The ecology of carex flacca schreb and carex panicea L.

Rieley, John, O.

THE ECOLOGY OF CAREX FLACCA SCHREB. AND CAREX PANICEA L..

A thesis submitted to

the University of Durham

for the degree of

DOCTOR OF PHILOSOPHY

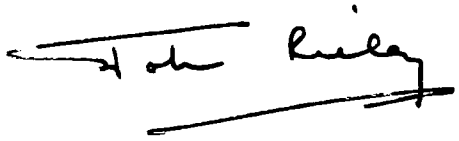
by

JOHN O. RIELEY
B. Sc. Glasgow.
(St. Cuthbert's)

School of Plant Biology,
University College of North Wales,
Bangor.

September 1967.

This thesis, which is entirely the result of my own work, has not been accepted for any degree and is not being submitted concurrently in candidature for any other degree.



CONTENTS.

ACKNOWLEDGEMENTS.

I wish to thank Professor D.H. Valentine for the provision of working facilities in the Botany Department at Durham during the period October 1963 to October 1966; and to my supervisor, Dr. D.J. Bellamy, I express my very great appreciation for his guidance and interest at all times during the course of this investigation.

I take this opportunity to thank also the various members of the technical staff of the botany department for valuable assistance given at different stages of the work, especially Mr. J. Redhead, Mr. R. Stuart and Mr. R. Swinhoe. I am deeply indebted to Miss E.M. Paton for reading and criticising the manuscript and to my wife for her encouragement and forbearance throughout.

Finally, thanks are due to the Natural Environment Research Council for financial support.

ABSTRACT.

The effect of pH, calcium and potassium on the performance of *Carex flacca* and *C. panicea* is investigated using tillers growing in solution culture. Performance is determined by changes in fresh weight, dry weight, leaf length and the uptake of mineral nutrients into the plants. Possible age response is taken into consideration by using tillers of two different initial sizes and seeds, as starting material.

No differential response due to initial age of the plant parts is detected. pH affects the final fresh and dry weights but not the relative concentrations of the elements present in the plant leaves. Above a certain external calcium concentration (about 50 p.p.m.) uptake of calcium by the plants greatly increases. Performance of both species increases with increase in external calcium concentration until the influx concentration is reached, and then it decreases. The germination and potassium variation experiments show that both species are very efficient in removing potassium from the culture solutions and maintaining a high internal concentration of this element. These observations could have important implications in natural plant communities. There is evidence to suggest that *Carex flacca* and *C. panicea* exhibit different responses

to calcium and pH which could lead to different ecological tolerances.

In a parallel study, the role of calcium and potassium in the nutrient dynamics of the two species is investigated over the two-year growing period. With progressive ageing, percentage potassium content decreases; total potassium increases over the first year, but falls sharply after flowering; both percentage and total calcium content increase steadily over the life span, but tend to decrease after fruiting. Analysis of different plant organs reveals considerable variation in the concentrations of calcium and potassium between adjacent parts of the same plant.

There is evidence to suggest that calcium and potassium re-cycle in different ways. Potassium is probably being supplied to the next generation of tillers from the parent plant, either by absorption from the substrate, or by translocation from dying leaves. Calcium, on the other hand, has to be absorbed by the tillers themselves when they have established their own root system.

Part. I.

INTRODUCTION.

The literature on the calcicole-calcifuge problem is extensive and conflicting. The existence of chalk plants and chalk-avoiding plants has been recognised for a long time, (WAHLENBERG, 1814; UNGER, 1836,). Much 'in vivo' and 'in vitro' observation has been carried out, and many reasons have been advanced to explain this division of plant tolerance. TANSLEY & ADAMSON, (1926), and STEELE, (1955), emphasised the varying degrees of fidelity of certain species on either calcareous or acid substrata and they suggested that the problem was different for each species. SALISBURY (1920), and WEBB & HART, (1945), stressed that many factors were involved. Comprehensive reviews have been published at intervals over the last 40 years summarising the different points of view: SALISBURY, (1920); LUNDEGARDH, (1931); WEBB & HART, (1945); HOU & MERKLE, (1950); RORISON, (1956); GRIME, (1960).

Among earlier reasons given for the delimitation of calcicoles (and calcifuges) was the physical nature of the soil on which the plants were growing. Physical features of calcareous soils are :- better drainage; a tendency to dry out in periods of drought; good aeration; high osmotic potential and a high percentage content of calcium carbonate with a correspondingly high pH, (HALL & RUSSELL, 1911; KRAUS, 1911,).

In Calluna vulgaris, a species with mycorrhizal roots, RAYNER, (1913), suggested that successful growth was dependent upon infection of the roots of the heather plant by the fungus at an early stage of development, and also upon subsequent healthy growth of the fungus. In this case the soil preferences shown by the plant were reputed to be dependent on the maintenance of a biological balance between the roots and the constituents of the microflora which surrounded them. Any factor which affected the growth of the fungal symbiont would indirectly influence the development of Calluna.

Current ideas on the calcicole-calcifuge problem revolve round the mineral composition of the respective soils, i.e. soil chemistry is takento be the most important factor, although all other habitat conditions are thought to exert a modifying influence,

(HOPE SIMPSON, 1938). The concept of the importance of chemical factors is not new, although carefully controlled culture experiments, linked with field data, are of more recent origin.

TRUOG, (1918), suggested that it was the calcium ion which was essential for the growth of calcicoles, while LUNDEGARDH, (1924), proposed low hydrogen ion concentration and MEVIUS, (1927), high hydroxyl concentration to be operative. PEARSALL & WRAY, (1927), suggested the ratio Ca/K+Na, as all important, and, thereafter, numerous chemical elements were suggested as being important :- potassium, (FLICHE & GRANDEAU, 1874); nitrogen, (BEAR, 1917, OLSEN, 1923); aluminium, (MIRASOL, 1920, CLYMO, 1962); iron, (MEVIUS, 1927); manganese, (LUNDEGARDH, 1931); phosphorus, (GORE, 1961, JAMES, 1962, HACKETT, 1965). Different workers have put stress on different elements, some of which are said to be required by certain plants, and others, if present in excess, are reputed to be toxic to plant roots leading to death and subsequent exclusion of the species, (HEWITT, 1948a, SPARLING, 1967).

CALCIUM

The two categories calcicole and calcifuge were broadly defined by HOPE SIMPSON, (1938). He regarded "calcicoles as species affecting the more important types of calcareous soils and rare or absent from acid soils, and calcifuges as the reverse". It has generally been accepted that, on the one hand, the over-riding common characteristic of the types of soil colonised by so-called calcicoles is the presence of large amounts of calcium carbonate; on the other hand, calcifuge habitats can be typified by the absence of calcium carbonate. No matter what other factors may be involved they must operate against the large background factor of presence or absence of calcium carbonate, and, consequently, high or low pH.

As a result of transplant and culture experiments, the level of exchangeable calcium in the soil has been shown to be of importance in the distribution of calcicoles by PEARSALL & WRAY, (1927), DE SILVA, (1934), BRADSHAW ET AL, (1958) and JEFFERIES & WILLIS, (1964). However, many authors have found that in the case of calcifuge plants the calcium level in the external medium had little effect upon growth and development of such species; GORE, (1961),

SNAYDON & BRADSHAW, (1961), JAMES, (1962), HACKETT, (1965). Inevitably, some exceptions to this generalisation have been reported. JEFFERIES & WILLIS, (1964), found that in solution culture Juncus squarrosus and Nardus stricta survived only in treatments containing low levels of calcium, and PEARSALL & WRAY, (1927), obtained similar results for Eriophorum angustifolium.

The results of experiments of different workers using different plants and techniques have led to some rather conflicting conclusions. RORISON, (1956 & 1960), SALISBURY, (1920), and PEARSALL & WRAY, (1927), found that there was a crucial phase during seedling development when soil chemical factors had a dominant influence compared with the physical nature of the soil or with competition, and, for the species which they investigated, it was the presence or absence of calcium, as calcium carbonate, with its dual role of calcium source and soil neutraliser which was the controlling factor. HACKETT, (1965), on the other hand, found that widely different supplies of calcium had insignificant effects on the establishment and growth of Deschampsia flexuosa ,a calcifuge*.

From the large volume of literature two general facts emerge :-

1. Calcicoles usually exhibit a strong response to calcium level in culture and transplant experiments, whereas calcifuges as a general rule do not; and chemical analysis of plants has indicated that the difference in response is due to an inability of calcicoles to absorb calcium from low solution concentrations.

2. Plants from acid habitats tend, in most cases, to be indifferent to calcium except in high dosage, when death may result, (PERKINS, 1961).

HYDROGEN ION CONCENTRATION

The effect of calcium carbonate on the hydrogen ion concentration of soils has been suggested as being an important factor controlling plant distribution, (SALISBURY, 1925). Many culture experiments have been carried out to investigate the effect of a variety of pH levels on the growth of different plant species : OLSEN, (1923, 1938a & b, 1953); DAVIDSON, (1927); ARNON ET AL, (1942); FAWZY ET AL, (1954); BOATMAN, (1962); HACKETT, (1964 & 1965).

ARNON, (1942), reported lower calcium and phosphate absorption by lettuce and tomato plants from strongly acid culture solutions, (pH 4 & 5), and also reduced phosphate absorption at pH 9; but he detected no profound effect on the uptake of magnesium, potassium or nitrate. In a later experiment, ARNON, (1942), also reported that between pH 4 and pH 8 fluctuations in pH could be tolerated by these plants, provided a sufficient supply of mineral nutrients was available. Growth (of tomato and lettuce) in acid nutrient solutions was favourably affected by increasing the concentration of calcium (added as calcium nitrate) in the nutrient solution, whereas at pH 6 the growth obtained at low and high calcium concentrations was equally favourable.

It would appear that in certain cases high calcium concentration can compensate for low pH, and vice versa. Similar responses to pH have also been reported by HACKETT, (1965), and JAMES, (1962). However, OLSEN, (1938b), using Deschampsia flexuosa, a calcifuge, (the same species was used by HACKETT) observed that although a high calcium concentration was not injurious to this species it was a true "acid soil plant" in the sense that it required a rather strong acid reaction in the culture medium in order to develop normally, and did not survive at all well in neutral or alkaline solutions.

It is now more fashionable to consider the effect of pH on the availability of certain essential elements rather than the physico-chemical effect of pH alone. It is generally considered that decrease in the pH of a soil decreases the solubility of iron to the point of deficiency (TRUOG, 1947), and, in fact, it has been shown that the iron content of plants has been increased by liming soil, (HOFFER & TROST, 1923; BENDER, 1941). The differential absorption of potassium and phosphorus at different pH levels has been studied by DAVIDSON, (1927), and the effect of pH on aluminium solubility by OLSEN, (1923). In work described by HOU & MERKLE, (1950), no effect of pH on aluminium uptake by plants could be detected, and SHEAR, (1938), found no increase in the aluminium content of plants as soil pH decreased.

ELEMENTS OTHER THAN CALCIUM

As stated above, deficiencies of elements necessary for normal growth, and the presence of others reputed to be toxic to plants have also been sited as factors controlling the distribution of calcicoles and calcifuges.

Iron

Iron chlorosis is a well-known example of the former. This has been investigated extensively by GRIME, (1960), but there is considerable debate concenrning the exact mechanism involved, (HEWITT, 1948b; BROWN & HOLMES, 1956; GAUCH, 1957).

Phosphorus

More recently the lack of available phosphorus has been taken to be an important factor in the failure of the establishment of calcicole species. BILLINGS, (1950), has described calcifuge vegetation, which on acid soils in North America is adapted to conditions of low available phosphorus which is a limiting factor in the success of other local species; BEADLE, (1954), has correlated the ecology of certain Eucalyptus species with their tolerance of low soil phosphate; and RORISON, (1956), has related

the failure of seedlings of the calcicole Scabiosa columbaria to establish themselves on acid soils to phosphate deficiency resulting from the external fixation of phosphate by aluminium.

Aluminium

Aluminium itself has come to be accepted as an element which may be important in the delimitation of these two categories of plants, (HOFFER & TROST, 1923; CLYMO, 1962; HACKETT, 1964 & 1965; SPARLING, 1967,). HARTWELL & PEMBER, (1918), suggested that in very acid soils, certain quantities of "active aluminium" were present which were held to be toxic to calcicolous plants, but MATSON & HESTER, (1933), have cautioned against simplification of the problem in this way and have proposed that the relationship of "the effect of soluble aluminium to plants is further complicated by the solubility and toxicity of manganese". More recent work on this aspect has been published by CLYMO, (1962), who carried out culture experiments with Carex demissa, a calcifuge, and C. lepidocarpa, a calcicole, to study the effects of varying levels of aluminium in the culture medium. His experiments showed that aluminium was toxic to C. lepidocarpa, but that C. demissa

was tolerant of fairly high levels. His experiments also indicated that C. lepidocarpa required a high calcium concentration for best growth. SPARLING, (1967), showed that Schoenus nigricans was capable of growing equally well in low and high calcium conditions but that it was extremely sensitive to aluminium ions, a concentration of 0.55 mg. Al/litre causing a 50% reduction in root growth.

Manganese

Various workers have reported that the percentage content of manganese in plants grown on calcareous or limed soils was less, compared to that present in plants grown on acid soil : MANN, 1930; McHARGUE ET AL, 1932; FRIED & PEECH, 1946; HALE & HEINTZE, 1946; HEINTZE, 1946; FUJIMOJO, 1948; and HOU & MERKLE, 1950, by analysis of plant material, determined that the percentage manganese in plants increased as soil pH decreased. The indications are that plants which grow on acid substrates are adapted to tolerate the higher concentrations of manganese available to them, but calcicole plants, which normally are not exposed to large amounts of manganese, cannot survive in such soils.

AIM OF THE RESEARCH AND CHOICE OF SPECIES

It would appear from this brief survey of the literature on the calcicole-calcifuge problem that, with regard to the possible explanations put forward by various authors, there is much contradiction and still much confusion. Different workers have used different species and methods of study, and have put more emphasis on one factor than on another. Some of this confusion may be due to the fact that culture experiments in the laboratory have rarely been correlated with field experiments or chemical analysis of field material to determine the behaviour of plants under natural conditions.

Recent ideas on this subject have tended to move away from the viewpoint, that calcium is the major factor delimiting calcicole and calcifuge species and towards the concept of differential responses to one or more of the other elements mentioned above. There is, however, still the fact that calcicoles grow in neutral to alkaline soils with high pH and high calcium content, while calcifuges, generally, are intolerant of such conditions, and are restricted to acid calcium deficient soils with a low pH. No matter how many explanations are put forward to explain the effects of other factors or chemical elements, the fact that, on the one hand, we have habitats deficient of calcium, and, on the

other, ones with excess, with a reasonable sharp ecological boundary between the two suggests that calcium itself must exert a very large influence, directly or indirectly, on the delimitation of these two categories. It was in an attempt to gather the relative data and to link these two essential aspects of the problem, the laboratory and the field, that this investigation to study the 'calcium effect' was begun.

The purpose of the culture experiments was to test the 'tolerance' of a number of species to varying calcium concentrations and pH levels. In order to control the ionic concentrations and pH of the culture media within narrow limits, these experiments were carried out in solution culture. It was intended to choose plants which grow naturally in conditions ranging from very acid, calcium deficient at one end of the scale, to alkaline, calcium-rich at the other, with plants from intermediate conditions in between.

The classic example of a cline of plant communities in relation to a cline of calcium levels is the extreme-rich fen to moss series of SJORS, (1948); DU RIETZ, (1949); & WITTING, (1947), (FIGURE 1.). This is a series of ecologically linked plant communities spanning the extremes of calcium-rich to calcium-deficient habitats and of pH. It was, therefore, decided to select a number of plants which find their optimum habitat in different mire types, and to

test their performance against various levels of calcium and pH under uniform environmental conditions. The fact that mire plants grow naturally in waterlogged habitats should ensure that their performance in water culture is not too far removed from their behaviour in nature.

A major criterion of plants for such comparative studies is that they should be similar morphologically(CLYMO, 1962), and, towards this end, species of Carex were chosen which covered the complete spectrum of the extreme-rich fen to moss series. Originally six species were chosen whose ecological amplitudes are indicated in FIGURE 2.. It was soon realised that only two species could be dealt with, if sufficient data was to be obtained in the time available for the investigation. The species chosen were Carex flacca and Carex panicea.

Reasons for choosing these two species.

1. They are similar morphologically and anatomically.

2. They cover the habitat range required.

3. They can, and often do, occur together.

4. Plants were easy to obtain in quantity within easy reach of Durham.

5. They can exist in relatively large populations.

FIGURE 1.

Extreme-rich fen to moss series of SJORS, (1948), DU RIETZ, (1949), and WITTING, (1947).

(Maucha diagrams from BELLAMY, (1967).

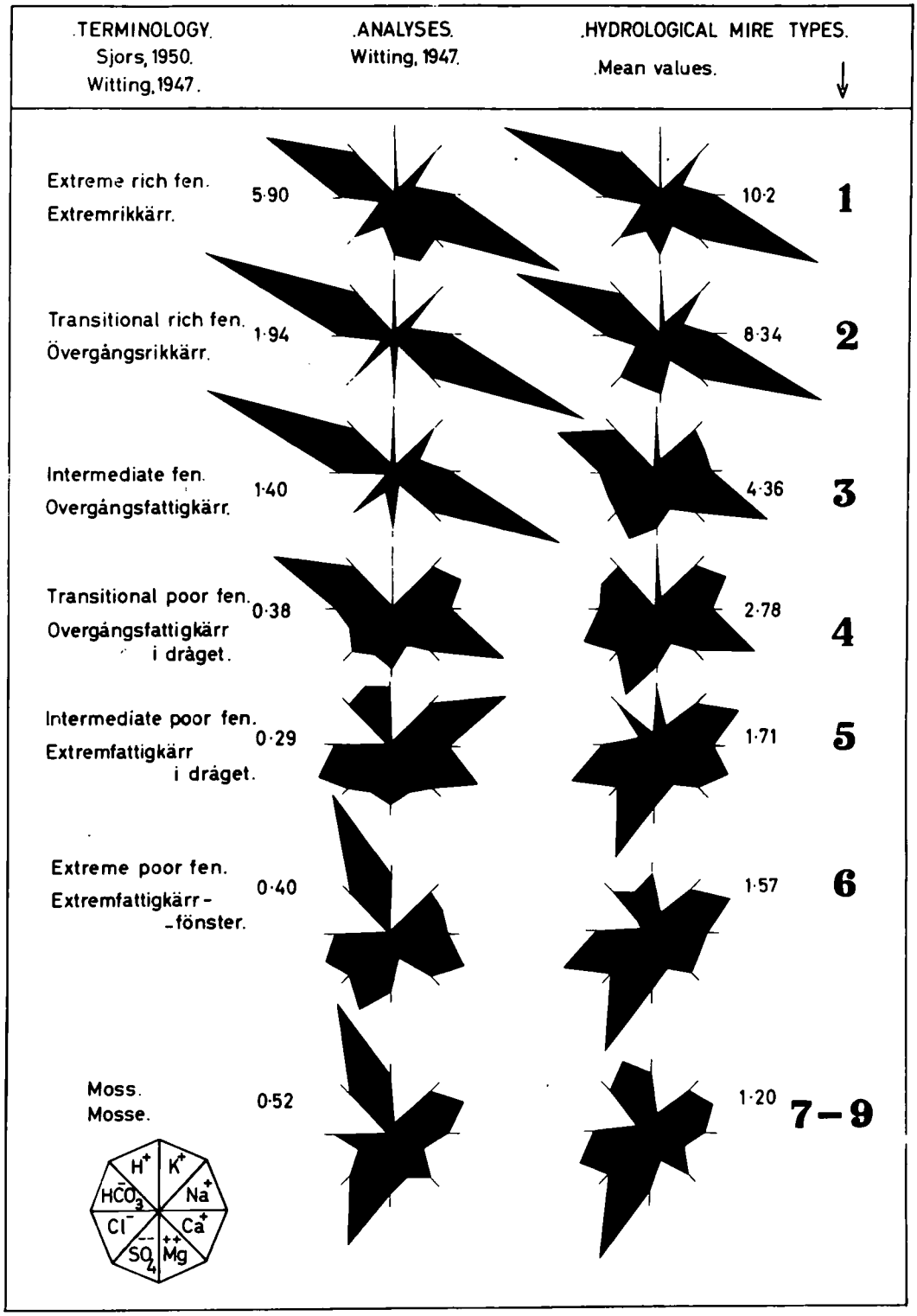
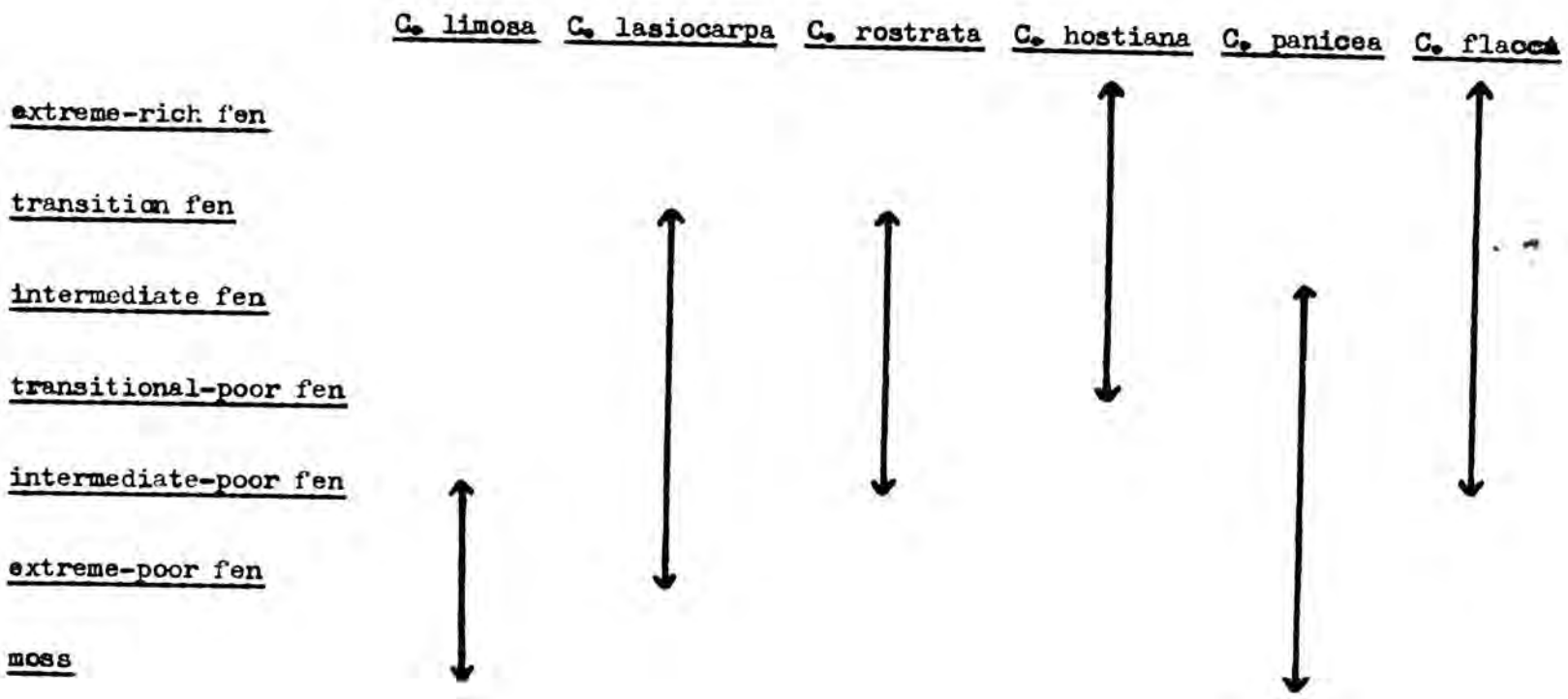

TERMINOLOGY.
Sjors, 1950.
Witting, 1947.
ANALYSES.
Witting, 1947.
HYDROLOGICAL MIRE TYPES.
Mean values.
Extreme rich fen.
Extremrikkärr.
5·90
10·2
1
Transitional rich fen.
Övergångsrikkärr.
1·94
8·34
2
Intermediate fen.
Övergångsfattigkärr.
1·40
4·36
3
Transitional poor fen.
Övergångsfattigkärr
i dråget.
0·38
2·78
4
Intermediate poor fen.
Extremfattigkärr
i dråget.
0·29
1·71
5
Extreme poor fen.
Extremfattigkärr-
-fönster.
0·40
1·57
6
Moss.
Mosse.
0·52
1·20
7–9
H+
K+
Na+
Ca++
Mg++
SO4--
Cl-
HCO3-

FIGURE 2.

Ecological amplitudes of the six *Carex* species originally chosen for study. (These have been determined by inspection of relevant phytosociological literature, SJORS, (1948 & 1950), DU RIETZ, (1949), WITTING, (1947) and BELLAMY, (1967).


C. limosa
C. lasiocarpa
C. rostrata
C. hostiana
C. panicea
C. flacca
extreme-rich fen
transition fen
intermediate fen
transitional-poor fen
intermediate-poor fen
extreme-poor fen
moss

MORPHOLOGY

Plants of both species consist of a sympodial rhizome system. Each rhizome terminates in a swollen stock which bears the leaves and forms a tufted aerial shoot with a phyllotaxis if $\frac{1}{3}$. Buds and roots are formed at the point where the stock bends and turns upwards. The length of individual rhizomes is very irregular (TABLES 2-5) ranging from practically zero to 15 cm.. In all cases, the leafy shoots formed at the ends of these rhizomes have been called 'tillers' throughout this investigation.

A stylised Carex flacca or C. panicea plant is shown in FIGURE 3, and the effect of the sympodial rhizome system on the spatial arrangement of subsequent generations of tillers is represented diagrammatically in FIGURE 4. Data on the number of leaves, number of rhizomes produced and maximum leaf length of mature plants from field populations is listed in TABLES 2-5.

Normally tiller development commences during the autumn from axillary buds on the stock. These remain small and below ground during the first winter, and elongate the following

spring to form a tuft of glaucous green leaves. The plant does not usually flower in this first summer, but overwinters above-ground without dying back appreciably (a few of the outer leaves die). In the second spring, further growth of the plant occurs with simultaneous development of the flowering spike. Flowering takes place during May - June, with fruit formation from June - August. After flowering, the mature tiller dies. The vegetative cycle of these two species spans two years and they may be referred to as 'biennial perennials'.

FIGURE 3.

Diagram of Carex tiller at the end of the first year's growth period.

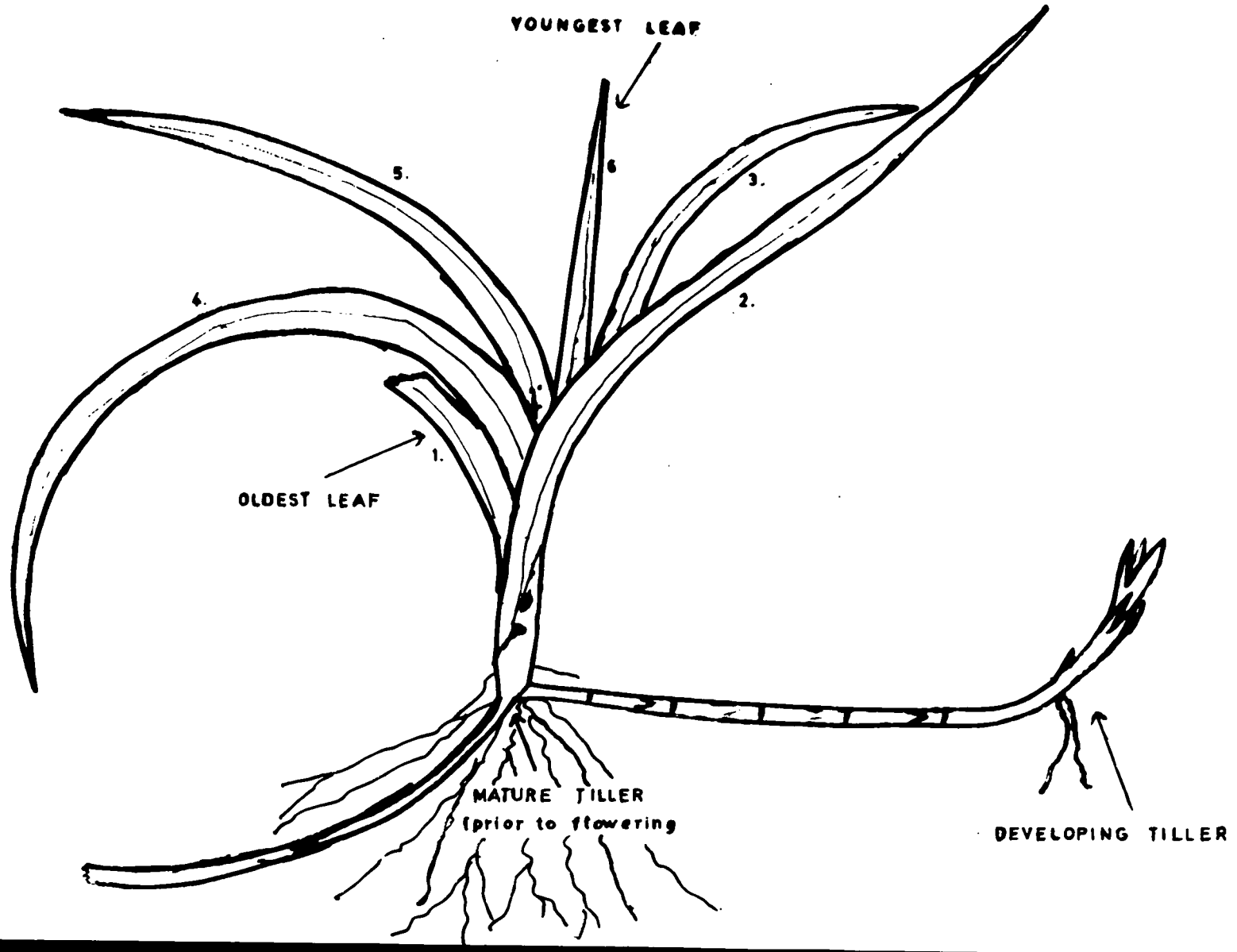

YOUNGEST LEAF
6.
5.
4.
3.
2.
1.
OLDEST LEAF
MATURE TILLER
(prior to flowering
DEVELOPING TILLER

FIGURE 4.

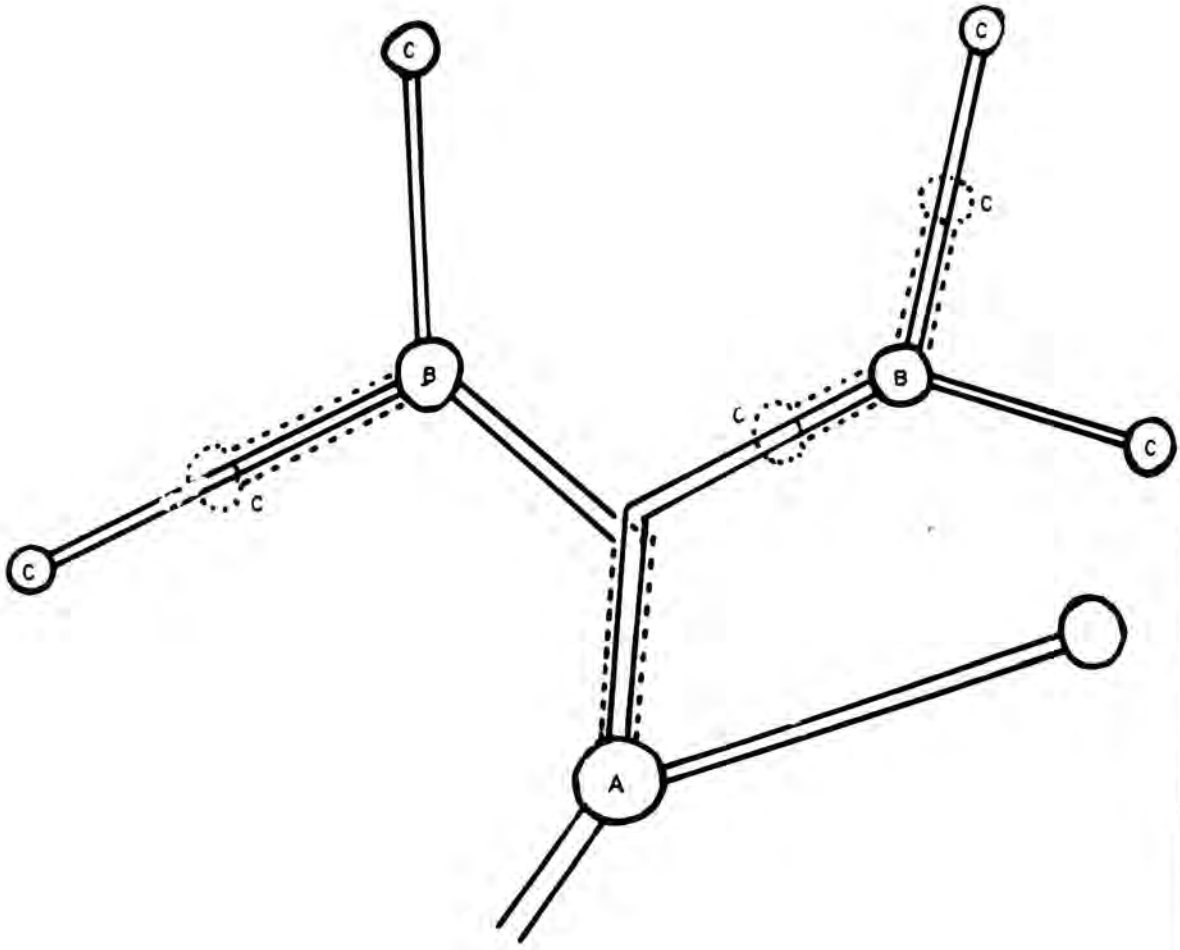
Diagrammatic representation of sympodial rhizome system of Carex tillers.

A - present year's flowering plant.

B - tiller at end of first year growth period (should flower in following summer)

C - developing tillers (very young).

For clarity, the actual arrangement of tillers in the substrate has been distorted. Subsequent tillers can be produced in the axils of leaves directly above tillers already formed.


C
C
C
B
B
C
C
C
C
A

APPROACH TO THE PROBLEM

Preliminary experiments were designed to try to answer the following questions.

1. What is the performance of these two species in relation to calcium supply and pH level?

2. Does calcium have a direct effect upon growth?
   (a) Can the two species obtain sufficient calcium for normal growth if it is in short supply?
   (b) Do they absorb excess calcium if it is available and with what result?
   (c) Is there an optimum calcium concentration in the external solution for growth of these two species?

3. Does calcium exert an indirect effect upon performance by influencing the uptake of other nutrients? (OLSEN, 1923; RICHARDS & SHIH, 1940; COLLANDER, 1941; MIDDLETON & RUSSELL, 1958; JACOBSON ET AL, 1960 & 1961; NIELSEN ET AL, 1963,). Most of the experiments studying the influence of calcium on the

absorption of other ions have been carried out on detached plant organs or tissue slices. Is there any evidence of a calcium effect in experiments using intact plants?

For the purpose of this investigation the term 'performance' is used to relate to different aspects of the behaviour of these two species under a variety of culture and habitat conditions. The parameters used to determine 'performance' are :- change in fresh weight and dry weight, fresh weight/dry weight ratio, leaf length, and change in the total and percentage content of the elements calcium, magnesium, sodium, potassium and phosphorus within the plants.

Part II

CULTURE EXPERIMENTS.

As stated above, conflicting results have been obtained by workers employing different study techniques. For this reason the techniques used in this investigation are described in detail in the body of the thesis before describing the experiments themselves.

No growth chamber was available for these experiments, so a cheap but effective one had to be constructed. This was built inside a large 'Dutch Light' greenhouse during October - December 1963, and the first experiments were commenced in January 1964. The chamber was subsequently enlarged in December 1964 to enable a greater variety of treatments to be applied at one time. Construction details of the growth chamber are given in detail in APPENDIX1.

THE CULTURE TECHNIQUE.

The substrate employed was colourless polythene chips supplied by Imperial Chemical Industries Ltd.. These were washed thoroughly with distilled water and autoclaved at 105°C for one hour before use. 3" plastic pots were filled with the chips and placed inside square polythene wash bowls, which were subsequently filled with the appropriate culture solution (FIGURE 5). Each plant pot was covered with a circle of black polythene, held in position with a rubber band. The edges of the circles of adjacent pots overlapped to reduce the amount of light reaching the surface of the culture solutions, in an attempt to minimise algal growth.

The culture solutions were changed weekly, and to simplify this procedure, the bowls of individual treatments were connected together by means of polythene tubing, welded to holes near their bases. To one end of each row of bowls a 40 litre aspirator was connected, and, at the other end, a tap was inserted to empty the bowls when required. By this technique, the culture solutions could be drained from one end and fresh culture solutions run in at the other, enabling a complete change to be carried out in about half an hour for the whole growth cabinet. In the enlarged

growth chamber, there were 14 rows of bowls, five in each row, allowing 14 different culture solution treatments to be applied at the same time to plants growing in adjacent rows of bowls. The complete unit contained 70 polythene bowls each with 9 plant pots which could hold three plants each. The capacity of the chamber was 70 x 9 x 3, i.e. 1890 plants at any one time if required.

Culture solution was run into each bowl until the level was about one inch below the tops of the plant pots ensuring that the polythene chips were kept permanently wet. To reduce further the possibility of algal growth, the top of the whole system, except for the plant pots, was covered with black polythene, as were the stock aspirators themselves. Slits were cut in the top of the polythene 'skirts' covering each plant pot, and through these were inserted the tillers under investigation into the polythene chips.

This technique is fundamentally one of water culture, in which additional support is provided for the plants by the sterilised polythene chips. This method has an advantage over those employing vermiculite or sand in that it enables the root systems of plants to be collected free from adhering substrate particles after each experiment by simply rinsing in distilled water.

Each change of culture solution required approximately 20 litres per treatment, and, as solutions were changed weekly, each aspirator (40 litre capacity) contained two week's supply of culture solution. The fact that the bowls contained a large excess of culture solution which was changed frequently, greatly reduced several sources of error in the culture technique.

1. pH drift was small, 4.2 increased to 5, and pH 7 dropped to 6.5 after a week.

2. The nutrient concentration was maintained at a fairly constant value over each week. (TABLE 1.)

3. It was thought unnecessary to aerate the culture solutions because of the large volumes of solution used and because of the large surface area of solution in each bowl.

FIGURE 5.

The culture technique.

THE CULTURE SOLUTION.

In carrying out these experiments, it was decided to use, as a basis, a well-tried and successful culture solution which gives an adequate supply of all the macro- and micronutrients required by plants for healthy growth. The culture solution chosen to form the basic medium was a modification of that used at the Long Ashton Agricultural and Horticultural Research Station (HEWITT, 1952). The final concentrations of the ions in the solutions were made up to be half of that recommended in the Long Ashton solution, except in the case of the ions, calcium and potassium, the concentrations of which were varied. Instead of supplying calcium as calcium nitrate, it was added as calcium chloride. In the potassium experiments potassium was added as potassium nitrate. As a result nitrate concentration also varied and to maintain the same nitrate level in all treatments appropriate quantities of sodium nitrate were added to make up the difference.

Concentrated stock solutions of each salt used were prepared and stored in $2\frac{1}{2}$ litre Winchester bottles. The concentration of these stock solutions was such that 100 ml. stock solution on dilution to 40 litres gave the required ionic concentration. This basic medium was bulked with appropriate quantities of calcium

chloride or potassium nitrate to give the required concentration of calcium or potassium for each experiment. pH was adjusted by the addition of sodium hydroxide.

Details of the exact amounts of each salt used in the preparation of the basic culture solution, and of the quantities of calcium chloride and potassium nitrate used in each treatment are given in APPENDIX 2.

COLLECTION AND PREPARATION OF PLANT MATERIAL.

Prior to each experiment, plants of *Carex panicea* were collected from blanket peat near Sunbiggin Tarn, Westmorland, and from a transition mire at Cassop, Co. Durham. *Carex flacca* was collected from a transition mire at Sunbiggin Tarn and from limestone grassland at Cassop. (Plants from this latter site were included to cover the extreme calcium-rich habitat.) On all of these sites, the species grow in large populations, and it is possible that they may be of restricted genetical origin. After collection, the plants were planted in boxes and kept in a heated greenhouse until required. Before use, they were thoroughly washed, and the tillers removed. Tillers of each species, selected by eye to be of approximately similar initial size (2-3 cm.), were rinsed in distilled water, surface dried, weighed and planted in the growth cabinet in the manner previously described. Before planting, any roots growing from the tillers were removed, so that each plant had to re-establish itself completely in the culture medium.

EXPERIMENT 1.

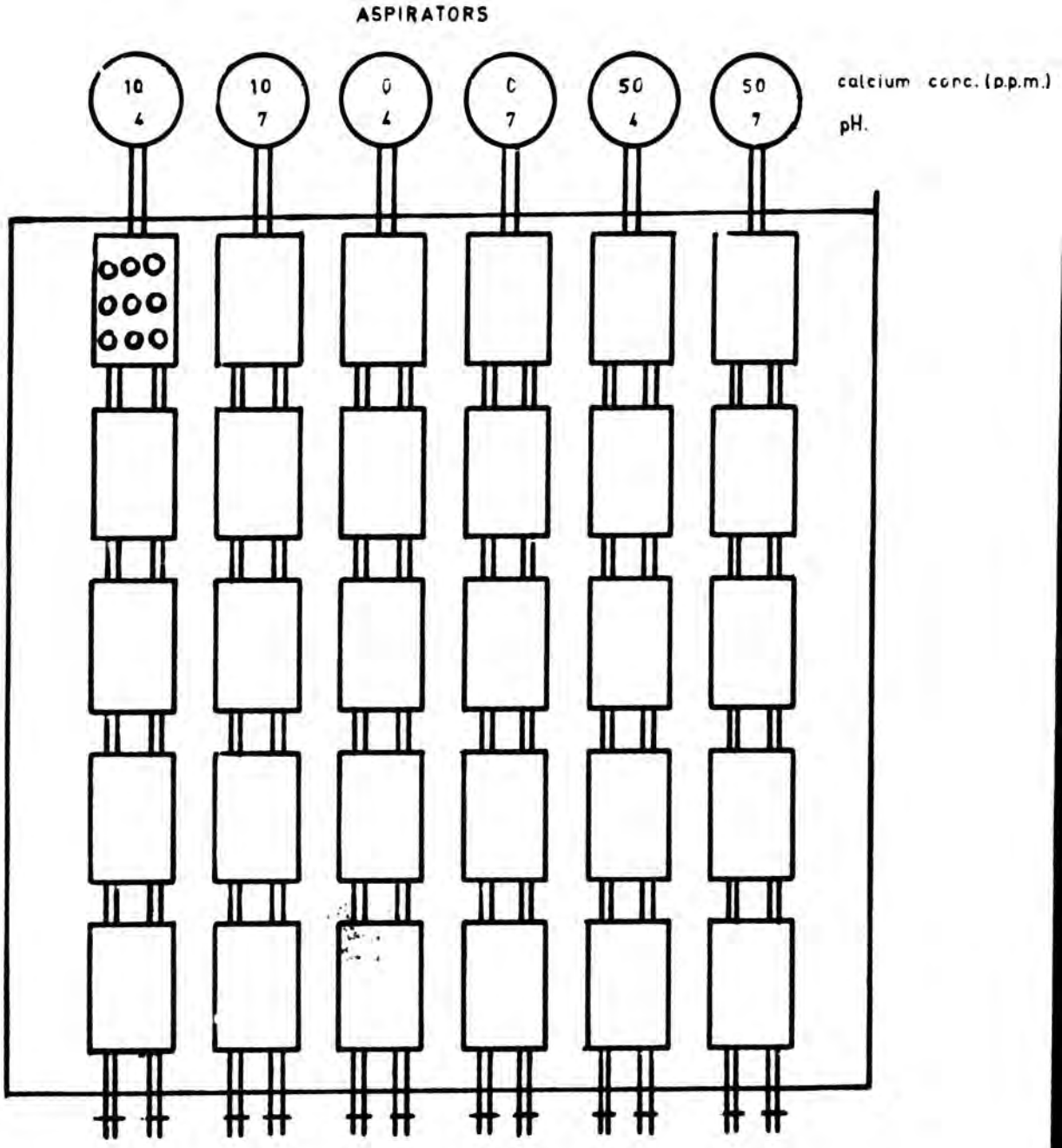
The object of this experiment was to investigate the performance of C. flacca and C. panicea tillers growing in culture solutions containing different calcium concentrations at different pH levels.

Since any variation in the concentrations of nitrate, potassium and phosphorus may produce pronounced effects on performance, the levels of these nutrients was maintained constant in all treatments. Calcium chloride was supplied in appropriate quantities to give final calcium concentrations of 0, 10 and 50 parts per million respectively. All of these solutions had an initial pH of 4.2, irrespective of the calcium concentration (BELLAMY & RIELEY, 1964). This pH (4.2) was maintained in one set of three 40 litre aspirators (covering the calcium range), while in a duplicate set pH was raised to pH 7 by the addition of sodium hydroxide solution.

The arrangement of the culture treatments within the growth cabinet is shown in FIGURE 6.

FIGURE 6.

Arrangement of culture treatments inside the growth chamber.


ASPIRATORS
10
4
10
7
0
4
0
7
50
4
50
7
calcium conc. (p.p.m.)
pH.

RESULTS

The results are detailed in APPENDIX 6, TABLES 7 & 8, and are presented in graph form in FIGURES 7, 8 & 9.

Fresh weight.

The graphs of *Carex panicea* from both collecting sites are similar. There is little change in fresh weight between 0 and 10 p.p.m. calcium at pH 4; (plants from the acid site show a slight increase, and those from the transition mire, a small decrease at 10 p.p.m.), but there is a very large increase in the 50 p.p.m. calcium treatment. At pH 7, on the other hand, there is a marked increase in fresh weight at the 10 p.p.m. calcium concentration (much greater than the value reached at the lower pH), and a further increase at 50 p.p.m.. It is interesting to note that at the highest calcium concentration there is virtually no difference between the final fresh weights of the plants growing at the two pH levels.

Carex flacca from the limestone grassland site (which was the only collecting site from which plants of this species were used in the preliminary experiment) exhibited the same type of response to calcium and pH as *C. panicea* over the lower

concentrations (0 and 10 p.p.m.), but differed from C. panicea in its behaviour at the 50 p.p.m. level. In this case, although the standard errors overlap, the trend is quite obviously towards an increase in fresh weight due to an increase in the external calcium concentration and to increase in pH level.

Dry weight.

There is little difference in the final dry weights of C. panicea plants originating from the acid site and grown in the extremes of pH. In plants from the transition mire, there is a suggestion of greater dry weight at the higher pH at the 10 p.p.m. calcium level.

C. flacca, on the other hand, shows a marked divergence in final dry weight at the 10 p.p.m. calcium concentration due to pH, and this pH effect increases at the 50 p.p.m. level. It is notable that there is no increase at all in final dry weight in of C. flacca plants at pH 4 between 10 and 50 p.p.m. calcium in the external solution.

Fresh weight/dry weight ratio

In all cases the shape of the graphs is similar. The ratio is higher at pH 4 than at pH 7 at the 0 p.p.m. calcium

level, but, with increase of the calcium concentration to 10 p.p.m., positions are reversed giving a higher ratio, or increased 'succulence', at the higher pH. At the higher calcium concentration, the ratio reached its highest values, and these appear to be independent of pH.

Chemical analysis.

The methods employed are described in full in APPENDIX 3.

Analysis of dry plant material of both species did not reveal any detectable differences in the concentrations of Calcium, magnesium, potassium, sodium or phosphorus due to either, difference in species, calcium concentration or pH, except in the 0 p.p.m. calcium solution, and this may have been due to the poor condition of the plants which survived this treatment. These results do, however, show the percentage concentrations of each of these elements present in the two species.

The most surprising fact about these results is that they show that the calcium level inside the plants does not increase (as a percentage of the total dry weight) with increased concentration of this element in the culture solutions over the range employed. This would seem to suggest that these plants exert

a 'buffering action' against the higher levels of calcium external to them, absorbing sufficient only to keep pace with increase in dry weight. All graphs indicate an increase in internal potassium and phosphorus concentration between 0 and 10 p.p.m. calcium, but, as has already been mentioned, this may have been due to the poor condition of the plants in the 0 p.p.m. treatment at the end of the experiment. These plants were chlorotic and many were dead and it is possible that leakage had taken place of these two elements from such plants, giving rise to the lower values detected.

FIGURE 7.

Experiment 1. -

Fresh weight and dry weight data.

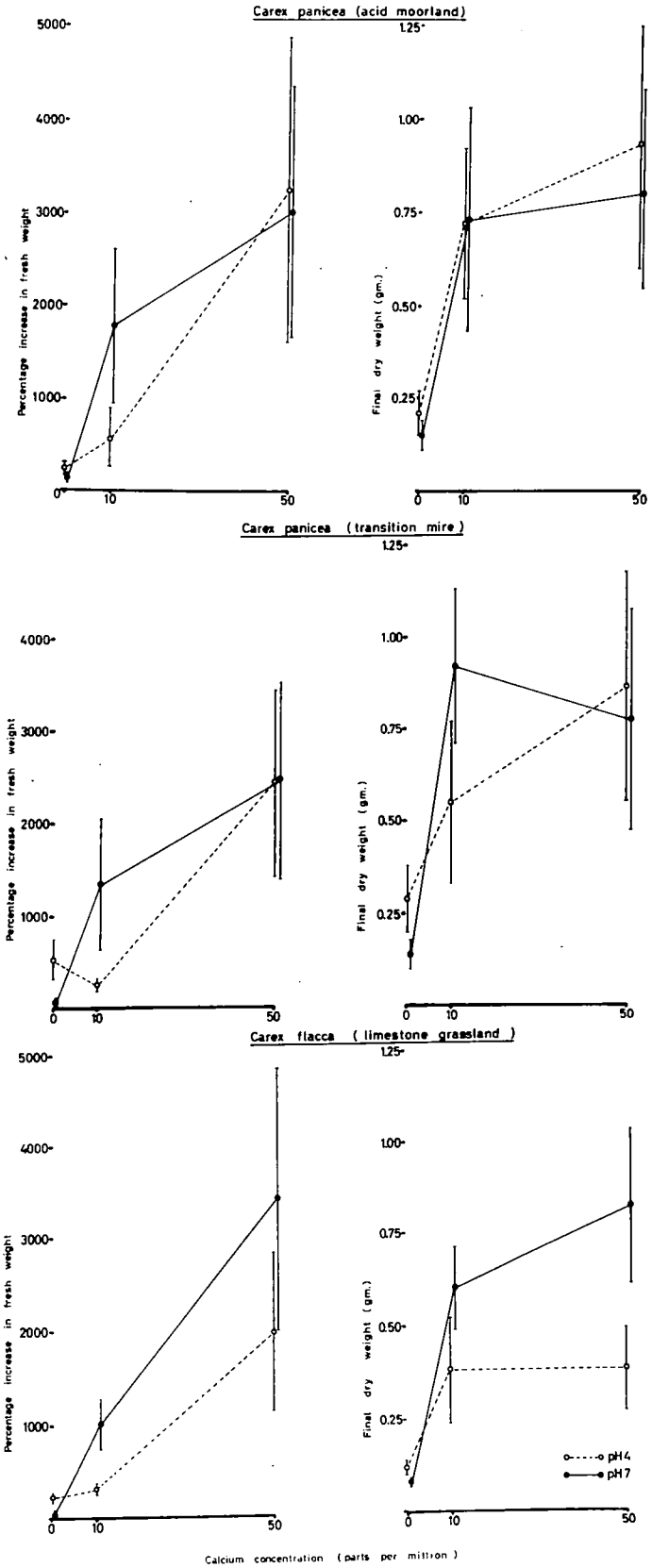
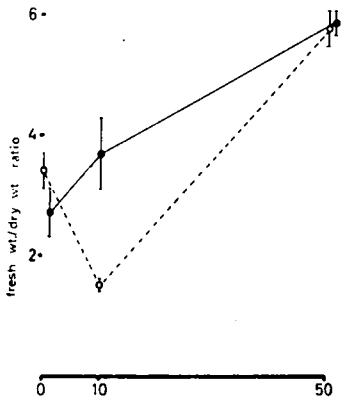

Carex panicea (acid moorland)
Percentage increase in fresh weight
Final dry weight (gm.)
Carex panicea (transition mire)
Carex flacca (limestone grassland)
Calcium concentration (parts per million)
pH4
pH7

FIGURE 8.

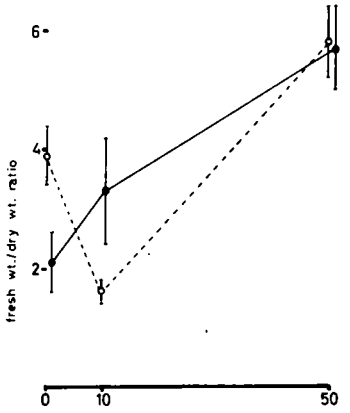
Experiment 1. -

Fresh weight/dry weight ratio.

Carex panicea (acid moorland)



Carex panicea (transition mire)



Carex flacca (limestone grassland)

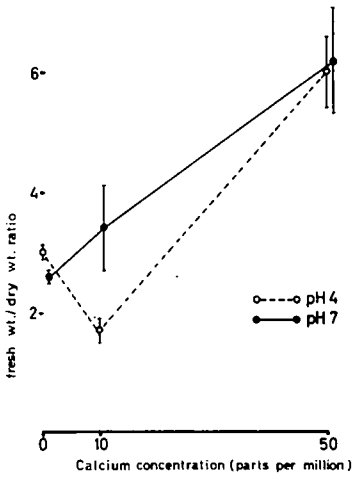
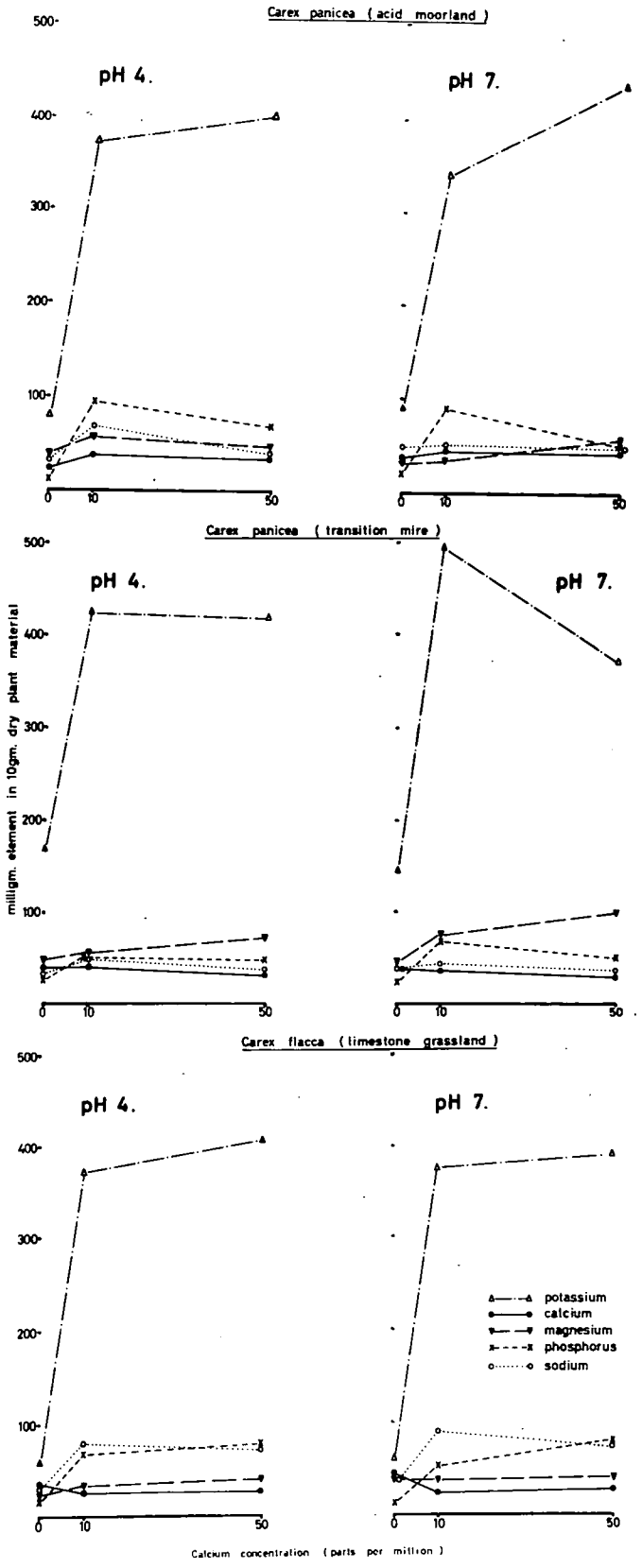


FIGURE 9.

Experiment 1. -

Chemical analysis data.


Carex panicea (acid moorland)
pH 4.
pH 7.
500
400
300
200
100
0
10
50
Carex panicea (transition mire)
pH 4.
pH 7.
milligm. element in 10gm. dry plant material
Carex flacca (limestone grassland)
pH 4.
pH 7.
potassium
calcium
magnesium
phosphorus
sodium
Calcium concentration (parts per million)

DISCUSSION OF EXPERIMENT 1.

There was no difference between the mineral contents of these two species attributable to difference in the pH of the external medium. However, some effect on the potassium and phosphorus contents was evident at the 0 p.p.m. calcium level. This effect was probably due to the absence of calcium from this particular nutrient solution since a later experiment containing only 0.5 p.p.m. calcium did not give rise to a similar low potassium concentration in the plants. Potassium and phosphorus are known to be very mobile in plant tissues, and dying plants or plant organs lose a proportion of both of these elements : JAMES, (1931); MITCHELL, (1936); PETRIE, (1934); ULRICH, (1943); WILLIAMS, (1955); PERKINS, (1961); PRITCHARD ET AL, (1964). It is also interesting to note that very high levels of potassium, compared to the other elements, were detected. Other workers have also commented upon the high levels of potassium found in plant tissues : FAGAN & WATKINS, (1932); THOMAS & TRINDER, (1947); OLSEN, (1948); MALMER, (1958).

There are two possible explanations to account for this apparently anomalous potassium value obtained in the absence of calcium from these culture experiments :

1. Potassium tends to vacate dying tissues. (The plants in this treatment soon showed signs of chlorosis and began to die.) This aspect of potassium will be dealt with at greater length in a later discussion.

2. It is possible that the absence of calcium resulted in diminished potassium uptake by the plants. VIETS, (1944), showed that a number of bivalent ions, including calcium, stimulated potassium absorption by excised barley roots. OVERSTREET ET AL, (1952), confirmed this effect of calcium on potassium uptake, and suggested that calcium had a stimulatory effect on the active transport of potassium, possibly by facilitating the breakdown of a K-carrier complex.

Carex panicea plants collected from the acid site were small and stunted. When tillers of these plants were grown in culture solutions deficient in calcium at either pH level they remained small. Tillers from the much larger plants collected from the transition mire (higher calcium and pH) performed no better on the calcium-deficient culture solution. C. panicea tillers grew much better at higher external calcium concentrations irrespective of original collecting site. These findings are in agreement with results of ARNON, (1942), who observed that plants of lettuce and tomato

could grow well under acid conditions provided sufficient nutrients, especially calcium and potassium, were available. He concluded that high calcium concentration could compensate for low pH.

SUMMARY AND INFERENCES.

The results of this experiment suggest :-

1. That *C. flacca* has become adapted to higher pH conditions in which it attains maximum performance (expressed as fresh weight and dry weight increase).

2. That *C. flacca* requires a higher calcium concentration than *C. panicea*, since even at pH 4 plants grown in the higher calcium solutions exhibit a larger percentage increase in fresh weight than those grown in the 10 p.p.m. calcium solution at pH 7.

3. That there may be a 'dehydrating' effect of low pH in the presence of a low calcium concentration.

4. That *C. panicea* is an adaptable species as far as mineral supply is concerned being able to survive in a wide range of calcium concentrations and pH levels, but with a different potential performance in each case. *C. flacca*, on the other hand, shows a marked preference for higher pH at all external calcium concentrations except the lowest one.

5. That both calcium concentration and pH are important factors influencing the performance of these two species in culture solution, and it is possible that their occurrence in nature is greatly dependent on them also.

QUESTIONS ARISING FROM AN ASSESSMENT OF THE RESULTS OF EXPERIMENT 1.

This preliminary experiment gave rise to several important questions which determined the course of the investigation.

1. In all cases there was a large difference in the performance of plants between 0 and 10 p.p.m. calcium and consequently this appeared to be a critical range of calcium concentration to study. What would be the performance of the two species at intermediate calcium concentrations?

2. Plants of both species continued to grow quite healthily at 50 p.p.m., the maximum calcium concentration employed in this experiment. What would be their reaction to higher calcium concentrations in solution culture? Is there a maximum calcium concentration for growth of these two species above which they cannot survive?

3. There was no increase in the percentage calcium concentration inside the plants but merely an uptake sufficient to keep pace with additional dry weight increase due to growth of the plants. Is there a maximum concentration of calcium in the external solution above which the 'buffering action' of the plants

ceases to be effective, leading to an increase in the relative calcium content of the plants?

4. As the chemical analysis graphs indicate, these plants contain very large quantities of potassium in their tissues, and they must, therefore, be very efficient in extracting this element from the growth medium. What would happen to the potassium content of plants growing in culture solutions in which potassium is varied over a low concentration range, especially when another essential element such as calcium is limiting?

5. Would the same responses to calcium concentration be exhibited by these two species at different stages of development?

6. How do these two species behave in the field under different conditions of nutrient supply? Is there a difference in performance on different sites?

7. Is there any detectable nutrient cycling in these plants, and, if so, can this be related to nutrient supply?

EXPERIMENT 2. VARIATION IN EXTERNAL CALCIUM CONCENTRATION.

The growth cabinet was increased in size to accomodate 14 different culture treatments. In this experiment a range of nine different calcium concentrations was employed, giving a series of concentrations in the range 0.5, 2.5, 5.0, 10, 20, 50, 100, 200, and 500 parts per million. In order to study the response of plants grown in culture from different initial stages of development, the tillers were divided by eye into younger (tillers 2-3 cm. long) and older tillers (larger ones between 5 and 6 cm. in length). Because of the large numbers of plants used in this experiment, no initial measurement of fresh weight was made because of the time it would have involved.

So that a more complete study of the 'with age' response could be made, a separate experiment was set up in a smaller growth chamber, to observe the effect of calcium concentration on germination and seedling establishment. Seeds of the two species were allowed to germinate on vermiculite, saturated with the culture solutions used above.

RESULTS.

Experiment 2.a. Performance of tillers of different ages.

(TABLES 9 & 10; FIGURES 10 - 12)

When removed from the growth chamber at the end of the experiment, all plants were weighed fresh, then dried to constant weight. Final leaf length and root length of all plants were measured, and the ratio of final fresh weight to final dry weight at each calcium concentration was calculated.

There was great variation in the final fresh weights and leaf lengths between plants at any one calcium concentration. (Greater variability resulted from the use of tillers than was anticipated.) Seeds were not used in the major experiements because of :-

(i) difficulty of germination, and,

(ii) plants grown from seed took a long time to reach a suitable size to provide sufficient material for chemical analysis.

Carex panicea.

(a) Fresh weight. (FIGURE 10.)

Performance of the plants from the acid site showed an increase from the 0.5 p.p.m. to the 10 p.p.m. external calcium, and then a gradual decrease at each successively higher calcium concentration until in the 500 p.p.m. solution, the final fresh weight was very low and, in most cases, the plants were dead. With plants collected in the autumn before the experiment was set up, the shape of the graph obtained for both young and old tillers was similar, indicating that the original age of the tillers had not made any appreciable difference to their performance. The plants collected a year earlier and kept in the greenhouse until required, gave a similar graph for the larger tillers as before, but the performance of the younger tillers was rather erratic.

Tillers of plants collected from the more calcium-rich transition mire habitat behaved differently from those from the acid moorland site, in that they had a much higher final fresh weight at lower calcium concentrations, with decrease in the final fresh weight above 5 p.p.m. calcium. Both young and old tillers responded similarly except that the younger tillers did not decrease in fresh weight until the calcium concentration exceeded 10 p.p.m..

(b) Dry weight. (FIGURE 10.)

In general, the final dry weights of these plants tended to follow the pattern of the final fresh weights but to a lesser degree. As final fresh weight increased, so did the dry weight but not always in the same proportion as is shown by the fresh weight/dry weight ratio.

(c) Leaf length. (FIGURE 11.)

The final lengths of the leaves of any one species from all treatments was about the same, apparently unaffected by calcium concentration. (There was, however, signs of chlorosis in plants grown in the very high and very low calcium concentrations.)

(d) Fresh weight/dry weight ratio. (FIGURE 12.)

In Carex panicea from the acid moorland site, this ratio was maintained at 4-5 up to an external calcium concentration of 20 p.p.m. after which it decreased at each higher calcium level. The ratio obtained for C. panicea plants from the transition mire decreased above 5 p.p.m. calcium.

Carex flacca.

(a) Fresh weight. (FIGURE 10.)

Plants collected from the transition mire site exhibited a much greater response to increasing calcium concentration than those from the limestone grassland. Older tillers from the former site maintained a high final fresh weight between calcium concentrations 10 to 200 p.p.m., with a sharp drop in fresh weight at the 500 p.p.m. calcium. This large increase was not so pronounced in the younger tillers, in which there was a more gradual increase in fresh weight from the 0.5 to the 20 p.p.m. calcium, and then a gradual decrease at subsequent higher concentrations. Plants from the limestone grassland site reached their maximum fresh weight at 20 p.p.m., and then dropped to a much lower weight in each succeeding calcium concentration, no plants surviving in the 500 p.p.m. solution. The younger tillers of C. flacca from the limestone grassland site behaved worse than any of the other plants of either species in any of the treatments. Only a few plants survived in certain treatments and from the results obtained it was not possible to detect any distinct differences in performance due to variation in calcium level. No Plants from this collection survived in calcium solutions containing more than 50 p.p.m. calcium.

(b) Dry weight. (FIGURE 10.)

As in the case of C. panicea, the final dry weights tended to follow increases and/or decreases in final fresh weight, but were not in proportion to them.

(c) Leaf length. (FIGURE 11.)

As before, these results were rather inconclusive, although the lengths of the leaves of older plants from the limestone grassland site were greater than the final leaf lengths of the younger tillers from the same site at each calcium concentration. These older tillers also showed an increase in length between 0.5 and 20 p.p.m. calcium, and a gradual decrease at higher calcium concentrations.

(d) Fresh weight/dry weight ratio. (FIGURE 12.)

In C. flacca, this ratio showed more variation than was evident for C. panicea. With C. panicea from Sunbiggin Tarn, the ratio increased from 0.5 to 10 p.p.m. calcium, reaching a value

FIGURE 10.

Experiment 2.a. -

Fresh weight and dry weight data.

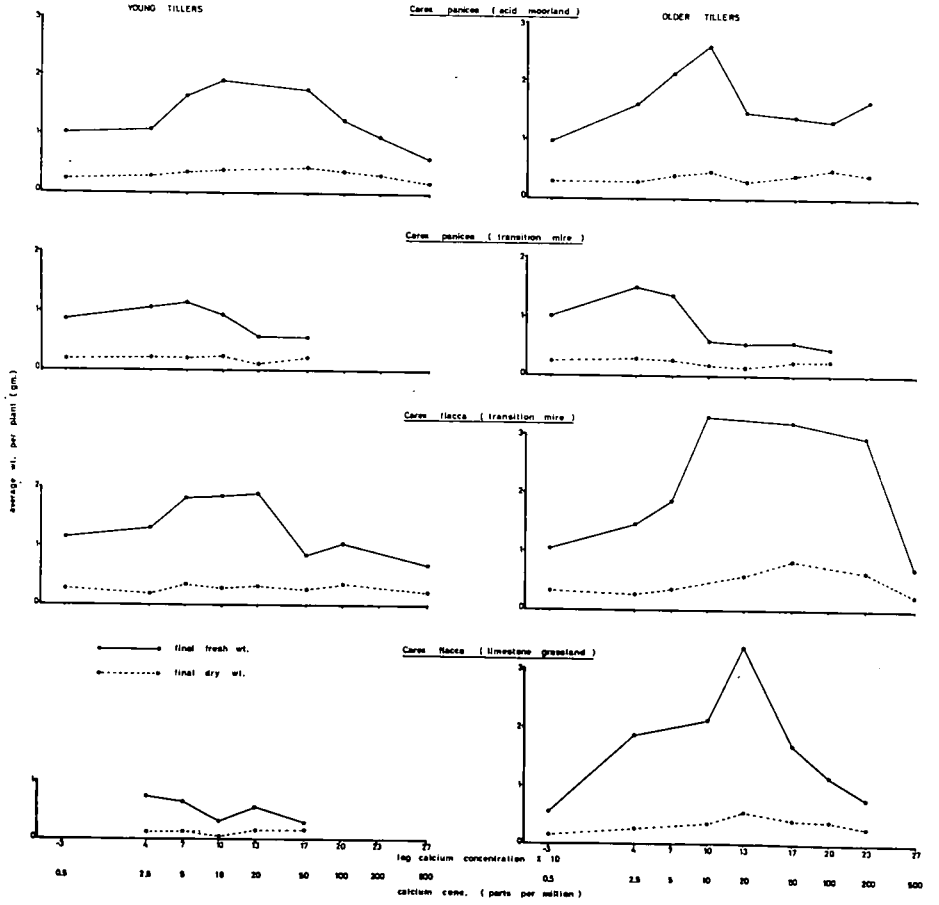

YOUNG TILLERS
OLDER TILLERS
Carex panicea (acid moorland)
Carex panicea (transition mire)
Carex flacca (transition mire)
Carex flacca (limestone grassland)
average wt. per plant (gm.)
final fresh wt.
final dry wt.
log calcium concentration x 10
calcium conc. (parts per million)

FIGURE 11.

Experiment 2.a.-

Maximum leaf length.

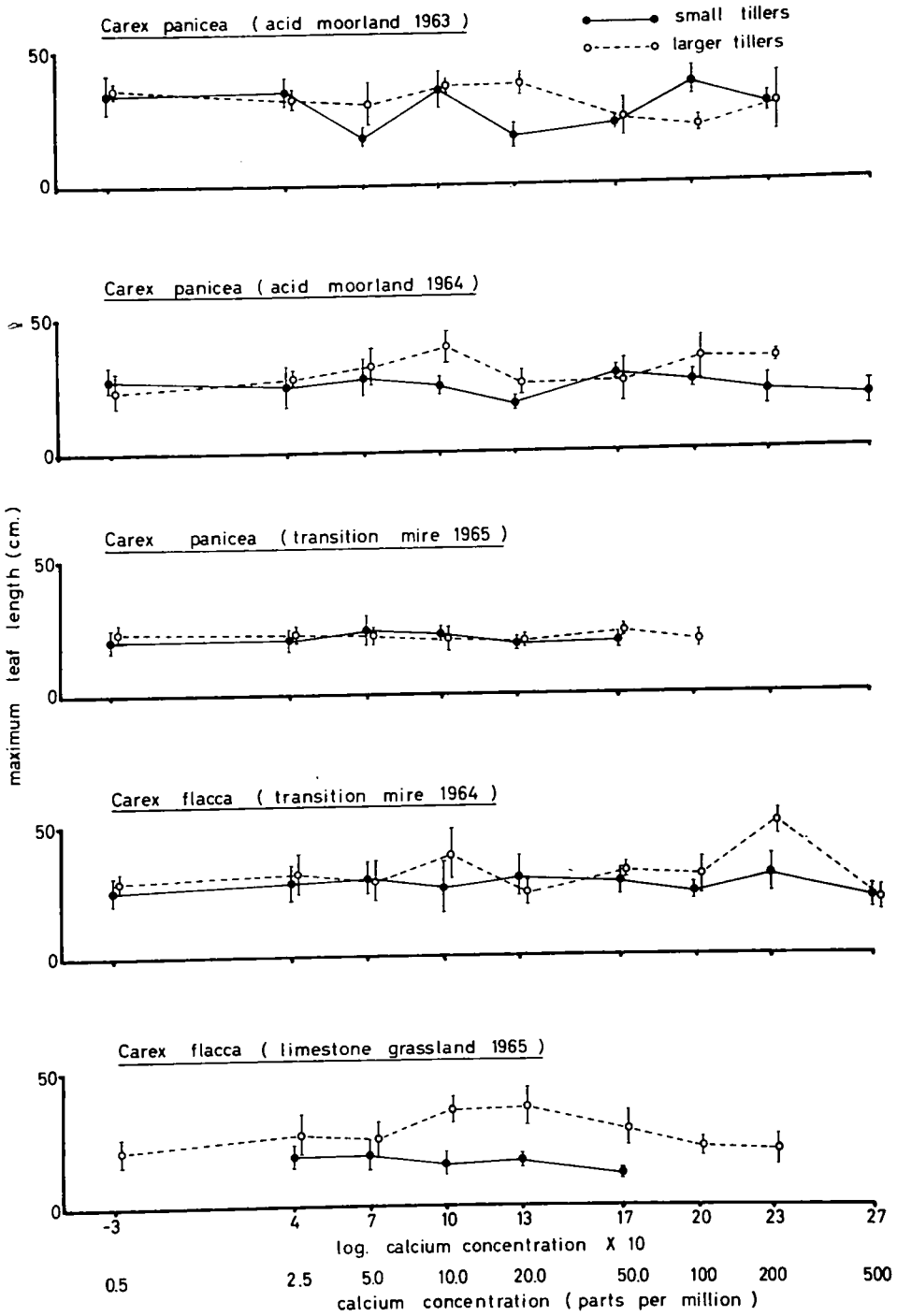
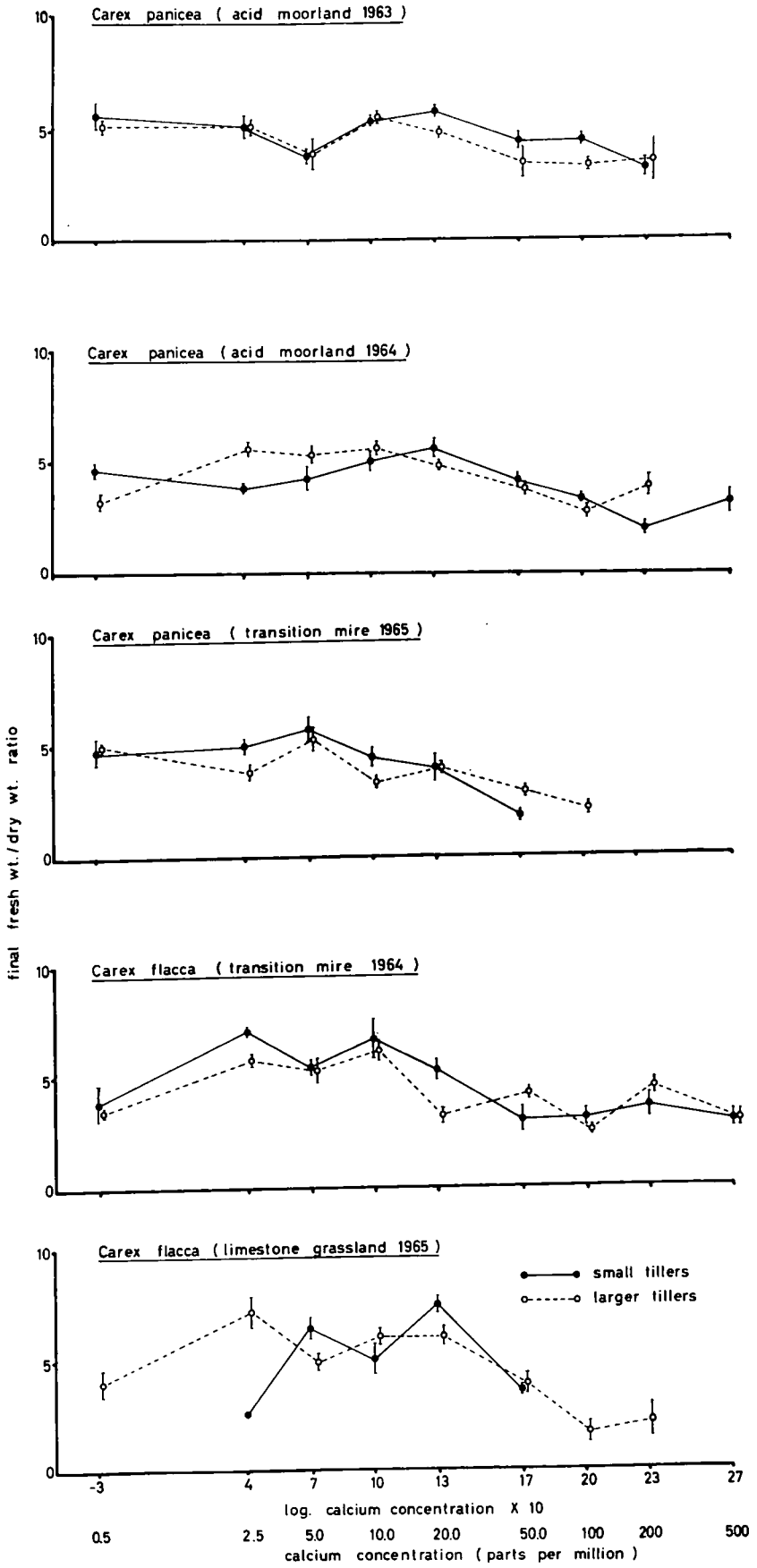

Carex panicea (acid moorland 1963)
small tillers
larger tillers
50
0
Carex panicea (acid moorland 1964)
50
0
Carex panicea (transition mire 1965)
50
0
maximum leaf length (cm.)
Carex flacca (transition mire 1964)
50
0
Carex flacca (limestone grassland 1965)
50
0
-3
4
7
10
13
17
20
23
27
log. calcium concentration X 10
0.5
2.5
5.0
10.0
20.0
50.0
100
200
500
calcium concentration (parts per million)

FIGURE 12.

Experiment 2.a. -

Fresh weight/dry weight ratio.


Carex panicea (acid moorland 1963)
Carex panicea (acid moorland 1964)
Carex panicea (transition mire 1965)
Carex flacca (transition mire 1964)
Carex flacca (limestone grassland 1965)
small tillers
larger tillers
final fresh wt./dry wt. ratio
10
5
0
-3
4
7
10
13
17
20
23
27
log. calcium concentration X 10
0.5
2.5
5.0
10.0
20.0
50.0
100
200
500
calcium concentration (parts per million)

of about 7 for both younger and older tillers. Above this concentration, there was a drop in the ratio to about 2.5 at higher calcium levels. The same pattern prevailed for C. flacca from Cassop, except that the decrease in the ratio did not occur until the calcium concentration exceeded 20 p.p.m.

(e) Chemical analysis of plants from Experiment 2.a.

The leaves of plants from each treatment were bulked together and analysed to determine whether, over the increased range of calcium concentrations there were any differences in the content of calcium, potassium and magnesium, these being three of the major elements liable to exhibit variation under the conditions of the culture experiments : calcium, because this was the element which was varied in the principal experiment; potassium, because of the large quantities of this element previously detected in these plants, and also because it was varied in concentration in the subsidiary experiment; and magnesium, because of its important role as a constituent element of chlorophyll.

The analytical results were calculated as milligrams of each element in 10 grams of oven-dried plant material, and also

as milligrams per 100 plants. Because of the large number of analyses involved replicate analyses were not carried out on every sample, but duplicate determinations were carried out on several different samples to find out the degree of variation which was likely to occur (TABLE 11). The techniques used in the plant analysis procedure are described in APPENDIX 3, and the results, which are detailed in full in TABLE 10, are summarised in FIGURES 13 and 14 (for calcium).

It was necessary to express the chemical analysis results both on a percentage and on a total basis for the following reasons :-

1. The percentage approach enables the relative concentrations of any one element to be determined in different plants or plant organs, grown on different nutrient solutions or collected from the field at different times of the year.

2. The total basis indicates the exact level of any element under similar conditions to those listed above. This latter approach is unaffected by what may be referred to as the 'dilution effect' of growth of the plant. During the active growth phases in a plant's life cycle dry weight increase may exceed increased absorption of nutrients from the substrate so that the same

proportion of chemical elements per unit dry weight of plant material as before is not maintained. The consequence of this is that although the total level of any one element may continue to increase during these growth phases, results calculated on a percentage basis indicate a decrease. This, however, is not a real decrease (loss), but an apparent one due to this 'dilution effect'.

Most of the earlier work on the chemical composition of plant material expressed the concentrations of the various elements on a percentage dry weight basis, which produced a false interpretation of how the plant was actually reacting to the nutrients available to it.

Authors who have based interpretation on a percentage basis only include : RIPPEL, (1927); JANSSEN & BARTHOLOMEW, (1929); PENSTON, (1931); FAGAN & WATKINS, (1932); McHARGUE & ROY, (1932); RICHARDSON, (1932); THOMAS & TRINDER, (1947). Those who have stressed the necessity for a total per plant approach include : SAMPSON & SAMISCH, (1935); PETRIE, (1934); MITCHELL, (1936); OLSEN, (1948).

RESULTS.

Potassium.

As in Experiment 1. this was the element present in greatest quantity in the plant tissues (between 200 and 350 milligrams per 10 grams dry plant material). No sharp increase in the percentage potassium content of the plants, from the lowest external calcium concentration to the next higher one was detected, and this might have been due to the fact that, in this case, the culture solution with the lowest calcium concentration contained 0.5 p.p.m. calcium, whereas, in the previous experiment no calcium at all was added (PAGE 30).

With C. panicea from Cassop there was a suggestion that potassium was being lost from the plants as the external concentration of calcium increased, but, in the case of plants collected from the acid site, no distinct pattern emerged.

Calcium.

Calcium was the element which showed the greatest variation and this was where the results of this experiment differed from the previous one. With increasing external calcium concentrations there was a very marked increase in the movement of calcium into

the plants. In Experiment 1. the highest calcium concentration used was 50 p.p.m.. It was only above this concentration that there was a marked influx of calcium in the second experiment.

Magnesium.

Magnesium, on the whole, remained constant throughout the complete range of calcium concentrations, lying between 20 and 50 milligrams per 10 gm. dry plant.

Sodium.

In every series of chemical analyses, control flasks were included to check for possible contamination during the digestion and analysis procedure. These flasks contained no plant material but the reagents were added as in the normal technique. These controls then underwent the usual processes of digestion, filtration, dilution and analysis. In the cases of calcium, potassium and magnesium there was no evidence of contamination, but in all control flasks sodium gave a sufficiently high reading to cast doubts on the sodium values obtained for the plant material (TABLE 6). In view of this the sodium results were discarded.

FIGURE 13.

Experiment 2.a. -

Calcium content of Carex panicea leaves.

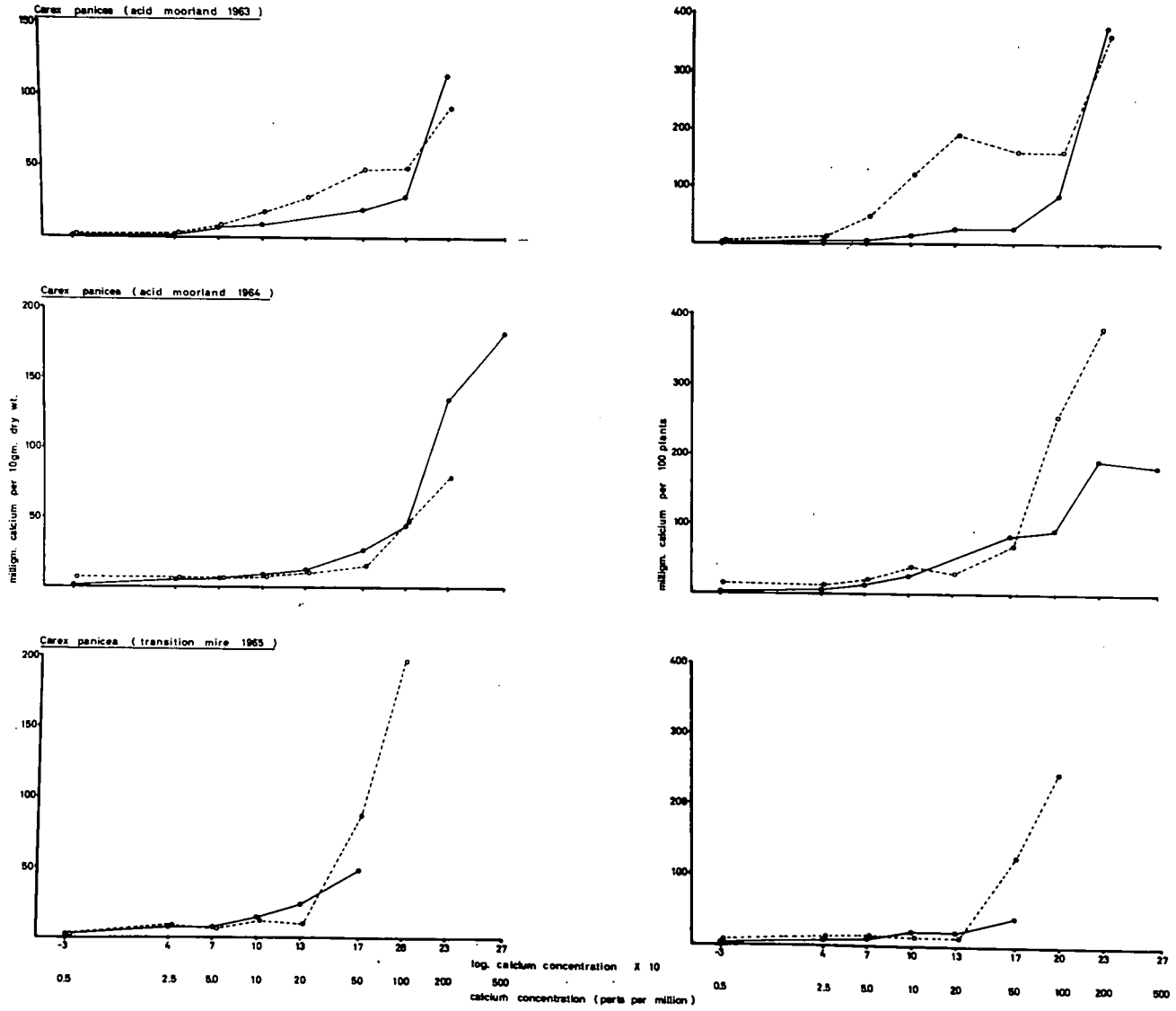
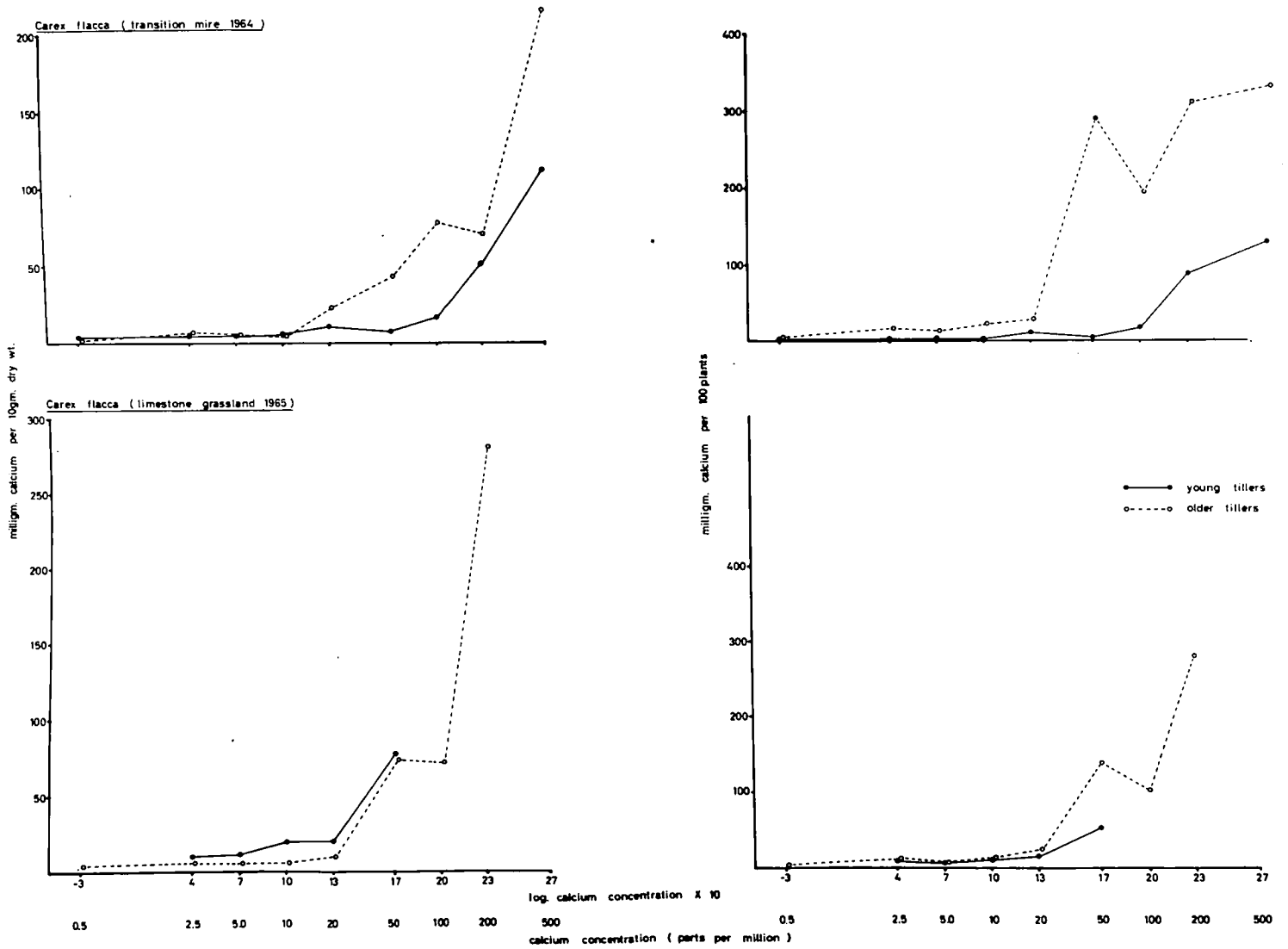

Carex panicea (acid moorland 1963)
Carex panicea (acid moorland 1964)
Carex panicea (transition mire 1965)
milligm. calcium per 10gm. dry wt.
milligm. calcium per 100 plants
log. calcium concentration X 10
-3 4 7 10 13 17 20 23 27
calcium concentration (parts per million)
0.5 2.5 5.0 10 20 50 100 200 500

FIGURE 14.

Experiment 2.a. -

Calcium content of Carex flacca leaves.


Carex flacca (transition mire 1964)
Carex flacca (limestone grassland 1965)
milligm. calcium per 10gm. dry wt.
milligm. calcium per 100 plants
young tillers
older tillers
log. calcium concentration X 10
-3
4
7
10
13
17
20
23
27
calcium concentration (parts per million)
0.5
2.5
5.0
10
20
50
100
200
500

Carex panicea from Cassop. (TABLES 9 & 10)

1. Percentage potassium content decreased from 300 to 190 mg./10 gm. in the younger tillers, and from 300 to 215 mg./10 gm. in the older tillers. The total potassium per 100 plants decreased from 3 mg. to 2 mg. in the younger tillers and from 7 mg. to 2.5 mg. in the older tillers.

2. Magnesium content was between 30 and 40 mg./10 gm. in the young tillers and between 25 and 40 mg./10 gm. in the older tillers. The total magnesium content per 100 plants exhibited very little variation, remaining almost constant throughout.

3. In the very young tillers calcium content increased gradually from 3 to 50 mg./10 gm. dry weight over the concentration range (FIGURE 13). (No plants survived in any of the treatments containing more than 50 p.p.m. calcium.) The actual increase per 100 plants was smaller, from 3 to 39 mg.. In plants grown from older tillers the calcium concentration remained steady at about 10-12 mg./10 gm. up to an external concentration of 20 p.p.m. calcium, and then showed a rapid increase in percentage content up to 195 mg./10 gm. at 100 p.p.m. calcium in the culture solution.

This increase in percentage calcium content was mirrored by a corresponding increase in actual calcium content per 100 plants which rose from 8 to 242 mg..

Carex panicea from Sunbiggin Tarn.

1. The concentration of potassium in plants collected in 1963, and kept in a greenhouse until used was very erratic, fluctuating wildly between successive external calcium concentrations. In the plants collected in 1964 potassium content tended to rise from the lowest external calcium concentration and then fell again from about 20 p.p.m. at each successively higher concentration.

2. Magnesium content of plants changed very little throughout the experiment.

3. Calcium content increased as external calcium concentration was raised, especially at the higher concentrations. This increase in percentage calcium content was gradual in both young and old tillers from plants collected in 1963⅓ and 1964 up to about 50 p.p.m. external calcium, and then a much

greater increase took place above 100 p.p.m.. No plants from these sites survived in the 500 p.p.m. calcium treatment. Similar results were obtained on a total basis.

Carex flacca. (TABLES 9 & 10)

The results of chemical analysis of C. flacca plants followed the same type of pattern as was shown by C. panicea, except that C. flacca plants survived in the highest calcium concentration used.

1. In all cases potassium exceeded all the other elements analysed in percentage concentration. (Except in older tillers of C. flacca from Cassop in the 200 p.p.m. external calcium.)

2. Magnesium remained fairly uniform throughout.

3. Calcium also showed similar trends to those in C. panicea. In tillers collected from the limestone grassland site, calcium content showed a marked increase in external solutions containing 50 p.p.m. calcium and above. This increase occurred in both young and old tillers.

Older tillers from the transition mire increased in internal calcium from about 50 p.p.m. external calcium, but in younger tillers, the large increase did not occur until the external concentration exceeded 100 p.p.m.. This might suggest that the younger tillers from this latter site exerted a greater 'buffering action' against excessive calcium (external) concentration than older plants.

It should be noted that young tillers from the limestone grassland site did not survive in culture solutions containing more than 50 p.p.m. calcium. This is not thought to be due to an intolerance of external calcium but to an inability of these tillers, collected from a relatively dry habitat to survive successfully in solution culture, where conditions may be adverse.

Experiment 2.b. Germination Experiment.

Since the percentage germination of Carex panicea was very low sufficient material for analysis was obtained only for C. flacca.

Root and leaf weight data are given in TABLE 12. Chemical analysis results are detailed in TABLE 13 and the calcium results are shown graphically in FIGURE 15.

1. Potassium content was again high compared to the other elements, and, as before, there was no regular pattern of variation with change in the external calcium concentration.

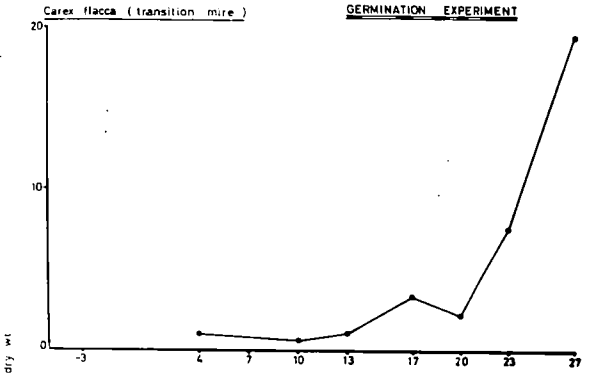
2. Magnesium content remained more or less constant.

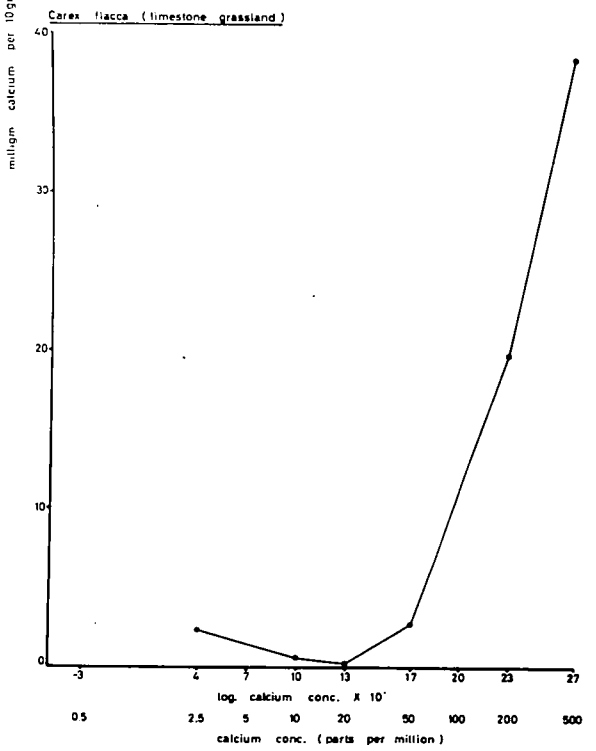
3. Calcium content of the seedlings increased rapidly when the external calcium concentration exceeded 50 p.p.m..

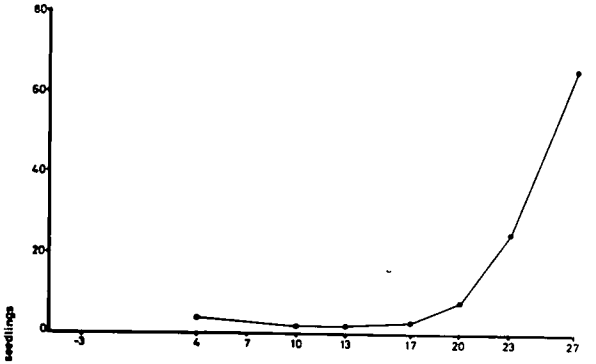
FIGURE 15.

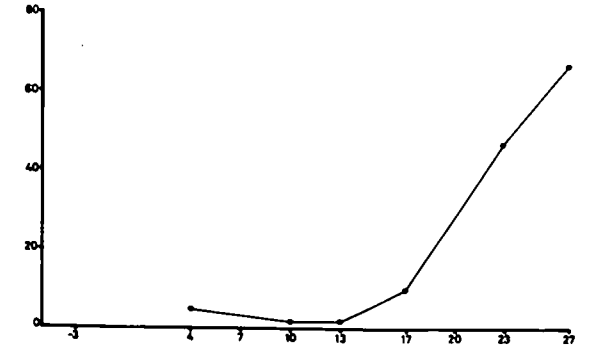
Experiment 2.b. -

Change in calcium content of developing seedlings.


Carex flacca (transition mire)
GERMINATION EXPERIMENT
20
10
0
-3
4
7
10
13
17
20
23
27


Carex flacca (limestone grassland)
milligm calcium per 10 gm dry wt
40
30
20
10
0
-3
4
7
10
13
17
20
23
27
log. calcium conc. X 10⁻
0.5
2.5
5
10
20
50
100
200
500
calcium conc. (parts per million)


80
60
40
20
0
-3
4
7
10
13
17
20
23
27


milligm calcium per 1000 seedlings
80
60
40
20
0
-3
4
7
10
13
17
20
23
27

SUMMARY OF EXPERIMENT 2.

1. Both species are indifferent to varying calcium concentration in the external solution up to 20 p.p.m..

2. Above 20 p.p.m. calcium is accumulated in increasing amounts as the external calcium concentration is raised, until the plants can no longer tolerate the high calcium concentrations and die. (This happens to tillers of both ages and to developing seedlings)

3. Potassium was the element present in greatest concentration in the leaves of these two species. No distinct pattern of potassium variation with changing external calcium concentration was detected except in C. panicea tillers collected from the transition mire.

4. Performance was not affected by the original age of the tillers. (But see previous comment on C. flacca from the limestone grassland site.)

5. Leaf length was not influenced by external calcium concentration.

6. Calcium showed considerable variation in the leaves of these plants especially when the external concentration of calcium exceeded 50 p.p.m..

7. No evidence was found of variation of internal magnesium content.

EXPERIMENT 3. VARIATION OF EXTERNAL POTASSIUM CONCENTRATION.

Because of the very high amounts of potassium present in all of the plant material analysed, it was thought probable these two Carex species either require fairly large quantities of potassium, (i.e. they would grow only on soils which have a high exchangeable potassium content), or else they would be extremely efficient in the uptake of the relatively small amounts of potassium available to plant roots in the substrate. Analysis of the soils from which these two species were collected in the field, in most cases, showed low exchangeable potassium content (TABLE 39).

The following experiment was designed to test the performance of C. flacca and C. panicea in culture solutions in which potassium was varied over a low concentration range, and in which calcium was maintained at a low level. The range of potassium concentrations chosen was 0.5, 1.0, 2.5, 5.0 and 10.0 p.p.m.. Calcium was maintained at the low concentration of 2.5 p.p.m. in all cases. The exact composition of these culture solutions is given in APPENDIX 2.

RESULTS.

Fresh weight and dry weight data for this experiment are given in TABLE 14. There was no correlation between increasing potassium concentration and final fresh or dry weight.

Chemical analysis results are given in TABLE 15 and the data for potassium content is summarised in FIGURES 16 & 17.

It can be seen that very low potassium concentration in the culture solution resulted in a correspondingly low potassium content in the plants (on a percentage and total basis). At each successively higher external potassium concentration a higher percentage of potassium was found in the plants. In the highest potassium concentration used (10 p.p.m.), the amount of potassium present in the plants at the termination of the experiment was equal to the greatest amount detected in plants from any previous experiment in which potassium had been supplied in much greater quantity. In fact, even at the 1 p.p.m. potassium level in the external solution, there was as much potassium in the plants as had been detected in some of the plants from other experiments. These plants must, therefore, be extremely efficient in absorbing potassium even when it is present in low concentration.

The graphs of total potassium content per 100 plants against potassium concentration in the culture solutions, although not so regular as those obtained for percentage content, show the same kind of increase in the plants.

Also in this experiment, calcium levels in the plants decreased as external potassium was raised (falling from 6 to 2 mg./10 gm. in most cases and from 10 to 2 mg./10 gm. in one instance). There was also evidence to suggest that internal magnesium content decreased as external potassium was increased.

FIGURE 16.

Experiment 3. -

Change in internal potassium content of Carex panicea with increase of potassium in the culture solution.

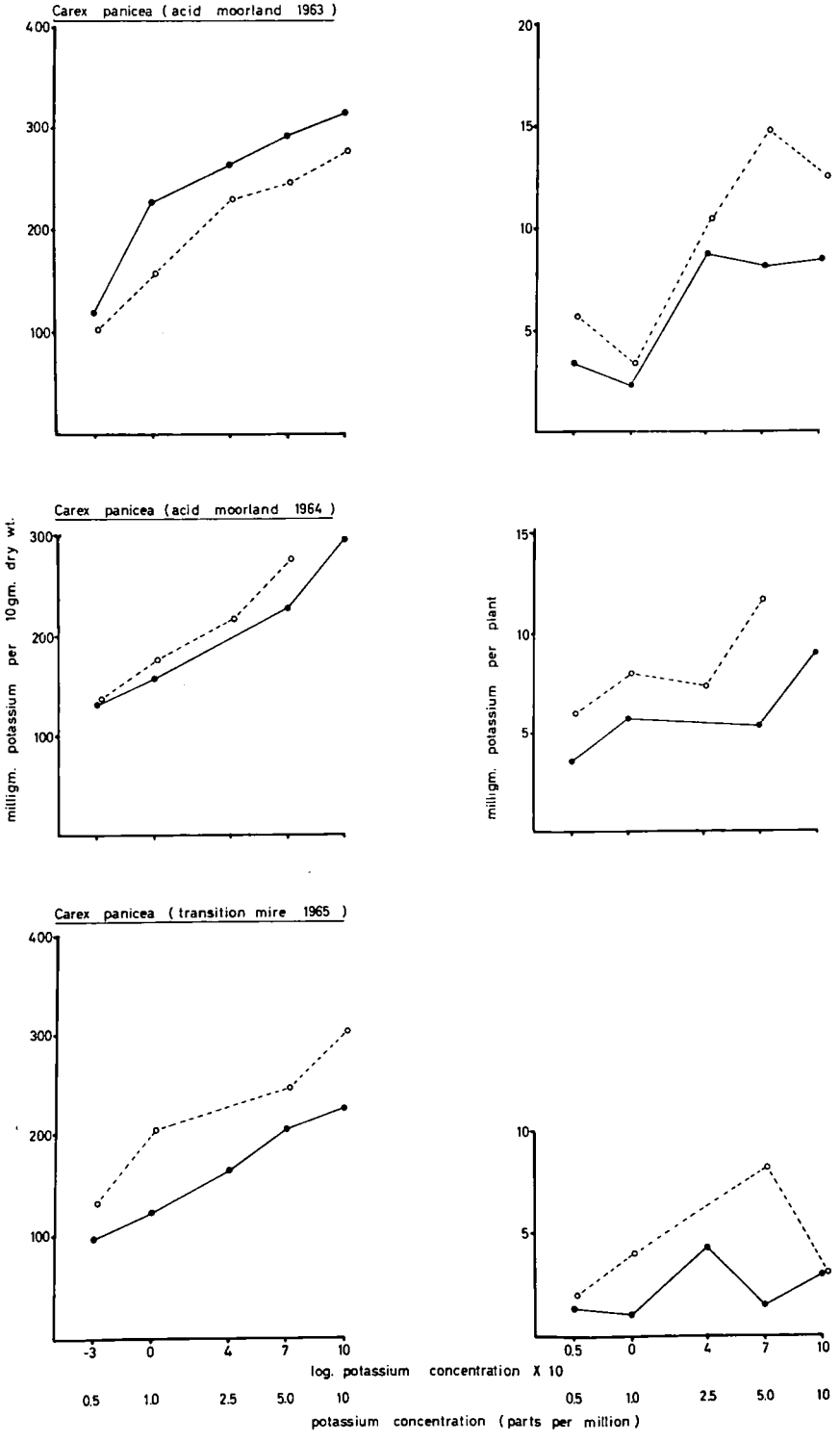
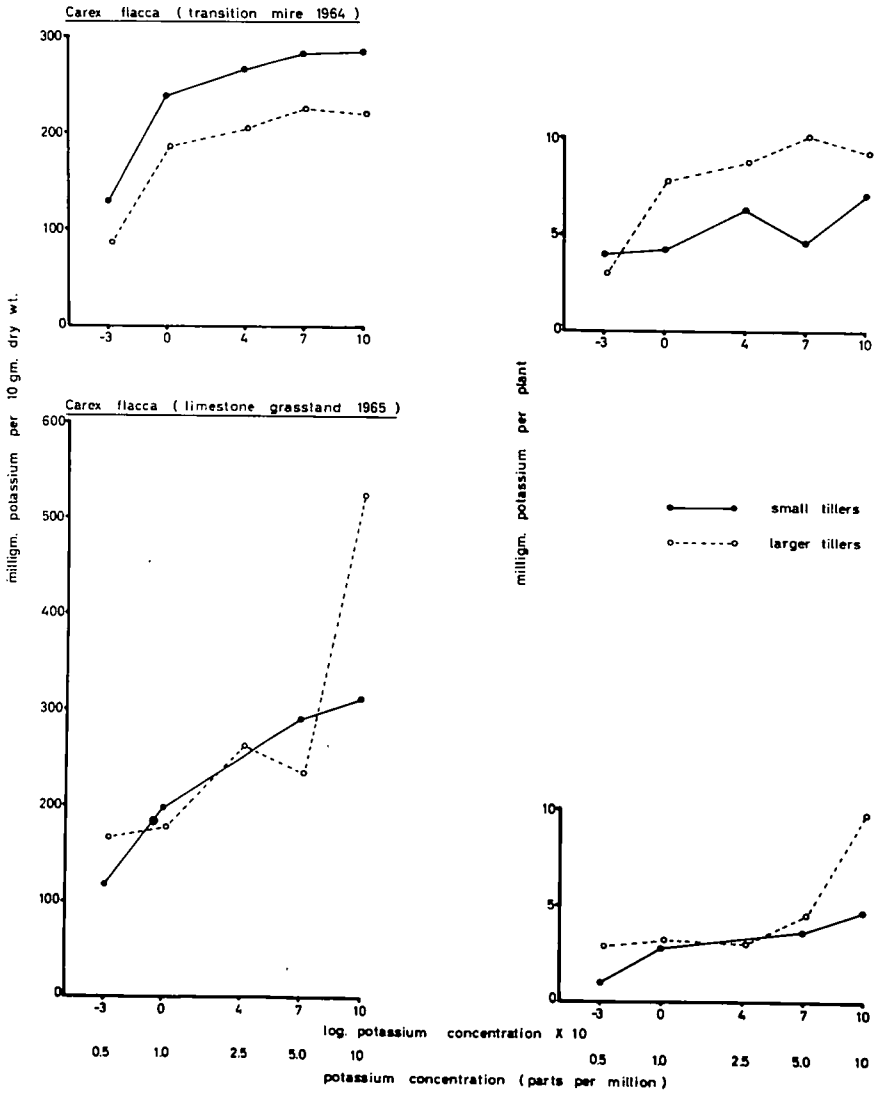

Carex panicea (acid moorland 1963)
400
300
200
100
20
15
10
5
Carex panicea (acid moorland 1964)
milligm. potassium per 10gm. dry wt.
300
200
100
15
10
5
milligm. potassium per plant
Carex panicea (transition mire 1965)
400
300
200
100
10
5
-3
0
4
7
10
0.5
0
4
7
10
log. potassium concentration X 10
0.5
1.0
2.5
5.0
10
0.5
1.0
2.5
5.0
10
potassium concentration (parts per million)

FIGURE 17.

Experiment 3. -

Change in internal potassium content of Carex flacca with increase of potassium in the culture solution.


Carex flacca (transition mire 1964)
Carex flacca (limestone grassland 1965)
milligm. potassium per 10 gm. dry wt.
milligm. potassium per plant
small tillers
larger tillers
log. potassium concentration X 10
0.5 1.0 2.5 5.0 10
potassium concentration (parts per million)

Summary of Experiment 3.

1. Percentage potassium content increased from the lowest external potassium concentration to the highest.

2. Calcium content of the plants tended to decrease from its original low value to an even lower one as external potassium concentration was raised.

3. Fresh weight and dry weight data showed no pattern of variation with variation in the external potassium concentration.

PART III.

NUTRIENT DYNAMICS

The object of this part of the investigation was to determine the levels of each of the major elements calcium, potassium, magnesium, sodium and phosphorus in the tissues of Carex flacca and Carex panicea under different environmental conditions in the field, and to determine whether or not the amounts of these nutrients varied over the two-year growth period. It was also intended to study the possibility of nutrient cycling within the two species.

Methods.

(a) Increment cropping.

Plants of both species were cropped from three localities over one growing period. The field stations which gave a range of calcium-rich to calcium-deficient habitats at both high and low altitude were Cassop Vale, Co. Durham; Sand Sike, Upper Teesdale, Co. Durham; and Tarn Moor, Sunbiggin Tarn, Westmorland. A brief description of these sites is given in APPENDIX 4.. XTkm

Plants were collected from all three sites on the same day, at fortnightly intervals, over the active growing and flowering period, from April until the end of July, and at less frequent intervals over the rest of the year. Whole plants were removed from the soil by means of a trowel, and transported to the laboratory in polythene bags. The plants were washed with tap water to remove adhering soil (or stored overnight in a cold room if separation could not be carried out immediately). The plants were then separated into the various parts: roots, rhizomes, dead tillers, young tillers, older tillers and flowering or fruiting stems. Each group of plant parts was

rinsed in distilled water, surface-dried, weighed, placed in paper packets, dried to constant weight and stored prior to chemical analysis.

Measurements were made of the fresh and dry weights of plants of both species at each collecting period and from the data obtained growth curves were constructed.

(b) Additional chemical analyses.

Plants from a stock collection kept in a greenhouse for several months were used in this investigation. These plants were separated into young tillers, mature tillers, roots and rhizomes as before. In addition, dead leaves were removed from some of the mature tillers, the remaining leaves of which were divided into dead leaf tips, photosynthetic laminas and colourless leaf sheathes. All of these fractions were analysed separately. This procedure was carried out to obtain a picture of the relative distribution of each element within the plant in more detail.

RESULTS.

(a) Increment cropping.

1. Growth curves.

Detailed results are given in TABLE 16. and these are summarised in FIGURE 18.. As expected they all show the same growth pattern differing in absolute values only. It can be seen from these graphs that although the two species are perennials, the growth curves bear out the supposition that individual tillers act as biennials, having two distinct growth phases with a resting period over the intervening winter. The most active growth period is between May and August in the first year, and between May and the end of June in the second year. After flowering, the plants lose weight as they die back.

At all sites Carex flacca shows an initial growth phase in the first year, maintains this level over winter, and then increases further in dry weight during the second year. Performance assessed as dry weight is greatest in the nutrient-rich Cassop site. Performance is rather poorer in the transition mire site at Sunbiggin Tarn, and is lowest in plants from the Sand Sike site. However, plants from all three sites show the two distinct growth pulses.

Carex panicea, on the other hand, does not have

exactly the same type of growth pulse as C. flacca.. During the first year tillers increase in dry weight but they lose some of this during the first winter. The following year they regain this 'lost' weight but plants from Sunbiggin Tarn and Sand Sike do not increase in dry weight beyond the maximum value reached in the first year. Plants from Cassop do show a marked second growth pulse.

2. Chemical analysis. (FIGURES 19 & 20; TABLES 17 & 18.)

As with the chemical analysis results of plants from the culture experiments, the chemical analysis data for the field material was expressed as a percentage of unit weight of dry plant material and as an absolute quantity per 100 plants.

The increases in dry weight mentioned above are paralleled by uptake of calcium, potassium, magnesium, sodium and phosphorus into the maturing plants. Sodium analysis was discontinued for the reasons given earlier. Phosphorus was determined in samples collected at the beginning of the investigation. However, as the study progressed it was not possible to keep pace with phosphorus determination on every sample and consequently analysis of this element was discontinued also. Of the remaining elements calcium and potassium showed the most marked variations in concentration over the growing period and the data obtained for these will be presented in greater detail.

Calcium

It can be seen from FIGURE 19. that calcium, expressed as total per plant is very low at the beginning of the first year's growing period, maintains a low value until May and then, coincident with the active growth phase, both species absorb more calcium, presumably, to keep pace with the amount required for increased cell-wall formation. Subsequently, the total calcium content shows a large increase from August, after which both additional growth and increase in calcium content stop during the winter. Percentage calcium also increases over this period, but the results are more variable. There is a further increase in total and percentage calcium during the second growth phase, continuing until the seeds set, about July - August.

Potassium.

The potassium content of Carex panicea and C. flacca shows considerable variation over the growing period. Percentage potassium content is high in the young plants (between 200 and 300 mg./10 gm. dry weight) and shows an increase at each succeeding collection period, reaching a peak about May, and, thereafter, decreasing consistently over the rest of the year. Analysis of mature tillers indicates that they have a percentage potassium content at the beginning of

the second growth phase equal to that present in the young tillers at the end of the first year. There is a slight rise in percentage potassium coinciding with the advent of the second growth phase (prior to flowering), and then it falls to a very low level after flowering and death of the plant (as low as 10 mg/10 gm. dry weight). The trend of absolute potassium content differs from that for the relative values. In developing tillers total potassium is very low, but percentage content is high, indicating that these very young shoots have a high concentration of potassium in small dry weight. Carex flacca always shows a pulse of potassium uptake with each growth pulse, both at Sunbiggin Tarn where exchangeable potassium in the soil is low and at Cassop where it is much higher (TABLE 21). Carex panicea, on the other hand, seems to absorb potassium mainly during the first growth phase and thereafter maintains this level, exhibiting no regular bimodal cycle of either growth or potassium uptake.

Potassium, calculated on a total K per plant basis, reveals the difficulty of interpreting the results of the percentage content of chemical elements in these plants. While percentage potassium content is at its highest in very young tillers, (in which one presumes there is much metabolic activity) total potassium per plant is at its lowest; and, whereas, percentage potassium decreases

as the tiller ages and increases in size, total potassium increases until flowering, and then falls rapidly. There is, however, evidence of a yearly rhythm in total potassium content, since the graphs indicate a decrease at the end of the first growth phase and an increase again in the second year prior to flowering.

From the analysis results of tillers and mature plants it can be seen that there is a pattern of nutrient increase and decrease (~~and decrease~~) throughout the year in the case of calcium and potassium. Neither magnesium, sodium nor phosphorus show any marked fluctuation on a percentage basis; they tended, for the most part, to remain within narrow limits for each cropping site. Magnesium content is much higher in plants cropped from the magnesian limestone site at Cassop.

Analysis results for roots and rhizomes proved to be rather inconclusive. It is impossible to calculate the amount of each element in a single root or system or rhizome because of the difficulty of removing complete root systems from the soil and also because of the irregularity of rhizome lengths. On a percentage basis, the levels of all the elements analysed for, remained rather constant and no pattern of variation over the year is evident.

The results of root and rhizome analyses have not been presented in graph form but are detailed in TABLE 19..

FIGURE 18.

Nutrient dynamics -

Growth curves.

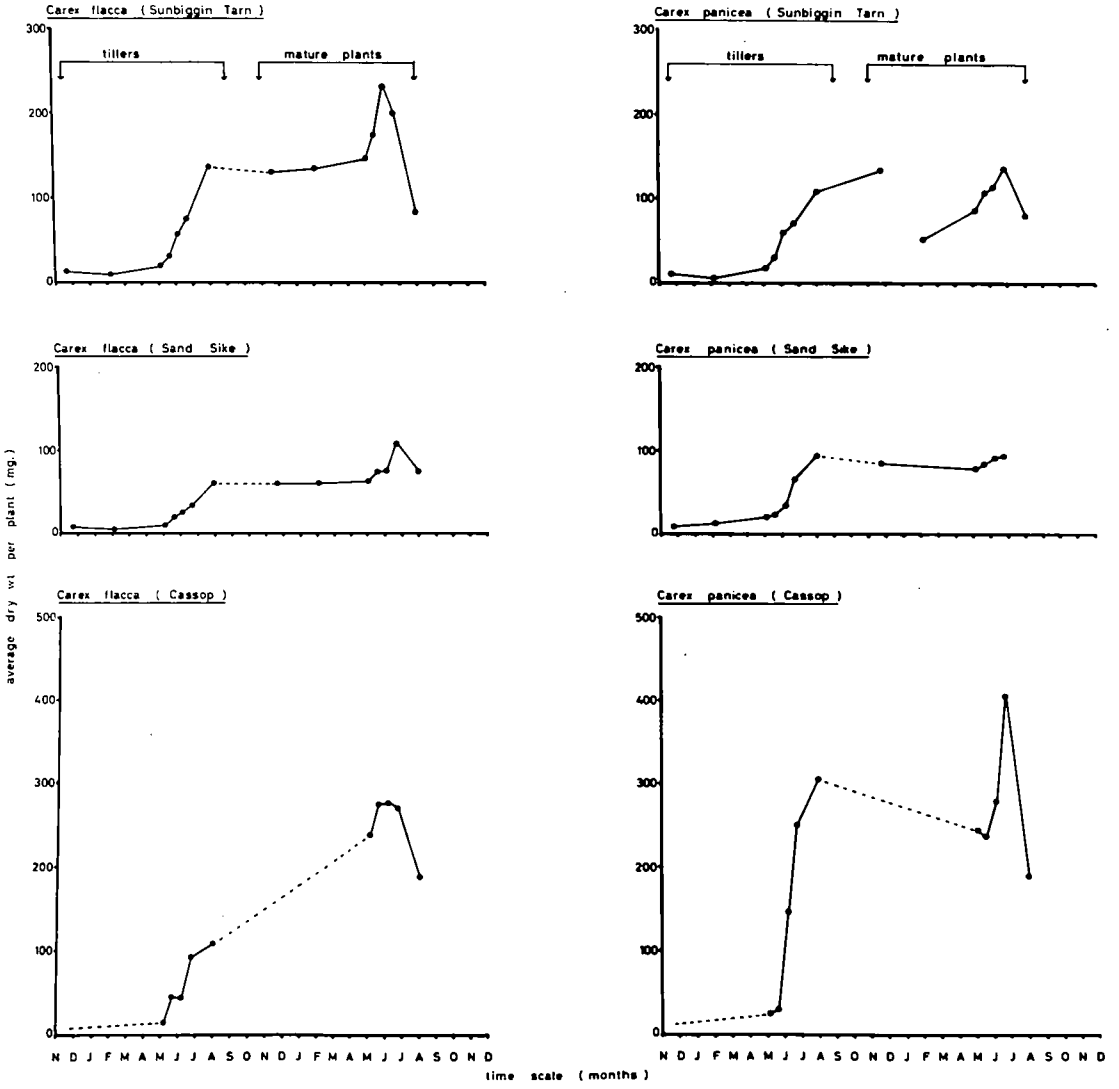

Carex flacca (Sunbiggin Tarn)
tillers
mature plants
Carex panicea (Sunbiggin Tarn)
tillers
mature plants
Carex flacca (Sand Sike)
Carex panicea (Sand Sike)
Carex flacca (Cassop)
Carex panicea (Cassop)
average dry wt per plant (mg.)
N D J F M A M J J A S O N D J F M A M J J A S O N D
time scale (months)

FIGURE 19.

Nutrient dynamics -

Variation in calcium content over the growing period.

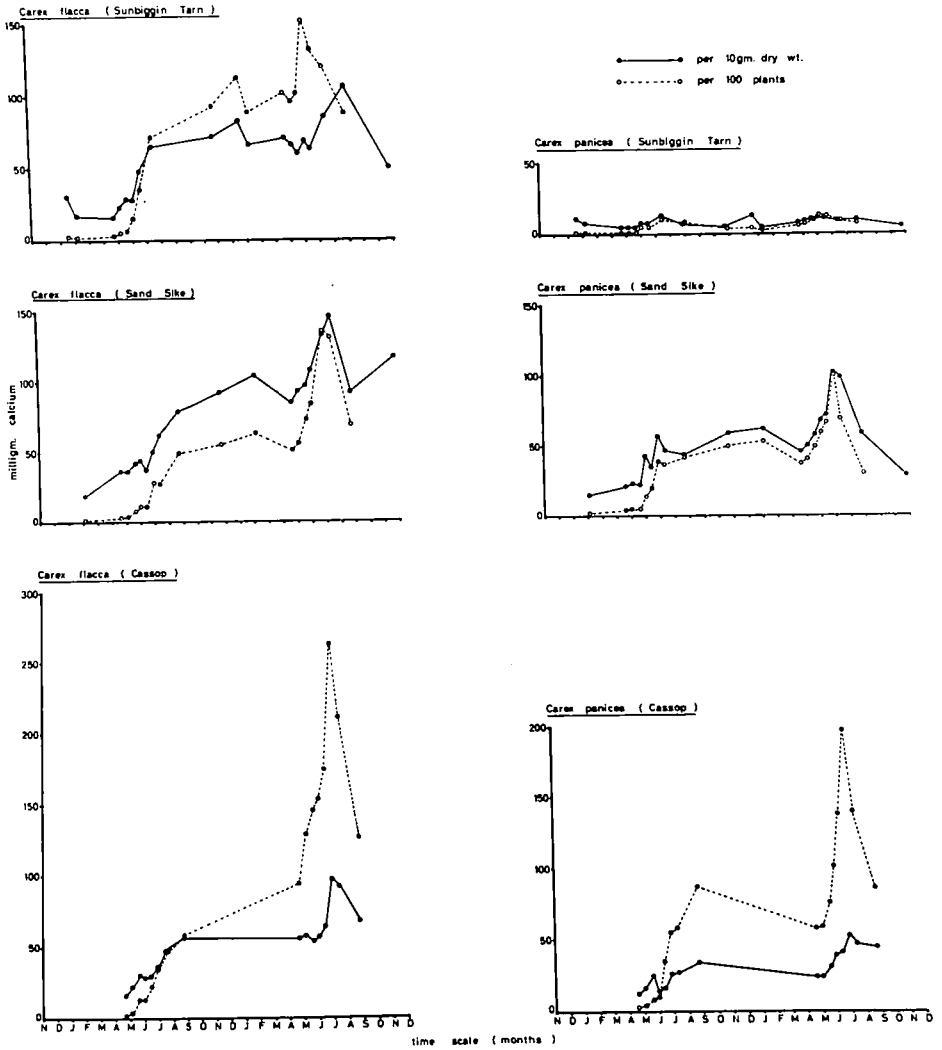
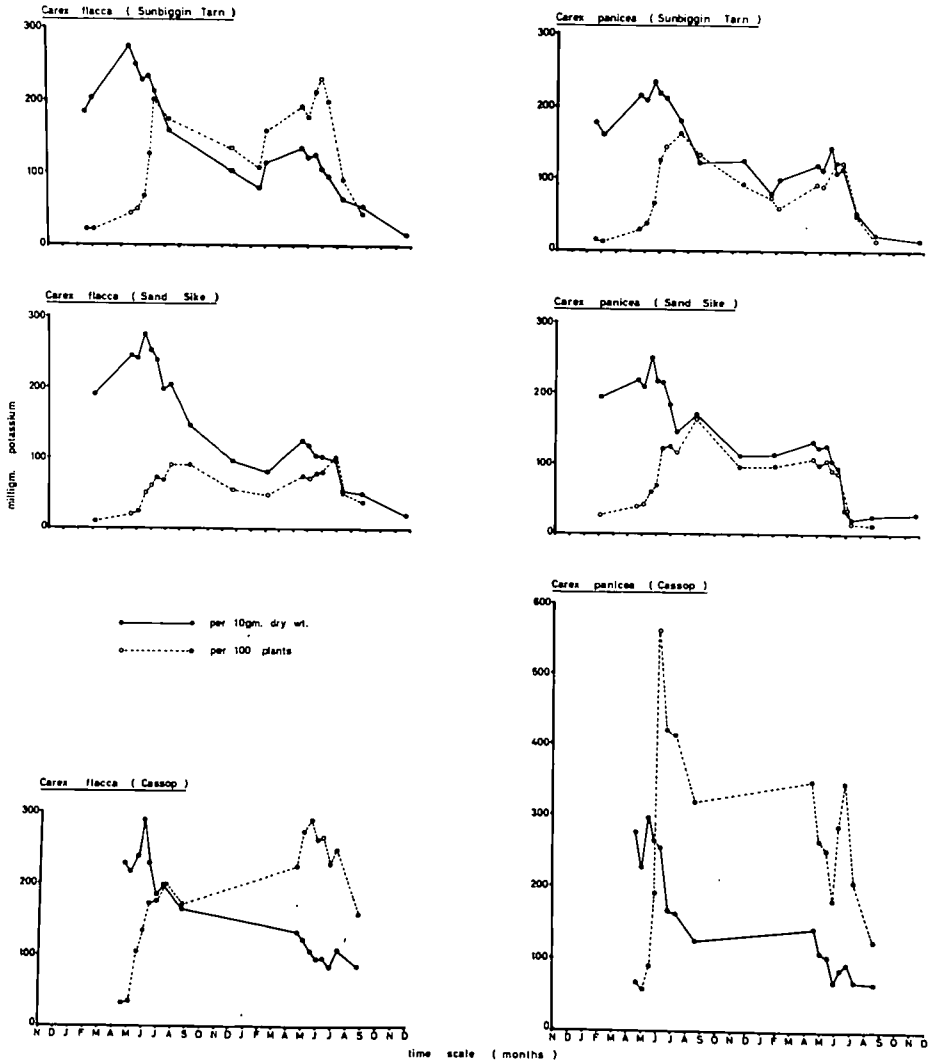

Carex flacca (Sunbiggin Tarn)
per 10gm. dry wt.
per 100 plants
Carex panicea (Sunbiggin Tarn)
Carex flacca (Sand Sike)
Carex panicea (Sand Sike)
milligm. calcium
Carex flacca (Cassop)
Carex panicea (Cassop)
N D J F M A M J J A S O N D J F M A M J J A S O N D
time scale (months)

FIGURE 20.

Nutrient dynamics -

Variation in potassium content over the growing period.


Carex flacca (Sunbiggin Tarn)
Carex panicea (Sunbiggin Tarn)
Carex flacca (Sand Sike)
Carex panicea (Sand Sike)
milligm. potassium
per 10gm. dry wt.
per 100 plants
Carex flacca (Cassop)
Carex panicea (Cassop)
N D J F M A M J J A S O N D J F M A M J J A S O N D
time scale (months)

(b) Additional chemical analyses.

The results are summarised in TABLE 20., from which can be seen the large differences in the concentrations of calcium and potassium, and to a lesser extent, magnesium, that exist between adjacent parts of the same plant, and even of the same leaf.

As an example, chemical analysis data for Carex panicea from Cassop will be used. All results are expressed on a percentage basis.

1. The plant as a whole. (FIGURE 21.)

Calcium

Calcium content is lowest in the roots, rhizomes and young tillers. It is highest in mature tillers. When the dead leaves are removed from mature tillers and analysed separately from the photosynthetic parts, calcium is found to be very high in the dead leaves, and very low in the remaining photosynthetic parts.

Potassium

Potassium, on the other hand, is lowest in the dead leaves and highest in the developing tillers. It is also high in the photosynthetic parts of the mature tillers.

Magnesium.

Magnesium does not vary so much in concentration as either calcium or potassium, but it appears to be higher in the mature tillers than in the roots, rhizomes or young tillers. Rather surprisingly, a higher percentage magnesium content is detected in the dead leaves than in the photosynthetic parts of the mature tillers.

2. Leaves. (FIGURE 22.)

Analysis of four leaf fractions, sheaths, lower photosynthetic lamina, upper photosynthetic lamina and dead tips show that calcium increases from a very low concentration in the sheaths to a very high level in the dead tips. Potassium is lowest in the dead tips and sheaths, and highest in the upper portion of the lamina adjacent to the dead tips. Magnesium is also highest in the upper lamina, and lowest in the sheaths.

From these results it is obvious that great care must be taken in the interpretation of results obtained by chemical analyses of whole plants, or even whole leaves. The average values

thus obtained will be entirely dependent on the proportion of living to dead material in the sample.

FIGURE 21.

Chemical analysis of different organs of *Carex panicea*.

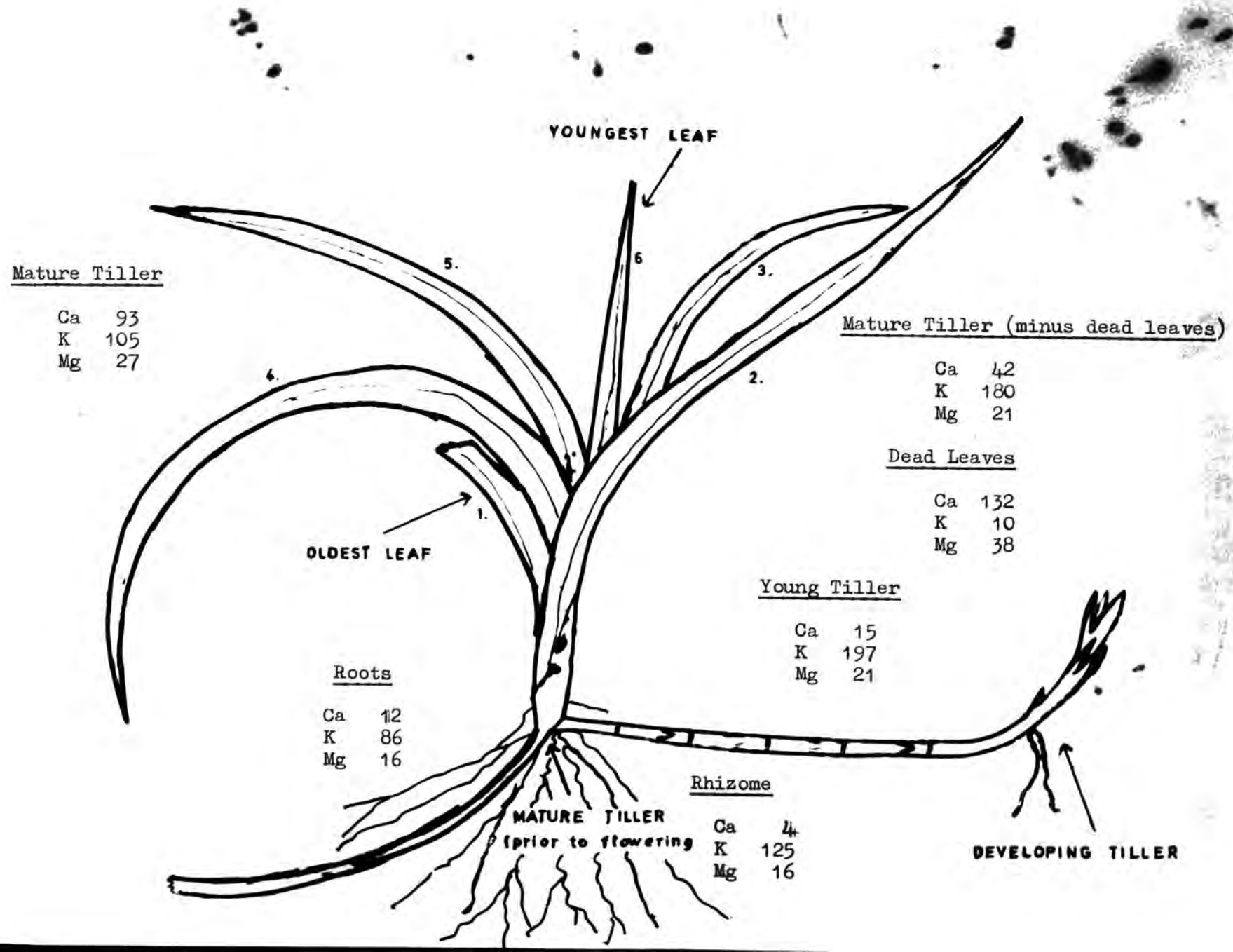
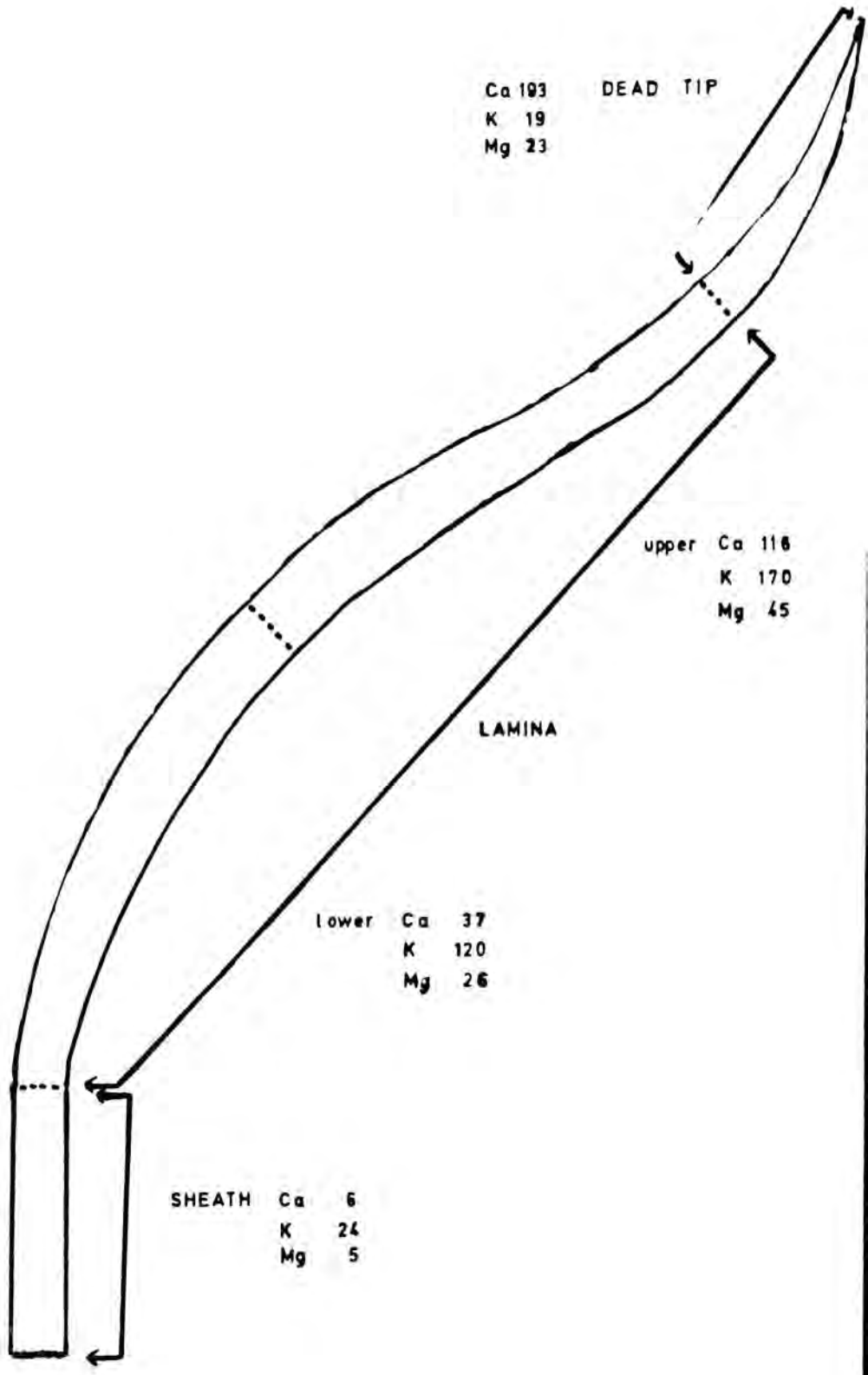

YOUNGEST LEAF
Mature Tiller
Ca 93
K 105
Mg 27
5.
6
3.
4.
2.
1.
OLDEST LEAF
Mature Tiller (minus dead leaves)
Ca 42
K 180
Mg 21
Dead Leaves
Ca 132
K 10
Mg 38
Young Tiller
Ca 15
K 197
Mg 21
Roots
Ca 12
K 86
Mg 16
Rhizome
Ca 4
K 125
Mg 16
MATURE TILLER
(prior to flowering
DEVELOPING TILLER

FIGURE 22.

Chemical analysis of different parts of individual leaves of Carex panicea. (results are expressed as mg./10gm. dry plant material.)


Ca 193
K 19
Mg 23
DEAD TIP
upper Ca 116
K 170
Mg 45
LAMINA
lower Ca 37
K 120
Mg 26
SHEATH Ca 6
K 24
Mg 5

DISCUSSION.

'Flow diagrams' have been constructed to represent the levels of calcium, potassium and magnesium present in Carex panicea and C. flacca plants at different stages of development over the two year growth cycle. The stages of development which were chosen for the various compartments of these diagrams were selected subjectively, but they are comparable for each species and element.

These stages are :-

A. First year tiller - maximum value of each element at the end of the first year's growth phase.

B. Mature plant - maximum value immediately before flowering.

C. Dead plant - lowest value detected after fruiting.

D. Very young tillers - content at youngest obtainable stage.

E. Fruiting stem - maximum content.

F. Seed - content per seed.

Because of the different habitat conditions prevailing at each collecting site, plants matured and flowered at different times, and, consequently, nonstandard collecting date could be selected as a reference for the nutrient dynamics diagram data. FIGURE 23. summarises the life cycle of these two species and appropriate values for calcium, potassium and magnesium have been substituted at each stage. FIGURES 24 & 25 From the difference in these values between adjacent stages, certain tentative suggestions can be made about the supply and distribution of these three major elements. The diagrams do not represent an exact picture since formation of new tillers and flowering stems is not an abrupt occurrence as depicted, but parallels the growth and nutrient absorption of the parent plant over a considerable period of time. All values listed in these diagrams refer to the average content of calcium, potassium or magnesium of 100 plants, tillers, flowering stems or seeds as the case may be. ~~The nutrient budgets~~ Because of the difficulty of expressing the chemical analysis results of roots and rhizomes on a total basis these nutrient

FIGURE 23.

Nutrient Dynamics flow diagram.

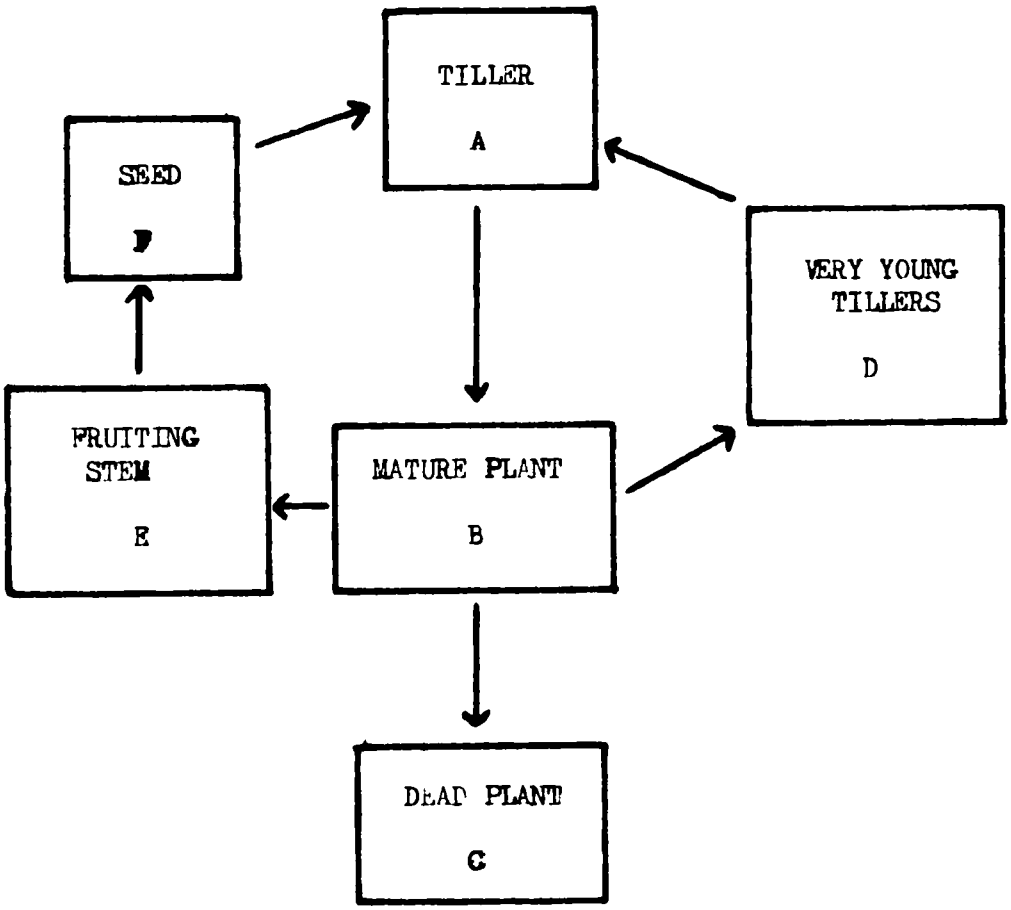
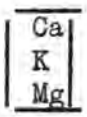

TILLER
A
SEED
VERY YOUNG
TILLERS
D
FRUITING
STEM
E
MATURE PLANT
B
DEAD PLANT
C

FIGURE 24.

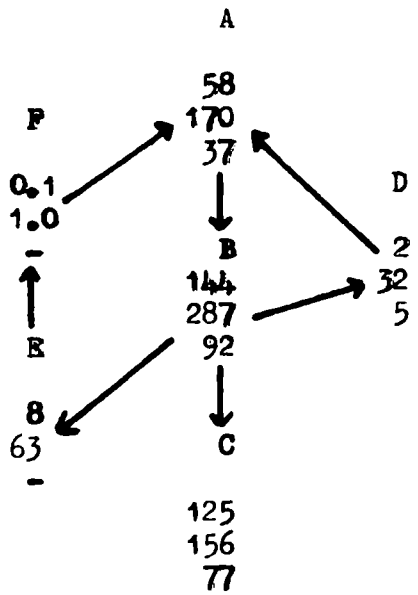
Nutrient dynamics flow diagram -
Carex flacca.
(values expressed as mg./100 plants.)

Key -

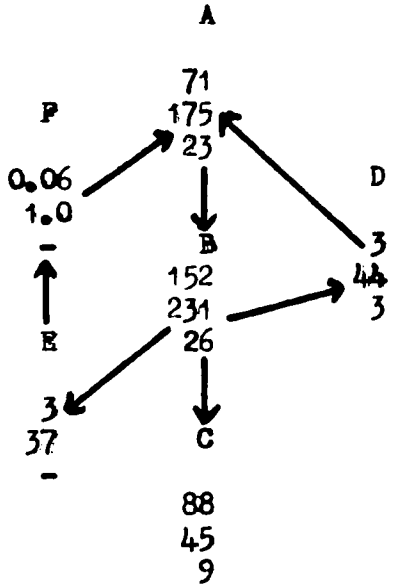


CAREX FLACCA

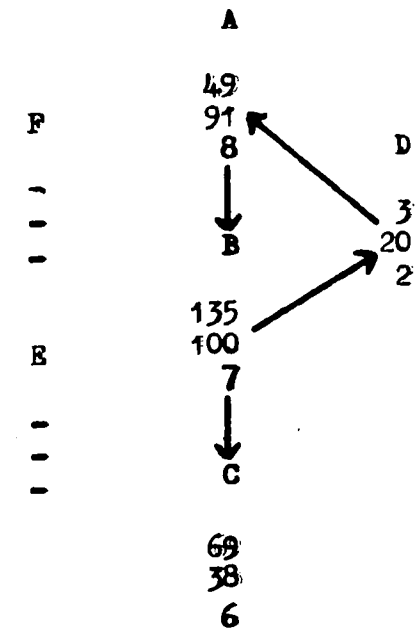
1. Cassop (limestone grassland.)



2. Sunbiggin Tarn (transition mire.)



3. Sand Sike (flush)



No values available for fruiting stems or seeds.

FIGURE 25.

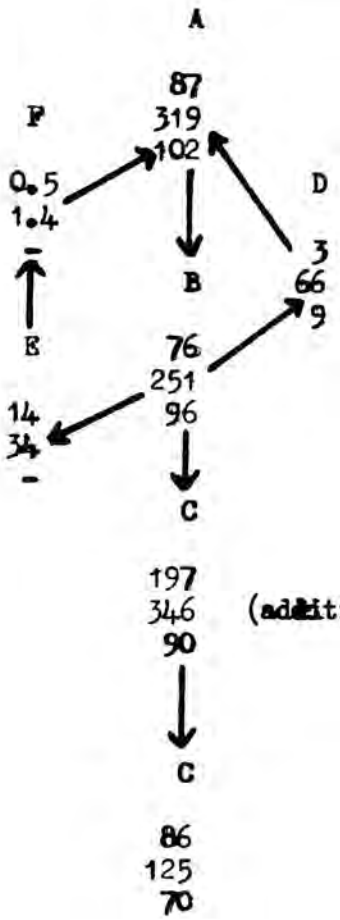
Nutrient dynamics flow diagram -
Carex panicea.
(values expressed as mg./100 plants.)

In the case of plants from Cassop the maximum values of the mature tillers were not reached immediately before flowering but occurred later. An additional stage has been incorporated in this diagram to take this into account.

Key -

CAREX PANICEA

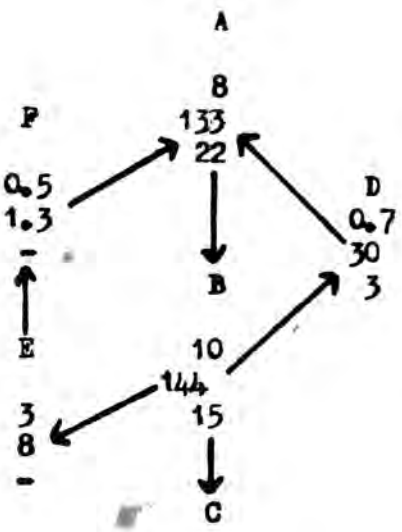
1. Cassop (transition mire.)



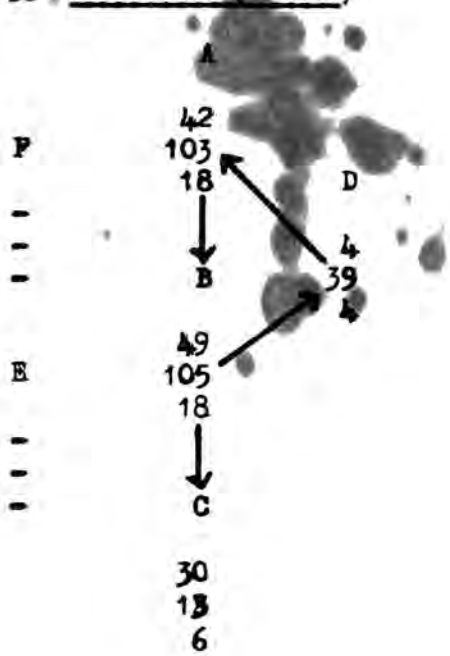
(additional stage)

No values available for fruiting stems or seeds.....

2. Sunbiggin Tarn (acid peat.)



3. Sand Sike (flush)



budgets have been presented for the above-ground parts of these plants only (plus newly emergent tillers).

Potassium.

On the whole, the amount of potassium in the fruiting stems corresponds to the potassium content per seed times the average number of seeds per plant. The potassium content per seed is relatively low, a factor which could lead to difficulty of seedling establishment and survival in areas with potassium deficient soils, or, in habitats in which competition for available potassium is high. On the other hand, the level of potassium in very young tillers is relatively high. Analysis of plants from subsequent cropping intervals during the growing season show that this value increases consistently as the tiller develops.

A very rough comparison can be made between the difference in potassium content of mature plants before and after fruiting (taking into consideration the potassium level in the fruiting stems), and the estimated amount of potassium potentially available for translocation to developing tillers. If one divides this amount of potassium by the potassium level detected in the very young tillers a number is arrived at which could approximate to the maximum possible number of tillers per plant.

Examples.

Carex flacca - Sand Sike.

Potassium decrease in mature plants after fruiting = 40 mg.

Potassium level in very young tillers = 20 mg.

The decrease could supply enough potassium for 2 tillers of this age.

Average number of tillers observed in the field = 2.

Carex flacca - Sunbiggin Tarn.

Potassium decrease = 150 mg.

level in young tillers = 44 mg.

decrease is sufficient to supply 3-4 tillers per plant.

Average number found in field = 2.

Carex panicea - Sand Sike.

Potassium decrease = 80 mg.

Level in young tillers = 40 mg.

Decrease is sufficient to supply 2 tillers per plant.

Average number found in field = 2.

Carex panicea - Sunbiggin Tarn.

Potassium decrease = 120 mg.

level in young tillers = 30 mg.

Decrease is sufficient to supply 4 tillers per plant.

Average number found in field = 2.

This is a very crude way of representing nutrient flux through a plant's life cycle, but it serves to illustrate what might be happening in nature.

The availability of potassium to the roots of a plant may be reflected in the absolute amount of this element detected in the plant itself, as can be seen from the varying levels of potassium found in the same species collected from different habitats. Thus Carex panicea collected from the transition mire site , with a relatively large supply of exchangeable potassium,contains a higher concentration of potassium in its leaves than Carex panicea from the acid moorland site. In this latter case, few seeds are set and the dead plants contain very little potassium at all. The emergent tillers from this acid site have a relatively high level of potassium and this is a good case for suggesting a 'shunting' mechanism for relaying potassium

to the actively growing parts where it is in greatest demand.

It is also possible that seed production is regulated by the amount of available potassium in the plant. The level of potassium in the seeds of plants from the acid site is similar to that in seeds from the sites richer in potassium, but the number of seeds produced in the former case is very much reduced. It would seem to be the case that the vegetative cycle receives preferential treatment with respect to available potassium.

Calcium

The flow diagrams for calcium differ from those for potassium in that calcium content is much less than potassium in the very young tillers and also in plants at the end of the first growth pulse. Analysis of plants from consecutive cropping intervals reveals that this low calcium level is maintained over the first 6 or 8 weeks and then increases steadily until it reaches the first year maximum. This increase corresponds with the time of formation of the root systems of the developing tillers.

In the cases of Carex flacca from Sunbiggin Tarn and C. panicea from Cassop, there is found to be a considerable

difference in calcium content between the second year peak and that detected after fruiting (60 mg. in the former and 100 mg. in the latter). Very little of this difference could be accounted for by new tiller formation, in fact, only between 6 and 10 mg. can be accounted for in this way. Assuming 3-4 tillers per plant, between 50 and 90 mg. (per 100 plants) calcium are unaccounted for and the most likely explanation is that this amount has been leached from the dead leaves and returned to the soil. It was also found that the fruiting stems and seeds contained less calcium than potassium, and germinating seeds would have to absorb almost all of their calcium requirements directly from the substrate.

Carex panicea plants from the acid site illustrate the situation under conditions of nutrient stress (when one or more elements are probably in short supply). In this case (for calcium) the maximum content of 11 mg./100 plants is reached by the end of the first year, drops to 10 mg. by the end of the second year, and decreases further to 7 mg. after fruiting. The difference of 3 mg. can be accounted for, by the amount of calcium present in the fruiting stem and seeds. The developing tillers has only 0.7 mg./100 plants, and this increased very slowly with age.

Magnesium

The trends in magnesium content over the year are similar to those for calcium. The concentration of this element is very low in the developing tillers

SUMMARY.

1. The growth curve data shows that although Carex panicea and C. flacca are perennials, individual tillers act as biennials.

2. With progressive ageing, percentage potassium content decreases; total potassium increases over the first year, but falls sharply after flowering; both percentage and total calcium content increase steadily over the two year period, but tend to decrease after fruiting.

3. Analysis of different plant organs reveals considerable variation in the concentrations of calcium, potassium and magnesium between adjacent parts of the same plant.

4. As the plants age there appears to be a change in their physiological properties which enables calcium to enter in greater quantity and accumulate prior to death of the plants, and, at the same time, allows potassium to leak out or be translocated away.

PART IV.

GENERAL DISCUSSION.

The culture experiments basically show :-

1. That both Carex panicea and C. flacca absorb the elements magnesium, potassium and phosphorus very efficiently even when another essential element, such as calcium, is present in very low or very high concentration. In both of these extremes, plants maintained similar levels of these three elements in their tissues, presumably because they were present in more than adequate supply.

The reasons for these uptake patterns are not altogether clear, but they may be connected with the permeability properties of the root cells and with the transport mechanisms within plants (EPSTEIN, 1961). JENNINGS, (1963), mentions that cations (especially calcium) can have a very marked effect upon the permeability properties of living cells. The 'antagonistic' properties of such cations when present in low concentration in the

medium external to the tissues involved is well known in reducing the toxic effects of other solutes. VIETS, (1944), found, for excised barley roots, that the absorption of potassium and bromide ions from a 5 mM solution of potassium bromide could be increased by the presence of calcium ions in the external medium up to a concentration of 22 m.e./litre. (This could help to explain the very low levels of potassium detected in plants from Experiment 1. in the absence of calcium from the culture solution.) Above this concentration of calcium, there was a decrease in the uptake of both potassium and bromide ions. VIETS, (1944), also found that calcium uptake increased with increasing concentration of calcium in the external solution. These results were confirmed by OVERSTREET ET AL, (1952), who showed further that potassium ions inhibit the uptake of calcium from an 0.0005N calcium chloride solution (i.e. from very low solution concentrations). There was no evidence of stimulation of calcium uptake over the range of potassium concentrations which they used (up to 100 m.e./litre potassium chloride). This inhibitory effect of potassium on calcium uptake in solutions containing low concentrations of calcium could account for the decrease in calcium content of plants from the potassium experiment (Experiment 3.).

2. Above a certain threshold concentration of external calcium (about 50 p.p.m.) uptake of calcium by the plants greatly increases, no longer keeping pace with growth of the plant, but flooding in uncontrollably.

3. The germination and potassium variation experiments show both species to be very efficient in removing potassium from the culture solutions and maintaining the internal concentration at the critical level of 200 mg./10 gm. dry plant material.

Up to and external calcium concentration of 20 p.p.m. it would appear that Carex panicea and C. flacca absorb only enough calcium to keep pace with increase in dry weight, and they do not accumulate excess from the pool of calcium available to them. They exert what may be termed a 'buffering action' against excess calcium, maintaining a balance between what is available externally and what is required for growth. Above a certain external concentration, which, in these particular experiments is 20 p.p.m. for C. panicea and 50 p.p.m. for C. flacca, this buffering property breaks down and calcium is absorbed in greater quantity. The magnitude of this influx of calcium increases with increasing external calcium

concentration until death of the plant results.

Since analysis of different plant parts shows that calcium is concentrated in the dead and dying tissues this could be regarded as a 'DEATH REACTION'. Because the levels of the other essential elements potassium, phosphorus and magnesium do not change significantly in the calcium experiments it would seem that calcium is having a direct effect, and is not acting through an effect on some other major ion, i.e. the plants are only under calcium stress in this experiment. In the field where other essential nutrient elements may be in short supply, calcium stress could produce a much greater differential effect between the performance of these species.

These culture experiments were carried out over a period of 12 weeks only, and they do not provide an exact comparison with field conditions, but they do give some indication of the possible role played by calcium in, or during, the ageing of these plants.

In nature, it is evident from chemical analysis of samples collected over a period of many months that the calcium content remains steady at a low concentration for 2-3 months after emergence (which would be about the age of the tillers used in the culture experiments); this is followed by a steady increase in calcium content over the remainder of the two year life span, reaching a peak

about the time flowering finishes. Thus, progressive ageing of these plants is associated with a corresponding increase in calcium content until the plant dies. After reaching this maximum value, calcium content decreases as the leaves gradually decay. In the culture experiments this 'calcium death effect' has been telescoped into 12 weeks by applying high calcium concentrations to the roots of these plants. This brings about an increase in uptake and accumulation of calcium, a process which continues until the plant dies.

These observations could have important ecological implications in natural plant communities. There is evidence from the culture experiments that Carex flacca and C. panicea exhibit different responses to calcium. In C. panicea, accumulation of calcium in the leaves commences at a lower external calcium concentration than for C. flacca. In most treatments, C. panicea does not survive in solutions containing more than 200 p.p.m. calcium, and, in one instance, no plants survived above 100 p.p.m. calcium.

Tolerance of a plant to calcium can be divided into three phases :-

1. The 'BUFFERED' phase, during which the plant maintains a

balance between what is available and what is actually required. If insufficient calcium is available, death results at this stage.

2. The 'INFLUX' phase, commencing above a certain threshold level of calcium, (or after a certain age of the plant) at the onset of which the plant's buffering power is destroyed and calcium is absorbed in amounts greater than is normally required for healthy growth.

3. The 'DEATH' phase, resulting in the death of the plant, or part of it, with subsequent loss of calcium from the tissues by leaching.

Performance of Carex panicea and C. flacca increases with increase in the external calcium concentration until the influx concentration is reached, after which performance decreases. Presumably different species have different influx points and death phase concentrations, which, in turn, will give rise to different ecological tolerances.

Nutrient dynamics and nutrient cycling.

There is evidence from the field data to suggest that the elements potassium and calcium re-cycle in different ways. Potassium reaches its highest value, or very near to it, by the end of the first year's growth pulse, and decreases to a much lower value after fruiting. At the same time, as the potassium level falls in the mature plants, it is increasing in the newly formed tillers, and, also, to a lesser extent, in the fruiting stem. It would appear, at least in the earlier stages of tiller development, until roots are formed, that potassium is supplied in sizeable quantities to the developing tillers via the parent plant, and it is possibly being transported from the dying leaves to the meristematic regions in the tillers. PENSTON, (1931), determined the relative concentration of potassium in different tissues of tomato by estimating the density of cobalt hexanitrite precipitate in the cells. He found that the tissues in which potassium was concentrated were :-

1. Apical meristems of roots and shoots.

2. Outer regions of the cortex, especially in stems, and to a lesser extent in roots.

3. Phloem.

4. Active green leaves.

5. Reproductive organs.

In early stages of development, he found that leaves had a very dense precipitate in all green cells. In yellow leaves, cells of the mesophyll lost their potassium and chloroplasts showed signs of disintegration, while elements of the vascular bundles were full of potassium not yet conducted away.

Much evidence has accumulated over the last 30 years indicating a decrease in potassium content of plant leaves with progressive maturity, and for redistribution of this element to other parts of the plant: RIPPEL, (1927); JAMES, (1931); FAGAN & WATKINS, (1932); RICHARDSON, (1932); WAGNER, (1932); PETRIE, (1934); SAMPSON & SAMISCH, (1935); ULRICH, (1943); THOMAS & TRINDER, (1947); OLSEN, (1948); BLACKMAN & RUTTER, (1949); THOMAS ET AL, (1952); GOODMAN & PERKINS, (1959); ALLEN & PEARSALL, (1963).

GOODMAN & PERKINS, (1959), found that in Eriophorum vaginatum potassium was much higher in living tissues than in dead parts, and they suggested that potassium might be translocated to the roots or to the immediate vicinity of the roots in the soil as the plants died to form a pool of available potassium. Analysis of root and rhizome material of C. panicea and C. flacca did not reveal any marked changes in potassium content corresponding to a loss from the leaves due to possible redistribution.

Since potassium appears to be washed out of dead or dying leaf material very quickly, (LONG ET AL, 1956; STENLID, 1958; TUKEY ET AL, 1958; BHAN ET AL, 1959; TUKEY & MORGAN, 1962; TUKEY & TUKEY, 1962; CARLISLE ET AL, 1965 & 1966.) it is possible that redistribution within the plant may not be the only pathway by which potassium can be re-cycled. Some potassium could be removed directly from the above-ground plant parts, to the substrate, by the leaching action of rainwater. Potassium would then have to be re-absorbed by the plant roots.

With the analysis of dead and living parts of individual leaves, it was not possible to calculate results on a 'per plant' basis, because many leaf parts of varying size had to be bulked for analysis, but it is possible that in the field, potassium is leached from leaves immediately they turn yellow and commence to die back.

However, these analyses were carried out on the leaves of plants kept in a heated greenhouse for a considerable period of time and were subjected to occasional watering only, and, consequently, they would not be exposed to continual leaching. It is open to question whether this irregular watering would be sufficient to remove the potassium directly from the leaves and further investigation of this possible effect will have to be carried out under controlled conditions.

The difference between the high levels of potassium found in plants and the very low levels of exchangeable potassium (compared with other elements) detected in many soils, indicates that these plants must be very efficient in removing potassium from their substrates. Even in the acid Sunbiggin Tarn peat with only 4 mg. potassium per 100 gm. oven dry peat, the concentration of potassium within the plants is still relatively high. Until developing tillers produce their own root systems, which may not be until several months after emergence, they must be entirely dependent upon the parent plant for their nutrient supply. Whether this supply comes from the soil via the root system of the parent plant, or by translocation from the dying leaves is still in doubt.

Evidence for and against translocation of potassium from ageing plant organs to developing ones is not very conclusive.

Most work on this aspect has involved estimating potassium as a percentage of the dry weight of plant material, and this does not take into account fluctuations in the dry weight due to carbohydrate change, and, in fact, what may be interpreted as a loss of potassium from percentage results may disguise an actual increase in total potassium content.

On a percentage basis WAGNER, (1932), MASON & MASKELL, (1931), and RIPPEL, (1927), have said that potassium accumulates in successive young leaves, and as each leaf ages and finally dies most of the potassium is translocated to leaves that are younger and situated higher in the plant. Finally they suggest that a certain amount migrates to the inflorescence, but when most of the leaves are senescent, the bulk of potassium in the plant is translocated from the leaves into the stem and passes into the roots, and a portion of it returns to the external medium. They imply that the later formed organs derive their potassium partly or wholly from earlier formed organs. Support for this point of view was provided earlier by JANSSEN & BARTHOLOMEW, (1929), who found that in potassium-starved plants potassium appeared to be transferred and localised in the meristematic and growing parts, and that dead leaves were relatively free of potassium. Later, however, MITCHELL, (1936), found that

in tree leaves total potassium increased throughout the year, while at the same time percentage potassium decreased due to the 'dilution effect' of growth already mentioned. On a total basis, he found that all the elements he analysed for, increased during the growing season and leaves fell before any backward loss was detected.

There is no direct evidence to support the translocation theory that could not equally well be explained by direct leaching from the plants and re-supply from the root system of established parent plants.

Reasons against redistribution of potassium within these plants :-

1. High percentage potassium levels on further investigation reveal low levels of total potassium.

2. No increase in the percentage potassium contents of the roots or rhizomes was detected.

3. Consistent decrease in percentage potassium often disguises an increase in total potassium.

4. In young tillers, very little increase in total potassium takes place until after roots have formed.

Evidence for redistribution:-

1. Total potassium decreases after flowering.

2. There is a sharp boundary between high percentage potassium in the living parts of the leaves and very low percentage potassium contents in adjacent dead parts.

3. There is a slight decrease in total potassium at the end of the first year's growth period, coincident with the emergence of new tillers.

4. Newly emergent tillers have no root system of their own, and must obtain their nutrient supply from the parent plant.

It is well established that the calcium content of plants is low in new tissues at the beginning of their growth, and, as the plant organs age, there is an increase in total and percentage calcium. Total calcium increases because the plant absorbs this element continually throughout its life cycle; and percentage, because this process of accumulation continues even after the plant organs have reached their maximum dry weight, so that further increase in total calcium leads to an increase in percentage calcium. During active leaf growth percentage calcium may remain steady, or even drop, as calcium uptake keeps pace with, or lags behind, increase in dry weight.

It is interesting to note that in plants collected from regions representing the two extremes of calcium concentration in the field, there are marked differences in the calcium contents of the plants. Carex panicea collected from the nutrient-deficient acid peat at Sunbiggin Tarn contains very little calcium, and the calcium content does not exhibit any significant seasonal variation over the two-year growth cycle. Plants from the calcareous Cassop Vale site show a very large increase in calcium content over the life span. Similar results are obtained for C. flacca from different sites. These results suggest that these two species can absorb

large quantities of calcium if it is available, but, when it is present in very low concentration, they are not such efficient a absorbers and accumulators of this element as they are of potassium. The results of other workers also show this tendency of calcium content of plant material to increase with age: FAGAN & WATKINS, (1932); McHARGUE & ROY, (1932); SAMPSON & SAMISCH, (1935); MITCHELL, (1936); OLSEN, (1948); WILL, (1957); PRITCHARD ET AL, (1964).

ALLEN & PEARSALL, (1963), found that calcium was not withdrawn from the leaves of Phragmites in the autumn as were other major elements, and they suggested that this might have been due to the fact that calcium was mainly present in plant material as insoluble pectates of the cell walls, and, as such, was immobile and unable to be translocated.

PETRIE, (1934), analysed tree leaves at different times during the growing season. He expressed his results both on a percentage and on a total basis. He found that calcium, as a percentage, declined during adolescence. This he explained by the fact that increase in growth must have exceeded rate of calcium uptake. After this period, calcium content increased again, thereafter remaining more or less constant. On a total basis, calcium increased until late senescence and then underwent no appreciable decline. He suggested that calcium was much less mobile in plants than potassium.

Calcium accumulated in the leaves but did not migrate out again so that calcium supplies for each successively formed organ must be derived directly from the external medium. He suggested further that the drift in absolute amounts of both potassium and calcium in individual leaves resembled the situation in the plant as a whole and implied that most of the calcium in the plant was fixed chemically and irreversibly in the living parts, and that loss of calcium was probably prevented by low mobility and continued fixation.

It may be that while leaves are still living and attached to the plant, no calcium is translocated away, but after death (and fall in the case of trees) calcium reverts to a soluble form and is leached out as the plant material decays. TAMM, (1951), however, adds a note of caution about placing too much weight on large percentage increases in calcium content of tree leaves, and suggests that such increases may only be apparent and largely due to a decrease in dry weight resulting from carbohydrate loss after death.

In Carex flacca and C. panicea calcium content decreases after the fruit have set and the leaves of the parent plant die. This decrease cannot be accounted for by the amount of calcium detected in the young tillers at this time. It would appear that calcium

is not being 'shunted' into the developing tillers (or into the seeds) but that the gradual decrease in calcium content after fruiting represents a direct loss from the dying leaves to the substrate, from which subsequent generations must absorb calcium directly. In habitats deficient in calcium this could lead to serious competition effects.

If we regard the sedge tiller as a biennial we would expect the following developmental scheme derived from the results of the culture experiments and from analysis of different parts of plants collected from the field.

GROWTH (1st. year)	DEATH OF PARTS OF THE PLANT
Uptake of potassium to obtain and maintain the optimum level.	Slight decrease in potassium.
Buffering against calcium.	Influx of calcium into dead parts.

REGROWTH (2nd. year)	DEATH OF PLANTS	DECAY
Further uptake of potassium to maintain optimum level.	Efflux of potassium.	Leaching of residual potassium and calcium.
Buffering against calcium uptake.	Influx of calcium.	

It is possible to postulate an overall scheme of growth and nutrient dynamics for these two species with respect to potassium and calcium (FIGURE 26). The data obtained from chemical analysis of field material supports this scheme in general (TABLES 17 & 18; FIGURES 27 & 28).

One major problem remains unsolved. Does calcium cause death, or simply flood in during the process of dying. The culture experiments point to the conclusion that calcium is the cause of death. Performance decreases at the higher external calcium concentrations; calcium floods in, but all other nutrients are present in the plant tissues in adequate quantity right up to the highest external calcium concentration at which plants survived. If the supposition that calcium causes death of these plants is true, then high external calcium concentration in nature could decrease the performance of a species at either growth pulse (by causing early death of plants during the first growth phase, but it may have more effect upon the second growth pulse when natural influx of calcium is greater). Consequently Carex panicea with its lower threshold tolerance would suffer more under conditions of high external calcium concentration than would Carex flacca, and it is possible that the former species could be excluded from habitats rich in calcium for this reason.

FIGURE 26

Theoretical nutrient dynamics and growth histogram for Carex panicea and C. flacca(calcium and potassium).

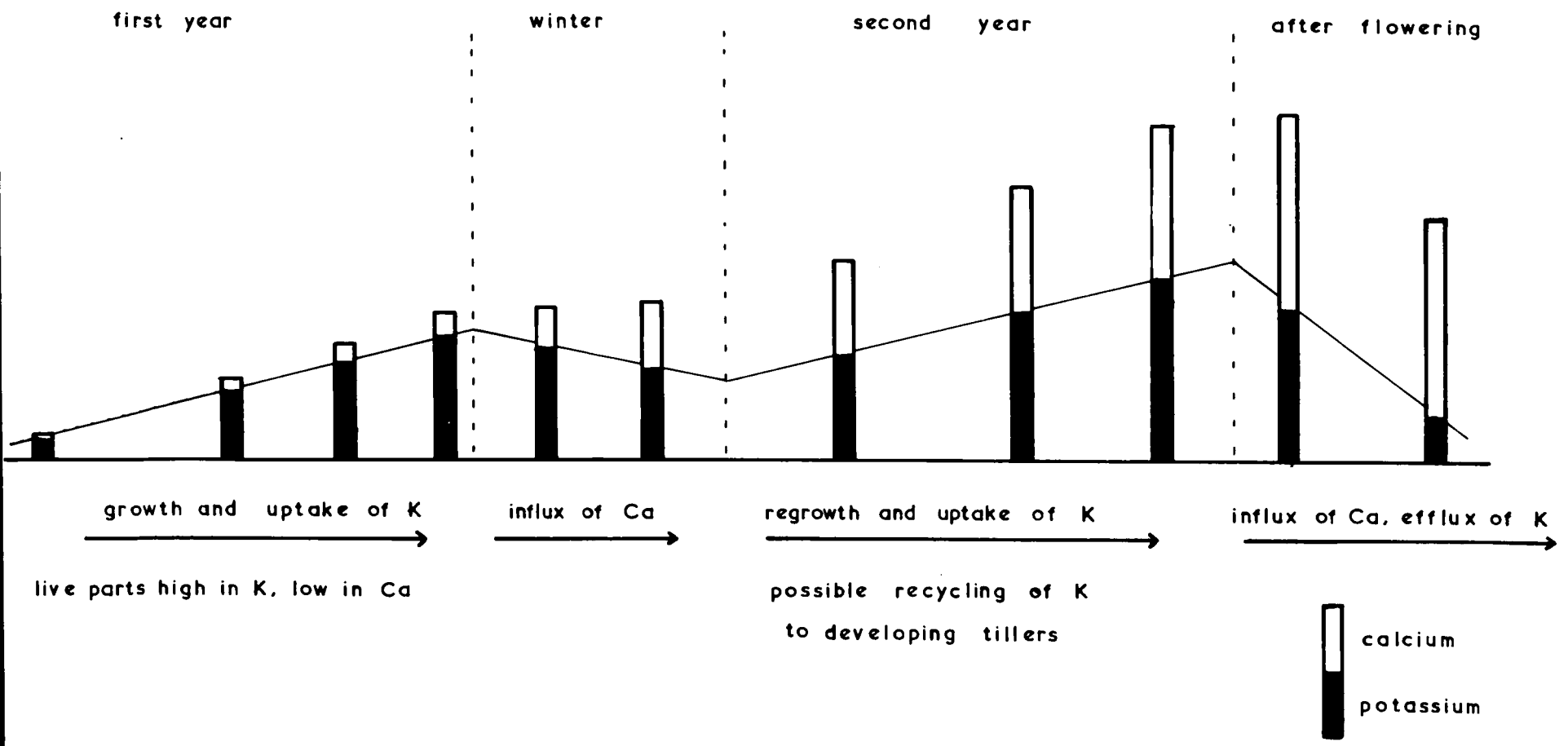

first year
winter
second year
after flowering
growth and uptake of K
influx of Ca
regrowth and uptake of K
influx of Ca, efflux of K
live parts high in K, low in Ca
possible recycling of K
to developing tillers
calcium
potassium

FIGURE 27.

Calcium/potassium histogram - *Carex flacca*.
(mg./100 plants.)

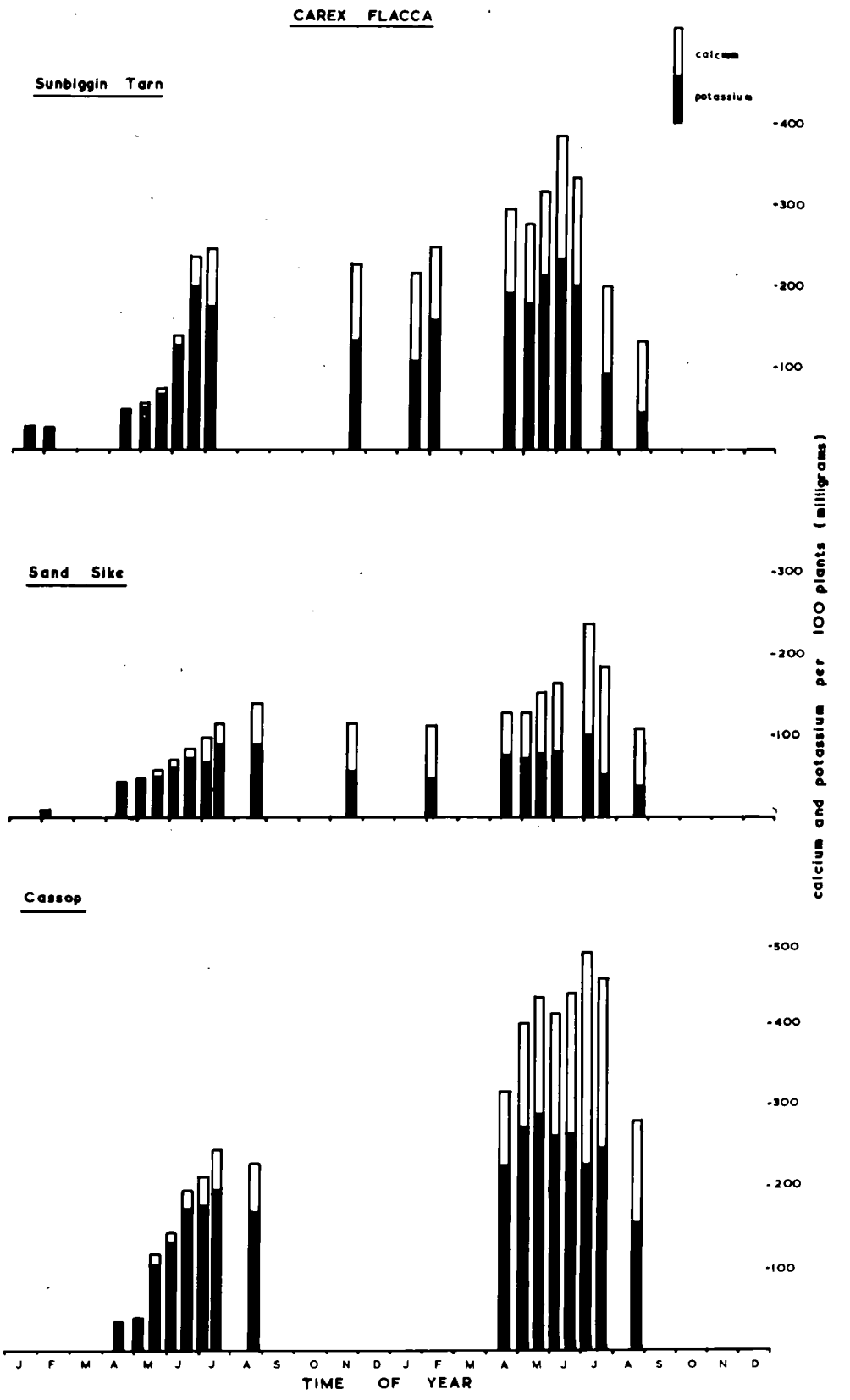
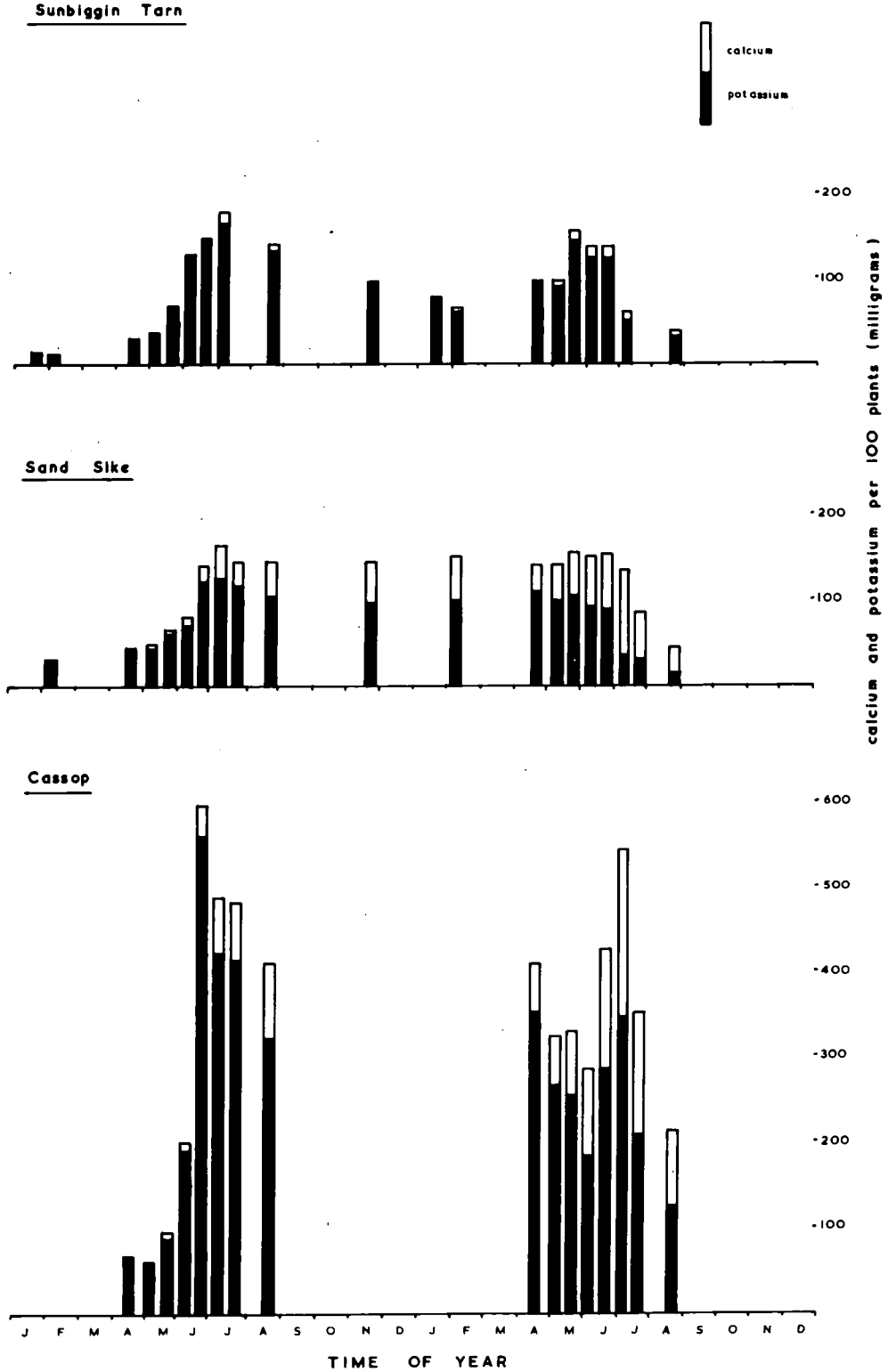

CAREX FLACCA
Sunbiggin Tarn
calcium
potassium
400
300
200
100
Sand Sike
300
200
100
Cassop
500
400
300
200
100
calcium and potassium per 100 plants (milligrams)
J F M A M J J A S O N D J F M A M J J A S O N D
TIME OF YEAR

FIGURE 28.

Calcium/potassium histogram - Carex panicea.
(mg./100 plants.)

CAREX PANICEA



CONCLUSIONS.

This work has proved several things.

1. The difficulty of working with genetically non-uniform material, although the similar general trends obtained with each species perhaps indicate that one should not be too sceptical.

2. The difficulty of working with species which cannot be easily grown from seed. However, such species have to be investigated eventually, and one cannot solve all ecological problems by working with 'perfect' material.

3. Interpretation of chemical analysis results must be approached with the greatest caution. Not only must analyses be carried out at each phase of the life cycle, but each part, both dead and alive of every organ, should be analysed separately if results are to be meaningful. What is required is a complete and detailed mineral balance sheet for each stage in the growth cycle. This would involve a tremendous

amount of work and whether or not the results obtained would justify the effort involved it is difficult to say at this stage.

4. This work has indicated that the calcium 'DEATH EFFECT' might be a fruitful sphere for further investigation and that it might be helpful in explaining the different ecological tolerances of these two sedges. One way of tackling this problem would be by carefully planned fertiliser experiments in the field and transplant experiments of the two species into 'alien ground', linked with the use of radioactive tracers to follow uptake and translocation of the major nutrient elements in detail.

PART V.

APPENDICES.

APPENDIX 1.

The growth chamber. (FIGURE 29.)

The base consisted of four teak benches, the legs of which were sunk in the floor of the greenhouse to make the whole unit stable, and also to lower the working surface to a convenient height. A framework of $3\frac{1}{2}$" x $3\frac{1}{2}$" angle iron was bolted to the bench tops to hold the side panels in position. These side panels were double-walled, consisting of black polythene mounted on a wooden framework, and were removeable to facilitate easy access to any part of the cabinet. The roof was made of "Claritex", polyglaze transparent sheet, supported at intervals by narrow wooden strips. Them bench tops were treated with wood preservative and covered with polythene sheet, to prevent water from the culture bowls warping or rotting them. Heating inside the cabinet was provided by a thermostatically controlled "Humex" air-heating wire secured round the perimeter and across the centre of the chamber on a wooden framework. Lighting was by 16 Phillips 400 watt mercury vapour horticultural lamps, mounted at regular intervals on a gantry

above the cabinet. There were regulated by three "Venner" time switches to provide lighting equivalent in length to that of a summer day. They were adjusted to switch on at 6 a.m., and off at 11 p.m. The space surrounding the chamber was heated, or cooled, by four $1\frac{1}{2}$ kilowatt fan heaters to keep the greenhouse temperature just below the level of 20°C maintained in the cabinet. These heaters were also thermostatically controlled, and two of them were fitted with perforated polythene ducts to ensure a more uniform distribution of heat throughout the greenhouse.

It was impossible to control temperature, light and humidity within narrow limits inside this growth chamber, and it was not intended to study the effects of these factors upon the growth of the plants in question. All that was required for the purpose of the experiments was that all plants in the growth chamber should be subject to identical conditions throughout one experimental run. Adequate supplies of heating and lighting were available to enable experiments to be carried out all year round. This technique allows strict comparisons to be made between the results of any one experiment only, and not between different experiments.

FIGURE 29.

The growth chamber.

APPENDIX 2.

The culture solution.

1. Calcium experiments.

Basic medium

salt	Wt. in gms. (for 40 litres, diluted nutrient)
KNO_3	4.04
$NaH_2PO_4 \cdot 2H_2O$	13.12
$MgSO_4 \cdot 7H_2O$	7.38
Ferric citrate	0.49
$MnSO_4 \cdot 4H_2O$	0.089
$CuSO_4 \cdot 5H_2O$	0.0096
$ZnSO_4 \cdot 7H_2O$	0.0116
H_3BO_3	0.0744
$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.0014

Calcium was added as calcium chloride ($CaCl_2 \cdot 6H_2O$) in amounts corresponding to the concentrations of calcium required in the respective culture solutions.

Wt. of $CaCl_2.6H_2O$ (gm.)	parts per million Ca^{++} in 40 litres of culture solution.
0.11	0.5
0.55	2.5
1.1	5.0
2.2	10.0
4.4	20.0
10.95	50.0
21.9	100.0
43.8	200.0
109.5	500.0

The final concentrations (p.p.m.) of the other lements in the basic culture solution was as follows :-

potassium	39
sulphur	24
nitrogen	20
phosphorus	20
magnesium	19
sodium	15
iron	2.8

manganese	0.55
copper	0.064
zinc	0.065
boron	0.37
molybdenum	0.019

The pH of the resultant nutrient solution was 4.2. In half of the treatments, in Experiment 1., the pH was raised to pH 7 by addition of appropriate quantities of sodium hydroxide solution.

2. Potassium experiment.

The basic culture solution was the same as before, except that calcium concentration was maintained at the low level of 2.5 p.p.m. by the addition of 0.55 gm. calcium chloride per 40 litres of culture solution. Potassium was varied, as potassium nitrate, and the concentration of nitrogen was maintained at the same level as in the basic medium by the addition of appropriate amounts of sodium nitrate.

Wt. of KNO_3 (gm.)	p.p.m. K^+ in 40 litres of culture solution.
0.323	0.5
0.646	1.0
1.615	2.5
3.23	5.0
6.46	10.0

Samples were taken from one batch of culture solutions before they were run into the culture bowls. Similar samples were collected from the culture solutions after one week in the growth chamber. Both batches of samples were analysed for calcium and potassium, and the results obtained are shown in TABLE 1.

The concentrations of these two elements changes during the week in the growth chamber, but not always in the direction that might have been expected. Calcium concentrations 'before and after' in the lower concentration ranges, up to 50 p.p.m. does not change very much over the week. Above this concentration, the level detected in the nutrient solution is greater at the end of the week than at the beginning, and it is thought that this increase

is brought about by evaporation of water from the solutions due to the large surface area of the bowls. In fact, evaporation may be compensating, to some extent, for removal of elements from the nutrient media.

Most of the potassium figures show the same pattern. The solutions were all prepared to contain 39 p.p.m. potassium, and they all contain approximately this amount. The potassium concentrations tend to increase slightly over the week in almost every case.

APPENDIX 3.

Chemical analysis techniques.

Determinations were made of the amounts of calcium, magnesium, sodium, potassium and phosphorus present in plant and soil samples. In the case of plant samples, this was calculated as a percentage amount of each element present in unit dry weight of dried plant material, and also as a total amount of each element per plant (or per 100 plants). In soils, each element was expressed in milligrams per 100 gm. oven dry soil. The methods employed were modified from the techniques described by PIPER, (1950); GORHAM, (1956), MACKERETH, (1963) and JEFFERIES & WILLIS, (1964). Analytical grade chemical were used throughout, and individual analysis techniques are described below.

I. PREPARATION OF SAMPLES.

1. Plant material.

Leaf material only was analysed from plants grown in the culture experiments as this was taken to give a truer representation of the nutrient status of the plants than the roots which were in constant contact with varying concentrations of nutrient solution.

Field material was separated, by means of a pair of fine-pointed dissecting scissors, into the various morphological parts :- roots, rhizomes, tillers, mature plants and flowering or fruiting stems. Each plant organ was analysed separately. In certain plant collections, the leaves themselves were sub-divided further into tips, laminas and sheaths, prior to analysis.

(a) Culture experiments.

After each experiment, plants were removed from the pots and washed in tap water to remove the polythene chips adhering to the roots, and then quickly rinsed in distilled water. The maximum leaf and root length of each plant was measured, after which roots were removed and both root and leaf portions were weighed and then dried in an oven at 80°C for 48 hours.

(b) Field collections.

After collection, plants were thoroughly washed in several changes of tap water to remove soil particles, and then rinsed in distilled water before separation of plant organs and drying as described above.

(c) Milling.

Prior to digestion all plant samples were ground to fine particle size in an "Apex" cutter mill to facilitate easier digestion of the material, and also to ensure homogeneity of the samples. No account was taken of possible contamination of the samples during milling (HOOD, 1944), since all samples were subjected to the same procedure and any error introduced in this way should have no relative significance.

(d) Digestion technique.

Approximately one gram of dried plant material (where available) was weighed, transferred to a 250 ml. conical flask and digested using a mixture of 20 ml. concentrated nitric acid, 5 ml. conc. hydrochloric acid and 5 ml. 60% w/v perchloric acid. Excess acid was removed by boiling on a heating rack in a fume

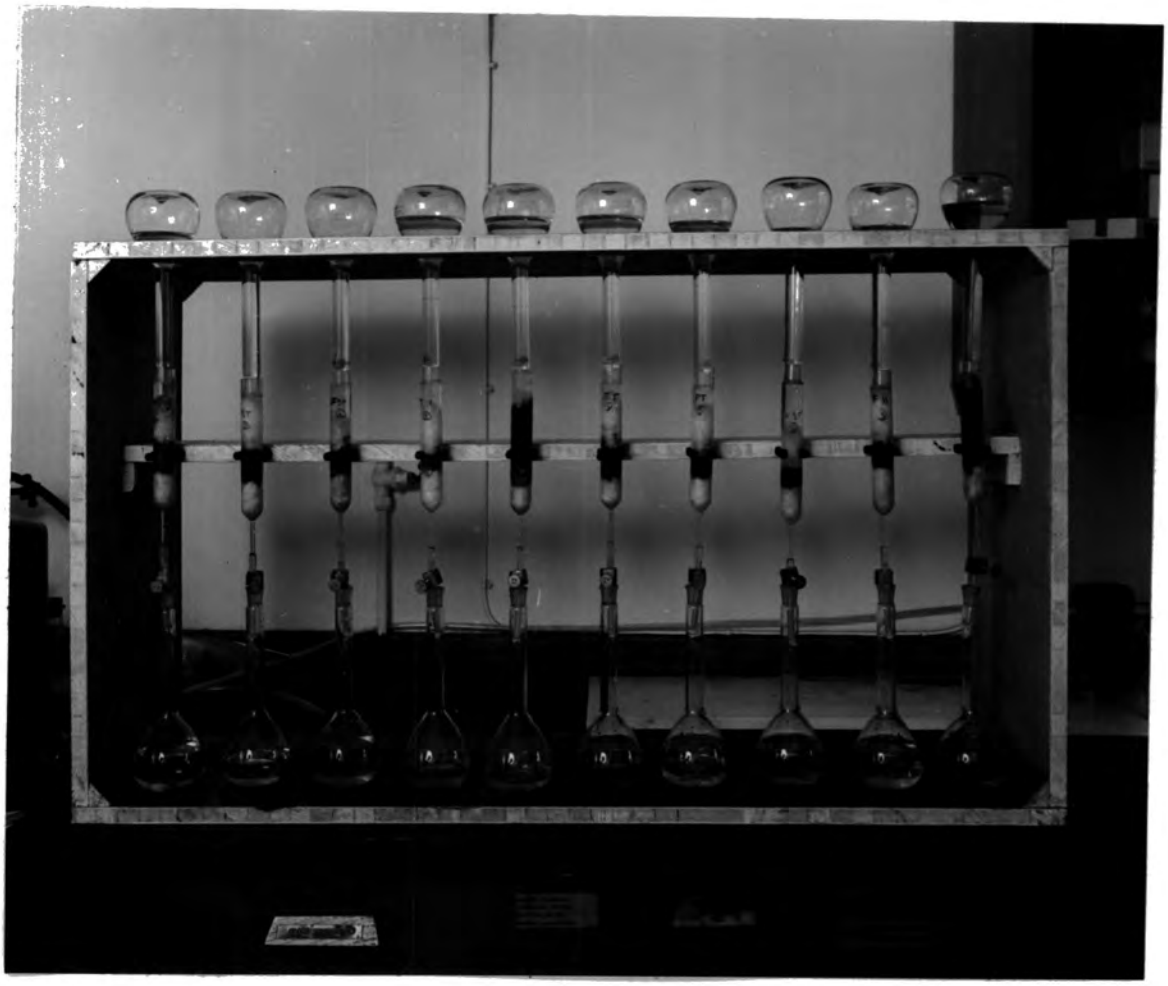
cupboard until only a small amount of perchlorate remained. The remaining solution was diluted with approximately 170 ml. of distilled water and filtered through a sintered glass filter, under suction, to remove silica. The filtrate was then made up to 250 ml. in a volumetric flask ready for analysis.

2. Soil samples.

After collection, the soil was spread onto cardboard trays and dried for 72 hours at 80°C and then passed through a 2 mm. sieve to remove the larger fragments. 2.5 gm. of dried soil was packed into a glass column and eluted with 250 ml. of N ammonium acetate solution (SCHOLLENBERGER & SIMON, 1945, FIGURE 30,). The flow rate was adjusted to 1-3 ml. per minute. The eluate was filtered and evaporated down to 100 ml. to remove excess ammonium acetate. 100 ml. conc. nitric acid and 70 ml. conc. hydrochloric acid were added and the mixture heated to remove the remaining ammonium acetate. Heating was continued until only about 5 ml. remained; 170 ml. distilled water was added, and the solution filtered and made up to 250 ml. as in the plant analysis procedure. (In

FIGURE 30.

Soil analysis leaching frame.



later analyses when an Atomic Absorption Spectrophotometer became available for the determination of calcium and magnesium, the addition of the concentrated nitric and hydrochloric acids with subsequent boiling to remove the ammonium acetate was ommitted, as it was then possible to determine all of the cations studied in this investigation on the original ammonium acetate leachate.) Phosphorus was not determined in these soil samples.

II. ANALYSIS TECHNIQUES.

Calcium, magnesium, sodium, potassium and phosphorus were determined in the solutions derived from the above preparation methods. Two different techniques were used during the course of this investigation for the determination of calcium and magnesium. The first was that described by JEFFERIES & WILLIS, (1964), employing ion-exchange chromatography to isolate individual ions, followed by versenate titration to estimate the concentration of calcium and magnesium. The second method used, which was much quicker and simpler, was by Atomic Absorption Spectrophotometry (DAVID, 1958 & 1959; ALLEN, (1958); KERR, 1960; ELWELL & GIDLEY, 1961,).

In all cases, sodium and potassium were determined using an "Eel" flame photometer (DEAN, 1960), and phosphorus by a modification of the stannous chloride ammonium molybdate technique (MACKERETH, 1963).

1. Separation and estimation of calcium, magnesium, potassium, sodium and phosphorus using ion-exchange chromatography.

(JEFFERIES & WILLIS, 1964, FIGURE 31.)

(a) Cation exchange resin Zeo-carb 225, 15% cross-linked and mean particle size 50u was freed from the cations under investigation by treatment alternately with 1 litre of 2N hydrochloric acid and 1 litre of 2N sodium hydroxide, followed by another 1 litre of 2N hydrochloric acid. The resin was then packed into glass columns 1.1 cm. in diameter, to a height of 10 cm., with glass wool plugs at the top and base of the resin beds. Before addition of a sample, the resin, in the hydrogen form, was first washed with distilled water (250 ml.) to remove surplus acid.

(b) 50 ml. samples of the test solutions were transferred to the columns and allowed to pass through the resin beds. Rate of flow

was adjusted to 1-3 ml. per minute, the eluates being collected for phosphorus analysis.

(c) 30 ml. of distilled water was then passed through the columns to remove phosphate present in the hold-up volume.

(d) The alkali and alkaline earth metals were separated by displacement chromatography by passing the following volumes and normalities of hydrochloric acid, in turn, through the columns.

(i) 45 ml. N HCl to remove sodium.
(ii) 40 ml. N HCl to remove magnesium.
(iii) 70 ml. 1.3N HCl to remove potassium.
(iv) 70 ml. 1.3N HCl to remove calcium.

(e) The bulk fractions were collected and excess acid removed by evaporation almost to dryness. The salts were re-dissolved in 2 ml. of 2N hydrochloric acid and the solution made up to exactly 250 ml. with distilled water. The concentration of both sodium and potassium was determined by flame photometry, and calcium and magnesium by versenate titration (CHENG & BRAY, 1951; CHENG ET AL, 1952,).

FIGURE 31.

Ion-exchange chromatography columns.

(f) In practice, it was found that the eluted fractions did not separate completely and contained a mixture of ions. This may have been due to slightly different particle size of the resin from that recommended by JEFFERIES & WILLIS, (1964), or to the fact that the hold-up volume in the leaching arm of the columns was too large, leading to overlap of the fractions coming off. In any case, the latter part of this procedure was modified.

Instead of trying to remove the cations under investigation as separate fractions, excess of hydrochloric acid was added to the resin columns in two batches - 100 ml. of N HCl followed by 150 ml. of 1.3N HCl - to remove all of the ions together. This bulk solution was evaporated and treated as before.

2. Estimation of sodium and potassium by flame photometry.

(DEAN, 1960.)

An Eel Mark II flame photometer was used for this purpose. Standard solutions were prepared, and the instrument was calibrated for sodium and potassium determinations respectively. Two ranges of standards were prepared for each element, 0-10 p.p.m. and 0-100 p.p.m., for use depending on the concentration of either

of these two elements in the sample solutions. In the preparation of these standard solutions, potassium chloride was used for potassium, and sodium chloride for sodium. From experience, it was found that the range most suitable for plant digest solutions was 0-10 p.p.m. for sodium, and 0-100 p.p.m. for potassium. For soil leachates 1-10 p.p.m. was quite adequate for potassium also. (In analyses of plant samples at the beginning of the investigation eluates from resin columns were analysed; later determinations were carried out on the plant digest solutions themselves without further treatment.

3. Spectrophotometric determination of phosphorus.

The instrument used was a "Hilger and Watts" Uvispek photo-electric spectrophotometer Mark 9 with a silica prism. The method of phosphorus determination was modified from the technique suggested by MACKERETH, (1963), for water analysis, which involves the measurement of the optical density of the blue colouration produced by the reaction of ammonium molybdate and stannous chloride with the phosphorus present in the sample.

The ammonium molybdate and stannous chloride reagents

were added by means of a 1 ml. syringes, that for the latter being drawn out to a fine point to enable delivery of very small quantities.

The spectrophotometer was calibrated using a series of standard solutions. Each solution was transferred to a 1 cm. silica absorption cell, and the extinction measured at 730u with a slit width of 0.025 mm. at maximum meter sensitivity. From the results obtained, a calibration curve was constructed. It was found that the graph was almost linear up to a concentration of 0.6 p.p.m. phosphorus, but above this concentration the graph curved rapidly, the instrument being unable to detect the difference between successively higher phosphorus concentrations satisfacorily. In practice, all sample solutions were diluted to lie within the range 0-0.6 p.p.m. phosphorus before measurement to ensure greater accuracy.

Considerable difficulty was experienced with acid digest solutions which were analysed without being passed through the resin columns. There was suppression of the blue colouration in the more concentrated phosphorus solutions which could only be attributed to the very low pH of these solutions.

4. Calcium and magnesium determination - I.

In the plant digest samples which were eluted on resin columns calcium and magnesium were estimated by titration with disodiumdihydrogenethylenediamine (versenate) (CHENG & BRAY, 1951; CHENG ET AL, 1952). To facilitate easier recognition of the end-point of the titrations a photo-electric assessment of the end-point was obtained using an "Eel" titrator coupled to a spot galvanometer. The titrator unit incorporates a rotating magnet, which activates a stirrer pellet in the sample beaker, thus ensuring adequate mixing of the test solution. A suitable narrow-band optical filter is selected from the range supplied. Readings are presented on the photo-extinction scale of the external galvanometer, the end-point of the titration being indicated by a large change in deflection, followed by almost constant readings.

Standardisation of the versenate solutions

10 ml. standard calcium solution were mixed with 10 ml. of distilled water and diluted to 1 litre; 1 ml. of this solution contained 10 ugm. Ca^{++}. To 20 ml. of this dilute calcium solution in a sample beaker was added 5 ml. N/100 sodium hydroxide solution

to raise the pH to between 10 and 12 (CHENG & BRAY, 1951,), and ammonium purpurate indicator added. The magnetic stirrer was adjusted to give a steady rate of mixing, and versenate solution was run in from a 2 ml. burette until the end-point was recorded on the galvanometer. Since 0.1 mg. calcium is equivalent to 1.00 ml. versenate, the burette reading should be exactly 2.00 ml.. Any difference is corrected for in the subsequent calculation.

Calcium determination.

20 ml. of unknown sample were measured into a sample beaker, 5 drops of indicator and 8 ml. N sodium hydroxide added. This solution was titrated slowly with versenate until the end-point was reached.

Calcium + magnesium determination.

A 20 ml. sample was pipetted into a sample beaker as before; a small spatula of eriochrome black T/ sodium chloride indicator mixture, and 8 ml. of N sodium hydroxide were added. Versenate solution was run in again until the end-point was recorded.

Calculation of results.

Calcium was determined from the 'calcium alone' titration, 1 ml. of versenate solution representing 0.1 mg. Ca^{++}, subject to any correction which the standardisation titration might have shown to be required. Magnesium was given in mg. magnesium per litre by $\frac{X \times 0.0608 \times 1000}{V}$, where V is the volume of the sample taken, and X is the difference between the calcium plus magnesium and the calcium only titrations.

Difficulties encountered in this method.

The method as suggested by CHENG & BRAY, (1951), for analysis of calcium and magnesium had to be modified because of the very low pH of the sample solutions (pH as low as 1.5) which tended to precipitate the indicator dye in the case of the ammonium purpurate, while the eriochrome black T indicator did not dissolve at all. Cheng et al, (1952), stressed the importance of pH for satisfactory determination by this method. They suggested a pH between 10 and 12 as most suitable. Consequently, the normal addition to natural waters of N/100 sodium hydroxide in the calcium alone titration,

and borate buffer in the calcium plus magnesium titration was inadequate to raise the pH anywhere near this value, and, instead, sufficient N sodium hydroxide was added in both cases to raise the pH to the required value for successful titration. This was found to be approximately 8 ml. N sodium hydroxide. If, on addition of this volume, the indicator still did not dissolve, then more N sodium hydroxide was added until it did. This further addition of sodium hydroxide reduced the sensitivity of the titration and obscured the end-point. This proved to be a very unsatisfactory method of determining calcium and magnesium in plant material.

5. Calcium and magnesium determination - II.

Later in this investigation into the mineral nutrient composition of plant material a 'Hilger and Watts' Atomic Absorption Spectrophotometer became available for use, and this gave a much more accurate and satisfactory estimation of calcium and magnesium. It also simplified the preparation procedure, eliminating the need to pass the sample solutions through resin columns and enabling many more analyses to be carried out in the same time as before.

The Atomic Absorption equipment xxx used in

conjunction with a suitable monochromator facilitates the evaluation of the relative absorption occurring when radiation of an appropriate frequency is passed through a population of free atoms. The sample solution is delivered into a spray chamber as a fine mist in an air stream, and is mixed in the burner with the fuel gas which in this case is acetylene. Free atoms are formed when the mixture is burned. Pulsed light from a hollow-cathode lamp, emitting the spectrum of the element to be determined, is passed through the flame and the monochromator, and the change in the absorption at a particular wavelength is detected electronically and recorded. Since the change in absorption is caused only by the presence of free atoms, the degree of absorption is generally propertional to the number of atoms present (ALLEN, 1958; DAVID, 1958 & 1959; ELWELL & GIDLEY, 1961,).

Calibration.

(i) Calcium

A stock solution of calcium carbonate containing 1000 p.p.m. calcium was prepared by adding 2.5 gm. calcium carbonate to 800 ml. of distilled water, adding 50 ml. N hydrochloric acid, and making the resulting solution up to 1 litre. A range of standard

calcium solutions covering the range 0-80 p.p.m. was prepared by appropriate dilution from the stock solution. These were sprayed, in turn, into the acetylene flame and a calibration graph prepared.

(ii) Magnesium.

A similar calibration curve was prepared for magnesium in the range 0-10 p.p.m. using suitable dilutions of a stock 1000 p.p.m. solution of Mg^{++} prepared by dissolving 10.135 gm. of magnesium sulphate ($MgSO_4.7H_2O$) in 1 litre of distilled water.

Determination of calcium and magnesium in sample solutions.

The Atomic Absorption Spectrophotometer was set up as described in the instruction manual using an air/acetylene flame. Samples of plant digest solution were analysed directly, the scale reading being noted and the concentration of calcium or magnesium obtained from the calibration graph. Calcium was determined at 4226Å and magnesium at 2852Å.

Sources of interference.

DAVID, (1959), found that the percentage absorption for calcium was greatly reduced in the presence of phosphorus. The magnitude of this interference was dependent upon both the calcium and the phosphorus concentrations in the sample. He found that in a solution containing 100 p.p.m. calcium, interference due to the presence of phosphorus did not present a serious problem below 10 p.p.m. phosphorus; in another experiment, however, he found that in a solution containing only 25 p.p.m. calcium, phosphorus caused marked depression of the percentage absorption of calcium in concentrations in excess of 4 p.p.m.. Davis suggested the addition of 6000 p.p.m. magnesium as magnesium chloride as an effective way of eliminating this interference. Other workers (ELWELL & GIDLEY, 1961) have suggested the addition of strontium or lanthanum chlorides to reduce phosphorus interference. It has also been mentioned by ELWELL & GIDLEY, (1961), that the higher temperature of the air/acetylene flame (compared with a coal-gas or propane flame), combined with an efficient atomiser which allowed only the smallest liquid droplets to pass into the flame, reduced further interference due to phosphorus. From experience of analyses of plant samples

it was found that both calcium and phosphorus contents exhibited considerable variation, and , consequently, in order to overcome possible interference sufficient 5% lanthanum chloride solution was added to each sample prior to analysis for calcium to produce a 1% solution.

DAVID, (1959), also detected a small reduction in calcium absorption due to the presence of sodium and potassium, and, to overcome this he suggested addition of a large excess of these two elements to both standard and test solutions. For the purpose of this investigation, since the reduction in percentage absorption due to sodium and potassium was so small, no additions were made to minimise possible interference due to them.

Advantages of Atomic Absorption Spectrophotometry.

Because of the large number of samples to be analysed, the use of the atomic absorption spectrophotometer greatly speeded up the analysis procedure, and, consequently the ion-exchange chromatography technique was discarded. This latter method was very lengthy, tedious and generally unsatisfactory, since the plant digest solutions had

to be passed through resin columns, the eluates collected for phosphorus analysis and the four ions, calcium, magnesium, sodium and potassium eluted off before final analysis. This led to a five-fold increase in the number of flasks required, and, as about 150 plant samples were analysed at a time this resulted in the used of 750 flasks, by the time all the ions were removed from the resin columns. The time involved was out of proportion to the number of results obtained. It was possible to elute a maximum of 20 samples per day on the apparatus available (any more would have been unmanageable anyway), and this number was not always attained. It took beteen 2 and 3 weeks to elute the individual ions from the columns (for all 150 samples), and then 600 flasks had to be evaporated to dryness and made up to a standard volume of 250 ml. prior to analysis. This took another week. Determination of calcium and magnesium by versenate titration involved another week each, phosphate a week, and sodium and potassium half a day each. This gives a total of 7 weeks in all. To this must be added the time required to acid wash the glassware and prepare the plant samples (drying, milling and weighing), another 3 weeks, giving a grand total of approximately 10 weeks for one batch of 150 plant samples. This assumes that one has nothing to do but chemical analysis.

The use of the Atomic Absorption Spectrophotometer reduced this time by almost 2/3. Calcium and magnesium could now be determined at the rate of 40-60 samples per hour directly on the initial plant digest solutions without further treatment. This procedure saved 2 weeks in time that would have been required for the versenate titrations, 3 weeks in eluting from the resin columns and 1 week, by not having to evaporate 600 solutions to dryness. This saved a total of 6 weeks; a saving in both time and glassware, with a resultant increase in accuracy.

APPENDIX 4.

Collecting Sites.

1. Tarn Moor, Sunbiggin Tarn, Westmorland.

Tarn moor is an area of undulating moorland lying to the west of Sunbiggin Tarn in central Westmorland (National Grid Reference NY 6707). It forms an uneven plateau about 250 metres (820 feet) above ordnance datum with ridges to the north and west rising to over 300 metres (980'). The drainage of the district is complex and there are numerous springs and swallow holes. The climate is wet, the annual rainfall being about 55 inches.

The numerous hollows of the plateau may contain deep peat, and support mires of different kinds, ranging from acid moss to mineral-rich fens.

Plants of the two species studied were collected from two different sites. Carex panicea was collected from an area of acid blanket peat (formed on glacial drift) situated on higher ground than the springs. The peat on this particular area had been eroded and it was being re-colonised, mainly by C. panicea. Few other species were present except for Carex nigra, Eriophorum angustifolium and E. vaginatum. The vegetation surrounding the erosion hollows was dominated by Calluna vulgaris.

Carex flacca was collected from a 'wet flush' which

was constantly inundated by mineral-rich water from a nearby spring (BELLAMY & RIELEY, 1967). In addition to C. flacca the most abundant species present were Carex hostiana, C. lepidocarpa, C. nigra, Eriophorum latifolium, Schoenus nigricans, Equisetum palustre, Primula farinosa and Succisa pratensis.

The vegetation of this area has been described in detail by HOLGATE, (1955 a & b)

2. Sand Sike, Upper Teesdale, Co. Durham.

The National Grid Reference of this site (1350 feet, 413 metres above ordnance datum) is NY 8330. Rainfall is between 50 and 55 inches per annum. MANLEY, (1942), emphasises the sub-arctic nature of the climate of the region.

The site from which Carex flacca was collected was an area of flood-bank by the side of the stream known as Sand Sike. This habitat consisted of a thin grassy turf on top of river-bed gravel which was subject to flooding after periods of heavy rainfall. Principal species associated with C. flacca were Primula farinosa,

Sesleria albicans, Carex panicea, C. dioica, Juncus articulatus, Saxifraga aizoides and Thymus drucei.

Carex panicea was collected from a flush adjacent to Sand Sike (on a south-facing slope) and draining into it. Associated species were Carex nigra, C. hostiana, C. flacca, and Sesleria albicans. A more detailed description of the Upper Teesdale region is given by PIGOTT, (1956) and VALENTINE, (1965).

3. Cassop Vale, Co. Durham.

This site is a disused quarry on magnesian limestone in central Durham. (National Grid Reference NZ 3338, 600 feet, 180 metres above ordnance datum.)

Carex flacca was collected from an area of dry limestone grassland covering the site of the former quarry workings. Associated species were Sesleria albicans, Carex caryophyllea and Anthoxanthum odoratum.

Carex panicea was collected from a transition mire, downhill from the Carex flacca area, into which water from the

magnesian limestone drains, maintaining a species-rich vegetation in the mire. Associated species were Carex flacca, C. hirta, Juncus articulatus, J. acutiflorus, Holcus mollis and Anthoxanthum odoratum.

APPENDIX 5.

Tables of results.

TABLE 1.

Chemical analysis of culture solutions before and after treatment.
(all values expressed as parts per million.)

Culture solution (Ca conc.)		calcium	potassium
0.5	b	0.5	37.5
0.5	a	0.1	55.0
2.5	b	4.0	39.5
2.5	a	4.5	44.5
5.0	b	5.5	40.0
5.0	a	5.5	54.5
10.0	b	11.0	41.0
10.0	a	8.0	39.0
20.0	b	18.0	39.0
20.0	a	19.0	51.0
50.0	b	55.0	39.5
50.0	a	52.0	36.0
100.0	b	95.0	41.0
100.0	a	105.0	38.5
200.0	b	190.0	37.0
200.0	a	210.0	45.5
500.0	b	504.0	37.5
500.0	a	600.0	49.0

b = before treatment
a = after treatment

TABLE 1. Chemical analysis of culture solutions before and after treatment.

TABLES 2 -5.

Morphological data.

Plant No.	No. of Rhizomes	Length of Rhizomes	No. of Leaves	No. of Dead leaves	Maximum leaf length
1.	1	11.0	6	1	21.0
2.	3	9.6,6.5	10	3	13.7
3.	3	12.7,5.9,1.7	10	4	12.3
4.	4	9.5,10.1,8.8	12	4	11.7
5.	3	7.5,6.3,4.0	11	4	10.7
6.	2	8.2,7.9	8	2	14.4
7.	1	10.4	8	2	12.4
8.	1	10.1	7	2	13.8
9.	1	10.3	10	2	10.4
10.	2	8.2,4.8	9	3	12.1
11.	1	12.0	11	4	11.5
12.	3	11.0,6.9,8.1	10	4	13.8
13.	2	9.5,6.4	8	2	19.0
14.	2	11.7,6.4	10	2	14.2
15.	2	9.9,7.5	9	1	13.3
16.	1	0.7	14	7	9.2
17.	1	14.0	13	6	7.9
18.	2	7.5,3.4	7	2	15.4
19.	2	9.3,8.4	9	2	10.4
20.	1	10.7	14	7	9.5
21.	3	5.2,9.6,1.5	12	5	9.9
22.	2	0.7	7	2	13.8
23.	1	9.3	8	3	16.4
24.	1	15.1	13	6	9.7
25.	1	7.8	7	3	14.1
mean values:		9.0 ± 2.8			12.8 ± 3.0

TABLE 2. Morphological data - Carex paniceа, Sumbiggim Tarn.

Plant No.	No. of Rhizomes	Length of Rhizomes (cm.)	No. of Leaves	No. of Dead leaves	Maximum Leaf length (cm)
1.	2	3.5	16	10	8.2
2.	3	3.8	15	3	8.4
3.	2	10.0, 4.0	11	4	9.8
4.	2	5.7	14	6	12.7
5.	1	1.3	10	5	14.0
6.	3	11.8, 3.2, 1.2	13	6	14.2
7.	2	3.0	9	5	11.7
8.	2	4.6	12	6	9.3
9.	2	3.9	14	7	8.5
10.	3	5.2	9	4	11.2
11.	1	4.3	10	4	9.9
12.	2	4.2, 2.6	9	4	8.8
13.	2	3.0	12	5	10.2
14.	1	1.3	10	3	12.0
15.	3	3.5, 2.7, 2.4	12	3	11.1
16.	3	3.8	10	5	16.8
17.	2	-	12	4	10.8
18.	2	-	11	5	5.6
19.	2	2.9	11	5	8.1
20.	2	6.0, 4.0	10	4	7.5
21.	1	-	8	2	7.3
22.	1	2.4	11	7	9.9
23.	1	-	10	5	8.3
24.	1	-	13	8	8.1
25.	1	-	7	3	8.0
mean values		4.4 ± 2.3			10.0 ± 2.5

TABLE 3. Morphological data - Carex paniced, Sand Silke.

Plant No.	No. of Rhizomes	Length of Rhizomes(cm.)	No. of Leaves	No. of Dead leaves	Maximum Leaf length (cm.)
1.	2	11.2	11	3	20.7
2.	2	12.1,1.1	8	3	14.7
3.	2	9.0	12	4	31.5
4.	2	10.1	12	5	14.2
5.	1	10.5	15	4	9.0
6.	2	12.6,9.5	8	3	16.1
7.	2	14.1,6.6	11	4	18.2
8.	1	9.5	8	3	18.2
9.	1	4.4	10⅓	4	24.8
10.	1	11.7	9	3	19.6
11.	1	4.5	11	5	19.6
12.	1	3.1	9	4	21.2
13.	2	7.9,1.7	8	4	16.3
14.	2	1.6	9	4	19.5
15.	2	0.5	9	3	20.8
16.	2	-	8	2	16.2
17.	1	15.4	13	5	21.5
18.	2	-	12	7	12.7
19.	4	4.9,2.0,1.8	13	7	14.8
20.	1	0.5	6	2	21.1
21.	2	5.0,4.5	10	3	15.7
22.	3	10.9,9.9,1.5	12	5	18.5
23.	1	9.3	9	3	14.6
24.	2	5.8	8	2	15.5
25.	2	6.3	9	4	17.0
mean values		8.4 ± 3.5			17.9 ± 4.6

TABLE 4. Morphological data - Carex flacca, Sunbiggin Tarn.

Plant No.	No. of Rhizomes	Length of Rhizomes (cm.)	No. of Leaves	No. of Dead leaves	Maximum Leaf length (cm.)
1.	4	2.7	13	3	7.8
2.	-	-	11	4	5.8
3.	2	4.4	8	3	8.3
4.	3	9.9	10	7	8.4
5.	1	3.1	-	8	9.6
6.	1	-	8	2	6.8
7.	2	-	9	3	7.7
8.	1	1.3	9	5	10.3
9.	-	-	10	8	6.3
10.	1	-	10	4	7.7
11.	1	-	9	3	10.4
12.	1	4.1	9	3	9.2
13.	2	[illegible]	9	5	8.5
14.	1	-	9	3	7.9
15.	-	-	13	9	6.1
16.	1	3.8	9	3	8.7
17.	2	10.2, 5.5	11	4	8.7
18.	-	-	8	3	9.6
19.	-	-	8	3	8.7
20.	-	-	9	4	12.5
21.	3	8.1, 8.1, 6.3	10	2	12.0
22.	2	2.4	11	2	9.2
23.	1	-	10	4	8.4
24.	2	3.8	10	4	10.7
25.	1	-	10	4	10.8
mean values:		5.4 ± 2.6			8.8 ± 1.6

TABLE 5. Morphological data - Carex flacca, Sand Sike.

TABLE 6.

Chemical analysis of control solutions.

Procedure	K	Ca	Na	P	Mg
soil analysis	0	1.3	3.9	-	0.8
plant analysis					
1.	0	1.5	1.4	0.025	0.1
2.	0.5	0.5	0.7	0	0.05
3.	0	0.1	-	0	0
4.	0	0.1	-	0	0.1
5.	0	0.03	0.9	-	0.025
6.	0	0.025	0.95	-	0.025

TABLE 6. Chemical analysis of control solutions (parts per million).

TABLES 7 & 8.

Results of experiment 1.

PC - *Carex panicea* from Cassop.

PT - *Carex panicea* from Sunbiggin.

FC - *Carex flacca* from Cassop.

Ref. No.	calcium conc. (ppm.)	mean % increase in fresh wt.	mean final dry wt. (gm.)	fresh wt/ dry wt.	calorific value (K cals/gm.) leaves	roots	% ash leaves	roots	pH of soln.
PC	0	420	0.24	3.9	4.24	4.28	3.6	5.3	
	10	250	0.55	1.6	4.18	3.96	5.8	9.8	4
	50	2825	0.84	5.7	4.99	4.23	5.0	6.1	
PC	0	61	0.12	2.5	4.43	4.53	4.2	4.9	
	10	1225	0.92	3.8	4.02	4.27	6.0	6.5	7
	50	2325	0.74	5.6	3.91	4.41	5.0	6.0	
PT	0	253	0.28	3.4	-	-	-	-	
	10	554	0.60	1.5	4.17	3.92	5.1	7.7	4
	50	3236	0.78	5.6	4.39	3.85	5.4	7.5	
PT	0	135	0.22	2.7	-	4.40	-	8.9	
	10	1600	0.65	3.5	4.43	4.44	2.4	7.1	7
	50	2315	0.80	5.4	4.15	3.87	5.3	6.6	
FC	0	167	0.09	3.0	-	-	-	-	
	10	303	0.33	2.1	-	-	-	-	4
	50	1840	0.38	5.8	-	-	-	-	
FC	0	11	0.08	2.4	-	-	-	-	
	10	890	0.60	3.3	-	-	-	-	7
	50	3020	0.75	5.6	-	-	-	-	

TABLE 7. Results of experiment 1.

TABLE 8. Chemical analysis results of Experiment 1.

Ref. No.	Phlorizium conc. (ppm.)	pH	Ca	K	Mg	Na	P
PC	●	4	39.9	169	47	33.8	28.7
	10		39.5	426	55	49.2	51.3
	50		32.8	417	70	35.3	48.9
PC	0	7	40.4	145	42	40.2	24.4
	10		35.7	497	73	44.1	51.3
	50		28.9	372	99	37.2	48.7
PT	0	4	22.2	78.8	37.8	31.5	9.5
	10		36.5	373	56.9	67.9	94.5
	50		35.2	403	47.1	38.7	68.8
PT	0	7	36.5	89.9	34.2	48.3	18.9
	10		43.5	342	31.7	51.3	89.8
	50		41.5	439	49.8	48.1	51.5
FC	0	4	37.4	60.4	24.0	32.0	19.3
	10		27.7	375	32.0	78.0	68.3
	50		26.6	406	41.0	73.0	77.5
FC	0	7	44.8	63.0	31.0	40.4	13.3
	10		24.4	377	39.0	91.3	53.2
	50		27.7	388	39.0	74.0	80.1

TABLES 9 & 10.

Results of Experiment 2.a.

PT63Y - Young tillers of C. panicea from Sunbiggin, collected in 1963.
PT63M - older tillers " " " " " " "
PT64Y - young tillers " " " " " " 1964.
PT64M - older tillers " " " " " " "
PC65Y - young tillers " " " Cassop " " 1965.
PC65M - older tillers " " " " " " "

FT64Y - young tillers of C. flacca from Sunbiggin collected in 1964.
FT64M - older tillers " " " " " " "
FC65Y - young tillers " " " Cassop " " 1965.
FC65M - older tillers " " " " " " "

Calcium concentration (p.p.m.)

1	-	0.5
2	-	2.5
3	-	5.0
4	-	10.0
5	-	20.0
6	-	50.0
7	-	100.0
8	-	200.0
9	-	500.0

TABLE 9. (i)½ Results of Experiment 2.a.

Ref. No.		mean fresh wt. (gm.)	mean dry wt. (gm.)	mean leaf dry wt.	Fresh wt./ dry wt.	mean max. leaf lth. (cm.)	No. of plants in sample.
PI63Y	1.	1.25	0.22	0.154	5.6 ± 0.6	33.9 ± 6.8	9
	2.	2.59	0.50	0.31	5.1 ± 0.5	33.6 ± 6.3	7
	3.	0.75	0.18	0.10	3.8 ± 0.3	18.6 ± 3.5	9
	4.	1.84	0.35	0.163	5.3 ± 0.1	34.5 ± 7.4	6
	5.	0.78	0.14	0.09	5.7 ± 0.2	17.3 ± 4.4	4
	6.	1.03	0.24	0.124	4.4 ± 0.4	22.2 ± 1.6	5
	7.	2.39	0.54	0.29¾	4.4 ± 0.2	36.9 ± 6.2	7
	8.	1.24	0.38	0.33	3.2 ± 0.4	28.6 ± 3.6	3
PI63M	1.	2.62	0.51	0.34	5.1 ± 0.3	34.7 ± 3.7	6
	2.	2.13	0.43	0.37	5.1 ± 0.4	31.6 ± 3.7	3
	3.	5.00	0.92	0.53	3.9 ± 0.7	29.8 ± 8.7	4
	4.	4.40	0.74	0.66	5.5 ± 0.3	37.3 ± 4.3	6
	5.	3.53	0.74	0.68	4.8 ± 0.2	37.1 ± 4.3	6
	6.	1.90	0.46	0.33	3.4 ± 0.8	23.7 ± 7.9	5
	7.	1.63	0.48	0.32	3.3 ± 0.3	21.1 ± 3.0	6
	8.	2.30	0.57	0.40	3.5 ± 1.0	29.3 ± 11.0	6
PI64Y	1.	1.01	0.29	0.165	5.6 ± 0.4	27.6 ± 4.3	6
	2.	1.07	0.28	0.087	3.8 ± 0.2	23.9 ± 7.0	6
	3.	1.64	0.35	0.198	4.2 ± 0.6	28.3 ± 6.8	6
	4.	1.90	0.38	0.295	5.0 ± 0.5	24.8 ± 2.0	2
	5.	0.61	0.11	0.090	5.5 ± 0.5	16.9 ± 1.8	4
	6.	1.77	0.43	0.303	4.1 ± 0.3	28.6 ± 2.7	4
	7.	1.24	0.37	0.208	3.3 ± 0.1	25.3 ± 3.0	4
	8.	0.96	0.31	0.143	1.9 ± 0.3	21.2 ± 5.9	4

TABLE 9. (ii) Results of Experiment 2.a.

Ref. No.		mean fresh wt. (gm.)	mean dry wt. (gm.)	mean leaf dry wt.	frsh wt./ dry wt.	mean max. leaf lth. (cm.)	No. of plants in sample.
PT64M	1.	0.97	0.29	0.203	3.2 ± 0.4	23.4 ± 6.1	4
	2.	1.61	0.29	0.208	5.6 ± 0.3	27.8 ± 2.0	4
	3.	2.12	0.39	0.350	5.3 ± 0.4	32.0 ± 6.8	4
	4.	2.60	0.66	0.553	5.6 ± 0.3	38.5 ± 6.9	3
	5.	1.47	0.50	0.290	4.8 ± 0.2	26.4 ± 4.3	3
	6.	1.39	0.50	0.460	3.7 ± 0.4	25.5 ± 8.1	3
	7.	1.31	0.50	0.440	2.7 ± 0.3	32.9 ± 7.7	4
	8.	1.65	0.40	0.383	3.9 ± 0.5	32.5 ± 1.8	3
PC65Y	1.	0.86	0.18	0.096	4.7 ± 0.6	20.2 ± 5.2	5
	2.	1.06	0.21	0.103	4.9 ± 0.4	20.3 ± 3.7	6
	3.	1.14	0.20	0.110	5.6 ± 0.6	23.5 ± 5.8	6
	4.	0.94	0.23	0.132	4.4 ± 0.5	21.9 ± 2.7	6
	5.	0.57	0.11	0.078	3.9 ± 0.6	16.8 ± 1.4	5
	6.	0.56	0.22	0.082	1.7 ± 0.3	19.2 ± 2.6	5
PC65M	1.	1.01	0.25	0.230	4.9 ± 0.2	23.3 ± 3.7	6
	2.	1.45	0.29	0.152	3.7 ± 0.4	21.7 ± 3.5	6
	3.	1.36	0.26	0.196	5.2 ± 0.5	22.2 ± 1.8	5
	4.	0.59	0.18	0.108	3.3 ± 0.3	19.8 ± 4.7	5
	5.	0.55	0.14	0.108	3.9 ± 0.2	19.3 ± 2.0	5
	6.	0.56	0.23	0.144	2.8 ± 0.3	22.5 ± 2.6	7
	7.	0.46	0.24	0.123	2.0 ± 0.3	19.1 ± 3.0	4

TABLE 9. (iii) Results of Experiment 2.a.

Ref. No.		mean fresh wt. (gm.)	mean dry wt. (gm.)	mean leaf dry wt.	fresh wt./ dry wt.	mean max. leaf lth. (cm.)	No. of plants in sample.
FT64Y	1.	1.15	0.27	0.099	3.8 ± 0.9	25.3 ± 6.0	7
	2.	1.30	0.18	0.075	7.0 ± 0.1	27.8 ± 7.0	4
	3.	1.81	0.34	0.113	5.3 ± 0.2	29.7 ± 6.1	9
	4.	1.84	0.27	0.063	6.6 ± 0.9	26.3 ± 9.6	11
	5.	1.89	0.31	0.102	5.2 ± 0.5	30.3 ± 7.3	9
	6.	0.84	0.25	0.063	2.9 ± 0.7	27.8 ± 5.1	8
	7.	1.04	0.34	0.111	3.0 ± 0.4	23.5 ± 3.2	8
	8.	1.53	0.43	0.173	3.5 ± 0.6	31.0 ± 6.8	7
	9.	0.68	0.22	0.116	2.9 ± 0.4	22.2 ± 3.6	5
FT64M	1.	1.04	0.31	0.230	3.4 ± 0.2	28.6 ± 4.4	4
	2.	1.46	0.26	0.227	5.7 ± 0.3	31.7 ± 8.4	3
	3.	1.85	0.35	0.255	5.2 ± 0.6	28.7 ± 8.1	4
	4.	3.30	0.57	0.428	6.1 ± 0.5	39.1 ± 9.5	4
	5.	0.71	0.23	0.130	3.1 ± 0.4	23.1 ± 5.0	3
	6.	3.20	0.82	0.665	4.1 ± 0.2	32.8 ± 2.0	2
	7.	1.07	0.43	0.250	2.4 ± 0.1	29.9 ± 6.8	4
	8.	2.95	0.64	0.443	4.4 ± 0.4	40.3 ± 4.4	4
	9.	0.71	0.24	0.153	2.9 ± 0.4	20.8 ± 4.9	3

TABLE 9. (iv) Results of Experiment 2.a.

Ref. No.		mean fresh wt. (gm.)	mean dry wt. (gm.)	mean leaf dry wt.	fresh wt./ dry wt.	mean max. leaf lth. (cm.)	No. of plants in sample.
FC65Y	1.	-	-	-	-	-	-
	2.	0.74	0.12	0.088	2.6 ± 0.3	18.4 ± 3.7	4
	3.	0.64	0.13	0.055	6.4 ± 0.5	18.2 ± 4.3	6
	4.	0.30	0.14	0.050	5.0 ± 0.7	15.1 ± 4.1	x 4
	5.	0.55	0.15	0.077	7.4 ± 0.4	16.4 ± 2.0	3
	6.	0.29	0.16	0.087	3.6 ± 0.2	11.3 ± 1.9	3
FC65M	1.	0.55	0.15	0.091	4.0 ± 0.6	19.6 ± 5.2	8
	2.	1.86	0.26	0.210	7.1 ± 0.7	26.4 ± 7.1	9
	3.	0.89	0.17	0.123	4.9 ± 0.4	23.9 ± 6.7	9
	4.	2.11	0.34	0.234	6.0 ± 0.4	35.2 ± 4.5	5
	5.	3.36	0.54	0.265	6.0 ± 0.5	35.6 ± 7.9	6
	6.	1.69	0.40	0.189	3.9 ± 0.5	28.0 ± 6.5	7
	7.	1.13	0.38	0.142	1.7 ± 0.5	20.5 ± 4.5	5
	8.	0.77	0.27	0.100	2.2 ± 0.8	19.5 ± 6.1	4

Ref. No.		Ca mg./10g.	K mg./10g.	Mg mg./10g.	Ca mg./100plts.	K mg./100pl.	Mg mg./100pls.
PT63Y	1.	0.5	308	26.0	8	474	40
	2.	2.0	200	23.7	62	620	74
	3.	6.9	287	28.4	69	287	28
	4.	9.2	308	28.1	150	502	46
	5.	-	-	-	-	-	-
	6.	20.3	272	24.4	252	337	30
	7.	29.3	342	23.9	846	988	69
	8.	114.0	275	20.1	3762	908	66
PT63M	1.	1.6	317	32.9	5.4	1078	112
	2.	2.7	275	24.3	12.7	1293	114
	3.	8.8	245	30.6	46.6	1299	162
	4.	18.2	159	28.9	120.1	1049	191
	5.	28.4	277	27.9	193.0	1884	190
	6.	48.3	238	24.3	159.0	785	80
	7.	49.5	247	21.3	158.0	790	68
	8.	90.6	272	17.6	362.0	1088	70
PT64Y	1.	0.44	237	29.1	0.73	391	48
	2.	5.3	211	34.8	4.61	184	30
	3.	6.2	230	30.5	12.3	455	60
	4.	8.7	263	32.1	25.7	776	95
	5.	12.8	213	31.5	11.5	192	28
	6.	27.2	236	23.6	82.4	715	72
	7.	43.7	226	267	90.9	470	56
	8.	135.0	191	19.6	193.1	273	28
	9.	183.0	194	18.3	183 .0	183	18
PT64M	1.	7.2	201	59.5	14.6	408	121
	2.	6.1	257	56.2	12.7	535	117
	3.	5.7	282	50.7	20.0	987	177
	4.	6.8	264	39.1	37.6	1460	216
	5.	10.1	287	50.2	29.3	824	146
	6.	14.7	244	34.0	67.6	1122	156
	7.	47.0	193	36.1	253.8	1042	195
	8.	78.6	204	50.3	379.6	985	243

TABLE 10. (i) Chemical analysis results for Experiment 2.a.

Ref.	No.	Ca mg./10g.	K mg./10g.	Mg mg./10g.	Ca mg./100pl.	K mg./100 pl.	Mg mg./100pl.
PC65Y	1.	2.8	300	38.4	2.7	288	37
	2.	8.1	285	38.1	8.3	294	39
	3.	8.2	260	39.2	9.0	286	43
	4.	14.9	238	34.2	18.7	314	45
	5.	24.1	227	31.8	18.8	177	25
	6.	47.8	239	33.6	39.2	196	28
PC65M	1.	3.3	302	25.1	7.6	695	58
	2.	8.6	314	29.8	13.1	477	45
	3.	7.4	269	27.6	14.6	527	54
	4.	11.7	246	29.8	12.6	482	32
	5.	10.1	285	24.6	10.9	308	27
	6.	87.2	228	29.5	125.6	328	43
	7.	197.0	214	38.5	242.3	242	47

TABLE 10. (ii) Chemical analysis results for Experiment 2.a.

Ref.	No.	Ca mg./10g.	K mg./10g.	Mg mg./10g.	Ca mg./100pl.	K mg./100pl.	Mg mg./100pl.
FT64Y	1.	3.6	319	58.9	3.6	316	58
	2.	5.3	270	47.0	4.0	203	35
	3.	4.6	309	52.6	5.2	349	59
	4.	6.7	328	48.3	4.2	207	30
	5.	10.8	320	47.2	11.0	326	48
	6.	8.2	327	32.7	5.2	206	21
	7.	17.2	266	28.8	19.1	295	32
	8.	51.8	297	25.2	89.6	514	44
	9.	113.0	226	17.9	131.1	262	21
FT64M	1.	2.4	278	29.5	5.5	639	68
	2.	7.4	256	29.2	16.8	581	66
	3.	5.5	267	25.3	14.0	681	65
	4.	5.3	285	20.2	22.7	1212	87
	5.	22.5	208	29.2	29.3	270	38
	6.	44.0	190	23.8	203.0	1264	158
	7.	78.6	199	28.8	196.5	498	72
	8.	71.0	261	11.8	314.5	1156	52
	9.	220.0	195	18.2	336.6	298	28
FC65Y	1.	-	-	-	-	-	-
	2.	9.5	294	34.2	8.3	257	30
	3.	11.3	304	33.8	6.2	167	19
	4.	19.0	313	40.2	9.5	157	20
	5.	20.0	266	28.1	15.4	204	22
	6.	77.2	193	40.0	51.7	129	27
FC65M	1.	4.2	315	33.4	3.8	288	31
	2.	5.4	333	32.6	11.3	699	69
	3.	5.2	311	30.6	6.4	383	38
	4.	5.4	309	19.4	12.6	723	45
	5.	9.4	302	17.9	24.9	800	48
	6.	73.3	340	20.0	138.5	643	38
	7.	70.9	279	24.7	100.7	396	35
	8.	280.0	239	28.9	280.0	289	29

TABLE 10. (iii) Chemical analysis results for Experiment 2.a.

TABLE 11.

Duplicate chemical analyses.

Ref. No.		K mg./10g.	Mg mg./10g.	Ca mg./10g.
PM	1.	111.2	9.0	52.0
	2.	112.5	10.3	53.8
FR	1.	50.1	7.0	43.7
	2.	49.8	7.1	45.3
PT	1.	165.8	21.5	35.7
	2.	156.7	23.4	41.4
PTy	1.	91.5	10.9	10.6
	2.	95.1	9.5	10.0

PM - Carex panicea, mature tillers.
FR - Carex flacca, roots.
PT - Carex panicea, tillers.
PTy - Carex panicea,, very young tillers.

TABLE 11. Duplicate chemical analyses.

TABLES 12 & 13.

Results of Experiment 2.b.

Ref. No.	calcium conc. (ppm.)	% germn.	total leaf dry wt. (gm)	total root dry wt. (gm.)	mean plant dry wt. (leaves)
FC	0.5	56	0.20	0.14	0.014
	2.5	36	0.19	0.17	0.021
	5.0	48	0.26	0.27	0.022
	10.0	52	0.39	0.34	0.030
	20.0	32	0.42	0.33	0.053
	50.0	44	0.40	0.38	0.036
	100.0	48	0.26	0.32	0.022
	200.0	40	0.24	0.19	0.024
	500.0	32	0.14	0.10	0.018
FG	0.5	4	0.029	0.066	0.029
	2.5	12	0.13	0.14	0.043
	5.0	20	0.25	0.31	0.050
	10.0	24	0.19	0.21	0.032
	20.0	24	0.13	0.09	0.022
	50.0	20	0.47	0.61	0.094
	100.0	20	0.19	0.22	0.038
	200.0	24	0.20	0.21	0.033
	500.0	32	0.27	0.20	0.034

FC - Carex flacca collected from Cassop, Co. Durham.
FG - Carex flacca, collected from Germany.

TABLE 12. Results of Experiment 2.b.

Ref. No.	calcium conc. (ppm.)	Ca	K	Mg	Ca	K	Mg
		mg./10gm.			mg./100plants		
FC	0.5	-	182	60.1	-	255	84
	2.5	2.4	202	59.8	5.1	426	126
	5.0	-	188	50.8	-	414	112
	10.0	0.6	117	33.5	1.8	351	101
	20.0	0.3	156	40.0	1.6	827	212
	50.0	2.8	211	56.1	10.2	768	204
	100.0	-	176	61.1	-	387	134
	200.0	19.7	167	45.4	47.3	401	109
	500.0	38.4	160	60.9	67.2	280	107
FG	0.5	-	199	59.8	6.2	577	173
	2.5	1.0	237	56.8	8.3	1026	246
	5.0	-	203	47.6	-	1015	238
	10.0	0.7	216	48.1	2.2	685	101
	20.0	1.1	163	53.1	2.4	353	115
	50.0	3.4	208	48.9	3.2	1955	460
	100.0	2.2	202	57.2	8.4	768	195
	200.0	7.6	197	52.9	25.3	656	176
	500.0	19.5	195	42.2	65.9	659	143

TABLE 13. Chemical analysis results for Experiment 2.b.

TABLES 14 & 15.

Results of Experiment 3.

Ref. No.	potassium conc. (ppm.)	mean fresh wt. (gm.)	mean dry wt. (gm.)	fresh wt./ dry wt.	mean maximum leaf lth. (cm.)
PT63Y	0.5	2.21	0.41	5.4	40.3 ± 2.2
	1.0	1.31	0.30	4.4	21.2 ± 10.5
	2.5	2.34	0.52	4.5	35.0 ± 6.2
	5.0	1.65	0.36	4.6	27.5 ± 8.0
	10.0	1.74	0.37	4.7	36.7 ± 5.2
PT63M	0.5	4.48	0.83	5.4	35.8 ± 8.7
	1.0	1.26	0.39	3.2	20.1 ± 1.6
	2.5	2.61	0.59	4.4	29.0 ± 3.8
	5.0	3.40	0.72	4.7	27.6 ± 6.0
	10.0	2.72	0.57	4.8	29.2 ± 3.6
PT64Y	0.5	1.70	0.29	5.9	33.2 ± 3.9
	1.0	1.47	0.33	4.5	31.6 ± 2.4
	2.5	-	-	-	-
	5.0	1.13	0.32	3.5	20.4 ± 4.7
	10.0	1.85	0.42	4.4	29.8 ± 13.3
PT64M	0.5	2.43	0.54	4.5	28.2 ± 5.7
	1.0	2.33	0.56	4.2	34.9 ± 1.4
	2.5	1.84	0.48	3.8	30.7 ± 7.0
	5.0	1.79	0.42	4.3	22.3
	10.0	-	-	-	-
PG65Y	0.5	0.81	0.23	3.5	27.3 ± 4.1
	1.0	0.44	0.17	2.6	16.3 ± 1.3
	2.5	0.37	0.20	1.9	18.7 ± 2.7
	5.0	0.26	0.14	1.9	16.0 ± 1.1
	10.0	0.56	0.21	2.7	17.9 ± 2.2
PG65M	0.5	0.92	0.23	4.0	30.2 ± 3.5
	1.0	1.04	0.28	3.7	27.0 ± 2.8
	2.5	1.00	0.32	3.1	20.8 ± 2.4
	5.0	1.82	0.44	4.1	30.0 ± 5.9
	10.0	1.01	0.28	3.6	24.7 ± 5.1

TABLE 14. Results of Experiment 3.

Ref. No.	potassium conc. (pp.)	mean fresh wt. (gm.)	mean dry wt. (gm.)	fresh wt./ dry wt.	mean maximum leaf lth. (cm.)
FT64Y	0.5	2.06	0.45	4.6	36.6 ± 7.1
	1.0	1.46	0.30	4.9	20.6 ± 8.3
	2.5	1.69	0.37	4.6	30.8 ± 6.4
	5.0	1.04	0.29	3.6	25.4 ± 5.2
	10.0	1.53	0.35	4.4	31.9 ± 5.8
FT64M	0.5	2.15	0.46	4.7	31.3 ± 10.7
	1.0	2.43	0.57	4.3	47.6 ± 6.1
	2.5	3.18	0.65	4.9	40.6 ± 13.7
	5.0	3.99	0.77	5.2	43.2 ± 13.8
	10.0	1.70	0.38	4.4	32.4 ± 7.9
FC65Y	0.5	0.65	0.16	4.1	19.1 ± 9.5
	1.0	0.99	0.27	3.7	21.5 ± 4.8
	2.5	0.57	0.24	2.4	23.6 ± 2.3
	5.0	0.95	0.24	4.0	20.8 ± 6.5
	10.0	1.00	0.25	4.0	23.7 ± 3.7
FC65M	0.5	1.19	0.27	4.4	28.0 ± 4.5
	1.0	0.93	0.30	3.1	24.1 ± 4.6
	2.5	0.65	0.23	2.8	29.4 ± 5.4
	5.0	1.05	0.32	3.3	22.2 ± 1.4
	10.0	1.02	0.28	3.6	23.7 ± 3.7

TABLE 14. (ii) Results of Experiment 3.

Ref. No.	potassium conc. (ppm.)	mean drywt. per plant (leaves)	Ca mg./10gm.	K mg./10gm.	Mg mg./10gm.	Ca mg./100plants	K mg./100plants	Mg mg./100plants
PT63Y	0.5	0.284	5.7	119	49.1	16.2	338	139
	1.0	0.204	2.5	227	41.0	5.2	464	84
	2.5	0.335	1.9	264	37.2	6.4	884	125
	5.0	0.287	1.9	287	25.2	5.5	824	72
	10.0	0.268	1.9	317	26.0	5.1	850	70
PT63M	0.5	0.557	6.4	103	52.8	35.7	574	294
	1.0	0.215	1.8	159	41.6	3.9	342	89
	2.5	0.455	4.0	231	35.9	18.2	1051	163
	5.0	0.600	2.4	247	40.5	14.4	1482	215
	10.0	0.448	1.8	278	23.7	8.1	1245	106
PT64Y	[illegible]	[illegible]	[illegible]					
	0.5	0.270	6.5	132	78.0	17.6	356	211
	1.0	0.238	4.0	158	48.5	9.5	566	115
	2.5	-	-	-	-	-	-	-
	5.0	0.233	2.7	227	35.3	6.3	529	82
	10.0	0.303	1.7	297	20.6	5.2	900	62
PT64M	0.5	0.433	10.6	138	54.8	45.9	598	237
	1.0	0.455	5.2	177	41.7	23.7	805	190
	2.5	0.377	4.5	218	38.8	15.2	735	131
	5.0	0.423	2.0	277	29.1	8.5	1172	123
	10.0	-	-	-	-	-	-	-
PC65Y	0.5	0.142	8.9	97	64.2	12.6	138	91
	1.0	0.078	6.0	123	39.8	4.7	96	31
	2.5	0.264	1.0	163	39.7	2.6	430	105
	5.0	0.075	0.8	204	39.1	0.6	153	29
	10.0	0.130	0.8	225	28.8	1.0	293	37
PC65M	0.5	0.155	6.7	131	48.6	10.4	203	75
	1.0	0.193	5.5	204	40.8	10.6	394	79
	2.5	-	-	-	-	-	-	-
	5.0	0.330	5.3	245	40.3	17.4	809	133
	10.0	0.147	4.2	302	23.5	6.2	444	35

TABLE 15. (i) Chemical analysis results for Experiment 3.

Ref. No.	potassium conc. (ppm.)	mean dry wt. per plant (leaves)	Ca mg./10gm.	K	Mg	Ca mg./100 plants	K	Mg
FT64Y	0.5	0.307	4.6	129	48.0	14.1	396	147
	1.0	0.179	1.7	239	36.0	3.0	428	64
	2.5	0.238	1.6	267	31.3	3.8	636	75
	5.0	0.165	1.6	281	24.8	2.6	464	41
	10.0	0.250	1.6	284	20.5	4.0	710	51
FT64M	0.5	0.298	1.8	86	34.7	5.4	257	103
	1.0	0.417	3.1	185	34.3	12.9	772	143
	2.5	0.425	1.7	205	23.2	7.2	871	99
	5.0	0.445	2.0	227	25.6	12.9	1010	165
	10.0	0.415	1.6	221	23.7	5.0	920	75
FC65Y	0.5	0.086	7.4	119	67.8	6.4	102	58
	1.0	0.140	5.1	198	44.0	7.1	277	62
	2.5	0.127	4.6	-	30.0	5.8	-	38
	5.0	0.125	3.9	290	40.6	4.9	363	51
	10.0	0.147	2.5	313	30.2	3.7	460	44
FC65M	0.5	0.176	4.9	166	53.4	8.6	292	94
	1.0	0.179	5.1	177	36.3	9.1	317	42
	2.5	0.114	5.3	262	32.2	6.0	299	37
	5.0	0.186	2.4	234	32.1	4.5	435	60
	10.0	0.186	4.8	522	25.0	8.9	971	47

TABLE 15. (ii) Chemical analysis results for Experiment 3.

TABLE 16.

Growth curve data.

Collection Date	Sumbiggin Tarn fresh wt. per 100plants (gm.)	Sumbiggin Tarn dry wt./ 100plants	Sand Sike fr. wt./ 100pl. (gm.)	Sand Sike dry wt./ 100pl.	Cassop fr. wt./ 100pl (gm.)	Cassop dry wt./ 100pl.	
20.11.64	5.7	1.4	2.9	0.8	-	-	FIRST YEAR TILLERS
6. 2.65	6.9	1.0	4.8	0.5	-	-	
3. 5.65	11.6	2.0	5.6	1.0	8.3	1.7	
17.5 .65	18.4	3.1	11.8	1.9	19.7	4.5	
31. 5.65	30.9	5.7	14.0	2.5	20.6	4.4	
13. 6. 65	38.3	7.6	16.6	3.4	33.0	9.3	
31. 7.65	69.7	13.7	30.1	6.1	45.7	10.9	
20.11.64	44.7	13.0	16.9	6.1	-	-	SECOND YEAR TILLERS
6. 2.65	48.0	13.5	27.2	6.1	-	-	
3. 5.65	67.0	14.7	31.3	6.3	81.9	23.8	
17. 5.65	85.6	17.4	43.5	7.7	105.2	27.4	
31. 5.65	101.3	23.2	36.8	7.7	103.4	27.8	
13. 6.65	93.5	19.9	48.5	10.8	83.4	27.0	
31. 7.65	47.2	8.2	34.0	7.5	70.9	18.8	

TABLE 16. (i) Growth Curve data - Carex flacca.

Collection Date	Sunbiggin Tarn fr. wt./ 100 pl. (gm.)	Sunbiggin Tarn dry wt./ 100pl. (gm.)	Sand Sike fr. wt./ 100pl. (gm.)	Sand Sike dry wt./ 100pl. (gm.)	Cassop fr. wt./ 100pl. (gm.)	Cassop dry wt./ 100pl. (gm.)	
20.11.64	4.1	1.1	4.2	0.9	-	-	FIRST YEAR TILLERS
6. 2.65	4.2	0.7	7.3	1.3	-	-	
3. 5.65	14.1	1.8	10.7	2.0	15.2	2.5	
17. 5.65	21.2	3.0	15.8	2.4	18.3	3.0	
31. 5.65	36.3	6.0	18.8	3.5	84.4	14.7	
13. 6.65	36.6	7.1	38.0	6.6	104.8	25.1	
31. 7.65	53.4	10.8	54.9	9.5	128.2	30.6	
20.11.64	42.3	13.5	35.6	8.6	-	-	SECOND YEAR TILLERS
6. 2.65	47.6	15.2	-	-	-	-	
3. 5.65	61.9	8.7	39.3	7.9	110.8	24.5	
17. 5.65	72.8	10.8	51.3	8.4	114.8	23.8	
31. 5.65	74.0	11.4	47.4	9.1	151.4	28.6	
13. 6.65	-	-	53.0	9.4	154.6	40.6	
31. 7.65	52.5	7.9	-	-	99.3	19.0	

TABLE 16. (ii) Growth Curve data - Carex panicea.

TABLES 17 & 18.

Nutrient dynamics data.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
	mg./10gm.				mg./100plants				
15. 1.65	31.1	185	17.9	-	3.7	22.2	-	-	FIRST YEAR TILLERS
6. 2.65	17.2	204	12.0	-	1.9	22.4	-	-	
19. 4.65	16.4	275	20.2	9.6	2.6	44.0	3.2	1.5	
3. 5.65	23.3	250	5.6	3.3	4.7	50.0	1.1	0.7	
17. 5.65	29.2	228	20.8	10.5	5.8	68.4	6.2	3.2	
31. 5.65	28.1	234	20.3	9.2	15.2	126	11.0	5.0	
13. 6.65	47.6	214	19.8	9.4	35.2	201	14.7	7.0	
11. 7.65	64.7	159	20.9	9.3	71.2	175	23.0	10.2	
20.11.65	72.0	103	10.7	-	93.6	134	13.9	-	
15. 1.65	83.4	80	7.2	-	108	107	9.7	-	SECOND YEAR TILLERS
6. 2.65	66.1	117	10.4	-	89.2	158	14.0	-	
19. 4.65	71.3	135	16.4	5.1	102	193	23.5	7.3	
3. 5.65	65.9	122	17.4	7.5	96.2	178	25.4	11.0	
17. 5.65	60.1	125	15.1	5.7	102	213	25.7	9.7	
31. 5.65	68.9	105	12.0	6.6	152	231	26.4	14.5	
13. 6.65	63.3	96	10.9	5.8	132	200	22.7	12.1	
11. 7.65	85.6	65	9.6	3.7	120	91	13.4	5.2	
21. 8.65	108	55	11.5	3.2	88.0	45	9.4	2.6	
20.11.65	49.9	16	11.7	-	-	-	-	-	

TABLE 17. (i). Nutrient dynamics data - *Carex flacca*, Sumbiggin Tarn.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
	mg./10gm.				mg./100 plants				
6. 2.65	19.1	191	11.8	-	1.0	9.6	-	-	FIRST YEAR TILLERS
19. 4.65	35.9	245	18.8	13.1	2.9	19.6	1.5	1.1	
3. 5.65	36.4	241	19.6	16.1	3.6	24.1	2.0	1.6	
17. 5.65	41.8	275	20.4	16.6	7.5	49.5	3.7	3.0	
31. 5.65	44.4	252	18.7	12.1	10.7	60.5	4.5	2.9	
13. 6.65	37.2	239	17.2	9.1	11.2	71.7	5.2	2.7	
27. 6.65	50.1	197	18.9	-	28.0	68.8	3.1	-	
11. 7.65	62.3	204	17.2	5.4	27.4	89.8	7.6	2.4	
21. 8.65	78.9	146	13.0	6.8	48.9	90.5	8.1	4.2	
20.11.65	92.3	96	8.3	-	55.4	57.5	5.0	-	
6. 2.65	104.1	80.7	8.6	-	62.5	48.4	5.2	-	SECOND YEAR TILLERS
19. 4.65	84.5	126	12.7	-	50.7	75.6	7.6	-	
3. 5.65	93.1	119	12.1	-	55.9	71.4	7.3	-	
17. 5.65	97.3	104	12.2	-	73.0	78.0	9.2	-	
31. 5.65	107.8	103	10.4	-	84.1	80.3	8.1	-	
27. 6.65	132.6	98	6.5	-	135.3	99.9	6.6	-	
11. 7.65	145.9	57	10.9	-	131.3	51.3	9.8		
21. 8.65	91.9	51	8.5	-	68.9	38.3	5.6	-	
20.11.65	116.7	20	7.5	-	-	-	-	-	

TABLE 17. (ii). Nutrient dynamics data - Carex flacca, Sand Sike.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
	mg./10gm.				mg./100plants				
19. 4.65	15.6	227	34.1	23.7	2.2	31.8	4.8	3.3	FIRST YEAR TILLERS
3. 5.65	21.6	216	28.8	18.7	3.5	34.6	4.6	2.9	
17. 5.65	29.6	237	32.8	10.1	13.0	104	14.4	4.4	
31. 5.65	28.3	288	33.8	5.2	21.8	133	15.6	2.4	
13. 6.65	29.0	228	39.5	11.2	34.4	171	29.6	8.4	
27. 6.65	36.2	184	28.7	-	47.4	198	27.3	-	
11. 7.65	47.4	198	44.7	7.2	58.1	170	44.7	7.2	
21. 8.65	55.9	163	35.8	6.6	58.1	175	37.2	6.9	
19. 4.65	54.6	131	29.2	6.3	92.8	223	49.6	10.7	SECOND YEAR TILLERS
3. 5.65	56.5	121	27.4	6.0	127	271	61.4	13.4	
17.5 .65	52.6	105	33.8	5.8	144	287	92.3	15.8	
31. 5.65	55.5	95	27.4	6.0	152	260	75.1	15.9	
13. 6.65	62.9	96	36.1	5.8	172	263	98.9	13.7	
27. 6.65	95.5	82.6	42.8	5.9	262	226	117	13.8	
11. 7.65	91.3	107	52.0	-	210	246	120	-	
21. 8. 65	66.5	83	41.0	6.1	125	156	77.1	11.5	

TABLE 17. (iii). Nutrient dynamics data - Carex flacca, Cassop.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
		mg./10gm.				mg./100plants			
15. 1.65	10.7	178	17.5	-	1.0	16.0	-	-	FIRST YEAR TILLERS
6. 2.65	7.6	161	9.6	-	0.6	12.9	-	-	
19. 4.65	5.0	216	20.8	7.7	0.7	30.2	2.9	1.1	
3. 5.65	5.0	210	20.4	6.7	0.9	37.8	3.7	3.0	
17. 5.65	5.1	237	20.4	6.8	1.4	66.4	5.7	1.9	
31. 5.65	7.9	219	23.8	5.2	4.5	125	13.3	3.0	
13. 6.65	7.7	212	23.6	7.0	5.2	144	16.1	4.8	
11. 7.65	12.9	181	20.2	8.5	11.6	163	18.2	7.7	
21. 8.65	7.2	123	20.5	8.6	7.8	133	22.1	9.3	
20.11.65	5.5	125	9.2	-	4.1	92.4	6.8	-	
15. 1.65	12.9	80	9.2	-	3.6	73.6	6.8	-	SECOND YEAR TILLERS
6. 2.65	4.1	99	7.0	-	3.1	60.0	5.3	-	
19. 4.65	7.7	120	15.5	5.6	5.9	92.4	11.9	4.3	
3. 5.65	8.9	113	14.3	6.3	7.1	90.4	11.4	5.0	
17. 5.65	9.6	144	15.1	6.3	9.6	144	15.1	6.3	
31. 5.65	10.5	109	13.0	5.4	11.9	123	15.0	6.3	
13. 6.65	11.2	114	15.4	5.6	12.0	122	16.5	6.0	
11. 7.65	9.1	53	9.4	8.6	8.5	50.0	8.8	8.1	
21. 8.65	9.5	22	6.3	3.5	6.7	15.4	4.4	2.5	
20.11.65	5.5	16.8	6.0	-	-	-	-	-	

TABLE 18. (i) Nutrient dynamics data - Carex panicea, Sunbiggin Tarn.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
	mg./10gm.				mg./100plants				
6. 2.65	14.7	197	11.7	-	1.9	25.6	-	-	FIRST YEAR TILLERS
19. 4.65	21.2	218	22.1	2.2	3.8	39.2	4.0	0.4	
3. 5.65	23.2	209	22.0	9.1	4.6	41.8	4.4	1.8	
17. 5.65	22.0	250	25.5	10.7	5.3	60.0	6.1	2.6	
31. 5.65	42.7	217	22.5	8.3	13.7	69.0	7.2	2.6	
13. 6.65	34.8	216	25.1	9.1	19.5	121	14.1	5.1	
27. 6.65	57.1	183	21.2	-	38.8	124	14.4	-	
11. 7.65	46.5	145	22.7	9.0	37.2	116	18.2	7.2	
21. 8.65	43.9	170	18.5	6.5	42.1	103	17.8	6.2	
20.11.65	58.7	111	12.7	-	50.5	95.3	10.9	-	
6. 2.65	62.0	113	10.3	-	53.3	96.8	8.9	-	SECOND YEAR TILLERS
19. 4.65	45.6	131	18.6	-	37.4	107	15.3	3.4	
3. 5.65	50.1	123	29.8	7.8	40.1	98.4	15.8	6.2	
17. 5.65	57.8	125	21.4	7.4	48.6	105	18.0	6.2	
31. 5.65	68.3	104	13.7	6.4	59.4	90.5	11.9	5.6	
13. 6.65	72.1	95	16.7	6.0	66.3	87.4	15.4	5.5	
27. 6.65	102.1	35	9.7	-	100.1	34.1	9.5	-	
11. 7.65	99.2	21	9.7	3.0	69.4	14.7	6.8	2.1	
21. 8.65	58.9	25	12.8	0.9	29.5	12.8	6.4	0.5	
20.11.65	28.5	28	7.8	-	-	-	-	-	

TABLE 18. (ii). Nutrient dynamics data - *Carex panicea*, Sand Sike.

Collection Date	Ca	K	Mg	P	Ca	K	Mg	P	
	mg./10gm.				mg./100 plants				
19. 4.65	11.8	276	38.3	13.1	2.8	66.2	9.2	3.1	FIRST YEAR TILLERS
3. 5.65	15.7	226	34.0	20.3	3.9	56.5	8.6	5.1	
17. 5.65	25.1	296	36.3	6.7	7.5	88.8	10.9	2.1	
31. 5.65	14.4	264	33.4	3.3	10.4	190	24.1	2.3	
13. 6.65	15.9	255	38.2	8.5	35.0	561	84.1	18.7	
27. 6.65	25.7	166	26.9	-	65.0	420	68.1	-	
11. 7.65	26.6	162	39.7	8.3	67.8	413	101.5	21.2	
21. 8.65	34.0	124	39.8	3.1	87.4	319	102.3	8.0	
19. 4.65	23.6	142	42.4	5.0	58.1	349	104.3	12.3	SECOND YEAR TILLERS
3. 5.65	24.2	108	31.2	5.9	59.1	263	76.1	14.4	
17. 5.65	31.3	103	39.2	6.9	76.4	251	98.0	16.8	
31. 5.65	38.5	68	33.6	4.0	102.4	181	89.4	10.6	
13. 6.65	41.2	85	31.6	5.9	138.0	285	106.0	19.8	
27. 6.65	53.2	93.4	24.3	-	196.8	346	89.9	-	
11. 7.65	46.7	69	39.1	4.8	140.1	207	117.3	14.4	
21. 8.65	45.1	66	36.8	4.0	85.7	125	69.9	7.6	

TABLE 18. (iii). Nutrient dynamics data - *Carex panicea*, Cassop.

TABLE 19.

Root and rhizome chemical analysis data.

Collection Date	ROOTS Ca	K	Mg	RHIZOMES Ca	K	Mg	
	Mg./10gm.			mg./10gm.			
15. 1.65	40.0	57.8	8.7	25.5	102	9.3	
6. 2.65	32.3	34.8	11.1	18.3	118	8.4	
19. 4.65	27.3	44.3	10.9	19.6	120	9.8	
3. 5.65	26.0	47.3	11.1	22.1	121	10.8	
17. 5.65	11.1	41.2	11.4	21.1	112	11.2	C. flacca
31. 5.65	25.0	47.1	9.7	26.7	103	9.2	Sumbiggin.
13. 6.65	21.1	57.0	9.4	23.3	119	9.8	
11. 7.65	28.4	53.6	9.5	24.4	71	6.8	
21. 8.65	38.4	52.0	9.3	22.4	76	7.5	
20.11.65	20.5	63.7	11.0	13.4	94	7.3	
6. 2.65	46.7	29.4	9.9	68.7	84.6	8.5	
19. 4.65	26.8	64.0	9.8	21.1	116	9.1	
3. 5.65	26.4	39	9.7	29.7	128	9.9	
17. 5.65	33.8	59	9.9	44.8	86	9.3	
31. 5.65	41.2	60	8.8	33.9	92	8.5	
13. 6.65	25.4	62	8.5	28.3	126	8.5	C. flacca
27. 6.65	36.2	48	7.2	27.5	85	7.0	Sand Sike.
11. 7.65	46.1	62	6.1	47.0	113	9.4	
21. 8.65	49.1	46	7.8	35.8	86	7.4	
20.11.65	45.9	50	7.0	37.3	84	6.7	
19. 4.65	47.3	56	27.1	30.5	103	17.5	
3. 5.65	35.7	63	24.8	21.9	91	17.5	
17. 5.65	70.4	56	36.6	24.0	115	21.2	
31. 5.65	42.4	86	26.6	36.5	136	24.0	C. flacca
13. 6.65	38.5	80	29.9	27.1	127	23.0	Cassop.
27. 6.65	103.3	87	63.3	21.0	145	30.5	
11. 7.65	83.8	115	62.2	52.9	153	39.2	
21. 8.65	60.0	81	40.5	66.1	129	25.5	

TABLE 19. (i). Root and Rhizome chemical analysis data.

Collection Date	ROOTS Ca	K	Mg	RHIZOMES Ca	K	Mg	
	mg./10gm.			mg./10gm.			
15. 1.65	5.2	88	9.3	3.9	107	8.3	
6. 2.65	1.9	99	6.6	2.4	117	6.0	
19. 4.65	2.5	106	13.3	2.3	116	9.5	
3. 5.65	2.6	85	10.4	2.3	99	8.3	
17. 5.65	-	-	-	3.3	97	9.7	C. panicea
31. 5.65	2.9	65	11.1	3.8	97	9.0	Sunbiggin.
13. 6.65	3.9	89	13.6	3.5	124	10.1	
11. 7.65	3.2	96	10.7	7.6	98	8.3	
21. 8.65	4.2	62	9.0	5.9	77	6.5	
20.11.65	3.0	71	9.3	3.9	107	8.3	
6. 2.65	23.3	67	12.5	-	-	-	
19. 4.65	17.8	61	14.0	10.8	100x	10.8	
3. 5.65	19.4	74	14.1	14.7	122	12.0	
17. 5.65	10.2	48	14.5	12.0	93	12.0	
31. 5.65	13.6	79	12.5	21.0	90	10.6	C. panicea
13. 6.65	23.5	83	13.4	26.8	118	10.7	Sand Sike.
11. 7.65	22.1	76	12.2	-	-	-	
21. 8.65	22.2	57	10.6	24.7	99	7.4	
20.11.65	20.2	80	11.1	8.1	114	8.6	
19. 4.65	12.4	67	27.9	8.8	131	20.1	
3. 5.65	14.3	60	16.2	9.3	103	18.8	
17. 5.65	13.2	42	23.9	14.0	87	21.9	
31. 5.65	13.5	46	19.2	13.1	97	17.2	
13. 6.65	11.1	51	20.0	12.6	93	19.1	C. panicea
27. 6.65	11.1	122	18.9	7.8	66	16.2	Cassop.
11. 7.65	13.2	71	19.1	17.5	74	17.4	
21. 8.65	16.9	70	26.0	10.0	120	17.9	

TABLE 19. (ii). Root and Rhizome chemical analysis data.

TABLE 20.

Additional chemical analysis of plant organs.

Plant organ	Ca	K	Mg	
		mg./ 10 gm.		
very young tillers	12.4	217	18.3	
older tillers	14.9	229	16.5	
mature tillers	98.8	125	21.0	
mature tillers (minus dead leaves)	58.1	183	21.3	
dead leaves	143.4	34	16.8	C. panicea Sumbiggin.
leaf tips	192.2	57	14.3	
leaf laminas	78.6	181	28.0	
leaf sheaths	22.2	181	16.7	
roots	18.8	107	17.4	
rhizomes	6.2	116	9.0	
young tillers	14.8	197	20.9	
mature tillers	92.4	105	26.8	
mature tillers (minus dead leaves)	42.2	179	21.2	
dead leaves	131.5	9.6	37.8	
leaf tips	192.9	19.3	23.2	C. panicea Cassop.
leaf laminas (upper)	115.5	170	44.8	
leaf laminas (lower)	37.4	119.7	25.8	
leaf sheaths	6.0	24.1	4.8	
roots	12.2	86	15.5	
rhizomes	3.9	125 T	11.3	
very young tillers	17.3	242	16.4	
older tillers	25.6	236	16.9	
mature tillers	68.9	171	25.1	
mature tillers (minus dead leaves)	40.7	212	24.7	C. flacca Cassop.
dead leaves	155.2	22.2	27.9	
leaf tips	135.0	71.1	30.0	
leaf laminas	45.2	111	25.9	
leaf sheaths	11.4	143	29.6	
roots	72.5	67.8	23.4	
rhizomes	23.3	140	16.5	

TABLE 20. Additional chemical analyses of plant organs.

TABLE 21.

Soil analysis data.

Sample origin.	Ca	K	Mg	Na
		mg./100gm. dry soil		
C. panicea site Sumbiggim Tarm	1.75	4.0	1.8	16.0
C. panicea site Cassop	613.5	85	96	17.8
C. flacca site Sumbiggim Tarm	343.5	2.5	12.0	28.5
C. flacca site Cassop	1133.5	10.0	215.8	34.5

TABLE 21. Soil analysis data.

TABLE 22.

Concentrations of elements in tillers before treatment in culture solutions.

Species and collection site	Ca	K mg./10gm.	Mg	P
C. flacca, Sunbiggin	37.9	194	33.2	9.2
C. flacca, Cassop	45.1	249	38.9	17.2
C. panicea, Sunbiggin	11.3	208	28.3	11.6
C. panicea, Cassop	21.5	352	34.4	9.6

TABLE 22. Relative concentrations of elements in tillers before treatment.

PART VII.

LITERATURE CITED.

ALLEN, J.E. 1958. Atomic absorption spectrophotometry with special reference to the determination of magnesium. Analyst, 83, 466.

ALLEN, S.E. & PEARSALL, W.H. 1963. Leaf analysis and shoot production in Phragmites. Oikos, 14, 176-189.

ARNON, D.I., FRATZKE, W.E. & JOHNSTON, C.M. 1942. Hydrogen ion concentration in relation to the absorption of inorganic nutrients by higher plants. Plant Physiol., 17, 515-524.

ARNON, D.I. & JOHNSTON, C.M. 1942. Influence of hydrogen ion concentration on the growth of higher plants under controlled conditions. Plant Physiol., 17, 525-539.

BEADLE, N.C.W. 1954. Soil phosphate and the delimitation of plant communities in eastern Australia. Ecology, 35, 370-375.

BEAR, F.E. 1917. A correlation between bacterial activity and lime requirement of soils. Soil Sci., 4, 433.

BELLAMY, D.J. 1967. Ecological studies on some European mire systems. Ph.D. Thesis, University of London.

BELLAMY, D.J. & RIELEY, J.O. 1964. The term 'base-rich' in ecology. Nature, 201, 946.

BELLAMY, D.J. & RIELEY, J.O. 1967. Some ecological statistics of a 'miniature bog'. Oikos, 18, 33-40.

BENDER, W.H. & EISENMENGER, W.S. 1941. Intake of certain elements by calciphilic and calciphobic plants growing in soils differing in pH. Soil Sci., 52, 297-307.

BHAN, K.C., WALLACE, A. & LUNT, O.L. 1959. Some mineral losses from leaves by leaching. Proc. Amer. Soc. Hort. Sci., 73, 289-293.

BILLINGS, W.D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the Western Great Basin. Ecology, 31, 62-74.

BLACKMAN, G.E. & RUTTER, A.J. 1949. Physiological and ecological studies in the analysis of plant environment. IV. The interaction between light intensity and mineral nutrient supply on the uptake of nutrients by the bluebell (Scilla non-scripta). Ann. Bot. Lond., N.S. ,13, 454-489.

BOATMAN, D.J. 1962. The growth of Schoenus nigricans on blanket bog peats. I. The response to pH and the level of potassium and magnesium. J. Ecol., 50, 823-832.

BRADSHAW, A.D., LODGE, R.W., JOWETT, D & CHADWICK, M.J. 1958. Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. J. Ecol., 46,749-757.

BROWN, J.C. & HOLMES, R.S. 1958. Iron supply and interacting factors related to lime-induced chlorosis. Soil Sci., 82, 507-519.

CARLISLE, A., BROWN, A.H.F. & WHITE, E.T. 1966. Litter fall, leaf production and the effects of defoliation by Tortrix viridana in a sessile oak (Quercus petraea) woodland. J. Ecol., 54, 65-85.

CARLISLE, A., BROWN, A.H.F. & WHITE, E.T. 1966. The organic matter and nutrient elements in the precipitation beneath a sessile oak(Quercus petraea) canopy. J. Ecol., 54, 87-98.

CHENG, K.L. & BRAY, R.H. 1951. Determination of calcium and magnesium in soil and plant material. Soil Sci., 72, 449-458.

CHENG, K.L., MELSTEAD, S.W. & BRAY, R.H. 1953. Removing interfering metals in the versenate determination of calcium and magnesium. Soil Sci., 75, 37-40.

CLYMO, R.S. 1962. An experimental approach to part of the calcicole problem. J. Ecol., 50, 707-731.

COLLANDER, R. 1941. Selective absorption of cations by higher plants. Plant Physiol., 16, 691-720.

DAVID, D.J. 1958. Determination of zinc and other elements in plants by atomic absorption spectroscopy. Analyst, 83, 655.

DAVID, D.J. 1959. Determination of calcium in plant material by atomic absorption spectrophotometry. Analyst, 84, 536.

DAVIDSON, J. 1927. Effect of hydrogen ion concentration on the absorption of phosphorus and potassium by wheat seedlings. Jour. Agric. Res., 35, 335-347.

DEAN, J.A. 1960. Flame photometry. McGraw-Hill. New York.

DE SILVA, B.L.T. 1934. The distribution of 'calcicole' and 'calcifuge' species in relation to the content in the soil of calcium carbonate and exchangeable calcium and to soil reaction. J. Ecol., 22, 532.

DU RIETZ, G.E. 1949. Huvudenheter och Huvudgränser i Svensk Myrvegetation. Sv. Bot. Tidskr., 43, 274-309.

ELWELL, W.T. & GIDLEY, J.A.F. 1961. Atomic absorption Spectrophotometry. Pergammon Press.

EPSTEIN, E. 1961. The essential role of calcium in selective cation transport by plant cells. Plant Physiol., 36, 437-444.

FAGAN, T.W. & WATKINS, M. 1932. The chemical composition of the miscellaneous herbs of pastures. Welsh J. Agric., 8, 144-151.

FAWZY, H., OVERSTREET, R. & JACOBSON, L. 1954. The influence of hydrogen ion concentration on cation absorption by barley roots. Plant Physoil., 29, 234-237.

FLICHE, P. & GRANDEAU, L. 1874. De l'influence de la composition chimique du sol sur la vegetation de Chataignier. Ann. d. Chimie et d. Physique. 354-379.

FRIED, M. & PEECH, M. 1946. The comparative effects of lime and gypsum upon plants grown in acid soils. Jour. Amer. Soc. Agron., 38, 614-623.

FUJIMOJO, C.K. & SHERMAN, G.D. 1948. Behaviour of manganese in the soil and the manganese cycle. Soil Sci., 66, 131-146.

GAUCH, H.G. 1957. Mineral nutrition of plants. Ann. Rev. Plant Physiol., 8, 31-63.

GOODMAN, G.T. & PERKINS, D.F. 1959. Mineral uptake and retention in cotton-grass (Eriophorum vaginatum L.). Nature, 184, 467-468.

GORE, A.J.P. 1961. Factors limiting plant growth on high level blanket peat. I. Calcium and phosphate. J. Ecol., 49, 399-402.

GORHAM, E. 1956. On the chemical composition of some waters from the Moorhouse Nature Reserve. J. Ecol., 44, 375-382.

GRIME, J.P. 1960. A study of a group of Derbyshire plants with particular reference to their nutrient requirements. Ph.D. Thesis University of Sheffield.

HACKETT, C. 1964. Ecological aspects of the nutrition of Deschampsia flexuosa (L) Trin.. I. The effect of aluminium, manganese and pH on germination. J. Ecol., 52, 159-167.

HACKETT, C. 1965. Ecological aspects of the nutrition of Deschampsia flexuosa (L.) Trin.. II. The effects of Al, Ca, Fe, K, Mn, N, P, and pH on the growth of seedlings and established plants. J. Ecol., 53, 315.

HALE, J.B. & HEINTZE, S.G. 1946. Manganese toxicity affecting crops on acid soils. Nature, 157, 554.

HALL, A.D. & RUSSELL, E.J. 1911. From LUNDEGARDH, (1931).

HARTWELL, B.L. & PEMBER, F.R. 1918. The presence of aluminium as a reason for the difference in the effect of so-called acid soil on barley and rye. Soil Sci., 6, 259-281.

HEINTZE, S.G. 1946. Manganese deficiency in peas and other crops in relation to availability of soil manganese. Jour. Agric. Sci., 36, 227-238.

HEWITT, E.J. 1948a. The resolution of the factors in soil acidity. The comparative effects of manganese and aluminium toxicities on some farm and market crops. A.R. Long Ashton Agric. Hort. Res. Stat., 58.

HEWITT, E.J. 1948b. Experiments on iron metabolism in plants. I. Some effects of metal-induced iron deficiency. A.R. Long Ashton Agric. Hort. Res. Stat., 58.

HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Commonw. Agric. Bur. Reading, England.

HOFFER, G.N. & TROST, J.F. 1923. The accumulation of iron and aluminium compounds in corn plants and its probable relation to root rot. Jour. Amer. Soc. Agron., 15, 323-330.

HOLDGATE, M.W. 1955a. The vegetation of some springs and wet flushes on Tarn Moor, near Orton, Westmorland. J. Ecol., 43, 80-89.

HOLDGATE, M.W. 1955b. The vegetation of some British upland fens. J. Ecol., 43, 389-403.

HOOD, S.L. ET AL. 1944. Mineral contamination resulting from grinding plant samples. Ind. Eng. Chem., 16, 202.

HOPE SIMPSON, J.F. 1938. A chalk flora of the lower greensand, its use in interpreting the calcicole habit. J. Ecol., 26, 218.

HOU, H. & MERKLE, F.G. 1950. Chemical composition of certain calcifugous and calcicolous plants. Soil Sci., 69, 471-486.

JACOBSON, L., HANNAPEL, R.J., MOORE, D.P. & SCHAEDLE, M. 1961. Influence of calcium on the selectivity of ion absorption processes. Plant Physiol., 36, 58-61.

JACOBSON, L., MOORE, D.P. & HANNAPEL, R.J. 1960. Role of calcium in the absorption of monovalent ions. Plant Physiol., 35, 352-358.

JAMES, D.B. 1962. Factors affecting the growth of Molinia caerulea on a calcareous soil. J. Ecol., 50, 521-527.

JAMES, W.O. 1931. Studies of the physiological importance of the mineral elements in plants. II. Potassium - its distribution, movement and relation to growth in the potato. Ann. Bot., 45, 425-442.

JANSSEN, G. & BARTHOLOMEW, R.P. 1929. The translocation of potassium in tomato plants and its relation to their carbohydrate and nitrogen distribution. J. Agric. Res., 38, 447-465.

JEFFERIES, R.L. & WILLIS, A.J. 1964. Studies on the calcicole-calcifuge habit. I. Methods of analysis of soil and plant tissues and some results of investigations on four species. J. Ecol., 52, 121-138.

JEFFERIES, R.L. & WILLIS, A.J. 1964. Studies on the calcicole-calcifuge habit. II. The influence of calcium on the growth and establishment of four species in soil and sand cultures. J. Ecol., 52, 691-707.

JENNINGS, D.H. 1963. The absorption of solutes by plant cells. Oliver & Boyd. Edinburgh.

KERR, J.R.W. 1960. The spectrophotometric determination of microgram amounts of calcium. Analyst, 85, 867-870.

KRAUS, G. 1911. Boden u. Klima auf Kleinsten Raum. From LUNDEGARDH, (1931).

LONG, W.G., SWEET, D.V. & TUKEY, H.B. 1956. Loss of nutrients from plant foliage by leaching as indicated by radioisotopes. Science, 123, 1039-1040.

LUNDEGARDH, H. 1924. Biochem. Zeitschr., 146, 564.

LUNDEGARDH, H. 1931. Environment and plant development. Arnold. London.

McHARGUE, J.S. & ROY, W.R. 1932. Mineral and nitrogen content of some forest trees at different times in the growing season. Bot. Gaz., 94, 381-393.

McHARGUE, J.S., & ROY, W.R. & PELPHREY, J.G. 1932. The iron, manganese, copper, zinc and iodine content of some important forage crops. Jour. Amer. Soc. Agron., 24, 562-565.

MACKERETH, F.J.H. 1963. Water analysis for limnologists. Freshwater Biol. Assoc., Sci. Publ. No. 21.

MALMER, N. 1958. Notes on the relation between the chemical composition of mire plants and peat. Bot. Not., 3, 276-288.

MANN, H.B. 1930. Availability of manganese and iron as affected by application of calcium and magnesium carbonates to the soil. Soil Sci., 30, 117-133.

MASON, T.G. & MASKELL, E.J. 1931. Further studies on transport in the cotton plant. I. Preliminary observations on the transport of phosphorus, potassium and calcium. Ann. Bot., 45, 125-173.

MATTSON, S. & HESTER, J.B. 1933. The laws of soil colloidal behaviour III. Soil Sci., 36, 229-244.

MAUCHA, R. 1932. Hydrochemische Methoden in der Limnologie. Die Binnengewässer 12. Stuttgart.

MEVIUS, W. 1927. Naturwiss. u. Landwirtsch. 2. From LUNDEGARDH, (1931).

MIDDLETON, L.J. & RUSSELL, R.S. 1958. The interaction of cations in absorption by plant tissues. J. Exp. Bot., 9, 115-127.

MIRASOL, J.J. 1920. Aluminium as a factor in soil acidity. Soil Sci., 10, 153-217.

MITCHELL, H.L. 1936. Trends in the nitrogen, phosphorus, potassium and calcium content of the leaves of some forest trees during the growing season. Black Rock For. Paper 1, (6).

NIELSEN, K.F. ET AL. 1963. A study of ion interactions in the uptake of nitrogen, phosphorus, potassium, calcium, chlorine and sulphur by corn. Soil Sci., 95, 315-321.

OLSEN, C. 1923. Studies on the hydrogen ion concentration of the soil and its significance to the vegetation, especially to the natural distribution of plants. Compt. Rend. Lab. Carls. Ed. Francaise, 15, 1-166.

OLSEN, C. 1938a. Water culture experiments with higher green plants in nutrient solutions having different concentrations of calcium. Compt. Rend. Lab. Carls. Ser. Chim., 22, 69-97.

OLSEN, C. 1938b. Growth of Deschampsia flexuosa in culture solutions (water culture experiments) and in soils with different pH values. Compt. Rend. Lab. Carls. Ser. Chim., 22, 405-411.

OLSEN, C. 1948. The mineral, nitrogen and sugar content of beech leaves and beech leaf sap at various times. Compt. Rend. Lab. Carls. Ser. Chim., 26, 197-230.

OLSEN, C. 1953. The significance of concentration for the rate of ion absorption by higher plants in water culture. IV. The influence of hydrogen ion concentration. Physiol. Plant., 6, 848-858.

OVERSTREET, R., JACOBSON, L. & HANDLEY, R. 1952. The effect of calcium on the absorption of potassium by barley roots. Plant Physiol., 27, 583-590.

PEARSALL, W.H. 1922. Plant distribution and basic ratios. The Naturalist, 269-271.

PEARSALL, W.H. & WRAY, E.M. 1927. The physiology and ecology of the calcifuge habit of Eriophorum angustifolium. J. Ecol., 15, 1-32.

PENSTON, N.L. 1931. Studies of the physiological importance of the mineral elements in plants. III. Study by microchemical methods of the distribution of potassium in tomato plants. Ann. Bot., 45, 673.

PERKINS, D.F. 1961. Mineral nutrient inter-relationships in Eriophorum vaginatum L.. Ph.D. Thesis, University of Wales, Swansea.

PETRIE, A.H.K. 1934. The drift of the content of potassium and calcium with age in plants. Austral. J. Exp. Biol. Med. Sci., 12, 99.

PIGOTT, C.D. 1956. The vegetation of Upper Teesdale in the north Pennines. J. Ecol., 44, 545-586.

PIPER, C. 1950. Soil and plant analysis. Waite Agric. Inst., Adelaide, Australia.

PRITCHARD, G.I., PIGDEN, W.J. & FOLKINS, L.P. 1964. Distribution of potassium, calcium, magnesium and sodium, in grasses at progressive stages of maturity. Can. J. Plant Sci., 44, 318-324.

RAYNER, M.C. 1913. The ecology of Calluna vulgaris. New Phytol., 12, 59-77.

RICHARDS, F.J. & SHIH, S.H. 1940. Physiological studies in plant nutrition. X. Water content of barley leaves as determined by the interaction of potassium with certain other elements. Ann. Bot., N.S. 4, 165-176.

RICHARDSON, A.E.V. 1932. Austral. Coun. Sci. Ind. Res. Bull., 66.

RIPPEL, A. 1927. Biochem. Z., 187, 272. From LUNDEGARDH, (1931).

RORISON, I.H. 1956. Ecological aspects of the calcicole-calcifuge concept. D. Phil. Thesis, University of Oxford.

RORISON, I.H. 1960. Some experimental aspects of the calcicole-calcifuge problem. I. The effects of competition and mineral nutrition upon seedling growth in the field. J. Ecol., 48, 585-599.

RORISON, I.H. 1960b. The calcicole-calcifuge problem. II. The effects of mineral nutrition on seedling growth in solution culture. J. Ecol., 48, 679-688.

SALISBURY, E.J. 1920. The significance of the calcicolous habit. J. Ecol., 8, 202.

SALISBURY, E.J. 1925. The incidence of species in relation to soil reaction. J. Ecol., 13, 149.

SAMPSON, A.W. & SAMISCH, R. 1935. Growth and seasonal changes in composition of oak leaves. Plant Physiol., 10, 739-751.

SCHOLLENBERGER, C.J. & SIMON, R.H. 1945. Determination of exchange capacity and exchangeable bases in soil - ammonium acetate method. Soil Sci., 59, 13-24.

SHEAR, G.M. 1938. The effects of soil reaction on the growth and chemical composition of annual garden flowers. Va. Agr. Exp. Stat. Tech. Bull., 63.

SJORS, H. 1948. Myrvegetation i Bergslagen. Acta Phytogeog. Suec., 21, 1-299.

SJORS, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos, 2, 241-258.

SNAYDON, R.W. & BRADSHAW, A.D. 1961. Differential responses to calcium within the species Festuca ovina L.. New Phytol., 60, 219-234.

SPARLING, J.H. 1967. The occurrence of Schoenus nigricans L. in blanket bogs. II. Experiments on the growth of S. nigricans under controlled conditions. J. Ecol., 55, 15-31.

STEELE, B. 1955. Soil pH and base status as factors in the distribution of calcicoles. J. Ecol., 43, 120-132.

STENLID, G. 1958. Salt losses and redistribution in higher plants. Encyclopedia of Plant Physiology, 4, 615-637.

TAMM, C.O. 1951. Seasonal variation in composition of birch leaves. Physiol. Plant., 4, 461-469.

TANSLEY, A.G. & ADAMSON, R.S. 1927. Studies in the vegetation of the English chalk. IV. A preliminary survey of the chalk grasslands of the Sussex Downs. J. Ecol., 15, 1-32.

THOMAS, B. ET AL. 1952. The ash constituents of some herbage plants at different stages of maturity. Emp. Jour. Exp. Agric., 20, 77.

THOMAS, B. & TRINDER, N. 1947. The ash components of some moorland plants. Emp. Jour. Exp. Agric., 15, 237-248.

TRUOG, E. 1918. Soil acidity. I. Its relation to the growth of plants. Soil Sci., 5, 169-195.

TRUOG, E. 1947. Soil reaction influence on availability to plants of nutrients. Soil Sci.,Soc. Amer. Proc., 11, 305-308.

TUKEY, H.B. & MORGAN, J.V. 1962. The occurrence of leaching from above-ground plant parts and the nature of the material leached. XVIth. Intern. Hort. Congr., Brussels, 153-160.

TUKEY, H.B. Jr. & TUKEY, H.B. 1962. The loss of organic and inorganic materials by leaching from leaves and other above-ground plant parts. In 'Radioisotopes in soil-plant nutrition studies', Intern. Atomic Energy Agency, Vienna, pp. 289-302.

TUKEY, H.B.Jr., TUKEY, H.B. & WITTWER, S.H. 1958. Loss of nutrients by foliar leaching as determined by radioisotopes. Proc. Amer. Soc. Hort. Sci., 126, 120-121.

ULRICH, A. 1943. Plant analysis as a diagnostic procedure. Soil Sci., 55, 101-112.

UNGER, F. 1836. Uber dem Einfluss des Bodens auf die Verteilung der Gewächse. From LUNDEGARDH, (1931).

VALENTINE, D.H. (Ed.) 1965. The natural history of Upper Teesdale. Northumberland & Durham Naturalists' Trust. Newcastle-upon-Tyne.

VIETS, F.G . 1944. Calcium and other polyvalent cations as accelerators of ion accumulation by excised barley roots. Plant Physiol., 19, 466-480.

WAHLENBERG, G. 1814. Tentamen de vegetatione et climate Helvetiae septentrionalis. From LUNDEGARDH, (1931).

WAGNER, H. 1932. Z. Pfanzenernähr Dung. u. Bodenk. A., 25, 48-102.

WEBB, D.A. & HART, E.V. 1945. Contributions toward an understanding of the calcicole and calcifuge habit in some Irish plants. Sci. Proc. Roy. Dublin Soc., 24, 1-10.

WILL, G.M. 1957. Variations in the mineral content of Radiata pine needles with age and position in the tree crown. N.Z. J. Sci. Tech. Bull., 38, 699-706.

WILLIAMS, R.F. 1955. Redistribution of mineral elements during development. Ann. Rev. Plant Physiol., 6, 25-42.

WITTING, M. 1947. Katjonsbestämningar i myrvatten. Bot. Not., 4, 287-304.