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A STUDY OF THE TAXONOMY OF Salicornia L.
IN IRELAND

by

IAN KEITH FERGUSON

A thesis submitted to the University of Dublin
for the degree of Doctor in Philosophy

September 1964



THESIS

380

I declare that the work herein now submitted as a thesis for the degree of Doctor in Philosophy of the University of Dublin, is entirely the result of my own investigations, apart from assistance and sources of information which are specifically acknowledged. I also certify that the work embodied in this thesis has not already been accepted in substance for any degree, and it is not being concurrently submitted as an exercise for a degree at any other university.

.....

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I wish to thank Professor D.A. Webb for his guidance and advice throughout this investigation. I would also like to thank him for his assistance in obtaining research grants so that I might undertake the investigation and for the generous allowance of time and facilities that I have had, during the tenure of the post of Assistant Curator of the Herbarium in the School of Botany, which enabled me to complete this work.

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CHAPTER I

Introduction

Introduction

The genus Salicornia is a notoriously difficult group. The number and nature of the taxa recognised, especially within the annual section of the genus, has varied considerably according to the differing conceptions as to what constitutes a species in this group.

There have been two main approaches to the taxonomy. The first was that adopted by many early workers which has been to regard all annual plants as belonging to one very variable species and this treatment has been used by many subsequent botanists who have had little acquaintance of the genus in the field. In the other approach there has been a tendency for the outlook to become more and more critical and the number of species described over the years is considerable.

This variable treatment of the genus may be attributed to a number of reasons. The first is because the vegetative and floral parts of Salicornia are very reduced and specialised and as a result it is not possible to use many of those characters which are usually of value for the discrimination of taxa in other genera. A second reason for the difficult nature of the taxonomy of the group is that the characters used for the recognition of species show very few correlated discontinuities and in general variation is continuous. One of the main reasons for this continuous variation appears to be the extreme plasticity of the plants in response to environmental factors. Furthermore, there is a tendency for

many plants to be cleistogamous, or if chasmogamous for self pollination to occur frequently and this type of breeding behaviour leads to the production of pure lines. The specialised habitat requirements namely a freedom from competition and a moist, saline soil, occur in a discontinuous manner along the coast in north west Europe. Discontinuous distribution acts as an isolating mechanism which prevents inter-colony gene exchange and thus contributes to the taxonomic difficulties of the group by causing local population or colony differentiation.

Taxonomic History

The first major investigation in the genus Salicornia was that of Woods' (1851) who described five annual species from the south coast of England. Other pioneer work that may also be mentioned is Dumortier's (1868) on the Belgium Salicornia and Duval-Jouve's classic account of the southern French species (1868).

Townsend (1903) revised Woods' work and he recognised six species in his account of the genus in the Flora of Hampshire.

Moss began a fresh study of the genus in Britain at the begining of this century and he published his results in Cambridge British Flora (1914). He described seven annual species and a number of hybrids and varieties. This work has provided the basis for most accounts of the genus until Ball & Tutin (1959) revised the taxonomy of the annual section of

the genus in Britain.

Wilmott & Miss Campbell (unpub.) began an extensive study of the British Salicornia after the first world war and they collected a considerable amount of information but unfortunately Wilmott died before any of the work was published. The notes that are at British Museum do show that he recognised a considerable number of new species and thought that up to fifty might be described from the British Isles. These workers appear to have seen little material from Ireland.

Ball & Tutin (1959) revised the annual section of the genus in the British Isles and sunk four of the previously described species and described four new species. These workers divide their species into two aggregates based on morphology correlated with chromosome number. They have made no extensive biometric studies of the range of variation of the characters which they use to distinguish the taxa that they recognise.

Dalby (1962) has published an account of the relationship between chromosome number and morphology. He has shown from experimental studies of individual plants that it is possible to determine chromosome number from morphology but that to do this it is necessary to examine a number of alternative characters as variation in many characters is continuous. Dalby has not attempted to treat population samples experimentally and he has not yet expressed any views on how his results compare with the taxonomic revision proposed by Ball & Tutin

(1959).

In recent years a number of workers on the continent have made studies of the genus Salicornia over small geographical areas. Nannfeldt (1955) working in Sweden has recognised two aggregates based on chromosome number in the Salicornia of the Baltic and described some of the variation that he has found.

Konig (1960) has published an account of the taxonomy of the genus in north west Germany. He also has divided the group into two aggregates recognised from morphology based on chromosome number but in contrast to Ball & Tutin treats his further divisions at subspecific rank.

Langlois (1961) has published the results of biometric studies of a number of characters measured on population samples from one locality in northern France. He has demonstrated that three groups may be recognised at this locality, however, he has not attempted to draw any definite conclusions from these results regarding the taxonomy of French Salicornia.
History of the Genus in Ireland.

The first record of the occurrence of the genus Salicornia in Ireland appears to be that of Threlkeld (1727) in Synopsis Stirpium Hibernicum where he reports that he has eaten pickled shoots of Kali geniculatum or Salicornia in the house of an Englishman in Dublin where it had been gathered plentifully about the city and preserved.

Mackay (1836) in Flora Hibernica describes two species, one an annual S. herbacea L. under which he gives two

varieties " α Stems erect" " β Stems procumbent" he cites S. herbacea E.Fl.v.1 22 - S. annua Sm. and S. acetaria Pallas as synonyms under the former and S. procumbens Sm. and S. prostrata Pall. as synonyms under the latter variety. The other species Mackay describes is a perennial S. radicans Sm.

The next important work relating to the flora of Ireland is that of Moore and More (1866) in Cybele Hibernica which records only one species S. herbacea L. and comments that the form S. procumbens Sm. is also frequent. These workers observe that S. radicans Sm. is included in Flora Hibernica with a locality at "strand at Narrow-water below Newry" but they fear that some form of S. herbacea has been gathered in this and other Irish stations given for S. radicans. Moore and More comment that Mackay's herbarium specimen is correctly named but they report not having found it at the alleged locality of "sea-shore Howth" and observe that many of Mackay's specimens are of little authority regarding locality.

Praeger (1901) in Irish Topographical Botany treats all annual Salicornia as belonging to one species S. herbacea L. and he records this from all maritime counties of Ireland except Leitrim. Moss (1914) in Cambridge British Flora in his extensive study of the genus in Britain describes seven annual species and a number of hybrids and varieties, however, he records only two of these as occurring in Ireland S. dolichostachya Moss and S. herbacea L.

Praeger (1934) in The Botanist in Ireland records

five species; S.europaea agg., S.dolichostachya Moss, S.stricta Dum., S.ramosissima Woods and S.pusilla Woods.

Webb (1943) in An Irish Flora treats the genus as consisting of one species S.europaea L. It is worth noting that he appears to be the first worker in the British Isles to use the correct Linnean name for the aggregate of annual species.

Tutin (1952) in Flora of the British Isles records three species as occurring in Ireland. S.dolichostachya Moss, S.stricta Dum. and S.ramosissima Woods.

Webb (1953) treats the genus as an aggregate of a large number of species and observes that six or seven are probably found in Ireland but their distribution is not yet known.

Ball and Tutin (1959) in their revision of the annual species of Salicornia in Britain record for Ireland only four of the eight species that they recognise; S.ramosissima Woods,? S.europaea L., S.pusilla Woods and S.dolichostachya Moss.

These workers have commented that plants of S.ramosissima from south and east Ireland differ from those occurring in England in being clear green becoming yellow tinged with pink to crimson and in the terminal spike being cylindrical and obtuse. They have found that these differences appear to be maintained in cultivation but have said further investigation is required. Ball & Tutin reported that Irish plants assignable to S.europaea L. appear to differ only in the larger terminal spikelets with 10-22 fertile segments.

Tutin (1962) in Flora of the British Isles follows the work of his earlier paper and has recorded the same four species for Ireland.

Ferguson (1962) reported the first authentic record for S.perennis Mill. in Ireland and has commented that there are two unlocalised specimens which are undoubtedly S.perennis in Mackay's Herbarium.

Webb (1963) has recorded three species for Ireland; S.pusilla Woods, S.perennis Mill. and S.europaea an aggregate comprised of 3-4 species probably. This account of the genus is based on the work of Ball & Tutin (1959), Tutin (1962) and Ferguson (1962 & unpub.)

Ferguson (1964) has reported a second station for S.perennis Mill. in Ireland and has commented that this species has probably always been present in Ireland but has been overlooked by botanists in the past as the two stations in Co. Wexford where this species has been found do not appear to have ever been visited by Praeger.

Ball (1964) in Flora Europaea has transferred S.perennis Mill. to the genus Arthrocnemum, he records six annual species of Salicornia for Ireland S.pusilla Woods, S.europaea L. S.nitens Ball & Tutin, S.fragilis Ball & Tutin, S.dolichostachya Moss subsp. dolichostachya and ? S.ramosissima Woods. It should be noted that Ball still seems doubtful whether S.ramosissima Woods occurs in Ireland or not.

The Purpose of This Study.

Although a number of extensive studies of the genus Salicornia have been made in Britain, as have been outlined, very little information is available concerning the number and nature of the taxa represented in Ireland, their distribution, and the extent of the variation within these taxa. Furthermore, Ball & Tutin (1959) have suggested that some Irish Salicornia differ from those that they have studied in Britain.

The purpose of this work was to study the variation in the genus Salicornia in Ireland by observation and measurement of selected characters in population samples from the field and then in cultivation. In the light of these studies it was hoped to determine whether it is possible to recognise distinct taxa in the genus. If this was found possible the purpose was to describe these, to demonstrate the extent of the discontinuities that exist between them and to record their distribution throughout the country.

The other object of the work was to correlate the results obtained with those of recent workers in Britain and north west Europe and to try and clarify as far as possible any confusion that exists in the taxonomy of the genus in the light of my experience of Irish Salicornia.

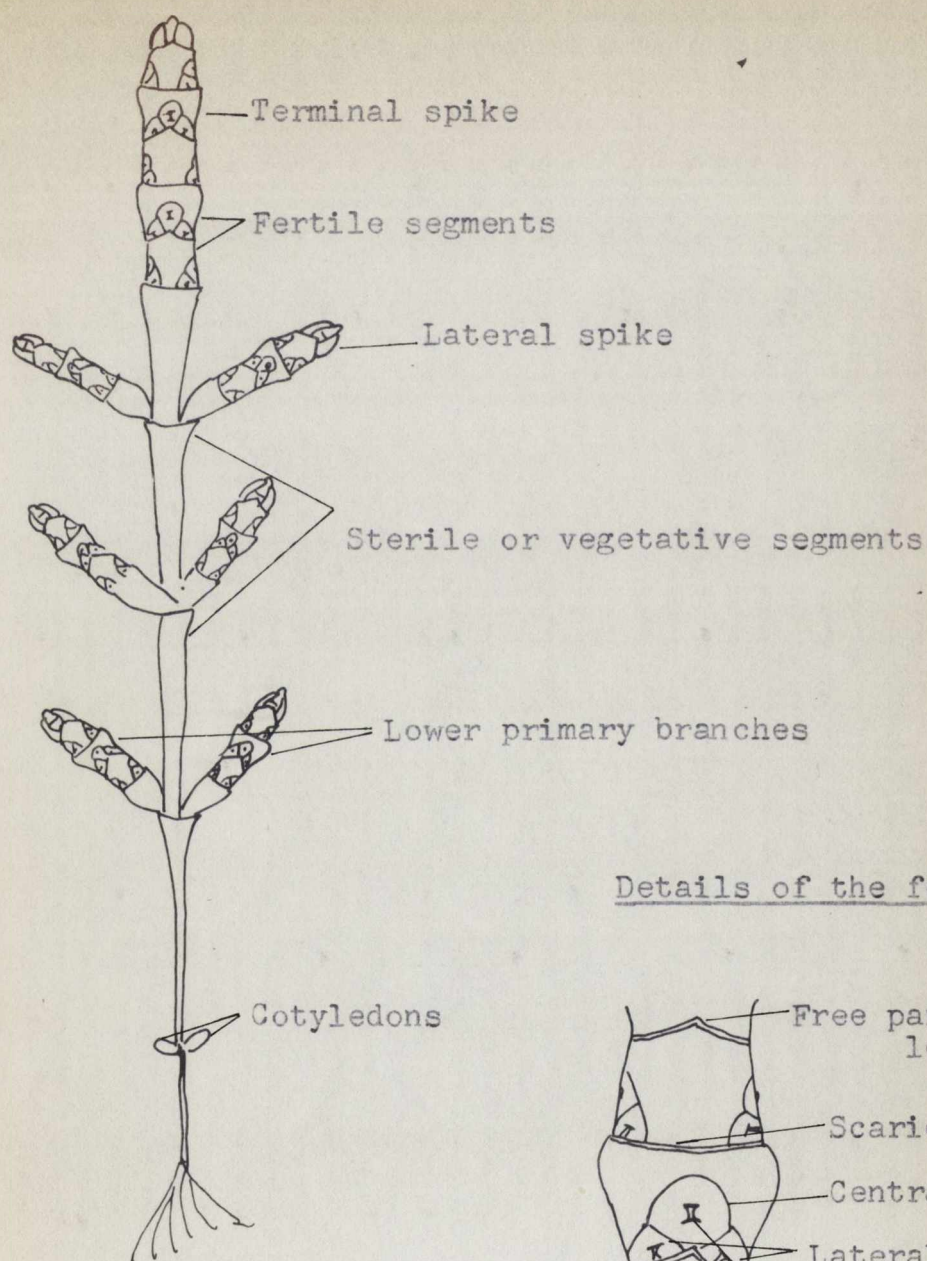
General Morphology

Salicornia L. is one of the most specialised representatives of the family Chenopodiaceae in north-west Europe. The genus is comprised of articulate, glabrous, annual or perennial herbs or dwarf shrubs. The leaves are opposite, decussate, amplexicaule, fleshy, with a short free portion extending upwards from the node and a larger portion below which is fused to the stem to form a green, succulent, false cortex the whole being referred to as a sterile or vegetative segment. The inflorescence is spicate, segmented, with opposite, decussate, almost free, bracts which subtend cymes of usually three flowers (rarely one). The flowers are very reduced, connate with and completely immersed in the fused bases of the succulent bracts of the segment; the perianth consists of three minute flaps. Stamens one or two; ovary solitary with two, branched, papillose, stigmas. The seeds have a thin membranous testa which is covered with curved or hooked hairs; endosperm is almost completely absent.

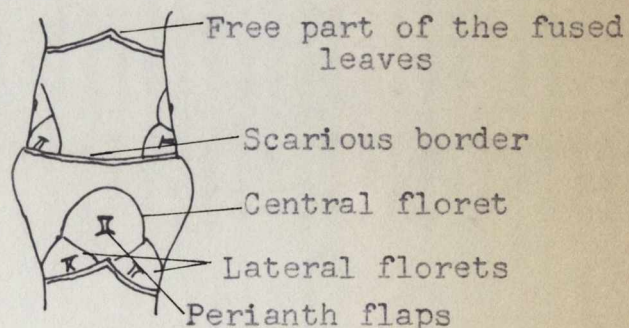
The general morphology of the plant is shown in Fig., 1 together with the terminology used in this work.

FIGURE I

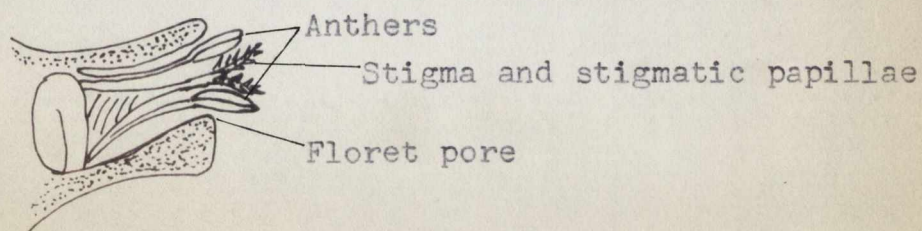
A simple and little branched Salicornia plant



Details of the fertile segments



A floret in section



A list of the supposed taxa of Salicornia present in Ireland with their diagnostic characters from the work of Ball (1964).

- (1) Arthrocnemum perenne (Mill.) Moss, (Salicornia perennis Mill.) Plant perennial, shrubby, all of the branches not ending in an inflorescence.
- (2) Salicornia pusilla Woods. Inflorescence with only one floret in a cyme, disarticulating in fruit.
- (3 - 4) S.europaea agg. Anthers 0.2 - 0.5 mm, often exserted: fertile segments with convex sides; lateral flowers smaller than the central.
- (3) S.europaea L. Lower fertile segments of the terminal spike 3 - 5 mm wide at the narrowest point. Leaves with a narrow scarious border not more than 0.1 mm wide.
- (4) ? S.ramosissima Woods. Lower fertile segments of the terminal spike 2 - 3.5 (- 4) mm wide (or less) at the narrowest point. Leaves with a conspicuous scarious margin 0.1 - 0.2 mm wide.
- (5 - 7) S.procumbens agg. Anthers (0.5) 0.6 - 1 mm, always exserted; fertile segments $\pm$ cylindrical sometimes with slightly concave sides; lateral flowers almost equalling the central.
- (5) S.nitens Ball & Tutin. Lower fertile segments of the terminal spike with a minimum diameter of 2 - 3.5 mm; plant usually becoming brownish or orange-purple.

- (6) S.fragilis Ball & Tutin, (S.stricta auct., pro parte, non Dumort.) Fertile segments usually greater than 3.5 mm in diameter. Terminal spikelets with 6 - 15 fertile segments $\pm$ cylindrical; plant green to yellowish-green rarely with red colouration.
- (7) S.dolichostachya Moss subsp. dolichostachya. Fertile segments usually greater than 3.5 mm in diameter at the base. Terminal spikelets with 12 - 30 fertile segments distinctly tapering at the apex. Plant dark green turning yellow in fruit. Branches arising at an angle of 60° - 90° curving upwards. Habit straggling to fastigate.

CHAPTER II

Methods and materials

Methods and Materials

The procedures outlined here relate to most parts of the work recorded in this thesis. Occasionally techniques applying only to particular studies have been described in the appropriate sections.

The choice and description of the main localities where material was collected for this study.

When the problem was commenced salt-marshes were chosen in six areas on the east and south coasts; Baldoyle, Rush and Bull Island in Co. Dublin, Tramore and Dungarvan in Co. Waterford and Comber in Co. Down. The marshes in these areas were selected because they were well developed and showed a wide range of habitats and it was considered that they would probably cover a high percentage of the variation in any taxa of Salicornia likely to be represented in Ireland. These areas were also chosen for convenience of revisiting throughout the course of the study.

In later seasons salt-marshes on the north and west coasts were investigated so that as far as possible the main areas studied were representative of a large part of the country.

<u>Population number</u>	<u>Locality</u>	<u>Species</u>	<u>Habitat</u>
1	Tramore, Co. Waterford	(<u>S.europaea</u>)	Salt-pans in the upper zones of mature marsh.
2	Rush, Co. Dublin	(<u>S.europaea</u>)	Open muddy shingle in the upper zones of developing marsh.
3	Bull Island, Co. Dublin	(<u>S.europaea</u>)	Salt-pans in the upper zones of mature marsh.
4	Rush, Co. Dublin	(<u>S.europaea</u>)	Salt-pans in the upper zones of mature marsh.
5	Ballyvaughan, Co. Clare	(<u>S.hibernica</u>)	Closed communities in the upper zones of mature marsh.
6	Dungarvan, Co. Waterford	(<u>S.europaea</u>)	Closed communities in the mid zones of mature marsh.
7	Kilcainin, Co. Galway	(<u>S.hibernica</u>)	Closed communities in the upper zones of mature marsh.
8	Tramore, Co. Waterford	(<u>S.hibernica</u>)	Closed communities and salt-pans in the upper zones of mature marsh.
9	Bull Island, Co. Dublin	(<u>S.dolichostachya</u>)	Levees in the lower zones of mature marsh.
10	Bull Island, Co. Dublin	(<u>S.fragilis</u>)	Salt-pans in the mid zones of mature marsh.
11	Bull Island, Co. Dublin	(<u>S.fragilis</u>)	Salt-pans in the mid zones of mature marsh.
12	Tramore, Co. Waterford	(<u>S.fragilis</u>)	Salt-pans and levees in the mid zones of mature marsh.

<u>Population number</u>	<u>Locality</u>	<u>Species</u>	<u>Habitat</u>
13	Tramore, Co. Waterford	(<u>S.fragilis</u>)	Open sandy mud in the lower zones of developing marsh.
14	Kilcainin, Co. Galway	(<u>S.fragilis</u>)	Levees in the lower zones of mature marsh.
15	Rush, Co. Dublin	(<u>S.dolichostachya</u>)	Open soft mud in the lower zones of developing marsh.
15a	Rush, Co. Dublin	(<u>S.dolichostachya</u>)	Open soft mud in the lower zones of developing marsh.
15b	Rush, Co. Dublin	(<u>S.dolichostachya</u>)	Soft mud among <u>Spartina</u> and <u>Puccinellia</u> in the lower zones of developing marsh.
15c	Rush, Co. Dublin	(<u>S.dolichostachya</u>)	Open soft mud in the lower zones of developing marsh.
16	Dungarvan, Co. Waterford	(<u>S.dolichostachya</u>)	Open soft mud in the lower zones of developing marsh.
17	Kilcainin, Co. Galway	(<u>S.europaea</u>)	Levees and closed communities in the mid zones of mature marsh.
18	Rush, Co. Dublin	(<u>S.fragilis</u>)	Levees and closed communities in the mid and lower zones of mature marsh.
19	Comber, Co. Down	(<u>S.fragilis</u>)	Levees and closed communities in the lower zones of mature marsh.
19a	Comber, Co. Down	(<u>S.fragilis</u>)	Levees and closed communities in the lower zones of mature marsh.

<u>Population number</u>	<u>Locality</u>	<u>Species</u>	<u>Habitat</u>
19b	Comber, Co. Down	(<u>S.fragilis</u>)	Open sandy mud in the lower zones of developing marsh.
19c	Comber, Co. Down	(<u>S.fragilis</u>)	Open sandy mud in the lower zones of developing marsh.
20	Baldoyle, Co. Dublin	(<u>S.europaea</u>)	Open muddy shingle in the upper zones of developing marsh.
21	Roundstone, Co. Galway	(<u>S.hibernica</u>)	Mainly in closed communities in the narrow strips of poorly developed marsh that occur in exposed inlets on the west coast.
22	Baldoyle, Co. Dublin	(<u>S.fragilis</u>)	Open soft mud among <u>Spartina</u> in the lower zones of developing marsh.
23	Comber, Co. Down	(<u>S.fragilis</u>)	Closed communities in the mid zones of mature marsh.
24	Island Mahee, Co. Down	(<u>S.europaea</u>)	Closed communities of mainly <u>Halimione</u> in the mid zones of mature marsh.
25	Limavady, Co. Derry	(<u>S.europaea</u>)	Salt-pans in the mid zones of mature marsh.
26	Ballyvaughan, Co. Clare	(<u>S.europaea</u>)	Closed communities in the mid zones of mature marsh.
27	Ballyvaughan, Co. Clare	(<u>S.fragilis</u>)	Levees and closed communities in the lower zones of mature marsh.
28	Tachumshin, Co. Wexford	(<u>S.fragilis</u>)	Open sandy mud in the lower zones of de- veloping marsh.

Population sampling technique.

During the first season samples of populations from stands chosen at random in six salt-marshes on the east coast were collected for biometric treatment of various characters. In later years the choice of populations sampled was subjective as discontinuities had been found to occur in the variation pattern of some of the characters investigated and it was necessary to try and ascertain whether these discontinuities resulted from the sampling technique or in fact were valid criteria for the recognition of taxa.

The method of sampling varied with the type of population selected. In apparently homogeneous populations of high density 25-50 plants were taken at random from an area of approximately one square metre. In populations of low density all the plants in a square metre were collected or, if a sufficient number of plants were not present the area was increased until a sample of 25-50 plants was obtained.

Obviously diseased and damaged plants were always rejected. In areas where two or more taxa appeared to be growing together a proportionally greater number of plants were collected care being taken to assure that a representative sample of each taxon was included.

Sampling was carried out at two main times, the first during August and early September when flowering was occurring and the second during October when most populations had set mature seed.

One of the main obstacles encountered in population

sampling was that it was difficult to collect material to study floral characters and to use this sample for cultivation experiments afterwards as no ripe seed is set usually when flowering is still occurring. Thus results obtained from the biometric treatment of cultivated population samples are based on samples from sites as near as possible to the original field sample and not from the actual sample itself. This procedure is justified as far as possible by comparison of biometric results from field samples of the same homogeneous population in different years and it was found that the results obtained do not differ greatly from year to year.

Cultivation and seed storage.

When the problem was commenced some preliminary investigations were made of methods of storage and of some of the conditions controlling germination of the seeds of Salicornia because it was considered that these factors might be important if successful cultivation experiments were to be conducted. (The results of these investigations are given in Appendix IV page 216) The results of these investigations showed that it was most satisfactory to dry entire plants and to store these at room temperature until time of sowing.

Plants were cultivated in ordinary garden compost made up of 3 parts loam, 1 part sand and 1 part leaf mould and were watered with artificial sea water made up from a modified formula of Brujewicy in Svendrup, Johnson and Fleming (1942). Plants were grown under two types of conditions (1) in a cool

greenhouse, (2) out of doors. Cultivation in the open was on the whole more satisfactory as the atmospheric conditions indoors often tended to be too dry during warm weather and the plants needed frequent overhead watering. However, material cultivated in the greenhouse was more suitable for study of the inheritance of some characters as for example habit, as plants grown indoors were free from the influence of environmental factors such as wind and rain.

Seeds were sown in March. Plants reached maturity in July and early August when cultivated indoors and during August and early September when grown in the open. Attempts were made to cultivate two generations of Salicornia in one year but this proved unsatisfactory (the results of these investigations are given in Appendix IV page 215).

Two main techniques for cultivation were used. The first was modified from that of Ball (1960a). Seedlings were grown in four inch earthenware flower pots and thinned at intervals to leave one or two plants finally to grow to maturity. The flower pots were stood in asbestos tanks filled with artificial sea water up to the level of the surface of the soil in the pots. The artificial sea water in the tanks was changed at 4-6 week intervals, drops in the water level in the tanks due to evaporation were corrected by periodic additions of tap water. This method was used to cultivate plants both in the greenhouse and out of doors. One of the limitations of the method was that it could only be used to study the variation of characters in single or small numbers of plants from

different populations grown side by side under similar conditions.

The other method of cultivation used was modified from that of Dalby (1956). Half size biscuit tins were filled with compost and soaked with sea water before sowing the seeds. Subsequently these were watered with artificial sea water at fortnightly intervals throughout the growing season. Plants cultivated by this method were only grown out of doors. This method of cultivation was used to study population samples and the entire progeny of individual plants.

Growth of diploid plants under all conditions of cultivation was more or less satisfactory though anthocyanin often failed to develop in plants grown indoors. Tetraploid plants tended to be rather small in cultivation and those grown as population samples in tins were rather "flabby" probably due to insufficient water. Tetraploid taxa from the lower zones of salt-marshes may require periodic submergence which they receive in nature for normal growth and development but this was difficult to arrange in the laboratory without more extensive facilities than those available for this study. There is a need for an extensive autecological study of the genus Salicornia.

Preservation of material.

Most of the results presented in this work have been obtained from observations and measurements of living material of Salicornia. It was found that fresh material could be stored

in polythene bags at room temperature for periods of up to one week and in a refrigerator at 4°C for periods of up to three weeks. However, all the material used in the study was preserved after examination in 2% formalin modified by the method proposed by Ball (1960b) lest it was necessary to refer to this again at some later stage. It was found also by comparison of the results obtained from fresh material with those obtained from preserved material that most of the characters investigated in this study, with the exception of colour, were not significantly altered by preservation.

Herbarium specimens prepared in the usual manner were found to be of little value, as has been found by other recent workers, because many of the important characters used for the recognition of taxa are lost on drying.

Material was also stored in a deep freeze at -14°C but this method was not found to be very satisfactory as the plants completely collapsed on thawing and then had to be discarded.

Some preliminary attempts were made to freeze dry material but no satisfactory technique was found with the equipment available. One of the difficulties that appears to have to be overcome is that the salt present in the plant reabsorbs moisture from the atmosphere at room temperature.

Chromosome Counts.

Root tip material was collected from seedlings germinated on moist filter paper at 19°C , or from seedlings or

mature plants in cultivation. It was pretreated in a saturated solution of Paradichlorobenzene for 2-3 hours and if it was not used immediately it was fixed in 1:3 acetic alcohol and stored in a deep freeze at -14°C until required.

Staining was by the Feulgen squash method of Darlington and La Cour (1960). Chromosome counts from satisfactory preparations of mitotic metaphase plates were recorded by camera lucida drawings and where possible by photographs. Preparations were made permanent by removal of the coverslip in 40% alcohol Darlington and La Cour (1960) or by freezing with CO_2 and "flicking" off the cover slip with a needle. The slide and coverslip were upgraded through the "alcohols" and mounted in Canada Balsam or Euparal Vert.

Pollen Fertility.

Pollen fertility was determined by the method of Stebbins and Valencia (1946) staining in lacto-phenol cotton blue for 1-2 hours and considering as viable only those pollen grains which stained a uniform dark blue. Those grains whose contents did not stain or stained only partially were considered as non-viable.

Measurements.

Plant height

Measurements were made from the cotyledons to the tip of the terminal spike.

Spikelet length

Measurements were made from the base of the first fertile segment.

Angle of branching

Measurements refer to the angle that the lower branches make with the main stem.

Pollen grain diameter

The diameter of 50 pollen grains from each cultivated plant and 250 pollen grains taken from a random sample of 10-20 mature anthers from a population sample were measured with a X 100 oil immersion objective. Only fertile grains were measured. Some pollen grains were found to be slightly oval in shape and in these circumstances the maximum diameter was measured.

Anther length

Where possible, five mature but undehisced anthers were measured from each plant in a population sample with a X 10 dry objective.

Seed length

A random sample of 250 seeds from a population sample of 25-50 plants were measured using a X 5 dry objective.

Scarious margin

Five measurements were made of the scarious margins of the fertile segments of each plant in a population sample using a X 10 dry objective.

Dimensions of the florets and fertile segments.

The dimensions of the central floret and the length, maximum and minimum diameters of the third fertile segment in

the terminal spike were measured using a X 3.2 dry objective.

All microscopic measurements were made with a calibrated X 8 eyepiece.

CHAPTER III

Investigation of characters

Chromosome number

The results of chromosome counts made from material of Irish Salicornia in the course of this study are given in Table 1. Two chromosome numbers have been found, a diploid number $2n = 18$ and a tetraploid number $2n = 36$ and there appears to be no variation in these numbers. The cytological investigations carried out in this work have not been very extensive. The chromosome number of only one representative of each homogeneous population sample was determined and this count was taken to represent the chromosome number of that population. This method was adopted because a considerable number of chromosome counts of Salicornia from the British Isles and north-west Europe have been published recently and all workers report a diploid number of $2n = 18$ and a tetraploid number of $2n = 36$ and the complete absence of any variation whatsoever from these numbers (see Table I & Figures II - VII). The results obtained in this work are in complete agreement with those of eight previous workers given in Table II.

Later in this study, when a clear correlation between chromosome number and certain morphological characters was found to exist, counts for some populations were not made the chromosome number being predicted from morphology.

The differences in chromosome number for two taxa reported by Dalby (1962) are the result of nomenclatural confusion and these are discussed in the section dealing with nomenclature (page 163).

TABLE I

Chromosome counts made from Irish Salicornia
by I.K.Ferguson

<u>Population Number</u>	<u>Species</u>	<u>Locality</u>	<u>Chromosome Number</u>
3	(<u>S.europaea</u>)	Bull Island, Co. Dublin	2n - 18
20	(<u>S.europaea</u>)	Baldoyle, Co. Dublin	2n - 18
2	(<u>S.europaea</u>)	Rush, Co. Dublin	2n - 18
1	(<u>S.europaea</u>)	Tramore, Co. Waterford	2n - 18
5	(<u>S.hibernica</u>)	New Quay, Co. Clare	2n - 18
8	(<u>S.hibernica</u>)	Tramore, Co. Waterford	2n - 18
22	(<u>S.fragilis</u>)	Baldoyle, Co. Dublin	2n - 36
11	(<u>S.fragilis</u>)	Bull Island, Co. Dublin	2n - 36
19	(<u>S.fragilis</u>)	Comber River, Co. Down	2n - 36
18	(<u>S.fragilis</u>)	Rush, Co. Dublin	2n - 36
13	(<u>S.fragilis</u>)	Tramore, Co. Waterford	2n - 36
12	(<u>S.fragilis</u>)	Tramore, Co. Waterford	2n - 36
9	(<u>S.dolichostachya</u>)	Bull Island, Co. Dublin	2n - 36
15	(<u>S.dolichostachya</u>)	Rush, Co. Dublin	2n - 36
-	(<u>S.dolichostachya</u>)	Dundalk Bay Co. Louth	2n - 36
-	(<u>S.pusilla</u>)	Bull Island, Co. Dublin	2n - 18
-	(<u>S.pusilla</u>)	Tramore, Co. Waterford	2n - 18
Also:-	(<u>S.fragilis</u>)	Foryd Bay, Caenvs., Wales	2n - 36

TABLE II

Chromosome numbers of European species of *Salicornia*

	Maude 1940	Konig 1939	Castro & Fontes 1946	Hambler 1954 & 1955	Nannfeldt 1955	Ball (in Lousley) 1957	Ball & Tutin 1959	Konig 1960	Jaworka (in Skalinska & alii) 1961.	Ball (in Love & Love 1961)	Dalby 1962	Ferguson Unpublis- hed
<i>S. europaea</i> L.	-	-	18	-	18	18	18	-	18	-	36	18
<i>S. obscura</i>												
Ball & Tutin	-	-	-	-	-	-	18	-	-	-	-	-
<i>S. ramosissima</i> Woods	-	18	-	18	-	18	18	18	-	-	18 36	-
<i>S. pusilla</i> Woods	-	-	-	16 ?	-	18	18	-	-	-	18	18
<i>S. nitens</i> Ball & Tutin	-	-	-	-	-	-	-	-	-	36	-	-
<i>S. lutescens</i>												
Ball & Tutin	-	-	-	-	-	-	36	-	-	-	-	-
<i>S. fragilis</i>												
Ball & Tutin	-	-	-	36 cf. B. & T. 1959	-	-	36	-	-	-	-	36
<i>S. dolichostachya</i>												
Moss	36	36	-	36	-	36	36	36	-	-	36	36
<i>S. strictissima</i>												
Gram	-	-	-	-	36	-	-	-	-	-	-	36
<i>S. leiosperma</i> Gram	-	-	-	-	36	-	-	-	-	-	-	-
<i>S. perennis</i> Mill.	18	-	18	18	-	-	-	-	-	-	18	-
<i>S. hibernica</i> Ferguson-	-	-	-	-	-	-	-	-	-	-	-	18

FIGURE IV

A representative of population 8

(*S. hibernica* Ferguson) Tremore, Co. Waterford

2n = 18

Illustrations of metaphase plates from root tip
squashes of Irish diploid Salicornia



| 5u |

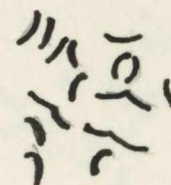


FIGURE II

A representative of population 3
(S.europaea L.) North Bull, Co.Dublin

2n = 18

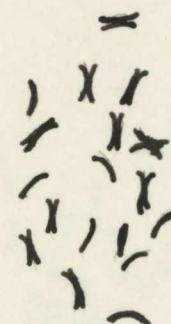


FIGURE III

S.pusilla Woods North Bull, Co. Dublin 2n = 18

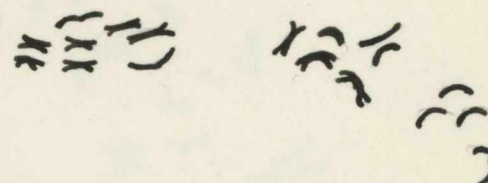
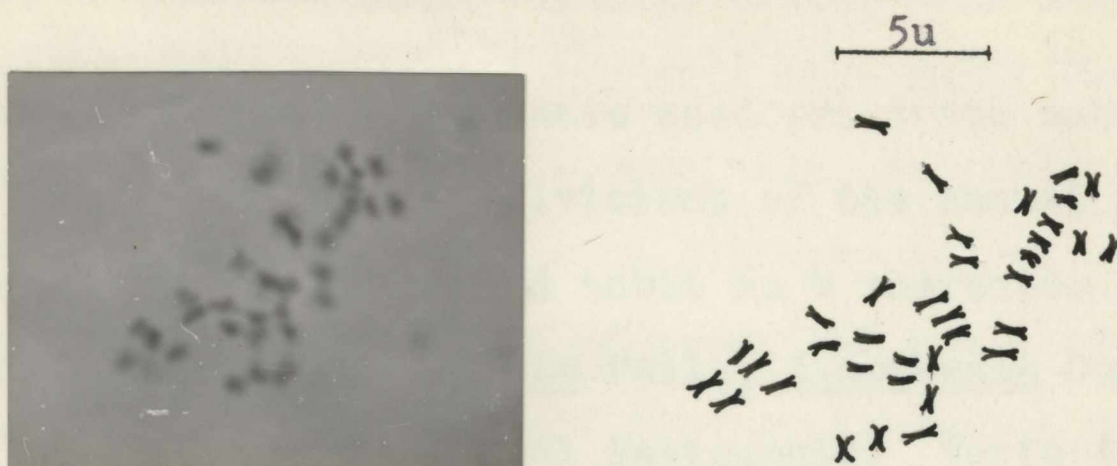


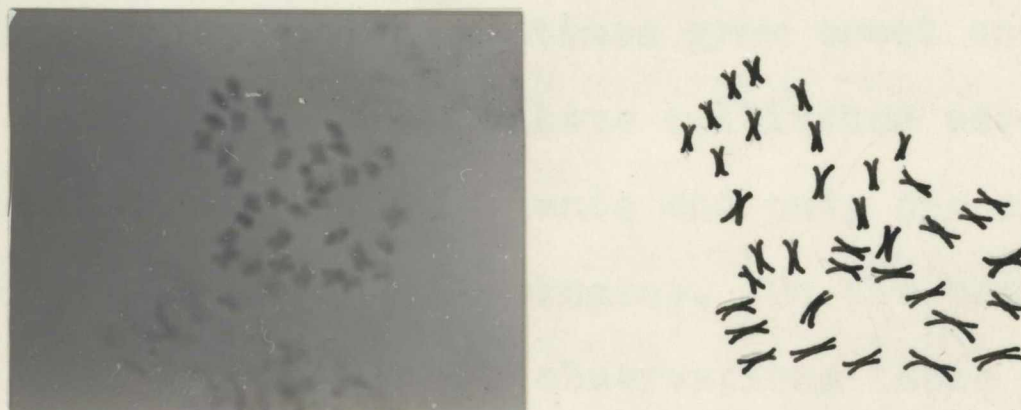
FIGURE IV

A representative of population 8
(S.hibernica Ferguson) Tramore, Co. Waterford

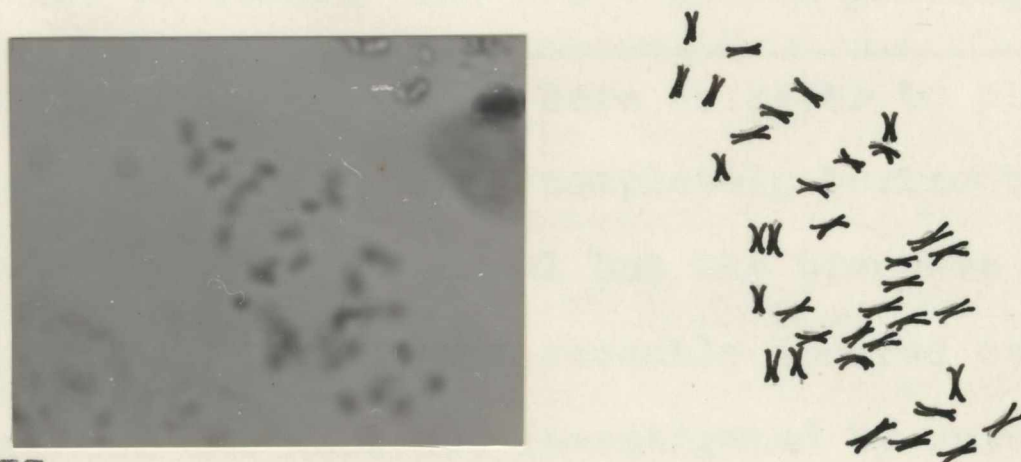
2n = 18

FIGURES V - VIIIllustrations of metaphase plates from root tip squashes of Irish tetraploid SalicorniaFIGURE V

A representative of population 18
(S. fragilis Ball & Tutin) Rush, Co. Dublin 2n = 36

FIGURE VI

A representative of population 15
(S. dolichostachya Moss) Rush, Co. Dublin 2n = 36

FIGURE VIII

S. dolichostachya Moss
Dundalk Bay, Co. Louth 2n = 36

Habit

Many previous workers have used prostrate habit as a basis for one of the primary divisions of the annual Salicornia. Moss & Salisbury (1914) have used habit as a character to distinguish three species S. prostrata Pall., S. appressa Dum. and S. smithiana Moss from other annual Salicornia. Tutin (1952) has recognised a prostrate aggregate comprised of the same three species. However, Dalby (1955 and 1956) has thrown considerable doubt on the value of this character for the recognition of species and has shown that the progeny raised in cultivation from prostrate parent plants may sometimes grow erect and sometimes prostrate. Ball & Tutin (1959) have cultivated seed from a considerable number of prostrate plants and only one collection of S. pusilla Woods gave prostrate progeny. On the basis of these results and other morphological observations these workers have sunk S. prostrata auct. angl., S. appressa Dum. and S. smithiana Moss with the previously described erect species S. ramosissima Woods.

The results of field observations made in this study have shown that prostrate* and erect plants growing side by side

* The term "prostrate" is used here to refer to plants which have all their branches growing completely horizontal. Plants where the main stem is horizontal but the branches have grown erect were thought to have been recently knocked over by environmental influences and were not investigated by cultivation experiments.

appear to be morphologically identical except that the former usually have their branches arising at a wide angle from the main stem while the latter rarely show this character. However, in some localities as for example at Baldoyle in Co. Dublin plants showing many combinations of habit and angle of branching have been observed; true prostrate plants, decumbent plants with their lateral branches horizontal, erect plants with their lower branches arising at a wide angle from the main stem and erect plants with their lower branches arising at an acute angle from the main stem. Also it has been observed in the field that plants showing a prostrate habit are associated with two particular types of habitat, the first occurring mainly on the east coast on open muddy shingle in the upper zones of developing salt-marshes, the second type of habitat occurs on the west coast in areas of exposed, poorly developed salt-marsh.

In this investigation progeny of prostrate plants were cultivated to assess the value of habit as a taxonomic character in the annual section of the genus Salicornia in Ireland and the results are set out in Table III.

All prostrate plants observed in the field and, investigated in cultivation experiments belonged to the diploid aggregate and the majority were assignable to the species S.europaea L. Prostrate plants of S.pusilla Woods were found at one locality but these were not extensively investigated. No prostrate plants were found which were assignable to the tetraploid aggregate. When this investigation was commenced it was

Table III shows the results of cultivation experiments with progeny raised from seed of prostrate parent plants collected at nine localities on the Irish coast.

Explanation of the symbols used in Table III

- Habit - P 1 - Main stems prostrate with all the branches completely horizontal.
- P 2 - Main stems decumbent with the lateral branches horizontal.
- E 1 - Main stems erect with the lower branches arising at an angle c. 45° .
- E 2 - Main stems erect with the lower branches arising at an angle c. 90° .
- E 3 - Main stems erect with the lower branches deflexed.

P 1

P 2

E 1

E 2

E 3

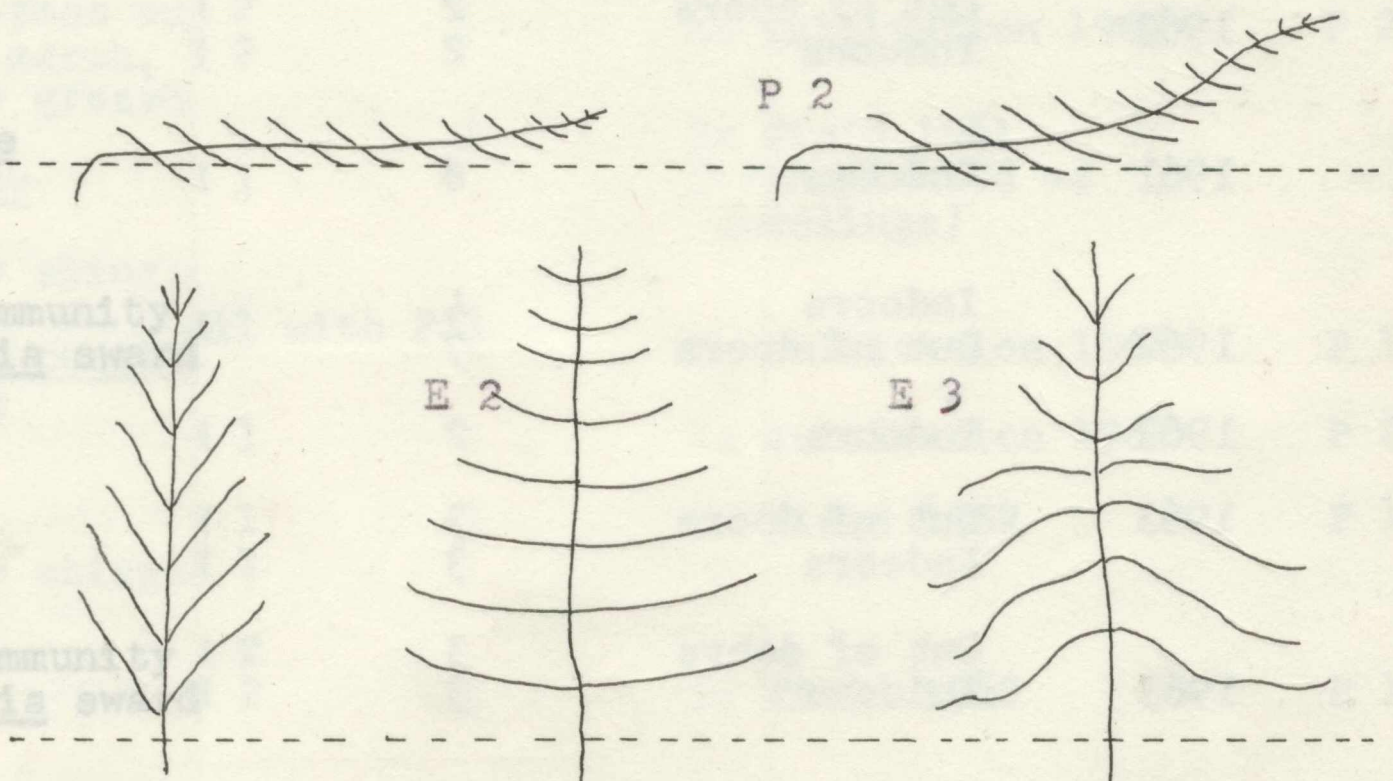


TABLE III

<u>Original habitat and locality</u>	<u>No. of parent plants used.</u>	<u>Immediate origin of parent plants</u>	<u>Habit of parent plant</u>	<u>Year of Cultivation</u>	<u>Cultivation conditions.</u>	<u>No. of progeny raised</u>	<u>Habit of progeny.</u>
<u>Baldoyle</u>	2	Ex field 1960	P 1	1961	Out of doors	4	P 2
Open muddy shingle	1	Ex field 1960	P 2	1961	Out of doors	2	E 1
	2	Ex field 1960	E 2	1961	Out of doors	6	E 1
	3	Ex cultivation 1961	P 2	1962	Indoors Out of doors	Seed failed to germinate.	
	4	Ex field 1961	P 1	1962	Out of doors	29	26 with P 2 3 with E 2
	1	Ex field 1961	P 1	1962	Indoors	2	E 2
	2	Ex cultivation 1962	P 2	1963	Out of doors	>100	All with P 2
	1	Ex cultivation 1962	P 2	1963	Indoors	2	E 2
	5	Ex field 1962	P 1	1963	Out of doors	>200	All with P 2
<u>Rush</u>	3	Ex field 1960	P 1	1961	Out of doors	6	3 with E 2 3 with P 2
Open muddy shingle	1	Ex cultivation 1961	P 2	1962	Out of doors	4	P 2
	3	Ex cultivation 1962	P 2	1963	Out of doors Indoors	2 2	P 2 P 2
<u>Roundstone</u>	8	Ex field 1961 (transplanted as seedlings)	-	1961	Indoors	8	P 1
Closed community of <u>Puccinellia sward</u>	3	Ex cultivation 1961	P 1	1962	Indoors Out of doors	4 7	All with P 1
	3	Ex cultivation 1962	P 2	1963	Indoors	2	P 1
<u>Costello</u>	3	Ex field 1962	P 1	1963	Out of doors Indoors	3 3	P 1 P 1
Closed community of <u>Puccinellia sward</u>	3	Ex field 1962	P 1	1963	Out of doors Indoors	3 3	P 2 P 2

Continued/

TABLE III continued

<u>Original habitat and locality</u>	<u>No. of parent plants used.</u>	<u>Immediate origin of parent plants</u>	<u>Habit of parent plant.</u>	<u>Year of Cultivation</u>	<u>Cultivation conditions.</u>	<u>No. of progeny raised</u>	<u>Habit of progeny.</u>
	3	Ex field 1962	P 1	1963	Out of doors Indoors	5 1	3 with P 1 2 with E 2 P 2
<u>Carna</u>	6	Ex field 1962	P 1	1963	Out of doors	>50	P 2
<u>Closed community of Puccinellia sward</u>	1	Ex field 1962	P 1	1963	Indoors	1	E 2
<u>Tramore</u>	3	Ex field 1962	P 2	1963	Out of doors Indoors	3 2	E 3 E 3
Open and partially colonised salt-pans in the upper zones of the salt-marsh.							
<u>Killyleagh</u>	2	Ex field 1961	P 1	1962	Out of doors Indoors	2 3	P 1 P 1
Open muddy shingle	2	Ex cultivation 1962	P 1	1963	Out of doors Indoors	2 1	P 2 E 2
<u>Kinsale</u>	3	Ex field 1962	P 1	1963	Out of doors	>50	P 2
Open salt-pans on reclaimed marsh, frequently grazed.	1	Ex field 1962	P 1	1963	Indoors	3	P 2
<u>Clonakilty</u>	1	Ex field 1962	P 1	1963	Out of doors	3	P 2
Open muddy shingle							
<u>Salicornia pusilla</u> Woods							
<u>Tramore</u>							
Open muddy shingle	1	Ex field 1961	P 1	1962	Indoors	1	P 2

considered that the underlying factors controlling the determination of the prostrate habit in Salicornia could have a purely environmental basis, or on the other hand, prostrate habit might be genetically controlled. However, the results set out in Table III suggest that the determination of habit cannot be explained simply in terms of either. For example sometimes prostrate habit appears to be purely a response to environmental conditions as is shown by some of the progeny of prostrate parent plants from Baldoyle, Carna, Costello and Rush which grew erect in cultivation. While the results from cultivation of material collected at Roundstone suggest that in this population habit is genetically controlled because all of the progeny grew prostrate from the cotyledonary stage under all conditions and over a number of generations (Plate I page 41).

The occurrence of intermediate conditions in habit suggested that in fact genetically prostrate and erect plants might exist in nature and that these were hybridising and many of the plants from which seed was collected and cultivated might be of hybrid origin. For example plants were observed in the field at Baldoyle which showed a complete range of habit, from fully prostrate to erect with a wide angle of branching. Also progeny raised from seed of prostrate parent plants collected at Rush, Kinsale, Clonakilty, Costello, Carna and Baldoyle behaved in a manner which might be interpreted as an intermediate condition for habit by growing upright at first in cultivation and then falling over and appearing decumbent or prostrate at maturity. However, the results in Table III show that the entire progeny

of prostrate parent plants from Kinsale, Carna and Baldoyle when cultivated in tins were entirely homogeneous in morphology and habit in the first generation in the case of plants from the two former localities and over a number of generations in the case of plants from the latter locality. These results do not support the existence of hybrid populations because if plants were of hybrid origin, variation in the habit of the progeny would be expected at least in the second generation in cultivation.

prostrate Breeding experiments were attempted between plants which were apparently genetically prostrate and genetically erect to study the behaviour of the resulting progeny. These unfortunately failed due to a lack of a satisfactory technique for emasculating cleistogamous flowers (see Chapter V page 135).

raised from The behaviour of progeny raised from seed originally collected at Baldoyle suggests that there may be some correlation between the conditions of cultivation and the response of the progeny. Here plants grown out of doors were decumbent while replicates grown indoors were erect but with their lower branches arising at an angle of c. 90° from the main stem (Plates 1c & 2b page 41). It seems that environmental conditions in cultivation such as wind and rain may have affected the habit of the progeny. In the field tidal currents and wave action would be additional environmental factors that could influence habit. This also seems to be the situation in the case of the response of the progeny cultivated from material collected originally at Killyleagh. During the first season progeny cultivated both indoors and in the open grew prostrate while plants grown the follow-

ing year from seed collected from plants cultivated the previous year grew decumbent or prostrate out of doors and erect indoors but with a wide angle of branching.

Angle of branching appears to be associated with prostrate habit but may be expressed independently of it. The progeny of prostrate parent plants raised from seed collected at Rush, Baldoyle and Killyleagh cultivated indoors grew erect but retained a wide angle of branching (Plate 2b page 43). No prostrate parent plants gave erect progeny with fastigate branching in cultivation although erect plants showing a wide angle of branching grown from seed collected at Baldoyle gave erect progeny with the lower branches making an acute angle with the main stem.

The behaviour of the progeny in cultivation which were raised from seed collected from prostrate plants from Tramore in Co. Waterford was very unusual (see Plates 3a & b page 43) and might be worth further investigation as these plants have only recently been found and thus have been in cultivation for only one season.

There appears to be some degree of genetic determination of habit in Salicornia though this may be influenced by environment. The degree to which prostrate habit is genetically determined seems to differ in plants from differing localities. For example plants from the west coast, from Roundstone and Costello, show a higher tendency towards having a genetically controlled prostrate habit than do plants from the east coast, from Rush and Baldoyle. The explanation for this may be associated to some extent with the habitat of the populations involved. Plants

on the east coast occur on open muddy shingle in the upper zones of developing salt-marsh. In these conditions competition is low and exposure is high due to uninterrupted wave and tidal action and these may act as environmental pressures favouring plants with a prostrate habit. Later, if the marsh develops and the area is colonised by other species this will tend to reduce exposure and increase competition and these conditions would seem to favour plants that had an erect habit. Thus it might be possible that the prostrate habit of plants occurring in developing salt-marshes may not have a very firm genetic basis. A possible explanation for the occurrence of a higher percentage of genetically prostrate plants on the west coast may be, that although prostrate plants occur in closed communities and the marshes are mature, the habitats are very exposed to strong wave and tidal action and also are grazed at frequent intervals. Here there appears to be a strong selection pressure favouring plants with a prostrate habit. Also conditions are less likely to change, due to the marshes being mature. The prostrate habit thus might tend to establish a firmer genetic basis. before these may be understood.

Turesson (1922) in an extensive study of the genotypical response of the plant species to the habitat in a large number of genera and species has reported results for species of Atriplex which are similar in many ways to those that have been found in the present study of Salicornia. He found that prostrate, ascending and erect forms occurred in Atriplex litorale and sometimes that the prostrate or ascending habit

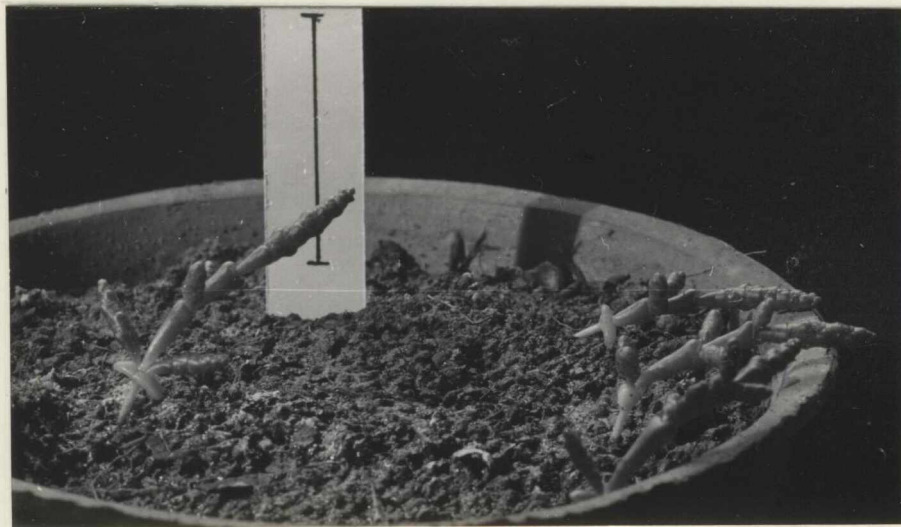
(a)
was genetically controlled and sometimes the result of environmental influences. Without cultivation it was impossible to determine which factor was controlling the expression of habit in any particular plant in the field. He found that prostrate forms were not directly modified to erect forms in cultivation but developed an ascending habit. However, ascending forms might become erect in cultivation and he showed that it was possible to induce prostrateness in ascending forms by increasing light intensity. Turesson explains the occurrence of the range in habit in Atriplex of the same species on the grounds that physiologically and genetically different races occur within the same systematic species.

The main result that may be concluded from these investigations is that habit is a variable character in the genus Salicornia and does not appear to be always genetically controlled or to be closely correlated with any other characters and it therefore cannot be regarded as having any classificatory value. It may also be concluded that the factors determining the expression of habit are very complex and need much further investigation before these may be understood.



(a)

Prostrate progeny cultivated indoors from seed of prostrate parent plants from Roundstone.



(b)

Prostrate progeny cultivated indoors in 1962 from seed of prostrate parent plants from Killyleagh.



(c)

Erect progeny with a wide angle of branching grown indoors in 1963 from seed of the cultivated prostrate plants shown in (b).



NOTE

The captions for Plate 2 (b) and (c) have been transposed due to a typographical error.

PLATE 2

(a)

A wild prostrate parent
plant from Baldoyle.



(b)

Decumbent progeny cultivated out
of doors from seed of a prostrate
parent plant from Baldoyle shown
in (a).



(c)

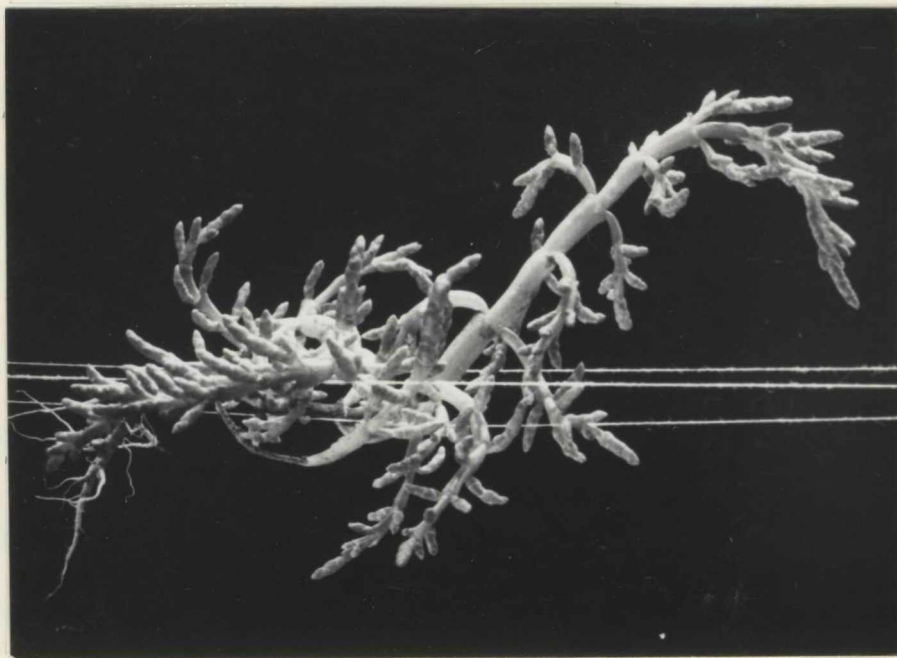
An erect progeny with a wide angle of branching, cultivated
indoors from seed of a prostrate parent plant from Baldoyle
shown in (a).



PLATE 3

(a)

A wild parent plant from Tramore with an unusual habit showing prostrate and deflexed branches.



(b)

Erect progeny with deflexed lower branches cultivated out of doors from seeds of plants resembling that shown in (a)



stem. The other species Branching belongs to the tetraploid aggregate. The presence or absence of well developed branching and the relationship of the length of the lower primary branches to the height of the main stem have been used as important taxonomic characters by workers in the past.

Moss (1914) describes a species S.gracillima as "little branched" and used this as a character to distinguish it from S.ramosissima though he described the degree of branching in the latter species as very variable.

Dalby (1956) in an extensive investigation of the relationship between the degree of branching and the environmental conditions has shown that unbranched, dwarf, highly coloured forms of the "S.gracillima" type have in cultivation been found to produce much larger and richly branched plants and he maintains that this dwarf condition is the ultimate reduced form of Salicornia due to competition and water shortage and he concluded that the dwarf habit and lack of branching were unreliable taxonomic characters.

Ball & Tutin (1959) believe that dwarf plants that have been called S.gracillima (Townsend) Moss are dwarf forms of S.ramosissima Woods and they have not maintained the epithet 'gracillima'. However, these workers have described two new species which they distinguish by the relationship between the length of the lower primary branches and the height of the main stem. The first species S.obscura is a diploid and is described as differing from S.europaea by the length of the primary branches being usually less than half the length of the main

stem. The other species S.fragilis belongs to the tetraploid aggregate and is distinguished from S.lutescens by the lower primary branches being rarely more than half the length of the main stem.

Later, Ball (1964) has sunk S.obscura with S.europaea and S.fragilis with S.lutescens and he ceases to use branching as a character of primary taxonomic significance.

Some preliminary cultivation experiments were carried out in this study to try and ascertain whether the dwarf red forms found in the upper zones of salt-marshes were the result of environmental influences or whether these characters had a genetic basis. Progeny raised from seed of dwarf, red, little branched plants found growing in dense stands in salt-pans in the upper zones of a marsh at Rush were more robust and freely branched than the parent plants and showed no tendency to develop red colouration in cultivation (Plates 4 a & b).

The results in Figure II show the variation found in 18 field populations of the ratio of the length of the lower primary branches to the height of the main stem. This variation in the degree of branching has been observed to be related to the habitat where the populations were sampled. For example populations sampled across a salt-pan where the plants grew in different degrees of density as populations 3, 4, 24 and 25 showed a wide degree of variation in branching, plants growing in dense stands in close competition were found to be little branched while others growing in open areas of the salt-pan were usually richly branched. Populations 15, 15a and 15b

FIGURE VIII
Ratio of the length of the lower primary branches
to the height of the main stem

Legend for Figure VIII

- Means of wild population samples of diploid plants.
- Means of wild population samples of tetraploid plants.
- Means of cultivated representatives or samples of diploid populations.
- Means of cultivated representatives or samples of tetraploid populations.
- | Standard deviation for each sample.
- ┌ Range of the measurements for each sample.

Details of the measurements from which the Figure has been drawn are given in the Tables in Appendix III.

Where more than two symbols of one kind occur together under one population number this indicates that the same population has been sampled more than once. This may apply to wild or cultivated population samples.

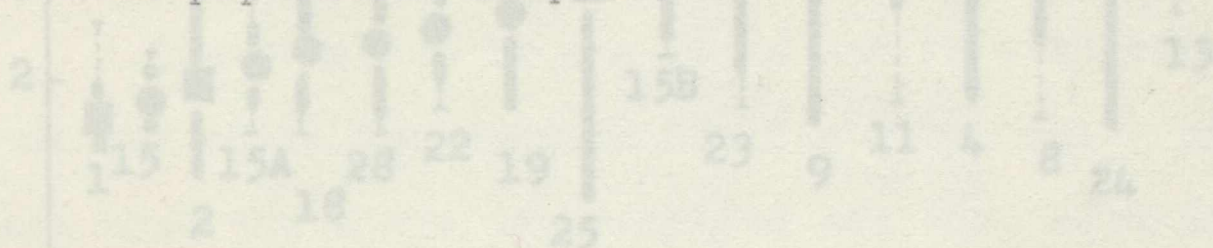
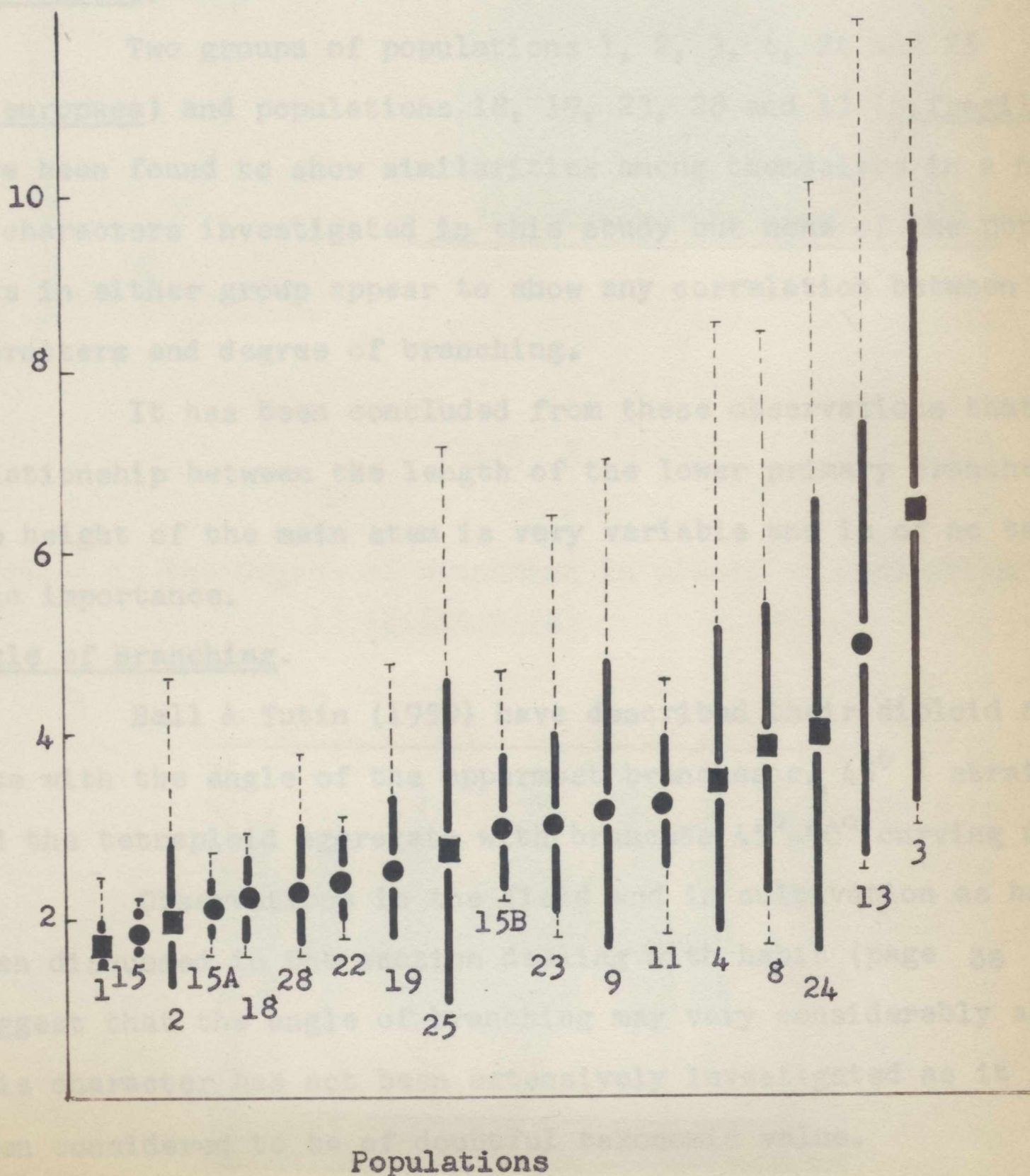


FIGURE VIII

Ratio of the length of the lower primary branches
to the height of the main stem

Values for
 the ratio



(S.dolichostachya) are all from the same locality but sampled from slightly different habitats, 15 and 15a were sampled from open, soft mud where little competition occurred while 15b was sampled from higher up the marsh growing among Puccinellia maritima. Competition has reduced the degree of branching in population 15b compared with 15 and 15a.

Some of the variation in branching in population 13 (S.fragilis) is shown in Plate 5

Two groups of populations 1, 2, 3, 4, 24 and 25 (S.europaea) and populations 18, 19, 23, 28 and 13 (S.fragilis) have been found to show similarities among themselves in a number of characters investigated in this study but none of the populations in either group appear to show any correlation between these characters and degree of branching.

It has been concluded from these observations that the relationship between the length of the lower primary branches and the height of the main stem is very variable and is of no taxonomic importance.

Angle of Branching.

Ball & Tutin (1959) have described their diploid aggregate with the angle of the uppermost branches c. $45^{\circ} \pm$ straight and the tetraploid aggregate with branches 45° - 90° curving upwards.

Observations in the field and in cultivation as has been discussed in the section dealing with habit (page 38) suggest that the angle of branching may vary considerably and this character has not been extensively investigated as it has been considered to be of doubtful taxonomic value.

PLATE 4

(a)

A representative of a population sample of dwarf, little branched parent plants of S. "gracillima" type.

(x 1/2)



(b)

More robust and freely branched progeny cultivated from a population sample of plants resembling that shown in (a).

(x 1/3)



PLATE 5

Variation in the degree of branching in plants of population 13 (S. fragilis)



Colour

Wilmott (pers. comm.) used colour extensively as a taxonomic character in his notes and descriptions of British Salicornia.

Ball & Tutin (1959) have been the only workers who appear to have emphasised colour as an important taxonomic character. These workers have distinguished their species S.nitens from the other species of the tetraploid aggregate, S.fragilis, S.lutescens, and S.dolichostachya which are usually green or yellowish-green in colour, by the tendency of this species to develop a brownish-purple to brownish-orange colour. Ball & Tutin distinguish S.ramosissima Woods from S.europaea L. by the former becoming a dark purplish-red colour while the latter species becomes yellow, red or pinkish.

Dalby (1962) has found a significant correlation between chromosome number and the presence of anthocyanin in 43 plants that he has examined. Anthocyanin is almost restricted to diploids though it does occur rarely in tetraploids. However, he emphasises that strictly it is the ability to produce anthocyanin in favourable circumstances that should be measured and not its actual appearance as he believes that environmental conditions may determine whether it is developed or not.

Observations on colour made in this work have shown that among tetraploid plants studied populations 15, 15a, 15b, 15c, 16 and 9 (S.dolichostachya) and populations 12, 13, 19b, 19c and 22 (S.fragilis) have never been found to develop anthocyanin either in the field or in cultivation.

The occurrence of anthocyanin in other tetraploid populations appears to be variable and may be influenced by the conditions under which the plants are growing. Populations 18, 19 and 19a (S. fragilis) growing at two different localities at Rush and Comber, on soft mud apparently high in reduced sulphides, were observed to develop anthocyanin at an early stage of growth and many plants were entirely dull pinkish-red in fruit. The progeny of some of these plants raised in cultivation showed only a faint flush of pink on the lower sterile segments. Population 23 (S. fragilis) growing on firm mud higher up the marsh from populations 19 and 19a was a shining, brownish-purple colour resembling descriptions of S. nitens Ball & Tutin. However, in cultivation the progeny of these plants showed only a faint flush of anthocyanin on the lower sterile segments. As mentioned earlier two other populations from Comber, 19b and 19c (S. fragilis) growing on open, sandy, mud, lower down the marsh from 19, 19a 23, were found to develop no anthocyanin in the field or in cultivation.

Among the diploid taxa populations 17 and 26 (S. europaea) and population 8 (S. hibernica) never developed anthocyanin either in the field or in cultivation. Populations 5 and 7 (S. hibernica) developed purplish-red colour around the florets and on the margins of the fused leaves. Progeny of these plants raised in cultivation were found to maintain this colour. The sterile segments of plants in these populations were observed both in the field and in cultivation to become a characteristic translucent yellowish-green colour in fruit.

progeny Population 1 (S.europaea) developed purplish-red colour on the florets and on the margins of the fused leaves and progeny raised in cultivation showed these colours also.

Cheshire Population 4 (S.europaea) showed no anthocyanin in the field but progeny in cultivation developed red colour on the lower sterile segments in early fruit and later the entire plants became bright red. Progeny cultivated a second year from seed from these bright red plants showed only a faint flush of colour on the lower sterile segments.

Plants of population 2 (S.europaea) were a bright red colour in the field late in fruit but progeny in cultivation only showed a tendency for the sterile segments to colour faintly before collapse.

Two otherwise apparently morphologically identical (S.europaea) colour forms, one developing anthocyanin the other without it, were observed in a number of localities on the west coast of Ireland. In cultivation progeny of parent plants of both forms from Carna in Connemara failed to develop anthocyanin while progeny of parent plants from Costello in Connemara maintained their distinct colours.

The results of cultivation of progeny raised from seed of populations 18, 19, 19a and 23 (S.fragilis) and population 2 (S.europaea) which showed well developed anthocyanin in the field but little in cultivation, suggest that environmental conditions especially the substrate may influence the expression of colour in some populations.

The development of anthocyanin in cultivation of

progeny of population 4 (S.europaea) is further evidence that environment may influence colour development. Ball (pers. comm.) has made similar observations on S.europaea L. at Parkgate in Cheshire where he found that this population failed to produce anthocyanin in some seasons while it has been highly coloured in other seasons. Ball attributes this varying colour development to environmental influences as temperature and sunlight during late summer and autumn.

It seems that the ability or lack of ability to produce colour may be genetically controlled in some populations. This appears to be situation in population 8 (S.hibernica) which failed to produce anthocyanin both in the field or in cultivation under a variety of conditions and over a number of years.

However, as Dalby (1962) has pointed out and this seems to be the case from many of the observations made in this work as for example population 4 and the results of cultivation of colour forms of S.europaea from western Ireland, that it is not the actual appearance of anthocyanin that should be measured but the ability of the plant to produce it.

Many of the results do not support Dalby's view that tetraploid populations rarely develop anthocyanin and diploid usually do, as tetraploid populations 18, 19, 19a and 23 (S.fragilis) showed the ability to develop anthocyanin while diploid populations 17 and 26 (S.europaea) and population 8 (S.hibernica) appear not to have got the ability to develop anthocyanin.

The results of investigations of colour in populat-

ion 23, which resembled S.nitens Ball & Tutin, suggest that colour cannot be used as a character of importance in distinguishing Irish plants assigned to this species.

Hambler (1958) comments that pigmentation has been regarded as an important character for diagnosis of species of Rhinanthus in the past. However, he has found after observations on cultivated plants and natural populations that this character is sometimes environmentally controlled and sometimes has a genetic basis and he has concluded that anthocyanin pigmentation does not provide any sound taxonomic character.

It may be concluded from the results obtained in this work that although some taxa do show a tendency to have characteristic pigmentation the development of anthocyanin cannot be regarded as a character of primary taxonomic importance as it sometimes appears to have a genetically controlled basis and sometimes is environmentally controlled.

Length of the terminal spike

Few workers appear to have used length of the terminal spikelet as a character of taxonomic importance. Moss (1914) has described S.dolichostachya as having considerably longer terminal spikes than other species of Salicornia occurring in Britain. Ball & Tutin (1959) have given measurements of the length of the terminal spike for the species that they describe and these measurements show a great deal of overlap. Both Ball & Tutin (1959) and Dalby (1956 & 1962) have reported the occurrence of robust diploid plants with long terminal spikes

but neither have attributed much taxonomic significance to these and believe that they are probably the result of favourable **environmental conditions.**

Measurements of the length of the terminal spike are dependent on the stage of growth of the plant as elongation of the inflorescence occurs between flowering and the ripening of seeds. Therefore only populations of approximately the same age and stage of growth may be compared.

Figures IXa and IXb show the results of measurements made in this work at two stages of growth. The first group of measurements were made when the lower fertile segments were in flower and the second group were made when the lower fertile segments were in fruit. These measurements show that some tetraploid populations have got longer terminal spikes than many of the diploid populations as for example population 13 (S.fragilis) and populations 15, 15a, 15b and 16 (S.dolichostachya) and this character may be of taxonomic value for distinguishing some populations of these taxa.

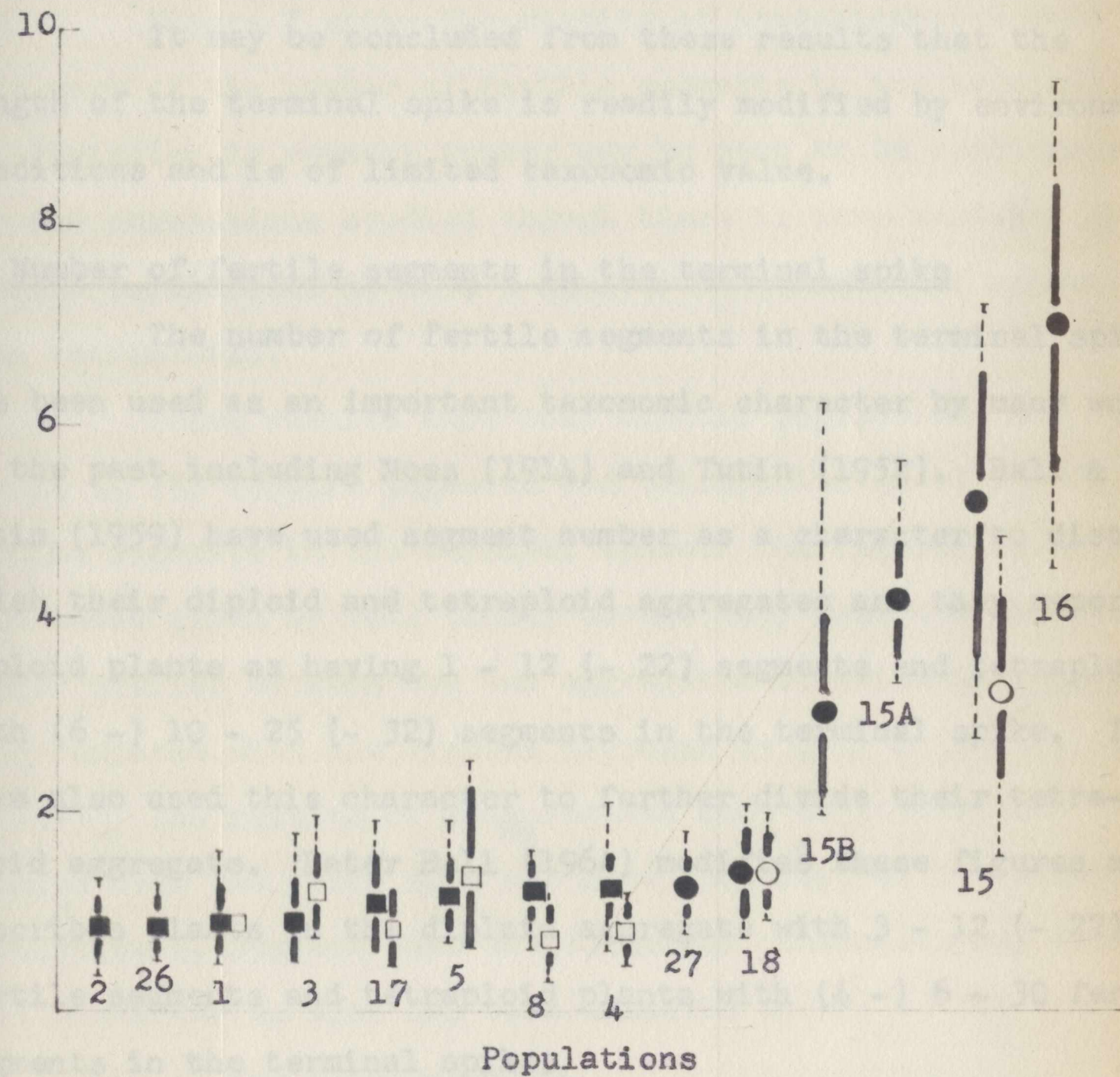
However, there are many populations which although showing differences in chromosome number show no significant difference in the length of the terminal spike.

The results of cultivation of progeny raised from seed collected from population samples shows that the mean length of the terminal spike of population samples may be significantly modified ($p = > 0.001$) by environmental conditions. This may be seen in populations 15, 19b, 8, 7 and 20 where apparently unfavourable environmental conditions of cult-

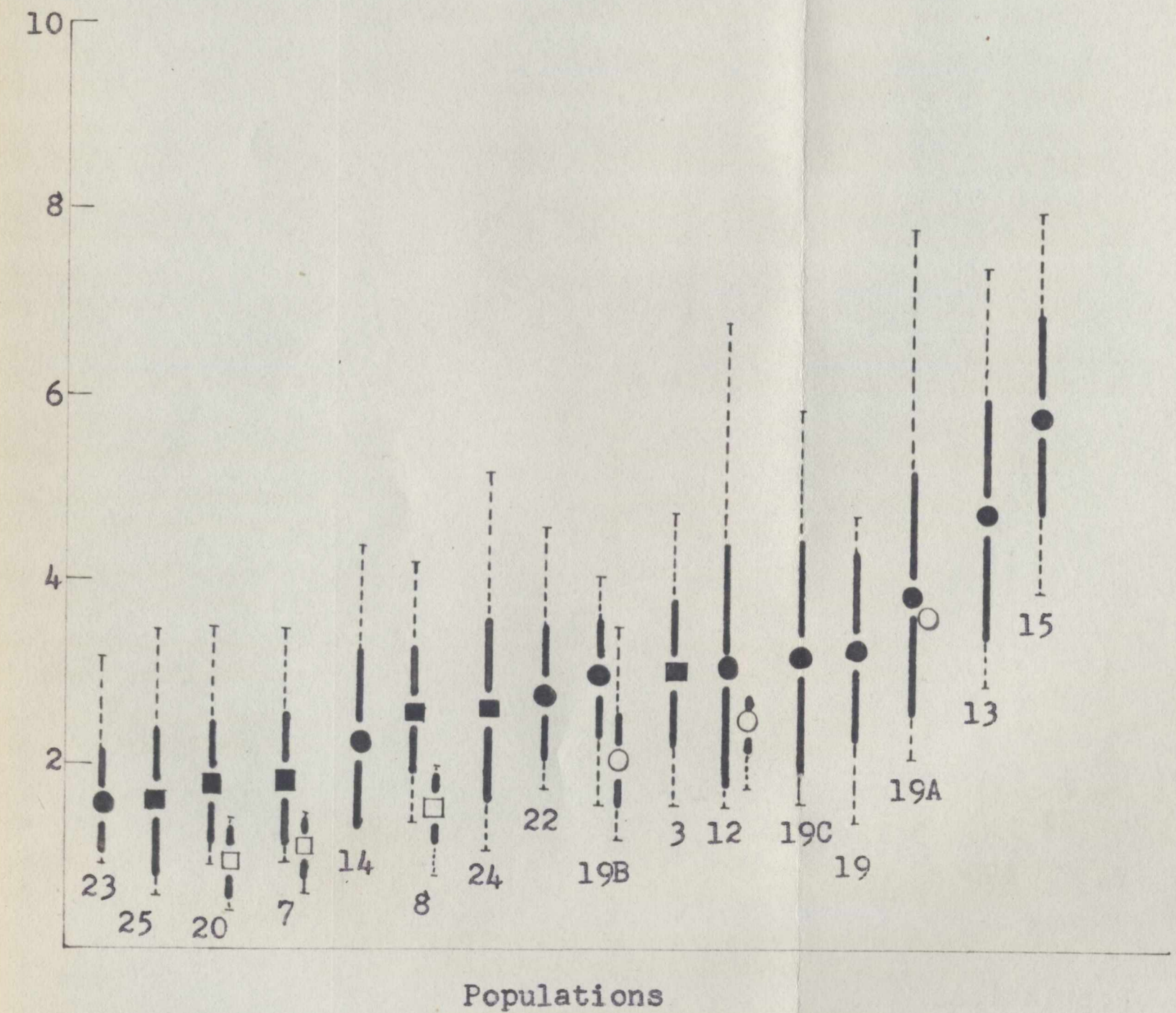
Length of the terminal spike (in cm)

Legend as in Figure VIII (page 46)

(a) Measurements made when the lower fertile segments were in flower.

Length of the
terminal spike
(in cm)

(b) Measurements made when the lower fertile segments were in fruit.

Length of the
terminal spike
(in cm)

ivation have produced significantly shorter terminal spikes in the progeny compared with those of the parent plants.

Occasional robust diploid plants with long terminal spikes have been quite frequently observed in the field and the progeny of parent plants collected from Rush, Bull Island and the Shannon Estuary have been raised in cultivation but in all cases these have not showed long terminal spikes.

It may be concluded from these results that the length of the terminal spike is readily modified by environmental conditions and is of limited taxonomic value.

Number of fertile segments in the terminal spike

The number of fertile segments in the terminal spike has been used as an important taxonomic character by many workers in the past including Moss (1914) and Tutin (1952). Ball & Tutin (1959) have used segment number as a character to distinguish their diploid and tetraploid aggregates and they report diploid plants as having 1 - 12 (- 22) segments and tetraploids with (6 -) 10 - 25 (- 32) segments in the terminal spike. They have also used this character to further divide their tetraploid aggregate. Later Ball (1964) modifies these figures and describes plants in the diploid aggregate with 3 - 12 (- 22) fertile segments and tetraploid plants with (4 -) 6 - 30 fertile segments in the terminal spike.

Ball (1964) describes the tetraploid species S.nitens with 4 - 9 fertile segments S.fragilis with 6 - 15 (- 22) fertile segments and S.dolichostachya with 12 - 30 fertile segments in

the terminal spike.

The number of segments in the terminal spike is related to the length of the spike but the results are not exactly similar as the length of the fertile segments vary in different taxa. However, the number of segments in the terminal spike is a more useful character as plants at different stages of development may be compared.

Figure X shows the results of investigations made in this work of the number of fertile segments in the terminal spike. The variation in segment number may be seen to be continuous for the populations studied though there is some tendency for diploid populations to have a smaller mean number of segments than tetraploids.

These results show that diploid populations may have 3 - 14 (- 19) fertile segments and tetraploids (4 -) 5 - 25 fertile segments in the terminal spike. The figures agree closely with those given by Ball (1964) though they show a considerably larger overlap between the two aggregates of Irish Salicornia when compared with the figures proposed by Ball & Tutin (1959).

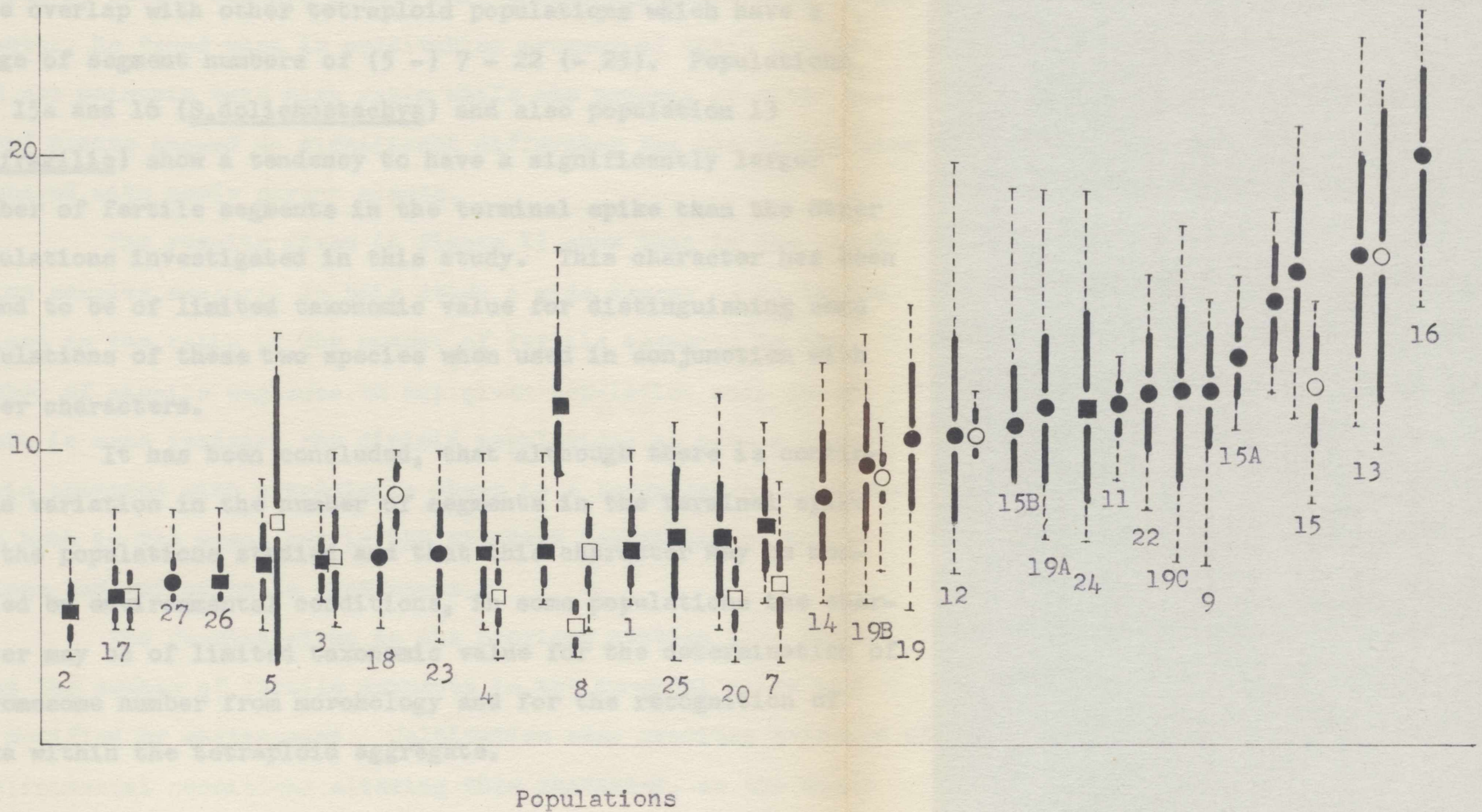
The results of measurements made on population samples over two years from the same locality, as for example population 8, suggest that environmental conditions may influence this character as also has been observed occurs in the case of the length of the terminal spike.

The results of cultivation of progeny show further evidence that in some populations the number of segments in the terminal spike may be significantly altered by environmental

FIGURE X

Number of segments in the terminal spike

Legend as in Figure VIII (page 46)

Segment
number

conditions as in populations 7, 8, 15, 18 and 20 ($p = > 0.001$) though in other populations this character is not significantly modified in cultivation as populations 3, 12, 13, 17 and 19b show.

Three tetraploid populations 18, 23 and 27 show a low mean segment number and a range of 4 - 10 fertile segments in the terminal spikelet. In this character these populations resemble S.nitens Ball & Tutin however, they do show a considerable overlap with other tetraploid populations which have a range of segment numbers of (5 -) 7 - 22 (- 25). Populations 15, 15a and 16 (S.dolichostachya) and also population 13 (S.fragilis) show a tendency to have a significantly larger number of fertile segments in the terminal spike than the other populations investigated in this study. This character has been found to be of limited taxonomic value for distinguishing some populations of these two species when used in conjunction with other characters.

It has been concluded, that although there is continuous variation in the number of segments in the terminal spike in the populations studied and that this character may be modified by environmental conditions, in some populations the character may be of limited taxonomic value for the determination of chromosome number from morphology and for the recognition of taxa within the tetraploid aggregate.

The ratio of the number of fertile segments
in the terminal spike to the number of
sterile segments in the plant.

Dalby (1962) appears to be the only worker to have used this ratio as a taxonomic character. He has applied it to 36 plants of known chromosome number and found a discontinuity occurred between diploid and tetraploid plants though a number of robust diploid plants fell within the tetraploid range. However, he found that in cultivation progeny of these plants did not maintain this high ratio while the progeny of other diploid plants showed no significant difference for the ratio, when compared with their parent plants.

The results given in Figure XI show that in the population samples measured in this study a wide degree of variation exists in the ratio of the number of fertile segments to the number of sterile segments, in any given population and, though there is some tendency for diploid populations to have a lower ratio compared with tetraploids there is a large degree of overlap both in the means and in the standard deviations of populations and variation is continuous.

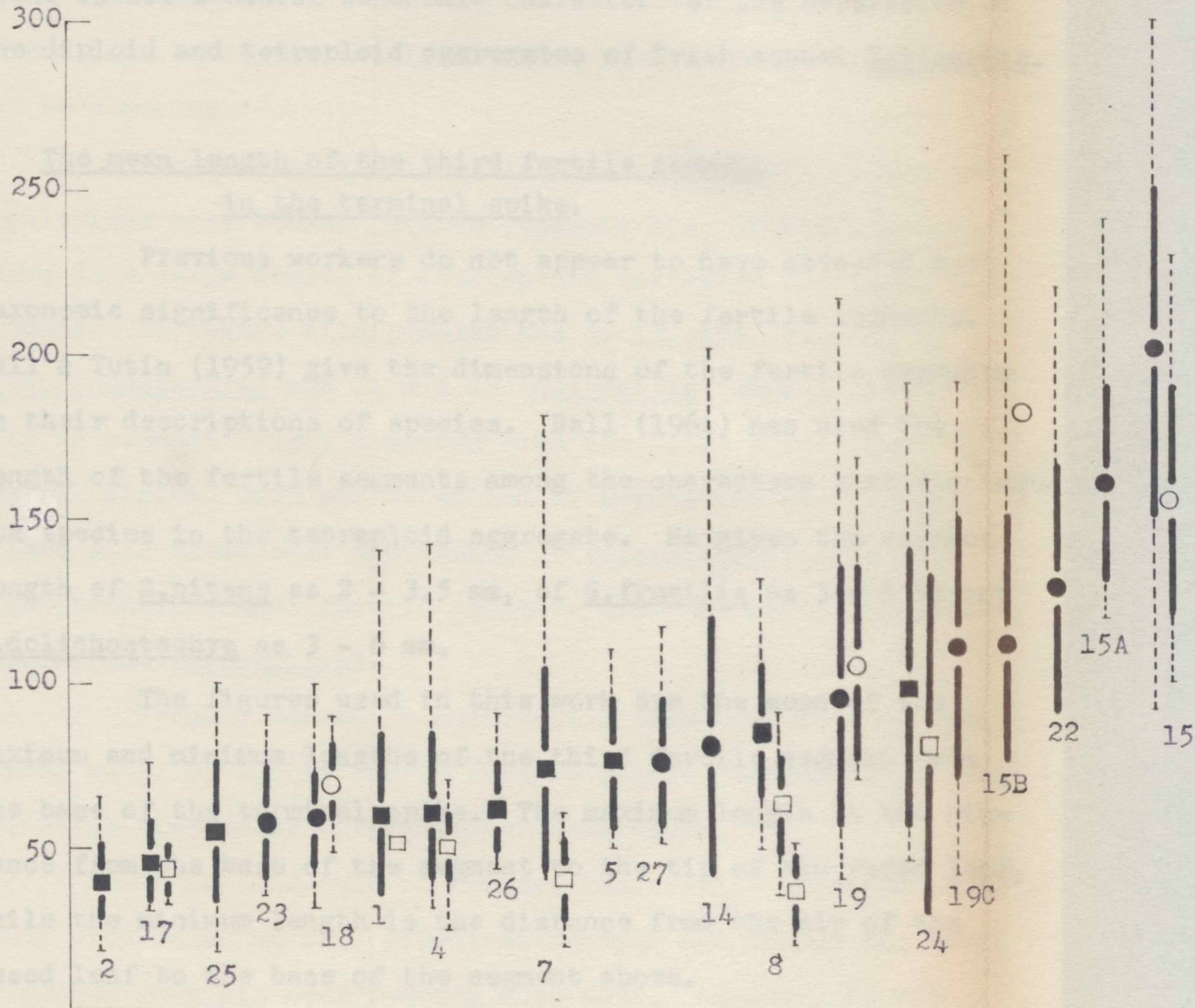
The results given in the previous section have shown that the number of fertile segments in the terminal spike may be modified by environment. Cultivation also provides evidence of environmental conditions altering this character, as the means of the ratio from progeny raised in cultivation have in many cases been significantly modified compared with the means of

FIGURE XI

The ratio of the number of fertile segments in the terminal spike to the number of sterile segments in the plant x 100.

Legend as in Figure VIII (page 46)

Values for
the ratio



Populations

their parents, this may be seen in populations 8, 15, 15b and 24 ($p = > 0.001$).

It has been concluded from these results, in disagreement with Dalby's findings, that the ratio of the number of fertile segments to the number of sterile segments in the plant is not a useful taxonomic character for the separation of the diploid and tetraploid aggregates of Irish annual Salicornia.

The mean length of the third fertile segment in the terminal spike.

Previous workers do not appear to have attached much taxonomic significance to the length of the fertile segments. Ball & Tutin (1959) give the dimensions of the fertile segments in their descriptions of species. Ball (1964) has used the length of the fertile segments among the characters that distinguish species in the tetraploid aggregate. He gives the segment length of S.nitens as 2 - 3.5 mm, of S.fragilis as 3 - 5 mm and S.dolichostachya as 3 - 6 mm.

The figures used in this work are the mean of the maximum and minimum lengths of the third fertile segment from the base of the terminal spike. The maximum length is the distance from the base of the segment to the tip of the fused leaf, while the minimum length is the distance from the tip of the fused leaf to the base of the segment above.

The length of the fertile segments is closely related to the length of the terminal spike and the number of segments in the terminal spike though these three characters are not

necessarily always interdependent. One of the main disadvantages of using this measurement as a taxonomic character is the same as that of using direct measurements of the length of the terminal spike as both are dependent on the stage of growth of the plants, because, elongation of the inflorescence occurs between flowering and the ripening of the seeds. Therefore only populations of approximately the same age and stage of growth may be compared.

The results in Figure XIIa and b show that tetraploid populations have longer fertile segments than diploids though there is a large degree of overlap and variation is almost continuous. In Figure XIIa, populations 9, 15, 15a, 15b and 16 (S.dolichostachya) and 14 and 18 (S.fragilis) show a discontinuity in segment length compared with the other populations which are all diploid with the exception of population 27 (S.fragilis). Figure XIIb shows that population 15 (S.dolichostachya) has significantly longer fertile segments than the other tetraploid populations (S.fragilis).

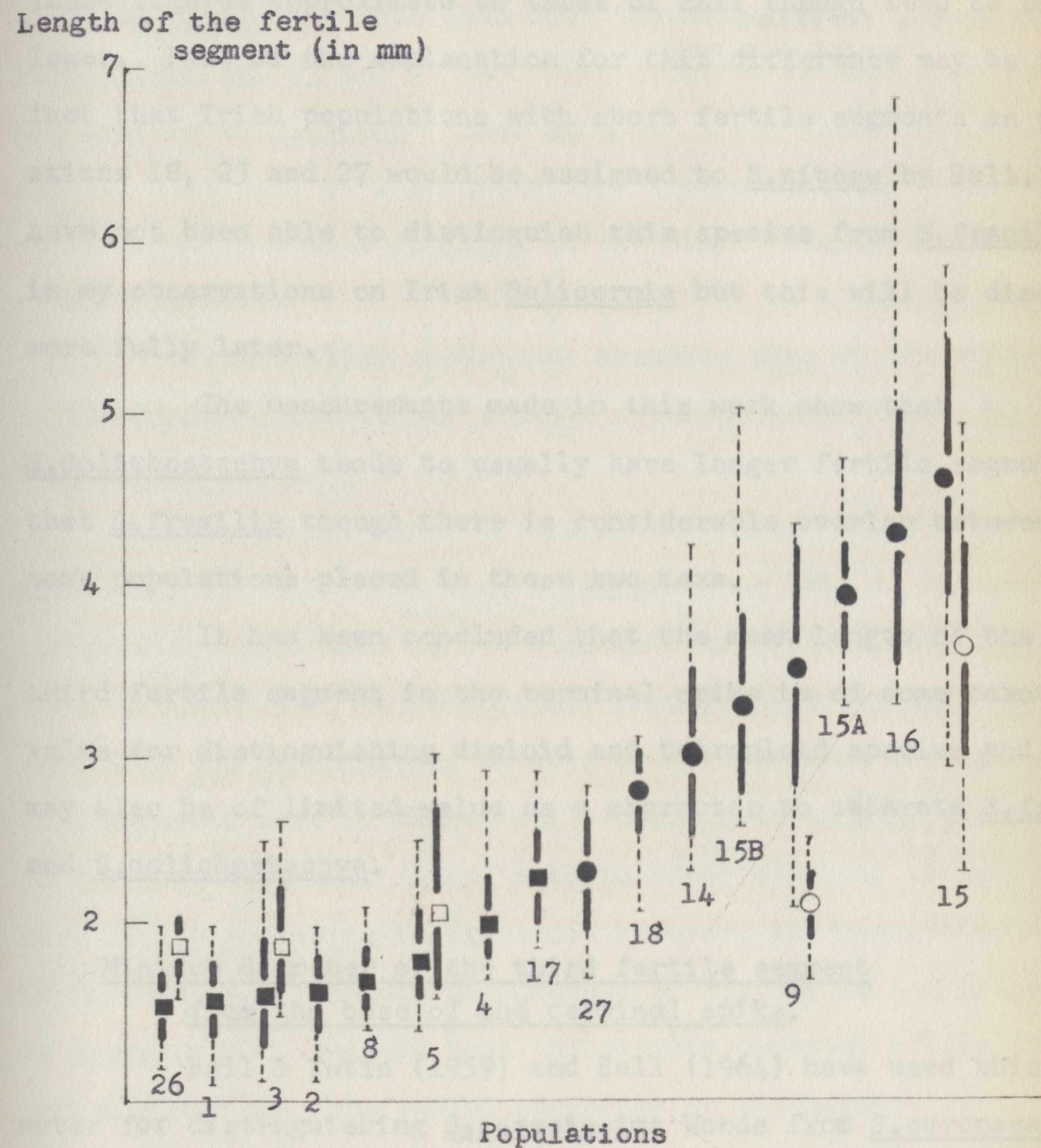
Progeny raised in cultivation show that in some populations as 8, 9, 12, 15 and 26 fertile segment length may be significantly altered by environmental conditions.

It is difficult to compare the results obtained in this study with those of Ball (1964) as he does not define the stage of growth when his measurements were made. However, if the range of measurements made in this work at both stages of growth are compared with those of Ball it may be seen that populations assigned to S.dolichostachya show a range of segment length of

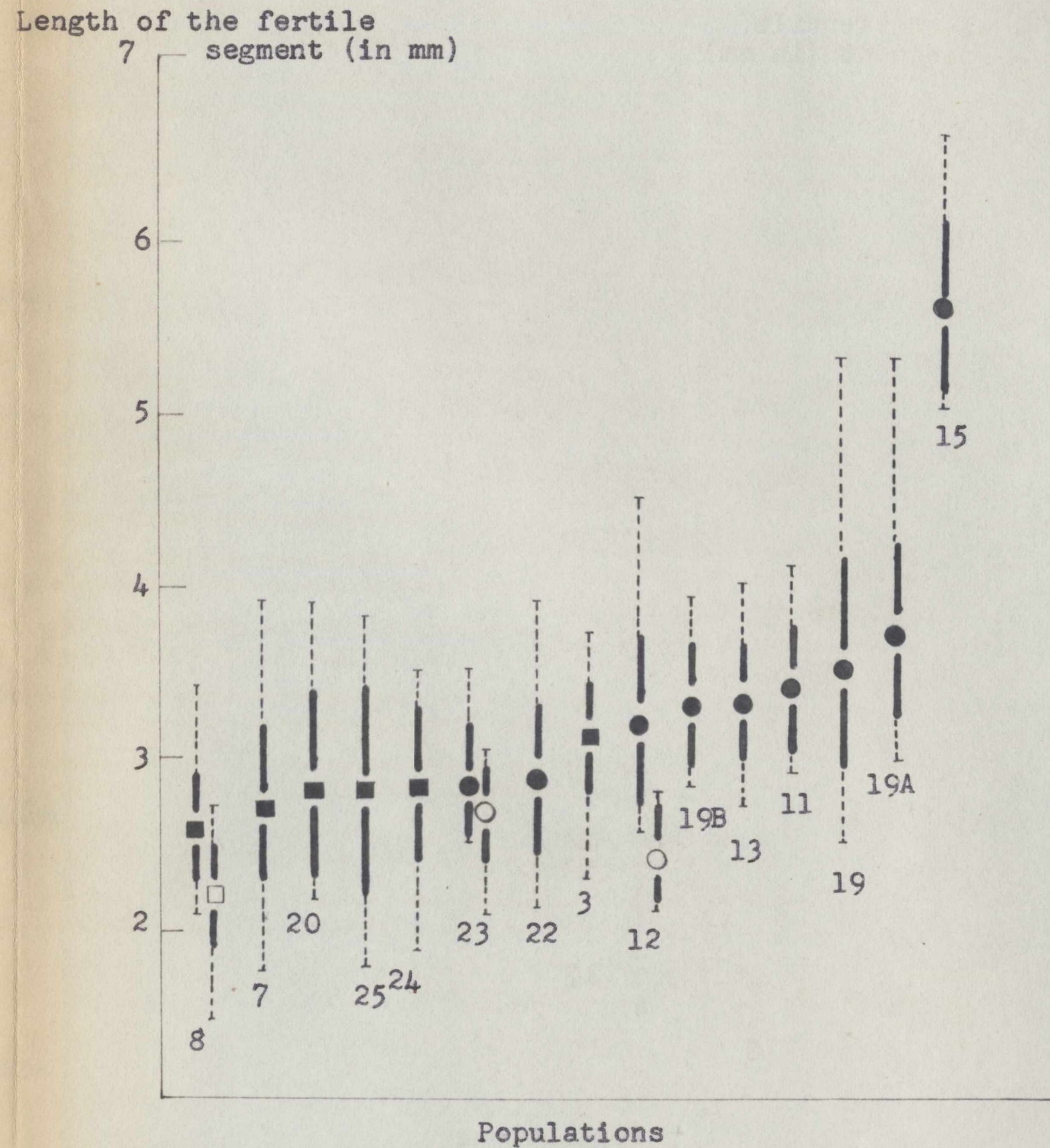
Mean length of the third fertile segment in the terminal spike (in mm).

Legend as in Figure VIII (page 46)

(a) Measurements made during flowering.



(b) Measurements made in early fruit.



(2 -) 2.5 - 6.5 mm which is very similar to that found by Ball. The range of measurements of the length of the fertile segments in S.fragilis found in this work fall between 2.0 - 4.5 (5.0) mm. These figures approximate to those of Ball though tend to be lower. Part of the explanation for this difference may be the fact that Irish populations with short fertile segments as populations 18, 23 and 27 would be assigned to S.nitens by Ball. I have not been able to distinguish this species from S.fragilis in my observations on Irish Salicornia but this will be discussed more fully later.

The measurements made in this work show that S.dolichostachya tends to usually have longer fertile segments than S.fragilis though there is considerable overlap between some populations placed in these two taxa.

It has been concluded that the mean length of the third fertile segment in the terminal spike is of some taxonomic value for distinguishing diploid and tetraploid species and it may also be of limited value as a character to separate S.fragilis and S.dolichostachya.

Minimum diameter of the third fertile segment
from the base of the terminal spike.

Ball & Tutin (1959) and Ball (1964) have used this character for distinguishing S.ramosissima Woods from S.europaea L. in the diploid aggregate and for distinguishing S.nitens Ball & Tutin from other species in the tetraploid aggregate. Ball gives the minimum diameter of S.ramosissima as 2.5 - 4 mm, of S.europaea as 3 - 5 mm, of S.nitens 2 - 3.5 mm and of S.

fragilis and S.dolichostachya as 3 - 6 mm.

Figure XIIIa shows that there is no discontinuity in the measurements of the minimum diameter in tetraploid populations of Irish Salicornia that have been investigated in this study. Populations 18, 23 and 27 have been observed to show some characters similar to S.nitens (pages 59 & 65) but these populations are not distinct, in this character, from many other populations which do not resemble S.nitens in the other diagnostic characters of that species.

Figure XIIIb shows that there is also no discontinuity in the minimum diameter of diploid populations of Irish Salicornia investigated in this study.

The measurements of the minimum diameter obtained in this study are all lower than those given by Ball as the range for tetraploid populations is 2 - 4 mm and for diploid populations 1.8 - 4.5 mm. This difference may be partially explained by the fact that the measurements in this study were made when the fertile segments were in flower while those made by Ball may refer to fruiting material. Also, Ball is doubtful about the occurrence of S.ramosissima in Ireland. However, the measurements made in this study on diploid populations 1, 17, 25, 24 and 3 assigned to S.europaea L. suggest that the minimum diameter of the fertile segments may not be a useful character to distinguish S. ramosissima from S.europaea if Irish Salicornia are considered.

It has been concluded from these results that the minimum diameter of the fertile segments is not a character of taxonomic value for the discrimination of taxa in Irish Salicornia.

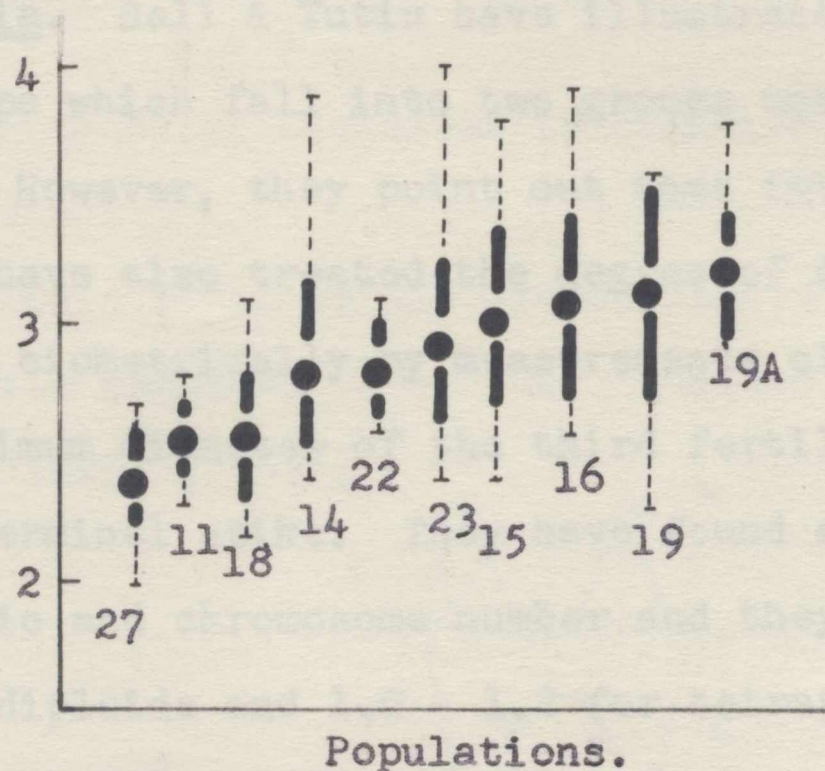
FIGURE XIII

Minimum diameter of the third fertile segment from
of the terminal spike (in mm),

Legend as in Figure VIII (page 46)

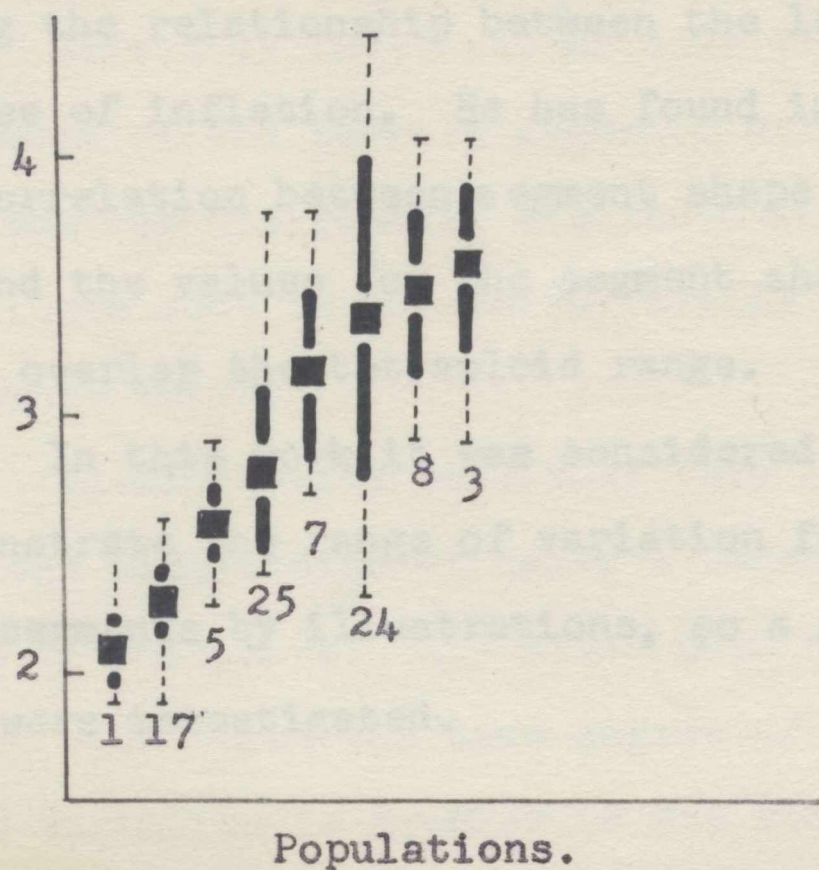
Minimum
Diameter
(in mm)

(a) Tetraploid populations



Minimum
Diameter
(in mm)

(b) Diploid Populations.



Morphology of the fertile segments.

Ball & Tutin (1959) appear to be the first workers to use the morphology of the fertile segments as a taxonomic character, although Wilmott (pers. comm.) has used this character extensively in his unpublished notes and descriptions of British Salicornia. Ball & Tutin have illustrated ten classes of segment shape which fall into two groups correlated with chromosome number. However, they point out that intergrading occurs. These workers have also treated the degree of inflation of the fertile segments biometrically by measurements of the ratio of the maximum/minimum diameter of the third fertile segment from the base of the terminal spike. They have found a correlation between this ratio and chromosome number and they give values of 1.1 - 1.4 for diploids and 1.0 - 1.2 for tetraploids.

Dalby (1962) has treated the morphology of the fertile segments biometrically and has proposed a segment shape index combining the relationship between the length of the segment and the degree of inflation. He has found in 39 plants measured that a correlation between segment shape and chromosome number occurs and the values for the segment shape index of very few diploids overlap the tetraploid range.

In this work it was considered impracticable to try and demonstrate the range of variation found in the shape of the fertile segments by illustrations, so a number of biometric methods were investigated.

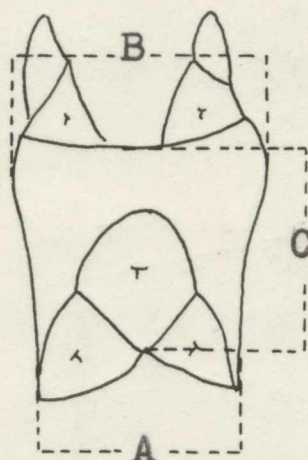
(i) An index $\frac{A + C}{2B} \cdot 100$ (letters as in diagram) below based on

that proposed by Dalby (1962) combining three measurements, the greater diameter, the lesser diameter and the length of the fertile segments.

(ii) An index $\frac{C}{B - A} \cdot 100$ based on the same three measurements

which it is suggested is simpler than that proposed by Dalby.

(iii) A simple ratio of the greater/lesser diameter of the fertile segments $\frac{B}{A} \cdot 100$ modified from that used by Ball & Tutin (1959),



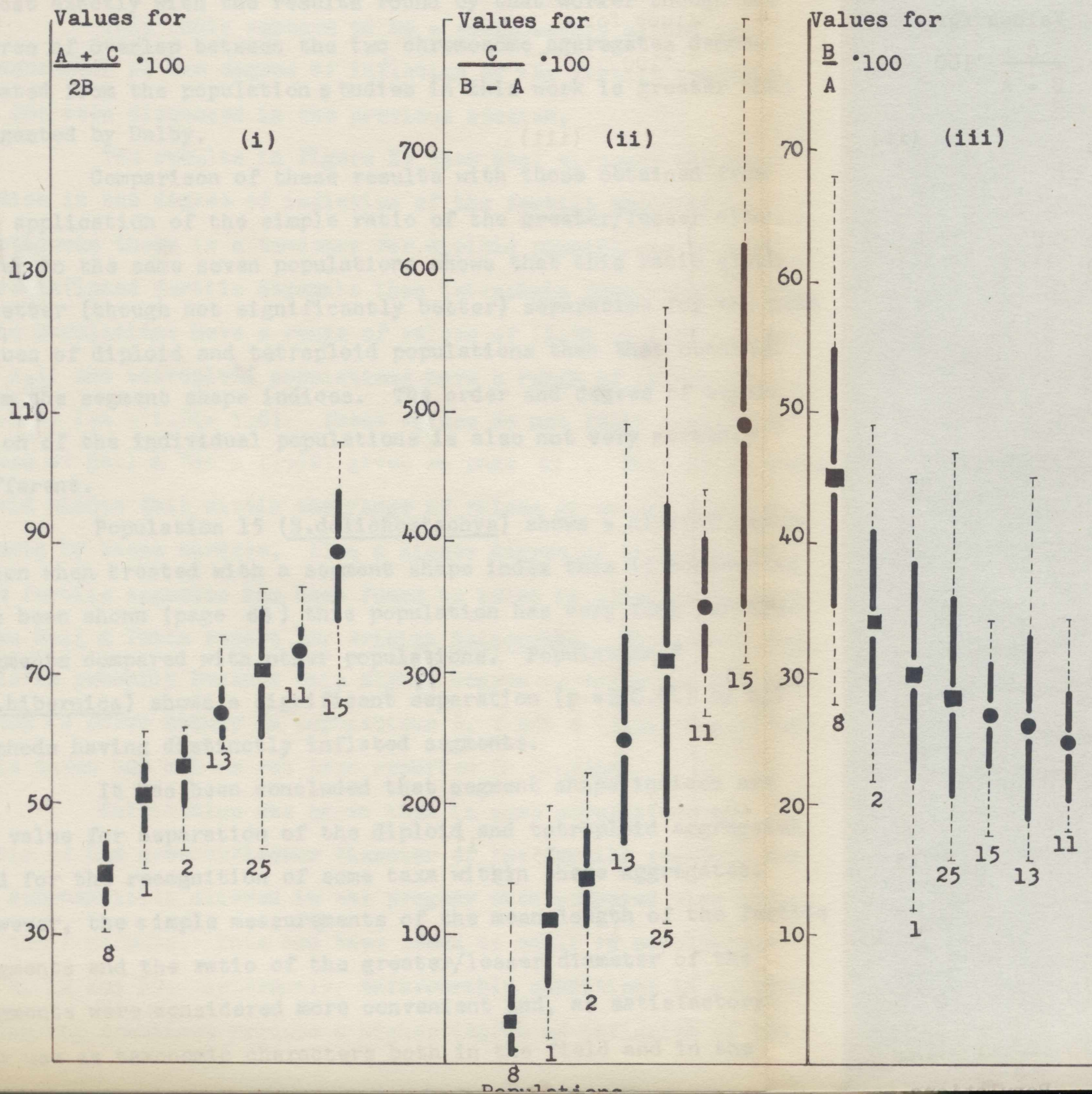
Trials of the three methods of biometric treatment of the shape of the fertile segments were conducted on seven populations and the results are shown in Figure XIV. All measurements were made on the third fertile segment from the base of the terminal spike.

These results show that very little difference occurs between the application of Dalby's segment shape index and that proposed in this work. All seven populations occur in the same order and show about the same degree of separation though the range of variation is greater in the results obtained from the

FIGURE XIV

Segment shape indices

Legend as in Figure VIII (page 46)



use of index (ii). The point of separation of diploid and tetraploid populations at about 60-65, using Dalby's index, corresponds almost exactly with the results found by that worker though the degree of overlap between the two chromosome aggregates demonstrated from the population studies in this work is greater than as has been discussed in the previous section, suggested by Dalby.

Comparison of these results with those obtained from the application of the simple ratio of the greater/lesser diameter to the same seven populations shows that this ratio gives a better (though not significantly better) separation for the mean values of diploid and tetraploid populations than that obtained from the segment shape indices. The order and degree of separation of the individual populations is also not very markedly different.

Population 15 (S.dolichostachya) shows a clearer separation when treated with a segment shape index this is because as has been shown (page 63) this population has very long fertile segments compared with other populations. Population 8 (S.hibernica) shows a significant separation ($p \geq 0.01$) by all methods having distinctly inflated segments.

It has been concluded that segment shape indices are of value for separation of the diploid and tetraploid aggregates and for the recognition of some taxa within these aggregates. However, the simple measurements of the mean length of the fertile segments and the ratio of the greater/lesser diameter of the segments were considered more convenient and, as satisfactory for use as taxonomic characters both in the field and in the

The ratio of the greater/lesser diameter of the
third fertile segment in the terminal spike

This ratio appears to be a satisfactory method of measurement of the degree of inflation of the fertile segments, as has been discussed in the previous section.

The results in Figure XV show that although the variation in the degree of inflation of the fertile segments is continuous there is a tendency for diploid populations to have more inflated fertile segments than tetraploid populations. Diploid populations have a range of values of (1.70 -) 1.55 - 1.20 (- 1.1) and tetraploid populations have a range of values of (1.5 -) 1.4 - 1.2(- 1.0). These values do not fully agree with those of Ball & Tutin (1959) given on page 68 . Many Irish tetraploid plants fall within the range of values given for diploid plants by these workers. Also a higher degree of inflation of the fertile segments has been found to exist in Irish Salicornia than Ball & Tutin report for British Salicornia. The reason for this is probably because this higher degree of inflation has been found to occur mainly in populations 5, 7 and 8 (S.hibernica) and this taxon has not as yet been reported in Britain.

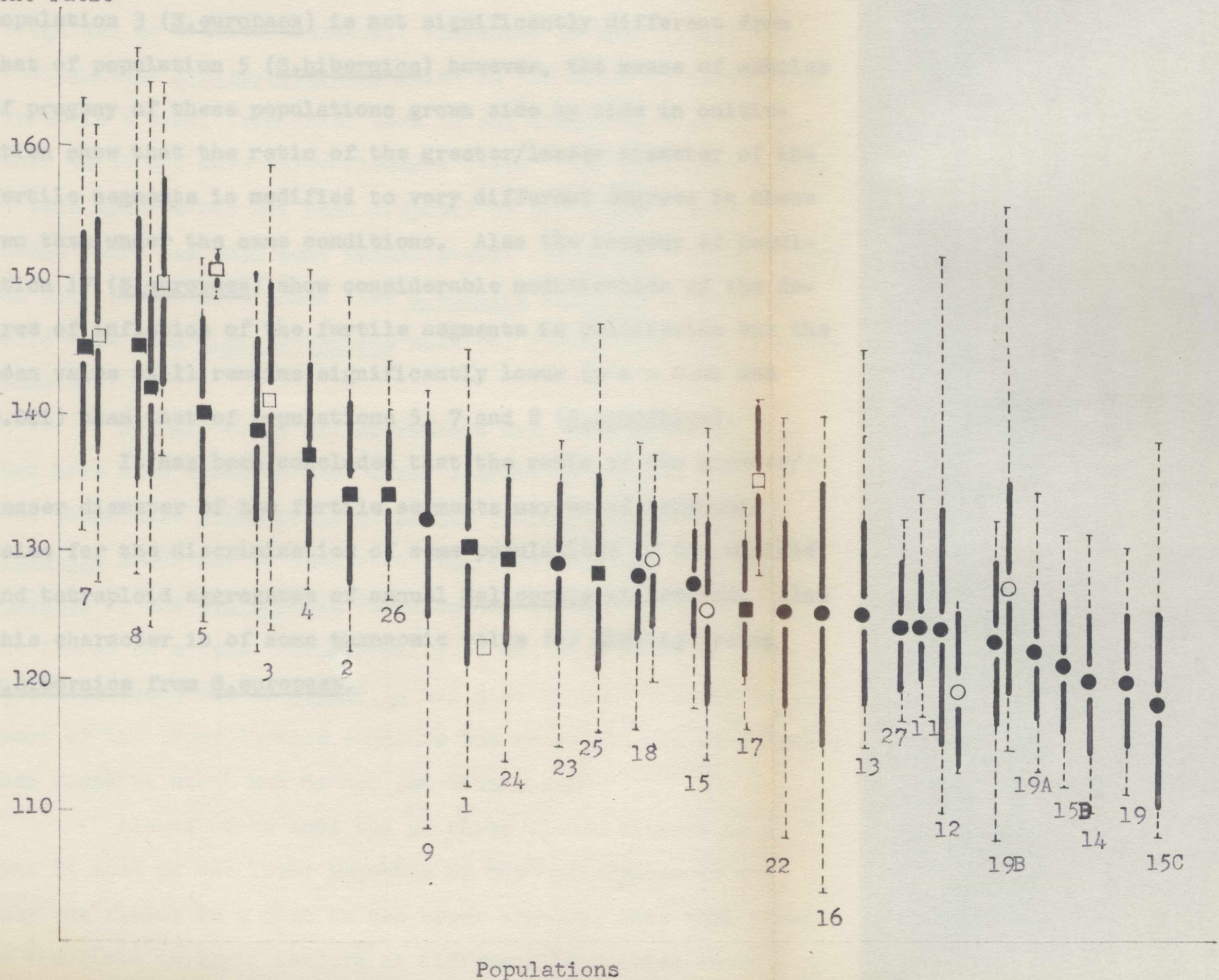
Cultivation has shown that in some populations the ratio of the greater/lesser diameter of the fertile segments may be substantially altered in the progeny when compared with that of their parents. This has been found to occur in populations 5, 8, 12 and 17. Apparently, unfavourable conditions in cultivation may sometimes produce a higher degree of inflation of the

FIGURE XV

The ratio of the greater/lesser diameter x 100 of the third
fertile segment in the terminal spike

Values for
the ratio

Legend as in Figure VIII (page 46)



fertile segments. However, in some populations this character has been found not to be significantly altered by cultivation as for example populations 3, 7, 15 and 18.

It is noteworthy that the mean value of the ratio of population 3 (S.europaea) is not significantly different from that of population 5 (S.hibernica) however, the means of samples of progeny of these populations grown side by side in cultivation show that the ratio of the greater/lesser diameter of the fertile segments is modified to very different degrees in these two taxa under the same conditions. Also the progeny of population 17 (S.europaea) show considerable modification of the degree of inflation of the fertile segments in cultivation but the mean value still remains significantly lower ($p = > 0.01$ and 0.001) than that of populations 5, 7 and 8 (S.hibernica).

It has been concluded that the ratio of the greater/lesser diameter of the fertile segments may be of taxonomic value for the discrimination of some populations of the diploid and tetraploid aggregates of annual Salicornia in Ireland. Also this character is of some taxonomic value for distinguishing S.hibernica from S.europaea.

The number of florets that occur in the cymes
of the fertile spikes

The variation that occurs in the number of florets in the cymes of the inflorescences (fertile spikes) was first recognised as a useful taxonomic character by Moss (1911) who distinguished S. disarticulata, which he described as having one floret in a cyme, from other taxa in the annual section of the genus which all have three flowered cymes. The taxonomic status of this species has not been disputed by any workers since, though there has been some nomenclatural confusion. Dandy (1958) and Ball (1960) have shown that S. pusilla Woods is an earlier valid name than S. disarticulata Moss for plants with one flowered cymes.

In this study all tetraploid taxa that occur in Ireland have been found to have three florets in a cyme. It has been found that populations of plants fitting descriptions of S. pusilla Woods may be separated from other diploid taxa (S. europaea L. and S. hibernica Ferguson) by the occurrence of only one floret in a cyme. Occasionally it has been observed that some inflorescences of S. pusilla may have lateral florets in the cymes of the lower fertile segments but these florets have always been found to abort and do not set viable seed.

Plants which have two or three viable florets in a cyme in some of the lower segments of the inflorescences and only one floret in a cyme in the upper segments have been found in the field in small numbers at different localities where S. europaea and S. pusilla were growing side by side. The

length and number of segments in the fertile spikes were found to be greater in these plants, which had a variable number of florets in a cyme, than in plants of typical S. pusilla. (See Plates 6 & 9).

The fertile spikes of typical specimens of S. pusilla Woods have always been observed to disarticulate at maturity. Some of the intermediate plants observed showed a tendency to disarticulate while others did not show this character. These observations suggested that S. europaea and S. pusilla may hybridise when growing side by side and, that the hybrids are viable. At one locality near Eastern Bridge between Belgooly and Kinsale in Co. Cork S. pusilla was found to be the only taxon of Salicornia present in the salt marsh. A large number of plants were examined at this locality but none were found with a variable number of viable florets in the cymes of the fertile spikes. This provided further evidence that the intermediate plants observed at other localities, where S. europaea and S. pusilla grew side by side, were in fact of hybrid origin.

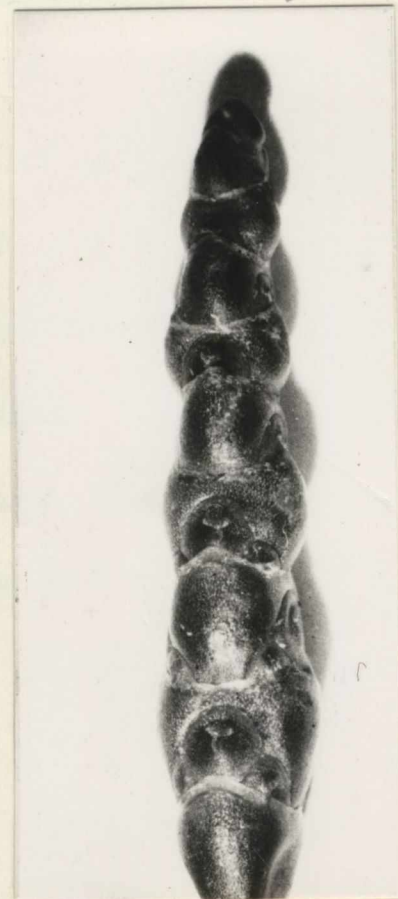
Twelve progeny were raised in cultivation from seed of five parent plants which were apparently intermediate in the character of the number of florets in a cyme. The intermediate parent plants were collected from Tramore and Dungarvan in Co. Waterford and from Middleton in Co. Cork. Eleven of the progeny raised were intermediate and closely resembled their parent plants while one of the progeny resembled typical S. pusilla. Though cultivation experiments were not extensive these results again suggest the existence of hybridisation between S. pusilla

An apparent hybrid between S.pusilla Woods and S.europaea L. showing a variable number of florets in the cymes of the segments. The lower three segments in the terminal spike show three florets while the upper segments have only one. The terminal spike is longer than in typical S.pusilla (Plate 9 page 173)

(Entire plant)
x 1/2



(Terminal spike)
x 5



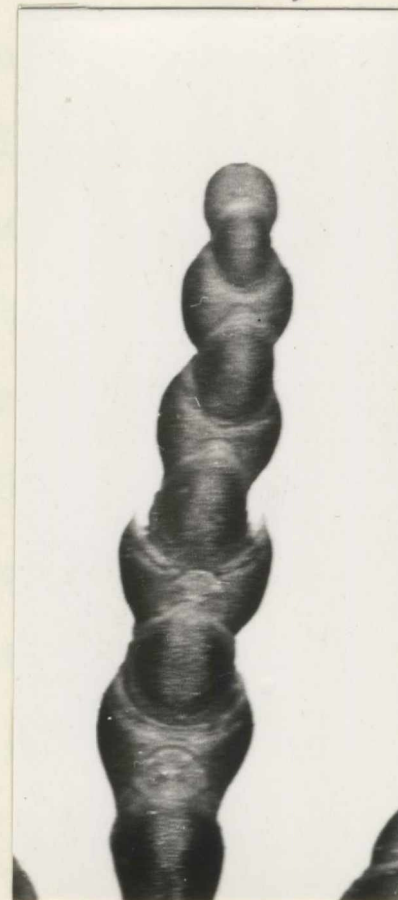
Cultivated progeny

The lower fertile segments in the terminal spike have three florets in a cyme the upper segments have only one.

(Entire plant)
x 1/2



(Terminal spike)
x 5



and S.europaea. It was not possible to observe in cultivation whether the fertile spikes disarticulated at maturity because the progeny of typical specimens of S.pusilla were never found to show this character in cultivation even when grown under a variety of conditions although they always set viable seed.

Apparently S.pusilla Woods occasionally hybridises with S.europaea where these two species grow together in the field, however the number of intermediate plants found in any of the populations studied is very low. It has therefore been concluded that the occurrence of one flowered cymes in the fertile spikes of S.pusilla Woods is a useful taxonomic character for the recognition of this species.

The degree of exposure of the florets

Ball & Tutin (1959) and Ball (1964) have described the visible part of the lateral flowers of each cyme as commonly appearing much smaller than the central flower in diploid taxa and, in tetraploid taxa, the visible part of the lateral flowers of each cyme almost as large as the central flower.

In this study it has been observed that in diploid taxa with three flowered cymes the central floret of the cyme is usually much larger than the visible part of the lateral florets while in tetraploid taxa the central floret of each cyme is usually only a little larger than the visible part of the lateral florets. These observations agree with the results of Ball & Tutin.

It has also been observed that the degree of exposure of the florets may be of value as a taxonomic character for the separation of taxa within the diploid aggregate. Plants of populations 5, 7 and 8 (S.hibernica) have usually more than half of the central floret and almost all of the lateral florets hidden by the fused leaves during flowering. Other diploid populations including 1, 2, 3, 4, 17, 20, 24 and 26 (S.europaea) have at least half of the central floret and about one third of the lateral florets visible during flowering.

It was not appreciated until late in this study that the degree of exposure of the florets might be a character of taxonomic importance and as a result it has not been treated biometrically. It seems possible that measurements of the distances between the tip of the fused leaves to the apex of the central floret and from the margin of the leaves to the top of the visible part of the lateral florets (refer to Figure I) could show a significant difference between populations in the diploid and tetraploid aggregates and also between plants in populations assigned to S.hibernica and S.europaea. It must be appreciated however, that some overlap in measurements of this character will occur between plants in both the two chromosome aggregates and between plants of the two diploid taxa as has been found in almost all of the characters investigated biometrically in this study. It is hoped that it may be possible to treat this character biometrically at some later stage.

tetraploid populations (75 - 195 - 215(- 270). Populations 15, 15a, 15b, 16 and 22 (S.dolichostachya) show central florets

The ratio of the length/width of the central floret
X 100 of the third fertile segment from the
base of the terminal spike.

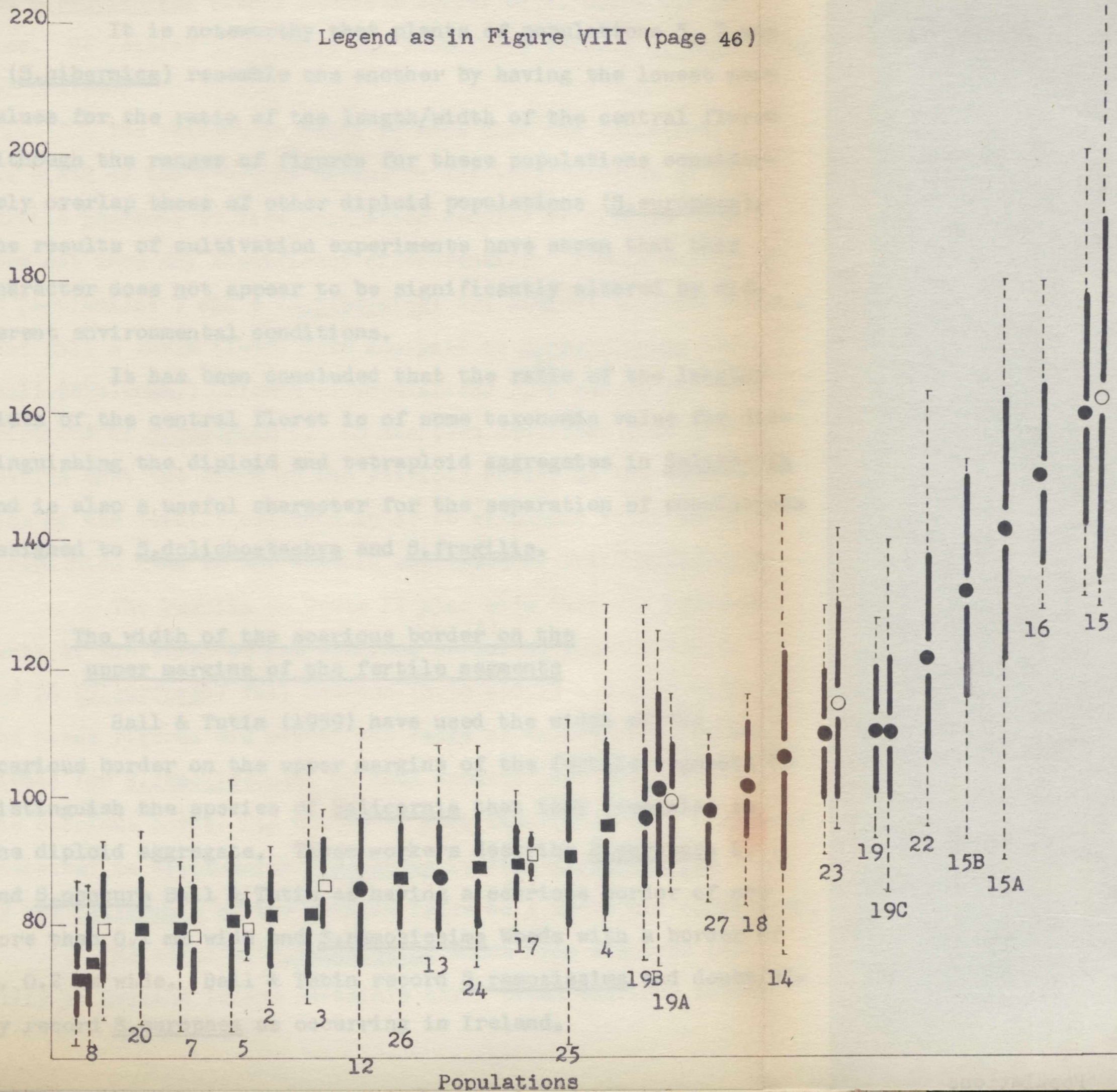
No previous workers appear to have attached much taxonomic significance to the shape of the central floret and this character has not been treated biometrically before. However, Moss (1912) describes the central floret as separating the lateral florets in S.dolichostachya and he uses this character to distinguish the species from other annual Salicornia. Ball & Tutin (1959) dismiss this character of Moss's as not being of any taxonomic value as they have found that degree to which the central floret separates the lateral florets is variable within plants of the same population. Ball & Tutin do give measurements of the dimensions of the central floret in their descriptions of the species of Salicornia that they recognise.

The results in Figure XVI show that the variation in the ratio of the length/width of the central floret X 100 is almost continuous. However, the distribution of the means of the ratios shows that there is some correlation between this character and the determined or predicted chromosome number of the population concerned. The central florets of tetraploid populations tend to be longer than broad when compared with those of diploid populations. The values for the ratios found in this study are diploid populations (80 -)85 - 130(- 150) and tetraploid populations (75 -)95 - 215(- 270). Populations 15, 15a, 15b, 16 and 22 (S.dolichostachya) show central florets

The ratio of the length/width of the central floret X 100
of the third fertile segment from the base in the
terminal spike

Values
for the
ratio

Legend as in Figure VIII (page 46)



that are one and a half times to twice as long as wide, while in other tetraploid populations (S.fragilis) the central florets are less than one and a half times as long as wide.

It is noteworthy that plants of populations 5, 7 and 8 (S.hibernica) resemble one another by having the lowest mean values for the ratio of the length/width of the central floret although the ranges of figures for these populations considerably overlap those of other diploid populations (S.europaea). The results of cultivation experiments have shown that this character does not appear to be significantly altered by different environmental conditions.

It has been concluded that the ratio of the length/width of the central floret is of some taxonomic value for distinguishing the diploid and tetraploid aggregates in Salicornia and is also a useful character for the separation of populations assigned to S.dolichostachya and S.fragilis.

The width of the scarious border on the upper margins of the fertile segments

Ball & Tutin (1959) have used the width of the scarious border on the upper margins of the fertile segments to distinguish the species of Salicornia that they recognise in the diploid aggregate. These workers describe S.europaea L. and S.obscura Ball & Tutin as having a scarious border of not more than 0.1 mm wide and S.ramosissima Woods with a border of c. 0.2 mm wide. Ball & Tutin record S.ramosissima and doubtfully record S.europaea as occurring in Ireland.

Later Ball (1964) modifies his earlier views and describes S.europaea with a scarious border of not more than 0.1 mm wide and S.ramosissima with a scarious border of c. 0.1 - 0.2 mm wide. He records S.europaea and doubtfully records S.ramosissima for Ireland.

The results in Table IV show that the variation in the width of the scarious border on the upper margins of the fertile segments of five population samples of diploid taxa does not show any significant discontinuity. Plants belonging to populations 7 and 8 (S.hibernica) are similar to Irish plants that Ball & Tutin (1959) have assigned to S.ramosissima Woods (Ball pers.comm.) Plants of populations 1, 4 and 26 fit descriptions of S.europaea L. It has been concluded from these results that the width of the scarious border on the upper margins of the fertile segments is of no taxonomic value for distinguishing taxa in the diploid aggregate of Irish Salicornia.

The results in Table IV also show that the measurements of the width of the scarious border of populations 1, 4 and 26 (S.europaea) fall between (0.10 -)0.13 - 0.19(- 0.20) mm and these figures are within the range of values given by Ball (1964) for S.ramosissima. It thus appears that the width of the scarious border may not be of much importance as a taxonomic character to distinguish S.europaea L. from S.ramosissima Woods if the Salicornia of the British Isles as a whole are considered.

Material of S.ramosissima Woods from its type locality at Hayling Island certainly has a broad scarious border

TABLE IV

The width of the scarious border on the upper margins of the fertile segments (in mm).

<u>Population number</u>	<u>Locality</u>	<u>Species</u>	<u>Number of Plants measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
26	Ballyvaughan	(<u>S. europaea</u>)	20	0.15	0.02	0.10-0.18
1	Tramore	(<u>S. europaea</u>)	20	0.16	0.03	0.12-0.20
4	Rush	(<u>S. europaea</u>)	25	0.16	0.02	0.14-0.20
7	Kilcainin	(<u>S. hibernica</u>)	42	0.17	0.03	0.10-0.21
8	Tramore	(<u>S. hibernica</u>)	15	0.17	0.02	0.12-0.21

In each plant five measurements were made from different segments

in the terminal spike.

of about 0.20 mm but plants of S.europaea from Parkgate in Cheshire and from Foryd Bay and Llandudno in Caernarvonshire have been found to have a scarious border that is greater than 0.10 mm broad.

It has been concluded from these observations that the width of the scarious border on the upper margins of the fertile segments does not warrant the importance attributed to it as a taxonomic character by Ball & Tutin.

Ball & Tutin (1959) have correlated chromosome number with stamen number and they describe the tetraploid species S.dolichostachya Moss and S.fragilis Ball & Tutin with (1 -)2 stamens in a floret and the diploid species S.europaea L. and S.ramosissima Woods with 0 - 1(- 2) stamens in a floret. Later Ball (1964) somewhat modified his views and described the diploid aggregate with "stamens 1 rarely 0 or 2" and the tetraploid aggregate with "stamens 1 - 2".

Table V shows the results of a preliminary investigation of stamen number in three population samples from Rush. Population 15 (S.dolichostachya) appears here to have a considerably higher number of florets with two stamens than have populations 18 and 4. Population 18 (S.fragilis) shows that in some cases anyway, plants belonging to the tetraploid aggregate have predominantly only one stamen in a floret. This result does not support the results of Ball & Tutin (1959) but is more in agreement with Ball's (1964) later views.

The observations made in this study and those of

Stamen number

Linneaus (1753) in his description of Salicornia used the presence of one stamen in the florets as an important character diagnostic of the genus. Smith (1813) described a species S.procumbens with two stamens in a floret. Moss & Salisbury (1914) described a species S.dolichostachya with only one stamen and S.herbacea (S.fragilis Ball & Tutin) and S. ramosissima Woods both with one to two stamens in a floret.

Ball & Tutin (1959) have correlated chromosome number with stamen number and they describe the tetraploid species S.dolichostachya Moss and S.fragilis Ball & Tutin with (1 -)2 stamens in a floret and the diploid species S.europaea L. and S.ramosissima Woods with 0 - 1(- 2) stamens in a floret. Later Ball (1964) somewhat modified his views and described the diploid aggregate with "stamens 1 rarely 0 or 2" and the tetraploid aggregate with "stamens 1 - 2".

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The observations made in this study and those of

TABLE V

The number of stamens in a floret recorded from population samples of three taxa occurring at Rush in Co. Dublin

<u>Population number</u>	<u>Species</u>	<u>Chromosome number</u>	<u>Number of plants</u>	<u>Number of florets examined</u>	<u>No. of florets with 1 stamen</u>	<u>No. of florets with two stamens</u>
2	(<u>S. fragillilis</u>)	2n = 18	14	178	174	10
15	(<u>S. dolichostachya</u>)	2n = 36	24	501	172	329
18	(<u>S. fragillilis</u>)	2n = 36	20	178	174	4

(Florets with no stamens were not recorded)

Ball & Tutin show that the material that Moss saw when he described S.dolichostachya in Cambridge British Flora as having only one stamen in a floret cannot have been typical of that species, yet the plant he illustrates is clearly S.dolichostachya and fits the original description. Moss's description of the diploid species S.ramosissima Woods as having two stamens in a floret also conflicts with recent results and Ball (1960) has postulated that Moss confused the data for these species when preparing account in Cambridge British Flora.

Stamen number was not investigated further as it was concluded that although this was of some taxonomic value for distinguishing S.dolichostachya the character is variable and of no taxonomic significance in the rest of the annual Salicornia. Also it was considered that there are other characters that have been investigated in this work which may be more readily used to distinguish S.dolichostachya.

The means of measurements of anther length from samples made of the same population in two successive years and from progeny of samples of populations raised in cultivation show, that this character may vary to some extent in the same population under different conditions. For example population 15 (S.dolichostachya) sampled in the field at the same locality over two successive years shows a significant difference ($p = > 0.001$) between the means of the measurements and this suggests that differing environmental conditions including

Anther length

Ball & Tutin (1959) appear to be the only workers to have used anther length as a taxonomic character in Salicornia. These workers have reported a correlation between this character and chromosome number and they have given the range of anther length of plants belonging to the diploid aggregate as 0.40 - 0.60 mm and for the tetraploid aggregate as 0.65 - 0.90 mm. Later, Ball (1964) has somewhat modified these measurements and he has given the anther length of diploid plants as 0.2 - 0.5 mm and of tetraploids as (0.5 -)0.6 - 1.0 mm.

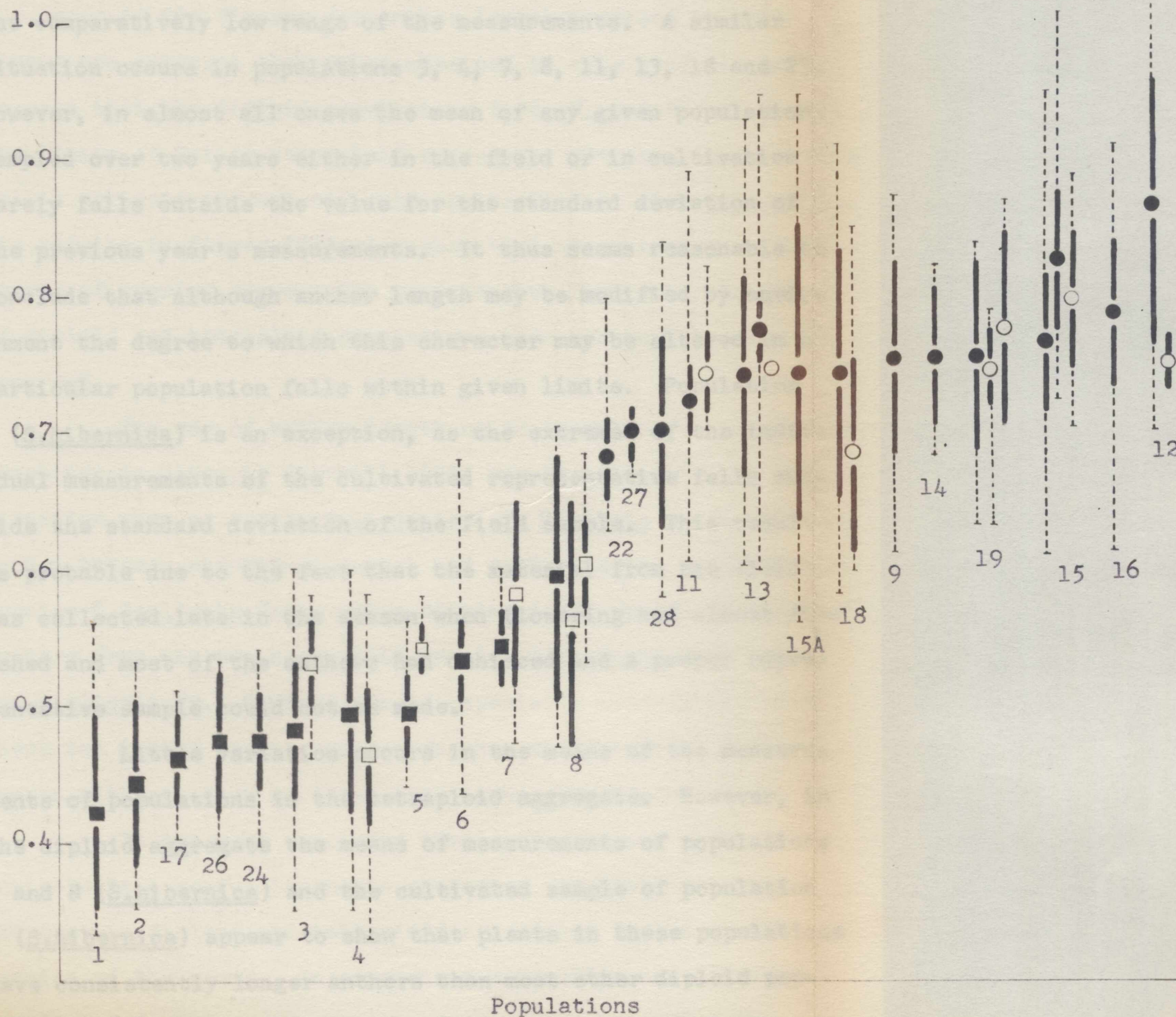
Figure XVII shows the results of measurements of anther length made in this study. The variation in anther length is almost continuous but there is a small discontinuity between the means of measurements of diploid and tetraploid populations. The full range of values for anther length found in this work are (0.33 -)0.35 - 0.68(- 0.70) mm in diploid populations and (0.56 -)0.65 - 0.96(- 1.05) mm in tetraploid populations.

The means of measurements of anther length from samples made of the same population in two successive years and from progeny of samples of populations raised in cultivation show, that this character may vary to some extent in the same population under different conditions. For example population 15 (S.dolichostachya) sampled in the field at the same locality over two successive years shows a significant difference ($p = > 0.001$) between the means of the measurements and this suggests that differing environmental conditions including

FIGURE XVII

Anther length (in mm)

Legend as in Figure VIII (page 46)

Anther length
(in mm)

perhaps light, temperature, and humidity may modify this character to some extent. It should be pointed out that tests of the level of significance in these circumstances will tend to give a high value because of the large size of the sample and the comparatively low range of the measurements. A similar situation occurs in populations 3, 4, 7, 8, 11, 13, 18 and 23. However, in almost all cases the mean of any given population sampled over two years either in the field or in cultivation rarely falls outside the value for the standard deviation of the previous year's measurements. It thus seems reasonable to conclude that although anther length may be modified by environment the degree to which this character may be altered in a particular population falls within given limits. Population 5 (S.hibernica) is an exception, as the extremes of the individual measurements of the cultivated representative falls outside the standard deviation of the field sample. This result is probable due to the fact that the material from the field was collected late in the season when flowering had almost finished and most of the anthers had dehisced and a proper representative sample could not be made.

Little variation occurs in the means of the measurements of populations in the tetraploid aggregate. However, in the diploid aggregate the means of measurements of populations 7 and 8 (S.hibernica) and the cultivated sample of population 5 (S.hibernica) appear to show that plants in these populations have consistently longer anthers than most other diploid populations (S.europaea). As a result of these observations

anther length has been used in this work to divide the diploid aggregate into two groups, one with anthers 0.49 - 0.70 mm long (S.hibernica) and the other with anthers 0.35 - 0.55 mm long (S.europaea). S.hibernica and S.europaea that are recognised in this study. If the figures for anther length proposed by Ball (1964) are compared with those obtained in this study it may be seen that the diploid populations 5, 6, 7, and 8 fall within the limits of Ball's tetraploid aggregate. It thus appears that Ball's criteria are not entirely applicable to Irish Salicornia. The results in Figure XVII also show that there is a greater degree of overlap between the measurements for anther length of diploid and tetraploid populations than has been previously reported.

The use of anther length as an important taxonomic character in Glyceria (Borrill 1956) may be analogous to the situation that occurs in Salicornia. In Glyceria a correlation occurs between chromosome number and anther length, the diploid species G.declinata Breb. being distinguished by its shorter anthers from the two tetraploid species G.fluitans (L.) R.Br. and G.plicata Fr. However, it is especially interesting that these two latter species show a further difference in anther length although they have the same chromosome number.

It has been concluded that anther length although variable is a useful taxonomic character for distinguishing between the diploid and tetraploid aggregates in the annual section of the genus. In comparison with other characters investigated in this study it is considered to be one of the

most reliable characters for the prediction of chromosome number from morphology. Also anther length has been considered to be of some taxonomic value for distinguishing between the two diploid taxa (S. hibernica and S. europaea) that are recognised in this study.

(1914) described the stigmas of S. perennis as bifid and of annual plants as tufted. Tutin (1952) has followed the descriptions given by Moss (1914). Moss (1954) in a paper primarily relating to South African Chenopodiaceae has redefined the genera Arthrocnemum and Salicornia and has made the new combination A. perenne (Mill.) Moss, and he uses stigma morphology as one of the important characters to distinguish these two genera. He described the stigmas in Arthrocnemum as bifid or trifid and in Salicornia as tufted.

In this work it has been observed that the stigma in S. perenne may be bifid or trifid; the branches are usually about 1 mm in length and often persistent after fertilisation (Figure XVIII).

In annual species of Salicornia the stigmas have been found to be variable even within the same plant being "tufted", (that is very shortly branched with branches often unequal in length) bifid, or trifid and often persistent (Figure XVIII & Plate 7). The stigmas of annual material collected in the field are usually shorter than those of S. perenne, with branches usually about 0.5 - 0.7 mm long. Tetraploid plants cultivated from seed from six populations; 10, 12, 13, 18, 19 and 19a (S. fragilis), produced stigmas with very long branches

Stigma morphology

Stigma morphology has been used by a number of previous workers as a taxonomic character to distinguish S. perennis Mill. from the annual section of the genus. Moss (1914) described the stigmas of S. perennis as bifid and of annual plants as tufted. Tutin (1952) has followed the descriptions given by Moss (1914). Moss (1954) in a paper primarily relating to South African Chenopodiaceae has redefined the genera Arthrocnemum and Salicornia and has made the new combination A. perenne (Mill.) Moss, and he uses stigma morphology as one of the important characters to distinguish these two genera. He described the stigmas in Arthrocnemum as bifid or trifid and in Salicornia as tufted.

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of more than 1 mm in length and indistinguishable from those of S.perennis (Figure XVIII). In diploid plants of populations 2, 3, 4 and 20 (S.europaea) and S.pusilla Woods the branches of the stigmas have been found to be usually shorter and more slender than those of S.perennis. However, the stigmas of these two species are very variable and in cultivation they have been found to be almost indistinguishable from those of S.perennis. X 40 approx.

It is noteworthy that these observations are in harmony with the illustrations in Smith's English Botany where S.perennis (t. 1691) and an annual species (t. 415) closely resembling S.fragilis Ball & Tutin (one of the tetraploid taxa recognised in the present study) are both depicted with trifid stigmas, though the branches of the former are longer. A third illustration (t. 2475) shows another annual species with a tufted stigma.

It has been concluded that stigma morphology is very variable in British Salicornia and is an unreliable taxonomic character.

Pollen grain diameter

FIGURE XVIII

Illustrations of stigmas of Salicornia sp.

X 40 approx.



(a) Stigma of S. perennis. (b) Stigma of an annual species in cultivation. (c) & (d) Stigmas of annual species collected in the field.

Pollen grain diameter

Ball & Tutin (1959) have found that a significant difference occurs between the pollen grain diameter of diploid and tetraploid plants. The figures they have found for diploid plants are (20 -)24 - 28(- 31) μ and for tetraploids (27 -)31 - 34(- 42) μ . Dalby (1962) has also found a correlation between pollen size and chromosome number and he has reported that a pollen diameter of 27.2 μ marks the change from diploid to tetraploid plants. Dalby has commented that this figure is lower than that given by Ball & Tutin and many of his tetraploid plants would fall within the diploid range given by these workers.

The results of measurements of pollen grain diameter obtained in this study are shown in Figure XIX. A discontinuity occurs in the means of the measurements at 28 - 29 μ and this is correlated with the determined or predicted chromosome number of the populations concerned. The ranges of the values found in this study are (20 -)22 - 28.5(- 31) μ for pollen grain diameter of diploid populations and (28 -)29 - 35(- 39) μ for tetraploid populations.

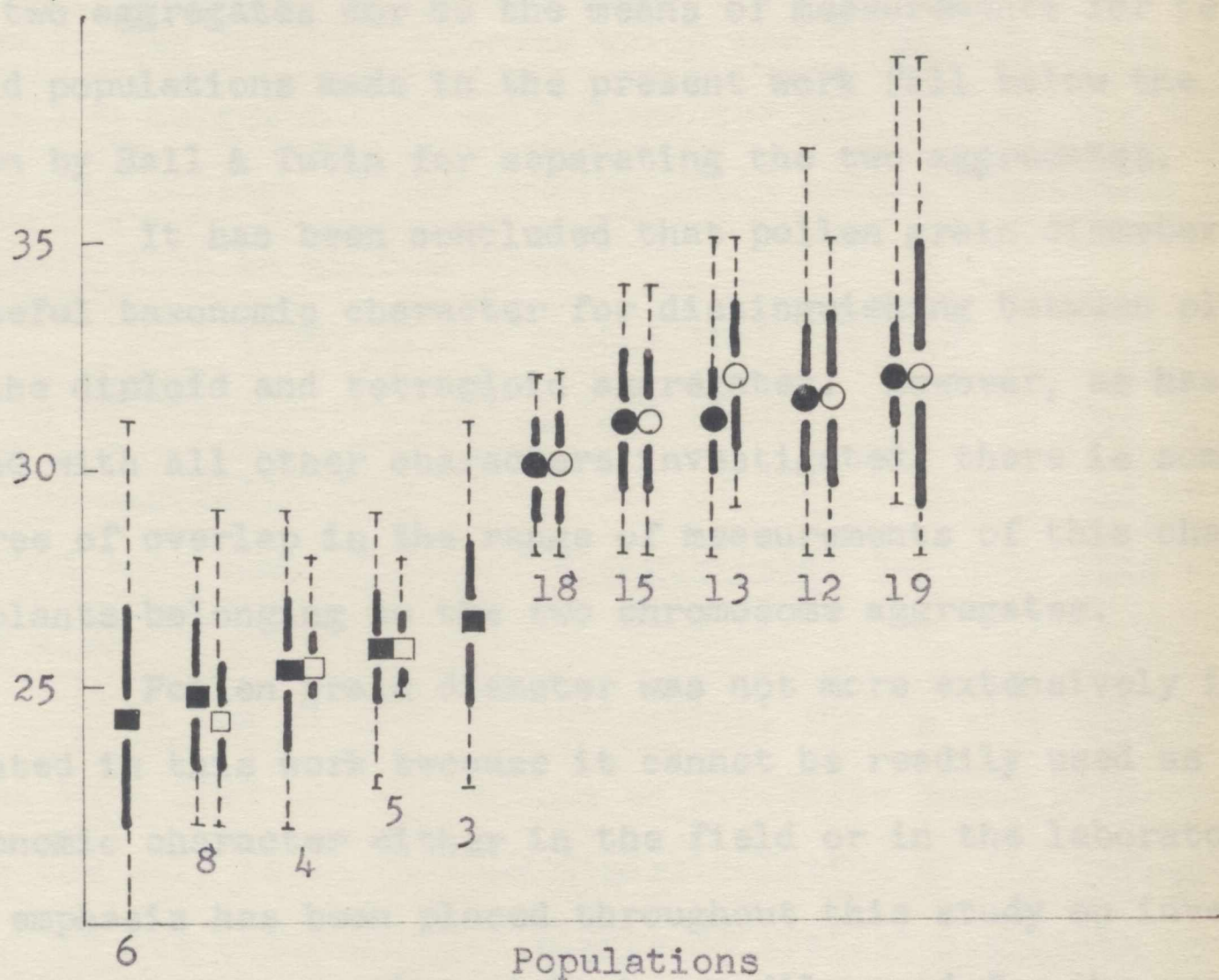
The results obtained from measurements made on cultivated representatives of the populations sampled suggest that pollen grain diameter is not modified by varying environmental conditions.

Figure XIX shows that the value for pollen grain diameter which distinguishes diploid and tetraploid plants lies between those obtained by the two previous workers (Ball &

FIGURE IXX

Pollen grain diameter (in μ)

Legend as in Figure VIII (page 46)

Pollen
diameter
(in μ)

Tutin have found a value of c. 29.5 μ , Dalby c. 27.2 μ and in the present study 28 - 29 μ). The explanation for the difference in these results may lie in differences in the sampling technique or in the mounting procedure of the pollen prior to measurement. Also Dalby's measurements were given as the volume of the pollen grains he measured while the results of Ball & Tutin and in the present study were measurements made of the largest diameter of each pollen grain. It is noteworthy that the means of none of the diploid populations measured in this study are greater than the figure given by Dalby for separating the two aggregates nor do the means of measurements for tetraploid populations made in the present work fall below the figure given by Ball & Tutin for separating the two aggregates.

It has been concluded that pollen grain diameter is a useful taxonomic character for distinguishing between plants of the diploid and tetraploid aggregates. However, as has been found with all other characters investigated, there is some degree of overlap in the range of measurements of this character in plants belonging to the two chromosome aggregates.

Pollen grain diameter was not more extensively investigated in this work because it cannot be readily used as a taxonomic character either in the field or in the laboratory and emphasis has been placed throughout this study on investigating characters that might be readily used for the recognition of taxa.

It has been concluded that the disarticulation of the infructescence is a useful taxonomic character for distinguish-

Disarticulation of the infructescence.

Moss (1911) in his original description of S. disarticulata (S. pusilla) stated that the disarticulation of the fertile spikes in fruit was a character diagnostic of the species. This character has been considered to be important for distinguishing S. pusilla from other annual Salicornia by most workers since.

Dalby (1963) has stated that S. pusilla is the only species of annual Salicornia in Britain where the infructescence disarticulates in fruit. He has shown that the seeds are dispersed in the cortical tissues which may float for up to three months and suggests that this character may account for the characteristic ecology of the species which occurs frequently along the drift line in salt-marshes.

Ball (1964 b) has stated that although the disarticulation of the fertile spikes is a useful character for distinguishing S. pusilla from other taxa of annual Salicornia he has observed that some plants of S. ramosissima may show this character also.

In the present investigation, plants with only one floret in a cyme and assignable to S. pusilla Woods were observed to be the only taxon to show disarticulation of the infructescens. It was observed that plants of typical S. pusilla never showed this character in cultivation though the plants set viable seed.

It has been concluded that the disarticulation of the infructescence is a useful taxonomic character for distinguish-

ing S.pusilla Woods from other annual Salicornia.

Seed length

The first worker to have measured the seeds of Salicornia appears to be Moss (1914). However, he gives a measurement for the length of the seeds for only one taxa S.dolichostachya of 1.7 mm. Tutin (1954) has used seed length as a character to distinguish three taxa and he has found measurements of 1.5 - 1.7 mm for S.dolichostachya, 1.5 mm for S.stricta and 1.4 mm for S.prostrata.

Nannfeldt (1956) has shown that there is a correlation between seed length and chromosome number in the Salicornia of the Baltic. He has given measurements of 1.4 - 1.8 mm for tetraploids and 1.0 - 1.5 mm for diploids.

Ball & Tutin (1959) have also found a correlation between seed length and chromosome number and they have given figures of 1.0 - 1.7 mm for the seed length of diploid populations and (1.3 -) 1.5 - 2.3 mm for tetraploid populations.

Konig (1960) working on German Salicornia has reported that the seeds of tetraploid plants are longer than those of diploid plants.

Dalby (1962) has found a correlation between chromosome number and seed length but he points out that there is a difference between the sizes of the seeds from the central and the lateral florets and his measurements have been made on seeds from the central florets only. He has reported considerable variation in the seed size of eighteen plants of known chromosome

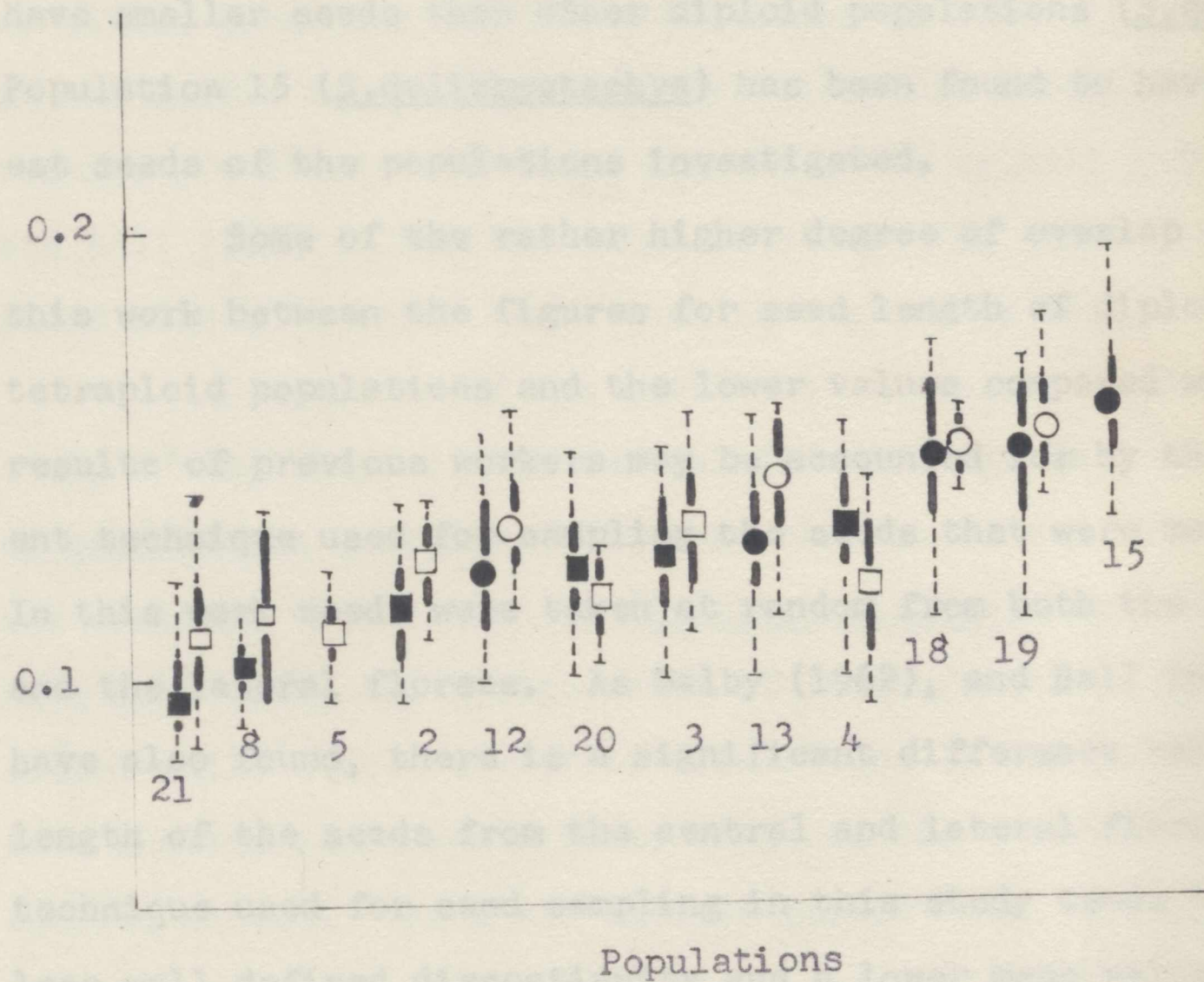
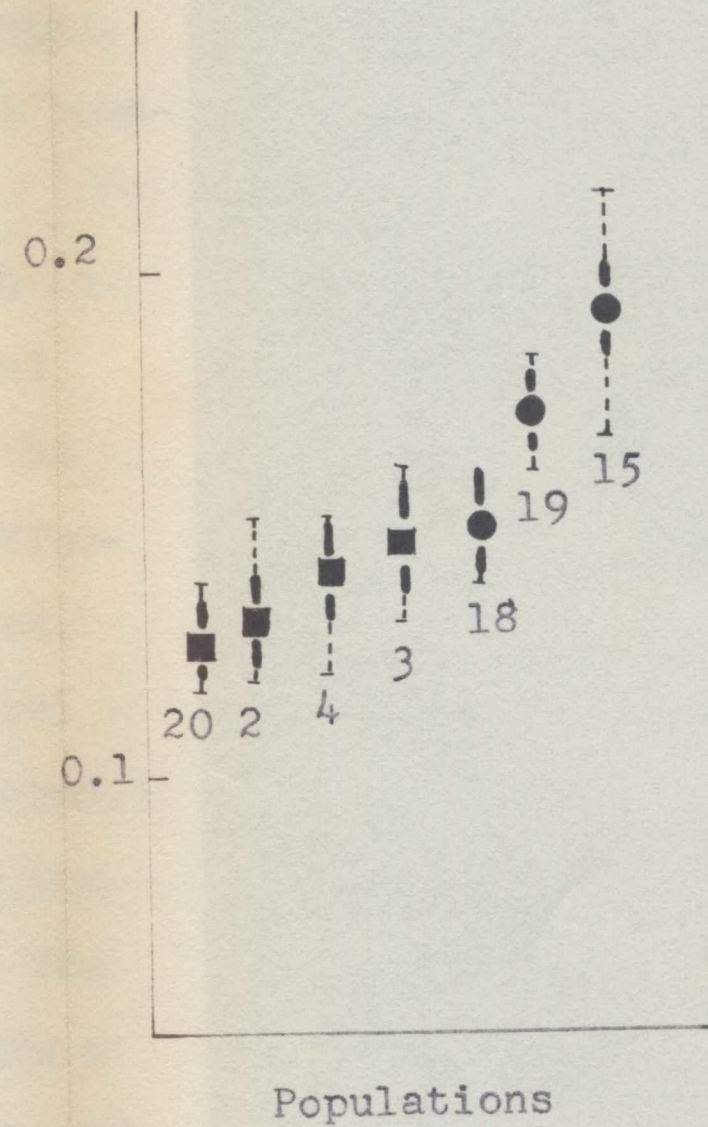
FIGURE XX

Seed length (in mm)

Legend as in Figure VIII (page 46)

(a) Seeds measured from all florets

(b) Seeds measured from the central florets only.

Seed length
(in mm)Seed length
(in mm)

number, the range that he has found is 1.0 - 2.0 mm in diploid plants and 1.2 - 2.3 mm in tetraploid plants.

The results in Figure XX show that there is a tendency for tetraploid populations to have longer seeds than diploid populations but there is a large amount of overlap between the measurements of populations of the two aggregates. It is noteworthy that populations 7, 8 and 21 (S.hibernica) show a tendency to have smaller seeds than other diploid populations (S.europaea). Population 15 (S.dolichostachya) has been found to have the longest seeds of the populations investigated. (Ball & Tutin (1959) and Ball (Some of the rather higher degree of overlap found in this work between the figures for seed length of diploid and tetraploid populations and the lower values compared with the results of previous workers may be accounted for by the different technique used for sampling the seeds that were measured. In this work seeds were taken at random from both the central and the lateral florets. As Dalby (1962), and Ball (pers.comm.) have also found, there is a significant difference between the length of the seeds from the central and lateral florets. The technique used for seed sampling in this study tends to give a less well defined discontinuity and a lower mean value for seed length for the two chromosome aggregates than that found by other workers. However, it has been considered that the results in this work do serve to show the variation and the degree of overlap, in this character, that exists between diploid and tetraploid populations and the results appear to be as useful as those

It has been concluded that seed length is really

of other workers though they are not comparable.

Cultivation has shown that seed length does not appear to be greatly altered by differing environmental conditions.

Figure XXb shows some preliminary measurements made on the seeds collected from the central florets only, for comparison with the results obtained by other workers. The range of values found for diploid populations is 1.20 - 1.50(- 1.55) mm and 1.38 - 2.00(- 2.13) mm for tetraploid populations. These results are similar to those figures given by Ball & Tutin (1959) and Ball (1964 a) but the range of values for diploid and tetraploid plants is still lower than that given by Dalby.

Comparison of the results of measurements made in this study of the shape of the central floret (page 82) with those of seed length suggests that these characters may be related to one another. Population 15 (S.dolichostachya) has been found to have long seeds and a high ratio of length/width of the central floret while other tetraploid populations 12 and 13 (S.fragilis) have shorter seeds and a lower ratio of the dimensions of the central floret. Among the diploid populations, 4 (S.europaea) has been found to have longer seeds and a high value for the ratio of the length/width of the central floret. These two characters are also perhaps related to the length of the fertile segments (page 63) as population 15 has been found to have very long fertile segments while populations 12 and 13 have comparatively short fertile segments.

It has been concluded that seed length is really

of very limited value for use as a taxonomic character for the separation of the diploid and tetraploid aggregates because of the very large degree of overlap that has been found to occur in the measurements made both in this study and by previous workers.

Salicornia.

Seed morphology

Seed morphology has been used by some early workers. However, Ball (1964 b) has stated that Miss Campbell's investigations were confined to the occurrence of 'stereoids' in the including Moss (1914) as a useful taxonomic character.

In this work seeds were examined from plants of different populations which were thought to represent distinct taxa. The characters examined were the density and structure of the hairs and the colour of the testa. No differences were observed in these characters between the seeds from any of the populations examined.

It was concluded that seed morphology was of no taxonomic value.

Anatomical characters.

The distribution of stereoids and spiral cells in the cortex

de Fraine (1912 in an extensive investigation of the anatomy of the genus has reported that 'stereoids' and spiral cells are present in the cortex of the fertile segments of some of the species she has investigated and are absent from others. The anatomical investigations made in this work were not very extensive but 'stereoids' were not found to be present. She has failed to find either type of cell in S.dolichostachya in any of the taxa that occur in Ireland. Spirally thickened cells were not found in the cortex of plants of populations S.disarticulata Moss (S.pusilla Woods) and S.gracillima Moss.

In the other annual species investigated de Fraine has found that only spiral cells occur.

Moss (1914) on the basis of de Fraines investigations has considered the occurrence and distribution of spiral cells and 'stereids' to be of taxonomic importance in the genus Salicornia.

Ball & Tutin (1959) report that Miss M.S. Campbell (unpublished) has thrown doubt on the value of this character. However, Ball (1964 b) has stated that Miss Campbell's investigations were confined to the occurrence of 'stereids' in the cortex and she did not investigate the presence of spiral cells. Ball has stated that in fact the presence or absence of spiral cells in the cortex of the fertile segments may be of taxonomic value for distinguishing between diploid and tetraploid plants. He has found that spiral cells always occur in plants of the diploid aggregate and also in small numbers in S.nitens Ball & Tutin and S.lutescens Ball & Tutin and sometimes in S.fragilis Ball & Tutin. In the latter species Ball has found that the occurrence of these cells is associated with the habitat of the population; spiral cells being absent when plants occur on soft mud and he has treated S.fragilis as being only an ecotype of S.lutescens. Ball has found that S.dolichostachya always occurs on soft mud and never has spirally thickened cells in the cortex.

The anatomical investigations made in this work were not very extensive but 'stereids' were not found to be present in any of the taxa that occur in Ireland. Spirally thickened cells were not found in the cortex of plants of populations

9, 15, 15a and 15b (S.dolichostachya). Spiral cells were found in very small numbers in populations 12, 13, 18 and 22 (S.fragilis). While populations 2, 3, 4, and 8 (S.europaea) and (S.hibernica) and S.pusilla Woods were found to have abundant spiral cells.

These results suggest that de Fraine was mistaken in reporting the presence of 'stereids' in S.pusilla and S.perennis but agree with the results of this worker in recording the absence of spiral cells in S.dolichostachya. The results also closely agree with those of Ball (1964 b).

It has been concluded that the presence or absence of spirally thickened cells in the cortex of the fertile segments may be a taxonomic character of some value for distinguishing the diploid and tetraploid aggregates but as has been observed with other characters throughout this investigation, many plants belonging to the two chromosome aggregates overlap in this character. This work has also shown that the absence of spirally thickened cells in the cortex is another character which distinguishes S.dolichostachya from the rest of the annual section of the genus.

(3) Characters considered to be of taxonomic importance either for distinguishing the two chromosome aggregates or taxa within these aggregates.

Number of segments in the terminal spike.

Mean length of the fertile segments.

Morphology of the fertile segments.

Number of florets in the cymes of the fertile seg-

A summary of results and conclusions

(1) Characters considered to be of little taxonomic value.

Habit.

Degree and angle of branching.

The ratio of the number of fertile segments in the

terminal spike to the number of sterile segments in the entire plant.

Minimum width of the fertile segments.

Width of the scarious margin.

Stigma morphology.

Seed morphology.

(2) Characters considered to be of only limited taxonomic value.

Colour.

Length of the terminal spike.

Stamen number.

Seed length.

Anatomy.

(3) Characters considered to be of taxonomic importance either for distinguishing the two chromosome aggregates or taxa within these aggregates.

Number of segments in the terminal spike.

Mean length of the fertile segments.

Morphology of the fertile segments.

Number of florets in the cymes of the fertile seg-

Degree of exposure of the florets.

The ratio of the length/width of the central floret.

Anther length.

Pollen diameter.

Disarticulation of the fertile spikes.

Among those characters that have been treated biometrically in this study it has been observed that there is a tendency for some populations (those assigned to S.hibernica and S.dolichostachya) to consistently show measurements that fall at the extremities of the variation while other populations (those assigned to S.europaea and S.fragilis) overlap and link these extremes and the variation in many of the characters is almost continuous with only ill defined discontinuities in the means. Those characters which have been used to separate S.pusilla Woods are an exception and do not show continuous variation.

Discrimination of taxa by analysis of pairs of characters

Figure 13 shows anther length of 22 wild and 4 cultivated populations plotted against the mean values for the ratio of the greater/lesser diameter of the fertile segments. The populations fall into two groups separated by a threshold value but the groups overlap in the means of measurements of the ratio of the greater/lesser diameter of the fertile segments. The diagram shows that in the digital characters populations 9, 7 and 8 (S.hibernica) have longer anthers and more isolated fertile segments than other populations (S.dolichostachya).

Discrimination of taxa by analysis of pairs of characters.

The results presented earlier in this work have shown that two chromosome numbers exist in the annual Salicornia in Ireland and that a number of morphological characters are correlated to varying degrees with these chromosome numbers. Throughout this investigation of the value of taxonomic characters, attention has been drawn to tendencies for particular populations to group together due to these populations being similar in many of the characters studied.

The purpose of this chapter is to try and show to what extent it is possible to distinguish the two chromosome aggregates and taxa within these aggregates by analysis of pairs of characters.

Discrimination of the CHAPTER IV aggregates.

Figure XXI a-d shows diagrams of the means of measurements of anther length made from population samples plotted against the means of measurements of four other characters.

Discrimination of taxa by analysis of pairs of characters

Figure XXI a shows anther length of 22 wild and 8 cultivated population samples plotted against the mean values for the ratio of the greater/lesser diameter of the fertile segments. The populations fall into two groups correlated with chromosome number but the groups overlap in the means of measurements of the ratio of the greater/lesser diameter of the fertile segments. The diagram shows that in the diploid aggregate populations 5, 7 and 8 (S.hibernica) have longer anthers and more inflated fertile segments than other populations (S.europaea).

Discrimination of taxa by analysis of pairs of characters.

The results presented earlier in this work have shown that two chromosome numbers exist in the annual Salicornia in Ireland and that a number of morphological characters are correlated to varying degrees with these chromosome numbers. Throughout this investigation of the value of taxonomic characters, attention has been drawn to tendencies for particular populations to group together due to these populations being similar in many of the characters studied.

The purpose of this chapter is to try and show to what extent it is possible to distinguish the two chromosome aggregates and taxa within these aggregates by analysis of pairs of characters.

Discrimination of the chromosome aggregates.

Figure XXI a-d shows diagrams of the means of measurements of anther length made from population samples plotted against the means of measurements of four other characters.

Figure XXI a shows anther length of 22 wild and 8 cultivated population samples plotted against the mean values for the ratio of the greater/lesser diameter of the fertile segments. The populations fall into two groups correlated with chromosome number but the groups overlap in the means of measurements of the ratio of the greater/lesser diameter of the fertile segments. The diagram shows that in the diploid aggregate populations 5, 7 and 8 (S.hibernica) have longer anthers and more inflated fertile segments than other populations (S.europaea).

FIGURE XXI

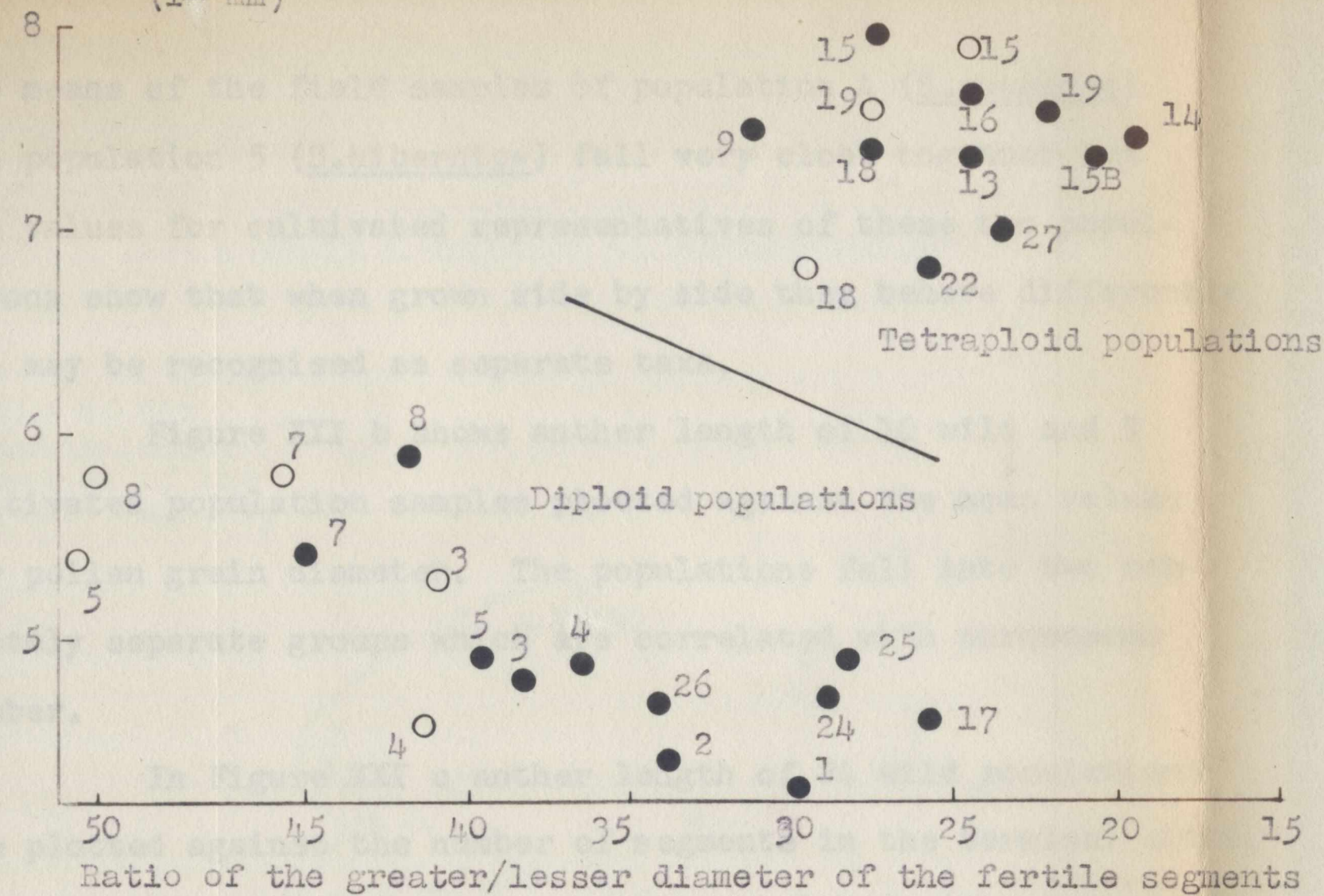
The mean values for:

- (a) anther length (in mm) plotted against the ratio of the greater/lesser diameter of the fertile segments of 22 wild and 8 cultivated population samples.
- (b) The mean values for anther length (in mm) plotted against pollen diameter (in μ) for 10 wild and 7 cultivated population samples.
- (c) The mean values for anther length (in mm) plotted against the number of segments in the terminal spike for 24 wild population samples.
- (d) The mean values for anther length (in mm) plotted against seed length for 9 wild and 4 cultivated population samples.

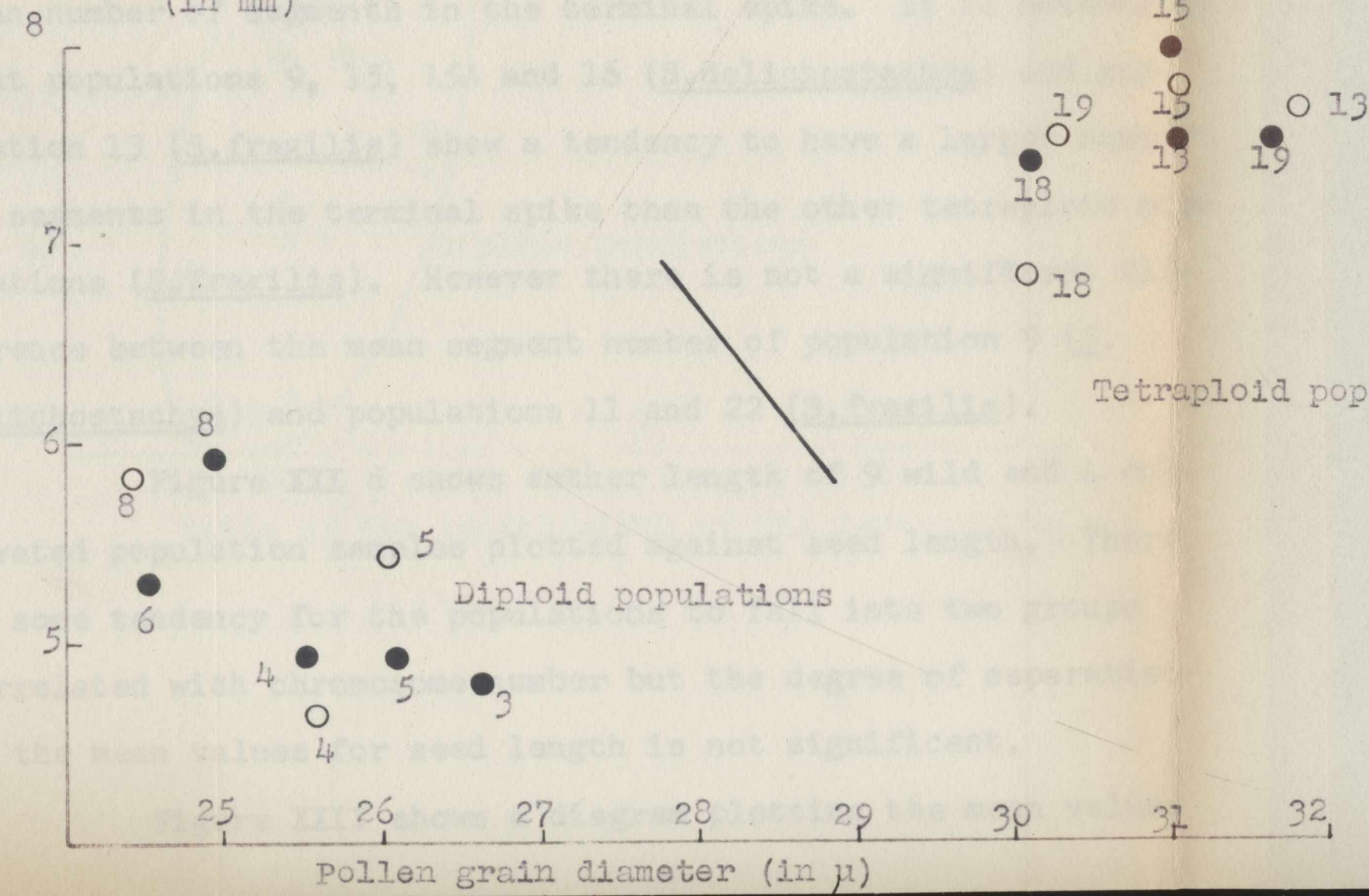
- - Means of measurements of wild population samples.
- - Means of measurements of cultivated population samples.

Anther length
(in mm)

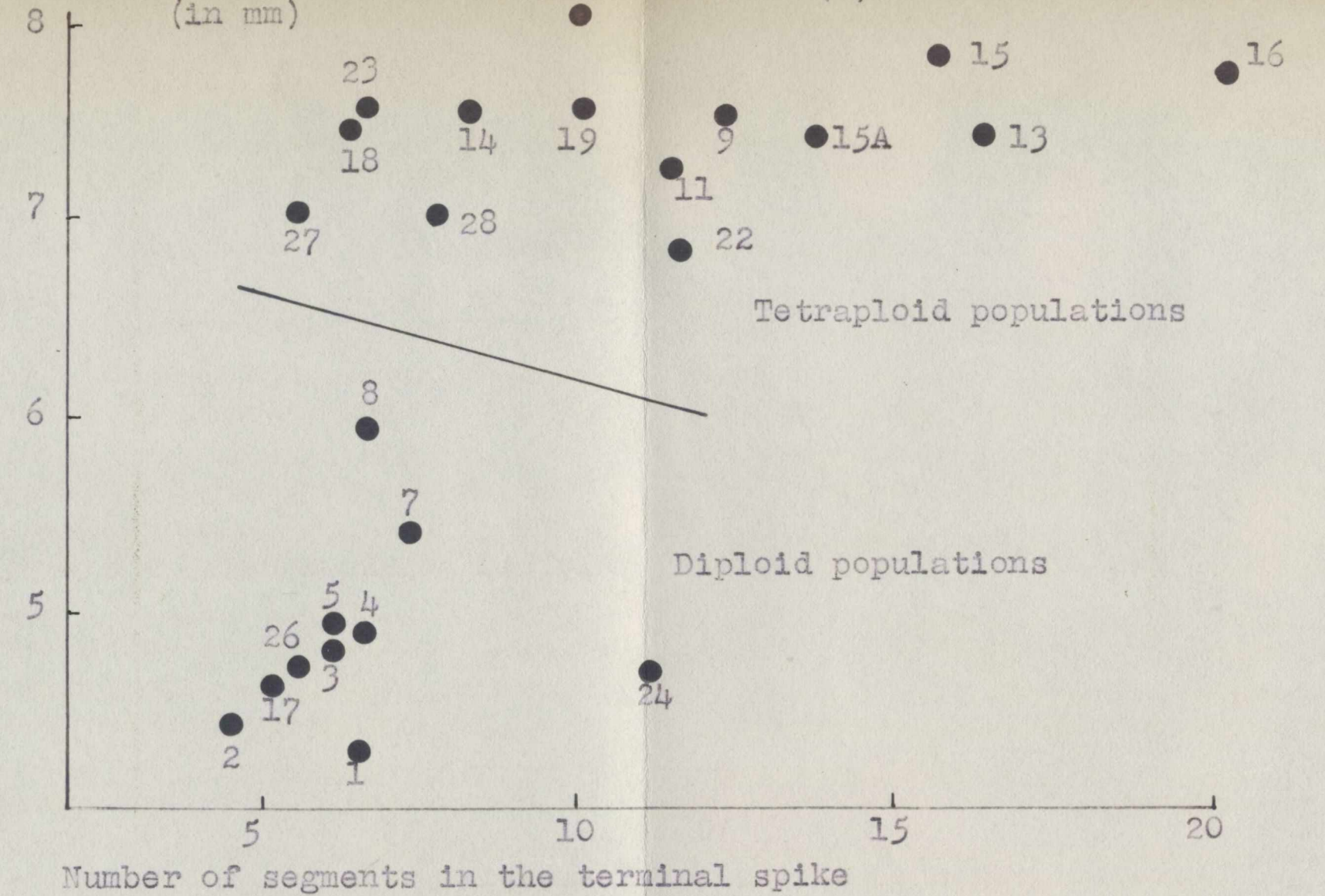
(a)



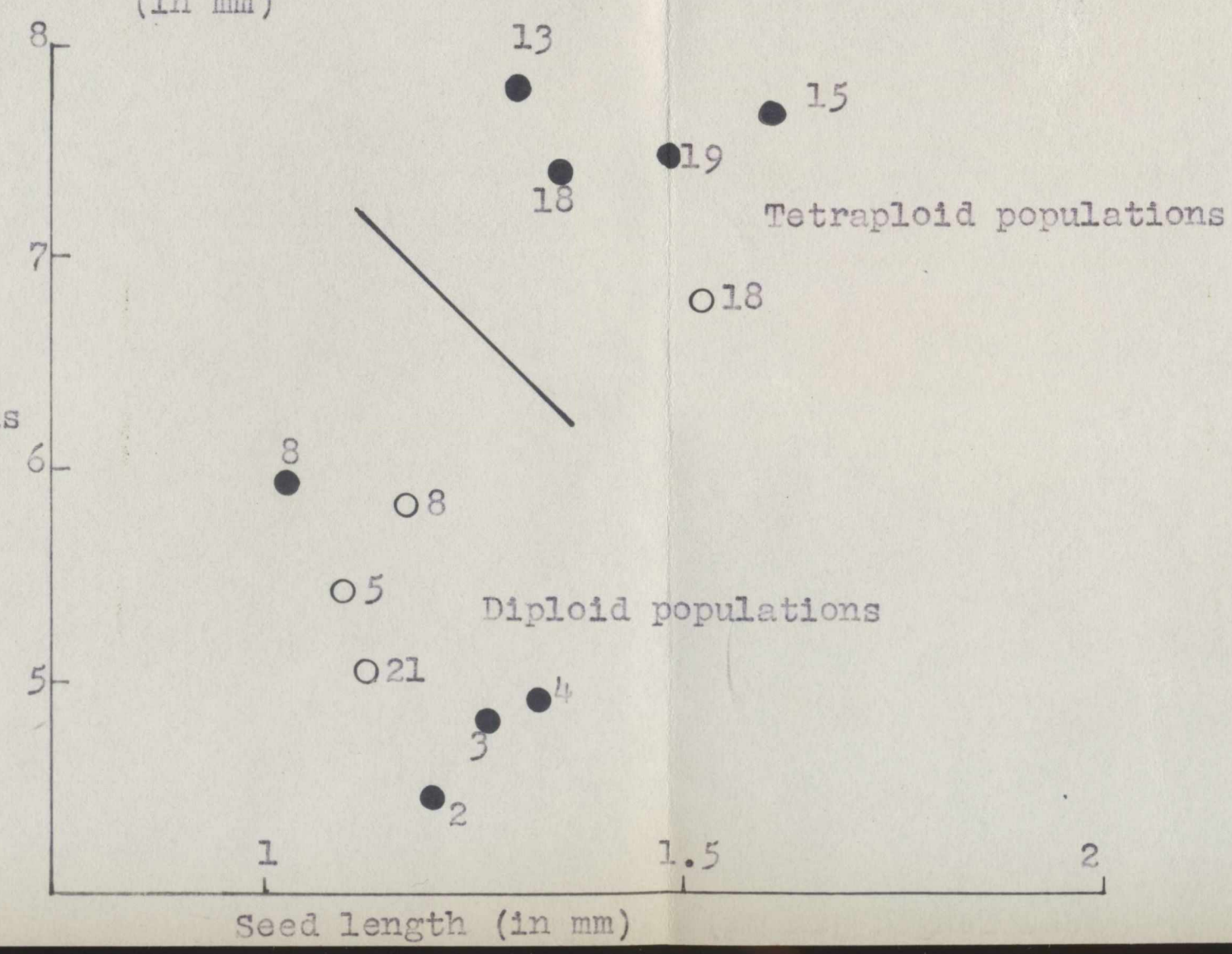
(b)

Anther length
(in mm)Anther length
(in mm)

(c)



(d)

Anther length
(in mm)

The means of the field samples of population 4 (S.europaea) and population 5 (S.hibernica) fall very close together but the values for cultivated representatives of these two populations show that when grown side by side they behave differently and may be recognised as separate taxa.

Figure XXI b shows anther length of 10 wild and 7 cultivated population samples plotted against the mean values for pollen grain diameter. The populations fall into two completely separate groups which are correlated with chromosome number.

In Figure XXI c anther length of 24 wild populations are plotted against the number of segments in the terminal spike. The populations fall into two groups correlated with chromosome number but many populations show considerable overlap in the mean number of segments in the terminal spike. It is noteworthy that populations 9, 15, 15A and 16 (S.dolichostachya) and population 13 (S.fragilis) show a tendency to have a larger number of segments in the terminal spike than the other tetraploid populations (S.fragilis). However there is not a significant difference between the mean segment number of population 9 (S.dolichostachya) and populations 11 and 22 (S.fragilis).

Figure XXI d shows anther length of 9 wild and 4 cultivated population samples plotted against seed length. There is some tendency for the populations to fall into two groups correlated with chromosome number but the degree of separation in the mean values for seed length is not significant.

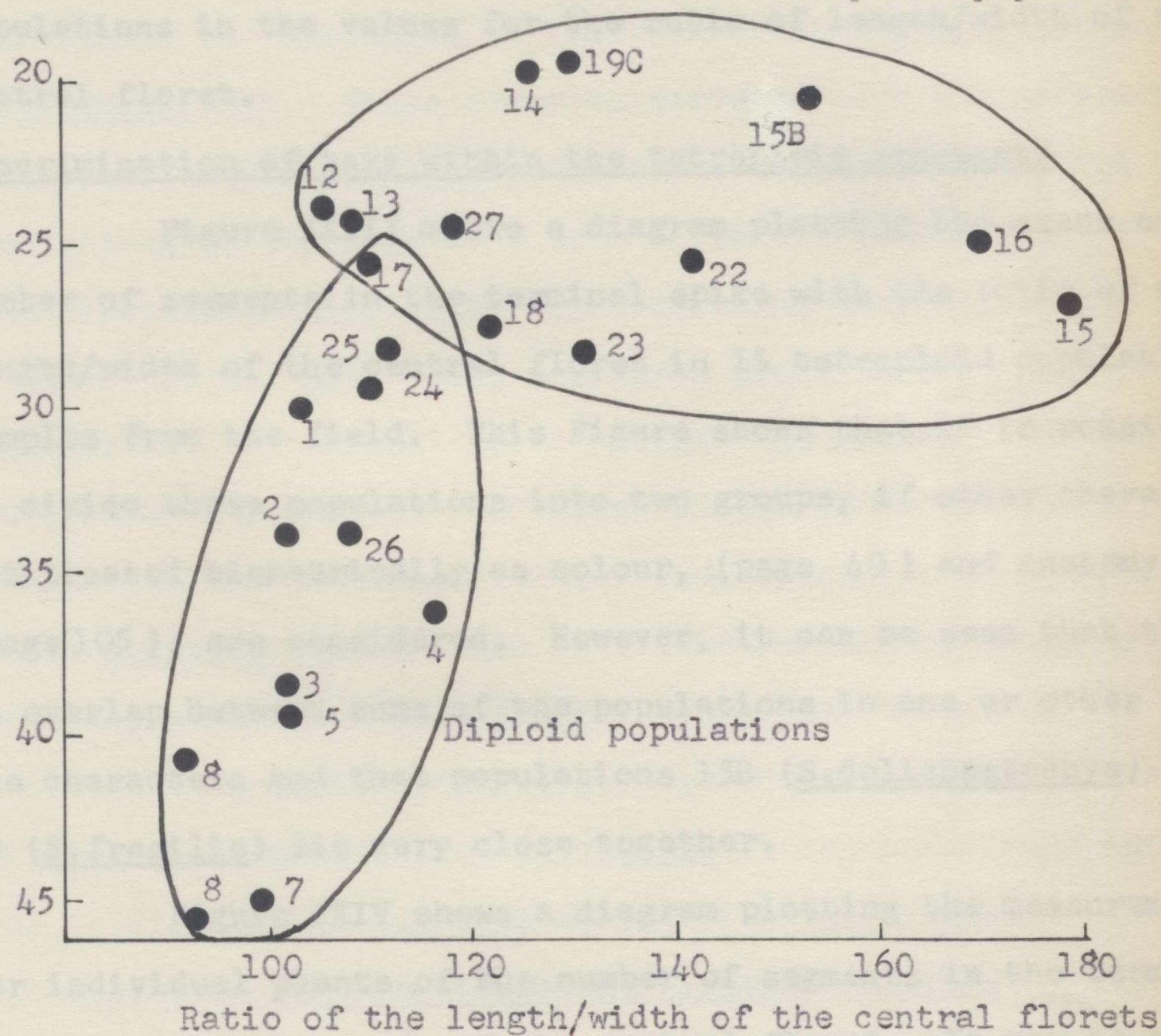
Figure XXII shows a diagram plotting the mean values

FIGURE XXII

The means of values for the ratio of the greater/lesser diameter of the fertile segments plotted against the ratio of the length/width of the central floret for 23 populations sampled in the field

Ratio of the
greater/lesser
diameter of the
fertile segments

Tetraploid populations



for population samples of the ratio of the greater/lesser diameter of the fertile segments against the ratio of the length/width of the central floret for 23 wild population samples. Again there is a tendency for the populations to fall into two groups correlated with chromosome number but these groups overlap. In the tetraploid aggregate populations 15, 15B and 16 (S.dolichostachya) show a tendency to separate from the other populations in the values for the ratio of length/width of the central floret.

Discrimination of taxa within the tetraploid aggregate

Figure XXIII shows a diagram plotting the means of the number of segments in the terminal spike with the ratio of the length/width of the central floret in 15 tetraploid populations samples from the field. This Figure shows that it is possible to divide these populations into two groups, if other characters not treated biometrically as colour, (page 49) and anatomy (page 105), are considered. However, it can be seen that there is overlap between some of the populations in one or other of the characters and that populations 15B (S.dolichostachya) and 22 (S.fragilis) lie very close together.

Figure XXIV shows a diagram plotting the measurements for individual plants of the number of segments in the terminal spike against the shape of the central floret. It may be seen from this diagram that it is possible to separate populations 15 and 16 (S.dolichostachya) from populations 13, 14 and 19C (S.fragilis) but population 15B (S.dolichostachya) and population 22 (S.fragilis) overlap and these characters can not be

used to separate all populations assigned to the two taxa. Figure XXV shows that it is possible to demonstrate biometrically a better degree of separation between population 22 and 15B by plotting the mean segment length of the fertile segments against the shape of the central floret. Population 18 (S. fragilis) has been plotted to show that population 22 still tends to overlap population 15B but that a larger number of individuals in population 22 fall nearer to S. fragilis than to S. dolichostachya. These examples serve to show the nature of the variation that exists in different characters measured in populations of the same taxa from different localities. It also demonstrates the difficulty in recognising taxa within the genus.

Figure XXVI shows a diagram plotting the number of segments in the terminal spike against the minimum width of the fertile segments of individual plants of 6 tetraploid population samples from the field. Populations 18, 23 and 27 resemble S. nitens Ball & Tutin in colour and in the shape of the fertile segments but this diagram shows that by use of the two important diagnostic characters proposed by Ball for distinguishing this species from S. fragilis it has been found impossible to distinguish S. nitens among Irish Salicornia.

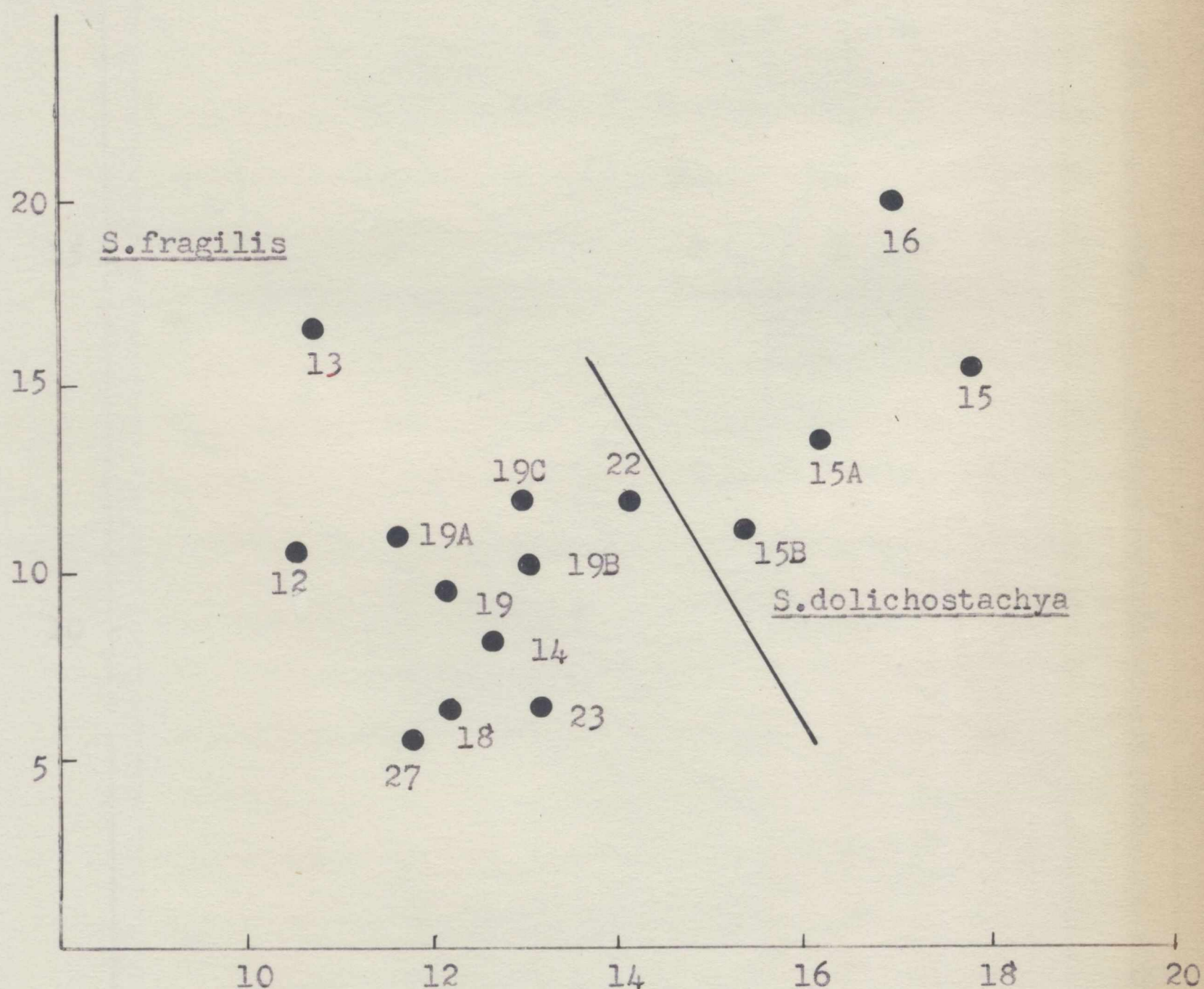
Discrimination of taxa within the diploid aggregate

In the discussion relating to Figure XXIa attention was drawn to the fact that populations 5, 7 and 8 (S. hibernica) were distinct in having longer anthers and more inflated fertile segments than other diploid populations. Figure XXVII shows a diagram plotting the anther length against the

FIGURE XXIII

The mean values for the number of segments in the terminal spike plotted against the ratio of the length/width of the central floret for 15 tetraploid populations sampled in the field.

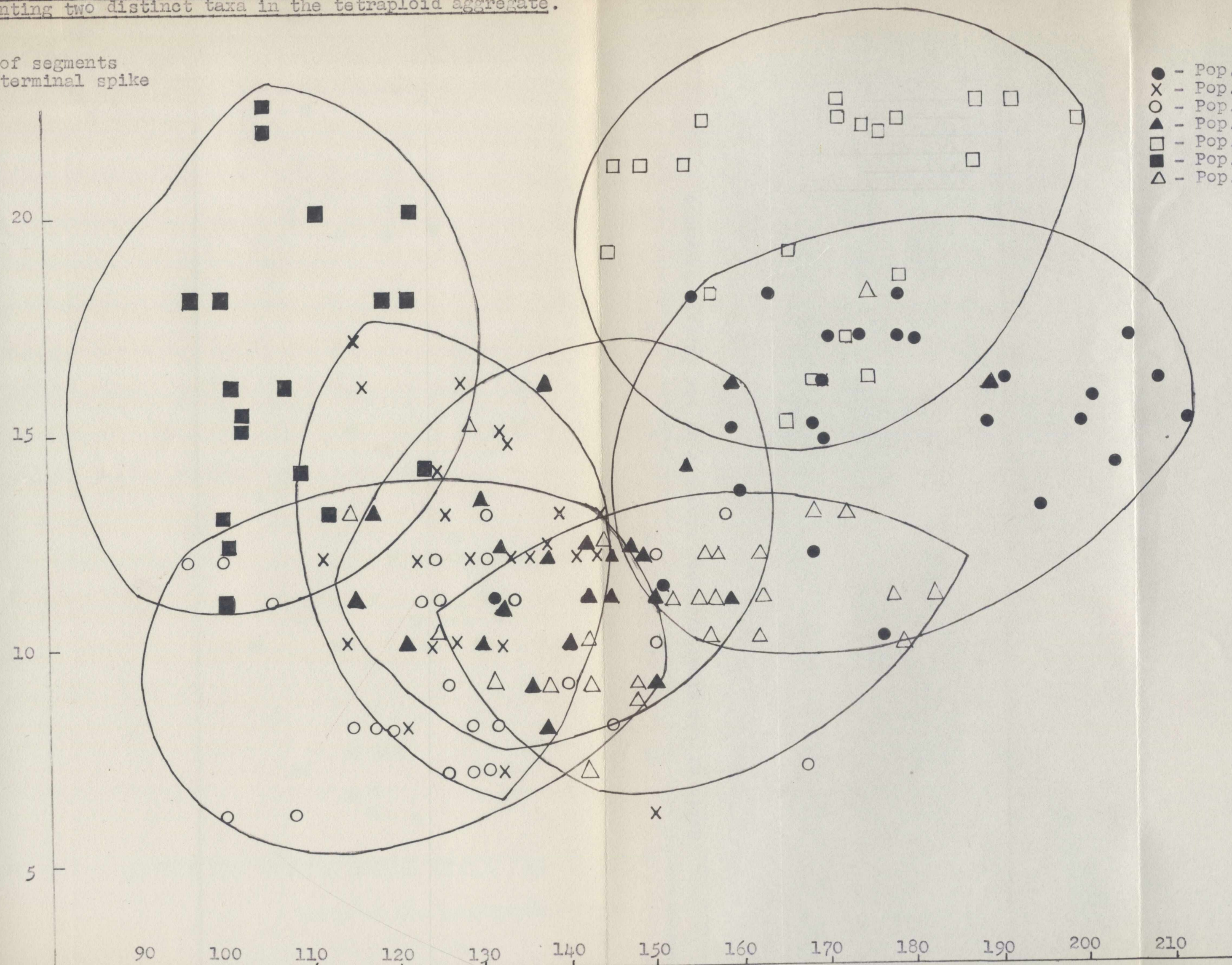
Number of
segments in
the terminal
spike



Ratio of the length/width of the central floret

Number of segments in the terminal spike plotted against the ratio of the length/width of the central florets of six population samples representing two distinct taxa in the tetraploid aggregate.

Number of segments
in the terminal spike



- - Pop. 15 *S. dolichostachya*
- × - Pop. 19C *S. fragilis*
- - Pop. 14 *S. fragilis*
- ▲ - Pop. 22 *S. fragilis*
- - Pop. 16 *S. dolichostachya*
- - Pop. 13 *S. fragilis*
- △ - Pop. 15B *S. dolichostachya*

Ratio of the length/width of the central florets of the third segment in the terminal spike

Mean length of the
fertile segments.

The length of the fertile segments plotted against the ratio
of the length/width of the central floret of three tetraploid
populations representing two taxa.

X - Pop.22 S.fragilis
● - Pop.15B S.dolichostachya
■ - Pop.18 S.fragilis

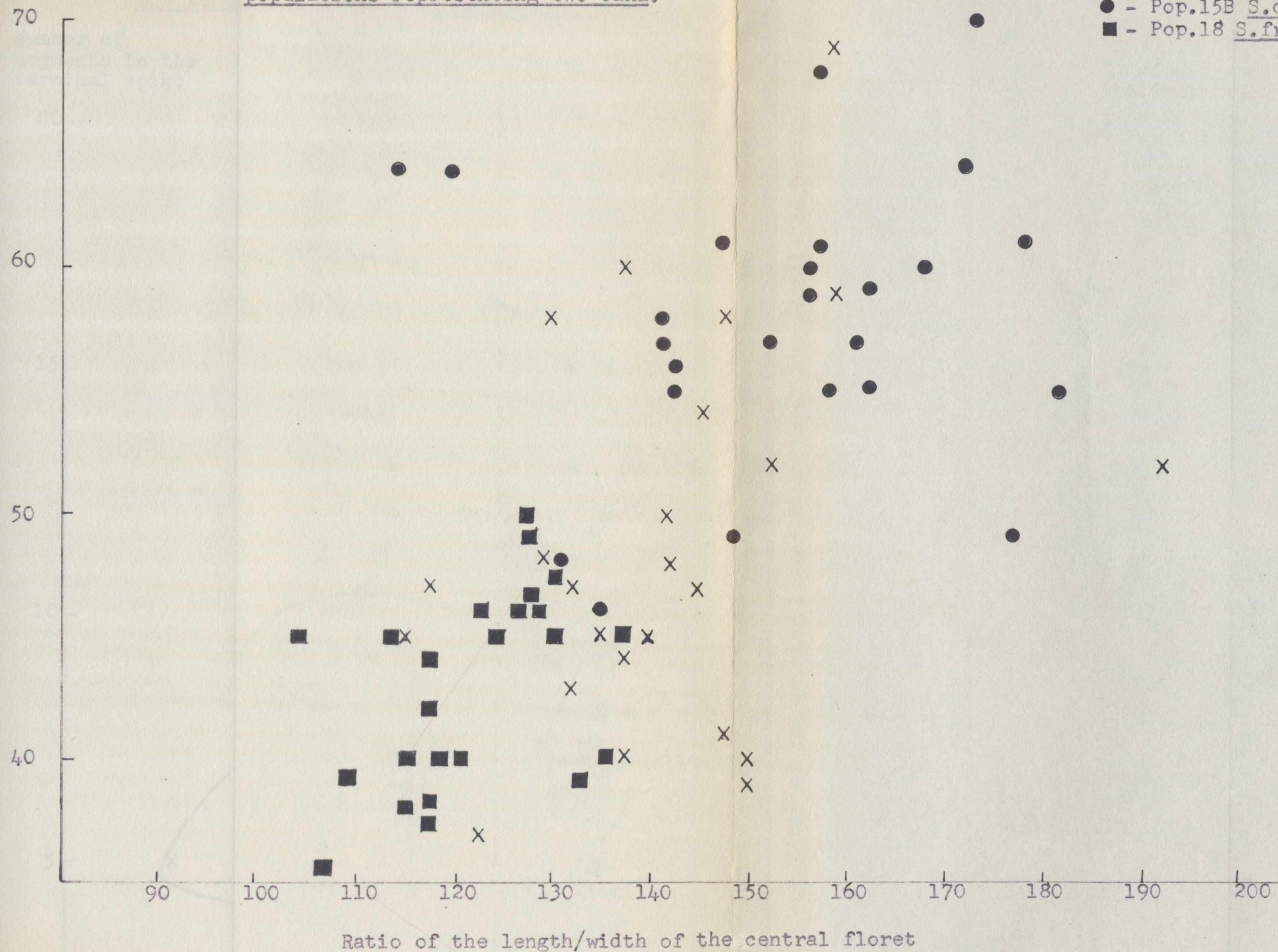


FIGURE XXVI

Number of segments in the terminal spike plotted against the minimum width of the fertile segments of six populations samples in the tetraploid aggregate

Number of
segments in the
terminal spike

- X- Pop.27 Ballyvaughan "S.nitens"
- Pop.19C Comber S.fragilis
- Pop.14 Kilcainin S.fragilis
- ▲- Pop.18 Rush "S.nitens"
- Pop.23 Comber "S.nitens"
- △- Pop.11 Bull Island S.fragilis

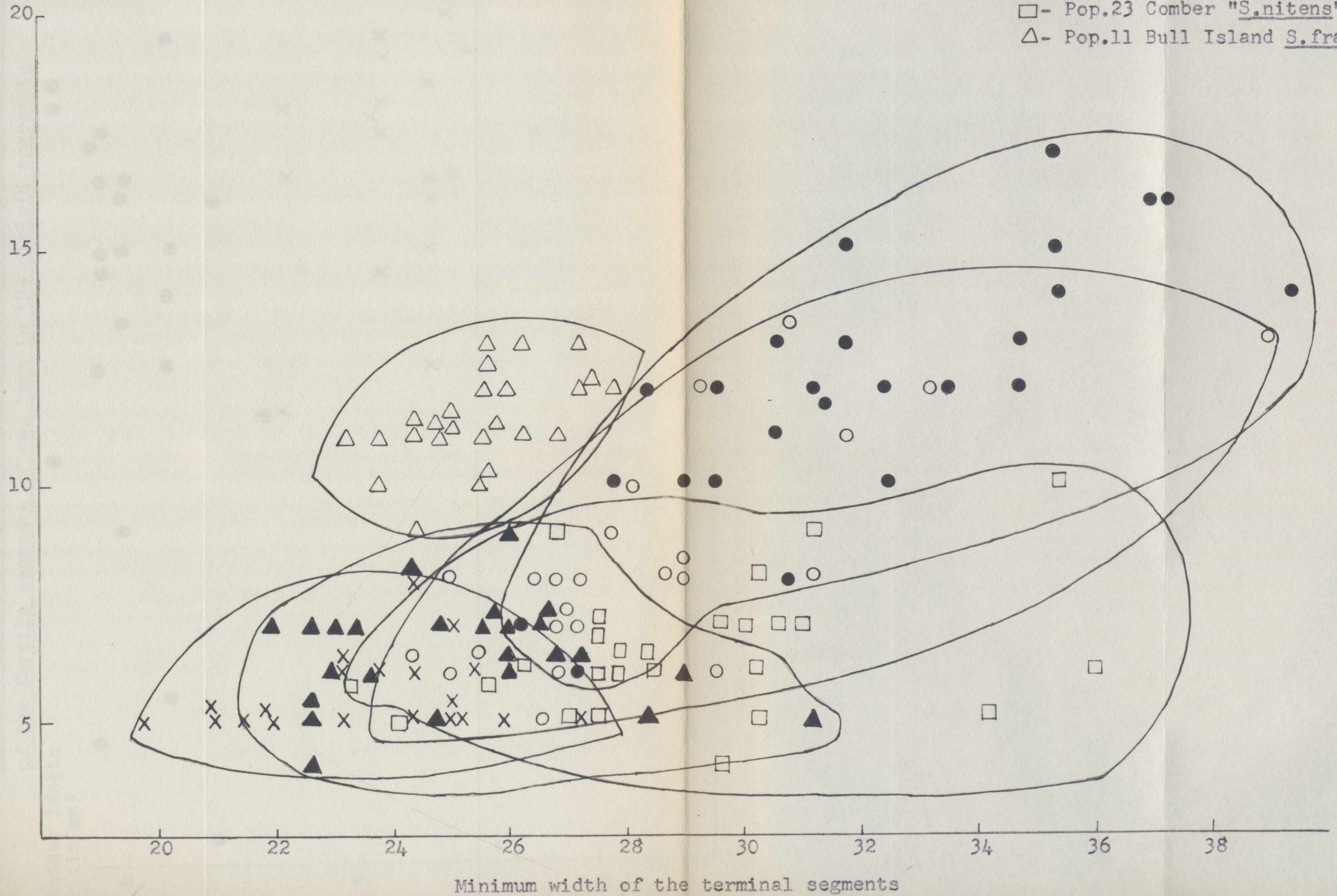
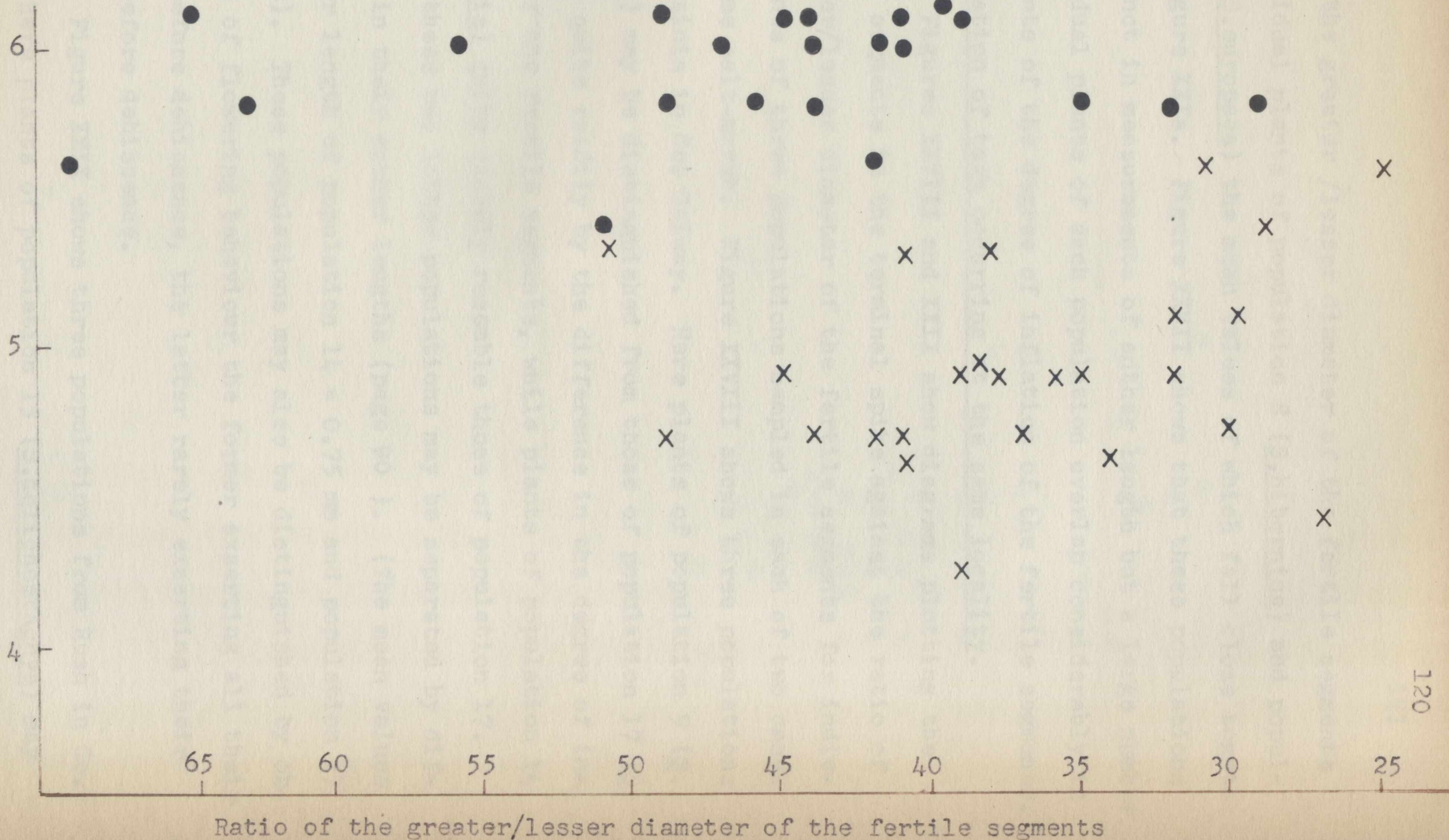


FIGURE XXVII

Anther length (in mm) plotted against the ratio of the greater/lesser diameter of the fertile segments of two taxa in the diploid aggregate

×- Pop.4 S.europaëa
●- Pop.8 S.hibernica

Anther length
(in mm)



ratio of the greater /lesser diameter of the fertile segments for individual plants of population 8 (S.hibernica) and population 4 (S.europaea) the mean values of which fall close together in Figure XXIIa. Figure XXVII shows that these populations are distinct in measurements of anther length but a large number of individual plants of each population overlap considerably in measurements of the degree of inflation of the fertile segments.

Discrimination of taxa occurring at the same locality.

Figures XXVIII and XXIX show diagrams plotting the number of segments in the terminal spike against the ratio of the greater/lesser diameter of the fertile segments for individual plants of three populations sampled in each of two cases in the same salt-marsh. Figure XXVIII shows three populations from Kilcainin in Co. Galway. Here plants of population 9 (S.hibernica) may be distinguished from those of population 17 (S.europaea) quite readily by the difference in the degree of inflation of the fertile segments, while plants of population 14 (S.fragilis) quite closely resemble those of population 17. However, these two latter populations may be separated by differences in their anther lengths (page 90). (The mean values for anther length of population 14 = 0.75 mm and population 17 = 0.46 mm). These populations may also be distinguished by observation of flowering behaviour the former exerting all their anthers before dehiscence, the latter rarely exerting their anthers before dehiscence.

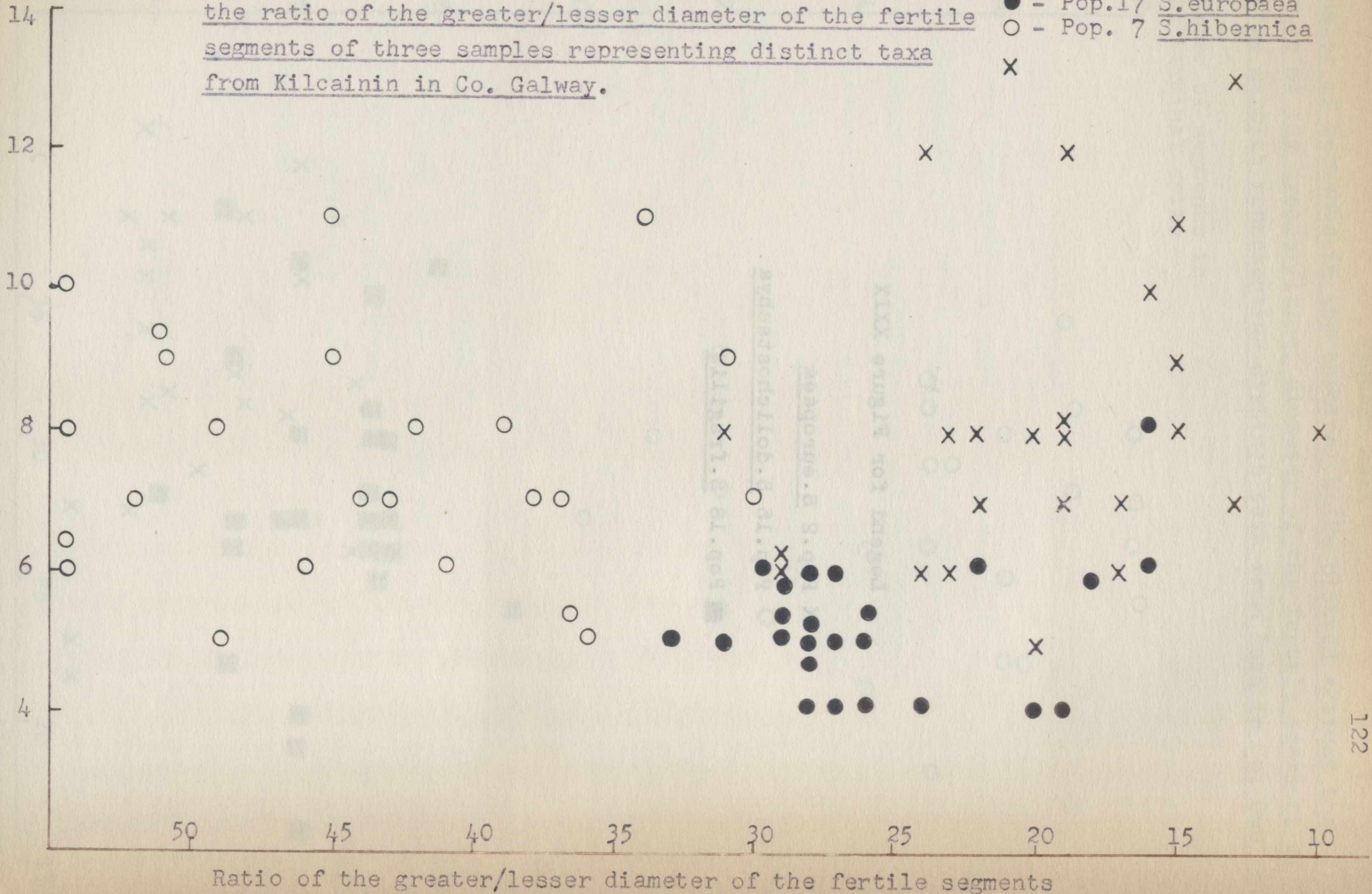
Figure XXIX shows three populations from Rush in Co. Dublin. Here plants of population 15 (S.dolichostachya) may

FIGURE XXVIII

Number of
segments in
the terminal
spike

Number of segments in the terminal spike plotted against
the ratio of the greater/lesser diameter of the fertile
segments of three samples representing distinct taxa
from Kilcainin in Co. Galway.

x - Pop.14 *S.fragilis*
● - Pop.17 *S.europaea*
○ - Pop. 7 *S.hibernica*

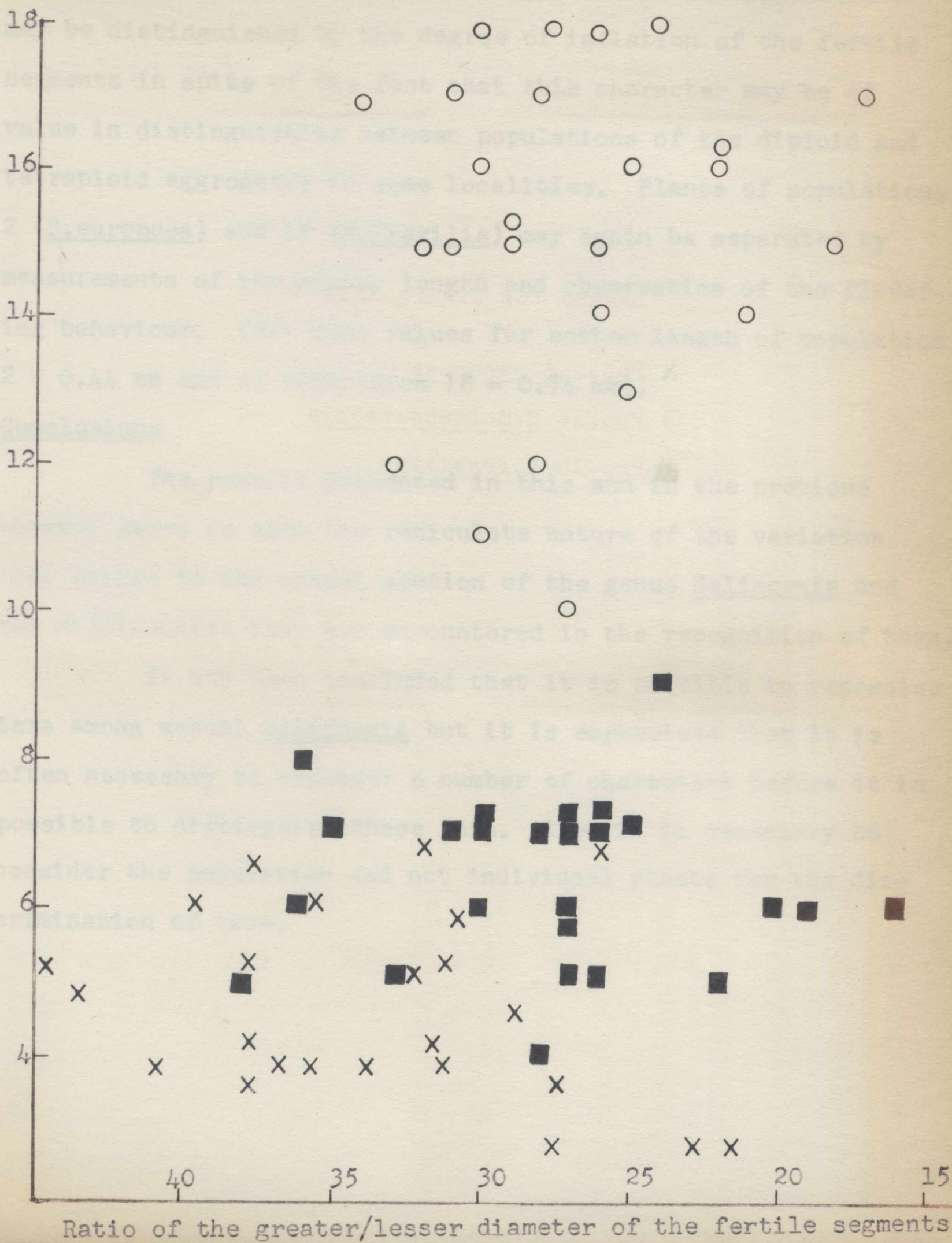


Legend for Figure XXIX

- X Pop.2 S.europaea
- O Pop.15 S.dolichostachya
- Pop.18 S.fragilis

Number of segments in the terminal spike plotted against the ratio of the greater/lesser diameter of the fertile segments of three samples representing distinct taxa from Rush in Co. Dublin.

Number of segments in the terminal spike



be readily distinguished from plants of the other two populations 2 (S.europaea) and 18 (S.fragilis) by the number of segments in the terminal spike though none of the populations may be distinguished by the degree of inflation of the fertile segments in spite of the fact that this character may be of value in distinguishing between populations of the diploid and tetraploid aggregates in some localities. Plants of populations 2 (S.europaea) and 18 (S.fragilis) may again be separated by measurements of the anther length and observation of the flowering behaviour. (The mean values for anther length of population 2 = 0.44 mm and of population 18 = 0.74 mm).

Conclusions

The results presented in this and in the previous chapter serve to show the reticulate nature of the variation that occurs in the annual section of the genus Salicornia and the difficulties that are encountered in the recognition of taxa.

It has been concluded that it is possible to recognise taxa among annual Salicornia but it is emphasised that it is often necessary to consider a number of characters before it is possible to distinguish these taxa. Also it is necessary to consider the population and not individual plants for the discrimination of taxa.

Floral development

The sequence of development of the reproductive organs has been used by some previous workers as a character to separate S. perennis from the annual section of the genus. Moss (1954) in an account of the South African Salicornia and the closely allied genus Arthrocnemum describes the flowers of the former as protandrous and those of the latter as protogynous. On the basis of this and other characters Moss transfers S. perennis Mill. to the genus Arthrocnemum. Ball (1964 a) confirms Moss' view that S. perennis is markedly protogynous, but he has found that the annual Salicornia are weakly protogynous. Ball (1964 b) although taking up Moss's new combination Arthrocnemum perenne (Mill.) Moss in Flora Europaea has stated that Delby (1962) and Ferguson (unpublished) have shown that the floral characters used by Moss are unsatisfactory.

CHAPTER V

Flowering behaviour and hybridisation experiments found, from observations in the field, to be protogynous. S. perennis has been in cultivation for a number of years but it has never flowered under these conditions.

Annual Salicornia of populations 15, 15A and 15B (S. dolichoetachya) and 12, 13, 18, 19 and 19A (S. fragilis) have been observed both in the field and in cultivation, to have their stigmas protrude just before the undeveloped anthers are exerted (Plate 7 b, seen in the two lateral florets of the lower segment), or to have the anthers and stigmas emerge simultaneously (Plate 7 c and d). This evidence suggests that

Inflorescences of annual tetraploid Salicornia spp. x 9 approx.

(a) Variation in Floral development (b) In the two lower lateral florets the stigma protrudes before the anthers; in the central florets immediately above, the anthers are dehiscing in contact with their stigmas.

The sequence of development of the reproductive organs has been used by some previous workers as a character to separate S.perennis from the annual section of the genus. Moss (1954) in an account of the South African Salicornia and the closely allied genus Arthrocnemum describes the flowers of the former as protandrous and those of the latter as protogynous. On the basis of this and other characters Moss transfers S.perennis Mill. to the genus Arthrocnemum. Dalby (1962) confirms Moss' view that S.perennis is markedly protogynous but he has found that the annual Salicornia are weakly protogynous. Ball (1964 b) although taking up Moss's new combination Arthrocnemum perenne (Mill.) Moss in Flora Europaea has stated that Dalby (1962) and Ferguson (unpublished) have shown that the floral characters used by Moss are unsatisfactory.

In this investigation S.perennis has been found, from observations in the field, to be protogynous. S.perennis has been in cultivation for a number of years but it has never flowered under these conditions.

Annual Salicornia of populations 15, 15A and 15B (S.dolichostachya) and 12, 13, 18, 19 and 19A (S.fragilis) have been observed both in the field and in cultivation, to have their stigmas protrude just before the undehisced anthers are exerted (Plate 7 b, seen in the two lateral florets of the lower segment), or to have the anthers and stigmas emerge simultaneously (Plate 7 c and d). This evidence suggests that

Inflorescences of annual tetraploid Salicornia spp. x 9 approx.

(a) Variation in stigma morphology, (b) In the two lower lateral florets the stigmas are protruding before the anthers; in the central florets immediately above, the anthers are dehiscing in contact with their stigmas. (c) Simultaneous development of anthers and stigmas in the lower central floret and in the dissected floret. (d) A further inflorescence showing simultaneous development of anthers and stigmas.

(a)



(b)



(c)



(d)



some annual Salicornia are weakly protogynous or homogamous. It has not been found possible to study floral development in diploid populations because these are frequently cleistogamous.

It has been observed that plants in cultivation and in the field may sometimes have unisexual flowers, one or other of the organs failing to develop. The stigmas have also been observed to frequently elongate and persist after fertilisation. This appears to occur after fertilisation has taken place as the stigmatic papillae in the plants examined have been found to have collapsed when elongation commences. This phenomenon may have contributed to misinterpretation in the past of the sequence of development of the anthers and stigmas.

It appears that floral development is genetically controlled as this character seems to be maintained in cultivation.

Davis & Heywood (1963) have quoted Erodium cicutarium as an example of plants where some races are protogynous while others are protandrous and this situation may be similar to that found in Salicornia. On the other hand it is possible that environmental factors may influence the order of maturation of the reproductive organs. Webb (pers. comm.) has observed that some species of Saxifraga which are normally protandrous may produce protogynous flowers when cultivated in the greenhouse under conditions of higher temperature. It seems that a great lack of information exists about the factors controlling the behaviour and development of the reproductive organs in flowering plants

as a whole and there is a need for experimental work not only on Salicornia but in a large number of other genera and families.

It has been concluded that though the results obtained in this work are limited and are not conclusive. It appears that floral development is variable and is not a reliable taxonomic character.

Exsertion of the anthers.

Ball & Tutin (1959) appear to be the first workers to use the differences in the behaviour of the anthers of flowering as a taxonomic character in Salicornia. These workers have described the tetraploid aggregate with anthers that are always exserted before dehiscence while plants in the diploid aggregate rarely if ever exsert their anthers before dehiscence. Ball & Tutin describe a diploid species S. obscura which has flowers that are usually cleistogamous. Ball (1964 b) has stated that the occurrence of dehiscent anthers within the flowers of diploid plants is sufficiently frequent to be a useful taxonomic character. The absence of such anthers however, cannot be taken to indicate that the plants are tetraploid. Ball has stated also that there is no direct or indirect evidence that dehiscent anthers occur within the flowers of tetraploid plants.

In this work a correlation has been observed between the chromosome number of plants and the behaviour of their anthers at flowering. Plants of the tetraploid populations, 12, 13, 15, 15A, 15B, 18, 23, 19, 19A and 19B have been found to

always exert their anthers before dehiscence occurs and it is possible to recognise tetraploid populations in the field by their yellow undehisced anthers protruding from the pores of the florets (Plate 7). Some variation in the behaviour of the anthers in diploid populations has been observed but they rarely if ever exert their anthers before dehiscence. Occasionally some plants in a diploid population may exert undehisced anthers but all the florets in a cyme have never been observed to exert undehisced anthers and florets in adjacent segments rarely exert their anthers before dehiscence.

It has been found that the behaviour of the anthers in diploid populations can be divided into two groups;

- (i) Plants where the flowers are completely cleistogamous the anthers persisting in the perianth. This has been observed in populations 8, 7, 5, (S.hibernica) 2, and plants from Dundalk Bay (S.europaea).
- (ii) Plants where the anthers are exerted after they have dehisced. This situation has been observed in populations 1, 3, 4 and 20. Population 21 (S.hibernica) and some plants from Connemara assigned to S. europaea have been observed to produce progeny in cultivation some of which behaved as type (i) and some as type (ii).

In cultivation progeny of population 8 remained fully cleistogamous (as type (i)) over a number of years under differing conditions. However, the progeny of populations 5 and 7 (S.hibernica) in cultivation during one season produced fully

cleistogamous flowers out of doors but when cultivated indoors the anthers were exerted after dehiscence.

These results suggest that sometimes environment may effect the occurrence of fully cleistogamous flowers as (i) and sometimes this character may have a genetic basis. Uphof (1938) has pointed out that cleistogamy can be induced by environmental influences such as temperature, humidity, nutrition and altitude. Cleistogamous and chasmogamous flowers may be produced on the same plant in different conditions; he has observed this in Specularia perfoliata where in early summer in cool wet weather the flowers are cleistogamous while later, on the same plant in drier conditions, chasmogamous flowers occur.

It has been concluded that exertion of the anthers is a useful taxonomic character for distinguishing between the diploid and tetraploid aggregates of the genus this is in agreement with the results obtained by Ball & Tutin (1959) and Ball (1964 a and b). The occurrence of cleistogamous flowers where the dehiscent anthers are retained in the floret in Salicornia is a complex character sometimes apparently being environmentally controlled and sometimes having a genetic basis but the investigations in this study are by no means conclusive and the factors that control this character are not fully understood and further detailed study is necessary.

Time of flowering

Differences in the times of flowering between taxa have been observed by a number of previous workers including Moss (1914) and Ball & Tutin (1959). Ball & Tutin have described the species belonging to the diploid aggregate as flowering in August and September and in the tetraploid aggregate they have described S.dolichostachya and S.lutescens as flowering in July-August, S.fragilis as flowering in August and S.nitens as flowering in September.

In this study populations 9, 15, 15A, 15B and 15C (S.dolichostachya) and populations 13 and 19 (S.fragilis) have been observed to flower both in the field and in cultivation two to three weeks earlier than other populations. In the field plants belonging to these populations may commence flowering in mid July and continue until late in August. Population 12 (S.fragilis) occurring at the same locality as population 13 but in a higher zone in the marsh commenced flowering in early September much later than plants of the latter population. It is also interesting that populations 18 and 23 (S.fragilis) which like population 12 resembled S.nitens Ball & Tutin in some characters, should flower late in the season fitting Ball & Tutin's description of this species.

Cultivation has shown that these differences in flowering times appear to be maintained in plants of different populations grown side by side under the same environmental conditions. This suggests that time of flowering is genetically controlled. It seems possible that the variation in flower-

ing time may be associated in some way with the degree and frequency of submergence and with the location in the salt-marsh of different populations of the same taxa. For example plants occurring in the lower and more exposed zones of a salt-marsh as population 13 may have been subjected to environmental pressures such as the necessity to have completed their life cycle before the onset of the autumn gales and selection has acted on populations in these lower regions of marshes to give earlier flowering.

Population It has been concluded, that although some taxa as S.dolichostachya do tend to flower earlier than others and this seems to be genetically controlled, time of flowering is variable within different populations of the same taxa and is not a reliable taxonomic character.

Pollen fertility

Dalby (1962) has found that the pollen of 28 plants from both the diploid and tetraploid aggregates has shown a fertility of between 85-100%. In one case he has found a fertility of only 18% and he suggests that the cause of this high percentage sterility is due to some genetic unbalance perhaps resulting from hybridisation of related but not identical biotypes.

The results of observations made on pollen fertility in this study are given in Table VI. These results show that there is a high degree of pollen fertility in the populations investigated.

It has been concluded that as there was a high degree

of pollen fertility a great deal of genetic unbalance did not exist in the material investigated. This suggested that hybridisation between different but closely related taxa did not appear to occur frequently at least in the populations studied in this work.

TABLE VI

The percentage of fertile pollen in cultivated
representatives of population samples

<u>Population number.</u>	<u>Species</u>	<u>Locality</u>	<u>Percentage of fertile pollen</u>
4	(<u>S.europaea</u>)	Rush	99%
3	(<u>S.europaea</u>)	Bull Island	93%
8	(<u>S.hibernica</u>)	Tramore	93%
5	(<u>S.hibernica</u>)	Ballyvaughan	98%
	(<u>S.pusilla</u>)	Tramore	93%
13	(<u>S.fragilis</u>)	Tramore	97%
18	(<u>S.fragilis</u>)	Rush	96%
12	(<u>S.fragilis</u>)	Tramore	87%
19	(<u>S.fragilis</u>)	Comber	97%
22	(<u>S.fragilis</u>)	Baldoyle	92%
9	(<u>S.fragilis</u>)	Bull Island	77%
15	(<u>S.dolichostachya</u>)	Rush	96%

Breeding behaviour

and were no longer Breeding behaviour and it seems that elongation Dalby (1962) has suggested that it is very likely that many annual forms of Salicornia are self-pollinated in nature, as ripe dehiscing anthers may be seen in contact with presumably receptive stigmas, and their pollen spilling on to the stigmatic papillae. However, his illustration does not show this very clearly. much more observation and experimental work is needed Dalby has shown that Salicornia pollen may be carried by wind in considerable quantities for short distances and he has suggested from this evidence that it is possible for hybridity to occur though it has not been proved. Dalby has also shown that self-compatibility is high in Salicornia and that there is little evidence of autonomous apomixis. and he states that the evidence in favour of sexual reproduction is strong though not conclusive. without completely mutilating the fleshy per In the present study it has been observed that self-fertilisation may frequently occur due to the high frequency of cleistogamous flowers in diploid plants. In tetraploid plants pollen from ripe dehiscing anthers has been seen, both in the field and in cultivated plants, spilling on to apparently receptive stigmas (Plate 7b). It has been observed in diploid plants in cultivation that the stigmas may be exerted after the anthers have dehisced within the floret. It seems that this elongation of the stigma is not a result of failure of self-pollination to occur because, as has been discussed earlier in this chapter (page 94), the papillae of stigmas that behaved in this manner that were examined were found to have collapsed

and were no longer apparently receptive and it seems that elongation and exsertion of the stigmas may not be a mechanism to assure that fertilisation occurs if self pollination fails, but is more likely a resulting effect from the development of the fertilised ovule.

The breeding behaviour of the annual Salicornia is not fully understood and much more observation and experimental work is needed.

Artificial hybridisation

Methods and materials

Hybridisations were mainly only attempted between plants which exserted their stamens before dehiscence as it was found extremely difficult to emasculate the flowers of plants which were cleistogamous without completely mutilating the fleshy perianth and causing the floret to die due to dehydration.

In female parent plants the florets which were to be used in attempted hybridisations were selected on separate inflorescences. Cymes were selected with florets which had anthers and stigmas that were not mature. The reproductive organs of the lateral florets were carefully removed and any cut surfaces were sealed with vaseline. The central florets were then covered with strips of thin polythene 2 cm broad, tied above and below the floret with thread. This procedure was adopted to prevent pollen from adjacent inflorescences reaching the stigma when it emerged. The anthers were removed before they dehisced, they were usually removed as they emerged from the floret pores.

The stigma was brushed with pollen from the male parent plant each day for 4 - 6 days beginning from the time when the stigma first appeared from the floret pores. The florets were kept covered with polythene strips for a further 7 - 10 days to assure that fertilisation had taken place and if it had not, to avoid any danger of self pollination occurring by pollen from anthers of florets on other parts of the plant reaching the stigma of the floret involved in the attempted hybridisation.

It was necessary to choose the characters that distinguish the parent plants with great care before hybridisation was attempted because, if this was not done the specialised and reduced nature of the plant resulting in so limited a number of useful, 'good' taxonomic characters could make it impossible to recognise whether progeny resulting from an attempted cross was in fact a hybrid or not.

To assist in determining whether the progeny resulting from an attempted cross was in fact a hybrid or not, seeds from the female parent plant from florets not involved in the hybridisation experiments were collected at the same time and were cultivated under similar conditions as the "hybrid" seeds to use for comparison with the believed hybrid progeny. In Table VII these seeds are referred to as "controls".

The column in Table VII entitled the "number of seeds set" refers to seeds with a dark brown testa covered with well developed hairs and which appeared viable at the time of collection.

TABLE VII

Results of attempted artificial hybridisations

<u>Female Parent</u>		<u>Male Parent</u>	<u>Number of attempted crosses</u>	<u>Number of seeds set</u>	<u>Behaviour of "hybrid" seeds in cultivation</u>	<u>Behaviour of "control" seeds in cultivation.</u>
(1) Rush Pop. No. 18 (<u>S.fragilis</u>)	X	Rush Pop. No. 15a (<u>S.dolichostachya</u>)	4	0	-	Good germination and growth.
(2) Rush Pop. No. 15a (<u>S.dolichostachya</u>)	X	Rush Pop. No. 18 (<u>S.fragilis</u>)	4	2	No germination	Good germination and growth.
(3) Rush Pop. No. 18 (<u>S.fragilis</u>)	X	Rush Pop. No. 15b (<u>S.dolichostachya</u>)	4	0	-	Plant failed to set any viable seed.
(4) Rush Pop. No. 15 (<u>S.dolichostachya</u>)	X	Comber Pop. No. 19 (<u>S.fragilis</u>)	4	0	-	No germination
(5) Comber Pop. No. 19 (<u>S.fragilis</u>)	X	Rush Pop. No. 15 (<u>S.dolichostachya</u>)	6	2	No germination	Good germination and growth.
(6) Rush Pop. No. 15a (<u>S.dolichostachya</u>)	X	Tramore Pop. No. 13 (<u>S.fragilis</u>)	4	2	One robust seedling germinated but died after 3 - 4 weeks.	Good germination and growth.
(7) Tramore Pop. No. 13 (<u>S.fragilis</u>)	X	Rush Pop. No. 15a (<u>S.dolichostachya</u>)	6	3	One seedling germinated and grew to maturity.	Good germination and growth.
(8) Comber Pop. No. 19a (<u>S.fragilis</u>)	X	Rush Pop. No. 15a (<u>S.dolichostachya</u>)	4	0	-	Good germination and growth.
(9) Tramore Pop. No. 13 (<u>S.fragilis</u>)	X	Comber Pop. No. 19a (<u>S.fragilis</u>)	4	2	No germination	Good germination and growth.
(10) Rush Pop. No. 15 (<u>S.dolichostachya</u>)	X	Rush Pop. No. 4 (<u>S.europaea</u>)	4	1	No germination	Good germination and growth.
(11) Baldoyle P. 2 in cult. (<u>S.europaea</u>)	X	Rush Pop. No. 4 E.1. (<u>S.europaea</u>)	2	0	-	Good germination and growth.

TABLE VII (continued)

<u>Female Parent</u>	<u>Male Parent</u>	<u>Number of attempted crosses</u>	<u>Number of seeds set</u>	<u>Behaviour of "hybrid" seeds in cultivation.</u>	<u>Behaviour of "control" seeds in cultivation.</u>
(12) Rush Pop. No. 4 E.1 (<u>S.europaea</u>)	X Baldoyle P. 2 in cult. (<u>S.europaea</u>)	2	0	-	Good germination and growth.
(13) Killyleagh P.1 in cult. (<u>S.europaea</u>)	X Rush Pop. No. 4 E.1 (<u>S.europaea</u>)	2	0	-	Good germination and growth.
(14) Rush Pop. No. 4 E.1 (<u>S.europaea</u>)	X Killyleagh P.1.in cult. (<u>S.europaea</u>)	2	0	-	Good germination and growth.

(For legend relating to (11) - (14) see Table III page 32)

The results obtained from artificial hybridisations attempted in the present study are shown in Table VII. These may be divided into three groups; they were:

- (1) Hybridisations where no seeds were set (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, and 14). As hybridisations were attempted between a robust plant of S.europaea L. from Ireland with long terminal spikelets which he used as male parent and a small spoked plant from an English locality. The resulting progeny had long terminal spikes and Ball concluded that this was a hybrid. However, it is felt that the result of the investigations, made in the present work, is a reservation in the length of the spike, some reservations as to whether in fact the progeny in this cross of S.europaea hybrid.
- (2) Hybridisations where apparently viable seeds were set but these failed to germinate in cultivation (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11). Controls usually did germinate and grow (2, 3, 4, 5, 6, 7, 8, 9, 10, 11).

Discussion of results and conclusions

Ball (1960 b) appears to be the only other worker to have attempted artificial hybridisations. He has experienced difficulties in developing a satisfactory technique for emasculating plants belonging to the diploid aggregate as has also been found in this study. Ball attempted a considerable number of crosses but found that a very low percentage of viable seed was set. One of the few successful crosses that he made was between a robust plant of S.europaea L. from Ireland with long terminal spikelets which he used as male parent and a short spiked plant from an English locality. The resulting progeny had long terminal spikes and Ball concluded that this was evidence that the plant was a hybrid. However, it is felt that as a result of the investigations, made in the present work, of the variation in the length of the spike, some reservations must be held as to whether in fact the progeny in this cross of Ball's was a hybrid.

The results obtained from artificial hybridisations attempted in the present study are shown in Table VII. These may be divided into three groups;

- (1) Hybridisations where no seeds were set (1, 3, 4, 8, 11, 12, 13, and 14).
- (2) Hybridisations where apparently viable seeds were set
- (3) In two but these failed to germinate in cultivation though controls usually did germinate and grow (2, 5, 10, and 11).

- (3) Hybridisations where seed was set and this germinated in cultivation (6 and 7).
- (1) Attempted crosses where no viable seed was set are inconclusive as the failure to set seed may have been due to a variety of reasons as for example the florets may have been damaged when emasculation was carried out, pollination may have failed to occur, or pollination may have occurred but fertilisation did not occur because of genetic incompatibility between the plants involved. Failure of the attempted crosses in diploids was most likely due to physical damage to the florets when emasculation was carried out as this was extremely difficult to perform.
- (2) Those results where apparently viable "hybrid" seed was set but failed to germinate in cultivation suggest, that it is possible that the taxa recognised as S. dolichostachya and S. fragilis in this study do not usually hybridise although fertilisation and seed set takes place there is some genetic unbalance which upsets normal seed germination and growth. The failure of the seeds to germinate may also be an effect of the environment in which they were cultivated but this seems to be unlikely as seeds collected from the same female parent plant and grown as controls germinated and grew normally.
- (3) In two cases the seeds resulting from attempted crosses germinated. It is significant that this occurred in the reciprocal crosses between two populations. However, in

one case the progeny died after it had formed two vegetative segments though the controls grew to maturity. In the other case the progeny grew to maturity but very closely resembled the female parent plant which was distinguishable from the male parent (S.dolichostachya) by its short fertile segments and more cylindrical spikelets and the shape of the central floret. This result is inconclusive the progeny may have been a hybrid but it seems more likely that self-fertilisation could have occurred at some stage during the experiment.

Very little may be concluded from the results of the artificial hybridisations attempted in this work. The results do suggest that plants assigned to S.dolichostachya and S.fragilis are frequently unable to hybridise and that also different races of apparently the same tetraploid taxa are sufficiently different genetically to be unable to cross. The results obtained in the present study contribute very little about the breeding behaviour of the species belonging to the diploid aggregate. Observation in the field, as has been discussed earlier in this work (page 76), has shown that, where S.pusilla Woods and S.europaea L. grow together, these species may hybridise though the frequency of hybrids is low. If Ball's results are considered they suggest that different races of S.europaea may hybridise and it seems possible that the genetic barriers that exist between races in this aggregate are not as great as those that appear to exist in the tetraploid aggregate. A possible

explanation for this is that in plants that are cleistogamous and where self-fertilisation is continually occurring there will not be great selection pressures to develop genetic barriers to prevent closely related taxa from interbreeding. In tetraploid populations where the anthers are exerted and there is a greater possibility of cross pollination occurring selection may act more rapidly to build up genetic isolation.

Key to the species of Salicornia in Ireland.

1. Perennial, with prostrate rooting branches; all the branches not ending with an inflorescence..1. S.perennis.
1. Annual, without rooting branches; all the branches ending in an inflorescence.
 2. Cymes mostly 1-flowered; fertile spikes disarticulating in fruit. 2. S.pusilla.
 2. Cymes 3-flowered; fertile spikes not disarticulating in fruit.
 3. Anthers 0.35 - 0.70 mm long; fertile segments inflated; central floret of cyme usually much larger than the visible part of the lateral florets.
 4. Anthers 0.49 - 0.70 mm long; fertile segments distinctly inflated; the greater diameter almost $1\frac{1}{2}$ times the lesser diameter; flowers cleistogamous; more than half the central floret and almost all of the lateral florets hidden by the fused leaves during flowering. 3. S.hibernica.
 4. Anthers 0.35 - 0.55 mm long; often exerted after dehiscence but sometimes cleistogamous; fertile segments convex but usually not distinctly inflated; at least half of the central and about $\frac{1}{3}$ rd of the lateral florets visible during flowering . .

Flowering and 4. S.europaea.

3. Anthers 0.65 - 0.95 mm long, always exerted

cylindrical before dehiscence fertile segments usually

Cymes three cylindrical and not inflated; central floret

of the cyme equal to or only a little larger

than the visible part of the lateral florets.

5. Fertile spikes with (4 -)6 - 12(- 24)

Habitat: salt-pans, closed segments; fertile segments 1.5 -

Distribution: known only 4.5 mm long, cylindrical or sometimes

Ireland; near Fethard-on-Sea slightly convex; the central florets

always less than $1\frac{1}{2}$ times as long as

broad. Plant yellowish-green or pink-

ish-red, rarely dark green.

In a posthumously 5. S.fragilis.

5. Fertile spikes with (9 -)12 - 25 seg-

ments; fertile segments (3.5 -)4.5 -

8.0(10) mm long often slightly concave

the central floret up to $1\frac{1}{2}$ - 2 times

as long as broad. Plant usually dark

green. 6. S.dolichostachya.

wings on the perianth, together with the mode of insertion of the

1. S.perennis Mill. Gard. Dict. ed. 8, no. 2 (1768); Ferguson,

Irish Nat. Journ. 14: 18 - 19 (1962) and 215 (1964); Webb,

An Irish Flora, ed. 4, 146 (1963); Ball in Flora Europaea

1: 102 (1964). The absence of albumen in the seeds

A small shrub with creeping woody stems forming tussocks up

to 1 m in diameter, also with short, erect, fleshy,

flowering and non flowering stems. Colour deep green often becoming brown or brownish-red. Fertile spikes cylindrical, blunt, 10 - 20 mm long, with 5 - 10 segments. Cymes three flowered, the central floret completely separating the lateral florets. Stamens two. Stigmas bifid or trifid. Flowers protogynous. (Plate 8 Appendix 1 and in page 173).

Habitat: salt-pans, closed communities, and muddy foreshores.

Distribution: known only from two localities in south-east Ireland; near Fethard-on-Sea and Duncormick in Co. Wexford. (Appendix II Figure 1 page 186).

In a posthumously published paper primarily concerned with South African Chenopodiaceae Moss (1948), transferred S. perennis Mill. to the genus Arthrocnemum and Ball (1964) has taken up this combination in Flora Europaea.

Arthrocnemum was first proposed by Moquin (1840), who included S. perennis Mill. in his original delimitation of the genus. Moquin uses the absence of albumen in the seed and of wings on the perianth, together with the mode of insertion of the florets, as characters to separate the genus from Salicornia. It seems doubtful however, whether these characters possess the validity which he attributed to them as they have been adopted by few subsequent botanists. The absence of albumen in the seeds does not seem to be constant throughout the traditional limits of the genus (Moss 1954). De Fraine (1912) in an extensive

investigation of the anatomy of the genus Salicornia makes no reference to any difference in the insertion of the florets between S.perennis Mill. and the annual species in the British Isles. In my own observations I have found that small differences do exist between S.perennis Mill. and the annual species of Salicornia in the British Isles in the shape of the florets and in the degree to which the central floret separates the laterals and also in the arrangement of the wings of the perianth. However, the former characters are very variable among annual Salicornia and it is doubtful whether they are sufficiently constant to serve as a basis for generic separation. Moss (1914) comments that the placing of S.perennis Mill. in the genus Arthrocnemum is curious, for this species possesses none of the characters of Moquin's genus. As mentioned earlier, Moss later changed his mind and transferred S.perennis to Arthrocnemum. In a later paper (Moss 1954) he redefined the two genera according to the following criteria.

Arthrocnemum: perennial; protogynous; stigma bifid;
some of the branches not terminating in
an inflorescence.

Salicornia: annual; protandrous; stigma tufted;
branches all terminating in an inflor-
escence.

Salicornia perennis Mill. certainly differs from the annual species of the British Isles in the first and last of these four characters. However, it has been shown in this work (Chapters III and V) that two of the characters that Moss uses

to separate Arthrocnemum from Salicornia, flowering behaviour and stigma morphology, are not constant for these two genera as they occur in Ireland. It is proposed that, in the light of these observations, the combination S.perennis Mill. be retained until the criteria for the definition of the genus Arthrocnemum can be considered once more in the light of knowledge of other related forms from a wider geographical area.

2. S.pusilla Woods Bot. Gaz. (London) 3: 30 (1851); Ball & Tutin, Watsonia 4: 200 (1959); Dalby, Proc. Bot. Soc. Brit. Is. 4: 470 (1962); Tutin in Flora of the British Isles ed. 2, 288 (1962); Perring & Walters, Atlas of the British Flora 87 (1962); Webb, An Irish Flora, ed. 4, 146 (1963; Ball in Flora Europaea 1: 102 (1964).

S.disarticulata Moss, Journ. Bot. Lond. 49: 183 (1911)

Annual, erect or prostrate up to 25 cm high often much branched and bushy. Plants yellowish-green, becoming purplish-red or reddish-brown in fruit or the sterile segments turning yellow before collapsing. Terminal spikelets 4 - 17 mm long, with 3 - 10 fertile segments, distinctly inflated. Cymes 1-flowered (occasionally plants occur which have two rudimentary lateral florets). Florets almost circular. Stamens usually 1; anthers usually exserted after dehiscence. Infructescence disarticulating and the seeds are dispersed still attached to the fleshy cortex of the fertile segments.

to just $2n = 18$. (Plate 9 Appendix I page 173).

Habitat: drift line and in closed communities in the upper regions of salt-marshes.

Distribution: locally frequent on the south and east coast; very rare elsewhere. Authentic records for this species were known for three localities on the south coast of Ireland (Perring & Walters 1962). This investigation has added twelve new localities for this species and confirmed one of those known. The distribution of S.pusilla in Ireland is very similar to that in Britain where this species is frequent along the south and south-east coasts, extending north on the east coast to a small number of stations at the mouth of the Humber estuary almost at the same latitude as the most northerly station for this species in Ireland (Appendix II, Figure 2 page 187).

S.pusilla Woods is clearly morphologically distinct from other annual diploid Salicornia in north-west Europe. However, Dalby (1956) has pointed out that apparently quite fertile putative hybrids occur when S.pusilla and S.ramosissima grow together. In this work (Chapters III and V) it has been shown that S.pusilla may apparently hybridise with S.europaea where these two species grow together. However, the frequency of hybrids is low, probably because of the regular occurrence of self-pollination in both these species (Chapter V). This factor together with the specialised form of seed dispersal and ecology which tend to isolate S.pusilla from other diploid taxa seem

to justify maintaining this taxon at specific rank.

Distribution: locally abundant in parts of the west, occasional in the south, unknown at present outside Ireland (Appendix

3. S.hibernica I.K. Ferguson sp. nov.

S.ramosissima quo ad pl.hibern. Ball & Tutin, *Watsonia* 4:
197 - 198 (1959).

Erect, very rarely procumbent, up to 25 cm high, typically freely branched and bushy but very variable and dwarf unbranched plants may occur in unfavourable habitats, sterile segments (5 -)7 - 11(- 14) in number. Plants typically yellowish-green sometimes with red or purplish-red colouration on the fertile segments, the sterile segments becoming translucent yellowish-green in fruit. Terminal spike 5 - 45 mm long, cylindrical, obtuse with (4 -)6 - 11(- 17) fertile segments. The third fertile segment from the base (in early fruit) 1.8 - 3.5 mm long with the greater diameter 3.5 - 4.5 mm and the lesser diameter 2.2 - 3.2 mm; foliar faces of the segments inflated, elliptical in transverse section; the ratio of the greater/lesser diameter 1.4 - 1.5. Free part of the leaf acute, hiding a little more than half of the central floret and almost completely hiding the lateral florets. Central floret 2.0 - 2.6 x 2.0 - 2.6 mm about as long as broad, lateral florets 1.9 - 2.0 x 1.9 - 2.0 mm. Flowers usually cleistogamous; anthers 0.49 - 0.70 mm long. Seeds 0.85 - 1.25 mm long. $2n = 18$. (Plates 10 and 11 Appendix I pages 174-175).

Habitat: well drained, open, sandy, mud pans and closed communities in the upper regions of salt-marshes.

Distribution: locally abundant in parts of the west, occasional in the south, unknown at present outside Ireland (Appendix II, Figure 3 page 188).

S. hibernica Ferguson sp. nov.

Erecta, rarius procumbens, usque ad 25 cm alta, segmentis sterilibus (5 -) 7 - 11(- 14), colore luteo-viride, interdum segmentis fertilibus rubro vel purpureo-rubro tinctis, segmentis sterilibus demum pellucidus. Spica terminalis 5 - 45 mm longa, obtusa, cylindrica, segmentis fertilibus (4 -) 6 - 11(- 17). Segmentia tertia fertilia a spicae basi (fructu nondum maturo) 1.8 - 3.5 mm longa, faciebus foliaribus inflatis, ut quidque transverse secatum formam manifeste ellipticam praebeet, diametro maiore (3.5 - 4.5 mm) diametrum minus (2.2 - 3.2 mm) paene dimidio excedenti. Pars libera folii acuta, flores laterales paene omnino, centralem partim obtegens. Flores centrales 2.0 - 2.6 x 2.0 - 2.6 mm, flores laterales 1.9 - 2.2 x 1.9 - 2.0 mm. Flores plerumque cleistogamae. Antherae 0.49 - 0.7 mm longae. Semina 0.85 - 1.25 mm longa. $2n = 18$. Typus in Herb. Coll. Trin., Dublin.: Tramore Co. Waterford. Leg. I.K. Ferguson September 1961.

of the scarious margins of the fused leaves (page 84), which is considered an important diagnostic character by Bell for

S.hibernica a S.europaea L. spicis obtusis, cylindricis, faciebus foliaribus inflatis, ut quidque transverse secatum formam manifeste ellipticam praebat, diametro maiore diametrum minus paene dimidio excedenti, parte libera folii acuta flores laterales paene omnino, centralam partim obtegente, floribus plerumque cleistogamis, antheris 0.49 - 0.7 mm longis, seminibus 0.85 - 1.25 mm longis discedit.

Ball & Tutin (1959) have stated that material from Ireland that they have assigned to S.ramosissima Woods differs from typical plants in being clear green becoming tinged pink to crimson and the terminal spikelets are cylindrical and obtuse. Ball (pers. comm.) has stated that plants from Galway Bay (that have been described as S.hibernica in the present study) are "difficult" and appear to be different from S.ramosissima Woods. He also comments that he has only once seen living material from this region and that he has never had Irish plants in cultivation which resemble those described as S.hibernica in this study.

S.hibernica does not resemble plants of S.ramosissima Woods, that I have seen from the type locality Hayling Island in Hampshire, during the course of this investigation, in the shape and dimensions of the fertile spikes and segments and in colour. Preliminary measurements made in this work of the width of the scarious margins of the fused leaves (page 84), which is considered an important diagnostic character by Ball for

distinguishing between S. ramosissima Woods and S. europaea L., have shown that there is no difference in measurements of this character between Irish plants of S. europaea L. and S. hibernica. Also, as has been pointed out earlier in this study (page 82), measurements of the width of the scarious border of the margins of the leaves of plants from North Wales assignable to S. europaea L. have thrown doubt as to whether this character warrents the taxonomic importance that Ball has attributed to it.

4. S. europaea L., Sp. Pl. 3 (1753); Ball & Tutin, *Watsonia* 4: 198 - 199 (1959); Tutin in Clapham, Tutin & Warburg, *Flora of the British Isles* ed. 2, 287 (1962); Ball in *Flora Europaea* 1: 102 (1964).

S. herbacea (L.) L., Sp. Pl. ed. 2, 5 (1763)

S. prostrata auct., pro parte non Pallas

S. pusilla auct., non Woods

S. gracillima (Townsend) Moss, *Journ. Bot. Lond.* 49: 182 - 183 (1911) pro parte

S. ramosissima auct., pro parte, non Woods

S. appressa Dumort., *Bull. Soc. Bot. Belg.*, 7: 334 (1868)
pro parte

S. smithiana Moss, *Journ. Bot. Lond.* 49: 183 - 184 (1911)
pro parte

S. obscura Ball & Tutin, *Watsonia* 4: 200 (1959)

S. patula Duval-Jouve, *Bull. Soc. Bot. Fr.* 15: 175 (1868)

S. brachystachya (G.F.W. Meyer) König, *Mitt. Fl.-Soz.*

Arbeitsgemeinschaft. N.F. 8: 11 (1960) pro parte

? S. stricta Dumort. Bull. Soc. Bot. Belg., 7: 334 (1868)

Erect, procumbent or prostrate, up to 35 cm high, typic-

ally freely branched and bushy but very variable and

often forming pure stands of simple little branched

plants in unfavourable habitats. Sterile segments (7 -)

9 - 15(- 18). Plant typically dark green the fertile

segments becoming pink, red or purplish in fruit, the

sterile segments becoming yellowish or diffuse pink some-

times the entire plant is flushed red. Terminal spike

5 - 50 mm long slightly tapering, obtuse or acute with

3 - 12 (19) fertile segments. Fertile segments (3rd from

the base measured in early fruit) 1.8 - 3.9 mm long, the

greater diameter 2.4 - 5.0 mm and the lesser diameter

2.0 - 4.5 mm, with the foliar faces of the fertile seg-

ments usually only slightly inflated: the ratio of the

greater/lesser diameter (1.1 -) 1.25 - 1.35(- 1.5). Free

part of leaf acute, with at least half of the central

floret and about one third of the lateral florets vis-

ible during flowering. Central floret 1.6 - 2.7 x 1.5 -

2.7 mm usually slightly longer than broad. Lateral

florets 1.7 - 2.0 x 1.7 - 2.1 mm. Anthers 0.35 - 0.55 mm

long, usually exerted after dehiscence, flowers occasion-

ally cleistogamous. Seeds 1.0 - 1.6 mm long. $2n = 18$.

(Plates 12 - 15, Appendix I pages 176 - 178).

Habitat: in most salt-marsh habitats, with the exception of the lower zones and soft muds.

Distribution: frequent in almost all salt-marshes throughout the entire country (Appendix II, Figure 4 page 189).

The nomenclature of the Salicornia from north-west Europe which are assignable to this species is very confused and the fact that dried material is almost valueless for identification has made typification very difficult. Linnaeus described four species of Salicornia in the first edition of Species Plantarum but only part of the type species Salicornia europaea & herbacea now remains in the genus Salicornia the rest have been transferred to new or other genera. In the second edition of Species Plantarum Linnaeus raised both varieties of his species S.europaea to specific rank and the epithet europaea was abandoned. However, under the rules of nomenclature S.herbacea (L.)L. is superfluous as it was a replacement for S.europaea L.

There is no sheet in the Linnean Herbarium labelled S.europaea but there is one labelled 'herbacea' with the figure '1' in Linnaeus's handwriting and a locality 'Gotland'. This appears to be the holotype of S.europaea. It is not possible unfortunately to identify this specimen, as mentioned above as is the case with many herbarium specimens of Salicornia preserved in the usual manner furthermore, the specimen is very young and is hardly yet in flower. Nannfeldt (pers. comm.) has stated that there is only one species at the locality in Gotland and that this is almost certainly diploid from its morphology,

though its chromosome number has not been counted. Under the circumstances it seems reasonable to refer to plants resembling those from Gotland as S.europaea L. Nannfeldt has seen detailed photographs of Irish diploid Salicornia which I believe to fit the descriptions of S.europaea L. and he has confirmed that these plants closely resemble those occurring on Gotland. This view is in agreement with those expressed by Ball (1960 a).

Pallas (1803) described two annual species of Salicornia, one, S.prostrata from his description and illustration appears to be assignable to the diploid aggregate. Recent workers including Moss and Salisbury (1914) and Tutin (1952) have regarded prostrate plants occurring in the British Isles as belonging to this species although the plant that Pallas originally described was from the Caspian Sea. The results of investigations of habit in this study have shown that it is very variable and is unreliable as a taxonomic character (page 30). These results are in agreement with those of Dalby (1955 and 1956) and Ball & Tutin (1959). Ball (pers. comm., 1964 a and 1964 b) has clarified the situation somewhat regarding the status of S.prostrata Pall. after examining living material of Salicornia from the Danube Basin and cultivating plants from seeds collected in that region. He attributes the epithet "prostrata" to plants which he believes to represent a distinct taxon which occurs only in eastern Europe.

Dumortier (1868) in an account of the Belgium Salicornia described four annual species. Two of these species were new S.appressa and S.stricta. The former has been

mainly distinguished by its prostrate habit which has been shown to be an unreliable taxonomic character and Ball & Tutin (1959) have included this species in S. ramosissima Woods. The results of the present study show that any Irish material to which the name S. appressa has been attributed must be included in S. europaea L.. S. stricta Dumort. is a more difficult problem because it is apparently impossible to identify the holotype, as Dumortier's specimens are immature and without locality (Ball 1960 a) and a number of authors have used this epithet in different senses, some referring to plants assignable to the diploid aggregate while others refer to plants assignable to the tetraploid aggregate.

Duval-Jouve (1868) published a study of the Salicornia of the Mediterranean coast of France at about the same time as Dumortier. This work gives extensive morphological and anatomical descriptions and illustrations. Two annual species were described one of which is clearly diploid S. patula the other tetraploid S. emerici. The former name has been taken up by Moss (1911) but he has reduced the rank to a form of S. europaea L. and cites S. patula Duv. Jouve and S. herbecea var. patula Buchenau among the synonyms. Langlois (1961) in a study of seed germination, habit, morphology and flowering in annual Salicornia from one locality in north-west France refers one of the taxa that he recognises to S. herbecea var. patula Moss. The specific epithet is incorrect as has been pointed out above but also the authority appears to be incorrectly cited as Moss did not apparently make this varietal combination. But more important, it

is emphasised in the present study that the type locality of Duval-Jouve's species is on the Mediterranean coast of France and though it has not been possible to examine material from this locality material has been examined from the Mediterranean from near Brindisi in Italy, which was collected as seedlings and grown in cultivation, and mature material from two stations in Corsica. All of this material appeared to be slender forms assignable to the diploid aggregate but did not seem to fall into the range of variation of any of the populations of Salicornia that I have seen in Ireland or Britain though, without a fuller biometric and experimental investigation of population samples from the Mediterranean it would be impossible to say with certainty that these plants represent a distinct taxon. It therefore seems inadvisable at present to use Duval-Jouve's names for Salicornia occurring on the north-west coast of Europe until the Salicornia of the Mediterranean have been more fully investigated.

Dalby (1956) has shown that the characters that distinguish S.gracillima (Townsend.) Moss from other diploid taxa, the dwarf and little branched habit, are the result of environmental influences such as competition, and water shortage. Ball & Tutin (1959) have included plants in S.ramosissima Woods which fit the original description of S.gracillima and occur at the type locality of this species. In the present study S.ramosissima Woods has not been recognised as occurring in Ireland and dwarf plants resembling descriptions of S.gracillima (Townsend.) Moss

have been treated as depauperated forms of S.europaea L. (1962). However, Herbarium specimens of Irish Salicornia which have been assigned to S.smithiana Moss and S.appressa Dumort. have been regarded in the present study as prostrate forms of S.europaea L. The record for S.pusilla Woods given in Praeger (1934) probably referred to this species in the same sense as that used by Townsend (1903) and Moss (1914). The description and illustration that Moss gives of S.pusilla shows that his interpretation of this species was a dwarf, poorly branched plant with three florets in a cyme. Irish plants of this description have been included in S.europaea L. in the present investigation. König cites S.ramosissima Woods, S.patula Duval-Jouve and Irish records for S.ramosissima Woods given by Druce (1911), Praeger (1934), Tutin (1952), Ball & Tutin (1959), Colgan (1961) and Tutin (1962) are mainly considered to refer to plants assigned to S.europaea L. in the present investigation.

König (1960) in a detailed account of the Salicornia of north-west Germany recognises two species one diploid, S.brachystachya Meyer with two sub species typica and gracilis Meyer, and the other tetraploid which will be discussed later. His illustrations suggest that German Salicornia do not differ very greatly from those of the British Isles, as might be expected, and the recognition of two aggregates separated by morphological characters based on chromosome number is in agreement with the results obtained in this work and with those of other

recent workers including Ball & Tutin (1959) and Dalby (1962), However, Konig's nomenclature needs some clarification, he rejects the Linnean names S.europaea and S.herbacea on the grounds that the description of the former in the first edition of Species Plantarum and the latter in the fifth edition of Species Plantarum differ and the concept of both names is thus ambiguous. It has been discussed above that the typification of S.europaea L. is quite possible provided that the plants found at Gotland to-day are accepted as being similar to the unidentifiable specimen from this locality numbered 1 and labelled "herbacea" in the Linnean Herbarium. Under S.brachystachya, which Meyer originally described as S.herbacea L. sub var. brachystachya, Konig cites S.ramosissima Woods, S.patula Duval-Jouve and S.gracillima (Townsend) Moss as synonyms. If Konig does not recognise S.europaea L. and S.ramosissima Woods as described by Ball & Tutin (1959) as distinct species, and wishes to lump these together, the epithet "europaea" seems to be the appropriate name for north German diploid Salicornia.

5. S.fragilis Ball & Tutin, *Watsonia* 4: 204 (1959); Tutin in Clapham, Tutin and Warburg, *Flora of the British Isles* ed. 2, 288 - 289 (1962); Ball in *Flora Europaea* 1: 102 (1964).

S.stricta auct., pro parte, non Dumort.

S.herbacea auct., pro parte, non (L.)L.

S.europaea auct., pro parte, non L.

S.lutescens Ball & Tutin, *Watsonia*, 4; 203 (1959)

S.nitens Ball & Tutin, *Watsonia*, 4: 204 (1959); Ball in *Flora Europaea* 1: 102 (1944)

S.emerici Duval-Jouve, *Bull. Soc. Bot. Fr.*, 15: 176 (1868)

Erect, up to 35 cm high, typically freely branched but variable and sometimes forming pure stands of small, slender, little branched plants in upper zone mud-pans and unfavourable habitats; sterile segments (5 -)7 - 14 (- 16). Plant typically green to yellowish green, the sterile segments becoming yellow and tinged pink, sometimes the entire plant may be dull pinkish-red or brownish purple with a smooth shining appearance. Terminal spikes (8 -)12 - 55(- 75) mm long cylindrical, obtuse, rarely slightly tapering with 5 + 16(-24) fertile segments. The third fertile segment from the base (in early fruit) 2.5 - 4.0(- 5.0) mm long, the greater diameter 2.5 - 5.0 mm wide and the lesser diameter 2.0 - 4.5 mm wide, usually cylindrical but sometimes the foliar faces of the leaves may be slightly inflated, the ratio of the greater/lesser diameter 1.2 - 1.3(- 1.4). Free part of the leaf acute, hiding about a quarter of the central floret and usually less than half of the lateral florets at the time of flowering. Central floret 1.5 - 3.0 x 1.2 - 2.4 mm usually a little longer than broad, lateral florets 1.4 - 2.6 x 1.0 - 2.2 mm. Anthers (0.6 -) 0.7 - 0.9(- 1.05) mm, always exerted before dehiscence. Seeds (1.0 -)1.25 - 1.5(- 1.7) mm long. $2n = 36$. (Plates 16-21, Appendix I pages 179-183).

Habitat: firm sandy mud in the lower zones and in salt-pans, levees and more or less closed communities in the mid and upper zones of salt-marshes.

Distribution: widespread and frequent on the south and east coasts where suitable habitats occur. (Appendix II, Figure 5 page 190).

Smith (1807) and 1813) recognised two annual species of Salicornia in the British Isles S.annua and S.procumbens and his descriptions and illustrations suggest that these epithets refer to plants that are now assigned to the tetraploid aggregate. The former species S.annua appears to resemble S.fragilis Ball & Tutin but Smith cites S.herbacea L. as a synonym which probably invalidates the name, also he gives no locality for the specimen which makes it difficult to try and identify the specimen with any certainty and there is no specimen in Smith's herbarium that is clearly the source of the illustration (Ball 1964 b). It is not possible either, to decide on the identity of the later species, S.procumbens, that Smith described as it is not well illustrated and is rather young. However, the locality is given as Yarmouth and it seems perhaps reasonable that if only one tetraploid taxon is represented at this locality, the epithet "procumbens" being the earliest valid name associated with plants assignable to the tetraploid aggregate could then be taken up to replace the name given to plants that resemble those occurring at Yarmouth.

done also. S.acetaria Pallas (1803) is an earlier name than S.procumbens for plants which, from the description and illustration given by the author suggest they are assignable to the tetraploid aggregate however, Pallas cites S.herbacea Linn. in synonymy which probably invalidates this name.

These views are more or less in agreement with those of Ball (1960 a and 1964 b).

Woods (1851) in an account of the British Salicornia recognises among his taxa a species S.herbacea L.. His description of this species suggests that he is referring to plants which are now placed in the tetraploid aggregate and thus S.herbacea sensu Woods is not synonymous with S.europaea L., as has been pointed out earlier, refers to diploid plants. S.procumbens sensu Woods clearly does not fit Smith's illustration and description and Wood's interpretation of this species is probably a procumbent form of a diploid taxon.

Duval-Jouve (1868) described a species S.emerici from the Mediterranean coast of France which is clearly assignable to the tetraploid aggregate from the descriptions and illustrations but it is not clear to which taxa it belongs and, as stated earlier (page 156) it seems unwise to take up Duval-Jouve's names to refer to plants from north-west Europe until more is known about the Salicornia of the Mediterranean.

Townsend (1903) refers to plants as S.stricta Dumort. which appear from his description to be assignable to the tetraploid aggregate. He probably used Smith's illustration of S.annua to identify S.stricta, as later authors appear to have

done also. The reason for this is because it is not possible to identify Dumortier's specimens as they are immature (Ball 1964 b) and Dumortier's description is very inadequate, but he cites S.annua Sm. as the only synonym of his species S. stricta. Dalby (1962) has described his concept of S.europaea

L. as a tetraploid. Moss (1911) describes a species S.europaea L. and from his description he appears to be referring to plants now placed in the tetraploid aggregate. He cites S.stricta Dumort. as a synonym. Later, Moss (1914) in Cambridge British Flora refers to two species which from his descriptions and illustrations are assignable to the tetraploid aggregate, S.herbacea L. and a new species S.dolichostachya Moss. The identity of the latter species has presented no difficulties and it would appear that S.herbacea sensu Moss (1914) is probably synonymous with S.fragilis Ball & Tutin.

The Irish records for S.stricta Dumort. given by Druce (1907) and Praeger (1934) probably refer to plants that are now assignable to the tetraploid aggregate as these workers more than likely used this epithet in the same sense as Moss and Townsend.

Konig (1960) has described two aggregates based on chromosome number in the annual Salicornia of north-west Germany. He has recognised one species and three subspecies in the tetraploid aggregate and he has elevated G.F.W. Meyer's var. stricta of S.herbacea L. to specific rank and points out that this name was published in 1824 and is an earlier one than that of Dumortier. However, as Ball (1964 b) points out, Dumortier in his

description of S.stricta cites only one synonym S.annua Sm. and he did not in any way refer to the variety stricta of Meyer so the identity of this variety is not relevant to the typification of the epithet "stricta" at specific rank.

Dalby (1962) has described his concept of S.europaea L. as a tetraploid species which as has been shown earlier is incorrect and he is using this epithet in the same sense as Woods, Townsend and Moss.

In the present investigation I have sunk S.fragilis Ball & Tutin with S.lutescens Ball & Tutin as I have visited the type locality of the former species at Leigh-on-Sea and I have also seen a considerable amount of material of S.lutescens from England that has been named by Ball (pers. comm.) and I have been unable to distinguish these species in the light of my experience of Irish Salicornia, as branching, length of the terminal spike and colour, the characters that Ball & Tutin (1959) have used to distinguish these two species, appear to be very variable and unreliable. In my opinion the epithet "lutescens" would have been more appropriate to adopt for this species as the nomenclatural type of S.fragilis is not a very typical representative of the species and both names were published at the same time. However, Ball (1964 b) has also sunk these two species and he has adopted the epithet "fragilis" so under the rules of nomenclature this must be adhered to.

In this work S.nitens Ball & Tutin has also been sunk into S.fragilis because populations have been found which appear to fall between these two species in the diagnostic

characters (Figure 16 page 119). S.nitens that I have seen at the type locality Hayling Island is certainly a very distinct population in the characters that Ball uses to separate this species from other tetraploid species. However, a number of populations have been found in this study which appear to be intermediate in different combinations of the characters that separate S.nitens from S.fragilis and I have thus been unable to accept S.nitens as a distinct species of the annual Salicornia in Ireland.

6. S.dolichostachya Moss, New Phytol., 11: 409 (1912); Moss in Moss & Salisbury, Camb. Brit. Fl., 2: 190 (1914); Praeger, Botanist in Ireland, 524 (1934); Tutin in Clapham, Tutin & Warburg, Fl. Brit. Isles ed. 1: 362 (1952); Ball & Tutin, Watsonia, 4: 202 (1959); Ball in Flora Europaea 1: 102 (1964).

S.stricta subsp. typica sensu König, Mitt. Fl.-Soz.

Arbeitsgemeinschaft. N.F. 8: 11 (1960)

Erect up to 40 cm high, usually fastigate with the lower primary branches about as long as the main stem, typically freely branched but variable and sometimes small plants with little or no branching may occur in dense stands; sterile segments 6 - 10(- 12). Plant dark green, sterile segments becoming dull yellow-green before collapsing. Terminal spike (30 -) 45 - 110(- 155) mm long, distinctly tapering obtuse or acute with (6-) 12 - 20

(- 31) fertile segments. The third fertile segment from the base (in early fruit) (2.5 -) 3.2 - 5.0 (- 6.8 mm long, with the greater diameter 3.0 - 5.0 mm and the lesser diameter 2.4 - 4.0 mm wide, usually nearly cylindrical but the foliar faces of the segments sometimes slightly concave, the ratio of the greater/lesser diameter (1.0 -) 1.2 - 1.3 (- 1.4). Free part of the leaf subobtusate, hiding about a quarter of the central floret and usually about a third of the lateral florets at the time of flowering. Central floret 1.5 - 2.2 x 2.5 - 4.3 mm, usually $1\frac{1}{2}$ - 2 times as long as broad, lateral florets 1.4 - 2.1 x 2.5 - 3.8 mm. Anthers 0.6 - 1.0 mm long, always exerted before dehiscence. Seeds 1.35 - 1.95 mm long. $2n = 36$. (Plate 22, Appendix I page 184).

Habitat: always in the lower zones of salt-marshes and usually occurring on open, soft mud and occasionally on levees.

Distribution: locally frequent on the east coast, rare on the west coast. (Appendix II, Figure 6 page 191). The distribution of this species is related to the type of habitat it is associated with, soft muds in the lower zones of salt-marshes. This type of habitat occurs more frequently on the south and east coasts where the estuaries are less exposed to strong tidal action and fine silty muds tend to develop more easily than on the west coast. This species has been reported from Co. Galway but I have not been able to find S.dolichostachya in this region.

Konig (1960) in his account of the annual Salicornia of north-west Germany describes a species S.stricta G.F.W.Meyer subsp. typica which appears from Konig's description and illustrations to closely resemble S.dolichostachya Moss. The nomenclature of S.stricta sensu Konig has been discussed in relation to that of the other tetraploid species recognised in the present study (page 162).

Plants that have been assigned to S.dolichostachya in the present investigation, when well grown, have usually been readily distinguishable from S.fragilis. However, many individuals of one dwarf population of S.dolichostachya from Rush (Pop. 15B) were difficult to separate biometrically from plants of some population of S.fragilis and this emphasises the importance of considering the population and not the individual in relation to the taxonomy of the genus.

General discussion

The reduced and specialised nature of Salicornia which has resulted in the absence of many of those characters, as for example leaves, calyx and corolla which are of considerable value for distinguishing taxa in other genera, has contributed to the taxonomic difficulties in this genus.

The results of this study have shown that very considerable variation occurs in the genus Salicornia. The nature of this variation does not seem to be attributable to one single factor but to a complex combination of a number of factors acting together. The extreme plasticity of the plants in response to environmental influences is one of the most important factors responsible for the variation in the genus. Some of

CHAPTER VII

General discussion

these effects of environmental influences have been deduced from comparative field studies and from plants grown in cultivation in standard conditions. For example investigations of habit (page 30) have shown that prostrateness may in some populations be purely a phenotypic modification however, in others the experiments have demonstrated the complexity of this character in that phenotypic modifications are paralleled by genotypic adaptations and sometimes the genetic basis of this character appears to show varying degrees of stability.

Another aspect of plasticity in the morphology of the genus which has contributed to the taxonomic difficulties is the occurrence of almost identical forms of different chromosome aggregates in the same habitat. Also the converse of this situation may occur where different forms of apparently the same

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The results of this study have shown that very considerable variation occurs in the genus Salicornia. The nature of this variation does not seem to be attributable to one single factor but to a complex combination of a number of factors acting together. The extreme plasticity of the plants in response to environmental influences is one of the most important factors responsible for the variation in the genus. Some of these effects of environmental influences have been deduced from comparative field studies and from plants grown in cultivation in standard conditions. For example investigations of habit (page 30) have shown that prostrateness may in some populations be purely a phenotypic modification however, in others the experiments have demonstrated the complexity of this character in that phenotypic modifications are paralleled by genotypic adaptations and sometimes the genetic basis of this character appears to show varying degrees of stability.

Another aspect of plasticity in the morphology of the genus which has contributed to the taxonomic difficulties is the occurrence of almost identical forms of different chromosome aggregates in the same habitat. Also the converse of this situation may occur where different forms of apparently the same

taxon may be found growing side by side in different habitats at the same locality. This has been observed in this investigation in such characters as colour, size, branching, length of the fertile spikes, time of flowering and in the number and shape of the fertile segments. Colour may be taken as an example of another character with a complex phenotypic and genotypic basis. The results in this work (page 50) have shown that it is not the actual appearance of anthocyanin that should be measured but the ability of the plant to produce it.

Investigations have shown that some of the variation in the group, especially in the diploid series, may be attributed to the breeding behaviour of Salicornia. Frequently plants have been found to be cleistogamous and also it seems likely that in plants with chasmogamous flowers self-pollination often occurs. Self-fertilisation will lead to increased homozygosity and to the production of pure lines. Also Salicornia has special ecological requirements, a permanently moist, saline soil and freedom from competition. These conditions occur only in salt-marshes in the British Isles and have a discontinuous distribution along the coast. Inter-colony gene exchange would thus be limited even if cross fertilisation did frequently occur. These factors perhaps also account to some extent, for the numerous, local and slightly different populations which are extremely hard to classify, that occur not only in Ireland but throughout north west Europe.

Among the annual Salicornia in Ireland two chromosome numbers have been found a diploid group and a tetraploid

group of plants. In considering these groups there do not appear to be any tetraploid populations which can be considered to be intermediate between two or more diploid populations and it thus seems that the tetraploid aggregate is not of recent origin, if this group is considered to be allopolyploid. The explanation of the morphological similarity between some diploid and tetraploid populations is that under certain environmental conditions similar phenotypes are produced from quite different genotypes. On the other hand, the explanation of the similarity between some diploid and tetraploid populations as S. fragilis and S. europaea may be that a tetraploid form arose from a population of S. europaea doubling its chromosome number or possibly from two closely similar but genetically distinct biotypes hybridising. This could be an explanation for the close similarity between diploid and tetraploid populations of S. fragilis and S. europaea which differ markedly only in the dimensions of some characters, as pollen grain diameter and anther length. However, the high percentage of pollen fertility found in plants investigated in this study suggests that again if the tetraploid aggregate is of autopolyploid origin it is not recent.

Speciation within the chromosome aggregates is perhaps easier to understand. In the diploid aggregate the most distinct taxon is S. pusilla and this is probably an extreme morphological and ecological variant of diploid populations assigned to S. europaea. Field observations have suggested that these species appear to be capable of hybridisation and are not apparently genetically isolated however, the method of seed dis-

persal of S.pusilla (Dalby 1963) probably acts as a mode ecological isolation. Furthermore, as is the case of S.hibernica which also appears to be an extreme form of S.europaea adapted to a particular habitat, many diploid populations are cleistogamous and self-fertilisation frequently occurs which would reduce selection pressure for genetic isolation. Cleistogamy may have arisen as an adaptation which assures that pollination, fertilisation and seed set occurs under less favourable conditions.

evolution In the tetraploid aggregate selection pressure perhaps may have acted towards developing genetical isolation especially in populations of S.fragilis and S.dolichostachya which occur together in the same marsh, as Dalby (1962) has shown that cross pollination is possible in plants with chasmogamous flowers.

The results of attempted hybridisations carried out in the present study seem to support this view especially where populations of S.fragilis and S.dolichostachya from the same locality did not set viable seed which germinated while attempted crosses between populations of S.fragilis and S.dolichostachya from different localities did set seed which germinated though the progeny did not grow to maturity.

justifiable If the origin of the tetraploid aggregate is considered to be autopolyploid, in spite of the fact that this phenomenon is not considered to have played a major role in the evolution of polyploid series in flowering plants as a whole (Heslop-Harrison 1953), S.dolichostachya may have arisen as a specialised ecotype to a particular habitat and has later become genetically isolated to some extent. S.fragilis occurs in more

varied habitats and the variation is more complex. Ball & Tutin (1959) have described three tetraploid species which in the present investigation are considered to all belong to one variable species. Part of the explanation for this treatment lies in the fact that these workers had considered the group over a limited geographical range. It appears from the results of this present study, that populations of the tetraploid aggregate assigned to S.fragilis are still in a condition of active evolution and some populations are more distinct than others. There is a need for more detailed cytological investigations and breeding experiments before the evolutionary history of the genus may be properly understood.

It has been concluded that the continuous and often reticulate pattern of variation of the characters in the populations studied have made the interpretation and delimitation of taxa within the genus often only possible if a number of different characters are considered independently and samples of populations are examined rather than individual plants.

Species have been recognised within the two chromosome aggregates, because treatment at subspecific rank does not seem justifiable as there is little geographical or ecological isolation, many of the taxa occurring commonly side by side in the same locality and often in more or less the same habitat.

However unsatisfactory it may seem to accept species which show a considerable amount of variation and overlap in many of the diagnostic morphological characters. It does seem necessary in difficult groups such as Salicornia that the

interpretation of the species concept cannot be too rigid if some sort of working order is to be introduced into what would otherwise be a very confused aggregate.

APPENDIX I

Photographs of the six species of Irish

Salicornia recognised in this study

S. peruviana Mill. Duncormick, Co. Wexford

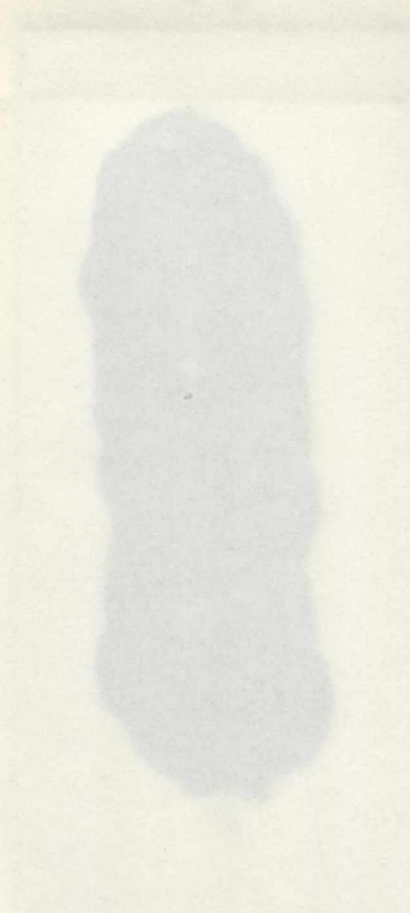
(Entire plant)

x 1/2



(Fertile portion)

x 3



APPENDIX I

S. pusilla Woods. Tramore, Co. Waterford

Photographs of the six species of Irish

Salicornia recognised in this study



S. perennis Mill. Duncormick, Co. Wexford

(Entire plant)
x 1/2

(Fertile spike)
x 5



PLATE 9

S. pusilla Woods. Tramore, Co. Waterford

(Entire plant)
x 1/2

(Terminal spike)
x 5



S. hibernica Ferguson

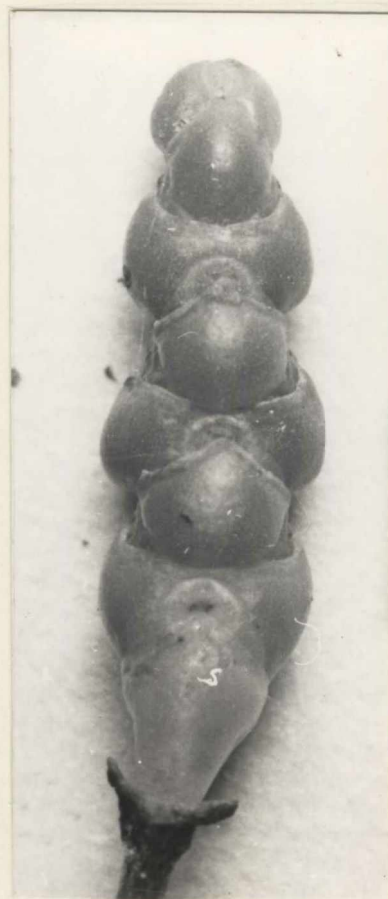
Tramore Co. Waterford

Wild parent.

(Entire plant)
x 1/2



(Terminal spike)
x 5



Cultivated progeny

(Entire plants)
x 2/3



(Terminal spike)
x 5



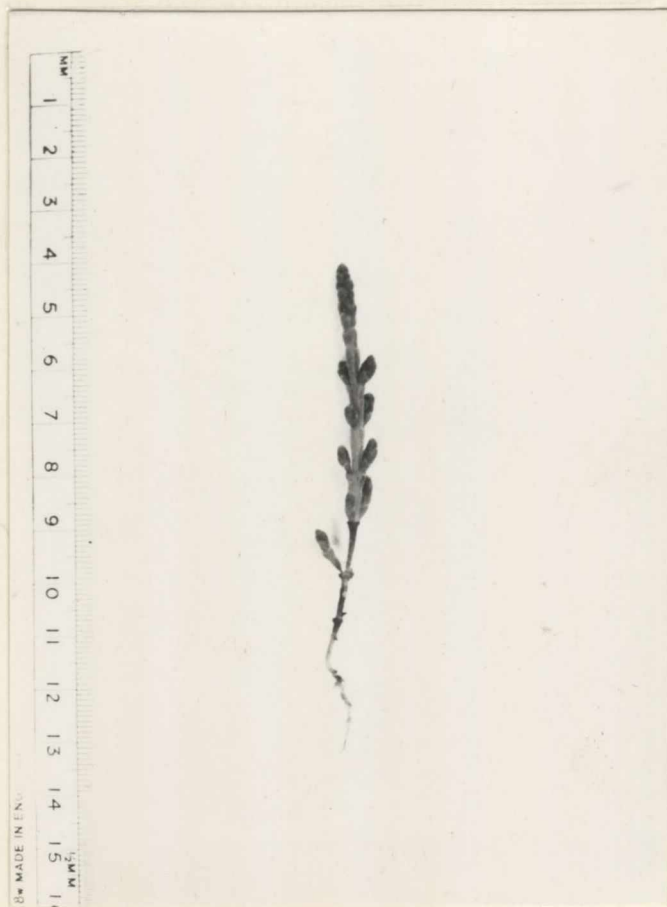
S.hibernica Ferguson

Ballyvaughan, Co. Clare.

Wild parent.

(Entire plant)
x 1/2

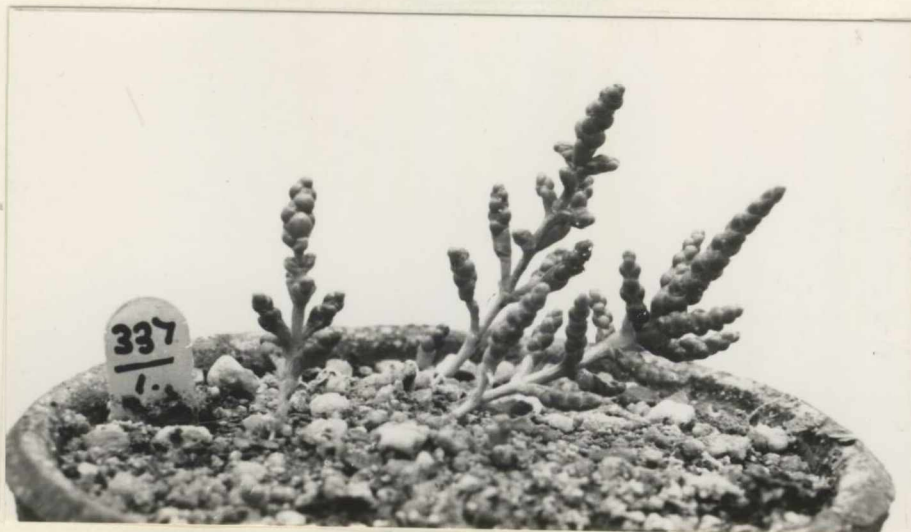
(Terminal spike)
x 5



Cultivated progeny

(Terminal spike)
x 5

(Entire plants)
x 2/3



S. europaea L.

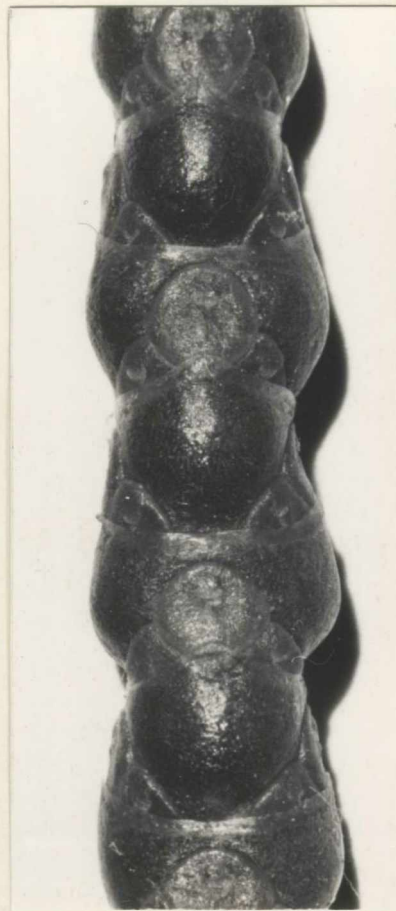
Rush, Co. Dublin (pop. 4)

Wild parent.

(Entire plant)
x 1/2



(Terminal spike)
x 5



Cultivated progeny.

(Entire plant)
x 2/3



(Terminal spike)
x 4

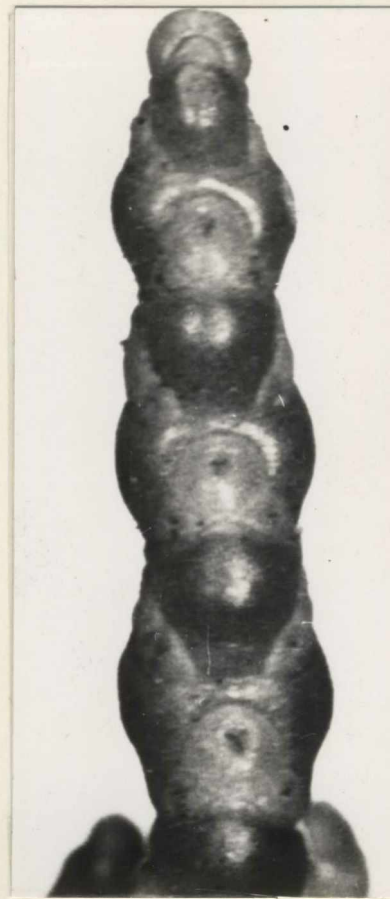


PLATE 13

S.europaea L.

Dollymount, Co. Dublin.

A little branched wild plant

(Entire plant)
x 1/2(Terminal spike)
x 5

PLATE 14

S.europaea L.

Rush, Co. Dublin.

A robust wild plant with short fertile spikes

(Entire plant)
x 1/2(Terminal spike)
x 5

S. europaea L.

Rush, Co. Dublin.

A robust wild parent plant with long fertile spikes.

(Entire plant)
x 1/2(Terminal spike)
x 5

Cultivated progeny

(Entire plant)
x 2/3(Terminal spike)
x 4

S. fragilis Ball & Tutin

Comber, Co. Down (pop. 19b)

(Entire plant)
x 1/2

(Terminal spike)
x 5



PLATE 17

S. fragilis Ball & Tutin

Comber, Co. Down (pop. 19)

(Entire plant)
x 1/2

(Terminal spike)
x 5



S. fragilis Ball & Tutin

Tramore, Co. Waterford, (pop. 12)

A wild parent plant resembling S. nitens Ball & Tutin in habit and the shape of the fertile segments.

(Entire plant)
x 1/2

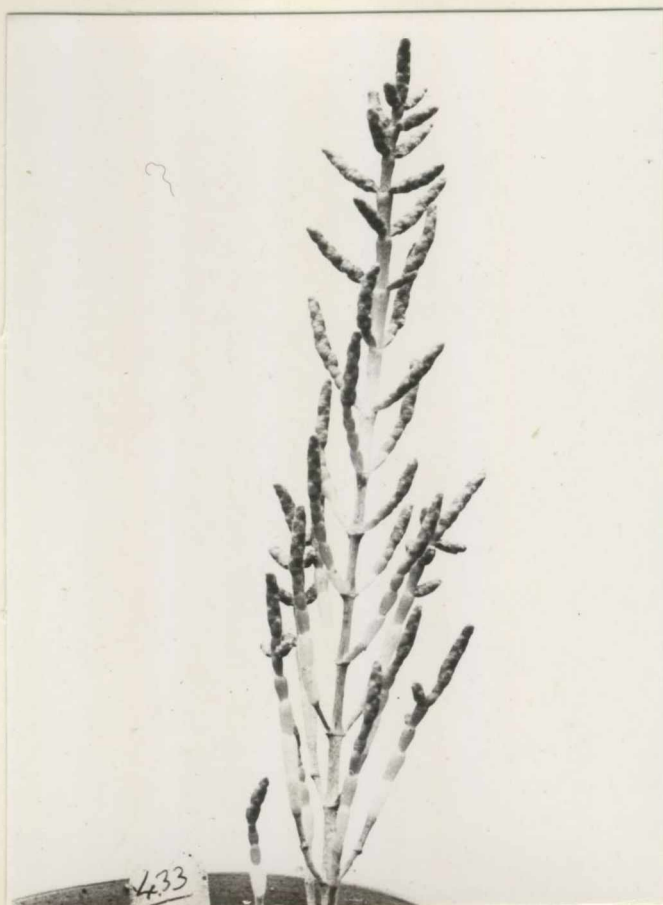
(Terminal spike)
x 5



Cultivated progeny with fertile segments that more closely resemble those of typical S. fragilis (Plates 16 and 17).

(Entire plant)
x 2/3

(Terminal spike)
x 5



S. fragilis Ball & Tutin

Dollymount, Co. Dublin (pop. 11)

A wild parent plant resembling S. nitens Ball & Tutin in habit and the very slender fertile spikes.

(Entire plant)
x 1/2



(Terminal spike)
x 5



Cultivated progeny

(Entire plant)
x 3/4



(Terminal spike)
x 5



S. fragilis Ball & Tutin

Rush, Co. Dublin (pop. 18)

A wild parent plant resembling S. nitens Ball & Tutin in colour and in the shape of the fertile segments.

(Entire plant)
x 1/2

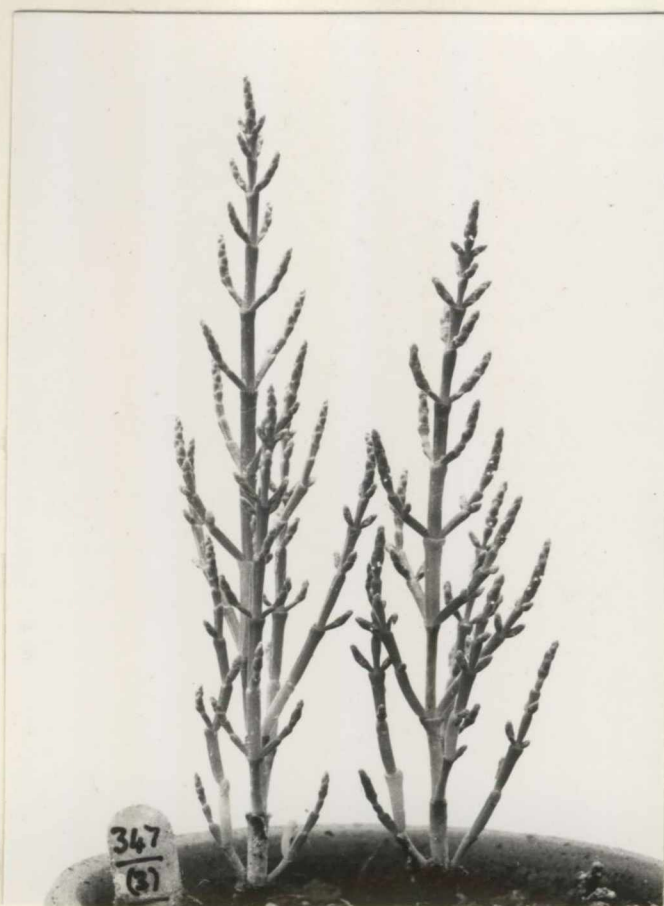


(Terminal spike)
x 5

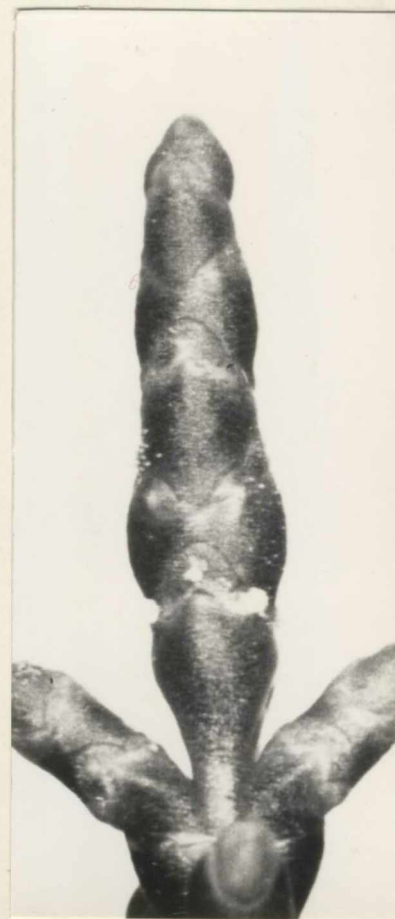


Cultivated progeny resembling the parent plant in shape of the fertile segments but not in colour.

(Entire plant)
x 2/3



(Terminal spike)
x 5



S. fragilis Ball & Tutin

Tramore, Co. Waterford (pop. 13)

A wild parent plant with long fertile spikes resembling
S. dolichostachya Moss

(Entire plant)
x 1/2

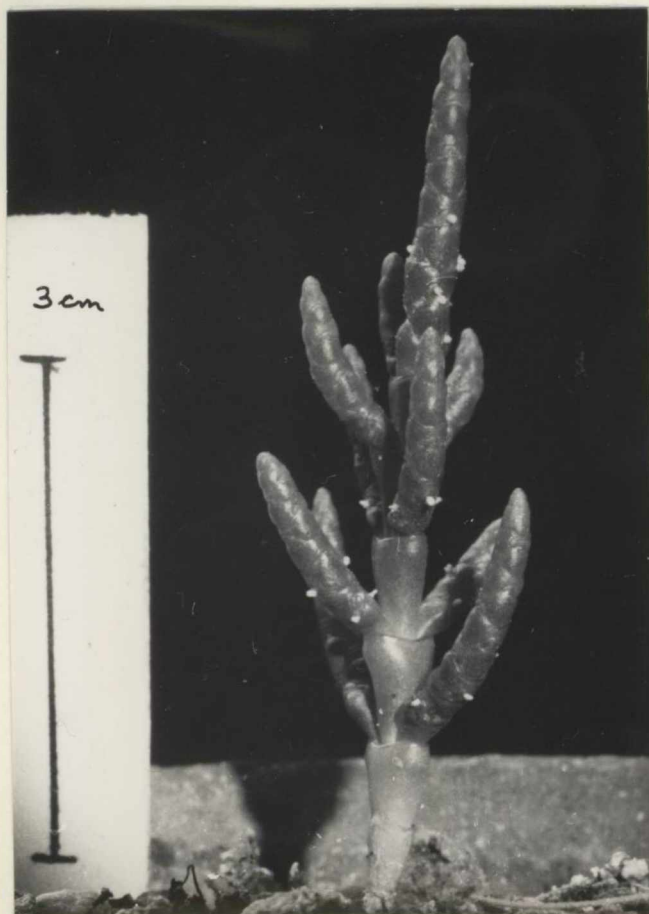


(Terminal spike)
x 5



Cultivated progeny

(Entire plant)
x 1 1/2



(Terminal spike)
x 5



S.dolichostachya Moss

Rush, Co. Dublin (pop. 15)

Wild parent

(Entire plant)
x 2/5

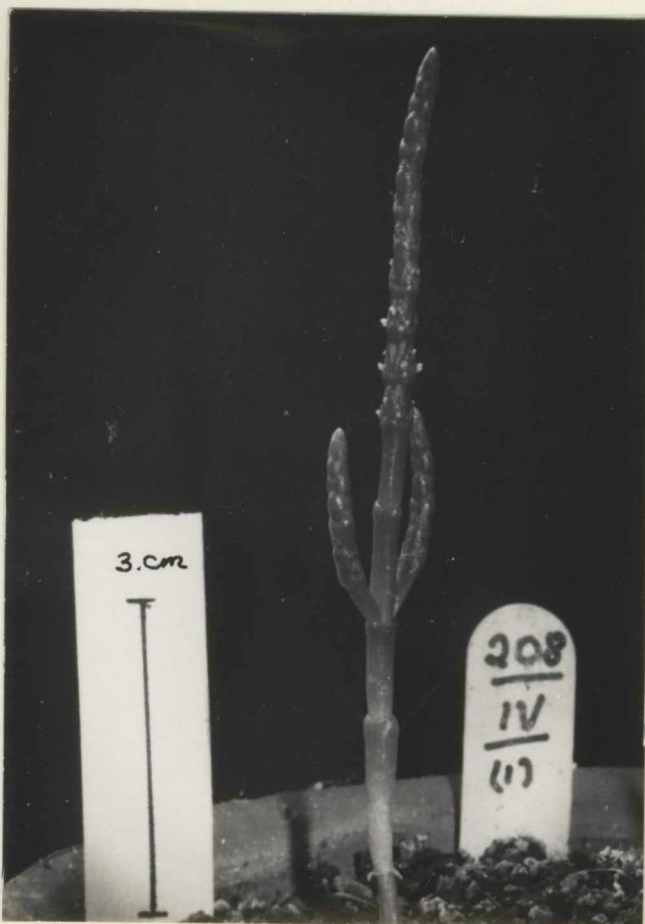


(Terminal spike)
x 5

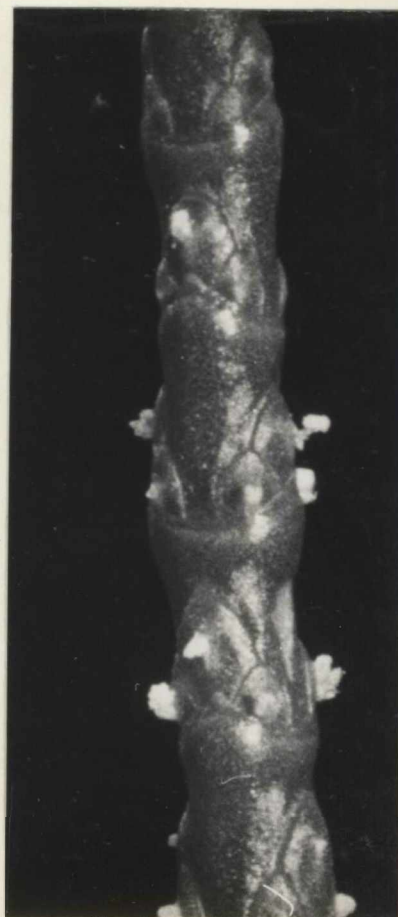


Cultivated progeny

(Entire plant)
x 1



(Terminal spike)
x 4



APPENDIX II

DISTRIBUTION IN IRELAND OF THE SPECIES OF *SALICORNIA* RECOGNISED IN THIS WORK

Figures 1-6 show the distribution in Ireland of the six species of *Salicornia* recognised in this study. Each circle is centred on the 10 kilometre square from which a record has been obtained. Open circles (occurring in Fig. 2 only) represent unconfirmed B.S.B.I. (1962) records. The vice counties, localities and 10 kilometre grid square records where each of the species occurs are given in the Table Distribution which follows the distribution maps.

FIGURE 1
The distribution of Salicornia in Ireland.

APPENDIX II

DISTRIBUTION IN IRELAND OF THE SPECIES OF SALICORNIA
RECOGNISED IN THIS WORK

Figures 1-6 show the distribution in Ireland of the six species of Salicornia recognised in this study. Each circle is centred in the 10 kilometre square from which a record has been obtained. Open circles (occurring in Fig. 2 only) represent unconfirmed B.S.B.I. (1962) records. The vice counties, localities and 10 kilometre grid square records where each of the species occurs are given in the Table which follows the distribution maps.

FIGURE I

The distribution of Salicornia perennis Mill. in
Ireland.



FIGURE 2

The distribution of Salicornia pusilla Woods in
Ireland.

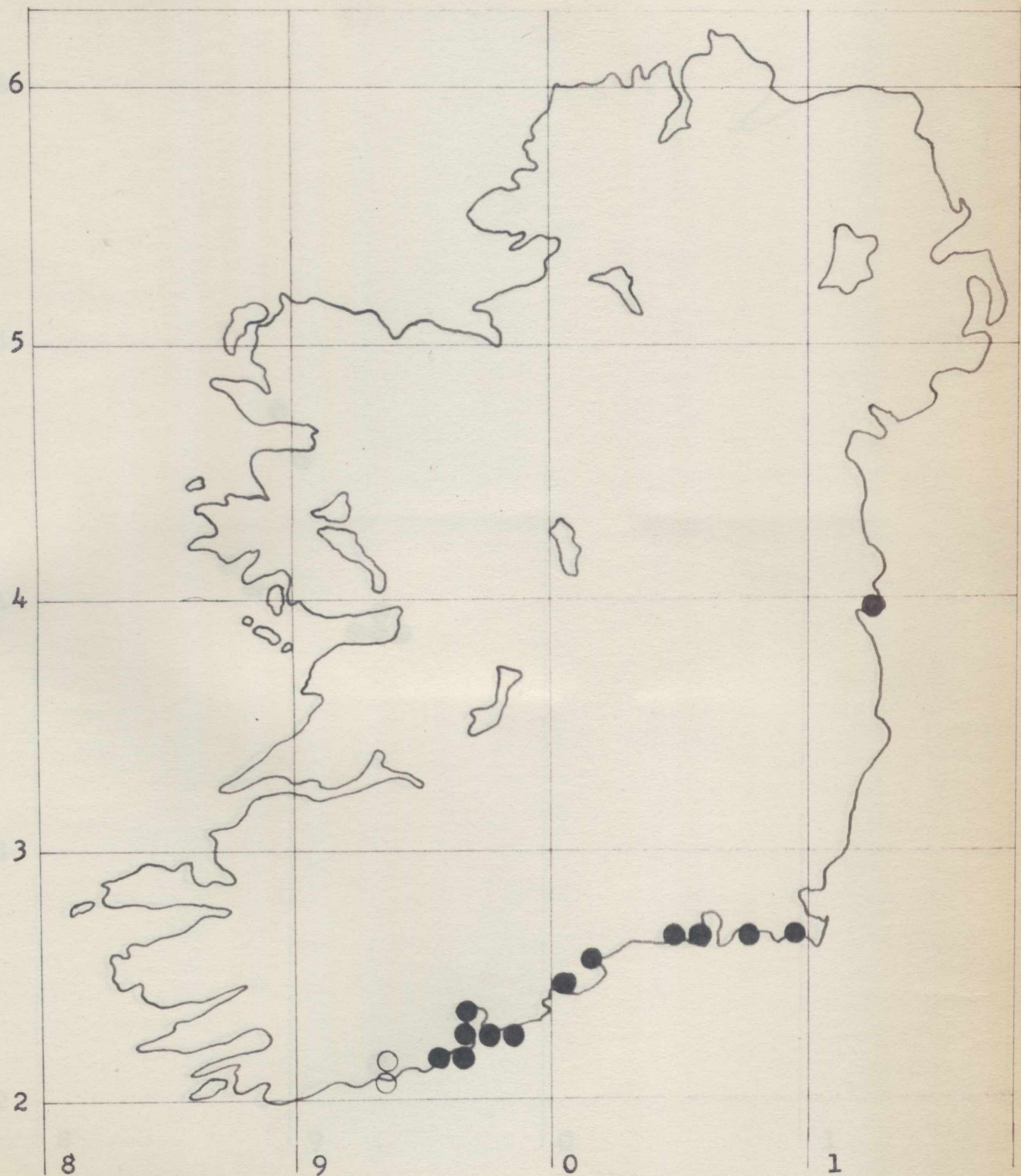


FIGURE 3.

The distribution of Salicornia hibernica Ferguson
in Ireland.

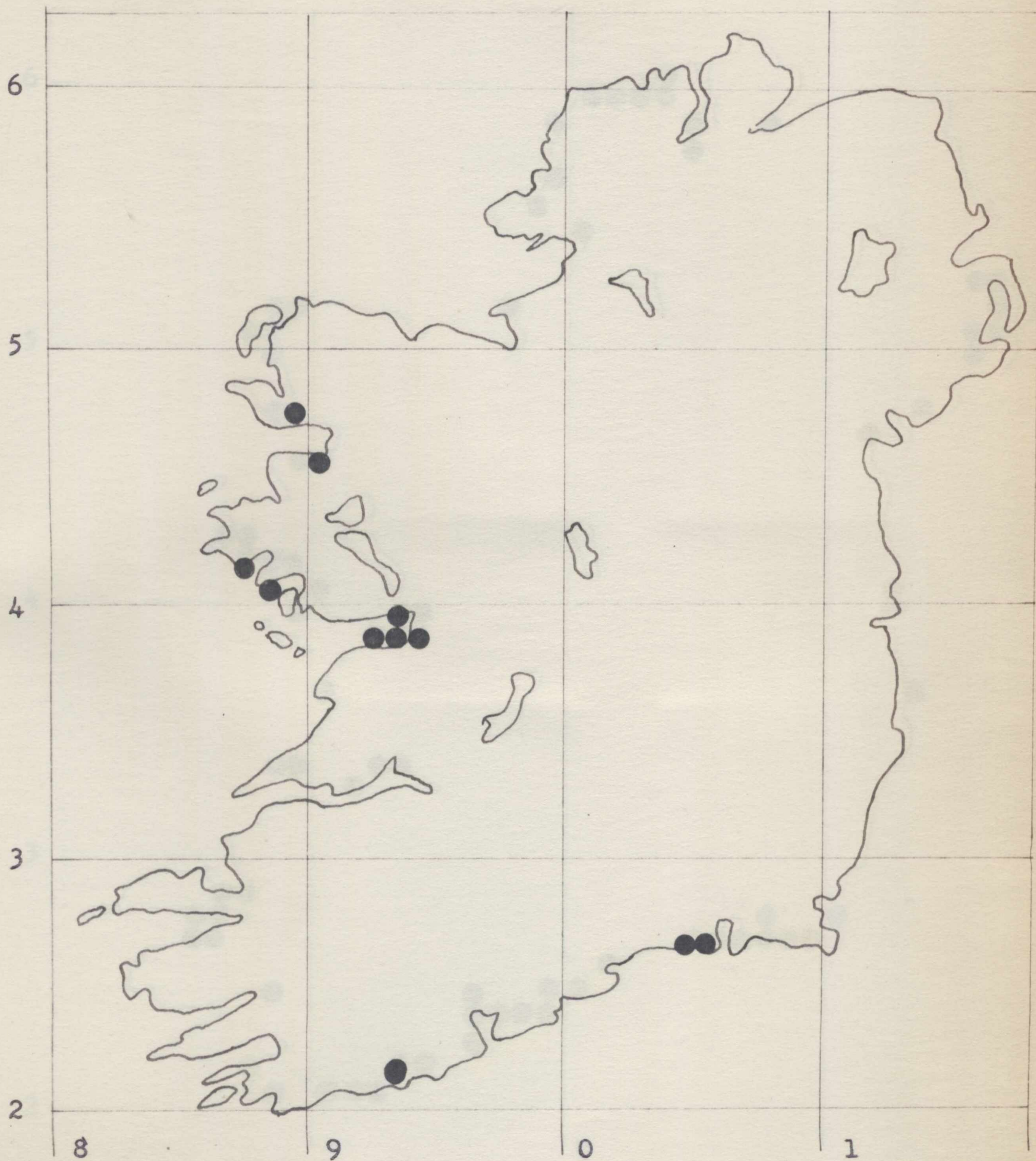


FIGURE 4.

The distribution of Salicornia europaea L. in Ireland.

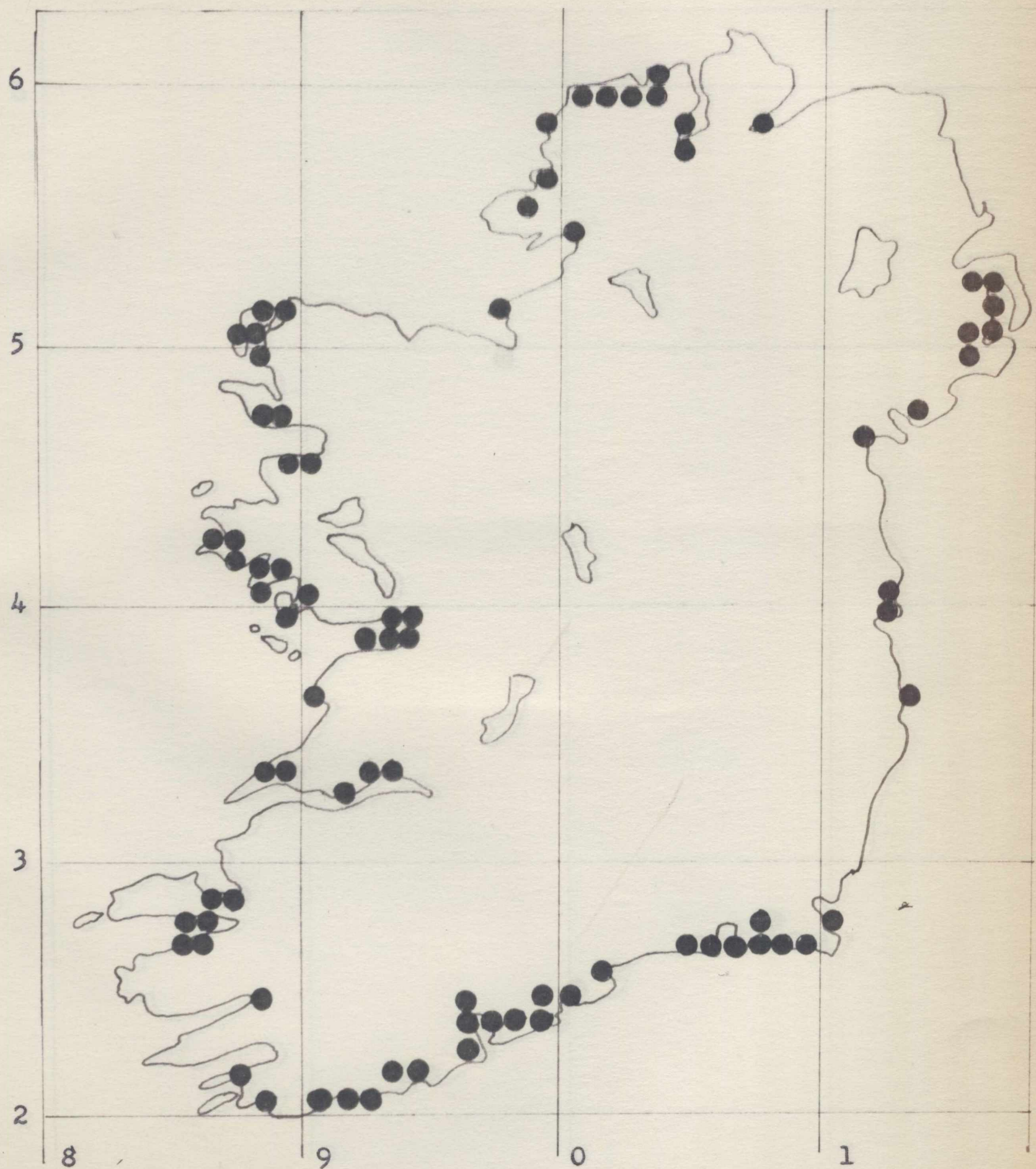


FIGURE 5.

The distribution of Salicornia fragilis P.W.Ball & Tutin
in Ireland.

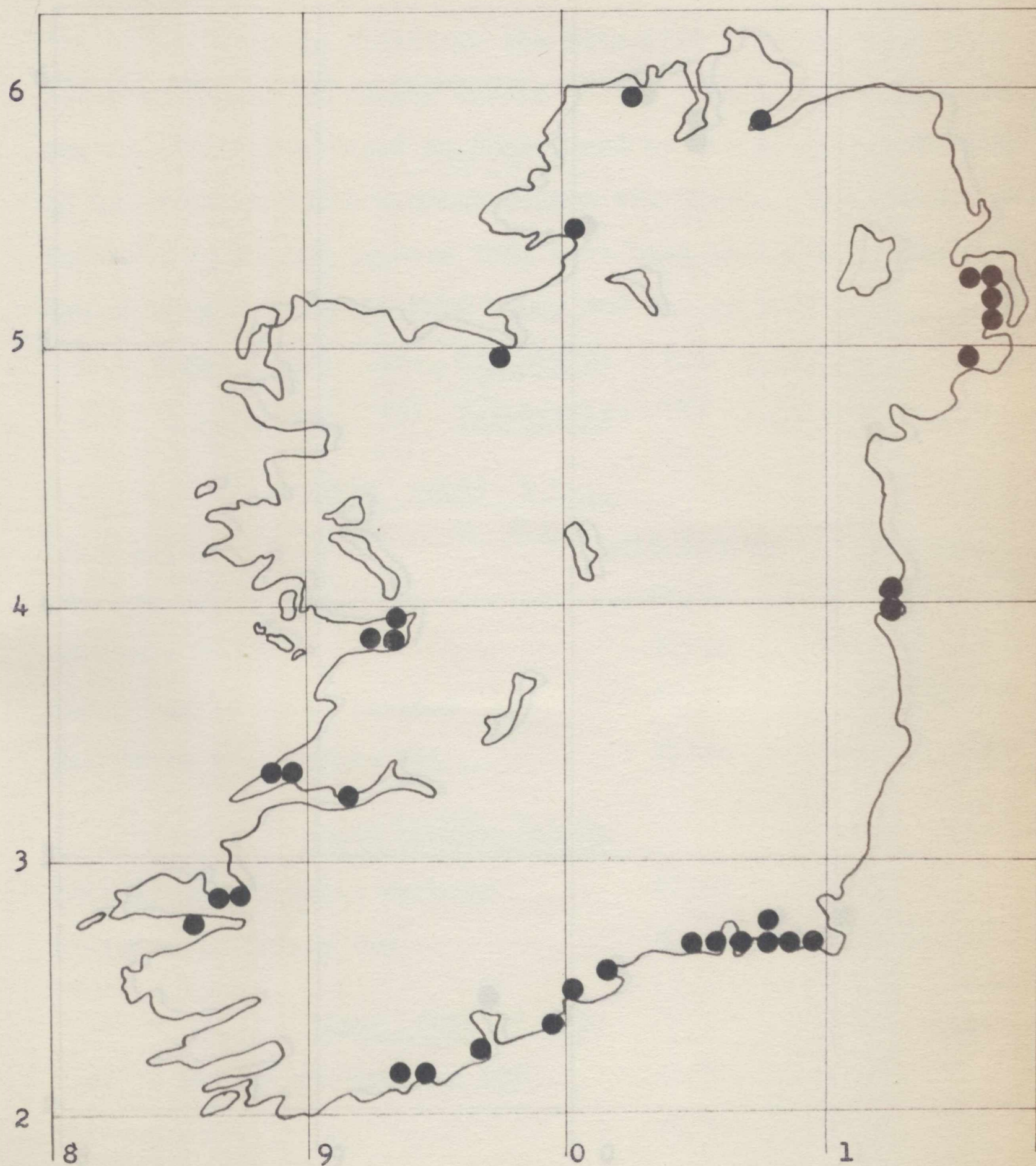
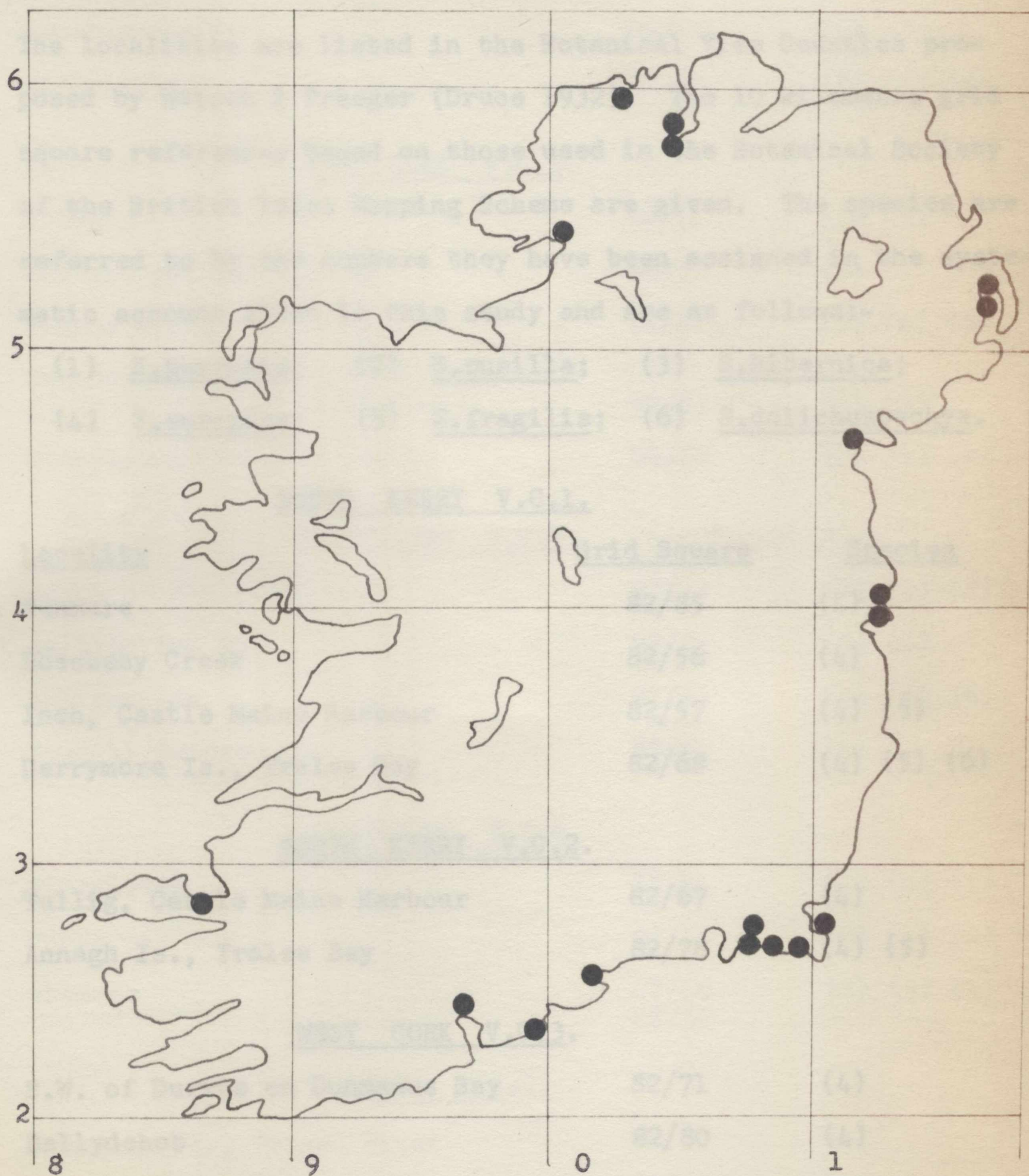


FIGURE 6.

The distribution of Salicornia dolichostachya Moss in
Ireland.



THE LOCALITIES IN IRELAND WHERE
THE SPECIES OF SALICORNIA RECOGNISED
IN THIS WORK HAVE BEEN FOUND

The localities are listed in the Botanical Vice Counties proposed by Watson & Praeger (Druce 1932). The 10 kilometre grid square references based on those used in the Botanical Society of the British Isles Mapping Scheme are given. The species are referred to by the numbers they have been assigned in the systematic account given in this study and are as follows:-

- (1) S.perennis; (2) S.pusilla; (3) S.hibernica;
 (4) S.europaea; (5) S.fragilis; (6) S.dolichostachya.

SOUTH KERRY V.C.1.

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
Kenmare	82/85	(4)
Rossbehy Creek	82/56	(4)
Inch, Castle Maine Harbour	82/57	(4) (5)
Derrymore Is., Tralee Bay	82/68	(4) (5) (6)

NORTH KERRY V.C.2.

Tullig, Castle Maine Harbour	82/67	(4) (4) (5)
Annagh Is., Tralee Bay	82/78	(4) (5) (5) (6)

WEST CORK V.C.3.

S.W. of Durrus on Dunmanus Bay	82/71	(4)
Ballydehob, Fergus River	82/80	(4)
Unionhall	92/00	(4)
Rosscarberry, nr. Labasheeda	92/10	(4)

WEST CORK V.C.3.
(continued)

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
Muckross Head Rd., Clonakilty	92/30	(4)
Courtmacsherry	92/31	(4)
Kilbrittain	92/31	(3) (4) (5)

MID CORK V.C.4.

Kinsale	92/41	(4) (5)
Eastern Bridge Kinsale	92/52	(2) (4) (5)
Minane Bridge	92/62	(2) (4) (5)
Owenboy River (c. 2 miles east of Carrigahne)	92/63	(2) (4)
Glanmire (c. 1 mile south)	92/64	(2) (4) (6)

EAST CORK V.C.5.

South of Middleton	92/73	(2) (4) (5)
Ballycotton Bay	92/83	(2) (4)
Ballymacoda	92/93	(4) (5) (6)
Youghal Bridge	92/94	(4)

WATERFORD V.C.6.

Kinsalebeg	02/04	(2) (4) (5)
Dungarvan Bay	02/15	(2) (4) (5) (6)
Tramore	02/46	(2) (3) (4) (5)

CLARE V.C.9.

Drumquin Pt., Fergus River	93/33	(4)
Killadysert	93/23	(4)
Goleen Bridge, nr. Labasheeda	93/12	(4)

CLARE V.C.9.
(continued)

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
Clonderlaw House, nr. Labasheeda	93/12	(4) (5)
Moyasta	83/93	(4) (5)
Blackweir Bridge, Poultnasherry Bay	83/83	(4) (5)
Lehinch	93/06	(4)
Newquay	93/38	(3) (4) (5)
Finavarra	93/28	(3) (4) (5)

WEXFORD V.C.12.

Rosslare Point	12/07	(4) (6)
Tacumshin Lake	02/96	(2) (4) (5) (6)
Duncormick	02/86	(1) (4) (5) (6)
Wellington Bridge	02/77	(4)
Garrycullen	02/77	(4) (5) (6)
Saltmills, Bannow Bay	02/76	(2) (4)
Fethard-on-Sea	02/76	(1) (4) (5) (6)
Near Ballygow (N. of Fethard)	02/66	(4) (5)

SOUTH-EAST GALWAY V.C.15.

Dunbuleann Bay, nr. Clarinbridge	93/48	(3) (4)
Tawin Island	93/39	(3) (4) (5)
Kilcainin House, Belmullet	93/39	(3) (4) (5)
Oranmore Saleen Harbour, Blacksod Bay	93/49	(4)
Saleen Harbour & Elly Bay	85/70	(4)
Near Pollatominish, Scrwaddacon Bay	85/91	(4)

WEST GALWAY V.C.16.

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
Rossaveel, Cashla Bay	83/99	(4)
Costello, Cashla Bay	84/90	(4)
Flannery's Bridge, Kilkieran Bay	84/91	(4)
Carna, Mweenish Bay	84/80	(3) (4)
Bunnahown, Bertraghboy Bay	84/81	(4)
Roundstone	84/71	(3) (4)
Ballinaboy, Mannin Bay	84/62	(4)

WICKLOW V.C.20.

Six Mile Point	13/36	(4)
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DUBLIN V.C.21.

North Bull, Dollymount	13/29	(4) (5) (6)
Baldoyle	13/29	(4) (5)
Malahide	14/20	(4)
Rush Estuary	14/20	(4) (5) (6)

WEST MAYO V.C.27.

Murrisk on Westport Bay	84/95	(4)
Killadangan, Westport Bay	94/05	(3) (4)
Mullaranny Strand	84/97	(3) (4)
Salia, Achill Island	84/87	(4)
Gweesalia, Blacksod Bay	84/89	(4)
Greenfield House, Belmullet	85/81	(4)
North of Saleen Harbour, Blacksod Bay	85/80	(4) (5) (6)
Saleen Harbour & Elly Bay	85/70	(4)
Near Pollatomish, Scruwaddacon Bay	85/91	(4)

SLIGO V.C.28.

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
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Road to Strandhill, Ballysadare Bay	94/79	(5)
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Grange	95/71	(4)
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LOUTH V.C.31.

Soldiers' Point, Dundalk Harbour	14/16	(4) (6)
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SOUTH DONEGAL V.C.34.

Carrick, nr. Laghy	05/04	(4) (5)
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Manorcunningham	05/47	(4) (6)
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NORTH DONEGAL V.C.35.

Tantallon	05/04	(4) (5)
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Maghera, Loughros Beg Bay	05/85	(4)
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Owenea River, N. of Ardara	95/96	(4)
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Annagary, The Rosses	95/98	(4)
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Derrybeg, Gweedore	05/09	(4)
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Ballyness Bay, nr. Falcarragh	05/19	(4)
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Creelough	05/29	(4) (5) (6)
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Carrickart	06/30	(4)
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Mulroy Bay, N. of Milford	05/39	(4)
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Aughnish Is., nr. Rathmelton	05/48	(4) (6)
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DOWN V.C.38.

Comber River	15/52	(4) (5)
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Castle Espie	15/62	(4) (5) (6)
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Island Mahee	15/61	(4) (5) (6)
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Killyleagh, Is. Taggart	15/60	(4) (5)
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Quoile Bridge, Downpatrick	15/50	(4)
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DOWN V.C.38.

(continued)

<u>Locality</u>	<u>Grid Square</u>	<u>Species</u>
Dundrum Bay	14/59	(4) (5)
Ballygowan, Carlingford Lough	14/37	(4)

DERRY V.C.40.

Ballykelly, nr. Limavady	05/78	(4) (5)
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APPENDIX III

Tables of measurements

TABLE I

Ratio of the length of the lower primary branches
to the height of the main stem.

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
1	Tramore	18	1.76	0.27	1.4 - 2.4
15	Rush	25	1.86	0.14	1.6 - 2.2
2	Rush	23	1.92	0.76	1.3 - 4.6
15A	Rush	25	2.08	0.33	1.6 - 2.7
18	Rush	25	2.17	0.63	1.8 - 2.7
28	Tachumshin	23	2.23	0.59	1.6 - 3.8
22	Baldoyle	25	2.39	0.45	1.8 - 3.1
19	Comber	49	2.53	0.68	1.7 - 4.8
25	Limavady	25	2.78	1.78	1.3 - 7.2
15B	Rush	24	2.99	0.67	2.2 - 4.7
23	Comber	25	3.00	0.99	1.9 - 6.4
9	Bull Island	25	3.20	1.62	2.0 - 7.0
11	Bull Island	24	3.24	0.68	1.9 - 4.6
4	Rush	25	3.52	1.73	1.8 - 8.5
8	Tramore	23	3.88	1.52	1.7 - 8.4
24	Island Mahee	25	4.12	2.53	1.82 - 10.1
13	Tramore	25	5.07	2.4	2.5 - 11.8
3	Bull Island	25	6.55	3.21	3.1 - 11.6
10	Tramore	25	6.75	1.5	4.5 - 9.5

APPENDIX III

Tables of measurements

TABLE I

Ratio of the length of the lower primary branches
to the height of the main stem. (cm)

Measurements made when the lower fertile segments were in flower.

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
1	Tramore	18	1.76	0.27	1.4 - 2.4
15	Rush	25	1.86	0.14	1.6 - 2.2
2	Rush	23	1.92	0.76	1.3 - 4.6
15A	Rush	25	2.08	0.33	1.6 - 2.7
18	Rush	25	2.17	0.63	1.8 - 2.7
28	Tachumshin	23	2.23	0.59	1.6 - 3.8
22	Baldoyle	25	2.39	0.45	1.8 - 3.1
19	Comber	49	2.53	0.68	1.7 - 4.8
25	Limavady	25	2.78	1.78	1.3 - 7.2
15B	Rush	24	2.99	0.67	2.2 - 4.7
23	Comber	25	3.00	0.99	1.9 - 6.4
9	Bull Island	25	3.20	1.62	2.0 - 7.0
11	Bull Island	24	3.24	0.68	1.9 - 4.6
4	Rush	25	3.52	1.73	1.8 - 8.5
8	Tramore	23	3.88	1.52	1.7 - 8.4
24	Island Mahee	25	4.12	2.53	1.82 - 10.1
13	Tramore	25	5.07	2.4	2.5 - 11.8
3	Bull Island	25	6.55	3.21	3.1 - 11.6
15	Cultivated	25	3.22	0.85	1.6 - 4.8
16	Dungarvan	20	6.92	1.4	4.5 - 9.5

TABLE IIa

Length of the terminal spike (in cm)Measurements made when the lower fertile segments were in flower.

<u>Population number</u>	<u>Locality</u>	<u>No. of plants measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
2	Rush	25	0.69	0.23	0.4 - 1.1
26	Ballyvaughan	20	0.8	0.17	0.6 - 1.1
1	Tramore	20	0.86	0.28	0.5 - 1.6
	Cultivated	1	0.9	-	-
3	Bull Island	25	0.9	0.34	0.5 - 1.8
	Cultivated	25	1.24	0.33	0.8 - 2.0
17	Kilcainin	25	1.09	0.26	0.7 - 1.9
	Cultivated	3	0.9	0.43	0.7 - 1.1
5	Ballyvaughan	25	1.1	0.3	0.7 - 1.9
	Cultivated	3	1.47	0.9	0.8 - 2.5
8	Tramore	25	1.04	0.2	0.7 - 1.5
	Cultivated	12	0.68	0.23	0.3 - 1.1
4	Rush	25	1.17	0.25	0.7 - 2.1
	Cultivated	15	0.88	0.2	0.5 - 1.2
27	Ballyvaughan	20	1.17	0.2	0.8 - 1.7
18	Rush	25	1.41	0.32	0.8 - 2.1
	Cultivated	25	1.40	0.23	1.0 - 2.0
15B	Rush	25	3.12	0.84	2.1 - 6.3
15A	Rush	25	4.2	0.46	3.4 - 5.6
15	Rush	25	5.18	1.34	2.7 - 7.2
	Cultivated	25	3.22	0.85	1.6 - 4.8
16	Dungarvan	20	6.92	1.4	4.5 - 9.5
15	Rush	8	10.33	2.6	8.1 - 15.5
14	Kilcainin	25	2.5	2.1	2.1 - 1.0
13	Coaher	25	2.9	1.0	1.0 - 1.0
	Cultivated	15	2.1	2.1	2.1 - 2.1
12	Coaher	25	10.7	2.6	5.2 - 13.4

TABLE IIb

Length of the terminal spike (in cm)
Measurements made when the lower fertile segments were in fruit.

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
2	Rush	25	4.5	0.82	3. - 7.
23	Comber	25	1.74	0.47	1.1 - 3.2
25	Limavady	25	1.84	0.8	0.6 - 3.5
20	Baldoyle	16	1.91	0.65	1.0 - 3.5
26	Cultivated	25	0.84	0.25	0.4 - 1.4
7	Kilcainin	25	1.93	0.63	1.0 - 3.5
	Cultivated	25	1.07	0.3	0.6 - 1.6
14	Kilcainin	25	2.28	0.9	1.4 - 4.4
8	Tramore	40	2.61	0.71	1.4 - 4.3
18	Cultivated	25	1.45	0.3	0.8 - 1.9
24	Island Mahee	25	2.7	1.03	1.1 - 5.3
22	Baldoyle	25	2.83	0.66	1.9 - 4.6
19B	Comber	25	2.92	0.7	1.6 - 4.1
	Cultivated	19	1.95	0.38	1.3 - 2.5
3	Bull Island	46	3.02	0.8	1.6 - 4.7
12	Tramore	30	3.1	1.2	1.5 - 6.8
	Cultivated	4	2.25	0.2	1.8 - 2.7
19	Comber	50	3.2	1.2	1.6 - 5.9
23	Comber	25	3.3	0.93	1.4 - 4.7
19A	Comber	49	3.9	1.2	2.1 - 7.9
	Cultivated	1	3.6	-	-
13	Tramore	18	4.7	1.3	2.9 - 7.4
15	Rush	8	10.33	2.6	8.1 - 15.5
14	Kilcainin	25	8.3	2.3	5. - 13.
19B	Comber	25	9.64	2.3	5. - 14.
	Cultivated	19	9.1	0.6	6. - 11.
19	Comber	50	10.3	2.6	5. - 15.
	Cultivated	25	11.7	11.9	-

TABLE III

Number of fertile segments in the terminal spike.

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
2	Rush	25	4.5	0.82	3. - 7.
17	Kilcainin	25	5.2	0.94	4. - 8.
	Cultivated	3	5.0	1.00	4. - 6.
27	Ballyvaughan	20	5.5	0.83	5. - 8.
26	Ballyvaughan	20	5.75	0.92	5. - 8.
5	Ballyvaughan	25	6.2	1.35	4. - 9.
	Cultivated	3	7.7	5.5	4. - 14.
3	Bull Island	25	6.3	1.06	5. - 8.
	Cultivated	25	6.44	1.44	4. - 10.
18	Rush	25	6.3	1.12	4. - 9.
	Cultivated	25	8.4	0.96	7. - 10.
23	Comber	25	6.4	1.4	4. - 10.
4	Rush	25	6.63	1.5	4. - 10.
	Cultivated	19	5.0	0.85	3. - 7.
8	Tramore 1962	25	6.68	1.34	5. - 10.
	1961	40	11.5	2.5	8. - 17.
	Cultivated 1962	12	4.3	0.9	3. - 5.
	1963	25	6.48	1.12	4. - 8.
1	Tramore	20	6.8	1.28	5. - 10.
25	Limavady	25	7.2	2.1	3. - 11.
20	Baldoyle	16	7.25	2.0	4. - 12.
	Cultivated	25	5.1	1.04	3. - 7.
7	Kilcainin	25	7.6	1.71	5. - 11.
	Cultivated	25	5.2	1.63	3. - 9.
14	Kilcainin	25	8.3	2.3	5. - 13.
19B	Comber	25	9.64	2.3	5. - 14.
	Cultivated	19	9.1	0.6	6. - 11.
19	Comber	50	10.3	2.6	5. - 15.
	Rush	25	58.0	13.7	33. - 100.
	Cultivated	25	68.2	11.9	50. - 90.

TABLE III
(continued)

<u>Population number</u>	<u>Locality</u>	<u>No. of plants measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
12	Tramore	30	10.3	3.2	6. - 20.
	Cultivated	4	10.5	0.87	10. - 12.
15B	Rush	25	10.9	2.1	9. - 18.
19A	Comber	49	11.3	2.7	7. - 19.
	Cultivated	1	20.0	-	-
24	Island Mahee	25	11.4	3.5	7. - 19.
11	Bull Island	25	11.4	1.4	9. - 13.
22	Baldoyle	25	11.88	2.2	8. - 16.
9	Bull Island	25	12.3	2.13	6. - 15.
19C	Comber	25	12.1	2.71	6. - 17.
15A	Rush	25	13.5	1.35	11. - 17.
15	Rush 1962	25	15.2	2.2	10. - 18.
19	Comber 1961	15	16.0	2.75	11. - 21.
	Cultivated	25	12.0	1.88	8. - 15.
13	Tramore	18	16.5	3.54	11. - 24.
	Cultivated	5	16.5	4.75	10. - 22.
16	Dungarvan	20	20.4	3.02	15. - 25.
15B	Rush	25	123.0	35.1	75 - 260
	Cultivated	2	183.0	-	-
22	Baldoyle	25	128.0	42.3	89 - 228
15A	Rush	25	160.75	31.4	120 - 242

TABLE IV

Ratio of the number of fertile segments in the terminal
spike to the number of sterile segments in the plant.

2	Rush	25	39.0	11.3	21. - 64.
17	Kilcainin	25	44.0	10.5	31. - 75.
	Cultivated	3	43.0	8.75	33. - 50.
25	Limavady	25	55.4	22.3	18. - 100.
23	Comber	25	57.3	15.1	36. - 90.
18	Rush	25	58.0	13.7	33. - 100.
	Cultivated	25	68.2	11.9	50. - 90.

TABLE IV
(continued)

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
1	Tramore	18	59.0	26	35 - 143
	Cultivated	1	50.0	-	-
4	Rush	25	60.0	24.8	29 - 143
	Cultivated	19	48.8	9.9	27 - 70
26	Ballyvaughan	20	63.0	12.8	45 - 88
7	Kilcainin	25	75.92	30.6	38 - 180
	Cultivated	24	37.96	10.8	20 - 60
5	Ballyvaughan	25	77.1	19.3	50 - 117
27	Ballyvaughan	20	78.6	17.6	50 - 114
14	Kilcainin	25	82.8	40.0	50 - 200
8	Tramore 1962	25	85.7	20.2	50 - 133
	Cultivated 1963	25	62.7	13.2	36 - 87
	Cultivated 1962	12	36.4	9.7	21 - 50
19	Comber	50	95.96	37.0	40 - 214
	Cultivated	19	102.6	28	70 - 167
24	Island Mahee	24	98.5	40.3	47 - 190
	Cultivated	4	79.0	55.9	38 - 162
19C	Comber	25	118.7	37.2	42 - 190
15B	Rush	25	123.0	35.1	75 - 260
	Cultivated	2	183.0	-	-
22	Baldoyle	25	128.0	42.3	89 - 228
15A	Rush	24	160.75	31.4	120 - 242
15	Rush	25	199.0	59	92 - 300
	Cultivated	25	153.0	36	100 - 230
	Rush	25	4.62	0.82	2.9 - 5.8
	Cultivated	25	3.6	0.63	2.3 - 4.9

TABLE Va

Mean length of the third fertile segment in the terminal spike
(in mm)

Measurements made during flowering

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
26	Ballyvaughan	20	1.54	0.17	1.2 - 2.0
	Cultivated	3	1.92	0.19	1.7 - 2.0
1	Tramore	20	1.53	0.22	1.03 - 2.0
3	Bull Island	25	1.61	0.34	1.1 - 2.5
	Cultivated	25	1.92	0.27	1.5 - 2.6
2	Rush	25	1.63	0.23	1.1 - 2.0
8	Tramore	25	1.68	0.19	1.4 - 2.1
5	Ballyvaughan	25	1.8	0.27	1.4 - 2.5
	Cultivated	25	2.11	0.57	1.6 - 3.0
4	Rush	25	2.02	0.25	1.7 - 2.9
27	Ballyvaughan	20	2.29	0.33	1.7 - 2.8
17	Kilcainin	25	2.30	0.30	1.9 - 2.9
18	Rush	25	2.80	0.25	2.1 - 3.1
14	Kilcainin	25	3.0	0.5	2.34 - 4.2
15B	Rush	25	3.34	0.47	2.6 - 5.0
9	Bull Island	25	3.5	0.7	2.1 - 4.8
	Cultivated	5	2.1	0.22	1.7 - 2.5
15A	Rush	25	3.88	0.32	3.3 - 4.7
16	Dungarvan	20	4.3	0.73	3.3 - 6.8
15	Rush	25	4.62	0.82	2.9 - 5.8
	Cultivated	25	3.6	0.63	2.3 - 4.9

TABLE Vb

Mean length of the third fertile segment in the terminal spike
(in mm)

Measurements made in early fruit

Tetraploid populations

<u>Population</u>	<u>Locality</u>	<u>No. of plants</u>	<u>Mean</u>	<u>Standard</u>	<u>Range</u>	
<u>number</u>	<u>Locality</u>	<u>measured</u>	<u>Mean</u>	<u>Deviation</u>	<u>Range</u>	
8	Tramore	40	2.6	0.26	2.1	- 3.4
	Cultivated	25	2.2	0.26	1.5	- 2.7
7	Kilcainin	25	2.7	0.43	1.8	- 3.9
20	Baldoyle	16	2.8	0.46	2.2	- 3.9
25	Limavady	25	2.8	0.56	1.8	- 3.8
24	Island Mahee	25	2.8	0.45	1.9	- 3.5
23	Comber	25	2.8	0.29	2.5	- 3.5
	Cultivated	19	2.64	0.26	2.1	- 3.0
22	Baldoyle	25	2.8	0.44	2.1	- 3.9
3	Bull Island	46	3.1	0.30	2.3	- 3.7
12	Tramore	30	3.2	0.50	2.6	- 4.5
	Cultivated	5	2.35	0.23	2.1	- 2.6
19B	Comber	25	3.3	0.34	2.9	- 3.9
13	Tramore	18	3.3	0.35	2.7	- 4.0
11	Bull Island	12	3.4	0.35	2.9	- 4.1
19	Comber	49	3.5	0.61	2.5	- 5.3
19A	Comber	49	3.7	0.52	3.0	- 5.3
15	Rush	8	5.6	0.48	4.96	- 6.6

Diploid populations

1	Tramore	20	2.1	0.15	1.9	- 2.44
17	Kilcainin	25	2.3	0.12	1.86	- 2.6
5	Ballyvaughan	25	2.6	0.15	2.32	- 2.9
25	Limavady	25	2.8	0.3	2.4	- 3.8
7	Kilcainin	25	3.2	0.3	2.7	- 3.8
24	Island Mahee	25	3.4	0.6	2.3	- 4.5
8	Tramore	40	3.5	0.3	2.9	- 4.1
3	Bull Island	46	3.6	0.3	2.9	- 4.1

TABLE VIa

Minimum diameter of the third fertile segment from
the base of the terminal spike (in mm)

<u>Tetraploid populations</u>					
<u>Population number</u>	<u>Locality</u>	<u>No. of plants measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
27	Ballyvaughan	20	2.38	0.19	1.97 - 2.73
11	Bull Island	25	2.55	0.12	2.3 - 2.8
18	Rush	25	2.55	0.24	2.2 - 3.1
14	Kilcainin	25	2.84	0.31	2.44 - 3.9
22	Baldoyle	25	2.84	0.19	2.6 - 3.1
23	Comber	25	2.9	0.3	2.44 - 4.0
15	Rush	25	3.02	0.35	2.38 - 3.83
16	Dungarvan	20	3.07	0.32	2.55 - 3.94
19	Comber	50	3.13	0.4	2.3 - 3.6
19A	Comber	25	3.23	0.25	2.9 - 3.8

TABLE VIb

Minimum diameter of the third fertile segment from the
base of the terminal spike (in mm)

<u>Diploid populations</u>					
1	Tramore	20	2.1	0.15	1.9 - 2.44
17	Kilcainin	25	2.3	0.12	1.86 - 2.6
5	Ballyvaughan	25	2.6	0.15	2.32 - 2.9
25	Limavady	25	2.8	0.3	2.4 - 3.8
7	Kilcainin	25	3.2	0.3	2.7 - 3.8
24	Island Mahee	25	3.4	0.6	2.3 - 4.5
8	Tramore	40	3.5	0.3	2.9 - 4.1
3	Bull Island	46	3.6	0.3	2.9 - 4.1

TABLE VII

Ratio of the greater/lesser diameter x 100 of the
Segment shape indices
 third fer... apike

(i)

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
8	Tramore	24	33	26.5	4 - 138
1	Tramore 1961	20	111	54.0	18 - 200
2	Rush 1962	25	144	41.0	56 - 225
13	Tramore	25	246	77.5	169 - 489
25	Limavady	25	307	119.6	109 - 578
11	Bull Island	25	348	55.0	268 - 443
15	Rush	25	493	140.0	308 - 800

(ii)

26	Ballyvaughan	20	134	4.9	126 - 144
8	Tramore	25	39.24	4.8	30 - 45
1	Tramore	20	51.20	5.05	40 - 61
2	Rush	24	55.20	4.86	43 - 61
13	Tramore	25	64.28	4.1	59 - 76
25	Limavady	25	70.28	10.04	43 - 83
11	Bull Island	25	73.44	3.16	69 - 82
15	Rush	25	89.68	9.6	69 - 105
15	Rush	25	127	4.4	118 - 134
	Cultivated	25	125	7.2	114 - 139
17	Kilcainin	24	126	4.7	116 - 133
	Cultivated	3	135	6.6	128 - 141
22	Baldoyle	25	126	7.3	108 - 140
16	Dungarvan	25	125	9.8	104 - 140
13	Tramore	18	125	6.8	115 - 145
27	Ballyvaughan	19	124	5.0	117 - 132
11	Bull Island	25	124	4.3	118 - 134
12	Tramore	29	124	9.0	110 - 152
	Cultivated	4	119	5.7	113 - 126

TABLE VII

(continued)

Ratio of the greater/lesser diameter x 100 of the
third fertile segment in the terminal spike

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
7A	Kilcainin	24	145	9.1	131 - 164
15B	Cultivated	25	146	9.2	127 - 162
8	Tramore 1961	40	142	7.1	124 - 165
14	1962	25	145	9.8	128 - 168
19	Cultivated	24	150	7.8	137 - 165
5	Ballyvaughan	25	140	7.6	124 - 152
	Cultivated	3	150	1.4	149 - 152
3	Bull Island	25	139	6.8	122 - 151
	Cultivated	25	141	8.8	124 - 159
4	Rush	25	137	6.6	127 - 151
2	Rush	24	134	6.7	122 - 149
26	Ballyvaughan	20	134	4.9	126 - 144
9	Bull Island	23	132	7.5	90 - 142
1	Tramore	20	130	8.5	120 - 145
	Cultivated	1	122	-	82 - 102
24	Island Mahee 1963	25	129	6.5	90 - 142
23	Comber	25	128.5	5.7	114 - 136
25	Limavady	25	128	7.4	115 - 138
18	Rush	25	128	5.4	116 - 138
5	Cultivated	24	129	4.6	120 - 137
15	Rush	25	127	4.4	118 - 134
2	Cultivated	25	125	7.2	114 - 139
17	Kilcainin	24	126	4.7	116 - 133
	Cultivated	3	135	6.6	128 - 141
22	Baldoyle	25	126	7.3	108 - 140
16	Dungarvan	25	125	9.8	104 - 140
13	Tramore	18	125	6.8	115 - 145
27	Ballyvaughan	19	124	5.0	117 - 132
11	Bull Island	25	124	4.3	118 - 134
12	Tramore	29	124	9.0	110 - 152
25	Cultivated	4	119	5.7	113 - 126

TABLE VII
(continued)

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of plants</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
19B	Comber	23	123	5.9	108 - 132
	Cultivated	19	127	8.0	114 - 156
19A	Comber	46	122	4.6	113 - 134
15B	Rush	25	120	5.0	112 - 131
14	Kilcainin	25	120	5.2	110 - 131
19	Comber	25	120	4.9	111 - 130
15C	Rush	35	118	7.2	108 - 138
14	Kilcainin	25	127	17.2	96 - 167
23	Comber	25	130	9.1	112 - 150
	Cultivated		135	14.6	117 - 162
19	Comber	49	131	10.2	106 - 160

TABLE VIII

The ratio of the length/width of the central floret of the
third fertile segment from the base of the terminal spike

8	Tramore 1962	40	92.8	6.5	82 - 102
	1961	39	95.4	6.6	82 - 102
16	Cultivated 1963	24	99.6	8.7	86 - 113
20	Baldoyle	16	99.4	7.8	85 - 115
7	Kilcainin	25	99.9	6.1	84 - 110
	Cultivated	25	98.6	8.7	89 - 117
5	Ballyvaughan	25	101	9.2	84 - 123
	Cultivated	3	99.7	4.6	97 - 105
2	Rush	25	102	6.9	88 - 113
3	Bull Island	46	102	9.4	88 - 125
	Cultivated	25	107	6.9	100 - 119
12	Tramore	30	106	10.1	74 - 131
26	Ballyvaughan	20	108	7.9	85 - 118
13	Tramore	18	108	8.5	97 - 124
24	Island Mahee	26	109.6	8.9	94 - 128
17	Kilcainin	24	110	5.7	100 - 121
	Cultivated	3	112	3.5	108 - 114
25	Limavady	25	111	11.0	81 - 132

TABLE IX

TABLE VIII

(continued)

<u>Population number</u>	<u>Locality</u>	<u>No. of plants measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
	Tramore		0.42		0.33 - 0.56
2	Rush		0.44	0.06	0.35 - 0.53
4	Rush	25	116	12.6	100 - 150
19B	Comber	25	122	13.9	94 - 146
19A	Comber	45	117	9.6	95 - 149
	Cultivated	9	120	8.5	107 - 136
27	Ballyvaughan	20	118	7.8	104 - 129
18	Rush	24	121.5	8.9	104 - 137
14	Kilcainin	25	127	17.2	96 - 167
23	Comber	25	130	9.1	112 - 150
	Cultivated	10	135	14.6	117 - 162
19	Comber	49	131	10.2	106 - 160
19C	Comber	25	130.6	9.95	113 - 148
22	Baldoyle	25	141.3	15.8	116 - 193
15B	Rush	25	154	17.3	114 - 182
15A	Rush	25	162	20.7	111 - 200
16	Dungarvan Bay	15	170	14.3	149 - 200
15	Rush	25	179	18.8	152 - 210
28	Cultivated	25	184	28.1	150 - 267
11	Bull Island	229	0.72	0.02	0.6 - 0.89
	Cultivated	7	0.74	0.03	0.7 - 0.82
13	Tramore 1961	149	0.77	0.02	0.6 - 0.95
	1962	252	0.74	0.07	0.6 - 0.93
	Cultivated	1	0.75	-	-
15A	Rush	189	0.74	0.11	0.56 - 0.95
18	Rush	195	0.74	0.09	0.58 - 0.91
	Cultivated	53	0.68	0.07	0.60 - 0.84
9	Bull Island	219	0.75	0.07	0.61 - 0.88
14	Kilcainin	7	0.75	0.05	0.68 - 0.82
19	Comber	51	0.75	0.07	0.63 - 0.91
	Cultivated 1962	26	0.74	0.03	0.63 - 0.91
	Cultivated 1963	12	0.77	0.07	0.67 - 0.88

TABLE IX
Anther Length (in mm)

<u>Population number</u>	<u>Locality</u>	<u>No. of anthers measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
1	Tramore	204	0.42	0.07	0.33 - 0.56
2	Rush	155	0.44	0.06	0.35 - 0.53
17	Kilcainin	19	0.46	0.03	0.4 - 0.51
26	Ballyvaughan	7	0.47	0.05	0.4 - 0.53
24	Island Mahee	20	0.47	0.03	0.4 - 0.54
3	Bull Island	163	0.48	0.05	0.35 - 0.6
	Cultivated	9	0.53	0.03	0.46 - 0.58
4	Rush	164	0.49	0.07	0.35 - 0.6
	Cultivated	69	0.46	0.05	0.33 - 0.58
5	Ballyvaughan	15	0.49	0.025	0.44 - 0.56
	Cultivated	4	0.54	0.02	0.53 - 0.58
6	Dungarvan	165	0.53	0.025	0.44 - 0.68
7	Kilcainin	4	0.54	0.025	0.51 - 0.6
	Cultivated	43	0.58	0.07	0.47 - 0.65
8	Tramore	214	0.59	0.09	0.47 - 0.7
	Cultivated 1962	48	0.56	0.09	0.51 - 0.65
	Cultivated 1963	50	0.60	0.025	0.53 - 0.68
22	Baldoyle	15	0.68	0.03	0.63 - 0.79
27	Ballyvaughan	5	0.7	0.02	0.67 - 0.72
28	Tachumshin	240	0.7	0.07	0.58 - 0.84
11	Bull Island	229	0.72	0.02	0.6 - 0.89
	Cultivated	7	0.74	0.03	0.7 - 0.82
13	Tramore 1961	149	0.77	0.02	0.6 - 0.95
	1962	252	0.74	0.07	0.6 - 0.93
	Cultivated	1	0.75	-	-
15A	Rush	189	0.74	0.11	0.56 - 0.95
18	Rush	195	0.74	0.09	0.58 - 0.91
	Cultivated	53	0.68	0.07	0.60 - 0.84
9	Bull Island	219	0.75	0.07	0.61 - 0.88
14	Kilcainin	7	0.75	0.05	0.68 - 0.82
19	Comber	51	0.75	0.07	0.63 - 0.91
	Cultivated 1962	26	0.74	0.03	0.63 - 0.91
	Cultivated 1963	12	0.77	0.07	0.67 - 0.88

TABLE IX
(continued)

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of anthers</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
15	Rush	193	0.77	0.05	0.61 - 0.95
		144	0.82	0.053	0.72 - 1.01
	Cultivated	48	0.79	0.053	0.7 - 0.89
16	Dungarvan	147	0.77	0.053	0.61 - 0.91
12	Tramore	148	0.86	0.10	0.7 - 1.05
	Cultivated	4	0.75	0.10	0.74 - 0.77

TABLE X

Pollen Grain Diameter (in μ)

The measurements have been made from a random sample of 250 pollen grains from wild population samples and 50 pollen grains from individual cultivated plants.

6	Dungarvan	24.4	2.6	20 - 31
8	Tramore	25.0	1.7	22 - 28
	Cultivated	24.6	1.3	22 - 29
4	Rush	25.6	1.7	22 - 29
	Cultivated	25.75	0.75	25 - 28
5	Ballyvaughan	26.2	1.3	23 - 29
	Cultivated	26.1	0.94	25 - 28
3	Bull Island	26.7	1.9	23 - 31
18	Rush	30.2	1.3	28 - 32
	Cultivated	30.3	1.3	28 - 32
15	Rush	31.0	1.7	28 - 34
	Cultivated	31.0	1.7	28 - 34
13	Tramore	31.0	1.3	28 - 35
	Cultivated	32.0	1.6	29 - 35
12	Tramore	31.4	1.7	28 - 37
	Cultivated	31.6	2.0	28 - 35
19	Comber	31.9	1.2	28 - 34
	Cultivated	30.3	1.3	28 - 32

TABLE XIa
Seed length (in mm)
Seeds measured from all florets

<u>Population</u> <u>number</u>	<u>Locality</u>	<u>No. of seeds</u> <u>measured</u>	<u>Mean</u>	<u>Standard</u> <u>Deviation</u>	<u>Range</u>
21	Roundstone	56	0.97	0.07	0.84 - 1.23
	Cultivated	106	1.12	0.12	0.87 - 1.42
8	Tramore	257	1.03	0.07	0.90 - 1.16
	Cultivated	42	1.16	0.19	1.00 - 1.39
7	Kilcainin	116	1.11	0.07	0.97 - 1.23
2	Rush	253	1.17	0.096	0.94 - 1.39
	Cultivated	107	1.27	0.07	0.10 - 1.40
12	Tramore	262	1.24	0.14	1.00 - 1.55
	Cultivated	88	1.36	0.08	1.16 - 1.61
20	Baldoyle	250	1.25	0.098	1.00 - 1.48
	Cultivated	105	1.20	0.08	1.03 - 1.30
3	Bull Island	261	1.26	0.10	1.03 - 1.52
	Cultivated	114	1.35	0.10	1.13 - 1.58
13	Tramore	248	1.30	0.11	1.03 - 1.58
	Cultivated	13	1.48	0.13	1.16 - 1.61
4	Rush	260	1.33	0.114	1.03 - 1.58
	Cultivated	106	1.22	0.14	0.97 - 1.45
18	Rush	262	1.47	0.144	1.13 - 1.74
	Cultivated	6	1.51	0.05	1.42 - 1.55
19	Comber	254	1.48	0.14	1.13 - 1.71
	Cultivated	29	1.56	0.105	1.39 - 1.81
15	Rush	254	1.59	0.1	1.35 - 1.96

TABLE XIb

Seed length (in mm)Seeds measured from the central florets only

<u>Population number</u>	<u>Locality</u>	<u>No. of seeds measured</u>	<u>Mean</u>	<u>Standard Deviation</u>	<u>Range</u>
20	Baldoyle	10	1.27	0.045	1.20 - 1.35
2	Rush	9	1.32	0.07	1.23 - 1.53
4	Rush	6	1.39	0.10	1.19 - 1.45
3	Bull Island	11	1.44	0.08	1.32 - 1.55
18	Rush	8	1.48	0.10	1.45 - 1.55
19	Comber	5	1.69	0.093	1.61 - 1.81
15	Rush	101	1.89	0.114	1.65 - 2.13

APPENDIX IV

Miscellaneous observations made in the course of
this study relating to the biology of the genus

Salicornia

Differences in the flowering time of different
and between different populations of the same
observed in the field in Salicornia. These
flowering time and the phenological response of
may be worth further investigation.

Some results of preliminary investigations of the
cultivation of Salicornia under conditions
of increased day length

The purpose of these investigations was to try and cultivate two generations of Salicornia in one year.

Seeds were sown in early December in a cool greenhouse. Germination occurred after 2-3 weeks and the material was then divided into two groups. The first was cultivated under conditions of ordinary daylength while the second received 14-15 hours illumination from fluorescent tubes giving 200ft. candles at the level of the plants. Growth was slow in the group grown in short days and the plants did not reach maturity any earlier than plants grown indoors from seeds sown in March. The seedling receiving increased illumination produced little or no vegetative growth but

APPENDIX IV

were of no value for taxonomic study. This response to increased illumination in the cotyledonary stage may be similar to that found by Cumm Salicornia in Chenopodium. He found that seedlings of a variety of C. rubrum could be induced to flower in the cotyledonary stage after a single dark period followed by constant illumination.

Differences in the flowering times of distinct taxa and between different populations of the same taxa have been observed in the field in Salicornia. These differences in flowering time and the photoperiodic responses of Salicornia may be worth further investigation.

Some results of preliminary investigations of the
cultivation of Salicornia under conditions
of increased day length

(2) The purpose of these investigations was to try and cultivate two generations of Salicornia in one year.

(4) Seeds were sown in early December in a cool greenhouse. Germination occurred after 2-3 weeks and the material was then divided into two groups. The first was cultivated under conditions of ordinary daylength while the second received 14-15 hours illumination from fluorescent tubes giving 200ft candles at the level of the plants. Growth was slow in the group grown in short days and the plants did not reach maturity any earlier than plants grown indoors from seeds sown in March. The seedling receiving increased illumination produced little or no vegetative growth but flowered at the cotyledonary stage and were of no value for taxonomic study. This response to increased illumination in the cotyledonary stage may be similar to that found by Cumming (1959) in Chenopodium. He found that seedlings of a variety of C. rubrum could be induced to flower in the cotyledonary stage after a single dark period followed by constant illumination.

Differences in the flowering times of distinct taxa and between different populations of the same taxa have been observed in the field in Salicornia. These differences in flowering time and the photoperiodic responses of Salicornia may be worth further investigation.

Seed storage

Four main methods of seed storage were investigated.

- (1) Entire plants dried and stored at room temperature.
- (2) Free seeds dried and stored at room temperature.
- (3) Entire plants stored moist in polythene bags at 4°C .
- (4) Free seeds stored in 2% saline at 4°C .

A high percentage germination exceeding 80% was obtained from seeds stored by all methods with the exception of those seeds stored in 2% saline. Storage of seeds in the presence of moisture as in methods (3) and (4) proved unsatisfactory for cultivation experiments as germination commenced even at 4°C after 12-14 weeks.

It was found most satisfactory to dry entire plants and store these at room temperature until time of sowing. Ball (per.com.) also has found this method the most satisfactory and he states that he has experienced little difficulty with the storage and germination of Salicornia seed.

Seeds stored dry showed 50% germination after two years and seeds obtained from fruiting plants stored in a deep freeze at -14°C showed a high percentage germination of about 80% after six months and 40% germination after 20 months.

Seeds germinate readily in the absence of salt small concentrations are necessary for normal growth and development.

Observations on the effects of salinity on seed germination.

(1) Baldoyle	No. of Seeds	% germination after 7 days at 20° C				% germination after 14 days at 20° C			
		H ₂ O	0.5%	2%	5% NaCl	H ₂ O	0.5%	2%	5% NaCl
<u>S. europaea</u> L.									
	50	98	90	10	0	No change			
	50	95	95	5	0	No change			
	50	60	60	0	0	No change			
(2) Bull Island									
<u>S. europaea</u> L.	50	98	95	20	0	No change			
	50	95	85	5	0	No change			

These results suggest that Salicornia seeds germinate readily in the absence of salt and that high concentrations of salt tend to inhibit germination. Brereton (person. com.) in an extensive study of conditions effecting the germination of Salicornia seeds has found that the percentage germination decreases with increase in the concentration of NaCl. Halket (1915) has shown that Salicornia in cultivation flourishes in the presence of a certain amount of salt but that growth is retarded in the complete absence of salt or if too high concentrations are present. It was concluded from these observations that though Salicornia seeds germinate readily in the absence of salt small concentrations are necessary for normal growth and development.

REFERENCES

- Ball, P.W. & Tutin, T.G. (1959). Notes on the annual species of Salicornia in Britain. Watsonia 4 : 193 - 205.
- Ball, P.W. (1960 a). The experimental taxonomy of Salicornia L. Ph.D. Thesis, University of Leicester.
- ERRATA
- Ball, P.W. (1960 b). Collection and preservation of Salicornia.
- "Ball (1964 a)" has been cited incorrectly in a number of instances as "Ball (1964)." page 1. Cambridge.
- Ball, P.W. (1964 b). A taxonomic review of Salicornia in Europe. Feddes Report. 69 : 1 - 8.
- Ball, P.W. (pers. comm.). The Hartley Botanical Laboratory, The University, Liverpool. 3.
- Borrill, M. (1956). A biosystematic study of some Glyceria species in Britain-Taxonomy. Watsonia 2 : 291 - 342.
- Brereton, A. (para. comm.). Department of Botany, University of North Wales, Bangor.
- Colgan, N. (1961). A supplement to Colgan's Flora of the County Dublin. Stationery Office, Dublin.
- Cumming, B.G. (1959). Extreme sensitivity of germination and photoperiodic reaction in the genus Chenopodium L.. Nat. Lond. 184 : 1044 - 1045.
- Dalby, D.H. (1955). Some variation in Salicornia and its significance, in Lousley, J.E. Species studies in the British Flora. London.
- Dalby, D.H. (1956). The nature of variation in the British annual glassworts (Salicornia spp.). Ph.D. Thesis, University of London.

Dalby, D.H. (1961). REFERENCES pusilla in Britain. Proc. Bot.

- Ball, P.W. & Tutin, T.G. (1959). Notes on the annual species of Salicornia in Britain. Watsonia 4 : 193 - 205.
- Ball, P.W. (1960 a). The experimental taxonomy of Salicornia L. Ph.D. Thesis, University of Leicester.
- Ball, P.W. (1960 b). Collection and preservation of Salicornia. Proc. Bot. Soc. Brit. Isles 3 : 392 - 393.
- Ball, P.W. (1964 a). Salicornia in Flora Europaea 1. Cambridge.
- Ball, P.W. (1964 b). A taxonomic review of Salicornia in Europe. Feddes Repert. 69 : 1 - 8.
- Ball, P.W. (pers. comm.). The Hartley Botanical Laboratory, The University, Liverpool. 3.
- Borrill, M. (1956). A biosystematic study of some Glyceria species in Britain-Taxonomy. Watsonia 3 : 291 - 298.
- Brereton, A. (pers. comm.). Department of Botany, University of North Wales, Bangor.
- Colgan, N. (1961). A supplement to Colgan's Flora of the County Dublin. Stationery Office, Dublin.
- Cumming, B.G. (1959). Extreme sensitivity of germination and photoperiodic reaction in the genus Chenopodium (Tourn.) L.. Nat. Lond. 184 : 1044 - 1045.
- Dalby, D.H. (1955). Some variation in Salicornia and its significance, in Lousley, J.E. Species studies in the British Flora. London.
- Dalby, D.H. (1956). The nature of variation in the British annual glassworts (Salicornia spp.). Ph.D. Thesis, University of London.

- Dalby, D.H. (1961). Salicornia pusilla in Britain. Proc. Bot. Fergusson, Soc. Brit. Is. 4 : 470.
- Dalby, D.H. (1962). Chromosome number, morphology and breeding behaviour in the British Salicorniae. Watsonia 5 : 150 - 162.
- Dalby, D.H. (1963). Seed dispersal in Salicornia pusilla. Nat. Lond. 199 : 197 - 198.
- Dalby, D.H. (pers. comm.). Imperial College, Botany Department, London University.
- Dandy, J.E. (1958). List of British Vascular Plants. London.
- Darlington, C.D. & Wylie, A.P. (1955). Chromosome atlas of flowering plants ed. 2. London.
- Darlington, C.D. & La Cour, L.F. (1962). The handling of chromosomes. London.
- Davis, P.H. & Heywood, V.H. (1963). Principles of Angiosperm taxonomy. Edinburgh & London. ed. 1. Facsimile 1957
- de Fraine, E. (1912). The anatomy of the Genus Salicornia. Lousley, J. Linn. Soc. (Bot.) 41 : 317 - 348.
- Druce, G.C. (1911). Phytogeographical excursion in the British Isles. Love, A. New Phyt. 10 : 318.
- Druce, G.C. (1932). A comital flora of the British Isles. Mackay, J. Arbroath. Flora Hibernica. Dublin.
- Dumortier, B.C. (1868). Bouquet du littoral Belge. Bull. Soc. Bot. Belge. 7 : 332 - 334.
- Duval-Jouve, J. (1868). Les Salicornia de l'Herault. Bull. Soc. Bot. France 25 : 132 - 140 and 165 - 178.
- Ferguson, I.K. (1962). Salicornia perennis Mill. in Ireland.

- Moss, C.E. Irish Nat. Journ. 14 : 18 - 19.
- Ferguson, I.K. (1964). A new station Salicornia perennis Mill. in Ireland. Irish Nat. Journ. 14 : 217.
- Halket, A. (1915). The effects of salt on the growth of Salicornia. Ann. Bot. 29 : 143.
- Hambler, D.J. (1954). Chromosome numbers in British Salicornia. Nat. Lond. 173 : 547.
- Hambler, D.J. (1958). Some taxonomic investigations on the genus Rhinanthus. Watsonia 4 : 101 - 116.
- * König, D. (1960). Beiträge zur Kenntnis der deutschen Salicornien. Mitt. flor.-soziol. Arb. Gemeinschaft., N.F. 8 : 5 - 58.
- Langlois, J. (1961). Croissance, Morphogenèse et Floraison de trois variétés de Salicornia herbacea L.. Bull. Soc. Lin. de Normandie 2 : 261 - 276.
- Linnaeus, C. (1753). Species Plantarum, ed. 1. Facsimile 1957 London.
- Lousley, J.E. (1957). The British flora during 1956. Nat. Lond. 179 : 351 - 353.
- Löve, A. & D. (1961). Chromosome numbers of central and north-west European plant species. Opera Bot. 5 : 1 - 581.
- Mackay, J.T. (1836). Flora Hibernica. Dublin.
- Moore, D. & More, A.G. (1866). Cybele Hibernica ed. 1 Dublin & London.
- Moquin, A. (1840). Chenopodearum monographica enumeratio. Paris
- Moss, C.E. (1911). Some species of Salicornia. J. Bot. 49 : 177-185.

- Moss, C.E. (1912). The International Phytogeographical Excursion in the British Isles. XII. Remarks on the characters and the nomenclature of some critical plants noticed on the excursion. *New Phytol.* 11 : 398 - 414.
- Moss, C.E. & Salisbury, E.J. (1914) Salicornia, in The Cambridge British Flora 2, Cambridge.
- Moss, C.E. (1948), in Barker, W.F., et al., *Plantae novae africanae*, ser. 28. *J.S.Afr. Bot.* 14 : 29 - 40.
- Moss, C.E. (1954), in Adamson, R.S. The species of Arthrocnemum and Salicornia in Southern Africa. *J.S.Afr. Bot.* 20 : 1 - 22.
- Nannefeldt, J.A. (1955). Nagot om Slakett Salicornia i Sverige. *Svensk. Bot.* 49 : 97 - 110.
- Nannefeldt, J.A. (pers. comm.). Institute of Systematic Botany of the University of Uppsala.
- Pallas, P.S. (1803). Illustrations plantarum imperfecte vel nondum cognitarum. Leipzig.
- Perring, F.H. & Walters, S.M. (1962). Atlas of the British Flora. London.
- Praeger, R.L. (1901). Irish Topographical Botany. Dublin.
- Praeger, R.L. (1934). The Botanist in Ireland. Dublin.
- Smith, J.E. (1807, 1815). English Botany, vols. 6, 24 and 35. London.
- Stebbins, G.L. & Valencia, J.I. & P.M. (1946). Artificial and natural hybrids in the Gramineae Tribe Hordeae I. Elymus, Sitanion & Agropyron. *Amer. J.Bot.* 33 : 338 - 351.

- Sverdrup, H.V., Johnson, M.W. & Fleming, R.H. (1942). The Oceans. Their physics, chemistry and general biology. New York.
- Threlkeld, C. (1727). Synopsis Stirpium Hibernicarum. Dublin.
- Turesson, G. (1922). The genotypical response of the plant species to the habitat. Heredity. 3 : 211 - 350
- Tutin, T.G. (1952), in Clapham, A.R., Tutin, T.G. & Warburg, E.F., Flora of the British Isles. ed. 1. Cambridge.
- Tutin, T.G. (1962), in Clapham, A.R., Tutin, T.G. & Warburg, E.F., Flora of the British Isles. ed. 2. Cambridge.
- Uphof, J.C.T. (1938). Cleistogamic flowers. Bot. Rev. 4 : 21 - 49.
- Webb, D.A. (1943). An Irish Flora. ed. 1. Dundalk.
- Webb, D.A. (1953). An Irish Flora. ed. 2. Dundalk.
- Webb, D.A. (1963). An Irish Flora. ed. 4. Dundalk.
- Webb, D.A. (pers. comm.). School of Botany, Trinity College, Dublin.
- Wilmott, A.J. (pers. comm.). Unpublished notes at the British Museum.
- Woods, J. (1851). (No title.) Bot. Gaz. 3 : 29 - 33.
- * Heslop-Harrison, J. (1953). New concepts of flowering plant taxonomy. London.