An Experimental Approach to Part of the Calcicole Problem
Author(s): R. S. Clymo
Source: *Journal of Ecology*, Vol. 50, No. 3 (Nov., 1962), pp. 707-731
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/2257478
Accessed: 11/06/2010 19:45

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=briteco.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Ecology*.

http://www.jstor.org

AN EXPERIMENTAL APPROACH TO PART OF THE CALCICOLE PROBLEM

By R. S. CLYMO*

Botany Department, University College, London

I. INTRODUCTION

The correlation of certain plant distributions with the presence or absence of calcium carbonate in the soil is well known. Hope-Simpson (1938) has defined as calcicoles 'species affecting the more important types of calcareous soil and rare on, or absent from, acid soils, and calcifuges as the reverse'. Other pairs of terms are also in use to describe the same observations. There is some danger that the semantic similarity of the terms may be taken to imply a reciprocally related explanation for each of the calcicole and calcifuge distribution types. With this reservation, the terms are useful as field descriptions, much as fever in medicine describes a class of symptoms with many underlying causes.

The experiments to be described have been concerned only with 'the calcicole problem'. Much work has been done on this subject and numerous summaries have been produced, *e.g.* by Black (1957), Grime (1960), Hartwell & Pember (1918), Hewitt (1952), Jensen (1952), Lundergårdh (1931), Rorison (1956), Russell (1961), Salisbury (1920), Schmehl *et al.* (1950), Steele (1955), Webb & Hart (1945), Wilde (1954) and Zlatnik (1928). To add another would serve no useful purpose. There are, however, four complicating factors, the importance of which has not been generally recognized. These affect the design of experiments, and must therefore be mentioned first of all.

First, as was pointed out by Salisbury (1920), most calcareous soils are well drained. He suggested that the calcicoles *Fagus sylvatica*, *Juniperus communis*, *Clematis vitalba*, *Buxus sempervirens*, *Helleborus foetidus* and the moss *Pleurochaete squarrosa* are really plants of well-drained soils. The calcicole status of beech and juniper is questionable (for example in the New Forest and Rothiemurchus Forest respectively) and the restriction of box to calcareous slopes may be related to the instability of these areas (Pigott & Walters 1953), but the possibility of such an explanation must be borne in mind, since most of the plants used to investigate the calcicole problem have been chalk downland plants.

Secondly, a number of plant taxa are calcicole only at the limits of their range. They may be called 'marginal calcicoles'. Praeger (1950) considered *Stellaria palustris*, *Arenaria verna*, *Sedum acre*, *Origanum vulgare* and *Primula veris* as calcicole in Ireland but not in Britain. A survey of the soil preferences of the plants used in earlier investigations of the calcicole problem is given in Table 1. The information has been condensed from accounts in various Floras.

It seems therefore that about two-thirds of these plants are calcicole in Britain in special circumstances; at the limit of their range, in well-drained soils, or as 'ruderals and weeds' in open disturbed ground. The experiments of Webb & Hart, and Steele

* Now at Botany Department, Westfield College, London, N.W.3.

appear to have been performed in conditions favouring physical and marginal calcicole behaviour (in a cool greenhouse and in a sandy soil respectively). Rorison's experiments

Table 1. *The soil preferences of plant taxa used in experiments on the calcicole problem*

Condensed from Floras. 1. Webb (1943) covering Ireland. 2. Clapham, Tutin & Warburg (1952) covering the British Isles. 3. Bonnier (1912-34) covering France, Switzerland and Belgium. 4. Hegi (1906) covering central Europe

Abbreviations. C = strong preference for calcareous soils; D = preference for dry soils; X = no marked preference for particular soils; ( ) = especially

Author	Species	1	2	3	4	Suggested summary
Zlatnik (1928)	Sesleria coerulea	C	C	C	CD	C
Webb & Hart (1945)	Geranium lucidum	↑ Calcicole by definition	X	X	X	X ?D
	Blackstonia perfoliata		C	C	C	C
	Origanum vulgare		(C)	(C)-X	C-X	Varies with climate
	Juncus inflexus		Basic or neutral	(C)		C
	Verbascum thapsus		(D)	X	D	D
	Hypericum perforatum		(C)	X	(C)	C
	Leontodon hispidus		(C)		X	?
	Poterium sanguisorba		C	X	C-X	Varies with climate
	Aquilegia vulgaris		C	(C)		C?
	Reseda luteola		(C)	X	(C)	C?
	Centaurea scabiosa		(C)	C-X	C-X	Varies with climate
	Erigeron acris	↓	D(C)	X	D	D
Steele (1955)	E. acris	DC	D(C)	X	D	D
	Iberis amara		DC	(C)	C	C
	Plantago media	X	Neutral soils	(C)	X	Plant of cultivation
	Veronica persica	X	X	X	X	Plant of cultivation
	Echium vulgare	Sandy places	D	X	D	D
	Sherardia arvensis	D	X	X	X	Plant of cultivation
	Carlina vulgaris	D	C	C-X	C-X	Varies with climate
	Galium verum	D	X	X	D	D
	Senecio viscosus		X	X	D	Plant of cultivation
	Pimpinella saxifraga	D(C)	D	X	D	D
Rorison (1956)	Asperula cynanchica	Rocky pastures sandhills	C	X	CD	C D?
	Scabiosa columbaria		CD	X	D	D
Miscellaneous	Zerna erecta	D	D(C)	C	C-(X)	Varies with climate
	Brachypodium pinnatum	D	C	X	D	Varies with climate D

in the field were also conducted on a sandy soil and a light calcareous soil. *Scabiosa columbaria* and *Asperula cynanchica* both fall into a group of plants which Perring (1960) found to be restricted more to south-west slopes in areas where rainfall is high.

This distribution does not appear to correlate well with the chemical factors studied but could be a function of the water or temperature factors.

Thirdly, in natural conditions on calcareous soils competition is almost universally present. The importance of this factor may be seen in Fig. 1 which shows a hypothetical case of the yields of two plant taxa in relation to some habitat factor (P). When grown separately the optimum for species Y is at a concentration *a* of P, whilst that of species X is at a higher concentration *b*. If grown together, however, X might be expected to suppress Y at all concentrations of P below *c*.

This example is much simplified, but has some relevance since there are several reports of calcicole plants growing best in conditions other than those in which they are found naturally (Hartwell & Pember 1918, Salisbury 1920, Tansley 1917, Webb & Hart 1945). It follows that much of the work which has been done with small selections of ions on single species is of no help in explaining the plant's ecology.

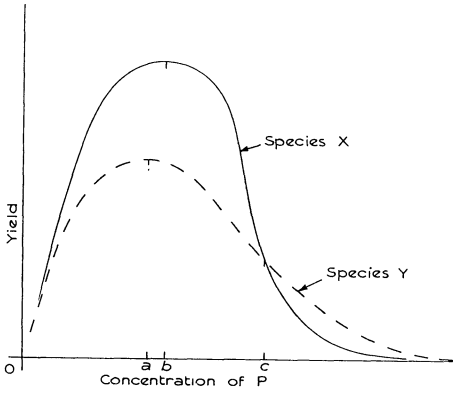

Fig. 1. Diagram showing growth response to concentration of factor P for two different species.

Fourthly, there is the difficulty of measuring success of a plant taxon. This is a complicated matter but is summarized below. Ideally experiments should be run for a minimum of several generations. In practice, if the plants produce an abundance of seed most of which does not survive to the reproductive stage, the production of dry weight by the individual plant is taken as a measure of success. This assumes that competitive ability is related mainly to bulk (the evidence on this point is meagre and inconclusive). The dry weight is thought to be a reasonable integrator of the whole plant's functioning, but it must obviously be used with caution.

Another criterion of success that is sometimes used is connected with deficiency or toxicity symptoms. The argument seems to run thus: Symptoms of toxicity or deficiency are seen in a plant in natural conditions. Similar symptoms can be produced in culture experiments by adding an often relatively large concentration of an ion *z* to the solution. Therefore, (a) the growth of the plant will be depressed in natural conditions where this ion occurs and (b) the plant will only be found where the ion *z* is absent or in very low concentration.

This argument has at least two major flaws. First the conclusion (a) is not necessarily true. Holliday *et al.* (1958) describe, without comment, a case where the lowest

concentration at which apparent boron toxicity symptoms occur is accompanied by an increase in yield compared with lower boron concentrations, and only at high boron concentrations, where the toxicity symptoms are severe, is there a decrease in yield. The same appears to be true of chlorosis. Grime (1960) states 'In only four' out of sixteen species 'is there evidence that a major reduction in vegetative or reproductive vigour is associated with chlorosis'. Secondly the conclusion (b) is not necessarily true, because of the modifying effects of competition already referred to.

It is thus apparent that the problem of calcicole behaviour must be delimited as much as possible if experimental results with ecological significance are to be made.

II. CHOICE OF PLANT TAXA

The choice of plant taxa is restricted for the reasons giv en already, and for some others The following conditions were set:

(a) The plants must grow naturally in wet habitats. This eliminates 'physical calcicoles' and allows the extrapolation of results obtained in water culture (which is most accurately and easily controlled) to natural conditions, with some confidence. It is of course necessary to check these extrapolations by field experiments and observations.

(b) The plants should show calcicole behaviour over their entire range. This condition eliminates marginal calcicoles with their attendant climatic interactions.

(c) The chosen plant taxa must have a fairly extensive distribution. If only a few small colonies of a plant taxon are known it is possible for them all to be on calcareous soils by the chances of random distribution. There are other historical and biotic explanations which may account for the distribution of uncommon plants which make them unsuitable for an investigation of this type. Besides this the collection of experimental material of uncommon plants is liable to be difficult and undesirable.

(d) The chosen plant taxa must be a morphologically similar pair with the same general habitat, one of which is calcicole and the other not (preferably calcifuge). If it is accepted that competition is most intense between closely related species then some of the effects of competition can be allowed for whilst the experiments are still manageable in size. There may, however, be effects of competition in natural conditions which can only be revealed in field experiments.

(e) Finally it is desirable although not essential that the plant taxa should be monocotyledonous. Such plants have easily separable offsets. They also have relatively small amounts of non-productive material and so respond (by dry weight measurements) more sensitively than plants with a large amount of purely structural material.

The plants which most nearly fit these requirements (in the British flora) are *Carex lepidocarpa* (calcicole) and *C. demissa* (tends to calcifuge), which are perhaps best considered as ecospecies in the group *C. flava* (sensu lato). There is a very small amount of gene interchange at the present time (Davies 1955, 1956). Plants of both taxa are found in wet, open habitats liable to disturbance such as forest rides, cart ruts, upland flushes, mowing fens or peat cuttings, and stream-sides. *C. flava* (sensu stricto) has been shown experimentally to require waterlogging for good growth and does not produce fruits if shaded (Elliott and Gregory pers. comm.). Observations in natural habitats would suggest that these are common features of *C. flava* (sensu lato).

III. METHODS

A. *Plant material collections*

About 40 000 seeds of each species were collected from the same site each year in July-September; *C. lepidocarpa* from Greywell Fen in Hampshire, and *C. demissa* from a ride in the New Forest. They were stored in a dark cool place and would germinate after the April following collection. More uniform germination is obtained by removing the utricles. The seeds were rubbed through a nest of sieves with a piece of wire gauze, and the chaff removed by winnowing and differential flotation. Smaller seed collections (about 200 seeds) were made from a wide geographic range for provenance tests.

Offsets were used in a few experiments. These proved eventually to be of little importance. *C. demissa* was collected from the same site as the seeds. *C. lepidocarpa* came from Etchinghill Fen in Kent. In the experiments with offsets measurements were made of the original fresh weight of all the offsets, and the dry weight of a sample covering the range of fresh weights. The ratio of fresh to dry weight was not significantly ($P = 0{\cdot}05$) dependent on the absolute size of the offset. The final dry weights were also measured. Because the dry weight increase in these experiments was about equal to the original dry weight the results are given as a percentage of the original weights. This reduces some of the differences attributable to the variation of growth potential with initial size.

B. *Chemical analyses*

These are described in Clymo (1960). Plant materials were wet ashed with a mixture of nitric, sulphuric and perchloric acids.

Nearly all the ion analyses were well-known procedures, mostly based on Mackereth (1957).

The phosphate method was that of Kaila (1955). Phosphomolybdic acid was formed in equinormal hydrochloric and sulphuric acids. In these conditions the colour is stable (after the first 15 minutes) for an hour at least, which facilitates analyses of large numbers of samples.

The iron and aluminium method was a slight modification of that of Davenport (1949). Both iron and aluminium form compounds with Ferron (7-iodo 8-hydroxy quinoline-5-sulphonic acid). The pH is important and is kept at 5·4 with an acetate buffer solution. At 310 mμ both Fe and Al compounds absorb light but at 600 mμ only the iron complex does so. Three standard curves (for Al 310 mμ, Fe 310 mμ and Fe 600 mμ) are made. Measurements on the unknown sample at 600 mμ then give the Fe concentration, the 310 mμ equivalent of this (from the standards) is subtracted from the observed 310 mμ reading and the difference is due to aluminium.

C. *Culture methods*

These are more fully described in Clymo (1960). Two systems were used. The first was of rectangular covered polystyrene tanks holding 1·2 l. of solution. The solutions were stirred without aeration by a pump which sucked the solution slowly up into a polythene tube and then shot it back rapidly. This was repeated eight to ten times a minute. Plants were suspended by filter paper rolls or cotton-wool plugs from twelve holes drilled in the lid. The whole apparatus was kept in a cool greenhouse. Dry weight

increases per plant per day were about the same in the tanks as in natural conditions. Solutions were renewed once or twice weekly and pH adjusted two to three times a week.

The second system was used for freshly germinated seedlings which were too small to be grown in the tanks. The seeds were held by surface tension on wet filter paper just above the solution level in 1 in. (2·5 cm) glass tubes. After 2-3 days the root hairs fixed them fairly securely to the filter paper. Solutions could be easily changed, but the roots were not in the dark (as they were in the tank system) nor was solution stirring practicable. The tubes were kept in conditions of controlled light, temperature and humidity.

There was a high correlation (R = 0·93 to 0·98) between root length and plant weight. Root length is the more accurate measurement and is usually given in the results.

The positions of both tanks and tubes were randomized each week.

IV. EXPERIMENTS, RESULTS AND COMMENTS

The experiments are not described in chronological order. The factors which have at one time or another been invoked to explain the calcicole habit are summarized in Fig. 2.

There are the primary effects, toxic or deficiency, of Ca^{++} and the inversely linked H^+. Then there are the secondary linked factors; the biological ones of ion antagonism with other cations, of metabolic antagonism with NO_3', and of correlated H^+ and 'organic toxins'; and the chemical ones involved in precipitation of insoluble hydroxides of iron

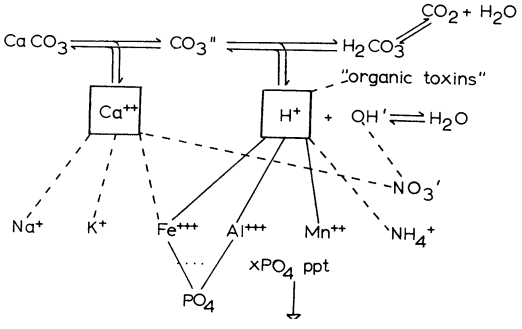

Fig. 2. Diagram of factors and their interrelations which may underlie calcicole behaviour. Chemical factors (full lines) result from ion equilibria in solution. Biological factors (dashed lines) include ion uptake antagonisms.

and aluminium when H^+ concentration is low. These are followed by tertiary effects on phosphate concentration (linked with iron and aluminium) owing to the insolubility of iron and aluminium phosphates. Finally (and not shown in Fig. 2) there may be biotic factors such as the restriction of snails to calcareous habitats.

This last possibility has not been investigated directly. In experiments described later both species were planted in a fen habitat and wet-heath habitat. No signs of browsing or other animal damage were seen in either habitat or of either species.

A. *Growth in natural waters and artificial solutions*

The first set of experiments were designed to answer the questions: Are there unrecognized substances in solution which seriously affect the growth of the *Carex* spp.,

and is the growth in culture similar to that in natural conditions? The basic idea of these experiments is simple. The growth of plants in natural solutions is compared with that in solutions made up to resemble the natural ones in concentration of defined ions. The experiments were made in the tanks.

Naturally grown offsets were used in the summer of 1958, and seedlings in 1959. In 1958 bulk soil water samples were collected at approximately 6-week intervals from Thursley Common, a wet-heath/valley-bog transition (grid ref. SU 907417), and Greywell Fen (grid ref. SU 720511), analogous to a Rich Fen in the du Rietz (1949) classification (see Clymo 1960 for details). In 1959 collections were made every 3 weeks and a further site was used on the margins of Fleet Pond (grid ref. SU 824553). This is a Poor

Table 2. *Ion concentrations in m.eq./l. of the first bulk water collections for experiments in 1958 and 1959*

	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Al^{+++}	Fe^{+++}	Mn^{++}	H^{+}	NH_4^{+}
Thursley 1958	0·35	0·078	0·31	0·047	0·11	0·07	<0·01	0·08	0·34
Greywell	5·03	0·35	0·35	0·038	–	–	<0·01	–	–
Thursley	0·12	0·35	0·65	0·026	0·23	0·64	<0·01	0·10	0·027
Fleet 1959	2·0	0·44	1·3	0·090	0·19	0·22	<0·01	–	0·14
Greywell	4·7	0·19	0·43	0·11	–	0·02	<0·01	–	0·12

	Cl'	SO_4''	NO_3'	PO_4'''	Weak acid salts	Total cations	Total anions
Thursley 1958	0·34	0·93	0·044	†0·016	–	1·39	1·33
Greywell	0·30	0·43	0·32	†0·016	*4·81	5·77	5·88
Thursley	1·33	0·85	0·020	†0·031	–	2·14	2·23
Fleet 1959	0·13	2·34	0·32	†0·20	0·92	4·38	3·91
Greywell	0·39	0·16	0·34	†0·13	*4·73	5·57	5·75

* 3·7 m.eq./l. bicarbonate.
† Decreased with storage to less than 0·01 m.eq./l.

Fen (du Rietz 1949). The solutions were filtered and stored in a cool dark place for 3 weeks before use. Solutions in the tanks were replaced each week. Just before first use each bulk collection was analysed for the concentration of Na^{+}, K^{+}, Ca^{++}, Mg^{++}, Mn^{++}, Fe^{+++}, Al^{+++}, NH_4^{+}, H^{+}, Cl', SO_4'', NO_3' and PO_4''', and artificial solutions made up with similar concentrations, any small unbalance of cations and anions being adjusted with Cl'.

It was discovered that phosphate in particular disappeared from the solutions during storage. Accordingly 0·016 m.eq./l. of sodium dihydrogen phosphate was added to each lot just before use. This is not a satisfactory procedure but there appears to be no suitable alternative.

Solution analyses of the first collections in 1958 and 1959 are shown in Table 2.

Subsequent collections were of approximately the same composition. The results of 12 weeks' growth are shown in Fig. 3.

In neither year is there any evidence that the growth of either species is affected by soluble factors other than those which were analysed. It may be concluded that, although organic toxins may on occasion limit the growth of plants they are not the general cause of the calcicole behaviour of *Carex lepidocarpa.*

There are significant differences in both years between the growth of plants in the fen and bog waters, and these are of the same sort as are found naturally.

Comparison between species is not possible in the 1958 experiment as the transplants

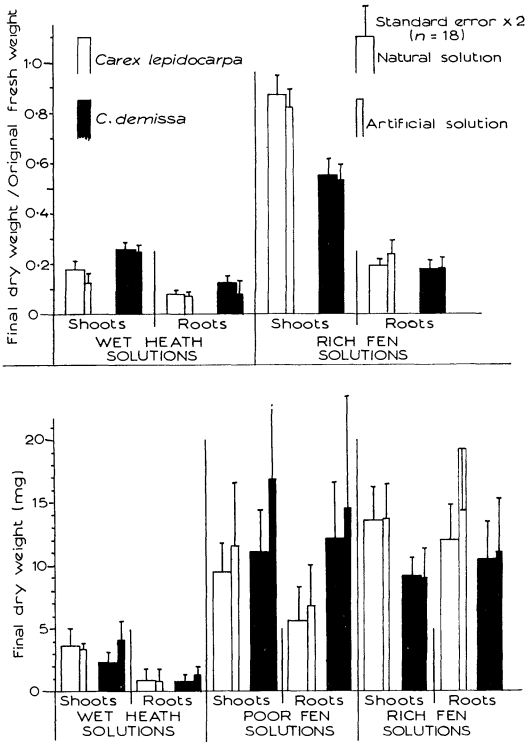

Fig. 3. Yield of *Carex lepidocarpa* (white) and *C. demissa* (black) in water culture. Natural soil water (wide columns) and artificial solutions resembling the natural ones (narrow columns) are compared from different habitats.

were of different initial sizes. In 1959 the plants were of the same initial size. In the Thursley water, neither species grows at all well. In the Fleet water, in which *C. demissa* is found naturally, *C. demissa* has grown better than *C. lepidocarpa.* The converse is true of growth in the Greywell water, though these differences are not significant.

It appears then that natural differences can be reproduced in water culture, and that it is the growth of the species relative to one another rather than their absolute growth which is important.

B. *The relative effects of pH, Ca^{++} concentration and toxicity or deficiency factors on growth*

The second set of experiments were designed to answer the questions: What is the relative importance of the direct H^+ and Ca^{++} concentration factors, and the indirect toxicity or deficiency factors? The experiments were made with offsets in the tanks with artificial wet-heath and fen waters. A series of pH adjustments to predetermined values between 3·5 and 7·6 was made with NaOH or H_2SO_4, the values being checked and if necessary adjusted every 2 or 3 days. The results are shown in Fig. 4. There was some drift of pH which is represented in Fig. 4 by the 'icebergs'. The long tails were produced in one period when 6 days passed between pH adjustments. Each series of solutions has a tendency to return to its 'natural' value. This is presumably related to the unequal flux of anions and cations between solution and plant.

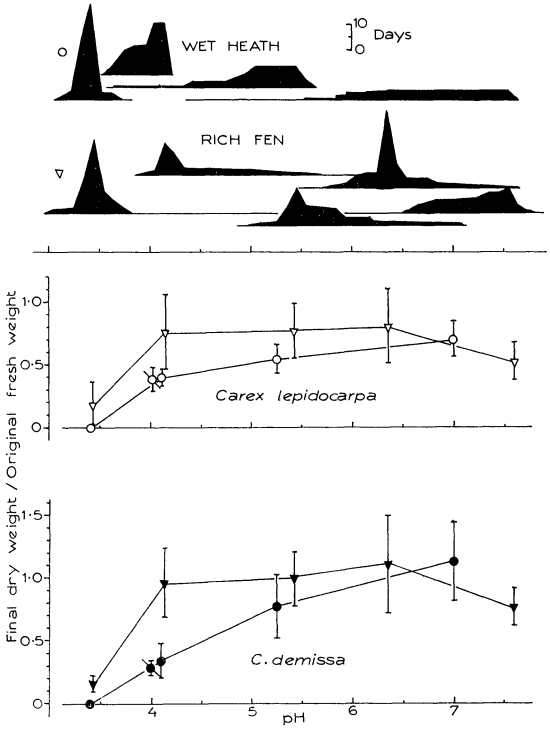

Fig. 4. Yield of offsets of *Carex lepidocarpa* (white) and *C. demissa* (black) in water culture with artificial fen and wet-heath soil waters with pH adjusted to various nominal values. The actual pH/time duration is shown by the 'icebergs'. The diagonally barred point at pH 4·0 shows the yield in solutions with excess Na_2SO_4 added.

In the fen series there is no evidence of a decrease in growth as measured by dry weight increase, of either species until the pH is less than 4. (At this pH there is 0·1 m.eq./l. of H^+ in solution—a concentration similar to that of other cations of metabolic importance.) This finding agrees with that of Arnon & Johnson (1942). There is no distinction between

the species, and, since the natural pH boundary between them is about 5·3-6·7 it seems unlikely that H^+ ion concentration is directly responsible for the calcicole behaviour of *C. lepidocarpa*—at least of the older plants.

In the wet-heath series there is an increase in growth as the pH rises, until there is no distinction between fen and wet-heath waters. This indicates that a high calcium concentration is not essential for the good growth of older plants. A control tank to which Na_2SO_4 was added in quantity larger than that used in pH adjustments produced the same growth as the corresponding experimental pH, so the increased growth at higher pH values is most plausibly attributed to the removal of some toxic substance. (A precipitate formed in these tanks.) Analyses showed that, of the ions included, Fe^{+++}, Al^{+++}, and Mn^{++} were removed in this way. There were also visual symptoms associated with the low pH wet-heath solutions. The roots were short, laterals were stubby and the whole root was often brown in colour.

Comparison between species is not possible, as the offsets were of differing initial weight ranges, but it seems that both are sensitive to the toxic factor in the concentration in the artificial wet-heath solution.

C. *Field experiments*

At this point a field check on these findings is desirable. Alteration of chemical conditions in the field is much more difficult and imprecise than in culture so the checks can only be applied at a few selected points. There were two field experiments designed to answer the questions: what are the relative importances of calcium and of H^+ (and pH-linked factors) on the growth of the two *Carex* spp.; and at what stage in the life cycle are these effects most pronounced? This second question is important when selecting the stage to work with in further culture experiments.

The experiments were made at Thursley Common on the wet heath, and at Greywell Fen. The results from Greywell were fragmentary owing to flooding, and the treatments there will not be detailed. At Thursley (in March 1958) ninety-six 1 m sq. plots were cleared of surface vegetation, with 1 m wide uncleared strips left between. One-third were treated with $CaCO_3$ (high Ca^{++}, high pH), one-third with $CaSO_4$ (high Ca^{++}, low pH) and one-third were left as controls. Treatments were randomized within blocks of twelve plots. There was also a factorial combination with and without phosphate, but this produced no significant differences in growth or seedling survival. The amounts of salts added were calculated to give 200 ppm Ca^{++} to a depth of 20 cm if they were all in solution at once. In fact this was not so, the concentration of Ca^{++} 12 weeks after treatment being about 50 ppm in both Ca^{++} treatments. The treatment was repeated in 1959. Weighed offsets were planted and a known number of seeds sown in the spring and counts made at intervals.

The results are shown in Figs. 5 and 6. The total dry weight of offsets and the fruit dry weights (Fig. 5) are considered first. As in the other experiments with offsets considerable differences occur between treatments *but* there is no significant difference between species. The observed effects are not, therefore, of any help in explaining the calcicole behaviour of *C. lepidocarpa.*

The seedling number counts in Fig. 6 are more helpful. The curves are compounded of germination and mortality curves. The seedlings were so small that it was not possible to count the number of dead ones accurately, as they dried up and blew away. Few dead

seedlings were noticed during the first 8 weeks of counts though they became much more numerous thereafter. There was no significant effect on numbers of either species in the first 10 weeks, when germination was the main process affecting numbers. When the hard and impermeable nature of the nutlet is considered this is not surprising, since the wall must be permeable before external chemical conditions can affect the young plant.

It seems clear that the factors affecting survival operate most effectively in the seedling stage, as Rorison (1960) showed.

The relatively high survival in 1958 of *C. lepidocarpa* on the plots with $CaSO_4$ added suggests a requirement for high Ca^{++}, unlike *C. demissa*. In 1959 this factor is masked by the toxic factor associated with low pH. This toxic factor has had some effect on *C. demissa* but far smaller than on *C. lepidocarpa*. No significance is attached to the differences

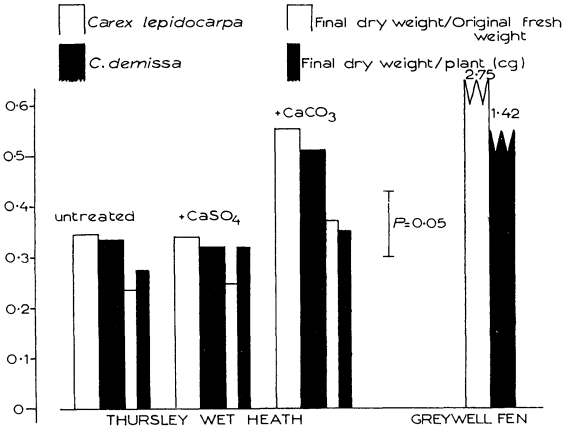

Fig. 5. Yield of offsets (wide columns) and fruits (narrow columns) of *Carex lepidocarpa* (white) and *C. demissa* (black) in a field experiment with addition of chemicals to the soil.

in initial percentage germination, since the final survival rate need only be a small fraction of the total seed production.

To summarize thus far, there appears to be a toxic factor in wet heath solutions which limits the survival and growth of both species, but of *C. lepidocarpa* much more than of *C. demissa*; and *C. lepidocarpa* needs a high Ca^{++} concentration for best survival and growth of seedlings. This effect can be masked by the toxicity effect and is not apparent in older plants. The effects observed in field experiments are consistent with those in culture.

D. *Identification of the toxic factor*

The next stage of the investigation is to discover which of the potentially toxic ions (Fe^{+++}, Al^{+++} and Mn^{++}) is operative in concentrations occurring naturally. These ions will be considered separately.

(i) *Manganese*

The concentration of Mn^{++} in the three experimental areas is less than 3 ppm. Nor has more than 3 ppm been found in any *C. flava* (sensu lato) site examined. Other investigators, for example Olsen (1935) find that 10-15 ppm are necessary to reduce dry

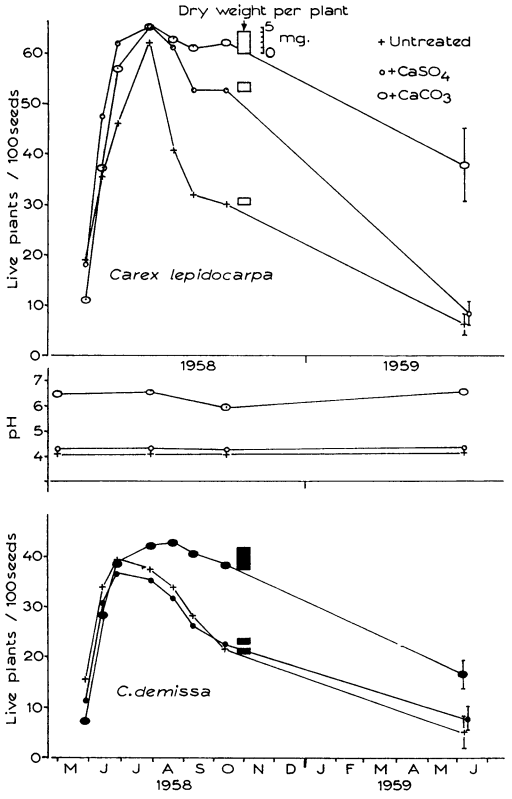

Fig. 6. Germination and survival curves for *Carex lepidocarpa* (white) and *C. demissa* (black) in a field experiment with addition of calcium carbonate (ovals), calcium sulphate (circles) or no addition (crosses) to the soil. Also shown are the mean plant dry weights corresponding to each treatment in October 1958, and the variation of pH with time and treatment.

Bars show ± twice the standard error of the mean (16 observations).

matter yields by 20%. Furthermore it is known that plants of wet places usually have a higher manganese content than those of dry habitats (Mayer & Gorham 1957), and it seems unlikely, therefore, that plants of wet places are more sensitive to manganese ions than those of dry places. Thus manganese ion concentration may be limiting *C. flava* (sensu lato) but is not likely to account for the calcicole habit of *C. lepidocarpa*. An experiment was made to examine this point. Seedlings in tubes were grown in a range of Mn^{++} concentrations. Details of the experiment follow.

56 days growth at 16° C with 12 hours light in each 24

Basic solution	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''
m.eq./l.	0·5	0·1	0·33	0·04	0·1	0·04
+1 ppm Fe^{+++}			Mn^{++}	varied	from	0-4 ppm

The results are shown in Table 3.

Table 3. *Results of an experiment on the effects of manganese on growth of seedlings*

Mn^{++} concentration (ppm)		0	0·1	0·5	1·0	2·0	4·0
Mean root length per plant (mm) ±Standard error ×2 (10 samples)	*Carex demissa*	91 ±21	104 ±13	101 ±22	89 ±18	101 ±14	50 ±22
	C. lepidocarpa	86 ±14	59 ±5	60 ±24	106 ±12	90 ±18	96 ±11

It is apparent that during the critical stage of growth, and over the range of Mn^{++} concentration found naturally, there are few significant effects on growth, and such as do occur are in the wrong sense to explain the calcicole behaviour of *C. lepidocarpa*. In this same experiment much larger effects were produced by other treatments.

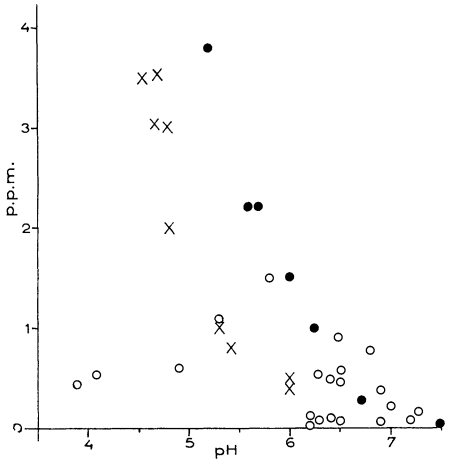

Fig. 7. Amounts of iron (crosses) and aluminium (circles) remaining in solution at various pH values. In the case of aluminium black circles represent experimentally determined values and open circles analyses of natural soil waters.

(ii) *Iron*

The same sort of general arguments which make it unlikely that manganese is the naturally important toxic ion apply to iron. These are the concentrations in natural habitats, accumulation in the plants, and the relatively high concentrations needed to produce toxicity symptoms in experiments. There is a further point concerned with the

pH/solubility curves of Fe^{+++} and Al^{+++}. These are shown in Fig. 7. They refer to what is essentially a wet-heath solution. (Similar curves were found by Magistad (1925), but Olsen (1958) found iron solubilities 10 to 1000 times smaller. The discrepancy is enormous but unexplained.)

Considerably more Al^{+++} is in solution, at a given pH, than Fe^{+++}. In the experiment in which the pH was varied, some reduction in yield was shown at pH 5·5 (approximately) where there is very little iron in solution though Al^{+++} was 1·5 ppm.

It has been suggested by Olsen (1958) that there is antagonism between Ca^{++} and Fe^{+++} uptake, so that Fe^{+++} could be toxic if the Ca^{++} concentration was low but the same concentration of Fe^{+++} would be harmless if Ca^{++} is high. The following experiment was made with seedlings in tanks to test this hypothesis.

84 days growth at 8·5-21° C, 350-400 foot candles, 12 hour day

Basic solution	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''	
	0·25	0·33	0·04	0·25 or 2·0	0·04	m.eq./l.

Ca^{++} 10 or 81 ppm Fe^{+++} 0·01 or 1·9 ppm.

The results are shown in Table 4. As with Mn^{++}, differences (between growth in 0·01 and 1·9 ppm of Fe^{+++}) are in the wrong sense for a toxicity effect on the calcicole species.

Table 4. *The results of an experiment to determine the interacting effects of iron and calcium on growth*

(a) Shoot dry weight/original fresh weight
(b) Root dry weight (mg)

	Ca (ppm)	*Carex lepidocarpa* (a)	*Carex lepidocarpa* (b)	*C. demissa* (a)	*C. demissa* (b)
Fe 0·01 ppm	10	0·81	0·149	1·65	0·386
	81	1·15	0·230	1·73	0·364
Fe 1·9 ppm	10	0·90	0·169	1·22	0·304
	81	1·23	0·265	1·20	0·341

(iii) *Aluminium*

That aluminium is the toxic factor was confirmed in a number of experiments. Two of these are shown below. Seedlings in tubes were used.

In the first experiment the interaction of pH, Ca^{++} concentration and Al^{+++} concentration was investigated.

54 days growth at 8-22° C in natural daylight (May-June)

Basic solution	Mg^{++}	K^{+}	NO_3'	PO_4'''	
	0·10	0·04	0·10	0·04	m.eq./l.
+0·2 ppm Fe^{+++}					
Variants of	pH	3·4	4·2	5·1	5·9	7·8
	Ca^{++}	3	9	27	81	ppm
	Al^{+++}	0	1	4	16	ppm

Not all the possible combinations were used, as this would have made the experiment too large. The ones which were used will be clear from the results which are shown in Table 5 and Fig. 8.

Table 5. *The results of an experiment on the effects of pH and calcium concentration on growth*

Measurements of mean length per plant in millimetres ± Standard error × 2 (10 samples)
The arrangement of results of each treatment is: *Carex lepidocarpa* root
C. lepidocarpa shoot
C. demissa root
C. demissa shoot

pH	Ca^{++} (ppm) 3	9	27	81
3·4	0 0			0 0
4·2	124 ± 39 51 81 ± 28 41			93 ± 21 45 65 ± 11 42
5·1	87 ± 30 44 118 ± 25 45			102 ± 51 28 76 ± 21 42
5·9	129 ± 32 42 169 ± 47 36	107 ± 37 52 74 ± 25 42	117 ± 27 43 104 ± 35 33	217 ± 50 39 127 ± 28 37
7·8	95 ± 27 47 107 ± 23 44	64 ± 39 37 107 ± 32 39	147 ± 32 46 90 ± 34 35	147 ± 48 49 114 ± 22 38

The results in Fig. 8 show that at pH 4·2 as little as 1 ppm of Al^{+++} is sufficient to reduce root growth of *C. lepidocarpa* by 90% over a wide range of Ca^{++} concentrations but root growth of *C. demissa* is much less affected. This is an important result.

By contrast there were no clear differences in the pH/Ca^{++} combinations as Table 5 shows. This experiment does confirm that in seedlings, as in older plants, a pH down to 4 is not of itself harmful.

The second tube experiment was designed to confirm the Al^{+++} toxic effect and to locate the area of critical interaction between the species in relation to Ca^{++} and Al^{+++} concentrations.

45 days growth at 7-21° C, 200-400 foot candles for 12 hours each day

Basic solution	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''	
	0·50	0·20	0·12	0·20	0·12	m.eq./l.
+0·1 ppm Fe^{+++}						
Variants of	Ca^{++}	20	30	40	ppm	factorially
	Al^{+++}	0	0·1	1·0	ppm	combined.

The results are shown in Fig. 9. They confirm that *C. lepidocarpa* only grows better than *C. demissa* when the concentration of Al^{+++} is very low *and* Ca^{++} is greater than about 30 ppm.

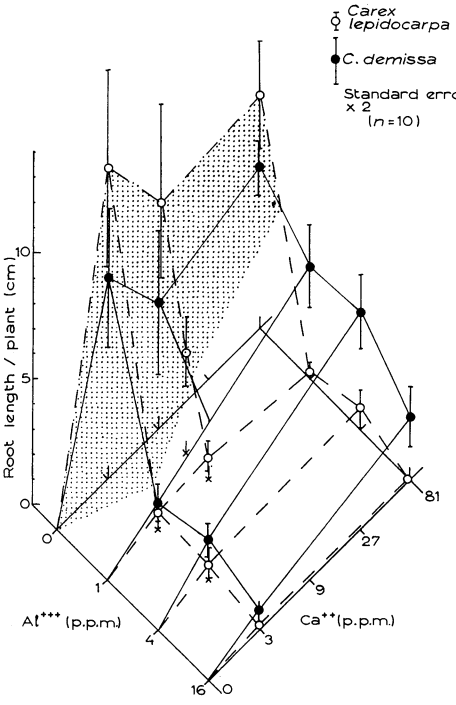

Fig. 8.

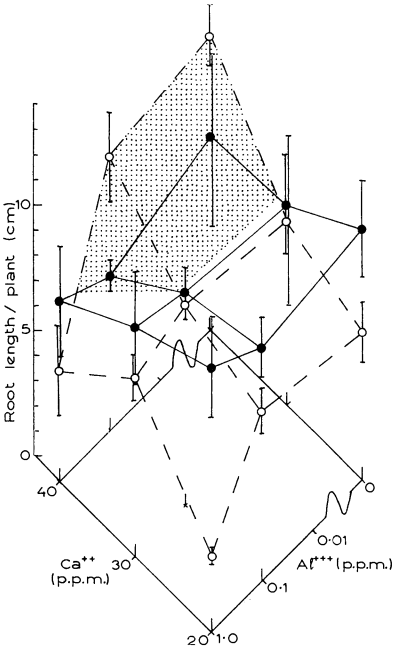

Fig. 9.

Figs. 8 and 9. Root lengths of seedlings of *Carex lepidocarpa* (white and dashed lines) and *C. demissa* (black and full lines) in relation to calcium and aluminium levels in water culture. In the dotted part *C. lepidocarpa* yields are greater than *C. demissa*.
Bars show ± twice the standard error of the mean (10 observations).

In all cases Al^{+++} produced the characteristic stunting and brown colour in *C. lepidocarpa* roots.

E. *Variation within the taxa*

The experiments so far described were all made with seed collected from one population of each species. It is important to discover how far these populations are typical of the whole. The following experiment was made to determine the sensitivity to Al^{+++} of samples from a wide geographic range of populations. Seedlings in tubes were used.

Grown for 40 days at 17·5° C, 290 foot candles for 12 hours each day

Basic solution	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''
	0·5	0·1	0·33	0·04	0·1	0·04 m.eq./l.

+1·0 ppm Fe^{+++} pH 4·4

Variants of Al^{+++} 0 0·5 5·0 ppm

Source of seed	Grid ref.		Height above sea level (ft) (1 ft = 0·3 m)
C. lepidocarpa			
Blackhead, Co. Clare	1	Ireland	400
Newbridge, Dublin	2		
Malham Tarn outflow	3	SD 8967	1250
Sunbiggin Tarn	4	NY 6707	825
Cothill Fen	5	SU 4600	250
Greywell Fen	6	SU 7251	275
Malham, Great Close Mire	7	SD 9067	1250
Blackhead, near sea	8	Ireland	10
Brook, Kent	9	TR 0744	175
Roydon Mire, Norfolk	10	TF 6822	25
C. demissa			
Brockishill 1957	A	SU 3011	100
Fritham Well	B	SU 3314	350
Brockishill, 1959	C		
Scar Close, Ribblesdale	D	SD 7577	1200
Voss, Norway	E	Norway	2800
C. flava			
Malham Fen	X	SD 8967	1250

The results are shown in Table 6.

Table 6. *The results of an experiment to determine the variation with provenance of sensitivity to the aluminium ion*

Measurements are mean root lengths per plant in millimetres ± Standard error × 2 (10 samples)

Site	0	0·5	5·0 ppm Al^{+++}
1	65 ± 7	52 ± 12	lost
2	112 ± 17	90 ± 10	
3	131 ± 40	30 ± 6	10 ± 2
4	138 ± 16	127 ± 10	24 ± 4
5	161 ± 34	95 ± 15	31 ± 3
6	163 ± 40	81 ± 12	22 ± 5
7	183 ± 37	73 ± 14	14 ± 6
8	191 ± 16	129 ± 10	lost
9	207 ± 10	112 ± 11	36 ± 4
10	330 ± ?	66 ± 15	19 ± 10
A	130 ± 18	154 ± 28	lost
B	169 ± 30	lost	73 ± 21
C	199 ± 42	162 ± 23	56 ± 15
D	lost	lost	57 ± 15
E	69 ± 10	101 ± 21	33 ± 5
X	186 ± 37	88 ± 12	17 ± 8

Some of the results were invalid (marked 'lost') because of attack of some of the tubes by a fungus—*Stachybotris* sp.

It is clear that 5 ppm Al^{+++} reduces root growth of *C. lepidocarpa* by roughly 80% in all cases, while the roots of *C. demissa* are much less affected (though there is some reduction). In all but two cases 0·5 ppm Al^{+++} reduced the growth of *C. lepidocarpa* roots, but not that of *C. demissa*. *C. flava* (sensu stricto) behaves very like *C. lepidocarpa*.

The differential response to low Al^{+++} concentrations, which seems to be the main cause of the calcicole behaviour of *C. lepidocarpa*, thus appears to be a general character of the two *Carex* spp.

V. THE APPLICABILITY OF THE EXPERIMENTAL FINDINGS TO NATURAL HABITATS

The conclusion has been reached from the experimental data that the most important single factor affecting the relative distribition in the British Isles of *C. lepidocarpa* and *C. demissa* is the concentration of aluminium in the soil water, with the Ca^{++} concentration as an important secondary factor. It is now necessary to return to the natural habitat and find out how far these conclusions are upheld.

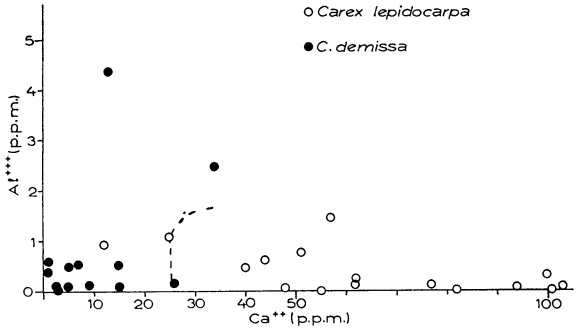

Fig. 10. Concentrations of calcium and aluminium in soil waters collected from natural habitats of *Carex lepidocarpa* (white) and *C. demissa* (black).

Soil water samples were collected especially from marginal or intermediate habitats. Chemical analyses were made of these (Clymo 1960). The Ca^{++}/Al^{+++} data (which give the most satisfactory separation of the species habitats) are shown in Fig. 10. One habitat of *C. lepidocarpa* at the edge of Roundstone Mire (Co. Galway) has a low Ca^{++} (12 ppm), critical Al^{+++} (0·95 ppm), but a high Na^{+} (28 ppm) owing to the nearness of the sea. It appears that in this habitat Na^{+} may to some extent compensate for Ca^{++}. The western Irish material is anomalous, or at least extreme, in other characters for example the development of the roots in the provenance experiment.

These soil water samples are point samples of a continuous variable. Also in most of the habitats the water was flowing, more or less slowly, so there will be ion flushing.

With these considerations in mind it can only be said that the data from natural habitats do not disagree with the experimental findings.

It may be concluded that in habitats suitable for *C. flava* (sensu lato), *C. demissa* is usually found where Ca^{++} is less than 30 ppm *or* Al^{+++} more than 0·5-1·0 ppm, while *C. lepidocarpa* is found where Ca^{++} is greater than 20 ppm *and* Al^{+++} less than 1 ppm.

It may seem that aluminium is quantitatively a rather esoteric element to be so influential. It is in fact the third most abundant element in the earth's crust (below silicon

and oxygen) and is a major constituent of clay minerals (Hutchinson 1943). Dust contains quite a lot of aluminium, and it is probably not a great exaggeration to say that wherever the pH is suitable in natural habitats the critical 1 ppm of aluminium will be found in solution. In Table 7 are some assorted analyses to illustrate this point.

Table 7. *The pH and aluminium concentration of water and peat samples from a variety of districts*

Place	pH	Al^{+++} ppm
I. of Lewis	7·0	0·21
I. of Lewis	5·3	0·19
W. Harris	6·0	0·21
S. Harris	5·9	0·22
Hartland	6·0	0·98
Hartland	5·9	0·97
Roydon	3·7	1·6
Roydon	3·9	4·1
Buxton Heath	4·4	14·8
Buxton Heath	4·4	4·7
Buxton Heath	3·9	1·5
Inverliever (Fraser 1933)	4	
Calluna peat		'exchangeable' Al and Fe 12·6
Scirpus peat		3·2
Eriophorum peat		3·3
Coom Rigg (Chapman 1961)	less than 5	9-58 in peat
Irish stations (data by courtesy of Mr J. H. Sparling)		
Woodford	4·7	1·10
Donegal 1.	4·0	0·60
2.	3·8	0·85
Owenanagh River, Mayo	4·1	0·40
Donegal 3.	4·2	0·90
Roundstone	5·2	1·0
Screeb	4·2	1·10
Fermoyle	3·8	0·95
Wicklow Mountains	3·8	1·40

VI. THE PHYSIOLOGICAL EFFECTS OF ALUMINIUM

A. *The state of aluminium*

The following experiment was made to determine in what form aluminium produces its toxic effect. Seedlings of *C. lepidocarpa* were grown in tubes.

Grown 45 days at 17·5° C, 290 foot candles for 12 hours each day

Basic solution	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''
	0·01	0·33	0·04	0·01	0·04 m.eq./l.
+1 ppm Fe^{+++}					
Variants	Ca^{++}	10 or 80 ppm			
	pH	4·2 or 7·6			
	Al^{+++},	2·0 ppm *or* AlEDTA,		2·0 ppm. Al *or* EDTA equivalent to AlEDTA.	

The results are shown in Table 8.

It appears rather surprisingly, that it is the amount of Al^{+++} in the ionic, or at least in the uncombined form, which is important. AlEDTA probably enters the cells, so the toxic action presumably cannot involve aluminium compounds with stabilities greater than AlEDTA, or less certainly $Al(OH)_3$.

Table 8. *The results of an experiment to determine the form in which aluminium is toxic to* Carex lepidocarpa

In treatments with Al^{+++} at pH 7·6 the precipitate of $Al(OH)_3$ was left in the solutions
Measurements are mean root lengths per plant in millimetres ± Standard error × 2 (10 samples)

Ca^{++}	10 ppm		80 ppm	
pH	4·2	7·6	4·2	7·6
EDTA	82 ± 10	76 ± 6	74 ± 14	73 ± 13
AlEDTA	77 ± 12	78 ± 10	76 ± 11	74 ± 7
Al^{+++}	32 ± 5	99 ± 14	33 ± 5	95 ± 11

B. *The site of action of aluminium*

In all the seedling experiments where aluminium toxicity was shown the growth of roots, measured by length or dry weight, was affected before shoot growth. Other reports have been made (for example Wright 1943) that shoot growth is more affected than root growth. The experiments on which these reports are based have included the complete growth cycle during which root/shoot interactions would develop and might well reverse the initial effects. In the present experiments root stunting was apparent within 2-3 days whilst shoot growth was not affected for several weeks.

A comparison of the anatomy and morphology of roots of *C. lepidocarpa* grown in solutions with or without 1·0 ppm Al^{+++} gave the following results.

		Without Al^{+++}	With Al^{+++} 1·0 ppm
Length		Long	Stunted (actual length varies with the growth period)
Diameter		Same ± 20%	
Root hairs	length	110	100
	No. per cm	About the same	
Lateral roots		No. per root about the same but + Al^{+++} has more per cm of root	
Epidermal cell length		121 ± 10	100 ± 9
Colour of root tip		Clear	Brown. Nuclei in the cells are visible without staining.

It appears that cell elongation has been little affected. Hence cell division must have been very much slowed down by Al^{+++}.

The accumulation of Al^{+++} (and Fe^{+++}) in the endodermis and to a smaller extent in

the cortex (Wright & Donahue 1953, Clymo 1960) is probably irrelevant to the main problem of accounting for root stunting if this is mainly owing to an inhibition of division in the apical region.

C. *The chemical effects of aluminium in the root*

It should be pointed out that the symptoms of root stunting are produced by factors other than Al^{+++}. The fungus *Stachybotris* sp. attacked some plants and caused root stunting very similar to that caused by Al^{+++}. Copper (approximately 3 ppm) has the same effect. It appears, therefore, that plant symptoms, as an indicator of chemical effects, must be treated with reserve. There have been a number of suggestions that aluminium acts by precipitating phosphate, either inside or outside the plant (for example Wright 1943, Wright & Donahue 1953, Rorison 1956). Rorison, whose work is the most immediately relevant, cites visual symptoms and the data in Table 9 in support of the hypothesis of phosphorus deficiency (induced by aluminium). The plants were *Scabiosa*

Table 9. *Extracts from results of Rorison's (1956) experiment in soil solutions*

Treatment	pH	D.W./plant (mg)	Root penetration (cm)	Phosphorus (mg/g dry weight) Root	Shoot
Calcareous sand	7·6	27	21·6	1·5	1·15
Acid (sand) $+Ca(OH)_2$	7·6	24	23·5	1·33	1·01
Acid $+NaOH$	7·6	19	19·5	1·22	1·01
Acid $+CaSO_4$	4·8	17	9·7	1·64	1·23
Acid sand	4·8	12	6·0	1·35	0·67

columbaria grown in soil solutions with various additives. The low concentration of phosphorus in the shoots of plants grown in acid sand solution is suggested to indicate P deficiency. But the concentration in acid sand $+CaSO_4$ is the highest of all. The pH is still low so Al^{+++} should still be in solution and calcium phosphate is itself relatively insoluble. There is in fact in this experiment some evidence of two effects, pH linked and Ca^{++} linked, such as have been shown for *Carex lepidocarpa*. If the growth in acid sand solution is taken as a base, the amelioration produced by other additions can be calculated:

Treatment	Effect owing to	Root length increase (cm)	Dry weight per plant (mg)
Acid sand		+ 0 (base 6·0)	+ 0 (base 12·0)
$+CaSO_4$	Ca^{++}	+ 3·7	+ 5
$+NaOH$	pH	+13·5	+ 7
	Total (Ca^{++}+pH)	+17·2	+12
$+Ca(OH)_2$	Ca^{++}+pH	+17·5	+12

Taken at their face value these data suggest that the pH effect is about three times as important as the Ca^{++} effect, that the roots are more affected than the shoots, and rather surprisingly that the effects are additive.

Returning to the possiblity of Al^{+++}/PO_4''' interaction. The following experiment was made with seedlings in tubes to discover the effects of very low external phosphate concentrations on early growth.

Grown 31 days at 17·5° C, 12 hour day

Basic solution	Ca^{++}	Mg^{++}		K^{+}	NO_3'		
	0·5	0·1		0·04	0·20		m.eq./l.
Variants	PO_4'''	0·001	0·004	0·020	0·05	0·20	m.eq./l.
	pH		4·2 or 7·6				

Also one treatment with PO_4''' 0·04 m.eq./l.+Al^{+++} 2 ppm.

The results are shown in Fig. 11.

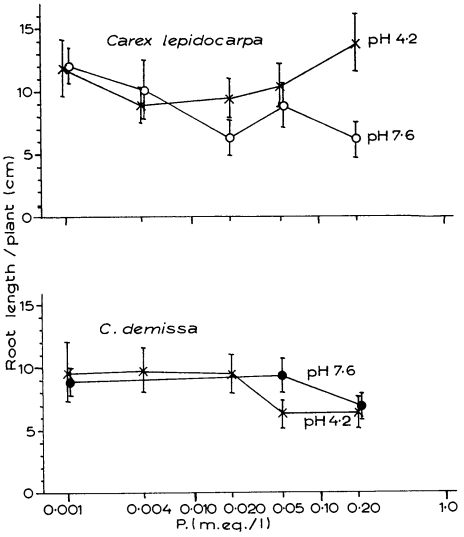

Fig. 11. Root lengths of seedlings of *Carex lepidocarpa* (white) and *C. demissa* (black) in water culture with various phosphate concentrations.

Bars show ± twice the standard error of the mean (10 observations).

The very low phosphate concentrations have had little effect on the root growth when compared with 2 ppm of Al^{+++}. Analysis showed that each seed contained 10-20 µg of phosphorus and this appears to be sufficient to support growth for 4 weeks at least. It is unlikely, therefore, that $AlPO_4$ precipitation is the explanation of root stunting in these experiments. Even when $AlPO_4$ is precipitated there is still a very small amount of PO_4''' in solution, and plant cells are known to be able to accumulate phosphorus by an active process when its external concentration is hardly detectable.

There are four other general points which concern the mechanism of aluminium action.

First, the experiment already described, in which AlEDTA produced no effect, indicates that if Al^{+++} does combine inside the cell it must be to form some compound less stable than AlEDTA.

Secondly, the effect is a graded one, suggesting a chemical concentration dependent mechanism, both in relation to Al^{+++} concentration for one species, and in tolerance by different species of Al^{+++}— some plant species are known to be aluminium accumulators (Hutchinson 1943).

Thirdly, the effect can be produced by such small amounts (and concentrations) of Al^{+++} that nearly every mechanism except enzyme inhibition seems unlikely on quantitative grounds.

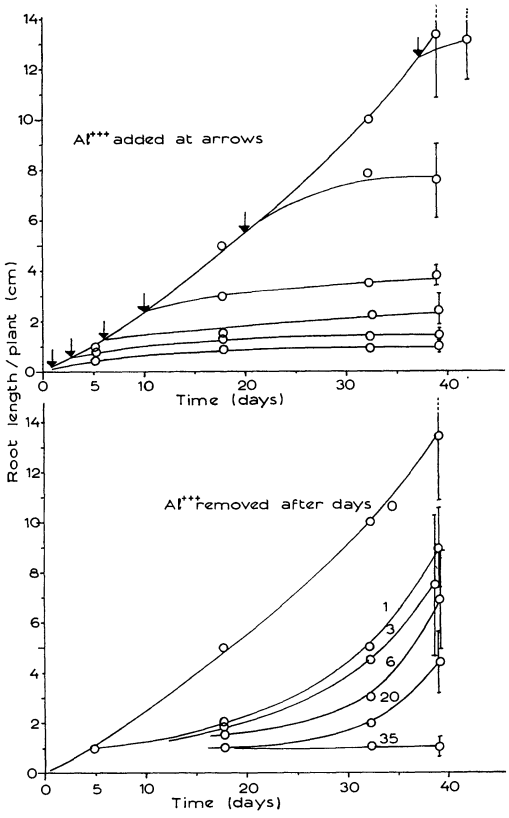

Fig. 12. Growth of roots of *Carex lepidocarpa* seedlings in water culture. In the upper part aluminium was added at the times marked by arrows. In the lower part a solution with aluminium was replaced by one without aluminium at the time (in days) shown by each curve.

Finally, the kinetics of Al^{+++} action indicate metabolic disturbance rather than for example exchange site saturation. The following experiment illustrates the kinetics. It was made with *C. lepidocarpa* in tubes.

17·5° C, 12 hour day

Basic solution	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	NO_3'	PO_4'''
	0·5	0·1	0·1	0·04	0·1	0·04 m.eq./l.
Variants	Al^{+++} 3 ppm added or removed after various intervals					

The results are shown in Fig. 12.

The toxic action is almost immediate, but there is a 10 day lag in recovery. This would seem to preclude a simple blockage of exchange sites.

SUMMARY

The calcicole problem is a multiple one. A careful selection of plant taxa for experiments was made, taking into account marginal and physical calcicole behaviour, the importance of competition, and the unreliability of visual symptoms. *Carex lepidocarpa* and *C. demissa* were selected.

Field and water-culture experiments indicate that in this case the most important factors are simple chemical ones. A factor present in low pH conditions, and toxic to *C. lepidocarpa* but less so to *C. demissa*, is identified as Al^{+++}. There is also a requirement by *C. lepidocarpa* for high Ca^{++} concentration. These effects are most important in the seedling stage.

The natural habitats of these two species can be separated at Al^{+++} about 1 ppm and Ca^{++} about 30 ppm.

Aluminium appears to act by preventing root cell division but it seems unlikely that this is directly connected with external phosphate precipitation.

ACKNOWLEDGMENTS

My thanks are due to the D.S.I.R. and University College London Committee for financial support, to Professor D. Lewis, F.R.S. for criticisms and facilities to perform the experiments, and most notably to Dr P. J. Newbould for his help and advice throughout the work.

REFERENCES

Arnon, D. I. & Johnson, C. M. (1942). Influence of hydrogen ion concentration on the growth of higher plants under controlled conditions. *Plant Physiol.* **17,** 525-39.

Black, C. A. (1957). *Soil–Plant Relationships.* Chapman & Hall, London.

Bonnier, C. (1921-34). *Flora Complète de France, Suisse et Belgique.* Paris.

Chapman, S. B. (1961). *Coom Rigg Moss.* Ph.D. Thesis, University of London.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1952). *Flora of The British Isles.* Cambridge University Press.

Clymo, R. S. (1960). *Causes of Calcicole Behaviour Illustrated Mainly in* Carex flava (s.l.). Ph.D. Thesis, University of London.

Davenport, W. H. (1949). Determination of aluminium in presence of iron. *Analyt. Chem.* **21,** 710-11.

Davies, E. W. (1955). The cytogenetics of *Carex flava* and its allies. *Watsonia,* **3,** 129-37.

Davies, E. W. (1956). The ecology and distribution of *Carex flava* and its allies in the British Isles. *Bot. Notiser*, **109**, 50-74.

Fraser, G. K. (1933). Studies of certain Scottish moorlands in relation to tree growth. *Forestry Commission Bulletin* **15**. H.M.S.O.

Grime, J. P. (1960). *A Study of the Ecology of a Group of Derbyshire Plants with Particular Reference to their Nutrient Requirements.* Ph.D. Thesis, University of Sheffield.

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**, 259-79.

Hegi, G. (1906). *Illustrierte Flora von Mittel-Europa.* Munich.

Hewitt, E. J. (1952). A biological approach to the problems of soil acidity. *Int. Soc. Soil Sci. Trans.* **1**, 107-18.

Holliday, R., Hodgson, D. R., Townsend, W. N. & Wood, J. W. (1958). Plant growth on 'Fly Ash'. *Nature, Lond.* **181**, 1079-80.

Hope-Simpson, J. F. (1938). A chalk flora on the lower Greensand: its use in interpreting the calcicole habit. *J. Ecol.* **26**, 218-35.

Hutchinson, G. E. (1943). The biochemistry of aluminium and of certain related elements. *Quart. Rev. Biol.* **18**, 1-29, 128-53 and 242-62.

Jensen, S. T. (1952). The liming problem. *Int. Soc. Soil Sci. Trans.* **1**, 93-106.

Kaila, A. (1955). Studies on the colorimetric determination of phosphorus in soil extracts. *Acta Agralia Fennica*, **83**, 25-47.

Lundegårbfh, H. (1931). *Environment and Plant Development* (Transl. E. ASHBY). Arnold, London.

Mackereth, F. J. H. (1957). *Water Analysis for Limnologists.* Freshwater Biological Association.

Magistad, O. C. (1925). The aluminium content of the soil solution and its relation to soil reaction and plant growth. *Soil Sci.* **20**. 181-226.

Mayer, A. M. & Gorham, E. (1957). The iron and manganese content of plants present in the natural vegetation of the English Lake District. *Ann. Bot. Lond.*, N.S. **15**, 247-63.

Olsen, C. (1935-38). Absorption of manganese by plants. 2. Toxicity of manganese to various plant species. *C. R. Trav. Carlsb., Ser. Chim.* **21**, 129-45.

Olsen, C. (1958). Iron uptake in different plant species as a function of the pH value of the nutrient solution. *Plant Physiol.* **11**, 889-905.

Perring, F. J. (1960). Climatic gradients of chalk grassland. *J. Ecol.* **48**, 415-42.

Pigott, C. D. & Walters, S. M. (1953). Is the box tree a native of England? In *The Changing Flora of Britain* (Ed. LOUSLEY).

Praeger, R. Ll. (1950). *Natural History of Ireland.* Collins, London.

du Rietz, G. E. (1949). Huvudenheter och huvudgränser i Svensk myrvegetation. *Svensk. Bot. Tidskr.* **43**, 274-309.

Rorison, I. H. (1956). *Some 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. *J. Ecol.* **48**, 585-99 and 679-88.

Russell, E. J. (1961). *Soil Conditions and Plant Growth.* 9th ed. Longmans, London.

Salisbury, E. J. (1920). The significance of the calcicolous habit. *J. Ecol.* **8**, 202-15.

Schmehl, W. R., Peech, M. & Bradfield, R. (1950). Causes of poor growth of plants on acid soils and beneficial effects of liming. *Soil Sci.* **70**, 393-410.

Steele, B. (1955). Soil pH and base status as factors in the distribution of calcicoles. *J. Ecol.* **43**, 120-32.

Tansley, A. G. (1917). On competition between *Galium saxatile* (*G. hercynicum* Weig.) and *G. sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *J. Ecol.* **5**, 173-79.

Webb, D. A. & Hart, A. V. (1945). Contributions towards an understanding of the calcicole and calcifuge habit in some Irish plants. *Sci. Proc. Roy. Dublin Soc.* N.S. **24**, 19-28.

Webb, D. A. (1943). *An Irish Flora.* Dundalgan Press, Dundalk.

Wilde, S. A. (1954). Reaction of soils: facts and fallacies. *Ecology* **35**, 89-92.

Wright, K. E. (1943). Internal precipitation of phosphorus in relation to aluminium toxicity. *Plant Physiol.* **18**, 708-12.

Wright, K. E. & Donahue, B. A. (1953). Aluminium toxicity studies with radioactive phosphorus. *Plant Physiol.* **28**, 674-80.

Zlatnik, A. (1928). Études écologiques et sociologiques sur la *Sesleria coerulea* et la Seslerion calcariae en Tchécoslovaquie. *Trav. de la Soc. Roy. des Sci. de Boheme, Cl. de Sci.* N.S. **8**, 1-116.

(*Received* 11 *November* 1961)