ABSTRACT

FACULTY OF SCIENCE

BOTANY

Doctor of Philosophy

A STUDY OF MORPHOLOGICAL VARIATION IN HALIMIONE PORTULACOIDES (L.) AELL. IN RELATION TO VARIATIONS IN THE HABITAT

by John Timothy Robin Sharrock

Mapping and transect work at three sites in the Hampshire basin indicated that the main habitat feature affecting the distribution and quantity of Halimione protulacoides was water content of the substrate, this being the result of several factors interacting: configuration of the area, height above Ordnance Datum and nature of the substrate.

Marked morphological differences were observed between plants growing on different substrates, three main types being recognised in the initial, subjective, examination: much-branched, non-rooting, prostrate, on pebble; prostrate, with much rooting, on sand; lax, upright and non-rooting, on mud. Since, with apparent relative genetical uniformity of Halimione in the Hampshire basin, there were indications of habitat differences affecting its morphology, separate objective multivariate analyses were carried out on habitat and morphology data.

These analyses showed that there was a high correlation between habitat and the morphology of Halimione portulacoides var. latifolia, with the three 'types' forming part of a continuous series. It

was also shown that _Halimione_ could tolerate a wide range of substrate water contents and occurred in a wide range of salt marsh communities.

Data collected in a wider survey, including areas with all three British varieties (_latifolia_, _parvifolia_ and _angustifolia_), were similarly analysed. It was shown that plants referable on leaf dimensions to the three varieties were also part of a continuous series morphologically; _parvifolia_ and _angustifolia_ are morphologically very distinct from one another, but _latifolia_ embraces the whole range of variation. There are also ecological differences, in that _parvifolia_ is limited to a sand substrate and _angustifolia_ is limited to a mud or pebble-and-mud substrate, while _latifolia_ is found in the whole range of substrates examined. _Parvifolia_ and _angustifolia_ are both distinct from _latifolia_ growing on the same substrate but the former most resembles _latifolia_ growing on sand and the latter most resembles _latifolia_ growing on pebble. The hypothesis is advanced that parts of a very plastic population of _Halimione portulacoides_ (sens. lat.) have become 'fixed' to form the two varieties _parvifolia_ and _angustifolia_.

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I. INTRODUCTION : THE GENERAL SCOPE OF THE INVESTIGATION

This investigation was originally planned as a study of the general autecology of *Halimione portulacoides*, especially in relation to the general factors affecting the distribution of *Halimione* within the salt marsh community. This species seemed of interest from two points of view. In the first place, its general ecological position in the salt marsh succession, and the factors affecting its distribution, were by no means clear; in the second, three morphologically distinguishable varieties - var. *latifolia*, var. *angustifolia* and var. *parvifolia* - had been described for Britain and the taxonomic status and specific habitat preferences of these varieties needed further investigation.

The initial work was carried out at the Hampshire basin marshes, partly because of their proximity to Southampton University and also because the lack of reference in the literature to varieties other than var. *latifolia* in the area suggested that there was likely to be relative genetical homogeneity and that the area was, thus, suitable for a preliminary investigation.

It soon became apparent, however, that there was considerable morphological variation in the plants from varying substrates even within the Hampshire basin itself and that this was apparently habitat-determined rather than genetically determined. The investigation of these morphological variations appeared not only to be a profitable feature for investigation but also an essential preliminary to any detailed autecological work.

In the event, the investigation of the correlation between morphology and habitat in the Hampshire basin proved so interesting that this was extended to cover areas where there was known genetical variability (where the three British varieties of *Halimione portulacoides* were known to occur) and the whole investigation was slanted away from the general autecology of *Halimione* and towards a numerical study of the interrelationships between habitat and morphology.

II. THE BACKGROUND

A. Brief literature review

1. General distribution of *Halimione portulacoides*

In the biological flora of *Halimione portulacoides*, Chapman (1950) shows that the northern limit of the distribution coincides approximately with the 60° July isotherm and, within this range, *Halimione* is a widespread salt marsh plant of the coasts of the southern half of Britain. A general review of the literature on salt marshes suggests that it usually occurs in the middle zones of established salt marsh. From wide field experience, Tansley (1949) places it between the Armerietum and Suaedetum in the salt marsh succession and, from similar experience, particularly in the east coast marshes, Chapman (1950) states that it makes its appearance, along with *Puccinellia maritima*, above the Asteretum and Limonietum and also (especially in the south-west and in Norfolk) often occurs as a pure zone just to the seaward side of dunes. Perraton (1953), working in a limited area on the Hampshire-Sussex border, observed that *Halimione* formed a zone from the upper Spartinetum and extended into the general salt marsh and sometimes extended beyond the lower fringe of the *Puccinellia maritima* zone, though his conclusion from this that the Halimionetum was a transition in the succession from the colonising Spartinetum to a general salt marsh community lacks documentation: from the evidence given, it could equally well be interpreted as a zonation with no successional significance. At Skallingens in the Netherlands, where *Halimione portulacoides* was invading the area, Iverson (1936) found that it had its optimum in the Puccinellietum. All accounts of the position of Halimione suggest that it forms a relatively narrow and well-defined zone, though it is particularly well-represented along creek edges and this is regarded by several authors (e.g. Chapman) as being its 'typical' habitat.

Chapman (loc. cit.), with a wide experience of British salt marshes, states that Halimione can be found growing successfully on a wide variety of substrata, from mud to sand, and even on shingle banks. In this latter case, Chapman cited an example at Blakeney Point, Norfolk, where he attributed the presence of Halimione to landward movement of the shingle bank covering up an area which was formerly general salt marsh, with the Halimione, but not the other salt marsh plants, surviving this change.

From field observations, mainly in the east coast marshes, Chapman (loc. cit.) regarded substrate water content as an important factor limiting distribution and suggested that young plants were particularly vulnerable to excessive substrate waterlogging. Marchant (1959), working at Hythe in Southampton Water, where Halimione is invading the Spartinetum, found some correlation between the distribution of Halimione, the marsh level and the substrate water content. This importance of substrate waterlogging as a factor limiting distribution is also emphasised by O'Reilly and Pantin (1957); from a comparison of North Bull Island and the neighbouring estuarine marshes of Co. Dublin, they conclude that the excessive waterlogging of North Bull Island is the reason for the absence of Halimione from this site. Although this particular correlation is largely based on negative evidence, the literature clearly suggests that the substrate water content is an important factor determining the distribution of Halimione and the good drainage of the creek edges is quoted as the reason for Halimione particularly thriving in these areas. The sensitivity to substrate waterlogging is frequently quoted as the main reason for Halimione being confined to relatively narrow limits of habitat conditions and forming defined zones in the salt marsh community.

Sedimentation is another factor which may affect the distribution and Beeftink (1959) associated the great increase in Halimione at Skallingens in the Netherlands (where Halimione was absent in 1909, a few plants were present in 1931 and by 1959 there was a well-established Halimionetum) with a corresponding increase in the sedimentation rate in the area, which he found H. portulacoides, but not many of the other salt marsh plants (including H. pedunculata), is able to withstand. Sedimentation may act not only through sheer physical accumulation of material over growing plants but also indirectly by altering the substrate composition and, thereby, the water relations.

As well as differing substrate conditions, other factors, such as grazing by animals, may play a part in determining the distribution of Halimione. The absence of Halimione from the apparently suitable marshes of Cardigan and Merioneth was correlated by Yapp and Johns (1917) with the high level of animal grazing in the area. Chater (*in litt.*), on the basis of transplant experiments, states that there are strong pointers to its spread being prevented by grazing and yet there are several heavily grazed areas where *Halimione* is abundant and several places on the Dovey where grazing is very rare and yet *Halimione* is not established. It is clear that more work on grazing effects is necessary. Chater (1962) has also concluded that grazing can have a great effect on the morphology of *Halimione*, causing a dwarf growth.

It is apparent from the literature that the range of the distribution of *H. portulacoides* is affected by a number of habitat factors, many interacting, though none are clearly defined in the literature, which consists largely of general observations.

2. The taxonomic situation

Three described varieties of *H. portulacoides* are found in Britain: var. *latifolia* (Gussone 1842), var. *angustifolia* (Gussone 1842) and var. *parvifolia* (Rouy 1910). These are briefly described as follows: var. *latifolia*: stems fairly elongated; lateral leaves oblong-lanceolate, green glaucescent; flower clusters in elongated spikes, separate, lax; sepals of fruiting calyx smooth, with no tubercules.

Var. *angustifolia*: stems slender, very much branched, often prostrate; leaves narrow, linear, silvery; small flower clusters drawn together in short spikes; sepals of fruit-bearing calyx often with basal obtuse tubercules (appressed).

Var. parvifolia: stem prostrate; leaves smaller and thicker than in the type.

Chapman (1937 and 1950) gives additional information, as follows:

Var. latifolia: laminae oblong or ovate-lanceolate, those of the main branches 3-4 times as long as broad; bracteoles up to 5 mm long by 4 mm broad, smooth or tubercled; flowers, fruits and seedlings abundant; probably an ecotype; maximum height 42 cm, minimum height 30 cm; internode length maximum 5 cm, minimum 0.3 cm, average 1.6 cm; leaf area maximum 532 sq cm, minimum 293 sq cm.

Var. angustifolia: laminae linear-lanceolate, 6-7 times as long as broad; flowers, fruits and seedlings abundant; maximum height 42 cm, minimum height 30 cm; internode length maximum 3.5 cm, minimum 0.3 cm, average 1.7 cm; leaf area maximum 227 sq cm, minimum 120 sq cm.

Var. parvifolia: a dwarf, prostrate, straggling undershrub 5-16 cm high; smaller in all its parts; leaves oblong or ovate-lanceolate; flowers, fruits and seedlings rare; reproduction chiefly vegetative; probably an ecotype; internode length maximum 3.1 cm, minimum 0.1 cm, average 1.0 cm; leaf area maximum 198 sq cm, minimum 101 sq cm; leaves 3-5 times as long as broad.

In addition, Aellen (1938), relying on leaf dimensions, describes the three varieties thus:

Var. latifolia: leaves broad, oval-lanceolate to broad eliptical, 3-4 times longer than broad, 1.0-1.5 cm broad.

Var. angustifolia: leaves linear-lanceolate, 6-7 times longer than broad, only 0.3 to 0.5 cm broad.

Var. parvifolia: in all parts smaller; leaves fairly long and oval-lanceolate.

It is clear from these descriptions that the three varieties are defined only in broad terms and identification of any particular specimen must be a subjective matter. All three varieties had, however, been recorded from Norfolk by Chapman (loc. cit.) but there was no reference in the literature to any variety except latifolia in the Hampshire basin.

B. Initial personal observations

General observations made in the course of the investigation on the position of Halimione in the salt marsh community and distribution in relation to the substrate are drawn together in this section.

In the Hampshire basin, casual observations confirmed those of Perraton (loc. cit.), that Halimione largely forms an intermediate zone between the Spartinetum and the general salt marsh, though persisting even into old, mature marsh, along with Aster, Limonium and Puccinellia, and even extending onto sea-walls and other grassy areas well above the upper limit of other salt marsh plants. On the East Coast, where the Spartinetum was often less well-developed, Halimione occupied the lowest levels of the salt marsh community or was largely confined to the creek edges. Halimione can, thus, cover almost the entire range of salt marsh, from the lowest to the highest levels.

While Chapman (loc. cit.), O'Reilly and Pantin (loc. cit.) and others all stress the importance of substrate water content in limiting the range of Halimione, a high degree of tolerance to this factor was found during the course of this investigation. At Hilbre Island in the Dee estuary, occasional plants were found growing on the sandstone cliff tops and at Needs Oar Point in the Hampshire basin Halimione is found in dry sandy-pebbly soils which are never subject to tidal submergence and have a maximum water content of less than 6 per cent. At the other extreme, Halimione is also apparently thriving in areas (e.g. Bursledon in the Hampshire basin) where the substrate water content never falls below 68 per cent. It appears that Halimione has a range of tolerance of substrate water content far in excess of that which the literature suggests. Rather than intolerance to high substrate water content, it appears more likely that this limits Halimione indirectly by delicately balanced interactions with other species, this, perhaps, especially affecting young plants.

It was noted that, especially on the east coast marshes, Halimione would often form an almost pure sward in areas where there was an apparently high rate of accretion. This may be comparable to the Skallingens situation, where Halimione was also able to tolerate a high rate of sedimentation which other plants could not tolerate. This appears to be the case whether the accretion is of sand or of silt and, although the indirect effects of accretion on the drainage and aeration of the substrate are undoubtedly important, this suggests that the rapid build-up of the substrate is less detrimental to Halimione than to other salt marsh species.

As indicated by Chapman (loc. cit.), Halimione was found on every variety of coastal substratum, from mud to sand and pebble. Chapman's explanation for the occurrence of Halimione on the shingle at Blakeney (viz. landward movement of the shingle over an established marsh) does not apply to another area: Needs Oar Point. Here it is more likely that the occurrence of Halimione on the shingle is due to erosion of the general salt marsh levels which were formerly overlying the shingle. If, as seems likely, this is the case, then it is clear that Halimione is able to withstand, equally, accretion or erosion of the substrate.

Grazing, quoted by Yapp and Johns (loc. cit.) as the probable reason for the absence of Halimione from the north Wales marshes, is heavy in parts of the Hampshire basin marshes, but these areas nevertheless still had an equal amount of Halimione to similar ungrazed areas and grazing would not appear to be a limiting factor in distribution, at least in the Hampshire basin.

While the factors suggested by the literature as important in determining the distribution of Halimione undoubtedly all play an important part, it is clear, even from casual observations, that their relative importance varies from locality to locality. While substrate water content may be an important limiting factor in a given locality, Halimione nevertheless has a great degree of tolerance to this factor. While generally forming a zone intermediate between the Spartinetum and general salt marsh, Halimione can be found lower down the salt marsh than any other species, bar Spartina, and higher up the salt marsh than any species, bar none. The tolerance of Halimione to accretion could be more relevant than the usual explanation of "good drainage" for the presence of Halimione especially on the levées of the creek edges, though the two must be interacting. On the other hand, Halimione was apparently one of the few plants to survive erosion at Needs Oar Point.

With this range of tolerance to substrate conditions and, hence, wide range over the whole spectrum of the salt marsh community, it would not be surprising if Halimione portulacoides exhibited a wide range of morphological variation. However, morphological variation within a species can either be genetically determined or arise as a direct response to variations in the habitat. In Halimione, the fact that similar forms had been recognised by several authors pointed to the existence of genetically distinct taxonomic entities and, in fact, plants showing the characteristics of all three varieties - latifolia, angustifolia and parvifolia were recognised on a short visit to Blakeney Point at the outset of the investigation. In contrast, in spite of the considerable morphological range exhibited by Halimione in the Hampshire basin, the initial survey of the area failed to produce any plants referable to the types angustifolia and parvifolia; it seemed possible, therefore, that plastic response within the variety latifolia was the cause of at least some of the morphological variation in this area.

III. PRELIMINARY SURVEY OF THE HAMPSHIRE BASIN MARSHES

A. The distribution of *Halimione portulacoides*

1. Introduction

All the salt marshes within a fifty-mile radius of Southampton were visited in a preliminary survey to investigate the extent and general status of *H. portulacoides* in the Hampshire basin and to investigate and determine the factors to which it is particularly reacting and which determine the limits of its distribution.

A map showing the locations of these marshes is given as Fig. 1 and brief details of some of the characteristics of these sites are given in Appendix I.

Three of the areas in the Hampshire basin were selected for initial investigation. In selecting the areas, three criteria were taken into account:

1. The presence of *Halimione* in sufficient quantity
2. The absence of appreciable disturbance by humans or grazing animals
3. Ease of access.

It was also desirable that the three areas should be of different substrates, so that a range of habitat conditions could be investigated.

On the basis of these criteria, three areas were chosen: (1) Fawley, Hampshire, with a mud substrate, (2) East Head, Sussex, with a sandy substrate and (3) Needs Oar Point, Hampshire, with a

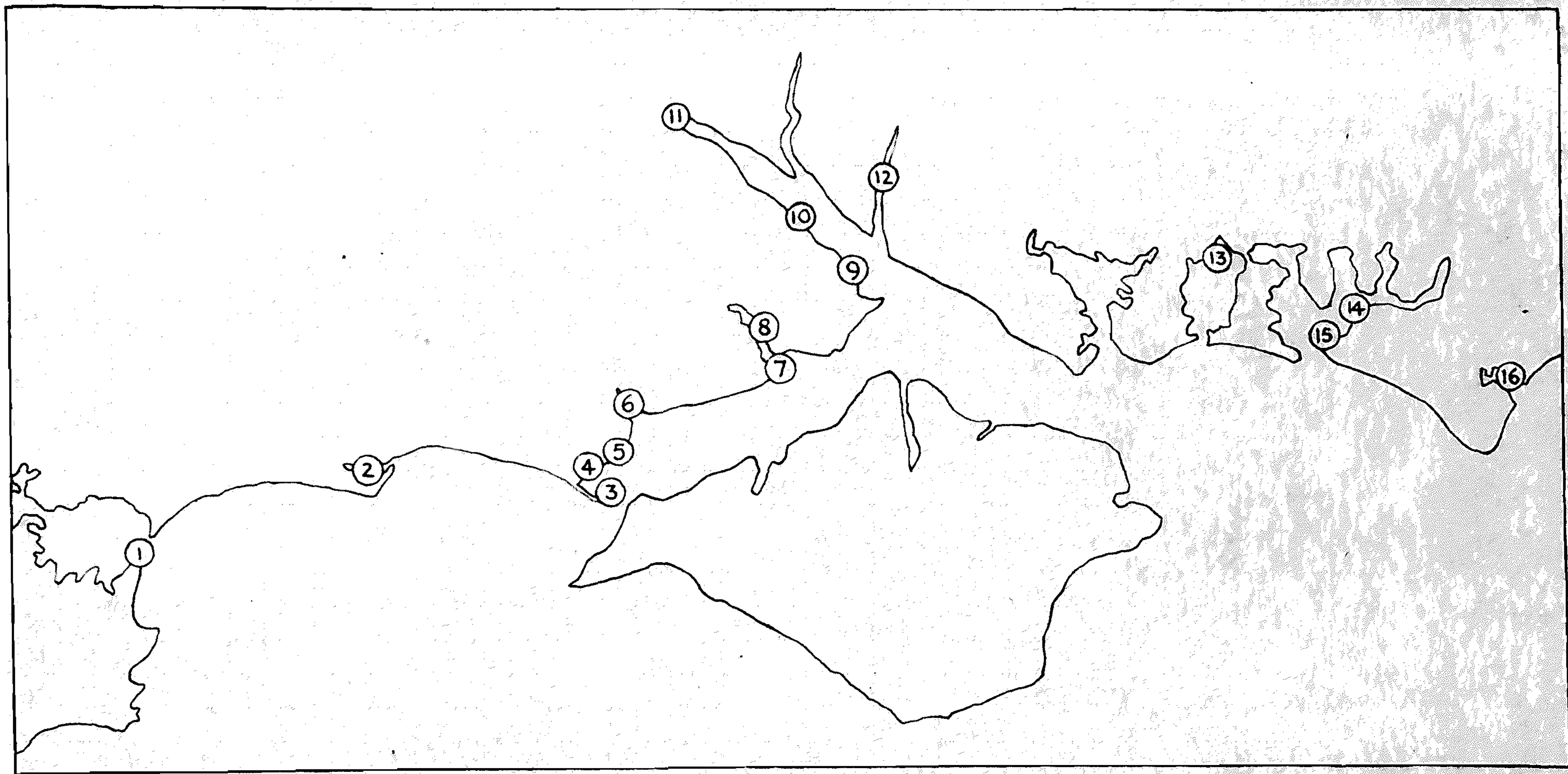


Fig. 1. Locations of the Hampshire basin marshes visited in the preliminary survey (see Appendix I)

pebble substrate. (These areas are numbered 9, 15 and 7, respectively, in Fig. 1 and Appendix I.)

2. Investigations in specific areas

a. Fawley

Superficial investigation of the Fawley site suggested that Halimione was mainly limited to the higher regions of the marsh. To investigate this objectively, a marsh segment of some 2,560 square metres was gridded, mapped and levelled with respect to Ordnance Datum from some 1,500 points and presence/absence data for Halimione was recorded for each quadrat within the gridded area. Maps drawn from these data are given showing the contours of the marsh segment at 10 cm intervals (Fig. 2) and the distribution of Halimione in relation to the 156 cm contour (Fig. 3). Comparison of these maps clearly indicates that, as appeared from a cursory examination, Halimione is indeed present mainly in the higher regions of the marsh.

However, a plot of the percentage of quadrats containing Halimione for each level of the marsh at 1 cm intervals (Fig. 4) indicates that the Halimione zone is not clear cut and has no sharp demarcation.

To obtain further evidence of this lack of clear delineation, Pearson's Ø correlation coefficients were calculated for heights at 2 cm intervals from Roman squares:

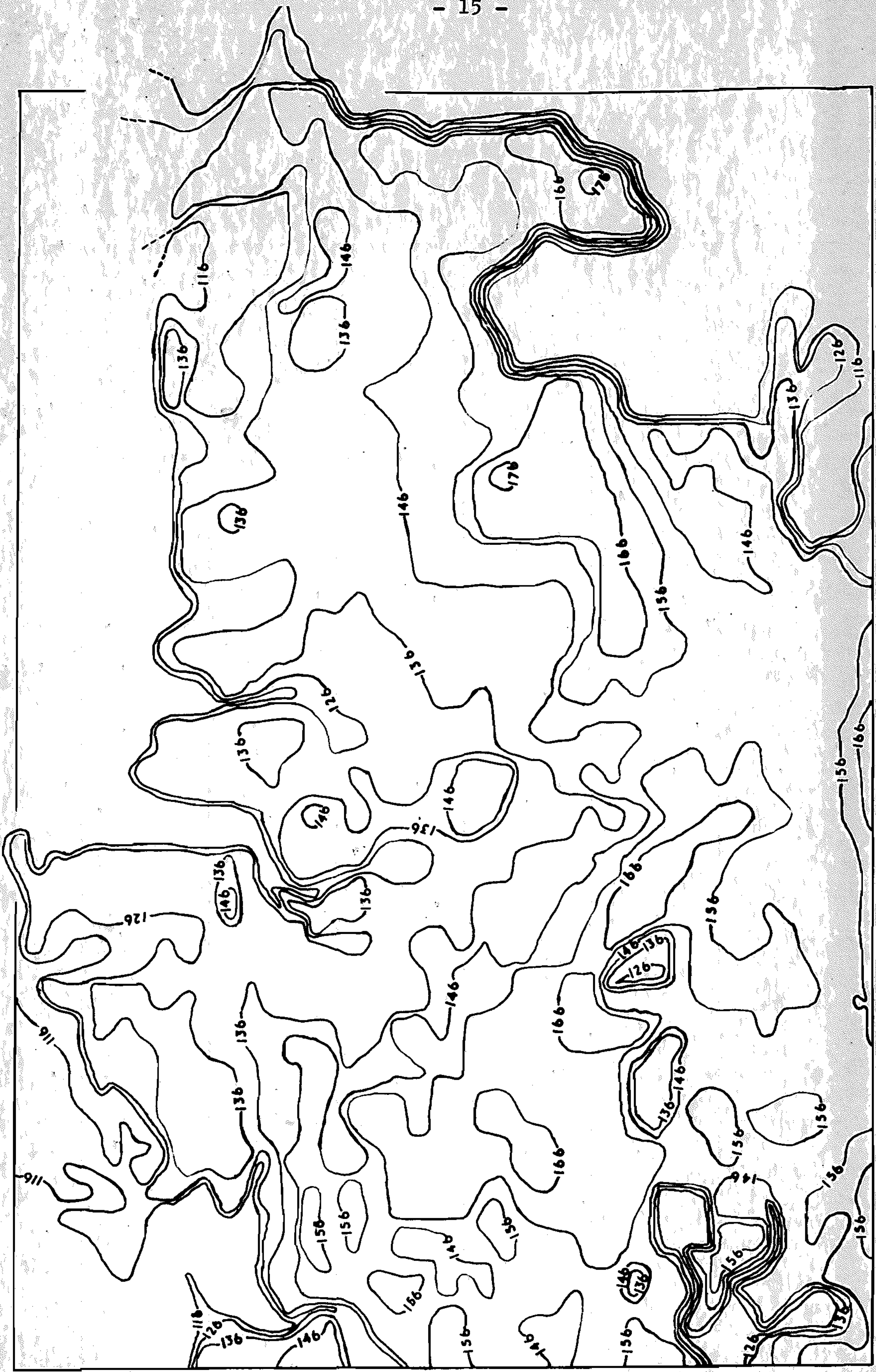


Fig. 2. Contour map of marsh segment at Fawley (contours in cm above O.D.)

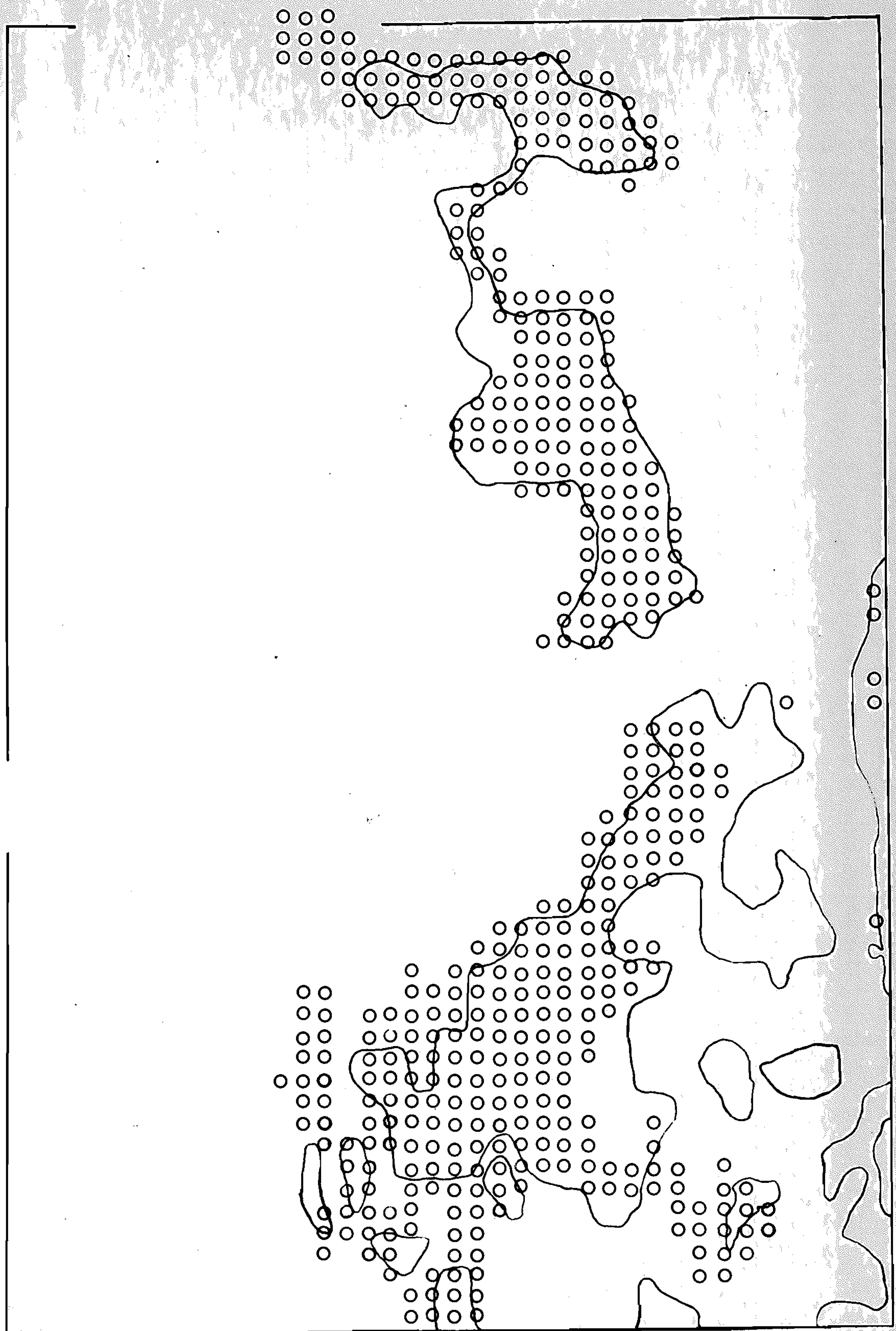
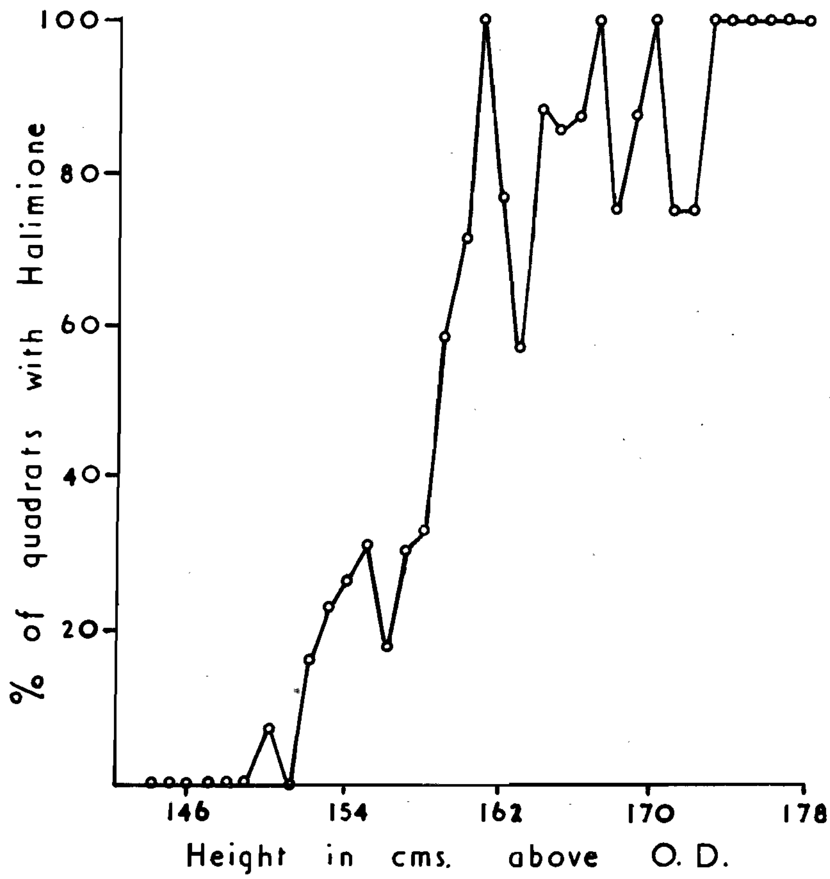


Fig. 3. Distribution of Halimione (open circles) in relation to 156 cm contour at Fawley (compare with Fig. 2)

Fig. 4. Graph of percentage of quadrats containing <u>Halimione</u> against height of the quadrats above O.D. (in cm).



	Halimione present	*Halimione* absent
Number of points above level	a	b
Number of points below level	c	d

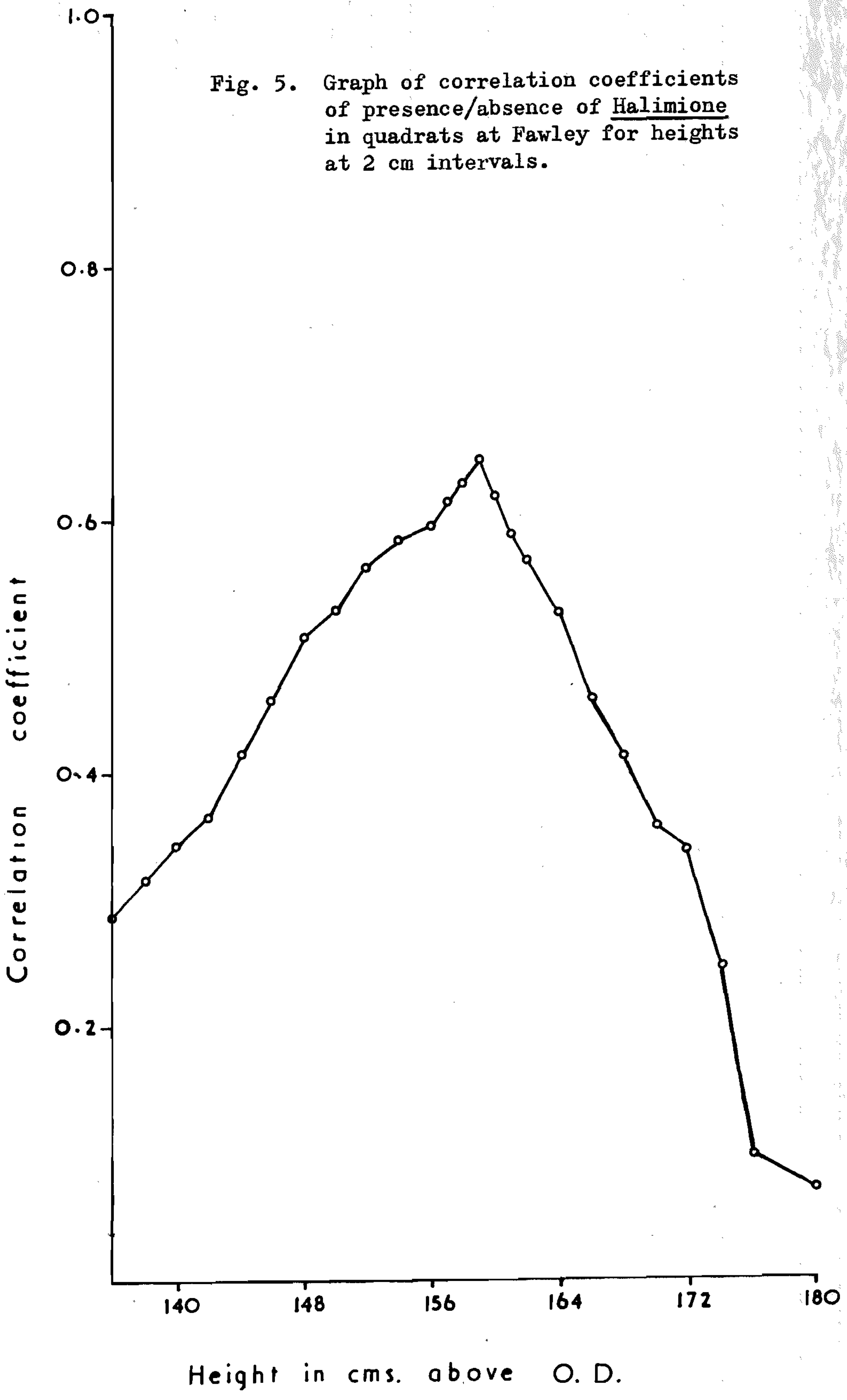
$$\text{Pearson's } \phi = \frac{ad - bc}{\sqrt{(a+b)(c+d)(b+d)(a+c)}}$$

This will only reach the maximum of unity if both b and c become equal to zero - in other words, if the *Halimione* distribution is completely determined by height and the edge is sharply defined, with *Halimione* never absent above a particular height and never present below it.

These ϕ determinations are plotted in Fig. 5 and the highest correlation coefficient is 0.65. Considering the visually-apparent correlation with height, this must be considered a relatively low value and it is clear that the division is not particularly sharp. Reference, now, back to the contour maps (Figs. 2 and 3) shows that this relative lack of correlation with height is due to the absence of *Halimione* from some relatively high regions where it might be expected to occur and presence in some relatively low regions where it might be expected to be absent.

A closer examination of these contour maps shows that the low-lying areas where *Halimione* is unexpectedly present are situated in areas where there is even lower ground to the seaward side and that the main areas of higher ground where *Halimione* is unexpectedly absent are bordered on their seaward side by even higher ground. This suggests a possible restriction on drainage and the possibility

Fig. 5. Graph of correlation coefficients of presence/absence of Halimione in quadrats at Fawley for heights at 2 cm intervals.



that substrate water content is just as important a factor as the actual height above Ordnance Datum, which only reflects the amount of water to be expected due to tidal submergence. This additional factor of restricted drainage could explain the relatively low value of correlation with height.

To investigate the importance of substrate water content, a line transect 30 metres long was set out across the marsh segment, levelled, the substrate water content determined and the presence or absence of Halimione noted for 31 points at metre intervals. The results of this survey are given in Fig. 6, which shows that Hamimione is growing in the highest area which also has the lowest water content.

To investigate this point further, healthy rooted Halimione cuttings were transplanted at each of the 31 points on the transect. After a year, the transect was examined and the position of the transplants which were still living was recorded. The situations of these is also indicated in Fig. 6. It is clear from this that Halimione is able to grow in areas at Fawley where it is not naturally present and that this potential distribution is more closely correlated with substrate water content than it is with height of the marsh.

It is clear that height of the marsh, general topography of the marsh, distance from creeks, substrate water content and allied factors are all interacting and all influence the distributional limits of Halimione even in a small area of salt marsh such as that investigated at Fawley.

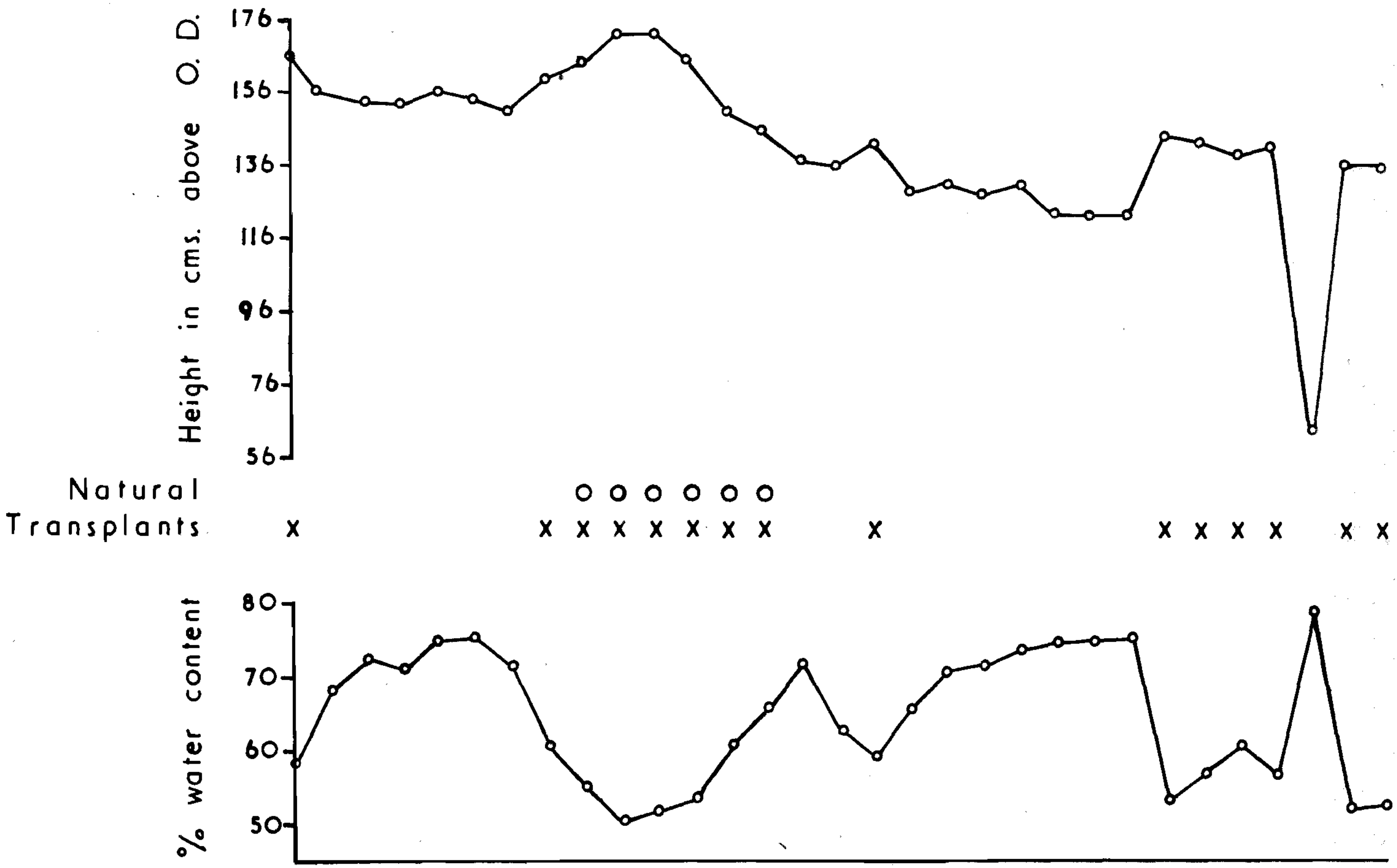


Fig. 6. Transect of marsh segment at Fawley, showing height of marsh, percentage water content of substrate, position of naturally occurring <u>Halimione</u> (open circles) and position of transplants surviving after one year (crosses)

b. East Head

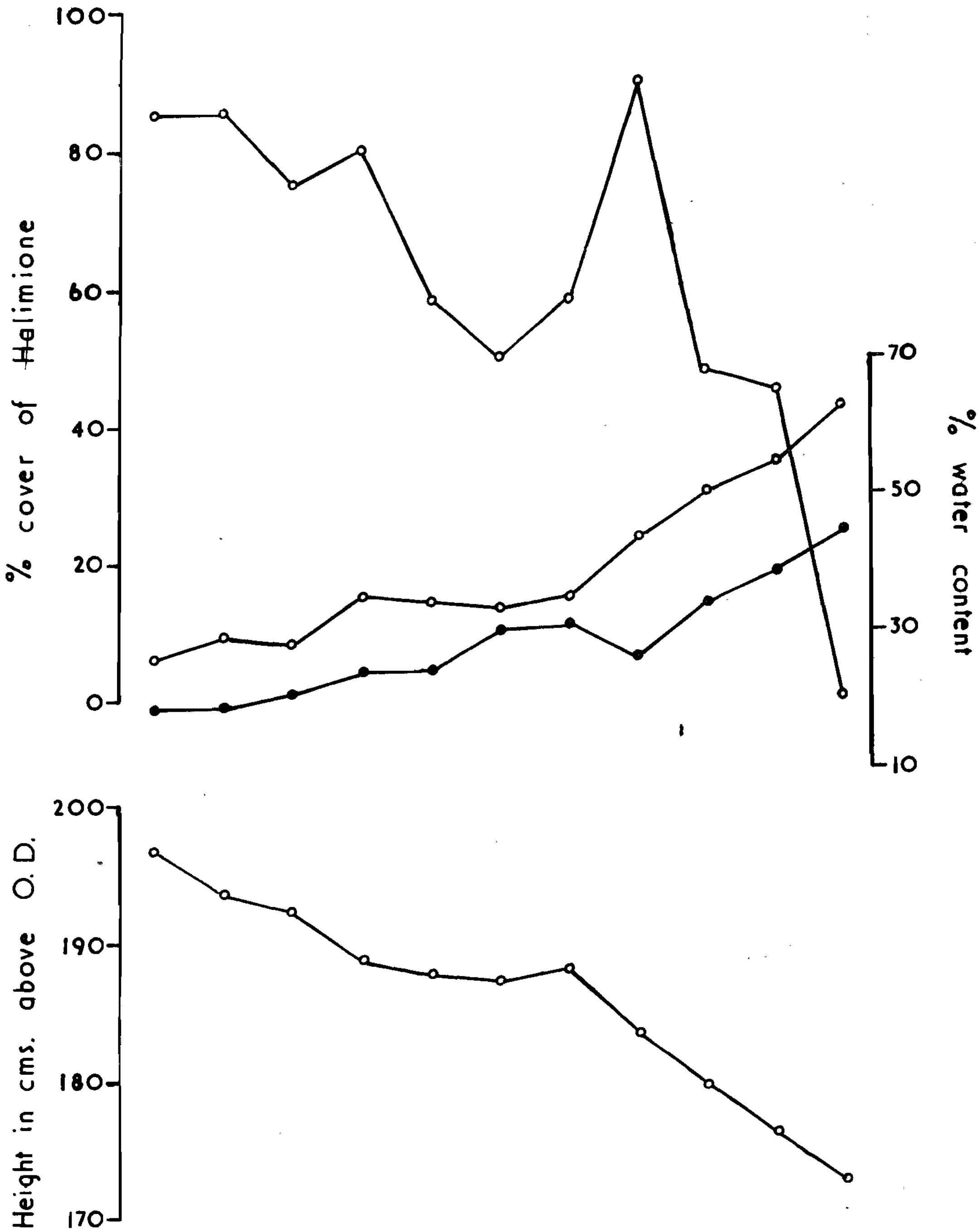
Following up the findings at Fawley, a belt transect of eleven adjoining metre-square quadrats was set out at East Head. The height above O.D., water content of the substrate at times of maximum emergence and submergence and the percentage cover of *Halimione* were obtained for each quadrat. The values of these are shown graphically in Fig. 7. The percentage cover values show a good deal of variation, but it is noticeable that the lowest values correspond to the most waterlogged conditions: not only at the lower levels, but also in quadrat 6, where the drainage is impeded by a rise in height at quadrat 7. It is noticeable that the highest percentage cover is in quadrat 8 which, although relatively low-lying, is on the steepest slope and, as is shown by the figure for emergence water content, has good drainage.

On the basis of this one transect across the sandy area at East Head, there is an indication that not only the mere presence of *Halimione*, but also the amount of the plant present is influenced by the substrate water content and that this is closely related to the height and also topography of the area.

c. Needs Oar Point

Data collected from Needs Oar Point in relation to a later, more detailed, survey may be used for a comparison with East Head. Ten scattered metre-square quadrats were laid out in a heterogeneous area. The substrate varied between mud, pebble with mud and pebble with coarse sand. The same measurements were made as at East Head,

Fig. 7. Transect at East Head, showing height of marsh, per cent cover of Halimione and per cent water content of substrate after maximum submergence (open circles) and maximum emergence (filled circles)



viz. height above O.D., substrate water contents at times of maximum submergence and emergence and percentage cover of Halmione. The results are given graphically in Fig. 8. Since the quadrats were scattered and not in a belt transect and because of the heterogeneity of the substrate, the data are less easily interpreted and the picture is far less clear. Nevertheless, the percentage cover is lowest at the lowest levels of the marsh, where there is also a high substrate water content, is at a maximum in the central region and is at a lower level on the highest (extremely dry) levels.

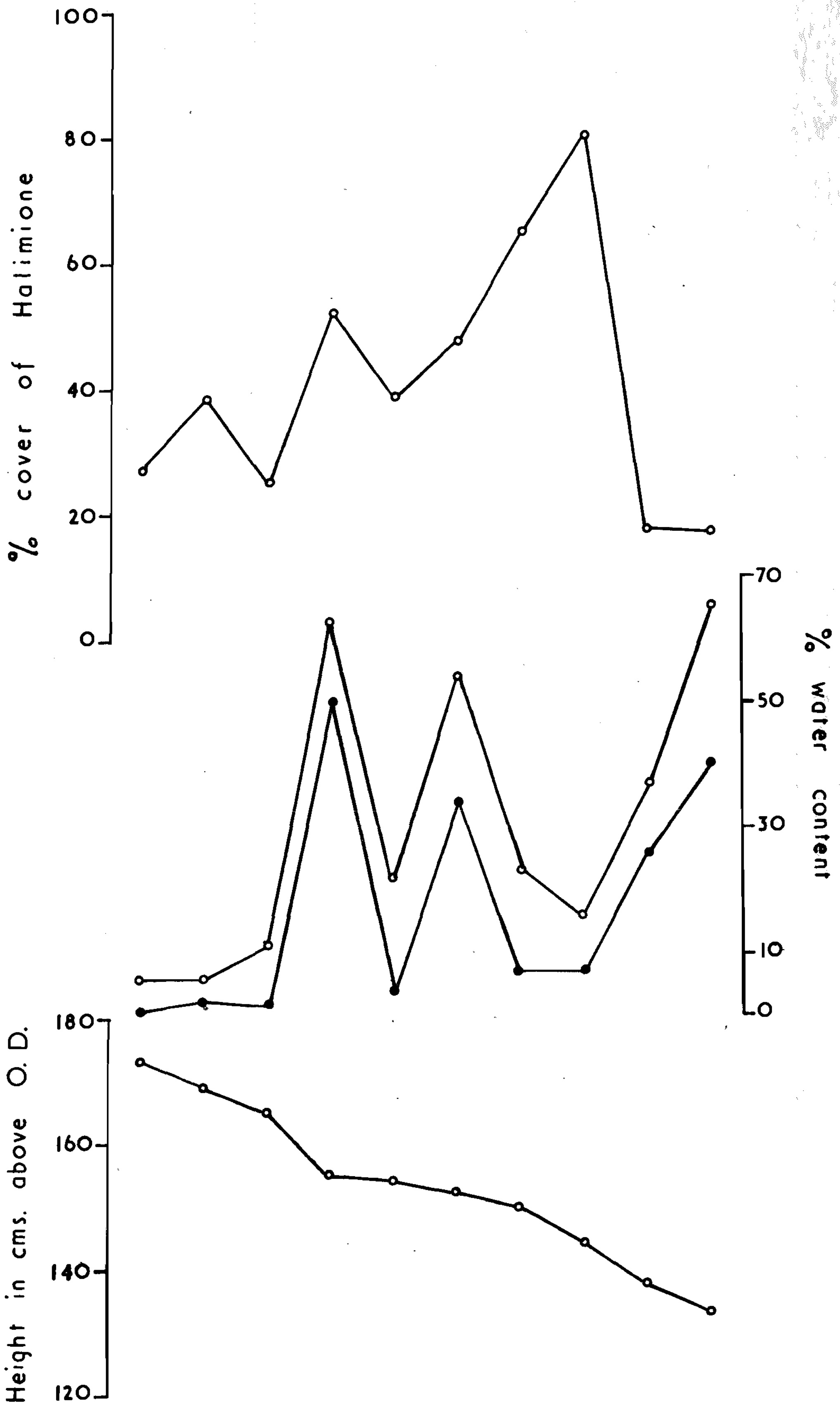
Although there is individual variation within the quadrats, as would be expected in a heterogeneous collection of quadrats, the effect of the substrate water content on the percentage cover of Halimione is suggested by those quadrats with an emergence water content of less than 10 per cent having an average percentage cover of 45 per cent and those with over 10 per cent having an average percentage cover of 35 per cent.

As at East Head, there is some indication from these few quadrats that the percentage cover of Halimione is influenced both by height of the marsh and by the substrate water content. The factors of substrate water content due to substrate texture and tidal submergence (i.e. height) and topographical configuration thus appear to be interacting.

3. Discussion

The detailed mapping of a sizeable marsh segment at Fawley indicated that Halimione was confined to the higher regions of this

Fig. 8. Quadrats at Needs Oar Point: as Fig. 7.



marsh but that the correlation with height was relatively poor (0.65) because of the unexpected absence from some high regions and unexpected presence in some low regions. More detailed work on one transect across the segment showed that the *Halimione* distribution was more closely related to the substrate water content than with height (the high regions where *Halimione* was absent having impeded drainage and the low regions where *Halimione* was present being well-drained). This correlation with substrate water content was even closer when the potential distribution of *Halimione* (as indicated by surviving transplants) was considered.

Short transects in two other areas (East Head and Needs Oar Point) gave indications that the amount of plant present (as indicated by the percentage cover) was also influenced by both height of the marsh above O.D. and the substrate water content.

Although the results from each area indicated that a high substrate water content was the factor limiting the lower limit of the growth of *Halimione*, the level of this was different at each site and *Halimione* nevertheless survived over a wide range of substrate water contents (in these areas, ranging from sites with never less than 64 per cent to sites with never more than 6 per cent) and the distribution of *Halimione* was clearly influenced by a number of interacting limiting factors.

B. Morphological variation in Halimione portulacoides

1. Morphological measurements

Although comparison with known *parvifolia*, *angustifolia* and *latifolia* showed that the Hampshire basin plants were all referable to var. *latifolia*, there appeared, merely from a cursory examination, to be considerable variation between plants from differing substrates. These differences in habit were largely caused by four features of the gross morphology:

1. The proportion of the plant lying prostrate and rooting at the nodes.
2. The proportion of the plant lying prostrate, but not rooting at the nodes.
3. The proportion of the plant growing vertically.
4. The degree of lateral branching.

Plants from a sandy substrate at East Head, a muddy substrate at Fawley and pebble substrate at Needs Oar Point were collected and these four features of their morphology were measured on specimens from each site. In addition, the general morphological differences visible in the field between the plants of each site were recorded.

The plants on a sandy substrate at East Head were low-growing, with most of the plant in a prostrate position, rooting at most nodes and with the only vertical portion being upward-growing lateral shoots. There was a considerable degree of lateral development, flowering appeared to be infrequent and the leaves were small. The plants formed a dense mat, with much intertwining of branches and interweaving of neighbouring plants and many stems were buried in the sand. The abundance of nodal rooting and the prostrate habit was attributed to deposition of sand over the plants, the area lying to the landward side of a spit.

On a muddy substrate at Fawley, the plants exhibited much less nodal rooting, a greater development of vertical shoots, more frequent flowering, larger leaves and longer internodes.

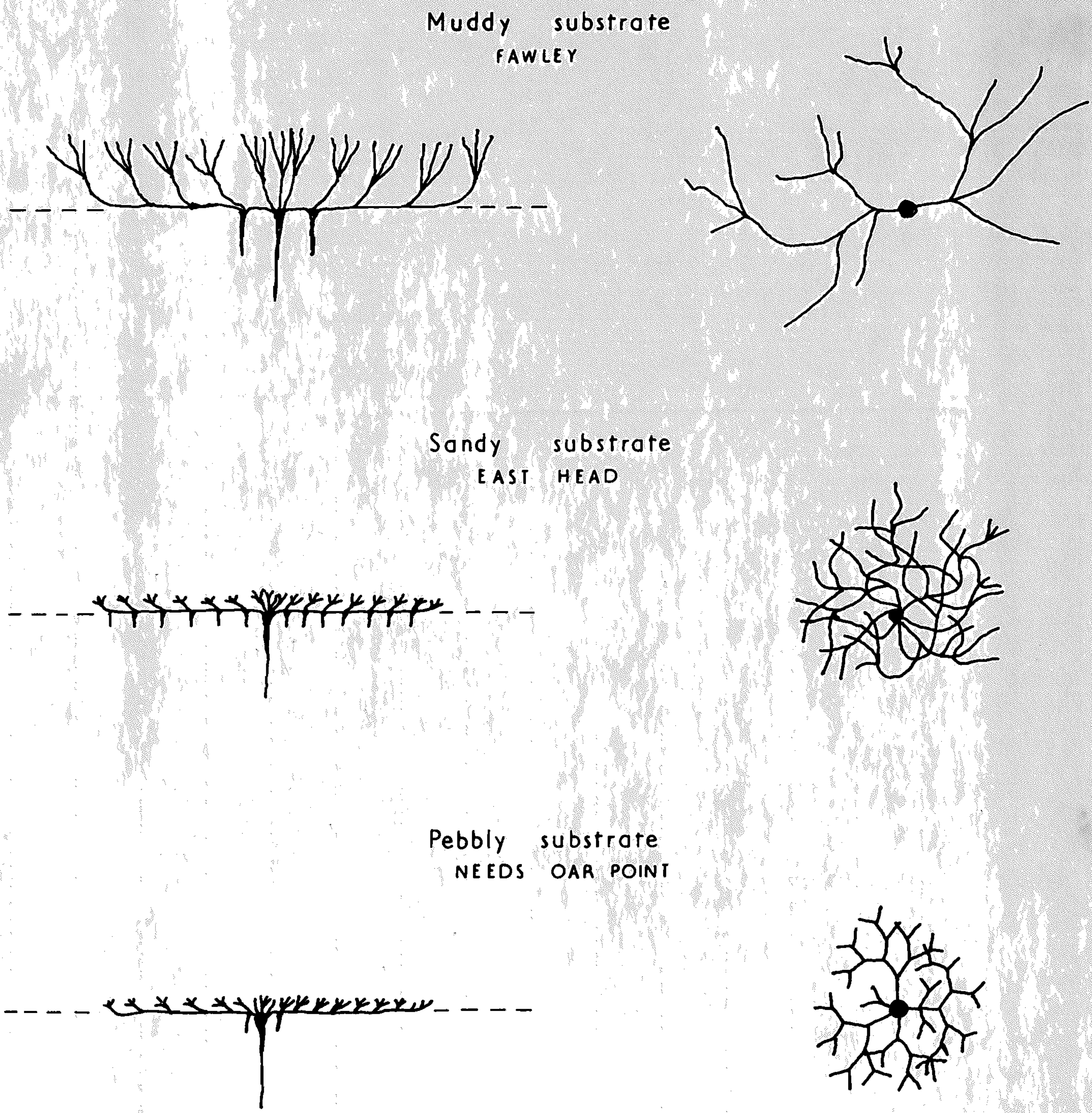
Plants growing on pebble at Needs Oar Point were almost entirely prostrate, but with virtually no nodal rooting or development of vertical shoots. These plants also showed a very great amount of branching, apparently due to mechanical damage to the apical buds (presumed to be due to shingle movement) leading to much lateral development and a "fan-like" habit.

From these results, brief descriptions of plants "typical" of sand, mud and pebble substrates were obtained. Diagrammatic representations of extreme forms of these three types are shown in Fig. 9.

Supporting the contention that the habit of Halimione varied depending upon the substrate were casual observations that plants growing on mud at East Head and Needs Oar Point resembled the type found at Fawley, that plants growing on sand in other localities resembled the East Head type and that plants growing on shingle at other sites resembled the very distinct Needs Oar Point type.

The observations and limited laboratory work, therefore, gave further evidence that the morphology of Halimione portulacoides is very variable, even within the Hampshire basin. Moreover this variation appeared, from superficial and subjective examination, to be correlated with differing substrata. The importance of various interacting factors such as height of the marsh, substrate water

Fig. 9. Diagrammatic representations of the three extreme types of habit of Halimione portulacoides found on muddy, sandy and pebbly substrates



content, topography of the marsh, etc. in relation to the distribution of Halimione was already evident and the connection between substrate and these factors of water relations made it obvious that consideration of all these factors would be necessary in any detailed study of the interactions between habitat and morphology.

2. Transplanting and pot-culture

Although the Hampshire basin plants were very variable, apparently correlated with the substrate conditions, it was still not clear whether the morphology of these distinct forms was modified by the habitat or whether genetically different forms were growing on these differing substrates.

In an attempt to resolve this, young plants from each of the three main substrates were transplanted to each of the other two substrates and, in addition, plants from each substrate were grown in pots under identical conditions.

After two years, the transplants exhibited habits indistinguishable from that of plants native to their new habitat and unlike that of plants in their original habitat. The plants in pot-culture were all identical in appearance after two years, despite having come from very different substrates.

Although these experiments were on a small-scale and the comparisons were largely subjective, on the basis of the measurements found to be specific to each type, these cultivation and transplanting experiments clearly suggested that (as had been suspected) the differing habitat conditions were modifying genetically homogeneous plants.

3. Discussion

The examination of Hampshire basin material confirmed that vars. parvifolia and angustifolia were absent and all specimens collected were referable to var. latifolia. At the same time, the morphology of these plants, all apparently latifolia, varied so considerably that entirely different habits were observable and these appeared to be correlated with the substrate - very different habits being typical of mud, sand and pebble.

Logical explanations for the modification of the "typical" habit of plants found on mud could be put forward to explain the habits of plants on sand and pebble substrates and limited transplanting from one substrate to another and small-scale pot-experiments confirmed the impression that the habitat conditions were modifying genetically similar material.

While it was apparent that the morphological variation was probably externally influenced by the habitat, it was also evident that the habitat factors involved were many and interacting and that any attempt to correlate the morphological variation with the associated habitat differences would have to consider all of them.

IV. ANALYSES OF DETAILED OBSERVATIONS FROM THE HAMPSHIRE BASIN MARSHES

A. Introduction

It has been seen in the preceding sections that cursory examination of *Halimione portulacoides* at various Hampshire basin sites indicated marked morphological differences between plants in different habitats, this variation being particularly marked between sites with different substrates. However, there is always the danger of subjective selection leading to unconscious selection of plants showing extreme characters; this is demonstrated by examples such as *Nymphaea alba* (Heslop-Harrison, 1953). In the present study, a completely objective collection of the data was required to eliminate any unconscious bias that might have entered the initial study. To this end, morphological measurements and information on habitat features were collected from metre-square quadrats at five Hampshire basin sites, measurements being made on the total *Halimione* content of each quadrat, and not on single plants as previously. At the same time, data were collected as to the other species associated with *Halimione* in the quadrats, to serve both as an indication of its general community relationships with other salt marsh plants and to provide additional indirect evidence as to the ecological factors at work throughout its range.

The five areas chosen for detailed study were: (1) Area 7, Needs Oar Point (pebble substrate); (2) Area 9, Fawley (muddy substrate); (3) Area 12, Bursledon (mainly very wet muddy substrate, with much *Spartina townsendii*); (4) Area 13, North

Binness Island (muddy substrate; an old high marsh with no Spartina colonisation); and (5) Area 15, East Head (sandy substrate). (The area numbers refer to Fig. 1.) Ten metre-square quadrats were laid out at each of these five diverse areas.

B. Relationship between habitat and the morphology of Halimione portulacoides

1. Data collection

a. Plant morphology

During the late summer of 1961, measurements were made on all the Halimione portulacoides plants within the fifty metre-square quadrats set out in the five Hampshire basin sites. A total of fourteen attributes were measured, as follows:

1. Total number of lateral branches
2. Total number of flowering apices
3. Total number of living vegetative apices
4. Total number of dead apices
5. Total length of 'prostrate-rooting' portion, in cm
6. Total length of 'prostrate non-rooting' portion, in cm
7. Total length of 'vertical' portion, in cm
8. Total number of nodes
9. Fresh weight in g of below-ground portion
10. Fresh weight in g of above-ground portion, excluding the leaves
11. Total number of leaves
12. Fresh weight of leaves, in g

13. Dry weight of leaves, in g

14. Percentage cover of quadrat by Halimione portulacoides

The total Halimione portulacoides content of each quadrat was transported in polythene bags and the analyses carried out in the laboratory. Attributes 5, 6 and 7 were determined by dividing the plants into prostrate and vertically growing portions and then further separating the prostrate portion into that which was rooting at the nodes and that which was not. The total length of each of the resulting three portions was then measured in cm. The dry weight of the leaves (13) was obtained after drying in an oven at 90°C until two consecutive weightings at 24 hour intervals did not differ. The percentage cover (14) was estimated by means of a metre-square quadrat frame gridded into 100 squares.

b. Habitat

It was clear from earlier work that many of what might be termed the "water relations factors" were interacting and all of those which could be accurately determined on as many as fifty samples were included, since it was impossible to separate the effect of one from that of another or give one prominence over another. In addition, the separation on substrate was given a more objective basis by inclusion of soil fractions. The selection of fourteen habitat factors for detailed measurement was governed by a compromise between those which were considered to be of most importance and those which could be readily and quickly determined on fifty samples. Those selected were as follows:

1. Distance from nearest creek

The distance of each quadrat from the nearest drainage creek was measured in cm.

2. Percentage water content (emergence)

Samples of soil were collected from each quadrat in air-tight screw-top bottles at periods of longest exposure from tides. The samples were weighed wet and again after drying at 90°C until two consecutive weighings at 24 hour intervals did not differ. The percentage water content was calculated from the loss in weight.

3. Percentage water content (submergence)

The same procedure was carried out as in 2, except that the samples were collected immediately after the period of maximum tidal submergence.

4. Percentage organic content

Approximate values for organic content of the soil were determined for each sample by ignition in a muffle-furnace at 900°C.

5. Height above Ordnance Datum

The height (in cm) above O.D. of each quadrat was obtained by levelling back to the nearest bench-mark. The results were always checked by at least one repeat set of levellings.

6. Percentage sodium content

The sodium content of the soil samples was determined by means of flame-photometry. A soil solution was obtained from each 0.5 g sample by extraction with acetic acid. (The potassium contents were also determined, but these were not used in the analysis since they were invariably approximately one tenth of the sodium value.)

7. Compactibility

The degree of compactibility of the substrate in each quadrat was obtained by use of the apparatus shown in Fig. 10. A solid cylindrical iron rod of diameter 1.3 cm was dropped vertically from a height of 30 cm through a hollow iron tube of internal diameter 1.5 cm which was held in a wooden tripod and kept vertical by reference to a plumb-line. The distance to which this iron rod penetrated the substrate was measured in cm. This was repeated ten times in different parts of each quadrat and the mean value was taken as the recorded measurement. A high value, thus, indicates high compactibility (i.e. a 'soft' substrate).

8. Speed of drainage

A metal tube of diameter 4.5 cm was embedded in the undisturbed substrate and 500 cc of sea-water was poured in. The time (in min) which this took to drain away was timed with a stop watch. A high value, thus, indicates a low speed of drainage.

9, 10, 11, 12, 13 & 14. Soil particle size

The separation of soil fractions in saline substrates may either be determined wet or dry. On the advice of Mr. A. Anning, Soil Analyst to the Department of Civil Engineering at Southampton University, the fractions were separated in oven-dried samples by means of British Standard sieves. The weight of each fraction was used to calculate the percentage of each particle size. The sieves used were of British Standard sizes 10, 25, 52, 72 and 200, of

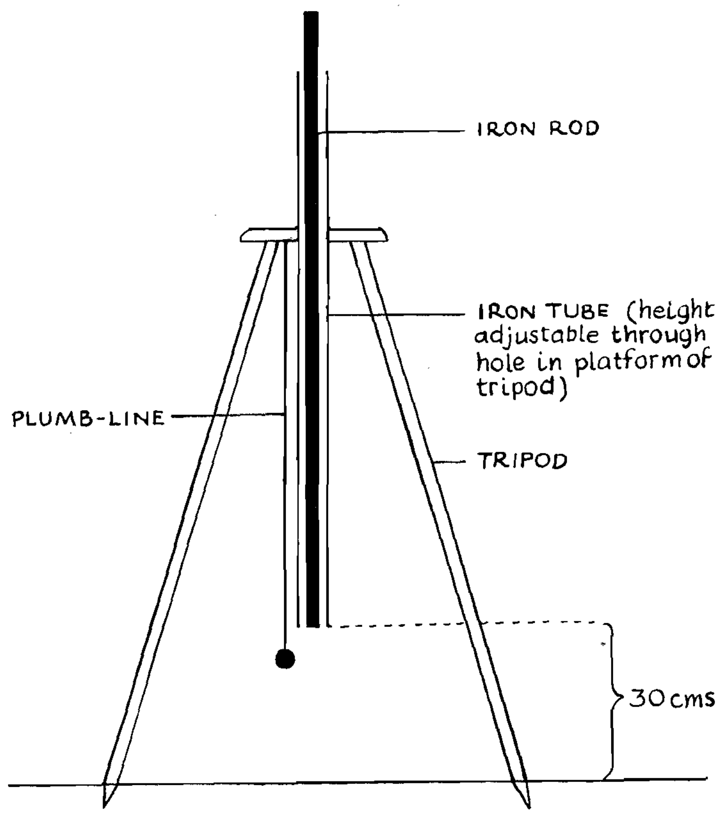


Fig. 10. Diagram of the apparatus used to measure compactibility

respective aperture width of 1676, 599, 116, 83 and 30 microns. This gave a separation into six fractions which, for convenience, will henceforth be termed "pebble", "coarse sand", "medium sand", "fine sand", "silt" and "clay", respectively.

2. Univariate appraisal

The data collected from the 50 quadrats in the Hampshire basin are given in tabular form in Appendices II and III. The distribution of these data is shown by means of histograms in Fig. 11. It will be seen that whereas some (such as percentage cover (14)) have a fairly symmetrical distribution, most of the remainder (such as number of nodes (8), number of flowering apices (2), etc.) follow a distinct "J" curve. A number of the histograms will also be seen to be discontinuous. This is most marked in the length of the vertical portion (7) and this is shown in detail in Fig. 12, the numbers referring to the respective quadrat numbers.

A detailed comparison of the composition of the blocks in the five most discontinuous histograms (numbers 2, 3, 7, 11 and 13) showed that nine groups of two or more quadrats always remain closely associated although these nine groups contain only just over half (29/50) of the quadrats and the others are completely scattered in relation to these groups. The nine groups of 29 quadrats which are closely associated with one another are shown in Table 1.

Although the quadrats within these groups are, by definition, similar in their values for dry weight of leaves, number of leaves, number of vegetative apices, number of flowering apices and length

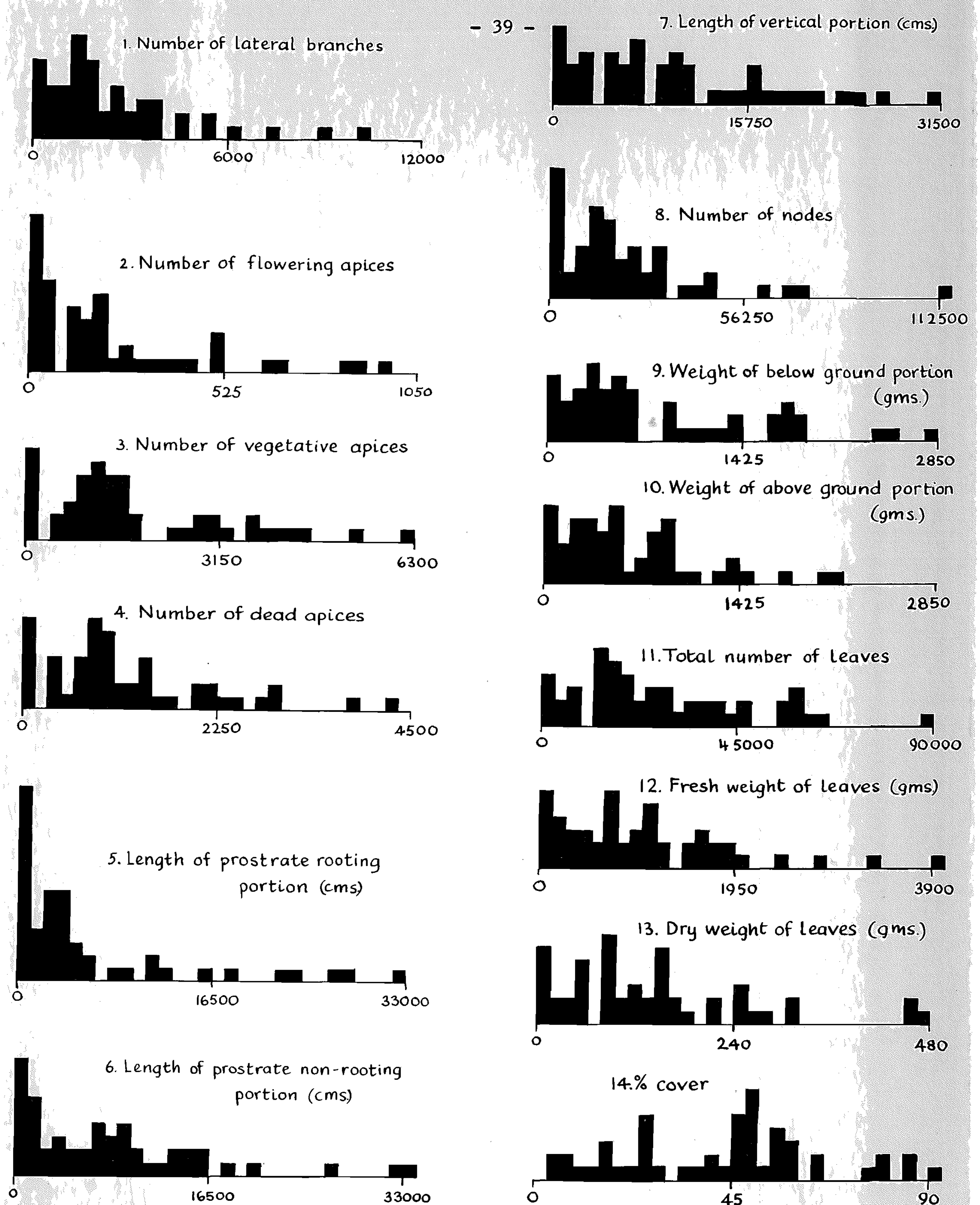


Fig. 11. Histograms showing distribution of the 50 Hampshire basin quadrats for each of the 14 morphological characters which were measured

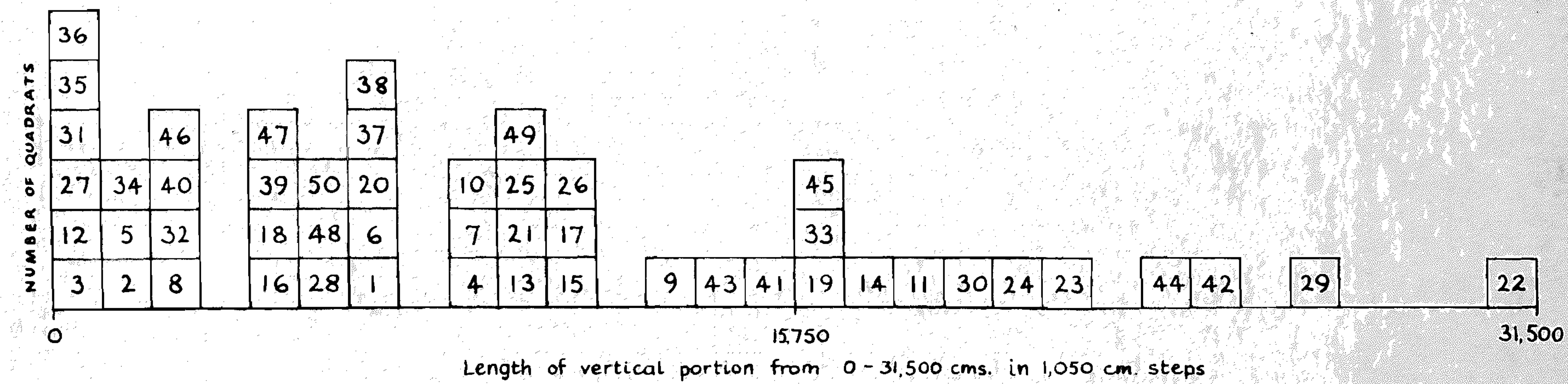


Fig. 12. Histogram of the distribution of the 50 Hampshire basin quadrats in relation to the length of the vertical portion

Table 1. Groups of quadrats consistently associated in discontinuous histograms

(Nine Groups of closely associated quadrats are given, listed by quadrat number and followed by the area in which the quadrat was located.)

Group I

3 Needs Oar Point
5 Needs Oar Point
46 East Head

Group II

11 Fawley
33 North Binness Island

Group III

12 Fawley
31 North Binness Island
34 North Binness Island
35 North Binness Island
36 North Binness Island

Group IV

13 Fawley
15 Fawley
21 Bursledon
25 Bursledon
26 Bursledon

Group V

16 Fawley
18 Fawley
28 Bursledon
37 North Binness Island
38 North Binness Island
39 North Binness Island

Group VI

20 Fawley
48 East Head

Group VII

23 Bursledon
30 Bursledon

Group VIII

41 East Head
45 East Head

Group IX

42 East Head
44 East Head

of the vertical portion, a comparison of the other characters and also of the habitat features of the quadrats shows that these are widely differing and that (apart from the characters upon which they are defined) the quadrats in each group have nothing in common.

Extensive comparisons of this type on all the data were carried out but no common pattern was in any way apparent. It would be tedious to give in full the details of these abortive comparisons and one is selected as an example.

Group V from Table 1 may be taken as an example. All these quadrats show relatively low values for the five characters by which they were grouped. Their values for the other nine morphology characters are given in Table 2. Perusal of these data reveals no pattern and the quadrats show little in common as regards these characters and they are just as diverse in their habitat characteristics, which are shown in Table 3.

The other groups similarly are not homogeneous when all the factors are taken into account. Thus, even exhaustive univariate comparisons of the data do not provide an adequate means of analysis, nor do they support the preceding impression of three main types of morphology associated with substrate composition. The failure to do so might, however, be due either to unconscious selection of extremes in the initial survey, falsely indicating the presence of distinct types, or to the separation of the types on a large number of characters simultaneously, this not being apparent in a univariate analysis of the mass of detailed measurements.

Table 2. Values of morphological measurements which were not used to define Group V, for the quadrats contained in Group V

							Other quadrats	
Quadrat numbers:	16	18	28	37	38	39	Min.	Max.
1. Number of side-branches	768	899	1,598	1,752	1,443	1,892	56	10,658
4. Number of dead apices	420	619	1,003	1,242	980	2,022	26	4,249
5. Length of prostrate-rooting (cm)	971	2,208	3,691	2,719	640	374	14	32,762
6. Length of prostrate non-rooting (cm)	7,564	3,304	14,962	5,036	4,345	9,559	131	33,498
8. Number of nodes	7,921	7,308	14,768	11,160	9,223	16,260	326	112,783
9. Weight below ground (g)	279	430	643	370	141	354	.7	2,801
10. Weight above ground (g)	363	511	546	416	415	688	8	2,175
12. Fresh weight of leaves (g)	690	741	776	634	574	560	16	3,900
14. Percentage cover	50	25	25	40	21	25	3	90

Table 3. <u>Values of habitat measurements for quadrats in Group V</u>

Quadrat numbers	16	18	28	37	38	39	Other quadrats Min.	Other quadrats Max.
1. Distance from nearest creek (cm)	1,460	200	290	370	270	250	0	1,460
2. % water content (emergence)	59.57	61.98	64.83	53.54	48.17	49.20	1.54	68.17
3. % water content (submergence)	61.51	66.24	72.67	63.98	61.60	59.26	5.78	78.25
4. % organic content	22.64	37.06	26.72	23.42	24.73	22.49	0.86	37.33
5. Height above O.D. (cm)	171.5	170.0	159.0	166.3	165.6	164.7	133.4	196.5
6. % sodium content	2.00	1.96	2.00	1.60	2.88	1.68	0.08	5.04
7. Compactibility (cm)	13.4	12.1	26.4	11.7	10.6	11.0	0.9	31.9
8. Speed of drainage (min)	27	24	60	37	40	36	1	140
9. % pebble	0.00	0.00	0.00	0.00	0.00	0.00	0.00	66.54
10. % coarse sand	1.39	3.95	1.16	0.98	2.34	0.67	0.00	10.72
11. % medium sand	15.37	10.10	18.83	5.91	1.34	9.11	0.74	40.82
12. % fine sand	6.58	10.90	5.71	2.67	4.39	6.94	1.14	28.56
13. % silt	38.52	51.72	32.15	47.71	31.11	22.10	1.60	55.27
14. % clay	38.14	23.33	42.35	42.73	60.82	61.18	0.53	61.58

Since the univariate approach to the morphological data had proved to be unproductive, no detailed univariate analysis was made of the habitat data.

3. Multivariate analyses

a. Introduction

Since it seemed likely that a combination of morphological characters, unlikely to be clearly recognisable in a univariate analysis, was important, multivariate analyses were undertaken. There was the expectation that, if it was combinations of characters which were important in separating differing habits, these were likely to show up in multivariate analysis where they had not been obvious in univariate appraisal.

b. Methods

The two methods of multivariate analysis carried out on these Hampshire basin data were Principal Component Analysis and Factor Analysis. Although the use to which these were put was experimental, the techniques themselves are well-known, expecially in the sociological and psychological fields (Thurstone 1947, Cattell 1952, Thomson 1956, etc.) and consequently it is not felt necessary to give detailed accounts of the methods and only a brief description follows.

It is theoretically possible to display the data in a space where the axes are attributes (variables) and the points are samples. This would be an "R space" representation. From correlations between the variables it is possible by Principal Component Analysis to arrive at a new set of orthogonal axes, defined by the cosines of the angles between the latent vectors, and associated with each of these is a value, the latent root, which is a measure of the amount of variation "accounted for" by each of the axes. Those axes which account for the majority of the variation can be selected and the individuals plotted with relation to these new axes. In Component Analysis, minor, repeated, variations may produce a picture which slightly obscures any underlying pattern and, to eliminate this, Factor Analysis is sometimes preferred.

Factor Analysis commences with the hypothesis that the common variation in the data (that is, not including error variation or any variation specific to a single variable) can be represented by a specific number of factors or axes. This is most often accompanied by a requirement for the simplest representation. These axes may be obtained by substituting communalities for the elements of the principal diagonal of the correlation matrix. Communalities are estimates of the amount of non-specific, non-error variance. In practice, subjective estimates of the communalities can be obtained from Principal Component Analysis. These are then substituted and new factors obtained from which a second estimation of the communalities is possible and the process iterated until the communalities converge to a constant value. The number of factors can also be subjectively estimated from Principal Component Analysis, if no *a priori* estimation is possible.

The factors obtained can be used as axes on which the individuals can be displayed, They are, however, orthogonal (uncorrelated) factors. If it is desired, as is normally the case, to make hypotheses on the nature of the factors with a view to testing such hypotheses by further analyses of some kind, the reality of orthogonal factors can be questioned, for in most biological data interactions are common and it is somewhat unrealistic to deal with completely uncorrelated factors. To remove this restriction and to provide the simplest possible description of the variables (at the cost of increasing the complexity of the factor interactions) rotation of the factors can be undertaken. In this case some criterion of finality of rotation (the "best" position) is required and the commonest criterion is that known as simple structure, due to Thurstone (1947).

In the absence of suitable computer programmes, rotation was done by hand, following Thurstone. Again, the individuals could be represented on these axes if such is required, although, if the identification of the factor is all that is required, this is not necessary.

Although the factors can strictly only be used to generate hypotheses and their "identification" with known features should only be tentative, it is often convenient to discuss these as if the identification were positive; this will frequently be done in the following sections.

The factors are conventionally given letters (A, B, C....) in decreasing order of importance and are given the suffix o if unrotated (orthogonal) and $_1$ if rotated.

c. Results

i. Morphology

37.41 per cent of the variation was extracted on three factors in Component Analysis. The three factors extracted 66.62 per cent, 15.89 per cent and 4.90 per cent, respectively. Factor Ao has, thus, by far the greatest significance and the third factor (Co) may virtually be ignored. The distribution of the attributes on these factors is shown in Figs. 13 - 15.

All the attributes are highly loaded on Factor Ao, indicating a close relationship between all the measurements and, hence, the homogeneity of the attributes, all of which refer to Halimione portulacoides. The range of variation is shown more clearly on Factor Bo, with length of prostrate-rooting portion, percentage cover, number of nodes, number of vegetative apices, number of side-branches and weight of below-ground portion all highly negative on this factor and number of flowering apices, length of prostrate non-rooting portion, weight of above-ground portion and fresh and dry weight of leaves all highly positive. This gives a clear impression of the two extreme types of plant: a compact, dense, low-growing, seldom-flowering, prostrate-rooting type and a non-compact, upright type with little nodal rooting and frequent flowering.

The distribution of the individuals (quadrats) on Factors Ao and Bo is shown in Fig. 16. Factor Ao is basically a measure of the amount of Halimione in the quadrat, while Factor Bo is a measure of

Fig. 13. Distribution of the 14 morphology attributes in relation to the Ao and Bo axes of Component Analysis (open circles) and Factor Analysis (filled circles) (The numerals refer to the morphology measurements listed on p. 37)

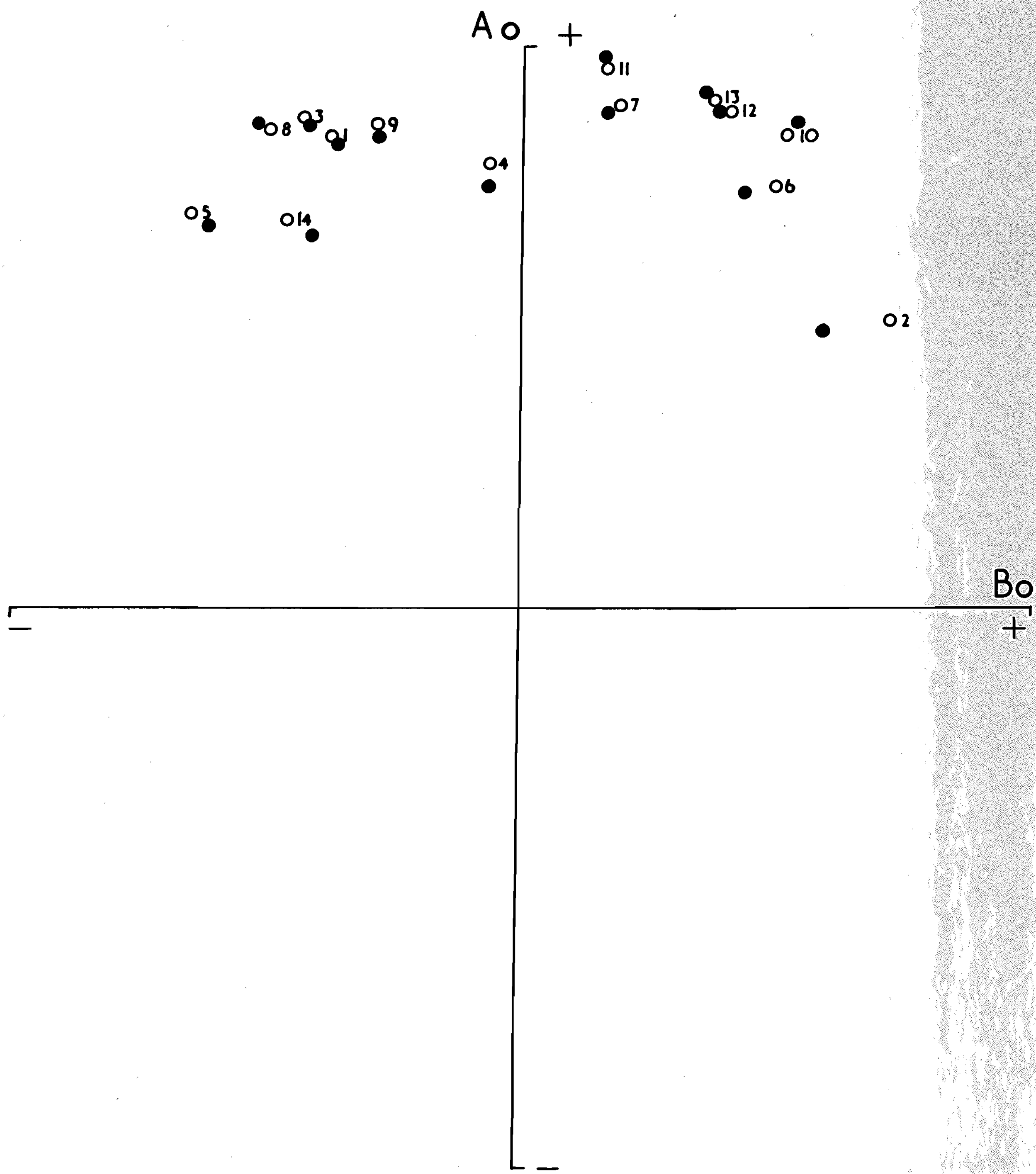


Fig. 14. Distribution of the 14 morphology attributes in relation to the Ao and Co axes of Component Analysis. (The numerals refer to the morphology measurements listed on p. 35)

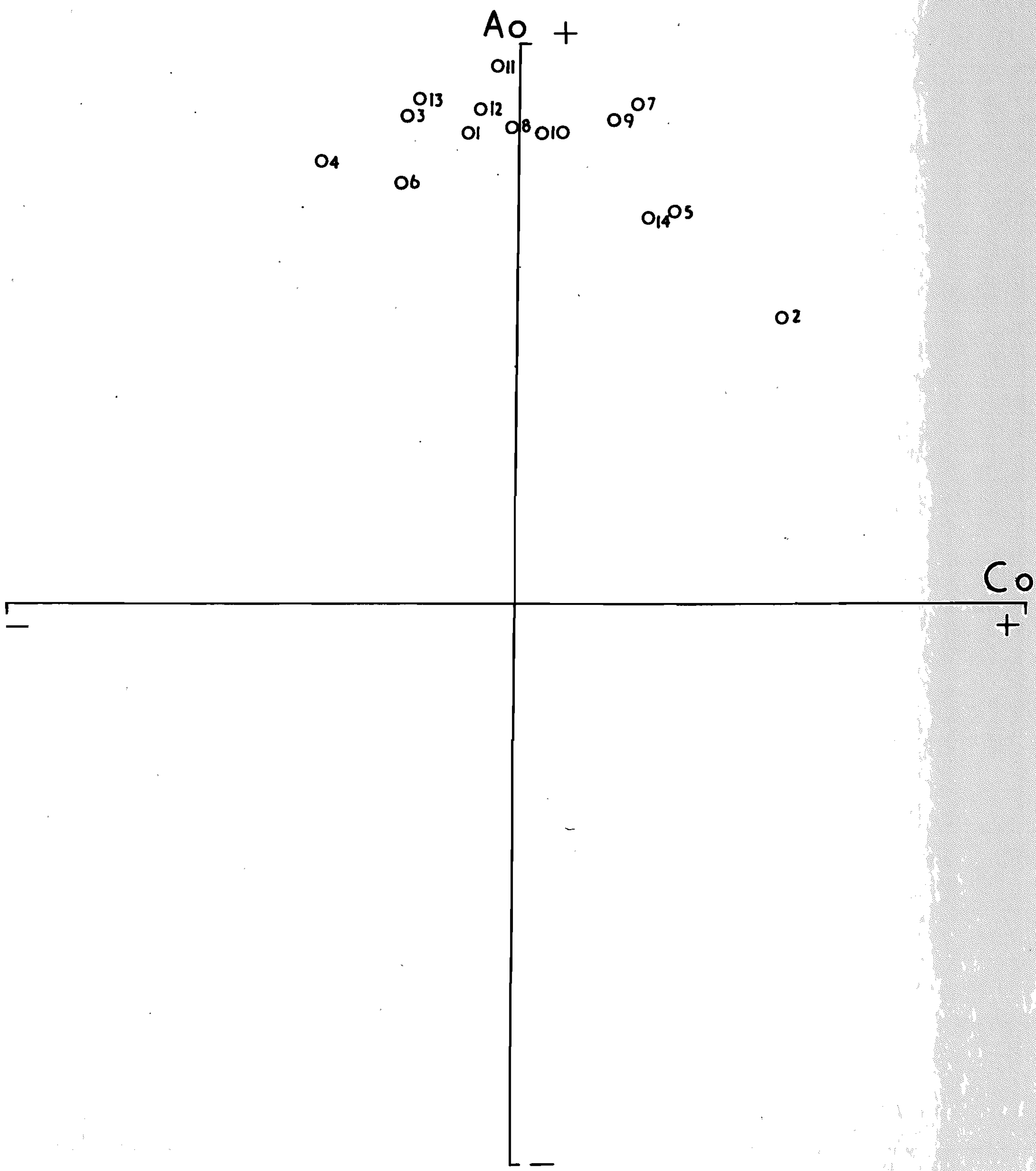
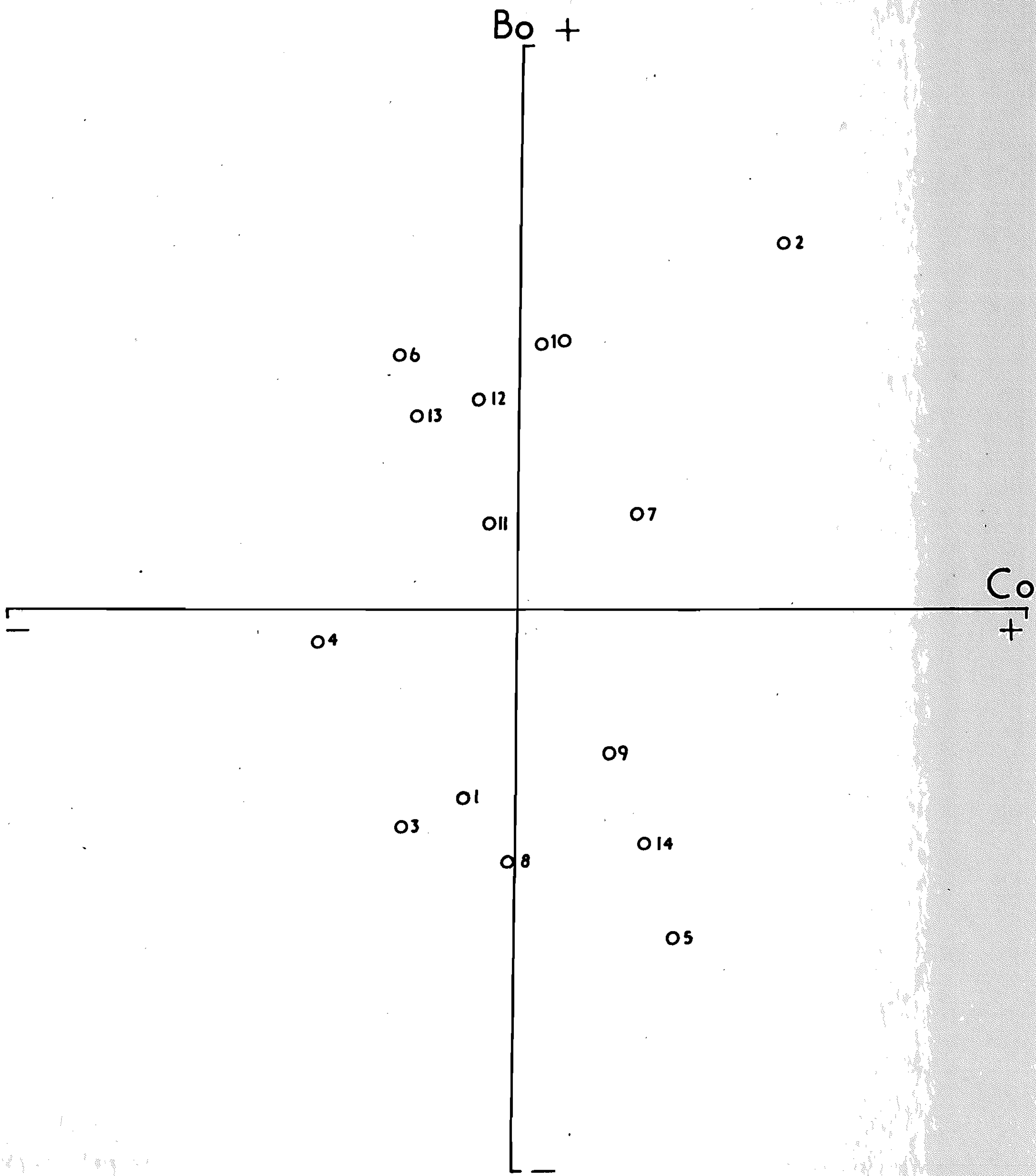


Fig. 15. Distribution of the 14 morphology attributes in relation to the Bo and Co axes of Component Analysis. (The numerals refer to the morphology measurements listed on p.33)



KEY TO SYMBOLS

	AREA	QUADRAT NUMBERS
○	Needs Oar Point	1 - 10
•	Fawley	11 - 20
●	Bursledon	21 - 30
∘	North Binness Island	31 - 40
x	East Head	41 - 50

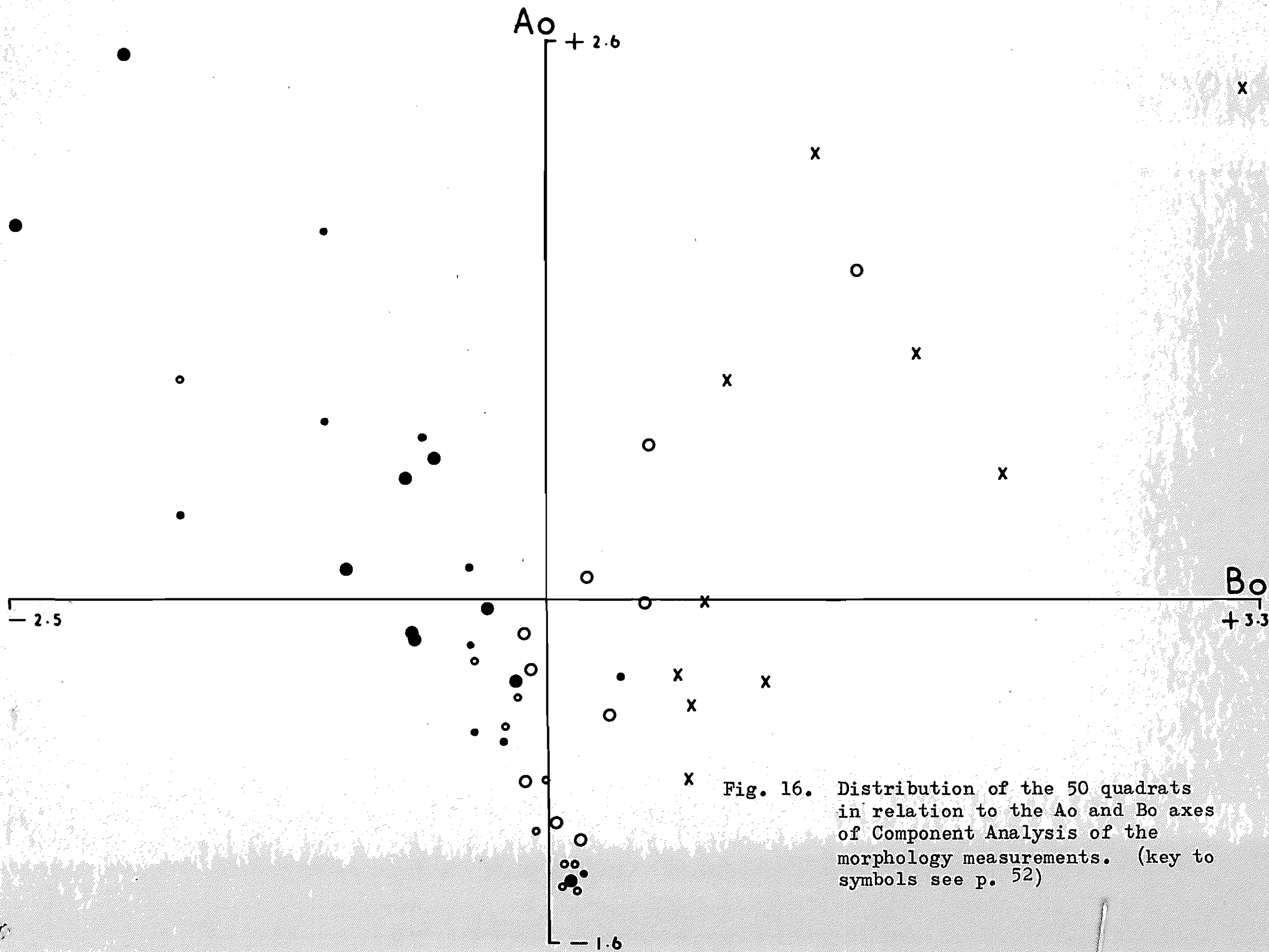


Fig. 16. Distribution of the 50 quadrats in relation to the Ao and Bo axes of Component Analysis of the morphology measurements. (key to symbols see p. 52)

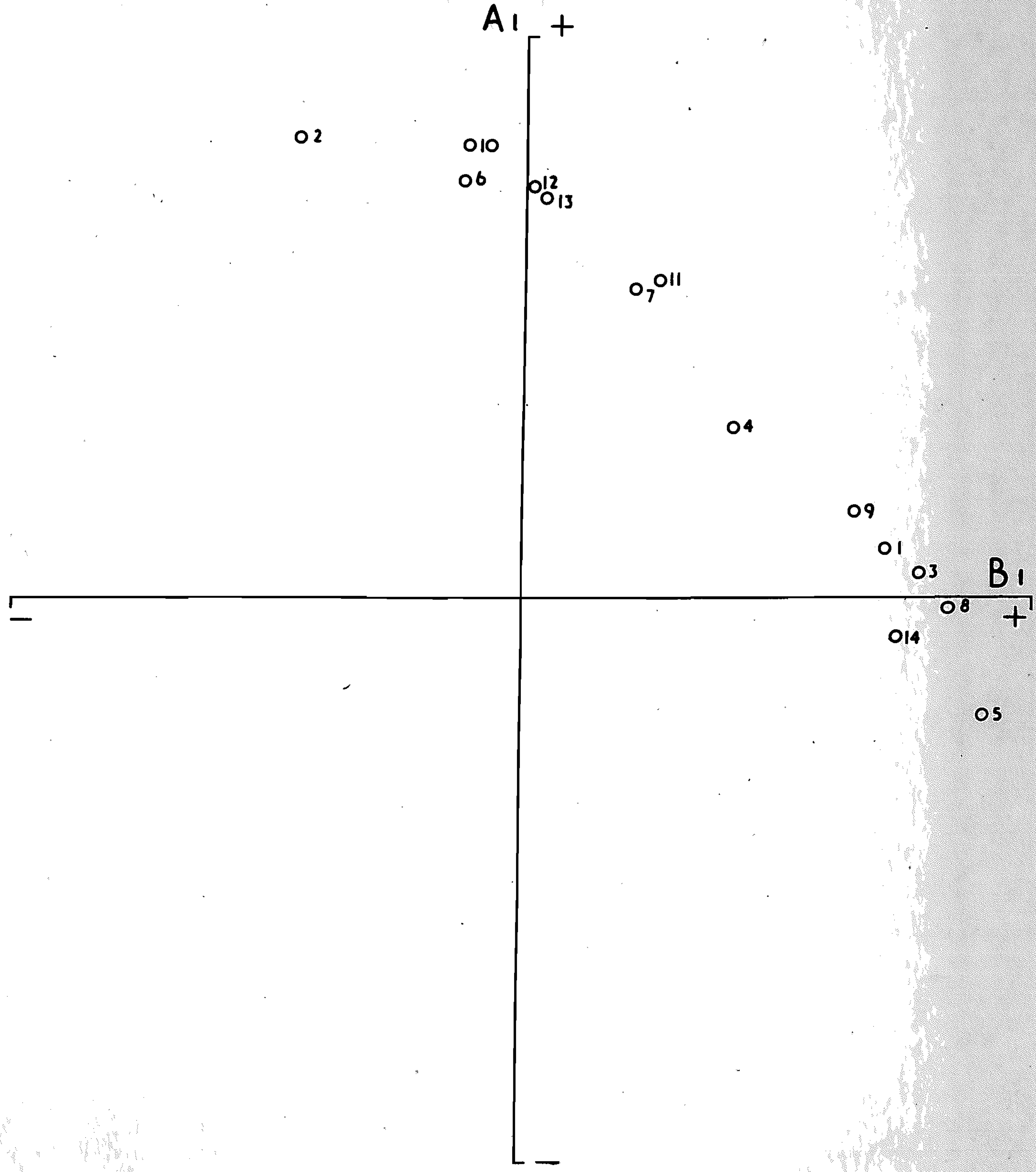
the general habit of the plant. The two extreme types of habit both give a high value for the amount of plant in the quadrat; the low, compact type because of the dense cover and the upright, lax type because of the bushy habit. In consequence, the quadrats form a "V-shaped" distribution, with the plants at East Head and Bursledon forming the extreme points of the "V". The continuous nature of the distribution confirms that the plants from all the five localities are all part of the same morphological population.

Factor Analysis, with communalities from five iterations in the diagonal, hardly alters the distribution of the attributes (Fig. 13).

Rotation of the axes was undertaken by hand calculation. Although separating the two types of habitat, this rotation was of little value in the identification of the factors when the attributes were plotted (Fig. 17). The rotation did, however, have the effect of "cleaning-up" the attribute distribution in aligning these more closely with the factors (ten attributes had loadings of less than 0.2 after rotation, compared with only six before rotation).

The range of variation of the habit of these Hampshire basin plants is demonstrated in Fig. 16 by their relative positions on factor Bo. A histogram of these quadrats plotted on their specifications on factor Bo (Fig. 18) shows the relatively normal distribution. Certainly, from this data, there is no suggestion that the Hampshire basin plants are in any way heterogeneous; the plants showing only the amount of variation that might be expected from a genetically similar series.

Fig. 17. Distribution of the 14 morphology attributes in relation to the rotated axes A_1 and B_1 (The numerals refer to the morphology measurements listed on p.35)



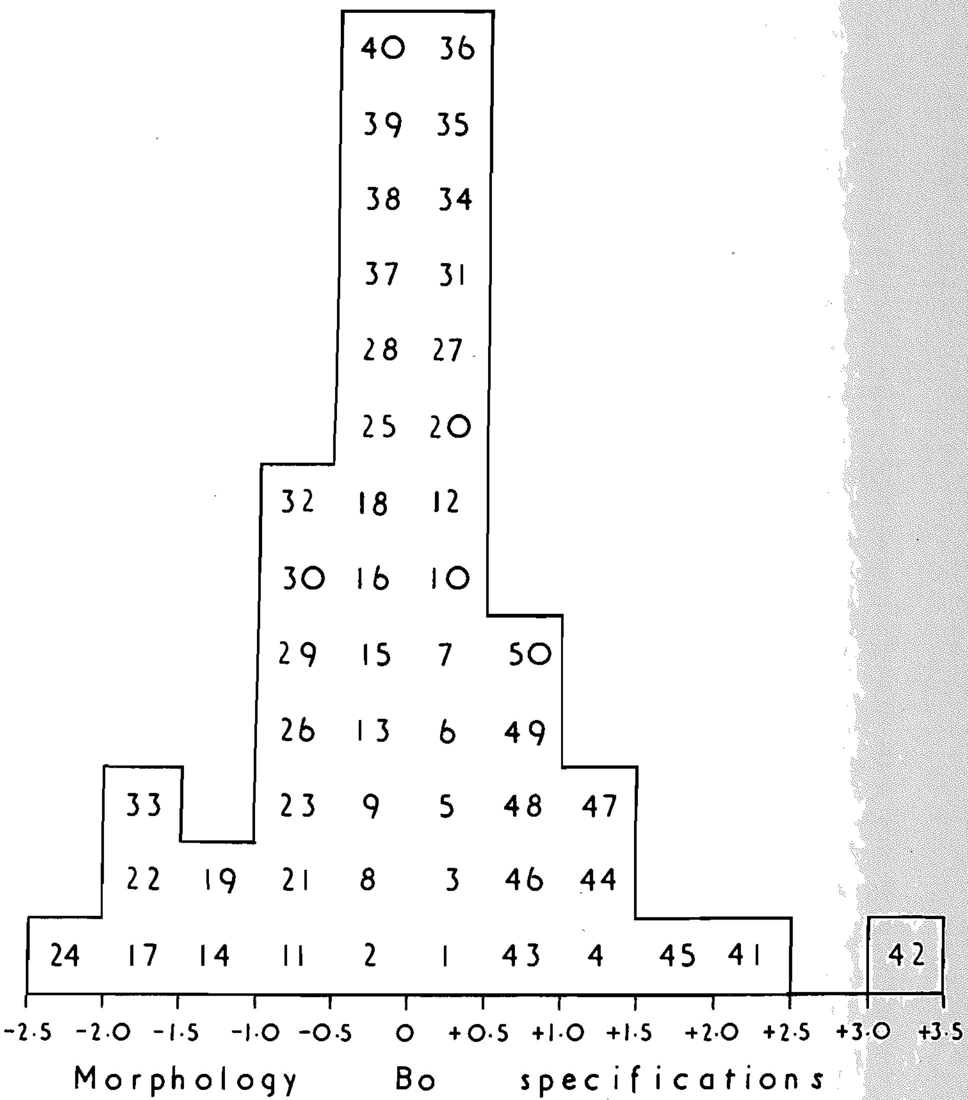


Fig. 18. Histogram of the distribution of the 50 Hampshire basin quadrats in relation to factor Bo of the Component Analysis of the morphological data.

ii. Habitat

In Component Analysis of the complete correlation matrix, 77.45 per cent of the variation was extracted on just three factors and the distribution of the attributes can, thus, be adequately represented in a three-dimensional model. Factor Ao accounted for 49.69 per cent of the variation, factor Bo 19.29 per cent and factor Co only 8.47 per cent. The distribution of the attributes in relation to these axes is shown in Figs. 19 - 21.

The attributes which are highly positive on factor Ao (compactibility, organic content, silt, clay, speed of drainage, etc.) are all those associated with a high water content. The attributes which are negative on factor Ao (pebble, coarse, medium and fine sand, height above O.D., etc.) are conversely all associated with a low water content. It is, thus, possible to tentatively identify factor Ao as a water content factor.

It is far less easy to identify the Bo axis. The height above O.D., fine sand and medium sand are all highly positive on Bo, while pebble, clay and coarse sand are negative. Although far from being proved, this factor could represent increasing exposure, with accretion and erosion as the two extremes. Factor Co, accounting for only 8.47 per cent of the variation, may safely be ignored.

The individuals (quadrats) are plotted on factors Ao and Bo in Fig. 22 and exhibit a distinct inverted "U-shaped" distribution. The extreme ends of the "U" are formed by the dry, pebbly quadrats

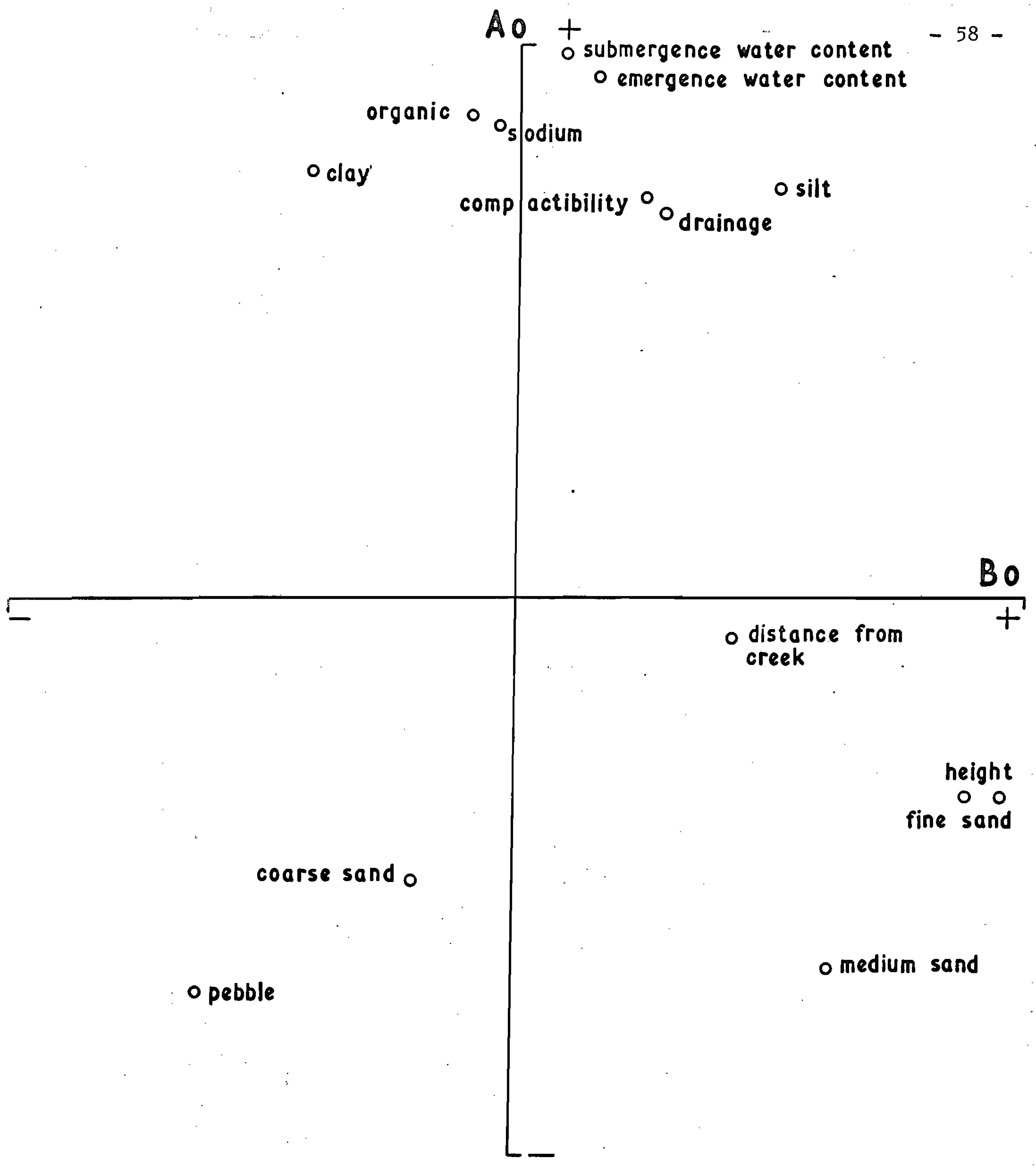


Fig. 19. Distribution of the 14 habitat attributes in relation to the Ao and Bo axes of Component Analysis

Fig. 20. Distribution of the 14 habitat attributes in relation to the Ao and Co axes of Component Analysis

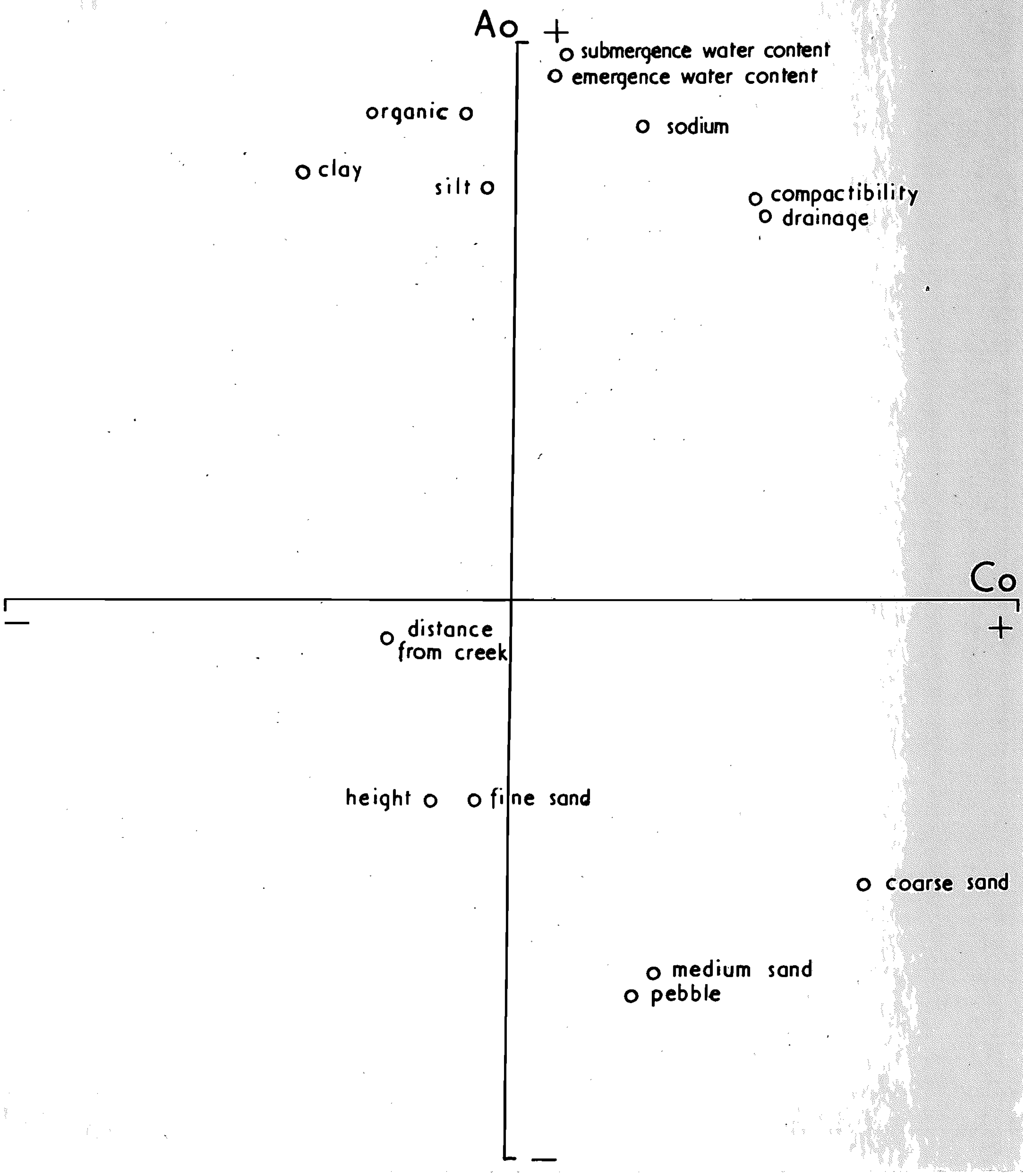
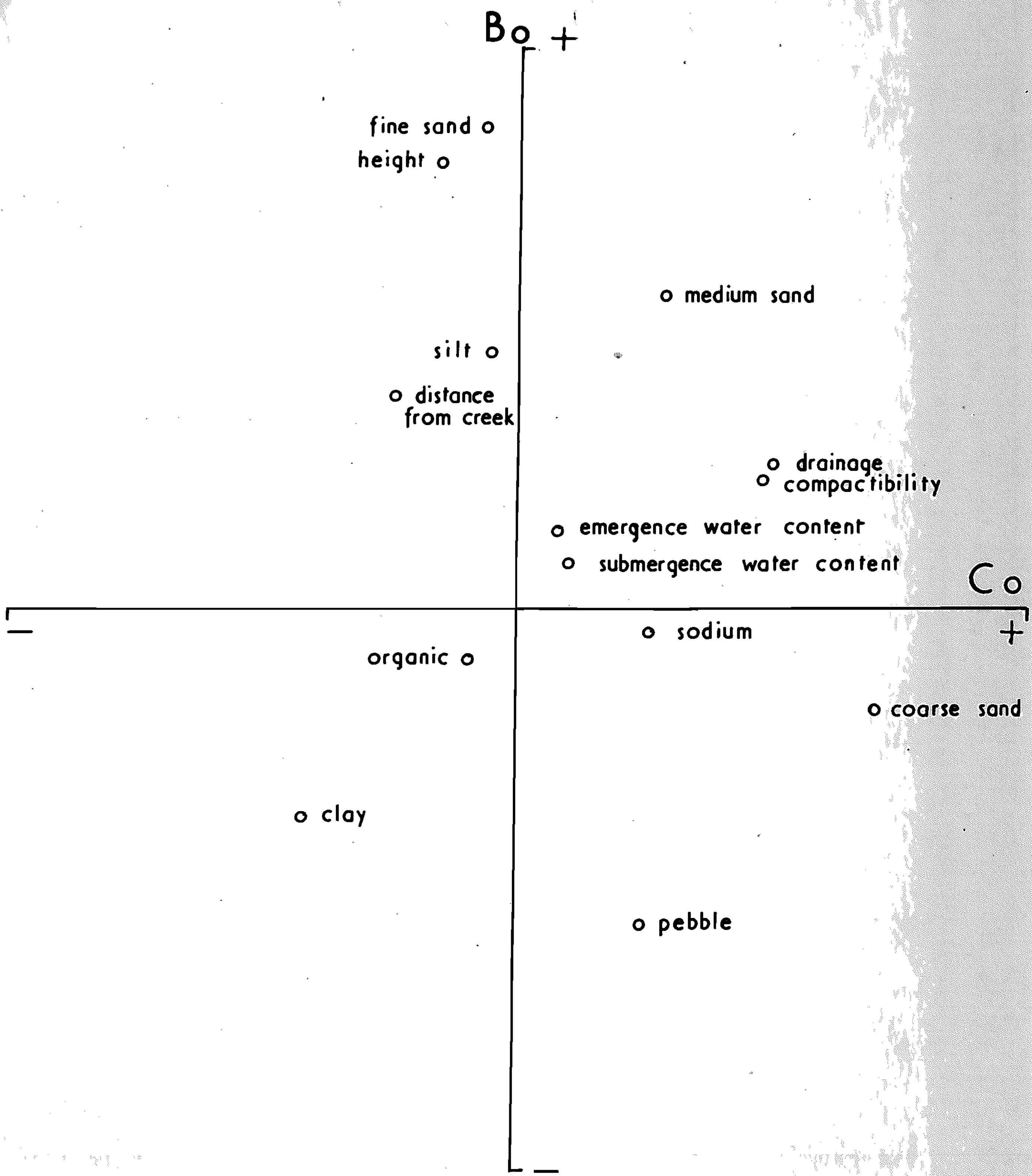


Fig. 21. Distribution of the 14 habitat attributes in relation to the Bo and Co axes of Component Analysis



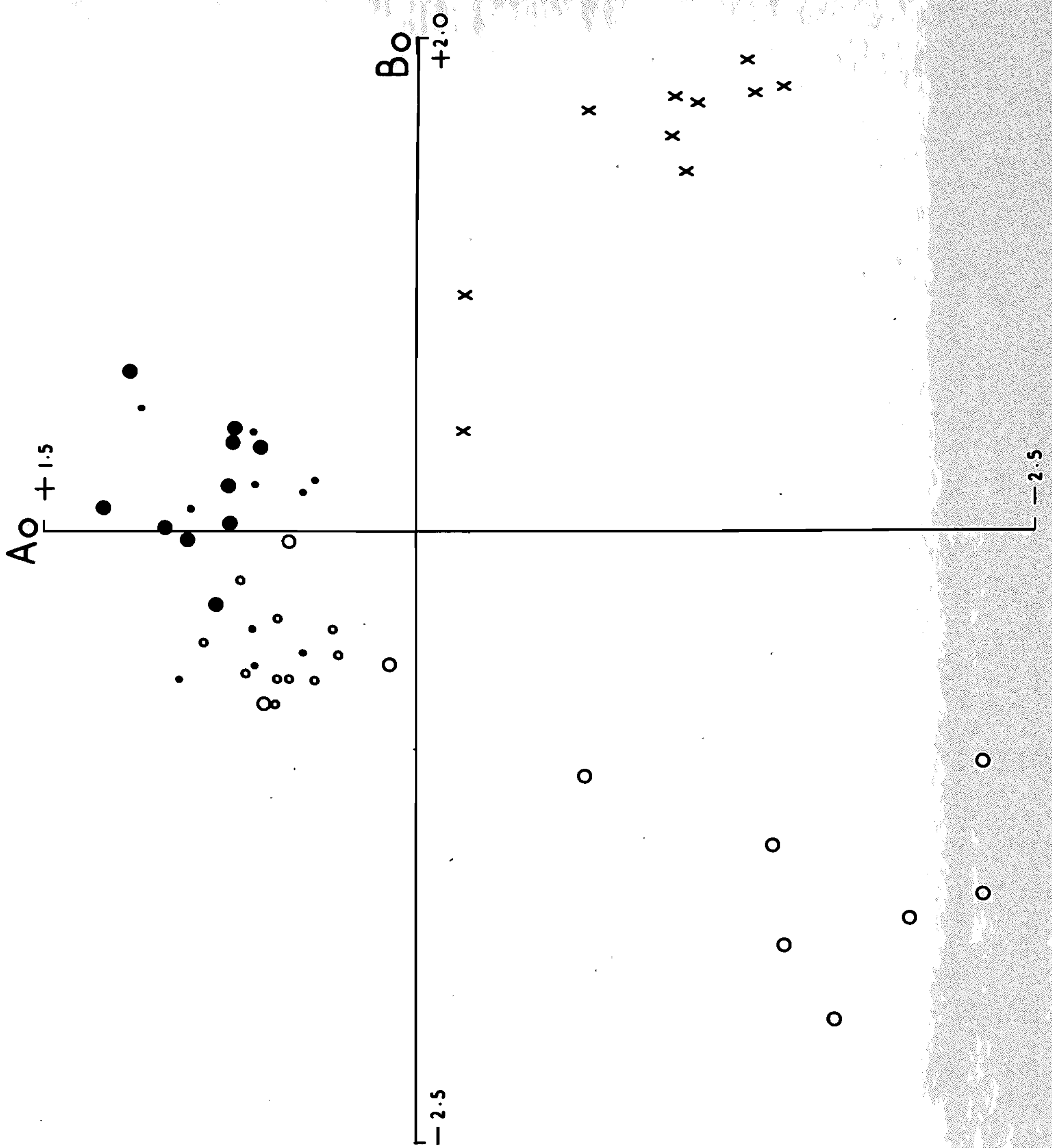


Fig. 22. Distribution of the 50 quadrats in relation to the Ao and Bo axes of Component Analysis of the habitat data (key to symbols on p. 52)

of Needs Oar Point and the dry, sandy quadrats of East Head. The bulk of the remaining quadrats form a cluster at the base of the "U" and consist of the wet, muddy quadrats, especially those at Fawley, Bursledon and North Binness Island. The small number of muddy quadrats at Needs Oar Point and East Head are also associated with the cluster at the base of the "U".

In order to see if there was any clearer underlying pattern, Factor Analysis of the data was undertaken (using communalities, calculated from five iterations from original estimates, in the diagonal of the correlation matrix).

The distribution of the attributes as shown by Factor Analysis is given in Fig. 23 and the values obtained by Component Analysis are also plotted for comparison. It is clear that there is virtually no difference between these two distributions, confirming that virtually all the relevant variation was utilised by the simpler Component Analysis and that there were no minor features masking the overall picture which would have made Factor Analysis necessary.

Rotation of the axes was carried out by hand computation, as described by Thurstone (loc. cit.). The distribution of the attributes in relation to these new rotated axes (now designated A_1 and B_1) is shown in Fig. 24.

The purpose of this procedure (to align the attributes more closely with the factors, and so make identification of the factors simpler) has clearly been achieved, though interpretation of the

Fig. 23. Distribution of the 14 habitat attributes in relation to the Ao and Bo axes of Component Analysis (open circles) and Factor Analysis (filled circles)

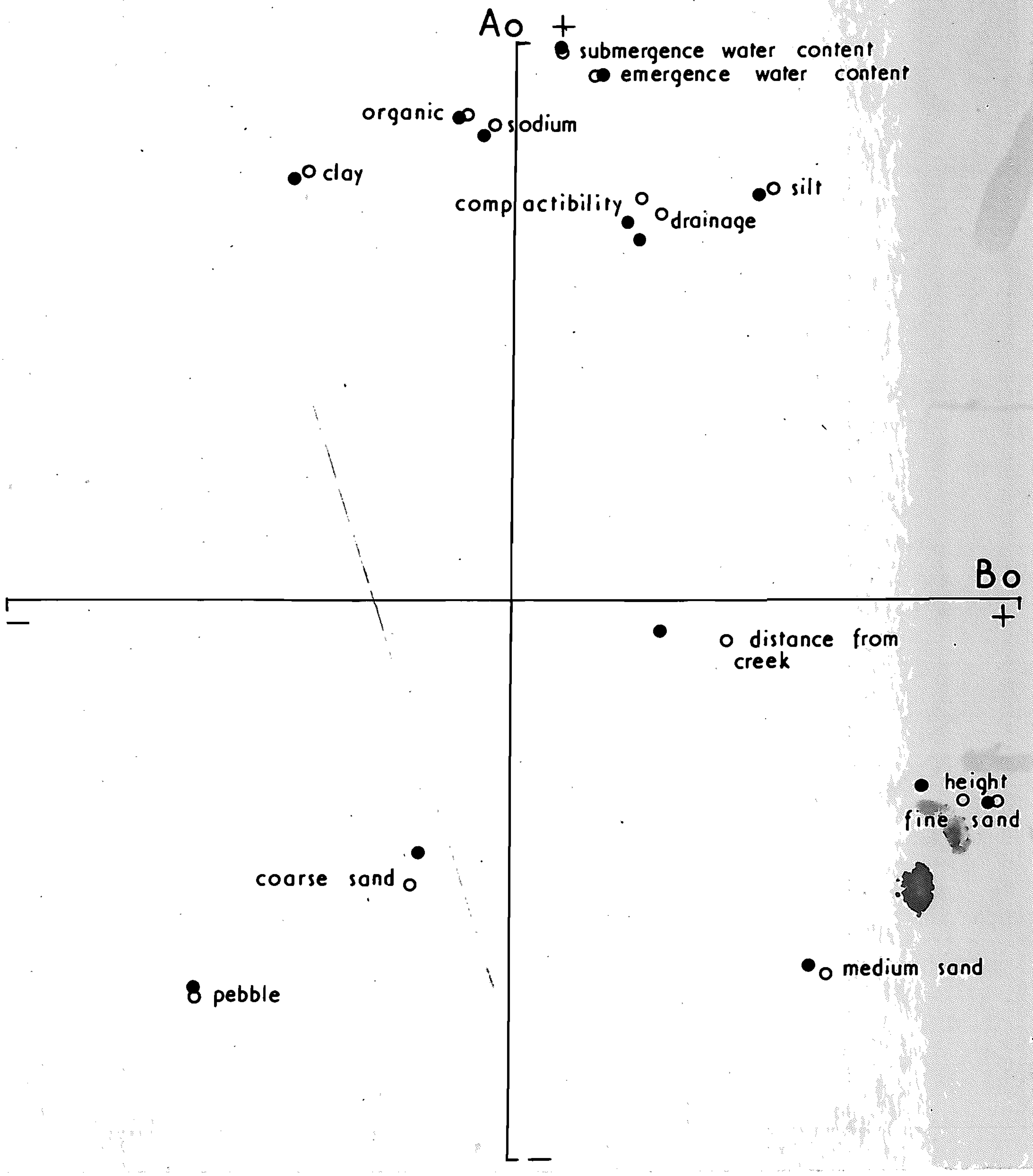
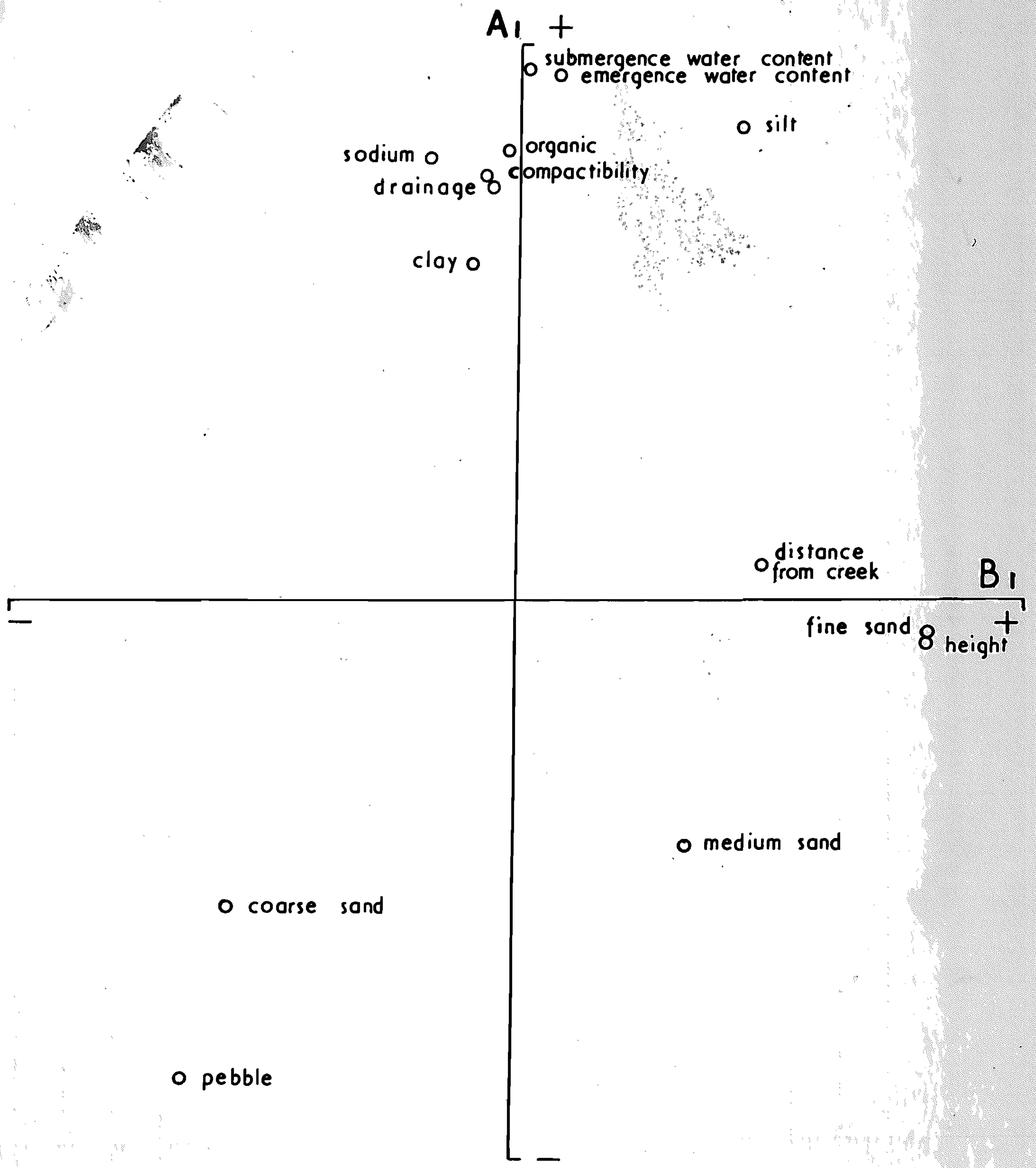


Fig. 24. Distribution of the 14 habitat attributes in relation to the rotated axes A_1 and B_1



factors (now correlated), is, in fact, not aided.

The distribution of the individuals (quadrats) specified on the rotated factors is shown in Fig. 25. The "U" formation of the unrotated factors has now closed up into an acute-angled "V", but the relative positions of the points are largely unchanged, though the dry East Head and Needs Oar Point quadrats are brought closer together and now form the end of an almost linear series with the muddy quadrats at the opposite end.

iii. The connection between morphology and habitat

The Principal Component and Factor Analyses have given a certain amount of information regarding the morphology and habitat, but the test for the hypothesised interrelationship lies in the correlation between these two sets of analyses.

The classical method of determining the correspondence between two separate analyses (such as those of habitat and morphology carried out here) is by undertaking Canonical Analysis. This takes each factor from one analysis and compares it in turn with each factor from the second analysis. Canonical Analysis is extremely complicated mathematically but could be undertaken, although no programme exists for use with a Pegasus computer. However, there are basic objections to the theory behind Canonical Analysis, quite apart from any computational difficulties. As already pointed out, the use of orthogonal factors can be objected to on the grounds that in biological work it is highly unlikely that two factors will ever be completely uncorrelated (this is,

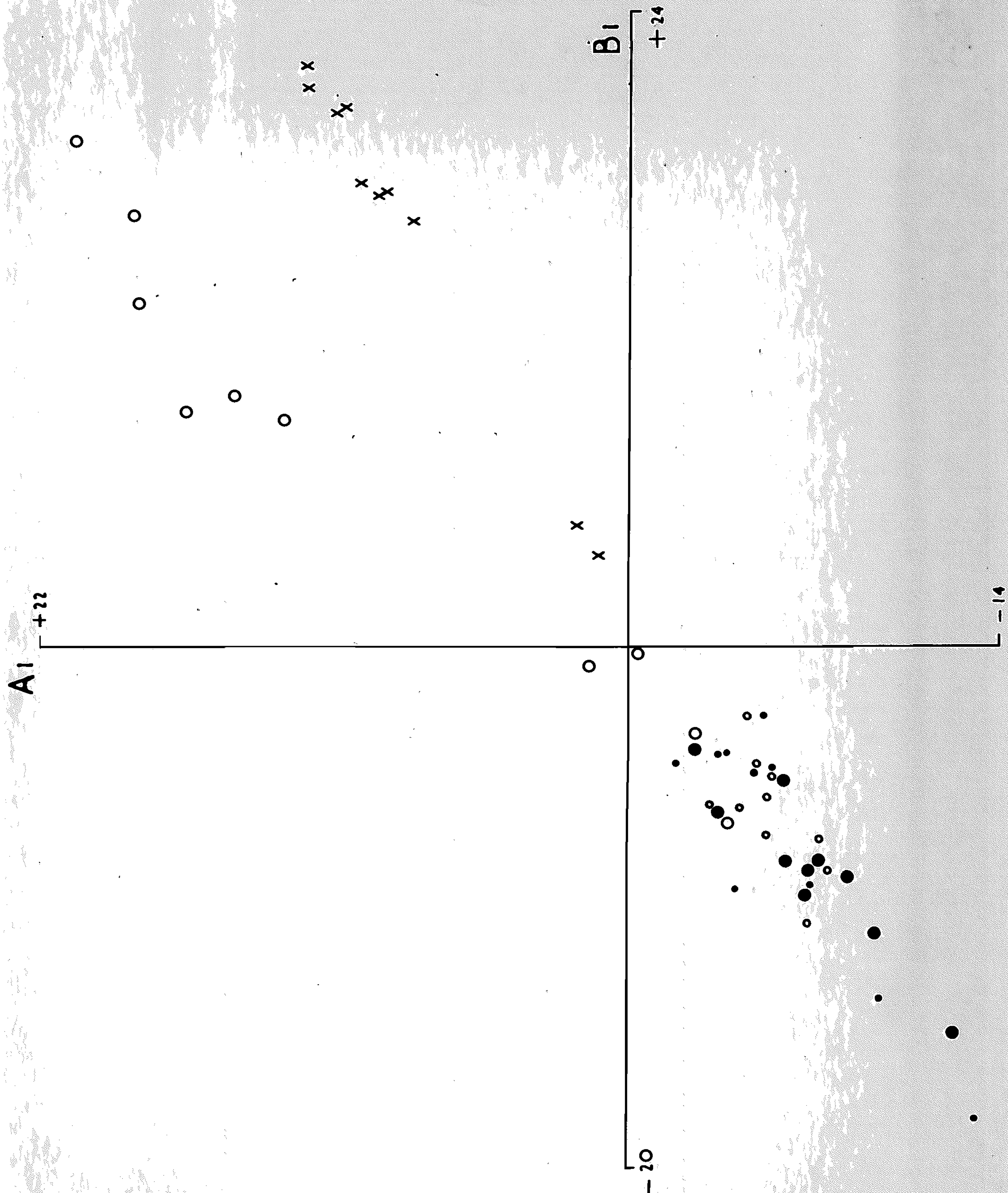


Fig. 25. Distribution of the 50 quadrats in relation to the rotated axes A_1 and B_1 (habitat) (key to symbols on p. 52)

indeed, one of the reasons for undertaking rotation of the axes). In Canonical Analysis, not only is there the assumption that every factor in each analysis is uncorrelated but also that each factor in one analysis is completely correlated with only one of the factors in the second analysis and is completely uncorrelated with the others. This is clearly unlikely to be the case and it was understood that the experience of other workers was that Canonical Analysis rarely, if ever, gave interpretable results. For these reasons, Canonical Analysis was discarded as a method and the two sets of analyses were compared separately.

As already shown, the morphology analysis produced a "V-shaped" distribution of the 50 quadrats, with the East Head and Bursledon quadrats forming the extreme tips of the two arms. In fact, along the morphology factor Bo, the series reads approximately East Head, Needs Oar Point, North Binness Island, Fawley, Bursledon. This closely approximates to a series of increasing substrate water content (except that Needs Oar Point is, on the whole, drier than East Head) and also with the distribution, especially, on habitat B_1 (except that here North Binness Island and Fawley are interchanged in their positions). It is clear, even from this superficial examination, that the morphology is closely related to the habitat.

It has already been pointed out that the morphological variation is mainly expressed by the distribution on Factor Bo and the relationship of this with the distribution of the same quadrats on Factors A and B in the habitat analyses should show the degree to which morphology is influenced by the habitat features which were measured.

The correlation coefficients were calculated between the specifications of the quadrats on each of the morphology and habitat factors. These are given in Tables 4 and 5.

As expected, there is little correlation between morphology Ao and any of the habitat factors, since the morphology factor appears to be mainly a measure of the amount of Halimione. The highest correlation is only +0.29, with the habitat factor Bo. There is, however, relatively high correlation between morphology Bo and each of the habitat factors. Considering that only a limited range of morphological features were measured on the plants and only a limited range of the features of the habitat were measured, the correlation between habit (as represented by morphology factor Bo) and habitat (as represented by the habitat factors) - up to +0.66 - is extremely high.

Scatter diagrams for each of the eight pairs of factors are given in Figs. 26 - 33; the ones with the greatest correlation are discussed below.

Taking the high negative correlation of morphology factor Bo and habitat factor Ao first (Fig. 28), the former has been identified as a measure of the habit, with the compact, dense, low-growing, seldom-flowering, prostrate-rooting type as the negative extreme and the converse lax, upright, frequent flowering type with little nodal rooting as the positive extreme. The latter (habitat factor

Table 4. Correlation coefficients between specifications of quadrats on unrotated morphology and habitat factors

Morphology factor	Habitat factor	Correlation coefficient
Ao	Ao	-0.16
Ao	Bo	+0.29
Bo	Ao	-0.59
Bo	Bo	+0.39

Table 5. Correlation coefficients between specifications of quadrats on rotated morphology and habitat factors

Morphology factor	Habitat factor	Correlation coefficient
Ao	A1	+0.18
Ao	B1	+0.24
Bo	A1	+0.54
Bo	B1	+0.66

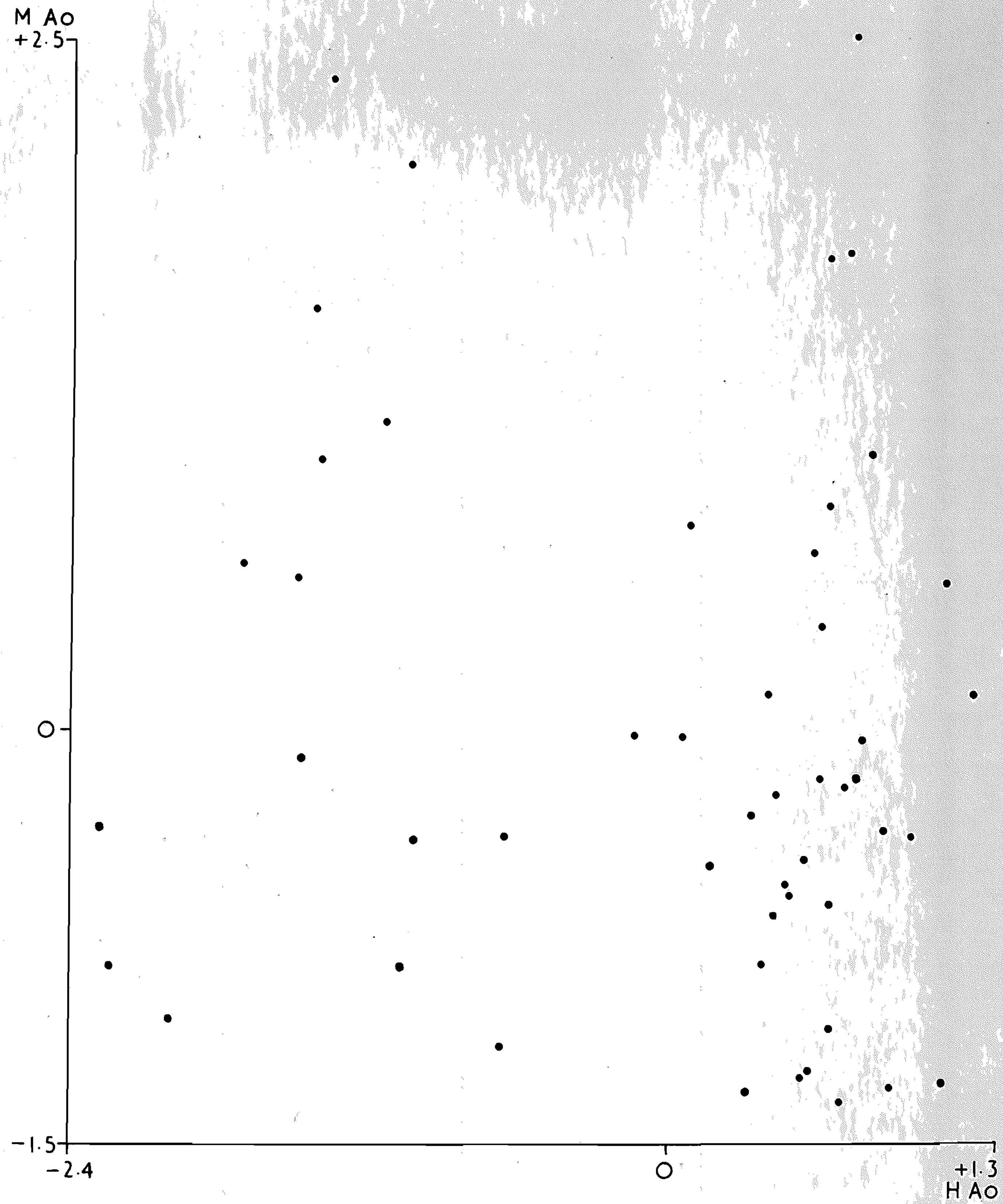


Fig. 26. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Ao and habitat Ao axes (r_{ij} = -0.16)

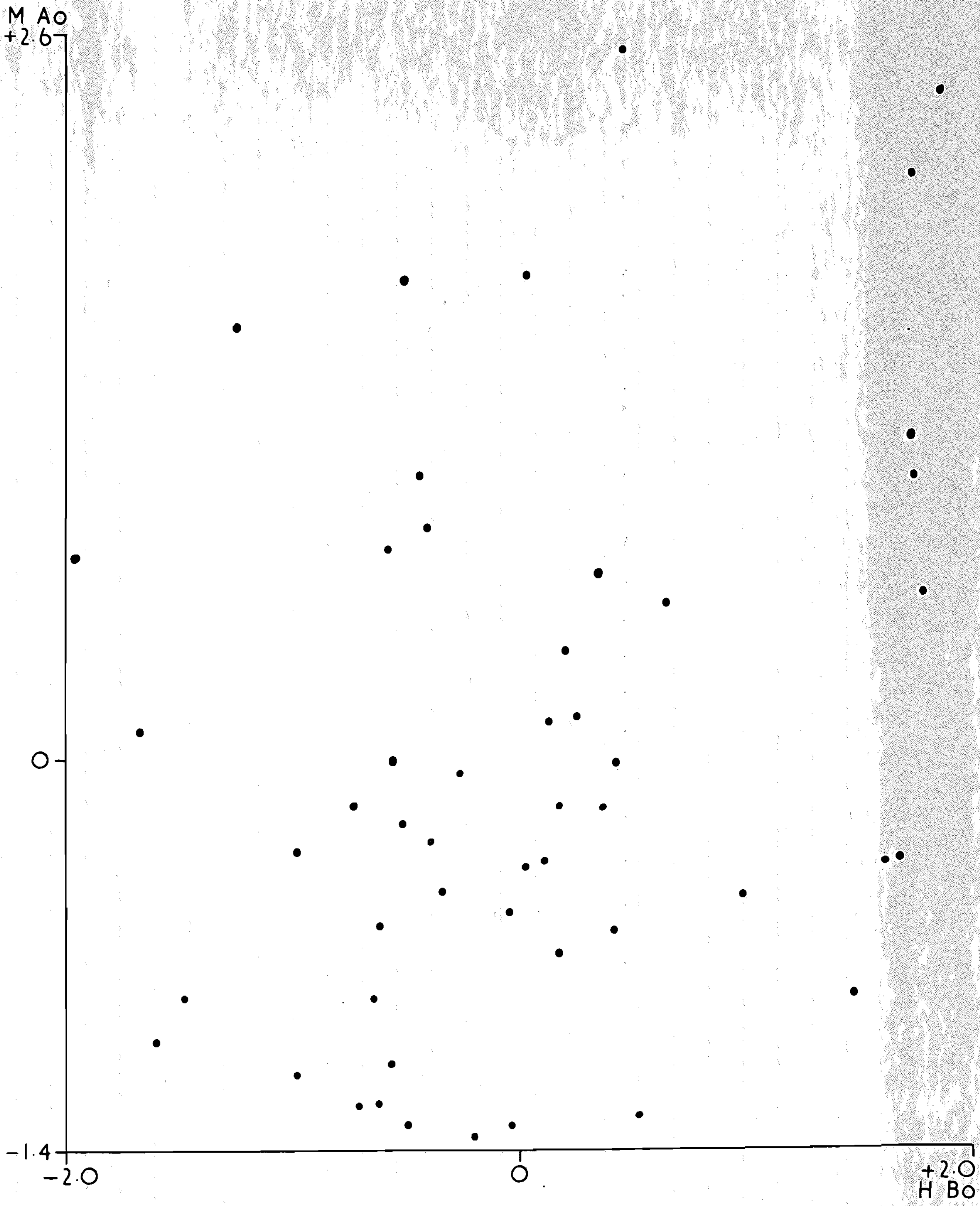


Fig. 27. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Ao and habitat Bo axes (r_{ij} = +0.29)

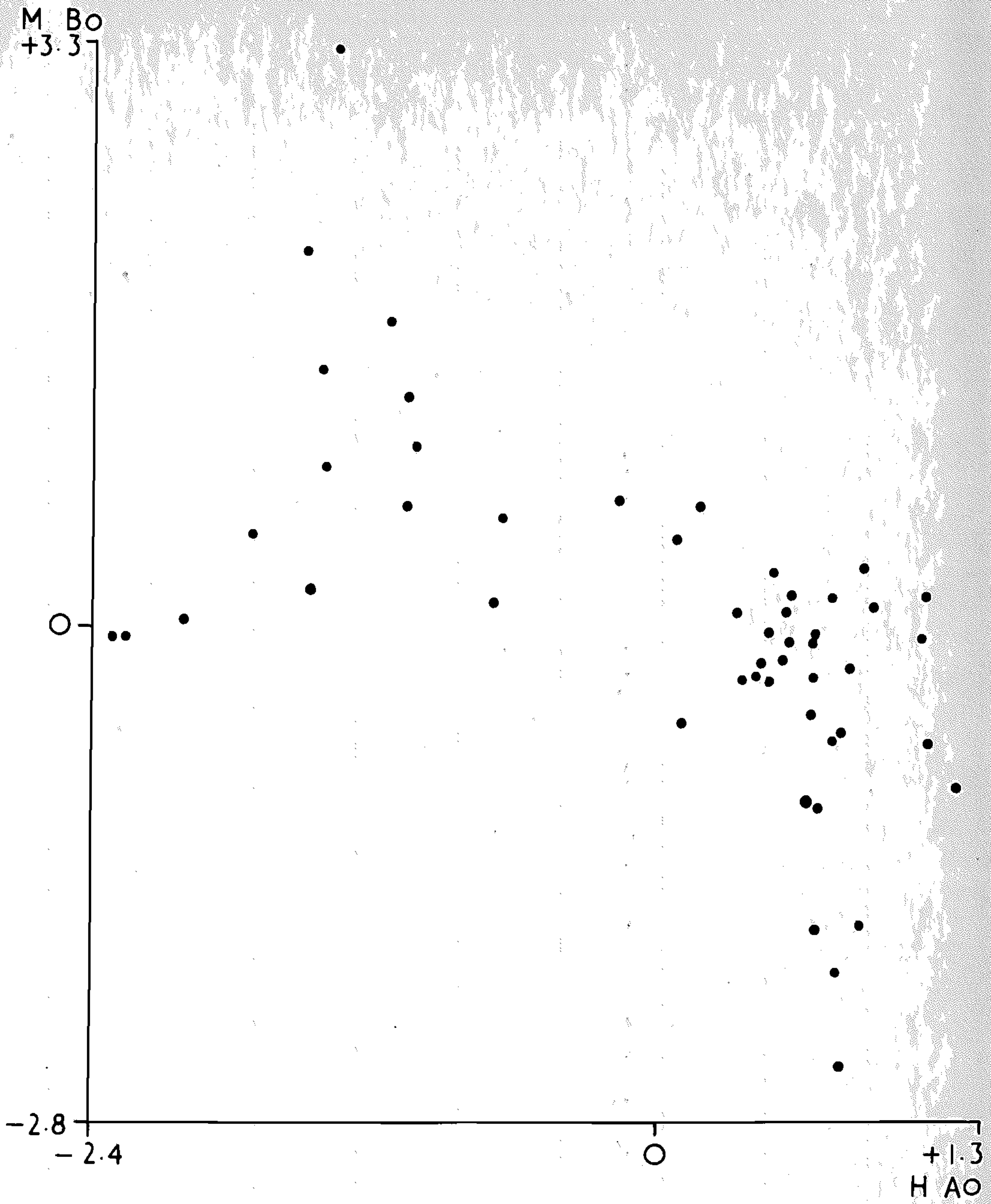


Fig. 28. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Bo and habitat Ao axes (r_{ij} = -0.59)

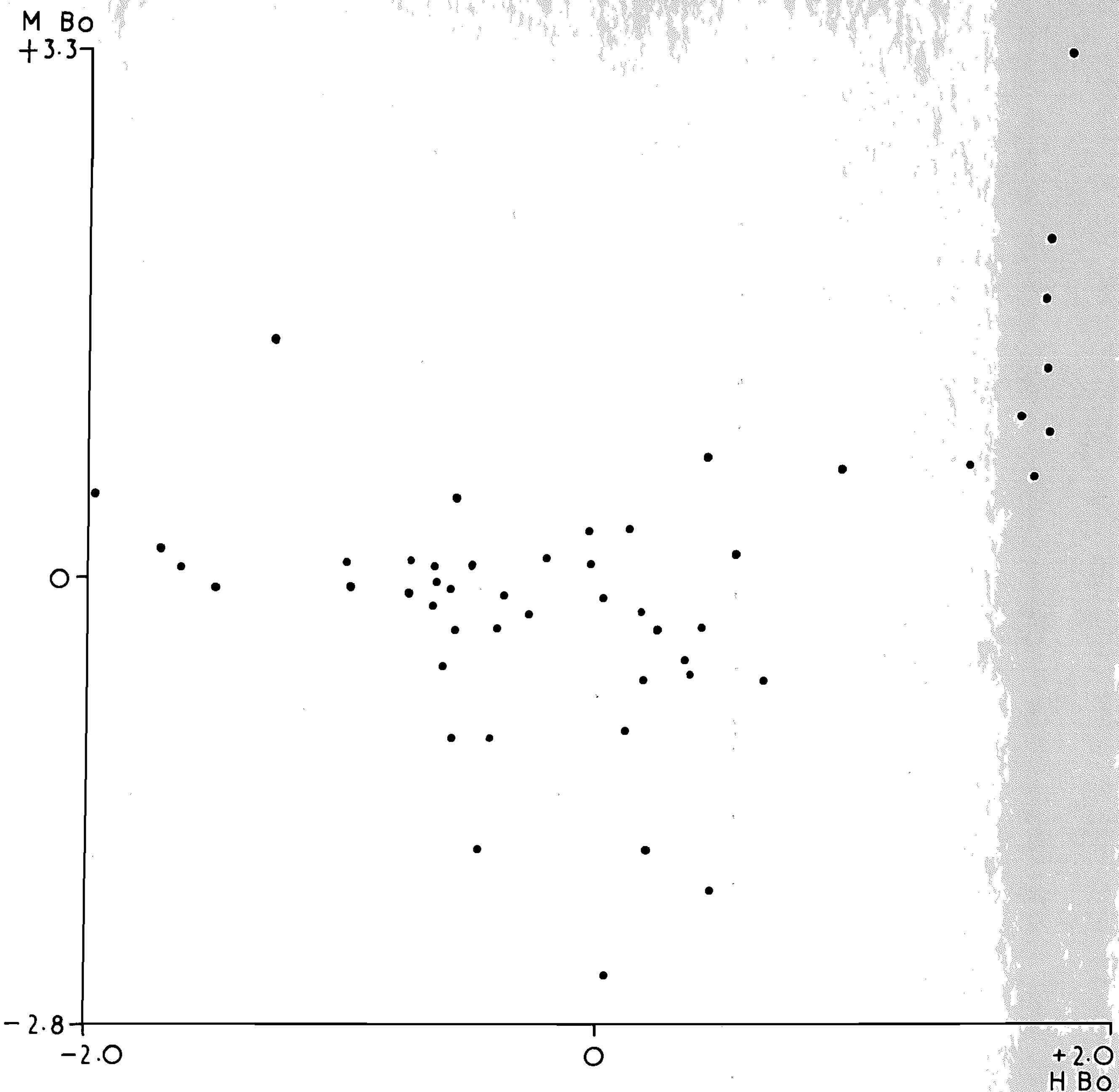


Fig. 29. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Bo and habitat Bo axes (r_{ij} = +0.39)

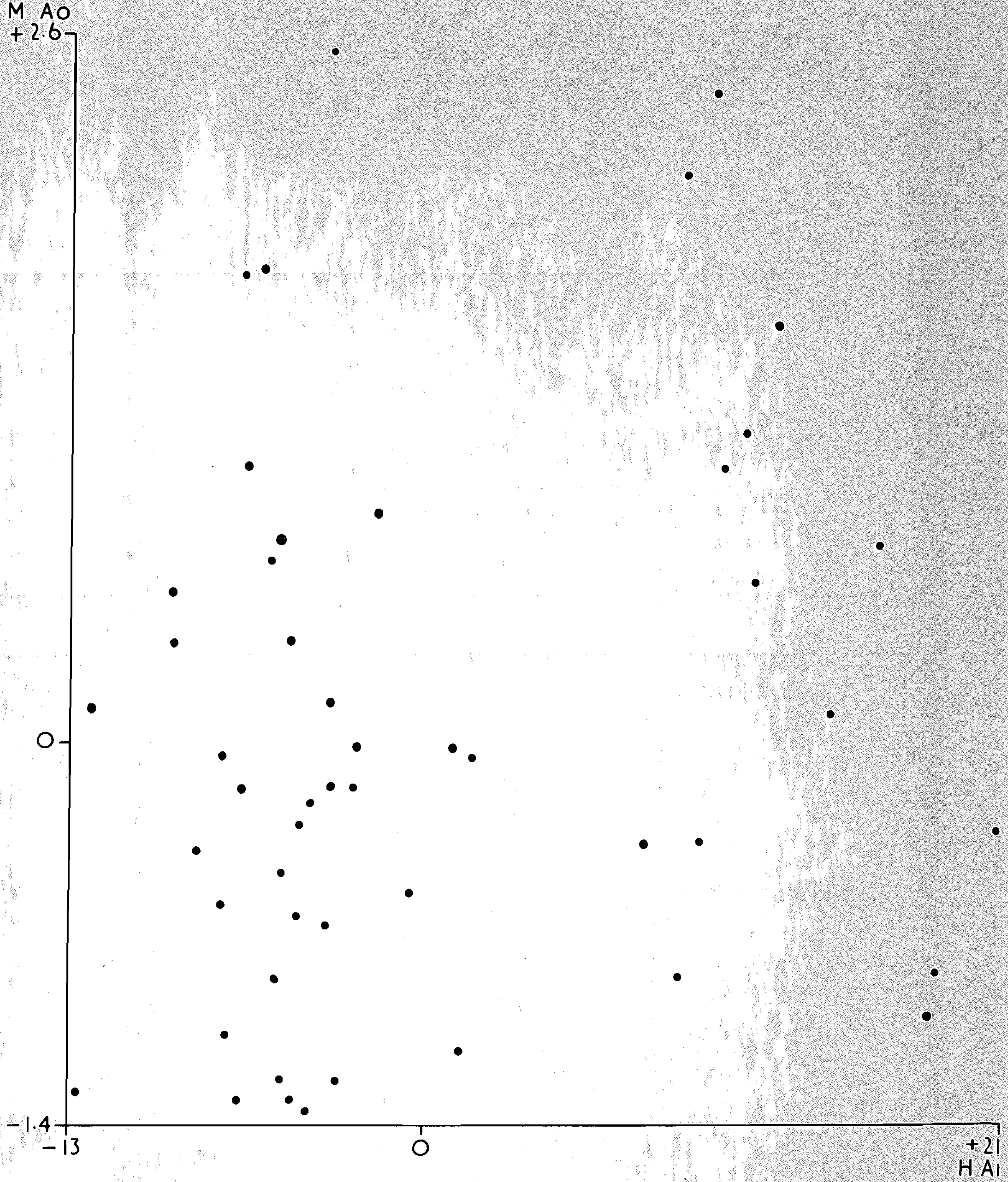


Fig. 30. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Ao and habitat A_1 axes (r_{ij} = +0.18)

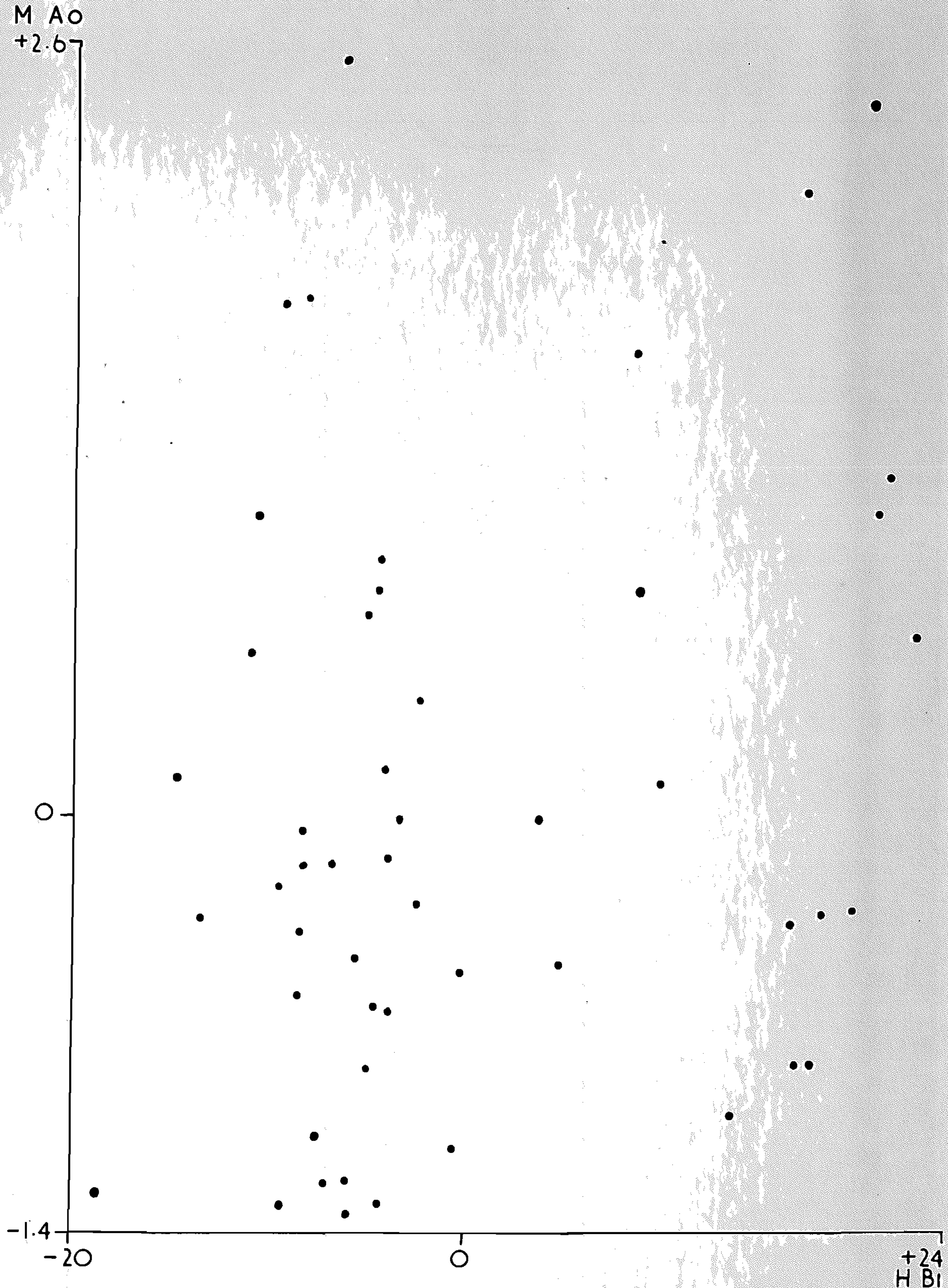


Fig. 31. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Ao and habitat B_1 axes (r_{ij} = +0.24)

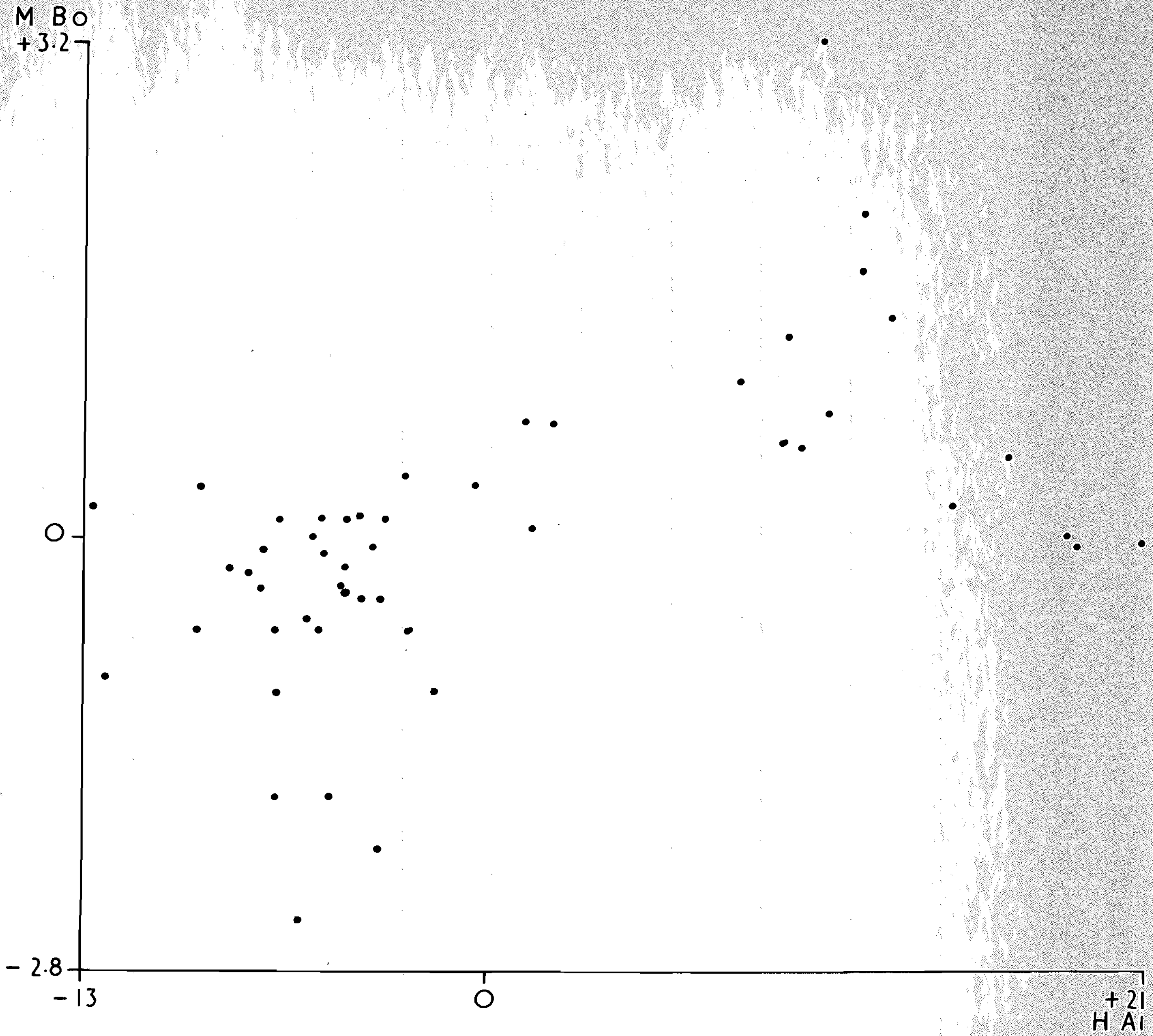


Fig. 32. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Bo and habitat A_1 axes (r_{ij} = +0.54)

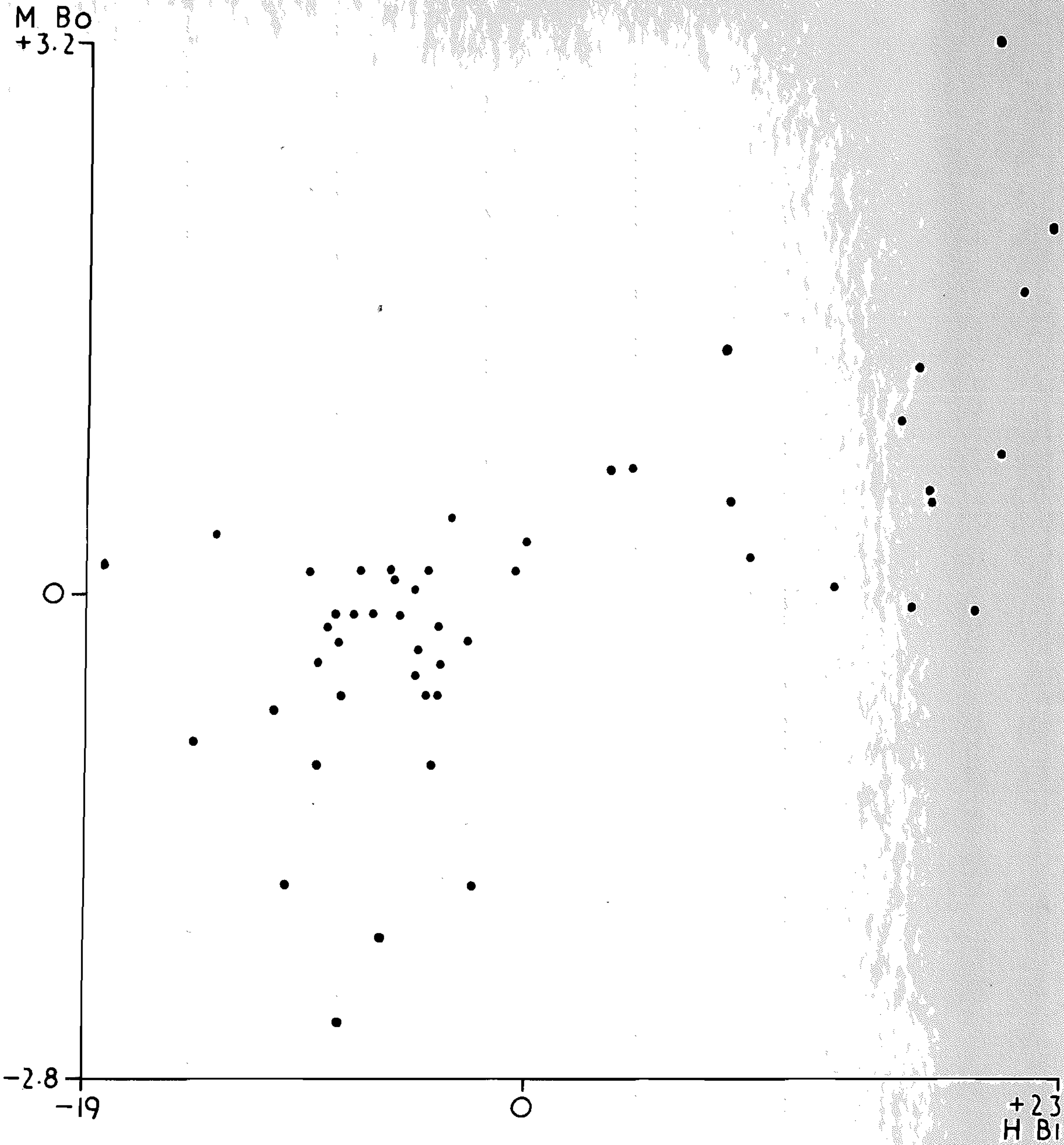


Fig. 33. Scatter diagram showing distribution of the 50 quadrats in relation to the morphology Bo and habitat B_1 axes (r_{ij} = +0.66)

Ao) has been identified as a drainage factor, with poorly drained soils positive and well-drained soils negative. The negative correlation between these two suggests that the morphological differences are closely linked with the habitat features associated with the habitat factor Ao. However, the negative correlation is difficult to reconcile with the positive correlation with habitat factor Bo and the "V" nature of the distribution of the individuals on these factors indicates that there are close interactions between the two and interpretation is consequently not clear.

The rotation of the habitat factors brought the individuals into an almost linear series (Fig. 25) and, with correlation between the two factors now allowed for and the high positive correlation between the morphology factor Bo and the rotated habitat factors A1 and B1 (Figs. 32 and 33), the interpretation is far clearer. The habitat features of a waterlogged substrate (see above) are now strongly correlated with the morphology characters of a large number of flowering apices, high weight of above ground portion, much non-rooting prostrate portion and a high weight of leaves, while the habitat features of a drier substrate (see above) are now strongly correlated with a large amount of prostrate-rooting, a large number of nodes, a high percentage cover, many vegetative apices, much lateral branching and a high amount of below ground portion.

This clearly indicates the association of a dense, compact, seldom-flowering plant with dry conditions and a laxer, frequently flowering plant with wet conditions.

C. Relationship between the habitat and other species associated with Halimione

1. Data collection

A total of 14 species additional to *Halimione portulacoides* (which was present in every quadrat) was found in the 50 Hampshire basin quadrats. These were as follows:

1. *Spartina townsendii* H. & J. Groves
2. *Limonium vulgare* Mill.
3. *Triglochin maritima* L.
4. *Puccinellia maritima* (Huds.) Parl.
5. *Salicornia stricta* agg.
6. *Festuca rubra* L.
7. *Agropyron pungens* (Pers.) Roem. & Schult.
8. *Armeria maritima* (Mill.) Willd.
9. *Glaux maritima* L.
10. *Plantago maritima* L.
11. *Spergularia marginata* (DC.) Kittel
12. *Juncus maritimus* Lam.
13. *Cochlearia officinalis* L.
14. *Aster tripolium* L.

In addition to simple presence or absence data, the percentage cover of each of these species was measured for each of the fifty quadrats and these data are given in Appendix IV.

2. Association analysis of species data

Since the species composition of a community is often a good indication of the substrate conditions, these associated species data were 'sorted' by means of the established technique of Association Analysis (Williams and Lambert 1959 and 1960).

Association Analysis is a technique for classifying individuals defined by the presence or absence of a number of attributes and the resulting groups can be used to generate hypotheses as to the underlying factors responsible for these groupings.

The basic data for Association Analysis consists of a population of individuals (in this case quadrats), each of which is distinguished by the presence or absence of various attributes (in this case the associated species). The object of the analysis is to divide the original population into the two most distinct groups. Both of these groups are then considered as separate populations and each is subdivided again. This process of subdivision is continued until a parameter (to be considered later) does not reach a previously selected minimum value.

The process is carried out by calculating the correlation coefficients between every possible pair of attributes within the population being considered. Then, for each attribute, the sum of all the correlation coefficients between it and all others is obtained and the attribute with the largest sum is the one selected to divide the population in two, those containing the attribute forming one group and those not containing it forming the other. After each division, any attribute which occurs in every individual of the remaining population (or which is completely absent) becomes indeterminate and is no longer statistically active in the analysis.

The parameter used to indicate the significance of each division is the highest individual χ^2. If this drops below a previously determined level the group of individuals being considered is designated final instead of being further subdivided.

Some comment is necessary regarding the use of a single attribute to divide the groups of individuals, since this inevitably leads to some misclassification in terms of overall similarity. Experience shows, however, that this is not great, and computational difficulties arise when alternative procedures are used. The limitations arising from the use of presence or absence data are also not great; limited work on fully quantitative data showing that the presence or absence of an attribute is usually of more importance than the quantity. (Lambert and Dale 1964; Lambert and Williams 1966).

Since the computation involved is large, the analysis is programmed for a Pegasus computer. The form of the programme sets limits on the number of attributes and individuals: only 76 attributes and about 1,680 individuals can be considered, but since the time of computation is linearly dependent on the number of individuals but dependent on the square of the number of attributes, this is not a serious drawback. In the present analysis, there were only 14 attributes and only 50 individuals so that the programme made no restriction on the analysis.

The description given above is for Normal analysis. It is equally valid to treat the attributes as individuals and the individuals as attributes: such an analysis being known as Inverse.

The results of the normal and inverse analyses can be combined in a two-way table which indicates the groups of species most relevant to specific groups of quadrats. The results of these analyses are presented in such a two-way table in Fig. 34.

The two-way table combining the results of the normal and inverse analyses (Fig. 34) gives one classification of the 50 quadrats into groups with similar floristic composition. The most distinct groups of quadrats are those defined (1) on presence of Armeria and Limonium, (2) on absence of Armeria and presence of Limonium, (3) on absence of both Armeria and Limonium but presence of Spartina and (4) on the absence of all three species.

It will be noted that the first of these groups consists entirely of eight of the ten quadrats from one area. These all contain Puccinellia, Limonium, Plantago and Armeria, while half also contain Aster, but none contains any of the other nine species. This is a very distinct group and shows that, floristically, the area (North Binness Island) is homogeneous and suggests that the habitat conditions may also be homogeneous.

The second main group is rather less well-defined, with Limonium (the defining species) the only species present in all quadrats, but Puccinellia, Salicornia and Spartina are present in many of the quadrats. The species composition suggests a rather wetter substrate than the first group and, in fact, eight of the ten Fawley quadrats are represented here and also the four lowest quadrats (which have

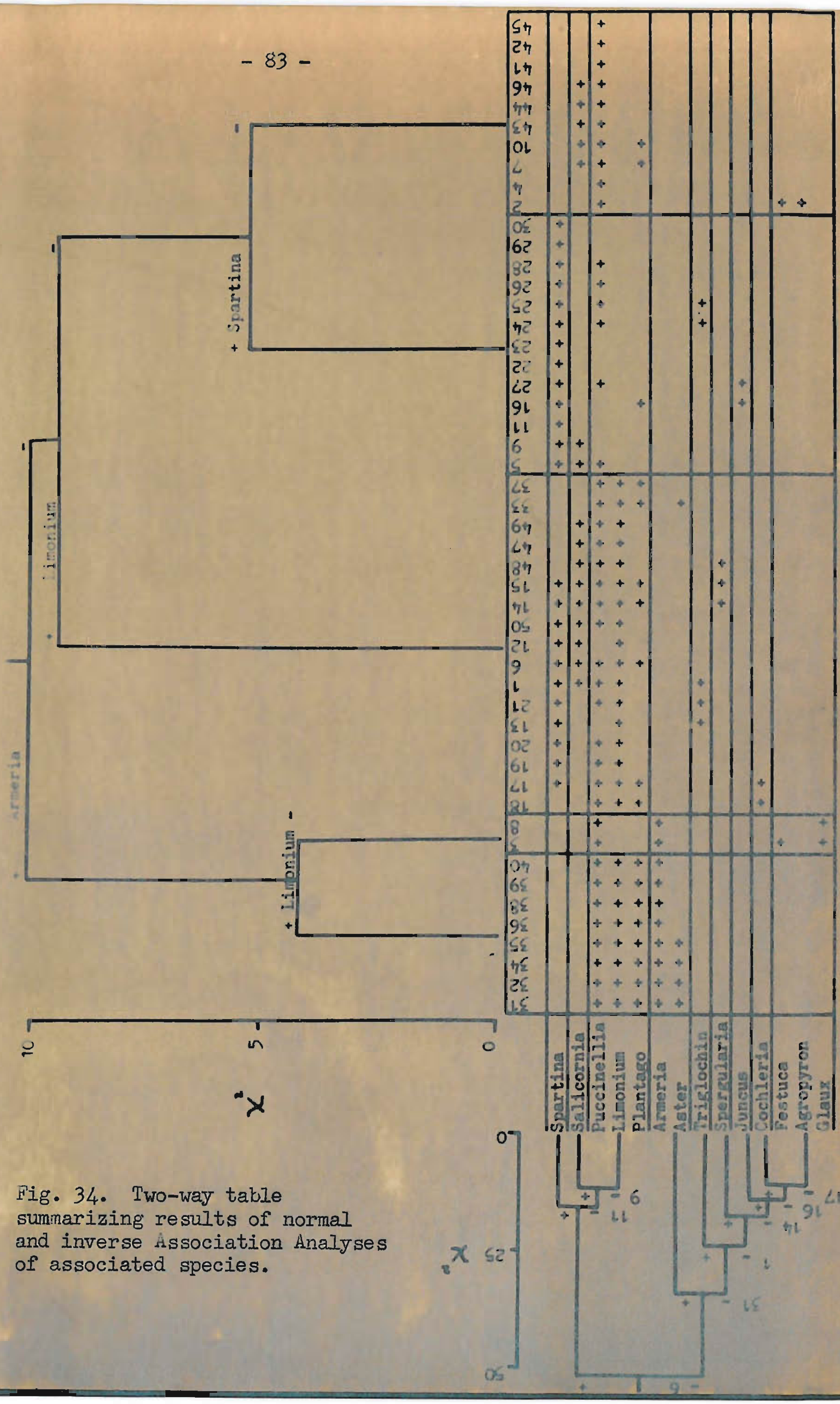


Fig. 34. Two-way table summarizing results of normal and inverse Association Analyses of associated species.

an increasingly muddy substrate) at the sandy area of East Head, though the group contains quadrats from all five sites.

The third main group, defined on the presence of Spartina but absence of Limonium and Armeria, suggests by its species composition an even more waterlogged substrate and, in fact, includes nine of the ten Bursledon quadrats, two from Fawley and two from Needs Oar Point. These are the areas where substrate water content is at its highest.

The fourth main group, where all the main species with the exception of Puccinellia are absent, is made up entirely of the higher East Head and Needs Oar Point quadrats, where Halimione is either forming an almost pure sward or is virtually the only plant on bare sandy-pebble substrate.

The normal Association Analysis, therefore, does tend to make a logical classification of the habitat, indirectly by use of the associated species. This grouping coincides closely with the grouping of the five sites which was made on substrate.

3. 'Canonical subdivision' of species and habitat data.

The presence or absence data of the associated species were used in Association Analysis to classify and define the habitat in terms of floristic composition. The percentage cover values, together with the numerical data on habitat, can also be used in a similar fashion (1) to classify, (2) to determine the most important features of the quadrats and (3) to test the possibility of application of true Canonical Analysis.

The sums of squares of correlation coefficients were calculated between each species with the other species, each species with the habitat features, each habitat feature with the other habitat features and each habitat feature with the associated species. The results of these calculations are shown in Table 6.

The highest $\Sigma\mathscr{C}^2$ is 6.66, for submergence water content with habitat. However, since it is the interaction between habitat and plants which is of interest, the division was made on *Spartina* (*Spartina* with habitat, 2.52). The data were therefore split in two on presence or absence of *Spartina* and new values calculated; these are shown in Tables 7 and 8.

The highest $\Sigma\mathscr{C}^2$ are 0.29 and 0.57, in both cases this being for submergence water content with habitat.

This type of analysis might be termed "canonical subdivision"; the data is given the opportunity of dividing on species only, on habitat only, or on the interaction between them. If a true canonical situation were present, one would expect the greater part of the information to reside in the interaction rectangles of the matrix; however, the division is in the "habitat only" part of the matrix and this suggests that the evidence is not primarily in the interaction. This "canonical subdivision", therefore, suggests that the rejection of canonical methods was correct and it provides an additional justification for the methods which were used in this investigation, viz. separate analyses with subsequent comparison.

Table 6. "Canonical subdivision": sums of squares of correlation coefficients

(a) Plants with habitat

Spartina	2.5200
Glaux	1.6704
Festuca	1.6420
Limonium	1.3804
Puccinellia	1.0461
Plantago	1.0394
Agropyron	0.8302
Salicornia	0.6589
Aster	0.4924
Armeria	0.4731
Triglochin	0.3435
Cochlearia	0.2642
Spergularia	0.2159
Juncus	0.1703

(b) Habitat with plants

% water (submergence)	1.3839
% water (emergence)	1.3522
% organic	1.3309
pebble	1.2126
clay	1.1306
silt	1.0464
compactibility	0.9923
% sodium	0.9152
speed of drainage	0.7775
medium sand	0.7498
fine sand	0.7091
coarse sand	0.4836
distance from creek	0.3816
height above O.D.	0.0344

(c) Habitat with habitat

% water (submergence)	6.6599
% water (emergence)	6.2785
% organic	5.5901
% sodium	5.2000
clay	4.7600
pebble	4.5121
silt	4.4553
compactibility	4.1089
medium sand	4.0824
speed of drainage	3.8803
fine sand	2.9567
height above O.D.	2.7208
coarse sand	2.5952
distance from creek	1.2523

(d) Plants with plants

Armeria	2.2128
Plantago	2.0377
Spartina	1.9404
Festuca	1.8903
Limonium	1.7878
Aster	1.7779
Agropyron	1.5815
Glaux	1.5446
Puccinellia	1.5307
Salicornia	1.4231
Spergularia	1.2904
Triglochin	1.2629
Cochlearia	1.1728
Juncus	1.1672

Table 7. "Canonical subdivision": sums of squares of correlation coefficients; after first division; + Spartina

(a) Plants with habitat

Salicornia	0.1096
Plantago	0.0872
Limonium	0.0558
Spergularia	0.0467
Puccinellia	0.0325
Cochlearia	0.0297
Triglochin	0.0179
Juncus	0.0111

(b) Habitat with plants

Compactibility	0.1143
Distance from creek	0.1118
% organic	0.0823
% water (emergence)	0.0817
speed of drainage	0.0573
height above O.D.	0.0475
coarse sand	0.0391
silt	0.0308
% water (submergence)	0.0304
% sodium	0.0243
pebble	0.0229
clay	0.0158
medium sand	0.0131
fine sand	0.0117

(c) Habitat with habitat

% water (submergence)	0.2359
% water (emergence)	0.1804
clay	0.1576
% sodium	0.1286
pebble	0.1282
speed of drainage	0.1250
compactibility	0.1165
medium sand	0.0937
silt	0.0906
height above O.D.	0.0891
% organic	0.0674
fine sand	0.0438
coarse sand	0.0399
distance from creek	0.0291

(d) Plants with plants

Plantago	0.1242
Spergularia	0.1037
Limonium	0.0982
Salicornia	0.0798
Puccinellia	0.0462
Cochlearia	0.0405
Juncus	0.0302
Triglochin	0.0293

Table 8. "Canonical subdivision": sums of squares of correlation coefficients; after first division; - Spartina

(a) Plants with habitat

Limonium	0.4559
Plantago	0.3670
Aster	0.1712
Glaux	0.1482
Armeria	0.1466
Festuca	0.1440
Salicornia	0.0929
Agropyron	0.0718
Cochlearia	0.0498
Spergularia	0.0220

(b) Habitat with plants

% organic	0.2493
clay	0.2460
% water (submergence)	0.2404
% sodium	0.2341
% water (emergence)	0.2275
medium sand	0.1940
compactibility	0.1650
speed of drainage	0.1507
fine sand	0.1455
pebble	0.1259
silt	0.1224
coarse sand	0.0947
height above O.D.	0.0784
distance from creek	0.0632

(c) Habitat with habitat

% water (submergence)	0.5330
% water (emergence)	0.5219
% organic	0.4826
clay	0.4515
compactibility	0.4441
% sodium	0.4425
speed of drainage	0.4008
pebble	0.3855
medium sand	0.3529
silt	0.3522
coarse sand	0.2681
fine sand	0.2098
height above O.D.	0.1949
distance from creek	0.1174

(d) Plants with plants

Plantago	0.1379
Limonium	0.1239
Armeria	0.1179
Festuca	0.1043
Aster	0.0878
Salicornia	0.0824
Agropyron	0.0695
Glaux	0.0656
Spergularia	0.0232
Cochlearia	0.0152

The very clearly defined division on submergence water content is an important piece of evidence that water content is the overriding factor in salt-marshes. Not only is the substrate water content the most important of the substrate conditions in any consideration of these but it is also the substrate factor having most influence on the floristic composition of the community.

The calculations also indicate that, of the salt marsh plants which were present in these quadrats, *Spartina* is the one most clearly influenced by the substrate conditions.

After the division on presence or absence of *Spartina*, substrate water content is the most important feature of the habitat in both groups. However, in the effect of habitat on the composition of the community, compactibility is most important in those areas supporting *Spartina* and organic content is most important in those areas lacking *Spartina*.

4. Discussion

Association Analysis of the associated species data classified the 50 Hampshire basin quadrats clearly into groups identifiable with positions in the salt marsh. *Halimione* was present in all of these quadrats and it is clear from this that *Halimione* exists in a wide range of communities, from the highest to the lowest in the salt marsh. This confirms the impression gained from the diverse statements in the literature, from general observations and from considerations of the varying substrate conditions in which *Halimione* was found.

The 'Canonical subdivision' calculations indicated that the habitat (substrate) conditions are of overriding significance. Of these, substrate water content is the most important in the salt marsh community. It is of particular interest that the substrate water content is the most important single feature within the '*Spartina* zone', as well as in the higher levels above it, in any consideration of the habitat factors in isolation. However, compactibility and organic content are, respectively, of greatest significance within and above the '*Spartina* zone', in any consideration of the effect on species composition of the community by the habitat factors. Compactibility, being a measure both of water content and of particle size, might be expected to have greatest significance in the lowest regions of the salt marsh. Similarly, organic content, being a measure of the 'richness' of the substrate and also an indication of the age of the salt marsh, could be expected to be of greatest significance in the higher regions of the salt marsh; indicating both the requirements of the species in the higher regions and also, perhaps, their position in the succession.

The fact that *Armeria* has the highest value in the 'plants-with-plants' portion of the matrix is of interest in that these quantitative calculations confirm the qualitative Association Analysis, where *Armeria* was the species upon which the first division was made.

V. EXTENDED SURVEY

A. Introduction

General observations and analyses of the data from the Hampshire basin had shown that *Halimione* extended over a wide range of substrates and existed in a wide variety of salt marsh communities. Within this wide range, *Halimione* showed marked differences in morphology. These differences in habit appeared to be closely correlated with differences in habitat, but the variation formed a continuous series. All this work had been carried out in the Hampshire basin, where var. *latifolia* was the only variety recorded in the literature and the only one found in the course of the investigation. In order to test the conclusions on a larger sample, to determine to what extent the Hampshire basin sites were representative (what proportion of the range of variation was covered by the Hampshire basin plants) and to determine the relative positions in the range of variation of the other two varieties (*angustifolia* and *parvifolia*), an extensive survey was carried out.

1. Choice of sites

Blakeney Point, Cley, Norfolk was chosen as the chief site for further detailed investigation because of the known presence there of *angustifolia* and *parvifolia*, in addition to *latifolia*. A smaller number of quadrats was also investigated at other sites with a variety of substrates: Gibraltar Point, Lincolnshire; Shellness, Isle of Sheppey, Kent; Rye Harbour, Sussex; Parkgate, Cheshire; and Hilbre Island, Cheshire. The fifty quadrats in the Hampshire basin were also included in the total of 250 quadrats which were investigated. The locations of these sites are shown in Fig. 35.

2. Selection of attributes

With a further 200 quadrats from which data were to be collected, it was necessary to reduce the number of attributes which were to be measured. The time factor necessitated that only those measurements which were quickly obtained could be used and, where a measurement that was considered essential was also time-consuming to determine, a modified technique had to be devised.

a. Morphology measurements

Five measurements were selected as being (1) representative of the extremes of the series found in the analyses of the Hampshire basin data and (2) determinable in the field. These were:

1. Length of the prostrate rooting portion (cm)
2. Length of the prostrate non-rooting portion (cm)
3. Percentage cover
4. Number of nodes
5. Weight of above ground portion (g)

These five measurements were all determined in exactly the same manner as the Hampshire basin measurements.

In addition to these five measurements, the leaf-length and leaf-width were also measured as being the easiest of several possible measurements diagnostic of the three varieties of *Halimione portulacoides*. In each case, the leaves from the third node from

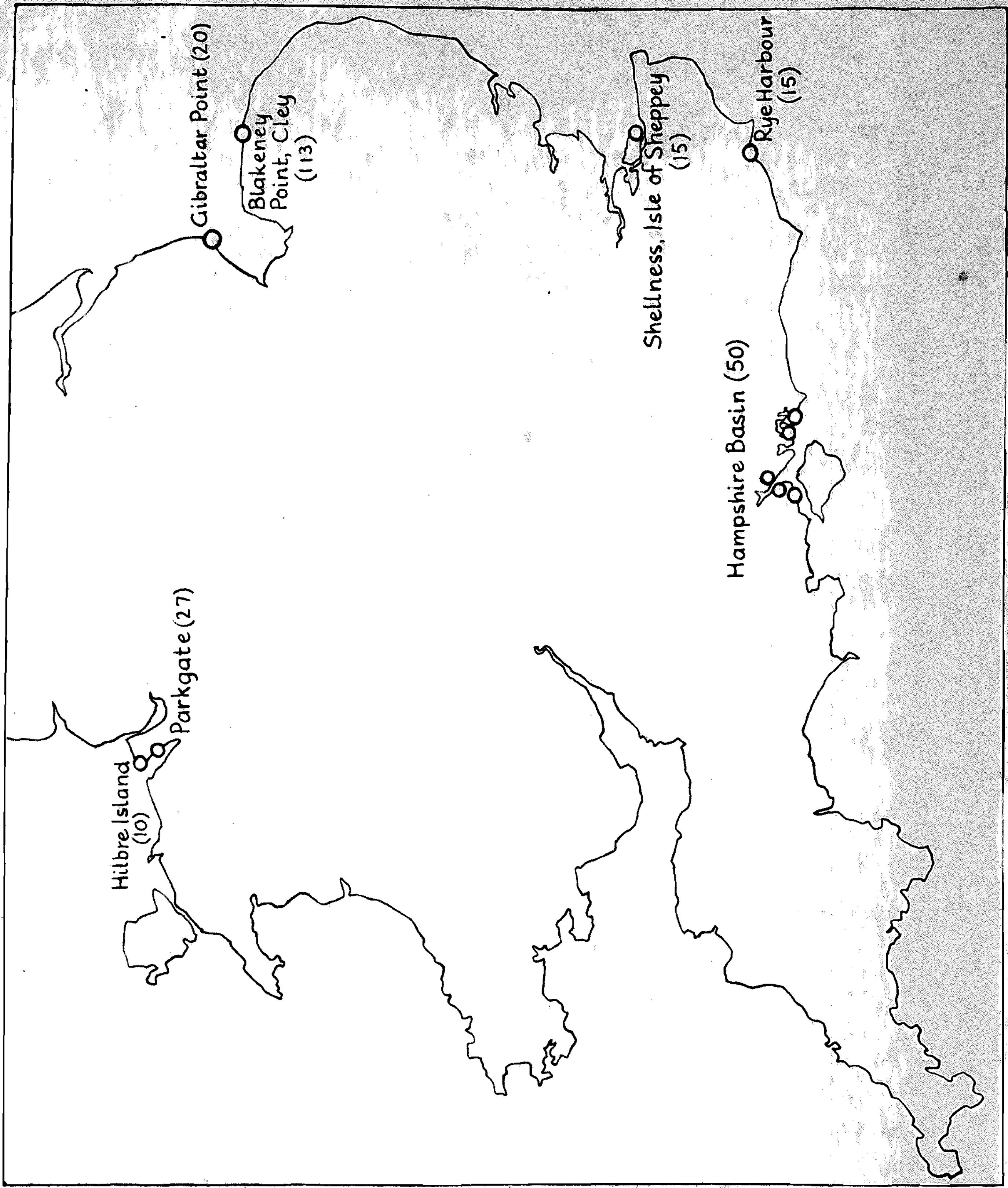


Fig. 35. Locations of extensive survey sites (number of quadrats at each site are shown in parenthesis)

the apex were measured and the mean for each quadrat calculated. These leaf measurements were also made on the Hampshire basin sites.

b. Habitat measurements

The most important feature in the earlier surveys had proved to be substrate water content. However, it was clearly impracticable to attempt to determine this on the greatly enlarged sample in the extended survey. It had also proved to be convenient to classify the areas on soil particle size, but here again it was clearly impracticable to carry out the lengthy drying, sieving and weighing techniques employed in the smaller survey.

The easy field-determination of compactibility led to its choice as a practical alternative to substrate water content and new, quicker techniques for soil fraction determinations were devised. The number of fractions determined was reduced from six to three by combining those previously known as 'coarse sand', 'medium sand' and 'fine sand' into one fraction, now designated 'sand', and combining 'silt' and 'clay' into one fraction, now designated 'clay'. In other words, only two sieves were employed: British Standard sizes 10 and 72. The material retained by size 10 being known as 'pebble', that retained by 72 as 'sand' and that passing through 72 as 'clay'. By this procedure, the actual amount of time spent sieving was considerably reduced. The drying and weighing (previously carried out in the laboratory) was, in this larger survey, carried out in the field. Each soil sample of approximately 100 g was rolled out on a large metal sheet and left to dry in the wind and sun. After sieving, each fraction was weighed on a rough balance.

Before the survey was undertaken, this method was tested on a sample 50 per cent of the Hampshire basin quadrats and the results obtained by the new, quicker method compared to the values previously obtained. These are shown in Table 9. The field determinations proved to be surprisingly close to the accurate measurements determined earlier, as is shown by the correlation coefficients between the two sets of values for each fraction: +0.9979, +0.9970 and +0.9991. The field determinations were, thus, justified as acceptable substitutes for the more accurate determinations.

B. Univariate appraisal

Since attempts at univariate analysis proved fruitless with the 50 Hampshire basin quadrats, the univariate approach was not attempted with the 250 quadrats in the extensive survey, except in relation to the leaf dimensions. Here there was the expectation that these measurements would be discontinuous, since leaf dimensions were one of the main features for separating the three varieties, examples of each of which were included in the data for the extensive survey.

The data on leaf dimensions are, therefore, plotted as histograms in Figs. 36 to 38. Quadrats containing plants distinguishable as vars. parvifolia and angustifolia are, respectively, cross-hatched and blacked-out. It will be apparent that, of the measurements made on the leaves, var. parvifolia is best defined upon leaf-length (this being 3-4 cm, as against 8 cm for the lowest value apart from these) and angustifolia upon the leaf-length/leaf-width ratio (this

Table 9. Percentages of each of the three soil particle fractions for 25 of the 50 Hampshire basin quadrats when determined (a) accurately in laboratory and (b) roughly in field

Quadrat No.	Pebble		Sand		Mud	
	a	b	a	b	a	b
1	0	0	13.66	12.8	86.34	87.2
3	61.30	63.6	32.34	30.3	6.36	6.1
5	6.09	6.1	16.60	18.4	77.31	75.5
7	57.76	59.2	26.40	23.5	15.84	17.3
9	0	0	19.19	17.5	80.81	82.5
11	0	0	5.23	5.1	94.77	94.9
13	0	0	22.53	23.3	77.47	76.7
15	0	0	24.75	26.3	75.25	73.7
17	0	0	26.12	28.0	73.88	72.0
19	0	0	28.67	30.7	71.33	69.3
21	0	0	33.31	36.4	66.69	63.6
23	0	0	31.25	33.0	68.75	67.0
25	0	0	19.67	21.0	80.33	79.0
27	0	0	28.20	29.3	71.80	70.7
29	0	0	24.94	25.5	75.06	74.5
31	0	0	20.10	20.8	79.90	79.2
33	0	0	7.11	8.1	92.89	91.9
35	0	0	17.73	19.2	82.27	80.8
37	0	0	9.56	11.0	90.44	89.0
39	0	0	16.72	18.2	83.28	81.8
41	0.13	0	64.55	65.7	35.32	34.3
43	0.59	1.0	59.54	60.4	39.87	38.6
45	0.21	0	69.68	70.7	30.11	29.3
47	0	0	58.21	59.6	41.79	40.4
49	0	0	34.65	35.7	65.36	64.3
Correlation coefficients (between a & b)	+0.9979		+0.9970		+0.9991	

Fig. 36. Leaf-length: histogram of the distribution of the 250 quadrats

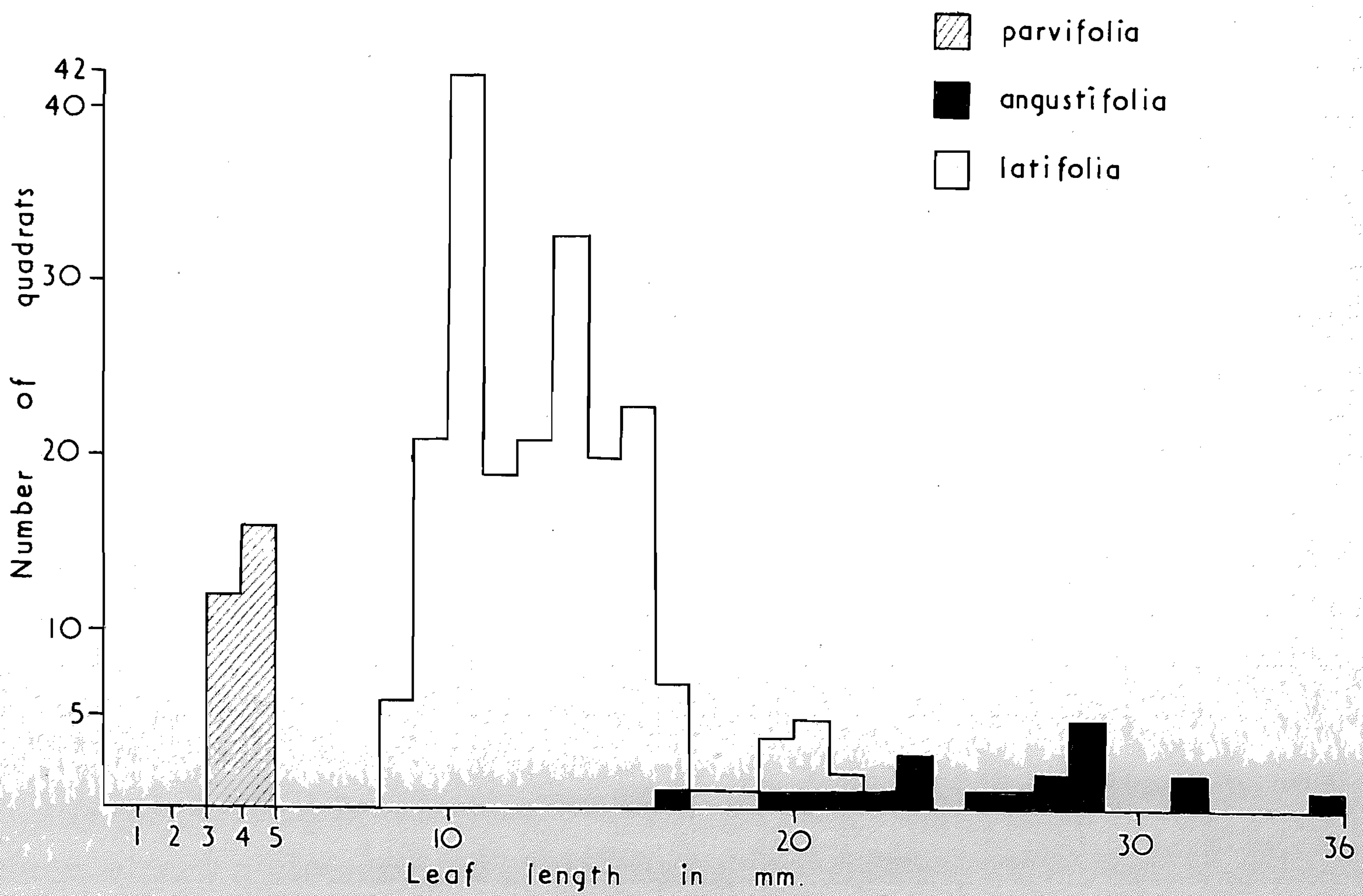


Fig. 37. Leaf-width: histogram of the distribution of the 250 quadrats

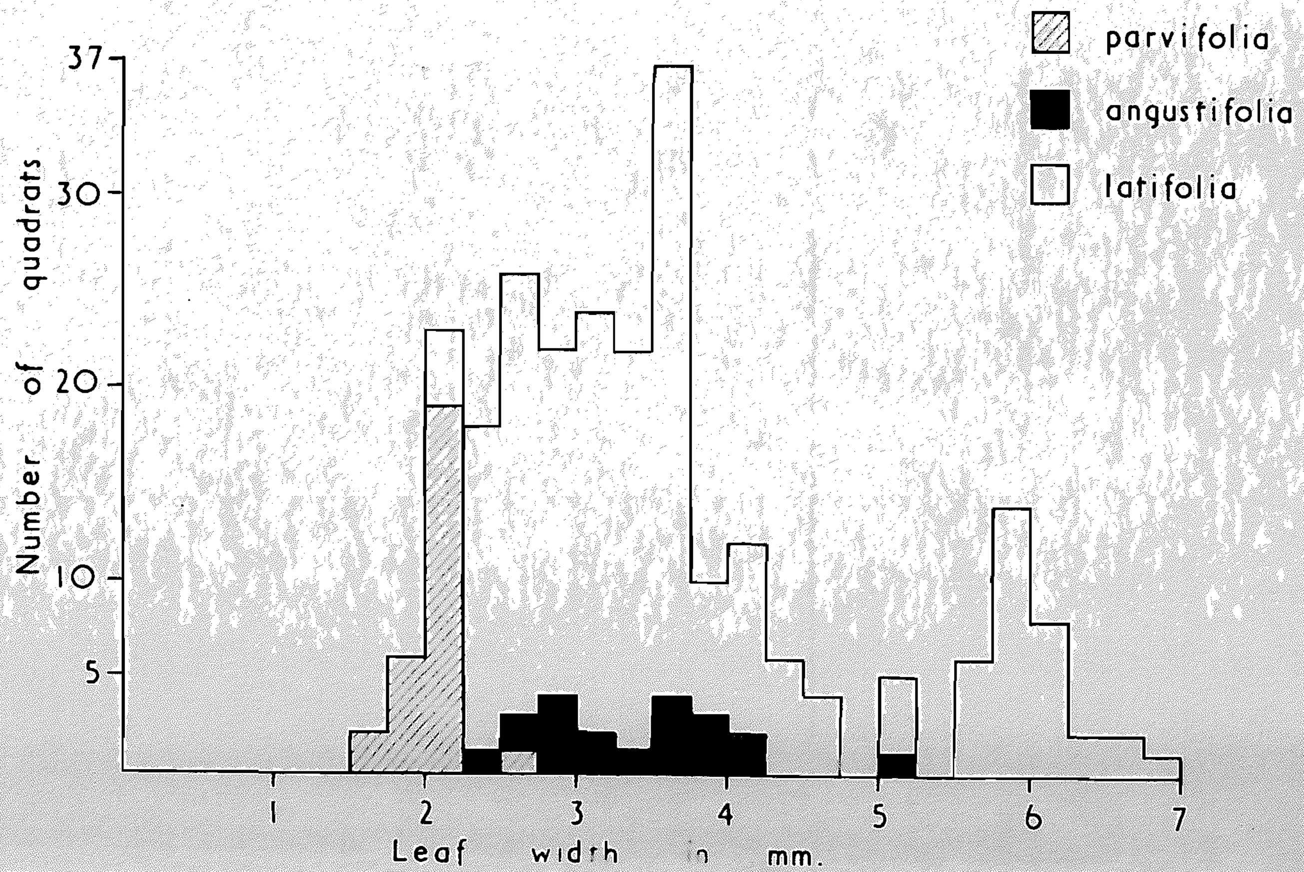
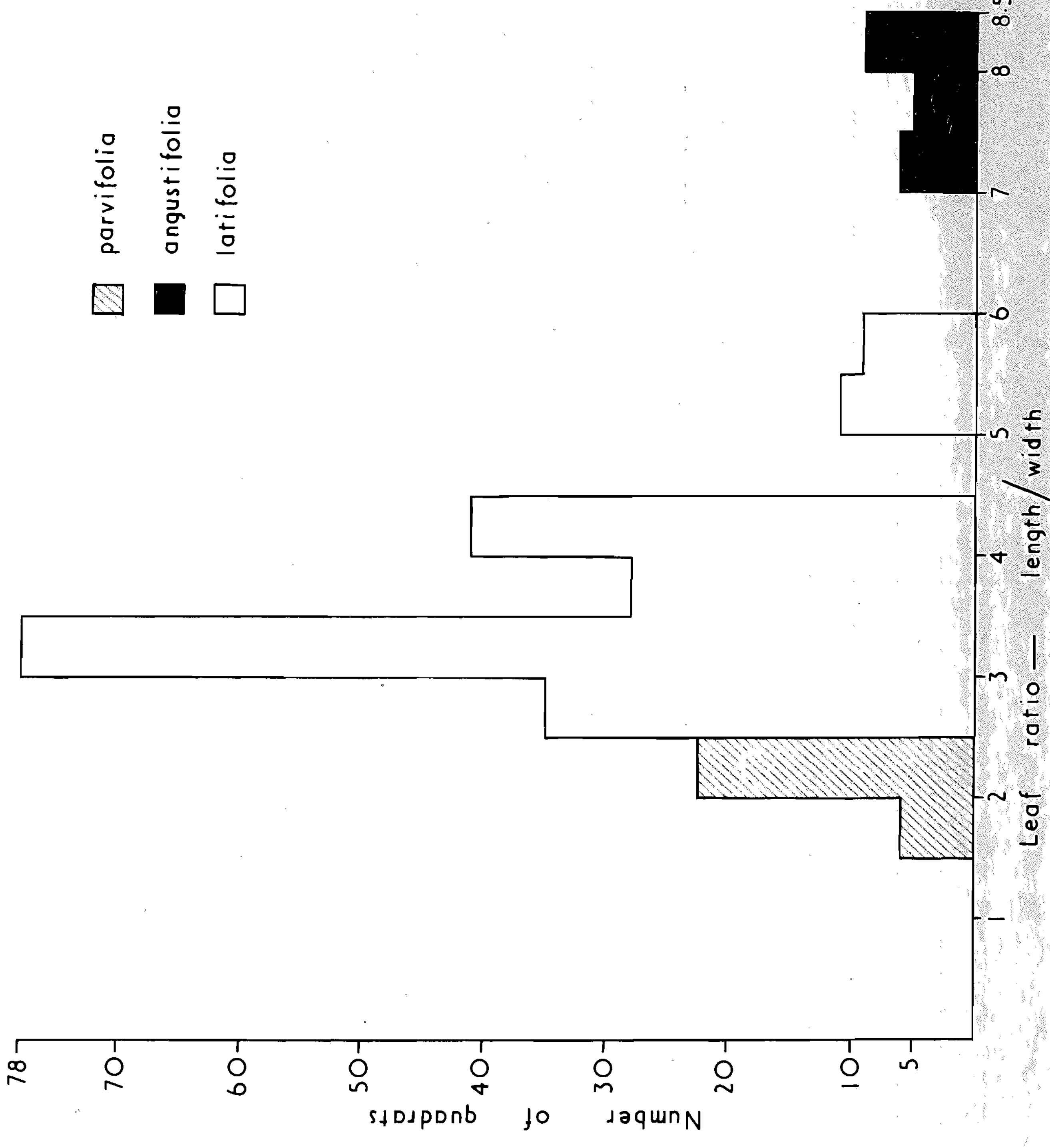


Fig. 38. Leaf-ratio: histogram of the distribution of the 250 quadrats



being 7.0 - 8.5 as against 6.0 for the highest apart from these). It is worth noting that no single leaf character appears to define these three varieties.

The quadrats separated thus by these criteria will, for convenience, subsequently be referred to solely by the labels parvifolia and angustifolia, without the intention of inferring that the plants within them show more than these leaf characters to separate them.

C. Multivariate analyses

1. Methods

The methods of analysis were identical to those employed on the pilot study, but Component Analyses only were undertaken, since experience showed that the further computation necessary for Factor Analysis was not justified by the small amount of additional information provided. Since, as was shown in the previous section, the leaf-length/leaf-width ratio gave a rather different picture from a consideration of the leaf-length and leaf-width separately, the Component Analyses of the morphological data were carried out twice: once with seven variables (including leaf-length and leaf-width separately) and once with six variables (with the leaf dimensions expressed as a ratio).

Although it was recognised that inclusion of a non-linear attribute such as leaf-ratio in a fundamentally linear analysis such as Component Analysis was to be avoided if possible, this was in fact done because of the importance of it in relation to the separation of those plants designated angustifolia.

2. Results

a. Morphology

In both of the two analyses, three factors were found to be sufficient to account for most of the variation: 78.45 per cent being extracted by three factors in the 7-variable analysis and 82.25 per cent in the 6-variable analysis. The following table shows the percentage of the variation extracted by the three most important factors in each case:

Table 10. Amount of variation (expressed as percentage of whole) extracted by each of the three most important factors in 7-variable and 6-variable Component Analyses

Factor	7-variable analysis	6-variable analysis
A	47.14	52.98
B	19.47	15.82
C	11.84	13.45
Total	78.45	82.25
Other 4 factors	21.55	Other 3 factors 17.75

The distributions of the attributes in relation to the three major factors in each of these analyses are shown in Figs. 39 to 44.

The specifications of the individuals make it possible to plot these in relation to each of the factors. The plots, each making up a three-dimensional model, are given as Figs. 45 - 47 for the 7-variable analysis and Figs. 48 to 50 for the 6-variable analysis.

In Figs. 45 to 50, the quadrats containing plants referable to

Fig. 39. Distribution of the 7 morphology attributes in relation to the Ao and Bo axes of Component Analysis

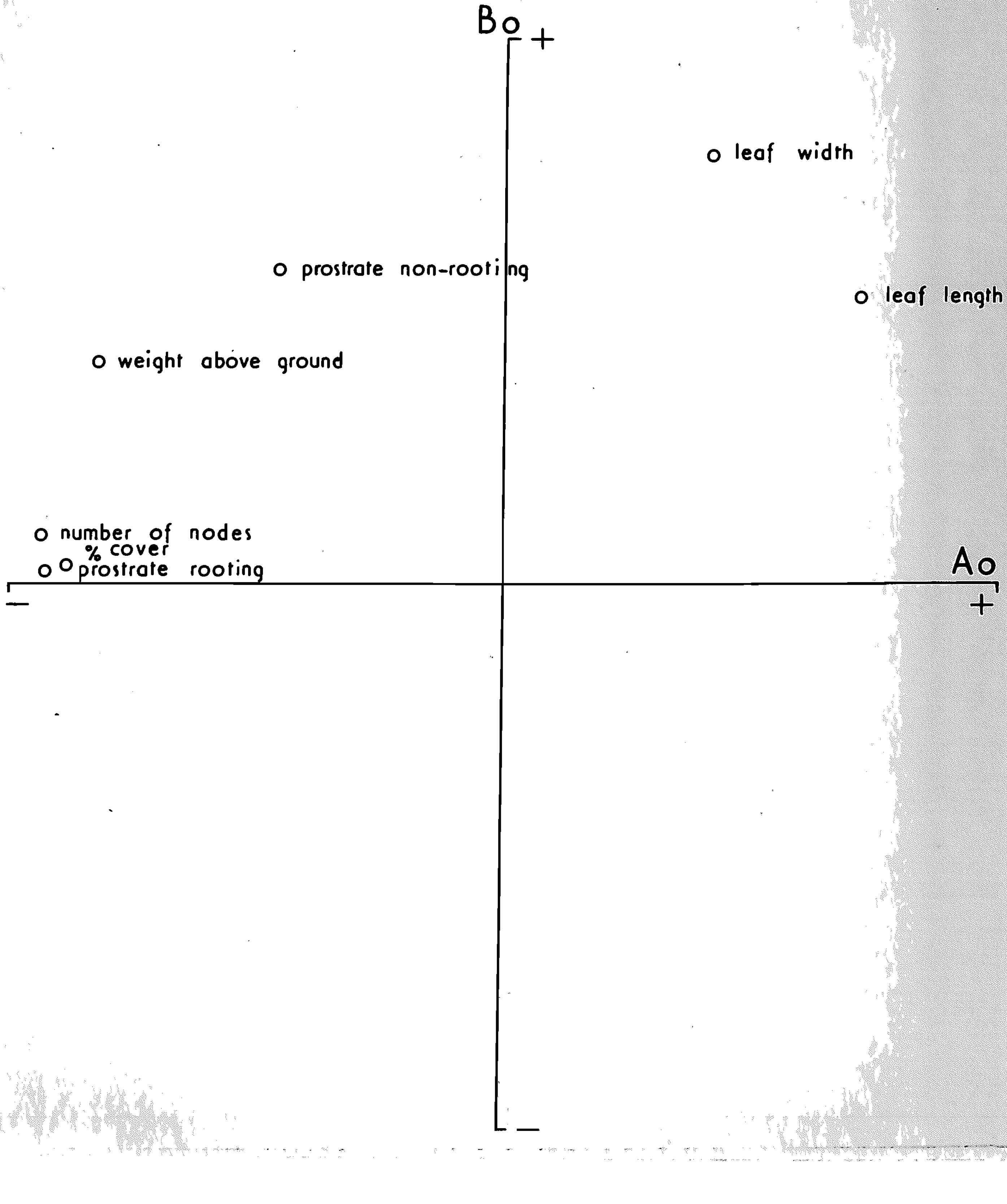


Fig. 40. Distribution of the 7 morphology attributes in relation to the Ao and Co axes of Component Analysis

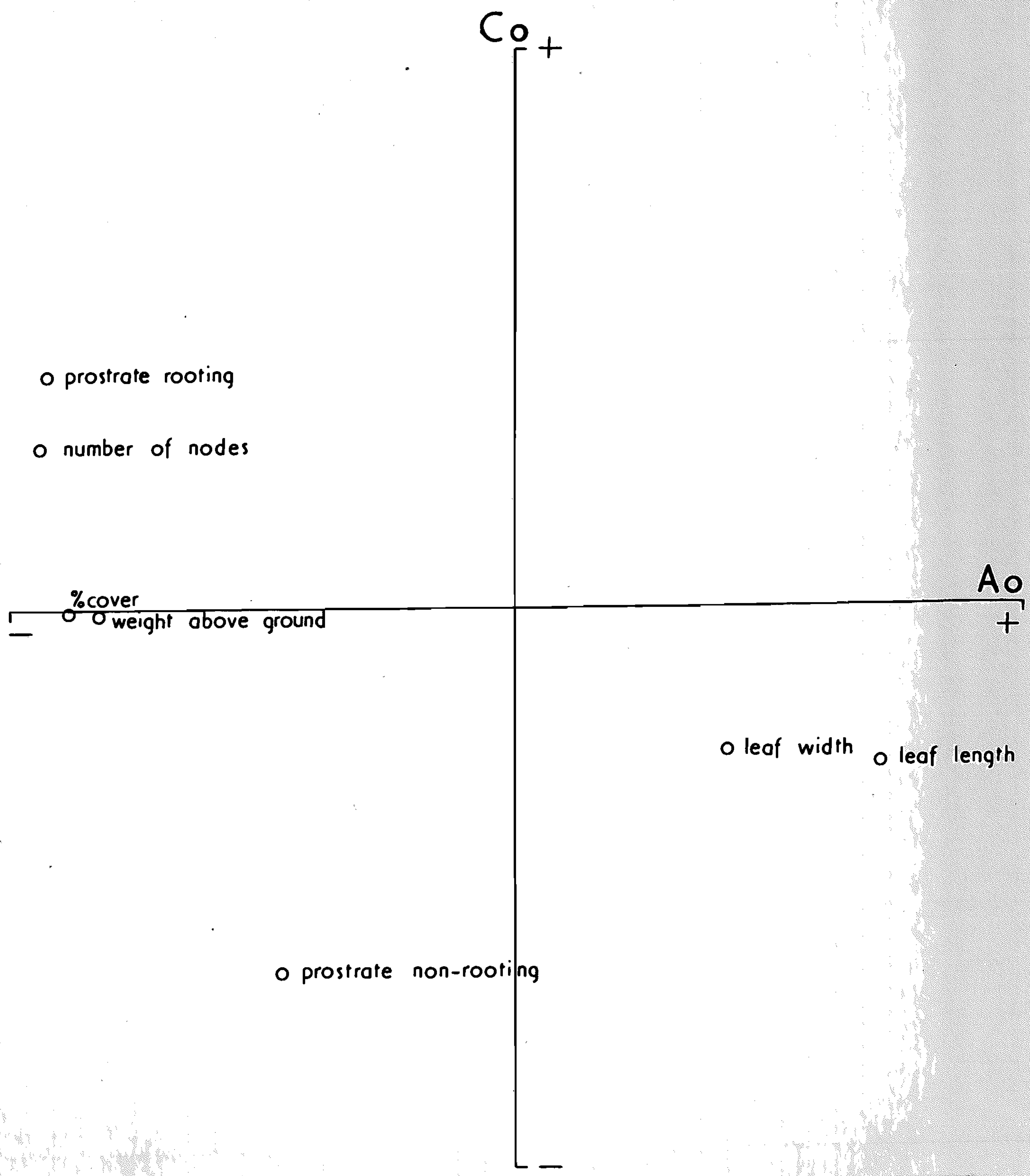


Fig. 41. Distribution of the 7 morphology attributes in relation to the Bo and Co axes of Component Analysis

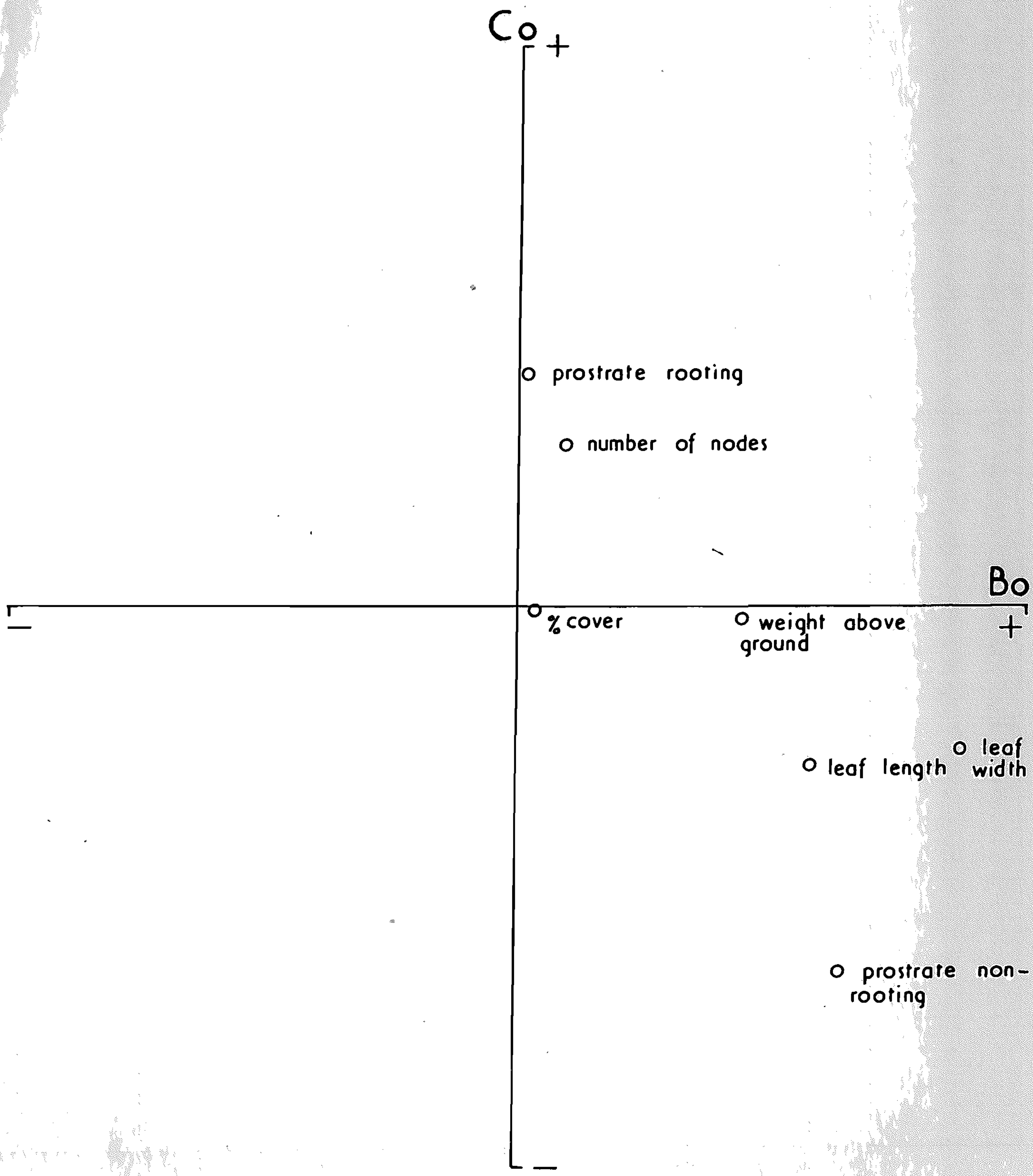


Fig. 42. Distribution of the 6 morphology attributes in relation to the Ao and Bo axes of Component Analysis

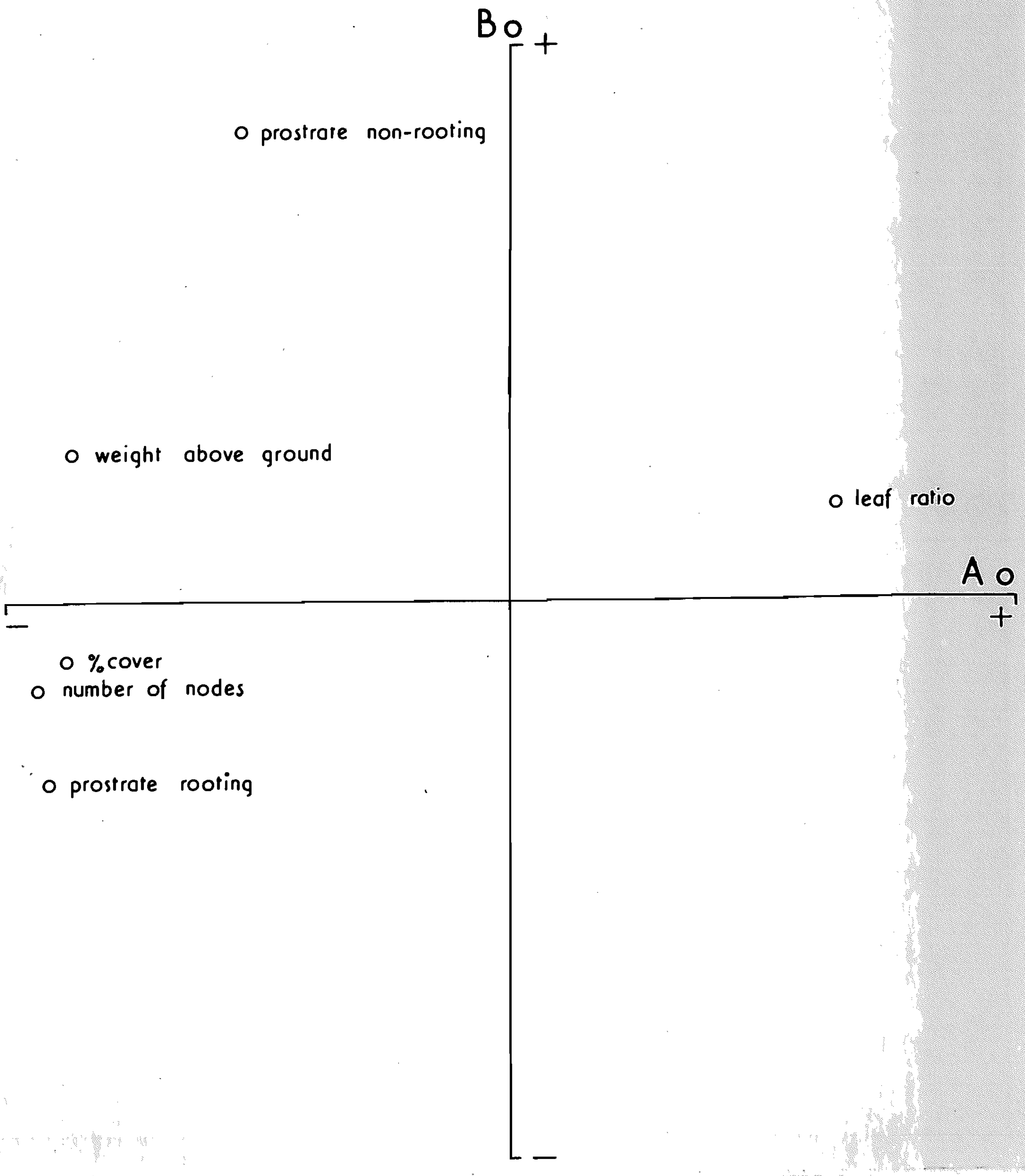


Fig. 43. Distribution of the 6 morphology attributes in relation to the Ao and Co axes of Component Analysis

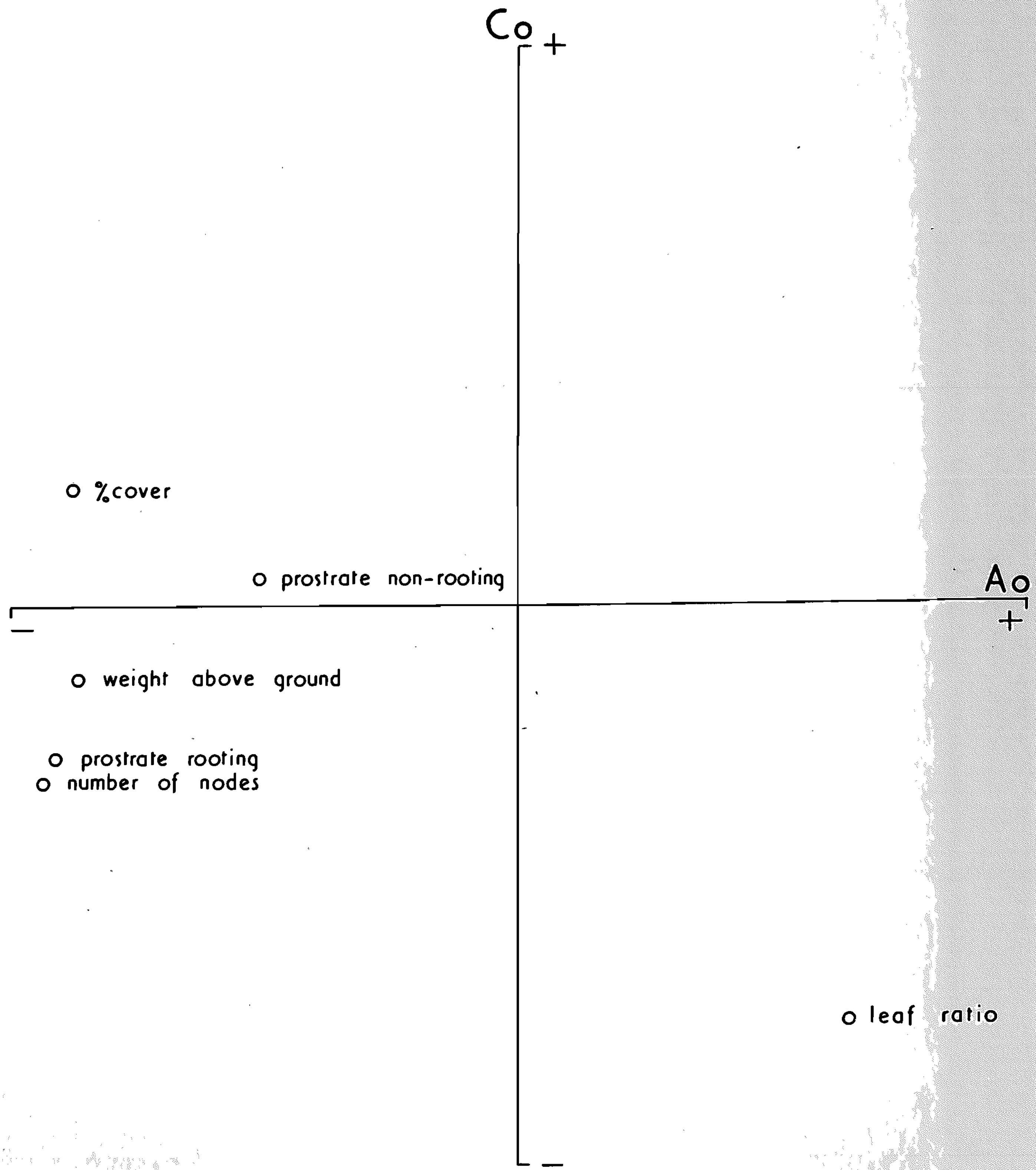


Fig. 44. Distribution of the 6 morphology attributes in relation to the Bo and Co axes of Component Analysis

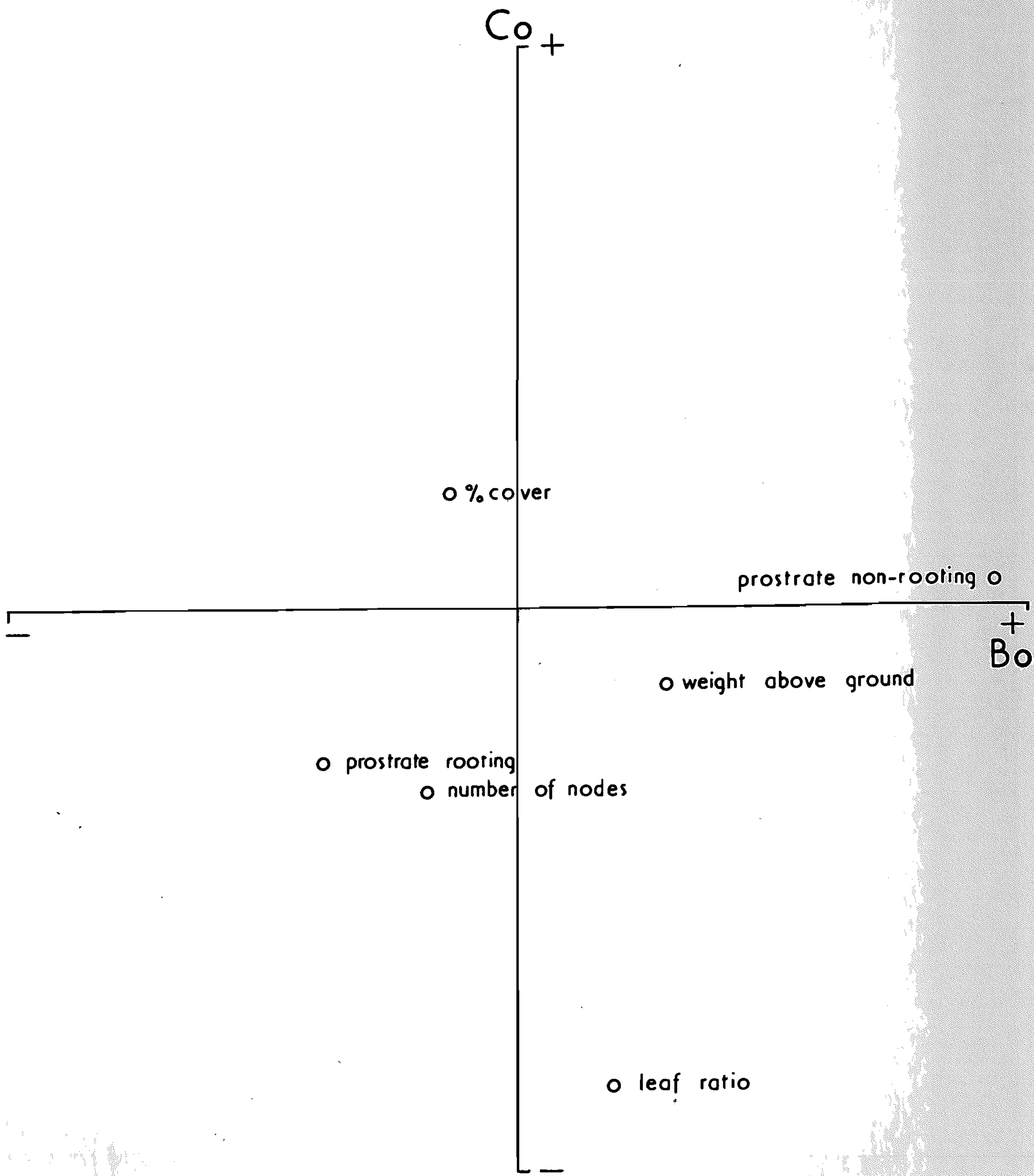


Fig. 45. Distribution of the 250 quadrats in relation to the Ao and Bo axes of Component Analysis (morphology; 7-variable). (Var. latifolia = dots; var. parvifolia = crosses; var. angustifolia = circles)

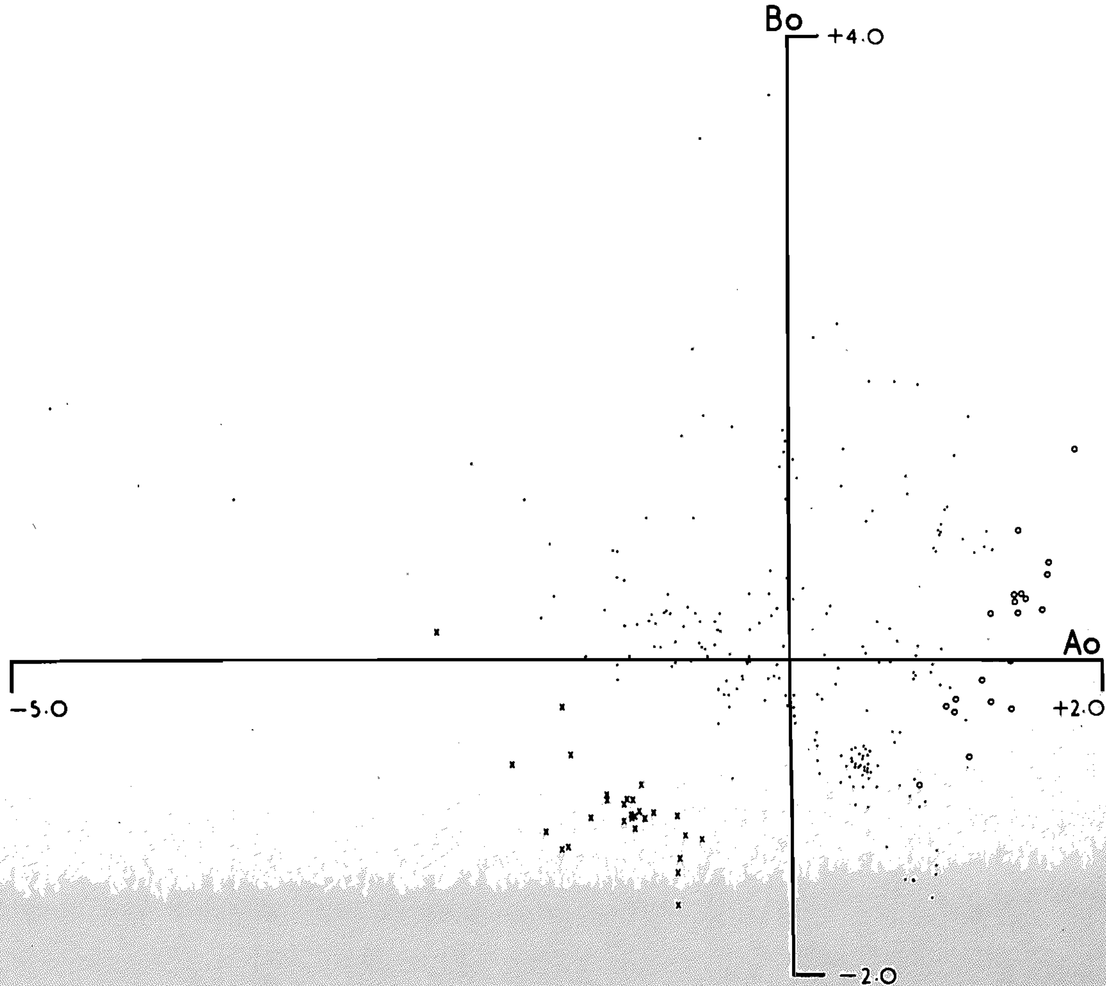


Fig. 46. Distribution of the 250 quadrats in relation to the Ao and Co axes of Component Analysis (morphology; 7-variable). (var. latifolia = dots; var. parvifolia = crosses; var. angustifolia = circles)

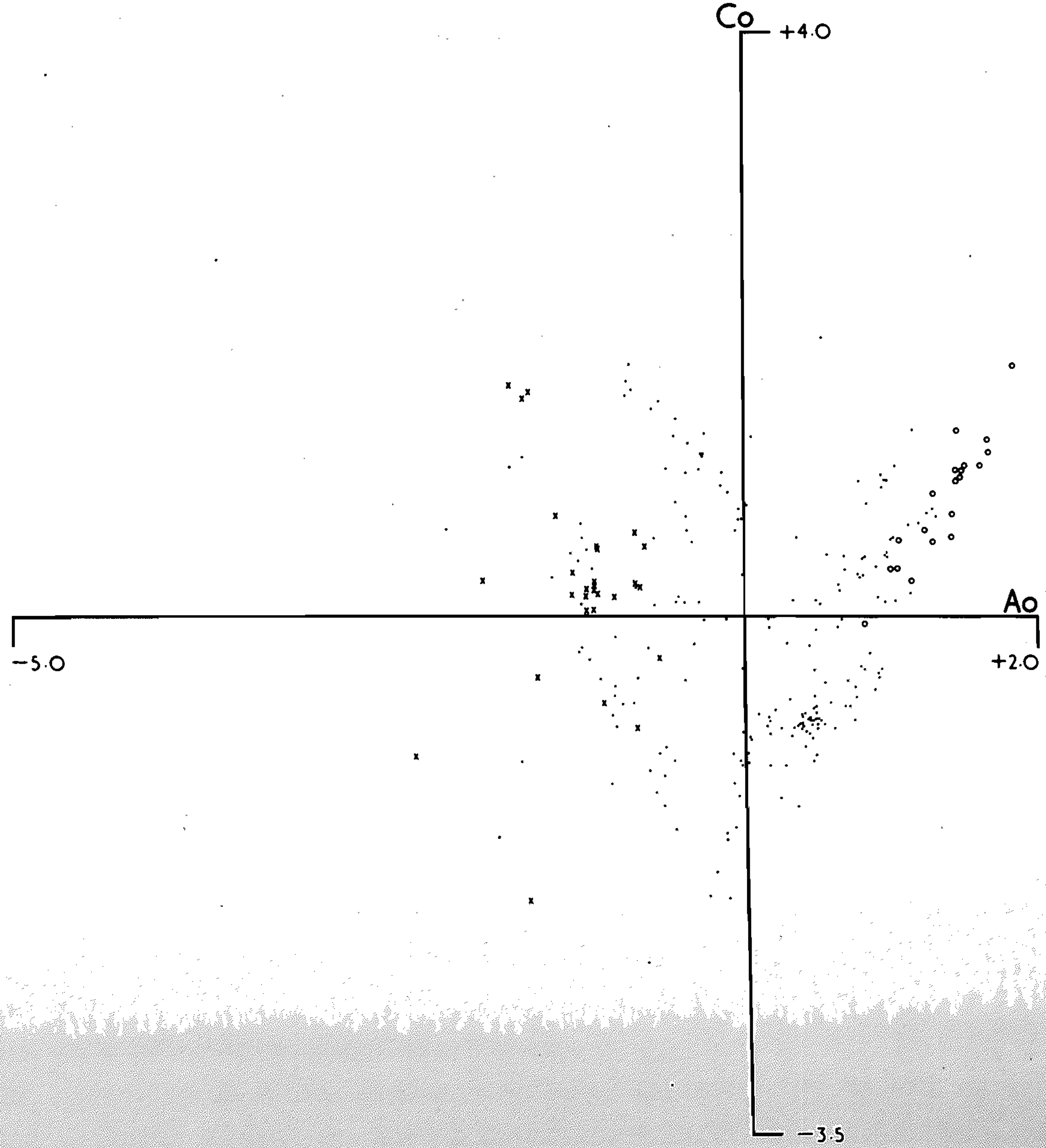


Fig. 47. Distribution of the 250 quadrats in relation to the Bo and Co axes of Component Analysis (morphology; 7-variable). (var. latifolia = dots; var. parvifolia = crosses; var. angustifolia = circles)

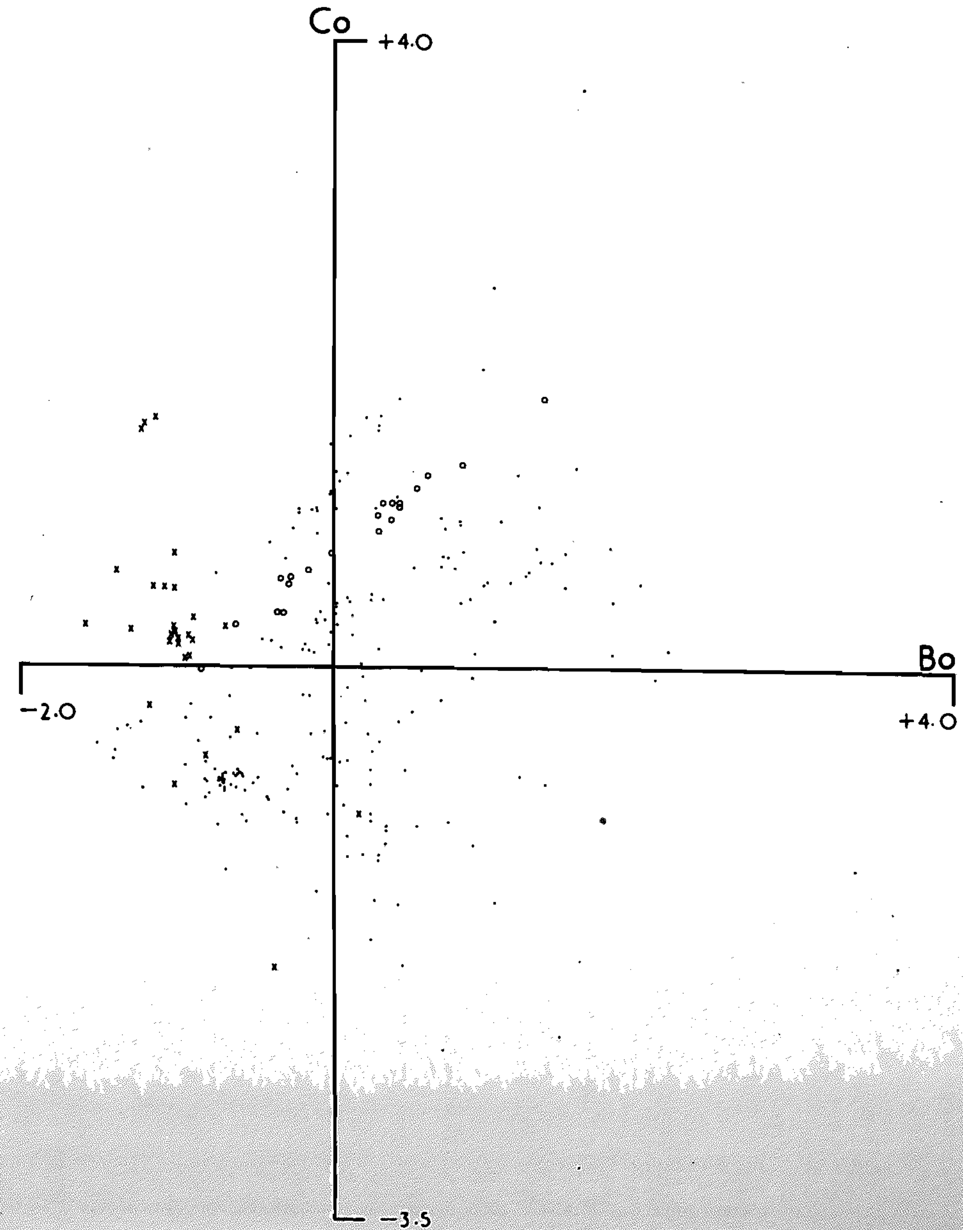


Fig. 48. Distribution of the 250 quadrats in relation to the Ao and Bo axes of Component Analysis (morphology; 6-variable). (var. <u>latifolia</u> = dots; var. <u>parvifolia</u> = crosses; var. <u>angustifolia</u> = circles)

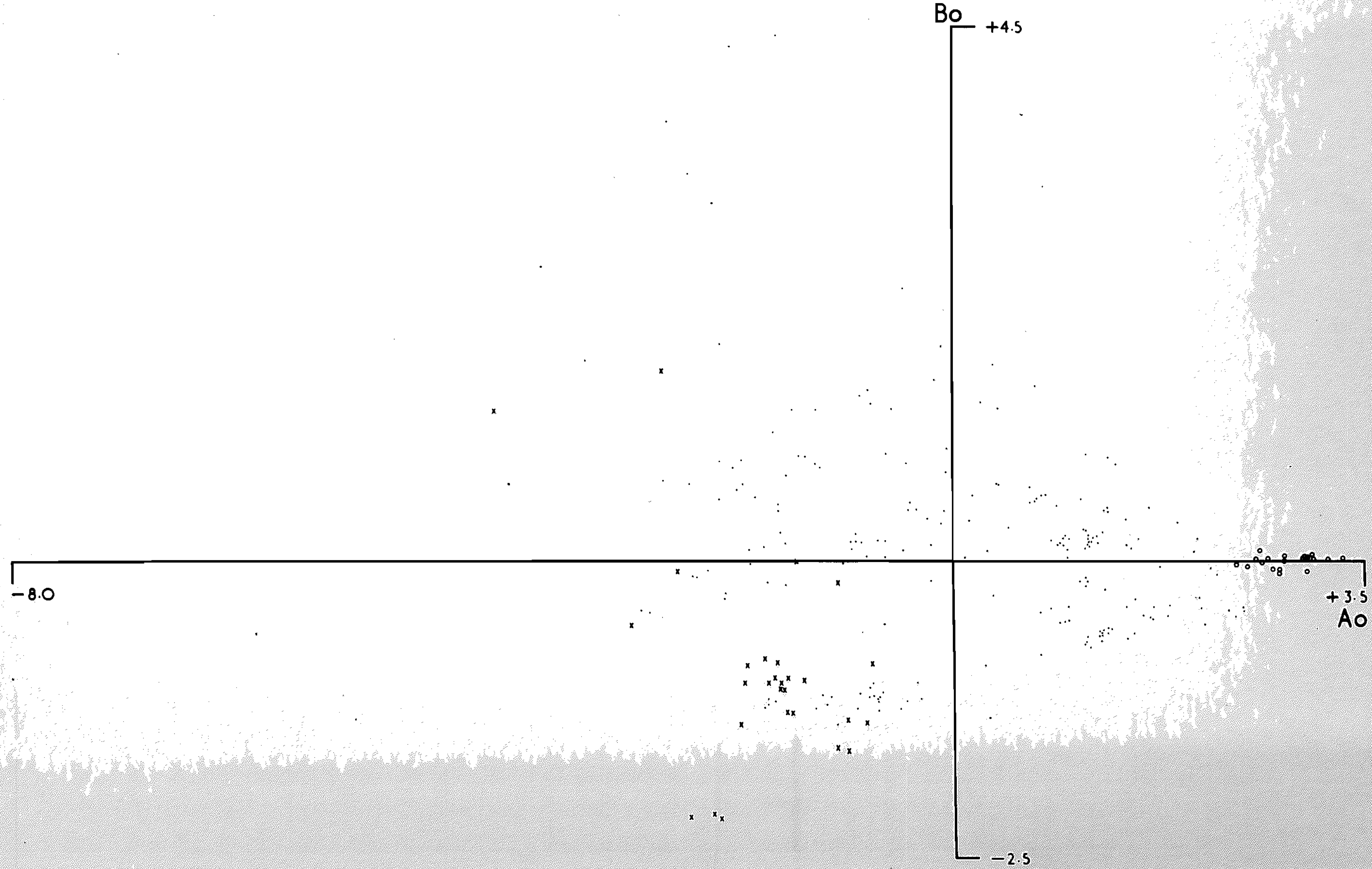


Fig. 49. Distribution of the 250 quadrats in relation to the Ao and Co axes of Component Analysis (morphology; 6-variable). (var. latifolia = dots; var. parvifolia = crosses; var. angustifolia = circles)

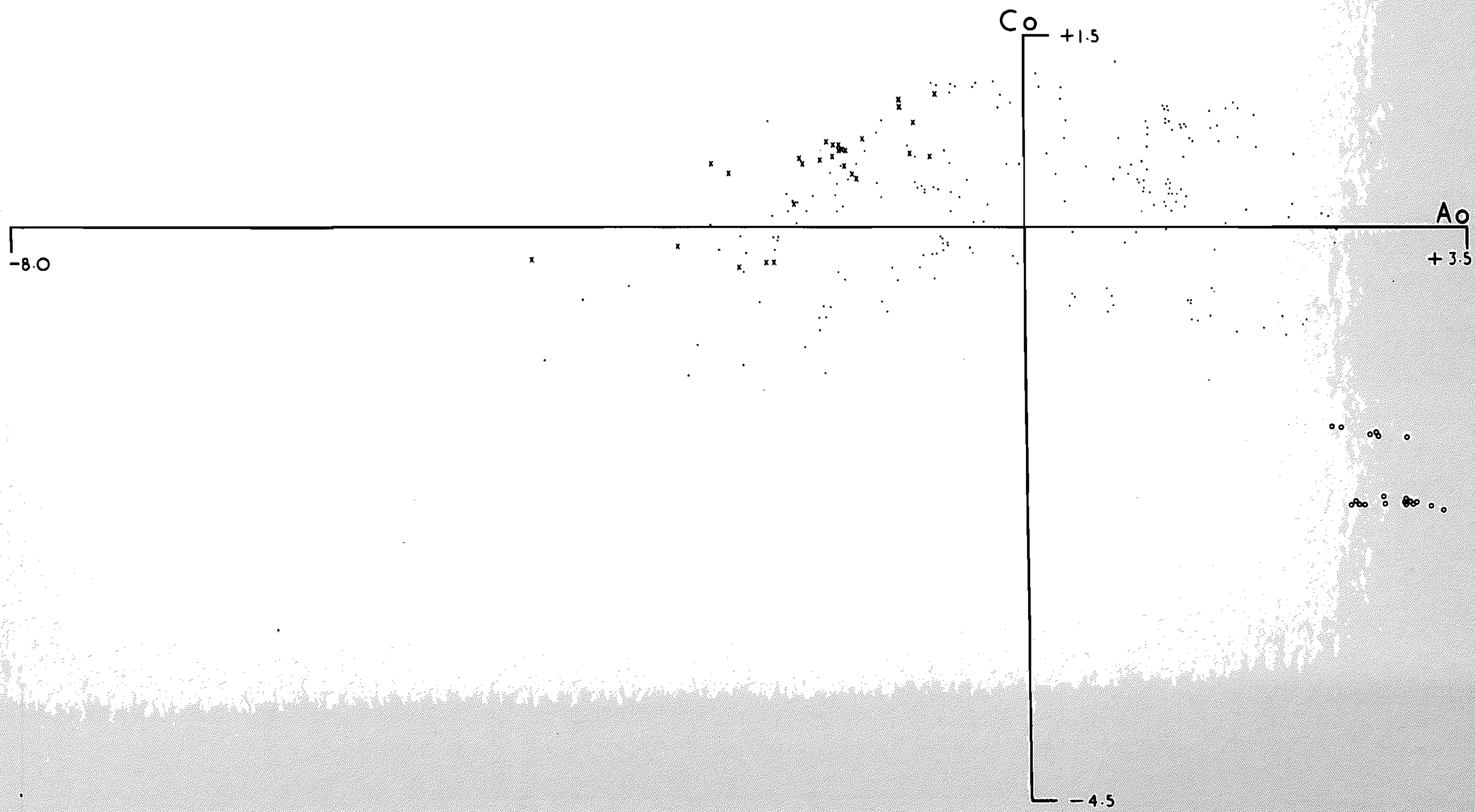
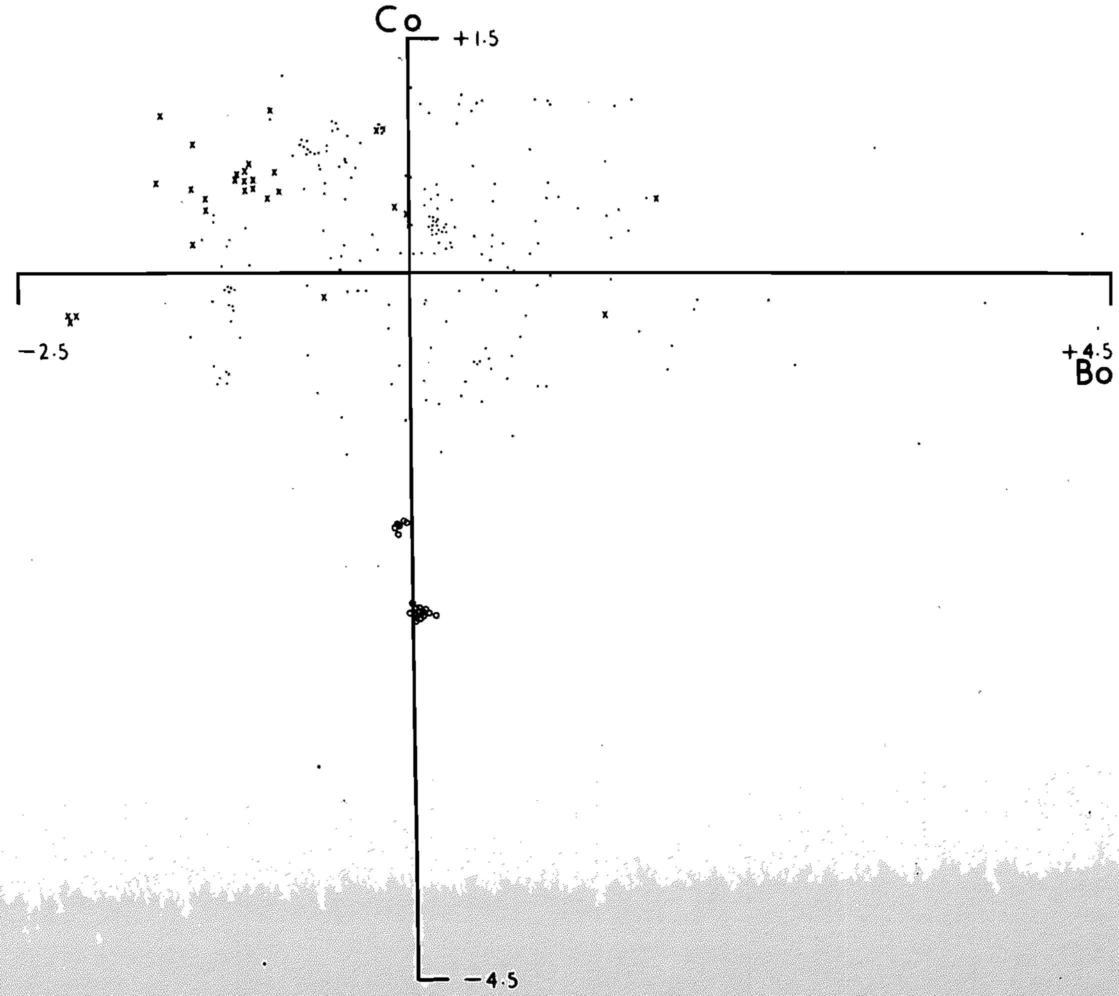


Fig. 50. Distribution of the 250 quadrats in relation to the Bo and Co axes of Component Analysis (morphology; 6-variable). (var. latifolia = dots; var. parvifolia = crosses; var. angustifolia = circles)



var. latifolia are indicated by dots, those referable to var. parvifolia by crosses and those referable to var. angustifolia by circles.

In the 7-variable analysis, the latifolia quadrats form an intermediate zone between angustifolia and parvifolia. The angustifolia quadrats are highly positive on the Ao axis, have a zero loading on Bo and are mainly positive on Co. The parvifolia quadrats are negative on Ao and Bo and largely positive on Co. The latifolia quadrats are largely intermediate between the parvifolia and angustifolia but, unlike them, many are negative on the Co axis. The three dimensional model is, thus, roughly, a solid, inverted cone, with the angustifolia and parvifolia quadrats being on opposite sides of an indented base. The parvifolia quadrats form a more distinct group than either of the other two varieties, not surprisingly since this analysis includes leaf-length, the character distinguishing parvifolia markedly from the other two varieties (Fig. 34).

In the 6-variable analysis, the latifolia quadrats again form an intermediate zone between angustifolia and parvifolia. The angustifolia quadrats are highly positive on the Ao axis, have a zero loading on Bo and are highly negative on Co. The parvifolia quadrats are negative on Ao, mainly negative on Bo and mainly positive on the Co axis. The latifolia quadrats are mainly intermediate between these two extremes. The three dimensional model is, roughly, 'discus-shaped', with the parvifolia quadrats forming the upper surface of one quadrant and the angustifolia quadrats being in a very distinct cluster below the opposite side of the 'discus'. The distinctness of the compact group of angustifolia quadrats is not surprising, since the 6-variable analysis includes leaf-ratio as one of the six attributes - the character distinguishing angustifolia markedly from the other two varieties.

Although, in each of the six two-dimensional figures, the clusters of angustifolia and parvifolia are distinct and completely separated from each other, their relation to latifolia is less distinct and they appear to merely form partially distinct extreme groups, considerably less distinct from the main group of quadrats than are some of the outlying extreme quadrats. However, the clusters of quadrats of parvifolia and angustifolia are, in fact, more distinct when the three-dimensional model is considered than they appear to be in the two-dimensional representations. The central cluster of quadrats (referable to var. latifolia) is not separated into distinct clusters: the variation within these plants thus being continuous.

By correlating the position of the parvifolia and angustifolia clusters in Figs. 45 to 50 with the attribute distributions in Figs. 39 to 44, it is possible to obtain descriptions of the habits of the two varieties. This comparison shows var. parvifolia to have a large amount of prostrate rooting, very little prostrate non-rooting, many nodes, a high percentage cover and short, narrow leaves with a low leaf-ratio (i.e. small, rounded leaves). On the other hand, var. angustifolia has little prostrate rooting, low percentage cover, few nodes and long leaves with a high leaf ratio (i.e. long, narrow leaves). The range between the dense, prostrate, compact, small-leaved parvifolia and the sparse, upright, lax, long-leaved angustifolia is almost entirely covered by the less distinct latifolia.

b. Habitat

With only four attributes, two factors in the Component Analysis extracted 86.85 per cent of the variation (the first extracting 56.13 per cent and the second 30.72 per cent). The distribution of the four attributes in relation to the two factors can, thus, be shown in two dimensions, and is given in Fig. 51. Pebble and sand are both highly positive on the Ao axis, pebble being positive on Bo and sand being negative on Bo. Both clay and compactibility are negative on the Ao axis.

With only four attributes, it is difficult to assign identities to the two axes and it is more convenient to make use of this analysis as a means of objectively dividing the quadrats into groups based on the four attributes simultaneously, rather than subjectively dividing them. This analysis is best regarded, therefore, as a means of sorting or classifying.

The specifications of the individuals on these axes enable all 250 quadrats to be plotted, and this display is shown in Fig. 52. The quadrats form a very distinct "V-shaped" distribution. Reference to Fig. 51 (and also perusal of the original data) shows that the two arms of the "V" are, respectively, quadrats with a substrate of pebble and of sand, and that the cluster at the base of the "V" consists of the quadrats with a muddy substrate.

Much the same type of "V-shaped" distribution was found in the

Fig. 51. Distribution of the four habitat attributes in relation to the Ao and Bo axes of Component Analysis

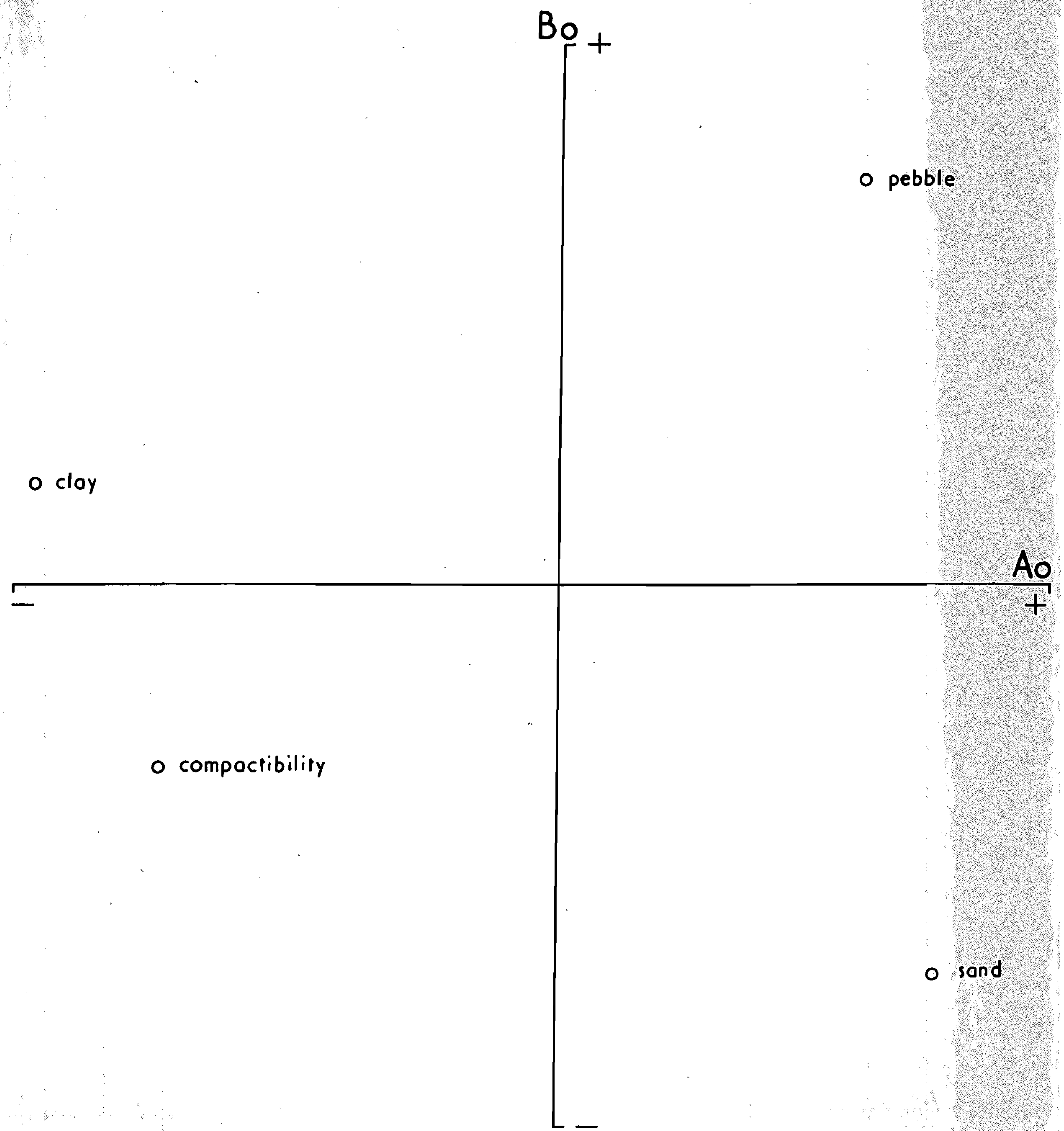


Fig. 52. Distribution of the 250 quadrats in relation to the Ao and Bo axes of Component Analysis. (habitat) (var. latifolia = dots; var. parvifolia = crosses, var. angustifolia = circles)

50 Hampshire basin quadrats in the pilot survey, when many more attributes were utilised in the analyses (c.f. Fig. 22) and this tends to confirm the contention that the most important single factor of the habitat (so far as these analyses are concerned) is the particle size of the substrate and justifies the use of particle sizes as the main attributes in these second analyses.

The distribution in Fig. 52 can lead to a more logical separation of the quadrats into three groups, based on all four of the attributes simultaneously, e.g. a division of the quadrats into (1) those negative on Ao, (2) those positive on both Ao and Bo, and (3) those positive on Ao and negative on Bo. However, the group negative on Ao is continuous with five quadrats just positive on Ao, these together forming a discrete group, with a marked gap between them and the other quadrats positive on Ao and negative on Bo. It appears logical to include these five quadrats with those negative on Ao. Hence, three groups may be defined which can, for convenience, be termed "pebble" (quadrats positive on Ao and Bo), "mud" (negative Ao, plus five quadrats just positive on Ao but appearing to be associated) and "sand" (positive Ao and negative Bo, less five quadrats just positive Ao but appearing to be associated with the group designated "mud").

c. The connection between morphology and habitat

Since Canonical Analysis was not undertaken, the most convenient means of demonstrating the connection between the habitat and the morphology of the plants is by plotting each separately and indicating the properties of the other on the same model. Thus, Fig. 52 shows the distribution of the 250 quadrats given by the Component Analysis of the habitat data, with the quadrats containing vars. latifolia, parvifolia and angustifolia shown by different symbols (dots, crosses and circles, respectively). It can readily be seen that both the parvifolia and angustifolia quadrats form discrete clusters and are, thus, confined to different, limited substrates. Quadrats containing var. parvifolia are confined solely to the areas where sand predominates. Similarly, the quadrats containing var. angustifolia are confined solely to the areas where the substrate is largely mud, or mud with pebble. The quadrats containing var. latifolia are far more widely spread and, as well as occurring in the same regions as parvifolia and angustifolia, they are found throughout the range of substrate conditions, from pebble, mud and sand regions. It is clear that var. latifolia is far less specific in its habitat requirements than either of the other two British varieties considered.

The effect of substrate conditions upon the morphology of var. latifolia is more conveniently demonstrated by plots of the distribution obtained by the morphology analyses with the three habitat types being indicated by different symbols. For the sake of clarity, the quadrats already referred to vars. parvifolia and angustifolia (shown already to be limited to sand and mud, respectively) are omitted. These simplified plots are shown in Figs. 53 to 58, with the quadrats largely with a pebble substrate

Fig. 53. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Ao and Bo axes of Component Analysis (morphology; 7-variable) ('mud' = dots; 'pebble' = circles; 'sand' = crosses)

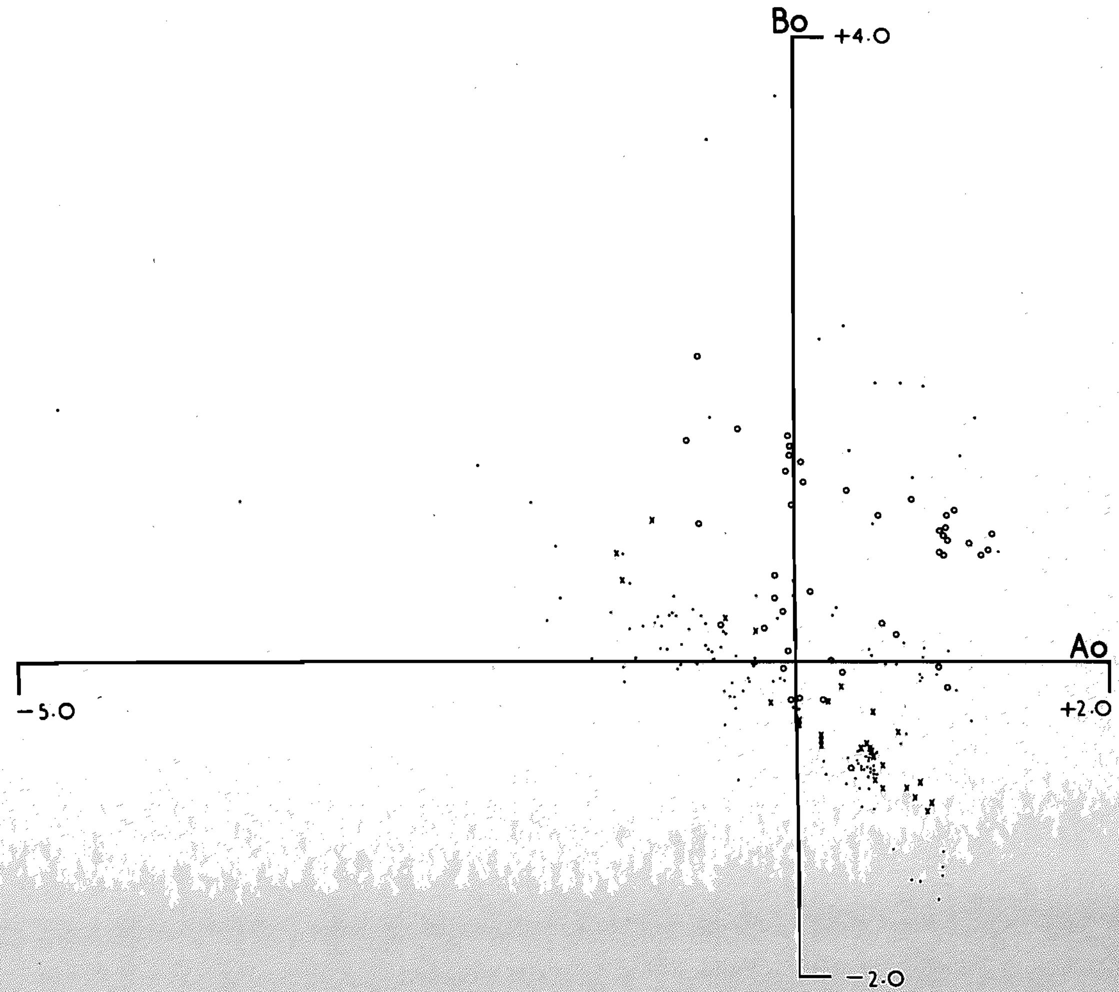


Fig. 54. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Ao and Co axes of Component Analysis (morphology; 7-variable). ('mud' = dots; 'pebble' = circles; 'sand' = crosses)

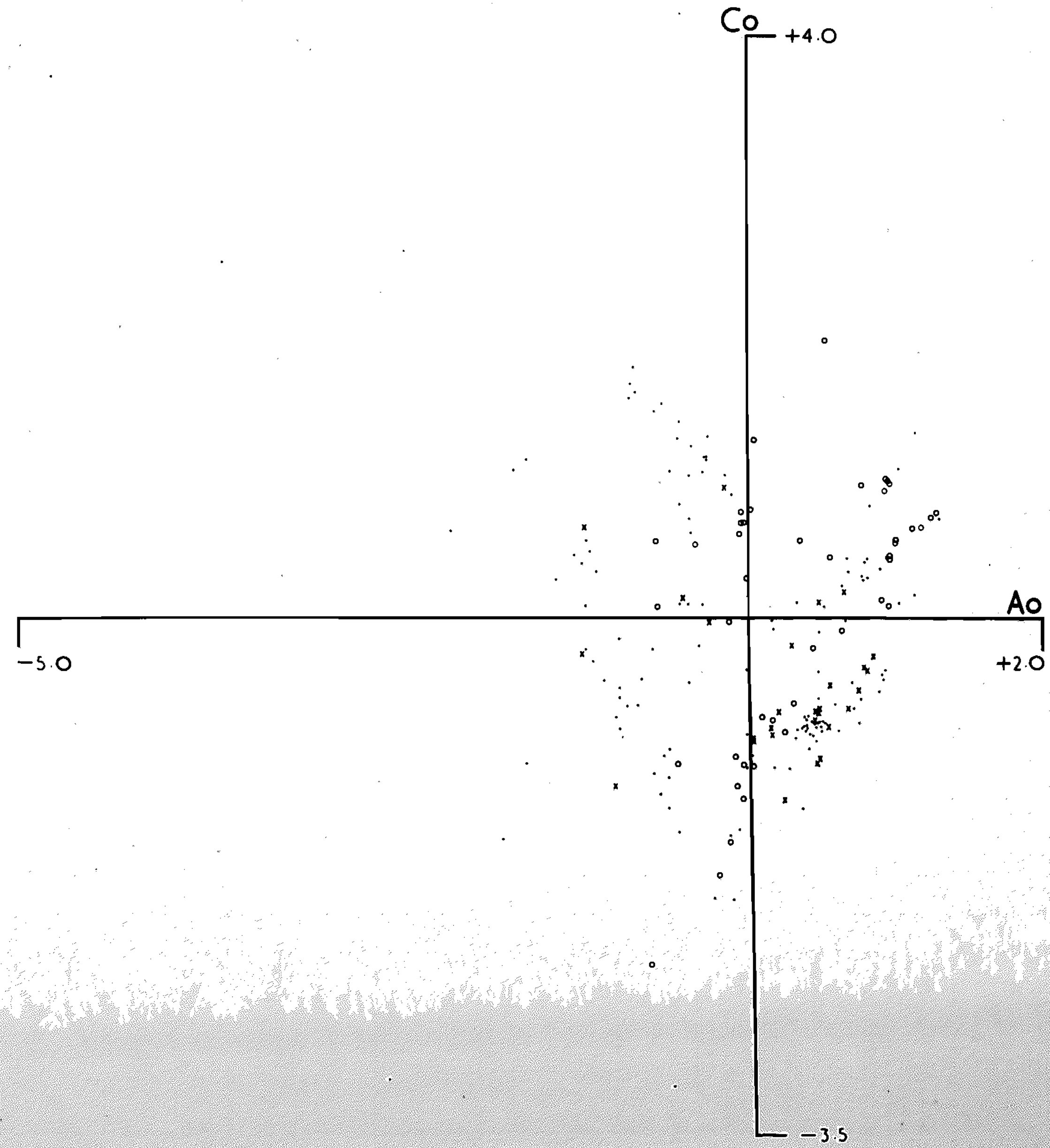


Fig. 55. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Bo and Co axes of Component Analysis (morphology; 7-variable). ('mud' = dots; 'pebble' = circles; 'sand' = crosses)

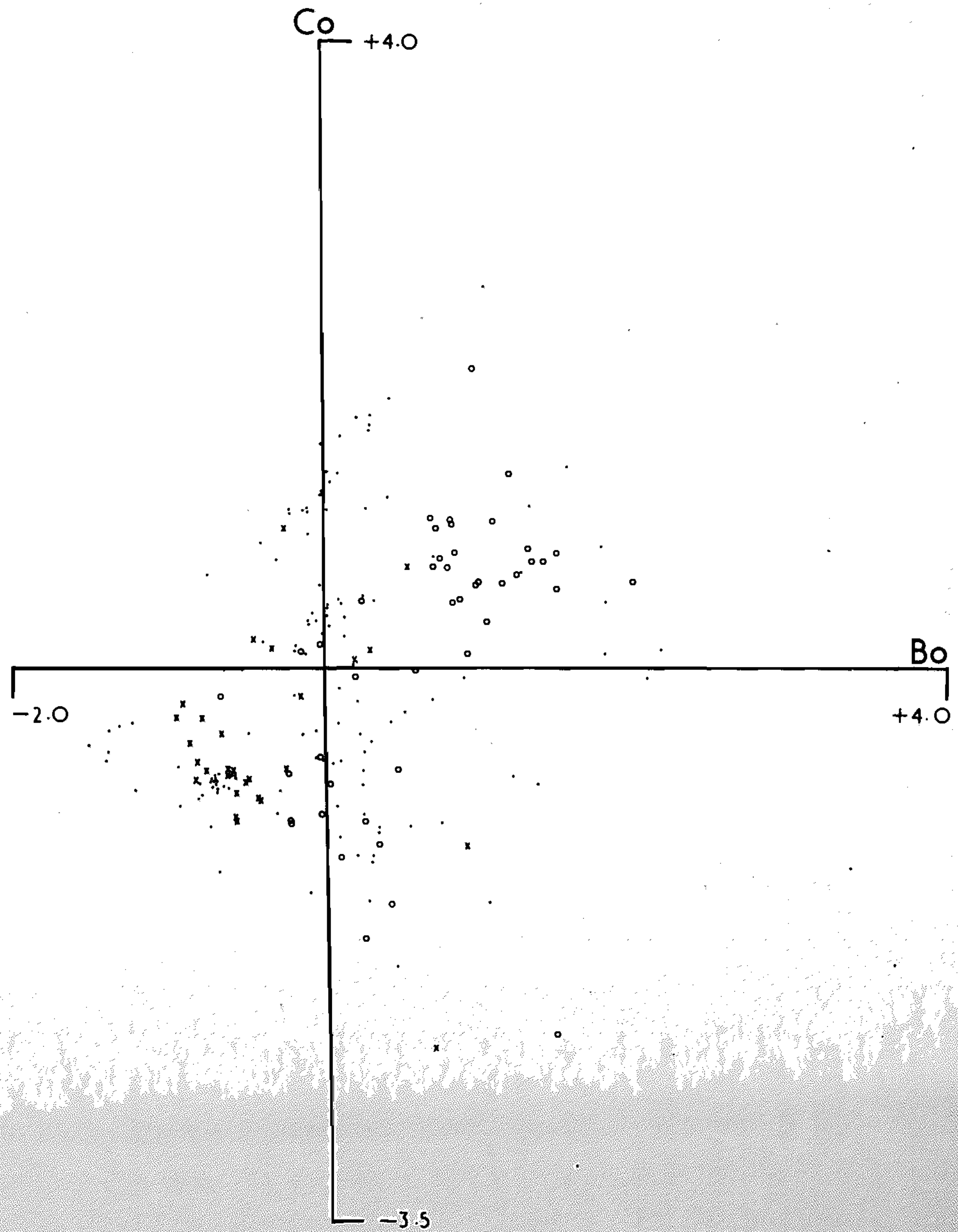


Fig. 56. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Ao and Bo axes of Component Analysis (morphology; 6-variable). ('mud' = dots; 'pebble' = circles; 'sand' = crosses)

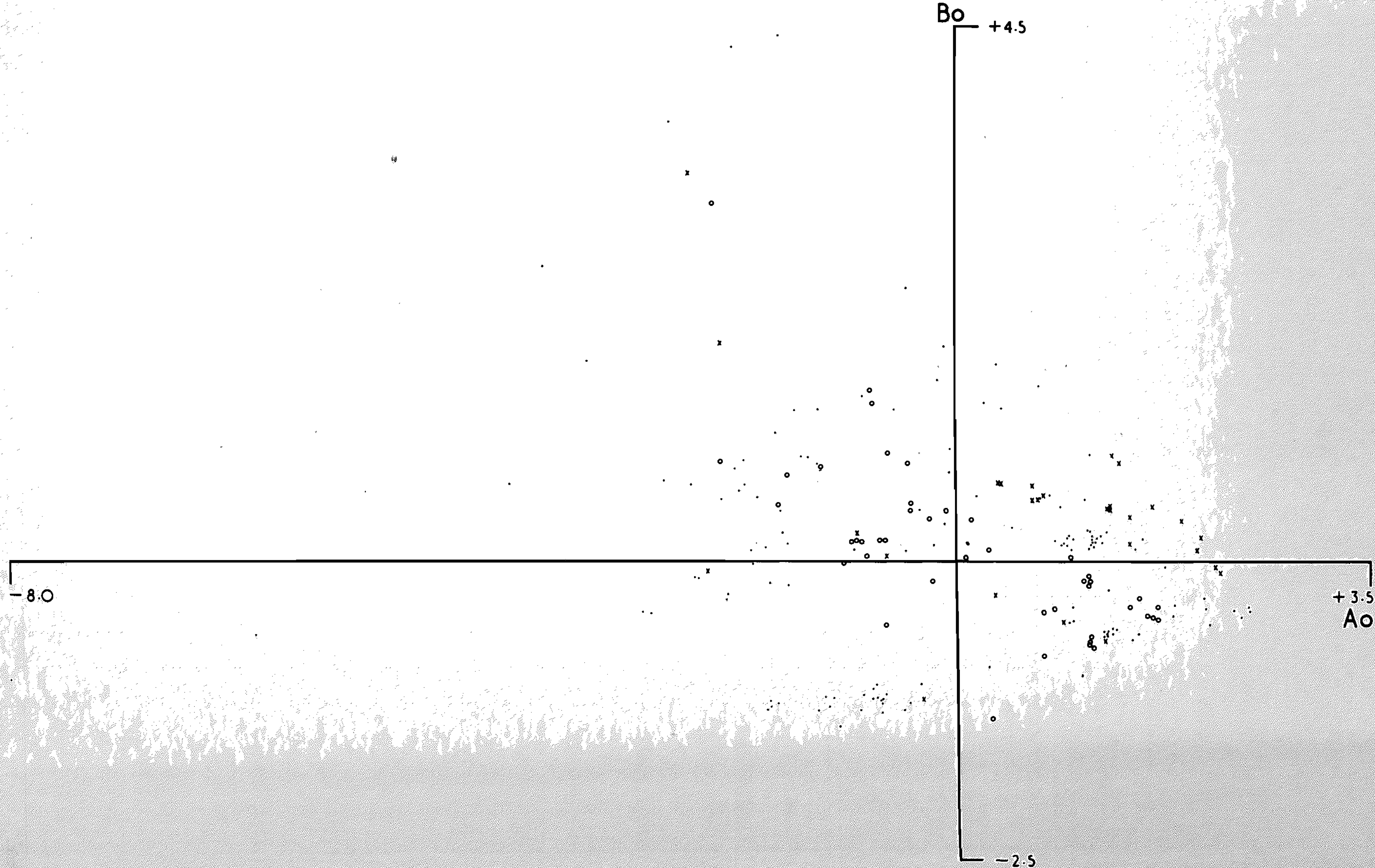


Fig. 57. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Ao and Co axes of Component Analysis (morphology; 6-variable). ('mud' = dots; 'pebble' = circles; 'sand' = crosses)

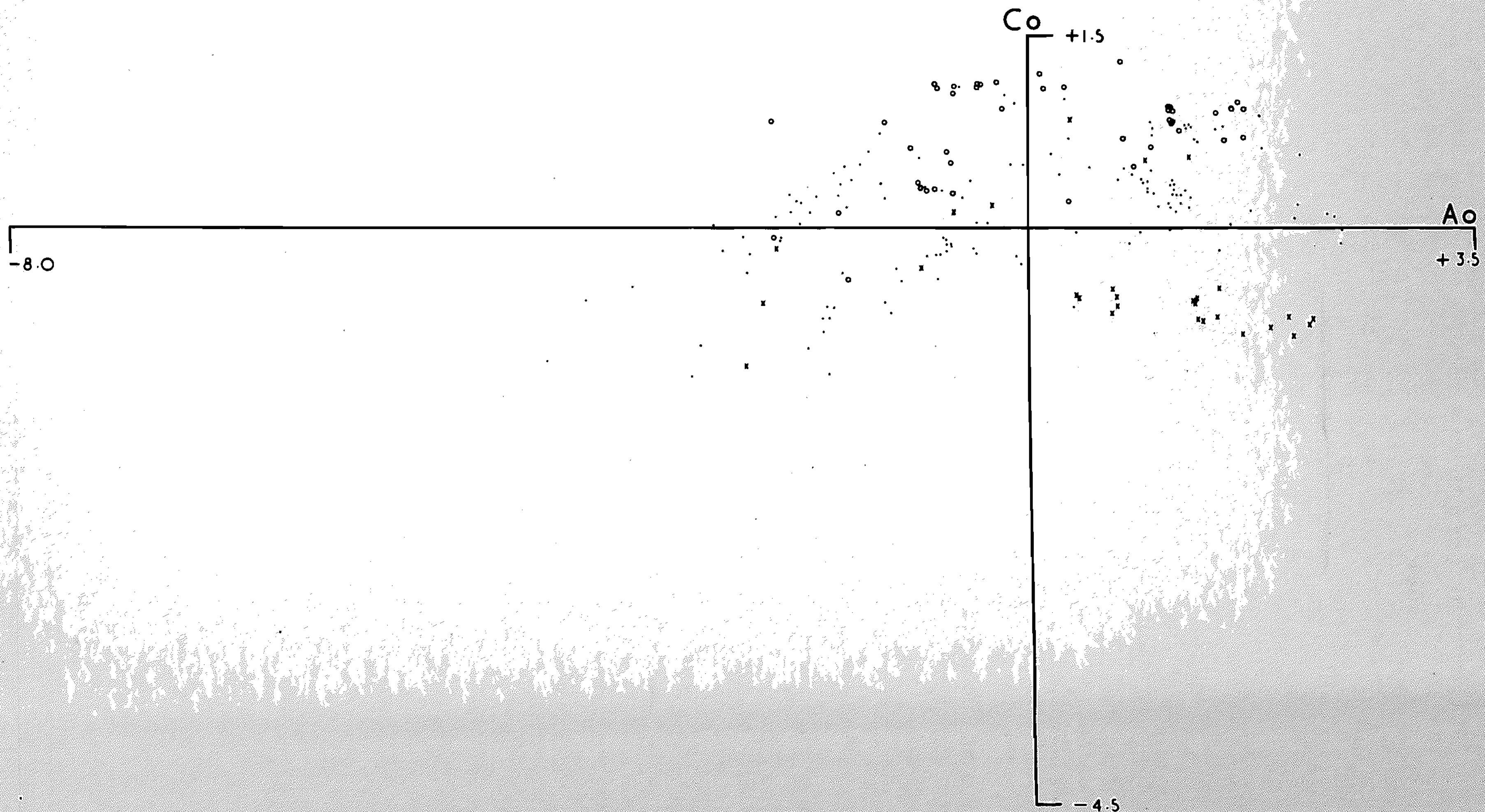
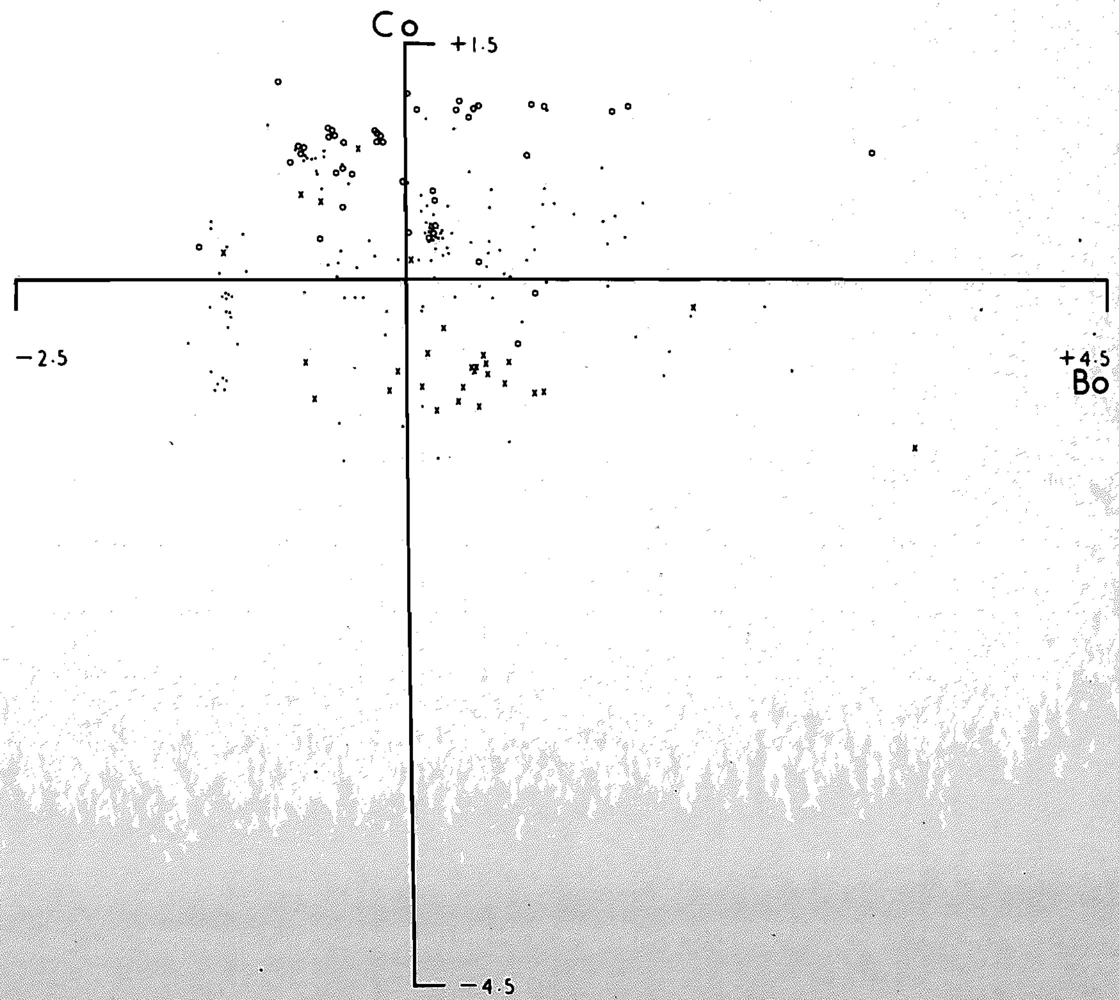


Fig. 58. Distribution of the 202 quadrats (vars. parvifolia and angustifolia omitted) in relation to the Bo and Co axes of Component Analysis (morphology; 6-variable). ('mud' = dots; 'pebble' = circles; 'sand' = crosses)



being indicated by circles, those with largely a sand substrate by crosses and those with largely a mud substrate by dots (a more detailed definition of these three divisions is given on p. 119).

There is far less distinction between these groups of quadrats divided on habitat than there is between the three varieties. However, despite the lack of discrete groups and the continuous nature of the variation within var. latifolia, the quadrats separated into "sand", "pebble" and "mud" on the basis of the habitat analysis are clearly supporting plants of slightly differing habit, as indicated in the morphology analyses.

In the 7-variable analysis (Figs. 53 to 55), the quadrats with a sand substrate are largely positive on the Ao axis, negative on the Bo axis and negative on the Co. The quadrats with a pebble substrate form a less clearly defined group and are distinct from the sand ones only on the Bo axis, where they are largely positive (only eight are negative and only five sand quadrats are positive).

In the 6-variable analysis (Figs. 56 to 58), the quadrats with a sand substrate are largely positive on the Ao and Bo axes and negative on the Co axis. The quadrats with a pebble substrate are, again, less clearly defined, though all but two are positive on the Co axis, whereas only five of the sand quadrats are positive.

The positions, in relation to the Bo axis in the 7-variable analysis and the Co axis in the 6-variable analysis, of the quadrats with sand and pebble substrates (as defined in the habitat analysis), enable the differences between the habits to be determined. Leaf width, leaf length and length of non-rooting prostrate portion are highly positive on Bo (7-variable) and Co (6-variable), while leaf ratio, length of rooting prostrate portion and number of nodes are highly negative on Bo (7-variable) and Co (6-variable).

Since the sand quadrats are mainly negative on both the Bo (7-variable) and Co (6-variable) axes, the habit of plants of var. latifolia growing on a sand substrate will tend towards a prostrate, much-rooting form, with many nodes (and hence short internodes) and with small, rather elongated leaves. Conversely, since the pebble quadrats are mainly positive on both the Bo (7-variable) and Co (6-variable) axes, plants of var. latifolia growing on a pebble substrate will tend towards a prostrate, but non-rooting, habit, with rather large, but not elongated leaves and with relatively few nodes (and hence longer internodes). The plants growing in muddy habitats tend to be mainly intermediate in their characteristics between those in sand and pebble substrates, but are far more variable, with extremes exceeding those found in other substrates and, in fact, the range of habit embraces the whole range of variation.

The analyses of the morphological data showed that, although the differences between vars. latifolia, angustifolia and parvifolia were slight, angustifolia and parvifolia both formed quite distinct and clearly defined groups, each with a quite different habit from the very variable latifolia (Figs. 45 to 50). Similarly, var. latifolia growing in sand and pebble substrates have differing habits but when growing in mud the habit is extremely variable and cannot be clearly defined (Figs. 51 to 56).

In considering the position of the three varieties, the most significant and relevant information is, perhaps, displayed in Fig. 52. This shows the distribution of the 250 quadrats in relation to the two main factors in the habitat analysis. In the display, the three varieties are indicated by different symbols and, while var. parvifolia is confined to a sand substrate and var. angustifolia to a mud substrate, var. latifolia is found in pebble, mud and sand substrates, including areas identical with those supporting vars. parvifolia and angustifolia.

Clearly, vars. parvifolia and angustifolia cannot merely be forms in which the morphology is modified by the habitat conditions, for (in this analysis) virtually identical habitat conditions are supporting plants with two distinct habits. While vars. parvifolia and angustifolia appear to be restricted (at least at the Blakeney Point site) to a limited range of substrate conditions, plants in these limited substrate conditions are not necessarily (on the evidence of the Component Analyses) of these varieties.

The evidence for this situation has, so far, been entirely based on the results from the Component Analyses. However, the indications were so clear that identical substrates can support plants of vars. parvifolia and latifolia or vars. angustifolia and latifolia that the area where all three were knownto occur (Blakeney Point) was revisited after the results of the analyses were complete. If the indications from the analyses were correct, there should be areas where plants with the morphological characteristics of two varieties could be found growing together. A careful search showed that occasional plants with all the characters of var. latifolia do occur within the sandy areas dominated by the completely distinct var. parvifolia. Although, at Blakeney Point, plants with the leaf characters of angustifolia were not mixed with latifolia, at Scolt Head Island plants apparently assignable to latifolia were found alongside apparent angustifolia.

From consideration of the three-dimensional models of the 7- and 6-variable analyses (Figs. 45-50 and 53-58), it is also possible to determine the morphological relationships of parvifolia and angustifolia with latifolia growing on sand, pebble and mud. In the 7-variable analysis, parvifolia is aligned rather nearer the latifolia growing on sand than that on pebble while angustifolia is clearly more closely associated with the latifolia growing on pebble. In the 6-variable analysis (which includes leaf-ratio), parvifolia is aligned more with the latifolia on pebble and the angustifolia is aligned with the latifolia on sand.

It is clear that latifolia growing on the same (sand) substrate as parvifolia more closely resembles parvifolia than angustifolia and that latifolia growing on the same (mud or mud-and-pebble substrate as angustifolia more closely resembles angustifolia than parvifolia, except in relation to leaf ratio, where the reverse is the case.

This same conclusion is reached when descriptions of the habits are compared, using the identifications of axes to define the groups. Both latifolia on sand and parvifolia are associated with a prostrate habit, with much nodal rooting, with many nodes (and, hence, short internodes) and with small leaves; the former, however, is associated with small elongated leaves and the latter with small rounded leaves. Both latifolia on pebble or mud-and-pebble and angustifolia are associated with little nodal rooting, with few nodes (and, hence, long internodes) and with small leaves; the former, however, is associated with large but not elongated leaves and the latter with long, narrow leaves and, whereas the former has a prostrate habit, the latter is more erect.

The habits of latifolia on various substrates, as defined from the Component Analyses of the extended survey data, therefore, are identical to the habits defined from the analyses of the Hampshire basin data and the extended survey completely confirms the results of the initial survey in this respect.

VI. CONCLUSIONS

A preliminary review of the literature suggested that *Halimione portulacoides* occupied limited zones in the salt marsh community and that its position was largely determined by the substrate water content. While observations tended to confirm this for restricted sites, a more extensive survey showed that the plant could tolerate widely differing substrate water contents (from < 6 per cent to > 68 per cent) and that, in various areas, *Halimione* occupied every position in the salt marsh from the upper regions of the Spartinetum to levels higher than that of any other salt marsh plant. Association Analysis of data of the species associated with *Halimione* in the Hampshire basin, moreover, showed that these species could be subdivided into distinct sets usually regarded as characteristic of different salt marsh conditions, thus giving additional evidence of the wide range of ecological tolerance exhibited by *Halimione*.

Cursory observations in the Hampshire basin showed that, although there was no reference to any variety other than *latifolia* in the literature, there was considerable morphological variation in the plants which occurred. The initial impression of three morphological types confined to distinct substrates - mud, sand and pebble - was objectively tested by analyses of habitat and morphological data. There was a high correlation between these, but the range of morphological variation was found to be continuous, the three 'types' merely being parts of a continuous morphological series from which they had been subjectively selected. The limited evidence available suggested that this morphological variation was habitat-induced in a very plastic, genetically-uniform, population.

The analyses indicated that plants growing on a substrate with a high substrate water content had a laxer and more upright habit, and flowered more frequently, than those on a substrate with a low water content, which were denser, more compact and seldom flowered. It is probable that a number of interacting factors effect these differences. The analyses of the habitat data showed that the drier substrates are divided into those with sand and those with pebble substrates. In the former, blowing sand is continually retained amongst the vegetation, burying the plants (this is indicated by the high values for 'below ground portion' for these plants). The plants surviving this process produce much vegetative growth and, in the dry conditions, the internodes are short. With most of the plant under the surface, there is much nodal rooting. In the latter (pebble substrate), it is probable that the prostrate habit is produced by mechanical damage (by wave action and/or pebble movement) of the apical buds and this also produces a much-branched habit, while the substrate movement prevents much nodal rooting. In the wetter substrates, it is probable that an entirely differenct set of factors are responsible for the morphological differences. In these regions, competition with other salt marsh species is more intense:

the wetter conditions and competition for light (especially in the Spartinetum) could lead to longer internodes and a generally laxer habit, while the lack of contact with the substrate, as the plant trails over other plants, could prevent nodal rooting. The fact that Halimione shows considerable plasticity and can respond to differences in habitat conditions by changes in its habit appears to be an important biological feature of the species, since its ability to produce markedly different growth forms under different environmental stresses could increase its general competitive equipment and power of survival.

The extension of the survey to cover diverse areas away from the Hampshire basin, as well as those in this region, confirmed that the morphological variation within Halimione portualcoides var. latifolia was closely related to the substrate, with a similar pattern emerging to that in the Hampshire basin. It also indicated that vars. parvifolia and angustifolia are morphologically very distinct from each other and that latifolia is largely intermediate between them though the latter embraces the whole range of variation and can resemble the other two varieties in gross morphology. However, while latifolia was found on the whole range of substrates examined, parvifolia was limited to a sand substrate and angustifolia to a mud or pebble-and-mud substrate. Moreover, while parvifolia and angustifolia are both morphologically distinct from latifolia growing on the same substrate, parvifolia most resembles latifolia growing on sand and angustifolia most resembles latifolia growing on pebble.

Despite the marked differences between parvifolia and angustifolia, the objective analyses carried out on the morphological data show clearly that they merely form two parts of the total range of morphological variation of Halimione portulacoides (sens. lat.) and that var. latifolia covers the whole range of variation and, indeed, embraces the range of both parvifolia and angustifolia. Simple examination of the leaf characters showed that leaf-length will separate parvifolia from the other two varieties and leaf-ratio will separate angustifolia from the other two varieties but that no single leaf measurement defines all three of the varieties, so that it is now open to question whether the three are taxonomically as distinct as the earlier literature implies.

Although the morphological characters used in the analyses were chosen more for their ecological significance than for their taxonomic significance, and the use of quadrat, rather than individual plant, data is more justifiable for ecological than taxonomic problems, the overall results nevertheless suggest that the morphological characters found in the plastic Halimione growing on sand and pebble substrates have become 'fixed' to some extent in the cases of parvifolia and angustifolia. This is also indicated by the similarity in morphology of plants referable to latifolia in substrates identical (as far as the features analysed are concerned) to those supporting parvifolia and angustifolia. The situation, where identical substrates can support plants which, on leaf characters, would be identified as two varieties, suggests that, as with Hieracium umbellatum (Turesson 1922), types characteristic of different habitats have become 'fixed'. The methods employed in this work do not allow for the resolution of this problem and a taxonomic approach would be necessary to elucidate the true nature of a situation which was not suspected when the investigation began.

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Appendix I. Brief details of Hampshire basin marshes visited

1. Studland, Dorset.

Substrate: Thin layer of sand overlying estuarine clay.

Status of *H. portulacoides*: Scattered plants, forming a narrow zone between *Spartina* and *Juncus*.

Topographical classification: Enclosed harbour; sheltered by sand-dunes; no drainage channels.

Disturbance: Holiday-makers and oil-pollution main disadvantages.

Access: Easy.

2. Christchurch Harbour, Hampshire.

Substrate: Estuarine clay.

Status of *H. portulacoides*: Scarce; vegetation mainly of fresh-water spp. associated with fresh-water inflow to harbour.

Topographical classification: Enclosed harbour.

Disturbance: Little; some grazing.

Access: Easy.

3. Hurst Castle, Hampshire.

Substrate: Thin layer of estuarine clay overlying shingle.

Status of *H. portulacoides*: Dense communities; dominating general salt-marsh, with *Aster* and *Limonium*.

Topographical classification: Small enclosed marshes, sheltered by shingle spits.

Disturbance: Negligible human disturbance.

Access: Difficult: over a mile of shingle spit to be traversed.

Appendix I (Cont.)

4. Keyhaven Marshes, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Limited to creek edges amongst upper Spartinetum.

Topographical classification: Partly sheltered by shingle spit.

Disturbance: Much disturbance by holiday crowds.

Access: Easy.

5. Pennington Marshes, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Absent; probably due to erosion.

Topographical classification: Open coast.

Disturbance: Little.

Access: Easy.

6. Lymington, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Scarce; limited to creek edges in upper Spartinetum.

Topographical classiiication: River estuary.

Disturbance: Little

Access: Easy

7. Needs Oar Point, Hampshire.

Substrate: Thin layer of estuarine clay overlying shingle.

Status of H. portulacoides: Narrow zone of almost pure Halimione with virtually no other salt-marsh plants above or below it.

Appendix I (Cont.)

Topographical classification: Sloping shore without marsh development; sheltered by shingle spit.

Disturbance: Little human disturbance; limited grazing by ponies and cattle.

Access: Easy (permit from Beaulieu Manor Office necessary).

8. Beaulieu River, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Scarce; occurs very occasionally in area dominated by extensive Spartinetum.

Topographical classification: River estuary.

Disturbance: Little.

Access: Easy.

9. Fawley, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Confined to higher areas of salt-marsh and creek edges.

Topographical classification: Estuarine; protected by extensive front of Spartinetum.

Disturbance: Little human disturbance; limited grazing by ponies and cattle.

Access: Easy (permit from Fawley Oil Refinery necessary).

10. Hythe, Hampshire.

Substrate: Estuarine clay (higher sand content than at Fawley).

Appendix I (cont.)

Status of H. portulacoides: Confined to higher areas of salt-marsh and creek edges.

Topographical classification: Estuarine; protected by extensive front of Spartinetum and by sand and shell banks.

Disturbance: Considerable: both human and by grazing animals.

Access: Easy.

11. Totton, Hampshire.

Substrate: Estuarine clay.

Status of H. portulacoides: Scattered over general salt-marsh.

Topographical classification: Estuarine.

Disturbance: Much pollution and increasing industrial encroachment.

Access: Easy.

12. Bursledon, Hampshire.

Substrate: Estuarine clay

Status of H. portulacoides: Scattered over general salt-marsh; Spartina invading.

Topographical classification: Flat estuarine marsh; some way up River Hamble.

Disturbance: Little.

Access: Easy.

13. North Binness Island, Hampshire.

Substrate: Estuarine clay; high organic content.

Status of H. portulacoides: Along creek edges and in irregular patches on flat marshes; Spartina only just invading.

Appendix I (cont.)

Topographical features: Sheltered within Langstone Harbour.

Disturbance: Little.

Access: Island can only be reached at low tide.

14. Chichester Harbour, Sussex.

Substrate: Estuarine clay with embedded rocks and bricks.

Status of H. portulacoides: Scattered plants along shore above Spartina zone.

Topographical classification: Wide harbour, hence little protection.

Disturbance: Little; some pollution.

Access: Easy.

15. East Head, Sussex.

Substrate: Sand dunes overlying estuarine clay.

Status of H. portulacoides: Dense, almost pure, Halimionetum on sand; Spartina on mud hardly invading sandy regions.

Topographical classification: Sheltered by sand-dune spit.

Disturbance: Some disturbance in summer from holiday-makers.

Access: Easy.

16. Pagham Harbour, Sussex.

Substrate: Estuarine clay.

Status of H. portulacoides: Scattered around shores; no one area with extensive Halimione.

Topographical classification: Sheltered harbour.

Disturbance: Little.

Access: Easy.

Appendix II. Morphological measurements made at Hampshire basin quadrats

a = number of lateral branches; b = number of flowering apices; c = number of vegetative apices; d = number of dead apices; e = length of prostrate rooting portion (cm); f = length of prostrate non-rooting portion (cm); g = length of vertical portion (cm); h = number of nodes; i = fresh weight of below ground portion (g); j = fresh weight of above ground portion (g); k = number of leaves; l = fresh weight of leaves (g); m = dry weight of leaves (g); n = percentage cover of quadrat by Halimione.

	a	b	c	d	e	f	g
Needs Oar Point							
1	3,245	60	3,026	1,180	6,382	7,063	7,266
2	817	160	881	689	463	1,649	1,263
3	704	56	596	380	148	1,508	643
4	4,704	280	4,481	952	27,443	11,983	8,409
5	496	24	512	143	656	1,823	1,368
6	2,177	126	1,025	849	3,274	2,375	7,003
7	3,011	120	2,883	2,212	4,242	837	8,613
8	1,729	223	1,538	1,986	1,283	4,166	2,689
9	1,853	198	1,853	909	4,058	1,457	13,018
10	3,523	361	3,121	2,284	11,012	6,761	8,808

Appendix II (cont.)

	a	b	c	d	e	f	g
Fawley							
11	2,410	639	1,605	881	8,222	8,220	18,431
12	81	11	98	29	301	410	409
13	1,244	119	1,489	319	2,488	6,049	9,487
14	3,842	159	3,728	2,761	1,524	33,498	16,974
15	2,368	409	1,437	1,488	2,769	12,818	10,610
16	768	180	786	420	987	7,564	4,947
17	1,884	503	1,416	864	971	10,110	10,707
18	899	139	722	619	2,324	3,304	4,728
19	2,880	319	2,408	2,165	2,208	17,898	16,281
20	1,444	1	1,565	663	5,886	8,220	6,816
Bursledon							
21	1,599	278	1,199	799	3,408	7,865	9,973
22	5,312	499	4,108	2,953	12,611	26,663	31,251
23	2,614	698	1,259	1,212	18,053	15,756	21,755
24	3,817	842	3,645	1,402	2,561	31,288	20,853
25	1,502	198	1,010	897	9,610	16,253	9,758
26	1,556	449	1,059	849	2,053	7,011	10,868
27	36	22	96	26	166	463	802
28	1,598	200	1,288	1,003	3,691	14,962	6,210
29	1,482	521	1,099	521	4,930	10,322	27,091
30	2,728	948	1,369	1,052	11,863	13,384	19,120

Appendix II (cont.)

	a	b	c	d	e	f	g
North Binness Island							
31	150	7	156	101	180	514	602
32	449	128	163	382	232	1,160	2,690
33	4,488	883	1,406	3,884	1,882	13,728	16,621
34	193	50	86	125	50	1,010	1,158
35	56	5	40	35	14	131	276
36	91	29	52	49	43	228	659
37	1,752	261	892	1,242	2,719	5,036	7,162
38	1,443	159	1,103	980	640	4,345	6,808
39	1,892	192	1,159	2,022	374	9,559	5,205
40	923	61	999	759	542	3,270	2,710
East Head							
41	5,254	2	3,951	1,202	23,614	3,554	15,512
42	10,658	198	6,156	2,460	32,762	8,842	24,449
43	6,109	43	3,173	1,748	16,150	5,749	14,260
44	8,811	146	5,407	4,249	22,020	20,012	23,258
45	7,555	2	4,408	2,905	27,854	9,502	16,211
46	1,172	28	814	723	3,577	962	2,583
47	3,552	2	2,757	1,411	4,710	2,000	5,152
48	2,576	47	1,879	1,452	4,073	4,440	5,709
49	3,754	46	2,566	1,554	4,205	15,311	10,358
50	1,921	23	1,561	1,029	4,563	9,641	5,781

Appendix II (cont.)

	h	i	j	k	l	m	n
Needs Oar Point							
1	21,968	553	543	25,503	841	130.0	47.5
2	3,296	208	320	14,416	384	50.1	27.0
3	2,321	193	204	6,304	248	34.8	25.5
4	70,226	1,849	840	60,704	2,072	246.4	65.0
5	3,641	98	95	3,418	202	29.0	17.5
6	12,118	512	305	18,670	468	62.5	52.0
7	16,831	920	530	33,619	1,081	160.0	39.0
8	12,738	383	502	29,987	736	80.0	38.0
9	16,488	399	466	27,953	960	149.0	17.0
10	33,641	1,732	651	45,167	1,666	208.0	80.0
Fawley							
11	30,803	1,224	774	55,366	1,906	268.0	54.0
12	1,225	375	22	1,410	61	6.5	6.0
13	12,665	340	500	25,968	1,200	158.0	43.0
14	47,440	1,680	1,298	63,085	2,784	464.0	48.0
15	23,084	1,020	722	32,264	1,100	184.0	48.0
16	7,921	279	363	13,480	690	88.0	50.0
17	13,814	541	1,418	41,681	1,692	248.0	14.0
18	7,308	430	511	14,488	741	92.0	25.0
19	27,664	856	999	44,440	2,421	318.0	45.0
20	19,212	616	308	17,624	940	92.0	46.0

Appendix II (cont.)

	h	i	j	k	l	m	n
Bursledon							
21	11,220	320	769	21,768	1,241	152.0	63.0
22	41,518	1,750	2,175	89,149	3,900	455.0	50.0
23	30,771	1,652	1,468	36,443	1,075	149.0	55.0
24	26,672	1,243	2,002	59,664	3,282	460.0	46.0
25	17,963	1,411	827	20,455	1,051	125.0	50.0
26	13,153	551	857	24,539	970	115.0	58.0
27	855	16	36	1,354	55	4.0	10.0
28	14,768	643	546	17,811	776	80.0	25.0
29	14,873	577	922	27,823	1,496	159.0	55.0
30	24,256	1,825	1,102	35,112	1,650	170.0	55.0
North Binness Island							
31	1,266	25	56	2,452	82	14.4	5.0
32	3,218	111	158	7,033	215	37.0	15.0
33	25,442	1,048	1,781	54,407	1,639	280.0	35.0
34	1,688	10	70	2,842	95	15.5	20.0
35	326	7	8	672	16	2.5	8.0
36	911	16	31	1,658	40	9.0	3.0
37	11,160	370	416	19,893	634	104.0	40.0
38	9,223	141	415	17,402	574	89.0	21.0
39	16,260	354	688	23,363	650	115.0	25.0
40	5,283	76	282	13,942	288	50.0	24.0

Appendix II (cont.)

	h	i	j	k	l	m	n
East Head							
41	46,518	1,410	245	36,010	775	130.0	85.0
42	112,783	2,385	905	59,040	1,786	250.0	85.0
43	37,752	2,801	890	45,556	1,480	220.0	75.0
44	72,750	1,800	1,350	57,908	1,835	315.0	80.0
45	63,040	2,555	891	39,556	1,160	150.0	58.0
46	15,626	327	105	8,730	201	27.0	50.0
47	20,041	460	220	15,152	400	62.0	58.0
48	16,126	627	365	16,776	335	95.0	90.0
49	30,501	925	395	20,014	780	100.0	48.0
50	22,674	537	223	13,151	480	55.0	45.0

Appendix III. Habitat measurements made at Hampshire basin quadrats

a = distance from nearest creek (cm); b = percentage water content (emergence); c = percentage water content (submergence); d = percentage organic content; e = height above O.D. (cm); f = percentage sodium content; g = compactibility (cm); h = speed of drainage (min); i to n = soil fraction percentages, designated pebble, coarse sand, medium sand, fine sand, silt and clay, respectively.

	a	b	c	d	e	f	g
Needs Oar Point							
1	550	34.22	53.98	19.72	152.2	1.38	7.4
2	680	1.07	5.86	1.89	173.0	0.08	0.9
3	430	1.54	11.42	1.48	165.0	0.24	1.9
4	260	6.93	23.21	5.09	150.1	0.44	4.0
5	160	26.28	37.28	13.01	137.0	0.94	6.1
6	560	49.72	63.34	36.53	155.4	1.96	8.0
7	300	4.07	22.22	2.86	154.0	0.56	3.3
8	730	2.89	5.78	0.86	169.4	0.32	3.7
9	100	40.06	65.02	24.49	133.4	1.78	14.5
10	340	7.64	16.27	2.62	144.3	0.40	1.8

Appendix III. (cont.)

	a	b	c	d	e	f	g
Fawley							
11	0	45.07	53.17	17.18	163.4	1.76	8.9
12	1,400	52.17	76.26	22.97	162.5	5.04	16.1
13	1,120	58.54	60.49	33.06	169.2	1.84	11.2
14	1,230	48.63	64.98	33.33	158.6	2.24	10.5
15	1,330	56.85	61.07	31.22	169.0	1.68	11.5
16	1,460	59.57	61.51	22.64	171.5	2.00	13.4
17	200	64.77	65.55	37.33	172.5	2.00	11.8
18	200	61.98	66.24	37.06	170.0	1.96	12.1
19	300	49.08	65.78	26.51	158.8	2.00	14.9
20	1,130	59.28	70.40	24.55	154.1	3.36	23.2
Bursledon							
21	80	54.19	69.29	27.12	160.5	2.00	10.2
22	200	62.53	68.66	24.98	163.1	1.86	21.1
23	160	56.48	65.99	26.65	163.1	2.00	21.8
24	190	58.56	67.70	28.13	161.7	2.00	16.0
25	190	56.40	68.59	24.65	162.6	2.56	17.7
26	220	62.50	68.00	25.13	160.1	2.16	21.6
27	190	56.91	71.42	28.60	158.6	1.70	27.3
28	290	64.83	72.67	26.72	159.0	2.00	26.4
29	390	58.55	78.25	31.69	160.6	4.24	31.9
30	490	68.17	76.72	15.21	159.4	2.72	31.3

Appendix III (cont.)

	a	b	c	d	e	f	g
North Binness Island							
31	650	49.74	63.41	28.70	166.8	2.00	9.9
32	730	53.99	65.29	30.71	163.8	1.20	13.0
33	740	54.49	69.10	25.62	162.6	1.70	13.3
34	670	47.75	62.93	29.23	167.0	1.98	10.2
35	570	49.73	67.33	24.36	165.6	1.96	10.0
36	470	48.43	58.29	24.09	165.8	1.50	10.5
37	370	53.54	63.98	23.42	166.3	1.60	11.7
38	270	48.17	61.60	24.73	165.6	2.88	10.6
39	250	49.20	59.26	22.49	164.7	1.68	11.0
40	230	44.81	60.33	23.95	164.6	1.98	12.4
East Head							
41	750	19.22	26.45	12.04	196.5	0.24	4.6
42	750	19.43	29.58	5.44	193.3	0.36	7.6
43	740	21.86	28.29	4.52	192.1	0.24	6.8
44	760	24.37	35.86	5.92	188.8	0.58	8.3
45	760	24.41	34.10	6.65	187.8	0.48	10.1
46	750	30.19	33.98	10.05	187.3	0.34	10.3
47	750	31.14	35.21	9.52	188.3	0.74	10.6
48	650	26.54	44.25	7.63	183.3	0.54	11.0
49	550	34.51	50.80	13.95	179.3	0.80	12.5
50	450	38.28	59.86	13.45	176.6	1.08	13.7

Appendix III (cont.)

	h	i	j	k	l	m	n
Needs Oar Point							
1	25	0.00	1.24	5.19	7.23	33.35	52.99
2	1	66.08	5.06	23.19	3.15	1.60	0.92
3	1	61.30	10.68	18.56	3.10	3.04	3.32
4	1	38.18	8.51	15.41	6.25	13.91	17.74
5	18	6.09	2.80	5.46	8.34	27.75	49.56
6	13	0.00	3.08	25.53	8.82	24.99	37.58
7	1	57.76	6.76	17.06	2.58	6.21	9.63
8	1	44.42	10.72	37.98	4.66	1.69	0.53
9	14	0.00	1.97	11.93	5.29	34.54	46.27
10	1	66.54	7.84	17.67	2.20	2.63	3.12
Fawley							
11	38	0.00	0.00	1.21	4.02	40.34	54.43
12	140	0.00	3.30	11.16	10.86	47.99	26.69
13	61	0.00	10.52	10.87	1.14	28.22	49.25
14	25	0.00	0.04	6.82	3.24	36.64	53.26
15	25	0.00	2.44	11.99	10.32	36.62	38.63
16	27	0.00	1.39	15.37	6.58	38.52	38.14
17	25	0.00	1.76	14.38	9.98	31.18	42.70
18	24	0.00	3.95	10.10	10.90	51.72	23.33
19	28	0.00	7.57	18.30	2.80	30.21	41.12
20	40	0.00	2.01	7.51	9.96	41.92	38.60

Appendix III (cont.)

	h	i	j	k	l	m	n
Bursledon							
21	60	0.00	5.72	22.01	5.58	47.43	19.26
22	62	0.00	9.00	19.27	9.05	43.77	18.91
23	57	0.00	2.32	17.84	11.09	32.91	35.84
24	58	0.00	3.89	14.82	3.49	55.27	22.58
25	59	0.00	1.88	15.30	2.49	36.35	43.98
26	62	0.00	4.37	11.90	11.55	41.78	30.40
27	60	0.00	6.47	14.18	7.55	29.53	42.27
28	60	0.00	1.16	18.63	5.71	32.15	42.35
29	58	0.00	2.28	13.96	8.70	32.00	43.06
30	60	0.00	1.23	13.28	11.62	47.54	26.33
North Binness Island							
31	38	0.00	7.39	10.97	1.74	25.16	54.74
32	40	0.00	0.04	5.30	2.85	30.23	61.58
33	36	0.00	4.36	0.74	2.01	48.15	44.74
34	38	0.00	4.40	6.35	1.43	27.91	59.91
35	40	0.00	4.40	8.40	4.93	40.89	41.38
36	36	0.00	1.16	7.28	3.68	33.93	53.93
37	37	0.00	0.98	5.91	2.67	47.71	42.73
38	40	0.00	2.34	1.34	4.39	31.11	60.82
39	36	0.00	0.67	9.11	6.94	22.10	61.18
40	39	0.00	0.51	9.59	2.07	30.11	57.72

Appendix III (cont.)

	h	i	j	k	l	m	n
East Head							
41	15	0.13	3.23	34.92	26.40	31.56	3.76
42	17	0.00	3.01	28.73	28.56	35.68	4.02
43	19	0.59	3.39	29.42	26.73	35.13	4.74
44	20	0.00	5.50	25.52	27.91	33.33	8.04
45	18	0.21	3.97	40.82	24.89	25.26	4.85
46	20	0.00	3.20	33.89	21.61	33.24	8.06
47	25	0.00	3.44	29.65	25.12	30.72	11.07
48	30	0.00	5.31	37.38	25.00	24.79	7.52
49	68	0.00	4.93	19.85	9.86	36.12	29.24
50	65	0.00	6.39	23.22	16.31	33.10	20.98

Appendix IV. Percentage cover values for associated species in the 50 Hampshire basin quadrats

The figures in the left hand column refer to the numbers of the quadrats: 1 - 10 Needs Oar Point; 11 - 20 Fawley; 21 - 30 Bursledon; 31 - 40 North Binness Island; 41 - 50 East Head.

The letters at the top of the columns refer to the individual species. The full scientific names are given on p. 79; the generic names are as follows: a = Spartina; b = Limonium; c = Triglochin; d = Puccinellia; e = Salicornia; f = Festuca; g = Agropyron; h = Armeria; i = Glaux; j = Plantago; k = Spergularia; l = Juncus; m = Cochlearia; n = Aster.

	a	b	c	d	e	f	g	h	i	j	k	l	m	n
1	15.3	18.4	12.9	41.0	16.4	0	0	0	0	0	0	0	0	0
2	0	0	0	11.5	0	43.9	15.3	0	0	0	0	0	0	0
3	0	0	0	22.8	0	16.4	0	29.3	12.9	0	0	0	0	0
4	0	0	0	50.2	0	0	0	0	0	0	0	0	0	0
5	12.9	0	0	14.2	36.9	0	0	0	0	0	0	0	0	0
6	18.4	11.5	0	48.4	18.4	0	0	0	0	5.7	0	0	0	0
7	0	0	0	45.0	26.6	0	0	0	0	5.7	0	0	0	0
8	0	0	0	17.5	0	0	0	39.8	10.0	0	0	0	0	0
9	67.2	0	0	0	22.8	0	0	0	0	0	0	0	0	0
10	0	0	0	50.8	26.6	0	0	0	0	8.1	0	0	0	0
11	43.9	0	0	0	0	0	0	0	0	0	0	0	0	0
12	49.6	5.7	0	0	12.9	0	0	0	0	0	0	0	0	0
13	46.1	8.1	8.1	0	0	0	0	0	0	0	0	0	0	0
14	43.9	20.3	0	18.4	14.2	0	0	0	0	8.1	5.7	0	0	0
15	11.5	43.9	0	26.6	10.0	0	0	0	0	5.7	8.1	0	0	0

Appendix IV. (cont.)

	a	b	c	d	e	f	g	h	i	j	k	l	m	n
16	42.1	0	0	0	0	0	0	0	0	8.1	0	33.2	0	0
17	5.7	17.5	0	22.8	0	0	0	0	0	30.0	0	0	14.2	0
18	0	10.0	0	33.2	0	0	0	0	0	16.4	0	0	12.9	0
19	33.2	12.9	0	36.9	0	0	0	0	0	0	0	0	0	0
20	45.0	10.0	0	32.6	0	0	0	0	0	0	0	0	0	0
21	45.0	10.0	12.9	33.2	0	0	0	0	0	0	0	0	0	0
22	45.0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	45.0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	42.7	0	18.4	11.5	0	0	0	0	0	0	0	0	0	0
25	45.0	0	10.0	10.0	0	0	0	0	0	0	0	0	0	0
26	40.4	0	0	11.5	0	0	0	0	0	0	0	0	0	0
27	55.6	0	0	11.5	0	0	0	0	0	0	0	26.6	0	0
28	60.0	0	0	12.9	0	0	0	0	0	0	0	0	0	0
29	42.1	0	0	0	0	0	0	0	0	0	0	0	0	0
30	42.1	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	18.4	0	18.4	0	0	0	27.3	0	50.8	0	0	0	10.0
32	0	16.4	0	22.8	0	0	0	26.6	0	47.9	0	0	0	11.5
33	0	8.1	0	42.1	0	0	0	0	0	22.8	0	0	0	12.9
34	0	11.5	0	45.0	0	0	0	23.6	0	25.1	0	0	0	14.2
35	0	11.5	0	23.6	0	0	0	33.2	0	22.8	0	0	0	11.5
36	0	31.9	0	12.9	0	0	0	43.9	0	39.2	0	0	0	0
37	0	17.5	0	50.8	0	0	0	0	0	12.9	0	0	0	0
38	0	35.7	0	33.8	0	0	0	24.4	0	25.1	0	0	0	0

Appendix IV (cont.)

	a	b	c	d	e	f	g	h	i	j	k	l	m	n
39	0	26.6	0	30.0	0	0	0	27.3	0	22.8	0	0	0	0
40	0	16.4	0	33.2	0	0	0	30.0	0	18.4	0	0	0	0
41	0	0	0	58.7	0	0	0	0	0	0	0	0	0	0
42	0	0	0	56.8	0	0	0	0	0	0	0	0	0	0
43	0	0	0	50.8	8.1	0	0	0	0	0	0	0	0	0
44	0	0	0	42.1	8.1	0	0	0	0	0	0	0	0	0
45	0	0	0	39.2	0	0	0	0	0	0	0	0	0	0
46	0	0	0	45.0	8.1	0	0	0	0	0	0	0	0	0
47	0	15.3	0	43.9	8.1	0	0	0	0	0	0	0	0	0
48	0	71.6	0	63.4	18.4	0	0	0	0	0	17.5	0	0	0
49	0	39.8	0	28.7	11.5	0	0	0	0	0	0	0	0	0
50	16.4	8.1	0	44.4	8.1	0	0	0	0	0	0	0	0	0

Appendices V and VI

The quadrat numbers in these appendices refer to the following localities:

1	-	12	Blakeney Point, Norfolk
13	-	22	Gibraltar Point, Lincolnshire
23	-	27	Hilbre Island, Cheshire
28	-	81	Blakeney Point, Norfolk
82	-	108	Park Gate, Cheshire
109	-	155	Blakeney Point, Norfolk
156	-	160	Hilbre Island, Cheshire
161	-	170	Gibraltar Point, Lincolnshire
171	-	185	Shellness, Isle of Sheppey, Kent
186	-	200	Rye, Sussex
201	-	210	Needs Oar Point, Hampshire
211	-	220	Fawley, Hampshire
221	-	230	Bursledon, Hampshire
231	-	240	North Binness Island, Hampshire
241	-	250	East Head, Sussex

Appendix V. Values of morphological measurements made on 250 quadrats of extensive survey.

a = leaf length (mm); b = leaf width (mm); c = length of prostrate rooting portion (cm); d = length of prostrate non-rooting portion (cm); e = % cover; f = number of nodes; g = weight of above ground portion (g).

	a	b	c	d	e	f	g
1	15.5	5.8	28530	12086	60	70200	800
2	15.4	5.7	36741	16243	71	87314	890
3	15.6	5.8	27493	10964	62	68992	780
4	14.2	3.6	36592	1300	100	30069	1211
5	15.2	3.8	45988	977	98	45135	1327
6	14.0	3.5	39212	1008	100	4008	1098
7	4.0	2.0	51607	593	74	153702	715
8	4.1	2.0	50018	629	83	165210	912
9	3.8	1.9	52111	607	75	152613	840
10	3.5	2.0	48713	1320	62	49236	901
11	3.8	2.5	39111	1098	80	48313	874
12	3.0	1.6	41263	2116	59	56100	890
13	10.8	2.8	2488	6049	43	12665	522
14	11.0	2.7	3650	7133	49	15163	503
15	10.9	2.7	2493	6123	51	12612	528
16	11.4	2.8	2965	6246	62	13100	592
17	10.8	2.7	3217	6918	45	17210	601
18	10.8	2.7	3002	6521	55	16230	584
19	10.6	2.8	2981	6266	58	12713	523
20	11.0	2.7	3111	6611	42	13127	520

Appendix V. (cont.)

	a	b	c	d	e	f	g
21	11.1	2.8	2681	6123	47	12641	560
22	10.8	2.8	2420	6000	51	11723	522
23	13.3	4.2	3017	1023	42	7013	500
24	12.6	4.3	5179	2000	52	9317	693
25	10.9	3.6	4230	1614	45	8463	327
26	14.0	4.7	2684	983	36	6159	222
27	13.7	4.6	3612	1111	44	7243	512
28	15.5	5.8	11012	6761	80	33652	982
29	16.2	6.0	1283	4160	38	12745	574
30	15.4	5.7	4242	841	39	16111	596
31	15.8	5.9	656	1827	17	3652	109
32	15.2	5.6	27445	11987	65	70216	870
33	16.0	5.9	170	1518	26	2311	234
34	15.5	5.8	465	1659	27	3314	352
35	15.6	5.9	4200	811	39	15691	600
36	15.8	6.0	1384	4060	38	12859	570
37	16.0	6.1	178	1562	26	2401	252
38	15.4	5.7	1280	4262	38	12759	582
39	15.6	5.9	27413	12085	65	70333	874
40	15.5	5.8	1226	4316	39	13714	594
41	16.1	6.0	42113	819	36	16610	569
42	15.7	5.9	4261	850	40	16161	589
43	15.5	5.8	26591	6412	62	71324	900
44	15.4	5.7	5937	612	36	13143	511

Appendix V (cont.)

	a	b	c	d	e	f	g
45	13.5	2.4	11216	9067	80	10162	700
46	13.5	2.5	8317	7423	50	7139	600
47	13.5	2.4	6216	6135	30	6149	257
48	13.5	2.5	10317	8416	75	11412	984
49	14.0	2.6	5367	4218	25	6132	198
50	13.0	2.3	8493	7615	35	10612	289
51	15.0	2.7	11613	9416	70	16143	981
52	13.5	2.5	15719	11111	80	17182	742
53	13.5	2.4	5381	4963	24	8173	182
54	13.5	2.5	10110	11162	35	18163	239
55	28.8	3.6	537	301	10	1400	99
56	19.9	2.5	1062	513	18	2793	198
57	23.1	2.9	985	549	17	3017	211
58	23.8	3.0	1362	584	25	5139	314
59	31.9	4.0	1674	961	30	7814	584
60	28.8	3.6	996	501	18	3612	235
61	20.3	2.9	1562	1051	28	6919	412
62	16.1	2.3	1816	1061	30	7148	501
63	35.1	5.0	974	459	18	3162	237
64	31.2	3.9	853	569	16	2710	124
65	23.2	2.9	259	109	5	989	85
66	21.6	2.7	1923	1419	30	8142	612
67	27.2	3.4	1740	1184	28	7193	514
68	25.6	3.2	1610	961	15	2612	128

Appendix V (cont.)

	a	b	c	d	e	f	g
69	28.7	4.1	842	421	8	1007	94
70	27.3	3.9	982	549	18	3612	235
71	26.7	3.8	1006	709	20	3814	264
72	28.9	3.6	1263	749	25	5612	318
73	28.0	3.5	964	459	19	3264	246
74	22.3	2.8	1873	140	29	8123	609
75	14.2	3.6	36584	1306	100	30162	1216
76	12.8	3.2	38617	1416	96	31216	1340
77	13.7	3.4	34617	1214	100	30061	1294
78	14.5	3.6	51463	2006	100	50162	2100
79	13.9	3.5	40019	1614	84	39816	1567
80	12.9	3.2	39167	1519	100	32614	1423
81	14.1	3.5	50001	1990	85	49918	1621
82	10.2	3.2	36585	1316	100	30262	1212
83	11.4	3.7	35142	1946	98	50123	1561
84	10.0	3.3	28167	1634	86	46139	1434
85	10.0	3.1	50165	10162	100	60123	1748
86	11.0	3.5	49312	17423	95	65124	1823
87	11.0	3.4	28416	18294	100	46150	1436
88	10.2	3.2	41763	12430	100	53601	1564
89	10.1	3.2	23914	16290	100	39406	1324
90	10.2	3.2	8198	10123	94	18162	681

Appendix V (cont.)

	a	b	c	d	e	f	g
91	10.3	3.3	28416	19245	85	47213	1498
92	10.3	3.3	8999	9120	100	17203	684
93	10.4	3.3	18998	18740	100	36159	1216
94	10.6	3.4	26142	16243	95	42604	1492
95	10.2	3.2	43864	15921	100	58162	1649
96	10.1	3.2	24669	10162	95	34201	1212
97	10.2	3.2	617204	27140	90	88193	2063
98	10.6	3.3	41620	16293	90	57602	1642
99	11.2	3.8	51742	18240	100	68120	1834
100	9.9	3.1	36592	15102	100	51203	1521
101	9.9	3.0	35142	14312	100	49620	1310
102	9.8	3.1	36174	13261	100	49203	1213
103	10.2	3.2	40162	17294	95	57209	1625
104	10.2	3.2	29968	16402	85	45163	1200
105	10.3	3.2	61610	32045	85	93104	2614
106	10.1	3.2	38124	17421	95	55162	1600
107	10.5	3.3	39214	16120	100	55621	1549
108	10.3	3.2	8894	1318	100	10314	500
109	15.5	5.8	468	1649	27	3299	704
110	14.9	5.0	11031	6760	81	33656	2317
111	15.4	5.7	27465	11992	65	70237	3920
112	16.0	5.9	4224	873	40	6813	1611
113	15.5	5.8	14523	5761	83	38742	2602

Appendix V (cont.)

	a	b	c	d	e	f	g
114	4.0	2.0	23664	359	85	67439	1216
115	3.8	1.9	32784	8830	85	172493	2153
116	3.7	1.9	16159	5742	75	47298	2316
117	3.5	1.7	22126	20032	80	92439	3147
118	4.1	2.0	27893	9567	58	83142	1990
119	4.2	2.1	34921	843	80	70198	2106
120	4.3	2.1	26174	931	85	54932	2416
121	4.0	2.0	36192	1046	74	74109	1982
122	4.0	2.0	16184	715	83	34928	2103
123	4.0	2.0	39284	10231	90	80984	2613
124	3.9	2.0	29841	1098	86	61214	2463
125	3.8	1.9	32121	2347	85	69280	2819
126	3.9	1.9	42614	999	80	86193	2314
127	4.0	2.0	28174	1067	82	60019	2618
128	3.7	1.8	29316	846	84	60008	2814
129	4.0	2.0	22139	1000	87	64810	2934
130	4.1	2.0	32149	4219	85	74198	2109
131	4.2	2.1	31621	20497	90	182439	3613
132	4.0	2.0	26284	399	91	59614	2865
133	4.0	2.0	29316	2210	85	74108	2104
134	4.0	2.0	28412	1010	85	68129	2367
135	3.9	2.0	31624	874	88	66193	2984
136	12.8	3.2	38524	1429	98	32161	1338
137	13.1	3.4	51263	1981	84	49823	1599

Appendix V (cont.)

	a	b	c	d	e	f	g
138	14.2	3.6	36592	1400	98	31016	1198
139	13.7	3.4	34651	1189	100	30083	1300
140	14.5	3.6	54136	2132	98	51923	2091
141	14.2	3.6	51320	2613	100	58132	1987
142	15.3	3.8	56126	2819	100	56241	1846
143	14.6	3.6	48132	1098	98	3998	1324
144	13.9	3.5	36914	1624	95	2974	1189
145	14.1	3.5	54921	2179	100	5134	1742
146	13.5	2.4	10319	8464	75	11692	974
147	13.5	2.5	8371	7432	50	7193	599
148	13.5	2.5	10109	11612	37	18613	241
149	13.8	2.5	3567	2418	25	2632	168
150	13.8	2.6	46193	37214	95	78193	841
151	13.4	2.4	8643	7519	48	12161	196
152	13.5	2.5	15791	11124	80	17212	735
153	13.5	2.5	8463	7532	51	7238	601
154	13.5	2.6	5448	4989	46	8123	584
155	13.5	2.4	3765	2314	28	2326	186
156	13.3	4.2	3071	1203	44	7130	488
157	13.5	4.5	4321	1164	46	8643	372
158	12.9	4.3	3162	1019	45	7642	498
159	13.4	4.5	5791	1986	51	9137	702
160	13.3	4.4	2846	893	39	6591	230

Appendix V (cont.)

	a	b	c	d	e	f	g
161	10.8	2.8	3124	6819	56	16327	569
162	11.5	2.9	2998	6301	63	13086	601
163	11.5	2.9	3112	6817	56	17310	587
164	10.8	2.8	2956	6624	63	13627	689
165	9.8	2.4	2483	6213	48	13712	531
166	10.1	2.6	3123	6591	43	13172	518
167	10.3	2.6	2695	6426	62	14201	601
168	11.2	2.9	2848	6490	45	16225	520
169	10.8	2.8	2418	6109	50	11803	520
170	10.8	2.8	2431	6213	50	12621	518
171	11.4	3.8	1078	11623	100	12006	2019
172	10.6	3.5	674	6132	98	6984	1079
173	12.3	4.1	1793	24617	100	27192	4123
174	11.6	3.8	796	8124	88	8061	1169
175	9.8	3.2	684	7932	90	7998	1659
176	10.4	3.5	1007	11065	95	9982	1824
177	11.5	3.8	655	6111	85	6008	1101
178	9.8	3.3	8592	9923	100	16524	3099
179	12.6	4.2	878	8492	100	9134	1856
180	9.7	3.2	741	7819	100	8019	1654
181	10.2	3.4	1009	15672	98	12196	2061
182	10.2	3.4	1326	8193	100	10006	1924
183	11.3	3.7	512	14612	100	12617	2100

Appendix V (cont.)

	a	b	c	d	e	f	g
184	12.4	4.1	618	11610	100	12123	1998
185	10.3	3.4	219	1017	95	961	175
186	8.4	2.8	26341	368	85	46984	1075
187	11.3	2.8	16260	5849	75	37786	2287
188	9.4	3.4	32854	8914	85	110119	2681
189	10.2	3.4	28534	7842	90	68192	1998
190	8.6	2.8	33962	8827	89	108642	2719
191	9.4	2.4	26984	7843	75	99164	2984
192	10.3	3.4	36841	9214	84	128931	6421
193	11.1	2.5	29642	5318	80	97812	3127
194	9.8	2.4	112630	8674	100	331009	7918
195	10.7	2.9	39841	7841	90	154832	2814
196	9.5	2.3	81723	6937	100	240198	6842
197	9.5	3.4	33841	8412	90	12816	2937
198	9.3	3.3	29356	6193	85	90172	3059
199	10.1	3.3	40016	7814	75	156120	2841
200	10.8	2.7	28137	9012	80	128172	2213
201	20.8	6.5	6382	7063	48	21968	1384
202	13.1	4.3	463	1649	27	3296	704
203	12.8	4.2	148	1508	26	2321	452
204	14.0	4.0	27443	11983	65	70226	2912
205	13.0	4.2	656	1823	18	3641	297
206	19.6	6.3	3274	2375	52	12118	773
207	13.4	4.4	4242	837	39	16831	1611

Appendix V (cont.)

	a	b	c	d	e	f	g
208	13.1	4.3	1283	4166	38	12738	1238
209	20.8	6.5	4058	1457	17	16488	1426
210	13.0	4.2	11012	6761	80	33641	2317
211	14.6	3.5	8222	8220	54	30803	2680
212	9.9	2.3	301	410	6	1225	83
213	14.6	3.5	2488	6049	43	12665	1700
214	14.7	3.5	1524	33498	48	47440	4082
215	14.5	3.5	2769	12818	48	23084	1822
216	14.6	3.5	987	7564	50	7921	1053
217	9.9	2.3	971	10110	14	13814	4010
218	9.9	2.3	2324	3304	25	7308	1252
219	11.6	2.9	2208	17898	45	27664	3420
220	9.9	2.3	5886	8220	46	19212	1248
221	20.5	6.2	3408	7865	63	11220	2010
222	19.8	6.3	12611	26663	50	41518	6075
223	18.7	6.1	18053	15756	55	30771	2543
224	21.0	6.9	2561	31288	46	26672	5284
225	16.5	5.2	9610	16253	50	17963	1878
226	15.4	5.0	2053	7011	58	13153	1827
227	12.6	4.0	166	463	10	855	91
228	17.4	5.2	3691	14962	25	14768	1322
229	19.2	6.0	4930	10322	55	14873	2418
230	20.5	6.2	11363	13384	55	24256	2752

Appendix V (cont.)

	a	b	c	d	e	f	g
231	9.7	2.5	180	514	5	1266	138
232	8.4	2.1	232	1160	15	3218	373
233	11.5	2.9	1882	13728	35	25442	3420
234	8.7	2.2	50	1010	20	1688	165
235	9.2	2.3	14	131	8	326	24
236	8.5	2.1	43	228	3	911	71
237	9.9	2.5	2719	5036	40	11160	1050
238	12.4	3.1	640	4345	21	9223	989
239	9.6	2.4	374	9559	25	16260	1338
240	8.7	2.2	542	3270	24	5283	570
241	12.0	3.5	23614	354	85	46518	1020
242	12.0	3.5	32762	8842	85	112783	2691
243	12.1	3.5	16150	5749	75	37752	2370
244	12.2	3.5	22020	20012	80	72750	3185
245	12.2	3.5	27854	9502	58	63040	2051
246	12.3	3.6	3577	962	50	15626	306
247	12.4	3.6	4710	2000	58	20041	620
248	12.5	3.7	4073	4440	90	16126	700
249	12.7	3.7	4205	15311	48	30501	1175
250	12.9	3.8	4563	9641	45	22674	703

Appendix VI. Values of habitat measurements made on 250 quadrats of extensive survey.

a = % pebble; b = % sand; c = % clay; d = compressibility (cm)

	a	b	c	d
1	38.18	1.20	60.62	4.0
2	29.30	4.31	66.57	3.9
3	40.03	1.01	58.96	4.1
4	0	3.26	96.74	9.8
5	0.10	2.36	97.54	11.2
6	0	2.84	97.16	10.0
7	0	79.32	20.68	5.4
8	0	81.46	18.54	5.6
9	0	86.35	13.65	4.9
10	0	76.53	23.47	5.7
11	0	83.20	16.80	5.0
12	0	80.02	19.89	5.1
13	0	16.20	83.80	11.2
14	0	18.53	81.47	11.3
15	0	10.42	89.58	8.1
16	0	8.73	91.27	15.6
17	0	18.21	81.79	12.9
18	0	9.43	90.57	13.2
19	0	7.28	92.72	10.0
20	0	11.40	88.60	9.9
21	0	12.30	87.70	11.6

Appendix VI (cont.)

	a	b	c	d
22	0	18.51	81.49	10.5
23	0	21.20	78.80	3.0
24	0	18.35	81.65	3.0
25	0	12.67	87.33	3.0
26	0	15.93	84.07	3.0
27	0	18.64	81.36	3.0
28	66.54	24.13	9.33	1.8
29	44.42	48.12	7.46	3.7
30	57.76	24.51	17.73	3.3
31	6.09	8.21	85.70	6.1
32	38.18	23.91	37.91	4.0
33	61.30	29.31	9.39	1.9
34	66.08	24.14	5.78	0.9
35	54.32	23.62	22.06	3.3
36	48.93	44.33	6.74	3.9
37	62.46	29.31	8.23	0.9
38	43.92	47.22	8.86	3.8
39	24.07	20.11	55.82	5.4
40	40.99	26.66	32.35	3.9
41	51.30	23.23	25.47	3.4
42	50.00	23.60	26.40	3.2
43	48.32	50.11	1.57	3.9
44	57.86	28.20	13.94	3.1
45	0	79.32	20.68	5.3

Appendix VI (cont.)

	a	b	c	d
46	0	81.46	18.54	5.6
47	0	80.00	20.00	5.1
48	0	83.20	16.80	5.0
49	0	76.50	23.50	5.7
50	0	77.61	22.39	5.4
51	0	78.52	21.48	5.9
52	0	79.36	20.64	4.8
53	0	80.17	19.83	6.9
54	0	82.01	17.99	5.4
55	6.13	8.34	85.53	4.1
56	0	9.21	90.79	8.7
57	0	15.36	84.64	6.5
58	0	8.92	91.08	7.4
59	14.30	7.41	78.29	3.6
60	0	2.36	97.64	8.2
61	0	18.47	81.53	9.1
62	1.00	9.86	89.14	5.2
63	0	10.11	89.89	3.6
64	0	2.10	97.90	7.9
65	0	15.21	84.79	8.4
66	0	8.67	91.33	7.9
67	0	9.34	90.66	7.8
68	4.74	5.67	89.59	5.8
69	8.35	16.52	75.13	3.2

Appendix VI (cont.)

	a	b	c	d
70	0	8.73	91.27	6.5
71	0	6.54	93.46	8.4
72	0	10.13	89.87	7.8
73	0	15.34	84.66	6.5
74	0	18.93	81.07	8.2
75	0	4.87	95.13	8.9
76	0	3.25	96.75	9.3
77	0	2.93	97.07	10.4
78	0	6.54	93.46	9.8
79	0	7.48	92.52	8.7
80	0	8.23	91.77	10.5
81	0	5.14	94.86	9.2
82	0	1.20	98.80	8.2
83	0	4.35	95.65	12.3
84	0	2.98	97.02	7.9
85	0	3.47	96.53	9.4
86	0	4.98	95.02	11.3
87	0	5.00	95.00	10.8
88	0	1.29	98.71	11.9
89	0	3.47	96.53	12.0
90	0	2.85	97.15	11.9
91	0	4.10	95.90	9.2
92	0	0.98	99.02	8.3
93	0	5.43	94.57	9.4

Appendix VI (cont.)

	a	b	c	d
94	0	3.47	96.53	10.1
95	0	4.01	95.99	10.3
96	0	3.27	96.73	10.5
97	0	4.82	95.18	11.9
98	0	1.98	98.02	12.1
99	0	2.32	97.68	11.4
100	0	1.85	98.15	7.3
101	0	1.76	98.24	8.9
102	0	5.00	95.00	8.0
103	0	4.86	95.14	8.0
104	0	3.12	96.88	12.0
105	0	2.19	97.81	11.0
106	0	1.08	98.92	11.8
107	0	2.01	97.99	9.3
108	0	1.05	98.95	8.9
109	66.18	6.00	27.82	0.9
110	65.34	5.98	28.68	1.0
111	39.99	18.24	41.77	3.9
112	58.47	1.67	39.86	2.5
113	71.24	9.84	18.92	0.8
114	0	70.13	29.87	4.1
115	0	81.92	18.08	5.2
116	0	69.99	30.01	6.1
117	0	81.24	18.76	4.0

Appendix VI (cont.)

	a	b	c	d
118	0	2.34	27.66	5.2
119	0	75.62	24.38	5.1
120	0	69.84	30.16	6.2
121	0	74.93	25.07	5.3
122	0	81.22	18.78	4.2
123	0	76.42	23.58	5.1
124	0	78.34	21.66	5.0
125	0	81.92	18.08	4.1
126	0	75.24	24.76	5.3
127	0	82.43	17.57	4.0
128	0	64.23	35.77	6.4
129	0	68.94	31.06	6.8
130	0	70.00	30.00	5.9
131	0	69.00	31.00	6.3
132	0	64.32	35.68	6.9
133	0	65.39	34.61	6.7
134	0	79.24	20.76	5.0
135	0	72.44	27.56	5.2
136	0	3.25	96.75	9.2
137	0	5.14	94.86	9.3
138	0	4.87	95.13	9.0
139	0	2.93	97.07	10.4
140	0	6.54	93.46	9.9
141	0	3.96	96.04	8.9

Appendix VI (cont.)

	a	b	c	d
142	0	4.63	95.37	9.0
143	0	7.84	92.16	9.3
144	0	2.98	97.02	9.2
145	0	1.99	98.01	8.4
146	0	69.99	30.01	6.0
147	0	81.22	18.78	4.1
148	0	81.92	18.08	4.2
149	0	68.94	31.06	6.7
150	0	69.84	30.16	6.3
151	0	70.00	30.00	5.9
152	0	79.24	20.76	5.1
153	0	81.24	18.76	4.1
154	0	72.44	27.56	5.2
155	0	76.42	23.58	5.0
156	0	18.65	81.35	3.0
157	0	19.84	80.16	3.2
158	0	20.34	79.66	3.1
159	0	15.99	84.01	3.5
160	0	18.21	81.79	4.2
161	0	10.42	89.58	8.0
162	0	18.21	81.79	12.8
163	0	8.17	91.83	15.2
164	0	9.34	90.66	17.4
165	0	10.65	89.35	8.6

Appendix VI (cont.)

	a	b	c	d
166	0	11.59	88.41	14.3
167	0	8.36	91.64	15.6
168	0	15.46	84.54	8.1
169	0	16.85	83.15	7.9
170	0	10.11	89.89	8.2
171	30.56	2.36	67.08	3.5
172	28.93	8.24	62.83	6.2
173	50.24	9.63	40.13	2.8
174	28.67	8.27	63.06	6.2
175	49.23	1.08	49.69	4.1
176	29.98	8.21	61.81	5.9
177	30.24	6.59	63.17	5.4
178	41.66	7.24	51.10	4.0
179	42.85	8.37	48.78	3.6
180	35.55	7.84	56.61	5.6
181	28.74	9.91	61.35	6.0
182	36.59	10.11	53.30	5.3
183	29.98	8.43	61.59	6.1
184	19.99	2.89	77.12	8.5
185	34.26	7.43	58.31	5.2
186	0	30.24	69.76	6.8
187	0	29.83	70.17	7.4
188	0	43.92	56.08	8.5

Appendix VI (cont.)

	a	b	c	d
189	0	40.18	59.82	9.2
190	0	30.19	69.81	9.5
191	0	43.21	56.79	7.8
192	0	31.24	68.76	8.2
193	0	33.65	66.35	8.4
194	0	35.67	64.33	6.5
195	0	37.92	62.08	7.3
196	0	39.84	60.16	7.2
197	0	40.12	59.88	6.0
198	0	38.24	61.76	7.1
199	0	36.12	63.88	8.1
200	0	34.86	65.14	9.2
201	0	13.66	86.34	7.4
202	66.08	31.40	2.52	0.9
203	61.30	32.34	6.36	1.9
204	38.18	30.17	31.65	4.0
205	6.09	16.60	77.31	6.1
206	0	37.43	62.57	8.0
207	57.76	26.40	15.84	3.3

Appendix VI (cont.)

	a	b	c	d
208	44.42	53.36	2.22	3.7
209	0	19.19	80.81	14.5
210	66.54	27.71	5.75	1.8
211	0	5.23	94.77	8.9
212	0	25.32	74.68	16.1
213	0	22.53	77.47	11.2
214	0	10.10	89.90	10.5
215	0	24.75	75.25	11.5
216	0	23.34	76.66	13.4
217	0	26.12	73.88	11.8
218	0	24.95	75.05	12.1
219	0	28.67	71.33	14.9
220	0	19.48	80.52	23.2
221	0	33.31	66.69	10.2
222	0	37.32	62.68	21.1
223	0	31.25	68.75	21.8
224	0	22.20	77.80	16.0
225	0	19.67	80.33	17.7
226	0	27.82	72.18	21.6

Appendix VI (cont.)

	a	b	c	d
227	0	28.20	71.80	27.3
228	0	25.50	74.50	26.4
229	0	24.94	75.06	31.9
230	0	26.13	73.87	31.3
231	0	20.10	79.90	9.9
232	0	8.19	91.81	13.0
233	0	7.11	92.89	13.3
234	0	12.18	87.82	10.2
235	0	17.73	82.27	10.0
236	0	12.12	87.86	10.5
237	0	9.56	90.44	11.7
238	0	8.07	91.93	10.6
239	0	16.72	83.28	11.0
240	0	12.17	87.83	12.4
241	0.13	64.55	35.32	4.6
242	0	60.30	39.70	7.6
243	0.59	59.54	39.87	6.8
244	0	58.63	41.37	8.3
245	0.21	69.68	30.11	10.1
246	0	58.70	41.30	10.3
247	0	58.21	41.79	10.6
248	0	67.69	32.31	11.0
249	0	34.65	65.36	12.5
250	0	45.92	54.08	13.7

Appendix VII. Analytical data

All the computer-tapes and computer type-outs for the Factor, Principal Component and Association Analyses are lodged with the Nature Conservancy, 19 Belgrave Square, London, S.W.1.