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THE SIGNIFICANCE OF THE CALCICOLOUS HABIT[1].

By E. J. SALISBURY.

One effect of soil conditions upon the plant, like that of the other factors of the environment, is to render particular species either more, or less, susceptible to the adverse influences, whatever their nature, which probably play their major rôle in the juvenile phases of development. It is well known that in the absence of competition, as when artificially planted and tended, many species will often grow in soils which they never occupy in a state of nature. For example many maritime species such as *Statice binervosa*, *S. humilis*, *Frankaenia laevis*, *Suaeda fruticosa*, or marsh plants such as *Alisma plantago Iris pseudacorus*, etc., can be grown for years and will even flourish in an ordinary garden soil. It is indeed probably infrequent for a species typically confined to one kind of soil to be totally unable to grow on any other soil than that on which it usually occurs, because of its direct inimical action; though extreme soil types such as the highly acid peats of our own country or the alkali soils of the United States afford instances where such direct action obviously occurs.

The fact that the vegetation of a given area may show a practically constant composition, as regards both its qualitative and quantitative floristic character, over a long period of years, bears witness to the stability of the balance between species and species. For each species and individual throughout the period of observation has been striving, so to speak, both by seed and vegetative propagation to conquer the ground occupied by its neighbours. Some idea of this stability can be gathered from the botanical analyses of the unmanured grass plots at Rothamsted furnished by Lawes, Gilbert and Masters (**36**). These showed that of the 50 species present on plot 3 in 1862, only four of the least important had disappeared fifteen years later, whilst only five additional species had appeared during that interval. Similarly the persistence of woodland species such as *Anemone nemorosa*, in a woodland area laid down to grass more than half a century ago, which is to be observed near Ayot in Hertfordshire, or the survival of cornfield weeds for more than 35 years after the cessation of cultivation, to which I have elsewhere called attention (**49**), still further emphasises the resistance which has to be overcome by invading species. Cockayne, writing of the New Zealand flora, has called attention to the absence of alien species from the virgin plant communities despite their success where the influence of man has modified the conditions of the environment (**12**, p. 147).

[1] Presidential Address to the London Intercollegiate Botanical Society. Delivered June 22, 1920.

There is thus a relative permanence in the plant community which is maintained even in associations whose constituents are largely annual species and where consequently the individuals themselves are periodically replaced. There must then be a very delicate balance between plant and plant, otherwise one or another would gradually oust its competitors. The soil conditions under which a species normally occurs and maintains itself in the wild state may be regarded as representing those which enable it to withstand the pressure of competition, and viewed thus we can appreciate that even slight edaphic distinctions or changes may profoundly modify the character of vegetation.

In considering so-called calcicolous species we must therefore recognise that we are dealing with plants which find a suitable home on calcareous soils without necessarily implying any obligatory association with, or even preference for, such soils apart from that imposed by climatic or biotic factors. Observations (cf. Christ **9**) on *Achillea atrata* and *A. moschata* afford an excellent example of this fact, for each in the absence of competition can apparently thrive on either a siliceous or calcareous type of soil, though when competing together *A. atrata* is strictly calcicole and *A. moschata* strictly silicicole (cf. also Tansley, **54**).

Calcareous soils exhibit certain characteristic features both of a chemical and physical nature. Of the former we may note the high proportion of soluble salts (for analyses see Hall and Russell, **27**) and the alkaline or neutral character of the soil solution. This neutralising effect of the presence of calcium is an important one in view of the continuous production of the so-called humus acids by the decomposition of the plant remains produced annually. These acids, whatever their nature, have been shown experimentally to be inimical to vegetable growth even in the case of species normally occurring on non-calcareous soil. O. Schreiner (**52**) has, for example, isolated from natural soils dihydroxystearic acid which is harmful to the growth of plants. G. B. Rigg (**45**), who prepared solutions from the decay products of the rhizomes of *Nymphaea*, found that even in a dilute state these had a toxic effect; but his most interesting observation for our present purpose is that the harmful effect was largely diminished by neutralisation of the solution. The well-known toxic effect of bog water (cf. Dachnowski, **15**) has been attributed, probably on adequate grounds, to these same acid products of decay. Moreover calcium salts even in very dilute solutions are especially effective in diminishing the toxic effect of inorganic solutions (cf. **13**). Such deleterious substances, whether organic or inorganic, may however affect the plant either directly or indirectly. Respecting their direct action the recent work of Truog and Meacham (**55**) has shown that acidity of the soil may influence the reaction of the plant juices. These authors determined electrically the hydrogen-ion concentration of the plant juices of species grown on limed and unlimed soil, and in twelve out of sixteen determinations the expressed juice of the plants grown on the unlimed soil exhibited the higher acidity; cf. also Clevenger (**11**) who found that the roots generally in limed soil had a lower acidity, though in some cases the tops were more acid. One need only recall the work of Bunzell (**6**) and Reed (**44**) showing the effect of variations in the acidity of the cell sap upon the enzyme activities of the plant, to emphasise how important, from this one aspect only, the reaction of the soil might be.

The researches of Dachnowski on the effects of acid and alkaline solutions on plants (**14**) showed that water absorption was diminished in acid media. Whilst too much stress must not be laid on the water of imbibition in relation to growth the work of MacDougal is very significant in this connection. This author has recently pointed out (**39**) that "the water relations of a cell mass in plants will naturally be determined by its protein-carbohydrate ratio, with the implied corollary that a varying capacity is displayed which may reach its maximum in a condition of acidosis, in forms rich in nitrogen, and in a neutralised, relatively salt-free condition in those in which the proportion of colloidal carbohydrate is relatively great." Since the normal plant cell contains but little nitrogenous material the imbibition of water by the biocolloids will be diminished if the cell sap becomes more acid and the rate of growth will presumably be retarded. As in many plants competition consists in 'choking out' the rate of growth may obviously be a determining factor in the plant's survival.

Lipman and Blair (**37**) have studied the effect of liming on the yield of non-leguminous crops and found that there was a gain per acre of 160 lbs. dry weight and 3 lbs. of nitrogen, though under these conditions there is an actual loss of nitrogen from the soil greater than where no lime was used. Further studies on leguminous crops however showed a very appreciable gain with liming and indicates a beneficial effect in rendering conditions favourable for nitrogen fixing organisms. Fred and Graul (**24**), employing *Trifolium pratense* and *Glycine hispida,* worked out the nitrogen balance-sheet for limed and unlimed plots and found that those receiving lime exhibited an increase in the amount of nitrogen fixed from the air. Their cultures were made on soils which were highly acid, the treated plots receiving sufficient lime to half neutralise in one case, and in the other to completely neutralise the acidity. In the case of red clover there was an increasing yield with decreasing acidity whilst with the Soy bean, a plant tolerant of appreciable soil acidity, the largest yield was obtained from the half-neutralised plot.

The experiments of Salter and McIlvaine (**51**) show that in water-culture conditions the maximum growth of wheat, Soy-bean (*Glycine*), *Medicago sativa,* and maize, corresponds to a hydrogen-ion concentration of about 5·94 P_H. When the reaction was approximately neutral the growth of wheat, Soy-bean, and maize was appreciably diminished but that of *Medicago sativa* was only slightly less. These authors concluded that for the plants named a slightly acid medium is most favourable for both germination and growth[1]. According to

[1] Cf., however, postscript on p. 215.

Hoagland (**30**) a P_H of even 5·0 is not unfavourable to barley at any stage of its growth and under less acid conditions the absorption of Ca, NO_3, PO_4 was diminished. It must however be borne in mind that the acid solutions were here obtained by means of inorganic substances under artificial conditions probably not paralleled by those of an acid soil. Nevertheless the results show that the tolerance of acidity varies with the species and that, isolated as a habitat factor, slight acidity may even be beneficial. Hutchinson and MacLennan (**31**, p. 98) who also worked with barley, but in soil cultures, obtained increasing yields until the soil was neutral.

Since the natural flora of a calcareous soil in this country usually contains a high proportion of leguminous species (*e.g. Lotus corniculatus, Onobrychis sativa, Trifolium* spp., *Anthyllis vulneraria, Hippocrepis comosa,* etc.) we can understand the advantages in respect to nitrogen supply through the increased activity of *B. radicicola.* Moreover as H. C. Christensen has shown (**10**) *Azotobacter* can only survive in a soil well supplied with calcium, and the extensive work of Hesselman (**29**) on nitrate and nitrite formation in forest soils has shown that types of humus poor in electrolytes, exhibit little or no nitrate formation, so that the plants present on such soils must be capable of assimilating nitrogen in the form of ammonia (cf. also Hutchinson and Miller (**32**) and literature there cited), whilst in mild humus, on the other hand, nitrate formation is active. Other indirect effects probably due to the chemical nature of the calcareous soil are the absence or reduced virulence of certain plant diseases. The classical instance is *Plasmodiophora* which appears to be naturally confined to acid soils, whilst diseases due to species of *Rosellinia* are stated to be more severe on acid soils. The calcicolous species of *Iris* are liable to severe attacks from *Heterosporium gracile* when grown on soil deficient in calcium (cf. Butler, **7**, pp. 117–124). On the other hand some diseases such as larch canker are reputed to be worse on chalky soils and *Calluna* mycorrhiza is adversely affected by the abundant bacteria (cf. Rayner, **43**). Our knowledge of the diseases of wild species, however, requires to be much more complete before we can judge of the influence of fungal diseases in determining distribution.

To summarise briefly the more obvious chemical effects: calcareous soil is free from the toxic effect of the products of decay whilst the neutral character of the substratum favours the development of bacteria rather than fungi, and in particular the nitrate forming organisms. The neutral reaction moreover favours the development of an abundant soil fauna (cf. Salisbury, **50**) and particularly earthworms which themselves reduce the acidity of the soil that passes through their bodies.

In opposition to these beneficial chemical effects the observations of Fliche and Grandeau (**23**) and of Röthe (**46**) have shown that, for certain silicicolous species at all events, the presence of calcium in considerable amount appears to diminish appreciably the absorption of potassium and it is well known that potassic manures are amongst the most profitable that can be applied to this type of soil.

The application of lime to soil has been assumed to bring about an increase in the available potash but the analyses of wheat grown on limed soil, furnished by Gaither (**25**) and MacIntire (**40**), indicate a depressing effect on the absorption of potassium which is in complete harmony with the results already quoted. It is also significant to note that amongst the American species cited by Fernald (**19**) as confined to soils rich in potassium are several British calcifuge species (*e.g. Solidago virgaurea* v. *alpina*, *Rubus chamaemorus*, *Viola palustris*, etc.). The data given by the last-named author also support the view that calcifuge species are, in part at least, plants demanding a considerable supply of potassium, since out of a total of 258 species, only 4·6 per cent. were found on calcareous soils and those rich in potassium and these species were of general occurrence. On the other hand 12·4 per cent. were absent from the calcareous soils but common to the potassic and magnesium soils.

Chatin (**8**) found that even 3 per cent. of calcium was inimical to *Castanea vulgaris*, though Weber concluded (**59**) that the calcium itself was not deleterious to silicicolous plants but rather the superabundance of the accompanying soluble salts. On highly calcareous soils some species exhibit chlorosis (cf. Tansley, **54**).

There is doubtless every degree of tolerance exhibited by different species for the types of soil ranging from the acid peat almost devoid of electrolytes generally, to the basic soil of a chalk down. It is important to realise that no hard and fast line can be drawn between silicicolous and calcicolous species, a fact well illustrated by the various cultivated leguminous plants. Some, for example the clovers, sainfoin, etc. appear to be intolerant of any appreciable acidity; others, like the soy-bean, appear to require a slight acidity for their maximum development whilst our wild *Lathyrus macrorhizus* is especially characteristic of oakwoods exhibiting a marked acidity and deficiency of soluble salts.

Turning our attention to the physical properties of calcareous soils perhaps the most important is their dryness (with the exception of some of the heavier clays and marls) at all seasons of the year. As pointed out by Hall and Russell (**27**, p. 104) the low productiveness of many chalky soils is due to exposure and lack of moisture rather than to any deficiency in plant food. This dryness is partly an outcome of the porosity and high absorptive capacity of the chalk sub-soil and rock (and to a less degree of the older limestones), which latter at its maximum saturation contains about 46 per cent. by volume of water (cf. Baldwin-Wiseman, **2**): also in part to the rapid decomposition of humus and consequent small amount present at any given time; and to the absence of colloidal clay from the surface layers owing to the flocculating effect of the basic salts. These latter are maintained in the surface (cf. Ames and Schollenberger, **1**), despite the leaching effect of rain-water charged with CO_2, by the salts returned to the soil from decaying vegetation and perhaps also through the concentration effect of evaporation on the soil solution (cf. Hall and Russell *l. c.* p. 103).

Various cereals grown by Hansteen-Cranner (**13**) in solutions of calcium nitrate exhibited a greater consumption of water, per grain of dry weight, and an augmented transpiration, as compared with plants grown in isosmotic solutions of potassium nitrate. The conditions of a water culture are so totally different from those in the field that one hesitates to accept the suggestion that this, rather than the physical characteristics of the soil, is the explanation of the xerophytic character of the calcicolous flora. But physiological drought of this kind may quite well be an added factor in the dryness of a habitat rich in calcium ions.

The same features which make for dryness also ensure good aeration and this in turn reacts upon the flora and fauna of the soil and possibly also tends to reduce acidity (**57**). The neutral reaction, as already noted, favours a rich bacterial flora, and also an abundant fauna, in consequence of which accumulation of humus is retarded through rapid oxidation and the surface layers are maintained naturally in good 'tilth' by the numerous earthworms, etc. which effect a continuous cultivation.

The problem before us as to what determines the favourableness of calcareous soils for calcicolous species is clearly a complex one and unlikely to be susceptible of explanation upon the basis of one single factor alone.

This preference, or it may well be local tolerance (*e.g. Pinus sylvestris* in Champagne is stated to occur as a calcicole through pressure of competition from silicicolous species), has been commonly attributed to the effect of calcium though Kraus (**33**) has urged the importance of the physical characters.

It is suggested that neither explanation is entirely true or entirely false, and that broadly calcicole species belong to two classes of which one embraces those that inhabit a calcareous soil chiefly owing to its physical features, whilst to the second category belong species for which the chemical characteristics appear to be the more important.

It is but rarely that we find a species strictly confined to one particular type of soil and never extending on to others. These very exceptions to what appears to be the general rule seem to provide the clue to the real underlying determinants. There are for instance a number of species normally calcicolous in this country which do occur also on soils that resemble the chalk in being well aerated and dry, but which contain little or no calcium and but a low proportion of mineral salts. For example the beech, so characteristic of the slopes of our chalk downs, also occurs in natural woods on well drained siliceous soils, as in *Quercus sessiliflora* woods in the south of England where it may even become locally dominant (cf. Tansley, **56**, in *Types of British Vegetation*, p. 102).

It is well known that the beech is intolerant of water-logged soils and its edaphic distribution is in complete harmony with this fact. Loudon (**38**, p. 1968) refers to this peculiarity and states that "the beech will grow on dry soils, including sand, gravel, and chalk, more freely than most other trees."

If, as we postulate, the main determining factor for the distribution of the beech is the physical character of the soil we should find, on the basis of the principles adumbrated above, that this tree attains its maximum altitude on dry, well aerated, so-called warm, soils such as calcareous strata supply, and we should moreover expect that restriction to calcareous soils, or those of a similar physical character, will be the more pronounced as we approach the northern limits of its distribution where the temperature is lower and the humidity of the soil relatively high.

Both these hypotheses seem to be borne out by the facts, for the beech forests in Switzerland attain to a higher altitude and the trees are better developed on soils rich in calcium than on soils in which it is deficient, and moreover the beech is very susceptible to aspect, attaining an altitude of over 1500 metres on slopes which face south, as compared with only 1100 metres on slopes which face north (cf. Röthe, **46** and Blytt, **3**).

The geographical distribution of this tree illustrates the same principle. On the continent, especially in the southern warmer regions (*e.g.* the Cevennes, Corsica), *Fagus sylvatica* flourishes on soils containing little or no lime (cf. Flahault, **20**, and Skene, **53**). In northern France it is markedly calcicolous whilst in this country and in Denmark (cf. Warming, **58**) it is almost entirely restricted to calcareous soils, or as we have noted above to soils of *similar physical character*. Flahault (**21**, **22**) cites a number of species which are regarded as calciphilous in northern France but which in the Cevennes are encountered growing upon non-calcareous soils. Amongst these we may note the following British species: *Clematis vitalba*, *Buxus sempervirens*, *Teucrium chamaedrys*, *Helleborus foetidus* and *Juniperus communis*. The fact that these species occur on siliceous soils in the warmer climate, suggests that they too occur on chalk because they find there the requisite physical conditions, not because of the chemical reaction or the large proportion of nutrient salts, an interpretation already advanced by Prof. Flahault.

It is worthy of note that even in these islands though the Juniper is chiefly found on chalk downs it is not confined to them but also occurs and flourishes on well drained sands and loams, as in Rothiemurchus forest, Inverness-shire, and on the Hythe beds of the Lower Greensand in the south of England, on gravelly soil almost destitute of calcium. Such calcicolous species may also occasionally be met with associated with *Calluna*, etc., where the latter is growing on well drained peat. It should however be pointed out that the occurrence of 'calcifuge' species on calcareous soils is often explicable as a consequence of leaching of the surface layers, or accumulation of humus at the surface, so that the youth of the 'calcifuge' plant, which is doubtless the critical period, is passed whilst rooted in the leached non-calcareous stratum. Once established, any diminished rate of growth due to subsequent extension of the root system into the calcareous subsoil would probably not materially reduce the powers of resistance to competition. Conversely plants which will not grow readily in a highly acid soil in the juvenile phase can often do so at a later stage of development, a fact well illustrated by the attempts to plant up acid peat with *Pinus sylvestris* (cf. Maxwell, **42**). Such facts indicate how little importance from this standpoint can be attached to the growth of species in unaccustomed types of soil which have not arisen there from seed, *in situ*; a caution particularly necessary in the case of planted trees, which generally attain to a considerable size (at least 2–3 years old) before being planted in their permanent quarters.

It is obvious that variations in climate modify the effect of the physical characters of a soil and lead, as we have already observed, to the occurrence of species on different soils in different climatic regions. Brenchley when studying the distribution of the weeds of arable land (**4**) noted a discrepancy which is perhaps to be explained on these grounds. She found that several weeds which are either calcifuge or occur on various types of soil in Bedfordshire, are more or less restricted to chalk in the west of England. The absence of the beech from most of the calcareous rocks of the West country is perhaps partly related to the higher rainfall and the lower porosity of limestone as compared with chalk; but the regeneration of this tree in Cornwall and Ireland, where, as Loudon observes (*l. c.* p. 1957), it attains an enormous size on the calcareous loams and sloping hill sides, seems to show that its absence is not due to climatic unsuitability but perhaps merely to its recent introduction. Moreover the observations of Fernald (**17**) have shown that in Newfoundland the soil distinctions are more important than the climatic differences. For though the silicicolous flora there has a southern facies whilst the calcicolous flora has an arctic facies, the calcicolous species are met with in the warmer calcareous region and the silicolous species in the colder areas of the south-east and south-west.

The writer is indebted to Dr Russell for calling his attention to two cultivated species which probably belong to the class of calcicoles whose distribution is mainly determined by the physical properties of the habitat. These are *Medicago sativa* and *Onobrychis sativa*. In respect to the latter it has been pointed out that stagnant water is fatal to the success of the crop (**5**), but whilst generally grown on chalky soils, where indeed it occurs as a wild species, good crops are obtained on clays and loams *where the climate of the district is dry and warm* (*l. c.* **5**, p. 1). Similarly Lucerne or Alfalfa, though regarded in this country as a crop requiring lime, produces good crops on ragstone soils with only 0·5 per cent. of calcium (cf. Hall and Russell, **27**, p. 124) whilst in France it is cultivated both on calcareous and siliceous soils. An appreciation of the significance of these facts might lead to a much more extended cultivation of these valuable fodder plants.

There is, however, apparently a second class of calcicolous species whose distribution would seem to be mainly determined by chemical rather than physical characters. To this category belong a number of plants that appear to be intolerant of, or at least unduly handicapped in competition by, acidity.

The writer has elsewhere pointed out (Salisbury, **48**, p. 99) that a number of trees and shrubs, which exhibit a marked calcicolous tendency, grow both on dry chalky soils and also in very damp or even aquatic habitats. Examples are furnished by *Fraxinus excelsior*, *Rhamnus catharticus*, *Acer campestre*, *Cornus sanguinea*, *Ligustrum vulgare*, *Sambucus nigra*, *Solanum dulcamara*, *Rubus caesius*, and many others. It is clear that these two extremes are as divergent as possible with respect to the water content of the soil or the concentration of soluble salts. *Solanum dulcamara*, which is a common constituent of chalk scrub, is not infrequent in acid sandy areas, where it occurs in ponds growing sometimes in more than a foot of water! The clue to such cases is probably furnished by a consideration of the acidity. The writer has shown (**48** and **50**) that in woods on acid soils the calcicolous *Mercurialis perennis* occurs either in dry areas with a high calcium content (or low acidity) or in damp areas where the lime requirement is high considered in terms of the unit weight of dry soil (total acidity) but is apparently ameliorated as a consequence of the high water content. Thus, considering total acidities, *Mercurialis perennis* has been found in areas with a lime requirement of from 0·24 per cent. to 0·72 per cent., the range for *Holcus lanatus* in the same area being 0·48 per cent.—0·62 per cent. But if we take into consideration the water content, then the respective ranges were proportional to 0·052 to 0·069 for *Holcus lanatus* and only 0·019 to 0·039 for *Mercurialis perennis*. The same feature of distribution has been noted for *Circaea lutetiana*, *Adoxa moschatellina* and *Allium ursinum*. The prevalence of the last named in the 'flushes' of woods on siliceous soils may well be related to the same factor. Massart (**41**, p. 81) cites an interesting example in the occurrence of *Sesleria coerulea* on chalk rocks in Belgium and also on tuffa which is always covered with water. *Rhamnus catharticus* is probably also a species whose distribution depends on the chemical characteristics of the soil. For whilst on the whole it is chiefly met with on the chalk it is also a pronounced feature of the East Anglian fens, where, as is well known, the water has an alkaline reaction with a high proportion of soluble salts.

In this connection it should be emphasised that even completely waterlogged soils need not necessarily become more acid though other attendant evils assert themselves. Very recently Gillespie (**26**) has shown that soils treated with excess of water may become less acid though exhibiting an increased reducing capacity which appears to have an injurious effect.

The association which Laurent has shown to exist between the distribution of *Viscum album* and calcareous soils (**34** and **35**) can scarcely be explained except on the basis of chemical action and the same is also probably true of

Thesium humifusum. An interesting case is discussed by Fernald (**18**) who attributes the distribution of *Pinus Banksiana* and *Thuja occidentalis* to chemical differences. Attempts to verify the injurious effects of acidity on 'chemical calciphiles' grown in pots in a laboratory were not very successful, owing to the unsuitability of the environment, which resulted in a marked diminution of the rate of growth as compared with plants in their natural habitat. The method adopted was to plant weighed clean rhizomes of *Adoxa moschatellina* and *Circaea lutetiana*, etc., in various types of soil and again weigh them after one season's growth. A large proportion of the specimens grown in acid soil died whilst where the weight at the end of the experiment was less than at the beginning the loss was usually greater in the more acid type of soil. In the case of two pairs however a definite gain was recorded and, so far as such meagre results can be relied upon, they indicate a markedly beneficial effect upon growth from neutralisation of the soil acidity.

Adoxa moschatellina	Original weight	Final weight	Percentage increase
Acid soil	0·11 gm.	0·13	18·1 %
Same soil neutralised with chalk	0·14 gm.	2·50	1400 %
Circaea lutetiana			
Acid soil	0·65 gm.	1·27	95 %
Same soil neutralised with chalk	0·57 gm.	2·50	338 %

All the cultures of *Ficaria verna* showed a decrease as compared with the original weight. The plants in very acid soils (real acidity P_H 5·6) died. Those in slightly acid soils had storage organs, at the end of the experiment, from 11 per cent. to 23 per cent. of the original weights, whilst those grown in neutral soils were from 24 per cent. to 30 per cent. of the original weights.

A great deal of experimental work requires to be done on the calcicolous flora, but the brief review of some of the facts of their occurrence here given seems to warrant their subdivision into two classes, between which however there is naturally no sharp line of demarcation. The one class frequents calcareous soils mainly on account of their physical characters and these may perhaps be appropriately termed *pseudo-calcicolous*. The second class is probably composed of species which are intolerant of high acidities and may consequently be termed *oxyphobic*. Climatic and biotic factors may, as has been noted, profoundly modify the relationships which are commonly observed between plant and soil so that the associations of calcicolous and silicicolous species which sometimes occur are perhaps more remarkable for their comparative rarity than for the fact of their occurrence.

The work of Hesselman previously referred to has indicated that some at least of the so-called calcifuge species assimilate nitrogen mainly in the form of ammonia, and are perhaps silicicolous owing to this faculty and the preponderance of nitrogen in this form on such soils. Similarly it is not improbable that some of the calcicolous species frequent calcareous soils owing to a high demand for nitrates which are especially abundant in a neutral medium containing calcium.

If it is factors such as acidity, nitrate content, or physical condition, etc. which determine these soil preferences it is clearly unreasonable to expect to find a total restriction of any but the most specialised forms to one particular soil type. On the contrary there will be all gradations of tolerance and the restriction will largely depend upon the rigour of the competition or other factors tending towards elimination in any given case. If the adverse factors tend to preponderate even a slight preference or tolerance for a particular soil type will weight the scale in the balance of survival and restriction will tend to be pronounced. Hence we find that at the climatic limits of a specie's range, whether geographic or altitudinal, soil preferences tend to become more clearly defined.

So, too, it seems to follow from the foregoing facts that contrary to the views expressed by earlier writers the solution of the problem of calcicoly is not to be found in one factor but perhaps in many, though possibly all comprised in the two main groups suggested. The very fact that the calcicole flora comprises plants belonging to no one geographic region, although in this country mainly southern, and belonging to the most diverse families, would in itself scarcely lead us to expect a uniform demand. Conversely there are closely related species which exhibit the most divergent preferences, as for instance *Rhamnus catharticus* and *Rhamnus frangula*, *Galium sylvestre* and *Galium saxatile*, *Rhododendron hirsutum* and *Rhododendron ferruginum*, *Sesleria coerulea* and *Sesleria disticha*, *Quercus Ilex* and *Quercus suber*, *Achillea atrata* and *Achillea moschata*, to which many more might be added. If closely allied species find the most suitable environment in such diverse habitats it is not surprising that the heterogeneous forms which comprise the calcicolous flora should make no uniform demand upon the soil.

Whilst our present knowledge when brought together appears to shed some light on this obscure problem it brings into prominence also the many lacunae which still require to be filled. In particular we need critical information regarding distribution. The much quoted exceptions in which calcicole species are met with on apparently non-calcareous soil are obviously worthless in the absence of a definite knowledge as to the calcium content of the soils in question, their physical condition, and above all their chemical reaction. Similarly the occurrences of calcifuge species on so-called calcareous soils are sometimes, at least, a consequence of leaching which thus in reality are no exception to the general rule. A striking example of this is seen in the heather-clad Hambledon Hills of Yorkshire, the soil of which is derived from the Lower Calcareous Grit of the Coralline series, in which, however, only a trace of calcium remains (cf. Elgee, **16**, p. 194, also Hanley, **28**). Furthermore in this connection it is essential that the smaller divisions of species should be critically separated since it is often just these microspecies which exhibit the most marked soil preferences.

Culture experiments are essential, but the fact that a species will tolerate certain chemical or physical conditions under the artificial protection of a laboratory experiment is no criterion of its success in competition with other species under these same conditions. Still less can the results of such experiments be considered as parallel with the conditions of nature when the whole life cycle, for at least two generations, is not passed in the experimental environment.

LITERATURE CITED.

(1) **Ames, J. W.** and **Schollenberger, C. J.** "Calcium and Magnesium content of Soil." *Soil Science*, **8**, pp. 323–325, 1919.

(2) **Baldwin-Wiseman** in *Q. Jour. Geol. Soc.* **63**, pp. 83–88, 1907.

Blair, A. W. *see* **Lipman.**

(3) **Blytt, A.** "Zur Geschichte der nordeuropäischen .besonders der norwegischen Flora." *Englers Jahrb.* 1893.

(4) **Brenchley, W. B.** "The Weeds of arable land in relation to the soils on which they grow." *Ann. Bot.* pp. 95–109, 1912.

(5) Board of Agriculture leaflet No. 280, 1916.

(6) **Bunzell, H. H.** "The relationship existing between the oxidase activity of plant juices and their Hydrogen-ion concentration." *Jour. Biol. Chem.* **28**, pp. 315–333, 1916.

(7) **Butler, E. J.** *Fungi and disease in plants.* Calcutta, 1918.

(8) **Chatin, H.** "Le Châtaignier. Étude sur les terrains qui conviennent à sa culture." *Bull. Soc. Bot. Fr.* 1870.

(9) **Christ, H.** *Das Pflanzenleben der Schweiz.* Basel, 1879.

(10) **Christensen, H. C.** "Studien über den Einfluss der Bodenschaffenheit auf das Bakterienleben und den Stoffumsatz im Erdboden." *Centralbl. für Bakt.* Ab. II. **43**, 1915.

(11) **Clevenger, C. B.** "Hydrogen-ion concentration of plant juices." *Soil Science*, **8**, pp. 227–242, 1919.

(12) **Cockayne, L.** *New Zealand Plants and their Story*, 2nd Edition. Wellington, 1919.

(13) **Cranner, B. Hansteen-.** "Über das Verhalten der Kulturpflanzen zu den Bodensalzen." *Jahrb. f. wiss. Botanik*, **53**, pp. 536–599, 1919.

(14) **Dachnowski, A.** "The effects of acid and alkaline solutions upon the water relations and the metabolism of plants." *American Jour. Bot.* **1**, pp. 412–439, 1914.

(15) **Dachnowski, A.** "The Peat Deposits of Ohio; their origin, formation and uses." *Geol. Survey Ohio*, Bull. 16, 1912.

(16) **Elgee, F.** *The Moorlands of N.E. Yorkshire.* Hull, 1912.

(17) **Fernald, M. L.** "The contrast in the Floras of Eastern and Western Newfoundland." *American Jour. Bot.* **5**, pp. 237–247, 1918.

(18) **Fernald, M .L.** "Lithological Factors limiting the ranges of *Pinus Banksiana* and *Thuja occidentalis.*" *Rhodora*, **21**, pp. 41–65, 1919.

(19) **Fernald, M. L.** "The soil preferences of certain alpine and sub-alpine plants." *Rhodora*, **9**, pp. 149–193, 1907.

(20) **Flahault, Ch.** *Distribution des Végétaux dans un coin du Languedoc.* Montpellier, 1893.

(21) **Flahault, Ch.** "La Flore et la Végétation de la France" in Coste, *Flore de France.* Paris, 1901.

(22) **Flahault, Ch.** "Les progrès de la géographie botanique depuis 1884, son état actuel, ses problèmes." *Progressus rei botànicae,* **1**, 1907.

(23) **Fliche, P.** and **Grandeau, L.** "De l'influence de la composition chimique du sol sur la végétation du Châtaignier." *Ann. d. Chimie et d. Physique*, pp. 354–379, 1874.

(24) **Fred, E. B.** and **Graul, E. J.** "Effect of inoculation and lime on Soy-beans." *Soil Science*, **7**, pp. 455–468, 1919.

(25) **Gaither, E. W.** "The effect of Lime upon the solubility of the soil constituents." *Jour. Indus. Eng. Chem.*, **2**, p. 315, 1910.

Gilbert, J. H. *see* **Lawes.**

(26) **Gillespie, L. J.** "Reduction potentials of Bacterial cultures and soils." *Soil Science*, **9**, pp. 199–215, 1920.

Grandeau, L. *see* **Fliche.**

Graul, E. J. *see* **Fred.**

(27) **Hall, H. D.** and **Russell, E. J.** *Agriculture and Soils of Kent, Surrey and Sussex.* London, 1911.

(28) **Hanley, J. A.** *The need for Lime on Yorkshire soils.* Leeds, 1918.

(29) **Hesselman, H.** "Studien över saltpeterbildningen..." Stockholm, 1917.

(30) **Hoagland, D. R.** "Relation of the concentration and reaction of the nutrient medium to the growth and absorption of the Plant." *Jour. Agric. Research*, **18**, pp. 73–117, 1919.

(31) **Hutchinson, H. B.** and **MacLennan, K.** "Studies on the Lime requirements of certain soils." *Jour. Agric. Sci.* **7**, pp. 75–105, 1915.

(32) **Hutchinson, H. B.** and **Miller, N. H. J.** "Direct assimilation of Ammonium salts by plants." *Jour. Agric. Sci.* **3**, Pt II, 1909.

(33) **Kraus, G.** "Boden und Klima auf kleinstem Raum." Jena, 1911.

(34) **Laurent, L.** *Bull. Soc. Roy. d. Belgique*, 1890.

(35) **Laurent, L.** *Bull. de l'Agriculture*, 1900.

(36) **Lawes, J. B.**, **Gilbert, J. H.** and **Masters, M. T.** "On the mixed herbage of permanent meadow." *Phil. Trans. Roy. Soc.* Pt IV, 1882.

(37) **Lipman, J. G.** and **Blair, A. W.** "The Lime factor in permanent soil improvement." *Soil Science*, **9**, pp. 83–114, 1920.

(38) **Loudon.** *Arboretum et Fruticetum.* London, 1838.

(39) **MacDougal, D. T.** "Hydration and Growth." Washington, 1920.

(40) **MacIntire, W. H.** "The influence of fertilizers upon the composition of Wheat." *Penn. Agric. Exp. St. Rep.* 1911.

MacLennan, K. *see* **Hutchinson.**

(41) **Massart, J.** *Esquisse de la Géographie Botanique de la Belgique.* Brussels, 1910.

Masters, M. T. *see* **Lawes.**

(42) **Maxwell, Sir Herbert.** *Scientific forestry for the United Kingdom.* London, 1918.

Meacham, M. R. *see* **Truog.**

Miller, N. H. J. *see* **Hutchinson.**

(43) **Rayner, M. C.** "The Ecology of *Calluna vulgaris*." *New Phytologist*, **12**, 1913.

(44) **Reed, G. B.** "The oxidases of acid tissues." *Bot. Gaz.* **57**, pp. 528–530, 1914.

(45) **Rigg, G. B.** "Decay and Soil toxins." *Bot. Gaz.* pp. 293–310, 1913.

(46) **Roth, A.** *Die Vegetation des Wahlenseegebietes.* Zürich, 1919.

(47) **Röthe, C.** "Über das Vorkommen der *Herniaria glabra* auf Dolomit-sand." *Ber. d. Nat. Ver. in Augsburg*, 1869.

Russell, E. J. *see* **Hall.**

(48) **Salisbury, E. J.** "The Oak-Hornbeam Woods of Hertfordshire." Parts I and II. *Journal of Ecology*, **4**, pp. 83–117, 1916.

(49) **Salisbury, E. J.** "The Ecology of Scrub in Hertfordshire." *Trans. Herts. Nat. Hist. Soc.* 1917.

(50) **Salisbury, E. J.** "The Oak-Hornbeam Woods of Hertfordshire." Parts III and IV. *Journal of Ecology*, **6**, pp. 14–52, 1918.

(51) **Salter, R. M.** and **McIlvaine, T. C.** "Effect of reaction of solution on germination of seed and on growth of seedlings." *Jour. Agr. Res.* **19**, pp. 73–95, 1920.

Schollenberger, C. J. *see* **Ames.**

(52) **Schreiner, O.** "The Organic constituents of Soils." *Science*, **36**, pp. 577–587, 1912.

(53) **Skene, M.** "The relation of Beech to edaphic factors." *Journal of Ecology*, **1**, p. 94, 1913.

(54) **Tansley, A. G.** "On competition between *Galium sylvestre* and *Galium saxatile* on different types of soil." *Journal of Ecology*, **5**, p. 113, 1917.

(55) **Truog, E.** and **Meacham, M. R.** "Soil Acidity; its relation to the acidity of the plant juice." *Soil Science*, **7**, pp. 469–474, 1918.

(56) *Types of British Vegetation.* Edited by A. G. Tansley. Cambridge, 1911.

(57) **Walker, S. S.** "The effect of aeration and other factors on the lime requirement of a mulch soil." *Soil Science*, **9**, 1920.

(58) **Warming, E.** *The Oecology of Plants.* (Eng. Ed.) Oxford. 1909.

(59) **Weber, C. A.** *Heimatbund an Elb und Wesermündung*, 1900.

POSTSCRIPT ON THE EFFECT OF SOIL REACTION ON GERMINATION.

The results of experiments upon the effect of reaction on germination have been somewhat conflicting. Salter and McIlvaine in the paper cited found that an acid reaction was beneficial, whereas Von Brehmer found that lime increased the germinating capacity of a number of Phanerogams ("The importance of lime as a plant food for seedlings,' *Gartenwelt*, Bd II, No. **14**, pp. 163–164, 1907). According to Claudell and Crochetell ("Influence of certain substances used as fertilisers on germination," *Ann. Agron.* **22**, pp. 131–142, 1896), an acid reaction is injurious to germinating seeds, and similar results were obtained by R. Tolf ("On the influence of humus soils on germination," *Tidskr. Landtmän*, v. **19**, pp. 387–390, 1898). The results of Promsey indicate, however, a beneficial action from dilute acids like that observed by Salter and McIlvaine ("The influence of acidity on germination," *Compt. Rend. Acad. Sci.* t. **152**, pp. 450–452, 1911, and "The rôle of acids in germination," *Bull. Soc. Nat. Agr. France*, t. **72**, pp. 916–922, 1912). Probably here too then the injurious or beneficial effect varies with the species.