

- 9 Dam, H. van, Suurmond, G., and ter Braak, C.J.F., Impact of acidification on diatoms and chemistry of Dutch moorland pools. *Hydrobiologia* 83 (1981) 425-459.
- 10 Drabløs, D., and Tollan, A. (Eds), Ecological impact of acid precipitation. Proc. int. Conf. Ecol. Impact Acid Precip., Norway 1980. SNSF project, Oslo-Aas 1980.
- 11 Focht, D.D., and Verstraete, D., Biochemical ecology of nitrification and denitrification. *Adv. Microb. Ecol.* 1 (1977) 135-214.
- 12 Fuhrer, J., Formation of secondary airpollutants and their occurrence in Europe. *Experientia* 41 (1985) 286-301.
- 13 Joranger, E., Schang, J., and Semb, A., Deposition of airpollutants in Norway, in: Ecological impact of acid precipitation, pp.120-121. Proc. int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Eds D. Drabløs and A. Tollan. Oslo-Aas 1980.
- 14 Heil, G.W., and Diemont, W.H., Raised nutrient levels change heathland into grassland. *Vegetatio* 53 (1983) 113-120.
- 15 Henriksen, A., A simple approach for identifying and measuring acidification of freshwater. *Nature* 278 (1979) 542-545.
- 16 Henriksen, A., Susceptibility of surface waters to acidification, in: Acid Rain/Fisheries, pp. 103-121. Proc. int. Symp. Acid Precip. Fish. Imp. Ed. R. E. Johnson. Am. Fish. Soc., Bethesda, Maryland 1982.
- 17 Leuven, R.S.E.W., den Hartog, C., Christiaans, M.M.C., and Oyen, F.G.F., Effects of acid precipitation on amphibians and fish, in: Zure regen: oorzaken, effecten en beleid, pp.184-186. Proc. Symp. Zure Regen, 's Hertogenbosch, 17-18 Nov.1983. Eds E.H. Adema and J. van Ham. Pudoc, Wageningen (1984).
- 18 Leuven, R.S.E.W., and Schuurkes, J.A.A.R., Effecten van zure, zwavel- en stikstofhoudende neerslag op zwak gebufferde en voedselarme wateren. Interim Report projects LB 130 and LB 131. Ministry of Housing, Physical Planning and Environment. Publikatiereeks Lucht 47 (1985).
- 19 Meent, D. van, Oosterwijk, J. van, and Aldenberg, T., RID-VEWIN, Meetnet regenwater 1978-1982. National Institute of Human Health and Environment (1984).
- 20 Nicholson, I.A., Cape, N., Fowler, D., Kinnaird, J.W., and Paterson, I.S., pH and sulphate content of precipitation over Northern Britain, in: Proc. int. Conf. Ecol. Impact Acid Precip., Norway 1980, pp. 142-143. Eds D. Drabløs and A. Tollan. SNSF project, Oslo-Aas 1980.
- 21 Overrein, L.N., Seip, H.M., and Tollan, A. (eds), Acid precipitation - Effects on forest and fish. Final Report SNSF project 1972-1980, 2nd edn. Oslo 1980.
- 22 Rebsdorf, A., Acidification of Danish soft waters, in: Proc. int. Conf. Ecol. Impact Acid Precip., Norway 1980, pp.238-239. Eds D. Drabløs and A. Tollan. SNSF project, Oslo-Aas 1980.
- 23 Roelofs, J.G.M., Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field observations. *Aquat. Bot.* 17 (1983) 139-155.
- 24 Roelofs, J.G.M., Clasquin, L.G.M., Driessen, J.M.C., and Kempers, A.J., De gevolgen van zwavel- en stikstofhoudende neerslag op de vegetatie in heideen heidevenmilieus, in: Proc. Symp. Zure Regen, 's Hertogenbosch, pp.135-140. Eds E.H. Adema and J. van Ham. Pudoc, Wageningen 1984.
- 25 Roelofs, J.G.M., Kempers, A.J., Houdijk, A.L.F.M., and Janssen, J., The effect of air-borne ammonium sulphate on *Pinus nigra* var. *maritima* in the Netherlands, *Pl. Soil* 84 (1985) 45-56.
- 26 Schoen, R., Wright, R., and Krieter, M., Gewässerversauerung in der Bundesrepublik Deutschland. *Naturwissenschaften* 71 (1984) 95-97.
- 27 Schuurkes, J.A.A.R., and Roelofs, J.G.M., De invloed van waterverzuring en stikstofverrijking op waterplantengemeenschappen in zwak gebufferde wateren, in: Proc. Symp. Zure Regen, 's Hertogenbosch, pp.177-179. Eds E.H. Adema and J. van Ham. Pudoc, Wageningen 1984.
- 28 Vanderborght, O.L.J. (Ed.), Proc., Symp. Acid Deposition and the Sulphur cycle, Brussel, June 1984. SCOPE, Belgium 1984.
- 29 Vangenechten, J.H.D., and Vanderborght, O.L.J., Acidification of Belgian moorland pools by acid sulphur-rich rainwater, in: Proc. int. Conf. Ecol. Impact Acid Precip., Norway 1980, pp.246-247. Eds D. Drabløs and A. Tollan. SNSF project, Oslo-Aas 1980.
- 30 Vangenechten, J.H.D., Puymbroeck, S. van, and Vanderborght, O.L.J., Acidification in Campine boglakes, in: Proc. Symp. Acid Deposition and the Sulphur Cycle, Brussel 1984, pp.251-262. Ed. O.L.J. Vanderborght. Scope, Belgium 1984.
- 31 Verloo, M., Cotterie, A., and Debaene, L., Soil acidity: contribution of acid rain, in: Proc. Symp. Acid Deposition and the Sulphur Cycle, Brussel 1984, pp.231-239. Ed. O.L.J. Vanderborght. Scope, Belgium 1984.

0014-4754/86/040351-07\$1.50 + 0.20/0
 © Birkhäuser Verlag Basel, 1986

The response of plants to acid soils

by I. H. Rorison

Unit of Comparative Plant Ecology (NERC), Department of Botany, The University, Sheffield S10 2TN (England)

Summary. Interactive effects between acid deposition and the rest of the environment are the key to further understanding. Although this article deals only with plant growth in relation to the chemical state of the soil and not with aerial effects, it is still possible to illustrate a number of interactions and patterns of response among both vascular and non-vascular components of vegetation. Evidence is examined with regard to plant age, pre-treatment and the nature of nutrient supply. It includes consideration of both effects of soil on plants and of plants on soil, notes both antagonisms and symbioses, and draws attention to inducible defence systems.

Key words. Aluminium; ammonium N; ion efflux; metal toxicity; mucilage; mycorrhizae; nodulation; nutrient deficiency.

Introduction

There is considerable concern over the effects of acid deposition on vegetation both by direct contact with aerial parts and through changes in the chemical state of the soil down the profiles in which plants root. This article will deal with plant growth in relation to the chemical state of the soil volume that is occupied and not with aerial effects. It should be stated at the outset that there is no single pattern of response shown by plants. Most

common crop plants have been selected and bred for rapid growth under fertile conditions and they lack the tolerance mechanisms necessary for survival in very acidic conditions.

Within the native populations of plants worldwide, however, there are those that are tolerant of a wide range of soil chemical conditions, including the suite of factors found in acidic soils.

Even within acidic soils the degree of acidity and the extent of associated toxicities varies according to the

geological origins of the soil's parent material. Biotic components also play a role from the various microbial populations⁴⁶ to the vascular plants with which they interact. The sloughing of organic matter and the efflux of inorganic ions into the soil from living organisms is all part of the interactive system which must be studied if we are to understand the implications of the acidification of soils.

Initially investigations were concentrated on the 'end-point' effects of single chemical factors on single crop¹⁶ or 'wild' plants⁴¹. Now, with greater interest in a functional approach, attention is concentrated on rates of reaction and upon interactive systems³⁹. In order to understand how plants survive it is necessary to know how they capture and utilize nutrients, often in the presence of competing and potentially toxic elements.

If soil acidity cannot be checked and it is necessary to select tolerant genotypes it is important to know how such tolerance is expressed. Evidence in the literature is widespread but accurate comparisons and interpretation requires an appreciation of individual sets of experimental procedures. Plant responses are particularly sensitive to age, pretreatment, and the source, composition and method of nutrient supply. Nevertheless, reviews of plant-soil acidity problems are frequent, e.g.^{10,26,42,44}.

Rather than provide a general outline of the problem yet again an attempt will be made to show how an appreciation of some of the interactive strands can lead to a fuller understanding than is possible from generalized statements based on single factor, single species, experiments. This includes a consideration of not only how acidification can affect plant growth, but also how certain aspects of plant growth can affect soil acidity.

Chemical characteristics of acidic soils which affect plant growth

Soil reaction

pH remains the most informative preliminary measurement to be made although definitive experimental evidence concerning the impact of H^+ ions and OH^- ions on plant growth is still awaited^{20,42}.

But it is known that as pH falls the solubility of several potentially toxic metal ions (Al^{3+} , Mn^{2+} and Fe^{3+}) increases⁵⁴. This solubility can also lead to nutrient deficiencies (e.g. of calcium, magnesium and phosphorus) because of the tendency of soluble ions to be leached or precipitated as metallic salts.

However, while the form and solubility of these elements is affected by soil pH, the form of two of them can, directly (calcium) and indirectly (nitrogen), have an effect on soil pH.

Nitrogen

First, considering nitrogen, it is widely reported that many, particularly uncultivated, soils contain a high proportion of organic forms which are unavailable to plants. Of the available inorganic forms ammonium nitrogen is the predominant source in acidic soils and nitrate in most others. This is understandable in terms of the pH optima of the bacteria involved in the nitrogen cycle¹ but there are exceptions⁴⁷.

There are two aspects of interest regarding the response of plants to these two forms of inorganic nitrogen:

1) the effect their uptake has on the pH of the rhizosphere;

2) the effect they have on the survival of the plant.

1. At its simplest this means that uptake of NO_3^- -N would increase the pH in the root zone of the plant since an efflux of OH^- ions would occur in order to maintain electrochemical balance³⁵. Conversely uptake of NH_4^+ -N would lead to a decrease in pH following the efflux of H^+ ions from the root (e.g. fig. 1).

It has been estimated that the efflux of H^+ ions from plant roots produces more acidity than any likely input of acid rain⁴⁸!

2) Vascular plants respond in an interesting way to these sources of nitrogen. Those normally restricted to acidic soils (e.g. *Deschampsia flexuosa* L.) are able to tolerate and utilize both NH_4^+ and NO_3^- provided that the pH of the root medium is kept acidic¹². At high pH values growth can be inhibited by supplying NO_3^- -N. Stunting is accompanied by a significant increase in tissue Ca concentrations⁴². This indicates a lack of a regulatory mechanism to control the passive uptake of Ca as found in plants adapted to highly calcareous soils²⁶. Again, plants which tolerate low pH and NH_4^+ -N have no problem with potassium uptake while plants adapted to less acidic media suffer from potassium deficiency attributed to an antagonism between NH_4^+ and K^+ ions during uptake¹². So in various ways the NH_4^+ form of nitrogen can be deleterious to the establishment and growth of plants not specially adapted to acidic conditions. On the other hand, plants capable of surviving acidic conditions not only tolerate NH_4^+ but also have enough of the enzyme nitrate reductase to be able to utilize any NO_3^- -N which may be present. The only recorded exceptions are some members of the Ericaceae which must depend largely on NH_4^+ -N¹⁴. Problems associated with the regulation of cellular pH are less severe when plants are dependent on symbiotic fixation of atmospheric N_2 . See under 'Biotic effects'.

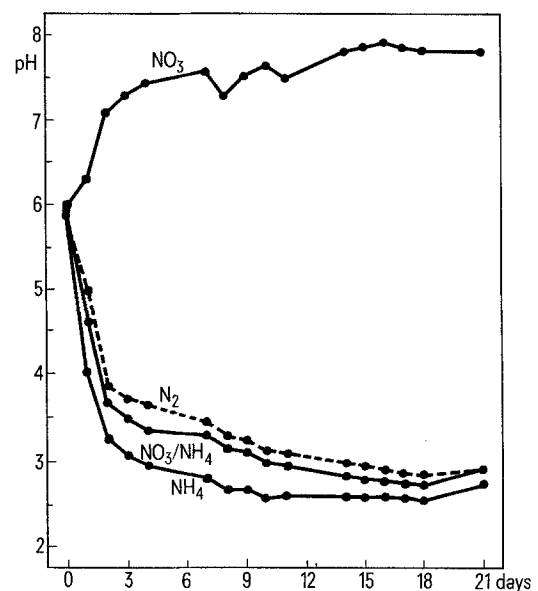


Figure 1. Time course of nutrient-solution pH during a 3-week growth period of *Abus glutinosa* on nutrient solutions with different N sources. N_2 signifies plants relying only on fixed nitrogen. NO_3^- , NO_3^-/NH_4^+ , NH_4^+ refer to plants receiving alternative supplies of inorganic N⁴⁹.

Calcium

Calcium as Ca^{2+} and CaCO_3 has a major regulatory role in the chemistry of the soil⁴⁴ and the response of plants to the element reflects this. Although it is required in smaller quantities than the other 'major' elements⁵³ differential responses to Ca^{2+} can be correlated with the pH of the soils on which the plants occur²⁵.

Experiments indicate that plants from soils low in Ca have evolved lower requirements for, and lower tolerances of, this element, compared with species from calcareous soils. Certainly leaf contents of Ca can be shown to relate to both soil pH and Ca content (fig. 2).

So increasing soil acidity, leading to the dissolution of CaCO_3 with the loss of Ca^+ ions and a drop in pH down the soil profile, can result in a change in the natural population of plants. Such leaching might not affect long-standing crops but would need to be taken into account in the establishment of any subsequent sowings.

Aluminium

As CaCO_3 is leached from the profile and acidity increases, aluminium becomes increasingly toxic to plants. It

dominates the cation exchange sites of clay minerals in soils below pH 4.5, replacing Ca^{2+} and Mg^{2+} and H and at the same time attracts phosphorus with its excess positive charges³.

In susceptible species aluminium can also interfere with the uptake and accumulation of Ca, Mg and P^{39,41}. The sites of interference may be outside the root and within either the apoplast or symplast²⁶.

In tolerant species aluminium is excluded from the symplast of roots and shoots and adequate amounts of essential nutrients including Ca and P are acquired because either (only) small amounts are required to maintain normal rates of growth or the plants benefit from a mycorrhizal association (see 'Biotic effects')⁶.

Since both Al^{3+} and NH_4^+ occur in acidic soil solutions to the detriment of many plants the possibility of interactions should be considered. Rorison⁴³ found (fig. 3), using flowing solutions in which pH was maintained at 4.5 ± 0.2 , that *Deschampsia flexuosa* (L.) Trin. was tolerant of NH_4^+ and Al^{3+} supplied singly or together, but susceptible to high Al^{3+} concentrations if supplied with

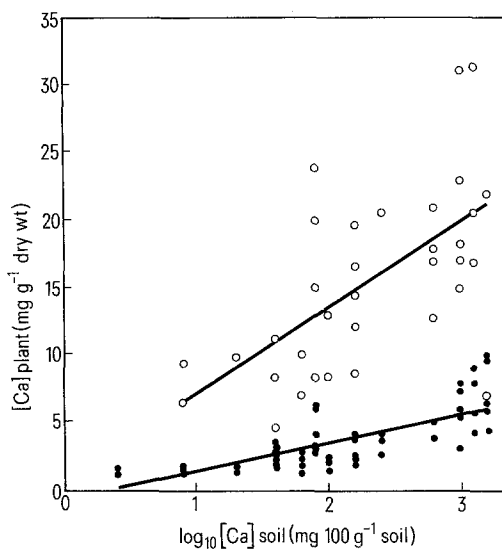


Figure 2. Relationships between exchangeable Ca concentrations in a range of soils and Ca concentrations in green-leaf tissue of a range of dicotyledonous (○) and monocotyledonous (●) species. Regression equations:

1) Dicots: $y = 0.83 + 6.31x$ ($p < 0.001$).

2) Monocots: $y = -1.17 + 2.31x$ ($p < 0.001$).

Material collected during a 14-day period in July 1969 and data taken from the unpublished UCPE Mineral Nutrient Survey. Species listed in increasing tolerance of calcareous soils.

Dicotyledonous species: *Vaccinium myrtillus* L.; *Potentilla erecta* (L.) Rauschel; *Galium saxatile* L.; *Lathyrus montanus* Bernh.; *Betonica officinalis* L.; *Campanula rotundifolia* L.; *Centaurea nigra* L.; *Lotus corniculatus* L.; *Poterium sanguisorba* L.; *Rumex acetosa* L.; *Veronica chamaedrys* L.; *Scabiosa columbaria* L.; *Succisa pratensis* Moench. Monocotyledonous species: *Deschampsia flexuosa* (L.) Trin.; *Festuca ovina* L.; *Nardus stricta* L.; *Molinia caerulea* (L.) Moench; *Agrostis tenuis* Sibth.; *Brachypodium pinnatum* (L.) Beauv.; *Sieglingia decumbens* (L.) Bernh.; *Anthoxanthum odoratum* L.; *Helictotrichon pratense* (L.) Pilger; *Holcus lanatus* L.; *Festuca rubra* L.; *Dactylis glomerata* L.; *Arrhenatherum elatius* (L.) Beauv. ex J. & C. Presl; *Carex flacca* Schreber; *Koeleria cristata* (L.) Pers.; *Bromus erectus* Huds.

Sites (surface pH (water) in parenthesis): Clumber (3.6); Ramsley Moor (3.6); Budby (3.7); Longshaw (3.6); Edale (3.6); Tideswell (4.8); Cadeby (7.4); Wardlow (4.3); Markland (7.4); Winnats south-facing slope (7.7); Lathkill Plateau (4.2); Lathkill north-facing slope (6.8); Lathkill south-facing slope (7.7). (Rorison and Robinson⁴⁴).

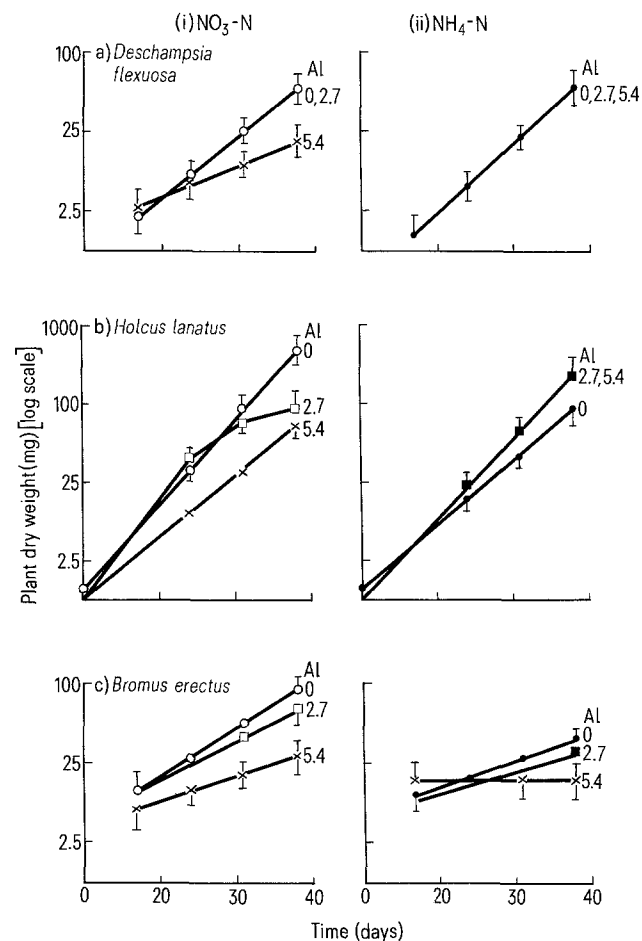


Figure 3. The mean yields of individual plants of (a), *Deschampsia flexuosa*, (b), *Holcus lanatus* and (c), *Bromus erectus* during 6 weeks' growth in response to different combinations of nitrogen and aluminium in a complete nutrient solution. Data are transformed to \log_e and curves fitted by the method of Hunt and Parsons¹⁹. The 95% C.L. are indicated when they exceed the dimensions of the symbols. Only curves that differ significantly from each other ($p < 0.05$) are included. Symbols: unfilled, $\text{NO}_3\text{-N}$ treatment; filled symbols $\text{NH}_4\text{-N}$ treatment. Al concentrations: (○, ●), zero (□, ■), 2.7 mg l^{-1} ; (×), 5.4 mg l^{-1} (Rorison⁴³).

NO_3^- . The growth of *Holcus lanatus* L., a species of wide edaphic distribution, was inhibited by NH_4^+ , relative to its growth on NO_3^- , but this was ameliorated by additions of Al^{3+} . *Bromus erectus* Huds. was also intolerant of NH_4^+ , and of Al^{3+} when supplied with NO_3^- . In this species, addition of Al^{3+} had no ameliorating effect upon NH_4^+ toxicity, and the results reflected its absence from acidic soils in the field.

These results contrast with previous findings on the Al tolerance of wheat cultivars¹¹, in which Al tolerance was linked with a capacity to increase rhizosphere pH in an unbuffered medium through excess NO_3^- uptake, thereby precipitating Al salts, and rendering Al unavailable. In a buffered soil, which was acidic enough for Al to be in solution and therefore potentially toxic: a), NO_3^- is unlikely to be the predominant N source: and b), even if it were, further evidence^{29,42} indicates that in acidic solutions whose pH is not allowed to drift, NO_3^- enhances Al uptake and toxicity, even in plants normally restricted to acidic soils (e.g. *Deschampsia flexuosa*). The results of Rorison⁴³, whilst not providing an incontrovertible explanation for the differences in plant distribution between acidic and calcareous soils, suggests that the relative roles of metal toxicity, N source and pH buffering in this problem need to be reassessed. A preliminary report of NH_4^+ and NO_3^- fertilizer additions to crops growing in acidic soils, and the subsequent effect of N uptake on soil pH illustrates some of the implications for agriculture²². Investigations into this problem that choose to ignore interactions, could lead to erroneous conclusions.

Manganese

Manganese is potentially as toxic as either aluminium or ammonium nitrogen, in acid media. But although it may be present in acidic soils in amounts that in laboratory cultures inhibit growth³⁰ it has not proved to be a major factor in the exclusion from acidic soils of plants of known sensitivity. Symptoms of manganese toxicity are rarely seen in the field for two main reasons. Firstly, Ca^{2+} , Fe^{3+} , Al^{3+} and Si^{32} and NH_4^+ ⁵² have all been shown to have an ameliorating effect on Mn as a possible toxin. Secondly, plants such as *Deschampsia flexuosa* tolerate high Mn concentrations in soil³⁴ or solution culture²⁷, whilst others, characteristic of less acidic conditions, do not³¹. Moreover, requirements for Mn are considered to be higher in plants from acidic soils than in those from calcareous soils⁸.

Under anaerobic conditions manganese may occur in the reduced state Mn^{2+} but again ameliorating effects of other elements appear to keep the potential toxicity in check.

Iron

In well-aerated soils of pH less than c. 3.5, ferric iron is likely to be toxic to many plants; above pH 3.5 its solubility is very low and toxicity unlikely⁴². In the reduced state Fe^{2+} it is soluble at pHs up to 6.0 and species tolerant of acidic conditions share with plants of marshland and other waterlogged habitats a resistance to iron toxicity. Recent work by Hendry and Brocklebank¹⁵ has shown that the mechanism of this tolerance is associated with the control of the activity of the enzyme, superoxide dismutase (SOD). So far three types of plant responses have been recorded: an iron exclusion response: induction of a complete enzyme defence system against Fe^{2+}

mediated oxygen radical formation; induction of an incomplete enzyme defence leading to radical attack and cellular damage.

Thus we are reminded that impeded aeration, however temporary, has an effect on the reduction-oxidation state of several key chemical elements which can also affect their influence on plant growth in acidic conditions. The extensive literature on acid sulphate soils becomes relevant at this point⁷.

Biotic effects

We have noted that linked with chemical features of the soil are several chemical reactions resulting from plant metabolism, such as the efflux of ions from roots. There are three other 'systems' which have a bearing on the plant's response to acidic conditions and may well reduce toxicities:

- 1) mucilage production
- 2) mycorrhizal associations
- 3) symbiotic N fixation (nodulation)

Mucilage

It has been reported¹⁸ that penetration into root meristems can be restricted by mucilage secreted in the apical root zones. It is suggested that there may be genotypic differences in the rate of secretion in response to exposure to aluminium, i.e. an exclusion mechanism similar to the one postulated by Rorison⁴² in which it was suggested that when internal or external metal concentrations reach critical levels, the synthesis of complexing agents (possibly pectates, cell wall proteins or organic acids) is induced. As yet there is only circumstantial evidence to support the hypothesis²⁶.

Mycorrhizae

Although the occurrence of mycorrhizal associations between fungi and vascular plants is widespread the consequences of the occurrence are much less well documented. Mycorrhizal associations are known to be beneficial to plant growth in infertile soils, particularly in the transfer of ions (such as phosphate) which diffuse slowly through the soil. However, both the fungal and higher plant components of the association may be susceptible to toxicities in the soil⁵⁰ and should be considered separately in order to understand fully the mechanisms of tolerance to acidic conditions. There are a number of other reasons why mycorrhizal associations may be ineffective in the field⁹ and these should also be borne in mind.

The types of mycorrhizal association which have been shown to be effective in the field include those formed with ericaceous plants growing in acidic or humus soils³⁶. Read and coworkers have demonstrated that resistance to metal toxins is provided by ericoid mycorrhizal infection and estimate that the fungus is an order of magnitude more tolerant than the host alone. They invoke the idea of metal binding by carboxylic acids of the matrix at a critical position in the host fungus interface. Such mechanisms have been predicted to operate also in plant roots^{40,44} and in lichen thalli⁵¹, but require experimental verification. There is still much that is not known about possible interactions between host, fungus and acidic environments.

Nodulation

Both leguminous and non-leguminous plants can benefit

from nitrogen fixed by associated rhizobia. This would be a considerable nutritional advantage in acidic soils if only most legumes were not susceptible to a number of soil acidity factors. The most frequently cited is aluminium^{40,17} which can be toxic at several stages in the association between rhizobium and legume¹.

Toxic effects of aluminium can also be increased because fixation of N 'within' the legume may cause an imbalance in the uptake of anions and cations leading to a net efflux of H⁺ ions into its rhizosphere. It has been calculated on the basis of cumulative efflux²³ that for each tonne of dry shoots produced by, respectively, lucerne, red clover and white clover, the equivalent of 80, 79 and 96 kg of lime (CaCO₃) would be required to neutralize the acidity produced at the root surface. Such localized increase in acidity could lead to increased solubility of aluminium and greater toxicity^{21,23}. However, some naturally occurring legumes, particularly species of *Ulex* and *Sarothamnus*, are well known as acidifiers of soils while being tolerant of acidic conditions themselves¹³. Among non-leguminous plants are some which grow and effectively fix nitrogen at very low pHs. Toelstra et. al.⁴⁹ showed a net efflux of H⁺ ions during N-fixation by *Alnus glutinosa*, amounting to 0.5 meq H⁺ n. mol⁻¹ N_{org} and normal growth recorded down to a pH of c. 2.8⁴⁹ (see fig. 1).

It is important to remember that there are not only inter- and intraspecific differences in the rate of acidification but that these differences will vary with the ontogeny of the plant also.

Plant adaptation to acidic conditions

Evidence from native species in the natural environment indicates a wide range of tolerance of metal toxicity and of nutrient deficiency. The plants most capable of surviving tend to be those with inherently slow rates of growth and low nutrient requirement⁵.

It has been suggested, on limited evidence, that such species are not more efficient in resource capture than faster-growing species but more careful husbanders of those resources⁵.

Certainly, there is extensive evidence that slow-growing plants from acidic environments have low nutrient optima⁵. However, detailed studies of root morphology have shown that slow-growing plants such as *Deschampsia flexuosa* can maintain a stable root-shoot quotient much better under infertile conditions than potentially faster-growing plants such as *Lolium perenne*^{37,38}. This is the result of a more efficient utilization and redistribution of dry matter in the form of finer roots and more root hairs. Other contributing factors are greater longevity of leaves and roots⁵, often combined with continuing growth during colder periods of the year⁴⁵. In this way slow-growing acid-tolerant species can out-produce less tolerant and potentially faster-growing species on acidic soils over the annual cycle.

Selection of genotypes of crop plants for tolerance to acidic conditions is well advanced and much valuable data are presented in the published records of two symposia which took place in 1976^{24,55}. It is encouraging to know that tolerance can be found among individuals of normal populations and there is a wealth of material among native plants still to be tapped⁵⁶.

While selection for tolerance is a relatively straightforward operation, the elucidation of physiological and genetical involvement is more difficult. Problems of relating laboratory findings to field conditions remain. The benefits of experimental controls have to be seen in the light of natural complexity and this is well illustrated, for example, in a consideration of the composition of nutrient media^{2,28}.

Endpiece

In the cool temperate climate of Britain leaching and soil acidification have occurred over millenia. However, there has been a tendency even in the soils with least neutralizing power such as the Lake District's⁴ for effects of both natural or agriculturally-induced acidification (as indicated by the pollen in tarn sediment) to have levelled out. As Pennington³³ reported: 'Our present state of knowledge of terrestrial vegetation suggests that a combination of acidifying processes had by c. 1800 AD produced a situation in the uplands of Cumbria where no further threshold of change was crossed as a result of burning fossil fuels.' Thus it is important to weigh carefully the effect on soil reaction that acid deposition might have in any one soil environment. Its effect must be considered alongside that of the hydrogen ions which are effluxed by plants and in the light of the already considerable concentration of hydrogen ions in acid soils.

Quantitative estimates are needed in order to gauge present and possible future effects on the survival and composition of both natural and introduced vegetation.

- Alexander, M., Effects of acidity on microorganisms and microbial processes in soil, in: Effects of Acid Precipitation on Terrestrial Ecosystems, pp. 363-374. Eds T. C. Hutchinson and M. Havas. Plenum Publishing Corporation, New York 1980.
- Asher, C. J., and Edwards, D. G., Modern solution culture techniques, in: Inorganic Plant Nutrition; Encyclopedia of Plant Physiology, New Series, vol. 15A, pp. 94-119. Eds A. Lauchli and R. R. Bielecki. Springer-Verlag, Berlin 1983.
- Bache, B. W., Soil acidification and aluminium mobility. *Soil use and Management 1* (1985) 10-14.
- Catt, J. A., Natural soil acidity. *Soil Use and Management 1* (1985) 8-10.
- Chapin, F. S., The mineral nutrition of wild plants. *A. Rev. Ecol. Systemat. 11* (1980) 233-260.
- Chapin, F. S., Patterns of nutrient absorption and use by plants from natural and man modified environments, in: Disturbance and Ecosystems, pp. 175-187. Eds H. A. Mooney and M. Godron. Springer-Verlag, Berlin 1983.
- Dost, H. (Ed.), Acid Sulphate Soil. Proceedings International Symposium on Acid Sulphate Soils, Wageningen 1972. International Institute of Land Reclamation and Improvement Wageningen 1973.
- Ernst, W., and Nelissen, H. J. M., Growth and mineral nutrition of plant species from clearings on different horizons of an iron-humus podzol profile. *Oecologia 41* (1979) 175-182.
- Fitter, A. H., Functioning of vesicular-arbuscular mycorrhizas under field conditions. *New Phytol. 99* (1985) 257-265.
- Foy, C., Chaney, R. C., and White, M. C., The physiology of metal toxicity in plants. *A. Rev. Pl. Physiol. 29* (1978) 511-566.
- Foy, C., and Fleming, A. L., The physiology of plant tolerance to excess available aluminium and manganese in acid soils, in: Crop Tolerance to Suboptimal Land Conditions, pp. 301-328. Ed. G. A. Jung. American Society of Agronomy, Madison 1978.
- Gigon, A., and Rorison, I. H., The response of some ecologically distinct plant species to nitrate- and ammonium-nitrogen. *J. Ecol. 60* (1972) 93-102.

- 13 Grubb, P. J., Green, H. E., and Merrifield, R. J. C., The ecology of chalk heath: its relevance to the calcicole-calcifuge and soil acidification problem. *J. Ecol.* 57 (1969) 175–212.
- 14 Havill, D. C., Lee, J. A., and Stewart, G. R., Nitrate utilisation by species from acidic and calcareous soils. *New Phytol.* 73 (1974) 1221–1231.
- 15 Hendry, G. A. F., and Brocklebank, K. J., Iron-induced oxygen radical metabolism in waterlogged plants. *New Phytol.* 101 (1985) 199–206.
- 16 Hewitt, E. J., A biological approach to the problems of soil acidity. *Trans. int. Soc. Soil Sci. Joint Meet. Dublin 1* (1952) 107.
- 17 Helyar, K. R., Effects of aluminium and manganese toxicities on legume growth, in: *Mineral Nutrition of Legumes in Tropical and Subtropical Soils*, pp. 207–231. Eds C. S. Andrew and E. J. Kamprath. CSIRO, Melbourne, Australia 1978.
- 18 Horst, W. I., Wagner, A., and Marschner, H., Mucilage protects root meristems from aluminium injury. *Z. Pfl. Physiol.* 105 (1982) 435–444.
- 19 Hunt, R., and Parsons, I. T., A computer program for deriving growth-functions in plant growth-analysis. *J. appl. Ecol.* 11 (1974) 297–307.
- 20 Islam, A. K. M. S., Edwards, D. G., and Asher, C. J., pH optima for crop growth. Results of a flowing solution culture experiment with six species. *Pl. Soil* 54 (1980) 339–357.
- 21 Israel, D. W., and Jackson, W. A., The influence of nitrogen nutrition on ion uptake and translocation by leguminous plants, in: *Mineral Nutrition of Legumes in Tropical and Subtropical soils*, pp. 113–129. Eds C. S. Andrew and E. J. Kamprath. CSIRO 1978.
- 22 Jarvis, S. C., Plant factors affecting acidity. 1982 Annual Report of the Grassland Research Institute, Hurley (1983) 22–23.
- 23 Jarvis, S. C., and Hatch, D. J., Rates of hydrogen efflux by nodulated legumes grown in flowing culture solution with continuous pH monitoring and adjustment. *Ann. Bot.* 55 (1985) 41–51.
- 24 Jung, G. A. (Ed.), *Crop Tolerance to Suboptimal Land Conditions*. ASA Special Publication Number 32. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Wisconsin 1978.
- 25 Jefferies, R. L., and Willis, A. J., Studies on the calcicole-calcifuge habit. II. The influence of calcium on the growth and establishment of four species in soil and sand cultures. *J. Ecol.* 52 (1964) 691–707.
- 26 Kinzel, H., Influence of limestone, silicates and soil pH on vegetation, in: *Physiological Plant Ecology*. III. Responses to the Chemical and Biological Environment. *Encyclopedia of Plant Physiology*, New Series, vol. 12C, pp. 201–244. Eds O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler. Springer-Verlag, Berlin 1983.
- 27 Mahmoud, A., and Grime, J. P., A comparison of the susceptibility of *Arrhenatherum elatius* (L.) Beauv. ex J. C. Presl, *Agrostis tenuis* Sibth., *Deschampsia flexuosa* and *Festuca ovina* L. to manganese toxicity. *Pl. Soil* 47 (1977) 559–565.
- 28 McCain, S., and Davies, M. S., The influence of background solution on root response to aluminium in *Holcus lanatus* L. *Pl. Soil* 73 (1983) 425–430.
- 29 McGrath, S. P., Growth and distribution of *Holcus lanatus* L. populations with reference to nitrogen source and aluminium. Ph.D. Thesis. University of Sheffield 1979.
- 30 Nazrul, A. K. M. I., Comparative ecology of plants in relation to soil moisture and mineral nutrition. Ph.D. Thesis, University of Sheffield (1976).
- 31 Nazrul-Islam, A. K. M., and Rorison, I. H., Effects of calcium and manganese concentrations varied separately on the growth and chemical composition of *Rumex acetosa*, *Molinia caerulea* and *Eriophorum angustifolium*. *Z. Pfl. Physiol.* 104 (1981) 467–474.
- 32 Peaslee, D. E., and Frink, C. R., Influence of silicic acid on uptake of Mn, Zn and Cu by tomatoes (*Lycopersicon esculentum*), grown on an acid soil. *Proc. Soil Sci. Soc. Am* 33 (1969) 569–571.
- 33 Pennington, W., Long-term natural acidification of upland sites in Cumbria: evidence from post-glacial lake sediments. 52th Annual Report of the Freshwater Biological Association, pp. 28–46. Freshwater Biological Association, Ambleside 1984.
- 34 Pigott, C. D., Soil formation on carboniferous limestone of Derbyshire. Relationship of soil to vegetation near Coombs Dale. *J. Ecol.* 58 (1970) 529–541.
- 35 Raven, J. A., and Smith, F. A., Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. *New Phytol.* 76 (1976) 415–431.
- 36 Read, D. J., The biology of mycorrhiza in the Ericales. *Can. J. Bot.* 61 (1983) 985–1004.
- 37 Robinson, D., and Rorison, I. H., A comparison of the responses of *Lolium perenne* L., *Holcus lanatus* L. and *Deschampsia flexuosa* (L.), Trin to a localized supply of nitrogen. *New Phytol.* 94 (1983) 263–273.
- 38 Robinson, D., and Rorison, I. H., A quantitative analysis of the relationships between root distribution and nitrogen uptake from soil by two grass species. *J. Soil Sci.* 36 (1985) 71–85.
- 39 Robson, A. D., and Pitman, M. G., Interactions between nutrients in higher plants, in: *Inorganic Plant Nutrition*. *Encyclopedia of Plant Physiology*, New Series, vol. 15A, pp. 147–180. Eds A. Läuchli and R. L. Bielecki. Springer-Verlag, Berlin 1983.
- 40 Rorison, I. H., The effect of aluminium on legume nutrition, in: *Nutrition of the Legumes*, pp. 43–62. Ed. E. G. Hallsworth. Butterworths Scientific Publications, London 1958.
- 41 Rorison, I. H., The effect of extreme soil acidity of the nutrient uptake and physiology of plants, in: *Acid Sulphate Soil*. Proceedings International Symposium on acid sulphate soils, Wageningen 1972, pp. 223–253. Ed. H. Dost. International Institute of Land Reclamation and Improvement, Wageningen 1973.
- 42 Rorison, I. H., The effects of soil acidity on nutrient availability and plant response, in: *Effects of Acid Precipitation on Terrestrial Ecosystem*, pp. 283–304. Eds T. C. Hutchinson and M. Havas. Plenum Publishing Corporation, New York 1980.
- 43 Rorison, I. H., Nitrogen source and tolerance of *Deschampsia flexuosa*, *Holcus lanatus* and *Bromus erectus* to aluminium during seedling growth. *J. Ecol.* 73 (1985) 83–90.
- 44 Rorison, I. H., and Robinson, D., Calcium as an environmental variable. *Plant, Cell Envir.* 7 (1984) 381–390.
- 45 Rorison, I. H., Peterkin, J. H., and Clarkson, D. T., Nitrogen source, temperature and plant growth, in: *Nitrogen as an Ecological Factor*. Symposia of the British Ecological Society 22, pp. 189–209. Eds J. A. Lee, S. McNeill and I. H. Rorison. Blackwell Scientific Publications, Oxford 1983.
- 46 Rovira, A. D., Bowen, G. D., and Foster, R. C. The significance of rhizosphere microflora and mycorrhizas in plant nutrition, in: *Inorganic Plant Nutrition*. *Encyclopedia of Plant Physiology*, New Series, vol. 15A, pp. 61–93. Eds A. Läuchli and R. L. Bielecki. Springer-Verlag, Berlin 1983.
- 47 Runge, M., Physiology and ecology of nitrogen nutrition, in: *Physiological Plant Ecology III*. Responses to the Chemical and Biological Environment. *Encyclopedia of Plant Physiology*, New Series, vol. 12C, pp. 163–200. Eds O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler. Springer-Verlag, Berlin 1983.
- 48 Sollins, P., Grier, G. C., McCorison, F. M., Cromack, J. Jr, Fogel, R., and Frederiksen, R. L., The internal element cycles of an old-growth Douglas-fir ecosystem in Western Oregon. *Ecol. Monogr.* 50 (1980) 261–285.
- 49 Troelstra, S. R., van Dijk, K., and Blacquièrre, T., Effects of N source on proton excretion, ionic balance and growth of *Alnus glutinosa* (L.) Gaertner: comparison of N₂ fixation with single and mixed source of NO₃ and NH₄. *Pl. Soil* 84 (1985) 361–385.
- 50 Trapp, J. M., Stahly, E. A., Benson, N. R., and Duff, D. M., Mycorrhizal deficiency of apple trees in high arsenic soils. *Hortic. Sci.* 8 (1973) 52–53.
- 51 Tuominen, Y., Studies on strontium uptake of the *Cladonia alpestris* thallus. *Ann. Bot. Fenn.* 6 (1967) 1–28.
- 52 Vlamis, J., and Williams, D. E., Manganese and silicon interaction in the Gramineae. *Pl. Soil* 27 (1967) 131–140.
- 53 Wallace, A., Frolich, E., and Lunt, A. R., Calcium requirements of higher plants. *Nature* 209 (1966) 634.
- 54 Woolhouse, H. W., Toxicity and tolerance in the responses of plants to metals, in: *Physiological Plant Ecology*. III. Responses to the Chemical and Biological Environment. *Encyclopedia of Plant Physiology*, New Series, vol. 12C, pp. 245–300. Eds O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler. Springer-Verlag, Berlin 1983.
- 55 Wright, J. J. (Ed.), *Plant Adaptation to Mineral Stress in Problem Soils*. A Special Publication of Cornell University Agricultural Experiment Station. Cornell University, Ithaca, New York 1977.
- 56 Wu, L., and Bradshaw, A. D., Aerial pollution and the rapid evolution of copper tolerance. *Nature* 238 (1972) 167.