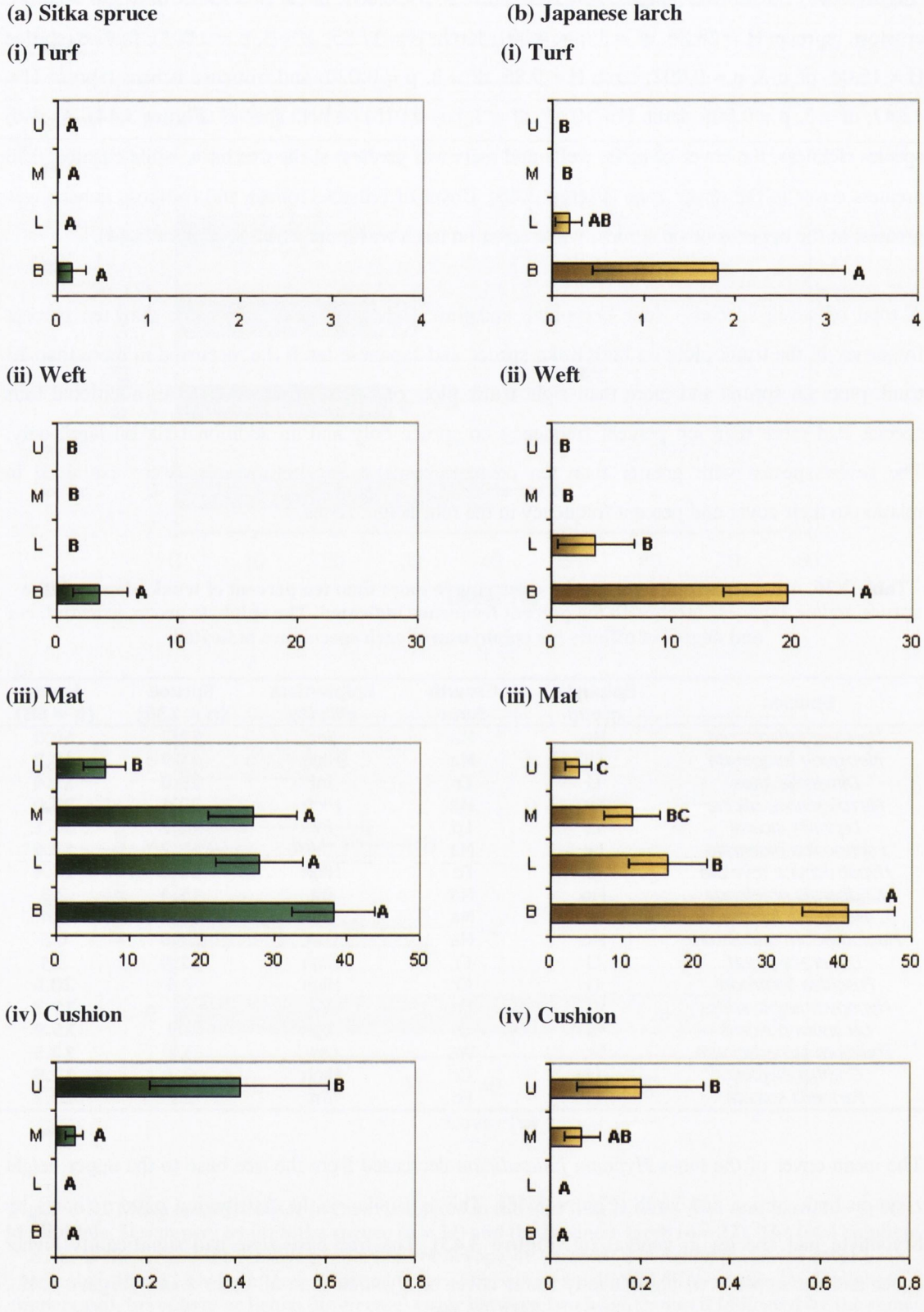


Figure 3.43 Mean cover of the (i) turf, (ii) weft, (iii) mat and (iv) cushion bryophyte growth forms in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter *N.B.* Horizontal scales vary among plots.

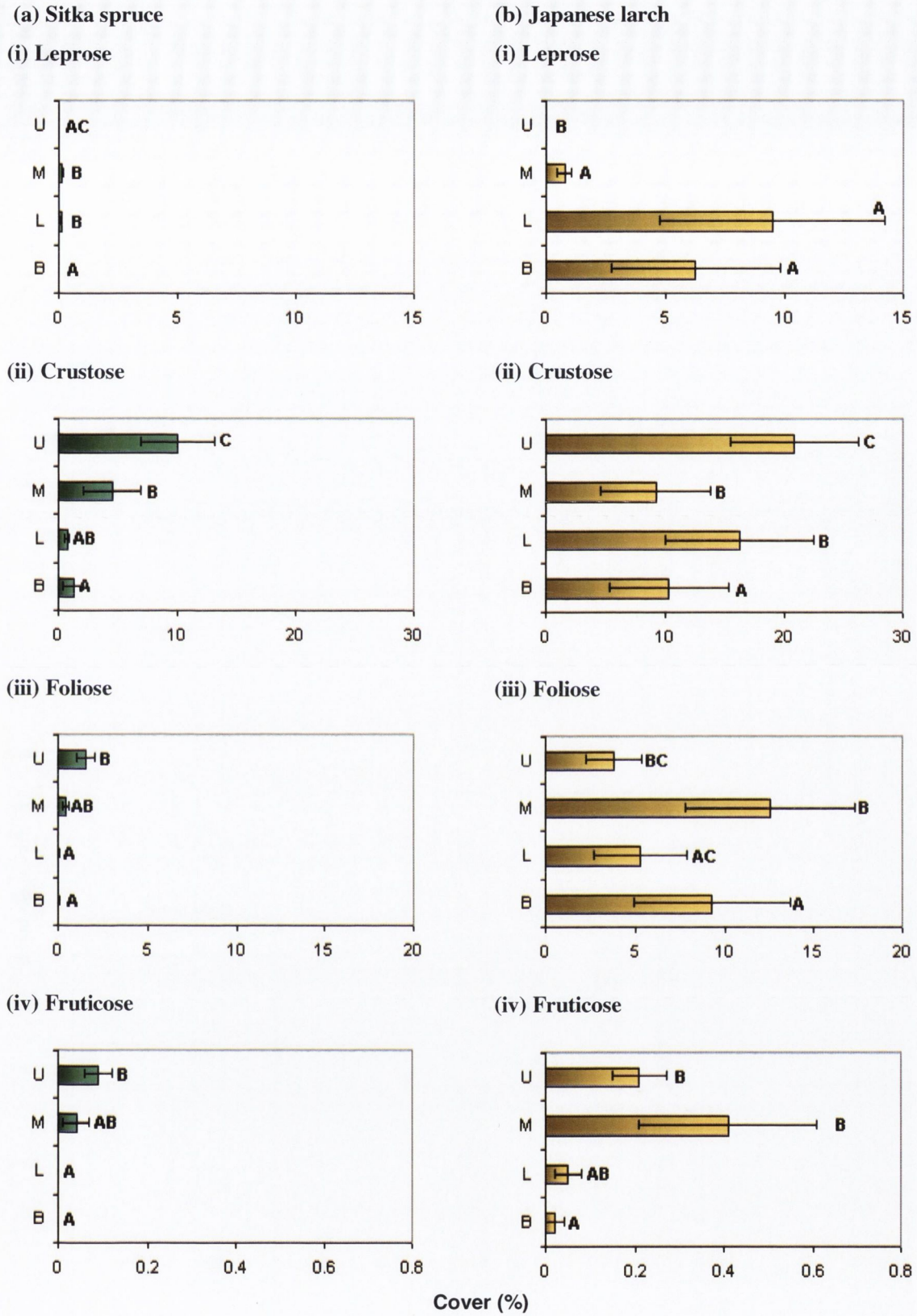
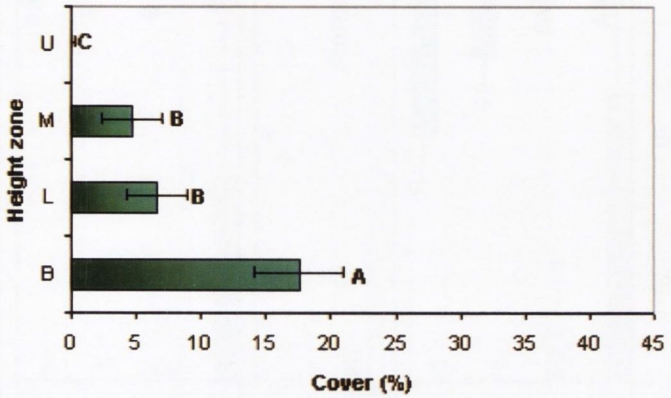
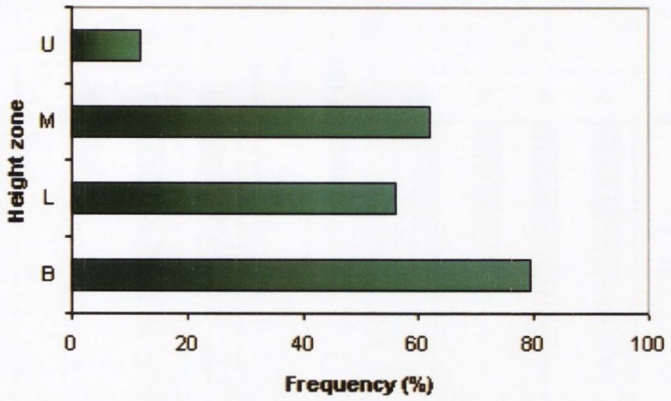


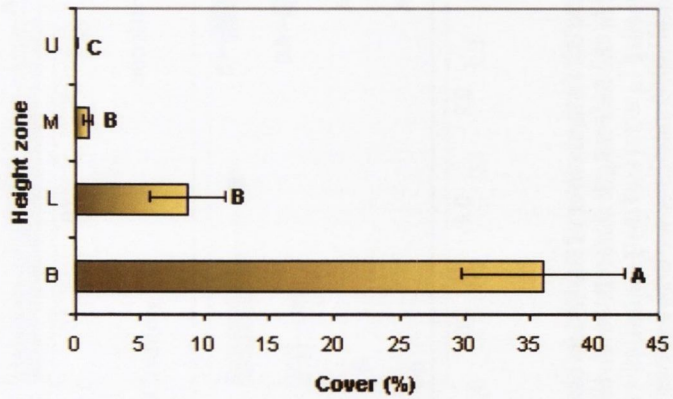
Figure 3.44 Mean cover of the (i) leprose, (ii) crustose, (iii) foliose and (iv) fruticose lichen growth forms in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter. *N.B.* Horizontal scales vary among plots.

(a) Sitka spruce





(b) Japanese larch



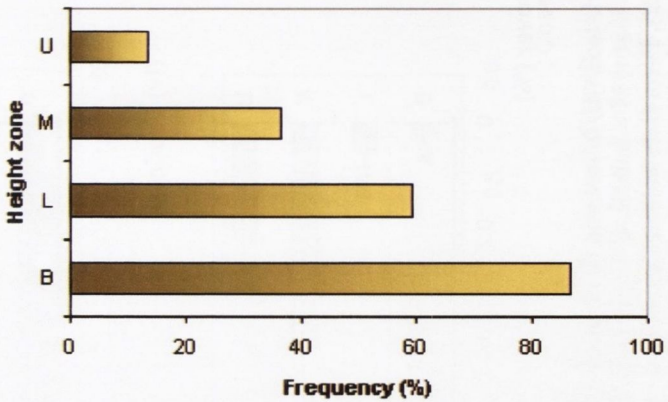


Figure 3.45 Mean cover and frequency of *Hypnum jutlandicum* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

The mean cover of the liverwort *Metzgeria temperata* was greatest in the middle zone on both spruce and larch (**Figure 3.46**). The middle zone had significantly greater cover than the tree base and lower zones on larch; however, there were no significant differences among the height zones on spruce. The large error bars for spruce indicate the large variation in cover among trees. There was significantly greater cover in the tree base (Mann-Whitney U test: $p = 0.002$) and lower zones (Mann-Whitney U test: $p < 0.001$) on spruce compared to larch (**Figure 3.46**). The pattern of frequency was similar to that for cover on larch, while on spruce the greatest frequency was in the lower height zone (**Figure 3.46**).

Mean cover of the crustose lichen *Dimerella lutea* increased from the tree base to the upper zone on spruce, with the middle and upper zone having significantly greater cover than the tree base and lower zones (**Figure 3.47**). On larch the greatest cover was in the middle zone but there were no significant differences among the four height zones (**Figure 3.47**). Cover on larch was very low and was lower than on spruce in all height zones but the difference was only significant for the upper zone (Mann-Whitney U test: $p = 0.002$). Percent frequency was greatest in the middle zone on both species (**Figure 3.47**).

Cover of the liverwort *Microlejeunea ulicina* (**Figure 3.48**) was greatest in the upper zone on spruce and in the middle zone on larch, but the large error bars indicate the large variation in cover among trees (**Figure 3.48**). Although cover of *Microlejeunea* was greater in every height zone on larch than on spruce, none of these differences between the two tree species were significant. Percent frequency on spruce increased from the tree base to the middle zone before decreasing again in the upper zone (**Figure 3.48**). On larch the maximum frequency was in the lower zone.

Lepraria incana, a leprose lichen, was absent from the tree base zone on spruce and the upper zone on larch (**Figure 3.49**). Mean cover was greatest in the middle height zone on spruce but overall cover was low. On larch, cover was greatest in the lower height zone but the large error bars indicate the large variation in cover in the tree base and lower zones. The cover of *Lepraria* was greater on larch than on spruce except in the upper zone; these differences were significant for the tree base (Mann-Whitney U test: $p < 0.001$) and lower zones (Mann-Whitney U test: $p = 0.009$) (**Figure 3.49**). As with cover, frequency was greatest in the middle zone for spruce and the lower zone for larch (**Figure 3.49**).

The liverwort, *Lophocolea bidentata* (**Figure 3.50**), was absent from the upper zone on spruce and from both the lower and upper zones on larch (**Figure 3.50**). The greatest cover was in the lower zone on spruce; however the only significant difference present was between the tree base zone and all other zones. The large error bars indicate the great variation in cover of *Lophocolea* among

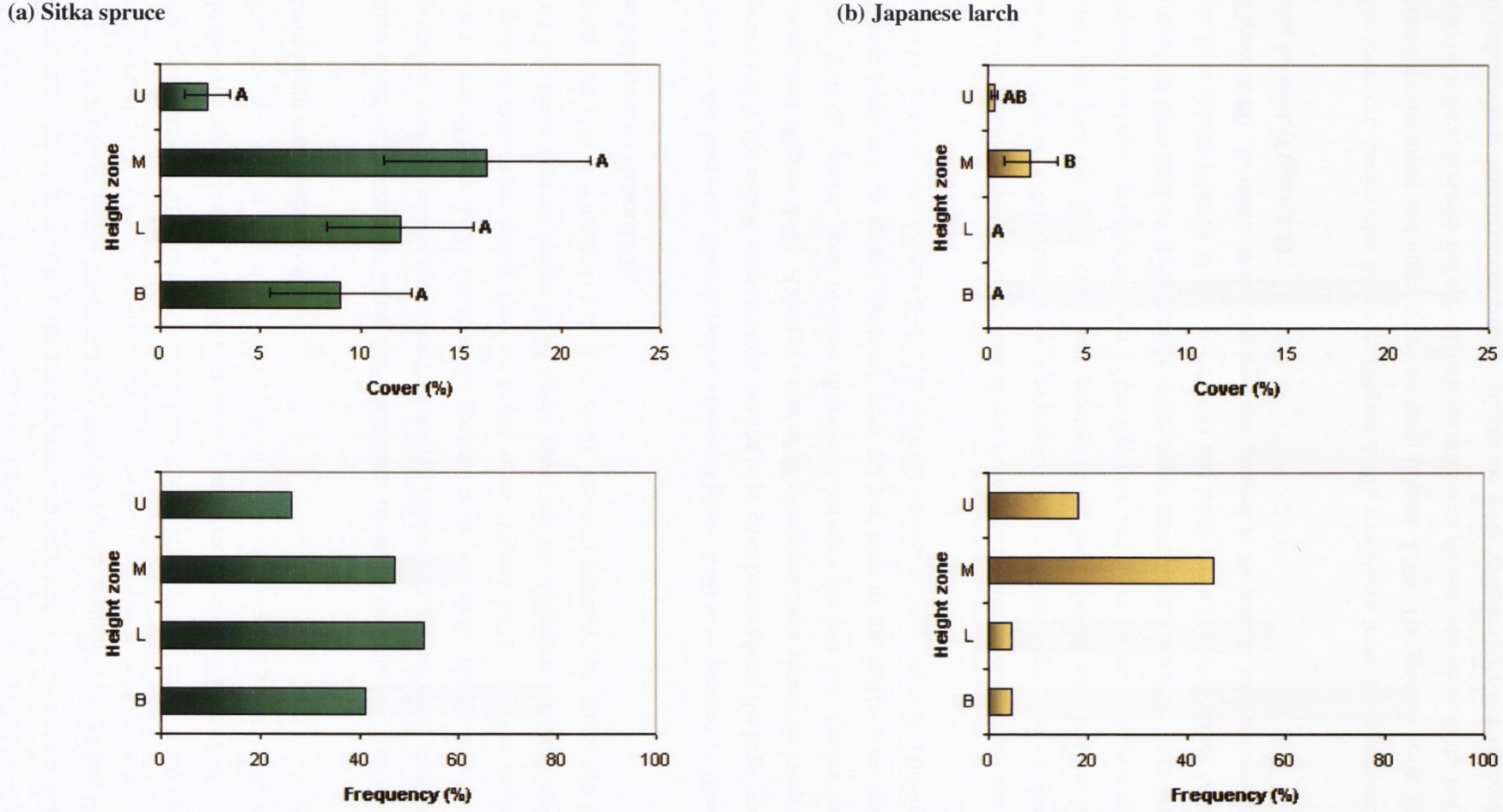


Figure 3.46 Mean cover and frequency of *Metzgeria temperata* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

(a) Sitka spruce

(b) Japanese larch

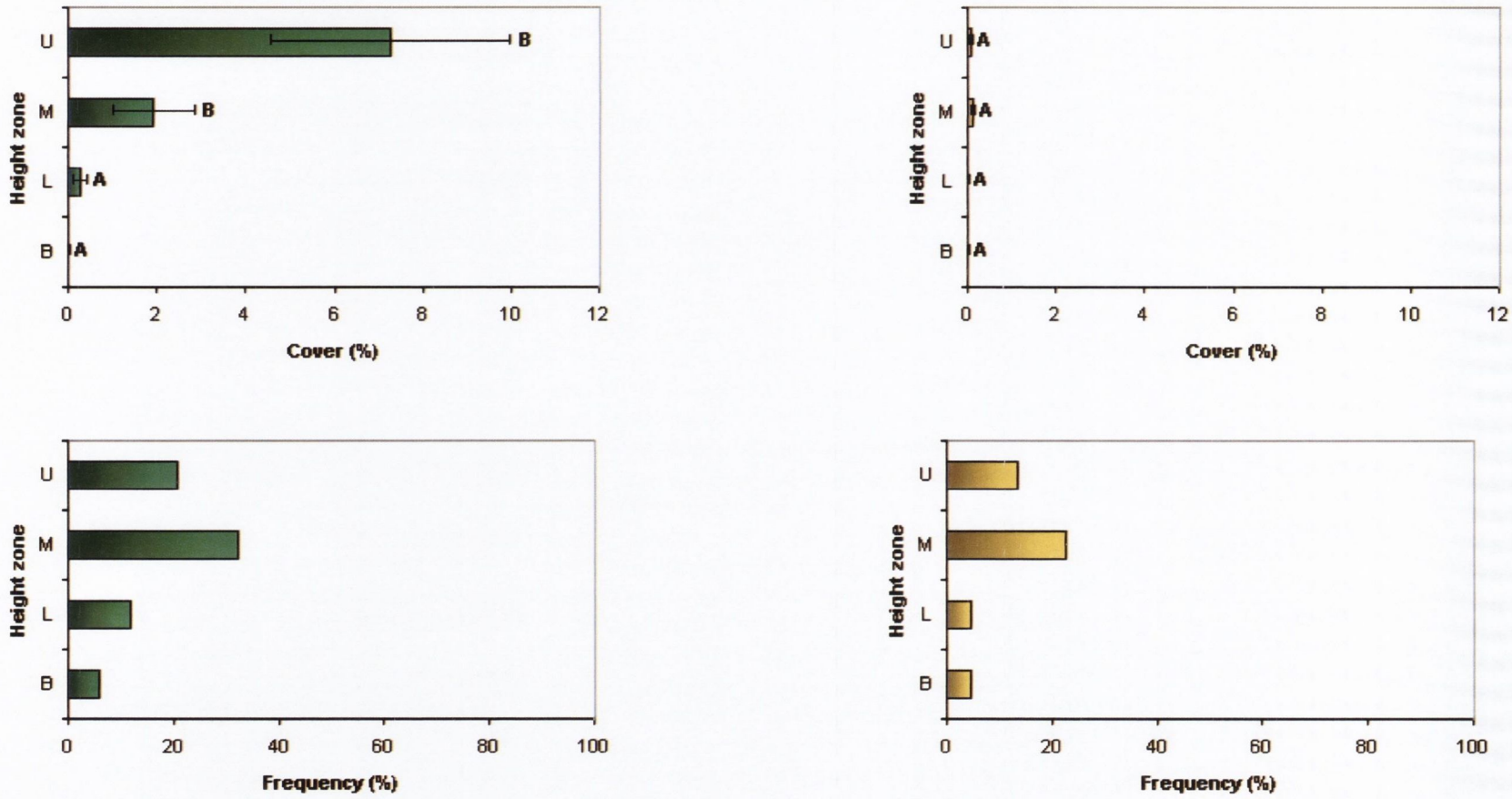


Figure 3.47 Mean cover and frequency of *Dimerella lutea* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

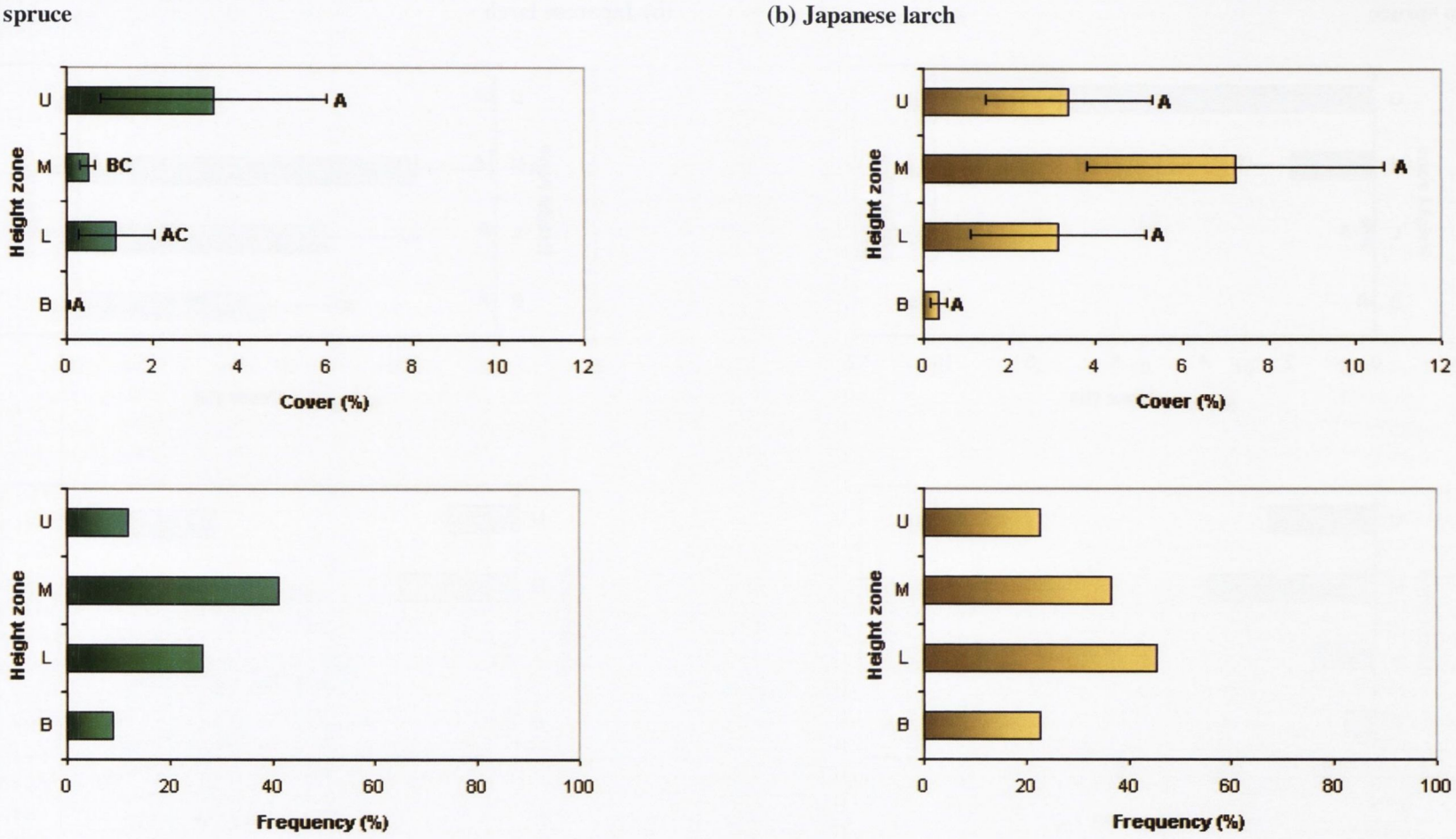


Figure 3.48 Mean cover and frequency of *Microlejeunea ulicina* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

(a) Sitka spruce

(b) Japanese larch

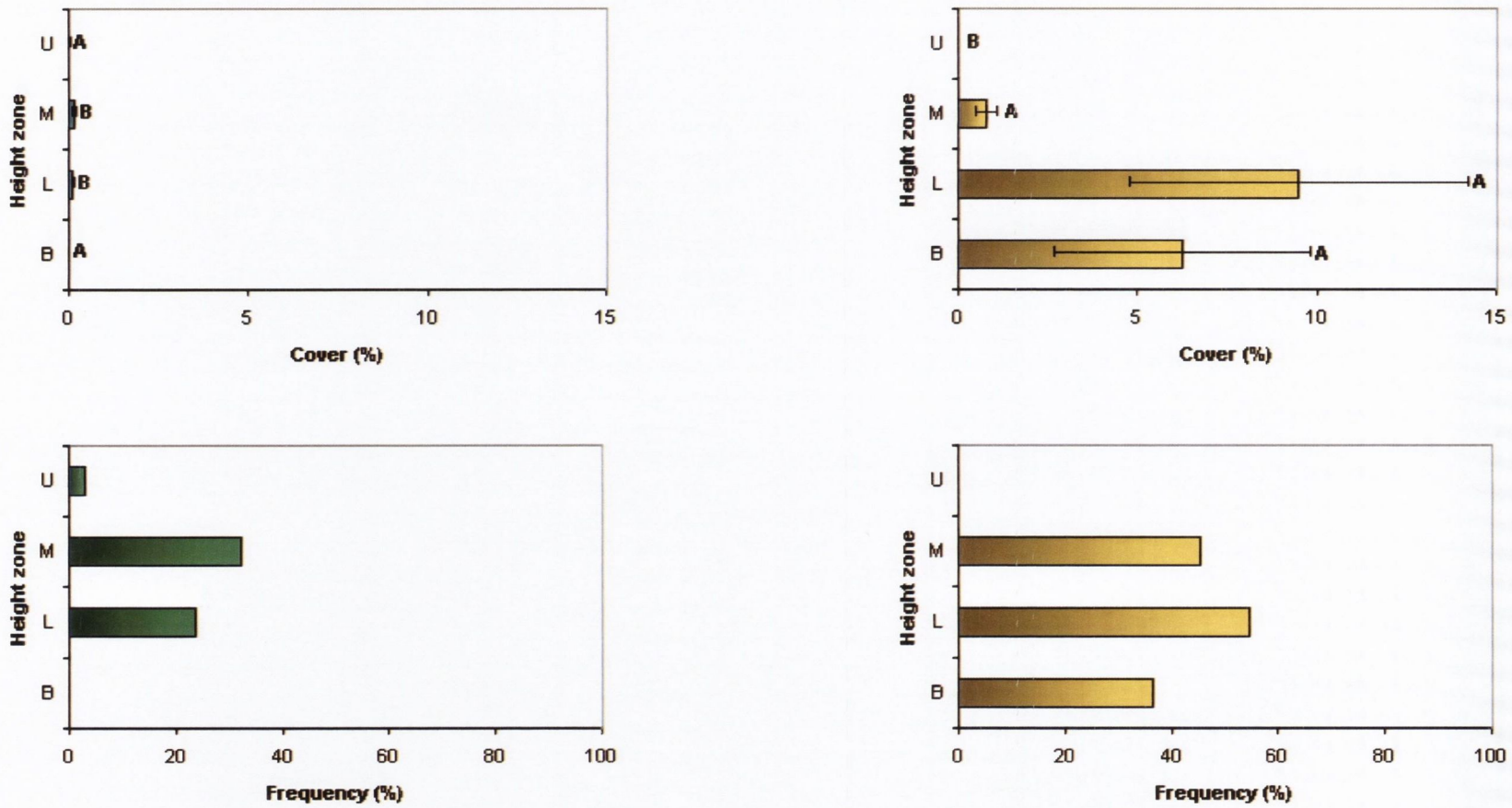
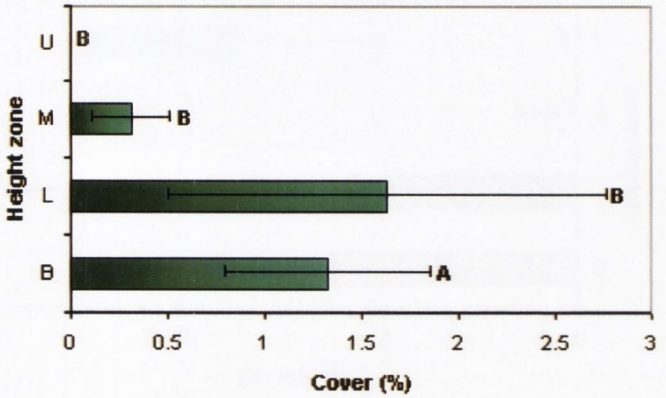
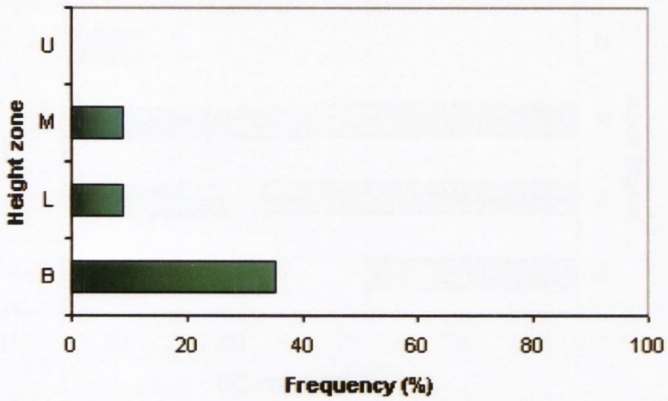


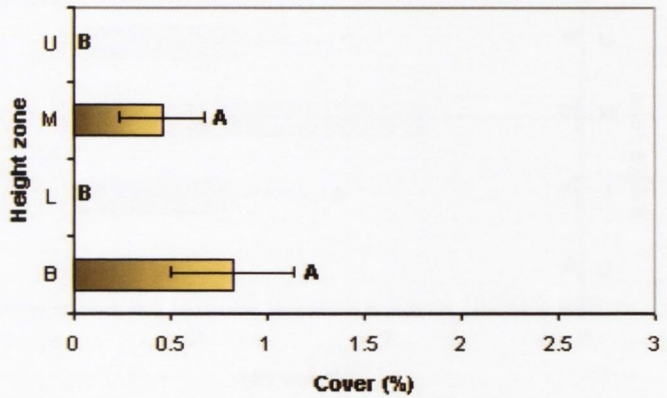
Figure 3.49 Mean cover and frequency of *Lepraria incana* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

(a) Sitka spruce





(b) Japanese larch



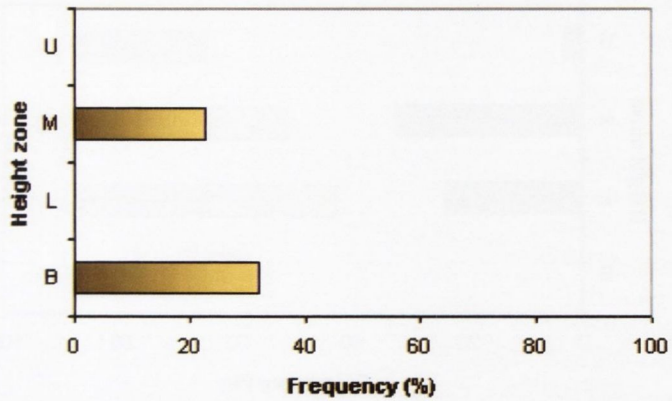


Figure 3.50 Mean cover and frequency of *Lophocolea bidentata* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

spruce trees. On larch the greatest cover was in the tree base zone (**Figure 3.50**). Percent frequency on larch followed the pattern of cover while on spruce the greatest frequency was at the tree base.

The foliose lichen *Hypotrachyna revoluta* was absent from the tree base zone on both tree species (**Figure 3.51**). On spruce, cover increased from the lower to the upper zones in a similar pattern to the distribution of total foliose lichen cover (cf. **Figure 3.44**). On larch, the greatest cover was in the middle zone, although there was great variation among trees, as indicated by the large error bars. The middle zone on larch had significantly greater cover than that on spruce (Mann-Whitney U test: $p = 0.021$) (**Figure 3.51**). Greatest frequency was in the upper zone on both tree species (**Figure 3.51**).

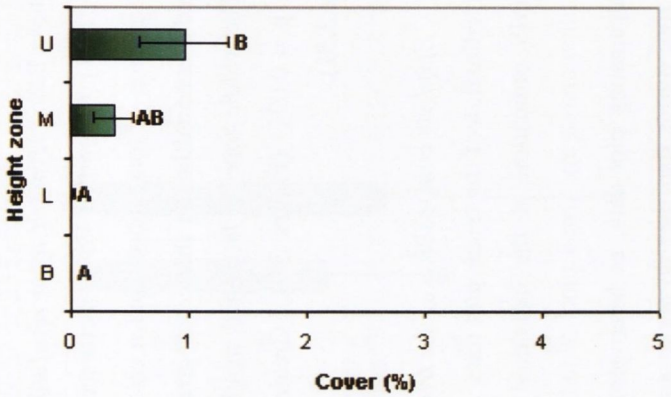
3.3.4.1 Epiphyte composition of the trunk plots

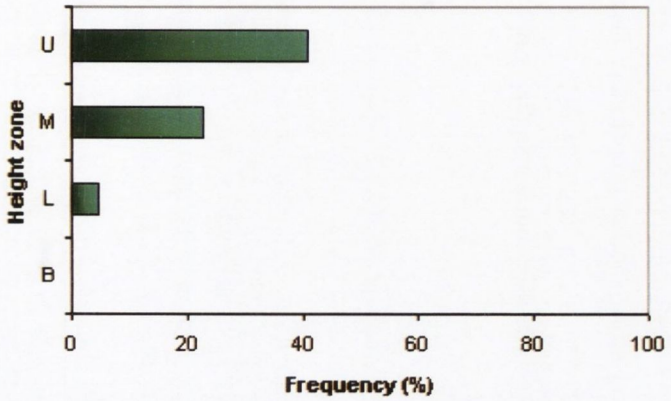
NMS Ordination of the trunk plot data

The NMS ordination of the individual trunk plots highlights the large variation in epiphyte composition among the trunk plots of individual trees (**Figure 3.52**). It also highlights the problem of amalgamating plot data, as heterogeneity among plots from individual trees or from the same height zone means that they do not group together in ordination space. Plots from the four height zones were separated along axis 2 to some extent. The tree base plots were most similar in epiphyte composition and were mainly grouped together toward the top of axis 2. The tree base plots located below axis 1 were from the trees with the 'lichen-dominated' epiphyte composition (CRUA1 and CURT1). Plots from all height zones on these trees were grouped together in ordination space and formed a reasonably distinct group towards the right hand side of axis 1 (**Figure 3.53**). The majority of the middle and upper plots positioned towards the top of axis two were from trees with the 'liverwort-dominated' epiphyte composition. Plots from all height zones on these trees were also grouped together in ordination space. The lower plots positioned towards the bottom of axis 2 were from trees with the 'bryophyte-poor' composition. A number of nearby plots from these trees contained no epiphyte species and so could not be included in the NMS ordination.

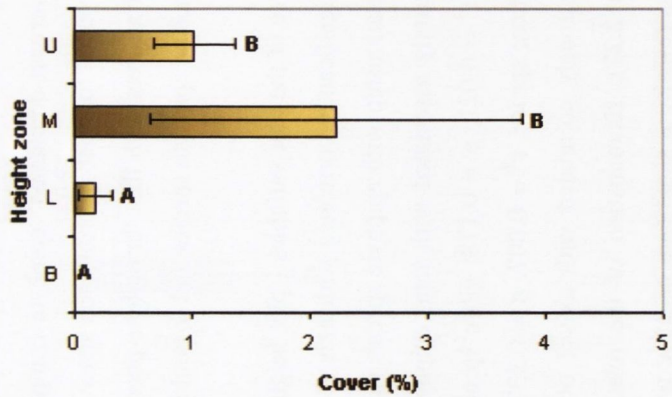
All three of the plot variables - plot height, tree girth at the centre of the plot and plot inclination - were significantly correlated with axis 1 of the NMS ordination of the plot data (**Table 3.27**), so their relationship with epiphyte species richness was examined further. However, none of these was significantly associated with total epiphyte richness (plot height: spruce, $r^2 = 0.007$, $p = 0.341$; larch, $r^2 = 0.021$, $p = 0.178$; girth: spruce, $r^2 = 0.003$, $p = 0.500$; larch, $r^2 = 0.001$, $p = 0.798$; inclination; spruce, $r^2 = 0.007$, $p = 0.332$; larch, $r^2 < 0.001$, $p = 0.884$). All three variables were more strongly correlated with axis 2 of the ordination, as were bryophyte and lichen richness (**Table 3.27**). Examination of the relationship between plot height and bryophyte and lichen richness revealed a significant negative relationship between bryophyte richness and plot height for spruce (although the relationship was weak) ($r^2 = 0.087$, $p < 0.001$), and for larch ($r^2 = 0.123$, $p =$

(a) Sitka spruce





(b) Japanese larch



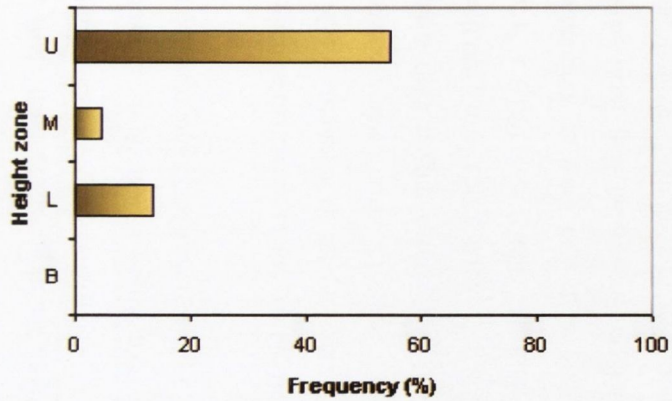


Figure 3.51 Mean cover and frequency of *Hypotrachyna revoluta* in the four height zones on the trunks of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in cover between two height zones if indicated by the same letter.

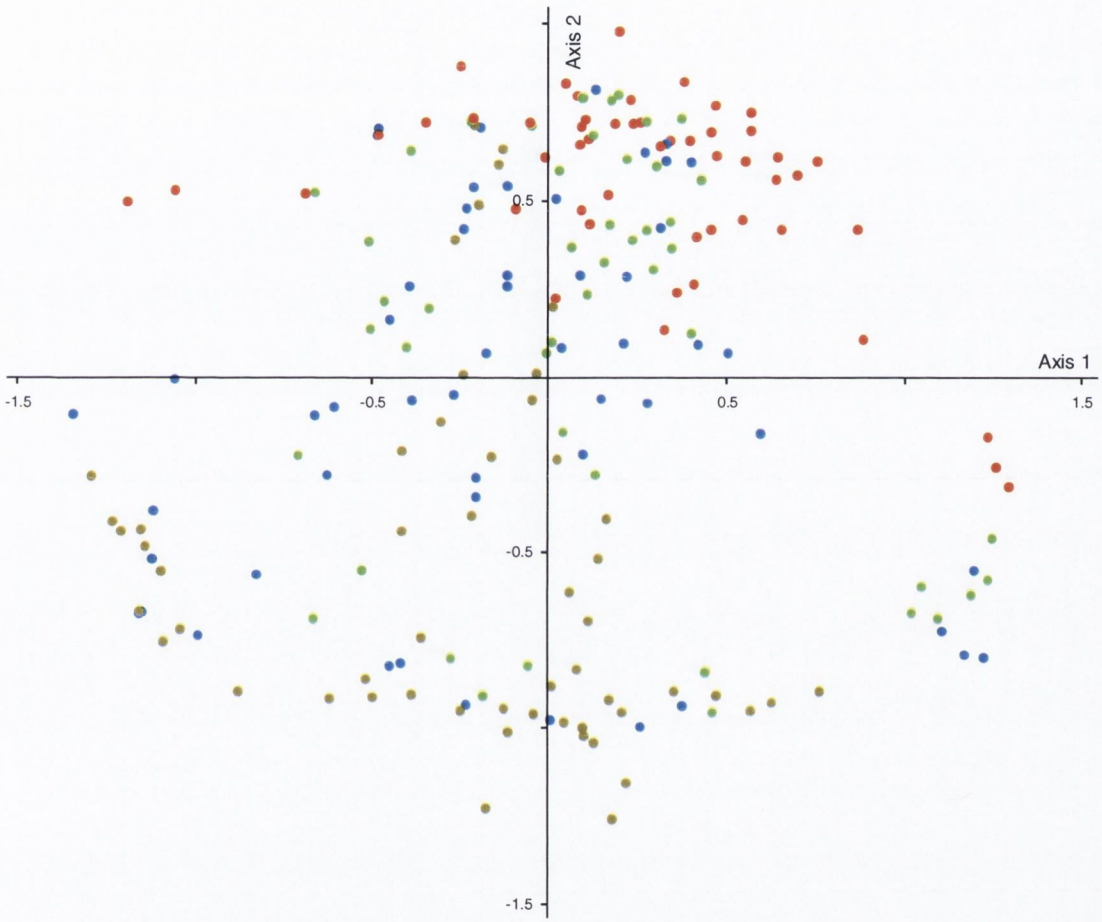


Figure 3.52 NMS ordination of the epiphyte composition of the trunk plots on the Sitka spruce and Japanese larch trees. The four height zones (tree base = red, lower = green, middle = dark blue, upper = gold) are indicated. Final stress for 3-dimensional solution = 21.71, final instability = 0.00049, axis 1 r^2 = 0.123, axis 2 r^2 = 0.137.

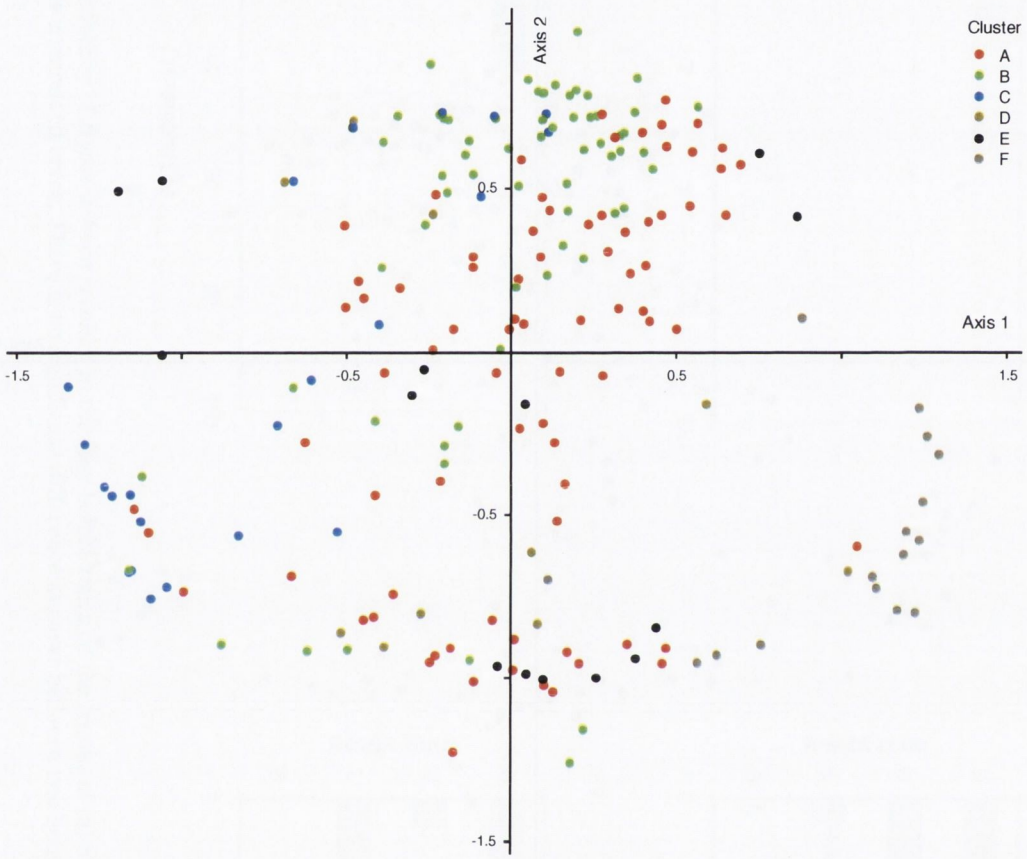


Figure 3.53 NMS ordination of the epiphyte composition of the trunk plots on the Sitka spruce and Japanese larch trees with the plots from trees in each of the six cluster groups (cf. Section 3.3.3.1) indicated. Refer to Figure 3.52 for details of the NMS ordination.

0.001) and a significant positive relationship between lichen richness and plot height for both spruce ($r^2 = 0.257$, $p < 0.001$) and larch ($r^2 = 0.278$, $p < 0.001$) (**Figure 3.54**). Both tree girth and inclination were weakly, but in many cases also significantly, associated with bryophyte richness (girth: spruce, $r^2 = 0.023$, $p = 0.077$; larch, $r^2 = 0.114$, $p = 0.001$; inclination: spruce, $r^2 = 0.006$, $p = 0.371$; larch, $r^2 = 0.074$, $p = 0.010$) and with lichen richness (girth: spruce, $r^2 = 0.075$, $p = 0.001$; larch, $r^2 = 0.099$, $p = 0.003$; inclination: spruce, $r^2 = 0.048$, $p = 0.012$; larch, $r^2 = 0.066$, $p = 0.015$) with the relationship being positive for bryophyte richness and negative for lichen richness in both cases.

Table 3.27 Pearson's correlations (r) between the axes from the NMS ordination (Figure 3.52) and selected diversity, cover and plot variables.

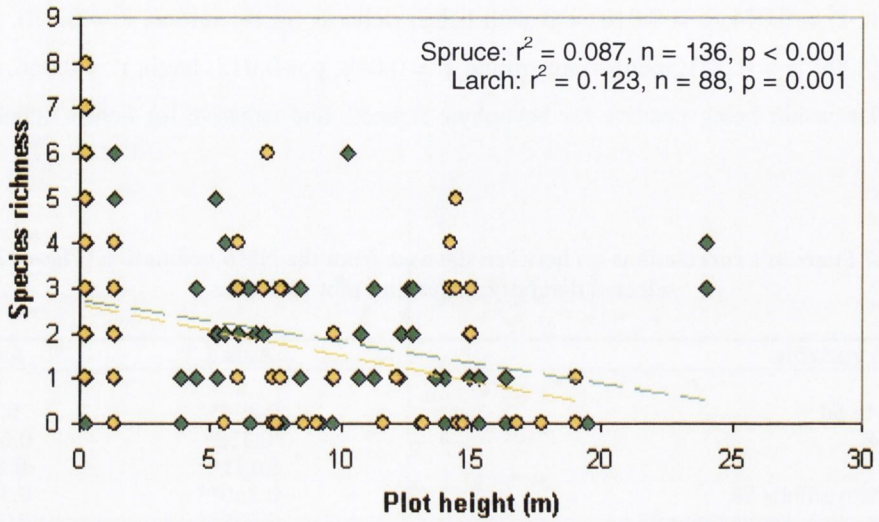
Correlation variable	Axis 1	Axis 2
Diversity:		
Total epiphyte SR	0.294**	0.015
Bryophyte SR	0.153*	0.613**
Lichen SR	0.171**	-0.605**
Low epiphytism affinity SR	0.350**	0.375**
Intermediate epiphytism affinity SR	0.325**	0.227**
High epiphytism affinity SR	-0.002	-0.355**
Total epiphyte 1/D	0.017	-0.132*
Bryophyte 1/D	0.102	0.520**
Lichen 1/D	0.095	-0.466**
Cover:		
Total epiphyte cover	0.455**	0.335*
Bryophyte cover	0.320**	0.581**
Lichen cover	0.218**	-0.400**
Plot:		
Plot height	-0.291**	-0.618**
Tree girth at centre	0.303**	0.372**
Inclination	0.133*	0.289**

Note. * indicates the correlation coefficient is significant at the $p < 0.05$ level and ** indicates significance at the $p < 0.01$ level.

To identify the discontinuities revealed by the ordination, cluster and indicator species analysis were used to divide the trunk plots into cluster groups (**Figure 3.55, Figure 3.56**). The plots of the number of cluster groups versus the average significance of the indicator species (**Figure 3.55a**) and the total number of significant indicator species (**Figure 3.55b**) suggest that the optimum number of clusters is ten or fourteen. The average significance of the indicator species is lowest for the ten cluster option ($p = 0.20$), while the number of significant indicators ($n = 38$) is highest for fourteen clusters. Examination of the NMS ordination plot suggested that the ten cluster option was the most sensible choice. The ten cluster groups are indicated on the NMS ordination plot (**Figure 3.57**). Indicator species analysis was used to identify species characteristic of each cluster group (**Table 3.28**).

The ten trunk plot cluster groups were examined in terms of certain diversity, cover and plot variables (**Table 3.29**). Cluster I was composed of mainly tree base and lower plots from both spruce and larch (cf. **Appendix 4**), with the spruce trees mainly from more heavily thinned stands.

(a)



(b)

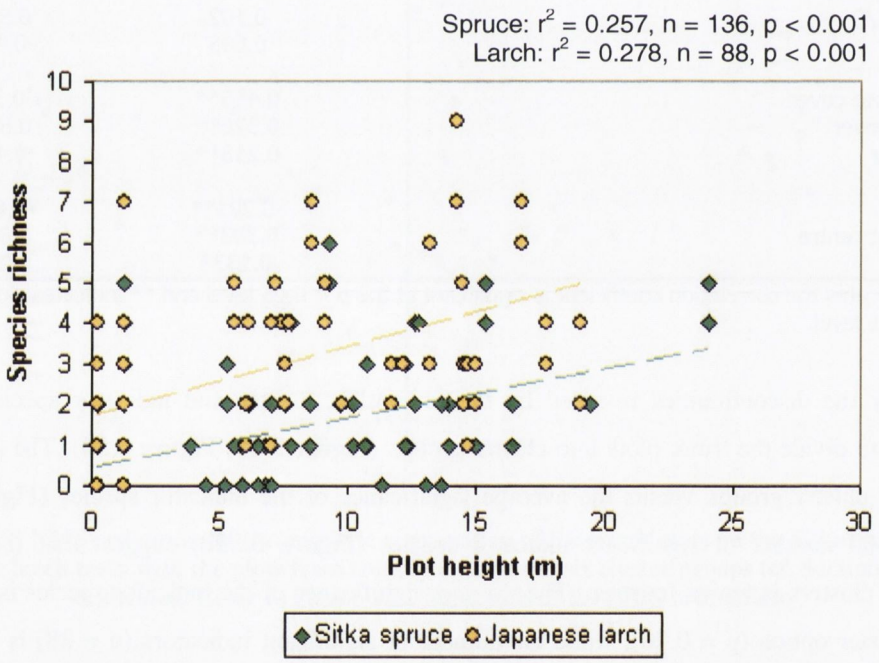
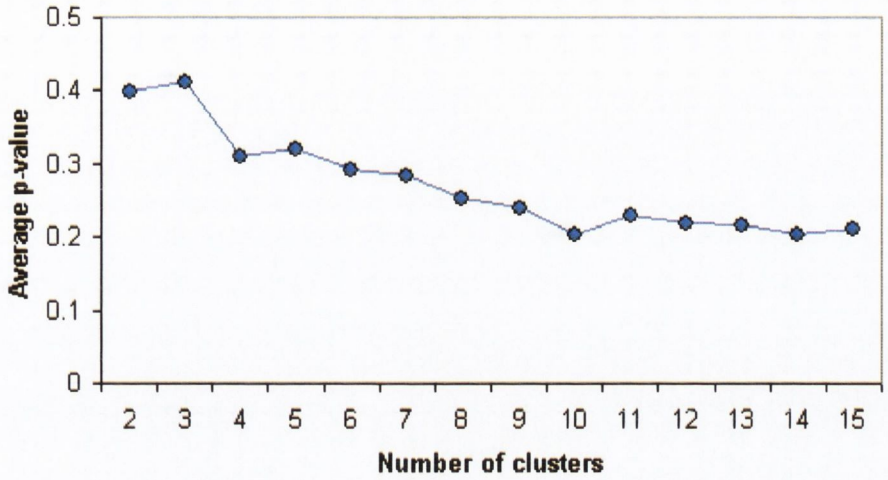


Figure 3.54 Relationship between plot height and (a) bryophyte and (b) lichen richness in the trunk plots on Sitka spruce (n = 136) and Japanese larch (n = 88).

(a)



(b)

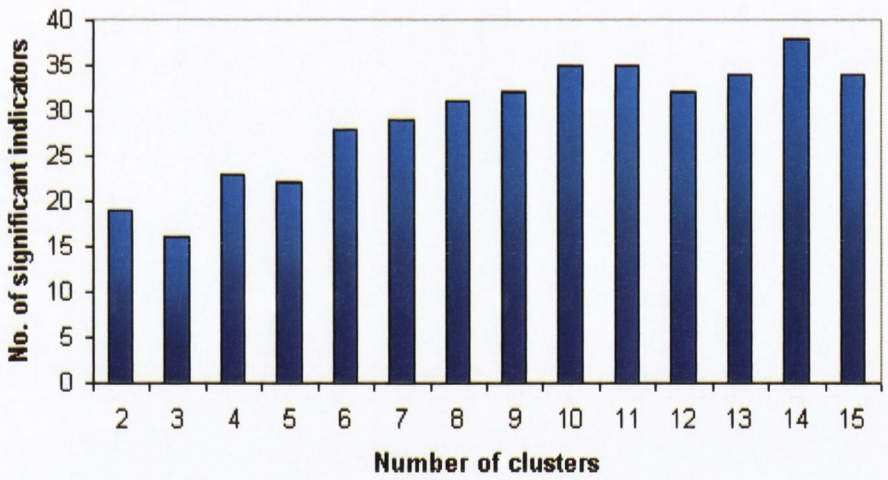


Figure 3.55 Graphs used to assess the appropriate number of cluster analysis groupings. Number of clusters is plotted against (a) average significance of the indicator species and (b) number of significant indicators. *Note*. Species indicators could not be derived for more than 15 clusters because further division caused at least one cluster to contain only one plot.

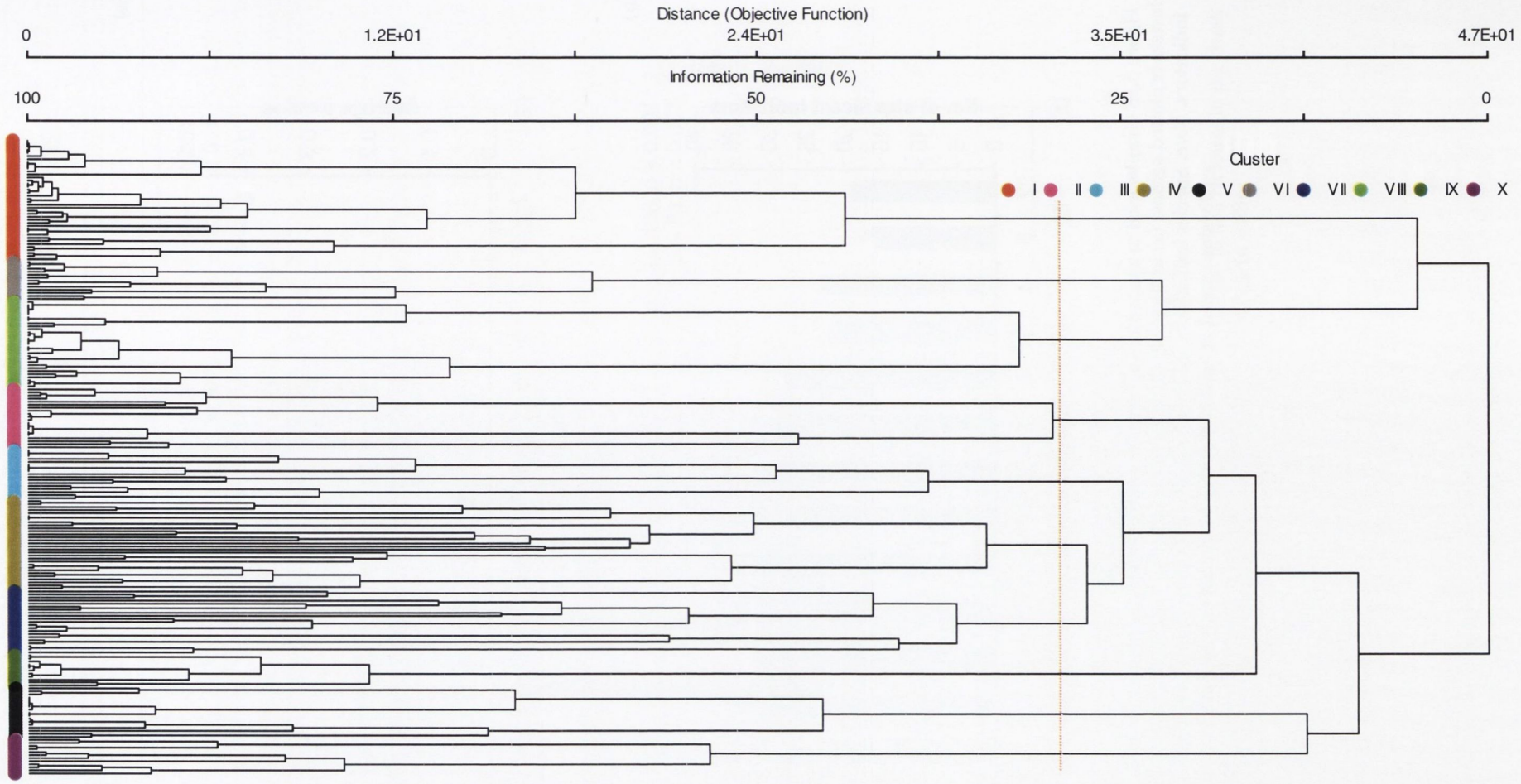


Figure 3.56 Cluster dendrogram of the trunk plots from the Sitka spruce and Japanese larch trees, scaled by Wishart's objective function and percent of information remaining. The position of the cut leading to the ten resulting clusters indicated in Figure 3.57is shown. (See Appendix 4 for a list of the trunk plots occurring in each cluster).

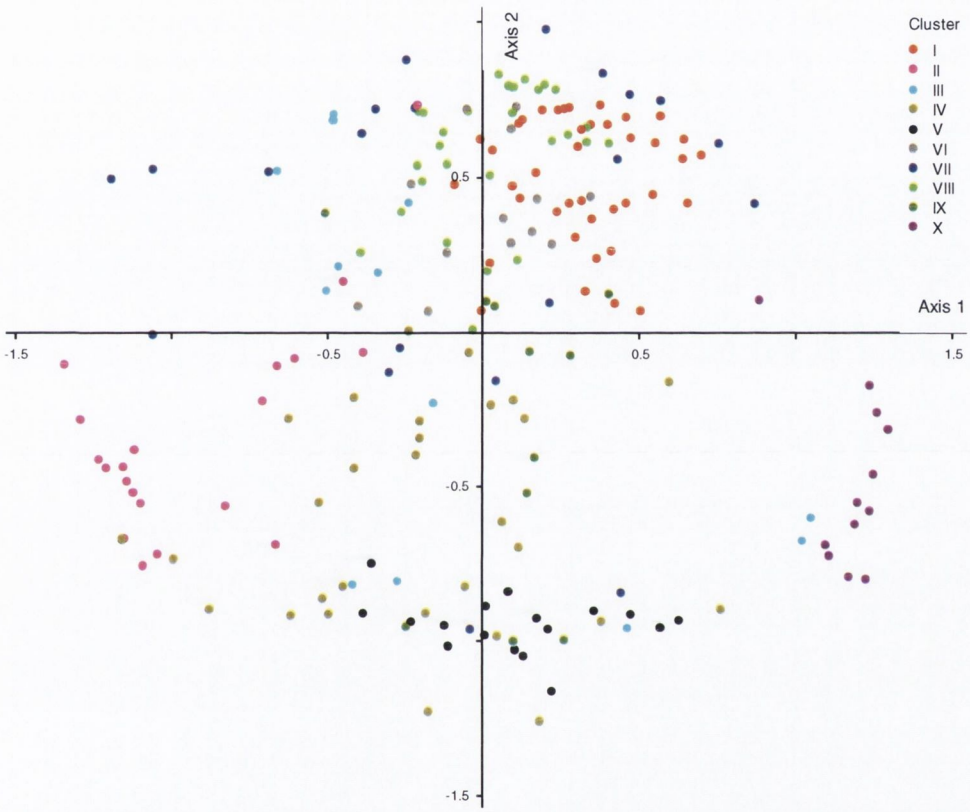


Figure 3.57 NMS ordination of the epiphyte composition of the trunk plots on the Sitka spruce and Japanese larch trees with the ten trunk plot cluster groups (cf. Figure 3.56) indicated. Refer to Figure 3.52 for details of the NMS ordination.

Table 3.28 The significant indicators for the trunk plot cluster analysis groups indicated in Figure 3.57. The indicator value (%) for each species in each of the six groups is shown and the highest indicator value is highlighted in bold. Only those species with an indicator value of 25% or more are included (cf. Section 3.2.3).

Species	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI	Cluster VII	Cluster VIII	Cluster IX	Cluster X
Hypnum jutlandicum	**64**	0	0	0	0	11	7	2	6	0
Isothecium myosuroides	**25**	0	0	0	0	0	0	0	0	0
Dimerella lutea	0	**91**	0	1	0	0	0	0	0	0
Dimerella pineti	0	**26**	0	0	0	2	0	0	0	0
Fuscidea lightfootii	0	0	0	0	**93**	0	0	0	0	0
Lecanora pulicaris	0	0	0	0	**75**	0	0	0	0	0
Kindbergia praelonga	0	0	0	0	0	0	**51**	5	0	0
Metzgeria temperata	2	0	0	0	0	4	0	**83**	0	0
Microlejeunea ulicina	0	0	0	1	0	0	0	0	**95**	0
Hypogymnia physodes	0	0	0	0	0	0	0	0	0	**98**
Lepraria incana	0	0	0	0	0	1	0	0	0	**79**
Platismatia glauca	0	0	0	0	0	0	0	0	0	**49**
Cladonia macilenta	0	0	0	0	0	0	0	0	0	**33**
Parmelia sulcata	0	0	0	0	1	0	0	0	0	**28**

Table 3.29 The mean (± standard error) of selected variables for the trunk plot cluster analysis groups shown in Figure 3.57. There is no significant difference between clusters for any variable if indicated by the same letter.

Variable	Cluster I (n = 40)	Cluster II (n = 20)	Cluster III (n = 16)	Cluster IV (n = 30)	Cluster V (n = 17)	Cluster VI (n =13)	Cluster VII (n = 21)	Cluster VIII (n = 29)	Cluster IX (n = 11)	Cluster X (n = 12)
Diversity:										
Total epiphyte SR	3.9^{a} (± 0.2)	3.0^{bc} (± 0.2)	2.2^{bd} (± 0.3)	4.3^{aef} (± 0.5)	3.8^{ace} (± 0.4)	4.9^{adef} (± 0.5)	5.1^{eg} (± 0.4)	4.0^{af} (± 0.3)	6.2^{fg} (± 1.0)	5.3^{dfg} (± 0.5)
Bryophyte SR	3.1^{a} (± 0.2)	1.4^{b} (± 0.2)	1.1^{c} (± 0.2)	1.2^{bc} (± 0.3)	0.3^{d} (± 0.2)	2.7^{ae} (± 0.3)	4.2^{f} (± 0.4)	3.2^{aef} (± 0.3)	3.2^{af} (± 0.5)	0.9^{bcd} (± 0.4)
Lichen SR	0.8^{a} (± 0.2)	1.6^{b} (± 0.1)	1.1^{ab} (± 0.3)	3.1^{cd} (± 0.4)	3.5^{ce} (± 0.4)	2.2^{bdf} (± 0.5)	0.8^{a} (± 0.2)	0.7^{a} (± 0.2)	3.0^{cef} (± 0.6)	4.3^{e} (± 0.5)
Total epiphyte 1/D	1.8^{ab} (± 0.1)	1.6^{abc} (± 0.1)	2.3^{abd} (± 0.3)	3.0^{cd} (± 0.3)	1.9^{ae} (± 0.1)	2.5^{d} (± 0.2)	2.2^{ad} (± 0.3)	1.5 ^{b} (± 0.1)	1.8^{abe} (± 0.2)	2.4^{de} (± 0.2)
Bryophyte 1/D	1.7^{a} (± 0.1)	1.3^{abc} (± 0.2)	1.1^{bcd} (± 0.2)	1.0^{bc} (± 0.2)	0.4^{f} (± 0.2)	1.9^{ae} (± 0.2)	2.3^{e} (± 0.2)	1.4^{a} (± 0.1)	1.4^{ad} (± 0.1)	1.2^{c} (± 0.2)
Lichen 1/D	0.8^{a} (± 0.1)	1.2^{b} (± 0.1)	1.2^{abc} (± 0.3)	2.2^{d} (± 0.2)	1.9^{cd} (± 0.1)	2.0^{cd} (± 0.3)	0.8^{a} (± 0.2)	0.9^{a} (± 0.1)	2.1^{cd} (± 0.4)	2.0^{cd} (± 0.2)
Cover:										
Total epiphyte cover (%)	59.9^{a} (± 3.8)	23.1^{bcd} (± 5.2)	1.1^{e} (± 0.3)	9.56^{f} (± 3.3)	18.4^{bc} (± 3.0)	10.45^{b} (± 1.8)	42.0^{cdh} (± 7.5)	49.8^{ag} (± 6.8)	38.6^{dg} (± 8.0)	63.3^{ah} (± 6.6)
Bryophyte cover (%)	59.4^{a} (± 3.8)	1.2^{b} (± 0.5)	0.4^{b} (± 0.1)	1.3^{b} (± 0.4)	0.1^{c} (± 0.1)	9.9^{de} (± 1.9)	30.6^{df} (± 7.2)	48.0^{af} (± 7.1)	31.8^{f} (± 7.1)	5.9^{bce} (± 2.2)
Lichen cover (%)	0.8^{a} (± 0.2)	22.2^{b} (± 5.2)	0.9^{ac} (± 0.4)	8.5^{d} (± 3.3)	18.4^{b} (± 3.0)	1.4^{ce} (± 0.4)	11.6^{acf} (± 5.9)	0.7^{a} (± 0.4)	7.2^{def} (± 2.5)	55.8^{g} (± 5.8)
Plot:										
Plot height (m)	1.3^{a} (± 0.5)	9.8^{b} (± 1.3)	2.7^{c} (± 0.8)	10.2^{b} (± 1.0)	12.2^{b} (± 0.8)	3.1^{cd} (± 0.8)	2.3^{ac} (± 0.7)	5.6^{def} (± 0.8)	10.5^{be} (± 2.6)	3.5^{cf} (± 1.2)
Tree girth at centre (cm)	137.9^{a} (± 9.4)	94.2^{b} (± 7.5)	89.6^{b} (± 7.1)	67.5^{c} (± 4.7)	50.5^{d} (± 3.1)	110.9^{b} (± 14.8)	103.9^{b} (± 10.0)	71.8^{ce} (± 3.7)	91.8^{be} (± 10.8)	132.4^{a} (± 6.7)
Inclination (°)	6.6^{a} (± 1.6)	1.1^{bc} (± 0.6)	2.2^{bc} (± 1.4)	0.1^{b} (± 0.4)	-0.6^{b} (± 0.8)	6.2^{ab} (± 3.8)	3.7^{ac} (± 1.7)	0.3^{b} (± 0.5)	0.9^{bc} (± 0.7)	1.2^{ab} (± 1.3)

The two significant indicators for this cluster were the moss species, *Hypnum jutlandicum* and *Isothecium myosuroides,* which are tolerant of shade, but also found in more exposed habitats (Hill *et al.*, 1994; Smith, 2004) (**Table 3.28**). The plots from this cluster had high bryophyte richness and low lichen richness on average (**Table 3.29**). Mean bryophyte diversity (1/D) was relatively high and mean bryophyte cover was the highest of all the cluster groups. The lowest mean plot height and highest girth and inclination for the plots in this cluster are an indication of the fact that these plots came mainly from the base and lower part of the tree where the trunk was often buttressed.

Cluster II consisted of mainly middle and upper plots, all from spruce trees. The majority of the plots came from trees in heavily thinned stands in the Wicklow cluster. The two significant indicators for this group, the crustose lichens *Dimerella lutea* and *D. pineti*, are both characteristic of shaded habitats (Dobson, 2005; Purvis *et al.*, 1992) (**Table 3.28**). The plots from this cluster were relatively species-poor on average but mean lichen cover was high (**Table 3.29**). The large mean plot height, combined with the relatively high mean girth, indicates that the plots came from large trees.

Cluster III contained trunk plots from a variety of height zones on trees from a number of stands, although they were mainly from the Wicklow cluster and mainly spruce trees; those plots from larch trees were mainly lower plots. They did not form a distinct group in the NMS plot (cf. **Figure 3.57**). There were no significant indicators for this group (**Table 3.28**) and the mean total epiphyte richness and cover was the lowest of all the cluster groups (**Table 3.29**).

Cluster IV contained middle and upper plots from spruce and larch trees from both the Cork and Wicklow clusters. There were no significant indicators for this group (**Table 3.28**), although *Colura calyptrifolia*, which is characteristic of humid habitats (Hill *et al.*, 1991; Paton, 1999) did occur in some of the plots from trees in the Cork cluster. Lichen richness and diversity were high in this cluster, but epiphyte cover was low on average (**Table 3.29**).

Cluster V consisted of upper plots, mainly from Wicklow cluster larch trees. The two significant indicators were crustose lichens (**Table 3.28**). *Fuscidea lightfootii* is characteristic of damp areas and *Lecanora pulicaris* is widely distributed (Dobson, 2005; Purvis *et al.*, 1992). Lichen richness and cover in this cluster were high, and bryophyte richness and diversity the lowest of all the clusters on average (**Table 3.29**).

Cluster VI consisted of tree base, lower and middle plots from larch trees and spruce trees, mainly from more heavily thinned stands. There were no significant indicators for this group (**Table 3.28**), but poorly developed *Parmelia s.l.* and *Cladonia* species, unidentifiable to species level, did occur in some of the plots. *Hypnum jutlandicum* was also present with low cover. The plots from this

cluster were relatively species-rich and had high diversity, but epiphyte cover was low on average (**Table 3.29**).

Cluster VII contained tree base and lower plots from dense spruce stands on peat and plots from all levels on spruce and larch trees from high rainfall areas. The single significant indicator for this group was the moss *Kindbergia praelonga*, which is tolerant of a range of conditions (Hill *et al.*, 1994) (**Table 3.28**). *Lejeunea cavifolia* and *Metzgeria fruticulosa*, both liverwort species characteristic of damp, humid situations (Paton, 1999), were also found in some of the plots in this group. The plots in this cluster had the highest bryophyte richness and diversity of all clusters on average and bryophyte cover was high. Although lichen richness was low, lichen cover was relatively high (**Table 3.29**).

Cluster VIII contained plots from all height zones from spruce trees in dense stands on peat or at high elevations with shaded aspects, with only a single plot from a larch tree. The liverwort indicator for this cluster, *Metzgeria temperata*, is characteristic of moist shaded situations (Paton, 1999) (**Table 3.28**). This was the most bryophyte-rich cluster and had high bryophyte cover, particularly of liverworts, but lichen richness and cover were low on average (**Table 3.29**).

Cluster IX contained lower, middle and upper plots, mainly from larch trees and all from the Cork cluster. The significant indicator for this group, *Microlejeunea ulicina*, is characteristic of humid situations (Paton, 1999) (**Table 3.28**). *Graphis scripta*, *Hypotrachyna revoluta* and *Frullania tamarisci* also occurred in a number of plots in this group. This was the most species-rich of the clusters and had both high bryophyte and lichen richness on average, with lichen diversity being particularly high (**Table 3.29**).

The final cluster, cluster X, contained the tree base, lower and middle plots from two larch trees from over-mature stands in Wicklow. There were five significant indicators for this group, with all five being lichens (**Table 3.28**). A number of these species were characteristic of acid substrates and a number were also particularly pollution tolerant (Dobson, 2005; Purvis *et al.*, 1992). This cluster was the most lichen-rich on average and had the highest lichen cover, but had low bryophyte richness; liverworts were absent (**Table 3.29**).

Trunk plot communities described

The NMS and cluster analysis have identified different species compositions in the trunk plots studied. This information was tabulated, with each distinct community informally named, and the indicators and the plot and stand types with which each community was associated being given (**Table 3.30**). The epiphyte community of the plots in cluster I was named the '*Hypnum jutlandicum* community' and that in cluster II the '*Dimerella*-dominated community'. The

Table 3.30 The epiphyte communities of the trunk plots studied. Each community is informally named and the indicators and the plot and stand types with which each community is associated are listed. (B = tree base, L = lower, M = middle, U = upper).

Cluster	Epiphyte community	Indicators	Plot type
I	'*Hypnum jutlandicum* community'	*Hypnum jutlandicum*, *Isothecium myosuroides*; High moss cover	B and L plots from larch stands and more heavily thinned spruce stands
II	'*Dimerella*-dominated community'	*Dimerella lutea*, *Dimerella pineti;* High cover of *Dimerella* species	M and U plots from heavily thinned spruce stands in the Wicklow cluster
III	'Species-poor community'	Low species richness and cover of epiphytes	B, L & M plots from spruce stands in the Wicklow cluster; L plots from Wicklow cluster larch stands
V	'*Fuscidea* and *Lecanora* community'	*Fuscidea lightfootii*, *Lecanora pulicaris;* High crustose lichen cover; Bryophytes scarce	U plots from Wicklow cluster larch stands
VII	*Kindbergia praelonga* community'	*Kindbergia praelonga*; High bryophyte richness	B & L plots from stands on peat or plots from all heights from spruce and larch stands in high rainfall areas
VIII	'*Metzgeria temperata* community'	*Metzgeria temperata*; High liverwort cover	B, L, M & U plots from spruce stands on peat or at high elevations on steep slopes with shady aspects
IX	'*Microlejeunea ulicina* community'	High cover of *Microlejeunea ulicina*; *Graphis scripta*; *Hypotrachyna revoluta*; *Frullania tamarisci*	L, M & U plots from larch stands, or silviculturally over-mature spruce stands, from wet sites in the Cork cluster
X	'Foliose and leprose lichen-dominated community'	*Hypogymnia physodes, Lepraria incana, Platismatia glauca, Cladonia macilenta, Parmelia sulcata;* Liverworts absent	B, L & M plots from heavily thinned silviculturally over-mature larch stands close to old woodland

community of the plots in cluster III was named the 'species-poor community'; a number of the nearby plots from the same trees contained no epiphyte species and so were excluded from the ordination. Clusters IV and VI did not have a well-defined epiphyte composition so were not included in the table. The epiphyte community of the cluster V plots was named the '*Fuscidea* and *Lecanora* community' and that of cluster VIII the '*Metzgeria temperata* community'. The community in the cluster IX plots was named the '*Microlejeunea ulicina* community' and cluster X the 'foliose and leprose lichen-dominated community'.

3.3.5 Distribution of epiphytes on branches

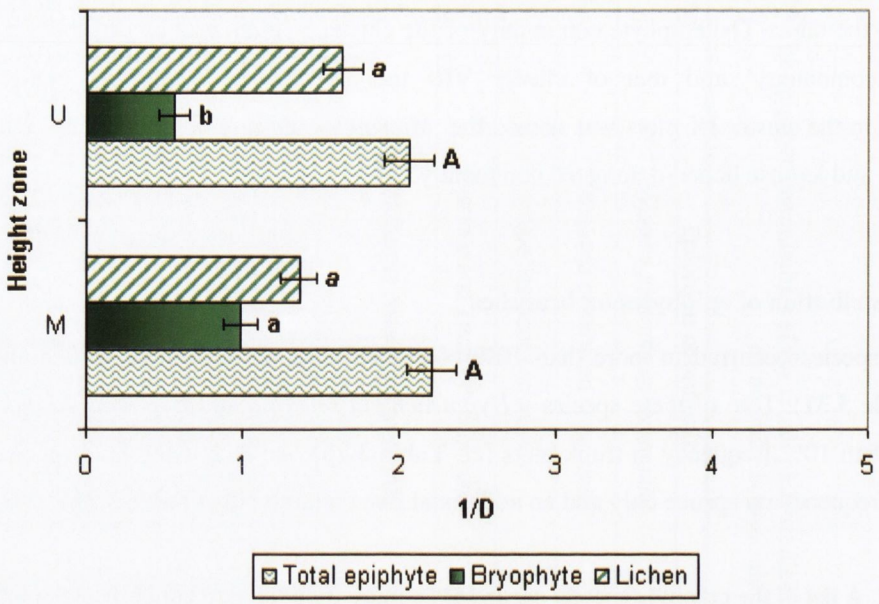
Only four species occurred in more than 10% of branch plots on both Sitka spruce and Japanese larch (**Table 3.31**). Two of these species – *Hypotrachyna revoluta* and *Hypnum jutlandicum* - also had more than 10% frequency in trunk plots (cf. **Table 3.26**). An additional three species had more than 10% frequency on spruce only and an additional five on larch only (**Table 3.31**).

Table 3.31. A list of the epiphyte species occurring in more than ten percent of branch plots on Sitka spruce and/or Japanese larch with the percent frequency indicated. The epiphyte group, growth form and affinity for epiphytism of each species are also indicated.

	Epiphyte group	Growth form	Epiphytism affinity	Spruce (n = 198)	Larch (n = 105)
Hypotrachyna revoluta	Li	Fo	High	**31.3**	**41.9**
Fuscidea lightfootii	Li	Cr	High	**22.2**	**50.5**
Ulota crispa s.l.	Mo	Cu	High	**16.2**	**17.1**
Hypnum jutlandicum	Mo	Ma	Int	**11.6**	**12.4**
Dimerella lutea	Li	Cr	Int	**23.7**	5.7
Metzgeria temperata	Lv	Ma	High	**19.7**	4.8
Microlejeunea ulicina	Lv	Ma	High	**10.1**	9.5
Lecanora pulicaris	Li	Cr	High	0.5	**24.8**
Trapeliopsis flexuosa	Li	Cr	Int	1.5	**23.8**
Hypogymnia tubulosa	Li	Fo	Int	6.1	**19.1**
Graphis elegans	Li	Cr	High	0.5	**14.3**
Pseudevernia furfuracea	Li	Fo	Int	0	**11.4**

The diversity and cover of epiphytes in the plots on the middle and upper branches of spruce and larch were compared. Species richness was not compared because of the difference in the cover of branches within each plot (cf. **Figure 2.3**). There was significantly higher bryophyte diversity (1/D) in the plots on the middle branches of spruce (Mann-Whitney U test: $p < 0.001$) and significantly higher total epiphyte (Mann-Whitney U test: $p < 0.001$), bryophyte (Mann-Whitney U test: $p = 0.001$) and lichen diversity (Mann-Whitney U test: $p < 0.001$) in the plots on the middle branches of larch (**Figure 3.58**). Total epiphyte and lichen diversity were significantly higher in the plots on the middle branches of larch than of spruce (Mann Whitney U test: total epiphyte, $p < 0.001$; lichen, $p < 0.001$) and bryophyte diversity was significantly higher in the plots on the upper branches of spruce than of larch (Mann-Whitney U test: $p = 0.022$).

(a)



(b)

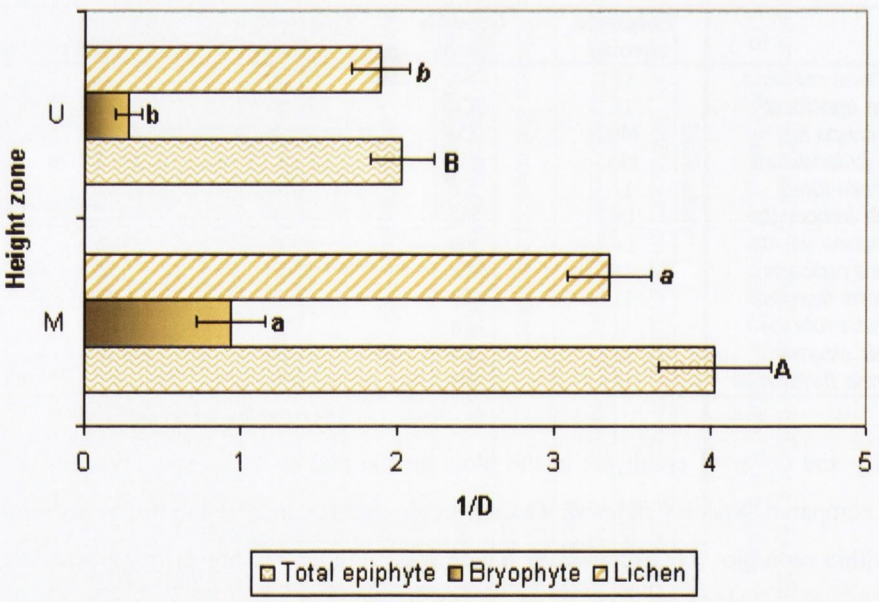


Figure 3.58 Mean diversity (1/D) of epiphytes in the plots on the middle (M) and upper (U) branches of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen (lowercase italic) diversity between the middle and upper branches if indicated by the same letter.

There was significantly higher total epiphyte (Mann-Whitney U test: $p < 0.001$) and bryophyte cover (Mann-Whitney U test: $p < 0.001$) in the plots on the middle branches of spruce than in those on the upper branches (**Figure 3.59**). On larch branches, bryophyte cover was significantly higher in plots on the middle branches (Mann-Whitney U test: $p = 0.001$) than in those on the upper branches. Bryophyte cover was significantly higher (Mann-Whitney U test: $p = 0.049$) and lichen cover was significantly lower (Mann-Whitney U test: $p < 0.001$) in plots on the middle branches of spruce than in those on larch. On the upper branches, total epiphyte cover was significantly higher in the plots on spruce (Mann-Whitney U test: $p < 0.001$) compared to larch, as was bryophyte cover (Mann-Whitney U test: $p = 0.011$), but lichen cover was significantly lower (Mann-Whitney U test: $p < 0.001$) compared to larch.

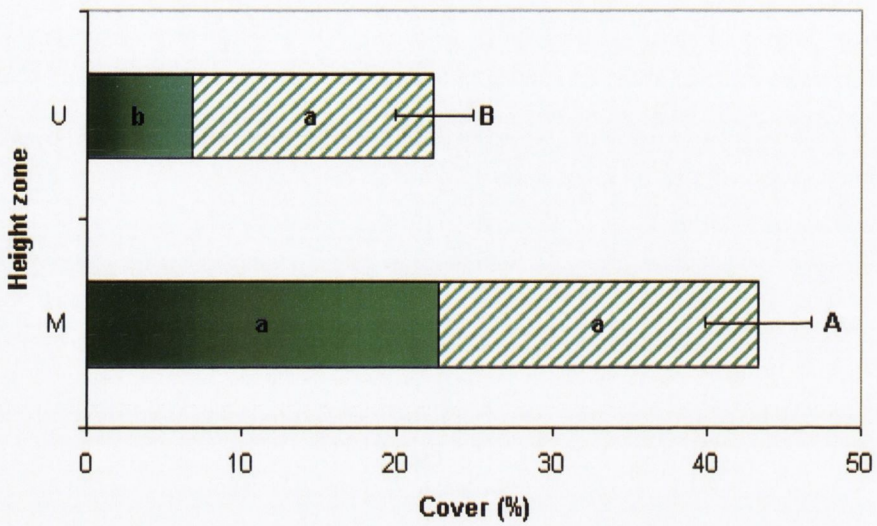
The percentage of inner, mid and outer branch plots containing epiphytes was examined on the middle and upper branches. On the middle branches, almost all the inner, mid and outer branch plots contained epiphytes on both tree species (**Table 3.32**). On the upper branches, while almost all the inner and mid branch plots contained epiphytes, a large proportion of the outer plots did not contain any epiphytes.

Table 3.32 The percentage of inner, mid and outer branch plots containing at least one epiphyte species on the middle and upper branches of Sitka spruce and Japanese larch.

		Inner	Mid	Outer
Spruce:				
	Middle	97.0	93.8	93.6
	Upper	91.2	100	58.8
Larch:				
	Middle	100	100	90.9
	Upper	95.5	100	42.9

The distribution of lichens in the inner, mid and outer plots on branches was examined. The middle and upper branches were examined separately. On the middle branches there were no significant differences in total epiphyte diversity among inner, mid and outer plots on spruce ($H = 0.767$, $df = 2$, $p = 0.681$) or larch ($H = 3.14$, $df = 2$, $p = 0.208$) (**Figure 3.60**). There were, however, significant differences in lichen diversity among plots on spruce ($H = 9.74$, $df = 2$, $p = 0.008$). Further examination revealed a significantly lower lichen diversity in the inner plots than in the mid or outer plots on the middle branches of spruce (**Figure 3.60**). On the upper branches there were significant differences in total epiphyte diversity among plots on both spruce ($H = 17.83$, $df = 2$, $p < 0.001$) and larch ($H = 17.81$, $df = 2$, $p < 0.001$) (**Figure 3.61**). There were also significant differences in lichen diversity among plots on spruce ($H = 23.34$, $df = 2$, $p < 0.001$) and both bryophyte ($H = 6.69$, $df = 2$, $p = 0.035$) and lichen diversity ($H = 17.27$, $df = 2$, $p < 0.001$) on larch. Further examination revealed that both total epiphyte and lichen diversity increased significantly from inner to mid plots, with a further significant decrease to their lowest levels in the outer plots (**Figure 3.61**). On larch total epiphyte, bryophyte and lichen diversity were significantly lower in

(a)



(b)

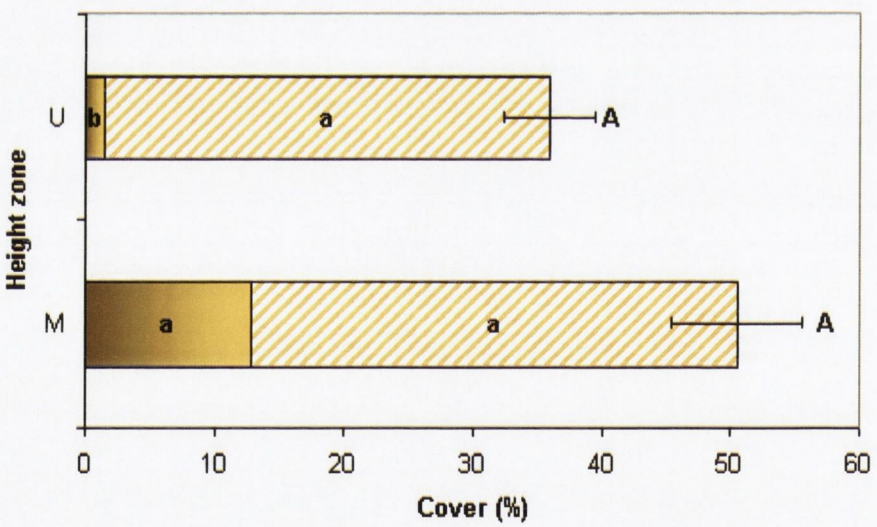
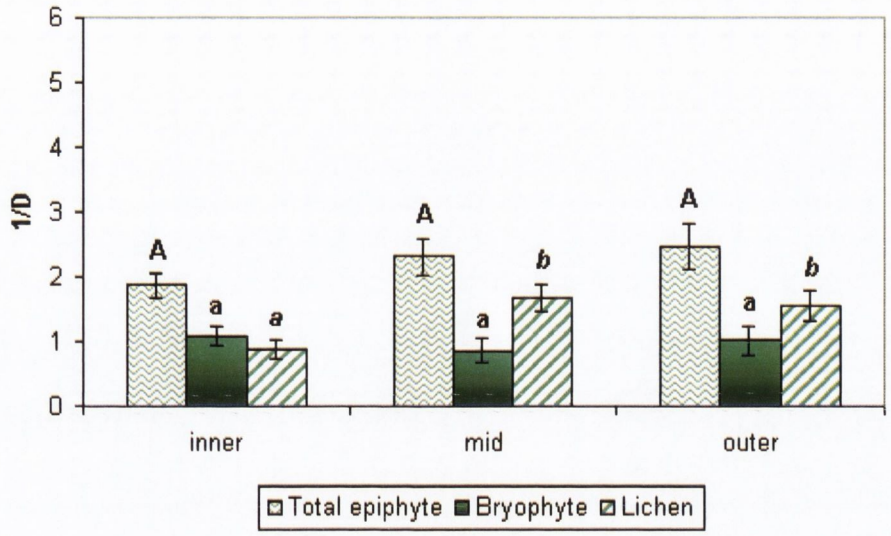


Figure 3.59 Mean cover of epiphytes in the plots on the middle (M) and upper (U) branches of (a) Sitka spruce (n = 34) and (b) Japanese larch (n = 22). Cover is expressed as a percentage of the cover of branches within each plot. The total cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. There is no significant difference in total (uppercase), bryophyte or lichen (lowercase) cover between the middle and upper branches if indicated by the same letter.

(a)



(b)

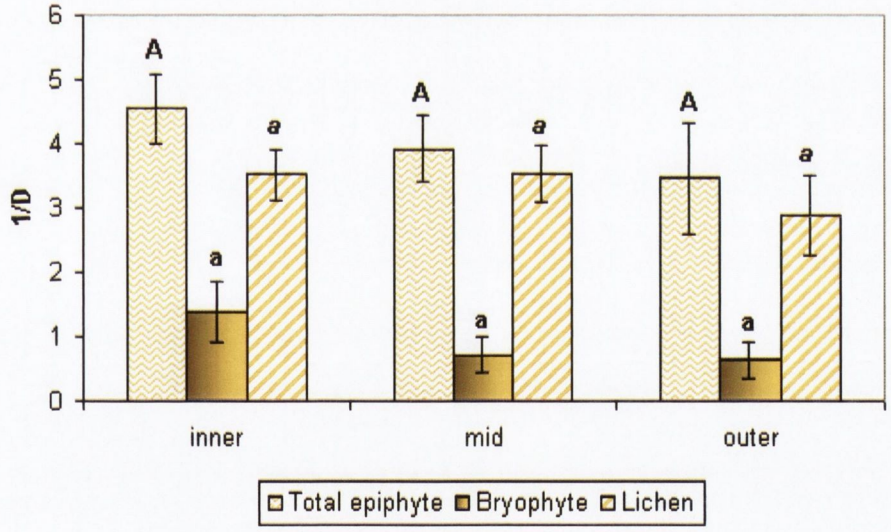
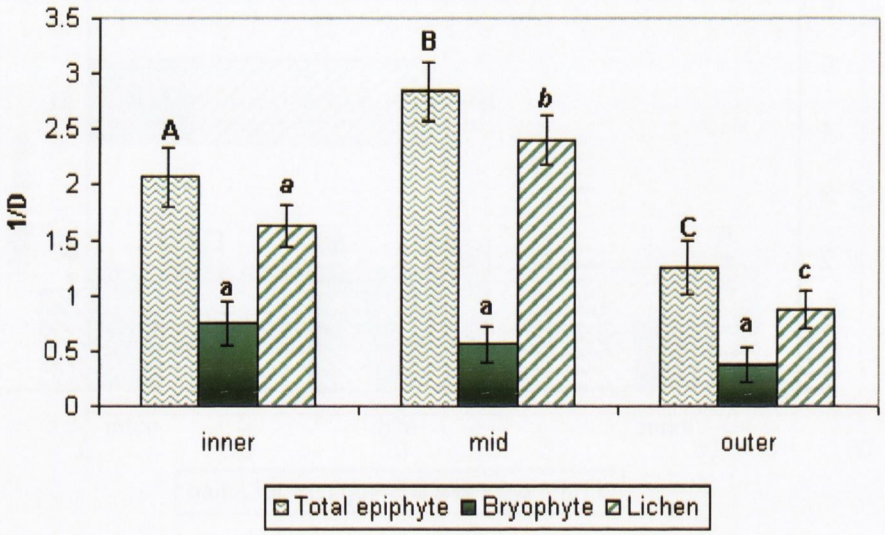


Figure 3.60 Mean Simpson's reciprocal diversity (1/D) in the inner, mid and outer plots on the middle branches of (a) Sitka spruce (n = 33, 32, 31) and (b) Japanese larch (n = 15, 14, 11). Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen diversity (lowercase italic) between bars if indicated by the same letter.

(a)



(b)

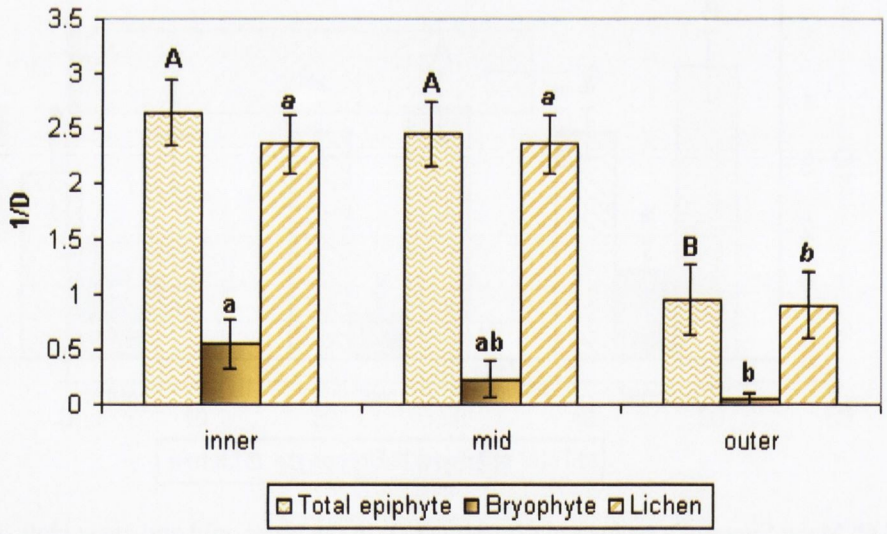


Figure 3.61 Mean Simpson's reciprocal diversity (1/D) in the inner, mid and outer plots on the upper branches of (a) Sitka spruce (n = 34, 34, 34) and (b) Japanese larch (n = 22, 22, 21). Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen diversity (lowercase italic) between bars if indicated by the same letter.

the outer plots than in the inner plots in all cases, with total epiphyte and lichen diversity also being significantly lower than in the mid branch plots.

On the middle branches, there were no significant differences in mean total epiphyte cover among the inner, mid and outer plots on spruce (H = 0.04, df = 2, p = 0.979) or larch (H = 3.37, df = 2, p = 0.186) (**Figure 3.62**). There were, however, significant differences in lichen cover among plots on both spruce (H = 7.27, df = 2, p = 0.026) and larch (H = 9.08, df = 2, p = 0.011). Further examination revealed a significantly lower lichen cover in the inner plots compared with the other two plots on both species (**Figure 3.62**). On the upper branches there were significant differences in total epiphyte cover (H = 9.92, df = 2, p = 0.007) and lichen cover (H = 12.10, df = 2, p = 0.002) among plots on spruce but not on larch (H = 3.81, df = 2, p = 0.149). There were, however, significant differences in bryophyte cover among plots on larch (H = 6.82, df = 2, p = 0.033). Further examination revealed a significantly lower total epiphyte and lichen cover in the outer plots compared with the other two plots on spruce (**Figure 3.62**). Bryophyte cover decreased from the inner to outer plots on both species and the difference between the outer and inner plots was significant on larch (**Figure 3.62**).

3.3.5.1 Epiphyte composition of the branch plots

NMS ordination of the branch plot data was not carried out as the large number of uncommon species meant that, when carrying out Monte Carlo testing, shuffling within the columns returned undefined distances more than the maximum 10,000 times. In order for this not to occur, a large number of species would have had to be removed from the matrix and it was considered that too much information would have been lost as a result. Cluster and indicator species analysis were used, however, to divide the branch plots into cluster groups (**Figure 3.63**, **Figure 3.64**). The plots of the number of cluster groups versus the average significance of the indicator species (**Figure 3.64a**) and the total number of significant indicator species (**Figure 3.64b**) suggest that the optimum number of clusters is six or eight. The average significance of the indicator species is lowest for the six-cluster option (p = 0.19), while the number of significant indicators (n = 31) is highest for eight clusters. It was decided that the eight-cluster option was the most sensible choice and indicator species analysis was used to identify species characteristic of each cluster group (**Table 3.33**). The eight branch plot cluster groups were examined in terms of certain diversity, cover and plot variables (**Table 3.34**).

Cluster i was composed of plots from both live and dead branches from larch stands and some more heavily thinned spruce stands, the majority of which were from the Wicklow cluster (**Appendix 5**). These were inner, mid and outer plots from both middle and upper branches, although there were slightly more outer branch plots, as indicated by the large distance from the trunk on average in this cluster (**Table 3.34**). Lichen richness and cover were relatively high but

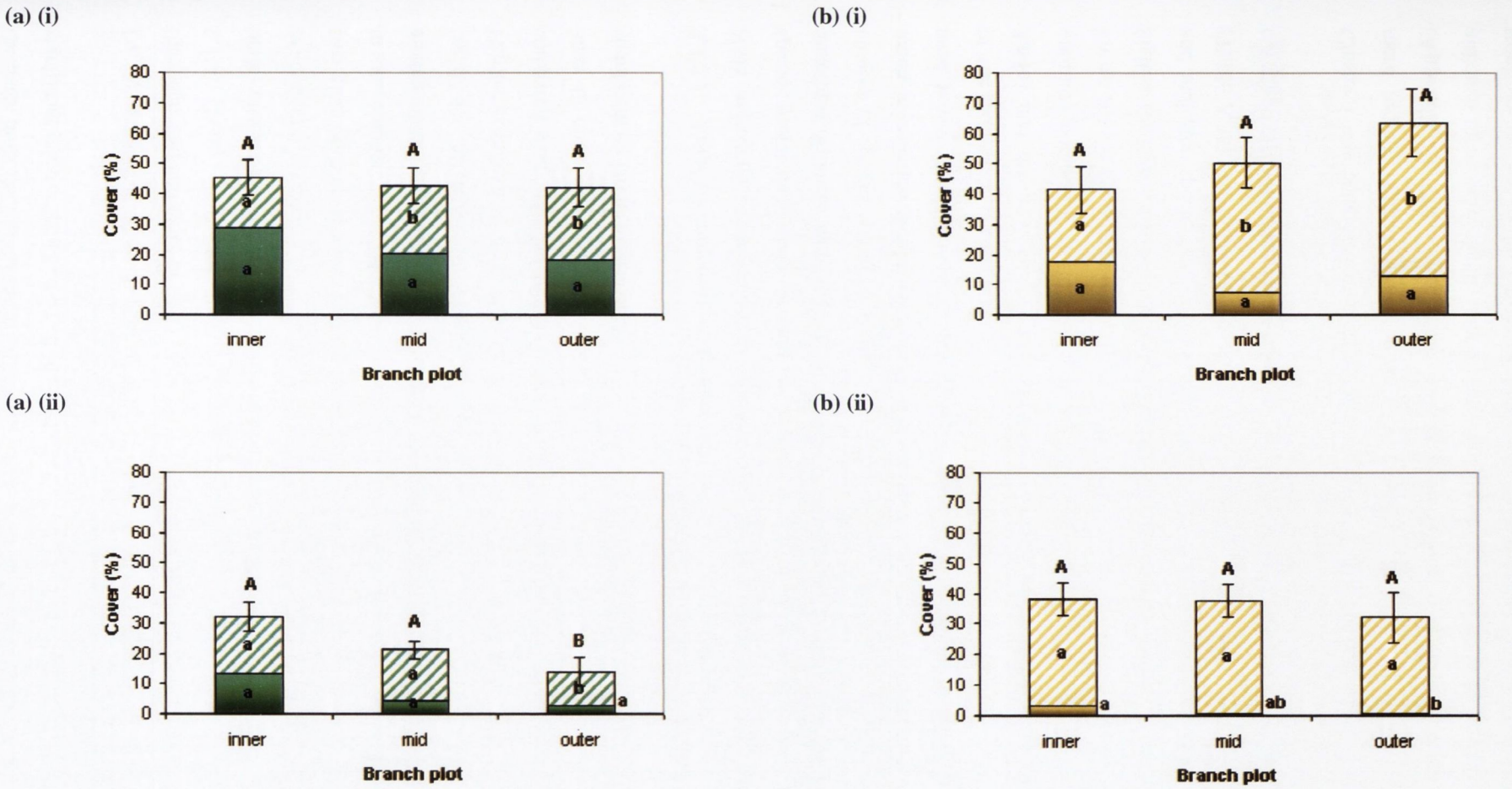


Figure 3.62 Mean cover of epiphytes in the inner, mid and outer plots on the (i) middle (M) and (ii) upper (U) branches of (a) Sitka spruce (M: n = 33, 32, 31; U: n = 34, 34, 34) and (b) Japanese larch (M: n = 15, 14, 11; U: n = 22, 22, 21). Cover is expressed as a percentage of the cover of branches within each plot. The total cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase) bryophyte or lichen (lowercase) cover between bars if indicated by the same letter.

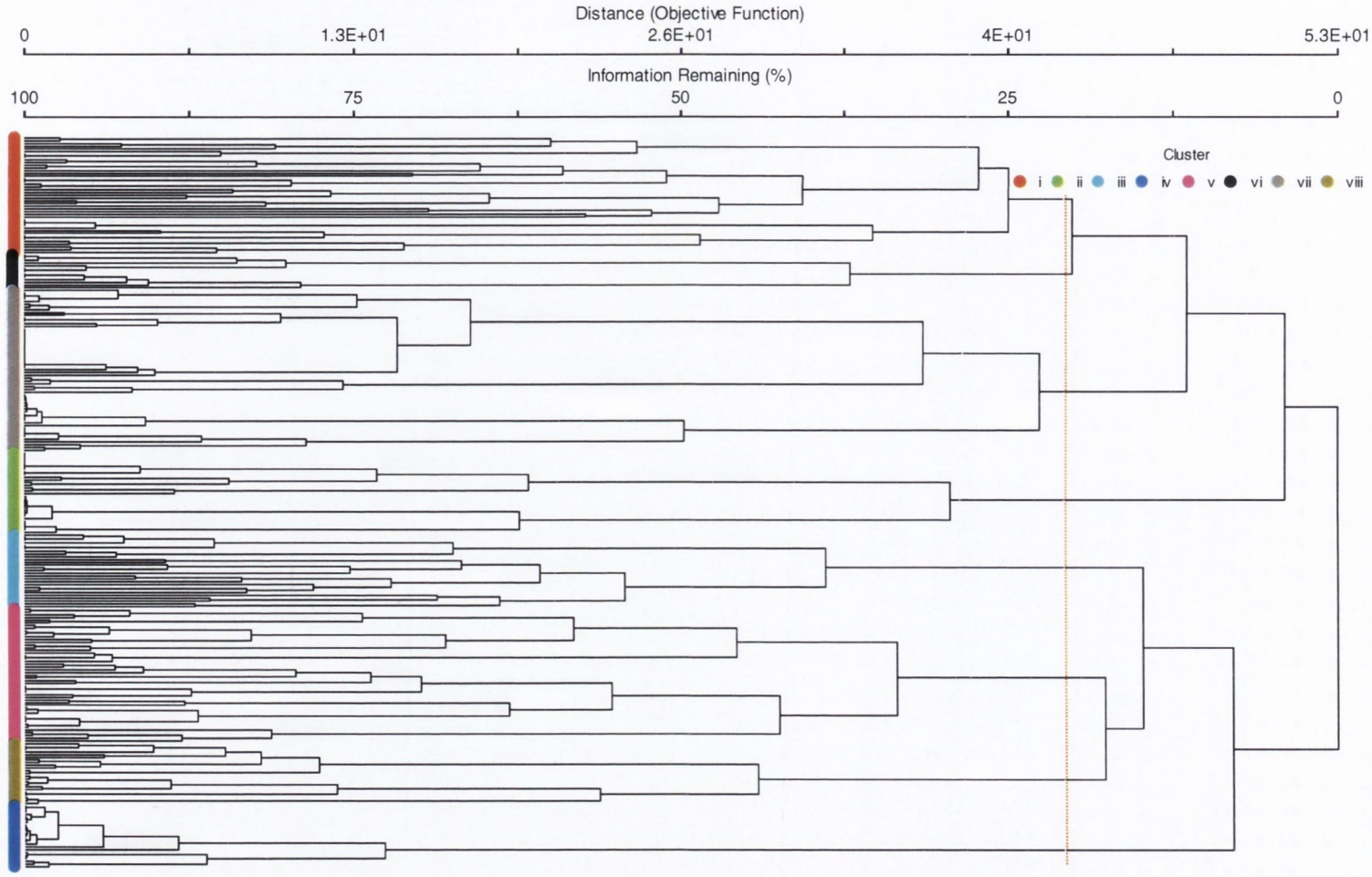
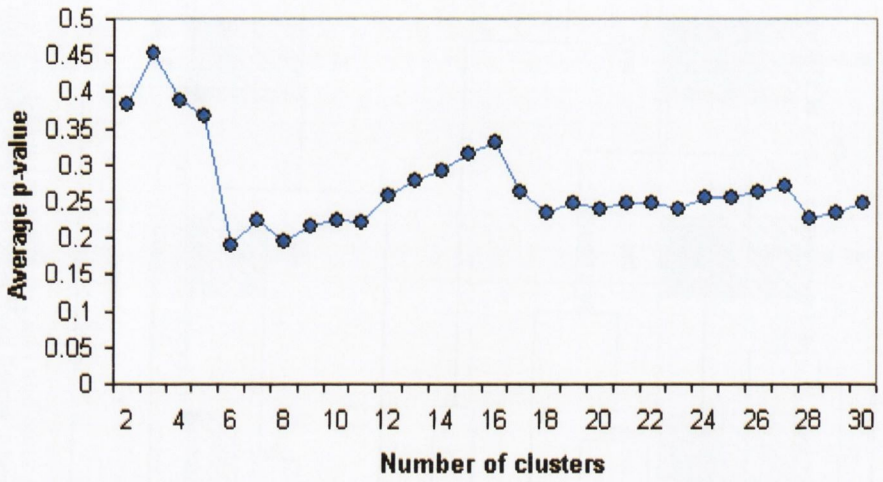


Figure 3.63 Cluster dendrogram of the branch plots from the Sitka spruce and Japanese larch trees, scaled by Wishart's objective function and percent of information remaining. The position of the cut leading to the eight resulting clusters is shown. (See Appendix 5 for list of plots occurring in each cluster).

(a)



(b)

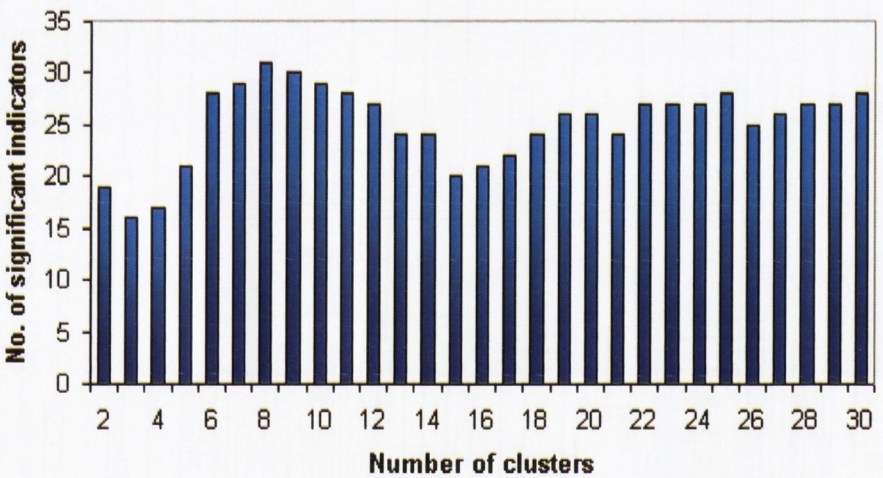


Figure 3.64 Graphs used to assess the appropriate number of cluster analysis groupings. Number of clusters is plotted against (a) average significance of the indicator species and (b) number of significant indicators. *Note*. Species indicators could not be derived for more than 30 clusters because further division caused at least one cluster to contain only one branch plot.

Table 3.33 The significant indicators for the branch plot cluster analysis groups indicated in Figure 3.63. The indicator value (%) for each species in each of the six groups is shown and the highest indicator value is highlighted in bold. Only those species with an indicator value of 25% or more are included (cf. Section 3.2.3).

Species	Cluster i	Cluster ii	Cluster iii	Cluster iv	Cluster v	Cluster vi	Cluster vii	Cluster viii
Dimerella lutea	0	**83**	1	1	2	0	0	0
Dimerella pineti	0	**34**	0	0	0	0	0	0
Microlejeunea ulicina	0	0	**38**	5	1	0	0	1
Ulota crispa s.l.	0	0	**36**	1	2	0	0	16
Metzgeria temperata	0	0	0	**88**	0	0	0	1
Lophocolea bidentata	0	0	0	**26**	0	0	0	0
Hypnum jutlandicum	0	0	1	**23**	12	0	0	1
Micarea peliocarpa	0	0	0	0	0	**62**	0	0
Gyalideopsis anastomosans	1	0	0	1	0	**36**	0	0
Fuscidea lightfootii	2	0	1	0	1	0	**63**	4
Lecanora pulicaris	0	0	0	0	1	0	**25**	1
Hypotrachyna revoluta	0	0	2	7	11	0	0	**69**
Trapeliopsis flexuosa	0	0	0	0	0	0	1	**44**
Graphis elegans	0	0	0	0	0	0	0	**36**

Table 3.34 The mean (± standard error) of selected variables for the branch plot cluster analysis groups shown in Figure 3.63. There is no significant difference between clusters for any variable if indicated by the same letter.

Variable	Cluster i (n = 43)	Cluster ii (n = 30)	Cluster iii (n = 27)	Cluster iv (n = 23)	Cluster v (n = 49)	Cluster vi (n = 13)	Cluster vii (n = 59)	Cluster viii (n = 23)
Diversity:								
Total epiphyte SR	3.3^{a} (± 0.3)	2.0^{b} (± 0.2)	5.3^{c} (± 0.6)	3.5^{a} (± 0.4)	3.3^{a} (± 0.3)	1.9^{b} (±0.2)	2.4^{b} (± 0.2)	5.3^{c} (±0.5)
Bryophyte SR	0.5^{a} (± 0.2)	0.2^{ab} (± 0.1)	2.3^{c} (± 0.2)	2.4^{c} (± 0.3)	1.0^{d} (± 0.2)	0^{b}	0.1^{b} (± 0.0)	1.4^{d} (±0.3)
Lichen SR	2.8^{ab} (± 0.3)	1.8^{a} (± 0.1)	3.0^{bd} (± 0.4)	1.2^{c} (± 0.2)	2.3^{ab} (± 0.2)	1.9^{ab} (±0.2)	2.3^{ab} (± 0.2)	4.0^{d} (±0.4)
Cover: *								
Total epiphyte cover (%)	34.0^{a} (± 5.0)	36.6^{a} (± 6.2)	36.5^{a} (± 6.8)	70.4^{b} (± 4.4)	28.0^{a} (± 4.0)	19.4^{c} (±7.9)	24.7^{ac} (± 2.7)	55.0^{d} (±5.1)
Bryophyte cover (%)	5.7^{a} (± 2.4)	1.5^{ab} (± 0.6)	21.8^{c} (± 4.6)	70.4^{d} (± 4.4)	13.6^{e} (± 3.1)	0^{b}	0.4^{b} (± 0.2)	11.9^{e} (±3.7)
Lichen cover (%)	28.2^{ac} (± 4.7)	36.6^{a} (± 6.2)	25.4^{ac} (± 5.4)	8.3^{b} (± 1.2)	20.3^{ac} (± 3.3)	19.4^{bc} (±7.9)	24.7^{ac} (± 2.7)	49.6^{d} (±4.4)
Plot:								
Distance from trunk (cm)	124.7^{ac} (± 18.5)	71.8^{ab} (± 12.0)	84.1^{a} (± 14.4)	36.6^{b} (± 7.8)	94.2^{a} (± 12.9)	149.2^{c} (±24.2)	100.2^{ac} (± 11.5)	89.2^{a} (±15.6)
Diameter of branch at centre (cm)	1.87^{ac} (± 0.21)	1.91^{ac} (± 0.19)	2.02^{ac} (± 0.30)	1.72^{ac} (± 0.18)	1.54^{a} (± 0.11)	1.24^{a} (±0.20)	2.66^{b} (± 0.18)	2.34^{bc} (±0.23)
Branch cover (%)	5.7^{a} (± 0.5)	5.9^{ac} (± 0.4)	5.8^{a} (± 0.7)	4.8^{a} (± 0.4)	5.1^{a} (± 0.3)	5.9^{ac} (±0.6)	8.4^{b} (± 0.5)	7.0^{bc} (±0.5)
Needle cover (%)	7.9^{a} (± 2.1)	1.3^{ab} (± 1.0)	4.5^{b} (± 2.1)	0.7^{b} (± 0.5)	7.7^{b} (± 2.1)	40.1^{c} (±7.4)	23.8^{c} (± 3.3)	5.4^{ab} (±3.0)
Proportion on dead branches (%)	48.8	60.0	66.7	82.6	59.2	7.7	15.3	56.5

Note. *Cover is expressed as a percentage of the cover of branches within each plot.

bryophyte richness and cover were quite low (**Table 3.34**). There were no significant indicators for this cluster group (**Table 3.33**).

Cluster ii contained plots mainly from middle branches and, where they did come from upper branches, they were almost all inner plots. The majority of plots came from dead branches (**Table 3.34**). All but two plots came from Wicklow cluster spruce trees, the majority of which were from heavily thinned stands. Epiphyte species richness, particularly bryophyte richness, was very low, but epiphyte cover was high and composed mainly of lichens (**Table 3.34**). The two significant indicators for this group were *Dimerella lutea* and *D. pineti* (**Table 3.33**), which were also significant indicators for trunk plot cluster II whose community was named the '*Dimerella*-dominated community' (cf. **Table 3.28** & **Table 3.30**).

The majority of plots in cluster iii were from dead middle branches, which came from larch stands in high rainfall areas in the Cork cluster and more heavily thinned spruce stands, some of which were in the Wicklow cluster. This cluster had the highest total epiphyte richness, which was made up of both high bryophyte and lichen richness (**Table 3.34**). The two significant indicators for this cluster were the bryophytes *Microlejeunea ulicina* and *Ulota crispa s.l.* (**Table 3.33**).

Cluster iv contained mainly inner plots from middle branches, as indicated by the shortest distance from the trunk on average for the plots in this group (**Table 3.34**). All but one plot came from branches on trees in spruce stands either on peat or at high elevations on steep slopes with shaded aspects. The majority of plots were from dead branches (**Table 3.34**). Bryophyte richness was relatively high and bryophyte cover was significantly higher than in all other groups (**Table 3.34**). The three significant indicators were the bryophyte species *Metzgeria temperata*, *Lophocolea bidentata* and *Hypnum jutlandicum* (**Table 3.33**); *Metzgeria temperata* is also a significant indicator for trunk plot cluster VIII whose community was named the '*Metzgeria temperata* community' (cf. **Table 3.28** & **Table 3.30**).

Cluster v contained plots from both living and dead, middle and upper branches, although the majority were from middle branches. The majority were also from spruce trees and from Cork cluster trees (**Appendix 5**). Lichen richness and cover were relatively high (**Table 3.34**). There were no significant indicators for this cluster (**Table 3.33**).

All of the plots in cluster vi were from spruce stands and these were mainly high-elevation stands in the Wicklow cluster (**Appendix 5**). The majority were outer branch plots and were mainly from the upper branches, as indicated by the low diameter at the centre of the plots and the large distance from the trunk (**Table 3.34**). Most were therefore on live branches, as indicated by the high needle cover in the plots (**Table 3.34**). Species richness was the lowest of all the clusters and bryophyte

species were absent. The two significant indicators for this group were the crustose lichens *Micarea peliocarpa* and *Gyalideopsis anastomosans*. *Micarea* is common in upland areas on acid bark, as well as on lignum, exposed peat and peaty debris, and *Gyalideopsis* is common on bark in moist sheltered woods (Dobson, 2005; Purvis *et al.*, 1992).

The majority of plots in cluster vii were from living branches, as indicated by the high needle cover in the plots (**Table 3.34**). The plots were mainly inner and mid plots from upper branches, with a number from trees in silviculturally over-mature spruce and larch stands, most of which were in the Wicklow cluster. The branch diameter in the plots was the highest of all cluster groups and the cover of branches within the plots was also relatively high (**Table 3.34**). Lichen richness and cover were high and bryophyte richness and cover low. The two significant indicators were the crustose lichens, *Fuscidea lightfootii* and *Lecanora pulicaris* (**Table 3.33**), which were also significant indicators for trunk plot cluster V, whose community was named the '*Fuscidea* and *Lecanora* community' (cf. **Table 3.28** & **Table 3.30**).

Cluster viii was composed mainly of inner and mid branch plots from dead and living, middle and upper branches, mainly from larch trees in the Cork cluster. It was the most lichen-rich cluster and had significantly higher total epiphyte and lichen cover than all other groups. The three significant indicators were all lichens, with the foliose lichen *Hypotrachyna revoluta* having the highest indicator value (**Table 3.33**).

Branch plot communities described

Cluster and indicator species analysis have identified different species compositions in the branch plots studied. This information was tabulated, with each distinct branch plot community informally named, and the indicators and the plot and stand types with which each community was associated being given (**Table 3.35**). The epiphyte composition of cluster i was not well defined so this cluster was not included in the descriptions. The epiphyte community in cluster ii was named the '*Dimerella*-dominated community' after the same community which occurred in some trunk plots. The community in cluster iii was named the '*Microlejeunea* and *Ulota* community'. Cluster iv was named the '*Metzgeria temperata* community' after the same community which occurred in some trunk plots. The epiphyte community of cluster v was not well defined so this cluster was not included in the descriptions. The community in cluster vi was named the '*Micarea peliocarpa* community'. The composition of cluster vii was named the '*Fuscidea* and *Lecanora* community' after the same community which occurred in some trunk plots. Cluster viii was named the '*Hypotrachyna revoluta* community'.

3.3.6 Effects of aspect on epiphytes

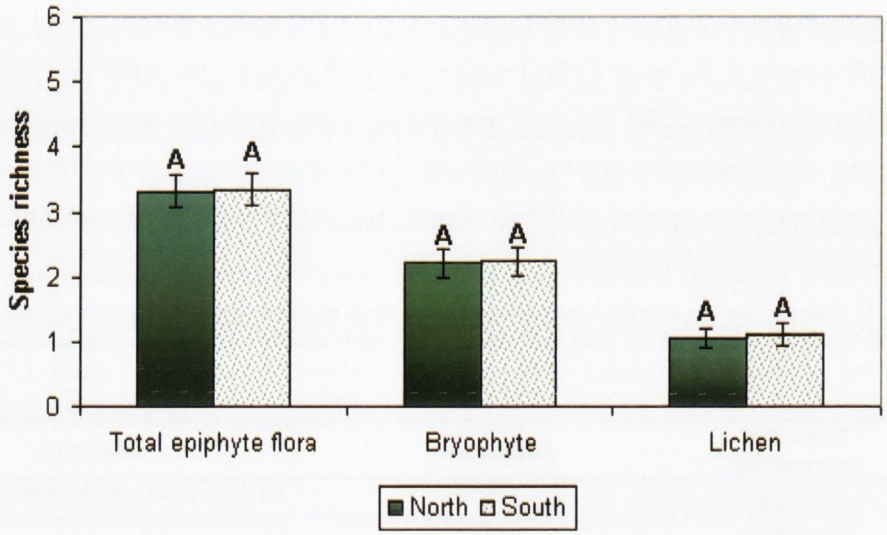
The differences in epiphyte richness, diversity and cover between the plots on the north and south sides of the trees were examined. There were no significant differences in mean total epiphyte, bryophyte or lichen richness between the trunk plots on the north and south sides of either the Sitka spruce or Japanese larch trees, although the higher lichen richness on the south side of larch approached significance (Wilcoxon signed ranks test: $p = 0.061$) (**Figure 3.65**). There were also no significant differences in diversity (1/D) between the trunk plots on the north and south sides of either tree species (**Figure 3.66**). On both tree species, mean bryophyte cover was higher on the north sides and mean lichen cover on the south sides of the trunks, however the difference was only significant for lichen cover on larch (Wilcoxon signed ranks test: $p = 0.028$) (**Figure 3.67**).

Table 3.35 The epiphyte communities of the branch plots studied. Each community is informally named and the indicators and the plot and stand types with which each community is associated are listed.

Cluster	Epiphyte community	Indicators	Plot type
ii	'*Dimerella*-dominated community'	*Dimerella lutea*; *Dimerella pineti*; High cover of *Dimerella*.	All plots from middle branches, inner plots from upper branches. Branches dead. Wicklow cluster spruce trees, from heavily thinned stands.
iii	'*Microlejeunea* and *Ulota* community'	*Microlejeunea ulicina*; *Ulota crispa s.l.*; High bryophyte and lichen richness and cover.	All plots from dead middle branches from larch stands and more heavily thinned spruce stands, mainly in the Cork cluster.
iv	'*Metzgeria temperata* community'	*Metzgeria temperata*; *Lophocolea bidentata*; *Hypnum jutlandicum*; High bryophyte cover	Inner plots from dead middle branches from trees in spruce stands on peat or at high elevations on steep slopes with shaded aspects.
vi	'*Micarea peliocarpa* community'	*Micarea peliocarpa*; *Gyalideopsis anastomosans*; Bryophytes absent	Mainly outer plots from living upper branches from spruce trees at high elevations in the Wicklow cluster.
vii	'*Fuscidea* and *Lecanora* community'	*Fuscidea lightfootii*; *Lecanora pulicaris*; High lichen richness and cover.	Inner and mid plots from living upper branches. Mainly silviculturally over-mature stands from the Wicklow cluster.
viii	'*Hypotrachyna revoluta* community '	*Hypotrachyna revoluta*; *Trapeliopsis flexuosa*; *Graphis elegans*; High lichen richness and cover	Inner and mid branch plots from all branches on larch trees in the Cork cluster.

Examination of the difference in mean species richness in the four height zones revealed a significantly greater total epiphyte richness in the trunk plots on the north than the south side of the trunk in the lower height zone (Wilcoxon signed ranks test: $p = 0.043$) and a significantly greater total epiphyte richness in the plots on the south side in the upper height zone on spruce (Wilcoxon signed ranks test: $p = 0.021$) but no significant differences in any height zone for larch (**Figure 3.68**). There were no significant differences in bryophyte or lichen richness in any height zone for either spruce or larch. There were no significant differences in total epiphyte, bryophyte or lichen diversity between the north and south sides of spruce in any height zone (**Figure 3.69**). There was, however, a significantly higher total epiphyte diversity in the plots on the south side of larch in the

(a)



(b)

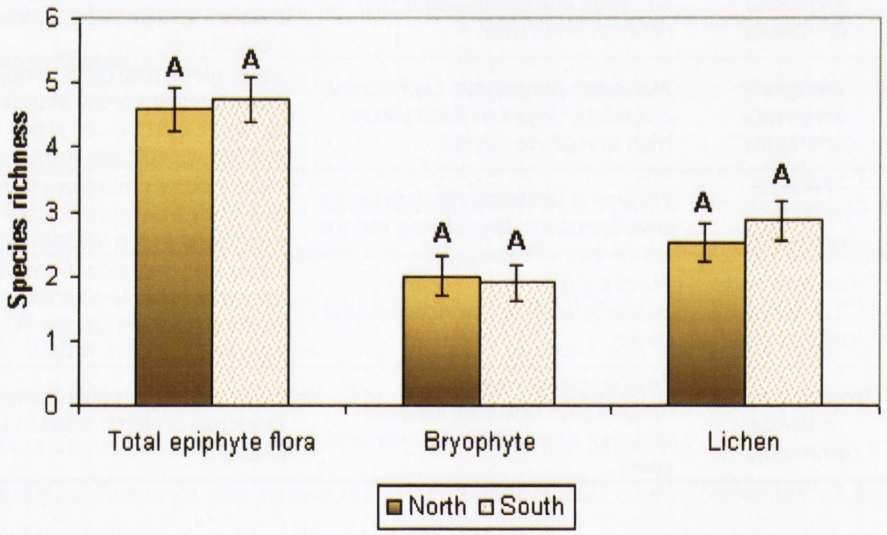
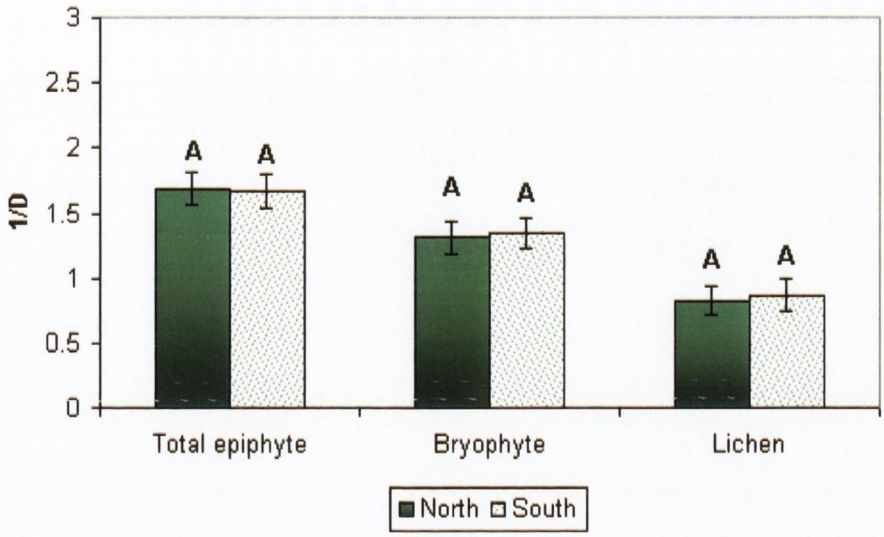


Figure 3.65 Mean total epiphyte, bryophyte and lichen species richness in the trunk plots on the north and south sides of (a) Sitka spruce (n = 68) and (b) Japanese larch (n = 44). Error bars indicate ± standard error. There is no significant difference in species richness between the two aspects if indicated by the same letter.

(a)



(b)

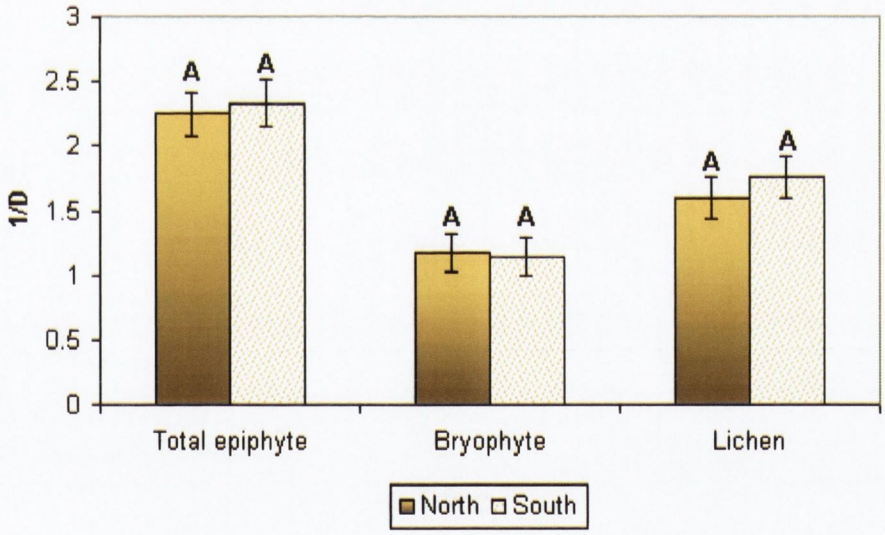
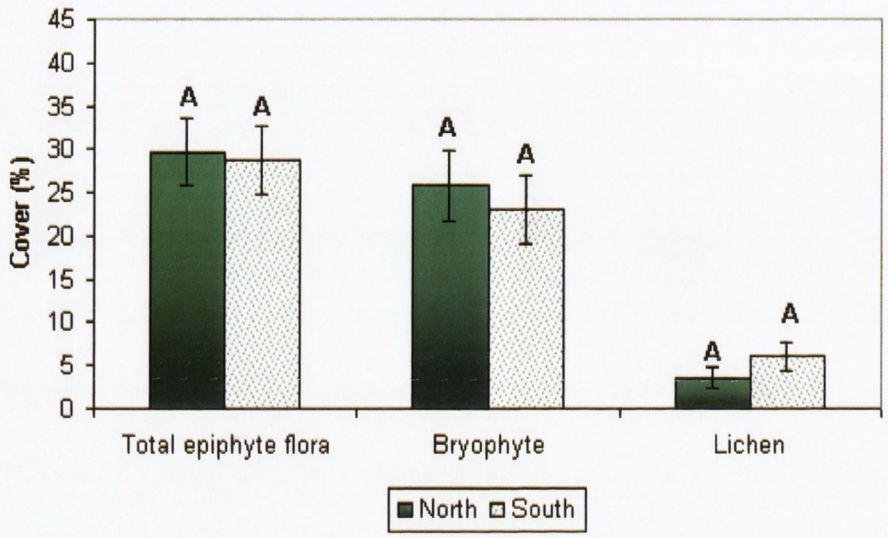


Figure 3.66 Mean total epiphyte, bryophyte and lichen diversity (1/D) in the trunk plots on the north and south sides of (a) Sitka spruce (n = 68) and (b) Japanese larch (n = 44). Error bars indicate ± standard error. There is no significant difference in diversity between the two aspects if indicated by the same letter.

(a)



(b)

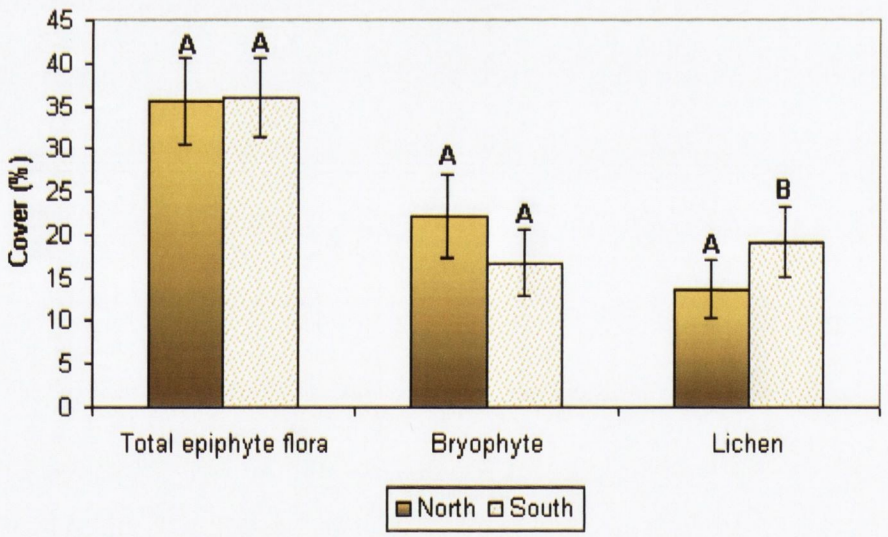


Figure 3.67 Mean total epiphyte, bryophyte and lichen cover in the trunk plots on the north and south sides of (a) Sitka spruce (n = 68) and (b) Japanese larch (n = 44). Error bars indicate ± standard error. There is no significant difference in cover between the two aspects if indicated by the same letter.

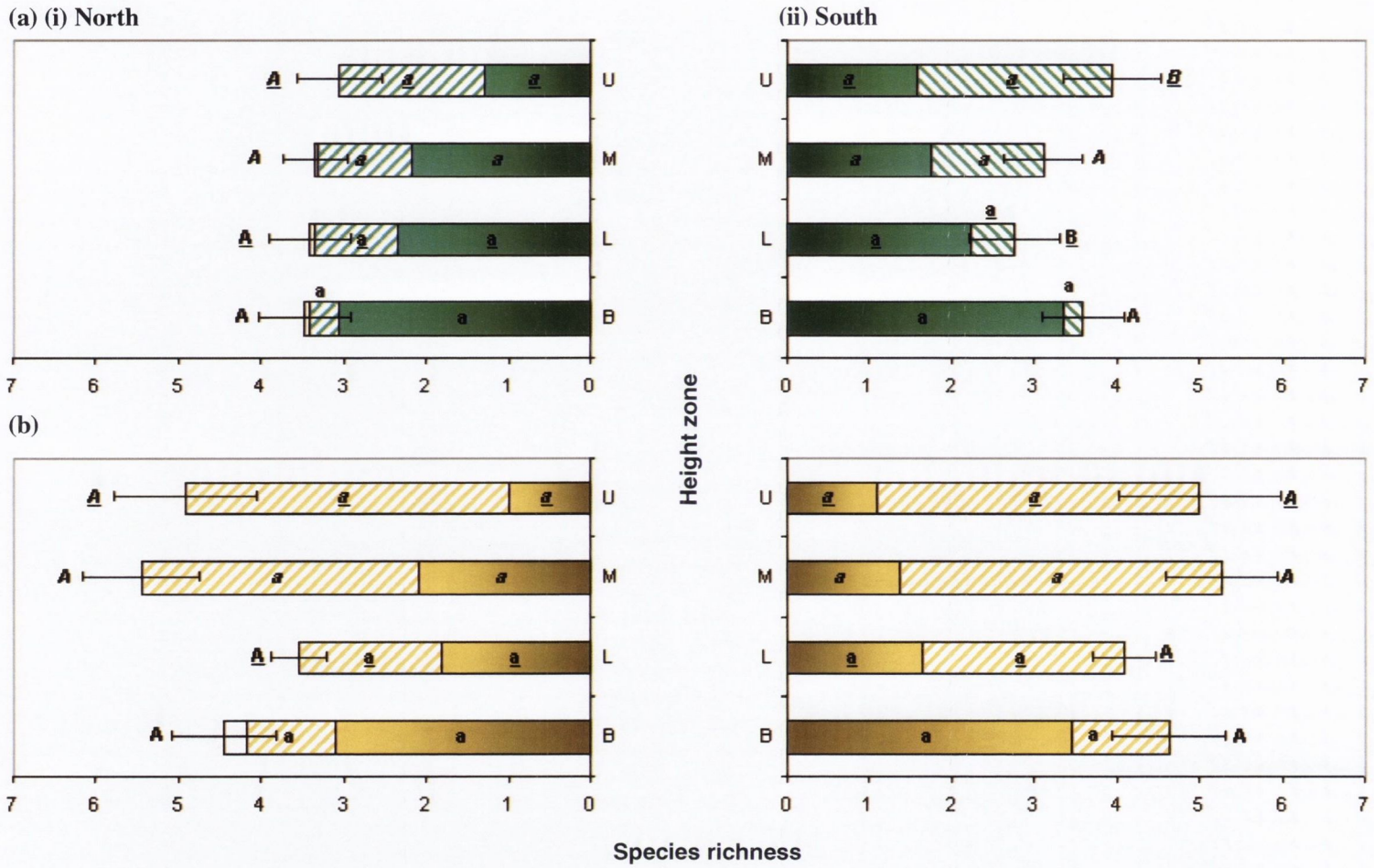


Figure 3.68 Mean epiphyte species richness on the (i) north and (ii) south sides of the trunks of (a) Sitka spruce (n = 17) and (b) Japanese larch (n = 11) in the four height zones (B = tree base, L = lower, M = middle, U = upper). The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) richness between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

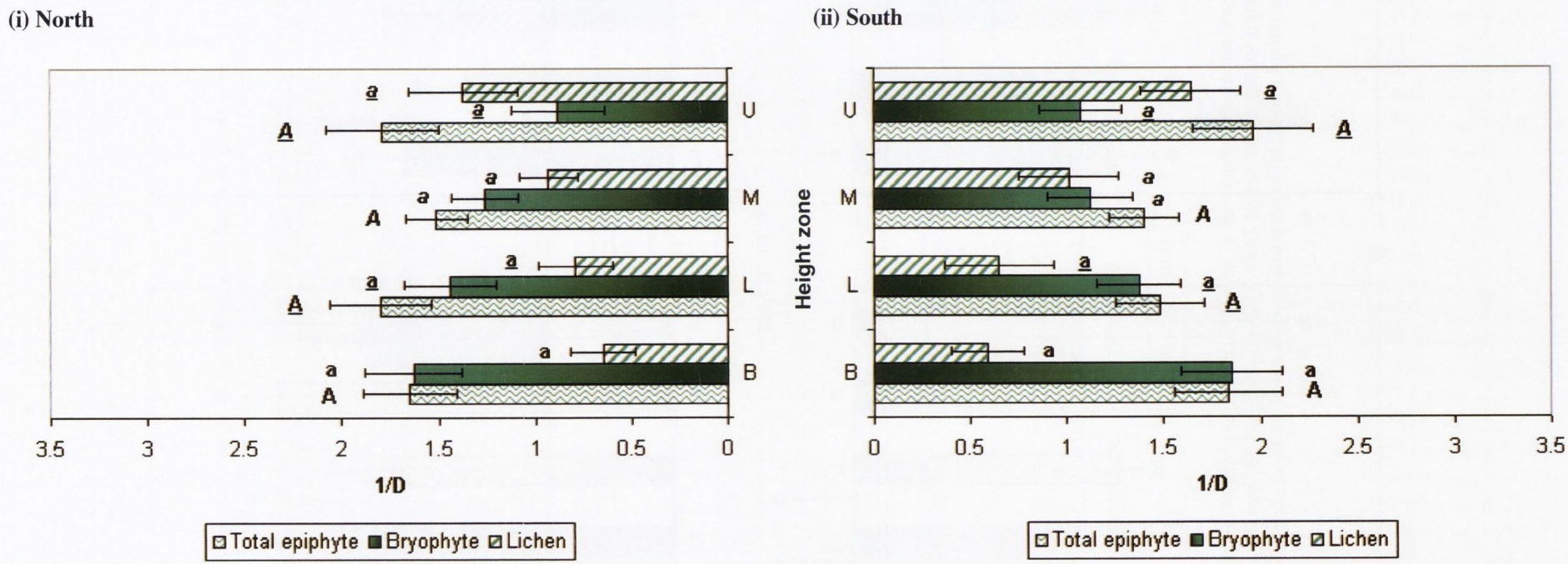


Figure 3.69 Mean epiphyte diversity (1/D) on the (i) north and (ii) south sides of the trunks of Sitka spruce in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 17). Total epiphyte, bryophyte and lichen diversity is shown. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) diversity between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

lower height zone (paired samples t-test: p = 0.046) and the difference in lichen diversity was close to significance (paired samples t-test: p = 0.057) (**Figure 3.70**). There was also significantly lower bryophyte diversity in the plots on the south side of larch in the middle height zone (Wilcoxon signed ranks test: p = 0.028). There were no significant differences in total epiphyte cover between the trunk plots on the north and south sides in any height zone on either spruce or larch (**Figure 3.71**). There was, however, significantly greater lichen cover in the plots on the south than the north sides in the upper zone on spruce (Wilcoxon signed ranks test: p = 0.009) and the greater bryophyte cover on the north side at the tree base on larch was close to significance (Wilcoxon signed ranks test: p = 0.056).

The situation on branches was different to that on trunks. Species richness was not compared as the area available for epiphyte colonisation differed among branch plots. However, diversity and cover, expressed as a percent of the cover of branches within each plot, were compared. There were no significant differences in total epiphyte, bryophyte or lichen diversity between the plots on the branches on the north and south sides of either Sitka spruce or Japanese larch (**Figure 3.72**). Total epiphyte cover was higher in the plots on the branches on the south side of the spruce trees than the north side, but not significantly so (Wilcoxon signed ranks test: p = 0.164). Lichen cover was significantly higher in the plots on the south side (Wilcoxon signed ranks test: p = 0.033) (**Figure 3.73**). There were no significant differences in cover between the branch plots on the north and south sides of the larch trees (**Figure 3.73**). When the middle and upper branches were examined separately, there were still no significant differences in diversity between the branch plots from the north and south sides of either spruce or larch (**Figure 3.74**). There was significantly higher lichen cover in the branch plots on the south side than the north side in the middle height zone on spruce (Wilcoxon signed ranks test: p = 0.023) but, as with the trunk plots, there were no significant differences between the plots on the north and south sides in either height zone on larch (**Figure 3.75**).

3.3.7 Bark physical and chemical properties

The preliminary study of the bark physical and chemical properties of the trunks of three Sitka spruce and three Japanese larch trees revealed a number of differences between the two species. Visual observation revealed that the bark of Sitka spruce was relatively smooth and thin. The bark at the base was thicker than that higher in the tree, especially in the oldest tree studied (COOM2). Resin blisters were present on the bark surface of two of the spruce trees studied (FURY2 and COOM2). At the base of all the trees studied, the bark was flaking off in circular pieces, although this was often obscured by heavy bryophyte cover (cf. **Photograph 3.2a**). The height to which this flaking was present varied and appeared to depend on the size of the tree, rather than the age, with larger trees having flaking bark higher on the trunk. MUNG2 and FURY2 were planted within a

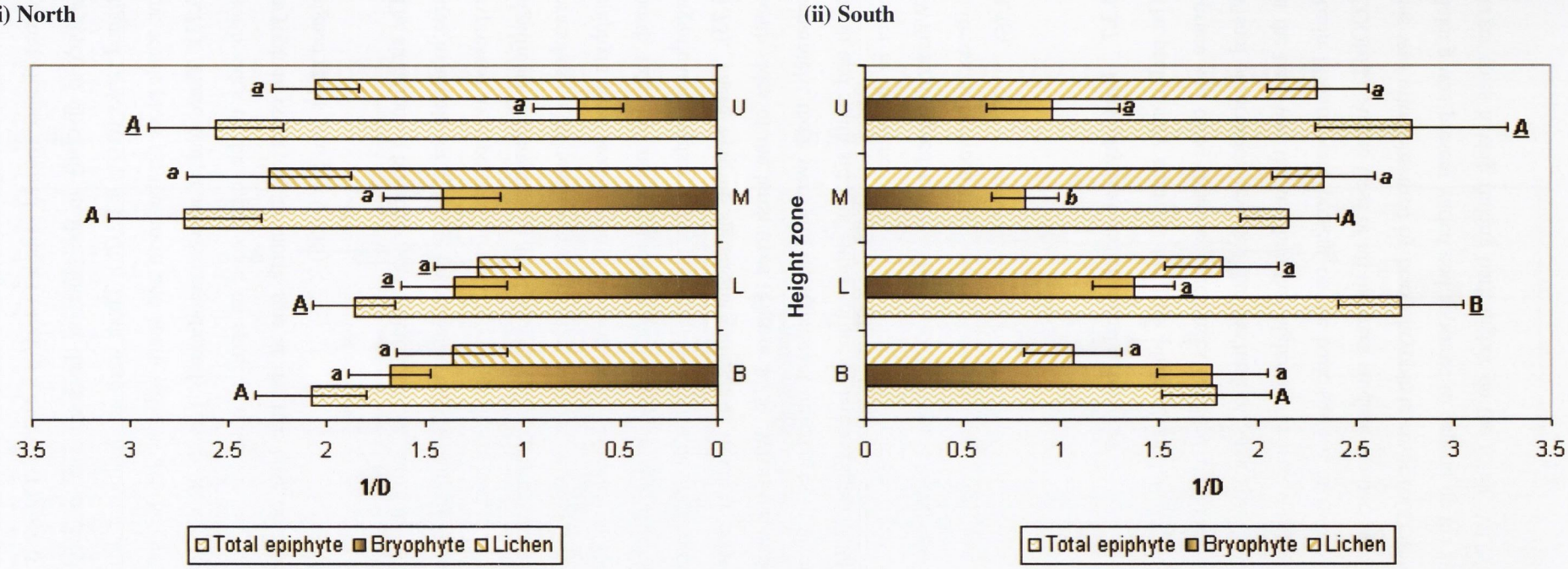


Figure 3.70 Mean epiphyte diversity (1/D) on the (i) north and (ii) south sides of the trunks of Japanese larch in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 11). Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) diversity between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

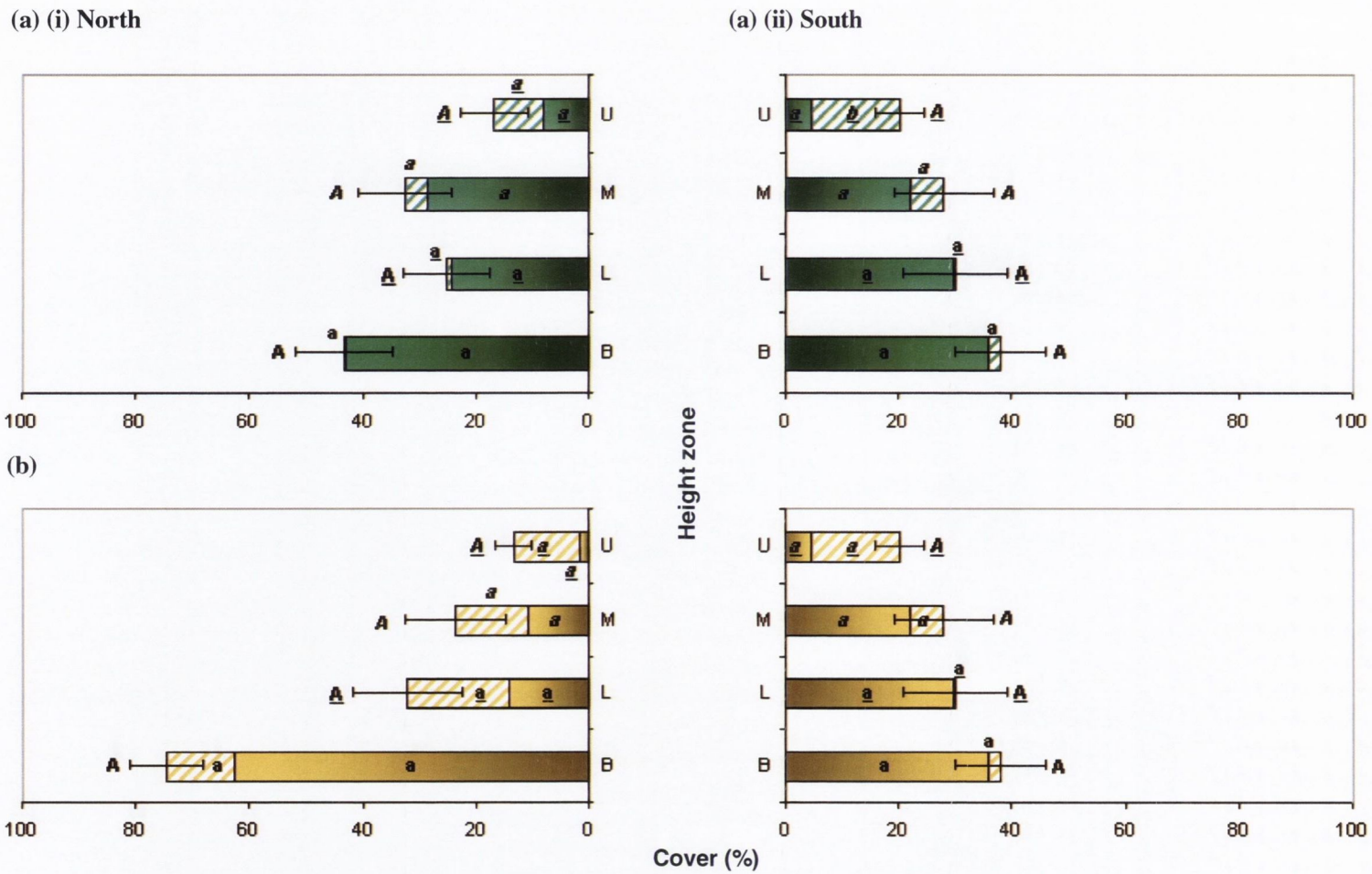
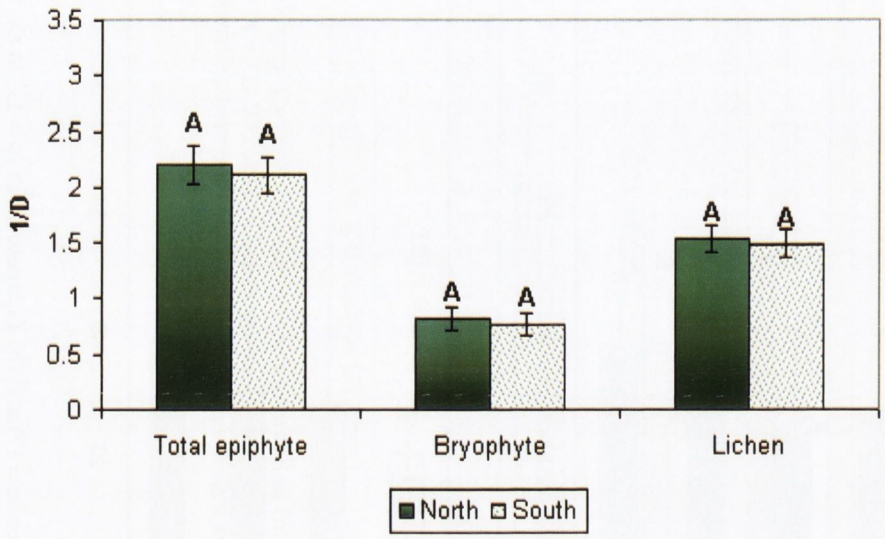


Figure 3.71 Mean epiphyte cover on the (i) north and (ii) south sides of the trunks of (a) Sitka spruce (n = 17) and (b) Japanese larch (n = 11) in the four height zones (B = tree base, L = lower, M = middle, U = upper). The total cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) cover between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

(a)



(b)

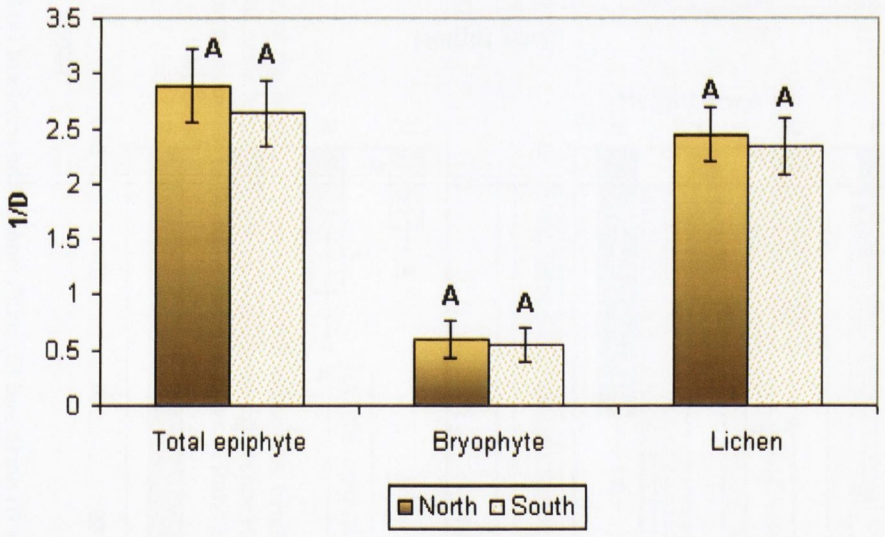
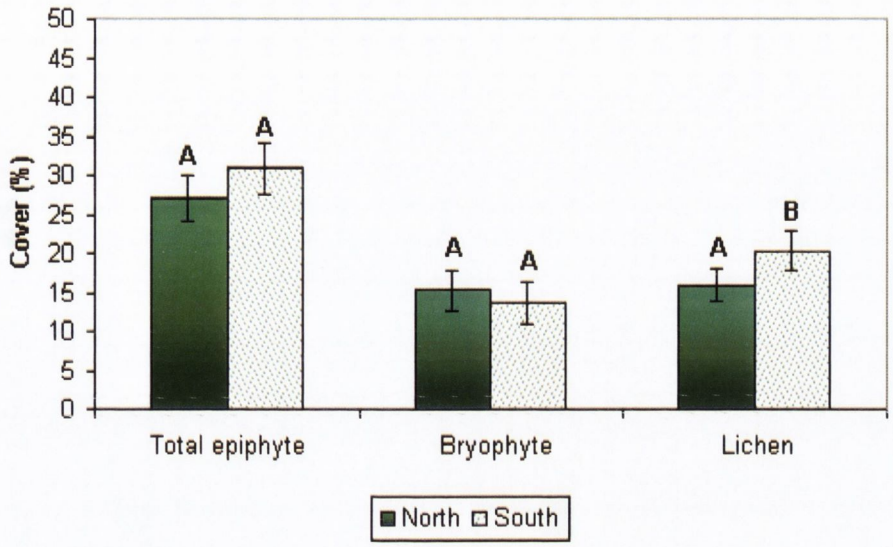


Figure 3.72 Mean total epiphyte, bryophyte and lichen diversity (1/D) in the branch plots on the north and south sides of (a) Sitka spruce (n = 96) and (b) Japanese larch (n = 46). Error bars indicate ± standard error. There is no significant difference in diversity between the two aspects if indicated by the same letter.

(a)



(b)

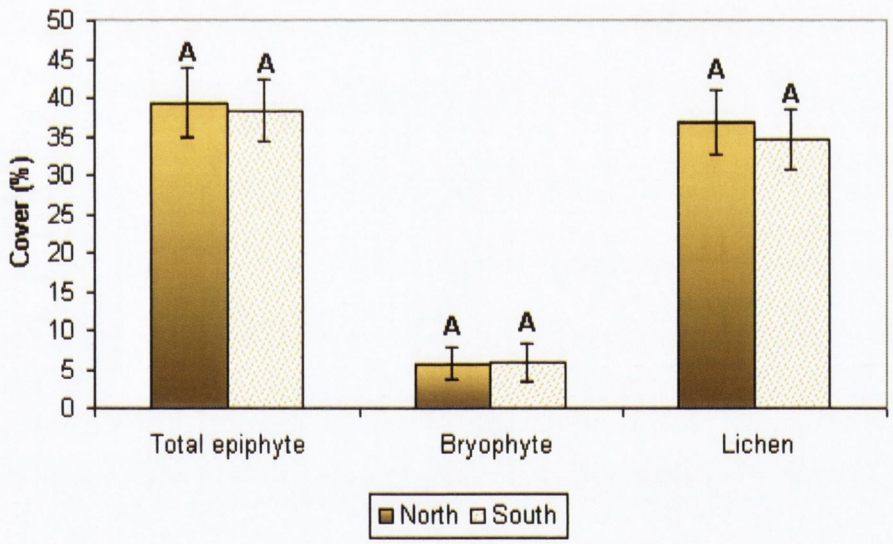


Figure 3.73 Mean total epiphyte, bryophyte and lichen cover in the branch plots on the north and south sides of (a) Sitka spruce (n = 96) and (b) Japanese larch (n = 46). Cover is expressed as a percentage of the cover of branches within each plot. Error bars indicate ± standard error. There is no significant difference in cover between the two aspects if indicated by the same letter.

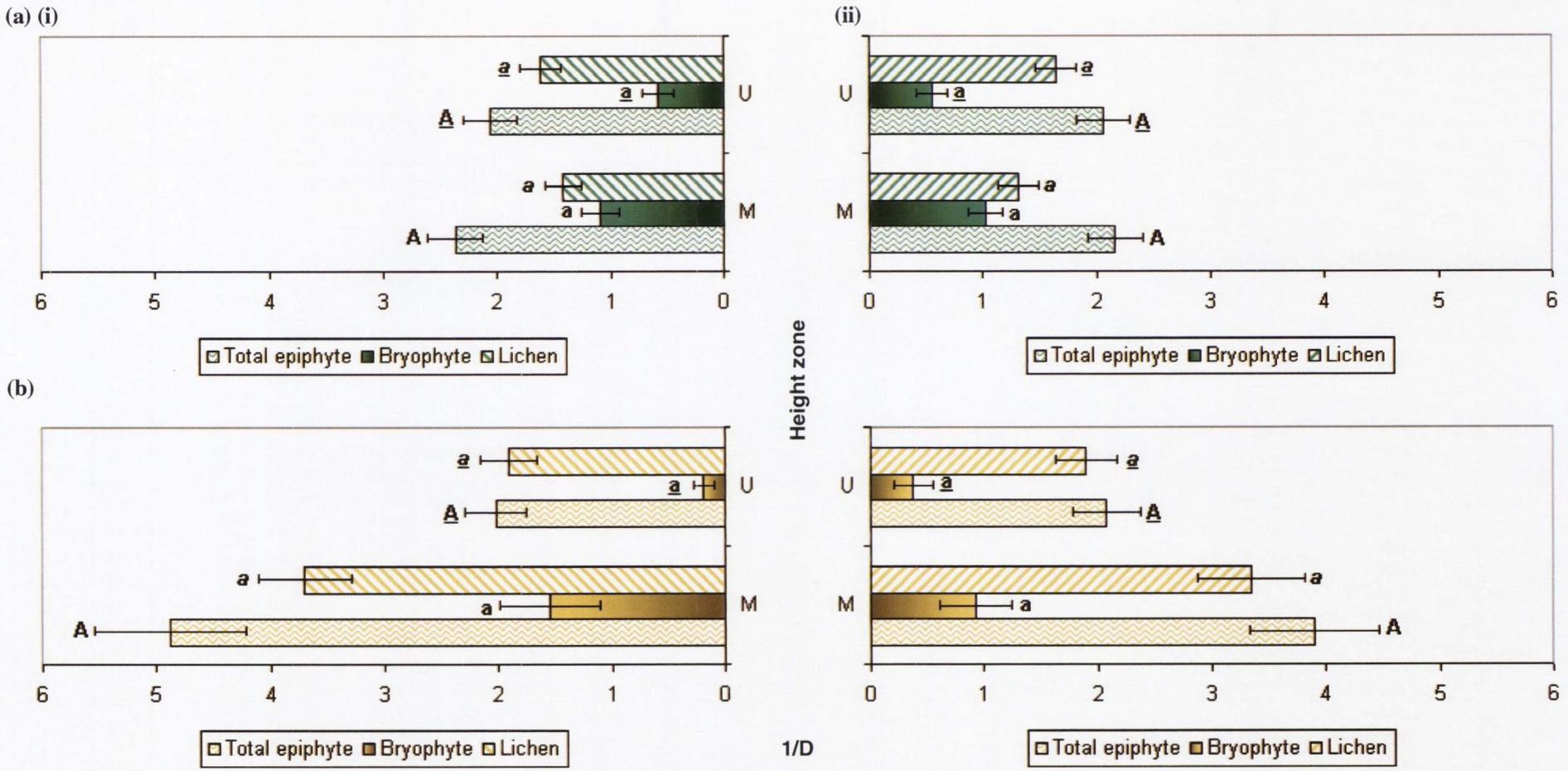


Figure 3.74 Mean epiphyte diversity in the plots on the middle (M) and upper (U) branches on the (i) north and (ii) south sides of (a) Sitka spruce (M: n = 45; U: n = 51) and (b) Japanese larch (M: n = 14; U: n = 32). Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen (lowercase italic) diversity between north and south in that height zone. Normal text compares M, and underline compares U.

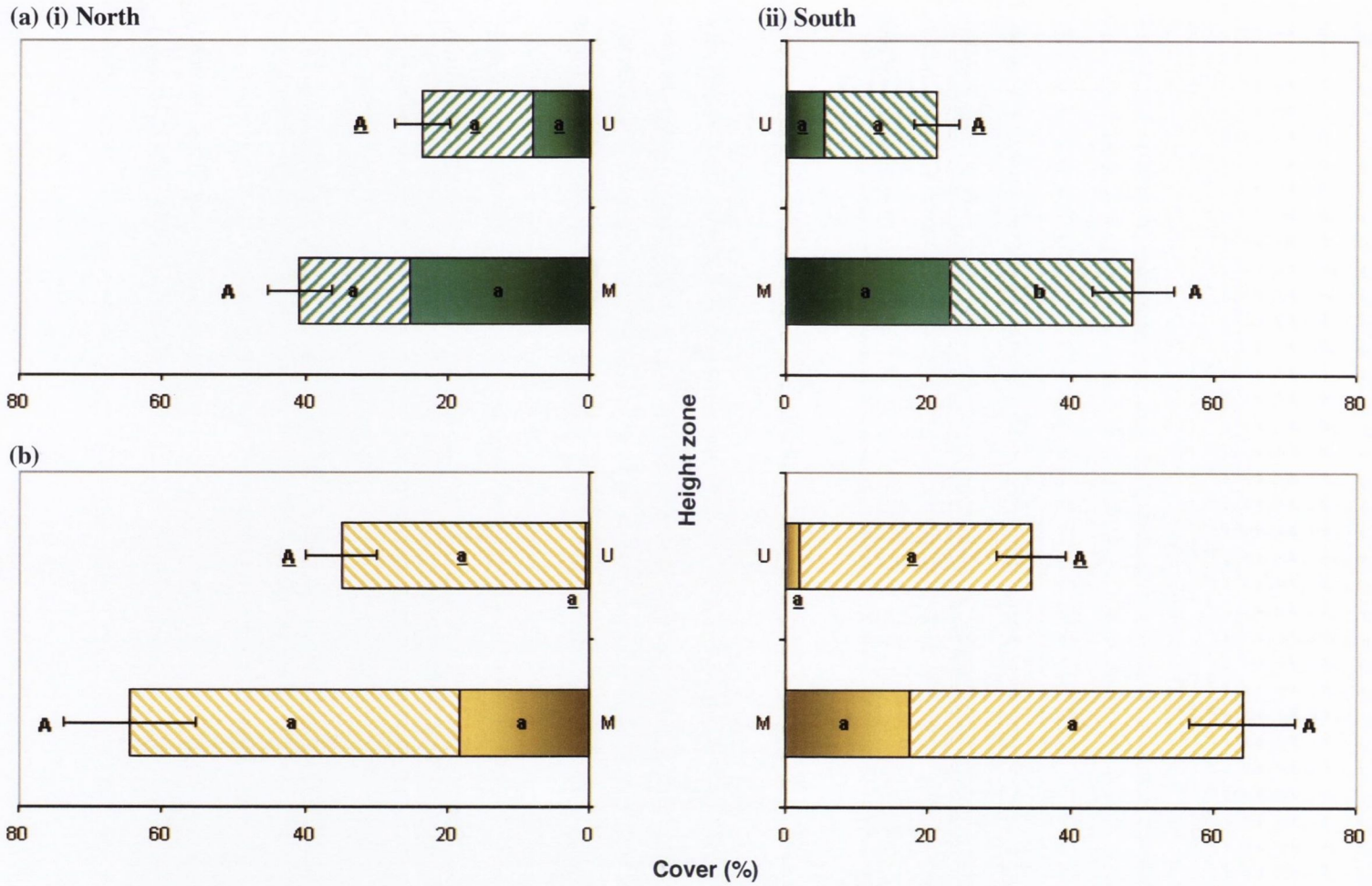


Figure 3.75 Mean epiphyte cover in the plots on the middle (M) and upper (U) branches on the (i) north and (ii) south sides of (a) Sitka spruce (M: n = 45; U: n = 51) and (b) Japanese larch (M: n = 14; U: n = 32). The total epiphyte cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) cover between north and south in that height zone. Normal text compares M, and underline compares U.

year of each other and yet MUNG2, the larger tree, had flaking bark to a proportionally greater height. None of the trees studied had large areas of flaking bark in the middle or upper plots, although the girdle scar at each annual branch whorl often had some cracking or flaking bark, especially where the branches emerged. In contrast to spruce, the bark of Japanese larch was thick and longitudinally fissured. Thin surface layers of the bark also were flaking or peeling off. The bark was thicker at the tree base but was similar in appearance throughout the height of the tree.

There were also chemical differences in the bark of the two tree species. Median bark pH was significantly higher in spruce (paired Samples t-test: $p = 0.014$) (**Figure 3.76**). The spruce tree at FURY (FURY2) had a significantly higher bark pH than the larch tree (FURY1) at the same site (paired samples t-test: $p = 0.004$) but there were no significant differences for the trees at MUNG or COOM (**Figure 3.77**). There were significant differences in pH among the different height zones on both spruce ($F_{3,23} = 3.20$, $p = 0.032$) and larch ($F_{3,23} = 5.86$, $p = 0.011$). Post-hoc testing revealed no significant differences among individual zones on spruce but on larch the lower zone had a significantly lower bark pH than the middle and upper zones (**Figure 3.78**). Regression analysis revealed a significant negative association of bark pH with both total epiphyte ($r^2 = 0.120$, $p = 0.016$) and bryophyte ($r^2 = 0.289$, $p < 0.001$) richness on the six trees studied (**Figure 3.79**).

The bark of the Japanese larch trees studied had a significantly greater water absorption capacity than the Sitka spruce trees (paired samples t-test: $p < 0.001$) (**Figure 3.80**). This was also the case for each pair of trees studied (paired samples t-test: MUNG, $p = 0.002$; FURY, $p = 0.004$; COOM, $p = 0.005$) (**Figure 3.81**). The water absorption capacity decreased from the tree base to the upper zones and there were significant differences among the zones on both tree species (spruce, $F_{3,23} = 6.53$, $p = 0.003$; larch, $F_{3,23} = 5.55$, $p = 0.006$). The tree base and lower zones had significantly greater water absorption capacity than the upper zone on both species (**Figure 3.82**). There was, however, no significant association of water absorption capacity with any of the species richness or cover variables.

3.3.8 Contribution of epiphytes to the overall flora of plantation forests

At the five stands where the ground flora was studied in addition to the epiphytic flora, the solely epiphytic flora made up an average of 40.3% (± 5.0se) of the total flora at the stands. Ground-dwelling lichens were not surveyed; however, although some ground-dwelling *Cladonia* species may have been present, they would have made little difference to the total species counts. The total area surveyed for ground flora was $100m^2$, while the aggregate area surveyed for epiphytes was a maximum of $2.5m^2$ and, since branch plots contained areas of empty space, not all this area was available for epiphyte colonisation. The stand at which epiphytes made the largest contribution to the overall flora was FURY2, a Sitka spruce stand in the Cork cluster, with solely epiphytic species

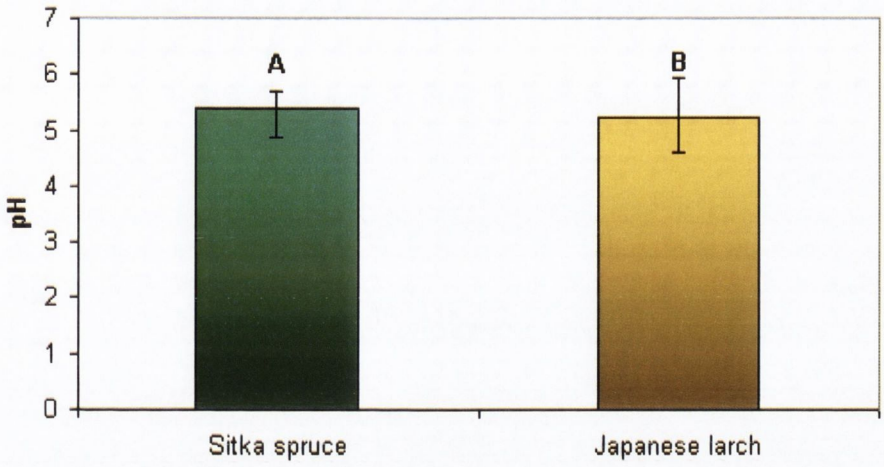


Figure 3.76 The median bark pH of the three Sitka spruce (n = 24) and three Japanese larch trees (n = 24) studied. Error bars indicate the pH range. There is no significant difference in pH between the species if indicated by the same letter.

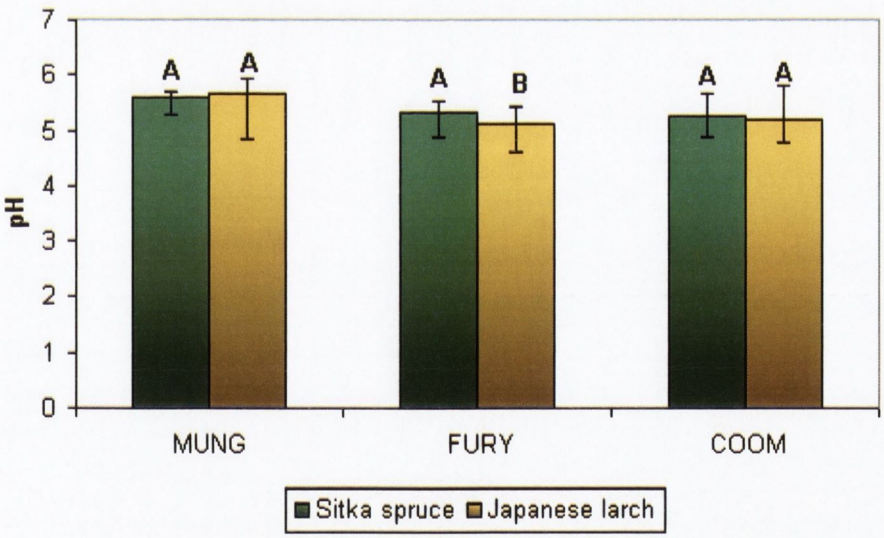
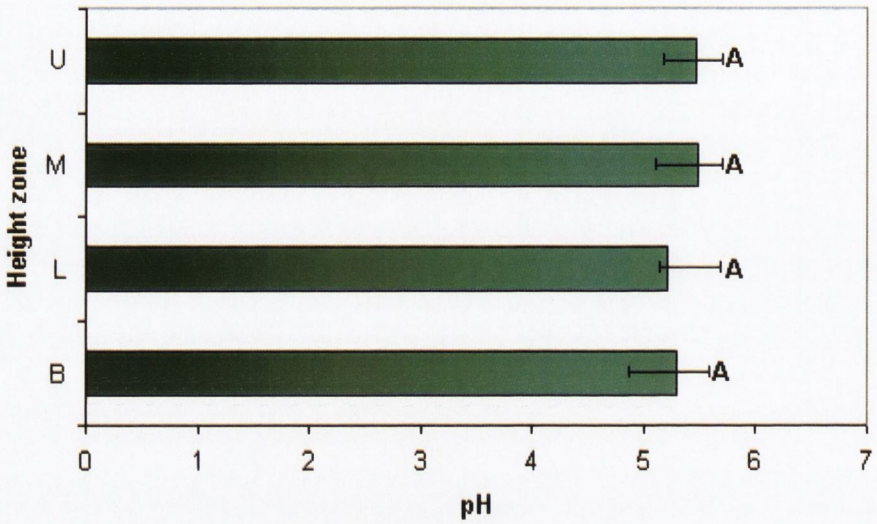


Figure 3.77 The median bark pH of the pairs of Sitka spruce (n = 8) and Japanese larch trees (n = 8) studied at each of the three sites. Error bars indicate the pH range. There is no significant difference in pH between the pairs of trees if indicated by the same letter.

(a)



(b)

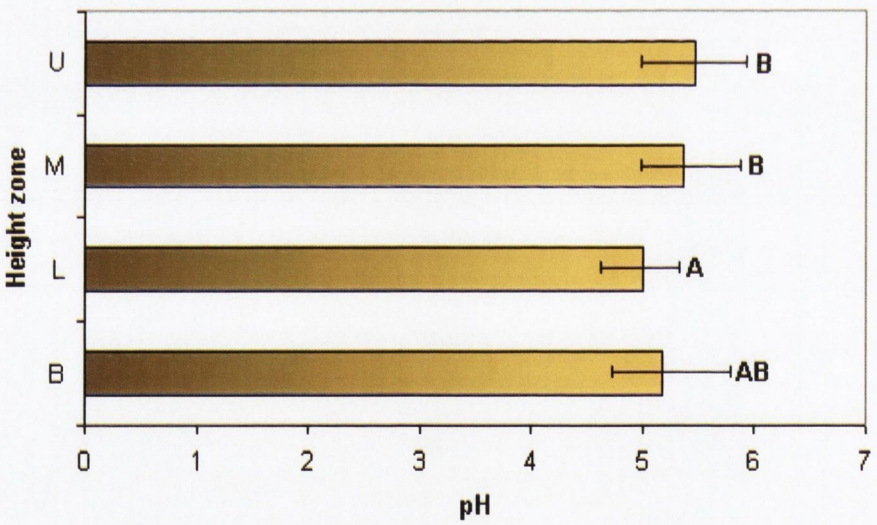
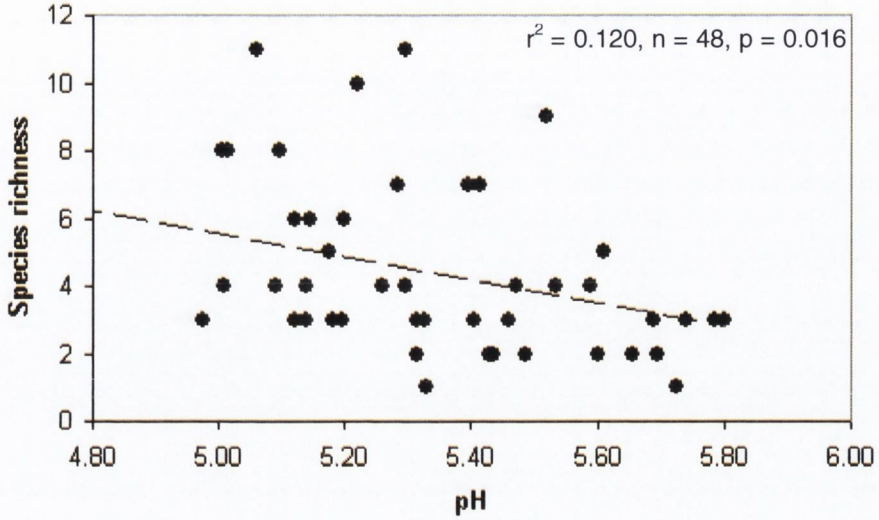


Figure 3.78 The median bark pH in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 6) on the three (a) Sitka spruce and (b) Japanese larch trees studied. Error bars indicate the pH range. There is no significant difference in pH between two height zones if indicated by the same letter.

(a)



(b)

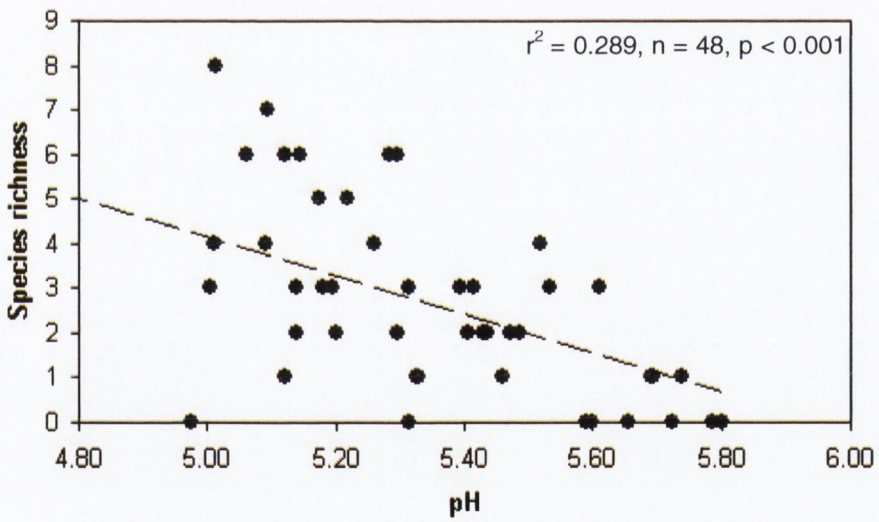


Figure 3.79 Relationship between bark pH and (a) total epiphyte and (b) bryophyte richness for the trunk plots on the three paired Sitka spruce and Japanese larch trees (n = 48).

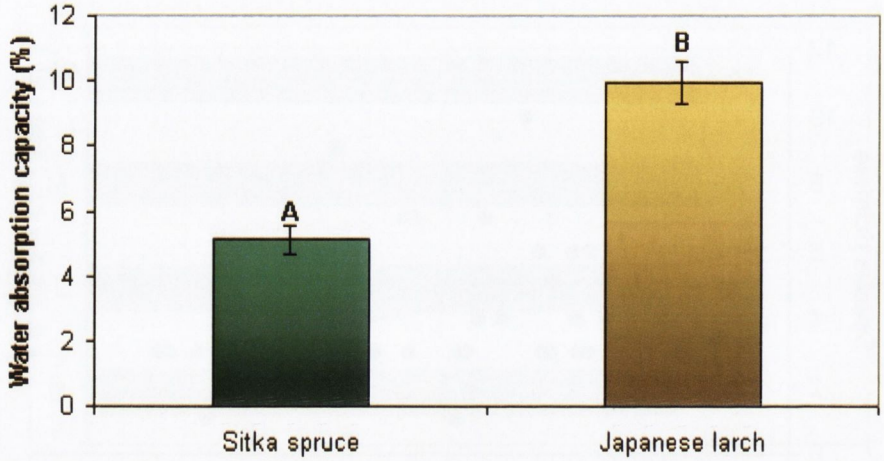


Figure 3.80 Mean water absorption capacity of the three Sitka spruce (n = 24) and three Japanese larch trees (n = 24) studied. Error bars indicate ± standard error and there is no significant difference between the two species if indicated by the same letter.

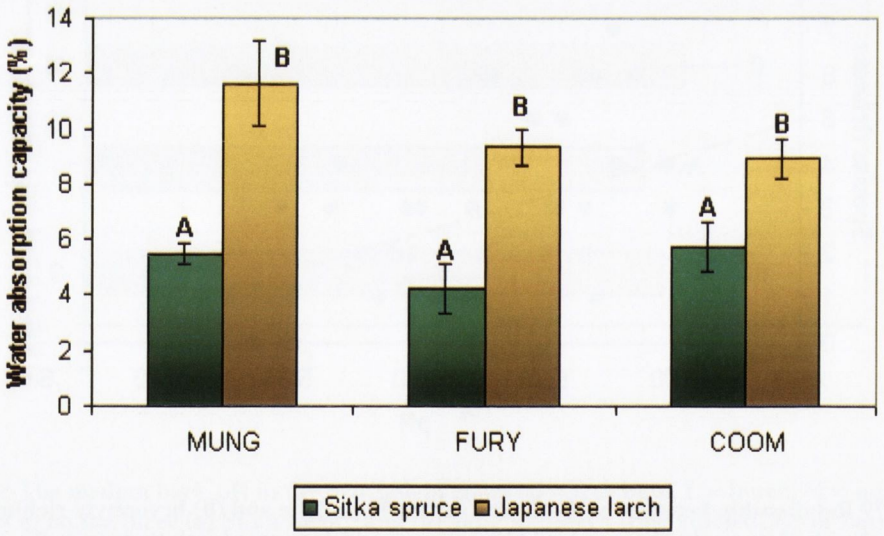
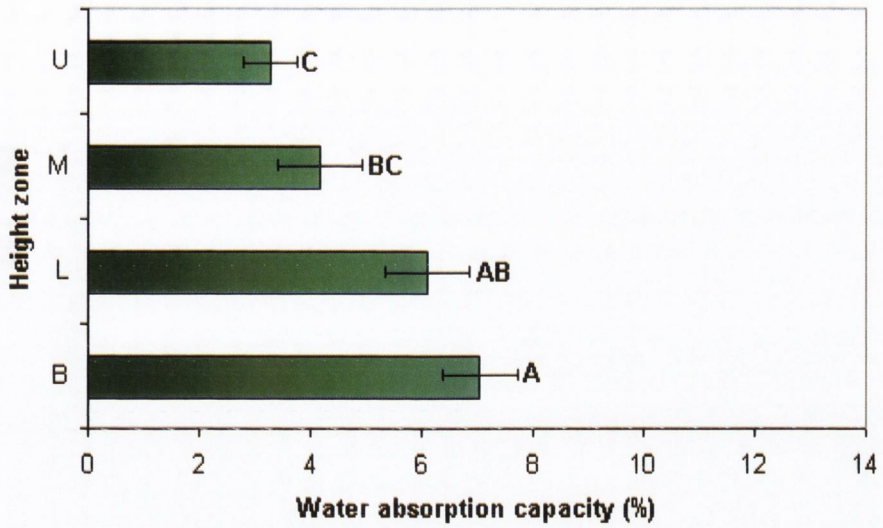


Figure 3.81 Mean water absorption capacity of the pairs of Sitka spruce (n = 8) and Japanese larch trees (n = 8) studied at each of the three sites. Error bars indicate ± standard error. There is no significant difference between the pairs of trees if indicated by the same letter.

(a)



(b)

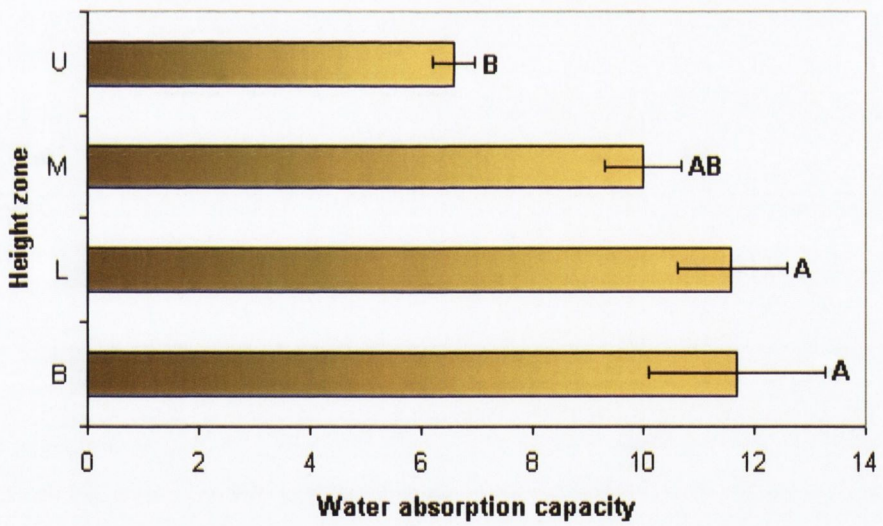


Figure 3.82 Mean water absorption capacity in the four height zones on the three (a) Sitka spruce (n = 6) and (b) Japanese larch trees (n = 6) studied. Error bars indicate ± standard error. There is no significant difference between two height zones if indicated by the same letter.

contributing 59.4% (**Figure 3.83a**). This stand had the poorest ground flora and richest epiphyte flora of all the stands studied and was the only Cork cluster stand at which ground flora and epiphyte data were collected. There was a degree of overlap in species between the ground and epiphytic floras. This was mainly as a result of a number of bryophyte species which occurred both on the ground and epiphytically. In two of the larch stands the epiphytic flora did not contribute any additional bryophyte species (**Figure 3.83b**). Overall, solely epiphytic bryophytes contributed an average of 17.3% (± 8.4se) of the bryophyte flora in these stands. Again, the stand at which epiphytes made the largest contribution to the total bryophyte flora was FURY2, with solely epiphytic bryophytes contributing 45.5% of the total bryophyte flora.

3.4 DISCUSSION

3.4.1 Epiphyte diversity

3.4.1.1 Effect of tree species

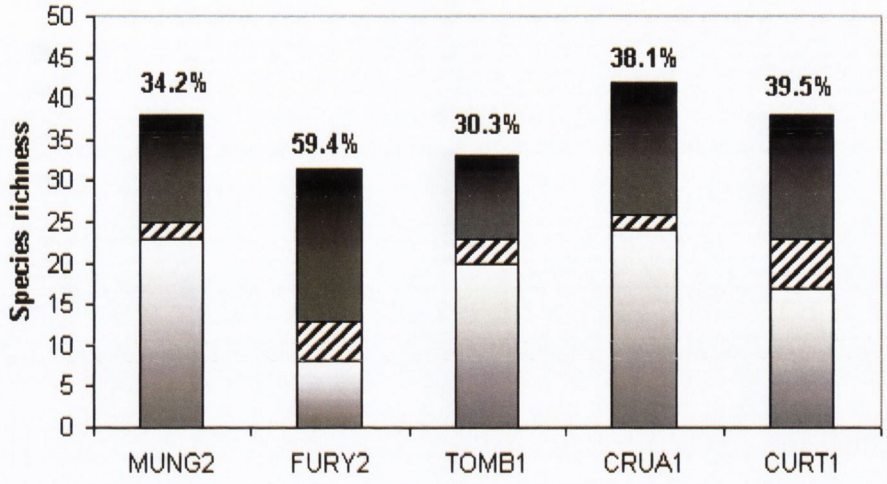
Tree diversity

The total number of species recorded was greater on Sitka spruce than on Japanese larch, mainly as a result of the greater number of bryophyte species recorded on spruce. However, more spruce trees were studied and this will have affected the total species count (Gaston & Spicer, 1998; Magurran, 1998). At the individual tree level, mean total epiphyte richness did not differ significantly between the two tree species. There was, however, a significantly higher lichen richness on larch. The most epiphyte-rich and lichen-rich flora was recorded on a spruce tree (KNOC2). A spruce stand was also the location of the most species-poor tree studied (TIKN1). The mean lichen diversity of all plots studied on each tree, according to Simpson's reciprocal, was significantly higher on larch and the most lichen-diverse flora on average was recorded on a larch tree.

Trunk diversity

There were more species recorded in total on larch trunks, despite the lower number of larch trees studied; this was mainly as a result of the greater number of lichen species recorded on larch. Significantly more total epiphyte and lichen species were recorded on average in the eight trunk plots on larch and lichen diversity and cover were significantly higher compared to spruce. Bryophyte richness, diversity and cover were higher on average on spruce, although not significantly so. Halonen *et al.* (1991) found that lichens were more abundant on the trunks of Scots pine (*Pinus sylvestris*) than of Norway spruce (*Picea abies*) in Finland. They concluded that the trunks of pine and spruce had different microclimates for lichens, with spruce trunks being more shaded and remaining moist longer than pines. Sitka spruce branches are known to retain their needles for six to eight years, although needles can be retained for up to eleven years (Norman & Jarvis, 1974), while Japanese larch is a deciduous species. This means that, as with Norway spruce and Scots pine, when comparing the trunks of Sitka spruce and Japanese larch, spruce

(a)



(b)

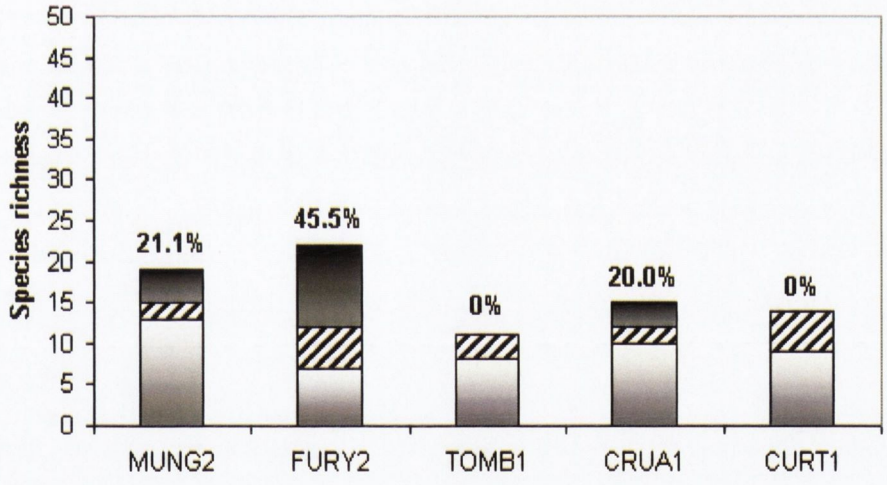


Figure 3.83 The contribution of epiphytes to the (a) total flora and (b) bryophyte flora at five stands (MUNG2 and FURY2 are Sitka spruce stands in the Wicklow and Cork clusters respectively and the remainder Japanese larch stands in the Wicklow cluster). The total flora is shown and the proportion of ground flora (light), epiphytic flora (dark) and species occurring both on the ground and epiphytically (hatched) are indicated. The percentage of the total flora contributed by solely epiphytic species is indicated above each bar.

trunks will be more moist and shaded. Most epiphytic lichens and a significant number of bryophytes are light-demanding and only a few species will dominate heavily shaded trunks (Rose, 1993). However, many bryophytes are also intolerant of desiccation (Trynoski & Glime, 1982). This means that the conditions present on larch trunks will have favoured many lichen species, while those on spruce will have favoured many bryophytes.

Whittaker's measure of beta diversity found no significant difference in beta diversity between spruce and larch trunks. However, Whittaker's measure appeared to produce ambiguous results for the epiphyte communities studied (cf. **Section 3.3.2.2**). This measure found TIKN1, a tree with a single epiphyte species on its trunk, occurring in a single trunk plot, to be the most β_w diverse tree studied. The negative relationship between beta diversity and species richness for spruce illustrates this point. Very species-poor floras, as were recorded on some spruce trees, tended to produce high β_w values.

Branch diversity

In contrast to the situation on trunks, more species were recorded in total on spruce branches; however, almost twice as many spruce branch plots were studied. More species were recorded on the branches of spruce than on the trunks, mainly as a result of more lichen species occurring on branches. Conversely, less species were recorded on larch branches than on their trunks. Esseen (1981) also recorded most lichens on dead or living branches with only a few on trunks in old spruce forests in central Sweden. Since spruce branches hold back showers and produce shade, branches will support more lichens than trunks (Halonen *et al.*, 1991). Spruce branches also have high number of strongly ramified twigs which provide a high number of attachment points, or habitat sites (Esseen, 1981). At the individual tree level, plots on larch branches had significantly higher lichen diversity and cover. This may be related to stand level differences in light levels, since lichens are generally more light-demanding (Rose, 1993).

Branch vitality appeared to have some importance in determining epiphyte diversity and abundance, with significantly higher bryophyte diversity and cover in plots on dead branches on both spruce and larch and significantly higher lichen diversity and cover in plots on dead branches on larch. However, with the majority of dead branches coming from the middle height zone, this was complicated by the effects of vertical position in the tree. There were no significant differences in diversity and cover between dead and living branches in the middle height zone, but in the upper height zone, dead branches had significantly higher total epiphyte, bryophyte and lichen diversity and cover than living ones on spruce, and higher total epiphyte and lichen diversity and cover on larch. Liu *et al.* (2000) found that the proportion of total lichen biomass on each tree that occurred on dead branches on Norway spruce and Scots pine in Finland was between 53% and 94%. Lang *et al.* (1980) observed that small young branches with abundant needles on *Abies balsamea* in New

Hampshire had fewer epiphytic species and less epiphyte cover than older portions of live branches and dead branches without needles. The relationship of branch vitality with epiphyte diversity and cover on spruce may not be as a result only of the nature of the dead substrate itself and the lack of needles, but rather the environmental conditions which led to the death of the branch, namely shade (Harris, 1990). The relatively low light levels and associated higher humidity may offer favourable conditions for epiphyte growth and survival. The fact that few species were restricted to dead branches, and those that were were not typical of dead wood (cf. **Section 3.3.2.3**), also suggests that it is the environmental conditions rather than the dead substrate that are important. All dead branches were in the early stages of decay and still retained their bark which may explain why those species found on dead branches were not typical dead wood species.

3.4.1.2 Effect of geographic location

The most epiphyte-, bryophyte- and lichen-rich floras were recorded on trees in the Cork cluster. At the individual tree level, the total epiphyte and bryophyte richness were significantly greater on the trees in the Cork cluster compared to those in the Wicklow cluster. This was also the case for both the trunk and the branches of the Cork cluster trees. Even the most species-poor Cork cluster trees almost equalled the most species-rich Wicklow cluster trees in total epiphyte richness (cf. **Figure 3.2**). A total of eight of the 15 trees from the Wicklow cluster had no bryophyte species in their branch plots. Mean bryophyte diversity, according to Simpson's reciprocal, of all plots studied on the trees was significantly higher in the Cork cluster; bryophyte diversity and cover were also significantly higher on both the trunks and branches. Bryophyte beta diversity, according to Whittaker's index, was however higher in the Wicklow cluster. This may be as a result of the tendency of this index to find very species-poor floras more beta diverse (cf. **Section 3.3.2.2**); alternatively it may suggest that the microenvironmental factors governing epiphyte composition are more uniform over the height gradient of the trees in Cork.

The overall picture produced is one of high bryophyte diversity on the trees in the Cork cluster. Diversity of lower plants is affected by climate (Hodgetts, 1996). The Cork and Wicklow clusters differ in their climate with a close to significantly higher estimated rainfall in the Cork stands (cf. **Section 2.6.1.1**). However, Humphrey *et al.* (2002) found that, in Britain, there was no difference in the bryophyte richness on deadwood between Sitka spruce plantations with >1500mm annual precipitation and those with 800-1500mm annual precipitation. The higher-precipitation stands in that study did have higher species counts of lichens on deadwood however. As well as having higher precipitation, the humidity in Cork is also higher, with fewer days with sun and more days with fog than in Wicklow (Met Éireann, 2006) (cf. **Section 2.6.1.1**). In addition, a number of Cork cluster stands were planted on peat, while the majority of the Wicklow cluster stands were planted on well-drained mineral soils. Kuusinen (1996b) suggested that, in Norway spruce (*Picea abies*) swamp-forest (or spruce mire) in Finland, the peat-layer, combined with extensive *Sphagnum*

cover, sustained a moister and more even microclimate than in adjacent mesic forests on mineral soil. A similar explanation was given by McCarthy (1980) for the apparent high atmospheric humidity in an alder-dominated marshland near Cork, the author suggesting it was the result of the evaporation of persistent ground water, and evapotranspiration from the soil, combined with the shelter of the surrounding forest. The Cork cluster stands planted on peat in the present study are also likely to have had high humidity levels. The fact that a number of the stands in the Cork cluster were unthinned and that the tree density in the Cork stands was higher than the Wicklow stands (although not significantly so) (cf. **Section 2.6.1.2**) will also have served to decrease the light levels in these stands, thereby increasing humidity. Frahm (2003) found that epiphytic lichens were characteristic of habitats with longer periods of desiccation than habitats with high bryophyte abundance. This means that bryophytes are likely to better adapted to the conditions prevailing in the Cork cluster stands.

3.4.2 Epiphyte composition

Sitka spruce and Japanese larch stands can support a reasonably diverse range of epiphyte species, including a few relatively rare species. The reporting of these rare species and the new vice-county records could be attributed, in part, to the under recording of lower plants in Ireland and particularly the under-recording of epiphytes, especially those at some height in trees. However, that is not to suggest that these rarities are necessarily commonly occurring and their discovery in young plantations planted on previously open areas is particularly noteworthy. The presence of two of the indicators of ecological continuity of woodland (cf. **Section 3.3.1.1**), in the absence of other indicator species, tells us little and is hardly surprising given that these are new plantations on previously unwooded sites.

3.4.2.1 Effects of tree species

There were slightly more species with a high affinity for epiphytism recorded on spruce; however, more spruce trees were studied. There were no significant differences between Sitka spruce and Japanese larch at the individual tree level in terms of the number of species with a high affinity for epiphytism they supported.

Many of the species recorded in this study appeared to be indifferent to host tree species. However, a number of species exhibited some degree of host specificity, being either restricted to or more common or abundant on one tree species than the other (Studlar, 1982a). While a large number of species were recorded only on one or other tree species, the fact that the majority of these species were recorded on only one individual tree means that their apparent host preference may have been a matter of chance. The majority of the more common species which occurred only on spruce were characteristic of moist, humid situations, as were the two significant indicators for spruce. Some

lichen species characteristic of well-lit situations were also only recorded on spruce, but these occurred only on the branches. Spruce trees have strong water absorbing centrifugal crowns, meaning that water is directed away from the trunks and they receive little rainwater (Barkman, 1958). Also, the preliminary investigation of the bark water absorption capacity found spruce to have a low water absorption capacity compared to larch. However, a favourable microclimate is known to make up for an unfavourable substratum, with high humidity compensating for poor water-holding capacity (Barkman, 1958). As previously stated, spruce trunks will be more moist and shaded than larch due to the year-round shade produced by the branches (Halonen *et al.*, 1991). Also, the spruce stands were denser (cf. **Section 2.6.1.2**) and the canopies probably closed, allowing little light to penetrate (Hale, 2001). The low insolation under spruce will decrease the risk of desiccation, thereby favouring species that require high humidity levels (Simmons & Buckley, 1991). A large proportion of the species restricted to spruce were only recorded in the Cork cluster. The fact that the climate in the Cork region is wetter and more humid (cf. **Table 2.6**) and the majority of Cork spruce stands have a high tree density and are planted on peat means that these spruce stands will have a particularly high atmospheric humidity.

In contrast to spruce, the more common species occurring only on larch were mainly foliose and fruticose lichen species. None of the species restricted to larch was characteristic of moist situations and a large proportion of them were recorded only in the Wicklow cluster. Larch trees are deciduous and stands of this species are more heavily thinned than spruce stands (Horgan *et al.*, 2004). Also, although it was not statistically significant, larch stands had a lower tree density than spruce stands in the present study. A more open canopy allows more throughfall, but rapid drying is allowed by the greater penetration of sunlight and freer air circulation (McCune & Antos, 1982). The result is likely to have been higher light levels and lower humidity within larch stands. Many lichens are known to be adapted to lower and more variable humidity (Pearson, 1969). However, the species with the highest indicator value for larch is characteristic of damp areas and other species requiring humid conditions are also recorded on larch. Although deciduous and more heavily thinned than spruce stands, larch stands still have low light levels compared to broadleaved deciduous stands (French, 2005). This means that they can support species requiring moist habitats, such as bryophytes, especially at the tree base. The preliminary investigation of the water holding capacity of the bark of the two tree species also showed a significantly greater water holding capacity for larch, which would facilitate colonisation by species requiring moist conditions. Bark water holding capacity has also been found to be important in determining host specificity (Barkman, 1958). However, the water absorption capacity values recorded for both tree species in the present study were quite low (cf. **Figure 3.80**) compared to even the lowest value recorded by Studlar (1982a) using the same methodology, which was for beech (*Fagus grandifolia*) at 10% weight gain per dry weight. The highest value reported in that study was for the relatively soft

rotting bark of red oak (*Quercus rubra*) at 80%. The only coniferous tree studied, hemlock (*Tsuga canadensis*), had a mean value of 21%.

Differences in bark texture may also have been important in determining host specificity. Rough-barked trees should support more species and have a greater range of microhabitats than smooth-barked trees (Studlar, 1982a). Spruce bark is smooth compared to larch bark and fruticose and foliose lichens, as well as many mosses, are known to need some bark roughness (Watson, 1936). Scaliness of bark has also been found to be important in determining epiphyte abundance (Barkman, 1958). However, the scaling bark of spruce did not appear to have a negative effect on epiphytes, as only the lower trunks of trees were scaling and these often had a dense covering of bryophytes. As the trees grow older and larger, scaliness may become a more important factor as a greater proportion of the trunk begins to scale.

A number of species restricted to larch were also characteristic of acid substrates. Larch bark has been reported to have pH values as low as 3.2 (Dobson, 2005) with eight-year-old Sitka spruce trees in Britain having pH values of 4.34 to 4.40 (Bates *et al.*, 1996). Although the median pH of larch bark in the present study was lower (more acidic) than for spruce, it had a greater range of pH values, with both the highest and lowest pH values recorded for larch. This meant there was a large degree of overlap in bark pH between the two species. Bark pH was negatively associated with total and bryophyte richness in the plots studied. This suggests that bark chemistry may be an important factor in determining epiphyte richness at the individual plot level, regardless of tree species. Bates & Brown (1981) concluded that the epiphytic floras of oak (*Quercus petraea*) and ash (*Fraxinus excelsior*) in southwest England responded to variations in bark acidity rather than to phorophyte-dependent nutritional factors. A number of the species restricted to larch trees were recorded only on the two oldest larch trees studied (CRUA1 and CURT1). Bark pH is known to decrease with age (Barkman, 1958), so the greater age of these trees may have resulted in a more acidic bark. A number of the species restricted to spruce were also quite pollution-sensitive while those restricted to or indicators of larch were pollution-tolerant. However, a number of the pollution-sensitive species were recorded only on spruce trees in the Cork cluster while a number of the pollution-tolerant species were recorded only on larch trees in the Wicklow cluster. This suggests that differences in the level of pollution between Wicklow and Cork cluster stands may have affected the epiphytic flora. Greater acidity and substantially higher annual deposition of the major ions have been recorded in the precipitation on the east coast compared to those recorded at west coast sampling stations (Bowman & McGettigan, 1994). The poor species richness of the spruce tree at TIKN may be attributable to its proximity to suburban Dublin and the resulting higher pollution levels. Other species restricted to larch and a number of its significant indicator species were quite widespread and common species. Their absence from spruce may have been as a result of light levels being too low in spruce stands.

3.4.2.2 Factors affecting overall epiphyte diversity and composition

The NMS ordination of the tree data highlighted the importance of tree species in determining the overall species composition, with some separation of Sitka spruce and Japanese larch trees. Geographic location was also shown to be important, with trees from the Cork and Wicklow clusters also being somewhat separated. However, trees from both geographic clusters were grouped together by cluster analysis in clusters A and B, and clusters A and E contained both spruce and larch trees. This indicates that there is a degree of overlap in species composition and that factors other than tree species and geographic location are important in determining that composition. The most important environmental factor determining species composition as identified by NMS was the estimated rainfall at each site (cf. **Section 3.3.3.1**). This factor was positively associated with total epiphyte richness for Sitka spruce but not Japanese larch. This suggests that factors other than high rainfall are important in producing species-rich larch stands. Lichen richness was also positively associated with rainfall for spruce stands. This agrees with the findings of Humphrey *et al.* (2002) that, in Britain, Sitka spruce stands with more than 1500mm annual precipitation had higher species counts of lichens on deadwood than those with 800-1500mm annual precipitation They attributed this to differences in moisture deficit (excess of evaporation over precipitation). While, in general, epiphytic lichens are adapted to lower and more variable humidity levels than bryophytes (Frahm, 2003; Pearson, 1969), they still require a significant level of humidity for growth. Bryophyte richness was not correlated with rainfall amount for either species. This also agrees with the findings of Humphrey *et al.* (2002) that climate zone was not the most important determinant of bryophyte richness. In that case, tree species was found to be the most important factor.

Elevation was also identified by NMS as an important factor determining epiphyte composition. In contrast to rainfall, elevation was negatively associated with species richness for spruce. However this was most likely related to the difference in elevation between Wicklow and Cork stands: the Wicklow sites had higher elevation (cf. **Section 2.6.1.1**) and lower species richness (cf. **Section 3.3.2.1**). There was a negative relationship found between lichen richness and elevation for the Cork cluster spruce stands. Other authors have found relationships between elevation and lichen biomass. Peck & McCune (1997) found that cyanolichen and green algal foliose lichen litter was higher in low-elevation (520-580m) sites in western Oregon, with alectorioid litter (pendulous lichen species in the genera *Alectoria, Bryoria* and *Usnea*) greatest in mid-elevation (1220-1340m) sites. Berryman & McCune (2000) also found cyanolichen biomass to be greatest at low elevations (470-950m) and forage lichen (pendulous fruticose lichen) biomass greater at higher elevations (950-1470m) in western Oregon. However, none of the sites in the present study was higher than 540m, and the Cork cluster spruce sites were no higher than 390m. Showman (1975) also found that site elevation was important in determining lichen distribution in Ohio and he related this to

the fact that high-elevation sites in this hilly region were more exposed to air pollution than sheltered lowland sites.

3.4.2.3 Overall epiphyte composition

Using the combined data from all plots on each individual tree, six groups of trees were identified by cluster and indicator species analysis, combined with NMS ordination, as having distinct overall epiphyte compositions. These cluster groups were used to produce descriptions of the overall composition of the epiphytes they supported. The composition of epiphytes on spruce trees belongs to four of the five composition types - 'moss-dominated', 'liverwort-dominated', '*Dimerella lutea*-dominated' and 'bryophyte-poor'. On the other hand, the composition of the epiphyte floras of larch trees belonged to only two of the composition types: 'moss-dominated' and 'lichen dominated'. This is probably partly an indication of the greater variation in planting site type and silvicultural regime for spruce than larch stands. Larch stands were mainly planted on dry to mesic sites while spruce stands were planted on sites which ranged from very poorly drained to dry. No larch stands were unthinned and the majority were heavily thinned while a number of spruce stands were unthinned (cf. **Section 2.6.1.2**). Also, no young (< 30 years) larch stands, equivalent to the spruce stands with the 'bryophyte-poor' epiphyte composition, were studied. However, differences in bark physical and chemical properties and in the canopy features of the two species are also likely to have played an important part.

The 'moss-dominated' epiphyte composition was recorded on trees from larch stands which are deciduous and, for silvicultural reasons, more heavily thinned (Horgan *et al.*, 2004), and heavily thinned spruce stands. They consequently had a relatively open canopy as indicated by their well-developed ground flora (cf. **Photograph 3.1**). This is likely to have resulted in intermediate humidity and light levels below the canopy. The high moss cover was mainly confined to the tree bases, while the crustose and foliose lichens were mainly recorded in the middle and upper trunk plots and on branches. The 'liverwort-dominated' epiphyte composition was recorded in stands which are likely to have had particularly high humidity and low light levels due to a combination of their density, planting on peat or shaded aspects. Mosses often had relatively high cover at the tree base and sometimes above this height, but liverwort cover was high, often to some height in the trees (**Photograph 3.2b**). The '*Dimerella lutea* dominated' epiphyte composition was recorded in heavily thinned spruce stands from Wicklow which had low rainfall, shaded aspects, and a relatively closed canopy, as indicated by the poor ground flora (**Photograph 3.3**). This is likely to have resulted in relatively low humidity and light levels below the canopy. This was quite a species-poor composition. The 'bryophyte-poor' epiphyte composition was recorded in young (< 30 years) dense stands which are likely to have had very low light levels below the canopy which prevented the development of a bryophyte flora (cf. **Photograph 3.4**). Crustose lichens occurred in the upper trunk plots and on branches. Overall species richness was relatively low. The 'lichen-

dominated' epiphyte composition was recorded only in two silviculturally over-mature larch stands in Wicklow. Light levels are likely to have been high and humidity levels low due to the deciduous nature of larch and the high levels of thinning (cf. **Photograph 3.5**). The lichen flora of these trees was quite distinct, as shown by the high number of significant indicators. The epiphyte composition of all the trunks plots on these trees was quite similar. The proximity of these stands to old woodland may have been an important factor in determining their distinctive epiphyte composition. French (2005) found that proximity to old woodland was important in influencing the number of woodland species that colonised the ground flora in Irish Sitka spruce stands, although a relationship was not found for larch stands. However, the richness of the floras at KNOC2 and COOM1, suggests that old woodland is not necessarily the only source of propagules, since neither of these stands were within 1km of old woodland. Hedgerows and areas of rough pasture with heather (*Calluna* spp.) or areas of gorse (*Ulex* spp.) may also act as propagule sources.

3.4.3 Vertical distribution

The overall epiphyte composition of the trees has been discussed. However, different epiphyte groups and species showed different patterns of distribution on the trees. On the trunk, the largest numbers of bryophyte species - mainly mosses - were recorded in total at the tree base on both spruce and larch. A number of bryophyte species were only recorded in the tree base and/or lower zones. Hale (1952), in his study of the cryptogamic epiphytes of broadleaved and coniferous species in southern Wisconsin, also found that tree bases were most important for bryophytes and over half the bryophytes he recorded at the base were restricted there. The tree base zone in the present study also had the highest mean bryophyte richness and cover. Trynoski & Glime (1982), studying the bryophytes of four broadleaved species in Michigan, also found species richness and cover of bryophytes to be greatest at the tree base. In the present study, bryophyte richness, diversity and cover decreased from the tree base to the upper zones on both spruce and larch. This pattern of decreasing bryophyte diversity with height was also recorded on Sitka spruce growing in its native range in California (Ellyson & Sillett, 2003). Light intensity, wind and evaporation all increase from the base to the top of a forest tree (Barkman, 1958). Bark water absorption capacity was also found to decrease from the tree base to the upper zones on both spruce and larch in the present study. This means that the bases of the trees will usually have the lowest light and highest humidity levels. The lower temperature and light compensation points of bryophytes means that, in cool humid microclimates, they will out-compete other epiphytes at the tree base (Studlar, 1982b). Larch had greater bryophyte cover at the tree base than spruce, with this difference close to significance. This may be due to the fact that the water absorption capacity of larch bark was significantly greater than that of spruce. Harris (1971) cited the thicker bark and higher water holding capacity of oak trees as the reason for their rich epiphyte flora on their lower trunk and lower horizontal branches. This factor, combined with the deciduous canopy and heavy thinning of

larch plantations, may provide the humidity levels required along with sufficient light levels to increase photosynthetic production and therefore increase bryophyte growth (Peck *et al.*, 1995).

All bryophyte growth forms, with the exception of cushions, were most abundant at the tree base and decreased in species richness and cover with height in the tree, as did the most commonly occurring bryophyte species; the moss mat *Hypnum jutlandicum*. Cushions were most abundant in the upper zone and were also common on the branches. Small cushions are often characteristic of tree crowns (Smith, 1982). The reason for this is that their cushion form assists with water retention, meaning the period of photosynthesis is extended; however, in their exposed habitat the time gained is often much reduced (Magdefrau, 1982). The mat form also assists with water retention, although in this case the less exposed habitat of these species means that the period of photosynthesis can be extended considerably (Magdefrau, 1982). Mats were by far the most abundant growth form encountered in the present study. Rough mats can be particularly drought resistant (Smith, 1982). Two of the most common liverwort mat species did not display the same pattern of distribution as mat species in general. *Metzgeria temperata* had greatest cover in the middle zone on both species and *Microlejeunea ulicina* in the upper zone on spruce and middle zone on larch. Smith (1982) has stated that appressed forms such as these are 'light-requiring'. This highlights the fact that, even within a given growth-form, species may show important differences in ecological requirements. Wefts were restricted to the tree base and lower zones, as were turfs on larch; a turf species was found in the middle height zone on spruce. The majority of species classified as having a low affinity for epiphytism were moss wefts and turfs, and the most species with a low affinity for epiphytism were recorded in the tree base zone. Wefts are considered to be 'shade-lovers' (Magdefrau, 1982) and generally occur at tree bases in warm humid areas (Smith, 1982). Turfs are typical of damp to wet habitats, such as spruce forest floors, and have particularly high values for capillary water conduction (Magdefrau, 1982).

In contrast to bryophytes, the largest number of lichen species was recorded overall in the upper zone on spruce and the middle zone on larch. A number of lichen species were recorded only in the upper zone. *Cladonia coniocraea* was unusual among lichen species in being recorded only at the tree base, as was *Cladonia macilenta* in being restricted to the tree base and lower zones. *Cladonia* species have been found to show a similar distribution pattern to bryophytes (Glime & Hong, 2002; Hale, 1955). Lichen richness and diversity were lowest on average in the tree base zone and increased to their highest value in the upper zone. Again, this increase in lichen diversity with height was seen on Sitka spruce in its native range (Ellyson & Sillett, 2003). In the present study, lichen cover also increased from the tree base to upper zone on spruce but not on larch. Lang *et al.* (1980) found a general increase in percent lichen cover with increasing height on *Abies balsamea* in New Hampshire. The upper zone will have the highest light and lowest humidity levels (Barkman, 1958). Since most epiphytic lichens are light-demanding (Rose, 1993) and are adapted

to lower and more variable humidity than bryophytes (Pearson, 1969) they are suited to the conditions present in the upper zone. The species with a high affinity for epiphytism were mostly lichens and they had their highest species richness in the upper zone.

All lichen growth forms, with the exception of leprose lichens, showed a similar pattern in the distribution of species richness to lichens in general, with greatest species richness in the upper zone. Harris (1971) found the maximum cover of *Usnea* species near the top of the tree on oak in south Devon. In the present study, while cover of these three groups was also highest in the upper zone on spruce, foliose and fruticose lichens had their greatest cover in the middle zone on larch. Lang *et al.* (1980) found that lichen cover peaked in the mid-canopy position in half the *Abies balsamea* stands they studied in New Hampshire and in the top-canopy position in the other half. Hale (1965) also found many foliose lichens to be absent from the higher parts of red maple (*Acer rubrum*) in Connecticut and lichen cover to be considerably lower at this height. The fact that more species in total were recorded in the middle height zone on larch suggests that conditions may be too extreme in the upper height zone for some lichen species (Hale, 1952). Leprose lichens had their greatest cover in the middle zone on spruce and lower zone on larch. *Lepraria* was found to be positively associated with bryophytes on the trunks of Sitka spruce growing in its native range (Ellyson & Sillett, 2003). Crustose lichens were the most abundant lichen growth-form encountered overall. These 'microlichens' are seldom included in ecological studies (Ellis & Coppins, 2006) despite the fact that they constitute the majority of Irish lichen species (Coppins, 2002). Because of their form, water loss is restricted to the upper surface and their closeness to the bark surface means they profit from surface water flow (Budel & Scheidegger, 1996). This means they can tolerate more exposed habitats. They have also been found to be negatively correlated with bryophytes, which can overgrow them (Ellis & Coppins, 2006). Fruticose lichens are at the other extreme in growth-form with a very high surface to volume ratio which means they have more rapid wetting and drying patterns (Budel & Scheidegger, 1996). This means they require wet, humid climates, or dry climates with regular dew or fog events. Although fruticose lichens were quite commonly encountered in the present study, they were often poorly developed and many were not identifiable to species level. The same was the also the case for many foliose lichens.

3.4.3.1 Factors affecting the epiphyte composition of the trunk plots

Plot height, tree girth at the centre of the plot and plot inclination were all identified by NMS ordination to be important to epiphyte diversity. However, although these variables were not found to be associated with total epiphyte richness, they were associated with bryophyte and lichen richness. Bryophyte richness was positively associated and lichen richness negatively associated with plot height. Both were also associated with girth and inclination, although only weakly so. Since tree girth decreases with height in the tree, associations with girth may actually be as a result of associations with plot height rather than with the size of the tree. Also, as trees with straight

trunks were chosen for study, inclination was close to zero in the majority of the plots, the main exceptions being the tree base plots, as the bases of the trunks were buttressed to a greater or lesser extent. This means that associations with inclination may also actually be as a result of associations with plot height. Although clear differences in the distribution of different epiphyte groups, growth forms and species in the different height zones were identified, distance from the ground is only a crude index of the plot environment (Parker & Brown, 2000). Taking the average values for each height zone will also have eliminated a large degree of the variability present among trees (Parker & Brown, 2000). The fact that plots from the four height zones were not clearly separated in the NMS ordination confirms that factors other than position on the tree are important in determining epiphyte composition.

3.4.4 Epiphyte plot composition

Cluster and indicator species analysis were used to identify groups of trunk and branch plots with distinct epiphyte floristic compositions. Eight groups of trunk plots and six groups of branch plots with distinct epiphyte communities were identified. The trunk plots with the '*Hypnum jutlandicum* community' were mainly tree base and lower plots from trees in larch stands and heavily thinned spruce stands, in which the light levels are likely to have been moderately high. At this level in the tree, humidity levels will be at their highest (Barkman, 1958) and, combined with the moderately high light levels, this is likely to have produced optimum conditions for moss growth (Peck *et al.*, 1995). A *Hypnum* dominated community, named the '*Hypnum cupressiforme* var. *filiforme* union' (a taxon now equated with *H. andoi* (Smith, 2004)) was also described by Phillips (1959) growing at breast height (1.37m) on beech (*Fagus sylvatica*), holly (*Ilex aquifolium*), European larch (*Larix decidua*), Scots pine (*Pinus sylvestris*), oak (*Quercus petraea*) and yew (*Taxus baccata*) in southern Ireland. *Hypnum andoi* was recorded in the present study, but not to the same extent as *Hypnum jutlandicum*, which was the most frequently encountered species overall (cf. **Table 3.26, Table 3.31**). Both Richards (1938) and Kirby & O'Connell (1982) found that *H. jutlandicum* was abundant on *Vaccinium myrtillus* but absent from trees in semi-natural woodlands in Killarney and Galway respectively. *H. jutlandicum* is reported to be a common species at tree bases in acid woods (Porley & Hodgetts, 2005). A pendulous form of this species was encountered on lodgepole pine (*Pinus* contorta) in a plantation in the west of Ireland (Doyle, 1987). The *Hypnum*-dominated 'union' described by Philips (1959) also contained *Isothecium myosuroides*, which was also a significant indicator for the '*Hypnum jutlandicum* community' in the present study.

The '*Kindbergia praelonga* community' was also mainly found in tree base and lower trunk plots but in wetter, denser sites. This meant that humidity levels are likely to have been high and light levels relatively low; as a result it appears that no one bryophyte species achieved dominance and a greater range of bryophyte species were found. Richards (1938) found *Kindbergia praelonga* to be

abundant at the bases of trees in shaded and humid oak woodland in Killarney. Kirby & O'Connell (1982) also found this species to be one of the dominant species on tree bases in a semi-natural oak woodland with hazel scrub in Galway. However, *Kindbergia* was not encountered by Phillips (1959) at breast height on a range of tree species in southern Ireland, including European larch and Scots pine. Another community dominated by bryophytes was the '*Metzgeria temperata* community'. However, unlike the previous two bryophyte-dominated communities, which were mainly restricted to the tree base and lower trunk plots, this community was found in plots from all height zones and in the inner plots of middle branches. The trees on which these plots occurred were growing in dense stands on peat or at high elevations with shaded aspects. This means that humidity levels are likely to have been particularly high. Barkman (1958) has noted that some 'zones' will reach higher above ground level in wet forests than in dry forests. This is probably due to the fact that the uppermost limit of trunk species is commonly determined by humidity (Cornelissen & ter Steege, 1989). The high humidity in these stands means that species normally restricted to the bases of the trees can occur at some height on the trunk. This phenomenon was also seen on Sitka spruce growing in its native range, where it is found in moist low-elevation forests. Bryophyte species were recorded higher on the trunks of these trees than is typical for those same bryophytes on trees elsewhere in the Pacific Northwest (Glime & Hong, 2002; Peck *et al.*, 1995). The indicator species for this group was *Metzgeria temperata*, which was first described by Kuwaha in 1976. Until recently all specimens of *Metzgeria temperata* were referred to *M. fruticulosa*. *M. fruticulosa* was recorded by Kirby & O'Connell (1982) in an oakwood with hazel scrub in Galway, but does not appear to have reached the dominance seen in the present study. It is possible that this is as a result of the high humidity levels in the stands in the present study where this community was found, particularly those planted on peat (cf. Kuusinen, 1996b; McCarthy, 1980).

Another bryophyte-dominated community found at some height in trees was the '*Microlejeunea ulicina* community'. It was found in lower, middle and upper trunk plots from larch trees or over-mature spruce trees from wet sites in Cork. Humidity levels are likely to have been relatively high in these stands, owing to their geographic location, but light levels are also likely to have been reasonably high. The resulting conditions appeared to be suitable for a number of bryophyte and lichen species. The tree base plots, and in some cases also the lower plots, on these trees had a '*Hypnum jutlandicum* community'. The vigorous moss species may have out-competed *Microlejeunea* and other less vigorous species lower in the tree. *Microlejeunea ulicina* was recorded on the lower trunks of trees in a Galway oakwood with hazel scrub by Kirby & O'Connell (1982). The community in the present study resembles the phytosociological lichen association *Graphidetum scriptae* which is found on moderately shaded smooth bark (James *et al.*, 1977). The species in that association are reported to require more strongly oceanic conditions (Coppins & Coppins, 2006), possibly explaining the restriction of the '*Microlejeunea ulicina* community' to

sites in the Cork cluster. The macrolichen species, such as *Hypotrachyna revoluta*, which occurred in the community in the present study would be viewed as 'pioneers' of subsequent successional stages, in this case most likely the *Parmelietum revolutae* which has been reported on *Larix* in Ireland (James *et al.*, 1977) (*Parmelia revoluta* is a synonym for *Hypotrachyna revoluta*). The '*Microlejeunea ulicina* community' also bears some resemblance to the bryophyte association *Scoparieto–Hypnetum filiformis* subassociation *microlejeueneetosum* described by Barkman (1958). In the Netherlands this association is found only in beech woods on loess and Barkman suggests that the more humid conditions created by the loess soils make up for the drier macroclimate in the stands. Another community in which *Microlejeunea ulicina* was an important component was the '*Microlejeunea* and *Ulota* community' (cf. **Table 3.35**). It was found in branch plots from larch stands and more heavily thinned spruce stands, mainly in the Cork cluster. Its composition also resembles the *Graphidetum scriptae* lichen association. The absence of *Ulota* as a significant indicator for the trunk plots may be due to the fact that the species only occurs on trunks where not too deeply shaded (Hill *et al.*, 1994).

Some tree base, lower and middle trunk plots were found to have a 'species-poor community'. Some of these plots came from trees in dense, unthinned spruce stands, in which light levels were likely to have been extremely low (cf. **Photograph 3.4**). This meant that even bryophyte species adapted to low light levels could not survive. Nearby plots from these trees contained no epiphyte species. The 'species-poor community' also occurred in lower plots from trees in Wicklow larch stands whose tree-base plots had a '*Hypnum jutlandicum* community'. The humidity levels in these stands are likely to have been particularly low, even at this height in the trees, because of the drier climate in Wicklow and the deciduous nature and heavier thinning of larch stands (**Photograph 3.1**). This meant that humidity levels were likely to be sufficient for vigorous bryophyte growth only at the tree base.

Plots with lichen-dominated floras were also found on the trees. The '*Dimerella*-dominated community' was found in middle and upper trunk plots, plots from middle branches and inner plots from upper branches from heavily thinned spruce stands, mainly in the Wicklow cluster (**Photograph 3.3**). Although light levels will be higher in these plots than at the tree base, the spruce canopy meant that plots were probably sufficiently shaded to support the shade-requiring *Dimerella* species. The closest phytosociological community to this would be the species-poor 'pre-Lobarion pioneer community' (James *et al.*, 1977). These communities usually lack many, or even all, of the macrolichens considered to be characteristic of the *Lobarion* community (James *et al.*, 1977). However, in the present study, almost all of the crustose lichen species were also absent so that it hardly resembled even the species-poor 'pre-*Lobarion* pioneer community'. Another community containing crustose lichens was the '*Fuscidea* and *Lecanora* community'. This was mainly found in upper trunk plots from Wicklow cluster larch stands (**Photograph 3.1**) and inner

and mid plots from the upper branches of silviculturally over-mature stands, also mainly in Wicklow. These plots are likely to have received higher levels of insolation than many of the plots studied due to both their geographic location and position on the trees. The form of the crustose lichens means that water loss is reduced, allowing them to survive in these lower humidity conditions (Budel & Scheidegger, 1996). This community resembles the *Lecanoretum subfuscae* association as it occurs in more shaded situations (James *et al.*, 1977), suggesting that, while light levels may have been higher in the plots with this community than in many of the plots studied, the plots were still relatively shaded. This association is considered to be a 'pioneer' community of well-lit twigs and young trees (James *et al.*, 1977) and occurs on the exposed twigs and thin branches of pine in Scottish native pinewoods (Coppins & Coppins, 2006). The '*Micarea peliocarpa* community' also had two crustose lichen species as significant indicators. This community was mainly found in outer plots from upper branches in high-elevation Wicklow cluster spruce stands. These plots are likely to receive the highest levels of insolation of all plots and also contain the youngest branches. A large proportion of outer plots from upper branches contained no epiphyte species (cf. **Table 3.32**). This cluster was the most species-poor of all clusters and bryophytes were absent from the plots. This may be due to a combination of the extreme microclimatic conditions and the shorter time available for epiphyte colonisation. *Micarea peliocarpa* was frequently encountered by McCarthy *et al.* (1986) on *Calluna vulgaris* growing in raised and blanket bogs in Ireland, where it was one of the first species to colonise the woody twigs.

A community containing foliose lichens was the '*Hypotrachyna revoluta* community' which was found in the inner and mid branch plots of Cork cluster larch trees. This community resembles the previously mentioned *Parmelietum revolutae* association, although the presence of *Graphis scripta* as a significant indicator means it might be considered intermediate between the *Graphidetum scriptae* and the *Parmelietum revolutae* (James *et al.*, 1977). *Hypotrachyna revoluta* also occurred in the '*Microlejeunea ulicina* community' in the trunk plots, but not to the same extent. Light levels will be higher on the branches than on the trunks but, due to the geographic location of the stands, humidity levels are also likely to be high. This will have favoured this foliose species as its greater surface area makes it more susceptible to water loss (Budel & Scheidegger, 1996). Some tree base, lower and middle trunk plots were also found to have a 'foliose and leprose lichen-dominated community'. These plots came from two trees from heavily thinned, silviculturally over-mature larch stands in Wicklow (**Photograph 3.5**). The light levels in these stands were likely to have been particularly high and humidity levels low. This meant that moss species did not reach high cover, even at the tree base, and liverwort species were absent. However, lichen species were able to flourish from the tree base to at least the middle height zone on the trees. Barkman (1958) has described a similar descent of 'zones' on trees at the edge of forest glades. The higher light levels allow lichen species to colonise lower levels on the trunk than they could have in stands with lower

below-canopy light levels. The community resembles the *Pseudevernietum furfuraceae* association, which is characteristic of trees with moderately acidic barks in well-lit situations and under pollution stress (James *et al.*, 1977). This association is found on pine in Scottish native pinewoods (Coppins & Coppins, 2006).

3.4.5 Distribution on branches

On both tree species there was significantly higher bryophyte diversity and cover in the plots on the middle branches compared with the upper branches. On spruce there was also significantly higher total epiphyte cover, and on larch significantly higher total epiphyte and lichen diversity, in the plots on the middle branches. Lyons *et al.* (2000) found that the lower crown branches of western hemlock (*Tsuga heterophylla*) in Washington state had consistently higher epiphyte cover than those in the middle and upper crown regions. They suggested that branch size was an important factor in this difference, since larger branches have an increased ability to intercept propagules, nutrients and moisture. In the present study, the difference in the age of the middle and upper branches may also have been an important factor, since a certain time lapse is required for the invasion and establishment of the epiphytic flora (Hale, 1952). Kershaw (1964) noted that the branches of birch (*Betula*), oak (*Quercus*), sycamore (*Acer*) and pine (*Pinus*) in Wales were bare of epiphytes until they reached 12-15 years of age. The same factors which seemed to affect the distribution of epiphytes on the trunk, namely lower humidity and higher light levels higher in the tree, are also likely to have affected the distribution of epiphytes on the branches in the same way. However, branch vitality may also have been important. As previously discussed, dead branches were found to have greater epiphyte diversity and cover than living branches (cf. **Section 3.4.1.1**). In the present study the majority of middle branches were dead, while the majority of upper branches were living. Liu (2000) also found that, in central Finland, the branches of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) in the lower canopy tended to be dead, while those in the upper part were living and actively growing. The difference in branch vitality between middle and upper branches may explain the greater diversity and cover on middle branches, although the effects of vitality and vertical position on the tree are difficult to separate.

On the middle branches, almost all the inner, mid and outer branch plots contained epiphytes, while on the upper branches, a large proportion of outer branch plots did not contain any epiphytes. Lyons *et al.* (2000) also found a lower proportion of outer branch plots to contain epiphytes than the inner or middle plots on western hemlock (*Tsuga heterophylla*) in Washington state. They also found that inner plots had the greatest epiphyte cover and outer plots the least. In the present study this was the case on the upper branches only. Bryophyte cover was greatest in the inner plots on both the middle and upper branches on both tree species and decreased to the middle and outer plots on all but the middle larch branches; on the upper larch branches this decrease was significant

and accompanied by a significant decrease in bryophyte diversity. Lyons *et al.* (2000) also found that the proportion of bryophytes decreased moving away from the trunk. This horizontal component to distribution was also found by Ellyson & Sillett (2003) on Sitka spruce branches in an old-growth redwood forest. They related this to the fact that exposure to desiccation is likely to increase along branches from the inner to the outer crown. The plots next to the trunk are likely to experience the shade of the branches above and protection from desiccation that plots further from the trunk do not have, thus favouring bryophytes. On the middle branches, lichen cover was significantly lower in the inner plots on both species and lichen diversity was also significantly lower in the inner plots on spruce. Lyons *et al.* (2000) also found that the proportion of alectorioid (pendulous lichen species in the genera *Alectoria, Bryoria* and *Usnea*) and 'other' lichens (non cyanolichen or alectorioid macrolichens) increased moving away from the trunk. They put this down to the effect of increasing light levels. However, on the upper branches in the present study, lichen diversity and cover were lowest in the outer plots; this difference was significant for all factors with the exception of cover on larch. A similar situation was found by Hilmo (1994) on young *Picea abies* trees in Norway, where the tips of branches had few species and low cover. Hilmo (1994) described branches as an axis of time where the age of the substrate increases from tip to base. Since a certain time lapse is required for the invasion and establishment of the flora (Hale, 1952), these outer plots may have been too young to have allowed epiphyte colonisation to take place.

3.4.6 The effects of aspect

There were no significant differences in the species richness or diversity of all plots on the north and south sides of the trunks or the branches of spruce and larch. However, the greater lichen richness on the south sides of larch trunks was close to significance and there was significantly higher lichen cover on the south side of the trunks of larch. The south side of trees will receive the most light due to the declination of the sun (Trynoski & Glime, 1982). Since most epiphytic lichens are light-demanding (Rose, 1993) they will flourish on this aspect. The greater bryophyte cover on the north side of larch at the tree base was close to significance. The north sides of the trees, particularly at the tree base, will have higher humidity than the south sides and this, combined with higher light levels in larch stands, are likely to have provided optimum conditions for bryophyte growth. The lack of any differences with aspect for spruce may be due to the fact that there is less variation in light levels between aspects in dense forests, with the shade of the crown also an important factor (Barkman, 1958). The high humidity levels in spruce stands may also have been important. Peck *et al.* (1995) found little difference in liverwort abundance with aspect on Sitka spruce growing on Hotsprings Island and related this to the high humidity of the site, which resulted in a relatively uniform distribution of moisture. When the different height zones on spruce were examined, there was significantly higher total epiphyte richness and lichen cover on the south

side in the upper height zone. At this height in the tree, even in a dense stand, light levels will be higher on the south side of the trunk. South facing middle branches on spruce also had greater lichen cover. This is again likely to be due to the higher light levels on the south-facing branches favouring the light-demanding lichen species. There was also significantly greater total epiphyte richness on the north side of spruce in the lower height zone. The cover of bryophytes was lower in the lower height zone than in the tree base or middle height zones on the north side of spruce (cf. **Figure 3.71**), although not significantly so. Competition is known to occur among epiphytes, particularly between bryophytes and lichens (Averis & Coppins, 1998). The lower bryophyte cover as outlined above may have allowed lichens and less vigorous bryophytes to colonise, thereby increasing the epiphyte richness.

3.4.7 Contribution to the overall flora

Epiphytes made up a substantial proportion of the total flora at the five stands studied, especially given the fact that the aggregate area studied for epiphytes was substantially less than that studied for ground flora species and that the trees studied were well grown and with vertical trunks. Awkwardly grown, leaning or damaged trees often have additional niches for epiphyte colonisation and therefore higher epiphyte diversity (B. Coppins, pers. comm.). There was a great deal of overlap in the bryophyte floras of the ground and the trees and, in two of the larch stands studied, epiphytic bryophytes did not contribute any additional bryophyte species. In these stands, it seems the bryophyte ground flora was able to extend up onto the trunks of the trees. Kirby & O'Connell (1982) also found the tree base communities in Shannawoneen Wood, Co. Galway to be extensions of the ground flora, with the majority of the species not recorded higher up on the trees. Few of the bryophyte species recorded in the present study had a high affinity for epiphytism, while the majority of lichen species did. This suggests that the contribution of the epiphyte flora to lichen species richness is likely to be much more important. This supports the findings of Kelly (2000) based on a preliminary survey of the epiphytes of five sessile oak (*Quercus petraea*) trees in Camillan wood, Killarney. He estimated that, while epiphytic bryophytes made up ca. 27.1% of the total bryophyte flora in the wood, epiphytic lichens made up ca. 78.6% of the total lichen flora. This contribution made by lichens may be particularly important in species-poor stands, such as the 'bryophyte-poor' stands surveyed in this study, where the ground flora was more or less absent (cf. **Photograph 3.4**). However, climatic conditions can cause differences in the proportion of epiphytes (Hosokawa, 1950). In dense, humid sites such as FURY2, which is planted on peat, epiphytic bryophytes can contribute substantially to the overall bryophyte flora and the overall epiphyte contribution to the total flora is also substantial.

3.4.8 Comparison to other studies

Given the few studies on epiphytes in Ireland and the complete lack of studies on the epiphytes of Irish forestry plantations, it is difficult to put the results of this study into context. The most comparable study is the work of Humphrey *et al.* (2002) comparing lichen and bryophyte communities of spruce and pine plantations with those of semi-natural pine and oak woodlands in Britain. They studied epiphytes up to 2m on trees, but reported only two bryophyte and two lichen species on substrates other than deadwood (*viz.* rocks and living trees) in mid-rotation (20-30 years) or mature (50-80 years) Sitka spruce plantations. However, the ages of the spruce stands in the present study mainly fell between the two age ranges cited above and a greater height range of the trees was studied. Bates *et al.* (1997), in their study of epiphytic bryophytes in a transect across southern Britain which included areas of coniferous plantations, found that, although Norway spruce (*Picea abies*) and species of pine (*Pinus* spp.) were frequently encountered, they supported epiphytes only infrequently.

Approximately one-third of the epiphyte species recorded in this study have not previously been reported in Irish epiphyte studies. This is not to suggest that none of them occur in semi-natural woodland or scrub habitats in Ireland, but is rather an indication of the under-recording of lower plants, and of epiphytes in particular. The epiphytic floras of the plantations were species-poor compared to semi-natural woodland. For example, Fox *et al.* (2001) recorded 61 species from 1.2m on the trunks of 21 oak trees at Brackloon wood, a semi-natural oakwood in Co. Mayo. In the present study 17 species were reported from the plots at 1.3m on spruce and 16 on larch. In the same study in Brackloon Wood, a total of 46 lichens were recorded on the entire surface of a single oak tree. The greatest number of lichen species recorded on any single tree in this study was 16, although the entire surface was not studied. Kirby & O'Connell (1982) recorded 94 species up to 2m on an unspecified number of trees of six different species in Shannawoneen wood, while a total of 53 species were recorded from the tree base and lower plots (0-0.5m and 1.05-1.55m) on the 40 trees in the present study. Folan & Mitchell (1970) recorded 93 lichen species from Derryclare wood compared with 59 lichen species from all sites in the present study.

Approximately two-thirds of the epiphyte species recorded in the present study were previously reported as epiphytes on various trees and shrubs in semi-natural woodland and scrub habitats in Ireland. For example, a number of the bryophyte species recorded by Phillips (1959) on a number of species in the southern half of Ireland were recorded. However, while elements of the bryophyte flora of semi-natural woodland and scrub are supported, it is important to consider the large number of species that were not encountered in the forestry plantations in this study. Of the list of twelve common epiphytic bryophytes given by Watson (1981), four were not recorded in the present study: *Dicranoweisia cirrata*, *Orthotrichum lyellii*, *Orthotrichum affine* and *Syntrichia laevipila*. Other epiphytic bryophyte species commonly reported from semi-natural habitats in

Ireland that were conspicuously absent were *Hypnum cupressiforme*, *Neckera complanata*, *Zygodon viridissimus* and *Plagiochila spinulosa*. A number of the above-mentioned bryophytes were characteristic species of the '*Neckera complanata* union' of Phillips (1959), recorded on trees in southern Ireland. He noted that this combination of species was absent from pine (*Pinus sylvestris*) and larch (*Larix decidua*), putting this down to a requirement for more moist, less acid conditions.

The epiphytic lichen flora, particularly at KNOC, was similar to the flora recorded on *Calluna vulgaris* growing mainly in raised and blanket bogs in Ireland (McCarthy *et al.*, 1986). This supports McCarthy *et al.*'s (1986) contention that *Calluna* is an important reservoir of epiphytic lichens, particularly in treeless areas. The presence of *Calluna* as a source of propagules may explain the richness of the flora of stands such as KNOC, which are not in close proximity to old woodland sites. *Calluna* is known to support minor components of the former epiphyte flora of pine in Ireland (H. Fox, pers. comm.). The most notable absentees from the lichen flora of the forestry plantations were cyanolichen species from the genera *Lobaria*, *Sticta*, *Pseudocyphellaria*, *Parmeliella*, *Pannaria*, *Nephroma*, or *Peltigera* which are considered to form part of the *Lobarion* community (Rose, 1988). Cyanolichens have a cyanobacterial photobiont, as opposed to the green algal photobiont of other species (Dobson, 2005). Managed forests, even of native tree species on ancient sites, have little evidence of these species (Rose, 1993). However, the conditions in planted forests are not necessarily unfavourable to their growth (Hilmo, 2002). Hilmo & Såstad (2001) sowed vegetative diaspores of old-forest lichen species, *Lobaria pulmonaria* and *Platismatia norvegica*, onto spruce twigs, which were transplanted into young planted (ca. 30 year old) forests and naturally regenerated old forests, both dominated by Norway spruce (*Picea abies*), in central Norway. The lichens established and grew as rapidly in the young forest as the old forest. This suggests that dispersal limitation is one important factor in explaining the absence of old-forest species in young stands, rather than unsuitable conditions for growth. These cyanolichen species do occur on spruce and other conifers in sheltered situations in the western Highlands of Scotland, especially where immediately adjacent to old-growth stands of hazel (*Corylus*) (B. Coppins, pers. comm.) however there is often little penetration of these species into the stands (Rose, 1993). The fact that cyanolichen species from the genera *Lobaria*, *Nephroma*, *Pseudocyphellaria* and *Sticta* occur on Sitka spruce in its native range (Ellyson & Sillett, 2003) also indicates that it is not an unfavourable host for these species.

Sitka spruce growing in its native range has been found to have a high affinity for epiphytes in general, and very large trees in old-growth redwood forests have been found to support more epiphytic biomass than has been previously reported from biomass studies of other conifer species on the west coast of the United States (Ellyson & Sillett, 2003). Their epiphyte flora is dominated by bryophytes (Ellyson & Sillett, 2003; Glime & Hong, 2002; Peck *et al.*, 1995) although large fern

mats containing *Polypodium* species are also supported (Ellyson & Sillett, 2003; Sillett & Bailey, 2003). *Polypodium* species are common epiphytes in semi-natural woodlands in Ireland (Kelly, 1981; Kirby & O'Connell, 1982). However, these species were absent in the present study. Juvenile pteridophyte species were recorded on two spruce trees, but the fact that no adult fern species were encountered during the course of the study suggests that they were 'accidental' epiphytes which would not have been able to reach maturity in their actual location (Benzing, 1990; Oliver, 1930).

3.5 CHAPTER SUMMARY

3.5.1 Epiphyte diversity

- Total epiphyte diversity did not differ between Sitka spruce and Japanese larch trees, although larch trees supported more lichen species. The most species-rich and lichen-rich epiphyte flora was recorded on a spruce tree however.
- Larch trees supported more lichen species overall on their trunks, despite the smaller number of larch trees studied, and the mean number of lichen species was higher in trunk plots on larch. There was no difference in the number of species recorded on branches between the two tree species.
- Trees in the Cork cluster had higher epiphyte diversity than those in the Wicklow cluster and this was the case for both trunks and branches.

3.5.2 Epiphyte composition

- Spruce and larch did not differ in the number of species with a high affinity for epiphytism they supported.
- Certain epiphyte species exhibited host specificity, with species specific to spruce characteristic of moist humid situations and those specific to larch consisting of a large proportion of foliose and fruticose lichen species. Although differences in bark physical and chemical properties and in the canopy features (evergreen vs. deciduous) of the two species is likely to have played an important role in this, differences between the two species in planting site type and silvicultural regime also appeared to be important.
- Trees with five distinct overall epiphyte compositions were identified in spruce and larch stands. They are the (1) moss-dominated, (2) liverwort-dominated, (3) *Dimerella lutea*-dominated, (4) bryophyte-poor and (5) lichen-dominated overall epiphyte compositions.
- Bryophyte richness, diversity and cover decreased from the tree base to the upper zone on the trunk; all bryophyte growth forms were also most abundant at the tree base with the exception of cushions, which were more abundant in the upper zone.
- Lichen richness, and diversity increased from the tree base to the upper zone on spruce and larch, as did the richness of all lichen growth forms, with the exception of leprose lichens.

Lichen cover increased with height on spruce while foliose and fruticose lichen cover peaked in the middle height zone on larch.

- Groups of trunk and branch plots with distinctive epiphyte communities were identified. These are the (1) *Hypnum jutlandicum*, (2) *Kindbergia praelonga*, (3) *Microlejeunea ulicina*, (4) species-poor and (5) foliose and leprose lichen-dominated communities found in the trunk plots only; the (6) *Metzgeria temperata*, (7) *Dimerella*-dominated, and (8) *Fuscidea* and *Lecanora* communities, found in both trunk and branch plots; and the (9) *Microlejeunea* and *Ulota*, (10) *Micarea peliocarpa* and (11) *Hypotrachyna revoluta* communities, found in the branch plots only.
- Bryophyte diversity and cover were higher in plots on the middle branches than the upper branches; however, the majority of middle branches were dead. Bryophyte cover was greatest in the inner plots on both middle and upper branches. The majority of outer plots on the upper branches contained no epiphyte species and the inner plots had the greatest epiphyte cover.
- There was greater lichen richness and cover on the south side of the trunks of larch; the difference in cover was significant and that in epiphyte richness close to significance. There was no difference in epiphyte richness, diversity or cover overall for spruce, although total epiphyte and lichen richness and cover were significantly higher on the south side in the upper height zone and total epiphyte richness was significantly higher on the north side in the lower height zone. Bryophyte cover was greater on the north side of larch at the tree base, although not significantly so.
- Lichen cover was higher in plots on south facing middle branches on spruce but there was no difference for larch.
- Epiphytes contributed a substantial proportion of the total flora at all stands examined; the great degree of overlap in bryophyte species between the ground and epiphytic floras means that the greatest contribution of epiphytes is to overall lichen richness.
- More species were reported in this study than previously reported in British conifer plantations; however, although plantations had many species in common with semi-natural woodland and scrub habitats, they were found to be species-poor relative to these habitats in Ireland. Certain bryophyte, cyanolichen and fern species were conspicuous by their absence in plantations.

3.5.3 Environmental factors

- Estimated rainfall received was positively associated with total epiphyte richness and lichen richness for spruce stands, but not for larch stands. However, elevation was negatively associated with total epiphyte richness for spruce.
- Plot height was negatively associated with bryophyte richness and positively associated with lichen richness on both tree species.

- The bark of the two species differed in its physical and chemical properties, although there was a great deal of overlap in bark pH between the species. Total epiphyte and bryophyte richness increased with decreasing pH, but water absorption capacity was not associated with epiphyte richness in the plots studied.

Chapter 4 Effects of open spaces on the epiphytes of Sitka spruce

4.1 INTRODUCTION

4.1.1 Open spaces in forestry plantations

Natural forests usually contain open treeless areas which can be either temporary canopy gaps caused by disturbance, or more or less permanent open spaces in areas that are unfavourable to tree growth because of waterlogged soils, rock outcrops or herbivory (Iremonger *et al.*, 2006). These open areas are important for the maintenance of good biodiversity levels in the natural forests of northwest Europe and North America (Peterken, 1996; Ratcliffe & Peterken, 1995). The availability and diversity of open space in plantation forests is often far less than in natural forests. In Ireland, where most forests consist of one or more even-aged stands (Joyce & O Carroll, 2002) light levels can decrease dramatically as the forest matures and the canopy closes (French, 2005; Smith *et al.*, 2005). Open spaces may be more important in these plantations for the survival of species of flora and fauna excluded from dark, closed canopy forests (Mullen *et al.*, 2003; Sparks *et al.*, 1996).

In Ireland, the importance of open space for biodiversity in forestry plantations has been recognised by the requirement in the *Forest Biodiversity Guidelines* (Forest Service, 2000b) that open space should make up 5-10% of the area of each forest. These open spaces can include ridelines, firebreaks, forest roads and turning bays, unplantable areas, areas left unplanted to facilitate powerlines or other utilities, and buffer zones for aquatic habitats and archaeological features. The *Code of Best Forest Practice* (Forest Service, 2000a) also suggests that open spaces should be proactively managed to capitalise on their biodiversity potential. The importance of open spaces for forest biodiversity is also recognised in Britain, where one of the four main strategies for enhancing biodiversity is protecting incorporated semi-natural open habitats, and linking these to permanent open space networks along with open habitats on second-rotation sites and beyond the forest (Hodge *et al.*, 1998).

Much of the research on open spaces in forestry plantations has been carried out in Britain and has focused on the use of existing networks of roads and rides to promote forest biodiversity (Carter & Anderson, 1987; Ferris-Kaan, 1995). It has been recognised that rides can provide a refuge for a range of communities typical of a site before planting and can be very species-rich (Sparks *et al.*, 1996). The width and orientation of these roads and rides has been found to be an important factor in determining the level of shade and therefore the range of species supported (Warren & Fuller, 1993). Studies of the ground flora of forest road edges in Ireland have also stressed the importance of road width for species diversity (Mullen *et al.*, 2003).

4.1.2 Open spaces and epiphytes

The presence of epiphytes within open spaces themselves is of course dependent on the presence of trees and shrubs. Neitlich and McCune (1997) found that gaps containing broadleaved trees and shrubs were important for epiphytic lichen diversity in managed conifer stands in Oregon. Where trees or shrubs are absent from an open space, it is the effect of the open space on the epiphytes of the planted trees surrounding the open space that is of interest. Rose (1974) has stated that most epiphytic lichens and a significant number of bryophytes are light demanding and that many will occur at or near the edges of woodlands, or along rides or glades. However, there have been no quantitative studies on the effects of open spaces on epiphytes in woodlands or plantation forests in Britain or Ireland.

One method of determining the effects of open spaces on epiphytes is to compare the epiphytes on trees at open edges with trees in the forest interior. A number of studies in Scandinavia and the United States have used this strategy (e.g. Esseen, 2006; Esseen & Renhorn, 1998; Hilmo, 2002; Kivisto & Kuusinen, 2000; Pearson, 1969; Renhorn *et al.*, 1997; Sillett, 1994; Sillett, 1995). The vast majority of these studies have looked at clearcut edges rather than natural edges. Esseen's (2006) study, however, has focussed on natural edges in a forest wetland mosaic. Pearson's (1969) study of a woodland surrounding a Minnesota bog is unusual in being a study of the epiphytes of the edge of a permanent internal open space.

4.1.3 Microclimate of the forest edge and interior

A forest edge is defined as an abrupt transition between two relatively homogeneous ecosystems, at least one of which is a forest (Matlack & Litvaitis, 1999). The forest edge has a width, which measures a marginal zone with an altered microclimate and different community structure from the forest interior (Matlack, 1993). Edge orientation will affect the width of the edge zone (Matlack & Litvaitis, 1999) as well as its microclimate (Chen *et al.*, 1995). The biggest influence on the microclimate of the forest edge is the step in topography it forms, but microclimate is also influenced by both the nearby forest and the adjacent open area (Geiger, 1965). Closed forest margins will have quite different microclimatic conditions to recently exposed edges (Matlack, 1993). If the edge adjoins an internal open space (i.e. a clearing, glade, road or ride), the size and configuration of this area will influence its microclimate. Small open spaces will have a relatively moderate microclimate, but above a certain size, the microclimate is subject to greater extremes (Geiger, 1965).

The forest edge is sometimes considered to have an intermediate microclimate between the forest interior and adjacent open area (Matlack & Litvaitis, 1999). However, the forest edge is only intermediate for certain microclimatic factors, and the highest variability is often found at the edge

(Chen *et al.*, 1993). Both forest edges and glades can have a more extreme microclimate than the forest interior or an open field (Barkman, 1958). In the forest interior there is an enclosed air space in the trunk area which has a transitional microclimate between the open air, from which it is separated by the crown area, and the ground below (Geiger, 1965). The microclimate of the forest interior can be heterogeneous, as can that of any open area it adjoins (Lieberman *et al.*, 1989). Microclimate will also vary with height in the tree (Barkman, 1958).

4.1.3.1 Light

The proportion of sunlight and shade is the first factor that determines the microclimate of the forest edge (Geiger, 1965). The light levels at the edge are strongly dependant on edge aspect and edge openness (i.e. degree of formation of a side canopy of foliage) (Matlack, 1993). More light enters at edges facing the equator in temperate zones and more penetrates under a high tree canopy than a low one (Matlack & Litvaitis, 1999). More light will also enter more open edges (i.e. those without a side canopy) (Matlack, 1993). When the forest edge is internal (i.e. adjoins a clearing, glade, ride or road), the width and orientation of the open space and the height of the surrounding trees will affect the amount of light received (Ferris-Kaan, 1995; Warren & Fuller, 1993). Light intensity will decrease with distance into the stand (Matlack & Litvaitis, 1999) and the zone of elevated light may extend only a short distance (Matlack, 1993). There may be a particularly abrupt gradient in mature forests (Davies-Colley *et al.*, 2000) with a dense side-canopy closing the edge to light (Matlack & Litvaitis, 1999). In the forest interior the light intensity will be lower than in the open, but the decrease in light will depend on the type of tree, the character of the stand, its age and its productivity (Geiger, 1965). Light intensity will also increase from the base to the top of trees (Barkman, 1958).

4.1.3.2 Temperature and air movement

The air and soil temperature at the edge is influenced by the amount of sunlight received and the wind profile (Geiger, 1965). Solar radiation causes soil heating, meaning that soil temperature gradients will mirror those of light exposure (Davies-Colley *et al.*, 2000). For this reason the amount of heat received by an edge is strongly influenced by the edge aspect and is much reduced on cloudy days (Geiger, 1965). Air temperature gradients extend further into the forest than soil temperature gradients (Chen *et al.*, 1995). In the forest interior, the forest canopy intercepts most of the solar radiation so there is little direct soil heating (Davies-Colley *et al.*, 2000). Temperature will increase with height in the tree and temperature variation will be largest at the base of the trunk and the top of the crown (Barkman, 1958). Daily averages of soil and air temperature are usually lower inside the forest than in the open or at the edge (Chen *et al.*, 1993). The temperature difference is greatest during the summer (Geiger, 1965). There is also diurnal variation with, from the edge into the forest, air temperatures usually decreasing during the day and increasing at night (Chen *et al.*, 1995).

The temperature difference between the forest and the open is the active influence the stand has over air movement. When a temperature difference builds up, a flow of air is produced to counteract this (Geiger, 1965). During the day, when the forest interior is cooler, air flows out as a forest breeze. However, the opposite does not occur at night due to the braking effect of the trees (Geiger, 1965). If the edge borders a sheltered clearing or glade, air heated in the clearing can move into the forest (Matlack & Litvaitis, 1999). A south-facing edge (in the northern hemisphere) can be substantially warmer during the day, as well as at night, than the adjacent forest or open area (Geiger, 1965).

The stand's passive influence over air movement is as an obstacle to airflow (Geiger, 1965). Moving air is forced up over the forest, causing an increase in wind speed at the edge (Matlack & Litvaitis, 1999). In an open stand, wind can penetrate in gusts but is slowed by the tree trunks (Geiger, 1965). Wind speed will decrease from the edge into the stand, depending on the relationship of edge orientation and wind direction (Chen *et al.*, 1995). In the forest interior, wind speeds vary little with height to about mid-canopy where they increase until reaching those of the open at some point above the canopy (Raynor, 1971). Clearings or glades will have wind protection up to a certain size, which depends on their width and the height of the surrounding trees (Geiger, 1965). A dense side-canopy will close the edge to air movement (Matlack & Litvaitis, 1999).

4.1.3.3 Humidity and precipitation

Two of the factors influencing humidity levels at forest edges are temperature and air movement. In a dense forest, or at a closed edge, sunshine and wind cannot penetrate to any significant effect, allowing the air in the trunk area to remain cool and moist (Geiger, 1965; Matlack & Litvaitis, 1999). The forest understorey will therefore be more humid than the adjacent open area (Matlack, 1993). However, although relative humidity is high in the trunk area, it is lower among the tree tops (Geiger, 1965). At edges adjacent to clearings, heated air can move into the forest from the clearing, lowering humidity (Matlack & Litvaitis, 1999). Relative humidity will increase from the edge into the forest. Gradients will be longer and steeper on clear, warm, dry days (Chen *et al.*, 1995).

Rain and fog droplets will drop out at forest edges leading to an increase in moisture accumulation in the edge zone (Matlack & Litvaitis, 1999). The amount of rain entering the edge zone will depend on the wind field, meaning that edges in wind shadow will also be in rain shadow (Geiger, 1965). The forest canopy will also remove fog droplets and the turbulence above the tree tops will cause some of this to fall into the forest (Geiger, 1965). However, fog precipitation makes up a small proportion of the water received within the forest compared with the edge. The understorey will receive less rainfall than the adjacent open area (Matlack, 1993).

4.2 METHODS

4.2.1 Measuring diversity, statistical analysis and ordination

Species richness, diversity and cover were assessed as in **Section 3.2.1**. Statistical analyses were also as carried out as in **Section 3.2.2** with quadratic regression used, in addition to linear regression, where the relationship between species diversity and environmental variables appeared to be unimodal. In comparing edge and interior trees, paired samples t-tests, or the non-parametric equivalent Wilcoxon signed ranks tests, were used. NMS ordination was carried out as described in **Section 3.2.3**. Cluster analysis was not used in this instance, although indicator species analysis was used to identify species characteristic of edge and interior trees.

4.3 RESULTS

4.3.1 Tree Diversity

A total of 24 trees were studied: one tree at the edge of an open space and one tree in the forest interior at twelve sites. A total of 68 species were recorded on these trees: 28 bryophyte, 39 lichen and one vascular plant species. Nine species were recorded on the open space edge trees that were not encountered on any of the forest interior trees. These consisted of four bryophyte and four lichen species encountered in the plots and an additional lichen species encountered on the studied branches outside the plots (cf. **Appendix 3**). The same number of species were recorded in total on the edge and interior trees, although slightly more bryophyte species were recorded on the edge trees and slightly more lichen species on the interior trees (**Table 4.1**). The cumulative species curve for these trees is beginning to reach a plateau (**Figure 4.1**), suggesting that the number of trees and plots studied was adequate to represent the overall epiphyte diversity in these Sitka spruce stands.

Table 4.1 The total number of epiphyte species recorded on all of the paired open space edge and forest interior trees and the total number of bryophyte, lichen and vascular plant species recorded.

	n	Total epiphyte	Bryophyte	Lichen	Vascular
Edge	12	55	26	29	0
Interior	12	55	22	32	1

The most species-rich (SR_C) tree was KNOC2, a forest interior tree from the Cork cluster, with an SR_C of 26 (**Figure 4.2**). This was also the most lichen-rich tree with a lichen SR_C of 16. The most bryophyte-rich tree was KNOC1, the open space edge tree from the same stand with a bryophyte SR_C of 13. The most species-poor tree was ATHN1, an open space edge tree from the Wicklow cluster with an SR_C of eight (**Photograph 4.1**). There were no significant differences in total epiphyte, bryophyte or lichen SR_C between the edge and interior trees (paired samples t-test: total

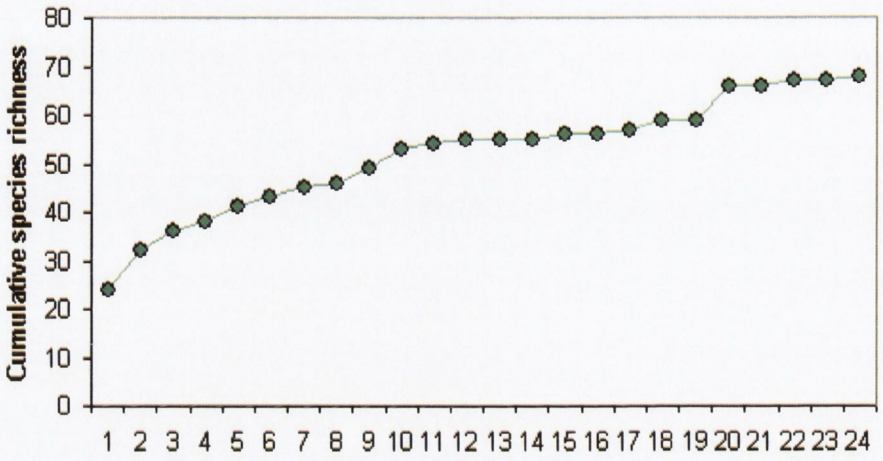


Figure 4.1 Cumulative species curve for the 24 Sitka spruce trees studied.

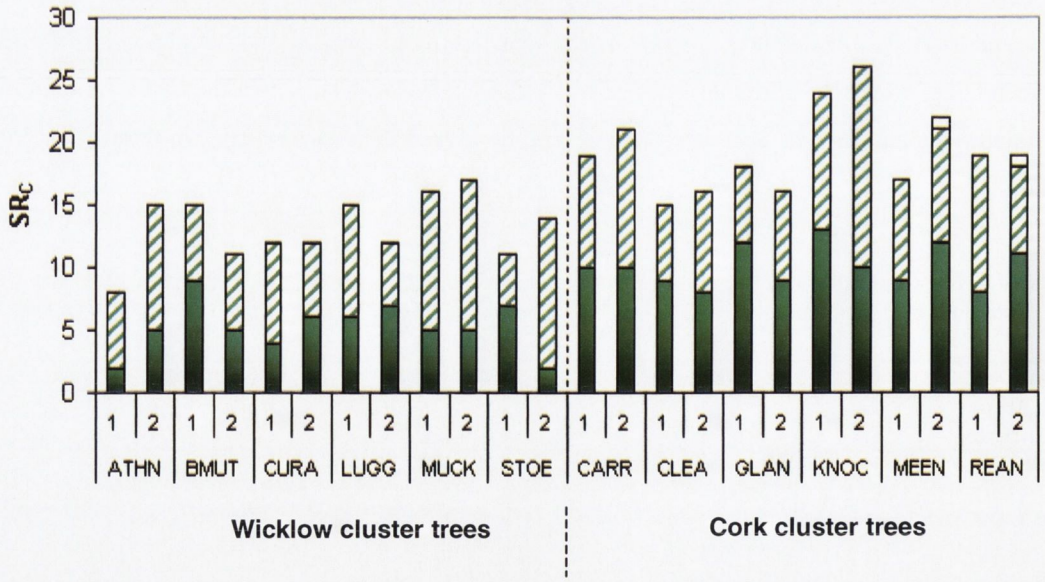


Figure 4.2 Epiphyte species richness (SR_C) of the pairs of trees studied (1 indicates an open space edge tree and 2 a forest interior tree). The total epiphyte richness is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant (unshaded) species are indicated.

Photograph 4.1 The glade at Athdown (ATHN), Co. Wicklow (GR O076 158); the adjacent stand is a 28-year-old Sitka spruce stand. The tree located to the right of the centre of the photograph (arrowed) was the open space edge tree studied (ATHN1). Note the live branches to the ground. (Photograph: Saoirse O'Donoghue)

epiphyte SR_C, p = 0.297; bryophyte SR_C, p = 0.695; lichen SR_C, p = 0.274) (**Figure 4.3**). There was also no significant difference in the species richness of species with a high affinity for epiphytism (SR_C) between the open space edge and forest interior trees (Wilcoxon signed ranks test: p = 0.414) (**Figure 4.4**). There was, however, a significantly greater number of species with an intermediate affinity for epiphytism on the forest interior trees (paired samples t-test: p = 0.041) and a greater, but not significant, number of species with a low affinity for epiphytism on these trees also (Wilcoxon signed ranks test: p = 0.619) (**Figure 4.4**).

The tree with the highest mean total epiphyte diversity of all plots (trunk and branch) studied ($1/D_M$) was KNOC1, an edge tree from the Cork cluster, with a $1/D_M$ of 3.9 (**Figure 4.5**). KNOC2, the interior tree from the same stand, was the most bryophyte diverse on average with a $1/D_M$ of 2.4. MUCK2, an interior tree from the Wicklow cluster, was the most lichen diverse on average, with a $1/D_M$ of 2.1. There were no significant differences in mean total epiphyte, bryophyte or lichen $1/D_M$ between the edge and interior trees (paired samples t-test: total epiphyte $1/D_M$, p = 0.389; bryophyte $1/D_M$, p = 0.428; lichen $1/D_M$, p = 0.290) (**Figure 4.6**).

There was a significant positive relationship between the total epiphyte richness and the mean total epiphyte diversity of both the edge ($r^2 = 0.687$, p = 0.001) and interior trees ($r^2 = 0.760$, $p < 0.001$) (**Figure 4.7**). This suggests that the more species-rich floras overall are more even at the plot level (i.e. no one species dominates in the plots).

4.3.2 Trunk diversity

A total of 46 species were recorded on the trunks of the trees: 26 bryophyte, 19 lichen and one vascular plant species. The total numbers of species recorded on the trunks of the edge and interior trees were similar (**Table 4.2**).

Table 4.2 The total number of epiphyte species and number of bryophyte, lichen and vascular plant species recorded on the trunks of the open space edge and forest interior trees.

	n	Total epiphyte	Bryophyte	Lichen	Vascular
Edge	12	40	23	17	0
Interior	12	37	21	15	1

The tree with the highest total epiphyte beta (β_w) diversity was STOE2, an interior tree from the Wicklow cluster, with a β_w of 5.8 (**Figure 4.8**). STOE2, the most bryophyte poor tree, also had the highest bryophyte β_w with the maximum value of 8.0. The tree with the highest lichen β_w was KNOC1, an edge tree from the Cork cluster, with the maximum value of 8.0. There were no significant differences in total epiphyte, bryophyte or lichen β_w diversity between the edge and

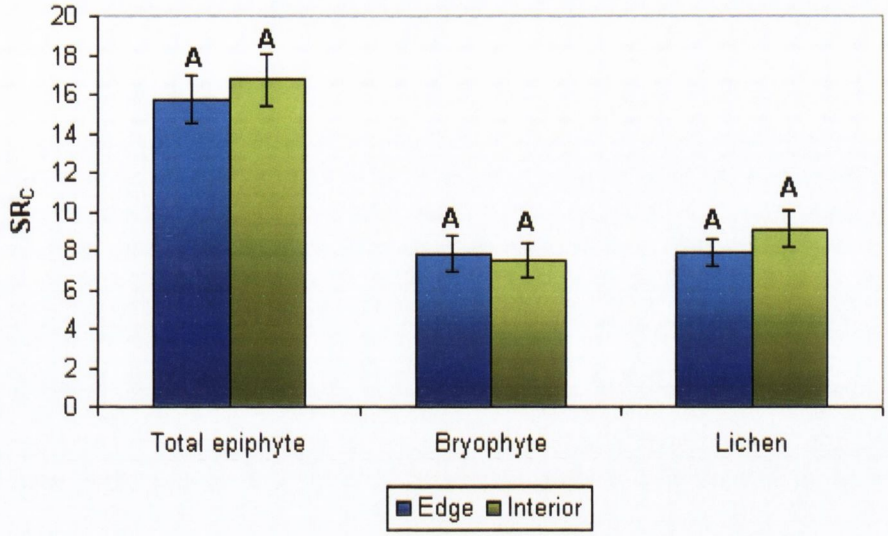


Figure 4.3 Mean epiphyte species richness (SR_C) of the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in species richness between bars if indicated by the same letter.

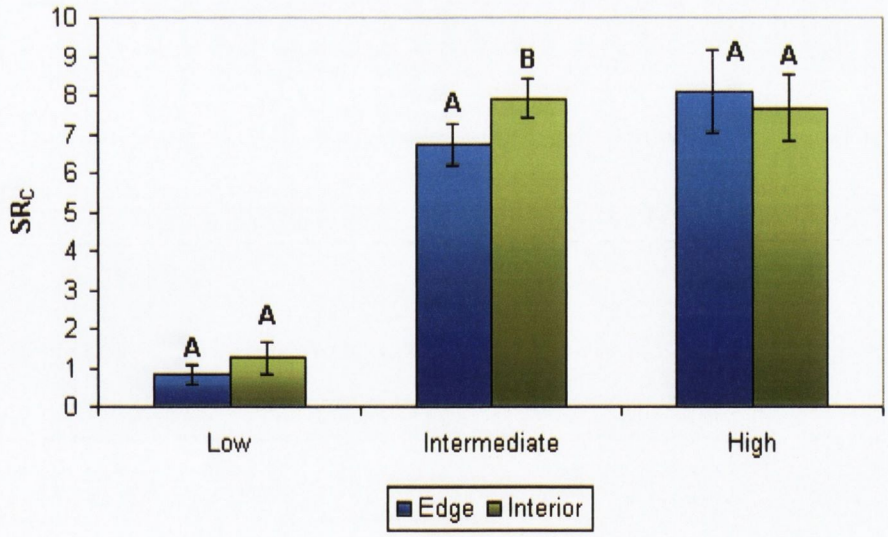


Figure 4.4 Mean epiphyte species richness (SR_C) of species with a low, intermediate and high affinity for epiphytism on the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in species richness between bars if indicated by the same letter.

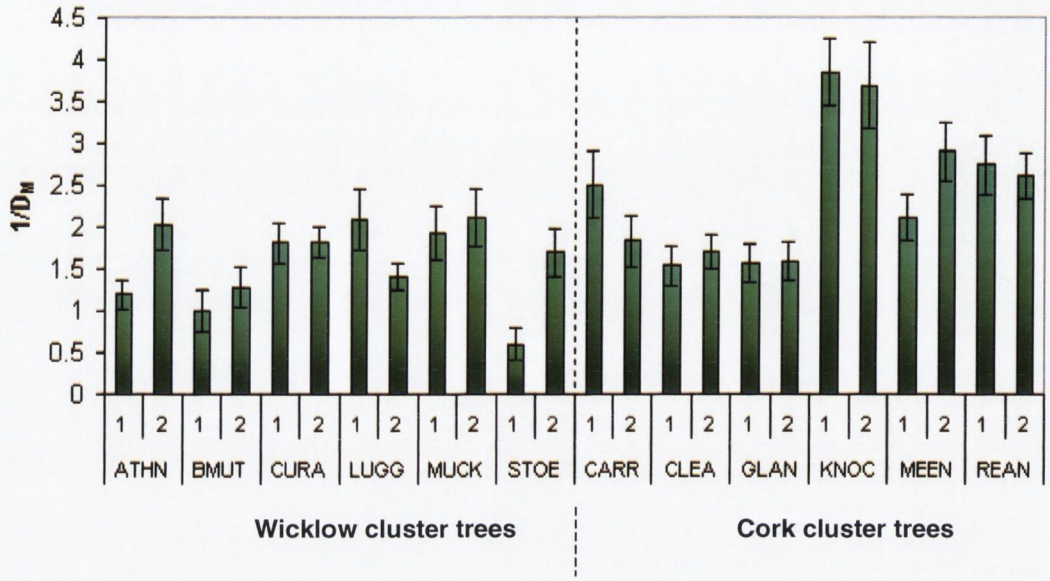


Figure 4.5 Mean Simpson's reciprocal diversity ($1/D_M$) of all plots studied (n = 20, except MUCK2, n = 18) on the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). Error bars indicate ± standard error.

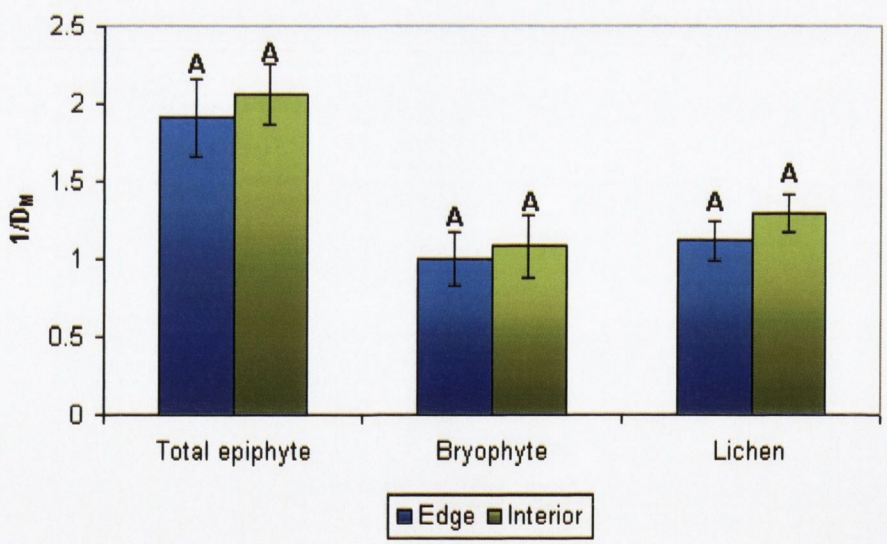


Figure 4.6 Mean of the mean Simpson's reciprocal diversity ($1/D_M$) of all plots studied on the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

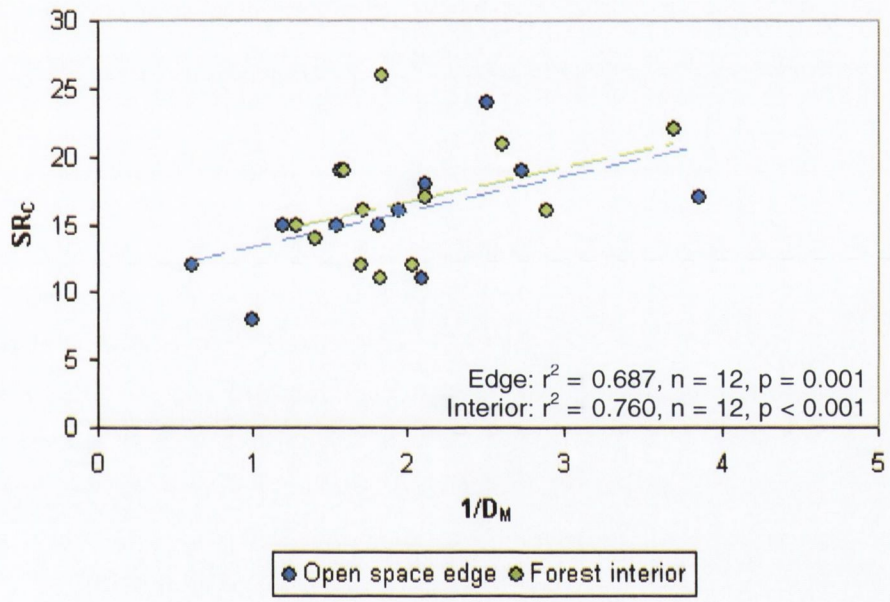


Figure 4.7 Relationship between the mean Simpson's reciprocal diversity ($1/D_M$) and the total epiphyte richness (SR_C) for the open space edge (n = 12) and forest interior trees (n = 12).

interior trees (paired samples t-test: total epiphyte β_w, $p = 0.259$; lichen β_w, $p = 0.321$; Wilcoxon signed ranks test: bryophyte β_w, $p = 0.622$) (**Figure 4.9**).

Eight trunk plots were studied on each tree, making a total of 192 trunk plots studied: 96 on the edge trees and 96 on the interior trees. The most species-rich trunk plot was an upper plot from REAN1 (TUs) (cf. **Section 2.3.1.1** for plot codes), an edge tree from the Cork cluster with a total epiphyte richness of twelve. This plot also had the highest lichen richness at nine species. Two tree base trunk plots from the interior tree, REAN2 (TBn and TBs), from the same site had the equal highest bryophyte richness at seven, along with an upper plot from an edge tree, KNOC1 (TUn). The highest mean total epiphyte richness (SR_{MT}) in the eight trunk plots and the highest bryophyte SR_{MT} was on REAN1 at 5.1 and 4.3 respectively (**Figure 4.10**). The highest lichen SR_{MT} was on MUCK2, an interior tree from the Wicklow cluster, at 2.8. There were no significant differences in the mean of the total epiphyte, bryophyte or lichen SR_{MT} between the edge and interior trees (**Figure 4.11**).

The most species-rich trunk plot, an upper plot from REAN1 (TUs), was also the most diverse plot with a 1/D of 5.7. The most bryophyte-diverse plot was a tree base plot from MEEN2 (TBn), a forest interior tree from the Cork cluster, with a bryophyte 1/D of 4.0. The most lichen-diverse plot was an upper plot from ATHN2 (TUn), a forest interior tree from the Wicklow cluster, with a lichen 1/D of 5.0. The highest mean total epiphyte and bryophyte diversity ($1/D_{MT}$) of all eight trunk plots was on KNOC1, at 2.9 (**Figure 4.12**) and 2.7 respectively. MUCK2 had the highest lichen $1/D_{MT}$ at 2.4. There were no significant differences in the mean total epiphyte, bryophyte and lichen $1/D_{MT}$ between the edge and interior trees (paired samples t-test: total epiphyte, $p = 0.209$; bryophyte, $p = 0.296$; Wilcoxon signed ranks test: lichen, $p = 0.385$) (**Figure 4.13**).

The highest mean total epiphyte cover ($Cover_{MT}$) in the eight trunk plots and the highest bryophyte $Cover_{MT}$ were recorded on REAN2, both at 71.9% (**Figure 4.14**). The highest mean lichen $Cover_{MT}$ was recorded on MUCK1 at 9.9% (**Photograph 4.2**), but lichen $Cover_{MT}$ on trunks was low overall (**Figure 4.14**). As with species richness (SR_{MT}) and diversity ($1/D_{MT}$), there was no significant difference in the mean $Cover_{MT}$ of the edge and interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.301$; bryophyte, $p = 0.176$; lichen, $p = 0.807$) (**Figure 4.15**).

Analysis of the relationship between species richness (SR_{MT}) and diversity ($1/D_{MT}$) revealed a significant positive relationship between these factors for both the edge ($r^2 = 0.747$, $p < 0.001$) and interior trees ($r^2 = 0.763$, $p < 0.001$) (**Figure 4.16a**). This suggests that the more species-rich epiphyte floras in the trunk plots are also more even (i.e. no one species dominates). No significant relationship was found between species richness (SR_{MT}) and cover ($Cover_{MT}$) for the edge trees (r^2

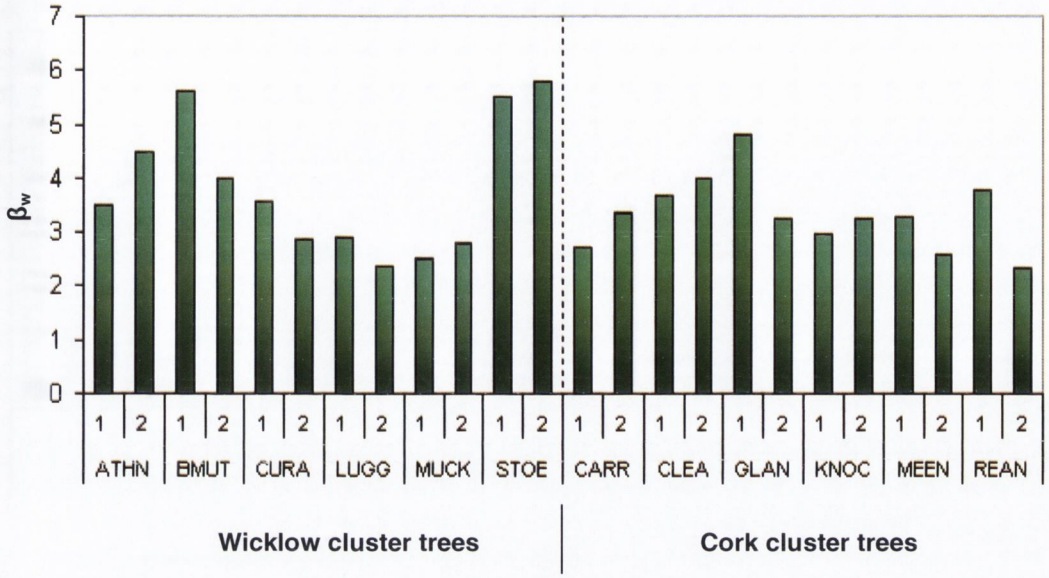


Figure 4.8 Total epiphyte beta (βw) diversity, according to Whittaker's index, on the trunks of the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree).

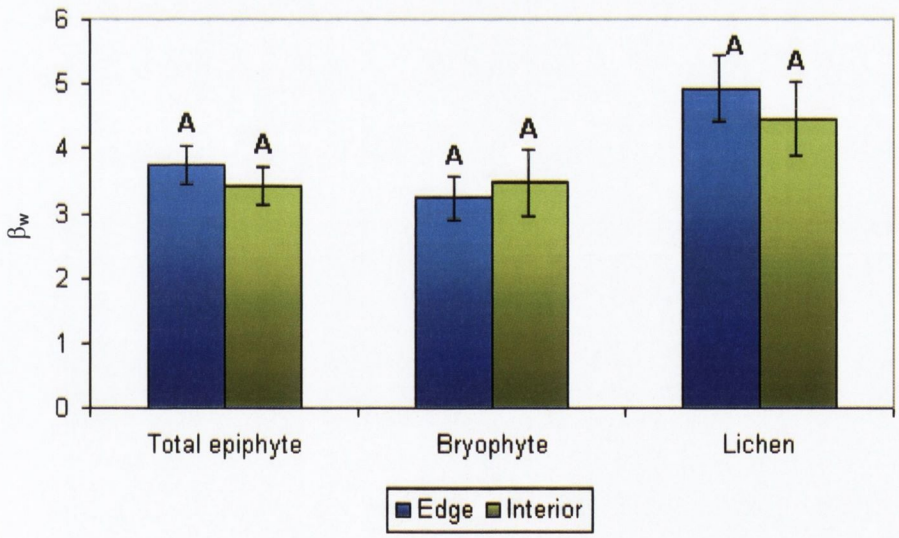


Figure 4.9 Mean beta diversity (β_w) of the trunks of the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in β_w diversity between bars if indicated by the same letter.

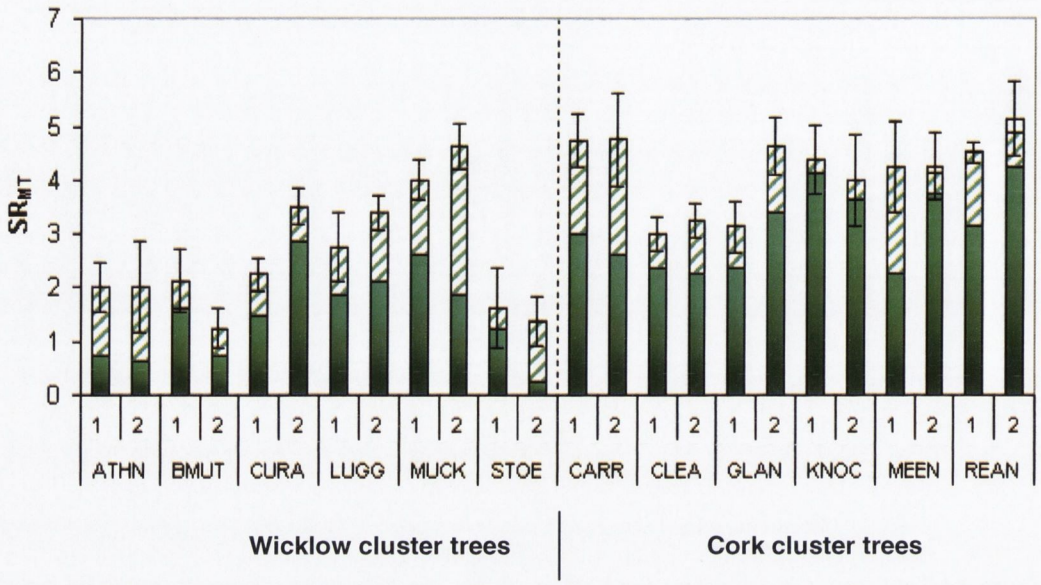


Figure 4.10 Mean epiphyte species richness (SR_{MT}) of the trunk plots (n = 8) on the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). The mean total epiphyte richness is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant (unshaded) species are indicated. Error bars indicate ± standard error.

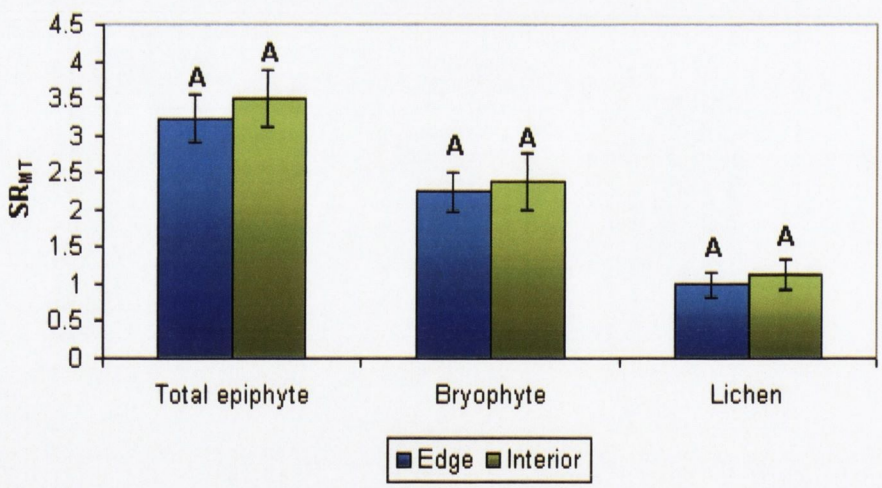


Figure 4.11 Mean of the mean epiphyte species richness (SR_{MT}) of the eight trunk plots on the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in species richness between the bars indicated by the same letter.

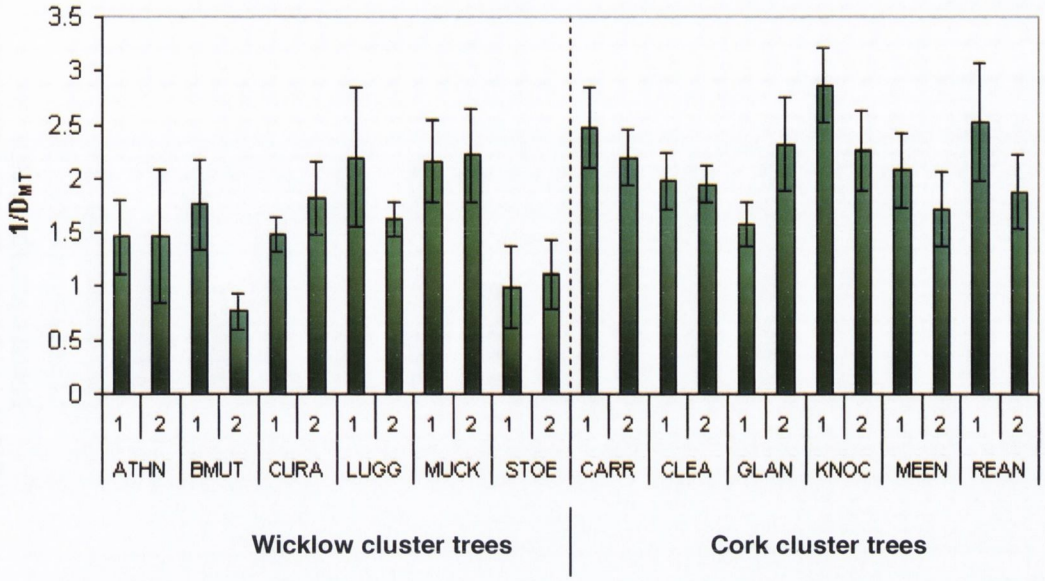


Figure 4.12 Mean Simpson's reciprocal diversity ($1/D_{MT}$) of the total epiphyte flora in the trunk plots (n = 8) on the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). Error bars indicate ± standard error.

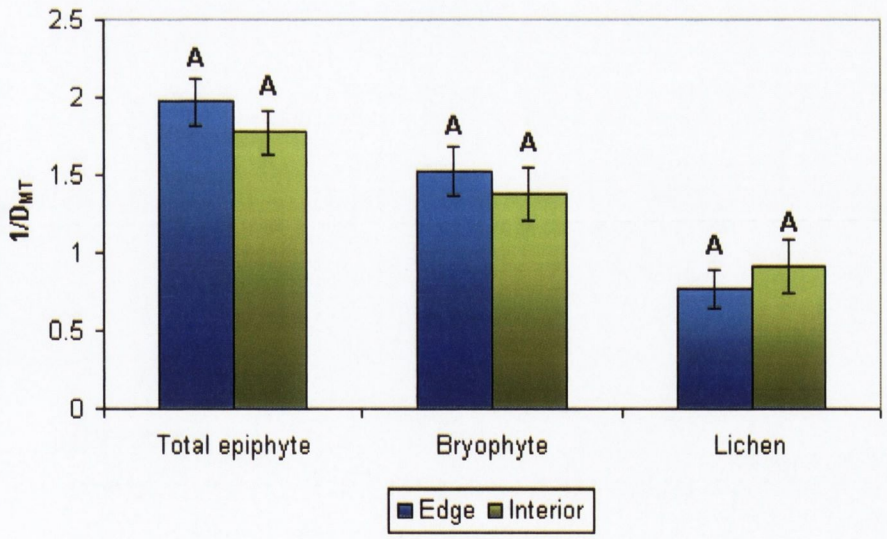


Figure 4.13 Mean of the mean Simpson's reciprocal diversity ($1/D_{MT}$) of the eight trunk plots on the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

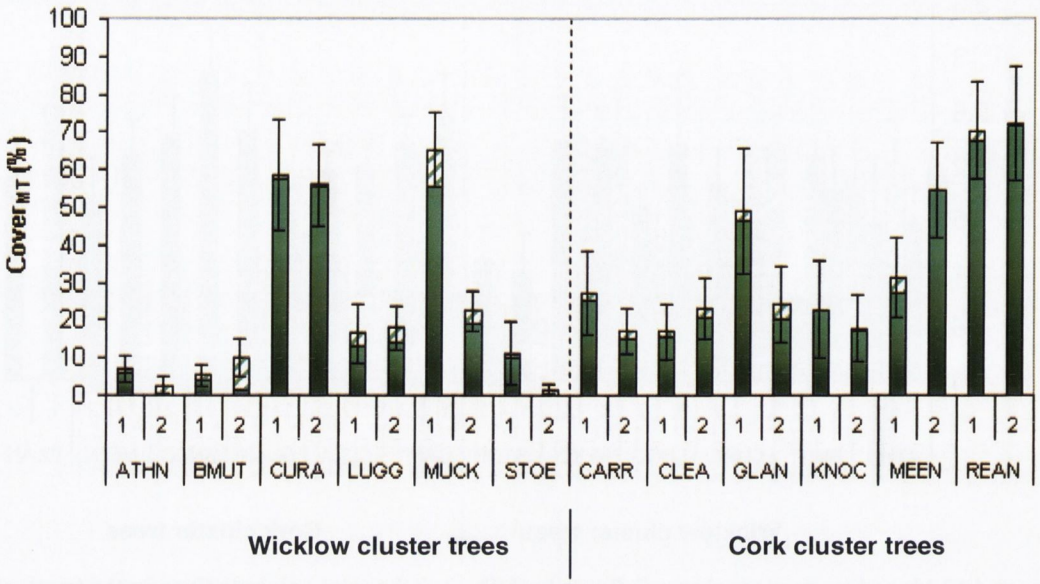


Figure 4.14 Mean epiphyte cover ($Cover_{MT}$) in the trunk plots (n = 8) of the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). The mean total epiphyte cover is shown and the relative proportions of bryophyte (solid shading), lichen (hatched shading) and vascular plant (unshaded) cover are indicated. Error bars indicate ± standard error.

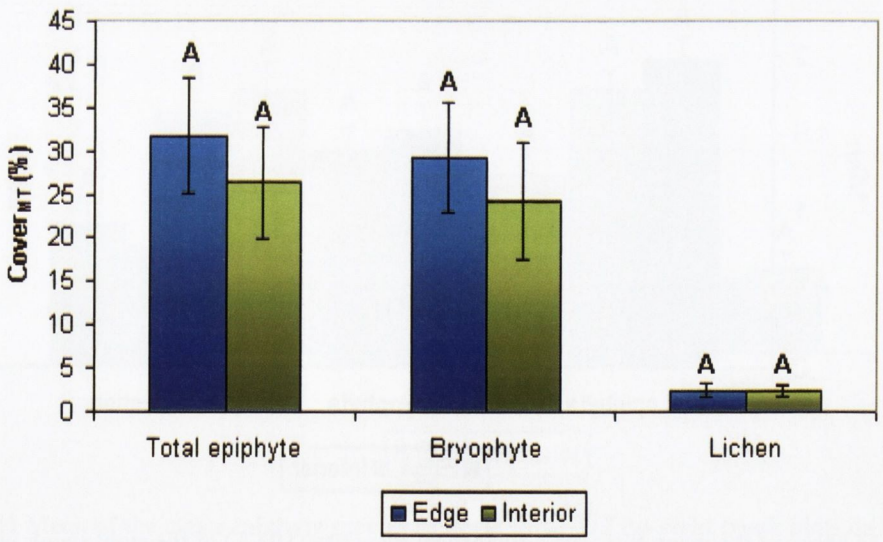


Figure 4.15 Mean of the mean cover ($Cover_{MT}$) in the eight trunks plots on the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in cover between bars if indicated by the same letter.

Photograph 4.2 Road at Mucklagh One (MUCK), Co. Wicklow (GR T083 864); a 42-year-old Sitka spruce stand. A tree was studied (MUCK1) at the edge of this road (to the left of the picture). Note the narrowness of the road and low light levels. (Photograph: Saoirse O'Donoghue).

= 0.220, p = 0.124) but there was a significant positive relationship found for the interior trees (r^2 = 0.369, p = 0.036) (**Figure 4.16b**).

4.3.3 Branch diversity

A total of 53 epiphyte species were recorded on the branches of the trees: 15 bryophyte and 38 lichen species. A similar total number of species were recorded on the branches of the open space edge and forest interior trees (**Table 4.3**). A total of four trees had no bryophyte species on their branches: three edge trees and one interior tree, all from the Wicklow cluster. A maximum of twelve branch plots were studied on each tree, making a total of 286 branch plots studied: 72 on the open space edge trees and 70 on the forest interior trees. (At MUCK2 only ten plots were studied, as one branch was only of sufficient length to accommodate a single plot). Plots were studied on living, moribund and dead branches. The vast majority of the plots on the edge trees were on living branches while just over half of those on the interior trees were on living branches (**Table 4.4**). All of the dead branches were from the middle height zone. The majority of the plots on the middle branches of the edge trees were on living branches while, on the interior trees, the majority of plots at this height were on dead branches (**Table 4.4**).

Table 4.3 The total number of epiphyte species and the number of bryophyte and lichen species recorded on the branches of the open space edge and forest interior trees.

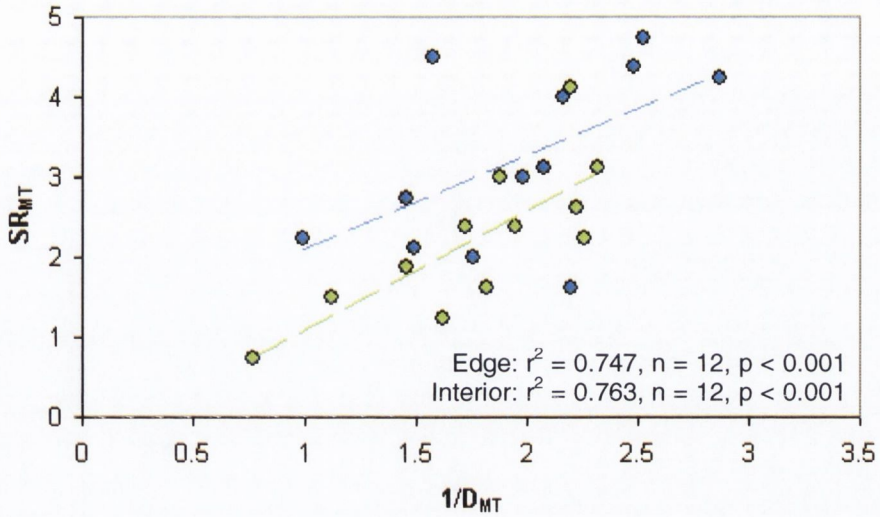
	n	Total epiphyte	Bryophyte	Lichen
Edge	12	40	13	27
Interior	12	38	10	28

Table 4.4 The number (and percentage) of branch plots from the middle and upper branches, and the total number of branch plots on living, moribund and dead branches on the open space edge and forest interior trees.

	n	Living	Moribund	Dead
Edge:				
Middle	72	48 (66.7%)	3 (4.2%)	21 (29.2%)
Upper	72	72 (100.0%)	0	0
Total	144	120 (83.3%)	3 (2.1%)	21 (14.6%)
Interior:				
Middle	70	6 (8.6 %)	9 (12.9%)	55 (78.6%)
Upper	72	72 (100.0 %)	0	0
Total	142	78 (54.9%)	9 (6.3%)	55 (38.7%)

The area available for epiphyte colonisation differed among branch plots (cf. **Figure 2.3**) so the mean epiphyte richness is not presented for branches. With this inequality in mind, the most species-rich branch plots were on an open space edge tree from the Cork cluster; KNOC1 had the most species-rich branch plots in terms of total epiphyte richness (BMs2, SR = 13) (cf. **Section 2.3.1.1** for plot codes), bryophyte richness (BMn1, SR = 8) and lichen richness (BMs2, SR = 8). The branch BMs was a living branch and BMn was a dead branch.

(a)



(b)

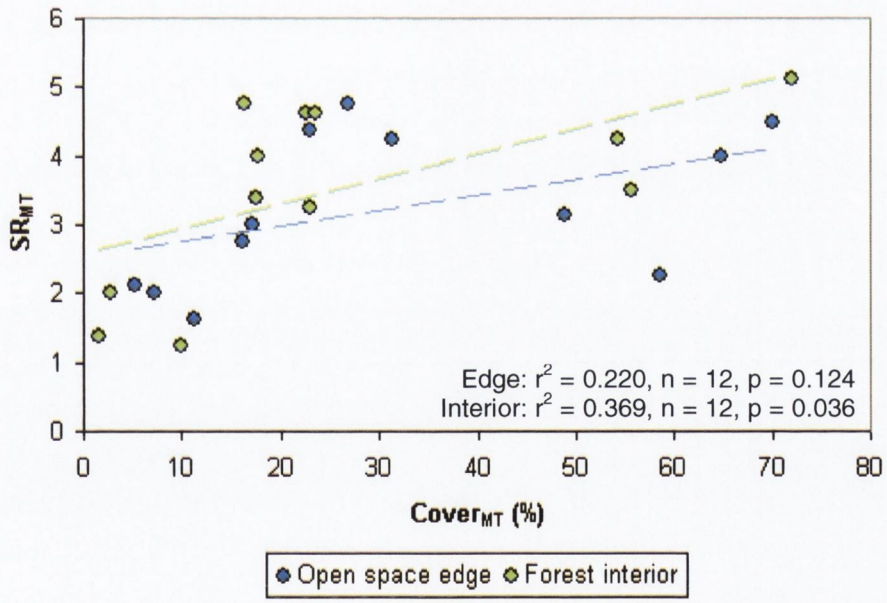


Figure 4.16 Relationship between (a) mean total epiphyte diversity ($1/D_{MT}$) and (b) mean total epiphyte cover ($Cover_{MT}$) and mean total epiphyte richness (SR_{MT}) in the eight trunk plots on the open space edge (n = 12) and forest interior trees (n = 12).

The most diverse branch plots were two plots from middle branches on KNOC2 (BMn2 and BMs3), a plot from an upper branch (BUs1) on the same tree and a plot from a middle branch on CARR1 (Mn1), each with a 1/D of 8.0. The most bryophyte diverse plots were plots from middle branches on CARR1 (Mn1) and KNOC1 (Ms2), each with a bryophyte 1/D of 5.0. Several plots from middle and upper branches had the joint highest lichen diversity of 5.0. The highest mean total epiphyte and bryophyte diversity ($1/D_{MB}$) in all branch plots was on KNOC2 at 4.7 (**Figure 4.17**) and 2.5 respectively. The highest lichen $1/D_{MB}$ was on the branches of KNOC1 at 3.0. There were no significant differences in mean total epiphyte, bryophyte or lichen $1/D_{MB}$ between the edge and interior trees (paired samples t-test: total epiphyte, $p = 0.194$; bryophyte, $p = 0.167$; Wilcoxon signed ranks test, lichen, $p = 0.519$) (**Figure 4.18**).

The highest mean total epiphyte cover ($Cover_{MB}$) on branches and the highest bryophyte $Cover_{MB}$ was on CURA2 at 57.6% and 51.3% respectively. This tree stood out from all other Wicklow cluster trees and, with both trees from REAN, stood out from all other trees in having particularly high bryophyte cover on their branches (**Figure 4.19**). The highest lichen $Cover_{MB}$ was on MEEN1 at 25.1%. There was a significantly higher total epiphyte $Cover_{MB}$ on the branches of the interior trees compared with the edge trees (paired samples t-test: total epiphyte $Cover_{MB}$, $p = 0.043$) but there was no significant difference in bryophyte or lichen $Cover_{MB}$; the difference in bryophyte $Cover_{MB}$ was close to significance (Wilcoxon signed ranks test: bryophyte $Cover_{MB}$, $p = 0.067$; paired samples t-test: lichen $Cover_{MB}$, $p = 0.455$) (**Figure 4.20**).

The epiphyte diversity and cover of the plots on living branches was compared with that on dead or moribund branches. There was significantly higher total epiphyte and bryophyte diversity (1/D) in plots on dead or moribund branches compared with those on living branches on the edge trees (Mann-Whitney U test: total epiphyte, $p = 0.034$; bryophyte, $p < 0.001$) and significantly higher bryophyte diversity on dead or moribund branches on the interior trees (Mann-Whitney U test: $p < 0.001$) (**Figure 4.21**). Total epiphyte, bryophyte and lichen cover were all significantly higher in plots on dead or moribund branches on both edge and interior trees (Mann-Whitney U test: total epiphyte cover edge, $p < 0.001$; interior, $p < 0.001$; bryophyte cover edge, $p < 0.001$; interior, $p < 0.001$; lichen cover edge, $p = 0.003$; interior, $p = 0.023$) (**Figure 4.22**). Since all of the plots on dead or moribund branches were in the middle height zone and all the upper branch plots were on living branches, the middle branches were examined separately. On the edge trees the higher total epiphyte diversity in plots on dead or moribund branches in the middle height zone was close to significance (Mann-Whitney U test: $p = 0.054$) and the higher bryophyte cover in plots on dead branches was significant (Mann-Whitney U test: $p = 0.007$) (**Figure 4.23a**). On the interior trees none of the differences in diversity were significant, although the higher bryophyte diversity on dead branches was close to significance (Mann-Whitney U test: $p = 0.079$) (**Figure 4.23b**). There was a significantly higher total epiphyte, bryophyte and lichen cover in plots on dead or moribund

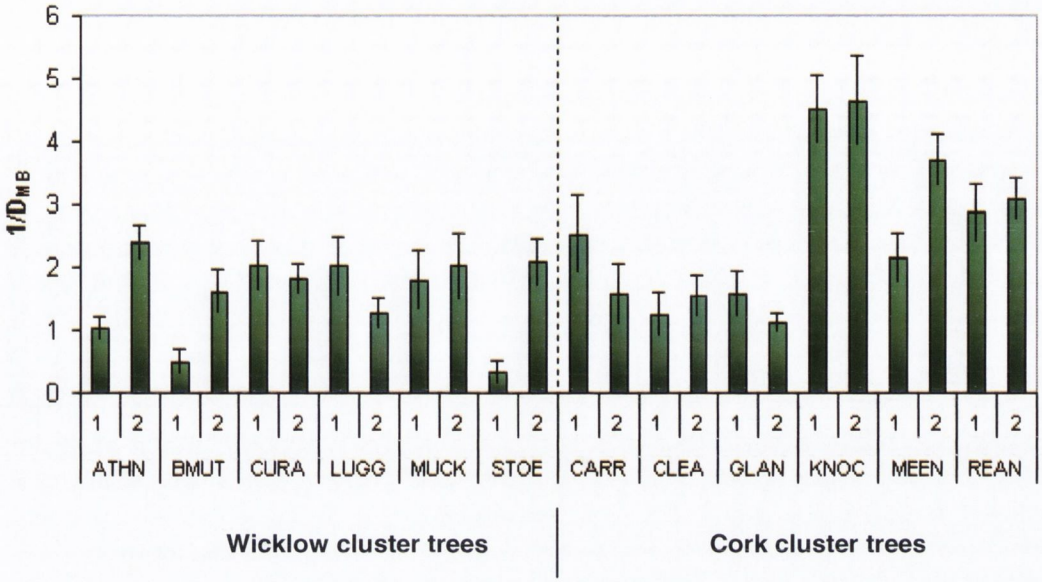


Figure 4.17 Mean total epiphyte diversity ($1/D_{MB}$) of all branch plots studied (n = 12, except MUCK2, n = 10) on the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). Error bars indicate ± standard error.

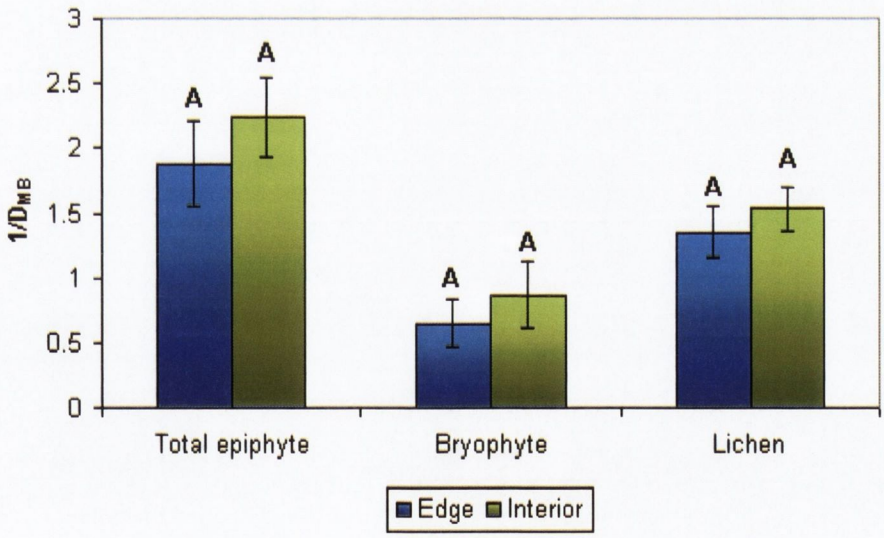


Figure 4.18 Mean of the mean epiphyte diversity ($1/D_{MB}$) of all plots studied on the branches of the open space edge (n = 12) and forest interior trees (n = 12). Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

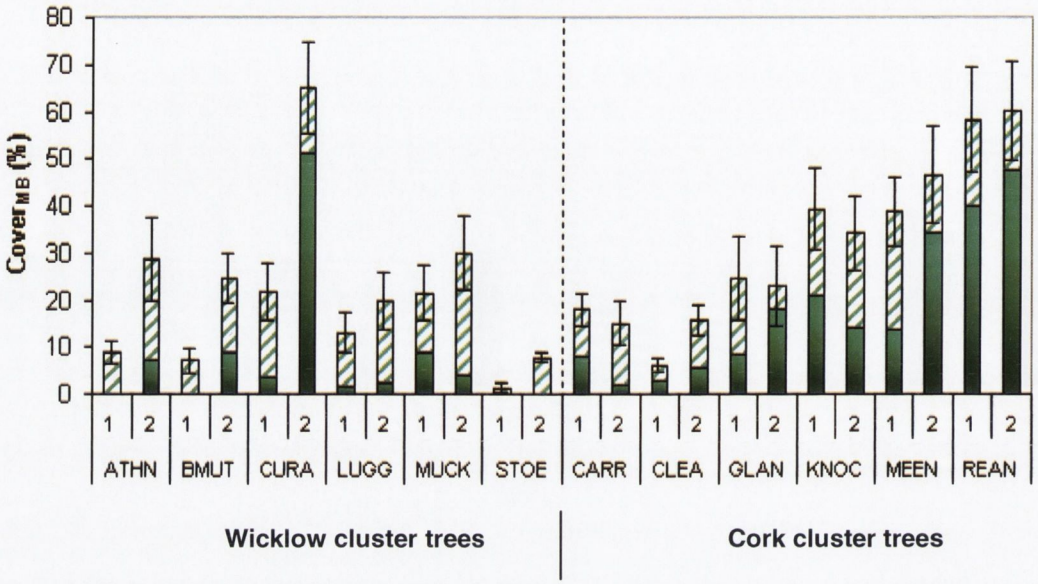


Figure 4.19 Mean epiphyte cover ($Cover_{MB}$) of all branch plots studied (n = 12, except MUCK2, n = 10) on the pairs of trees (1 indicates an open space edge tree and 2 a forest interior tree). Cover is expressed as a percentage of the cover of branches within each plot. The mean epiphyte cover is shown and the relative proportions of bryophyte (solid shading) and lichen cover (hatched shading) are indicated. Error bars indicate ± standard error.

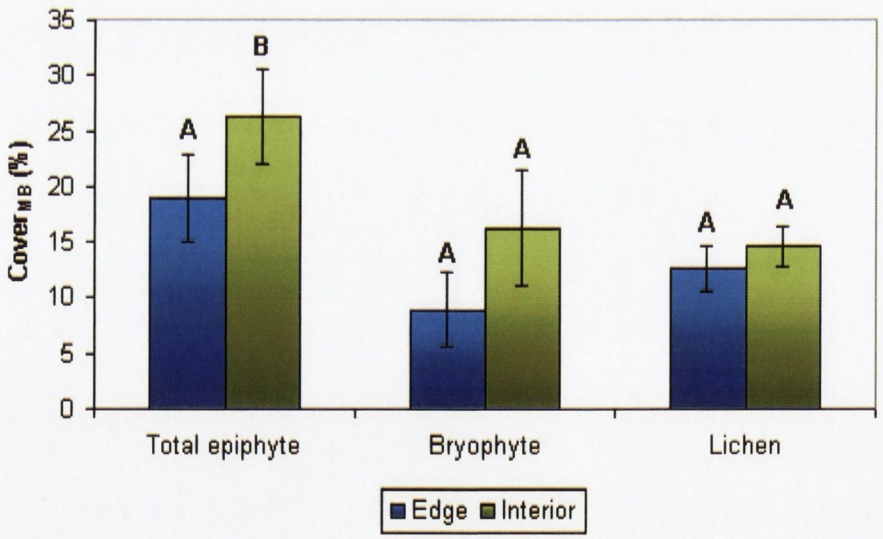
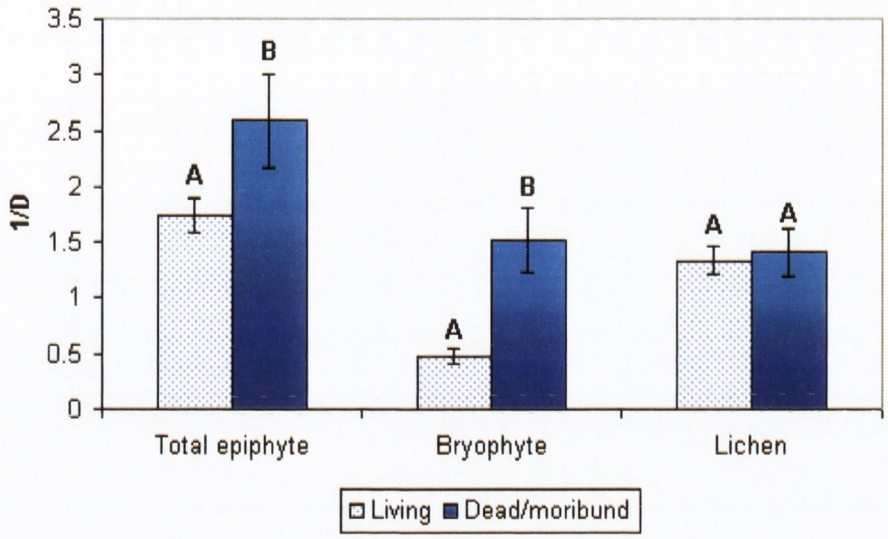


Figure 4.20 Mean of the mean epiphyte cover ($Cover_{MB}$) of all plots studied on the branches of the open space edge (n = 12) and forest interior trees (n = 12). Cover is expressed as a percentage of the cover of branches within each plot. Error bars indicate ± standard error. There is no significant difference in cover between bars if indicated by the same letter.

(a)



(b)

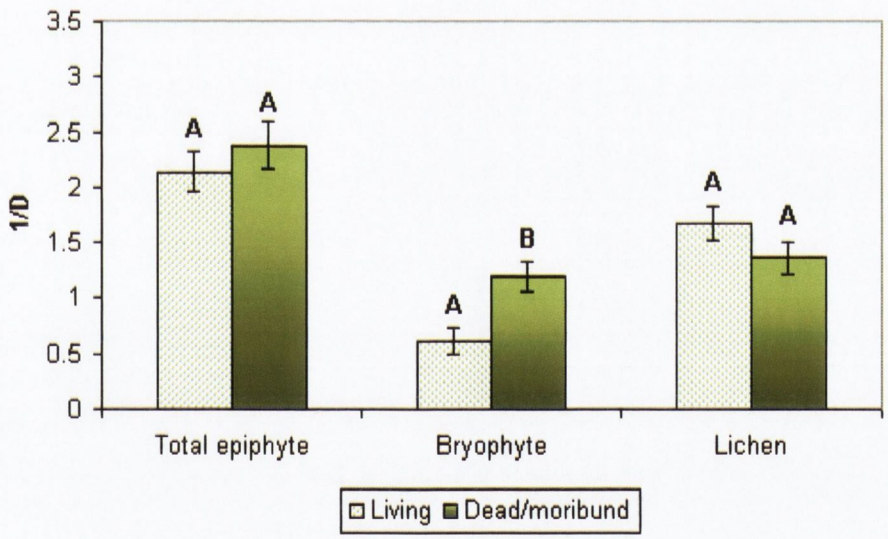
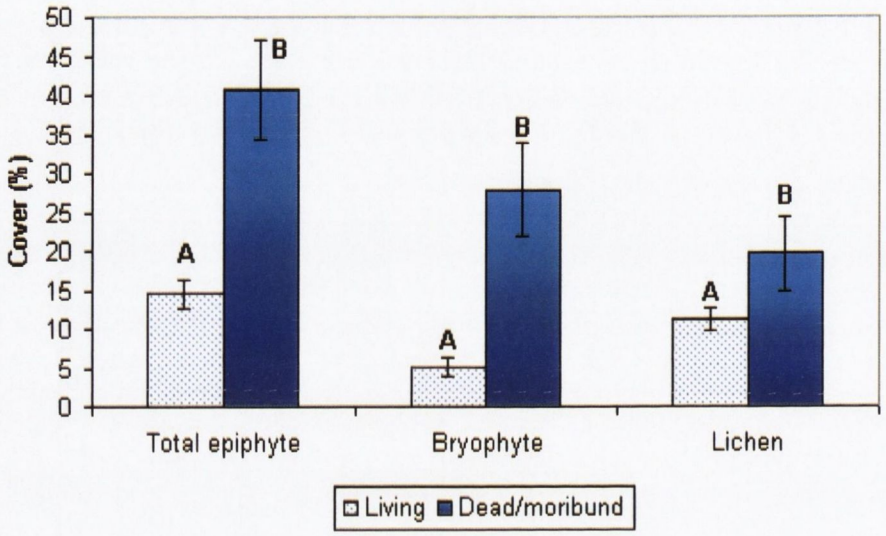


Figure 4.21 Mean Simpson's reciprocal diversity (1/D) of all plots on living and dead or moribund branches on the (a) open space edge (living: n = 120, dead/moribund: n = 24) and (b) forest interior trees. (living: n = 78, dead/moribund: n = 64) Error bars indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

(a)



(b)

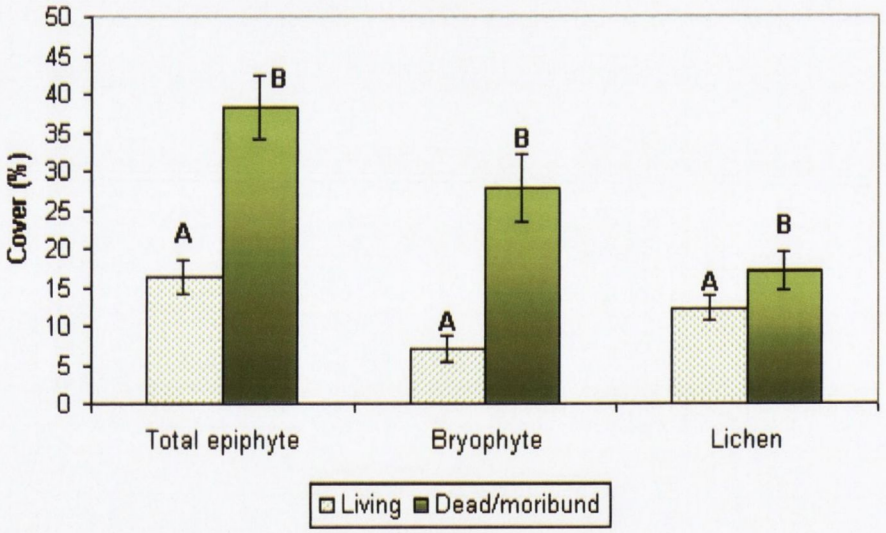
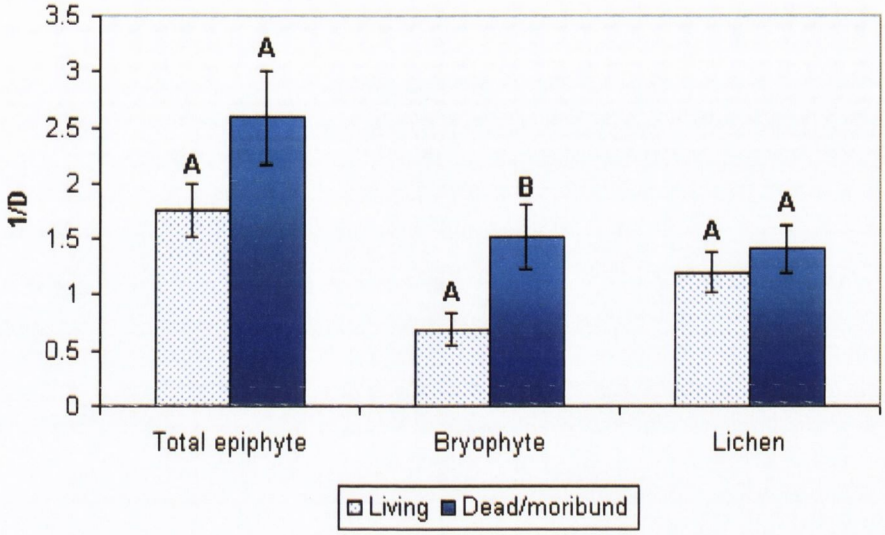


Figure 4.22 Mean cover in all plots on living and dead or moribund branches on the (a) open space edge (living: n = 120, dead/moribund: n = 24) and (b) forest interior trees (living: n = 78, dead/moribund: n = 64). Error bars indicate ± standard error. There is no significant difference in cover between bars if indicated by the same letter.

(a)



(b)

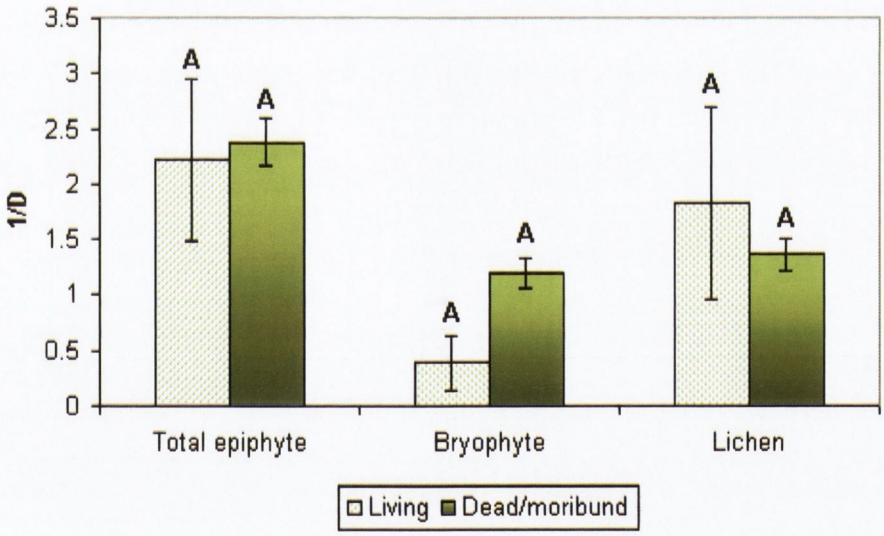


Figure 4.23 Mean Simpson's reciprocal diversity (1/D) in all plots on living and dead or moribund branches from the middle height zone on the (a) open space edge (living: n = 48, dead/moribund: n = 24) and (b) forest interior trees (living: n = 6, dead/moribund: n = 64). Error bar indicate ± standard error. There is no significant difference in diversity between bars if indicated by the same letter.

branches in the middle height zone on the edge trees (Mann Whitney U-test: total epiphyte, $p < 0.001$; bryophyte, $p < 0.001$; lichen, $p = 0.003$) but, although cover was greater on the dead or moribund branches on the interior trees, this difference was not significant (**Figure 4.24**). However, few living branches were studied in the middle height zone on interior trees (cf. **Table 4.4**).

4.3.4 Comparison of the open space edge and forest interior trees

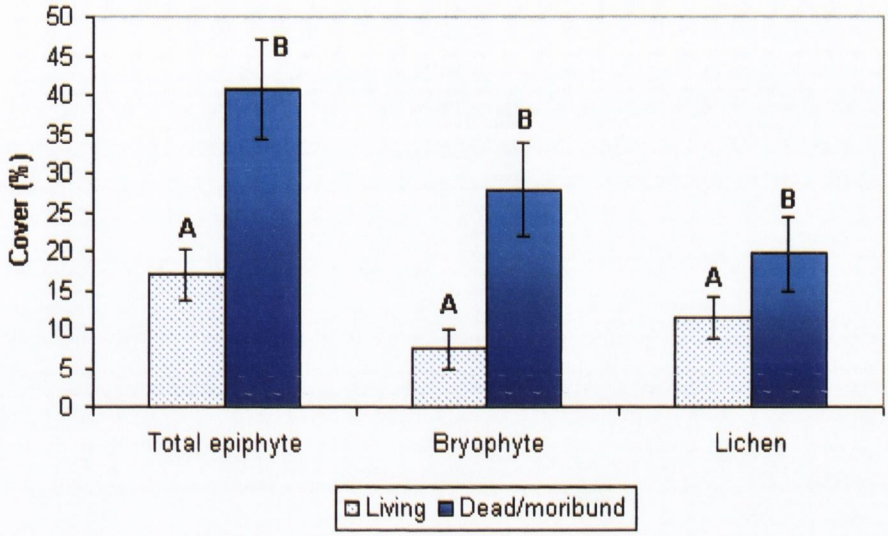
A total of 14 species were recorded on the open space edge trees only - seven bryophyte and seven lichen species - and a total of 15 on the forest interior trees only – two bryophyte, twelve lichen and one vascular plant species. However, ten of the species recorded only on the edge trees and twelve of those recorded only on the interior trees were recorded only on one of the trees studied. Of the remaining seven species, only one occurred on more than two trees (**Table 4.5**). All of the species recorded only on the edge trees were quite common on substrates other than bark and in situations other than woodland. *Campylopus introflexus* is usually a colonist of bare peat and is relatively rare on trees (Hill *et al.*, 1992), *Isothecium myosuroides* is a shade tolerant plant of well-drained hard substrates but is also found in exposed situations (Hill *et al.*, 1994; Smith, 2004), *Ulota phyllantha* can be found on rocks, walls, trunks or branches (Hill *et al.*, 1994) and *Usnea flammea* can be found on soil, rocks, wood and trees (Purvis *et al.*, 1992). Those species recorded only on the interior trees were also varied in their substrate preferences. *Trapeliopsis flexuosa* is usually found on hard wood (Purvis *et al.*, 1992), although it is sometimes also found on bark in polluted areas (Dobson, 2005). *Thuidium tamariscinum* is found in a wide range of moist habitats (Hill *et al.*, 1994). Indicator species analysis revealed no significant indicators for either open space edge or forest interior trees.

Table 4.5 A list of the species recorded only on either the open space edge or forest interior trees and recorded on more than one tree studied. The epiphyte group, growth form and affinity for epiphytism of each species are shown and the number of trees on which each species was recorded is indicated.

Species	Epiphyte group	Growth form	Epiphytism affinity	Edge	Interior
Campylopus introflexus	Mo	Tu	Low	**2**	0
Isothecium myosuroides	Mo	We	Int	**2**	0
Ulota phyllantha	Mo	Cu	High	**2**	0
Usnea flammea	Li	Fr	Int	**2**	0
Trapeliopsis flexuosa	Li	Cr	Int	0	**3**
Thuidium tamariscinum	Mo	We	Low	0	**2**
Juvenile pteridophyte	Va	-	-	0	**2**

A total of eight species - five bryophyte and three lichen species - had more than ten percent frequency on both the edge and interior trees (**Table 4.6**). An additional two species had more than ten percent frequency on the edge trees only and an additional three on the interior trees only. Three species, *Hypotrachyna revoluta*, *Ulota crispa s.l.* and *Frullania dilatata*, had much higher percent frequency on the open space edge trees than the forest interior trees. *Hypotrachyna*

(a)



(b)

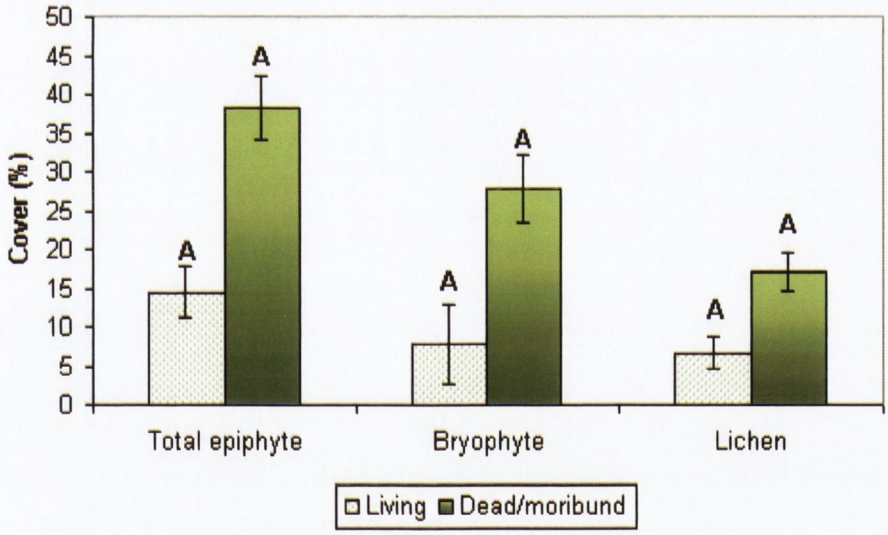


Figure 4.24 Mean cover in all plots on living and dead or moribund branches from the middle height zone on the (a) open space edge (living: n = 48, dead/moribund: n = 24) and (b) forest interior trees (living: n = 6, dead/moribund: 64). Error bars indicate ± standard error. There is no significant difference in cover between bars if indicated by the same letter.

revoluta is found on wayside and woodland trees and is quite widespread (Dobson, 2005; Purvis *et al.*, 1992), *Ulota crispa s.l.* is found in damp humid woodlands where not too deeply shaded and not subject to competition from strongly growing pleurocarps (Hill *et al.*, 1994; Smith, 2004) and *Frullania dilatata* is usually found in sheltered and rather dry situations (Hill *et al.*, 1991). Four species, *Plagiothecium undulatum*, *Microlejeunea ulicina, Kindbergia praelonga* and *Dimerella lutea*, had notably higher percent frequency on the forest interior trees. *Plagiothecium undulatum* is found in woods and on shaded banks (Smith, 2004), *Microlejeunea ulicina* is usually found in very humid sites (Paton, 1999) and *Dimerella lutea* is found in humid shaded situations (Purvis *et al.*, 1992). *Kindbergia praelonga* can be found in open to deeply shaded, damp or dry habitats (Hill *et al.*, 1994).

Table 4.6 A list of the epiphyte species occurring in more than ten percent of trunk plots on the open space edge or forest interior trees, with the percent frequency indicated. The epiphyte group, growth-form and affinity for epiphytism of each species are indicated.

Species	Epiphyte group	Growth form	Epiphytism affinity	Edge (n = 96)	Interior (n = 96)
Hypotrachyna revoluta	Li	Fo	High	**20.8**	**11.5**
Ulota crispa s.l.	Mo	Cu	High	**18.8**	9.4
Frullania dilatata	Lv	Ma	High	**12.5**	4.2
Fuscidea lightfootii	Li	Cr	High	**12.5**	**10.4**
Metzgeria temperata	Lv	Ma	High	**49.0**	**47.9**
Lepraria incana	Li	Lp	Int	**17.7**	**16.7**
Hypnum jutlandicum	Mo	Ma	Int	**55.2**	**55.2**
Metzgeria furcata	Lv	Ma	Int	**12.5**	**13.5**
Lophocolea bidentata	Lv	Ma	Int	**13.5**	**14.6**
Plagiothecium undulatum	Mo	Ma	Low	9.4	**13.5**
Microlejeunea ulicina	Lv	Ma	High	**11.5**	**16.7**
Kindbergia praelonga	Mo	Ma	Int	7.3	**19.8**
Dimerella lutea	Li	Cr	Int	6.3	**21.9**

4.3.4.1 NMS ordination of the open space edge and forest interior trees

The NMS ordination (**Figure 4.25**) was based on the sum of the cover of the epiphyte species in all trunk and branch plots on each tree. As was suggested by the indicator species analysis (cf. **Section 4.3.4**), there is no clear separation of edge and interior trees and other factors appeared to be more important in determining species composition. Axis 1 separated Wicklow and Cork cluster stands to some extent. Trees with high bryophyte cover were grouped together at the top right of the NMS graphic (cf. **Table 4.7**). These stands also had low amounts of total incident radiation.

Some of the pairs of edge and interior trees are located close to one another in ordination space, indicating a similar species composition, while others are more widely separated (**Figure 4.25**). The interior trees whose overall epiphyte composition was named 'liverwort-dominated' (cf. **Section 3.4.2.3**) were positioned close to the edge trees from the same stands at the top right of the NMS graphic, suggesting a similar overall epiphyte composition. LUGG2, whose overall epiphyte composition was named 'moss-dominated', was located close to LUGG1, also suggesting a similar species composition. Although BMUT2, whose overall epiphyte composition was named

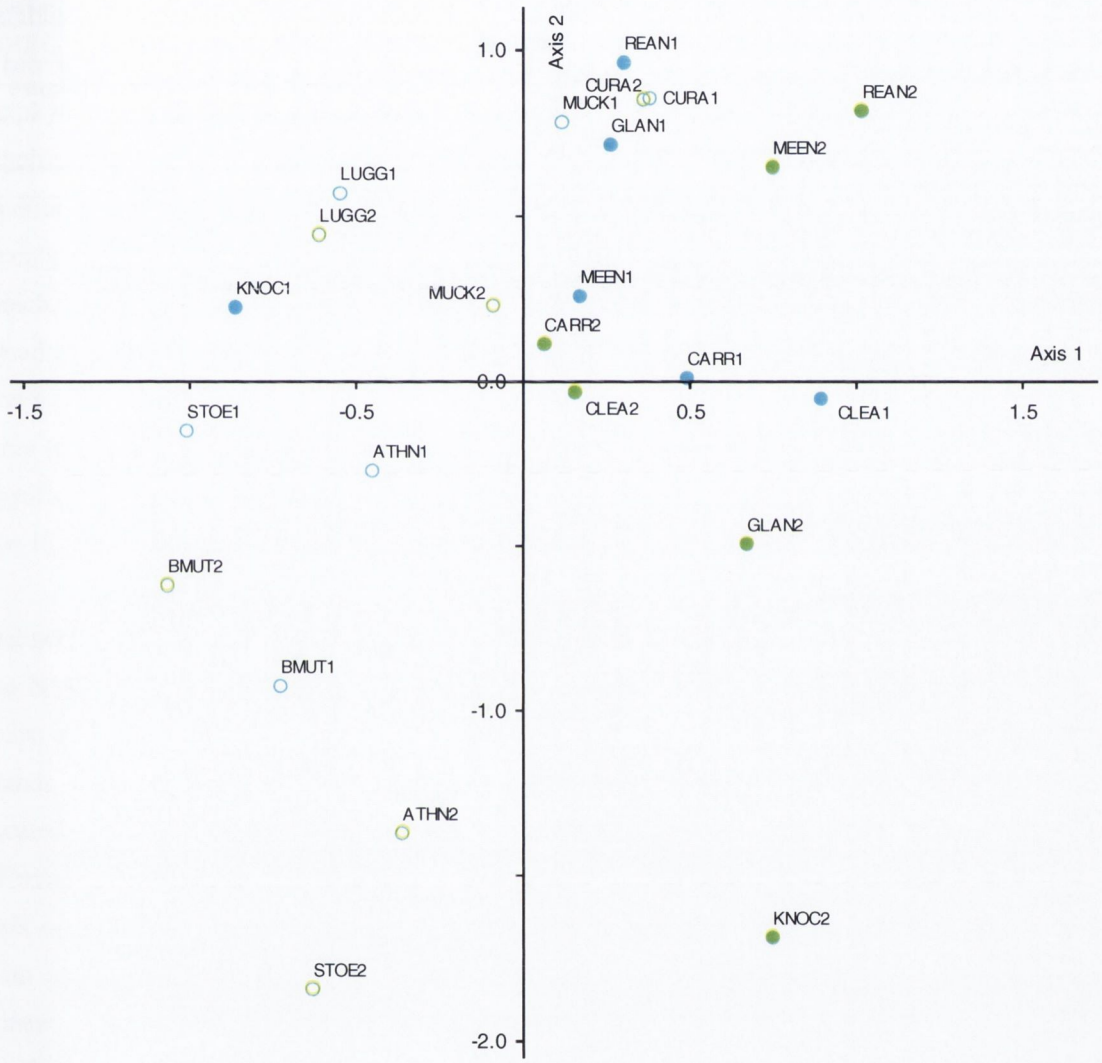


Figure 4.25 NMS ordination of the open space edge (blue) and forest interior trees (green) according to the sum of the epiphyte plot cover data for each tree. Wicklow (unshaded) and Cork cluster (shaded) trees are indicated. Final stress for the 2-dimensional solution = 17.47, final instability = 0.00047, axis 1 r^2 = 0. 279, axis 2 r^2 = 0.438.

'*Dimerella lutea*-dominated', was located close to BMUT1, *Dimerella lutea* did not reach the dominance it achieved on the interior tree on its edge counterpart. The edge trees from the stands where the floras of the interior trees were named 'bryophyte-poor' were not positioned close to the interior trees and, while their floras were still relatively bryophyte-poor, bryophytes did achieve some cover in the tree base and lower plots on the south side of these trees. The separation of the two trees from KNOC indicates that the floras, despite being quite species-rich, are quite dissimilar.

Table 4.7 Pearson's correlations (r) between the axes from the NMS ordination of all trees (Figure 4.25) and selected diversity, cover, tree, stand, site and open space variables.

Correlation variable	Axis 1	Axis 2
Diversity:		
Total epiphyte SR_C	0.434*	-0.005
Bryophyte SR_C	0.401	0.244
Lichen SR_C	0.186	-0.298
Low epiphytism affinity SR_C	0.258	0.251
Intermediate epiphytism affinity SR_C	0.651**	0.023
High epiphytism affinity SR_C	0.112	-0.116
Total epiphyte $1/D_M$	0.380	0.075
Bryophyte $1/D_M$	0.513*	0.276
Lichen $1/D_M$	0.069	-0.099
Trunk total β_w diversity	-0.460*	-0.555**
Trunk bryophyte β_w diversity	-0.582**	-0.668**
Trunk lichen β_w diversity	0.176	-0.085
Cover:		
Trunk total epiphyte $Cover_{MT}$	0.598**	0.763**
Trunk bryophyte $Cover_{MT}$	0.624**	0.756**
Trunk lichen $Cover_{MT}$	-0.254	0.043
Branch total epiphyte $Cover_{MB}$	0.429*	0.428*
Branch bryophyte $Cover_{MB}$	0.492*	0.428*
Branch lichen $Cover_{MB}$	0.032	0.145
Tree:		
Age	0.339	0.449*
DBH	-0.173	0.292
Height	0.142	0.382
Height to 1st live branch	0.155	0.032
Stand:		
Tree density	0.481*	0.073
Average DBH	-0.446*	0.062
Basal area	0.143	0.025
Site:		
Elevation	-0.231	-0.072
Aspect	0.081	0.331
Slope	-0.072	0.096
Estimated rainfall	0.087	-0.236
Area of old woodland	-0.395	0.084
Distance to old woodland	0.420*	-0.032
Total incident radiation	-0.408*	-0.530**
Open space:		
Canopy openness	-0.306	-0.417*
Total transmitted radiation	-0.349	-0.456*

Note. * indicates the correlation coefficient is significant at $p < 0.05$ and ** indicates significance at $p < 0.01$.

The relationship between the environmental variables with significant correlations with axis 1 of the NMS ordination (**Table 4.7**) and species richness was examined further. There was a significant positive relationship between tree density and total epiphyte richness (SR_C) on the interior trees (r^2

= 0.384, p = 0.032) but not the edge trees (r^2 = 0.150, p = 0.213) (**Figure 4.26**). The relationship between tree density and bryophyte SR_C was close to significance on both the edge (r^2 = 0.296, p = 0.068) and interior trees (r^2 = 0.326, p = 0.053) (**Figure 4.26**). There was also a significant negative relationship between average DBH and total epiphyte richness on the interior trees (r^2 = 0.341, p = 0.046).

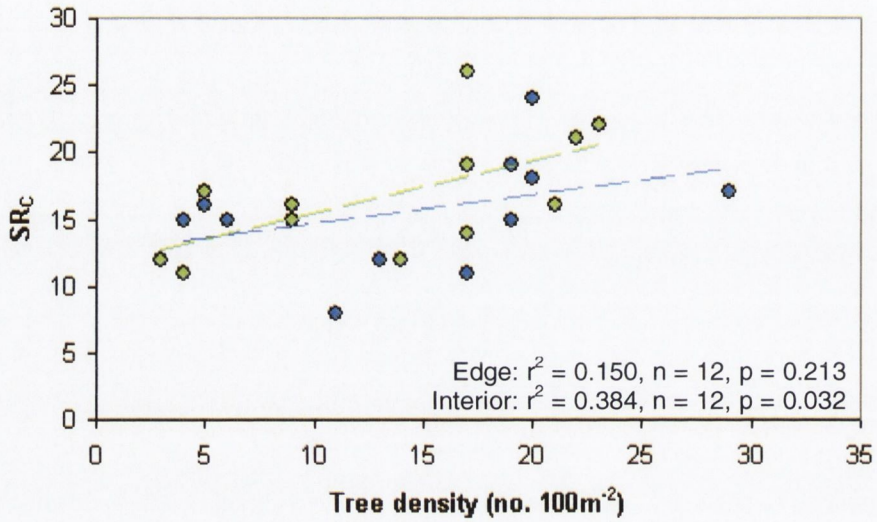
As only four of the twelve sites were within 1km of an area of old woodland, it was difficult to establish whether any relationship was present between this factor and species richness (SR_C). There appeared to be a negative relationship between total radiation incident on each site and total epiphyte and bryophyte richness (SR_C) but linear regression revealed that this was not statistically significant for edge (total epiphyte: r^2 = 0.104, p = 0.304; bryophyte: r^2 = 0.002, p = 0.896) or interior trees (total epiphyte: r^2 = 0.009, p = 0.769; bryophyte: r^2 = 0.052, p = 0.477). This was mainly as a result of the pair of trees from MUCK and CURA, two sites in the Wicklow cluster, which, despite having the lowest incident radiation, had only moderate epiphyte richness. Quadratic regression revealed a significant unimodal relationship between total incident radiation and total epiphyte richness for the edge trees (r^2 = 0.660, n = 12, p = 0.008) but not the interior trees (r^2 = 0.154, n = 12, p = 0.472) (**Figure 4.27a**). The relationship with bryophyte richness was significant for both edge and interior trees (edge: r^2 = 0.672, n = 12, p = 0.007; interior: r^2 = 0.586, n = 12, p = 0.019) (**Figure 4.27b**).

Neither canopy openness nor total transmitted radiation was significantly correlated with axis 1 of the NMS ordination (**Table 4.7**). To examine the effects of the open space variables on the edge trees, a separate NMS ordination of these trees was carried out (**Figure 4.28**). Wicklow and Cork stands were again separated on axis 1 of the ordination. Trees with high bryophyte cover were located to the top right of the NMS graphic and tended to have low canopy openness and low levels of transmitted radiation. Again, none of the open space variables was significantly correlated with axis one of the ordination (**Table 4.8**). However, two of the variables were negatively correlated with axis two, which was also strongly positively correlated with epiphyte cover (**Table 4.8**). Linear regression revealed a significant negative relationship between total epiphyte cover in the trunk plots ($Cover_{MT}$) of the edge trees and both canopy openness (r^2 = 0.354, p = 0.041) and total radiation transmitted (r^2 = 0.414, p = 0.024) at the centre of the open space (**Figure 4.29**).

4.3.5 Vertical distribution of epiphytes

The distribution of epiphyte species in the four height zones was examined on the edge and interior trees. The overall number of species recorded on the trunk at each of the height zones on the trees was greatest in the upper zone on both the edge and interior trees, as was the total number of lichen species (**Figure 4.30**). There was a lower or equal number of bryophyte species recorded in all

(a)



(b)

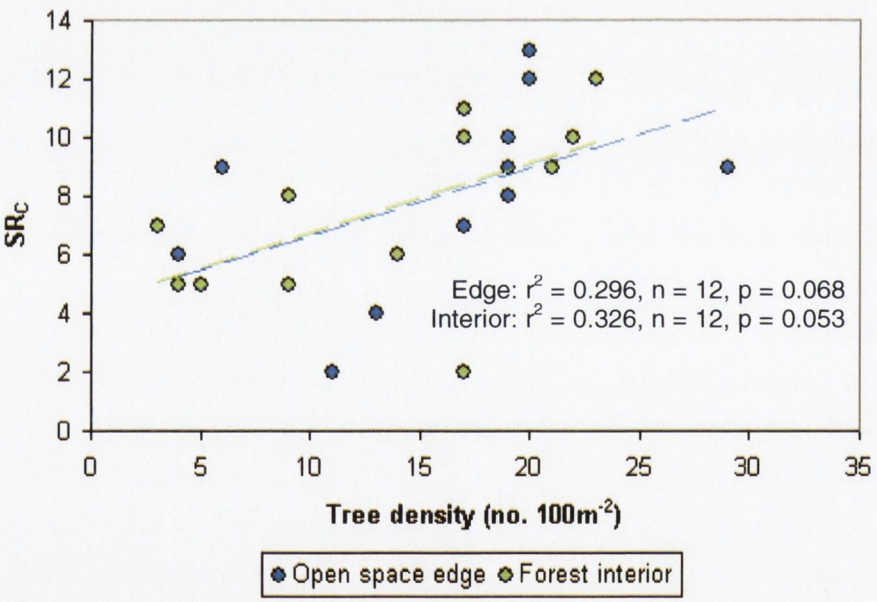
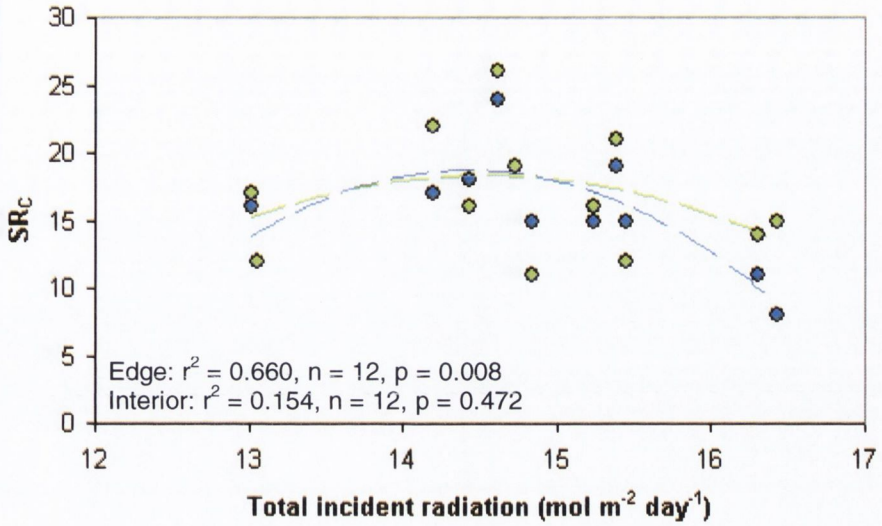


Figure 4.26 Relationship between tree density and (a) total epiphyte and (b) bryophyte species richness (SR_C).

(a)



(b)

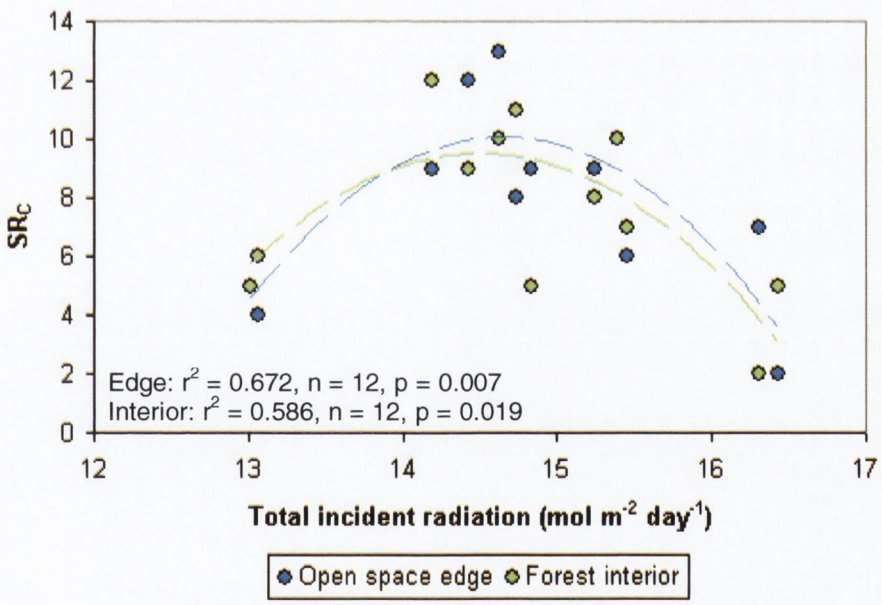


Figure 4.27 Relationship between total radiation incident on each site and (a) total epiphyte and (b) bryophyte species richness (SR_C).

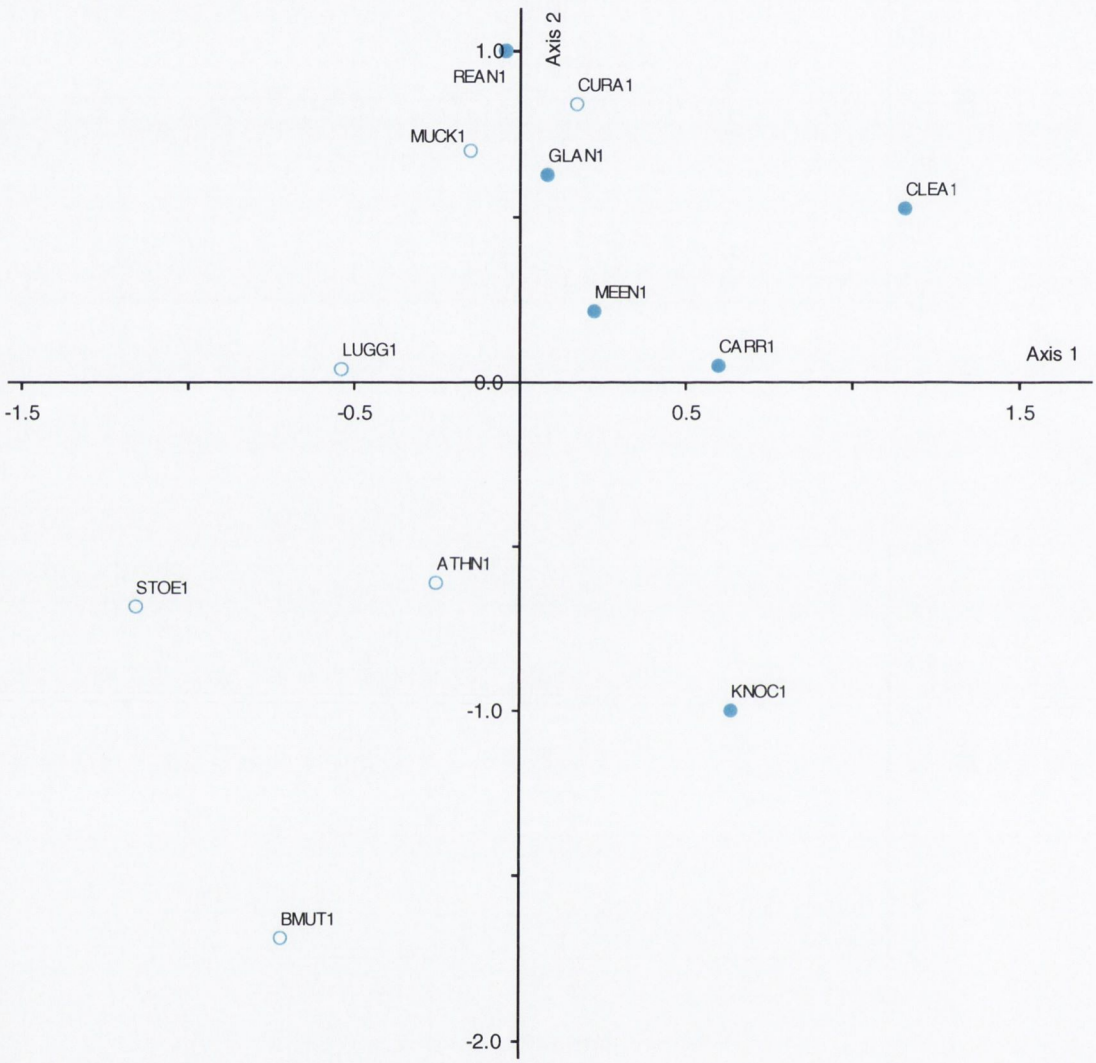
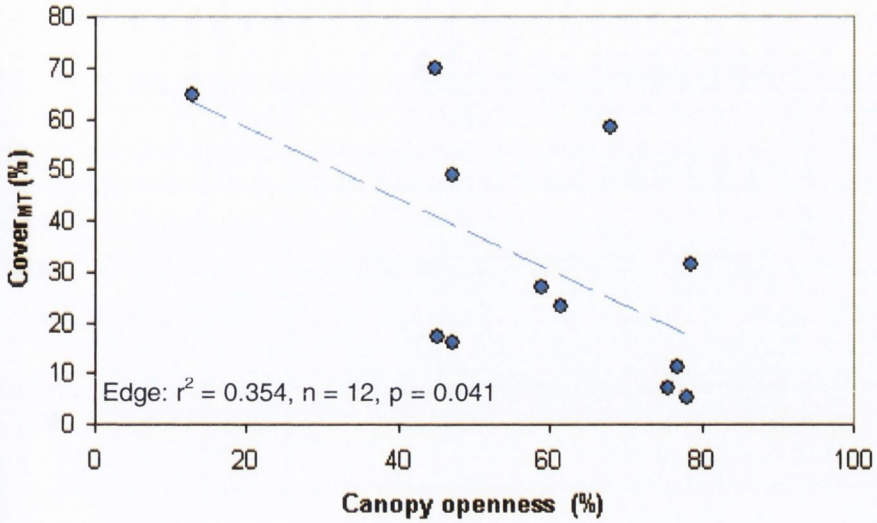


Figure 4.28 NMS ordination of the open space edge trees according to the sum of the epiphyte plot cover data for each tree. Wicklow (unshaded) and Cork cluster trees (shaded) are indicated. Final stress for the 2-dimensional solution = 8.35, final instability = 0.00047, axis 1 r^2 = 0. 320, axis 2 r^2 = 0.489.

(a)



(b)

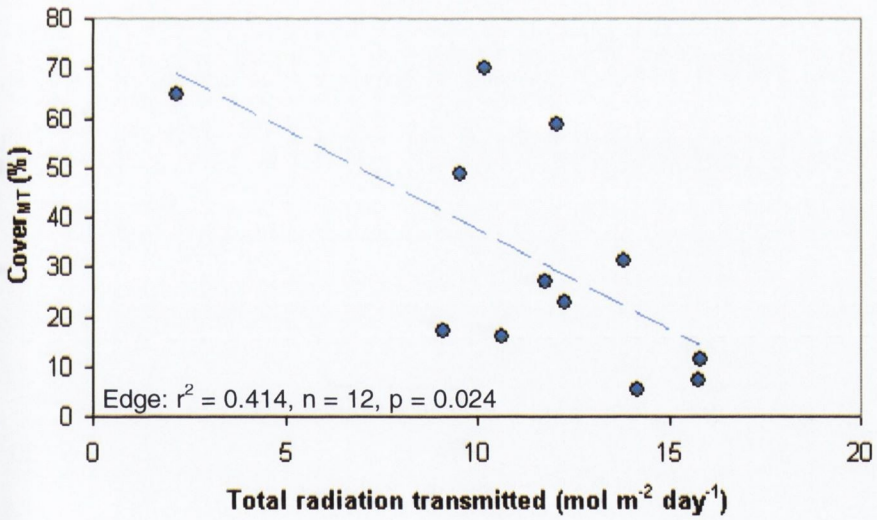
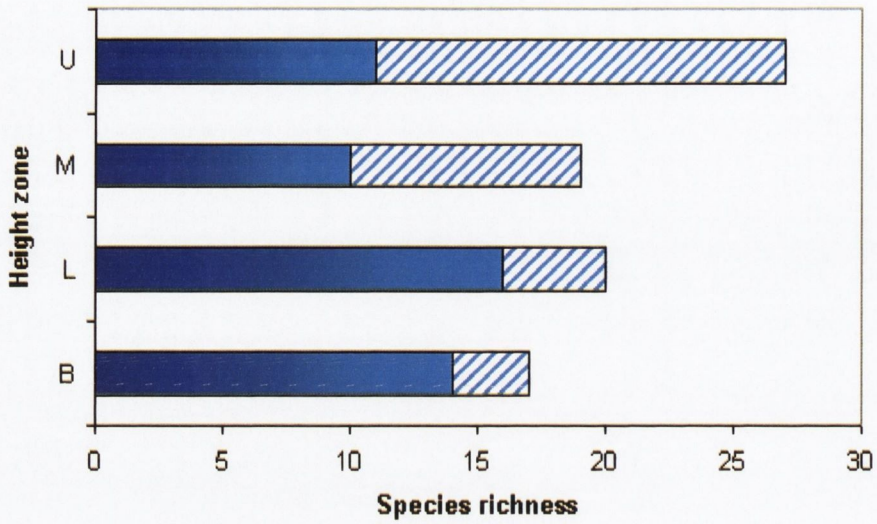


Figure 4.29 Relationship between (a) canopy openness and (b) total radiation transmitted at the centre of the open space and the mean total epiphyte cover in the trunk plots ($Cover_{MT}$) of the open space edge trees.

(a)



(b)

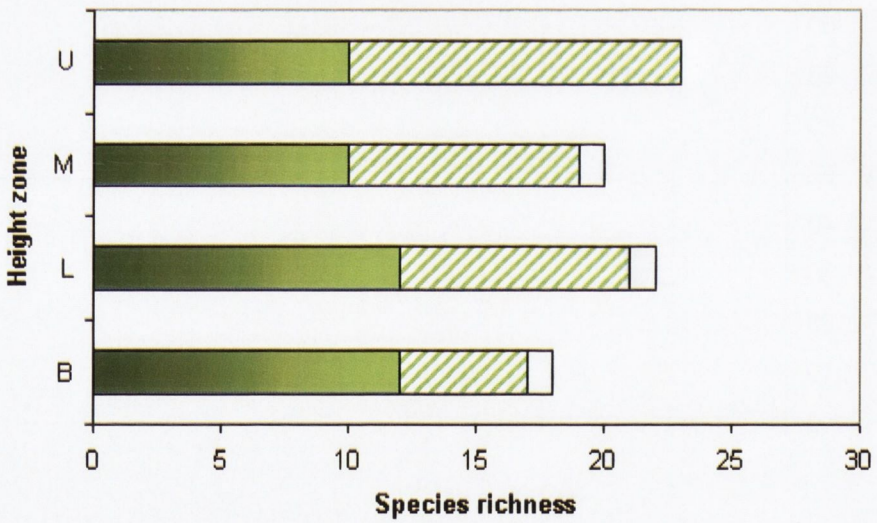


Figure 4.30 Overall number of species recorded in the four height zones (B = tree base, L= lower, M = middle, U = upper) on the trunks of all (a) open space edge and (b) forest interior trees. The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species are indicated.

height zones on the interior trees compared to the edge trees, while there was a lower or equal number of lichen species recorded in all height zones on the edge trees, with the exception of the upper zone. When the bryophyte and lichen species were further split into their different growth forms (cf. **Section 2.4.1** and **Appendix 3**) we can see that bryophyte wefts were only recorded in the tree base and lower zones on both edge and interior trees (**Figure 4.31**). Turfs were recorded only in the middle zone on the interior trees, but in all but the upper zone on the edge trees. Fruticose lichens were only present in the upper zone on the forest interior trees while they were present in both the middle and upper zones on the edge trees. (**Figure 4.32**)

Table 4.8 Pearson's correlations (r) between the axes from the NMS ordination of the open space edge trees (Figure 4.28) and selected diversity, cover and open space variables.

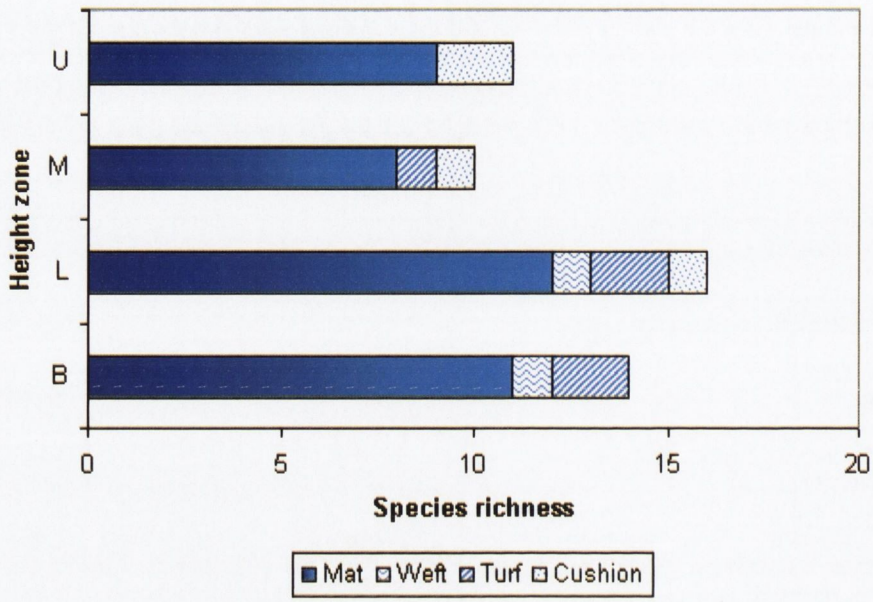
Correlation variable	Axis 1	Axis 2
Diversity:		
Total epiphyte SR_C	0.491	0.070
Bryophyte SR_C	0.397	-0.154
Lichen SR_C	0.334	0.336
Total epiphyte diversity ($1/D_M$)	0.561	0.173
Bryophyte diversity ($1/D_M$)	0.507	0.159
Lichen diversity ($1/D_M$)	0.574	0.226
Trunk total β_w diversity	-0.542	-0.423
Trunk bryophyte β_w diversity	-0.490	-0.503
Trunk lichen β_w diversity	0.176	-0.085
Cover:		
Trunk total epiphyte $Cover_{MT}$	0.192	0.799**
Trunk bryophyte $Cover_{MT}$	0.215	0.795**
Trunk lichen $Cover_{MT}$	-0.130	0.391
Open space:		
Open space width	0.183	0.113
Canopy openness	-0.248	-0.597*
Total transmitted radiation	-0.300	-0.599*

Note. * indicates the correlation coefficient is significant at $p < 0.05$ and ** indicates significance at $p < 0.01$.

A similar pattern as seen for total species richness was seen for mean species richness in each height zone (**Figure 4.33**). Bryophyte richness decreased and lichen richness increased with height on both edge and interior trees. There were significant differences in total epiphyte richness among the four height zones on the edge trees ($H = 9.00$, $df = 3$, $p = 0.029$) but not on the interior trees ($H = 0.56$, $df = 3$, $p = 0.905$) (**Figure 4.33**). There were also significant differences in lichen richness among the four height zones on the edge trees ($H = 37.47$, $df = 3$, $p < 0.001$), and, despite the lack of a significant difference in total epiphyte richness, there was a significant difference in bryophyte and lichen richness among the four height zones on the interior trees (bryophyte $H = 10.92$, $df = 3$, $p = 0.012$; lichen $H = 28.06$, $df = 3$, $p < 0.001$). Further testing revealed a significantly greater total epiphyte and lichen richness in the upper height zone of the edge trees compared with all other zones (**Figure 4.33**). Lichen richness was also significantly greater in the upper zone compared with all other zones on the interior trees.

As with species richness, bryophyte diversity decreased and lichen diversity increased with height on the forest interior trees, although the situation on the open space edge trees was not as clear-cut

(a)



(b)

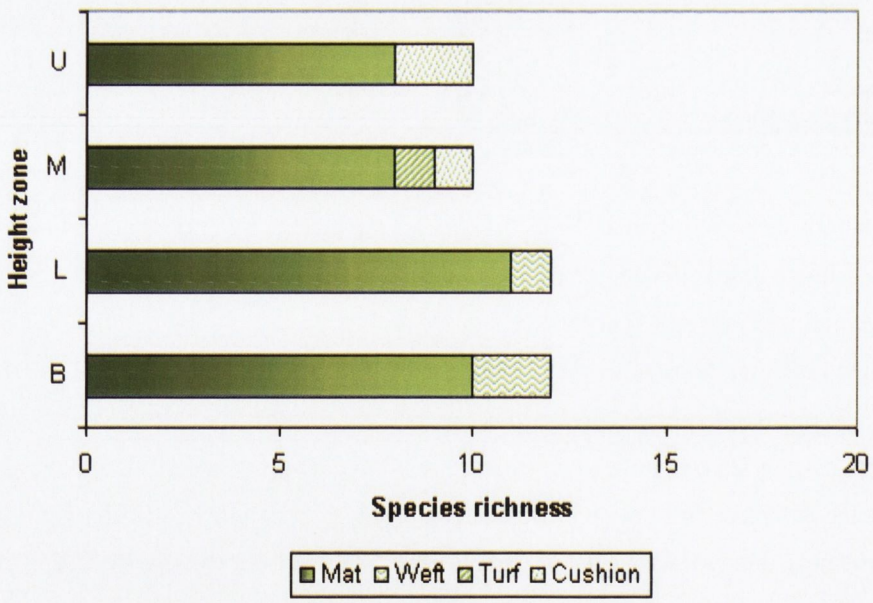
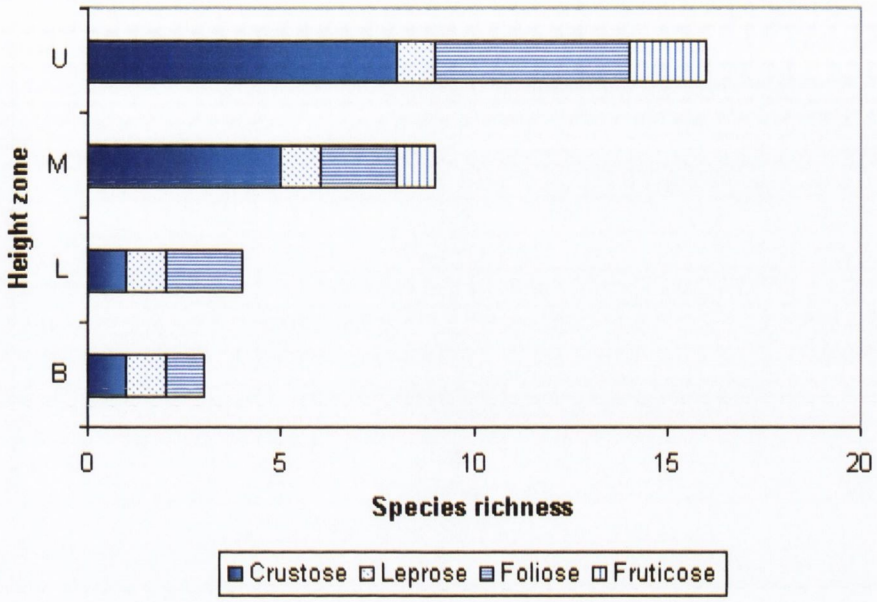


Figure 4.31 Relative proportions of the four bryophyte growth forms making up the overall bryophyte species richness in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of the (a) open space edge (n = 12) and (b) forest interior trees (n = 12).

(a)



(b)

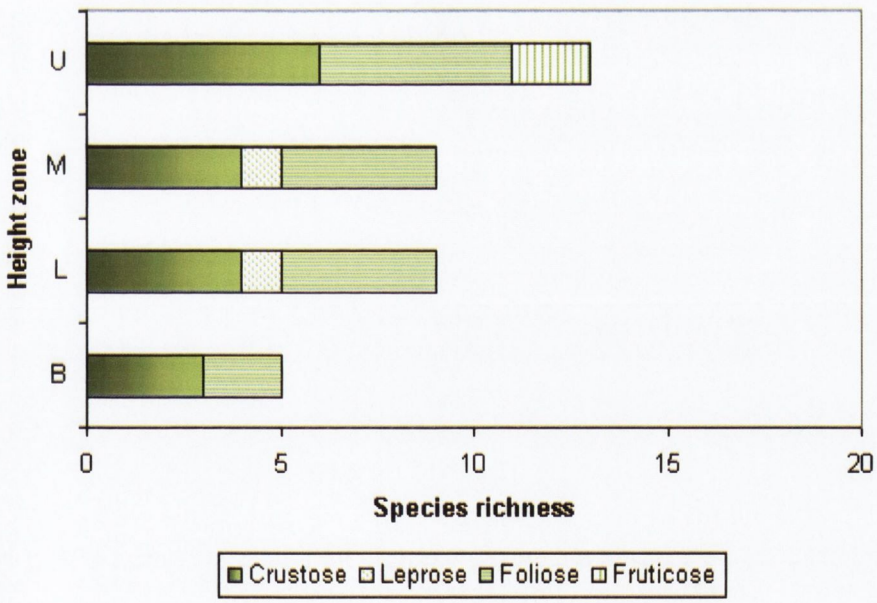
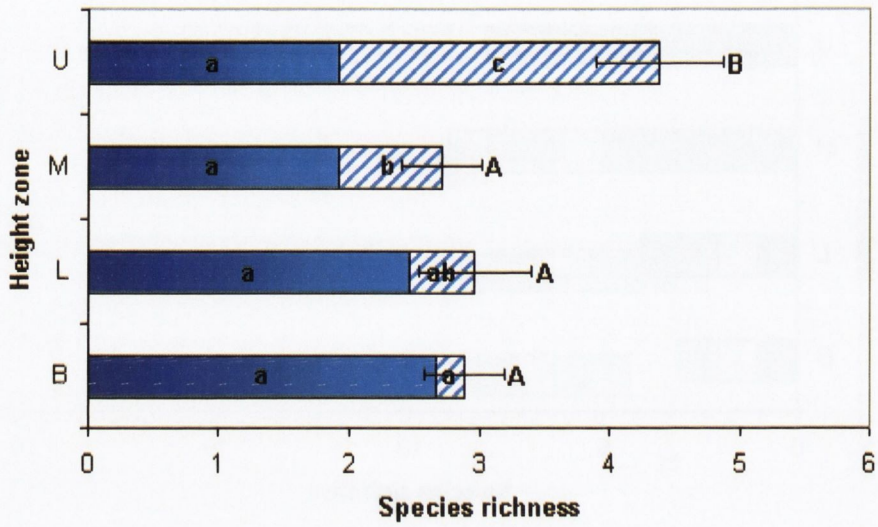


Figure 4.32 Relative proportions of the four lichen growth forms making up the overall lichen species richness in the four height zones (B = tree base, L = lower, M = middle, U = upper) on the trunks of the (a) open space edge (n = 12) and (b) forest interior trees (n = 12).

(a)



(b)

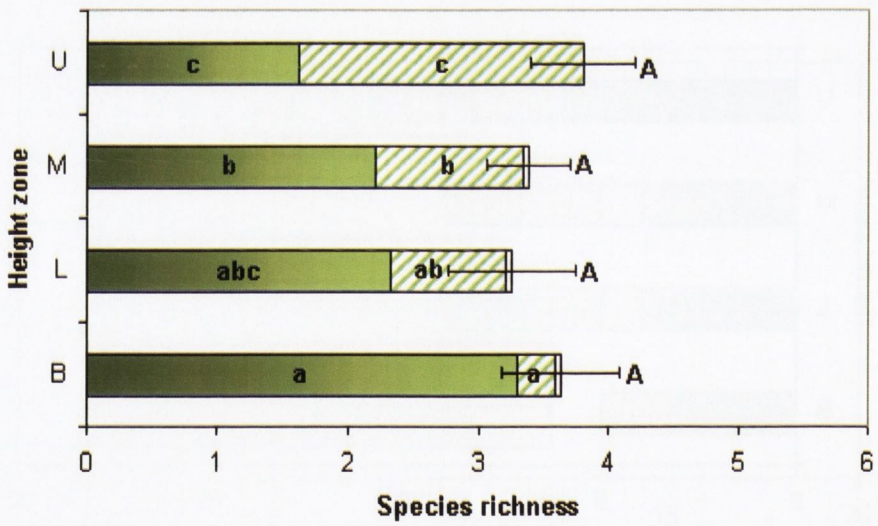


Figure 4.33 Mean epiphyte richness in the trunk plots in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 24) on all (a) open space edge and (b) forest interior trees. The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species (unshaded) are indicated. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) richness between two height zones if indicated by the same letter.

(**Figure 4.34**). There were significant differences in total epiphyte diversity among the four height zones on the edge trees (H = 11.11, df = 3, p = 0.011) but not on the interior trees (H = 2.29, df = 3, p = 0.515) (**Figure 4.34**). There were also significant differences in lichen diversity among the height zones on both the edge (H = 34.91, p < 0.001) and interior trees (H = 26.52, p < 0.001), but no significant differences in bryophyte diversity on either edge or interior trees (edge, H = 0.893, p = 0.827; interior, H = 5.557, p = 0.135). Further testing revealed a significantly greater total epiphyte and lichen diversity in the upper zone of the edge trees compared with all other zones (**Figure 4.34**). Lichen diversity was also significantly greater in the upper zone than all other zones on the forest interior trees.

There were significant differences in total epiphyte cover among the four height zones on the edge trees (H = 15.07, df = 3, p = 0.002), but not on the interior trees (H = 4.02, df = 3, p = 0.259) (**Figure 4.35**). There were, however, significant differences in bryophyte and lichen cover on both the edge (bryophyte cover, H = 25.24, df = 3, p < 0.001; lichen cover, H = 34.43, df = 3, p < 0.001) and interior trees (bryophyte cover, H = 13.03, df = 3, p = 0.005; lichen cover, H = 36.56, df = 3, p < 0.001). Bryophyte cover was significantly lower, and lichen cover significantly higher, in the upper zone than in all other zones on both trees (**Figure 4.35**). Total epiphyte and bryophyte cover were higher in the tree base and lower zones on the edge trees than on the interior trees and the difference was significant for the tree base (paired samples t-test: total epiphyte cover, p = 0.017; bryophyte cover, p = 0.020).

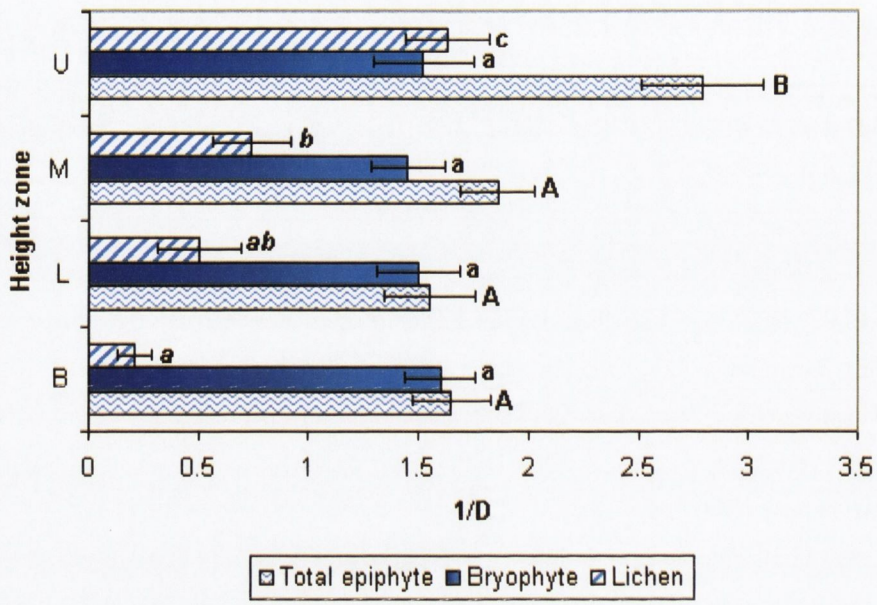
4.3.5.1 Epiphyte composition of the trunk plots

NMS ordination of the trunk plot data

The NMS ordination of the trunk plot data from the edge and interior trees (**Figure 4.36**) again highlights the variation in the species composition of the trunk plots. Axis 2 separates the plots from the four height zones to some extent. The strong correlation of plot height with this axis confirms this (**Table 4.9**). Plots at the top of axis two were characterised by high bryophyte cover. The group of mainly tree base and lower forest interior trunk plots which contained the '*Hypnum jutlandicum* community' (cf. **Section 3.3.4.1**) were located at the top left of the NMS graphic with the same plots from the open space edge trees from many of the same sites. Also grouped with them were tree base and lower plots from the south side of some edge trees whose forest interior counterparts had either a '*Metzgeria temperata* community' or 'species-poor community'. All these plots also had a '*Hypnum jutlandicum* community', with many of the plots from the south side of the edge trees also characterised by the presence of *Hypnum andoi*.

The plots from all heights on the forest interior trees with a '*Metzgeria temperata* community' were grouped together towards the top right hand side of the graphic along with tree base, lower and middle plots from the edge trees from the same sites which contained the same community. At the

(a)



(b)

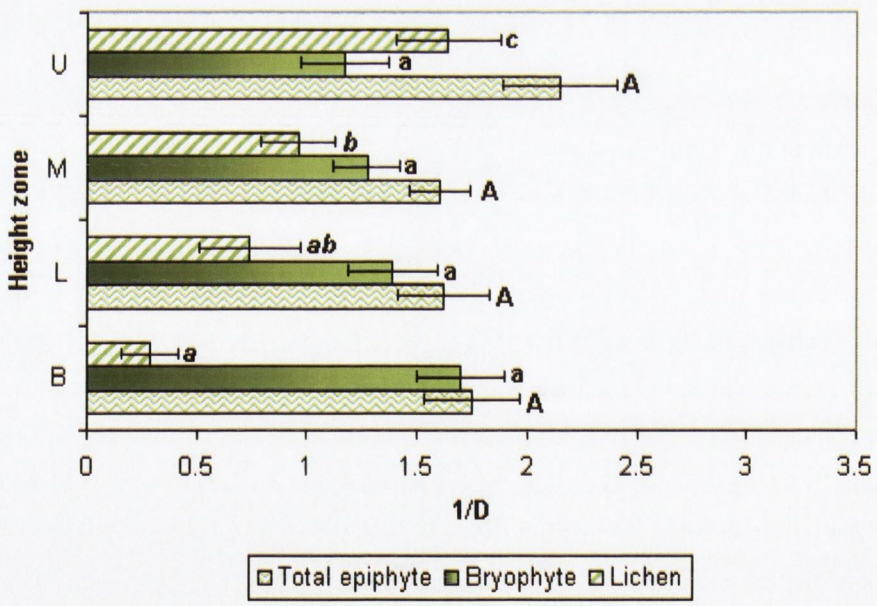
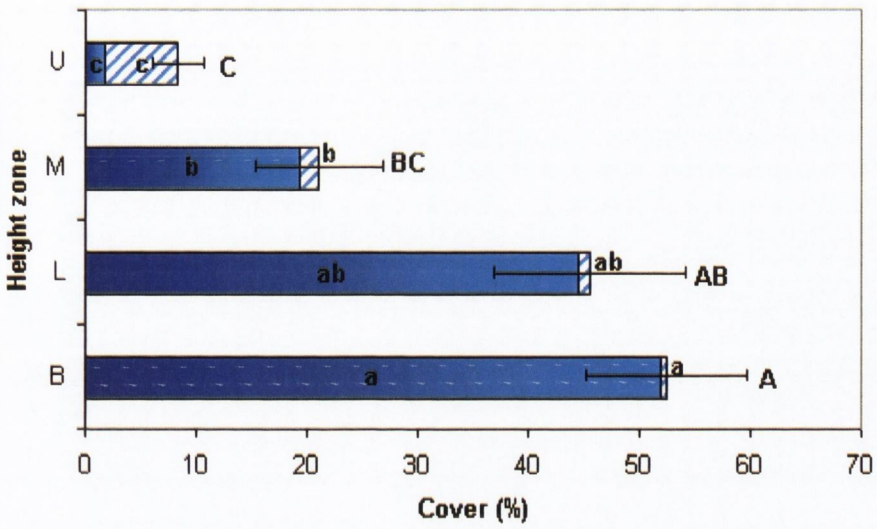


Figure 4.34 Mean epiphyte diversity (1/D) in the trunk plots in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 24) on all (a) open spaced edge and (b) forest interior trees. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase), bryophyte (lowercase) or lichen (lowercase italic) diversity between two height zones if indicated by the same letter.

(a)



(b)

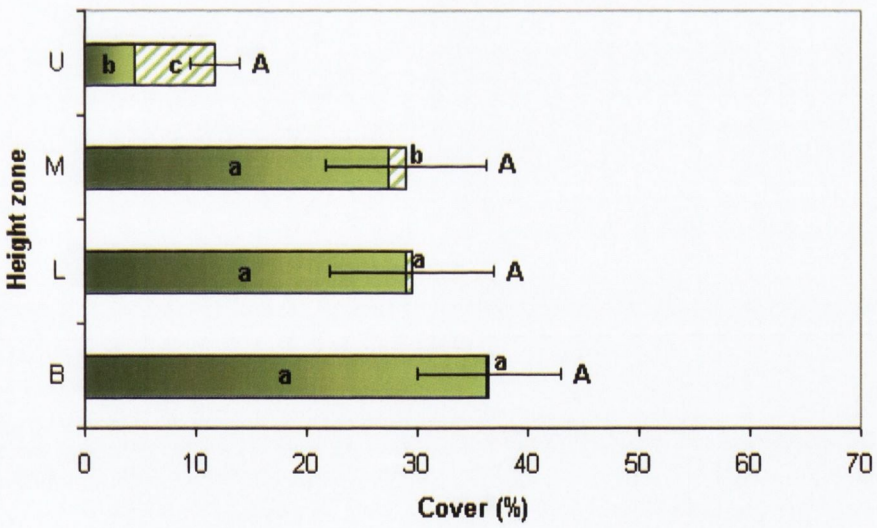


Figure 4.35 Mean epiphyte cover in the trunk plots in the four height zones (B = Tree base, L = Lower, M = Middle, U = Upper) (n = 24) on all (a) open space edge and (b) forest interior trees. The total epiphyte cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. There is no significant difference in total epiphyte (uppercase) or bryophyte and lichen (lowercase) cover between two height zones if indicated by the same letter.

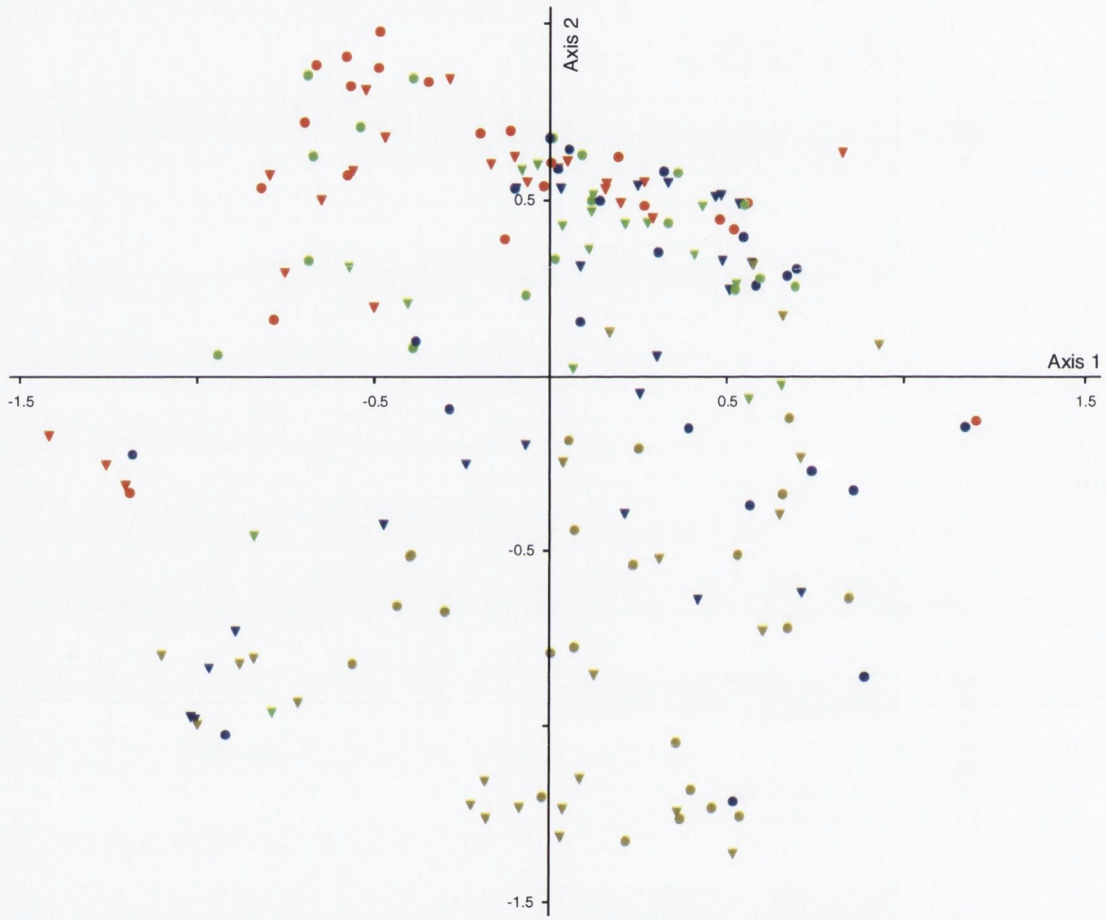


Figure 4.36 NMS ordination of the epiphyte composition of the trunk plots on the open space edge (circles) and forest interior trees (triangles). The four height zones (Tree base = red, Lower = green, Middle = dark blue, Upper = gold) are indicated. Final stress for the 3-dimensional solution = 19.25, final instability = 0.00049, axis 1 r^2 = 0. 116, axis 2 r^2 = 0.236.

bottom left of the NMS graphic, the group of middle and upper plots from forest interior trees with a '*Dimerella*-dominated community' were also grouped with three plots from edge trees which contained the same community. A group of middle and upper trunk plots, mainly from open space edge trees, but also including the two upper plots from a forest interior tree (KNOC2), were scattered in the centre of the NMS graphic and were characterised by the presence of *Frullania dilatata* and *Ulota crispa s.l.*. *F. dilatata* is relatively desiccation tolerant (Paton, 1999) and *Ulota* is found on trunks only where not too shaded (Hill *et al.*, 1994). Another group of middle and upper trunk plots scattered towards the bottom right of the graphic were mainly edge tree plots from the majority of the Cork cluster sites and some Wicklow cluster sites at high elevations. These were characterised by the foliose lichens *Hypotrachyna revoluta* and *Hypogymnia tubulosa*, both widespread lichen species found in both open and woodland situations (Dobson, 2005; Purvis *et al.*, 1992).

Table 4.9 Pearson's correlations (r) between the axes from the NMS ordination of the trunk plots (Figure 4.36) and selected diversity, cover and plot variables.

Correlation variable	Axis 1	Axis 2
Diversity:		
Total epiphyte SR	0.112	-0.004
Bryophyte SR	0.028	0.460**
Lichen SR	0.106	-0.513**
Low epiphytism affinity SR	-0.056	0.303**
Intermediate epiphytism affinity SR	-0.249**	0.316**
High epiphytism affinity SR	0.361**	-0.372**
Total epiphyte 1/D	-0.016	-0.206*
Bryophyte 1/D	-0.095	0.309**
Lichen 1/D	0.097	-0.473**
Cover:		
Total epiphyte cover	0.012	0.564**
Bryophyte cover	0.025	0.619**
Lichen cover	-0.069	-0.375**
Plot:		
Plot height	0.174	-0.688**
Tree girth at centre	-0.222*	0.653**
Inclination	-0.146	0.317**

Note. * indicates the correlation coefficient is significant at $p < 0.05$ and ** indicates significance at $p < 0.01$.

4.3.5.2 Epiphyte composition of the branch plots

The '*Dimerella*-dominated community', which was present on the middle branches of the Wicklow cluster spruce trees (cf. **Section 3.3.5.1**), was also present in four plots on branches from the edge trees; these were mainly middle branches on trees from the same stands. The '*Microlejeunea* and *Ulota* community', which was present on the branches of a number of the forest interior spruce trees, was also found on the edge trees from the same stands. The '*Metzgeria temperata* community', found on the branches of forest interior trees from spruce stands on peat or at high elevations with shaded aspects, was also found mainly on middle branches from the edge trees from the same sites. The '*Fuscidea* and *Lecanora* community', present mainly on the upper branches of some forest interior spruce trees, was also present mainly on the upper branches on the edge trees, although *Lecanora pulicaris* was not as important a component of this community on

spruce as it was on larch (cf. **Section 3.3.5.1**). The '*Micarea peliocarpa* community', found on upper branches in high elevation Wicklow cluster spruce stands, was also present on the upper branches of the edge trees from the same stands. Plots on the middle and upper branches, mainly on edge trees from more heavily thinned stands, contained a community characterised by the presence of the foliose lichen, *Physcia tenella*, which is common in well-lit situation (Dobson, 2005).

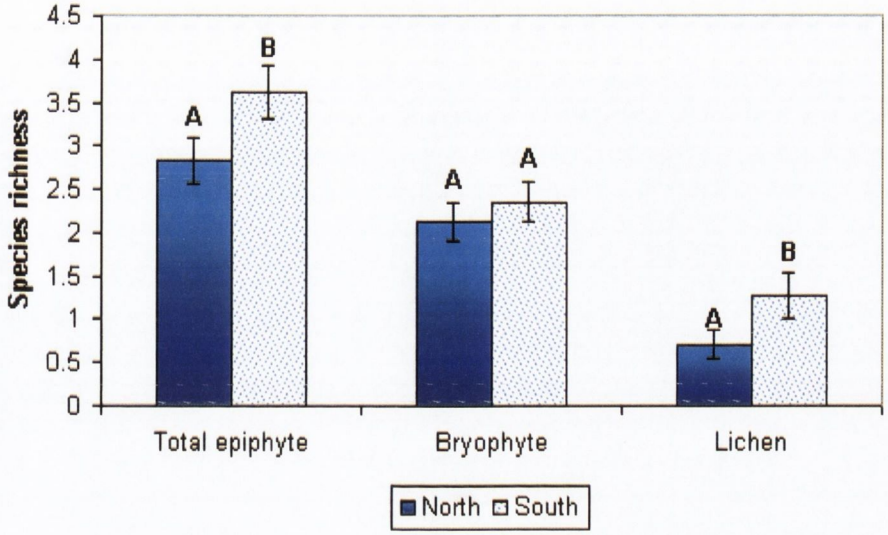
4.3.6 The effects of aspect on epiphytes

There was a significantly greater total epiphyte and lichen richness in the plots on the south side of the trunks of the edge trees than in those on the north side (Wilcoxon signed ranks test: total epiphyte, $p = 0.016$; lichen, $p = 0.004$) but no significant difference in bryophyte richness (Wilcoxon signed ranks test: bryophyte, $p = 0.407$) (**Figure 4.37a**). In contrast, there were no significant differences in total epiphyte, bryophyte or lichen richness between the north and south sides of the trunks of the interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.893$; bryophyte, $p = 0.737$; lichen, $p = 0.364$) (**Figure 4.37b**). The significantly greater total epiphyte and lichen richness on the south side of the edge trees was not as a result of an increase in species richness relative to the south side of the forest interior trees, as there was no significant difference in total epiphyte, bryophyte or lichen species richness between the south sides of the edge and interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.998$; bryophyte, $p = 0.899$; lichen, $p = 0.808$). The difference was as a result of a significantly lower total epiphyte and lichen richness on the north side of the edge trees in comparison to (i) the north side of the interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.018$; bryophyte, $p = 0.199$; lichen, $p = 0.008$) and (ii) the south side of the edge trees.

There was a significantly higher lichen diversity (1/D) in the plots on the south side of the trunks of the edge trees (Wilcoxon signed ranks test: $p = 0.019$) and the greater total epiphyte diversity on the south side was close to significance (Wilcoxon signed ranks test: $p = 0.070$) (**Figure 4.38a**). In contrast, there were no significant differences in total epiphyte, bryophyte or lichen diversity between the north and south sides of the trunks of the interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.761$; bryophyte, $p = 0.613$; lichen, $p = 0.413$) (**Figure 4.38b**). As with species richness, the difference in lichen diversity was as a result of a lower diversity on the north side of the edge trees compared with the north side of the interior trees (Wilcoxon signed ranks test: $p = 0.010$); there was no significant difference in lichen diversity between the south sides of the edge and interior trees (Wilcoxon signed ranks test: $p = 0.992$).

As with species richness and diversity, there was significantly greater total epiphyte, bryophyte and lichen cover on the south side of the trunks of the edge trees compared with the north side (Wilcoxon signed ranks test: total epiphyte cover, $p < 0.001$; bryophyte cover, $p = 0.008$; lichen

(a)



(b)

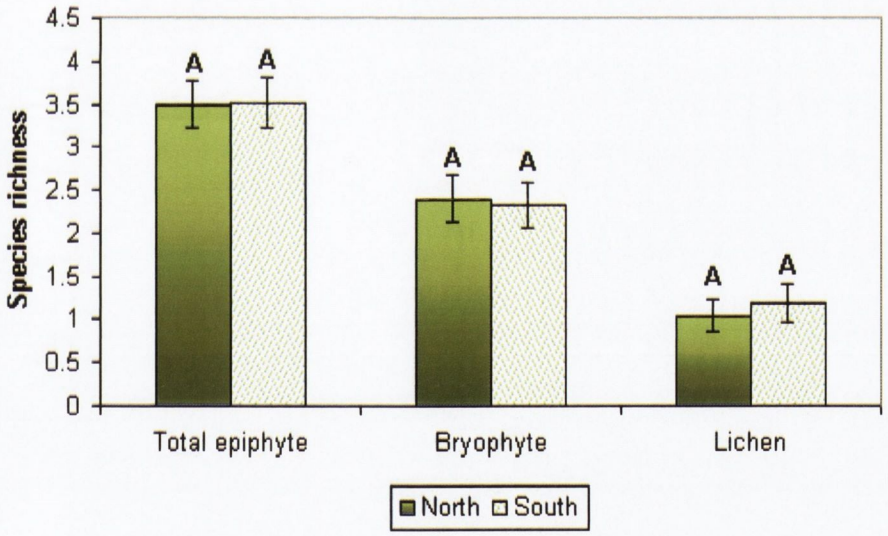
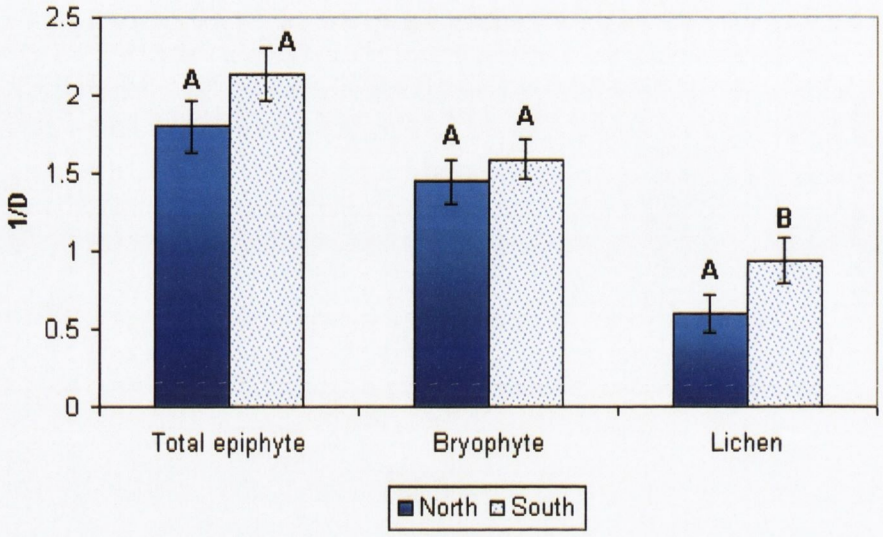


Figure 4.37 Mean total epiphyte, bryophyte and lichen species richness in the trunk plots on the north (n = 48) and south sides (n = 48) of the (a) open space edge and (b) forest interior trees. Error bars indicate ± standard error. There is no significant difference in species richness between the two aspects if indicated by the same letter.

(a)



(b)

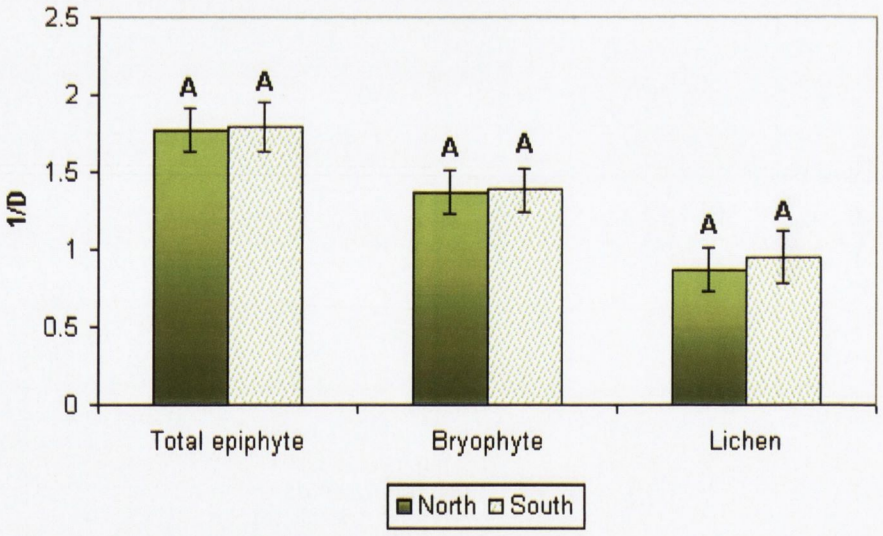


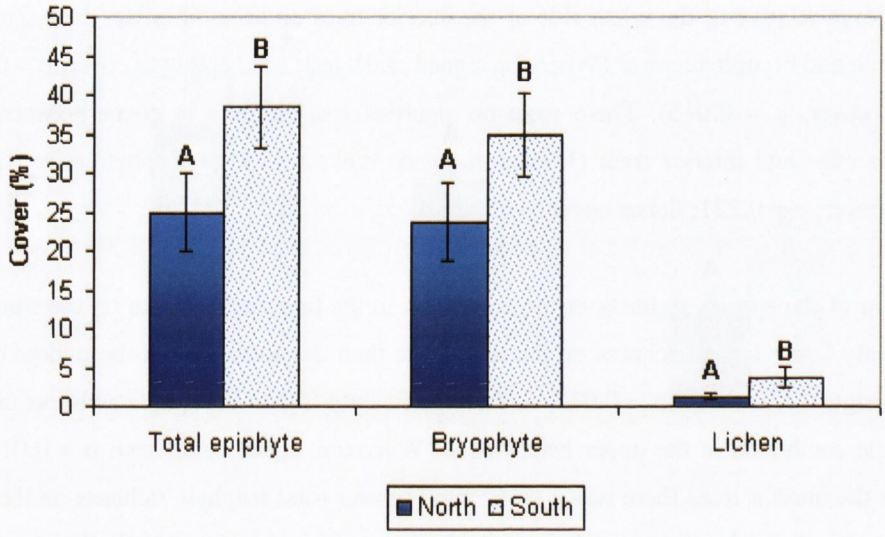
Figure 4.38 Mean total epiphyte, bryophyte and lichen diversity (1/D) in the trunk plots on the north (n = 48) and south sides (n = 48) of the (a) open space edge and (b) forest interior trees. Error bars indicate ± standard error. There is no significant difference in diversity between the two aspects if indicated by the same letter.

cover, p = 0.016) (**Figure 4.39a**). Again, in contrast, there were no significant differences in total epiphyte, bryophyte or lichen cover between the north and south sides of the trunks of the interior trees (Wilcoxon signed ranks test: total epiphyte cover, p = 0.908; bryophyte cover, p = 0.473; lichen cover, p = 0.344) (**Figure 4.39b**). In contrast to the situation with species richness and diversity, the significantly greater cover on the south side of the edge trees was as a result of increased cover relative to the south side of the interior trees and the difference was significant for total epiphyte and bryophyte cover (Wilcoxon signed ranks test: total epiphyte cover, p = 0.025; bryophyte cover, p = 0.015). There were no significant differences in cover between the north sides of the edge and interior trees (Wilcoxon signed ranks test: total epiphyte cover, p = 0.373; bryophyte cover, p = 0.221; lichen cover, p = 0.777).

Examination of the species richness of the edge trees in the four height zones on the trunk revealed a significantly lower lichen richness on the north side than the south side in the middle height zone (Wilcoxon signed ranks test: p = 0.031) and a significantly higher bryophyte richness on the north side than the south side in the upper height zone (Wilcoxon signed ranks test: p = 0.016) (**Figure 4.40a**). On the interior trees there was a significantly lower total epiphyte richness on the north side than the south side in the upper height zone (paired samples t-test: p = 0.042) (**Figure 4.40b**). As with species richness, there was a significantly lower lichen diversity on the north side than the south side in the middle height zone (Wilcoxon signed ranks test: p = 0.024) and a significantly higher bryophyte richness on the north side than the south side in the upper height zone on the edge trees (Wilcoxon signed ranks test: p = 0.027) (**Figure 4.41**). There were no significant differences in diversity between the north and south sides of the interior trees (**Figure 4.42**). The difference in cover between the north and south sides in the four height zones was more striking. There was a significantly greater total epiphyte and bryophyte cover on the south side of the edge trees at both the tree base (paired samples t-test: total epiphyte, p = 0.020; bryophyte, p = 0.027) and lower height zones (Wilcoxon signed ranks test: total epiphyte, p = 0.008; bryophyte, p = 0.024) (**Figure 4.43a**). On the interior trees there was a significantly greater total epiphyte and lichen cover on the south side than the north side in the upper height zone (Wilcoxon signed ranks test: total epiphyte, p = 0.006; lichen, p =0.023) (**Figure 4.43b**).

The situation in the branch plots was different from that in the trunk plots. Species richness was not compared as the area available for epiphyte colonisation differed among branch plots (cf. **Figure 2.3**). However, diversity and cover, expressed as a percentage of the cover of branches within each plot, were compared. There were no significant differences in diversity between the plots on the north and south facing branches on either the edge (Wilcoxon signed ranks test: total epiphyte, p = 0.340; bryophyte, p = 0.169; lichen, p = 0.562) or interior trees (Wilcoxon signed ranks test: total epiphyte, p = 0.635; bryophyte, p = 0.989; lichen, p = 0.701) (**Figure 4.44**). When the plots on branches on the north side of the edge trees were compared with those on the north side of the

(a)



(b)

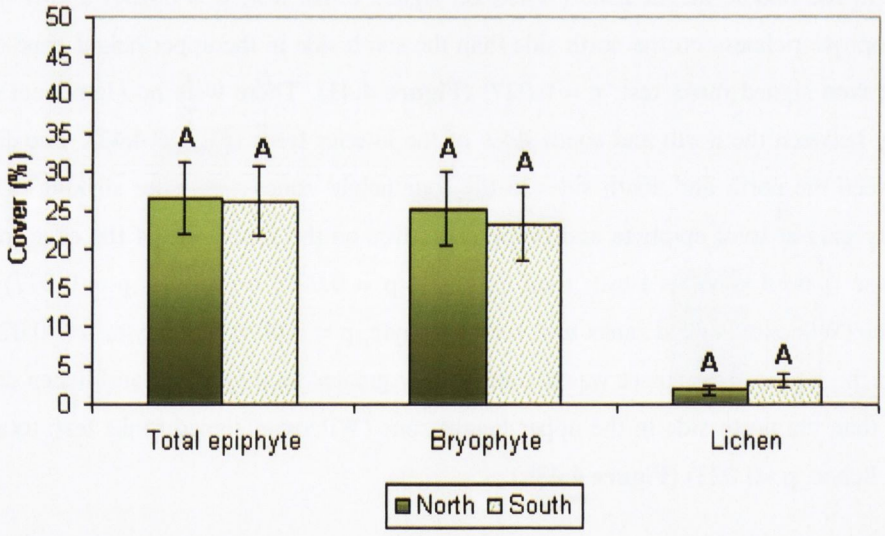


Figure 4.39 Mean total epiphyte, bryophyte and lichen cover in the trunk plots on the north (n = 48) and south sides (n = 48) of the (a) open space edge and (b) forest interior trees. Error bars indicate ± standard error. There is no significant difference in cover between the two aspects if indicated by the same letter.

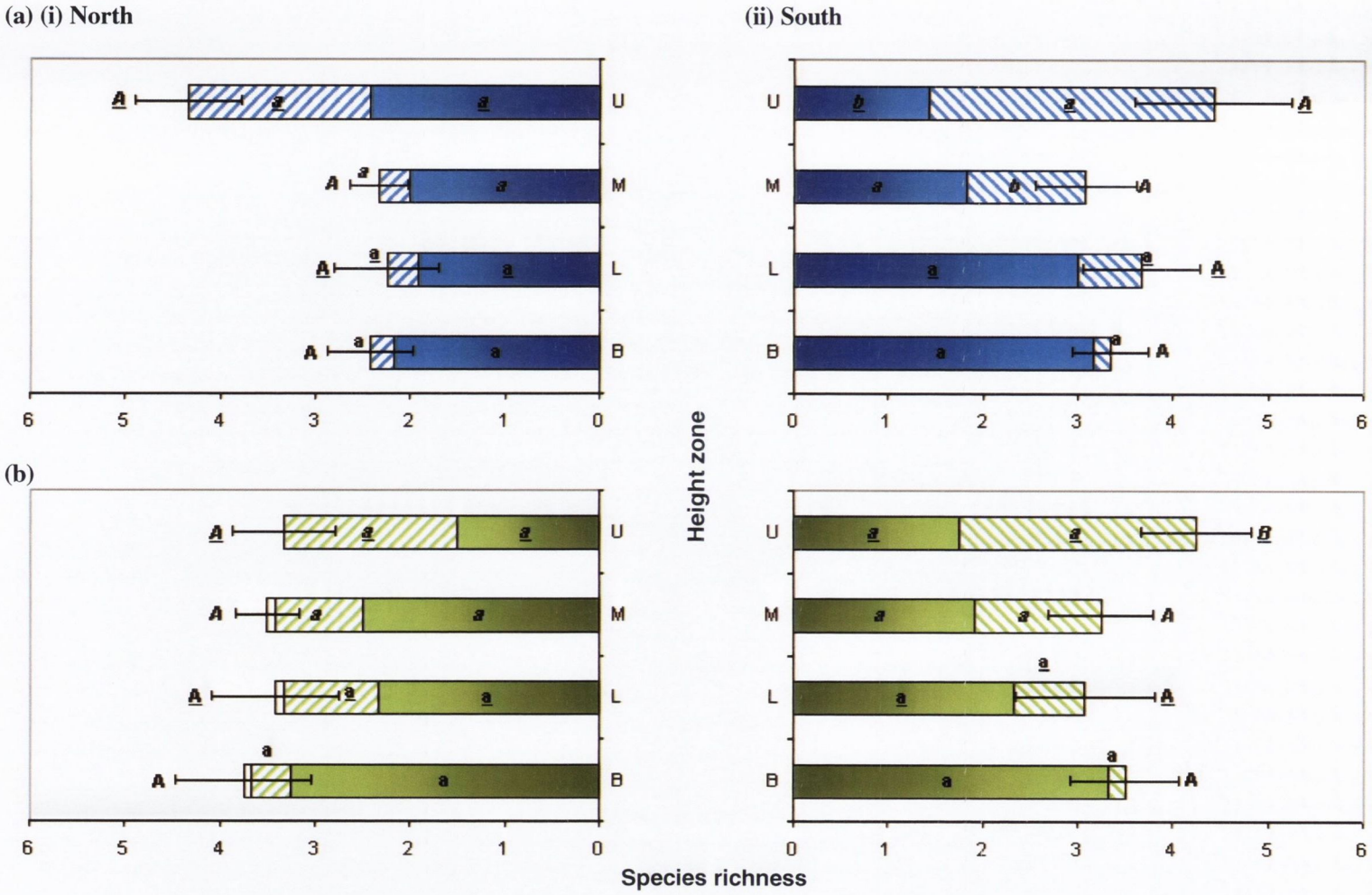


Figure 4.40 Mean epiphyte species richness on the (i) north and (ii) south sides of the trunks of the (a) open space edge (n = 12) and (b) forest interior (n = 12) trees in the four height zones (B = tree base, L = lower, M = middle, U = upper). The total epiphyte richness is shown and the relative proportions of bryophyte (shaded), lichen (hatched) and vascular plant species (unshaded) are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) richness between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

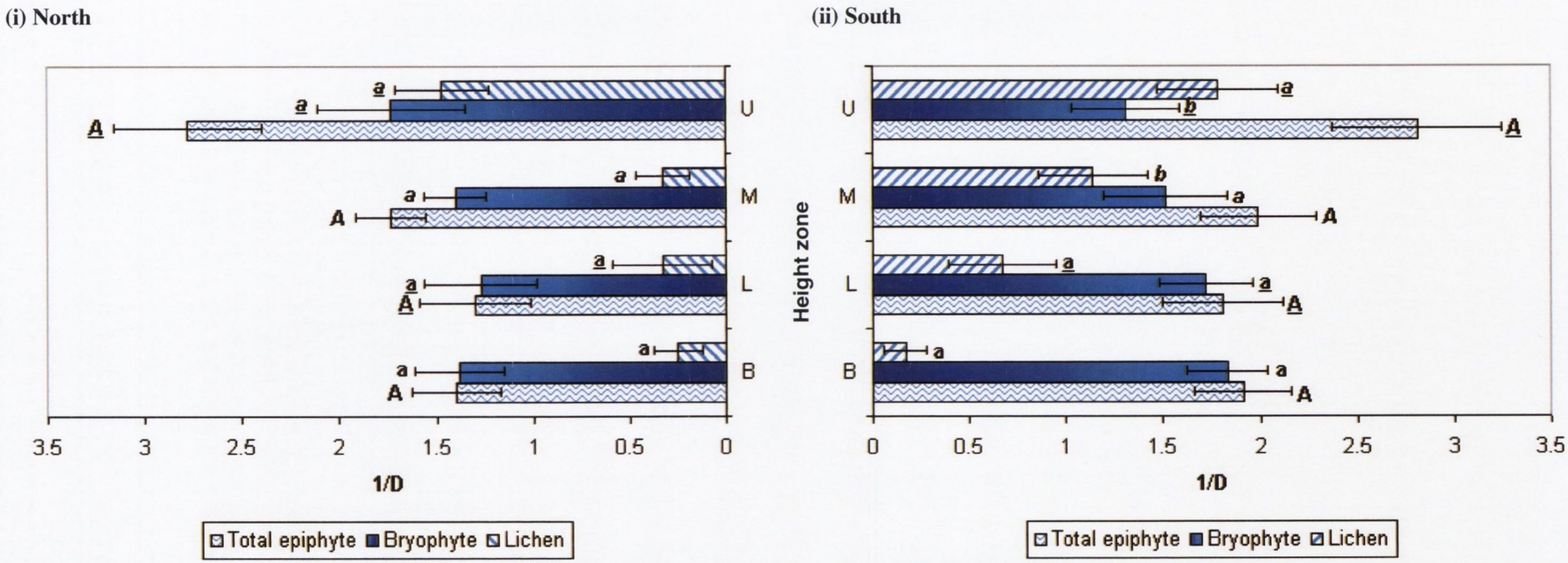


Figure 4.41 Mean epiphyte diversity (1/D) on the (i) north and (ii) south sides of the trunks of the open space edge trees in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 12). Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) diversity between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

(ii) North

(ii) South

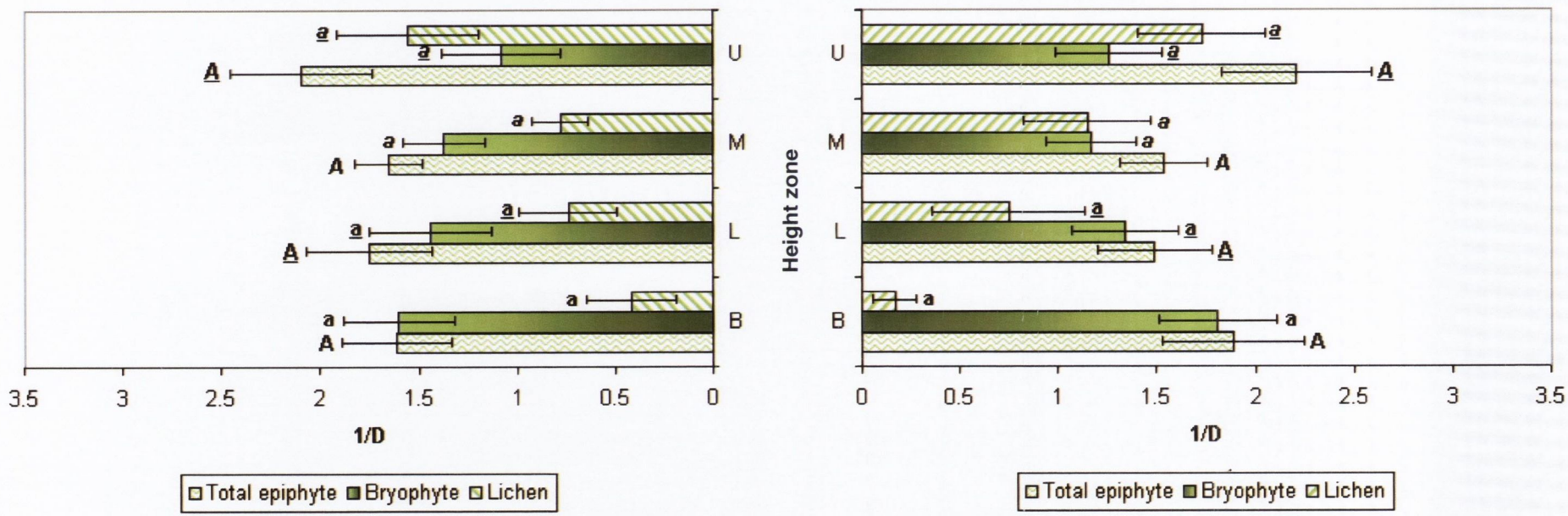


Figure 4.42 Mean epiphyte diversity (1/D) on the (i) north and (ii) south sides of the trunks of the forest interior trees in the four height zones (B = tree base, L = lower, M = middle, U = upper) (n = 12). Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) diversity between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

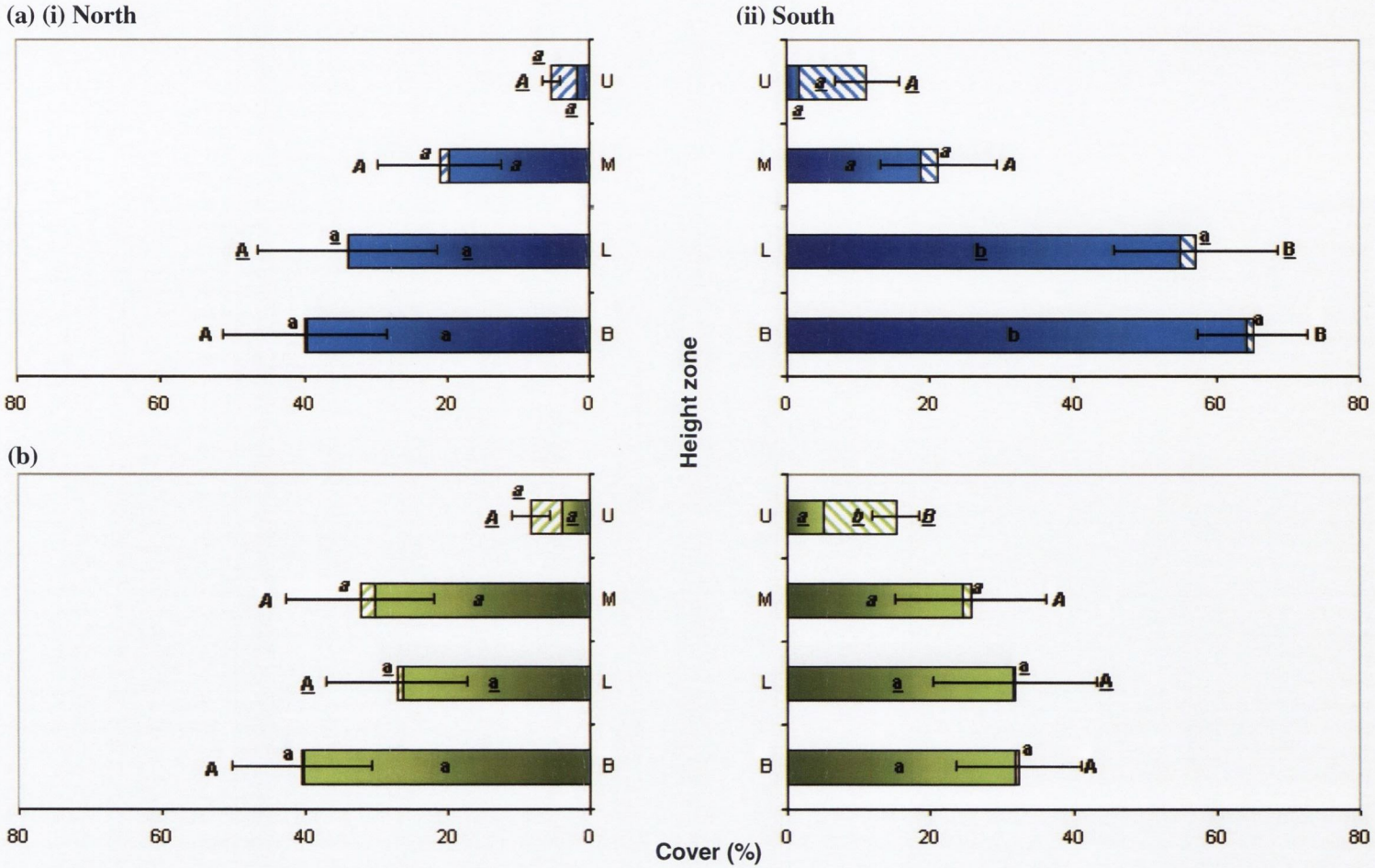
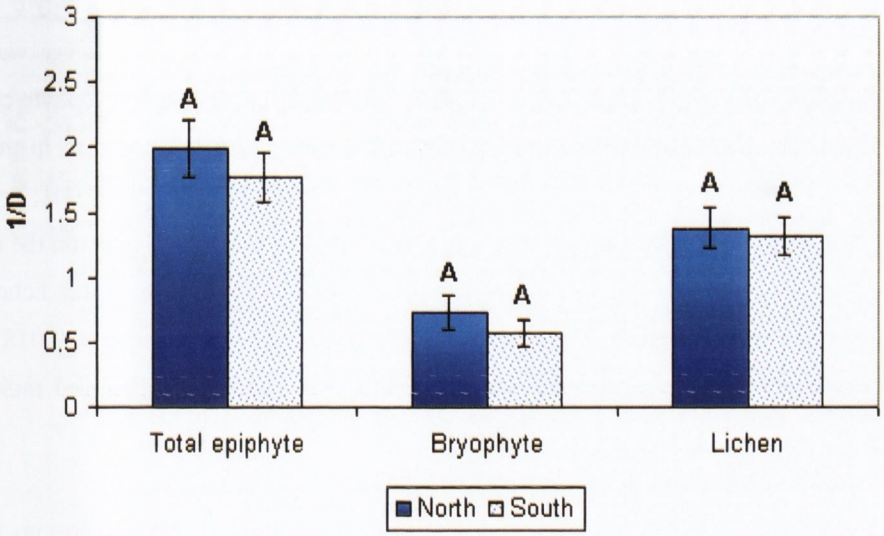


Figure 4.43 Mean epiphyte cover on the (i) north and (ii) south sides of the trunks of the (a) open space edge (n = 12) and (b) forest interior trees (n = 12) in the four height zones (B = tree base, L = lower, M = middle, U = upper). The total cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) cover between north and south in that height zone. Normal text compares B, underline compares L, italic compares M and underline italic compares U.

(a)



(b)

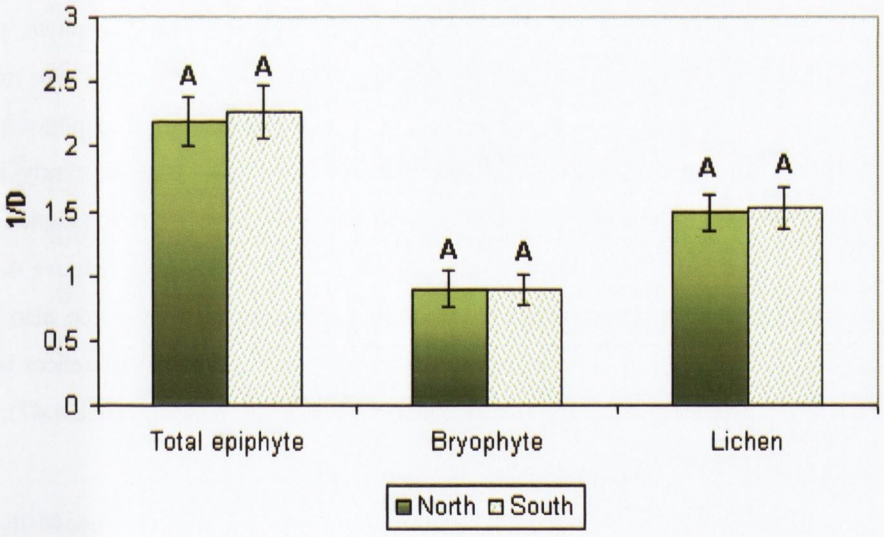


Figure 4.44 Mean total epiphyte, bryophyte and lichen diversity (1/D) in the branch plots on the north and south sides of the (a) open space edge (n = 72) and (b) forest interior trees (n = 70). Error bars indicate ± standard error. There is no significant difference in diversity between the two aspects if indicated by the same letter.

interior trees, a significantly greater lichen diversity was found on the interior trees (Wilcoxon signed ranks test: $p = 0.010$). There were no significant differences in diversity between the plots on branches on the south side of the edge and interior trees. In contrast to the situation on trunks, total epiphyte, bryophyte and lichen cover were lower in the branch plots on the south side of the edge trees than on the north side (**Figure 4.45a**). The difference for total epiphyte cover was significant (Wilcoxon signed ranks test: $p = 0.017$) and that for bryophyte cover was close to significance (Wilcoxon signed ranks test: $p = 0.056$). The total epiphyte and bryophyte cover in the branch plots on the south side of the edge trees was also significantly lower than in those on the south side of the interior trees (Wilcoxon signed ranks test: total epiphyte, $p = 0.001$, bryophyte, $p < 0.001$). There were no significant differences in cover between the branch plots on the north sides of the edge and interior trees. On the interior trees there was a significantly higher lichen cover in the branch plots on the south side of the trees (Wilcoxon signed ranks test: $p = 0.018$) and total cover was also higher on the south side but not significantly so (Wilcoxon signed ranks test $p = 0.158$) (**Figure 4.45b**).

When the middle and upper branches were examined separately, there were no significant differences in total epiphyte, bryophyte or lichen diversity between the plots on the north and south facing branches in either height zone on either the edge (Wilcoxon signed ranks test: middle, total epiphyte, $p = 0.263$; bryophyte, $p = 0.097$; lichen, $p = 0.470$; upper, total epiphyte, $p = 0.918$; bryophyte, $p = 0.763$; lichen, $p = 0.963$) or interior trees (Wilcoxon signed ranks test: middle, total epiphyte, $p = 0.888$; bryophyte, $p = 0.775$; lichen, $p = 0.904$; upper, total epiphyte, $p = 0.477$; bryophyte, $p = 0.627$; lichen, $p = 0.494$) (**Figure 4.46**). There was a significantly lower total epiphyte (Wilcoxon signed ranks test: $p = 0.032$) and bryophyte cover (Wilcoxon signed ranks test: $p = 0.011$) in the plots on the south facing middle branches of the edge trees (**Figure 4.47**). In the upper height zone there was a significantly lower lichen cover on the south side also (Wilcoxon signed ranks test, $p = 0.031$). On the interior trees there were no significant differences between the plots on the north and south sides in either the middle or upper height zones (**Figure 4.47**).

4.4 DISCUSSION

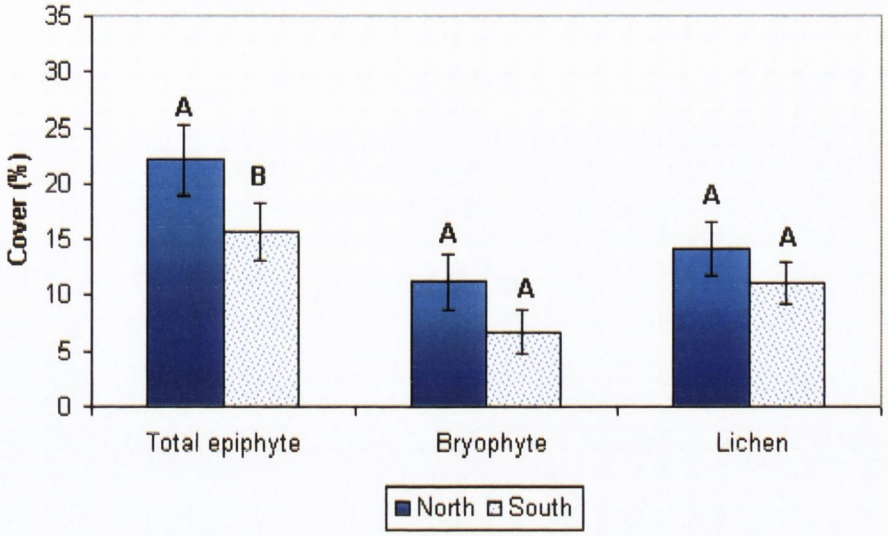
4.4.1 Epiphyte diversity

4.4.1.1 Effect of open spaces

Tree diversity

The same number of species were recorded in total on the open space edge and forest interior trees. At the individual tree level, there were also no significant differences in the total epiphyte, bryophyte or lichen richness between the edge and interior trees, nor was there a difference in the mean diversity of all plots studied on the edge and interior trees, as measured by Simpson's reciprocal.

(a)



(b)

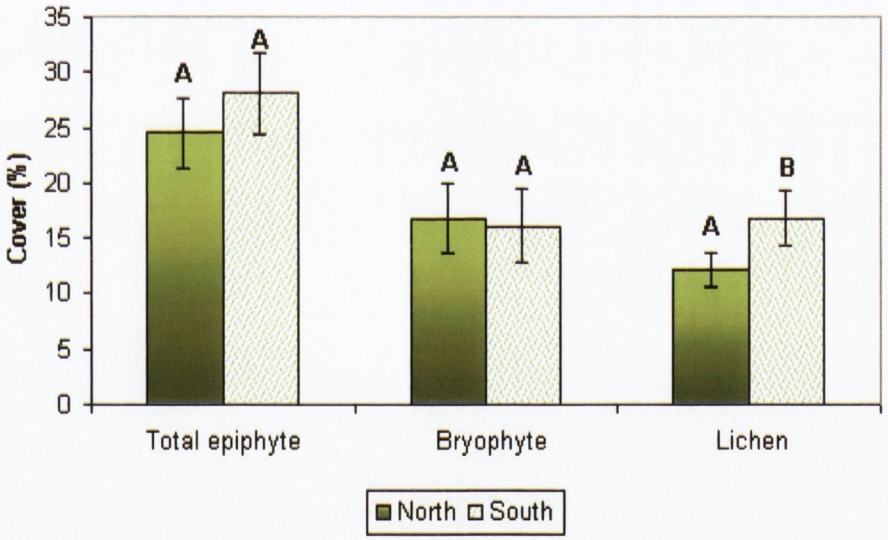


Figure 4.45 Mean total epiphyte, bryophyte and lichen cover in the branch plots on the north and south sides of the (a) open space edge (n = 72) and (b) forest interior trees (n = 70). Cover is expressed as a percentage of the cover of branches within each plot. Error bars indicate ± standard error. There is no significant difference in cover between the two aspects if indicated by the same letter.

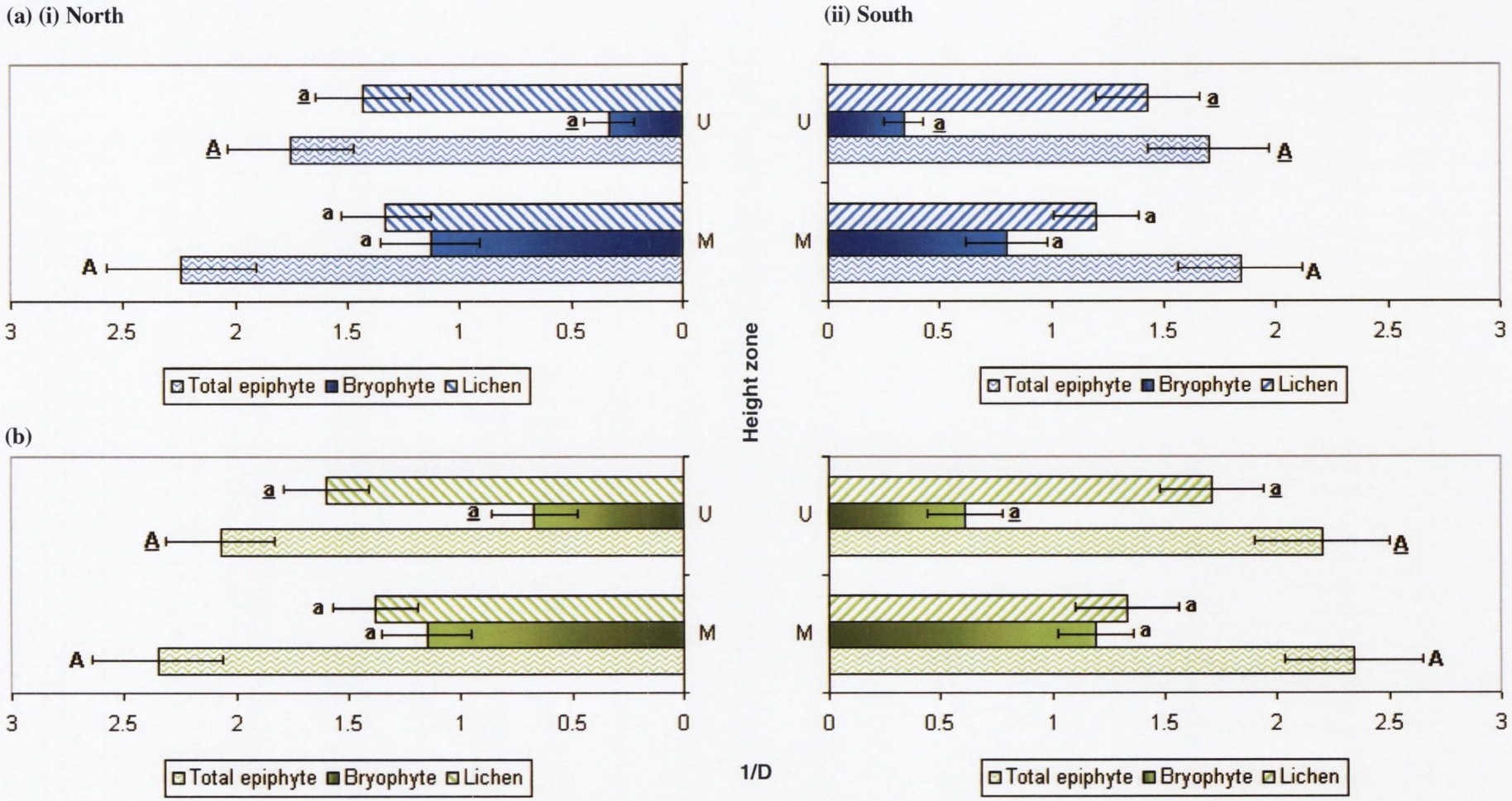


Figure 4.46 Mean diversity in the plots on the middle (M) and upper (U) branches on the (i) north and (ii) south sides of the (a) open space edge (M & U: n = 36) and (b) forest interior trees (M: n = 34, U: n = 36). Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) diversity between north and south in that height zone. Normal text compares M, and underline compares U.

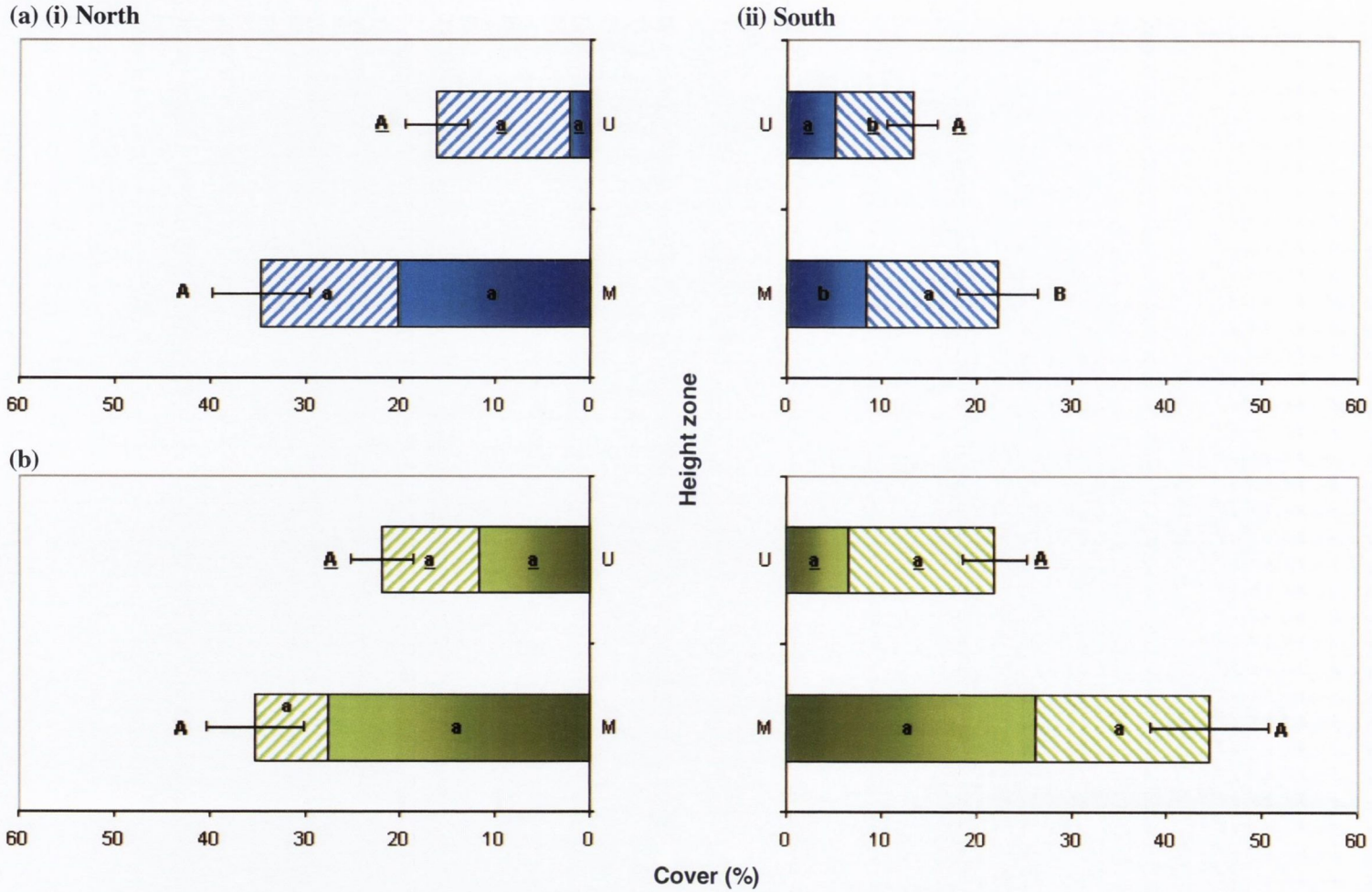


Figure 4.47 Mean epiphyte cover in the plots on the middle (M) and upper (U) branches on the (i) north and (ii) south sides of the (a) open space edge (M & U: n = 36) and (b) forest interior trees (M: n = 34, U: n = 36). The total epiphyte cover is shown and the relative proportions of bryophyte (shaded) and lichen (hatched) cover are indicated. Error bars indicate ± standard error. Bars with the same letter indicate no significant difference in total epiphyte (uppercase), bryophyte or lichen (lowercase) cover between north and south in that height zone. Note that normal text compares M, and underline compares U.

Trunk diversity

The total number of species recorded on the trunks of the edge and interior trees was similar and, at the individual tree level, there were no significant differences in the mean total epiphyte, bryophyte or lichen richness or diversity of the plots on the trunks of the edge and interior trees. There were also no significant differences in total epiphyte, bryophyte or lichen beta (β_w) diversity between the edge and interior trees. However, as previously noted (cf. **Section 3.4.1.1**) Whittaker's beta diversity measure was found to generate ambiguous results for species-poor floras. There was no significant difference in the mean cover of the eight trunk plots on each tree. There was, however, a significant positive relationship between mean species richness and mean cover in the eight trunk plots for the interior trees, but this relationship was not significant for the edge trees. This suggests that the open spaces are having an effect on the epiphyte cover of the edge trees which is not affecting the species richness of these trees.

Branch diversity

A similar total number of species were recorded on the branches of the open space edge and forest interior trees. There were also no significant differences in the mean total epiphyte, bryophyte or lichen diversity of all plots on branches at the individual tree level between edge and interior trees. However, there was a significantly higher mean total epiphyte cover in the branch plots on the interior trees than in those on the edge trees, and the difference in bryophyte cover was also close to significance. However, more plots were studied on dead branches on the forest interior trees and total epiphyte, bryophyte and lichen cover were found to be significantly higher on dead branches. As discussed in **Section 3.4.1.1**, branch vitality appeared to be important to epiphyte diversity and cover with both measures higher on dead branches (cf. Lang *et al.*, 1980; Liu *et al.*, 2000).

The overall picture produced is of no difference in epiphyte diversity between edge and interior trees. A number of studies have compared the edge and interior of forests in relation to epiphytes . Some of these studies have found reduced abundance (Esseen & Renhorn, 1998) or diversity (Kivisto & Kuusinen, 2000) of epiphytes at the edge compared with the forest interior. However, these studies have looked at edges created by clearcutting, rather than edges present from the planting stage, and the effects were mainly due to the effects of wind damage (Esseen & Renhorn, 1998) and sudden exposure to high levels of irradiance (Kivisto & Kuusinen, 2000). Closed forest margins will have quite different microclimatic conditions to recently exposed edges (Matlack, 1993). Esseen (2006) studied natural edges in a forest wetland mosaic and found reduced abundance of *Alectoria sarmentosa* at the edge. However, the sampled edges were open and exposed to prevailing winds and it was concluded that disturbance by wind was the most plausible explanation for the low abundance of the lichen at these sites. Pearson (1969) studied the natural edge of a permanent internal open space consisting of a bog and its surrounding woodland and found that the cover of epiphytic lichens was significantly higher on trees at the edge than in the

surrounding woodland. This he related to the lower humidity and higher light levels at the edge. However, no such differences between edge and interior trees were apparent in the present study. This is similar to the results of Iremonger *et al.* (2006) from sites that included those in the present study. They found spider assemblages at the edge (tree base) of open spaces in mature Sitka spruce stands to be indistinguishable from those two metres and five metres away in the forest interior. One possible reason for this is the fact that the majority of the edges studied had live branches over their entire height (cf. **Photograph 4.1**). These branches formed a side-canopy which closed the edge to light and air movement (Matlack & Litvaitis, 1999) resulting in an abrupt transition in light levels and light related factors at the edge and no significant gradient in these factors into the forest (Matlack, 1993). This side-canopy will also shade the trunk (Halonen *et al.*, 1991) and inner branches of the open space edge trees, resulting in lower light levels here than might otherwise be expected. The portions exposed to the higher light levels will mostly be small young branches with abundant needles, and, as discussed previously, these have been found to have fewer species and less cover than older portions of live branches and dead branches without needles (cf. **Section 3.4.1.1,** Lang *et al.*, 1980).

4.4.2 Epiphyte composition

4.4.2.1 Effects of open spaces

There was no significant difference in the number of species with a high affinity for epiphytism supported by the edge and interior trees. However, significantly more species with an intermediate affinity for epiphytism were recorded on the forest interior trees. This suggests that the microclimatic conditions present on the edge trees are sometimes too extreme for those species not primarily found in epiphytic habitats. The highest variability in microclimate is often found at the edge (Chen *et al.*, 1993).

A number of species were recorded only on either the edge or interior trees, but few of these species were recorded on more than one tree. This means that their apparent preference for edge or interior trees may have been a matter of chance. The more common species recorded only on the edge trees were wide ranging in their habitat preferences and were not characteristic of woodland habitats. This suggests that they are either tolerant of, or require, the higher light and lower humidity conditions which are likely to be present at the edge (Pearson, 1969). Those recorded only on forest interior trees were more characteristic of moist shaded habitats. In dense forests, or at closed edges, the lack of any significant penetration of sunshine and wind means the air in the trunk area will remain cool and moist (Geiger, 1965; Matlack & Litvaitis, 1999). This will favour species adapted to low light and high humidity levels. There were, however, no significant indicator species for either edge or interior trees, indicating that the floras of edge and interior trees as a whole are not distinct. However, some of the more common species did have greater percent

frequency on either edge or interior trees. The species with greater constancy on edge trees had less requirement for shade, while those with greater constancy on the interior trees required more humid shaded situations. The size, configuration and aspect of the open spaces varied considerably among sites, which will have resulted in variation of the microclimatic conditions present on the edge trees (compare **Photograph 4.1** & **Photograph 4.2**). The microclimate in the forest interior will also vary considerably among stands (Lieberman *et al.*, 1989), as will the microclimate at different heights in the tree (Barkman, 1958). The resulting variation between and among both edge and interior trees may explain why few species are restricted to one or other location.

4.4.2.2 Epiphyte composition of the trunk and branch plots

The NMS ordination of the trunk plots indicated that the '*Hypnum jutlandicum* community' identified in the trunk plots on the forest interior trees (cf. **Table 3.30**) was also present on many open space edge trees. However, a number of these trunk plots were from the south side of edge trees whose forest interior counterparts did not have plots with the '*Hypnum jutlandicum* community'. This suggests that the light levels in the interior of these stands may have been too low for even for *Hypnum jutlandicum*, which is adapted to deeply shaded conditions (Smith, 2004). *Hypnum andoi*, which was not recorded regularly in the forest interior plots, commonly occurred in plots on the south side of the edge trees. This species was the main component of the '*Hypnum cupressiforme* var. *filiforme* union' (a taxon now equated with *H. andoi* (Smith, 2004)) described by Phillips (1959) growing at breast height (1.37m) on beech (*Fagus sylvatica*), holly (*Ilex aquifolium*), European larch (*Larix decidua*), Scots pine (*Pinus sylvestris*), oak (*Quercus petraea*) and yew (*Taxus baccata*) in southern Ireland. The presence of *H. andoi* on the south side of the edge trees suggests that this species may require higher light levels than are present in the interior of many spruce stands.

The '*Metzgeria temperata* community', identified in the trunk and branch plots of some forest interior trees, was also present in trunk and branch plots on the edge trees from the same stands. However, none of these edge trees had this flora in their upper trunk plots, most likely because the higher light and lower humidity levels at the edge (Pearson, 1969) and at this height in the trees (Barkman, 1958) produced conditions unfavourable to *Metzgeria temperata*, which is characteristic of damp shaded habitats and is intolerant of prolonged desiccation (Hill *et al.*, 1991; Paton, 1999; Smith, 1990). Plots with the '*Dimerella*-dominated community' were mostly restricted to forest interior trees, although a handful of plots from edge trees from the same stands, and three plots from MUCK1, which was located next to a narrow road on a site with a shaded aspect (cf. **Photograph 4.2**), also had this flora. *Dimerella lutea* was also one of the species with higher percent frequency on the interior trees. This suggests that higher light and lower humidity levels are present on the edge trees at the sites in question and that these conditions are unfavourable to

Dimerella, which is common in damp or humid, shaded situations (Dobson, 2005; Purvis *et al.*, 1992).

The '*Microlejeunea* and *Ulota* community' present in the branch plots of some forest interior trees was also present on the edge trees from the same stands. The '*Fuscidea* and *Lecanora* community', present mainly on the upper branches of some forest interior spruce trees, was also present mainly on the upper branches on the edge trees, although *Lecanora pulicaris* was not as important a component of this community on spruce as it had been on larch (cf. **Section 3.3.5.1**). This may be related to the lower light levels in spruce stands, as *Lecanora* is common in more well-lit habitats (Dobson, 2005; Purvis *et al.*, 1992). The '*Micarea peliocarpa* community', found on the upper branches in high elevation Wicklow cluster spruce stands, was also present on the upper branches of the edge trees from the same stands.

A number of middle and upper trunk plots on the edge trees had two distinct epiphyte communities that had not been encountered in a significant number of trunk plots on the interior trees. One group of plots, characterised by the presence of *Ulota crispa s.l.* and *Frullania dilatata*, was similar to the '*Microlejeunea* and *Ulota* dominated' community seen on the branch plots in its bryophyte species composition but *Graphis* was absent from all but one plot, meaning it resembled the *Ulotetum bruchii* described by Barkman (1958) more than the *Graphidetum scriptae* described by James *et al.* (1977). The second group of plots, characterised by the foliose lichens *Hypotrachyna revoluta* and *Hypogymnia tubulosa*, had a flora similar to the '*Hypotrachyna revoluta* community' found in some branch plots, however, the absence of *Graphis scripta* and *Trapeliopsis flexuosa* and the presence of *Hypogymnia tubulosa* made it differ from that community and from the *Parmelion revolutae* association described by James *et al.* (1977). The middle and upper branches of the edge trees also had a distinct epiphyte community not encountered in a significant number of branch plots on the forest interior trees. This community was characterised by the presence of the foliose lichen, *Physcia tenella*. This community resembles the *Physcietum adscendentis* association, which is found on nutrient enriched bark in Britain and Ireland (James *et al.*, 1977). These three communities, which were more or less restricted to edge trees, are all characterised by photophilous and desiccation tolerant species which were much less common in the forest interior of most spruce stands, most likely due to the lower light levels found there (Hale, 2001). Rose (1974) has suggested that many epiphytes will occur at or near edges of woodlands or along rides or glades because of their light-demanding nature. Vanderpoorten *et al.* (2004) observed preferences for edges for many obligate bryophytes in broadleaved forests and Norway spruce (*Picea abies*) plantations in Belgium and France.

4.4.3 Factors affecting epiphyte diversity and composition

The NMS ordination highlighted the fact that factors other than a trees' location at the edge of an open space or in the forest interior are important in determining epiphyte composition. Geographic location appeared to be important, with general separation of trees from the Wicklow and Cork clusters. The differences in climate and planting site type between the two clusters have previously been discussed (cf. **Section 3.4.1.2**). One of the important factors affecting epiphyte richness identified by the NMS ordination was tree density. However, the positive relationship between tree density and total epiphyte richness was only significant for the forest interior trees, although the relationship for bryophyte richness was close to significance for both the edge and interior trees. The lack of a relationship with total epiphyte richness for the edge trees suggests that the influence of the open spaces on the epiphyte flora of these trees is overriding that of tree density. Dense forests are usually considered to be too dark for epiphytes (Rose, 1992). Peck & McCune (1997) found that lichen biomass on retained old-growth trees was negatively correlated with the density of the surrounding forest. However, Hazell *et al.* (1998) found that two bryophyte species growing on aspen (*Populus tremula*) were positively affected by higher density of Norway spruce (*Picea abies*) in the surrounding plantation. A more open canopy allows more throughfall, but rapid drying is allowed by the greater penetration of sunlight and freer air circulation (McCune & Antos, 1982). Since many bryophytes are adapted to low light levels and have a low tolerance to desiccation (Trynoski & Glime, 1982) they are better adapted to the conditions in denser stands. However, extreme levels of shade, as were seen below the canopy in ATHN (cf. **Photograph 3.4**), will exclude bryophytes, as well as lichens. Many of the dense unthinned stands were on very wet sites and were unthinned for stability reasons. This is likely to have resulted in even more humid conditions in these stands (cf. **Section 3.4.1.2**; Kuusinen, 1996b; McCarthy, 1980). It is also possible that the lack of thinning was favourable to the development of the epiphyte flora in these stands, as epiphytes are known to be sensitive to forest operations (Mitchell *et al.*, 2002). The significant negative relationship between average DBH and total epiphyte richness is most likely also an effect of tree density rather than tree size, since the inverse relationship between tree growth and competition means that trees in dense stands will be smaller.

Total radiation incident on each stand was also identified by NMS to be an important factor affecting epiphyte diversity. Iremonger *et al.* (2006) found that bryophyte and lichen species richness in the ground flora of open spaces, which included those in the present study, decreased with increasing solar radiation. However, although the relationship between total incident radiation and total epiphyte and bryophyte richness appeared to be negative for most stands in the present study, two stands with very low incident radiation also had low species richness. The significant relationship revealed by quadratic regression suggests that this relationship may be unimodal and that there is an optimum level of incident radiation, above and below which bryophyte richness is negatively affected. However, the lack of data from stands with incident radiation levels between

13 and 14molm^{-2}day^{-1} (cf. **Figure 4.27**) means that this can only be speculation. Matlack (1993) found that local radiation load was the main factor determining the forest microenvironment of sites in eastern USA because of its direct relationship with factors such as vapour pressure deficit, temperature and litter moisture. However, Bates (1992) found radiation to be less important than bark moisture relations and bark chemistry in determining community composition on *Quercus* and *Fraxinus* in Scotland. In the present study, it appears that radiation was an important factor in determining epiphyte diversity, particularly of bryophyte species, regardless of whether the trees were at the edge of on open space or in the forest interior.

None of the open space variables was significantly correlated with axis 1 of the NMS ordination. Nor were they significantly correlated with axis 1 of the separate ordination of the edge trees, again suggesting the open spaces are having little effect on overall epiphyte diversity or composition. However, there were significant negative relationships between mean total epiphyte cover in the trunk plots of the open space edge trees and both canopy openness and total radiation transmitted to the centre of the open space. It is likely that trees at the south-facing edge of large open spaces, that allow a large proportion of the total radiation to be transmitted to the centre of the open space, will have less wind protection and experience higher temperatures, and therefore have lower humidity levels (Geiger, 1965). These conditions will be less favourable to bryophyte growth.

4.4.4 Vertical distribution and the effect of open spaces

Clear patterns in vertical distribution were evident on both the open space edge and forest interior trees. The greatest overall number of epiphyte species were recorded in the upper zone on both edge and interior trees. Mean bryophyte richness decreased on average from the tree base to the upper zone and mean lichen richness increased on both edge and interior trees. On the interior trees, this resulted in a more or less constant total epiphyte richness and diversity over the height of the trees. However, on the edge trees there was a significantly greater lichen richness and diversity in the upper zone, leading to a significantly greater total epiphyte richness and diversity at this height. Pearson (1969) found lichen cover on the trees at the edge of a woodland surrounding a Minnesota bog was significantly higher than in the woodland interior. This he attributed to the higher light intensity and lower humidity at the edge. As previously noted, it appears that the dense side-canopy produced by the live branches over the entire height of the edge trees shades the trunks of the edge trees. However, in the upper height zone, light levels are still likely to be high and humidity low, favouring lichen species which are often light demanding (Rose, 1993) and are adapted to lower and more variable humidity (Pearson, 1969).

As with epiphyte richness, mean bryophyte cover also decreased from the tree base to the upper zone, and lichen cover increased. Again, this meant there were no significant differences in total

epiphyte cover among the height zones on the interior trees, while on the edge trees, total epiphyte cover was significantly higher in the tree base and lower zones than in the upper zone. Total epiphyte and bryophyte cover were also significantly higher in the tree base zone on the edge trees than in the same zone on the interior trees. One might expect that the edge trees would receive the most light and have the lowest humidity (Pearson, 1969), and that, as a result, the conditions would not favour bryophytes which are found in habitats with shorter periods of desiccation than lichens (Frahm, 2003). However, the presence of live branches from the base of the edge trees meant that the tree base and lower zones on the edge trees were generally quite shaded. This, combined with the fact that humidity and bark water absorption capacity are highest at the tree base (Barkman, 1958) and there is an increase in moisture accumulation at the edge (Matlack & Litvaitis, 1999), may have resulted in relatively high humidity levels. While many bryophytes are adapted to low light levels (Trynoski & Glime, 1982), they still require a certain minimum level and are virtually excluded by very low light levels (cf. **Photograph 3.4**). In the present study, larch trees in the forest interior were found to have greater bryophyte cover at the tree base than spruce (cf. **Figure 3.42**). It is likely that this was as a result of higher light levels in the larch stands. While the tree base zone on the edge trees is shaded by live branches, some penetration of light is likely to have occurred. This may have led to higher light levels at the base of the edge trees compared to the interior trees. The result may have been optimised light and humidity levels, which led to greater photosynthetic production, and therefore increased bryophyte growth on the edge trees (Peck *et al.*, 1995). Those trees at the edges of large open spaces which transmitted high levels of radiation were an exception, as humidity levels may have been too low in these cases (cf. **Section 4.4.3**).

4.4.5 Aspect and the effect of open spaces

There was little difference in species richness, diversity or cover between the north and south sides of the forest interior trees. The main difference was a higher total epiphyte richness and total epiphyte and lichen cover on the south side in the upper height zone. Since light levels will be higher on the south side of the trunk (Trynoski & Glime, 1982) and in the upper height zone (Barkman, 1958) this difference was not surprising, given that most epiphytic lichens are light demanding (Rose, 1974). However, there were more striking differences seen on the open space edge trees. There was a significantly greater total epiphyte richness and lichen richness and diversity on the south side of the trunks of the edge trees compared with the north side. However, this was as a result of a lower species richness and diversity on the north side, compared to the north side of the forest interior trees, rather than a higher species richness on the south side. When the four height zones were examined separately, lichen richness and diversity were lower on the north side in the middle height zone, and bryophyte richness and diversity were higher on the north side in the upper height zone. The dense side-canopy present at the edge of the majority of the open spaces may have resulted in the north sides of the trunks of the edge trees being more shaded than

the north side of the interior trees, which did not have live branches until higher in the tree. The resulting lower light and higher humidity levels, particularly higher in the tree, may have favoured bryophytes and negatively affected lichens.

There were also significant differences in cover between the north and south sides of the edge trees, although in this case it was as a result of total epiphyte and bryophyte cover being higher on the south side of the edge trees compared with the south side of the interior trees. This was mainly as a result of the greater total epiphyte and bryophyte cover in the tree base and lower plots on the south side of the edge trees. As previously discussed, this may have been as a result of increased light levels in combination with favourable humidity provided by the low live branches which provided optimum conditions for bryophyte growth. The tree base and lower plots from the south side of some of the edge trees were grouped together in the NMS ordination of the trunk plots data and contained the '*Hypnum jutlandicum* community'. Some of their forest interior counterparts did not have plots with the '*Hypnum jutlandicum* community'.

On the branches, there were no significant differences in diversity between plots on north and south facing branches on either the open space edge or forest interior. However, as with the trunk plots, lichen cover was significantly higher on the south facing branches on the interior trees. As with the trunk, this is likely to be related to the higher light levels on the south side of the trees which will favour lichens. However, on the edge trees total epiphyte cover was lower on the branches on the south sides compared to the north sides, and to the south sides of the interior trees. The branches on the south sides of the edge trees, particularly the upper branches, are likely to receive the highest light intensity and have the lowest humidity (Pearson, 1969). These conditions may be too extreme for bryophytes and even certain lichens. In addition, all the branches on the south side of the edge trees were also living, while some of the south facing branches in the middle height zone on the forest interior trees were dead or moribund. Living branches were found to have lower cover of epiphytes than dead or moribund branches (cf. **Section 3.3.2.3**).

4.5 CHAPTER SUMMARY

4.5.1 Epiphyte diversity

- No differences in epiphyte diversity were found between open space edge and forest interior trees or in the diversity on the trunks and branches of these trees.
- Forest interior trees had greater epiphyte cover on their branches. However, more plots were studied on dead branches on the interior trees and dead branches were found to have more epiphyte cover than living branches.

4.5.2 Epiphyte composition

- The forest interior trees supported more species with an intermediate affinity for epiphytism, suggesting that the microclimatic conditions present on some of the edge trees may be too extreme for species not primarily found in epiphytic habitats.
- Few species recorded only on edge or interior trees were recorded on more than one tree and no significant indicators for edge or interior trees were found. However, some of the species with greater percent frequency on the edge trees had less requirement for shade while those with greater frequency on the interior trees required more humid shaded situations.
- While the '*Hypnum jutlandicum* community', '*Metzgeria temperata* community', '*Microlejeunea* and *Ulota* community', '*Fuscidea* and *Lecanora* community' and '*Micarea peliocarpa* community' were present in plots on both edge and interior trees, the '*Dimerella*-dominated community' was mainly restricted to interior trees. Middle and upper trunk and branch plots with communities characterised by either bryophyte or foliose lichen species adapted to higher light and lower humidity levels were mainly restricted to edge trees.
- Epiphyte richness, diversity and cover were relatively constant in all height zones on the interior trees. However, the greater lichen richness and diversity in the upper zone of the edge trees meant that epiphyte richness and diversity were significantly greater in this zone. Epiphyte cover was significantly higher in the tree base and lower zones on the edge trees.
- Epiphyte richness differed little with aspect on the forest interior trees. However, total epiphyte richness and lichen richness and diversity were significantly lower on the north side of the trunks of the edge trees and epiphyte cover was higher on the south side, mainly as a result of the higher bryophyte cover in the tree base and lower zones. These differences are considered to be related to the presence of live branches over the entire height of the edge trees which produced optimum conditions for bryophyte growth on the south side of the lower trunk and conditions detrimental to lichens on the north side.
- Lichen cover was significantly higher on the south than the north facing branches on the forest interior trees but lower on the south than the north facing branches of the edge trees.

4.5.3 Environmental factors

- Other factors, particularly geographic location, were more important in determining epiphyte composition than location at the edge of an open space or in the forest interior.
- Tree density was positively associated with total epiphyte and bryophyte richness; however, many of the dense unthinned stands were on very wet sites. Very dense forests virtually excluded epiphytic bryophytes, although lichens were present higher in the trees.
- Total radiation incident on each stand was also found to be important to total epiphyte and bryophyte diversity, most likely as a result of its effect on microclimate. However, the

relationship appeared to be unimodal, with low epiphyte diversity in stands exposed to both high and low levels of radiation.

- The size and configuration of open spaces appeared to have an effect on epiphyte cover, with large open spaces which allowed large amounts of radiation to be transmitted resulting in low cover on the trunks of the edge trees.

Chapter 5 Conclusions

5.1 INTRODUCTION

At the beginning of this thesis a number of aims and objectives were set out (cf. **Section 1.7**). These are revisited in the following section, with the main findings summarised. Forest management methods which may enhance the potential of these plantations to provide habitats for epiphytes are discussed. The constraints on the present study are outlined and opportunities for further research are suggested.

5.2 AIMS OF THE STUDY

The main aims of this research were to characterise the diversity of the epiphyte flora of Irish forestry plantations and to determine whether they provide an alternative habitat for native woodland epiphyte species. Prior to the inception of the BIOFOREST project, no work had been published on epiphytes in Irish forestry plantations. Also, little work had been carried out in forestry plantations in Britain or in the rest of Europe. While in Europe plantations account for an average of only 3% of the total woodland area, in Ireland and in Britain the proportion of plantations are exceptionally high (approximately 94% and 71% respectively) (Anon., 2003). This means that plantations are potentially of greater importance for epiphytes, and other woodland groups, than in regions containing large areas of semi-natural forests. This research is therefore innovative and aims to address this major information gap.

A number of distinctive epiphyte communities were identified in the trunk and branch plots studied and these were described and related to communities previously described in Ireland, Britain and the rest of Europe. The plantations in the present study did not appear to be inheriting species of the *Lobarion* community, which is believed to be the major 'climax' community of epiphytes in the post-glacial forests of Europe (Rose, 1988). However, some trunk plots on larch and some branch plots on both spruce and larch in the present study had a community similar to the 'pioneer' *Lecanoretum subfuscae* association and the trunk plots of two silviculturally over-mature larch trees had communities similar to the *Pseudevernietum furfuraceae* association; both these communities are found on pine in Scottish native pinewoods (Coppins & Coppins, 2006).

Compared with two previous studies on epiphytes in British plantations (Bates *et al.*, 1997; Humphrey *et al.*, 2002), and to work from mainland Europe (Vanderpoorten *et al.*, 2004) it appears that plantations in Ireland are relatively rich in epiphytes and particularly in epiphytic bryophytes. This may be related to the climatic conditions present on the island. Ireland has an oceanic climate and, despite the east-west gradient in rainfall, the coastal mountain belt mean that even the driest areas are still wetter than most parts of lowland England (Ratcliffe, 1968). The result is one of the richest bryophyte floras in Europe, particularly of Atlantic bryophytes (Holyoak, 2003). Studies in wet areas of the Pacific Northwest have shown that, where sufficient moisture is available, conifer

species, which are lacking in epiphytic bryophytes in drier regions, quite commonly support rich bryophyte communities (Glime & Hong, 2002). This could explain the relative bryophyte richness of the stands in the present study. Spruce stands from low elevation sites in the Wicklow cluster, which would have been the driest sites studied, were quite species-poor, despite the fact that many were silviculturally over-mature.

It is unlikely that non-native conifer plantations will develop an epiphytic flora characteristic of native broadleaves (Humphrey *et al.*, 2002), particularly of dispersal-limited species such as cyanolichens. Esseen *et al.* (1996) have suggested that the limited amount of substrate (i.e. small branches) available to lichens and the relatively short period of time for lichen colonization and growth provided by young branches are important factors limiting the abundance of lichens in managed stands. Dettki and Esseen (2003) have modelled the long-term effects of forest management on epiphytic lichens in northern Sweden. Their results suggest that even-aged silvicultural systems with a 110-year rotation can only support a low amount of pendulous lichens, and that short rotations (60-year) are detrimental to epiphyte communities. It is likely that diversity in plantations would increase with time (Humphrey *et al.*, 2002). Price & Hochachka (2001) found that, while macrolichens were absent from Sitka spruce and western hemlock (*Tsuga heterophylla*) stands less than 70 years old in British Columbia, alectorioid (pendulous lichen species in the genera *Alectoria, Bryoria* and *Usnea*) and cyanolichen abundance increased with stand age thereafter, at least up to 120 years. Some of the stands in the present study that had been left beyond silvicultural maturity were quite species-rich; particularly some lichen-rich larch stands.

5.3 OBJECTIVES OF THE STUDY

The first objective of the present study was to examine differences in the epiphyte diversity of Sitka spruce and Japanese larch stands. Although total epiphyte diversity did not differ between the two species, larch was found to have greater lichen diversity. However, the most epiphyte-rich and lichen-rich flora was found on a spruce tree. The two tree species did not differ in the number of species with a high affinity for epiphytism they supported. However, certain species did exhibit host specificity for either spruce or larch. This indicates that plantations containing both spruce and larch stands will be more diverse than those containing only one or other species. It is important to consider, however, that the differences in epiphyte composition between the two species identified in the present study may be related, in part, to differences in planting site type. The majority of larch stands were planted on dry to mesic sites, while the majority of spruce stands were planted on peat and/or at high elevations. The small sample size, as indicated by the large number of uncommon species, may also have been an important factor. However, the differences in bark physical and chemical properties and in the canopy features of the two species (evergreen versus

deciduous) are clearly also of great importance in determining the epiphyte composition of the two species.

Spruce stands were the location of the two relatively rare bryophyte species recorded in the present study: *Daltonia splachnoides* and *Plagiothecium laetum*. *Daltonia* has a European distribution classed as 'Hyperoceanic Southern-temperate' (Smith, 2004), meaning it is not only more or less restricted in its European range to the Oceanic zone but also markedly western within that zone (Hill & Preston, 1998). Its discovery in a conifer plantation parallels the spread of the Oceanic liverwort *Colura calyptrifolia* in south and central Wales (Bosanquet, 2004). In the latter case the reported spread has been on to willows almost exclusively growing in or close to conifer plantations. Bosanquet (2004) suggests three possible explanations for this: that conifer cover protects *Colura* more effectively from harmful frosts than deciduous cover; that conifers act as more efficient spore traps than deciduous trees; or that conifers provide constantly humid conditions. *Colura* has also recently been recorded on spruce trees at the same Welsh sites, as well as in southern Scotland and the English Lake District (B. Coppins, pers. comm.). *Colura*, and two additional Oceanic bryophytes, *Frullania teneriffae* and *Ulota phyllantha*, were also encountered on Sitka spruce in the present study; *Colura* was also found on larch trees in the Cork cluster. This suggests that spruce plantations can provide suitable habitats for Oceanic bryophyte species.

The second objective of the present study was to assess the contribution made by epiphytes to overall plant diversity in Sitka spruce and Japanese larch plantations. While this investigation was preliminary and focussed only on well grown trees with vertical trunks, it was found that epiphytes contributed a substantial proportion of the total flora at all stands examined (a mean of 40.3%). A great deal of overlap in the bryophyte flora of the ground and the trees was identified. However, although epiphytic bryophytes do not contribute a great deal to overall bryophyte diversity in drier sites, in seems that in wet sites they can make a substantial contribution. The contribution of epiphytic lichens to the overall lichen flora was great in all stands. The poor ground flora diversity of closed canopy Sitka spruce plantations has been described (French, 2005; Smith *et al.*, 2005); the trees in the two dense closed canopy stands (ATHN2 and STOE2) which virtually lacked ground flora species (cf. **Photograph 3.4**) were still poor in epiphytic bryophytes, but their epiphytic lichen floras were relatively diverse.

The final objective of the present study was to assess the effect of open spaces within forestry plantations on epiphyte diversity. No differences in epiphyte diversity were found between open space edge and forest interior trees. Some differences in epiphyte composition were identified, with certain species having greater percent frequency on either edge or interior trees. Middle and upper trunk and branch plots on the edge trees also contained epiphyte communities, characterised by photophilous or desiccation tolerant species, which had not been encountered to a significant extent

on interior trees. The main effect of open spaces was on the epiphyte cover of the edge trees. This appeared to be related to a combination of increased light levels and the presence of live branches over the entire height of the south sides of the edge trees, which produced optimum conditions for bryophytes at the tree bases and lichens in the upper zone.

5.4 PLANTATION MANAGEMENT

While the identification of management recommendations was not the primary focus of this research, a number of observations can be made regarding plantation management for epiphyte diversity. Some of the main factors identified as being important to epiphyte diversity in this study, such as rainfall, elevation and radiation levels, are beyond the control of forest managers. However, other factors are within their control. As mentioned above, the host specificity exhibited by certain epiphyte species means that plantations containing both spruce and larch stands will be more diverse than those containing only one or other species. The planting of a mixture of canopy species has been recommended as a method of enhancing ground flora diversity in plantations (French, 2005; Smith *et al.*, 2005). In that case, non-intimate mixtures of species were recommended, as intimate mixes are more difficult to manage (Horgan *et al.*, 2004) and it is more likely that one species will have an over-riding influence on the ecology of the stand. Mixed plantings, intimate or non-intimate, were not specifically examined in the present study. However, one stand (CLEA) which contained 80% Sitka spruce and 20% lodgepole pine (*Pinus contorta*) as an intimate mixture appeared to be heavily influenced overall by the shade cast by the spruce trees, while the areas of larch in another stand (MUNG1) which contained 80% Japanese larch and 20% Sitka spruce as a non-intimate mixture had conditions similar to other larch stands. Therefore it seems that non-intimate mixes would also be more suitable for enhancing epiphyte diversity.

A number of silviculturally over-mature stands (> 50 years) were surveyed in the present study (cf. **Table 2.2**). While the trees from over-mature Wicklow cluster spruce stands on dry sites (MUNG2 and MUIN1) were quite species-poor, a tree from a stand in the Cork cluster in a high rainfall area (COOM2) was quite species-rich and supported *Pyrrhospora quernea*, which is common on oaks in 'old woodland' situations (Dobson, 2005). An over-mature larch stand from the Cork cluster (COOM1) was not particularly species-rich compared with other Cork cluster larch stands, but it did support a number of lichen species not found in other stands, including *Anisomeridium ranunculosporum* which is found in old, shaded woodland (Dobson, 2005). Two larch trees from over-mature stands in Wicklow (CRUA1 and CURT1) were particularly lichen-rich, especially in foliose and fruticose lichens, and had a distinct flora similar to that of pine in native Scottish pinewoods. This suggests that over-mature spruce stands in high rainfall areas and over-mature larch plantations may be important for overall epiphytic lichen diversity. This agrees with the

recommendation for enhancing ground flora diversity in plantations, that a proportion of stands be retained beyond commercial maturity (French, 2005; Smith *et al.*, 2005).

Tree density was one of the factors identified as being important to epiphyte diversity in spruce stands, with denser stands having greater bryophyte richness. This appears to conflict with the recommendation that, to enhance their ground flora diversity, spruce stands be rigorously thinned to prevent canopy closure (French, 2005; Smith *et al.*, 2005). The lower light and higher humidity levels in dense stands appeared to favour bryophytes. Hazell *et al.* (1998) found that two bryophyte species growing on aspen (*Populus tremula*) were positively affected by higher density of Norway spruce (*Picea abies*) in the surrounding plantation. It is important to note, however, that many of the dense stands in the present study were planted on very wet sites and, despite approaching commercial maturity (32-43 years after planting), were unthinned for stability reasons. The resulting high humidity may have played a part in the diversity of their bryophyte and overall epiphyte floras. The two younger (28-29 years after planting), dense, unthinned stands in the present study (ATHN and STOE) were found virtually to exclude epiphytic bryophytes. However, the positive effects of the constant humidity provided by dense spruce stands on bryophyte diversity cannot be ignored and requires further investigation. In contrast, heavily thinned, silviculturally over-mature larch stands appeared to be important for lichen diversity.

While open spaces within Sitka spruce plantations did not appear to affect overall epiphyte diversity, they did appear to benefit certain photophilous and desiccation-tolerant species. In the younger, unthinned stands (ATHN and STOE), open spaces had a positive effect on bryophyte diversity, with bryophytes present on the edge trees while they were virtually excluded from the forest interior. However, the dense side-canopy formed by the edge trees appeared to minimise most of effects of the open spaces on the epiphytic flora. While open spaces within larch stands were not studied, it was observed that larch trees at the edges of roads often had high cover of foliose and fruticose lichens. Native broadleaved species often occurred within the open spaces in the spruce plantations and were observed to support a range of epiphytic species. These observations lend support to the promotion of open spaces within forestry plantations as a method of enhancing biodiversity (French, 2005; Iremonger *et al.*, 2006; Smith *et al.*, 2005).

5.5 CONSTRAINTS ON THE PRESENT STUDY

While this research has addressed a major gap in our information on epiphytes in forestry plantations, it has only begun to address the many different aspects of epiphyte diversity and the factors affecting this diversity. The major constraint on this project has been time. The studying of epiphytes using tree-climbing techniques is a time-consuming and physically demanding method, with each tree taking approximately one day to sample and many additional laboratory hours

required to identify species unidentified in the field. This meant that the study had to be restricted to two tree species: Sitka spruce and Japanese larch. These species were selected because of their importance as plantation species in Ireland and because of their contrasting life-form characteristics. They are not necessarily representative of all plantation tree species or even of all plantation conifers. Also, with the exception of the pairs of trees studied adjacent to open spaces, only a single tree was studied in each stand. The study of more trees in each stand would have allowed for better characterisation of the epiphyte flora at the stand level. The study of more open spaces, and of open spaces in larch plantations, would also have given a better understanding of the effect of different types and sizes of open spaces on the epiphyte flora.

The investigation of epiphyte communities has been restricted to bryophytes, lichens and, where they occurred, vascular plants. Free-living algae and non-lichenised fungi were also encountered during the course of this study but were not considered. Although Barkman (1958) has reported that the number of epiphytic algae and fungi in any epiphyte association in Europe are small, they were commonly encountered in the present study. Therefore, significant elements of epiphyte biodiversity were omitted. Also, although a preliminary investigation of the contribution of epiphytes to overall plantation diversity was made in this study, further work combining studies of ground flora and epiphytes would build on this work and help to identify the extent to which factors important for high epiphyte diversity were also important for ground flora diversity.

The original sampling design of selecting sites in two geographic clusters was employed to reduce the effects of large-scale environmental variation. However, considerable variation still existed between the Sitka spruce and Japanese larch stands studied. The majority of the Sitka spruce stands studied were selected for the purpose of BIOFOREST project 3.1.3 as a whole and the presence of open spaces in these stands was the major limiting factor determining selection. When the author came to select the larch stands at a later date, the lack of availability of mature larch stands in the two geographic clusters meant that little choice was available. Most notably, larch stands at the lower end of the age range were not present. The site types the larch stands were planted on were also quite restricted compared to the spruce stands. Fewer larch stands were studied, mainly as a result of time constraints.

This study has concentrated on mature stands and, although a handful of stands left beyond the normal felling age were also studied, no long rotation (>100 years) stands were included. This is mainly as a result of the scarcity of long-rotation stands in Ireland. Although there are only a limited number of such stands, their study would add significantly to the understanding of the effects of longer rotations on the epiphyte flora.

Another major limitation of this study was the limited investigation of environmental variables. The measurement of the incident and transmitted radiation of the open space sites studied proved to be informative. Further measures of microclimatic factors, such as the light and humidity levels in different stands and at different heights in the tree, would have added considerably to the understanding of the factors determining epiphyte distribution. The study of the physical and chemical properties of spruce and larch bark was preliminary and further work would also add to the understanding of the observed differences in the epiphyte flora of the two species.

5.6 OPPORTUNITIES FOR FURTHER STUDY

Many opportunities for future work have arisen out of this study and out of the fact that little previous work had been carried out on epiphytes in forestry plantations in Ireland and the rest of Europe. The study of epiphytes in areas outside the two geographic clusters concentrated on in this study would build on the data already collected. Adding additional plantation species such as broadleaved species, and native broadleaved species in particular, would provide a much broader picture. Of the factors identified as being important to epiphyte diversity, tree density is one factor that can be controlled by forest managers. An examination of the epiphyte diversity at different thinning intensities would add greatly to the understanding of how best to manage plantations for epiphytes, particularly as the findings of the present study appear to conflict with the recommendations for enhancing the ground flora diversity of plantations. In terms of open spaces, the majority of the edges examined in this study were closed edges. However, at one of the sites studied, broadleaves had been planted between the edge studied and the open space, preventing closure of the edge. Further study of edges with fringing broadleaves would add greatly to the information on the effect of open spaces within spruce plantations on epiphyte diversity. A study of the epiphytes of broadleaved trees and shrubs within open spaces would give a clearer picture of the overall contribution made by open spaces to epiphyte diversity. Last, but by no means least, while semi-natural woodland and scrub is a minority habitat in Ireland, basic research on the epiphytes of these habitats is urgently needed in order to put any studies of Irish forestry plantations into context and to give a better understanding of how to manage both woodlands and plantations for epiphyte diversity.

References

Acebey, A., Gradstein, S.R., & Kromer, T. (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology*, **19**, 9-18.

Anon. (1995) *Interim Report on the Follow-up of the Second Ministerial Conference. Ministerial Conference on the Protection of Forests in Europe.* Ministry of Agriculture and Forestry, Helsinki.

Anon. (2003) *State of Europe's Forests 2003.* MCPFE, Vienna.

Anon. (2005a) *Larch (*Larix decidua *Mill.,* Larix kaempferi *(Lamb.) Carr).* Forest Service, Dublin.

Anon. (2005b) *Sitka spruce (*Picea sitchensis *(Bong.) Carr.).* Forest Service, Dublin.

Averis, A.B.G. & Coppins, A.M. (1998) *Bryophytes, Lichens and Woodland Management in the Western Highlands.* Scottish Natural Heritage.

Barker, M.G. & Pinard, M.A. (2001) Forest canopy research: sampling problems, and some solutions. *Plant Ecology*, **153**, 23-38.

Barkman, J.J. (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes.* Van Gorcum, Assen.

Bates, J.W. (1982) Quantitative Approaches in Bryophyte Ecology. In *Bryophyte Ecology* (ed A.J.E. Smith), pp. 1-44. Chapman and Hall, London.

Bates, J.W. (1992) Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. *Journal of Ecology*, **80**, 163-179.

Bates, J.W. & Brown, D.H. (1981) Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* in a maritime area of south west England. *Vegetatio*, **48**, 61-70.

Bates, J.W., McNee, P.J., & McLeod, A.R. (1996) Effects of sulphur dioxide and ozone on lichen colonization of conifers in the Liphook forest fumigation project. *New Phytologist*, **132**, 653-660.

Bates, J.W., Proctor, M.C.F., Preston, C.D., Hodgetts, N.G., & Perry, A.R. (1997) Occurrence of epiphytic bryophytes in a 'tetrad' transect across southern Britain. I. Geographical trends in abundance and evidence of recent change. *Journal of Bryology*, **19**, 685-714.

Beers, T.W., Dress, P.E., & Wensel, L.C. (1966) Aspect transformation in site productivity research. *Journal of Forestry*, **64**, 691-692.

Begon, M., Harper, J.L., & Townsend, C.R. (1990) *Ecology: Individuals, Populations and Communities*, 2nd edn. Blackwell Science, Oxford.

Benzing, D.H. (1990) *Vascular Epiphytes: General Biology and Related Biota.* Cambridge University Press, Cambridge.

Berger, W.H. & Parker, F.L. (1970) Diversity of planktonic Foraminifera in deep sea sediments. *Science*, **168**, 1345-1347.

Berryman, S. & McCune, B. (2000) Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data. *Journal of Vegetation Science*, **17**, 157-170.

Bosanquet, S.D.S. (2004) *Colura calyptrifolia* in Wales. *Field Bryology*, **82**, 3-5.

Bowman, J.J. & McGettigan, M. (1994) Atmospheric deposition in acid sensitive areas of Ireland - the influence of wind direction and a new coal burning electricity generation station on precipitation quality. *Water, Air and Soil Pollution*, **75**, 159-175.

Bradshaw, R.H.W. & Hannon, G.E. (1988) Human Influence in the Decline of the Irish Forest Ecosystem. In *Human Influence on Forest Ecosystems Development in Europe* (ed F. Salbatino). ESF FERN-CNR, Piatagora Editrice, Bologna.

British Lichen Society (2007) *Lichens and Lichenicolous Fungi List* http://www.thebls.org.uk/content/checklist.html

Budel, B. & Scheidegger, C. (1996) Thallus Morphology and Anatomy. In *Lichen Biology* (ed T.H. Nash), pp. 37-64. Cambridge University Press, Cambridge.

Burns, K.C. & Dawson, J. (2005) Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. *Austral Ecology*, **30**, 883-891.

Cameron, T. (2002) 2002: the year of the 'diversity-ecosystem function' debate. *TRENDS in Ecology & Evolution*, **17**, 495-496.

Carter, C.I. & Anderson, M.A. (1987) *Enhancement of Lowland Forest Ridesides and Roadsides to Benefit Wild Plants and Butterflies. Research Information Note 126.* Forestry Commission, Farnham.

Chen, J., Franklin, J.F., & Spies, T.A. (1995) Growing season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74-86.

Chen, J.Q., Franklin, J.F., & Spies, T.A. (1993) Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, **63**, 219-237.

Church, J.M. (1996) *Red Data Books of Britain and Ireland.* Joint Nature Conservation Committee, Peterborough.

Church, J.M., Hodgetts, N.G., Preston, C.D., & Stewart, N.F. (2001) *British Red Data Books Mosses and Liverworts.* Joint Nature Conservation Committee, Peterborough.

Coillte Teoranta (2002) *Environmental and Social Report 2001.* Coillte Teoranta, Dublin.

Coillte Teoranta (2005) http://www.coillte.ie/managing_our_forests/forest_facts/facts_national .htm

Coppins, A. & Coppins, B.J. (2002) *Indices of Ecological Continuity for Woodland Epiphytic Lichen Habitats in the British Isles* British Lichen Society, London.

Coppins, B.J. (2002) *Checklist of Lichens of Great Britain and Ireland* British Lichen Society, London.

Coppins, B.J. & Coppins, A.M. (2006) The lichens of the Scottish native pinewoods. *Forestry*, **79**, 249-259.

Cornelissen, J.H.C. & ter Steege, H. (1989) Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology*, **5**, 131-150.

Coroi, M., Skeffington, M.S., Giller, P., Smith, C., Gormally, M., & O'Donovan, G. (2004) Vegetation diversity and stand structure in streamside forests in the south of Ireland. *Forest Ecology and Management*, **202**, 39-57.

Cross, J.R. (1987) Status and value of native broadleaved woodland. *Irish Forestry*, **44**, 81-88.

Cross, J.R. (1998) An outline and map of the potential natural vegetation of Ireland. *Applied Vegetation Science*, **1**, 241-252.

Culberson, W.L. (1955) The corticolous communities of lichens and bryophytes in the upland forests of N. Wisconsin. *Ecological Monographs*, **25**, 215-231.

DAFRD (2000) *CAP Rural Development Plan 2000-2006 Ireland.* Department of Agriculture Food and Rural Development, Dublin.

Davies-Colley, R.J., Payne, G.W., & van Elswijk, M. (2000) Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*, **24**, 111-121.

Dettki, H. & Esseen, P.-A. (2003) Modelling long term effects of forest management on epiphytic lichens in northern Sweden. *Forest Ecology and Management*, **175**, 223-238.

Dettki, H. & Esseen, P.A. (1998) Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography*, **21**, 613-624.

Dickinson, C.H. & Thorp, T.K. (1968) Epiphytic lichens on *Corylus avellana* in the Burren, County Clare. *Lichenologist*, **4**, 66-72.

Dobson, F.S. (2005) *Lichens: An Illustrated Guide to the British and Irish Species*, 5th edn. Richmond, Slough.

Doyle, G.J. (1987) *Hypnum jutlandicum* Holmen and Warncke growing as a pendulous epiphyte on *Pinus contorta* in a plantation in the west of Ireland. *Lindbergia*, **12**, 73-75.

Doyle, G.J. & Moore, J.J. (1982). Floristic Changes in Developing Conifer Plantations Growing on Blanket Peat in the West of Ireland. In *Struktur und Dynamik von Wäldern* (ed H. Dierschke), pp. 699-716. J. Cramer, Vaduz.

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.

Ellis, C.J. & Coppins, B.J. (2006) Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography*, **33**, 1643-1656.

Ellyson, W.J.T. & Sillett, S.C. (2003) Epiphyte communities on Sitka spruce in an old-growth redwood forest. *Bryologist*, **106**, 197-211.

EPA (2004) *Ireland's Environment 2004.* Environmental Protection Agency, Wexford.

Esseen, P.-A. (1981) Host specificity and ecology of epiphytic macrolichens in some central Swedish spruce forests. *Wahlenbergia*, **7**, 73-80.

Esseen, P.-A. (2006) Edge influence on the old-growth forest indicator lichen *Alectoria sarmentosa* in natural ecotones. *Journal of Vegetation Science*, **17**, 185-194.

Esseen, P.-A. & Renhorn, K.-E. (1998) Edge effects on an epiphytic lichen in fragmented forests. *Conservation Ecology*, **12**, 1307-1317.

Esseen, P.-A., Renhorn, K.-E., & Pettersson, R.B. (1996) Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecological Applications*, **6**, 228-238.

Eversman, S., Johnson, C., & Gustafson, D. (1987) Vertical distribution of epiphytic lichens on three tree species in Yellowstone National Park. *Bryologist*, **90**, 212-216.

Fahy, O. & Gormally, M. (1998) A comparison of plant and beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecology and Management*, **110**, 263-273.

Farmer, A.M., Bates, J.W., & Bell, J.N.B. (1990) A comparison of methods for the measurement of bark pH. *Lichenologist*, **22**, 191-197.

Ferris-Kaan, R. (1995) Management of Linear Habitats for Wildlife in British Forests. In *Nature Conservation 4: The Role of Networks* (eds D.A. Saunders, J.L. Craig & E.M. Mattiske), pp. 67-77. Beatty & Sons, Surrey.

Ferris, R. & Carter, C. (2000) *Managing Rides, Roadsides and Edge Habitats in Lowland Forests. Forestry Commission Bulletin 123.* Forestry Commission, Edinburgh.

Fitzpatrick, H.M., ed. (1966) *The Forests of Ireland: An Account of the Forests of Ireland from Early Times until the Present Day.* The Society of Irish Foresters, Bray.

Folan, A.C.M. & Mitchell, M.E. (1970) The lichens and lichen parasites of Derryclare wood Connemara. *Proceedings of the Royal Irish Academy*, **70(B)**, 163-170.

Folke, C., Holling, C.S., & Perrings, C. (1996) Biological diversity, ecosystems, and the human scale. *Ecological Applications*, **6**, 1018-1024.

Forest Service (1996) *Growing for the Future: A Strategic Plan for the Development of the Forestry Sector in Ireland.* Department of Agriculture Food and Forestry, Dublin.

Forest Service (2000a) *Code of Best Forest Practice - Ireland.* Forest Service, Department of the Marine and Natural Resources, Dublin.

Forest Service (2000b) *Forest Biodiversity Guidelines.* Forest Service, Department of the Marine and Natural Resources, Dublin.

Forest Service (2000c) *The Irish National Forestry Standard.* Forest Service, Department of the Marine and Natural Resources, Dublin.

Forest Service (2003) *National Report to the Fourth Session of the United Nations Forum on Forests.* Forest Service, Wexford.

Fox, H., Cullen, M., Little, D.J., Ryan, M., Ciarruiz, P., Dwyer, R., & Boyle, G.M. (2001) *Vegetation Monitoring and Botanical Survey of Brackloon Wood, Westport, Co. Mayo.* Forest Ecosystem Research Group, Department of Environmental Resource Management, University College Dublin, Dublin.

Frahm, J.-P. (2003) Climatic habitat differences of epiphytic lichens and bryophytes. *Crypotgamie, Bryologie*, **24**, 3-14.

Franks, A.J. & Bergstrom, D.M. (2000) Corticolous bryophytes in microphyll fern forests of south-east Queensland: distribution on Antarctic beech (*Nothofagus moorei*). *Austral Ecology*, **25**, 386-393.

Frazer, G.W., Canham, C.D., & Lertzman, K.P. (1999) *Gap Light Analyzer 2.0* Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

French, L.J. (2005) *Ground Flora Communities in Ireland's Plantation Forests: Their Diversity, Structure and Composition*. PhD Thesis, University of Dublin, Trinity College, Dublin.

Garvey, L.M. (1998) *Light Levels in Tomies Wood, Killarney and their Effect on the Photosynthesis of* Rhododendron ponticum *L.* PhD Thesis, University of Dublin, Trinity College, Dublin.

Gaston, K.J. & Spicer, J.I. (1998) *Biodiversity: An Introduction* Blackwell Science, Oxford.

Geiger, R. (1965) *The Climate Near the Ground* Harvard University Press, Cambridge, Massachusetts.

Gentry, A. & Dodson, C. (1987) The contribution of non-trees to tropical forest species richness. *Biotropica*, **19**, 145-156.

Gerson, U. & Seaward, M.R.D. (1977) Lichen-Invertebrate Associations. In *Lichen Ecology* (ed M.R.D. Seaward). Academic Press, London.

Gimingham, C.H. & Birse, E.M. (1957) Ecological studies on growth-form in bryophytes: I. Correlations between growth-form and habitat. *Journal of Ecology*, **45**, 533-545.

Glime, J.M. & Hong, W.S. (2002) Bole epiphytes on three conifer species from Queen Charlotte Islands, Canada. *Bryologist*, **105**, 451-464.

Gradstein, S.R. (1995). Diversity of Hepaticae and Anthocerotae in Montane Forests of the Tropical Andes. In *Biodiversity and Conservation of Neotropical Montane Forests* (ed S.P. Churchill, H. Balslev, E. Forero & J.L.Luteyn), pp. 321-334. The New York Botanical Gardens, New York.

Gradstein, S.R., Griffin III, D., Morales, M.I., & Nadkarni, N. (2001) Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia*, **23**, 203-212.

Gradstein, S.R., Hietz, P., Lucking, R., Lucking, A., Sipman, H.J.M., Vester, H.F.M., Wolf, J.H.D., & Gardette, E. (1996) How to sample the epiphytic diversity of tropical rain forests. *Ecotropica*, **2**, 59-72.

Gustafsson, L. & Eriksson, I. (1995) Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology*, **32**, 412-424.

Hale, M.E. (1965) Vertical distribution of cryptogams in a red maple swamp in Connecticut. *Bryologist*, **68**, 193-197.

Hale, M.E., Jr. (1952) Vertical distribution of cryptogams in a virgin forest in Wisconsin. *Ecology*, **33**, 398-406.

Hale, M.E., Jr. (1955) Phytosociology of corticolous cryptogams in the upland forests of southern Wisconsin. *Ecology*, **36**, 45-63.

Hale, S.E. (2001) Light regime beneath Sitka spruce plantations in northern Britain: preliminary results. *Forest Ecology and Management*, **151**, 61-66.

Hale, S.E. & Edwards, C. (2002) Comparison of film and digital hemispherical photography across a wide range of canopy densities. *Agricultural and Forest Meteorology*, **112**, 51-56.

Halonen, P., Hyvarinen, M., & Kauppi, M. (1991) The epiphytic lichen flora on conifers in relation to climate in the Finnish middle boreal subzone. *Lichenologist*, **23**, 61-72.

Harris, A.S. (1990) *Picea sitchensis* (Bong.) Carr., Sitka spruce. In *Silvics of North America* (eds R.M. Burns & B.H. Honkala), Vol. 1. Conifers, pp. 260-267. USDA Forest Service, Washington, DC.

Harris, G.P. (1971) The ecology of corticolous lichens. I. The zonation on oak and birch in south Devon. *Journal of Ecology*, **59**, 431-439.

Hazell, P., Kellner, O., Rydin, H., & Gustafsson, L. (1998) Presence and abundance of four epiphytic bryophytes in relation to density of aspen (*Populus tremula*) and other stand characteristics. *Forest Ecology and Management*, **107**, 147-158.

Herbert, T.J. (1987) Area projections of fisheye photographic lenses. *Agricultural and Forest Meteorology*, **39**, 215-233.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427-432.

Hill, M.O. & Preston, C.D. (1998) The geographical relationships of British and Irish bryophytes. *Journal of Bryology*, **20**, 127-226.

Hill, M.O., Preston, C.D., & Smith, A.J.E. (1991) *Atlas of the Bryophytes of Britain and Ireland. Volume I. Liverworts (Hepaticae and Anthoceratae).* Harley, Colchester.

Hill, M.O., Preston, C.D., & Smith, A.J.E. (1992) *Atlas of the Bryophytes of Britain and Ireland. Volume II. Mosses (except Diplolepideae).* Harley, Colchester.

Hill, M.O., Preston, C.D., & Smith, A.J.E. (1994) *Atlas of the Bryophytes of Britain and Ireland. Volume III. Mosses (Diplolepideae).* Harley, Colchester.

Hilmo, O. (1994) Distribution and succession of epiphytic lichens on *Picea abies* branches in a boreal forest, central Norway. *Lichenologist*, **26**, 149-169.

Hilmo, O. (2002) Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest. *Ecography*, **25**, 329-335.

Hilmo, O. & Sastad, S.M. (2001) Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biological Conservation*, **102**, 251-259.

Hodge, S.J., Patterson, G., & McIntosh, R. (1998) The Approach of the British Forestry Commission to the Conservation of Forest Biodiversity. In *Assessment of Biodiversity for*

Improved Forest Planning. Forest Sciences Series 51; European Forest Institute Proceedings 18 (eds P. Bachmann, M. Kohl & R. Paivinen) pp. 91-101 Kluwer Academic, Dortrecht.

Hodgetts, N. (1996) *The Conservation of Lower Plants in Woodland.* Joint Nature Conservation Committee, Peterborough.

Holyoak, D.T. (2003) *The Distribution of Bryophytes in Ireland: An Annotated Review of the Occurrence of Liverworts and Mosses in the Irish Vice-Counties, Based Mainly on the Records of the British Bryological Society.* Broadleaf Books, Dinas Powys.

Holz, I., Gradstein, S.R., Heinrichs, J., & Kappelle, M. (2002) Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. *Bryologist*, **105**, 334-348.

Hong, W.S. & Glime, J.M. (1997) Comparison of phorophyte communities on three major tree species on Ramsey Island, Queen Charlotte Islands, Canada: bryophyte vs lichen dominance. *Lindbergia*, **22**, 21-30.

Horgan, T., Keane, M., McCarthy, R., Lally, M., & Thompson, D. (2004) *A Guide to Forest Tree species Selection and Silviculture in Ireland*, 2nd edn. COFORD, Dublin.

Hosokawa, T. (1950) Epiphyte quotient. *Botanical Magazine Tokyo*, **63**, 18-20.

Houle, A., Chapman, C.A., & Vickery, W.L. (2004) Tree climbing strategies for primate ecological studies. *International Journal of Primatology*, **25**, 237-260.

Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., & Harding, K. (2002) Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation*, **107**, 165-180.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577-586.

Hyvarinen, M., Halonen, P., & Kauppi, M. (1992) Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. *Lichenologist*, **24**, 165-180.

Iremonger, S., Gittings, T., Smith, G.F., Wilson, M., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D.L., Giller, P.S., O'Sullivan, A., Neville, P., Mitchell, F.J.G., O'Donnell, V., Kelly, T., & Dowding, P. (2006) *Investigation of experimental methods to enhance biodiversity in plantation forests.* Report for COFORD and EPA.

James, P.W., Hawksworth, D.L., & Rose, F. (1977) Lichen Communities in the British Isles: A Preliminary Conspectus. In *Lichen Ecology* (ed M.R.D. Seaward), pp. 295-413. Academic Press, London.

Jarvis, A. (1999) *Quantifying the Hydrological Role of Cloud Deposition onto Epiphytes in a Tropical Montane Cloud Forest, Colombia.* B.S. Dissertation, Kings College London, London.

Jesberger, J.A. & Sheard, J.W. (1973) A quantitative study and multivariate analysis of corticolous lichen communities in southern boreal forests of Saskatchewan. *Canadian Journal of Botany*, **51**, 185-201.

Johansson, D. (1974) Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica*, **59**, 1-129.

Joyce, P.M. & O Carroll, N. (2002) *Sitka spruce in Ireland.* COFORD, Dublin.

Kelly, D.L. (1975) *Native Woodland Vegetation in Western Ireland with Especial Reference to the Region of Killarney*. PhD Thesis, University of Dublin, Trinity College, Dublin.

Kelly, D.L. (1981) The native forest vegetation of Killarney south-west Ireland: an ecological account. *Journal of Ecology*, **69**, 437-472.

Kelly, D.L. (2000) Charting Diversity in a Killarney Oakwood: Levels of Resolution in Floristic Recording, and the Effects of Fencing and Felling. In *Biodiversity: The Irish Dimension* (ed B.S. Rushton), pp. 76-94. Royal Irish Academy, Dublin.

Kelly, D.L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S.O., & Marcano-Berti, L. (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology*, **20**, 643-666.

Kershaw, K.A. (1964) Preliminary observations on the distribution and ecology of epiphytic lichens in Wales. *Lichenologist*, **2**, 263-276.

Kirby, E.N. & O'Connell, M. (1982) Shannawoneen Wood, County Galway, Ireland: the woodland and saxicolous communities and the epiphytic flora. *Journal of Life Sciences of the Royal Dublin Society*, **4**, 73-96.

Kivisto, L. & Kuusinen, M. (2000) Edge effects on the epiphytic lichen flora of *Picea abies* in middle boreal Finland. *Lichenologist*, **32**, 387-398.

Kuusinen, M. (1996a) Epiphyte flora and diversity of basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist*, **28**, 443-463.

Kuusinen, M. (1996b) Importance of spruce swamp-forests for epiphyte diversity on *Picea abies* in southern and middle boreal Finland. *Ecography*, **19**, 41-51.

Lang, G.E., Reiners, W.A., & Pike, L.H. (1980) Structure and biomass dynamics of epiphytic lichen communities of balsam fir forests in New Hampshire. *Ecology*, **61**, 541-550.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd English edn. Elsevier, Amsterdam.

LichenIreland (2007) *Checklist of Irish Lichens* http://www.habitas.org.uk/lichenireland/splist.asp

Lieberman, M., Liberman, D., & Peralta, R. (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**, 550-552.

Little, D.J., Boyle, G.M., Ryan, G., & Farrell, E.P. (2001). *Intensive Monitoring of an Oak Woodland in Western Ireland: Development of an Irish Ecological Monitoring Network (IEMN).* COFORD, Dublin.

Liu, C., Ilvesniemi, H., & Westman, C.J. (2000) Biomass of arboreal lichens and its vertical distribution in a boreal coniferous forest in central Finland. *The Lichenologist*, **32**, 495-506.

Lyons, B., Nadkarni, N.M., & North, M.P. (2000) Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. *Canadian Journal of Botany*, **78**, 957-968.

Magdefrau, K. (1982) Life-forms of Bryophytes. In *Epiphytes and Epiliths* (ed A.J.E. Smith), pp. 45-58. Chapman and Hall, London.

Magurran, A.E. (1998) *Ecological Diversity and its Measurement* Chapman and Hall, London.

Magurran, A.E. (2003) *Measuring Biological Diversity* Blackwell, Oxford.

Martin, N.M. (1938) Some observations on the epiphytic moss flora of trees in Argyll. *Journal of Ecology*, **26**, 82-95.

Matlack, G.R. (1993) Microenvironment variation within and among forest edge sites in the eastern United-States. *Biological Conservation*, **66**, 185-194.

Matlack, G.R. & Litvaitis, J.A. (1999) Forest Edges. In *Maintaining Biodiversity in Forest Ecosystems* (eds L. Malcolm & J.R. Hunter), pp. 210-233. Cambridge University Press, Cambridge.

May, R.M. (1975) Patterns of Species Abundance and Diversity. In *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 81-120. Harvard University Press, Cambridge.

McCarthy, P.M. (1980) Vertical zonation of lichens on alder (*Alnus glutinosa* (L.) Gaertn.) near Cork, Ireland. *Scientific Proceedings, Royal Dublin Society, Series A*, **6**, 397-405.

McCarthy, P.M., Mitchell, M.E., & Schouten, M.G.C. (1986) Lichens epiphytic on *Calluna vulgaris* (L) Hull in Ireland. *Nova Hedwigia*, **42**, 91-98.

McCune, B. (1990) Rapid estimation of abundance of epiphytes on branches. *Bryologist*, **93**, 39-43.

McCune, B. (1993) Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, **96**, 405-411.

McCune, B., Amsberry, K.A., Camacho, F.J., S. Clery, C.C., Emerson, C., Felder, G., P.French, Greene, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G.G., Pendergrass, K., Peterson, E.B., Peterson, E.T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Shaw, D., Turner, R., & Widner, M. (1997) Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *Northwest Science*, **71**, 145-152.

McCune, B. & Antos, J.A. (1981) Correlations between forest layers in the Swan Valley, Montana. *Ecology*, **62**, 1196-1204.

McCune, B. & Antos, J.A. (1982) Epiphyte communities of the Swan Valley, Montana. *Bryologist*, **85**, 1-12.

McCune, B. & Mefford, M.J. (1997) *PC-ORD for Windows 3.17* MjM Software, Glenedon Beach, Oregon.

McCune, B. & Mefford, M.J. (1999) *Mulitvariate Analysis of Ecological Data* MjM Software, Oregon.

McCune, B., Rosentreter, Ponzetti, & Shaw, D. (2000) Epiphyte habitats in an old conifer forest in western Washington, USA. *Bryologist*, **103**, 417-427.

McEntee, M.A. (1980) A revision of the equation relating sunshine hours to radiation income for Ireland. *Irish Journal of Agricultural Research*, **19**, 119-125.

McEvoy, T. (1944) Irish native woodlands: their present condition. *Irish Forestry*, **1**, 27-35.

McGee, G.G. & Kimmerer, R.W. (2002) Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. *Canadian Journal of Forest Research*, **32**, 1562-1576.

Met Éireann (2006) http://www.met.ie/climate/30year-averages.asp

Mitchell, A.W., Secoy, K., & Jackson, T., eds. (2002) *The Global Canopy Handbook: Techniques of Access and Study in the Forest Roof*, 1st edn. Global Canopy Programme, Oxford.

Mitchell, F. & Ryan, M. (1997) *Reading the Irish Landscape.* Town House, Dublin.

Mitchell, F.J.G. (1995). The Dynamics of Irish Post-Glacial Forests. In *Woods, Trees and Forests in Ireland* (eds J.R. Pilcher & S.S. Mac an tSaoir), pp. 13-22. Royal Irish Academy, Dublin.

Mitchell, M.E. (1964) Lichens occurring on *Arbutus* at Killarney. *Irish Naturalists Journal*, **14**, 277-278.

Moe, B. & Botnen, A. (2000) Epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* in four different habitats at Grinde, Leikanger, western Norway. *Plant Ecology*, **151**, 143-159.

Moore, S.E. & Allen, H.L. (1999). Plantation Forestry. In *Maintaining Biodiversity in Forest Ecosystems* (eds L. Malcolm & J.R. Hunter), pp. 400-433. Cambridge University Press, Cambridge.

Mullen, K., Fahy, O., & Gormally, M. (2003) Ground flora and associated arthropod communities of forest road edges in Connemara, Ireland. *Biodiversity and Conservation*, **12**, 87-101.

Muller, K. (2001) Pharmaceutically relevant metabolites from lichens. *Applied Microbiology and Biotechnology*, **56**, 9-16.

Nadkarni, N. (1994) Diversity of species and interactions in the upper tree canopy of forest ecosystems. *American Zoologist*, **34**, 70-78.

Nadkarni, N.M. & Matelson, T.J. (1989) Bird use of epiphyte resources in neotropical trees. *The Condor*, **91**, 891-907.

Nadkarni, N.M., Merwin, M.C., & Nieder, J. (2001) Forest canopies, plant diversity. *Encyclopedia of Biodiversity*, **3**, 27-40.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.J., & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-736.

Nagendra, H. (2002) Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography*, **22**, 175-186.

Neitlich, P.N. & McCune, B. (1997) Hotspots of epiphytic lichen diversity in two young managed forests. *Conservation Biology*, **11**, 172-182.

Nieder, J., Prosperí, J., & Michaloud, G. (2001) Epiphytes and their contribution to canopy diversity. *Plant Ecology*, **153**, 51-63.

Norman, J.M. & Jarvis, P.G. (1974) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong) Carr). III. Measurements of canopy structure and interception of radiation. *Journal of Applied Ecology*, **11**, 375-398.

O'Connell (1990) Origins of Irish Lowland Blanket Bogs. In *Ecology and Conservation of Irish Peatlands* (ed G.J. Doyle). Royal Irish Academy, Dublin.

O Carroll, N. (2004) *Forestry in Ireland: A Concise History.* COFORD, Dublin.

Oliver, W.R.B. (1930) New Zealand epiphytes. *Journal of Ecology*, **18**, 1-50.

Palmer, M.W. (1986) Pattern in corticolous bryophyte communities of the North Carolina piedmont: do mosses see the forest or the trees? *Bryologist*, **89**, 59-65.

Parker, G.G. & Brown, M.J. (2000) Forest canopy stratification - is it useful? *The American Naturalist*, **155**, 473-484.

Paton, J.A. (1999) *The Liverwort Flora of the British Isles* Harley Books, Colchester.

Pearson, L.C. (1969) Influence of temperature and humidity on distribution of lichens in a Minnesota bog. *Ecology*, **50**, 740-746.

Peck, J.E., Hong, W.S., & McCune, B. (1995) Diversity of epiphytic bryophytes on 3 host tree species, Thermal Meadow, Hotsprings Island, Queen-Charlotte-Islands, Canada. *Bryologist*, **98**, 123-128.

Peck, J.E. & McCune, B. (1997) Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications*, **7**, 1181-1187.

Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285-307.

Pentecost, A. (1998) Some observations on the biomass and distribution of cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains, Uganda. *Global Ecology and Biogeography Letters*, **7**, 273-284.

Peterken, G.F. (1981) *Woodland Conservation and Management.* Chapman and Hall, London.

Peterken, G.F. (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions.* Cambridge University Press, Cambridge.

Pettersson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-E., & Sjoberg, K. (1995) Invertebrate communities in Boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation*, **74**, 57-63.

Phillips, E.A. (1959) Bark bryophyte unions in southern Ireland. *Bryologist*, **62**, 24-31.

Phillips, R., ed. (1980) *Grasses, Ferns, Mosses & Lichens of Great Britain and Ireland.* Pan Books, London.

Pike, L.H., Rydell, R.A., & Denison, W.C. (1977) A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area and their distribution. *Canadian Journal of Forest Research*, **7**, 680-699.

Pócs, T. (1982) Tropical Forest Bryophytes. In *Bryophyte Ecology* (ed A.J.E. Smith). Chapman and Hall, London.

Porley, R.D. & Hodgetts, N.G. (2005) *Mosses and Liverworts.* Collins, London.

Price, K. & Hochachka, G. (2001) Epiphytic lichen abundance: effects of stand age and composition in coastal British Columbia. *Ecological Applications*, **11**, 904-913.

Purdy, K. & Ferris, R. (1999) *A Pilot Study to Examine the Potential Linkage Between and Applications of Multiple Woodland Datasets: A GIS Based Analysis, Rep. No. 298.* Joint Nature Conservation Committee, Peterborough.

Purvis, O.W., Coppins, B.J., Hawksworth, D.L., James, P.W., & Moore, D.M. (1992) *The Lichen Flora of Great Britain and Ireland.* Natural History Publications and The British Lichen Society, London.

Rackham, O. (2005) Questions to Ask of Irish Native Woodland In *Ireland's Native Woodlands. Conference proceedings.* (eds C. Doyle & D. Little), pp. 11-18. Woodlands of Ireland, Dublin.

Ratcliffe, D.A. (1968) An ecological account of Atlantic bryophytes in the British Isles. *New Phytologist*, **67**, 365-439.

Ratcliffe, P.R. & Peterken, G.F. (1995) The potential for biodiversity in British upland spruce forests. *Forest Ecology and Management*, **79**, 153-160.

Raynor, G.S. (1971) Wind and temperature structure in a coniferous forest and a contiguous field. *Forest Science*, **17**, 351-363.

Renhorn, K.-E., Esseen, P.-A., Palmqvist, K., & Sundberg, B. (1997) Growth and vitality of epiphytic lichens. I. Response to microclimate along a forest edge-interior gradient. *Oecologia*, **109**, 1-9.

Rhoades, F.M. (1981) Biomass of epiphytic lichens and bryophytes on *Abies lasiocarpa* on a Mt. Baker lava flow, Washington. *Bryologist*, **84**, 39-47.

Rhoades, F.M. (1995). Nonvascular Epiphytes in Forest Canopies: Worldwide Distribution, Abundance, and Ecological Roles. In *Forest Canopies* (eds M.D. Lowman & N.M. Nadkarni), pp. 353-408. Academic Press, California.

Richards, P.W. (1938) The bryophyte communities of a Killarney oakwood. *Annales Bryologici*, **11**, 108-130.

Richardson, D.H.S. (1987) Lichens as Pollution Indicators in Ireland. In *Biological Indicators of Pollution* (ed D.H.S. Richardson). Royal Irish Academy, Dublin.

Richardson, D.H.S. & Young, C.M. (1977) Lichens and Vertebrates. In *Lichen Ecology* (ed M.R.D. Seaward). Academic Press, London.

Roberts, M.R. & Gilliam, F.S. (1995) Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications*, **5**, 969-977.

Rose, F. (1974) The Epiphytes of Oak. In *The British Oak: Its History and Natural History* (eds M.G. Morris & F.H. Perring). E.W. Classey, Faringdon.

Rose, F. (1988) Phytogeographical and ecological aspects of *Lobarion* communities in Europe. *Botanical Journal of the Linnean Society*, **96**, 69-79.

Rose, F. (1992) Temperate Forest Management: Its Effects on Bryophyte and Lichen Floras and Habitats. In *Bryophytes and Lichens in a Changing Environment* (eds J.W. Bates & A.M. Farmer), pp. 211-233. Oxford University Press, New York.

Rose, F. (1993) Ancient British woodland and their epiphytes. *British Wildlife*, **5**, 83-93.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time.* Cambridge University Press, Cambridge.

Schmitt, C.K. & Slack, N.G. (1990) Host specificity of epiphytic lichens and bryophytes: a comparison of the Adirondack Mountains (New York) and the southern Blue Ridge Mountains (North Carolina). *Bryologist*, **93**, 257-274.

Seaward, M.R.D. (1994) Vice county distribution of Irish lichens. *Biology and Environment-Proceedings of the Royal Irish Academy* **94B**, 177-194.

Shannon, C.E. & Weaver, W. (1949) *The Mathematical Theory of Communication.* University of Illinois Press, Urbana, Illinois.

Showman, R.E. (1975) Lichens as indicators of air quality around a coal-fired power generating plant. *Bryologist*, **78**, 1-6.

Sillett, S.C. (1994) Growth rates of two epiphytic cyanolichen species at the edge and in the interior of a 700-year-old Douglas fir forest in the western Cacades of Oregon. *Bryologist*, **97**, 321-324.

Sillett, S.C. (1995) Branch epiphyte assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas fir canopy in Western Oregon. *Bryologist*, **98**, 301-312.

Sillett, S.C. & Bailey, M.G. (2003) Effects of tree crown structure on biomass of the epiphytic fern *Polypodium scouleri* (Polypodiaceae) in redwood forests. *American Journal of Botany*, **90**, 255-261.

Sillett, S.C., Rambo, T.R. (2000) Vertical distribution of dominant epiphytes in Douglas-fir forests of the central Oregon Cascades. *Northwest Science*, **74**, 44-49.

Simmons, E.A. & Buckley, G.P. (1991). Ground Vegetation Under Planted Mixtures of Trees. In *The Ecology of Mixed Species Stands of Trees* (eds M.G.R. Cannell, D.C. Malcolm & P. Robertson), pp. 211-231. Blackwell Scientific, Oxford.

Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.

Smith, A.J.E. (1982) Epiphytes and Epiliths. In *Bryophyte Ecology* (ed A.J.E. Smith), pp. 191-227. Chapman and Hall, London.

Smith, A.J.E. (1990) *The Liverworts of Britain and Ireland.* Cambridge University Press, Cambridge.

Smith, A.J.E. (2004) *The Moss Flora of Great Britain and Ireland.* Cambridge University Press, Cambridge.

Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., Pithon, J., O'Donnell, V., McKee, A.-M., Iremonger, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Giller, P.S., & Kelly, T. (2005) *Assessment of Biodiversity at Different Stages of the Forest Cycle.* Report for COFORD and EPA. http://www.coford.ie/iopen24/pub/pub.Project_files/312Report.pdf

Sparks, T.H., Greatorex-Davies, J.N., Mountford, J.O., Hall, M.L., & Marrs, R.H. (1996) The effects of shade on the plant communities of rides in plantation woodland and the implications for butterfly conservation. *Forest Ecology and Management*, **80**, 197-207.

SPSS (2001) *SPSS for Windows 11.0.1.* SPSS Inc.

Stace, C. (1997) *New Flora of the British Isles.* Cambridge University Press, Cambridge.

Studlar, S.M. (1982a) Host specificity of epiphytic bryophytes near Mountain Lake, Virginia. *Bryologist*, **85**, 37-50.

Studlar, S.M. (1982b) Succession of epiphytic bryophytes near Mountain Lake, Virginia. *Bryologist*, **85**, 51-63.

Tilman, D., Wedlin, D., & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 130-137.

Trynoski, S.E. & Glime, J.M. (1982) Direction and height of bryophytes on four species of northern trees. *Bryologist*, **85**, 281-300.

Uliczka, H. & Angelstam, P. (1999) Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography*, **22**, 396-405.

UNEP (1992) *Convention on Biological Diversity.* United Nations Environmental Programme, Nairobi.

Universität Hamburg (2007) *Checklists of lichens and lichenicolous fungi in Europe* http://www.biologie.uni-hamburg.de/checklists/europe/europe_l0.htm

Vanderpoorten, A., Engels, P., & Sotiaux, A. (2004) Trends in diversity and abundance of obligate epiphytic bryophytes in a highly managed landscape. *Ecography*, **27**, 567-576.

Warren, M.S. & Fuller, R.J. (1993) *Woodland Rides and Glades: Their Management for Wildlife*, 2nd edn. Joint Nature Conservation Committee, Peterborough.

Watson, E.V. (1981) *British Mosses and Liverworts*, Third edn. Cambridge University Press, Cambridge.

Watson, W. (1936) The bryophytes and lichens of British woods. Part II. Other woodland. *Journal of Ecology*, **24**, 446-478.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213-215.

Wiegleb, G. (2002) *The Value of Biodiversity.* http://www.tu-cottbus.de/BTU/Fak4/AllgOeko/Forschung/value-phil-11.pdf

Wilson, M.V. & Schmida, A. (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology*, **72**, 1055-1064.

Wolf, J.D.H. (1993) Epiphyte Communities of Tropical Montane Rain Forests in the Northern Andes. I. Lower Montane Communties. In *Ecology of Epiphytes and Epiphyte Communities in Montane Rain Forests, Columbia.* University of Amsterdam, Amsterdam.

Wolf, J.H.D. & Flamenco-S, A. (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, **30**, 1689-1707.

Woods, R.G. & Coppins, B.J. (2003) *A Conservation Evaluation of British lichens.* British Lichen Society, London.

Appendices

Appendix 1 The estimated rainfall, area of old woodland within 1km, distance to old woodland, area of buildings grouped within 3km, distance to buildings grouped and pre-afforestation habitat of each stand (cf. Section 2.3.3 for details).

Site Codes	Estimated Rainfall ($mmyr^{-1}$)	Area of old woodland (ha)	Distance to old woodland (m)	Area of buildings grouped (ha)	Distance to Buildings (m)	Pre-afforestation habitat
ATHN1&2	1300	0	1001	0	3001	Rough pasture
BMUT1&2	1100	0	1001	0	3001	Rough pasture
CURA1&2	1300	0	1001	0	3001	Furze/Bracken
LUGG1&2	900	93.0	0	110.0	635	Old woodland
MUCK1&2	1500	0.6	933	0	3001	Furze/Bracken
MUIN1	1100	0	1001	0	3001	Furze/Bracken
MUNG2	1100	1.9	143	0	3001	Furze/Bracken
STOE1&2	1800	26.3	536	0	3001	Rough pasture
TIKN1	1100	0.8	759	378.6	1613	Furze/Bracken
CARR1&2	1500	0.1	771	0	3001	Furze/Bracken
CLEA1&2	1300	0	1001	0	3001	Rough pasture
COOM2	2400	0	1001	0	3001	Furze/Bracken
FURY2	1800	0	1001	0	3001	Furze/Bracken
GLAN1&2	1300	0	1001	0	3001	Rough pasture
KNOC1&2	1500	0	1001	0	3001	Rough pasture
MEEN1&2	1500	0	1001	0	3001	Rough pasture
REAN1&2	1300	0	1001	0	3001	Rough pasture
AGHA1	1500	0	1001	0	3001	Rough pasture
CRUA1	1300	19.3	164	13.4	2336	Furze/Bracken
CURT1	1500	9.8	576	0	3001	Furze/Bracken
GAPP1	1500	13.2	512	0	3001	Rough pasture
MUNG1	1100	1.9	488	0	3001	Furze/Bracken
TOMB1	1500	0	1001	0	3001	Furze/Bracken
COOM1	2400	0	1001	0	3001	Rough pasture
FURY1	1800	0	1001	0	3001	Furze/Bracken
GLAN3	1300	0	1001	0	3001	Rough pasture
GOUN1	1300	0	1001	0	3001	Furze/Bracken
LAHA1	1300	3.1	183	0	3001	Rough pasture

Appendix 2 The tree density, mean DBH and basal area from the 10m x 10m plot surrounding each tree (cf. Section 2.3.2) and the height and DBH of each tree studied.

Tree Code	10m x 10m plots			Studied trees	
	Tree density (no. $100m^{-2}$)	Mean DBH (cm)	Basal Area (m^2100m^{-2})	Tree height (m)	Tree DBH (cm)
ATHN1	11	28.6	0.77	12.0	40.5
ATHN2	9	24.9	0.52	14.2	31.4
BMUT1	6	38.2	0.72	21.0	45.7
BMUT2	4	33.2	0.35	22.5	34.8
CURA1	13	24.3	0.72	21.0	45.8
CURA2	14	20.1	0.47	15.6	27.1
LUGG1	4	37.2	0.46	20.0	51.9
LUGG2	3	31.9	0.24	19.0	34.7
MUCK1	5	40.5	0.66	26.2	45.2
MUCK2	5	32.7	0.42	22.8	35.9
MUIN1	4	45.0	0.80	29.4	49.1
MUNG2	7	29.0	0.52	24.2	37.9
STOE1	17	19.8	0.83	11.0	24.7
STOE2	17	19.2	0.8	11.2	24.9
TIKN1	7	50.1	0.69	20.6	38.4
CARR1	19	22.8	0.94	26.0	41.8
CARR2	22	19.2	0.70	20.85	26.0
CLEA1	19	21.3	0.86	13.4	33.2
CLEA2	9	23.0	0.45	16.4	30.4
COOM2	3	48.1	0.58	35.4	62.1
FURY2	6	25.7	0.33	21.0	30.6
GLAN1	20	18.9	0.66	18.0	47.6
GLAN2	21	18.4	0.60	19.35	25.9
KNOC1	20	17.5	0.58	15.0	25.7
KNOC2	17	17.6	0.43	15.45	23.3
MEEN1	29	17.2	0.74	16.2	34.8
MEEN2	23	17.3	0.59	16.8	24.9
REAN1	19	24.3	0.98	21.3	34.5
REAN2	17	18.1	0.48	18.0	22.9
AGHA1	10	21.8	0.40	19.8	27.0
CRUA1	3	35.2	0.23	25.8	42.6
CURT1	4	37.9	0.64	25.2	44.2
GAPP1	4	30.1	0.29	21.6	34.8
MUNG1	3	26.2	0.16	22.4	28.8
TOMB1	12	16.8	0.29	17.8	25.7
COOM1	4	24.8	0.26	29.3	46.5
FURY1	6	31.5	0.48	22.5	33.8
GLAN 3	7	24.6	0.34	18.5	25.9
GOUN1	4	27.6	0.25	21.3	32.4
LAHA1	7	27.6	0.43	23.0	29.6

Appendix 3 A list of the epiphyte species recorded in this study. The epiphyte group (bryophytes: Mo = moss and Lv = liverwort; lichens: Li; vascular plants: Va), growth form (bryophyte: Cu = cushion, Ma = mat, Tu = turf, We = weft; Lichen: Cr = crustose, Lp = Leprose, Fo = Foliose, or Fr = Fruticose) and affinity for epiphytism (Low = primarily found in non-epiphytic habitats, Int = occurring in both epiphytic and non-epiphytic habitats, High = primarily found in epiphytic habitats) of each species is given. Their occurrence on Sitka spruce and Japanese larch and in the Wicklow and Cork clusters is indicated: * indicates species found only on the open space edge Sitka spruce trees, + indicates additional species found outside the plots on the studied branches.

Species	Epiphyte Group	Growth Form	Epiphytism affinity	Spruce	Larch	Wicklow	Cork
Atrichum undulatum	Mo	Tu	Low	√		√	
Campylopus flexuosus	Mo	Tu	Low		√		√
Campylopus introflexus	Mo	Tu	Low	√*		√	√
Cryphaea heteromalla	Mo	Ma	High	√*			√
Daltonia splachnoides	Mo	Cu	Int	√			√
Dicranum scoparium	Mo	Tu	Int		√	√	√
Hypnum andoi	Mo	Ma	Int	√	√	√	√
Hypnum jutlandicum	Mo	Ma	Int	√	√	√	√
Hypnum resupinatum	Mo	Ma	Int	√	√	√	√
Isothecium myosuroides	Mo	We	Int	√	√		√
Kindbergia praelonga	Mo	Ma	Int	√	√	√	√
Mnium hornum	Mo	Tu	Int	√*		√	
Plagiothecium laetum	Mo	Ma	Int	√		√	
Plagiothecium undulatum	Mo	Ma	Low	√	√	√	√
Pseudoscleropodium purum	Mo	We	Low		√	√	
Pseudotaxiphyllum elegans	Mo	Ma	Low	√	√	√	√
Rhytidiadelphus loreus	Mo	We	Low	√	√	√	√
Rhytidiadelphus squarrosus	Mo	We	Low		√	√	
Thuidium tamariscinum	Mo	We	Low	√	√	√	√
Ulota crispa s.l.	Mo	Cu	High	√	√	√	√
Ulota phyllantha	Mo	Cu	High	√*			√
Calypogeia muelleriana	Lv	Ma	Low	√			√
Colura calyptrifolia	Lv	Ma	Int	√	√	√	√
Frullania dilatata	Lv	Ma	High	√	√	√	√
Frullania tamarisci	Lv	Ma	Int	√	√		√
Frullania teneriffae	Lv	Ma	Int	√			√
Lejeunea cavifolia	Lv	Ma	Int	√			√
Lophocolea bidentata	Lv	Ma	Int	√	√	√	√
Metzgeria fruticulosa	Lv	Ma	High	√		√	√
Metzgeria furcata	Lv	Ma	Int	√	√	√	√
Metzgeria temperata	Lv	Ma	High	√	√	√	√
Microlejeunea ulicina	Lv	Ma	High	√	√	√	√
Radula complanata	Lv	Ma	High	√			√
Anisomeridium biforme	Li	Cr	High	√			√
Anisomeridium polypori	Li	Cr	High	√			√
Anisomeridium ranunculosporum	Li	Cr	High		√		√
Byssoloma subdiscordans	Li	Cr	Int	√*			√
Candelariella reflexa	Li	Cr	High	√		√	
Dimerella lutea	Li	Cr	Int	√	√	√	√
Dimerella pineti	Li	Cr	High	√	√	√	√
Diplotomma alboatrum	Li	Cr	Int		+		+
Fellhanera bouteillei	Li	Cr	Int	√		√	√
Fuscidea lightfootii	Li	Cr	High	√	√	√	√
Graphina ruiziana	Li	Cr	High	√	√		√
Graphis elegans	Li	Cr	High	√	√	√	√
Graphis scripta	Li	Cr	High	√	√	√	√
Gyalideopsis anastomosans	Li	Cr	High	√	√	√	√
Lecania cyrtella	Li	Cr	High	√		√	
Lecanora chlarotera	Li	Cr	High	√	√		√
Lecanora pulicaris	Li	Cr	High	√	√	√	√
Lecidella elaeochroma	Li	Cr	High	√	√		√
Micaria lignaria	Li	Cr	Int	√		√	√
Micaria peliocarpa	Li	Cr	Int	√	√	√	√
Micaria prasina	Li	Cr	Int	√	√	√	√

Phaeographis smithii	Li	Cr	High	√	√		√
Pyrrhospora quernea	Li	Cr	High	√			√
Rinodina biloculata	Li	Cr	High	√			√
Rinodina roboris	Li	Cr	High	+			+
Thelotrema lepadinum	Li	Cr	High		√		√
Trapeliopsis flexuosa	Li	Cr	Int	√	√	√	√
Trapeliopsis granulosa	Li	Cr	Low		√		√
Lepraria incana	Li	Lp	Int	√	√	√	√
Cladonia chlorophaea	Li	Fo	Low	√	√		√
Cladonia coniocraea	Li	Fo	Int		√	√	
Cladonia macilenta	Li	Fo	Int		√	√	
Evernia prunastri	Li	Fo	High	√	√	√	√
Hypogymnia physodes	Li	Fo	Int		√	√	
Hypogymnia tubulosa	Li	Fo	Int	√	√	√	√
Hypotrachyna laevigata	Li	Fo	High	+			+
Hypotrachyna revoluta	Li	Fo	High	√	√	√	√
Melanelia exasperata	Li	Fo	High		+	+	
Melanelia fuliginosa ssp. *glabratula*	Li	Fo	High	√		√	
Parmelia saxatilis	Li	Fo	Int		√	√	
Parmelia sulcata	Li	Fo	Int	√	√	√	√
Parmotrema chinense	Li	Fo	Int	√			√
Physcia adscendens	Li	Fo	Int	√			√
Physcia aipolia	Li	Fo	High	√*		√	
Physcia tenella	Li	Fo	High	√	√	√	√
Platismatia glauca	Li	Fo	Int		√	√	
Pseudevernia furfuracea	Li	Fo	Int	√	√	√	
Punctelia subrudecta	Li	Fo	Int	√			√
Xanthoria parietina	Li	Fo	Int	+*			√
Xanthoria polycarpa	Li	Fo	High	√*		√	
Ramalina farinacea	Li	Fr	High	√	√	√	√
Ramalina fastigiata	Li	Fr	High	√			√
Usnea cornuta	Li	Fr	High		√	√	√
Usnea esperantiana	Li	Fr	High	√			√
Usnea filipendula	Li	Fr	High	√	√		√
Usnea flammea	Li	Fr	Int	√*			√
Usnea fragilescens	Li	Fr	High		√	√	
Usnea glabrescens	Li	Fr	High		√	√	
Usnea subfloridana	Li	Fr	High		√	√	
Juvenile pteridophyte	Va	-	-	√			√
Oxalis acetosella	Va	-	Low		√	√	√
Rubus fruticosus agg.	Va	-	Low		√		√

Appendix 4 A list of the trunk plots occurring in the ten cluster analysis groups indicated in Figure 3.56.

Cluster I	(Cluster I)	Cluster VI	Cluster VIII	Cluster II	Cluster III	Cluster IV	Cluster VII	Cluster IX	Cluster V	Cluster X
LUGG2TBn	GOUN1TBn	BMUT2TBs	MUCK2TLs	LUGG2TLs	ATHN2TBs	ATHN2TUn	STOE2TBn	GLAN3TLn	ATHN2TUs	CRUA1TBn
GAPP1TBs	COOM2TBs	MUCK2TLn	CURA2TMs	BMUT2TMn	ATHN2TMs	GAPP1TMn	KNOC2TBn	GLAN3TLs	TOMB1TUs	CRUA1TBs
TOMB1TBn	LAHA1TBs	MUCK2TMs	MEEN2TUs	MUNG2TMs	BMUT2TBn	GLAN3TUn	KNOC2TBs	GLAN3TMs	CRUA1TUs	CRUA1TLn
AGHA1TBs	GOUN1TBs	CARR2TLn	GLAN2TMn	MUIN1TLn	TOMB1TLn	FURY2TUs	MEEN2TBn	COOM1TUs	TOMB1TUn	CURT1TLn
MUNG2TBn	GOUN1TLn	MUCK2TBs	GLAN2TMs	LUGG2TUn	ATHN2TMn	CLEA2TUn	GLAN2TBs	COOM2TLn	AGHA1TUn	CRUA1TLs
GLAN3TBs	FURY1TBn	CARR2TLs	REAN2TUn	CLEA2TMs	KNOC2TLn	BMUT2TMs	GLAN2TLn	COOM2TUs	TOMB1TUs	CURT1TLs
FURY2TLn	FURY1TBs	AGHA1TMn	MEEN2TUn	LUGG2TMn	KNOC2TLs	CARR2TUn	GLAN2TLs	FURY1TMn	AGHA1TUs	CURT1TBn
AGHA1TBn	COOM2TBn	MUIN1TBn	GLAN2TUn	LUGG2TMs	MUNG2TLs	STOE2TMs	LAHA1TMn	FURY1TMs	CURT1TUs	CURT1TBs
GAPP1TBn		GLAN3TMn	FURY2TUn	LUGG2TUs	AGHA1TLs	MUNG1TMn	COOM1TBn	FURY1TUn	GAPP1TUn	CRUA1TMn
MUNG1TBn		GOUN1TMn	CURA2TLs	MUNG2TMn	STOE2TLn	CRUA1TUn	MEEN2TLn	COOM1TMn	GAPP1TUs	CRUA1TMs
COOM2TMs		LAHA1TLs	REAN2TBn	CLEA2TMn	REAN2TUs	TOMB1TLs	GLAN2TBn	COOM2TUn	STOE2TUs	CURT1TMn
LAHA1TBn		AGHA1TMs	MEEN2TMn	BMUT2TUn	GAPP1TLn	TOMB1TMn	GLAN3TBn		MUNG1TUs	CURT1TMs
LUGG2TBs		MUNG2TLn	REAN2TMn	MUNG2TUs	STOE2TMn	GAPP1TLs	FURY2TBn		GAPP1TMs	
LUGG2TLn			REAN2TMs	MUIN1TMn	TIKN1TLn	MUIN1TLs	FURY2TBs		MUNG1TUn	
AGHA1TLn			MEEN2TMs	BMUT2TUs	MUNG1TLn	COOM1TUn	KNOC2TMn		GLAN3TUs	
MUNG1TBs			CURA2TMn	MUNG2TUn	MUNG1TLs	CURT1TUn	KNOC2TMs		CLEA2TUs	
FURY2TLs			MEEN2TBs	MUIN1TUs	MUNG1TMs	COOM1TMs	KNOC2TUn		GLAN2TUs	
MUIN1TBs			FURY2TMn	MUNG2TBs		STOE2TUn	KNOC2TUs			
FURY1TLs			REAN2TBs	MUIN1TUn		MUCK2TUn	COOM1TBs			
MUCK2TBn			REAN2TLn	MUIN1TMs		MUCK2TUs	COOM1TLs			
TOMB1TBs			REAN2TLs			FURY1TUs	COOM1TLn			
CLEA2TBs			CLEA2TLs			CARR2TMn				
GOUN1TLs			MEEN2TLs			CARR2TMs				
MUCK2TMn			CURA2TUn			LAHA1TUs				
CLEA2TBn			CLEA2TLn			CARR2TUs				
CURA2TBs			CARR2TBs			LAHA1TUn				
CURA2TBn			CURA2TUs			LAHA1TLn				
CARR2TBn			FURY2TMs			LAHA1TMs				
CURA2TLn			GOUN1TMs			GOUN1TUn				
FURY1TLn						GOUN1TUs				
COOM2TLs										
COOM2TMn										

Appendix 5 A list of the branch plots occurring in the eight branch plot cluster analysis groups indicated in Figure 3.63.

Cluster i	(Cluster i)	Cluster vi	Cluster vii	(Cluster vii)	Cluster ii	Cluster iii	Cluster v	(Cluster v)	Cluster viii	Cluster iv
LUGG2BMn1	LUGG2BMn3	ATHN2BUn1	ATHN2BUs1	CARR2BUn1	LUGG2BMn2	LUGG2BUs2	ATHN2BMs1	MUNG2BMs2	MUCK2BMn1	ATHN2BMn2
MUNG1BMn2	MUCK2BUs1	ATHN2BUn2	STOE2BMn2	GLAN3BUs2	LUGG2BMs2	BMUT2BUn1	BMUT2BMs1	MEEN2BUn2	MUCK2BMs1	CURA2BMn1
AGHA1BMs1	CARR2BMn3	ATHN2BUn3	MUNG1BMn1	STOE2BUs1	LUGG2BMs3	GLAN2BMn3	GLAN2BMs1	MEEN2BUn3	LAHA1BUn1	CURA2BMs1
MUIN1BUn2	COOM2BMs3	STOE2BUs2	MUNG1BUn1	MUNG1BUn2	BMUT2BMn1	KNOC2BMs1	COOM2BMn2	STOE2BMs2	REAN2BMs3	REAN2BMn1
MUIN1BUs2	CURA2BUs3	STOE2BMn1	MUCK2BMn3	TOMB1BUn1	BMUT2BMs2	KNOC2BMn1	AGHA1BMn2	LAHA1BUn3	COOM2BUn1	MEEN2BMn1
LUGG2BUn2	MEEN2BMs3	MUCK2BUn3	STOE2BUn1	TOMB1BMs1	STOE2BMs1	FURY2BMs3	AGHA1BMn3	FURY2BMn3	COOM2BUs1	MEEN2BMn2
MUIN1BUn3	GLAN2BMn2	CURA2BUn3	MUNG2BUn2	GAPP1BMs3	MUNG2BMn1	BMUT2BMn3	REAN2BUn1	MUCK2BUn2	GAPP1BMs1	GLAN2BMn1
MUIN1BUs3	FURY2BUs1	BMUT2BUn3	FURY2BUs2	CURT1BUs3	ATHN2BMn3	BMUT2BUs1	REAN2BUs2	MUCK2BUs2	COOM2BUs2	CURA2BMn2
STOE2BMn3	KNOC2BUn3	STOE2BMs3	ATHN2BUs3	BMUT2BUn2	MUNG2BUs1	BMUT2BMs3	MEEN2BMn3	MEEN2BUs3	GAPP1BMs2	CURA2BMn3
CURA2BUn2	CLEA2BMs3	STOE2BUn3	GAPP1BMn2	CLEA2BUs1	LUGG2BUn1	KNOC2BMn2	MEEN2BMs2	CARR2BUs1	GOUN1BUs1	CURA2BMs2
FURY1BUn1	REAN2BUn2	FURY2BUn3	GLAN2BUs2	COOM1BUn2	ATHN2BMn1	KNOC2BMs3	MEEN2BUs1	CARR2BUs2	AGHA1BMs2	CURA2BMs3
FURY1BUs1	REAN2BUs3	FURY2BUs3	CARR2BUn2	CLEA2BUs2	CURA2BUs2	KNOC2BMn3	MEEN2BUs2	MUNG1BUs3	LAHA1BUn2	REAN2BUs1
COOM2BMs2	REAN2BUn3	MUCK2BMn2	GLAN3BUs1	MUNG1BUs2	MUNG2BMn2	KNOC2BUn1	GLAN3BMs1	AGHA1BUn2	GLAN3BMn2	CURA2BUn1
FURY1BUn3			FURY1BUs2	COOM1BUs2	CLEA2BUn1	KNOC2BUn2	CARR2BMn1	AGHA1BUn3	GOUN1BUn1	CURA2BUs1
CURT1BMs3			BMUT2BUs2	FURY2BUn2	MUNG2BUs2	KNOC2BUs1	COOM2BMn1	CLEA2BMn1	GOUN1BUs2	FURY2BMs1
TOMB1BMs2			STOE2BUn2	GAPP1BUn1	AGHA1BMn1	FURY1BMn1	LAHA1BMn1	CLEA2BMn2	LAHA1BUs1	MEEN2BUn1
TOMB1BMs3			GLAN2BUn1	GAPP1BUn2	LUGG2BMs1	COOM2BUn3	BMUT2BMn2	CARR2BMn2	GLAN3BMs2	FURY2BMn1
GAPP1BMn1			GLAN2BUn2	GAPP1BUs1	LUGG2BUs1	FURY1BMn3	CLEA2BMs1	FURY2BMn2	GOUN1BUn2	REAN2BMn2
CRUA1BMs2			GLAN2BUs1	CRUA1BUs2	ATHN2BMs3	FURY1BMs1	GLAN2BMs3	CLEA2BMs2	GLAN3BMs3	REAN2BMs1
FURY1BUs3			GLAN2BUs3	KNOC2BUs2	MUNG2BMn3	FURY1BMs2	FURY1BMn2		GLAN3BUn2	REAN2BMs2
CRUA1BMn2			TOMB1BUn2	AGHA1BUn1	MUNG2BMs3	FURY1BMs3	ATHN2BUs2		GLAN3BMn3	REAN2BMn3
CRUA1BMn1			TOMB1BUs2	CRUA1BUn1	MUIN1BMs1	COOM2BUn2	GOUN1BUn3		GLAN3BUn1	MEEN2BMs1
CURT1BMs2			GAPP1BUs2	AGHA1BUs1	MUIN1BUn1	KNOC2BMs2	GLAN2BMs2		FURY1BUn2	GLAN3BMn1
CRUA1BMn3			MUNG1BUs1	CRUA1BUn2	MUIN1BUs1	KNOC2BUs3	COOM2BUs3			
CRUA1BMs1			COOM1BUs3	CURT1BUn2	ATHN2BMs2	CARR2BMs1	GOUN1BMn2			
CURT1BMs1			FURY2BUn1	CURT1BUs2	MUIN1BMn1	COOM1BUn1	GOUN1BUs3			
CRUA1BMs3			TIKN1BUn2	AGHA1BUs2	MUIN1BMn2	COOM1BUs1	GOUN1BMn1			
CRUA1BUs1			TIKN1BUs1	CURT1BUn1	MUIN1BMn3		LAHA1BUs2			
FURY2BMs2			TIKN1BUs2	CURT1BUs1	MUIN1BMs3		CLEA2BMn3			
COOM2BMs1			CLEA2BUn2		MUIN1BMs2		MUNG2BMs1			