Effect of soil acidity on trees and plants as expressed by the (Ca+Mg+K)/Al ratio

Harald Sverdrup and Per Warfvinge
Department of Chemical Engineering II, Lund Institute of Technology
Box 124, University Chemical Center, S-221 00, Lund, Sweden .

2nd revised edition

Effect of soil acidity on growth of trees and plants as expressed by the (Ca+Mg+K)/Al ratio

.

Exccecutive summary

This text lists values for BC/Al limits for different trees and wild plants and crop plants in Europe and East Asia, to be used in the calculation of critical loads of acidity for terrestrial ecosystems.

Scientific summary

The quantitative tolerance to Al in acid soils as expressed by root growth in culture or field stem growth as a function of soil solution (Ca+Mg+K)/Al molar ratio has been determined for different plant species. Different BC/Al limts for different coniferous trees such as spruce, fir, pine, larch and pacific conifers, different temperate deciduous tree species such as beech, birch, maple, oak, aspen, alder and willow, different tropical and subtropical trees and bushes such as teak, orange, peach, cotton, eucalyptus, guapira, tea and coffee, as well as many different types of wild and cultivated grasses, herbs and legumes. The tolerance was determined using data from laboratory bioassays. Data on growth and soil chemistry from field research sites was combined to yield estimates of the response of growth to soil solution aluminium under field conditions.

The tolerance can be modeled for all plants investigated by using one of three different ion exchange models, expressed in terms of the soil solution (Ca+Mg+K)/Al molar ratio. Different parameters have been tried, individually and in combinations suggested by the theoretical analysis. The study was focused on several diagnostic soil chemistry parameters;

- pH

- Al-concentration,

- Ca/Al, (Ca+Mg)/Al, (Ca+Mg+K)/Al

- (Ca+Mg+K)/(Al+H), (Ca+Mg+K)/(Al+2H), (Ca+Mg+K)/(Al+3H)

In the combined expressions, K was added on an equivalent basis, implying that K was given one half of the antagonistic power of Ca and Mg towards Al and H. The most consistent correlations to growth effect parameters is obtained using (Ca+Mg+K)/Al or(Ca+Mg+K)/(Al+3H). The results strongly suggests that the ratio reflects the relationship between ions desireable to the plant versus those that are undesired. For practical uses such as critical loads BC/Al-ratio appear as the most practical, and the parameter best supported by laboratory data.

The results suggests that trees and ground vegetation react to Al according to patterns that can be interpreted as root uptake of nutrients proportional

to root surface conentrations, where the surface concentrations of base cations and Al are controlled by three distinct ion exchange mechanisms. The results may reflect basic differences in how the different plants actually take up nutrients from the soil solution. The laboratory $(Ca+Mg+K)/Al$ ratio is relevant for field conditions when applied to the uniform conditions in each soil layer, as can be shown for German data. The net effect on the plant will be the effect of the BC/Al damage function integrated over all soil layers penetrated by the plant root. For calculations of critical loads of acid deposition to forest ecosystems, a general value of $(Ca+Mg+K)/Al \geq 1.0$ seems well chosen for European and North American forests.

The theoretical evaluation of the results have lead to kinetic expressions for base cation uptake by plants according to a type of modified Michaelis-Menten kinetics, where the saturation coefficient is influenced by soil acidity parameters. Differences in response to soil acidity such as the unspecific response (spruce and firs, grasses) and the Vanselow response (pine, and deciduous trees and certain domesticated plants), is parallelled by basic differences in the uptake kinetics for base cations in these plants.

Contents

1 Preface

This work was initiated as a part of critical loads work in Sweden, Europe and East Asia. During the work with critical loads in Europe, a critical limit BC/Al=1 was suggested used in the calculations by Dr. Wim de Vries and collaborators at the Winand Staring Centre in Wageningen, Netherlands. The value was based on an earlier idea by Dr. Berhard Ulrich at the University of Göttingen. The limit was applied in the calculation of critical loads for the Netherlands, and incorporated in the European procedure without being challenged. In the Swedish critical loads project, it was felt that it was necessary to review the experimental foundation for the use of the BC/Al-limit and address what a proper value might be.

This report is very much the work of other persons than the authors. This work contains a synthesis of the results of many that have toiled in laboratories and greenhouses for a long time, laboriously determining the individual response to Al of many, many trees and plants. Without all the colleagues that worked hard for many years, we would have had nothing to make a synthesis on. We are grateful for their efforts, and appreciate the great care generally taken to ensure accurate and reliable results.

The idea of relating the growth response of trees in particular to acidification by using the (Ca+Mg+Al)/Al ratio, in daily speech known as the "calcium-aluminium ratio", must be credited to Professor Emeritus Dr. Bernhard Ulrich of the University of Göttingen in Germany. Even if it could be admitted that others had a similar idea far earlier, it was still him that turned it into a widespread tool for relating soil chemistry to the biology of trees. Later, the concept was recycled by Dutch scientists into the critical loads mapping work. Ultimately, this has become the tool upon which a large part of the efforts to reduce emissions of sulphur and nitrogen are based.

What Prof. Ulrich realized like many others, is that plants are significantly affected by the surrounding chemical environment. In afterthought it is evident to most ecologists that this must be so, growth of individual plants and vegetation species composition depend on factors such as feedbacks between plants and the chemical and physical environment in the soil.

In the period 1920-present, the nitrogen deposition has increased four-fold over allmost all of Europe due to inceasing emissions from automobiles, agriculture and industry. At the same time forestry practices also improved significantly, resulting in the best growth ever seen in the forests of Europe. The improved management practices has succeeded in better utilisation of available N in the soil for growth. This has not been without economic profit, and it could be regarded as an unplesant revellation if the increasing growth was something that can not be sustained in the future. Acidification of soils caused by deposition of ammonium, nitric and sulfuric acid, is at present promoting

forest growth in many areas, more N promotes growth, soil acidification makes base cations in the soil ion exchange complex available in the soil solution. The final result may be nutrient deficiencies and severe forest reductions in growth potential. Despite a history of better and bigger growths until present, acid deposition and forest damage due to acid soils does indeed exist, and it must be taken seriously by the forest industry and forest research.

At the present time, the general feeling in environmental management policymaking is that traditional forest research has failed to provide a mechanistic link between soil acidity parameters and forest vitality. First of all, vitality as a parameter is unsatisfactorily defined, and therefore vitality cannot be measured more than semi-quantitatively. Parameters like optimal growth in the absense of pollutants and soil acidity, needle loss, crown density cannot be measured with any accuracy. The noise in the signal measured is most often larger than the signal sought for, hence nothing can be seen even if the signal was there. The tool for field observation are not adequate for the problem. Secondly, the use of integrated biological and chemical models for interpreting the available data around the problem has been sparse, making data penetration superficial. Simple linear regressions or stepwise multiple regressions simply do not suffice to discover mechanistical relationships in non-linear systems.

Numerous pieces of a large puzzle lie before us, small independent pieces of research:

- acid deposition causes acidification of the soil

- acidification of the soil result in high soil solution Al concentrations

- high soil solution Al concentrations do harm growth of seedlings of individual plant species in the laboratory

- all plants examined in laboratory experiments show sensitivity towards Al at some level

- root damage on trees in laboratory experiments result in growth rate changes

- needle loss in the field can be connected to growth rate change for individual trees

- decreased needle mass in the field imply decreased growth of that stand

- trees in the field show increased needle losses in areas receiving high acid deposition

The scope of this study was to try to link some of the pieces, in order to put together a part of this puzzle, where many pieces are available.

2 Preface to the second edition

When this book appeared for the first time in 1993, the whole edition was gone within two months. The report has been strongly critisized as well as highly praised and it has initiated at least two reviews we know of (Favourable; Cronan and Grigal 1995; Critical; Eldhuset and Nygaard, 1995). Our goal has been that of providing support for using limits to set levels of no effect, rather than adressing level of effect, something not always realized by our critics.

In the review of several European acidification research programmes, it has concluded during review discussions that forest research has failed to provide a conclusive link between soil acidification and forest decline parameters. And it must be concluded that it is indeed pretty obvious that trees cannot tolerate just any level of Al concentration in the soil solution or any BC/Al ratio below those indicated by laboratory experiments. The definite link has not be convincinly established, however, nor has tree vitality under field conditions been successfully defined in a unique way that allows it to be measured with any accuracy worth while. It is obvious that most researchers do think links exists, but the links have not been found yet, probably because of inadequate methodology. Laymen and owners of small forest properties have little doubt that links exist, and in qualitative terms, they appear to have some understanding of it.

Nobody likes to be told that they have failed, and forest researchers are no exception (It does not matter much that the excuses for no success so far, might be fully valid and acceptable). Worried forest owners wants answers to their questions, and not explanations why they cannot get an answer "just now". The issues of soil acidity, aluminium and BC/Al ratios have thus become by convenience "controversial", and later confirmative results of a link will be viewed extra critically by those who felt they were pointed out as having "failed" at the earlier attempt.

Maybe it has been premature to conclude that forest researchers failed to establish the link. Maybe they did, but did not see this because of lack of adequate methodology and evaluation tools. Many times we could indeed find good correlations between labvoratory data and effects by screening the data differently and more critically, than the original authors and by using non-linear mathematical expressions. Fundamental was that the same theory is consistently applied to all available experiments.

This report has caused the initiation of several Swedish field studies that either have the objective to search for connections between soil acidity parameters (pH, Al, BC/Al-ratio) and tree vitality (growth, yellowing, needle loss, crown thinning, sap bleeding). Maybe they will lead to useful response expressions for field conditions, or to new explanations why such expressions can be different for field conditions, or whether additional or other parameters

should be used for field conditions. Hopefully the poor state of measuring tree vitality can be significantly improved in the future, maybe through remote sensing technologies.

We are greatful to all those that helped us update the second edition, and we hope it has lost some of its faults. We have proof-read it to correct several spelling and typographical errors. Plant ecologist Gudrun Berlin of the Department of Plant Ecology at Lund University helped us revise all latin names and translate all into consistent English names, as well as update any latin name redundancies and latin name mispellings.

Our critical load mapping colleague for Europe, Dr. Wim de Vries at the Winand Staring Centre, Wageningen, Netherlands, contributed several useful comments and thoughts, and inspired many ideas.

Prof. Dr. Dianwu Zhao of the Eco-Environmental Institute at the Chinese Academy of Sciences, Beijing, China, added a large amount of new data based on Chinese experiments, not otherwise available to us for linguistic reasons.

The main purpose of the book was always to be useful, and to be used as a handbook to the sensitivity-numbers for different plants, helping those mapping ecosystem sensitivity to soil acidification.

3 Introduction

3.1 Acidification and forest damage

Observation of forest damage such as defoliation, discoloration, growth decrease and tree dieback has been recorded in European forests during the 1980's and 1990's. Currently, annual or periodic regional surveys of forests health are conducted and the geographical extent of forest damage is mapped (For Germany and the United States see the review by by Krahl-Urban 1988; for Norway the survey of by Solberg 1991; A European overview is given by Moseholm 1988; a survey of Sweden is presented by Wijk et al., 1991; some remarks on the Canadian situation is mentioned by Tomlinson et al. 1985; for an early warning in Germany see the work by Ulrich 1983). The acidification of the soil has been linked with acidic deposition, and changes in soil chemistry over time has been observed (Ulrich 1983; Chen et al. 1973; Tamm and Hallbäcken, 1985; Johnston et al., 1986; Falkengren-Grerup, 1987; Falkengren-Grerup et al. 1990; Warfvinge et al. 1993). Soil acidification releases Al into the soil solution, something that was linked with forest damage, and which is the subject of this text.

Many factors influence growth and health status of trees in a forest (Fig. 1). Most of the factors are related to the trees access to energy and nutrients, they act as promotors when abundant, and retarders when in short supply. A few of them are retarders only. Together these factors determine growth. In a forest stand, competition between trees and with other vegetation for resources and energy also become important.

Some of these factors may vary with time, but have fairly constant average values in the long term. Typical of such factors are temperature, water and light. Over very long times, factors like patogens, insects and disasters like forest fires also will tend to even out. The variation between years may be very large but the average over decades or centuries vary very little, if any. This is significant since the generation time for a tree is normally close to a century and several generaltions is easily half a millennia. This puts great emphasis on the long term perspective. Others many vary significantly on an annual basis as well as they may have appeared or disappeared within a shorter timeframe. Examples of such factor are air pollution and soil acidification. The focus of this study is the part played by soil acidification, mainly as induced by acid deposition.

3.2 The critical load

The critical load was defined at the Skokloster 1988 Critical Load Workshop as: **"The maximum input of acidic deposition to an ecosystem which will not cause long term damage to ecosystem structure and function"**,
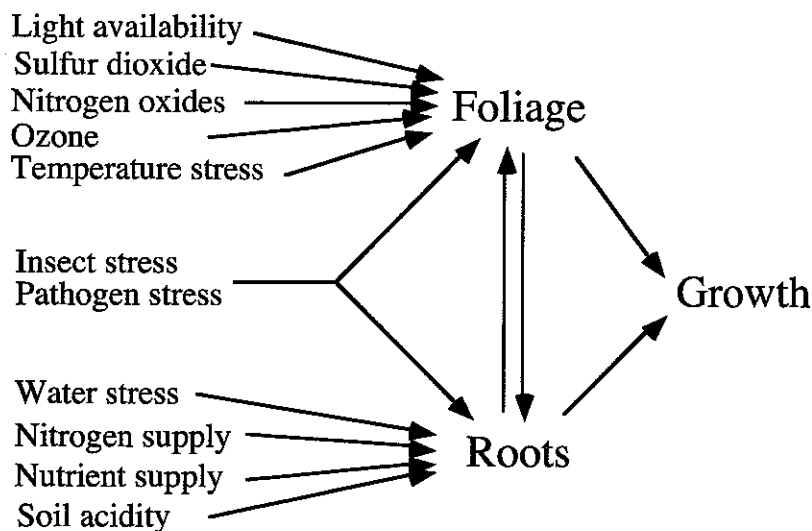
Figure 1: Many factors influence growth and health status of trees in a forest. Some influence the root, others above-ground plant parts. Some of the factors are part of nature, others are related to the interactions of landuse and pollution with the ecosystem.

The *critical load*, is being calculated for European forest ecosystems (Nilsson and Grennfelt, 1988, Sverdrup and Warfvinge 1988; Sverdrup, de Vries and Henriksen, 1990; Hettelingh et al., 1991) as well as for ecosystems in general in Eastern Asia, and in particular China (Kuylenstierna et al., 1993; Hettelingh et al., 1993). Mapping of Critical Loads in Europe and Asia rests upon the ability to be able to define at which stage acidification of soils will affect trees, tree growth and forest ecosystems, ground vegetation by changing competition in the ground flora and affecting the growth of crop plants. The mapping exersize in Asia encompasses very different ecosystems such as taiga, temperate forests, boreal deciduos forests, mediterranian woodlands, steppe, savannah, deserts, alpine landscapes, tundra, tropical forests, mangrove swamps and rain forests. This puts a large demand on the ability to specify the chemical limits to soil acidity for a very wide variety of plants and trees.

The demand for a certain reduction in deposition is linked to the elements in the calculation of the critical load. The calculation of the critical load is composed of a series of elements:

1. Assessment for an ecosystem type

2. Selection of an indicator plant specie for the ecosystem

3. Critical chemical limit for the indicator plant

4. Calculation of the critical load of acidity

5. Reduction required in present acidic deposition

Since each element in the procedure depends on the preceeding element, a change in indicator species or chemical limit will automatically change the required reduction. Postulating a smaller required reduction is equivalent to postulation a higher tolerance of the plant to acid deposition. Claiming trees used as indicator species to be tolerant to Al is equivalent to demanding less reduction in the present acid deposition.

3.3 The critical limit

The calculations of critical loads involve a series of steps where for each ecosystem type, an indicator plant or indicator animal species is selected (Fig. 3. Chemical limits in terms of chemical conditions must be given for the indicator species used. Calculation of critical loads for forest ecosystems, use trees as indicator species. European and Asian critical load calculations use the soil solution ratio between $(Ca+Mg+K)$ and Al in the soil as the critical parameter, assuming that a limit of $(Ca+Mg+K)/Al \geq 1.0$ will protect the forest ecosystem from damage. This value was first suggested by Ulrich (1983) and was first suggested used as the critical limit for critical loads by Schulze et al., (1987) and confirmed by the Skokloster Workshop on critical loads in 1988. Both Ulrich and Schulze et al. published only limited amounts of data to support their conclusion. Ulrich's initial proposal was mainly supported by field observations and the work of Rost-Siebert (1987). Our study is mainly a response to the 1988 Skokloster decision to use BC/Al=1. The limiting value has primarily been derived from data in the literature, where it was observed that high Al concentrations in the soil solution affect plant uptake of base cations, N and P or growth of seedlings (Asp and Berggren, 1990; Cronan et al., 1990; Huetterman and Ulrich, 1984; Ingestad et al., 1984; Schulze, 1987; Sverdrup et al., 1990; Tomlinson II, 1983; Ulrich, 1984, 1985; Ulrich and Matzner, 1983; Ulrich et al., 1984). A large amount of literature can be found on the subject, and a comprehensive list will be given in the data section.

One of the major problems in applying the $(Ca+Mg+K)/Al$-ratio to critical load calculations and estimates of soil acidification impacts on field tree growth, has been the interpretation of laboratory bioassay results in relation to field conditions. Laboratory bioassay conditions may differ significantly from field conditions, in the field a large number of confounding factors

make actual measurement of simultaneous (Ca+Mg+K)/Al-ratio and growth change notoriously difficult. Critical loads in Europe have been mapped using (Ca+Mg+K)/Al=1.0 for all tree species (Sverdrup et al. 1990; Hettelingh et al., 1991). In Asia a variety of different values has been used, selected after ecosytem type and indicator plants with limiting values available. This study elaborates on the principles and preliminary results outlined in an earlier study by the Sverdrup et al., (1991). The conclusions reached in this study are based on much more data from a wider range of literature, and differ somewhat from earlier results.

It is important to realize that the limit is set from a no-effect perspective. Thus the limit is set at a value where it is possible to say that there is a low probability of having an adverse effect. Several researchers have drawn in doubt whether there will be an effect at the values we indicate, thus implying that the effect threshhold is lower. We therefore conclude that they strongly support our conclusion that at the Al-levels suggested by the BC/Al-limit, there will be low probability of adverse effects, and that the suggested BC/Al-limit for critical load calculations gives adequate protection from soil acidification.

3.4 SMB calculation formula

The equations are derived from a from a mass balance for acidity. This leads to the basic equation:

$$CL = ANC_W - ANC_L \tag{1}$$

where ANC_W =   Alkalinity production due to weathering   eq/ha yr
             CL   =   Critical load of acidity   eq/ha yr
             ANC_L =   ANC leaching   eq/ha yr

In this equation the limiting ANC leaching is determined by the maximum permitted leaching of H and Al, from a simplified expression of ANC:

$$ANC_L = -H_L^+ - Al_L^{3+} \tag{2}$$

where Al_L =   Al leaching   eq/ha yr
             H_L =   H$^+$ leaching   eq/ha yr

The limiting Al-flux in the equation is determined by the molar BC/Al-ratio applied. This leads to:

$$Al_L^{3+} = \frac{BC_L}{(BC/Al)_{crit}} \tag{3}$$

where BC_L =   Base cation leaching   eq/ha yr
             $(BC/Al)_{crit}$ =   BC/Al ratio used as limit

Stand site characteristics
Climate conditions
Water supply conditions

Yield
table
growth

Foliage

Growth
effect

Nitrogen supply
Base cation supply
Soil acidity

Roots

Growth
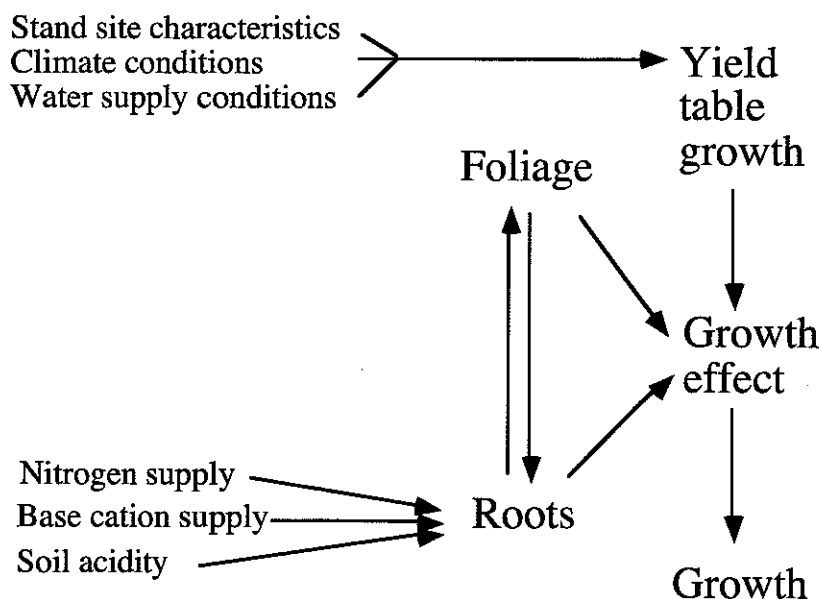
Figure 2: Basic approach to include soil acidity feedback on uptake used in calculations of critical loads in the PROFILE model. The response model used in PROFILE is based on the results presented in this report.

The base cation leaching is calculated from a mass balance:

$$BC_L = BC_{W(CaMgK)} + BC_D - BC_U \qquad (4)$$

where BC_D =   Base cation deposition   eq/ha yr
        $BC_{W(CaMgK)}$ =   Weathering rate of Ca+Mg+K   eq/ha yr
        BC_U =   Base cation uptake   eq/ha yr

In the mass balance equation for base cations, approximatelty 30% of released base cations from weathering are Na, providing no protection against Al for plants. The production of Ca, Mg and K from weathering is:

$$BC_{W(CaMgK)} = x_{BC} \cdot ANC_W \qquad (5)$$

where x_{BC} =   Fraction of weathering as Ca+Mg+K   0.7
        ANC_W =   Neutralization rate due to weathering   eq/ha yr

Before calculation can start, two conditions must be fulfilled. First some base cations will escape uptake due to plant physiological limitations (2 meq/m^3). This minimum leaching can however, not be larger than what is available from weathering and deposition:

$$BC_{min} = Q \cdot [BC]_{min} \tag{6}$$

Q is percolation, $[BC]$ is the limiting concentration for uptake, provided there is enough, if:

$$BC_{min} > x_{BC} \cdot ANC_W + BC_D \tag{7}$$

then:

$$BC_{min} = x_{BC} \cdot ANC_W + BC_D \tag{8}$$

The other condition is that uptake cannot be larger than what is available for uptake, if:

$$BC_U > x_{BC} \cdot ANC_W + BC_D - BC_{min} \tag{9}$$

then:

$$BC_U = x_{BC} \cdot ANC_W + BC_D - BC_{min} \tag{10}$$

This Al leaching can be written as:

$$Al_L^{3+} = 1.5 \cdot \frac{(x_{BC} \cdot ANC_W + BC_D - BC_U)}{(BC/Al)_{crit}} \tag{11}$$

Operationally the H^+ concentration can be calculated using the gibbsite equation:

$$[H^+] = (\frac{[Al]^{3+}}{K_{gibb}})^{1/3} \tag{12}$$

where K_{gibb} = Gibbsite coefficient   300 m^6/eq^2 (-pK(gibb)=8.5)

Accordingly, the limiting H^+-concentration corresponding to a certain Al concentration in the soil is calculated from the Al^{3+}-flux calculated above, dividing by the flow and the gibbsite coefficient:

$$[H^+]_{limit} = (\frac{Al_L^{3+}}{Q \cdot K_{gibb}})^{1/3} \tag{13}$$

By inserting the expression for the Al-limiting flux in the expression and multiplying with flow Q to get from H^+-concentration to flow, we get:

$$H_L^+ = (1.5 \cdot \frac{x_{BC} \cdot ANC_W + BC_D - BC_U}{(BC/Al)_{crit} \cdot Q \cdot K_{gibb}})^{1/3} \cdot Q \tag{14}$$

The modified SMB equation for Critical load of acidity in eq/ha yr thus becomes:

$$CL = ANC_W + (1.5 \cdot \frac{(x_{BC} \cdot ANC_W + BC_D - BC_U)}{(BC/Al)_{crit} \cdot K_{gibb}})^{1/3} \cdot Q^{2/3}$$

$$+ 1.5 \cdot (\frac{(x_{BC} \cdot ANC_W + BC_D - BC_U)}{(BC/Al)_{crit}}) \tag{15}$$

For many plants, the BC/H ratio may be significant, especially in soils with very high content of organic material or in soils where the rooting depth is very low. Then Al concentrations may be very low, and the H^+-ion concentration will be the determining factor. Due to the construction of the response mechanism, once a BC/Al limit has been established, then the same numerical value can be applied as the limiting BC/H limit.

The limiting H^+-flux is determined by the molar BC/H-ratio applied. This leads to:

$$H_L^+ = \frac{BC_L}{(BC/H)_{crit}} \qquad (16)$$

The base cation leaching is calculated from a mass balance:

$$BC_L = BC_{W(CaMgK)} + BC_D - BC_U \qquad (17)$$

Inorganic Al is generally close to zero in peaty soils and bogs. Filling in the equation:

$$CL = ANC_W + H_L^+ \qquad (18)$$

give the full expression for peat and bogs:

$$CL = ANC_W + \frac{0.5 \cdot (x_{BC} \cdot ANC_W + BC_D - BC_U)}{(BC/H)_{crit}} \qquad (19)$$

The factor 0.5 in Eq 24 and 1.5 in Eq. 15 derives from the conversion of critical loads and base cation concentrations in equivalents to molar ratio. The SMB equations are based on the following assumptions:

- The soil profile is assumed to be one stirred tank

    - The same gibbsite coefficient is assumed to apply through the soil profile
    - The weathering rate is evenly distributed over the soil profile
    - Uptake is evenly distributed over the soil profile

- The weathering rate is independent of chemical conditions

- The BC/Al ratio is assumed to have a value such that the value of ANC_L always is negative.

Most of these assumptions can be omitted by using integrated soil chemistry models. The most frequently used model in Europe for this purpose is the PROFILE model. It calculates the critical load over 4 soil layers in the regional version. There are several handbooks and guidance manuals available for calculating critical loads (The Mapping Manual, UN-ECE-1990; The Mapping Vademecum by Hettelingh and de Vries 1991, Mapping Critical Loads by Sverdrup, Henriksen and de Vries 1990 as well as several reports by de Vries and Sverdrup 1988-present)

4   Objectives

Quantitative connections between soil state parameters and forest health would be highly desirable, as they would permit quantitative assessments of potential damage to European forests under different acid deposition scenarios.

The objectives of this study is to quantify and document the link between soil acidification as expressed by soil solution Al-, Ca-, Mg-, K-, H-concentrations and the soil solution $(Ca+Mg+K)/Al$ molar ratio. The objective is to derive quantitative expressions for growth and mortality of trees and plants, based on soil chemistry. Specific values for different species need to be quantified, in order to allow for calculation of critical loads of acidity, considering that different tree and plant species may be used as indicators for different ecosystems. Secondly, similar damage functions for crown thinning and yellowing will be sought for. The relation between field observations of forest decline and results obtained in laboratory bioassays will be investigated for quantitative information.

5   Basic assumptions

It is assumed that laboratory experiments on tolerance of plants to soil Al and acidity measure tolerance properties of different plant species. It is assumed that these tolerance properties are applicable to the field situation, if the difference in conditions between field and laboratory can be accounted for. It is assumed that this difference can be accounted for with soil chemistry models.

Laboratory
bioassay
experiments

Literature data on
tolerance to soil
acidity

Vegetation
map

Synthesis
(BC/Al-ratios)

Ecosystem
class

BC/Al-ratios for
occurring plants

Ecosystem plant
inventory using
Asian flora

Ocurring plants

Distribution of
critical limits

Distribution
of plants

Protection level cutoff
in the critical limit
distribution

Protection level
cutoff in plant
distribution

BC/Al-ratios for
indicator plants

Indicator plant
and limit

Ecosystem
BC/Al-limit

SMB
model

Critical
load

Weathering rate map

Figure 3: Flow chart for the derivation of a BC/Al-limit for ecosystems and
how this is connected to the critical load calculation.
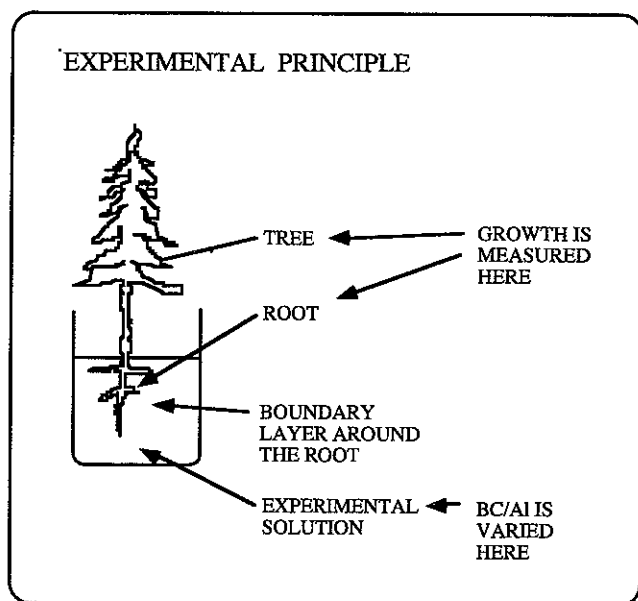
Figure 4: Basic setup for observing effect of soil acidity and Al on plant growth. The empirical correlations are derived by plotting observed plant growth against bulk BC/Al-ratio. This procedure bypass any effects taking place in the boundary layer between the bulk of the solution and the root surface, they are included in the correlation between growth versus solution composition.

6   Data

6.1   Experimental design

All experiments followed the same basic outline in their setup, with a few exceptions. The basic design is shown in Fig 4. The experimental solution varied between the different experiments, consisting of an aqueous solution, sometimes added as solution only, sometimes to sand culture and sometimes a complete soil culture was used. Growth was measured directly on the plant, the BC/Al ratio was varied in the bulk composition of the experimental solution. Thus any effects taking place in the boundary layer between the bulk of the solution and the root surface, is included in the response of growth versus solution composition.

The experiments by the Swedish researcher Göransson and his colleagues utilized a special design, where the nutrient solution was sprayed directly on to roots suspended in air in a chamber (Göransson and Eldhuset, 1987).

There are some basic diffrereces between the different basic experimental setups, and these are:

- Spray culture. The plant is grown in air and the root is sprayed with the experimental nutrient solution. The real composition of the solution film on the roots is very difficult to sample and determine. Organic exudates may build up in the very small solution volume. Experimental results are difficult to evaluate exactly and are very difficult to extrapolate to field conditions.

- Hydroponic culture. Organic plant exudates may build up in the solution during long experiments and slowly complex the Al added. Extrapolation to field conditions difficult.

- Sand culture. Sand culture experiments are often drained and organic plant exudates may be efficiently removed. The soil solution can be exactly determined. May sometimes be extrapolated to field conditions. Can be artificially infected with mycorrhiza.

- Soil culture. The added solutions change due to soil reactions and ion exchange. The solution used for watering as well as the soil solution must be analysed regularly. Drainage allow organic exudates to reach steady state concentrations which may be estimated or measured. Can be artificially infected with mycorrhiza. The results can readily be extrapolated to field conditions.

Experience from reviewing results show that results from hydroponic culture, sand culture and soil culture are generally consistent, and often quantitatively very similar. The spray culture experiments generally give large problems when an evaluation relevant to field conditions is wanted. Assumptions that cannot be checked must be made. For more details on individual experimental designs, we would like to refer to the individual published reports. As always, some reports describe the experimental methods very carefully and clearly, while others leave the reader none the wiser.

6.2   Data sources, laboratory experiments

Data on the reaction of different plants to soil chemistry was taken from the literature, and in several cases, data was further evaluated before use. Most of the data have been derived from pot experiments with seedlings and juvenile plants, and related to root growth and measurements of root length increase after certain time intervals in the experiment. Observations of growth changes from the field could be puzzled together with soil chemistry data from independent studies from the same sites, in order to create the whole picture for

several sites. Mitchell (1977) and Polunin (1980) was consulted on classification of different tree species. The data for each type of plant, was taken from the following references:

- Norway spruce (*Picea abies*), red spruce (*Picea rubens*), black spruce (*Picea mariana*), white spruce (*Picea glauca*); sitka spruce (*Picea sitchensis*);

  Abrahamsen, 1984; Arp and Quimet, 1986; Asp et al., 1988; Evers 1983; Gobran et al., 1991; Godbold and Huetterman, 1986; Göransson and Erikson, 1991; Göransson and Eldhuset 1991; Haus et al., 1988; Haus and Ulrich, 1988; Hutchinson et al., 1986; Huetterman and Rost-Siebert, 1984; Ingestad et al., 1984; Johnson, 1988; Joslin and Wolfe, 1988, 1989a, b; Keltjens and Loenen, 1989; Markkonen-Spiecker, 1985; McCormac and Canavera, 1980; McCormack and Steiner, 1978; van Praag and Weissen, 1985; van Praag et al., 1985; Quattie and Schier, 1990; Rehfuess, 1988; Ryan et al., 1986; Rodhe, 1987; Rost-Siebert, 1983; Ryan, 1985, 1986; Schier, 1984; Schulze, 1987; Schulze et al., 1989; Smit et al., 1987; Spicker, 1990; Steiner 1978; Stienen and Bauch, 1988; Sumner et al, 1987; Tischner 1983; Ulrich, 1983, 1984, 1987; Ulrich et al., 1984; Tomlinson II, 1983; Ulrich and Matzner, 1983.

- Silver fir (*Abies alba*), fraser fir(*Abies fraseri*), balsam fir(*Abies balsamea*), faber fir(*Abies fabri*);

  Becker, 1991; Bonneau, 1991; Bruck, 1988; Cronan et al, 1989; Entry et al., 1987; Haus and Ulrich, 1988; Krahl-Urban et al. 1988; Ma, 1991; Rehfuess, 1988; Schier, 1984.

- Scots pine (*Pinus sylvestris*), armand pine (*Pinus armandii*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), loblolly pine (*Pinus taeda*), aleppo pine (*Pinus halepensis*), masson pine (*Pinus massonii*), monterey pine (*Pinus radiata*), pitch pine (*Pinus rigida*), longleaf pine (*Pinus palustris*), slash pine (*Pinus elliottii*), sand pine (*Pinus clausa*), scrub pine (*Pinus virginiana*);

  Barnard et al, 1989; DeWald et al., 1990; Driscoll et al., 1985; Göransson and Eldhuset 1987; Göransson and Erikson, 1991; Jordan et al., 1990; Johnson and Taylor, 1989; Humpreys and Truman, 1963, Hutchinson et al., 1986; Keltjens and van Loenen, 1989; Kowalkowski, 1987; Ma, 1991; MacDonald et al., 1986; McCormick and Steiner, 1978; Matziris and Nakos, 1978; Nosko et al., 1988; Schädele et al., 1986; Ryan et al., 1986; Tepper et al., 1989; Truman et al., 1986, Williams, 1982.

- Western hemlock (*Tsuga heterophylla*), douglas fir (*Pseudotsuga menziesii*), larch (*Larix decidua*); western red cedar (*Thuja plicata*), northern

white cedar (*Thjua occidentalis*); mandarin fir (*Cunninghamia lanceolata*), Chinese fir (*Schima superba*);

Keltjens and van Loenen, 1989; Kowalkowski, 1987; Ryan et al., 1986a, b; Smit et al, 1989. Liao and Chen, 1991.

- Silver birch (*Betula pendula*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), European beech (*Fagus sylvatica*), American beech (*Fagus grandifolia*), white willow (*Salix alba*), oak (*Quercus robur*), pin oak (*Quercus palustris*), red oak (*Quercus rubra*), European alder (*Alnus glutinosa*), aspen (*Populus tremula*), honey locust (*Gleditsia triachantos*), autumn olive (*Elaeagnus umbellata*), sugar maple (*Acer saccharum*), heather (*Calluna vulgaris*), European elder or black elder (*Sambucus nigra*), rhododendron (*Rhododendron ponticum*), rowan (*Sorbus aucuparia*), hornbeam (*Carpinus betulus*) Norway maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*), white ash (*Fraxinius excelsior*);

  Asp and Berggren, 1990; Cronan et al, 1989; Gobran et al., 1991; Göransson and Eldhuset, 1987; Hutchinson et al., 1986; Kelly et al., 1990; Keltjens and van Loenen, 1989; Kirkpatrick et al., 1975; Matzner et al., 1986; McCormick and Steiner 1978; McCormick and Amendola, 1983; Neiztschke and Runge 1985; Persson and Majdi, 1991; Powers, 1927; van Praag and Weissen, 1985; van Praag et al., 1985; Rasmussen, 1986; Rost-Siebert, 1984; Steiner et al., 1979, 1984; Schädele et al., 1986, Sucoff et al., 1987, 1990; Tepper et al., 1989; Tyler 1987; Thornton et al., 1986a,b, 1990; Ulrich, 1987; Wittig; 1986; Wolfe and Joslin, 1989.

- Teak (*Tectona grandis*), peach (*Prunus persica*), sweet orange (*Citrus sinicum*), lemon (*Citrus limone*), Japanese mandarin (*Citrus natsudaidai*), cotton (*Gossypium hirsutum*), coffee (*Coffea arabica*), guapira (*Guapira olfersiana*), eucalyptus (*Eucalyptus gummifera*), grape wine (*Vitis vinifera*); tea (*Camellia sinensis*);

  Adams and Lund, 1966; Drechsel, 1987; Edwards et al., 1976; Forsline, 1983; Haas, 1966; Hue et al., 1986; Konishi et al., 1985; Liebig et al., 1942; Lin and Myhre, 1989; Mullette, 1974; Pavan and Bingham, 1982; Pavan et al., 1982; Sanhueza et al., 1988; Worku et al 1982; Yokomizo and Ishara, 1973.

- Heath rush (*Juncus squarrosus*), False brome (*Brachypodium sylvaticum*), Wavy hair-grass (*Deschampsia flexuosa*), Tufted hair-grass (*Deschampsia cespitosa*), Upright brome (*Bromus erectus*), Lesser hairy brome (*Bromus benekenii*), Yorkshire fog (*Holcus lanatus*), Redtop (*Agrostis stolonifera*), Common Bent (*Agrostis capillaris*), Crab grass (*Digitaria*), Remote

sedge (*Carex remota*), Kentucky bluegrass or Smoth meadow-grass (*Poa pratensis*), Annual meadow-grass (*Poa annua*), Wood meadow-grass (*Poa nemoralis*), Swe; "Storgröe" (*Poa remota*), Swe;"Trampgröe" (*Poa supina*), Meadow foxtail (*Alopecurus pratensis*), Meadow fescue(*Festuca pratensis*), Perenial rye-grass (*Lolium perenne*);

Andersson and Brunet, 1993; Gilbert and Pember, 1934; Hackett, 1965; Helyar and Andersson, 1971; McLean and Gilbert 1927; Pegtel, 1987; Runge, 1986; Rode, 1988; Rorison, 1985; Rengel and Robinson 1990a, b; Schuurkes et al., 1986; Varco and Sartain, 1988.

- Arnika (*Arnica montana*), American cranberry (*Vaccinium macrocarpon*), foxglove (*Digitalis purpurea*), majoram (*Origanum vulgare*), wood avens (*Geum urbanum*), wall lettuce (*Mycelis muralis*), heath bedstraw (*Galium saxatile*), sweet woodruff (*Galium odoratum*), may lily (*Maianthemum bifolium*, wood sorrel (*Oxalis acetosella*), chichweed (*Trientalis europaea*), yellow wood anemone (*Anemone ranunculoides*), wood anemone (*Anemone nemorosa*), lily-of-the-valley (*Convallaria majalis*), ramsons (*Allium ursinum*), wild strawberry (*Fragaria vesca*), zigzag clover (*Trifolium medium*), alfalfa (*Medicago sativa* var. falcata), alfalfa or black medick (*Medicago sativa* var. lupalina), cowslip (*Primula veris*), columbine (*Aquilegia vulgaris*), peach-leaved bellflower (*Campanula persicifolia*), wood leek (*Allium album*), common valerian (*Valeriana officinalis*), common dandelion (*Taraxacum officinale*), autumnal hawkbit, (*Leontodon autumnalis*), chickweed (*Stellaria media*), mouse-ear chickweed (*Cerastium fontanum*), selfheal (*Prunella vulgaris*), yellow bristle-grass (*Setaria pumila*):

Andersson 1993; Gilbert and Pember, 1934; Medappa and Dana, 1970; Pegtel, 1987; Powers, 1927; Pratt, 1966; Rode, 1988; Runge, 1986.

- Wheat (*Triticum aestivum*), rye (*Secale cereale*), barley (*Hordeum vulgare*) rice (*Oryza sativa*), sorghum (*Sorghum sativa*), sweet corn or maize (*Zea mays*), bush vetch (*Vicia sepium*), horse bean (*Vicia faba*), cowpea (*Vignia unguiculata*), subterranean clover (*Trifolium subterraneum*), white clover (*Trifolium repens*), yellow lupin (*Lupinus luteus*), alfalfa (*Medicago sativa*), soya bean (*Glycine max*); garden lettuce (*Latuca sativa*):

Ahmad and Tan, 1986; Andrew et al, 1973; Aniol, 1983; Alva et al., 1985, 1986a, b; Cambraia et al., 1983; Enyedi and Kuja, 1986; Grauer and Horst, 1990; Gilbert and Pember, 1934; Guerrier, 1982; Howeler and David, 1975; Horst et al, 1983; Horst und Göppel, 1986; Hutchinson et al, 1986; Jarvis and Hatch, 1986; Lee and Pritchard, 1984; Matsumoto and Yamaya, 1986; Moore and Patrick, 1989; Moore et al, 1990; Moore

and Patrick, 1989; Noble et al., 1988a, b; Parker et al., 1988a, b, 1989;
Pegtel, 1986; Ragland and Coleman, 1959; Rengel and Robinson, 1989;
Suhayda and Haug, 1986; Schuurkes et al, 1986; Varco and Sartain, 1986;
Wright et al., 1989.

Information of a more general type was derived from Kandler and Miller,
1991; Kowalkowski 1987; Barnard et al 1990. Several of the studies cited
above, compare growth and growth reductions to Al soil solution concentra-
tions only. When one investigator reports significant growth changes at 2.5
mg/l, whereas another reports no change until 15 mg/l Al or more, then this
difference can often be traced back to differences in Ca, Mg and K concentra-
tions of the soil solution of the bioassay. More often than not, K concentrations
will be several orders of magnitude larger than seen in nature. This is caused
by the use of "Ingestad ideal nutrient solutions" or similar compositions, rather
than something similar to the natural soil solution composition. This implies
that K concentrations may be in the range of 5-20 mg/l, wheras in the soil,
more than 1-2 mg/l is seldomly observed. It is a consistent pattern that the
growth effect expressed as a function of (Ca+Mg+K)/Al ratio instead of Al
concentration alone will generally remove most of the difference between such
studies on the same plant species.

Several Asian trees have been screened for soil acidity sensitivity by Chi-
nese researchers. The screening has been based on field surveys and estimates
of visible damage (needle loss and discoloration) as well as experimental bioas-
says. These experiments and results have not been published in the West, but
the Chinese Academy of Science made transcripts of the reports in Chinese
language with the results available to this study. The study involve 89 major
tree species occurring throughout Far East Asia. (We have not been able to
determine the English name for all of them). The study is especially valuable
as it covers species not covered in any other study, it conserns Asian trees,
and because it is to a large degree based on field studies of actual damage to
trees in areas affected by acid rain and soil acidification.

6.3 Data quality

Several of the data sets used come from experiments not completely controlled
in all conditions or with the experimental design not fully described in the liter-
ature. It must therefore be cautioned that all data are not of the same quality
and accuracy, and the uncertainties involved are in many cases completely
unknown. The growth rate information is a mixture of data from seedling
experiments in real soil in pots, from sand culture experiments, from seedlings
in nutrient solution and young plants in pots. Root growth is both root elong-
ination and root weight increment. Most of the bioassay experiments used

nutrient solutions with Ca+Mg+K concentrations in the range of either 0.1-0.3 mMol/l or around 1-3mMol/l, corresponding to 4-16 mg/l expressed as Ca respectively 40-160 mg/l as Ca. In the field, most podzols and soils with pH below 5.5 seldom exceed a concentration of 0.3 mMol/l of Ca+Mg+K in the soil solution, 0.03-0.05 mmol/l is rather typical. For spruce and other plants that follow the valence unspecific mechanism, these experimental differences are of minor importance. But for deciduous trees and pines, the effect of the Ca+Mg+K concentration on the damage function must be considered when the results are evaluated.

The number of plants used in the studies are not always specified. For several species, the response isoterms are results from tests on a large number of plants, for the most important european trees examples include: Norway spruce n>3,800, red spruce n>800, white spruce n>800, black spruce n>800, loblolly pine n>1,000, scots pine n>3,800, jack pine n>1,600, aleppo pine n>390; beech n>500. The available information has been listed in Tabs. 2-8.

Coniferous trees		Deciduous trees	
Reference	(Ca+Mg+K) mmol/l	Reference	(Ca+Mg+K) mmol/l
Markonen-Spiecker, 1986	2.2	Thornton et al., 1989	0.25
Tischner et al., 1983	1.65	Sucoff et al., 1989	0.1-0.8
McDonald et al., 1986	0.2-0.5	Wolfe and Joslin, 1989	0.1-8.7
Hutchinson et al., 1986	0.27-1.1	Göranson and Eldhuset 1987	0.219
Keltjens and van Loenen, 1989	0.6	Pavan et al., 1983	0.07-7.0
Truman et al., 1986	0.45	Thornton et al., 1990	0.75
Asp et al., 1988	0.2	Thornton et al., 1991	0.75
van Praag and Weissen, 1985	1.45-2.9	van Praag and Weissen, 1985	1.45-2.9
Ohno et al., 1990	0.21-0.31	Edwards et al., 1976	1.0
Schädele et al., 1986	12.0	DeWald et al., 1990	0.6-1.5
McCormick et al, 1978	4	McCormick and Steiner, 1978	4
Humpreys and Truman, 1964	7.0	Adams and Lund 1966	0.25-5.0
Arp and Quimet, 1986	2.0	Neitschke and Runge, 1985	0.025-0.5
Williams, 1985	0.12-0.5	Mulette, 1975	0.75
Rost-Siebert, 1985	0.05-5.0	Rost-Siebert, 1985	0.05-5.0
Hütterman and Ulrich, 1983	1.63	Haas, 1934	6.0
Ilvesniemi, 1991	0.1-1.0	Yokomizu and Ishihara, 1973	2.1
Liao and Chen, 1990	0.3-3.0	Kruger and Sucoff, 1987	0.005-0.25
Arovaara and Ilvesniemi 1990	1.52-0.152	Arovaara and Ilvesniemi 1990	1.52-0.152
Göranson and Eldhuset 1991	0.04	Leibig et al, 1942	5.0
Evers, 1983	4.11	Hütterman and Ulrich, 1983	1.63
		Hue et al., 1986	0.25
		McCormick and Amendola, 1983	4
		Steiner et al., 1980, 1984	4

Table 1: Concentrations of Ca+Mg+K used in some of the laboratory assay experiments. The values for conifers range from 0.2 to 12 mmol/l, for deciduous trees from 0.005 to 7.0 mmol/l.

Reference	Tree species	n	BC/Al levels
Göransson and Eldhuset, 1991	Norway spruce	1540	6
van Praag and Weissen, 1985	Norway spruce	21	4
Tischner et al., 1983	Norway spruce	160	4
Evers, 1983	Norway spruce	80	4
Markkonen-Spiecker, 1986	Norway spruce	250	4
Spiecker, 1985	Norway spruce, field	40	3
Landmann, 1990, Becker 1991, Bonneau 1991	Norway spruce, field	1,000	3
Söderberg, 1993	Norway spruce, field	16,375	5/10*
Asp and et al., 1988	Norway spruce	36	4
Ilvesniemi, 1992	Norway spruce	1250	10
Arovaara and Ilvesniemi, 1990-1	Norway spruce	360	6
Arovaara and Ilvesniemi, 1990-2	Norway spruce	45	15
Arovaara and Ilvesniemi, 1990-3	Norway spruce	45	15
Hutchinson et al., 1986	Red spruce	420	6
McQuattie and Schier, 1990	Red spruce	32	4
Raynal et al., 1990	Red spruce	160	5
Schier, 1985	Red spruce	57	5
Hutchinson et al., 1986	Black spruce	420	6
Hutchinson et al., 1986	White spruce	420	6
Nosko et al., 1988	White spruce	85	4
Ryan et al. 1986	Sitka spruce	126	9
Spiecker, 1985	Silver fir, field	40	3
Landmann, 1990, Becker, 1990 m.m.	Silver fir, field	1,000	3
Schier, 1985	Balsam fir	25	5
Liao and Chen, 1991	Schimia fir	80	4
Liao and Chen, 1991	Mandarin fir	80	4
Keltjens and van Loenen, 1989	Larch	105	7
Keltjens and van Loenen, 1989	Douglas fir	105	7
Ryan et al. 1986	Douglas fir	126	9
Ryan et al. 1986	Western hemlock	126	9
Ryan et al. 1986	Western red cedar	126	9

Table 2: Examples of number of conifers used in the experiments (n) and number of BC/Al used in the experiments for different types of coniferous trees. (*;levels of needle loss)

Reference	Tree species	n	BC/Al levels
Göransson and Eldhuset, 1991	Scots pine	1540	6
Keltjens and van Loenen, 1989	Scots pine	105	7
Ilvesniemi, 1992	Scots pine	1250	10
Arovaara and Ilvesniemi, 1990-1	Scots pine	360	6
Arovaara and Ilvesniemi, 1990-2	Scots pine	45	15
Arovaara and Ilvesniemi, 1990-3	Scots pine	30	10
Tischner et al., 1983	Scots pine	160	4
McCormick and Steiner, 1978	Scots pine	120	10
Söderberg, 1993	Scots pine, field	15,600	5/10[*]
Hutchinson et al., 1986	Jack pine	420	6
McDonald et al., 1986	Jack pine	1,296	5
Hutchinson et al., 1986	White pine	420	6
Matziris and Nakos	Aleppo pine	390	3
Jordan, 1985	Loblolly pine, field	200	3
Raynal et al., 1990	Loblolly pine	160	5
Schädele et al., 1986	Loblolly pine	168	7
Humphreys and Truman, 1964	Loblolly pine	10	5
Paganelli et al. 1987	Loblolly pine	230	6
Williams, 1982	Loblolly pine	100	5
Williams, 1982	Sand pine	100	5
Williams, 1982	Longleaf pine	100	5
McCormick and Steiner, 1978	Pitch pine	120	10
McCormick and Steiner, 1978	Scrub pine	120	10
Humphreys and Truman, 1964	Monterey pine	153	5
Williams, 1982	Slash pine	100	5
Humphreys and Truman, 1964	Slash pine	39	5

Table 3: Examples of number of pine used in the experiments (n) and number of BC/Al used in the experiments for different types of coniferous trees. ([*];levels of needle loss)

Reference	Tree species	n	BC/Al levels
Keltjens and van Loenen, 1989	Birch	105	7
Göransson and Eldhuset, 1987	Birch	840	9
Steiner et al., 1980	Paper birch	162	9
Steiner et al., 1984	Paper birch	27	3
McCormick and Steiner, 1978	Paper birch	120	10
McCormick and Amendola, 1978	Paper birch	24	4
McCormick and Steiner, 1978	Gray birch	120	10
McCormick and Steiner, 1978	Yellow birch	120	10
Keltjens and van Loenen, 1989	European oak	105	7
DeWald et al., 1990	Red oak	40	5
Thornton et al., 1989	Red oak	100	4
McCormick and Steiner, 1978	Red oak	120	10
McCormick and Steiner, 1978	Pin oak	120	10
van Praag and Weissen, 1985	European beech	101	4
Thornton et al., 1989	European beech	60	4
Neitztshe and Runge 1985	Europen beech	720	5
Thornton et al., 1986	Sugar maple	100	4
Steiner et al., 1984	Popular	27	3
Steiner et al., 1984	Popular	24	4
McCormick and Steiner, 1978	Alder	120	10
Sucoff et al., 1989	Honey locust	132	4
Wolfe and Joslin, 1989	Honey locust	243	16
Thornton et al., 1985	Honey locust	100	4
Schädele et al., 1986	Honey locust	144	7
McCormick and Steiner, 1978	Autumn olive	120	10
Powers, 1926	Rhododendron	5	5
Lin and Myhre, 1990	Citrus, field	225	5
Haas 1937	Citrus	105	7
Liebig et al., 1942	Citrus	24	4
Hueh et al., 1986	Cotton, field	96	6
Pavan et al., 1982	Coffee	30	5
Pavan et al., 1983	Coffee	35	5
Konishi et al. 1985	Tea	21	7
Drechsel et al., 1991	Liberia teak, field	35	5
Drechsel et al., 1991	Benin teak; field	40	5
Mulette, 1975	Eucalyptus	40	5
Kirkpatric et al., 1976	Peach	50	5
Edwards et al., 1976	Peach	40	4

Table 4: Examples of number of plants used in the experiments and number of BC/Al used in the experiments for different types of deciduous trees and a few ground vegetation species.

Reference	Species	Number of plants	BC/Al levels
Rode, 1988	Juncus	96	6
Pegtel, 1987	Deschampsia	96	6
Rode, 1988	Deschampsia	96	6
Hackett, 1965	Deschampsia	134	12
Rorison, 1985	Deschampsia	144	4
Hackett, 1965	Alopecurus	45	3
Hackett, 1965	Festuca	45	3
Hackett, 1965	Lolium	45	3
Rode, 1988	Carex	96	6
Varco and Sartain, 1966	Poa	72	9
Rengel and Robinson, 1990	Annual ryegrass	36	3
Helyar and Anderson, 1972	Perennial ryegrass	80	8
Rorison, 1985	Holcus	144	4
Rorison, 1985	Bromus	144	4
Andersson and Brunet, 1993	Bromus–BC/Al	8	270
Andersson and Brunet, 1993	Bromus–BC/H	5	135
Gilbert and Pember, 1934	Smooth crabgrass	210	9
Gilbert and Pember, 1934	Rough crabgrass	132	9
Gilbert and Pember, 1934	Kentucky bluegrass	60	5
Gilbert and Pember, 1934	Agrostis	72	5
Gilbert and Pember, 1934	Agrostis	36	5
McLean and Gilbert, 1927	Agrostis	24	5
Helyar and Anderson, 1972	Phalaris	80	8
McLean and Gilbert, 1927	Phalaris	24	4

Table 5: Examples of number of plants used in the experiments and number of BC/Al used in the experiments for different types of grass species.

Reference	Species	Number of plants	BC/Al levels
Medappa and Danna 1970	Vaccinium	270	9
Rode, 1988	Heather	96	6
Rode, 1988	Galium	96	6
Andersson, 1993	Galium	6	324
Rode, 1988	Digitalis	96	6
Rode, 1988	Origanum	96	6
Rode, 1988	Geum	96	6
Rode, 1988	Mycelis	96	6
Gilbert and Pember, 1934	Mouse-ear chickweed	96	7
Gilbert and Pember, 1934	Chickweed	90	6
Gilbert and Pember, 1934	Dandelion	96	4
Gilbert and Pember, 1934	Hawkbit	144	7
Gilbert and Pember, 1934	Selfheal	54	5
Powers, 1926	Spearmint	24	4
Pegtel, 1987	Arnica	24	4
Andersson, 1993	Allium	4	160
Hutchinson et al., 1986	Cladina	180	6
Hutchinson et al., 1986	Pleurozium	180	6

Table 6: Examples of number of plants used in the experiments and number of BC/Al used in the experiments for different types of ground vegetation species.

Reference	Species	Number of plants	BC/Al levels
Aniol, 1983	Wheat	288	9
Ahmad and Tan, 1986	Wheat	80	4
Parker et al., 1989	Wheat	64	4
Wright et al., 1989	Wheat	100	20
McLean and Gilbert, 1927	Barley	30	4
Horst und Göppel, 1986	Barley	36	6
Horst und Göppel, 1986	Rye	36	6
McLean and Gilbert, 1927	Rye	60	4
Moore et al., 1990, More and Patrick, 1989	Rice, field	88,000	10
Howeler and Cadavid, 1976	Rice	100,000	4
McLean and Gilbert, 1927	Sorghum	30	4
Ligon and Pierre, 1932	Sorhum	54	5
Guerrier, 1982	Sorghum	132	6
Alva et al., 1986	Soya	400	20
Parker et al., 1989	Soya	32	4
Ahmad and Tan, 1986	Soya	80	3
Alva et al., 1986	Soya	720	6
Andrew et al., 1973	Soya	96	4
McLean and Gilbert, 1927	Oats	60	4
McLean and Gilbert, 1927	Corn	9	3
Ligon and Pierre, 1932	Corn	54	5
Horst et al., 1983	Cowpea	144	4

Table 7: Examples of number of plants used in the experiments and number of BC/Al used in the experiments for different types of crops.

Reference	Species	Number of plants	BC/Al levels
Alva et al., 1986	Subterranean clover	400	20
Helyar and Anderson, 1972	Subterranean clover	80	8
Helyar and Anderson, 1972	White clover	80	8
Jarvis and Hatch, 1986	White clover	360	4
Lee and Pritchard, 1984	White clover	28	7
Powers, 1926	Alsike clover	4	4
Andrew et al., 1973	Simple clover	96	4
Andrew et al., 1973	Rueppel clover	96	4
Andrew et al., 1973	White clover	96	4
Alva et al., 1986	Alfalfa	400	20
Helyar and Anderson, 1972	alfalfa	80	8
Andrew et al., 1973	Temperate alfalfa	96	4
Andrew et al., 1973	Tropical alfalfa	96	4
Powers, 1926	Alfalfa	16	4
Andrew et al., 1973	Alfalfa	96	4
Andrew et al., 1973	Alfalfa	96	4
Horst und Göppel, 1986	Horse bean	24	6
Horst und Göppel, 1986	Yellow lupin	24	6
Alva et al., 1986	Sunflower	400	20
Brown et al., 1950	Potatoes	16	4
Brown et al., 1950	Tomatoes	16	4
Pierre and Stuart, 1932	Garden lettuce	44	3
Ligon and Pierre, 1932	Garden lettuce	54	5
McLean and Gilbert, 1927	Garden lettuce	132	7
McLean and Gilbert, 1927	Beets	40	3
McLean and Gilbert, 1927	Carrots	10	4
McLean and Gilbert, 1927	Radish	6	4
McLean and Gilbert, 1927	Turnip	5	4
McLean and Gilbert, 1927	Cabbage	40	5
Andrew et al., 1973	Desmodium	96	4
Andrew et al., 1973	Macroptilium	96	4
Andrew et al., 1973	Lotononis	96	4
Andrew et al., 1973	Stylosanthes	96	4
Powers, 1926	vetch	20	4

Table 8: Examples of number of plants used in the experiments and number of BC/Al used in the experiments for different types of crops.

7 Theory

Uptake of any nutrients to plants is a multi-stage processes. Several different types of processes are involved, and the slowest step in the process chain will determine the total uptake rate. The rate limiting step may differ for the same plant, depending on the conditions. For plant growth *Liebig's law* must be obeyed; The nutrient in least supply will determine the maximum growth rate G_{max}. Several effects are additive, the actions of nutrients, water and chemistry:

$$G_{max} = f(Nutr) \cdot g(Water) \cdot j(Chemistry) \tag{20}$$

where $f(Nutr)$ is the action of nutrient avalability, $g(Water)$ is the action of water availability on root function and soil avaliability, and $j(Chemistry)$ the effect of soil chemistry. The nutrient limitation is given by a function of different types of nutrient and water as a nutrient:

$$f(Nutr) = \min_{i=nutrients} \sum_{j=1}^{4 \, layers} \frac{W_{j,i} + D_{j,i} - L_{j,i}}{G_{max} \cdot x_i} \tag{21}$$

x_i is the content of the nutrient i (base cation, nitrogen, water, trace elements) in the tree. W is weathering, D is deposition and L is runoff. Consumption from intermittent storage such as ion exchange or soil moisture is excluded, since such sources are not sustainable. If the amount required by the plant is less than the amount available, then the function has the value 1, and this nutrient will not limit growth. $g(Water)$ is the efficiency function of the root dependent on water, it has the form of a Freundlich isotherm.

Growth of plants and production of biomass is directly proportional to nutrient uptake, since different elements are incorporated in biomass in relatively fixed concentrations and proportions. Under normal undisturbed or unpolluted ecosystem conditions, plant growth is mainly determined by water, nitrogen, temperature or light availability.

In terms of the uptake process flowchart in Fig. 5, it can be seen that water availability influences soil solution concentrations and mass flow as well as sap flow in the plant. Under rare optimal light, water and temperature conditions, growth may consume nutrients to the degree where diffusion in the root vicinity can become rate limiting. Root ion exchange of nutrients is normally not rate limiting in normal soil conditions, with little anthropogenic acidification. For most natural European forests, the normal condition is that the forest should be nitrogen limited. Then N availability in the soil solution and the solute flow of N will be the growth rate limiting step. Historically, N input to European forest ecosystems were 1/5 to 1/10 of the present 1990 input. Base cations under most conditions are available in sufficient supply. However, under soil acidification conditions, other positively charged ions besides Ca,
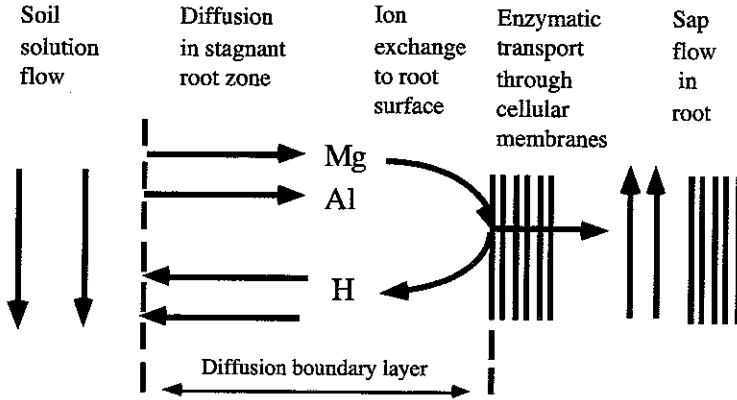
Figure 5: Uptake of nutrients necessary for growth of plants occur through a series of processes, each of which may be rate limiting, depending on the conditions in the soil and the geometry of the root boundary layer.

Mg and K start to appear in the soil solution in high concentrations (Al, H, Fe), and the ratio of these ions to base cations and P is greatly changed. The changed solution concentrations and ion ratios will result in a different surface composition of adsorbed ions on the root surfaces. The transport mechanisms taking ions through the root membrane into the sap in the root, depend on the availability of necessary nutrient ions on the outer surface of the root membranes. With uptake of base cations like Ca or Mg severely restricted due to low root surface concentration, uptake of base cations and phosphorus may become growth limiting instead of nitrogen.

Fig. 6 show a conceptual model for tree growth a process. According to this view, maximum growth is ultimately limited by plant physiology. The first regulator of growth is light, since this is significant for total energy available to the plant. Temperature will modify the chemical processes involved in photosynthesis and energy conversion. Water will affect the efficiency of the root apparatus as well as transport of substance internally in the plant. These factors will modify physiological maximum growth to a maximum possible growth given the light, temperature and water conditions. Availability of nutrients as applied in "*Liebig's law*" regulates potential growth to real growth, ignoring environmental retarding effects. Under acidification, soil aluminium and acidity may further limit growth.
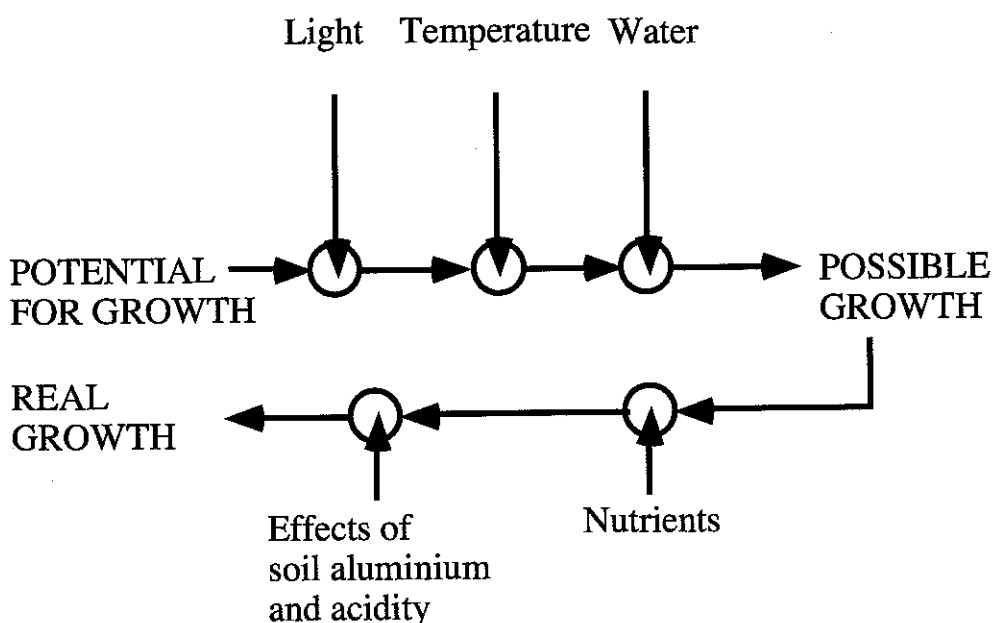
Light   Temperature Water

POTENTIAL → POSSIBLE
FOR GROWTH   GROWTH

REAL
GROWTH

Effects of   Nutrients
soil aluminium
and acidity

Figure 6: Conseptual model for tree growth as a process. According to this view, growth is ultimately limited by plant physiology. The first regulator of growth is light, since this is significant for total energy available to the plant. Temperature will modify the chemical processes involved in photosynthesis and energy conversion. Water will affect the efficiency of the root apparatus as well as transport of substance internally in the plant. These factors will modify physiological maximum growth to a maximum possible growth given the light, temperature and water conditions. Availability of nutrients as applied in "*Liebig's law*" regulates potential growth to real growth, ignoring environmental retarding effects. Under acidification, soil aluminium and acidity may further limit growth.

7.1   Earlier model approaches considered

Earlier models for tree growth (Ågren, 1983; Aber et al., 1991; van Dam, 1992; Nye and Tinker, 1977) have tended to model growth as a function of mass flow and availability of nitrogen, water and light. This concept will work well in forest stands only affected by such factors, untouched by pollution or large soil chemistry changes over time. The light/nitrogen limitation concept has however failed to predict or explain forest decline caused by soil acidification, due to the fact that important processes and couplings to soil chemistry are missing in these earlier models. Incorporating such connections lead to predictive capability concerning soil acidifiaction effects (Bossel et al., 1985).

The concept of Nye and Tinker (1977) assumes ion exchange at the root surface to be the step preceding uptake. The next step is uptake of adsorbed ions from the root surface according to first order or Michaelis-Menten kinetics:

$$r_{up} = k_{up} \cdot \frac{X_{BC}}{X_{BC} + K_M} \qquad (22)$$

Uptake from theouter root surface through the cell wall into the plant is actively regulated by the plant. But transport from the bulk of the liquid to the outer root surface is passive with respect to the plant and governd by physical prosesses such as flow, convection and diffusion. Combining this with surface concentration control by ion exchange as outlined earlier, or by a simple Langmuir adsorption isotherm for base cation adsorption:

$$Ads_{BC} = Ads_{max} \cdot \frac{[BC]}{[BC] + K_{ads1}} \qquad (23)$$

We can derive an uptake expression, used by several authors earlier (Nye and Tinker, 1977; Gherini et al., 1990; van Oene, 1993), by inserting in the Michaelis-Menten expression, assuming:

$$\frac{Ads_{max}}{CEC} = X_{BC,max} \qquad (24)$$

yields:

$$r_{up} = \left(\frac{k_{up} \cdot X_{BC,max}}{X_{BC,max} + K_M}\right) \cdot \frac{[BC]}{[BC] + \left(\frac{K_M \cdot K_{ads1}}{X_{BC,max} + K_M}\right)} \qquad (25)$$

This traditional view of uptake does not envision any drastic variation in Al in the soil, nor that there may be interactions between ions at adsorption sites on the root. It cannot predict what would happend if Al were to change significantly, and it cannot predict what increased Al in soils would do to tree growth. This implies that these traditional uptake models cannot predict any change in growth due to soil acidification. They simply assume that soil

acidification does not occur. In unpolluted soils, there will be much Al in the exchange complex, but very little in solution. When there is a significant increase in soil solution Al, then the basic assumptions concerning BC uptake are no longer valid. Under such conditions, adsorption of Al to the root will increase and this will change the amount of adsorbed BC at a certain soil solution concentration. Adsorption of both BC and Al must be considered:

$$Ads_{BC} = Ads_{max} \cdot \frac{[BC]}{[BC] + K_{ads1}} \tag{26}$$

$$Ads_{Al} = Ads_{max} \cdot \frac{[Al]}{[Al] + K_{ads2}} \tag{27}$$

The amount of adsorbed BC must now share space on the root with Al, the fraction of adsorbed BC is::

$$X_{BC} = \frac{Ads_{BC}}{Ads_{BC} + Ads_{Al}} \tag{28}$$

This can be inserted in the Michaelis-Menten expression for uptake traditionally used:

$$r_{up} = \left(\frac{k_{up}}{1 + K_M}\right) \cdot \left(\frac{[BC^{2+}]}{[BC^{2+}] + [Al^{3+}] \cdot \left(\frac{K_M}{1+K_M}\right) \cdot \left(\frac{[BC^{2+}]+K_{ads1}}{[Al^{3+}]+K_{ads2}}\right)}\right) \tag{29}$$

K_M is the Michaelis-Menten half-rate-saturation coefficient. The full Michaelis-Menten expression of Nye and Tinker (1977) may possibly not be necessary, the first order approximation of it may suffice, because uptake will level off when the surface is saturated with BC.

At this point it is not reasonable to continue with purely empirical adsorption isotherms, when ion exchange expressions derived from the law of mass action are available (Vanselow, Gaines-Thomas, Gapon e.t.c.).

7.2 Model assumptions

It is assumed that base cation uptake can become uptake rate limited in severely acidified soils, and soils receiving high nitrogen deposition. It is assumed that this can be described by a model where uptake is dependent on absorbed amount of the ions taken up on the root. The surface ion exchange effect can be expressed to a large part by using the soil solution ratio between the divalent base cations Ca, Mg, K and Al. (This is often referred to as the "Ca:Al-ratio" in the literature, even if it is understood that it should comprise Ca, Mg and K, as "Al" should rather be understood as the sum of all inorganic charged Al-species (Bonneau, 1990)). In the continuation we will sometimes use the notation BC=Ca+Mg+K. It becomes increasingly more difficult for

the plant to take up the necessary base cations from the soil solution when soil acidification occur, due to the increased concentration of H^+ and Al^{3+} in relation to base cations. The following assumptions form the basis of the (Ca+Mg+K/Al)-response functions extracted from the experimental data:

- Uptake of base cations is proportional to the adsorbed amount of Ca, Mg and K on the root surfaces active in uptake.

- Al may disturb the uptake mechanisms at the root surface, by competition at adsorption sites, in the root membrane and cytoplasm.

- The concentration at the root surface is controlled by an adsorption mechanism, analogous to ion exchange between the major soil solution constituents Al^{3+}, Ca^{2+}, Mg^{2+}, K^+ and H^+ ions.

The ion exchange analogy is proposed with special reference to Asher, (1987); Bolt (1982); Cronan, (1991) and Morris et al., (1989) but also with respect to earlier studies (Sverdrup et al., 1990, 1992) and results presented by Bingham, (1979); Christensen, (1984a, b); Cronan et al., (1989); Cutler and Rains, (1974); Eriksson (1988, 1989); Goyer, (1988); Hütterman and Ulrich (1984) and Ulrich, (1983, 1984).

- Growth is reduced if the possible uptake of BC is lower than what is required to physiologically match the potentially avaialable uptake of N (i.e. Liebig's law applies to trees and BC and N uptake).

In addition to the causes given above, high soil solution concentrations may cause denaturalisation of extracellular and intracellular enzymes and by immobilization of P in the soil. This is not incorporated in the assumed mechanisms and the kinetics derived thereof. The value of the (Ca+Mg+K)/Al-ratio in the soil solution is coupled to uptake of base cations, chemical weathering, base cation deposition and acid deposition. Uptake will tend to make Ca+Mg+K smaller in the soil, weathering and atmospheric deposition of Ca+Mg+K will tend to increase it, whereas acidification will tend to increase Al. Thus the net effect of forest growth and acidification may be similar with respect to the (Ca+Mg+K)/Al-ratio, even if the damage mechanisms are very different on the molecular level at the root-soil solution interface. In the short term perspective, (Ca+Mg+K)/Al ratios and soil acidification aspects are of interest for forest stand health and vitality, in the long term for forest productivity and hence commercial value.

7.3   Uptake kinetics

The uptake of Ca, Mg and K here represented as BC, is governed by a kinetic equation based on soil solution concentration of base cations, usually a

Michaelis-Menten expression. When base cations are limited in supply, but under conditions favorable for uptake, then uptake will be concentration dependent, approaching zero order when base cations are available in large supply. When growth is restricted by some other nutrient, uptake will also be zero order. However under acidic soil conditions the availability of base cations may become restricted by supply or by the chemical conditions in the soil which would allow other constituents of the soil solution to compete for root receptor sites. Uptake U is expressed as a function of a plant physiologically determined maximum uptake, modified by soil moisture and soil chemistry functions. Growth is proportional to nutrient uptake, limited according to "*Liebig's law*" and regulation by climatic factors such as light, temperature and soil water availability:

$$G_{min} = \frac{U_{limit}}{x_{limit}} \cdot f(light) \cdot f(\theta) \cdot f(T) \qquad (30)$$

$f(\theta)$ is the soil water availability function, which has been described elsewhere (Sverdrup et al., 1992). Modifiers taking into account the effect of temperature ($f(T)$) and light $f(light)$ have been omitted for simplicity in the following text. When N or P is present in large quantities, then this can temporarily affect the growth capacity of the plant, for U_{limit}, *Liebig's law* prevails, in the long run. Under growth conditions restricted by soil acidification, uptake become dependent on the amount of base cation adsorbed at the tree root:

$$U = k \cdot BC_{ads} \qquad (31)$$

where U is the uptake rate, k is the uptake rate coefficient. The amount of adsorbed base cation at the root is given by the adsorption capacity CEC_{root}, the available root surface and the base cation saturation at the root exchange sites:

$$BC_{ads} = A_{root} \cdot CEC_{root} \cdot X_{BC} \qquad (32)$$

BC_{ads} is the adsorbed amount base cations, A_{root} is the total active surface at full wetting of the roots, X_{BC} is the fraction of the adsorption sites on the root occupied by Ca and Mg, CEC_{root} the adsorption capacity (keq/m^2 root) and U the uptake rate. The effective root surface is defined as the root surface exposed to water in the soil to the degree where the water is also in contact with other soil constituents supplying nutrients. The maximum uptake U_{max} as limited by the Michaelis-Menten expression only, is occurring at full base cation saturation at the root surface, when X_{BC}=1.0. U_{max} is basically dependent on the cation exchange capacity, specific active surface area and the transport rate through the membranes of the root. If the proper expressions are combined, the kinetic uptake equation is derived:

$$U = U_{max} \cdot X_{BC} \qquad (33)$$

Changes in root mass over time as the tree grows imply a change in A_{root} over time. The non-specific divalent adsorption is assumed to occur analogously either to Gapon, Vanselow equilibrium ion exchange, or valence unspecific ion exchange.

Uptake of Ca, Mg and Al and their soil solution seem to be strongly coupled, the uptake of K and NH_4 affect each other mutually, but are less sensitive to Al interference. Phosphorus as PO_4 and NO_3 are also taken up in a series of similar events, mainly as negative ions.

In multi-layer assessments, it will be necessary to consider that the BC/Al value is not uniform down through the soil profile. This will allow the plant to partially reallocate uptake to other soil layers, if the conditions become adverse for uptake in a particular layer. However if the PROFILE model is used (Sverdrup and Warfvinge, 1988; Warfvinge and Sverdrup, 1992), uptake in any layer will be limited by actual supply. In a long term perspective, nature will limit this to the amount available from weathering in that particular layer plus any percolate in excess of 15μeq/l. Thus under conditions where base cation supply is limiting growth, the limiting uptake will be:

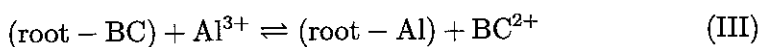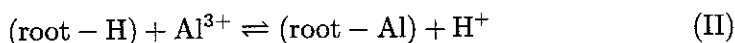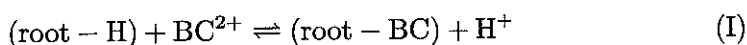$$U_{limit} = \min_{j=N,P,Ca,Mg,K} \sum_{i=1}^{layers} u_{crit,i}(j) \cdot f(\frac{BC}{Al})_i \qquad (34)$$

$u_{crit,i}$ is maximum uptake possible in layer i of nutrient j. The critical uptake is determined by availability of the nutrient in the soil. For N, deposition, fixation and decomposition of organic matter is the most important sources. For P and base cations, weathering and atmospheric deposition are most important in the long term, in a shorter perspective, ion exchange may be an important source. For considerations of long term availability, i_{ex} and i_{decomp} must be set to zero.

$$u_{crit,i} = i_W + i_E X + i_{DECOMP} + i_{DEP} - i_L \qquad (35)$$

where i_w is release rate due to weathering of nutrient (i=N, P, Ca, Mg, K), i_{dep} is input of i from the atmosphere, i_L is the amount leached at the bottom of the root zone of nutrient i. The effect of the above description of uptake kinetics is that the tree will compensate for a lowering of BC/Al ratio in the B-layer, by increasing uptake from other layers. Fine root mass will be reallocated in the soil over longer time periods to soil layers with better BC/Al ratio as long as this is possible. When the amount available in a certain layer is not corresponding to the amount uptake reallocated to that layer by the plant, and no other layer can supply the missing amount, then growth is reduced. Thus the plant will try to optimize its uptake.

7.4   The valence unspecific mechanism

For a valence unspecific reaction the ion exchange matrix is indifferent to the valence of the adsorbing ions, the matrix behaves as an infinite continuum of receptor sites. This implies that whenever a base cation is absorbed, one H^+ or Al is released, and the difference in change somehow adjusted for by some at present unknown process:

$$(\text{root} - \text{H}) + BC^{2+} \rightleftharpoons (\text{root} - BC) + H^+ \tag{I}$$

$$(\text{root} - \text{H}) + Al^{3+} \rightleftharpoons (\text{root} - Al) + H^+ \tag{II}$$

$$(\text{root} - BC) + Al^{3+} \rightleftharpoons (\text{root} - Al) + BC^{2+} \tag{III}$$

the valence unspecific selectivity coefficients for root exchange become:

$$K_{H/BC} = \frac{X_{BC}}{X_H} \cdot \frac{[H^+]}{[BC^{2+}]} \tag{36}$$

$$K_{H/Al} = \frac{X_{Al}}{X_H} \cdot \frac{[H^+]}{[Al^{3+}]} \tag{37}$$

$$K_{BC/Al} = \frac{X_{Al}}{X_{BC}} \cdot \frac{[BC^{2+}]}{[Al^{3+}]} \tag{38}$$

where X_i is the exchanged fraction of substance i, the parameters in brackets concentrations and K the selectivity coefficients.

The equation for divalent base cations uptake by trees is obtained by combining the growth rate equation with the expression for X_{BC} and the expressions for adsorbed fraction of base cation, substituting for the selectivity coefficients depending on reaction type. This may be used to solve for X_H and X_{Al}, assuming BC, Al and H to be the dominating ions on the surface:

$$X_{BC} = 1 - X_{Al} - X_H \tag{39}$$

to give for the exchanged amount Al and the exchanged amount H: We will search for an expression for the base saturation at the root, since this affects uptake as shown earlier:

$$U = U_{max} \cdot X_{BC} \tag{40}$$

by rearranging the selectivity expressions, to expressions for exchangeable H and Al at the root as function of the base saturation X_{BC}:

$$X_H = X_{BC} \cdot \frac{1}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]} \tag{41}$$

$$X_{Al} = X_{BC} \cdot K_{H/Al} \cdot \frac{[Al^{3+}]}{[BC^{2+}]} \tag{42}$$

These are then filled in Eq. 19:

$$X_{BC} = 1 - X_{BC} \cdot K_{H/Al} \cdot \frac{[Al^{3+}]}{[BC^{2+}]} - X_{BC} \cdot \frac{1}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]} \qquad (43)$$

This can be rearranged to:

$$X_{BC} \cdot (1 + K_{H/Al} \cdot \frac{[Al^{3+}]}{[BC^{2+}]} + \frac{1}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]}) = 1 \qquad (44)$$

Further rearrangement yields:

$$X_{BC} = \frac{1}{1 + K_{H/Al} \cdot \frac{[Al^{3+}]}{[BC^{2+}]} + \frac{1}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]}} \qquad (45)$$

By multiplying with BC we get

$$X_{BC} = \frac{[BC^{2+}]}{[BC^{2+}] + K_{H/Al} \cdot [Al^{3+}] + \frac{1}{K_{H/BC}} \cdot [H^+]} \qquad (46)$$

The response function f(BC/Al) is defined using Eq. 13, setting:

$$f(BC/Al) = \frac{U}{U_{max}} = X_{BC} \qquad (47)$$

By changing the notation for the coefficients, the response function f(BC/Al) can be given by:

$$f(BC/Al) = \frac{[BC^{2+}]}{[BC^{2+}] + K_{Al} \cdot [Al^{3+}] + K_H \cdot [H^+]} \qquad (48)$$

It can be seen that this is the Micaelis-Menten equation for uptake of base cations. The difference is that the saturation coefficient is dependent on competing ions for uptake positions, such as H and Al. Theoretically, any ion not usefull for uptake will have this effect. The expression indicate that Al and H^+ will decrease uptake proportional to the soil solution H^+ and Al concentrations. This can rearranged to;

$$f(BC/Al) = \frac{(BC/(Al + p \cdot H))}{(BC/(Al + p \cdot H)) + K_{US}} \qquad (49)$$

This can also be expressed in terms of the BC/Al-ratio, ignoring the additional effect of pH;
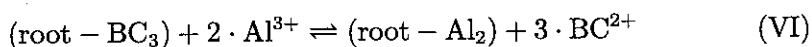
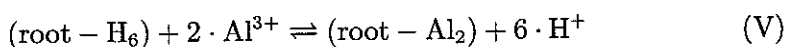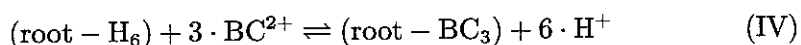$$f(BC/Al) = \frac{(BC/Al)}{(BC/Al) + K_{US}} \qquad (50)$$

Under conditions with no Al present in the soil the expression is transformed to:

$$f(BC/H) = \frac{(BC/H)}{(BC/H) + K_{US}} \tag{51}$$

The valence unspecific mechanism imply that there is no BC-antagonism against Al beyond the first order relation, and there is only one isotherm in terms of BC/Al ratio regardless of Ca or Mg concentration.

7.5   The Vanselow mechanism

For a variant of the Vanselow type of reaction, the root ion exchange matrix is a viewed as a polydentate valence specific substrate. During reaction a rearrangement of the solid phase has to occur, so that three BC^{2+}-ions or two Al^{3+}-ions can be tied to a hexa-valent binding site with double bonds (Warfvinge, 1988). The reaction stoichiometry suggested is:

$$(root - H_6) + 3 \cdot BC^{2+} \rightleftharpoons (root - BC_3) + 6 \cdot H^+ \tag{IV}$$

$$(root - H_6) + 2 \cdot Al^{3+} \rightleftharpoons (root - Al_2) + 6 \cdot H^+ \tag{V}$$

$$(root - BC_3) + 2 \cdot Al^{3+} \rightleftharpoons (root - Al_2) + 3 \cdot BC^{2+} \tag{VI}$$

The Vanselow selectivity coefficients become by application of the law of mass action, considering that the activity of a phase in an ideal mixed crystal depend on the molar fraction of the species:

$$K_{H/BC} = \frac{2 \cdot X_{BC}}{X_H} \cdot \frac{[H^+]^6}{[BC^{2+}]^3} \tag{52}$$

$$K_{H/Al} = \frac{3 \cdot X_{Al}}{X_H} \cdot \frac{[H^+]^6}{[Al^{3+}]^2} \tag{53}$$

$$K_{BC/Al} = \frac{3 \cdot X_{Al}}{2 \cdot X_{BC}} \cdot \frac{[BC^{2+}]^3}{[Al^{3+}]^2} \tag{54}$$

The Vanselow mechanism imply that the root surface receptors have a fixed valence of hexagonal orientation. This could suggest the coordination of water Ca-, Mg- and Al-complexes to receptor sites.

$$X_H = X_{BC} \cdot \frac{2}{K_{H/BC}} \cdot \frac{[H^+]^6}{[BC^{2+}]^3} \tag{55}$$

$$X_{Al} = X_{BC} \cdot \frac{2 \cdot K_{BC/Al}}{3} \cdot \frac{[Al^{3+}]^2}{[BC^{2+}]^3} \tag{56}$$

This is inserted in Eq. 19 to yield:

$$X_{BC} = 1 - X_{BC} \cdot \frac{2 \cdot K_{BC/Al}}{3} \cdot \frac{[Al^{3+}]^2}{[BC^{2+}]^3} - X_{BC} \cdot \frac{2}{K_{H/BC}} \cdot \frac{[H^+]^6}{[BC^{2+}]^3} \qquad (57)$$

$$X_{BC} = \frac{1}{1 + \frac{2 \cdot K_{BC/Al}}{3} \cdot \frac{[Al^{3+}]^2}{[BC^{2+}]^3} + \frac{2}{K_{H/BC}} \cdot \frac{[H^+]^6}{[BC^{2+}]^3}} \qquad (58)$$

For a Vanselow root ion exchange mechanism reaction, the growth inhibition expression can be derived by the same rearrangement of the terms mathematically as was demonstrated for the unspecific response mechanism.

The response expression is:

$$f(BC/Al) = \frac{[BC^{2+}]^3}{[BC^{2+}]^3 + K_{Al} \cdot [Al]^2 + K_H \cdot [H]^6} \qquad (59)$$

By use of the gibbsite assumption, H can also be totally eliminated from the expression;

$$[Al^{3+}]_{eq} = K_{Gibb} \cdot [H^+]^3_{eq} \qquad (60)$$

K_{Gibb} is the coefficient for soil solution Al equilibrium with gibbsite. The K_{Gibb} value for the rooting zone of the plant is used in the equation. The equation is not valid if such conditions prevail that the gibbsite equilibrium approximation no longer hold. Without Al present the expression is reduced to:

$$f(BC/H) = \frac{[BC^{2+}]^3}{[BC^{2+}]^3 + K_H \cdot [H]^6} \qquad (61)$$

The full expression may be simplified by using the gibbsite expression, to:

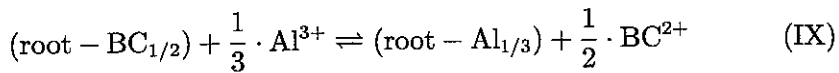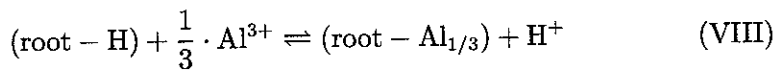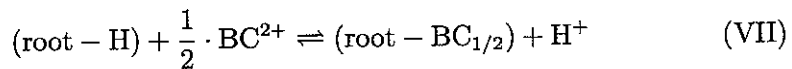$$f(BC/Al) = \frac{[BC^{2+}]^3}{[BC^{2+}]^3 + K_V \cdot [Al]^2} \qquad (62)$$

The Vanselow mechanism imply a strong antagonistic effect of Ca, Mg and K against Al, as well as a strong effect of the BC/Al-ratio on growth, since it is second order with respect to this ratio. This also implies that plants with this type of reaction should react strongly with their uptake of base cations to changes in the base cation concentration. A change will have relatively stronger effect on the uptake in relation to plabnts with the unspecific response. This can be seen if the expression is rearranged in terms of the BC/Al ratio:

$$f(BC/Al) = \frac{[BC^{2+}] \cdot (BC/Al)^2}{[BC^{2+}] \cdot (BC/Al)^2 + K_V} \qquad (63)$$

This implies that there is several different isoterms for the same BC/Al-ratio depending on the soil solution BC concentration.

7.6   The Gapon mechanism

The Gapon ion exchange mechanism imply ion exchange of equivalent charges. Each BC^{2+}-ion or Al^{3+}-ion is bound by single bonds to binding sites which maintain their valence at -1. The stoichiometry of the ion exchange reactions occurring at the root between the surface, H^+, BC^{2+} and Al^{3+} are for a Gapon reaction:

$$(\text{root} - \text{H}) + \frac{1}{2} \cdot BC^{2+} \rightleftharpoons (\text{root} - BC_{1/2}) + H^+ \qquad \text{(VII)}$$

$$(\text{root} - \text{H}) + \frac{1}{3} \cdot Al^{3+} \rightleftharpoons (\text{root} - Al_{1/3}) + H^+ \qquad \text{(VIII)}$$

$$(\text{root} - BC_{1/2}) + \frac{1}{3} \cdot Al^{3+} \rightleftharpoons (\text{root} - Al_{1/3}) + \frac{1}{2} \cdot BC^{2+} \qquad \text{(IX)}$$

For the Gapon reaction the selectivity coefficients become after applying the law of mass action using single bonded H^+, BC^{2+} and Al^{3+} and charge fractions on the ion exchange matrix:

$$K_{H/BC} = \frac{X_{BC}}{X_H} \cdot \frac{[H^+]}{[BC^{2+}]^{1/2}} \qquad (64)$$

$$K_{H/Al} = \frac{X_{Al}}{X_H} \cdot \frac{[H^+]}{[Al^{3+}]^{1/3}} \qquad (65)$$

$$K_{BC/Al} = \frac{X_{Al}}{X_{BC}} \cdot \frac{[BC^{2+}]^{1/2}}{[Al^{3+}]^{1/3}} \qquad (66)$$

Rearrangement of the equation yields:

$$X_H = \frac{X_{BC}}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]^{1/2}} \qquad (67)$$

$$X_{Al} = K_{BC/Al} \cdot X_{BC} \cdot \frac{[Al^{3+}]^{1/3}}{[BC^{2+}]^{1/2}} \qquad (68)$$

This is filled in Eq. 19:

$$X_{BC} = 1 - \frac{X_{BC}}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]^{1/2}} - K_{BC/Al} \cdot X_{BC} \cdot \frac{[Al^{3+}]^{1/3}}{[BC^{2+}]^{1/2}} \qquad (69)$$

The expression for the base saturation at the root uptake surface sites is:

$$X_{BC} = \frac{1}{1 + \frac{1}{K_{H/BC}} \cdot \frac{[H^+]}{[BC^{2+}]^{1/2}} + K_{BC/Al} \cdot \frac{[Al^{3+}]^{1/3}}{[BC^{2+}]^{1/2}}} \qquad (70)$$

For a Gapon root reaction mechanism, the uptake inhibition expression is:

$$f(BC/Al) = \frac{[BC^{2+}]^{1/2}}{[BC^{2+}]^{1/2} + K_G \cdot [Al]^{1/3} + K_H \cdot [H^+]} \qquad (71)$$
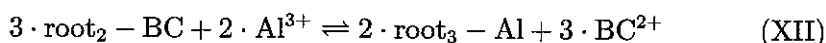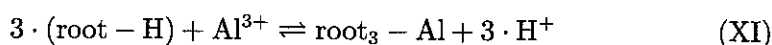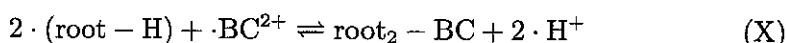
It can be shown that by using the gibbsite expression, the equation may be reformed to:

$$f(BC/Al) = \frac{[BC^{2+}]^{1/2}}{[BC^{2+}]^{1/2} + K_G \cdot ([Al] + p \cdot [H^+])^{1/3}} \qquad (72)$$

where p is the ratio between the Gibbsite coefficient and the H/BC ion exchange selectivity coefficient at the root surface. The Gapon mechanism, which may be the most common mechanism for cation ion exchange on dead organic matter in soils (Warfvinge 1988), imply charge surface balance and charge exchange. This seems to seldom occur on parts of living plants.

7.7   The Gaines-Thomas mechanism

No ion exchange analogy can be investigated without trying the Gaines-Thomas equation, since it has been applied in many soil chemistry models. The Gaines-Thomas reaction mechanism leads to an expression intermediate between the unspecific response expression and the Vanselow expression, with the exception that the reaction sites maintain their valence at -1. This imply that BC^{2+} ions are bound to two single bond sites by single bonds.

$$2 \cdot (root - H) + \cdot BC^{2+} \rightleftharpoons root_2 - BC + 2 \cdot H^+ \qquad (X)$$

$$3 \cdot (root - H) + Al^{3+} \rightleftharpoons root_3 - Al + 3 \cdot H^+ \qquad (XI)$$

$$3 \cdot root_2 - BC + 2 \cdot Al^{3+} \rightleftharpoons 2 \cdot root_3 - Al + 3 \cdot BC^{2+} \qquad (XII)$$

The Vanselow selectivity coefficients become by application of the law of mass action:

$$K_{H/BC} = \frac{X_{BC}}{X_H^2} \cdot \frac{[H^+]^2}{[BC^{2+}]} \qquad (73)$$

$$K_{H/Al} = \frac{X_{Al}}{X_H^3} \cdot \frac{[H^+]^3}{[Al^{3+}]} \qquad (74)$$

$$K_{BC/Al} = \frac{X_{Al}^2}{X_{BC}^3} \cdot \frac{[BC^{2+}]^3}{[Al^{3+}]^2} \qquad (75)$$

By rearranging the selectivity expressions, the amount of exhangeable H and Al is given, and inserted in Eq. 19:

$$X_H = \frac{X_{BC}^{1/2}}{K_{H/BC}^{1/2}} \cdot \frac{[H^+]}{[BC^{2+}]^{1/2}} \tag{76}$$

$$X_{Al} = K_{BC/Al}^{1/2} \cdot X_{BC}^{3/2} \cdot \frac{[Al^{3+}]}{[BC^{2+}]^{3/2}} \tag{77}$$

Let:

$$Y_{BC}^2 = X_{BC} \tag{78}$$

Then Y_{BC} is found as the solution of the equation:

$$Y_{BC}^3 + Y_{BC}^2 \left(\frac{[BC]^{3/2}}{K_{BC/Al} \cdot [Al]}\right) + Y_{BC}\left(\frac{[H] \cdot [BC]}{K_{H/BC} \cdot K_{BC/Al} \cdot [Al]}\right) - \frac{[BC]^{3/2}}{K_{BC/Al} \cdot [Al]} = 0 \tag{79}$$

The Gaines-Thomas response type expression has the following approximate asymptotic solution:

$$f(BC/Al) = \frac{[BC^{2+}]^{3/2}}{[BC^{2+}]^{3/2} + K_{GT} \cdot [Al]} \tag{80}$$

This isotherm differ in practice little from the unspecific expression, but retains a small antagonistic effect of Ca and Mg towards Al in addition to the 1:1 built into the BC/Al ratio.

7.8   Empirical expressions

The general equations for the damage functions can all be expressed in terms of the BC/Al-ratio in order to highlight any additional antagonistic effects. This may also be seen as an purely empirical formula based on a form such as:

$$f(BC/Al) = \frac{[BC^{2+}]^n}{[BC^{2+}]^n + K_{Exp} \cdot ([Al^{2+}] + p \cdot [H^+])^m} \tag{81}$$

equivalent to:

$$f(BC/Al) = \frac{[BC^{2+}]^{n-m} \cdot (BC/(Al + p \cdot H)^m}{[BC^{2+}]^{n-m} \cdot (BC/(Al + p \cdot H)^m + K_{Exp}} \tag{82}$$

where n and m would be exponents and K_{Exp} a coefficient to be determined experimentally. For analysis of the data, BC/(Al+p· H) is offered as the parameters we should be using when plot response versus soil acidity. This implies that there is several different isoterms for the same BC/Al-ratio depending on the soil solution BC concentration when n and m are different. An important consequence of using an empirical expression is that valid resonse curves can be determined, even if the actual mechanism of response on the molecular level is totally unknown.

7.9   Discussion

When conditions prevail where the soil solution concentration of Al becomes insignificant, then the expression is reduced to:

$$f(BC/Al) = \frac{[BC]^n}{[BC^{2+}]^n + K \cdot p^m \cdot [H^+]^m} \tag{83}$$

or expressed in terms of the BC/H ratio:

$$f(BC/Al) = \frac{(BC/H)^{n-m}}{(BC/H)^{n-m} + K \cdot n^m} \tag{84}$$

The relationship between BC/Al-limit and the BC/H-limit can be determined at the point where the response functions have the same value:

$$f(BC/Al) = f(BC/H) \tag{85}$$

This is obtained by setting Eq. 44 equal to Eq. . From this the relation between the BC/H-limit and the BC/Al-limit can be derived.

$$(\frac{BC}{Al})_{limit} = \frac{1}{p} \cdot (\frac{BC}{H})_{limit} \tag{86}$$

For the "unspecific" response type, p=1, the BC/H-limit is equal to the BC/Al-limit. For the Vanselow response p=3, the BC/H-limit is equal to the 3 times the BC/Al-limit. For the Gapon response p=1 (Jönsson et al. 1995).

Turning back to the theoretical derivation of the expressions at the beginning of the book, we remember that Nye Tinker (1977) suggested the generic Michaelis-Menten expression for uptake:

$$r_{up} = k_{up} \cdot \frac{X_{BC}}{X_{BC} + K_M} \tag{87}$$

In our treatment of the uptake process, we arrived at something similar, starting from first order uptake expression for base cations, assuming the adsorbed amount on the root outside to be the presence felt by the inside of the plant:

$$r_{up} = k_{up} \cdot X_{BC}, \tag{88}$$

and invoking not only uptake of BC but also competition between Al, H and BC at the surface for uptake acceptor sites, we could show that the uptake expression is:

$$r_{up} = k_{up} \cdot f(BC/Al) \tag{89}$$

or written fully out:

$$r_{up} = k_{up} \cdot \frac{[BC^{2+}]^n}{[BC^{2+}]^n + K_M} \tag{90}$$

This is a Michaelis-Menten rate expression, based on concentration of substrate in the soil solution ! The half-rate saturation coefficient of the Michaelis-Menten expression in this approach is affected by the presense of the competing ions Al and H in the soil solution:

$$K_M = K_{Exp} \cdot ([Al^{2+}] + p \cdot [H^+])^m \tag{91}$$

The difference from the earlier Michaelis-Menten expression as suggested by Nye and Tinker (1977) is that the old expression ignore soil chemical conditions beyond BC availability, this expression also includes the effect of Al and H in the soil solution. The response function derived here will have no effect if other nutrients will be more limiting than base cations when constricted by Al and H effects. It is thus the maximum uptake capacity that is constricted by these functions. The maximum uptake capacity of the particular root system may be difficult to estimate.

7.10 Summary of expressions

The general equations for the damage functions can all be expressed in terms of the BC/Al-ratio in order to show any extra antagonistic effects. In summary the following expressions are available:

$$f(BC/Al) = \frac{[BC^{2+}]^n}{[BC^{2+}]^n + K([Al^{3+}] + p \cdot [H^+])^m} \tag{92}$$

where n and m would be exponents and K_{Exp} a coefficient to be determined experimentally. From the theoretical considerations made above, the following values have been suggested. These values have been confirmed for grasses in this study using the studies of Anderson and Brunett (1993) and later also for fungi and bacteria in laboratory culture (Jönsson et al., 1994):

Parameter	n	m	p
Unspecific	1	1	1
Vanselow	2	3	3
Gapon	1/2	1/3	1
Gaines-Thomas	1.5	1	1

Experimental data is required to determine which of the response types apply to a certain damage function. Experimental data seem to indicate that uptake of N and P is also restricted by the Al response. Other surface reaction stoichiometries than those shown above were tested, but no one fitted the data reasonably well, except the ones given above.

8 Example of evaluation procedures

For most of the studies reported here, we did not use the evaluation of the original author. All primary data was completely reevaluated whenever possible. In this process, sometimes a different conclusion from the one by the original authors would be reached. This was necessary, however, in order to evaluate all data consistently, using the same theory.

8.1 Experiments from Finland on spruce and pine

The evaluation procedure will be illustrated using the studies of Arovaara and Ilvesniemi (1990) on Norway spruce and scots pine and one study on Norway spruce and scots pine by Ilvesniemi (1992).

In both studies a solution composition based on Ingestads ideal nutrient ratio was used. Arovaara and Ilvesniemi (1990) studied growth response in 3 experiments. Experiment 1 for Norway spruce and scots pine, involved six Al levels (0, 10, 20, 50, 75, 100 mg Al/l) and concentrations of N, K, P, Ca, Mg of 100, 45, 14, 6,6 mg/l. Experiment 2 for Norway spruce and scots pine, involved five Al levels (0, 20, 50, 100, 150 mg Al/l) and three nutrient levels based on concentrations of N, K, P, Ca, Mg of 100, 45, 14, 6,6 mg/l in strengths of 1/1, 1/3, and 1/10. Experiment 3 involved five Al levels (0, 5, 10, 20, 50 mg Al/l) and three nutrient levels for Norway spruce (1/2, 1/6, 1/20) and two nutrient levels for scots pine (1/2, 1/20), based on concentrations of N, K, P, Ca, Mg of 100, 45, 14, 6, 6 mg/l. In all experiments, pH was kept constant at 3.8.

Ilvesniemi (1992) studied the effect of two nutrient levels (1/5 and 1/50) on Norway spruce and scots pine and five Al levels (0, 5, 10, 20, 50 mg Al/l).

The data has been listed in the Tables 9-13. Tabs. 9, 11 and 13 show the data as derived directly from the reference. Tabs.10 and 12 show the data after our normalization of the numbers according to biomass produced in the 1/1 nutrient level experiments. This in order to relate the data all to the same standard. For Norway spruce in experiment 3, the Arovaara and Ilvesniemi (1990) state a growth of 8.2 mg to be the reference growth of the unaffected plants.

First the data was plotted as growth versus Al concentration, as can be seen in Fig. 7. There is not a good correlation between growth and Al in the soil solution. If growth response is plotted versus Ca/Al instead a better correlation is obtained. The best correlation is obtained by plotting (Ca+Mg+K)/Al. The base cations were added in equivalents, giving K one half the protective power of Ca and Mg against Al. This was done as it was felt that K does have a somewhat smaller antagonistic effect than Ca. The same evaluation proceedure was applied to the spruce data. Growth response against Al alone gives a poor correlation. The spruce experiments of Arovaara and Ilvesniemi

| Tree | Level | Growth, mg | | Relative growth in % of control | | | | |
| | | Aluminium concentration, mg/l | | | | | | |
		0	5	10	20	50	100	150
Pine 2	1/1	36.6			102	81	70	50
Pine 3	1/2	8.2	95	93	93	71		
Pine 2	1/3	34.9			79	73	61	53
Pine 2	1/10	29.0			80	79	59	55
Pine 3	1/20	7.2	93	77	74	82		
Spruce 2	1/1	26.8			63	66	49	73
Spruce 3	1/2	6.9	98	111	98	102		
Spruce 2	1/3	17.7			82	73	101	69
Spruce 3	1/6	7.2	102	92	102	79		
Spruce 2	1/10	18.5			81	92	99	78
Spruce 3	1/20	6.6	109	125	108	77		

Table 9: The original data as reported by Arovaara and Ilvesniemi (1990), experiment 2 and 3.

(1990) apparently contain inconsistencies as can be seen from the table and Fig. 8 even if growth response is plotted against BC/Al.

This apparent problem of inconsistency was resolved by plotting growth response versus $(Ca+Mg+K)/Al$, but dividing up the experiments according to seedling age or total amount of biomass produced at the time of the experiment. Experiment one of Arovaara and Ilvesniemi (1990) was 1 year old and exposed to Al for 1/2 year. Experiment two of Arovaara and Ilvesniemi (1990) was 3 years old and exposed for 1/2 year. Experiment three of Arovaara and Ilvesniemi (1990) was 2 years old and exposed for 1/2 year. Experiment four of Ilvesiniemi (1992) was 1 year for pine and 1/2 year for spruce old and exposed for 1/2 year. It can now be seen from Fig. 10 that older seedlings of Norway spruce are possibly more resistant to Al, the scatter is unfortuneately to large for us to be quite certain. Or the plants that produced more biomass show more variation in their resistance. The data of Ilvesniemi (1992) and Arovaara and Ilvesniemi (1990) cannot really detect the reason why some experiments gave less sensitivity than others.

Tree	Level	Relative growth in % of control Aluminium concentration, mg/l							
		0	5	10	20	50	75	100	150
Pine 1	1/1	100		99	106	89	84	66	
Pine 2	1/1	100			102	81		70	50
Pine 3	1/2	100	95	93	93		71		
Pine 2	1/3	95			75	69		58	50
Pine 2	1/10	79			63	62		46	43
Pine 3	1/20	82	68	65	72				
Spruce 1	1/1	100		96	94	77	53	43	
Spruce 2	1/1	100			63	66		49	73
Spruce 3	1/2	84	82	93	82		85		
Spruce 2	1/3	66			54	48		67	45
Spruce 3	1/6	87	88	75	88		68		
Spruce 2	1/10	69			56	63		68	53
Spruce 3	1/20	80	87	100	86		62		

Table 10: The data of Arovaara and Ilvesniemi (1990) in experiment 1, 2, 3 normalized with respect to total biomass in the 1/1 nutrient solution experiment. For Spruce in experiment 3, the authors state a growth of 8.2 mg to be the reference growth of the unaffected plants.

Tree, origin	Level	Growth, mg	Relative growth in % of control			
			Aluminium concentration, mg/l			
		0	5	10	20	50
Spruce 4, South	1/5	151	66	36	19	7
Spruce 4, Central	1/5	114	68	43	30	10
Spruce 4, East	1/5	127	79	48	30	8
Spruce 4, South	1/5	87	64	36	22	10
Spruce 4, South	1/50	47	75	55	37	28
Spruce 4, Central	1/50	43	65	50	46	25
Spruce 4, East	1/50	47	56	48	41	27
Spruce 4, South	1/50	34	60	50	39	22

Table 11: The original data of Ilvesniemi (1992) for pine of different geographical origin in Finland.

Tree, origin	Level	Growth, mg	Relative growth in % of control			
			Aluminium concentration, mg/l			
		0	5	10	20	50
Spruce 4, South	1/5	100	66	36	19	7
Spruce 4, Central	1/5	100	68	43	30	10
Spruce 4, East	1/5	100	79	48	30	8
Spruce 4, South	1/5	100	64	36	22	10
Spruce 4, South	1/50	31	23	17	11	9
Spruce 4, Central	1/50	37	24	19	17	9
Spruce 4, East	1/50	37	21	17	15	10
Spruce 4, South	1/50	39	23	20	15	9

Table 12: The data of Ilvesniemi (1992) normalized with respect to the growth of biomass in 1/5 nutrient experiment.

Tree	Level	Growth, mg	Relative growth in % of control Aluminium concentration, mg/l			
		0	5	10	20	50
Pine 4	1/5	92	100	93	100	86
Pine 4	1/50	55	36	37	35	25

Table 13: The original data of Ilvesniemi (1992) for scots pine.

Experiment Experiment	Biomass mg dwt	Plant mg dwt	Age yrs
Pine 4	120	6	1
Pine 1	930	15	1
Pine 3	8	8	2
Pine 2	33	35	3
Spruce 4	30	4.8	1/2
Spruce 1	245	4.1	1
Spruce 3	7.2	7.2	2
Spruce 2	22	26	3

Table 14: Age of seedlings at the beginning of each experiment. The total amount dry biomass produced in each experiment. Estimated average plant weight in the control experiment.
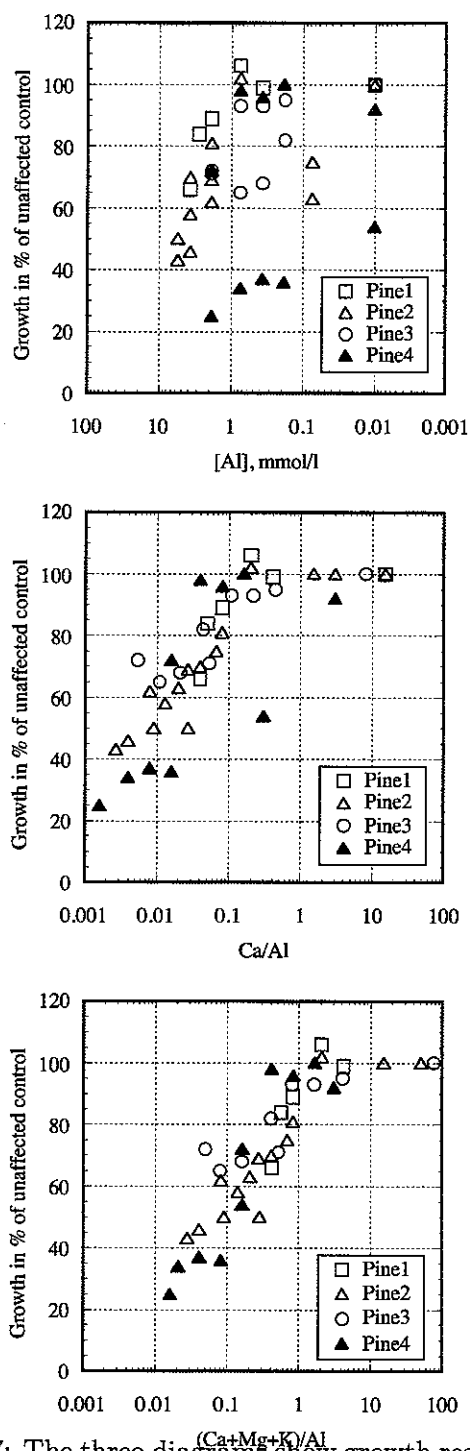
Figure 7: The three diagrams show growth response for scots pine as compared to the Al concentrations in 4 experiments by Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992). It can be seen how best consistency is obtained by relating response to the (Ca+Mg+K)/Al ratio.
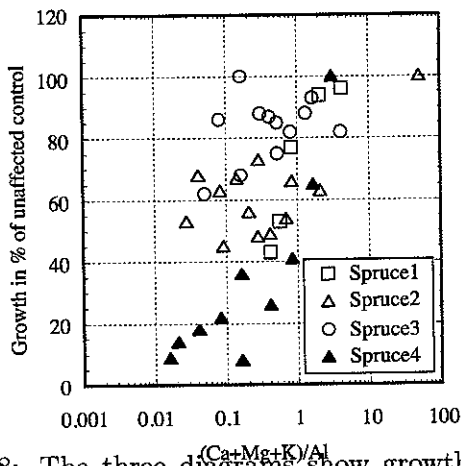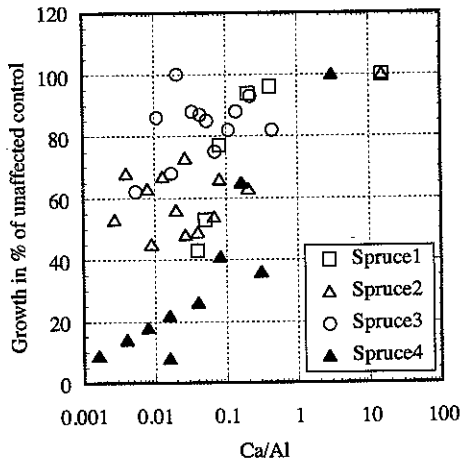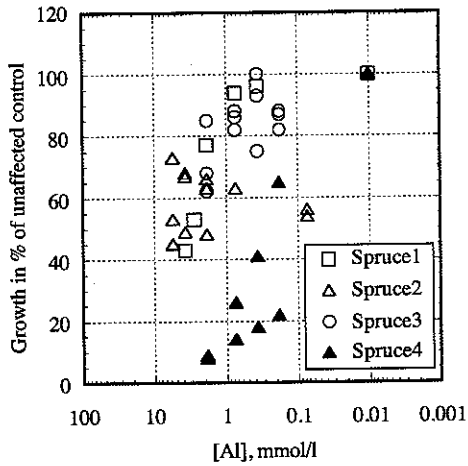
Figure 8: The three diagrams show growth response for Norway spruce as compared to the Al concentrations in 4 experiments by Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992). It can be seen how best consistency is obtained by relating response to the (Ca+Mg+K)/Al ratio. The response in these experiments show more spread for spruce than other experiments found in other studies.
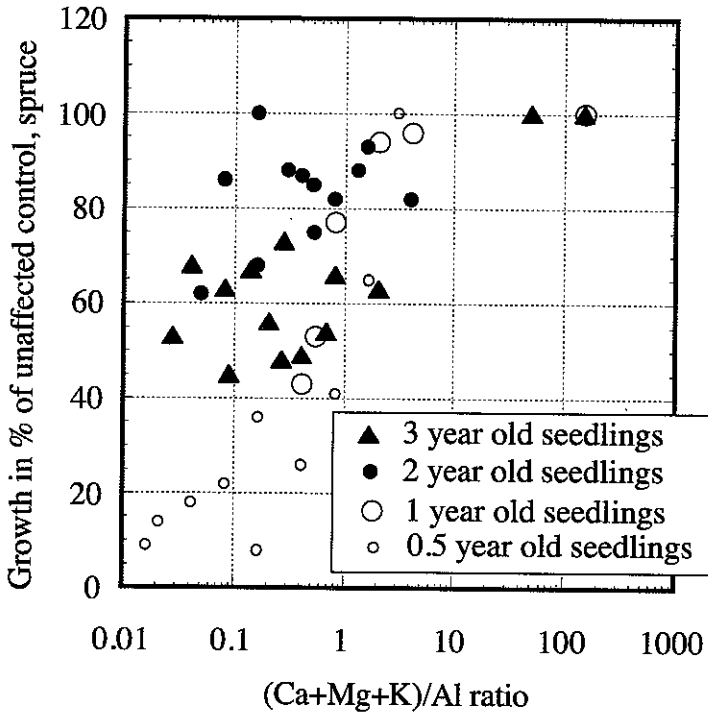
Figure 9: If the data of Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992) is split up according to seedling age, then the picture become clearer. Very young seedlings appear to be less resistant to Al than older.
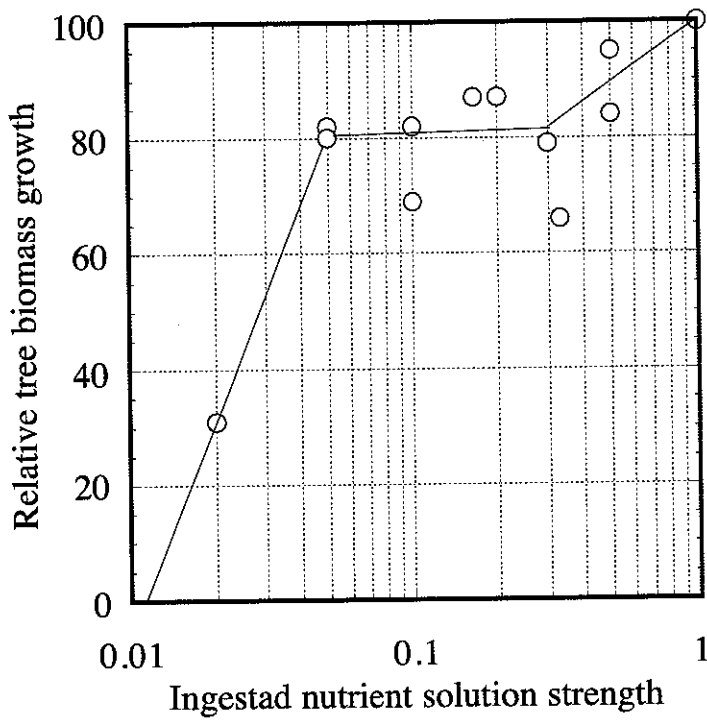
Figure 10: The dependence of growth on nutrient solution concentration be investigated by using data from Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992).

8.2   Experiments from Sweden on pine, spruce and birch

The study of Göransson and Eldhuset (1987) warrant extra explaining, as it employed a special methodology, and as it tested scots pine plants with and without mycorrhiza on the roots. The method used for growing plants was by setting them in specially designed chambers where the roots were sprayed with a nutrient solution. Thus the root was only covered with a thin film of liquid. This causes a problem for interpretation as the solution concentration on the root may not be the same as in the solution sprayed. A very dilute solution was used, with nutrients in Ingestad proportions. The concentrations were in mg/l of N, K, P, Ca, Mg; 10, 6.6, 1.32, 0.7 and 0.85 mg/l, a total base cation concentration of 0.219 mmol/l, excluding Na. The spray solution contained 0, 1, 3, 6, 10, 15 mmol/l Al. The roots were sprayed at two nutrient supply rates, near optimum and at a rate called constant stress, being 40% of the near optimum. Göransson was consulted by per letters and telephone in order to clarify the excact nature of his experiments and clarify the differences between his earlier and our present interpretations of the material.

In Tab. 15, the data for Birch has been listed. Göransson and Eldhuset measured the Ca/Al ratio at the root surface. Data must be used cautionously as root biomass was also included in the analysis. Thus the ratio is a mixture of ratio in the root biomass and ratio in the solution covering the root surface. The ratio between Ca+Mg+K and Ca is 12 in the experiments, and this was used to recalculate the Ca/Al into (Ca+Mg+K)/Al ratio. Thus a connection between growth in the biostat and (Ca+Mg+K)/Al ratio in the solution at the root surface could be established. The result is very consistent with the results from other studies.

The data for Norway spruce from experiments by Göransson and Eldhuset (1987) was more difficult to interprete, since no Ca/Al at the root surface was not reported. The base cation concentration used in this experiment was very low, K, Ca and Mg was 0.0313, 0.0052 and 0.0031 mmol/l, a total base cation concentration of 0.04 mmol/l. In order to translate the solution (Ca+Mg+K)/Al ratio to the corresponding ratio on the root surface, the ratio z between BC/Al(root) and BC/Al(spray) was determined from the experiment on birch. This yield a set of ratios shown in Tab. 16. The use of the ratios in this way results in a substantial uncertainty, but appears to be the only option available, unless new data is produced. For spruce and pine only BC/Al ratios inside the root is available. Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992) relates to soil solution composition, whereas Göransson and Eldhuset (1991) relates to root surface solution concentration, and are thus not completely comparable. It can be seen that the spruce data of Arovaara and Ilvesniemi (1990) show a significant spread, but both experiments fall in the same range of BC/Al ratios. For comparison with data from other studies,

Experiment	(Ca+Mg+K)/Al Spray	Ca/Al Root	(Ca+Mg+K)/Al Root	Birch % growth
Optimum	1.35	0.5	6	100
	0.19	0.08	1	71
	0.07	0.06	0.72	54
	0.036	0.03	0.36	39
	0.0216	0.03	0.36	12
Stress	1.35	0.5	6	100
	0.19	0.13	1.56	87
	0.07	0.17	2.04	52
	0.036	0.06	0.72	47
	0.0216	0.03	0.36	21
	0.0144	0.01	0.12	12

Table 15: Data from experiments by Göransson and Eldhuset (1987) on birch (*Betula pendula*).

only the data from experiments on three year old seedlings were used (Fig. 14).

A comparison between experiments with scots pine without mycorrhiza and scots pine with mycorrhiza, revealed no difference in the response of growth to soil solution Al, as can be seen in Fig. 26.

8.3 Experiments from Germany on Norway spruce

A few experiments were designed in such a way that the effect of the H-ion on Norway spruce could be investigated. We selected the experiments by Tischner et al., (1985), Markonen-Spiecker (1985), and Evers (1983). All worked with Norway spruce seedlings and Tischner (1985) also with small plants.

In all experiments different types of nutrient solution was used. Tischner et al., (1983) used a Hoagland solution, Markonen-Spiecker (1985) an Ingestad solution and Evers (1983) a modified Hoagland solution. Typical for these solutions are that they have very high K concentration, in general solutions with very high ion strength. The experiments were hydroponic solution experiments (Evers, 1983 and Markonen-Spiecker 1985) or sand culture (Tischner et al., 1985).

[Al] mmol/l	z	$z \cdot BC/Al$(spray)	Spruce	Pine	Pine and Mycorrhiza
0.16	8.3	2.08	100	100	100
0.2	8.3	1.66	100		
0.3	8.3	1.11	78		
1	8.2	0.33	51	84	
3	29	0.38	33	93	91
6	20	0.13	30	87	84
10	17	0.07	21	56	70
15	8.3	0.022	38	46	46
30	8.3	0.01		34	43

Table 16: Data from experiments by Göransson and Eldhuset (1987) on Norway spruce and scots pine with and without mycorrhiza.

The experiments can be used to evaluate how K should be incorporated in the expression. There is a tendency towards better consistency in the plots if K is included for experiments with low ion strength. But for concentrated solutions, it is apparent that K is lass relevant in the BC/Al ratio. Unfortuneately, many of the experiments were carried out with so unrealistic K concentration levels with respect to field conditions, that it must have been evident from the very beginning that the results of the experiments would not be easily transfered to field conditions.

From the diagrams in Fig. 11 and 12 it is evident that for spruce, K is not as efficient in counterreacting the effect of Al as Ca and Mg. The plots of effects against (Ca+Mg)/Al as the soil acidity variable give bettter consistency than plotting effects against (Ca+Mg+K)/Al.

The incorporation of H in the expression was also tried. The variables BC/Al (assuming no significant effect of H), BC/(Al+H) (assuming H to have effect on a atom by atom basis) and BC/(Al+3*H) (assuming H to have effect on a charge basis) the was tried. For Norway spruce, BC/(Al+H) give slightly better consistencies than excluding it or including it times 3. This is consistent with the unspecific response type for Norway spruce, and confirm other similar findings. The differences are small, mostly because the small pH range available in these experiments. It can be concluded that ignoring the effect of the H-ion on Norway spruce, has a marginal effect for assessing the sensitivity to soil acidity in mineral soils. For iorganic soils with little or no

pH	[H] mM	% growth remaining for [Al] mM				
		0	0.5	1.0	2.0	5.0
3	1	83	65	60	45	-
3.5	0.316	100	67	66	57	48
4	0.1	100	94	85	67	-
4.5	0.0316	(70)	-	67	65	-

Table 17: Norway spruce (*Picea abies*), stem weight, small plants, Tischner et al., (1985)

Al, this aspect may become very important.

The correlation between BC/Al and growth effect is better than the correlation between effect and Al concentration alone (Fig. 13). The diagrams show that the effect of Al on growth of seedlings is equal to that of H, in absolute terms, on a molar basis, for Norway spruce. The implications for field conditions is that the limiting Al concentration is reached first or the limiting BC/Al ratio. H-ion concentrations comparable to those active for Al imply a soil pH of 3-3.2. Such low soil pH values rarely occur.

pH	[H] mM	[BC] mM	[Al] mM	% growth remaining for clones used			
				I	II	III	IV
3.8	0.16	2.19	0	100	100	(100)	100
3.8	0.16	2.19	1.48	100	95	97	82
3.8	0.16	2.19	2.96	45	77	59	76
3.8	0.16	2.19	4.44	34	41	88	27

Table 18: Markonen-Spiecker (1985), Norway spruce (*Picea abies*), seedlings, root weight

pH	[H] mM	[BC] mM	% growth remaining for [Al] mM			
			0	0.2	1.0	1.5
3.5	0.316	4.34	-	-	-	73
3.5	0.316	4.34	-	-	-	97
3.5	0.316	4.34	-	-	-	72
3.5	0.316	4.34	-	-	-	68
3.8	0.16	4.34	100	-	98	-
3.8	0.16	4.34	100	-	86	-
3.8	0.16	4.34	100	-	78	-
3.8	0.16	4.34	100	-	77	-
4.5	0.0316	4.34	100	88	-	-
4.5	0.0316	4.34	100	100	-	-
4.5	0.0316	4.34	100	98	-	-
4.5	0.0316	4.34	100	100	-	-

Table 19: Evers (1983), Norway spruce (*Picea abies*), seedlings, seedling root weight
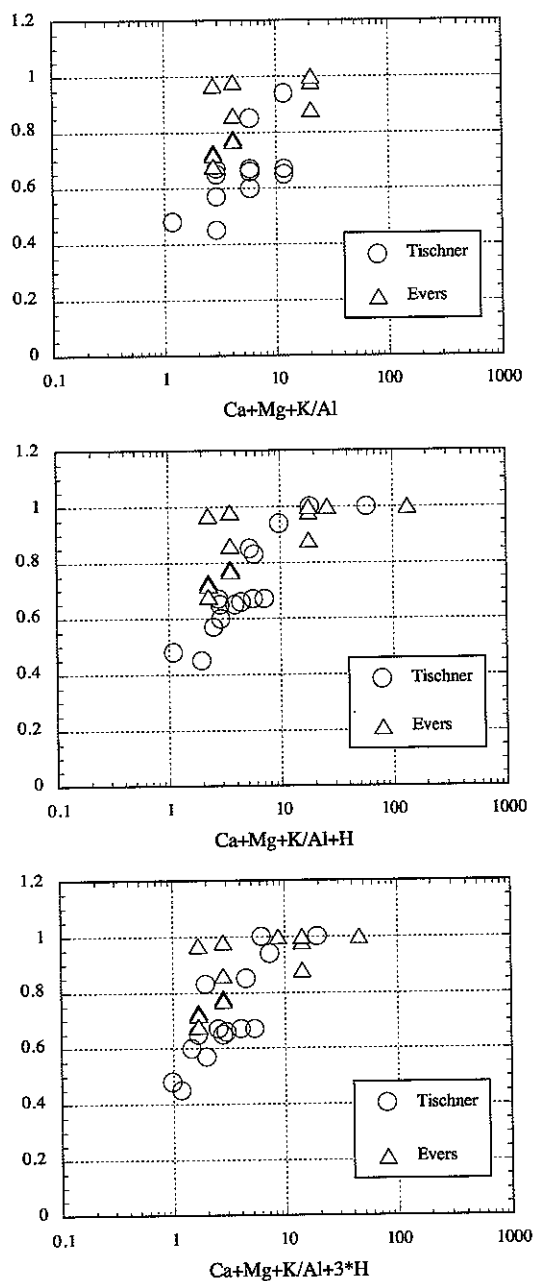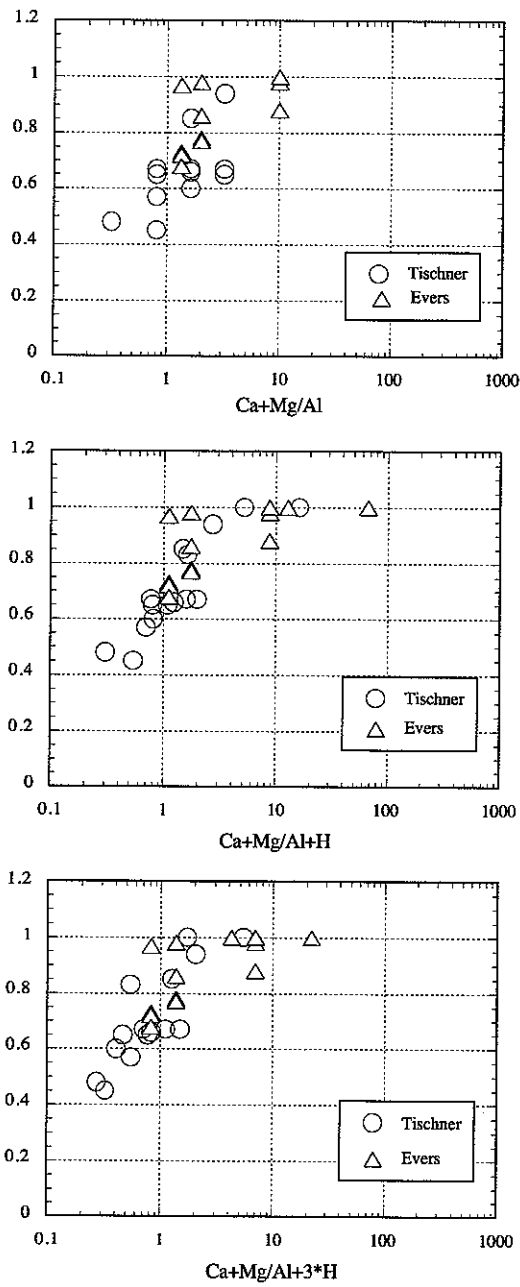
Figure 11: Test of different effect parameters on experiments on Norway spruce (*Picea abies*) performed by Tischner et al., (1985) and Evers (1983). The effect parameter tested is $(Ca+Mg+K)/(Al+ p \cdot H)$ where p vary from 0 to 3.

Figure 12: Test of different effect parameters on experiments on Norway spruce (*Picea abies*) performed by Tischner et al., (1985) and Evers (1983). The effect parameter tested is $(Ca+Mg)/(Al+ p \cdot H)$ where p vary from 0 to 3. K has been excluded.
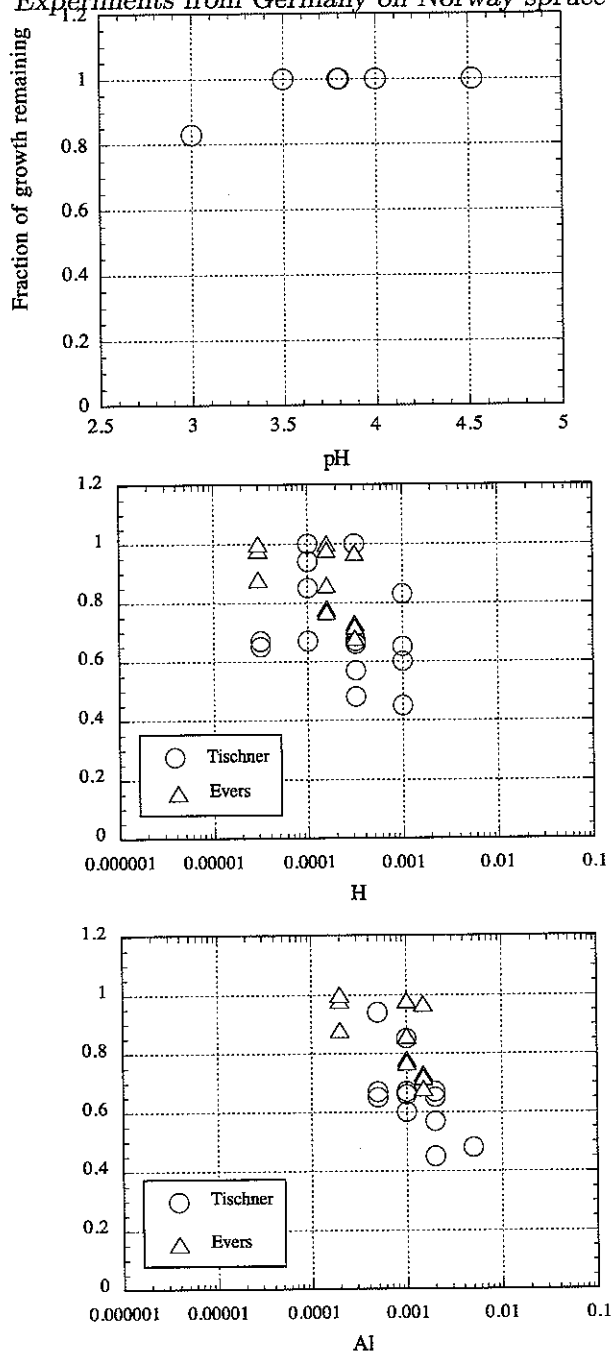
Figure 13: The relationship between individual parameters such as pH, the soil solution of H and Al and growth for Norway spruce (*Picea abies*). The upper diagram involve experiments with no Al present. The middle diagram show dependence on H-ion, but include different Al levels. The bottom diagram show the dependence on Al at different soil pH values.

9   Laboratory results for trees

9.1   Conifers

The data used in this study was when needed normalized by using the control experiments. The example explained for Swedish and Finnish data, illustrates how data was interpreted. Total biomass production, plant weight,root weight, or root elogination was used in the order listed, depending on what was available. The whole shape of the curve can be determined for a majority of the species investigated.

9.1.1   Spruce

Fig. 14 show the results from laboratory assays for Norway spruce (*Picea abies*), excluding the data of Arovaara and Ilvesniemi (1990). In the diagram the white dots represents Scandinavian studies, and black dots German studies using Norway spruce. It is apparent that there is no significant difference in the response with respect to plant origin. Root growth decline in laboratory experiments by Abrahamsen, (1984) as a function of soil solution BC/Al for Norway spruce is shown in Fig. 20. The relation is based on Ca only as Mg concentrations were not available. Assuming the soil solution concentration of Mg to be equal to the concentration of Ca would make the results of this experiment equal to other results for Norway spruce. The data suggests that there may be an additional antagonistic effect of Ca in addition to the 1:1 BC/Al effect suggested by other data.

The goodness of fit of the response function has been illustrated in Fig. 16. It can be seen that the response function has a standard deviation of +/-20%. The correlation of observed experimental points to the empirical response best fit function is $r^2 = 0.67$.

Fig. 15 shows the response of red spruce (*Picea rubens*). The sensitivity of Red spruce and Norway spruce appear to be identical. balsam fir and sitka spruce, red spruce, black spruce and White spruce are North American tree species.

Fig. 17 show the response for sitka spruce (*Picea sitchensis*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*). It can be seen that sitka spruce, white spruce and black spruce are very tolerant to Al.

All the spruce species investigated consistently follow the unspecific mechanism. The data of Arovaara and Ilvesniemi (1990) and Ilvesniemi (1992) was stratified with respect to seedling age as was seen from Fig. 10, only data for the younger seedlings were used in the comparisons, as the rest show too much scatter.

Entry et al. (1987) investigated the response of the mycorrhiza associated with balsam fir. It appears to show the same response as balsam fir, as can

be seen by comparing Fig. 18 and Fig. 27.

Fraser fir appear to quantitatively follow the exact same decline pattern in Vermont and New York as red spruce, and within very narrow limits. This was used to set the sensitivity of fraser fir equal to that of red spruce (Krahl-Urban et al., 1988; Hutchinson et al., 1986; McCormack and Steiner, 1978). For white, sitka and black spruce, K=0.13, for red and Norway spruce, K=0.33 gave the best fit.

Fig. 20 show results from experiments by Abrahamsen et al., (1984), which may indicate a slight additional antagonism of Ca in addition to the 1:1 of the BC/Al ratio. This leaves a possibility for the unspecific mechanism to in reality be a Gaines-Thomas mechanism, even if the other data is not sufficiently accurate to decide the issue, nor do the response data scatter particularly much between experiments with differing BC concentration. Fig. 42 show the results as compared to field growth response data, and the shift towards higher tolerance to Al in the field is evident.
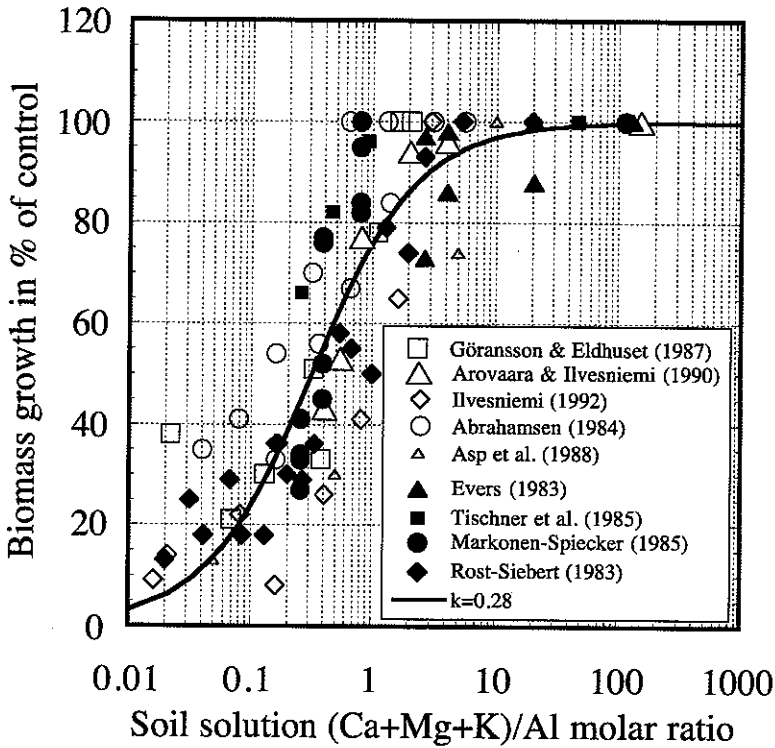
Figure 14: The relation between laboratory observations of growth decline and root growth decline in laboratory experiments for Norway spruce (*Picea abies*) including all available data. White dots respresents trees of Scandinavian studies, black dots German studies. There is no significant difference between Scandinavian and German trees.
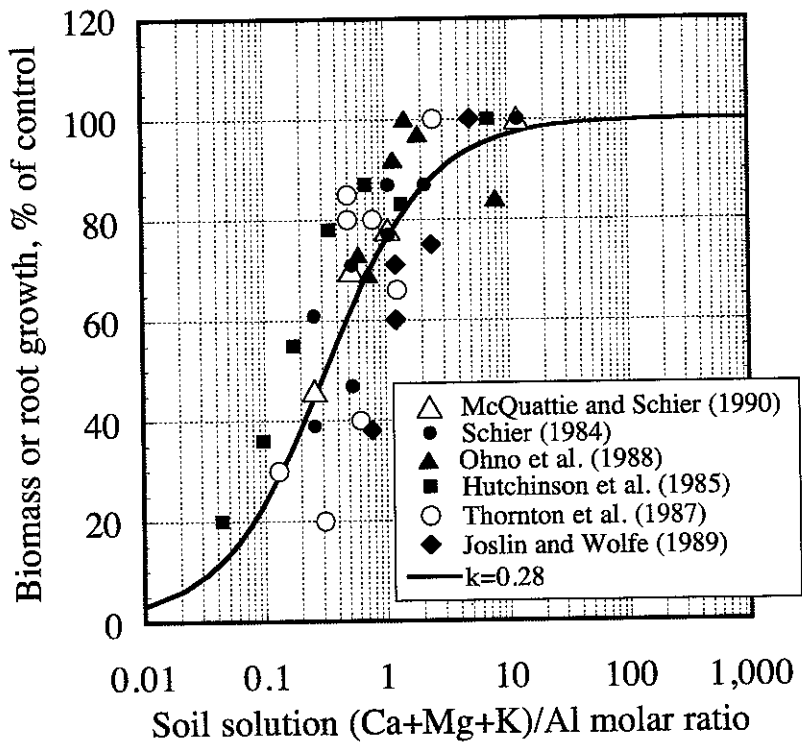
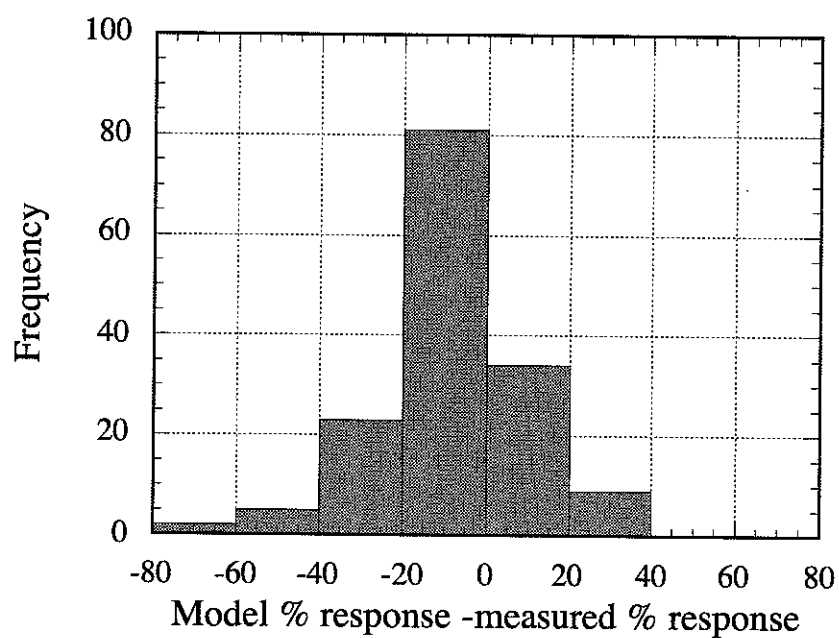Figure 15: Response to soil Al in laboratory experiments for red spruce (*Picea rubens*).

Figure 16: Distribution of observed points around the response function. The scatter is a normal distribution, the standard deviation is $+/-15\%$. The correlation coefficient is $r^2=0.67$
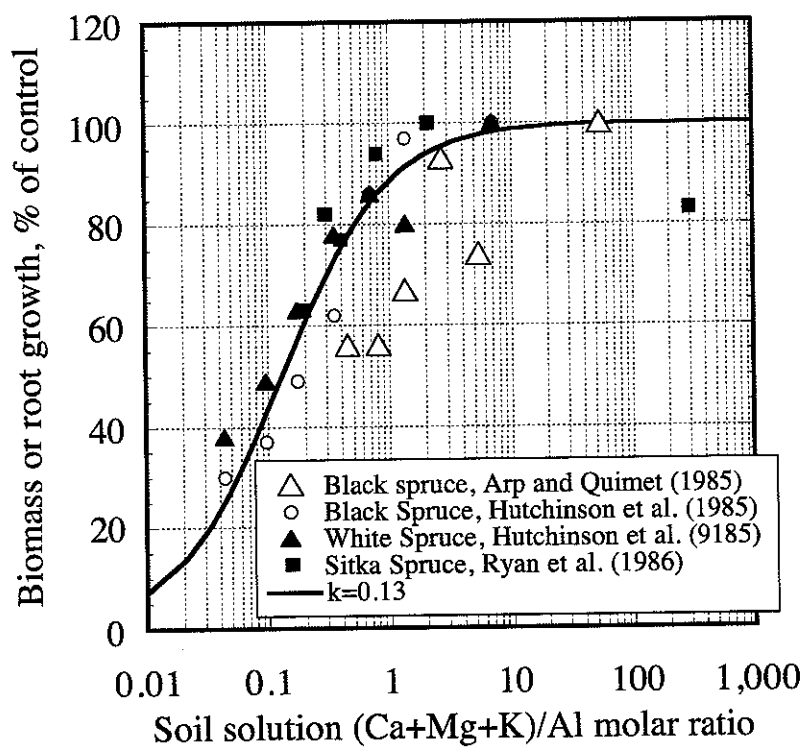
Figure 17: Response to soil Al in laboratory experiments for different types of spruce; white spruce (*Picea glauca*), black spruce (*Picea mariana*) and sitka spruce (*Picea sitchensis*).
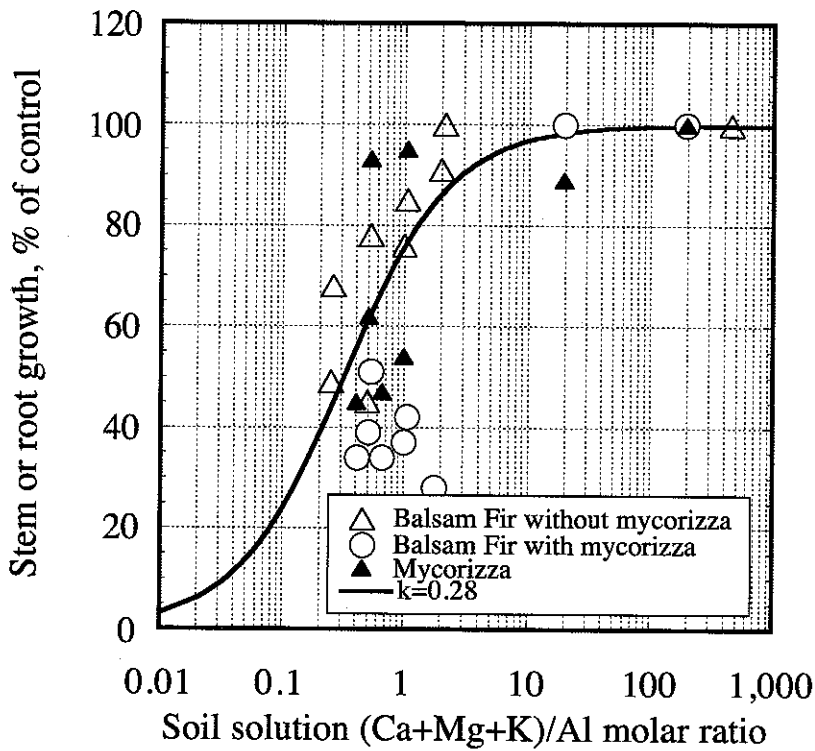
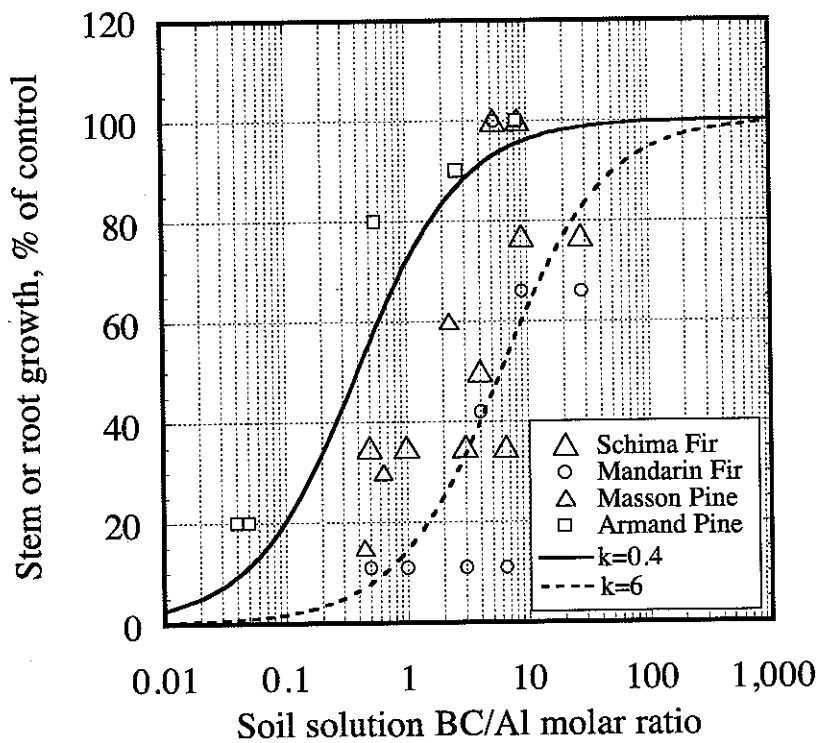Figure 18: Response to soil Al in laboratory experiments for balsam fir (*Abies balsamea*).

Figure 19: The response data for different Chinese fir and pine species such as masson pine (*Pinus massonii*), Chinese fir (*Schima superba*), mandarin fir (*Cunninghamia lanceolata*) and armand pine (*Pinus armandii*). The data for masson and armand pine is field data on stem growth.
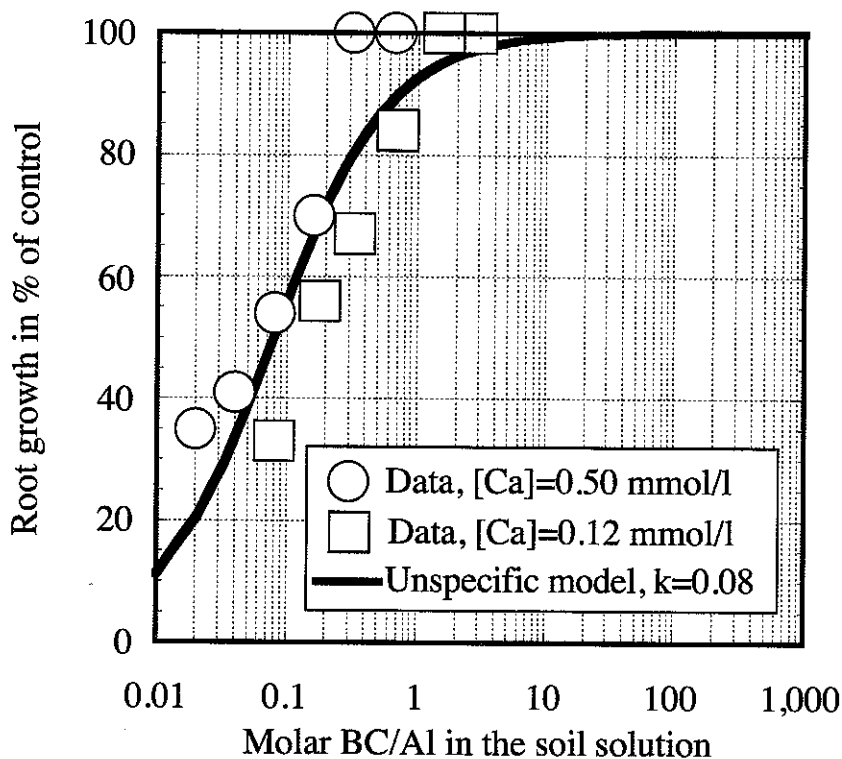
Figure 20: Growth decline in laboratory experiments by Abrahamsen, (1984) as a function of soil solution BC/Al for Norway spruce. The data suggests that there may be an additional antagonistic effect of Ca in addition to the 1:1 BC:Al effect suggested by other data.

9.1.2 Pines

Fig. 21 show the response to Al as observed in laboratory assays for different types of pine such as scots pine (*Pinussylvestris*, armand pine (*Pinus armandii*), masson pine (*Pinus massoniana*), aleppo pine (*Pinus halepensis*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), longleaf pine (*Pinus palustris*), monterey pine (*Pinus radiata*) and loblolly pine (*Pinus taeda*).

Fig. 22 show the data available for scots pine only. There is significant scatter visible when all data is shown unstratified this way, and can serve to illustrate some of the variance in results between experiments. The scatter can be shown to be caused by natural variation in the plant material used, differences in medium pH, and differences between experimental setups where organic exudates can build up and where they are removed by drainage. The black symbols in the diagram all represent Scandinavian studies, the other are German studies (Tischner 1983, Keltjens and van Loenen 1989) or a North American study (McCormick and Steiner 1978). The data of Keltjens and van Loenen (1989) show a very steep response, a similar response was also recorded for other species in their experiments. Their results should be used with caution, since they are not completely consistent with other studies.

In Fig. 23 scots pine data was excluded. It can be seen how the pines are divided in two levels of sensitivity to Al. Armand, aleppo, monterey and white pine appear as more resistant. The data for armand and masson pine come from field data and may also be subject to alternative interpretations of the baseline data. Thus the sensitivity for armand and masson pine is only approximate, the plants may be significantly more sensitive.

Pines seems to follow the Vanselow mechanism, with the exception of the data by Arovaara and Ilvesniemi (1990), which indicate less sensitivity and unspecific response. The responses cluster including plants with semi-quantitative data, into two groups with respect to Al sensitivity.

Data from experiments by Göransson and Eldhuset (1991) show that there is no difference in response between trees infected with mycorrhiza and plants witout mycorrhiza (Fig. 26). This confirms the same type of result obtained for balsam fir. Aleppo pine is a subtropical pine species occurring throughout the Eastern Mediterranian and Middle East area. White pine, pitch pine, monterey pine, longleaf pine, slash pine, sand pine, jack pine and loblolly pine are North American pine species, pitch pine, monterey pine, longleaf pine, masson pine and armand pine occur in subtropical regions such as southern United States, southern China and East Asia. Whether the pine has needles in groups of 2, 3 or 5 does not seem to be connected to sensitivity.
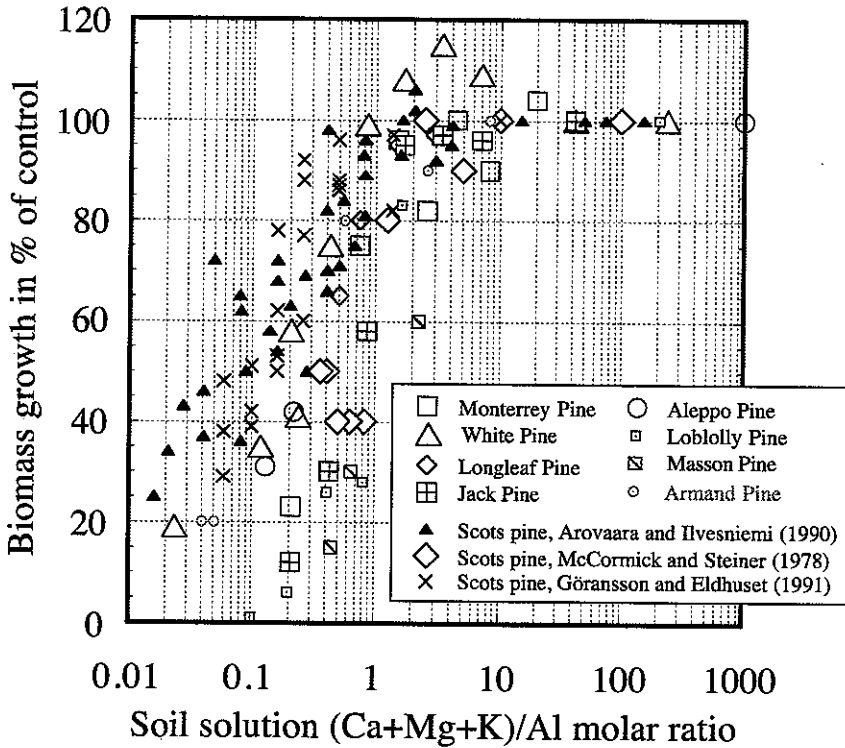
Figure 21: All response data available for different pine species such as armand pine (*Pinus armandii*), masson pine (*Pinus massoniana*), aleppo pine (*Pinus halepensis*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), scots pine (*Pinus sylvestris*), longleaf pine (*Pinus palustris*), monterey pine (*Pinus radiata*) and loblolly pine (*Pinus taeda*).
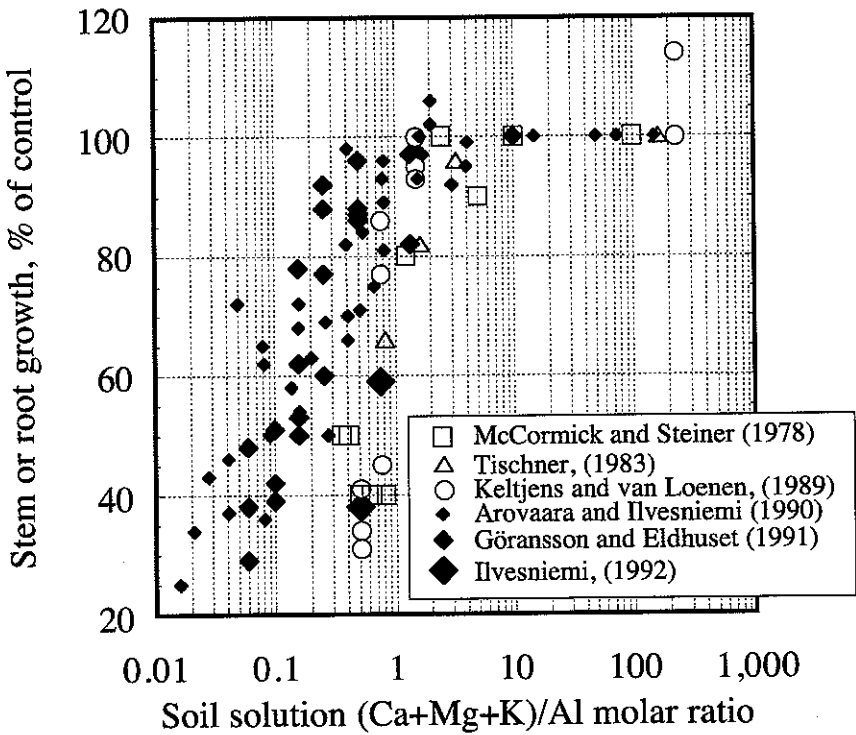
Figure 22: The response data for scots pine (*Pinus sylvestris*) according to different studies. Black symbols represents Scandinavian studies.
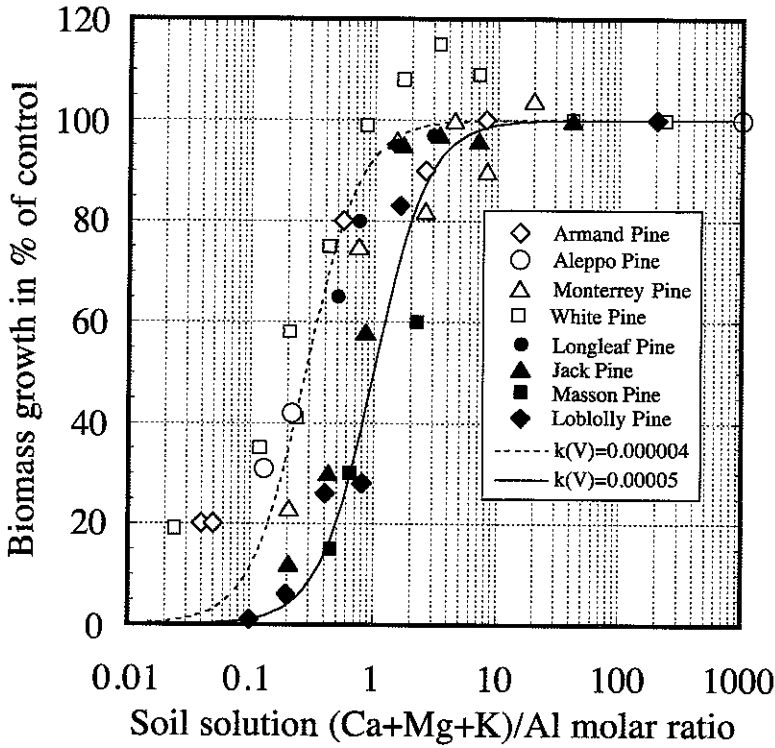
Figure 23: The response data for different pine species except scots pine, show a Vanelow type of response to soil Al, such as armand pine (*Pinus armandii*), masson pine (*Pinus massoniana*), aleppo pine (*Pinus halepensis*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), longleaf pine (*Pinus palustris*), monterrey pine (*Pinus radiata*) and loblolly pine (*Pinus taeda*).

9.1.3 Other conifers and cypresses

Fig. 19 show results for Chinese fir and mandarin fir as compared to masson pine and armand pine. Chinese fir and mandarin fir show the same sensitivity to Al as Norway spruce. Armand pine and masson pine are among the most sensitive of the pines.

American Pacific coast conifers such as western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) are shown in Fig. 24. Hemlock, red cedar and trees of the cypress type appear to be very resistent to soil Al.

Larch (*Larix decidua*) and douglas fir (*Pseudotsugas menziesii*) is shown in Fig. 25. Two different studies (Ryan et al., 1988a,b and Keltjens and van Loenen, 1989) yield somewhat different sensitivities for douglas fir. The study of Keltjens and van Loenen (1989), showed significant mortality with increasing Al for douglas fir and larch, but near insensitivity for the surviving fractions in the experiments. The study of Keltjens and van Loenen (1989) used one year nursery plants. Keltjens and van Loenen 1989 also obtained results for pine which also showed pecularities. Ryan et al., (1988) found more insensitivity to soil solution Al than Keltjens and van Loenen, (1989). Data for larch and douglas biomass represent total biomass production in the experiments, including mortality. One possibility is that the results of Ryan et al. (1988) should be given more weight, giving douglas fir the same sensitivity as hemlock.

9.1.4 Mycorrhiza

Mycorrhiza is considered to be an important part of the root system of a tree, and the tree and mycorrhiza fungus live in a symbiosis. Mycorrhiza is generally seen as a kind if integrated extension of the root system, and may be as large or larger than the root system it self. The mycorrhiza system is generally considered to be very important for the nutrient collecting capability of the tree, and anything that could affect the functioning of the mycorrhiza system would be of interest.

Accordingly, a few experiments have been designed to study the effect of soil acidity of roots without mycorrhiza and trees with roots infected with mycorrhiza. The data available for balsam fir (Entry et al., 1987) and scots pine (Göransson and Eldhuset, 1987) may seem to suggest that mycorrhiza is of no relevance for the response to Al whether the root is infected by mycorrhiza or not. Entry et al., (1987) showed the effect of soil acidity and Al directly on mycorrhiza and other soil microorganisms. Similar results were also obtained for bacteria (Ohno et al. 1988). The response isotherm for mycorrhiza alone appears to be similar to that of spruce and pine (Figs. 26, 18, 27).

For 3 different species mycorrhiza, the Vanselow response type was found

and K(Vanselow)=000.5, yielding a BC/Al limit of 1. For the fungi (*Actiniomycetes*), K=0.00005 and BC/Al-limit= 2. The response for several bacteria was also found, it was very sensitive K(Vanselow)=0.02 and BC/Al-limit=6. The same types of responses are found for fungi and bacteria as for trees without any exception. This has far-reaching consequences for the interpretation of the empirically observed response functions.

A much more comprehensive review of the response of soil fungi and soil bacteria involved in organic matter decomposition has been carried out by Jönsson et al. (1994). We would recommend this to the reader working with mycorrhiza and soil microorganism reaction to soil acidity. That investigation show bacteria in general to be very sensitive to soil acidity, and fungi showed sensitivity comparable to that of Norway spruce. It also show that the response equations apply to soil microorganisms.

9.1.5   Response functions and critical limits

Plant species, latin name, type of Al damage mechanism, coefficient of the response function, and BC/Al ratio at which growth has been reduced to 80% of normal is listed for conifers in Tab. 20. It approximates the BC/Al-limit for reduction to 90% of normal growth under field conditions.
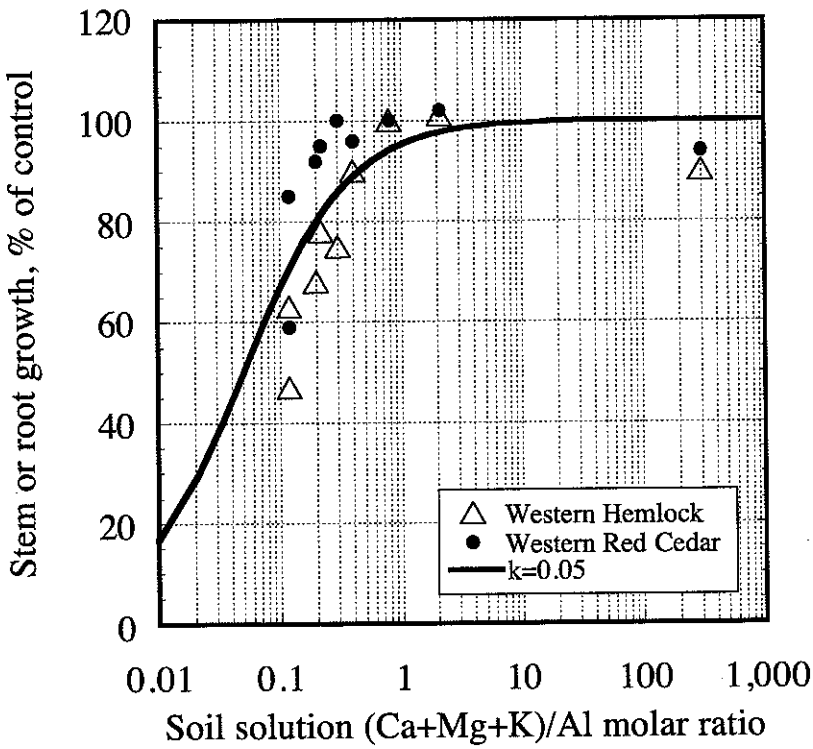
Figure 24: The response data for two American Pacific coast conifers, western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). The data was taken from seedling experiments by Ryan et al., 1989a, b and Keltjens and van Loenen, (1989).
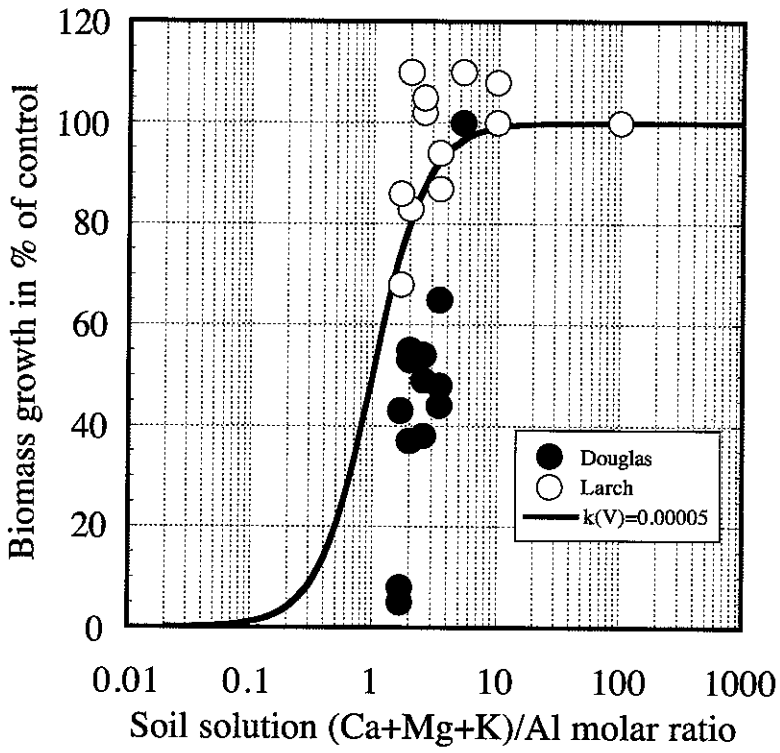
Figure 25: The response data for larch (*Larix decidua*) and douglas fir (*Pseudotsugas menziesii*).
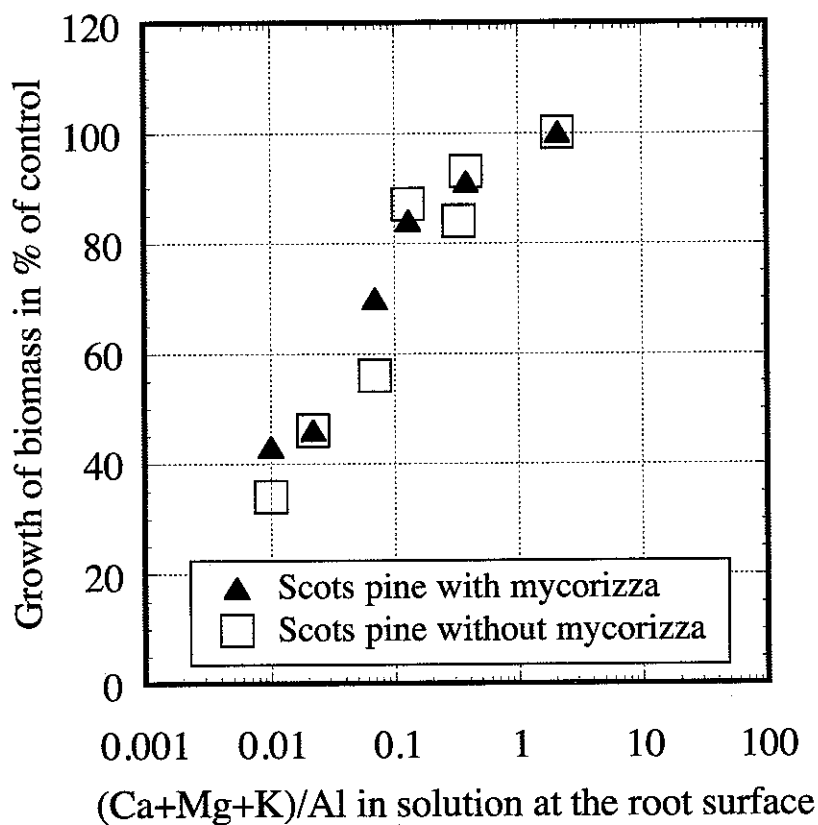
Figure 26: A comparison between experiments with scots pine without mycorrhiza and scots pine with mycorrhiza, revealed no difference in the response of growth to soil solution Al (Göransson and Eldhuset 1987). There is a near 1:1 correspondence between the response to Al for pine with and without mycorrhiza. It does not appear as mycorrhiza does much to offer the plant extra protection.

Figure 27: The response data for different types of mycorrhiza on balsam fir, actinomycetes and soil bacteria. Data suggests that mycorriza is equal or more sensitive to soil Al than the tree. THis suggests that the symbiosis of mycorrhiza may be seriously disturbed by soil acidification.

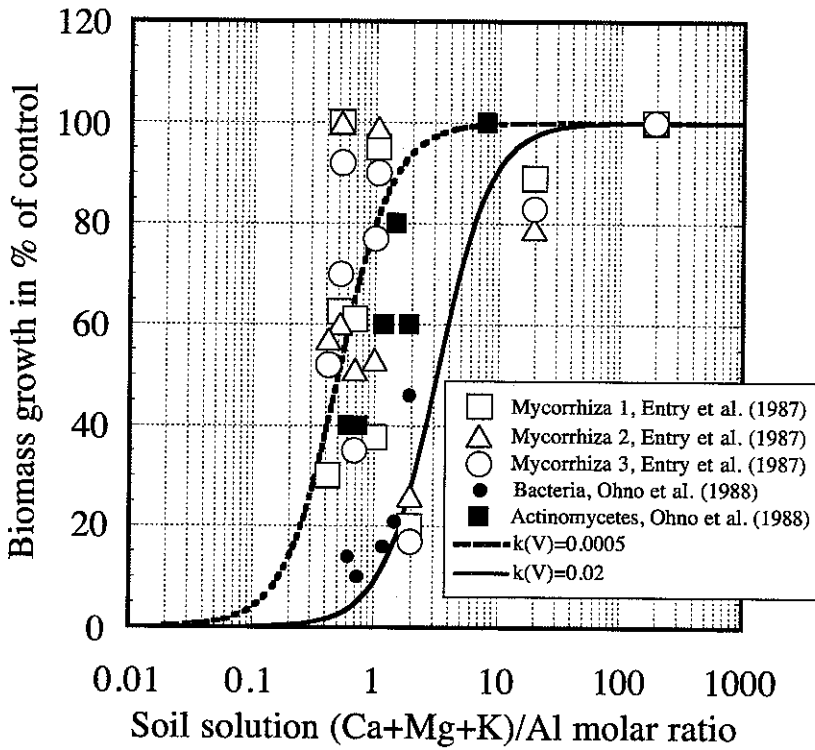| English	Latin name	Reaction type	K-value	BC/Al(crit)
Sitka spruce	*Picea sitchensis*	Unspecific	K=0.1	0.4
White spruce	*Picea glauca*	Unspecific	K=0.2	0.5
Black spruce	*Picea mariana*	Unspecific	K=0.25	0.8
East Siberian fir	*Abies nephroleptis*	n.d.	n.d.	1
Szechuan fir	*Abies recurvata*	n.d.	n.d.	1
Himalayan fir	*Abies pindrow*	n.d.	n.d.	1
Grand Himalayan fir	*Abies spectabilis*	n.d.	n.d.	1
Western Szechuan Chinese fir	*Abies squamata*	n.d.	n.d.	1
Himalayan spruce	*Picea smithiana*	n.d.	n.d.	1
Bhutan spruce	*Picea spinulosa*	n.d.	n.d.	1
Altai spruce	*Picea obovata*	n.d.	n.d.	1
Balsam fir	*Abies balsamea*	Unspecific	K=0.3	1.1
Norway spruce	*Picea abies*	Unspecific	K=0.35	1.2
Red spruce	*Picea rubens*	Unspecific	K=0.35	1.2
Fraser fir	*Abies fraseri*	Unspecific	K=0.35	1.2
Silver fir	*Abies alba*	n.d.	n.d.	1.4
Faber fir	*Abies fabri*	n.d.	n.d.	2
Shensi fir	*Abies chensiensis*	n.d.	n.d.	10
Yunnan Chinese fir	*Abies delavayi*	n.d.	n.d.	10
Western Chinese fir	*Abies fargesii*	n.d.	n.d.	10
Central China spruce	*Picea bractyla*	n.d.	n.d.	10
Likiang spruce	*Picea likiangensis*	n.d.	n.d.	10
Chinese fir	*Schima superba*	Unspecific	K=2	10
Mandarin fir	*Cunninghamia lanceolata*	Unspecific	K=6	20
White pine	*Pinus strobus*	Vanselow	K=0.000002	0.5
Aleppo pine	*Pinus halepensis*	Vanselow	K=0.000002	0.5
Slash pine	*Pinus elliottii*	Vanselow	K=0.000002	0.5
Sand pine	*Pinus clausa*	Vanselow	K=0.000004	0.6
Shortleaf pine	*Pinus echinata*	n.d.	n.d.	0.6
Monterey pine	*Pinus radiata*	Vanselow	K=0.0008	0.8
Armand pine*	*Pinus armandii*	Vanselow	K=0.000015	1*
Arolla pine	*Pinus cembra*	n.d.	n.d.	1
Dwarf mountain pine	*Pinus mugo*	n.d.	n.d.	1
Scots pine	*Pinus sylvestris*	Vanselow	K=0.00002	1.2
Scrub pine	*Pinus virginiana*	Vanselow	K=0.00002	1.2
Pitch pine	*Pinus rigida*	Vanselow	K=0.00002	1.2
Jack pine	*Pinus banksiana*	Vanselow	K=0.00003	1.5
Loblolly pine	*Pinus taeda*	Vanselow	K=0.00003	1.5
Longleaf pine	*Pinus palustris*	Vanselow	K=0.00005	2
Ponderosa pine	*Pinus ponderosa*	n.d.	n.d.	2
Red pine	*Pinus resinosa*	n.d.	n.d.	2
Masson pine**	*Pinus massonii*	Vanselow	K=0.0001	4
Western red cedar	*Thuja plicata*	Vanselow	K=0.0000001	0.09
Northern white cedar	*Thuja occidentalis*	n.d.	n.d.	0.1
Western hemlock	*Tsuga heterophylla*	Vanselow	K=0.0000003	0.2
Douglas fir	*Pseudotsuga menzerii*	Vanselow	K=0.0000004	0.3
Japanese cedar	*Cryptomeria japonica*	n.d.	n.d.	1
Larch	*Larix decidua*	Vanselow	K=0.00005	2

Table 20: Response type and estimated aluminium response coefficients for pine and other conifers. The BC/Al-limit represents growth reduced to 80% of unaffected. *: BC/Al_{crit}=0.5, based on field estimate. **: BC/Al_{crit}=2.0 under field conditions.

English name	Latin name	Method	Sensitivity class	Estimated BC/Al(crit)
Oriental thuja	*Thuja orientalis*	F&BA	Strong	0.3
Chinese junipher	*Junipherus chinensis*	F&BA	Strong	0.3
Mourning cypress	*Chamaecyparis funebris*	F&BA	Strong	0.3
Yew pine	*Podocarpus macrophyllus*	F&BA	Strong	0.3
Japanese black pine	*Pinus thunbergiani*	F&BA	Relatively strong	0.7
Masson pine	*Pinus massonii*	F	Slightly sensitive	4*
Mandarin fir	*Cunninghamia lanceolata*	F	Slightly sensitive	20*
Deodar cedar	*Cedrus deodora*	F	Slightly sensitive	1.4
Japanese cedar	*Cryptomeria japonica*	F	Slightly sensitive	1.4
Chinese yew	*Taxus chinensis*	F	Slightly sensitive	1.4
Loblolly pine	*Pinus taeda*	F	Slightly sensitive	1.5*
Swamp cypress	*Taxodium disticum*	F	Sensitive	2
Dawn redwood	*Metasequoia glyptostroboides*	F	Very sensitive	6

Table 21: Relative tolerance of coniferous trees to acid deposition as screened in Chinese bioassays (BA) and as derived from field surveys (F). * represents values estimated in accurate laboratory experiments.

9.2   Deciduous and broadleaf trees

9.2.1   Temperate and boreal trees

Fig. 28 show the bioassay response for European birch or silver birch (*Betula pendula*), the American species; paper birch (*Betula papyrifera*), grey birch (*Betula populifolia*) and yellow birch (*Betula alleghaniensis*). There is good consistency between experiments, despite differences in base cation concentrations and birch species. Silver birch is more tolerant to Al than paper birch and aspen. Paper birch is more sensitive than European beech, European oak and sugar maple. There is good consistency between the results of Göransson and Eldhuset (1987) and the other results, despite fundamental differences in experimental design.

Aspen (*populus tremula*) and European alder (*Alnus glutinosa*) is shown in Fig. 29. Alder appear to be significantly more sensitive than birch, beech and oak. Data was taken from from McCormick and Steiner, 1978; Steiner et al., 1980, 1984; and McCormick and Amendola, 1983.

Fig. 30 show a comparison between laboratory bioassay results for European oak (*Quercus robur*) and American red oak (*Quercus rubra*). Both trees show the same response.

Fig. 31 show response data for European beech (*Fagus sylvatica*) and American beech (*Fagus grandifolia*) from laboratory bioassays in Germany and Sweden, as compared to the available field data. beech apparently follow the Vanselow response mechanism, and show little elasticity in its response to Al as compared to spruce. This implies that there is a small distance from

initial growth decline to a full dieback. The data was taken from Rost-Siebert, 1983; Asp and Berggren, 1990; field data from Ulrich (1984). American beech appear to be slightly more tolerant to soil acidity than its European relative.

Fig. 32 show laboratory bioassay results for sugar maple (*Acer saccharum*), trees from Northeastern United States and Eastern Canada. The tree is used for commercial collection of maplesyrup. Both stem growth and root growth data are shown and indicate the same response.

Fig. 33 show laboratory data for two North American bushes, honey locust (*Gleditsia triachantos*) and autumn olive (*Elaeagnus umbellata*), a relative of hawthorn. Alder is included for comparison. The soil acidity response of honeylocust is comparable to the response of sugar maple in terms of Al sensitivity, whereas the bush autumn olive is much more sensitive.

Crack willow (*Salix fragilis*) seem to be the only temperate tree discovered so far to follow the Gapon mechanism. It shows a large elasticity in the response to Al, making the determination of a limiting Al concentration less meaningful. The data is shown in Fig. 39. The large elasticity implies that even if growth is significantly affected by Al, the tree will still survive without difficulty, adjusting to a lower growth activity level.

9.2.2 Tropical and subtropical trees

Fig. 34 show the response of teak (*Tectona grandis*) in Nigerian plantations as compared to guapira (*Guapira olfersiana*), and eucalyptus (*Eucalyptus gummifera*), all are trees belonging to subtropical or tropical climate. Guapira is a tree of the tropical mountain cloud-forest in Venezuela, South America. It grows under very humid conditions. It appears as if eucalyptus is the most sensitive of the three tree species to soil acidity when this is expressed as the $(Ca+Mg+K)/Al$ ratio.

Fig. 35 shows the data for cotton (*Gossypium hirsutum*). For cotton, two different interpretations are available of the base cation data. The one giving a smooth response curve was chosen before the interpretation giving a discontinuity in the curve.

Sour orange (*Citrus aurantium*) and Japanese mandarin orange (*Citrus natsudaidai*) is shown in Fig. 36. The data originate from both seedling experiments, younger trees and trees several years old in a Japanese nursery.

Peach (*Prunus persica*) is shown in Fig. 37. Peach is a fruit tree found in subtropical areas, originating from the southern slopes of the Caucasus mountains. Peach is closely related to apricot, plum and cherry. The Al sensitivity is comparable with honey locust and beech. The experiments were carried out on young trees in pots.

The response data for tea (*Camillia sinensis*) is shown in Fig. 38. Tea is reportedly tolerant to Al, and it can take up large amounts of Al in its

leaves and purge it by letting the leaves fall. The response to soil acidity is apparently of the unspecific type. The diagram show the response to Al at two P levels in the nutrient solution. Much P seem to make the plant more tolerant to Al. The response curve has a peculiar form, sinking at low and high BC/Al ratios. Why this happends is not understood at the moment, but it is possible that Al may complex P in a form not readily available to the plant. In the experiments reviewed, growth of eucalyptus as well as tea declined at Al concentrations below 0.3 mM/l for unknown reasons.

Coffee (*Coffea arabica*) is the only tree beside crack willow (*Salix fragilis*) so far discovered to follow the Gapon mechanism. Coffee is a tree preferring tropical climate. Both tree species both show a large elasticity in the response to Al as is illustrated in Fig. 39. This explains the good success of coffe on tropical lateritic red soils. It also indicates that increasing the BC/Al ration may increase growth of the tree. How this affects the crop of coffe beans could not be determined.

9.2.3   Response functions and critical limits

Plant species, latin name, type of Al response mechanism, coefficient of the response function, and BC/Al ratio at which growth has been reduced to 80% of normal is listed for leaf trees in Tab. 22. It approximates the BC/Al-limit for reduction to 90% of normal growth under field conditions.
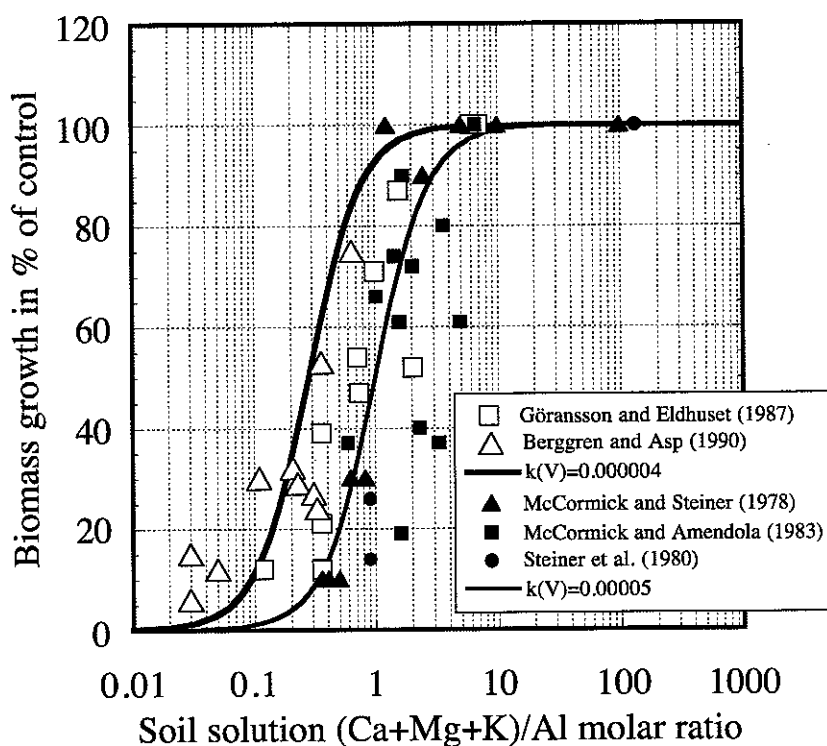
Figure 28: Comparison of response data from individual bioassay experiments for silver birch (*Betula pendula*) shown as white dots and lumped results for American birch species shown as black dots, for the North American species paper birch (*Betula papyrifera*), grey birch (*Betula populifolia*) and yellow birch (*Betula alleghaniensis*).
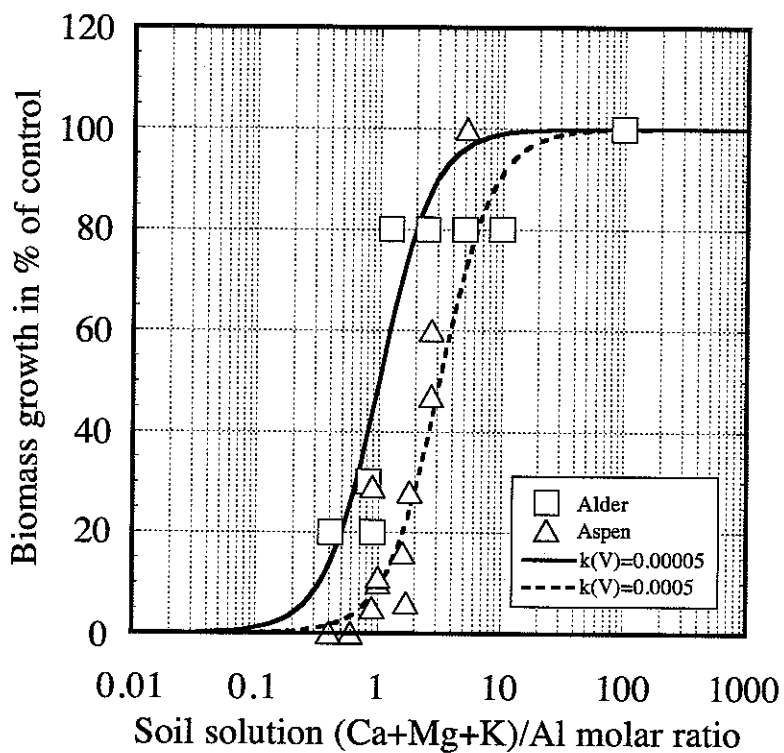
Figure 29: The response data for alder (*Alnus glutinosa*) and aspen (*populus tremula*).
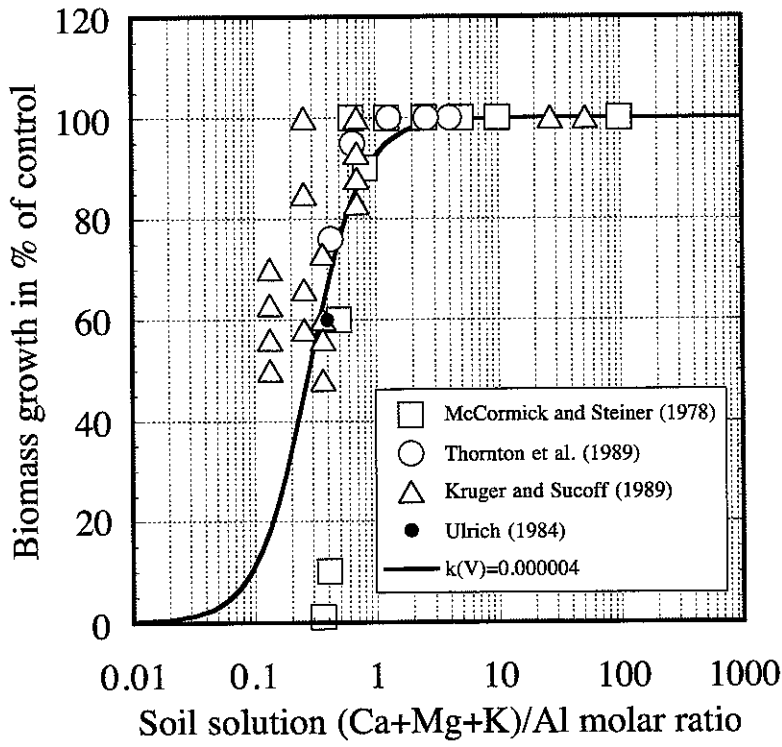
Figure 30: The relation between field observations of growth decline for oak (*Quercus robur*), red oak (*Quercus rubra*) as a function of BC/Al ratio. German field data for oak has been included (Black dot, Ulrich 1984).
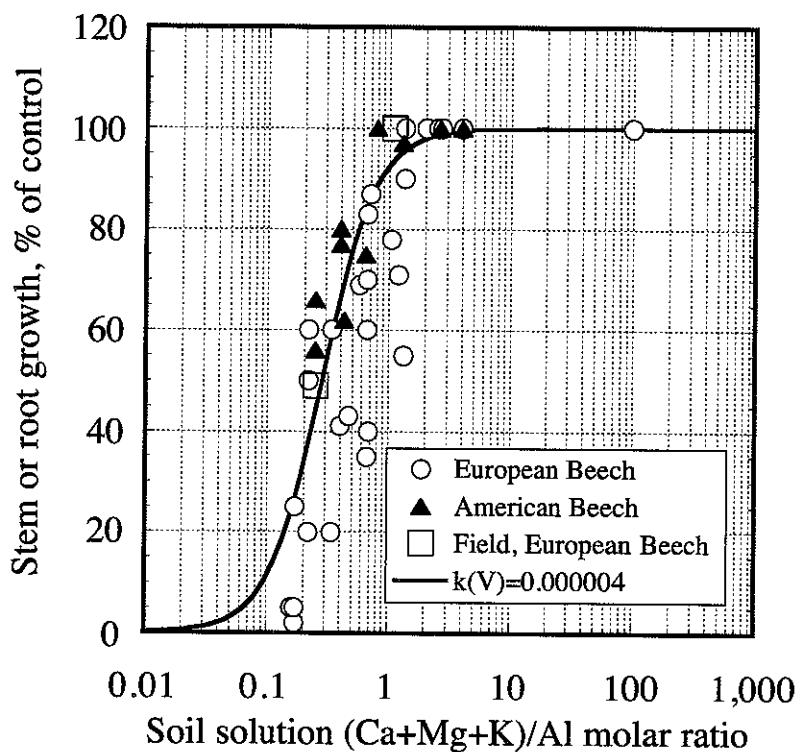
Figure 31: The relation between laboratory experiments and field observations of growth decline for European beech (*Fagus sylvatica*), American beech (*Fagus grandifolia*) in relation to the BC/Al ratio.
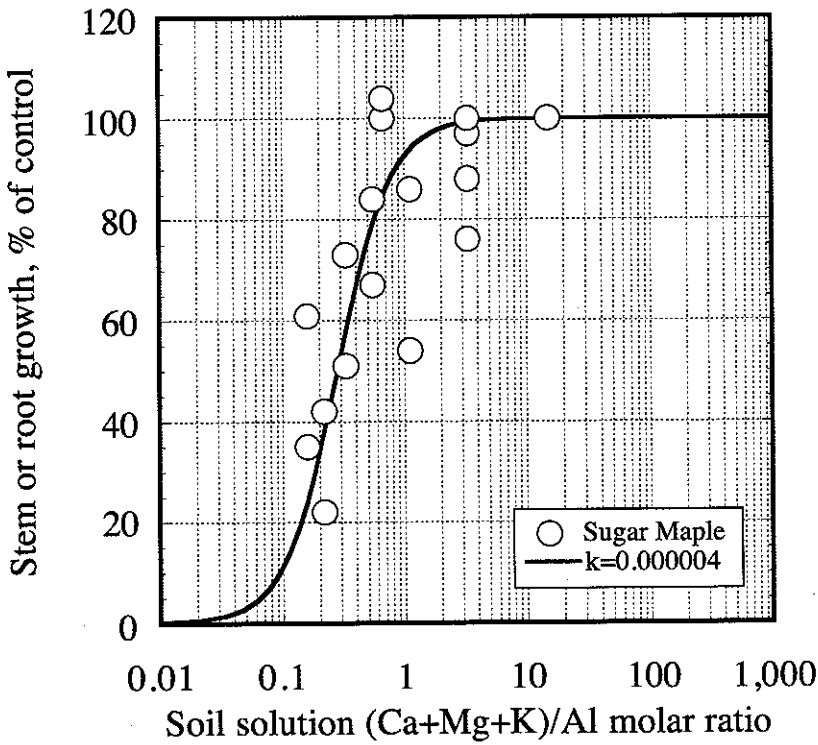
Figure 32: The response data for sugar maple (*Acer saccharum*). The data was taken from Thornton et al., 1986.
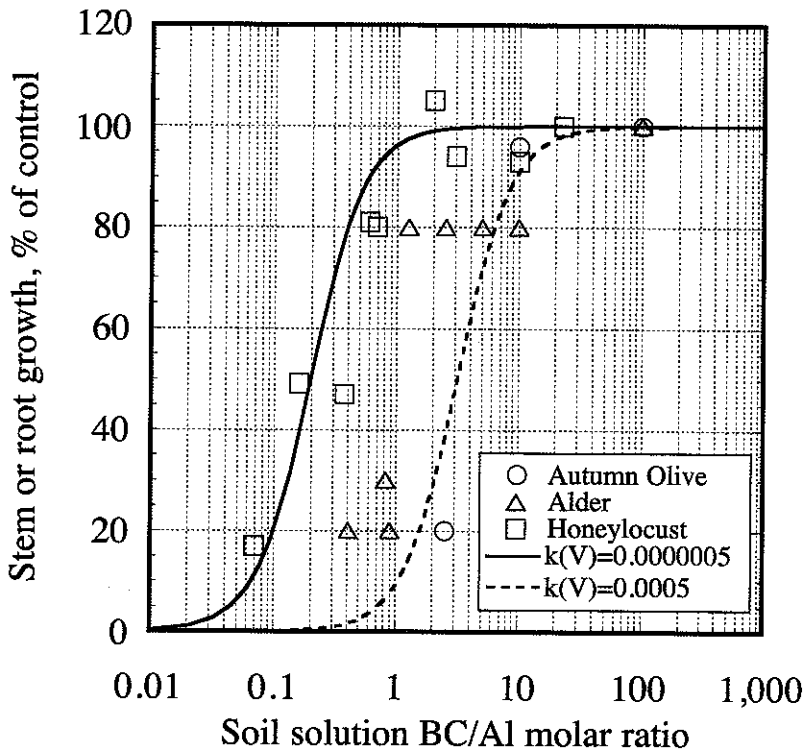
Figure 33: The response data for honey locust or (Swe; korstörne) (*Gleditsia triachantos*) and autumn olive (*Elaeagnus umbellata*). Autumn olive, a North American bush related to hawthorn and rowan. Honeylocust and autumn olive appear follow the Vanselow mechanism. The data was taken from Sucoff et al., 1989; Thorton et al, 1985, 1983.
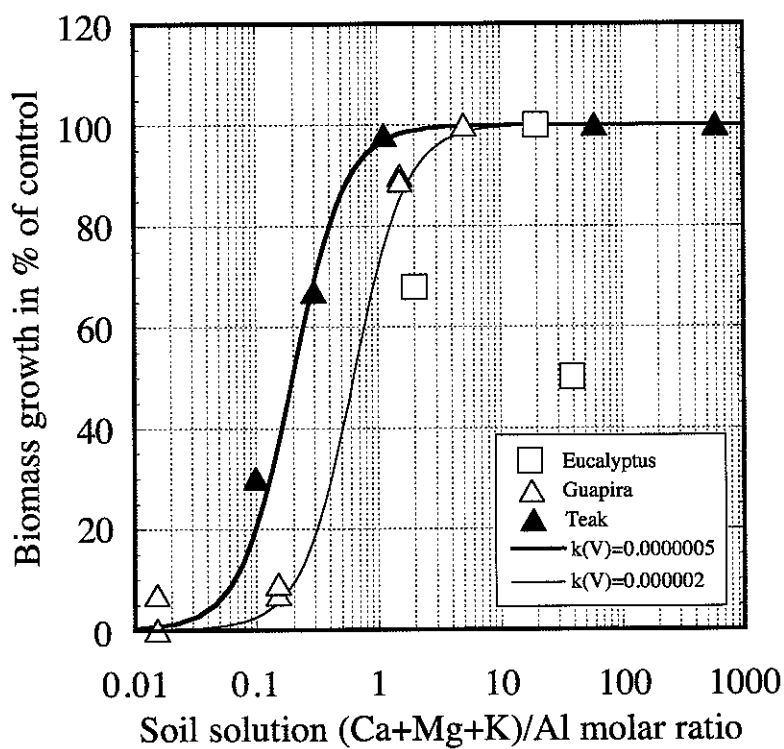
Figure 34: The response data for Nigerian teak (*Tektona grandis*). Eucalyptus (*Eucalyptus gummifera*) and Venezuelan guapira (*Guapira olfersiana*), a cloud-forest tree.
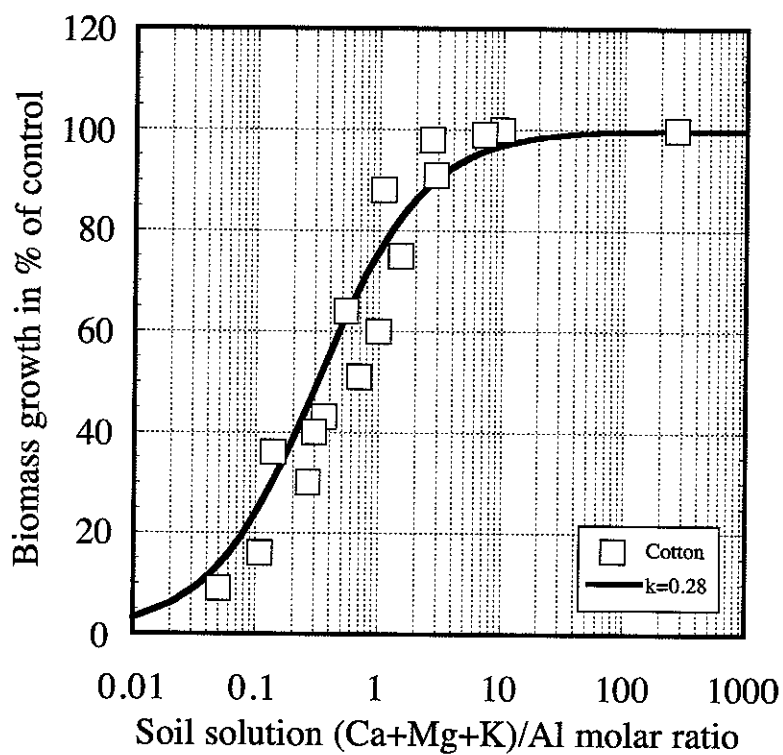
Figure 35: The response data for domesticated Indian cotton (*Gossypium hirsutum*).
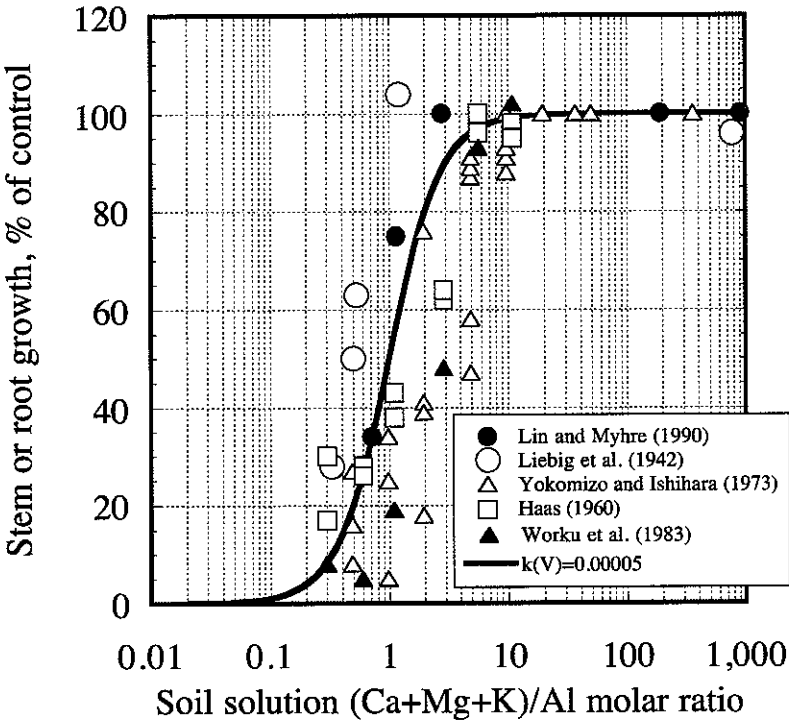
Figure 36: The response data for sweet orange (*Citrus sinensis*) and Japanese mandarin orange (*Citrus natsudaidai*).
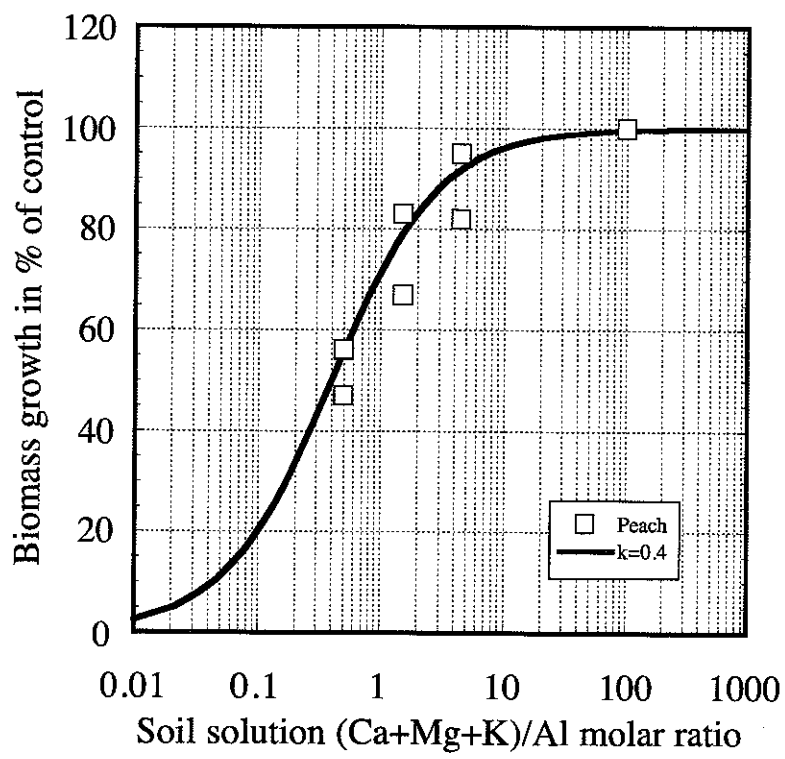
Figure 37: The response data for peach (*Prunus persica*).
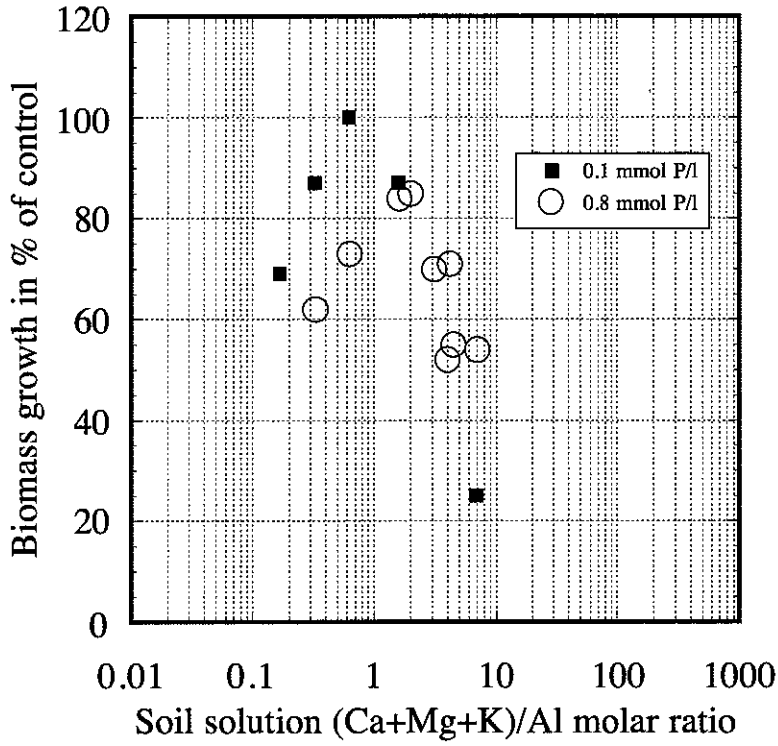
Figure 38: The response data for Chinese tea (*Camillia sinensis*). The diagram show the response to Al at two P levels in the nutrient solution. Much P seem to make the plant more tolerant to Al.

Figure 39: Response data for crack willow (*Salix fragilis*) and coffee (*Coffee arabica*). willow and coffee were the only plants of those investigated that showed behavior according to the Gapon mechanism. The large elasticity implies that even if growth is significantly affected by Al, the tree will still survive without difficulty, adjusting to a lower growth activity level.

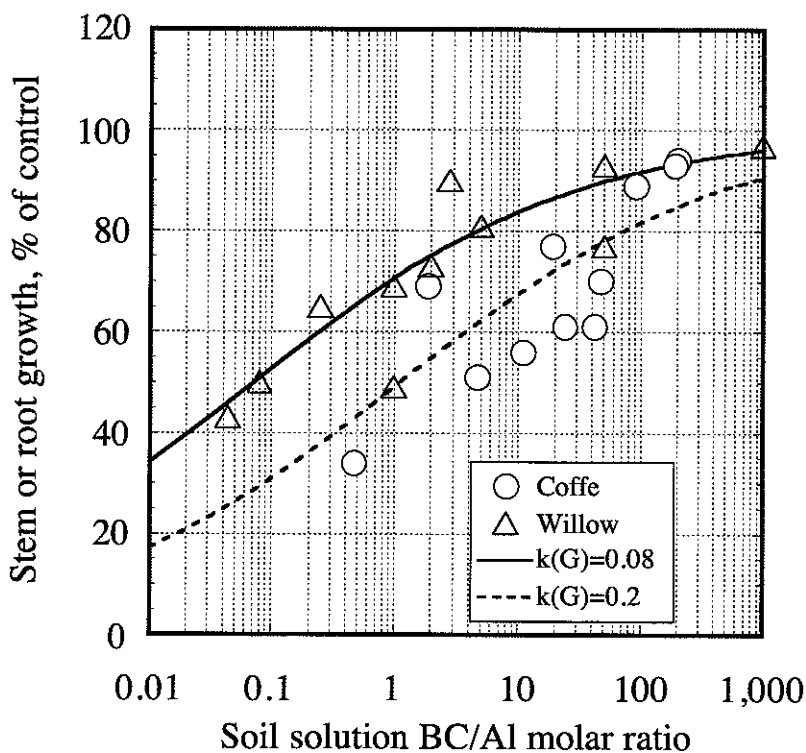| Plant species	Latin name	Reaction type	K-value	BC/Al(crit)
Honey locust	*Gleditsia triachantos*	Vanselow	K=0.0000005	0.4
Grape wine	*Vitis vinifera*	n.d.	n.d.	0.5
Teak	*Tectona grandis*	Vanselow	K=0.000004	0.6*
Sugar maple	*Acer saccharum*	Vanselow	K=0.000004	0.6
Norway maple	*Acer platanoides*	n.d.	n.d.	0.6
Oak	*Quercus robur*	Vanselow	K=0.000004	0.6
Red oak	*Quercus rubra*	Vanselow	K=0.000004	0.6
Pin oak	*Quercus palustris*	Vanselow	K=0.000004	0.6
Fire cherry	*Prunus cerasus*	n.d.	n.d.	0.6
Silver birch	*Betula pendula*	Vanselow	K=0.000006	0.8
American beech	*Fagus grandifolia*	Vanselow	K=0.000004	0.6
Beech	*Fagus sylvatica*	Vanselow	K=0.000004	0.6
Rowan	*Sorbus aucuparia*	n.d.	n.d.	0.6-1
Cotton	*Gossypium hirsutum*	Unspecific	K=0.3	1.2
False acacia	*Robinia pseudoachacia*	n.d.	n.d.	1.2
Chinese tea	*Camillia sinensis*	Unspecific	K=0.4	1.4
Peach	*Prunus persica*	Unspecific	K=0.4	1.4
Guapira	*Guapira olfersiana*	Vanselow	K=0.000002	1.4
Hornbeam	*Carpinus betulus*	n.d.	n.d.	1.4
Lime	*Tilia cordata*	n.d.	n.d.	1.4
Black Alder	*Alnus glutinosa*	Vanselow	K=0.00005	2
Paper birch	*Betula papyrifera*	Vanselow	K=0.00005	2
Gray birch	*Betula populifolia*	Vanselow	K=0.00005	2
Yellow birch	*Betula alleghaniensis*	Vanselow	K=0.00005	2
Sour orange	*Citrus aurantium*	Vanselow	K=0.00005	2
Wattle	*Acacia*	n.d.	n.d.	1.4-2
Black Elder	*Sambucus nigra*	n.d.	n.d.	1.9
White ash	*Fraxinius exelsior*	n.d.	n.d.	2
Eucalyptus	*Eucalyptus gummifera*	Vanselow	K=0.00006	2.8
Japanese mandarin orange	*Citrus natsudaidai*	Vanselow	K=0.0003	3
Rhododendron	*Rhododendron ponticum*	Vanselow	K=0.0004	4.5
Crack willow	*Salix fragilis*	Gapon	K=0.08	5
European alder	*Alnus glutinosa*	Vanselow	K=0.0002	5
Aspen	*Populus tremula*	Vanselow	K=0.0005	6
Autumn olive	*Elaeagnus umbellata*	Vanselow	K=0.0005	6
Coffee	*Coffea arabica*	Gapon	K=0.2	75

Table 22: Response type and estimated aluminium response coefficients for different species of deciduous trees and bushes ordered according to relative sensitivity. The BC/Al-limit represents growth reduced to 80% of normal. * BC/Al=0.35 based on a field value for stem growth. n.d. represents values derived from a combination of the quantitative data in this study and the semi-quantitative data of Cronan et al., (1989); Kowalkowski (1987) and Ulrich (1985), as well as unpublished data.

English name	Latin name	Method	Sensitivity class	BC/Al(crit)
Chestnut	*Castanopis sclerophylla*	F&BA	Strong	0.3
	Michelia macclurei		Strong	0.3
Horsetail	*Casuarina equisetifolia*	F&BA	Strong	0.3
Assam rubber tree	*Ficus elastica*	F&BA	Strong	0.3
Tall Fig	*Ficus altissima*	F	Strong	0.3
Chinese Sabinia	*Sabina chinensis*	F&BA	Strong	0.3
Chinese waxleaved privet	*Ligustrum lucidum*	F&BA	Strong	0.3
Forest osman	*Osmanthus forrestii*	F&BA	Strong	0.3
Japanese tea	*Camellia japonicum*	F&BA	Strong	0.3
Chinese tea	*Camellia sinensis*	F&BA	Strong	1.4*
Oil tea	*Camellia oleifera*	F&BA	Strong	0.3
Orange	*Citrus deliciosa*	F&BA	Strong	0.3
Sweet orange	*Citrus sinensis*	F&BA	Strong	2*
Ebony	*Diospyros kaki*	F&BA	Strong	0.3
Sharon rose	*Hibiscus syriacus*	F	Strong	0.3
Tarim poplar	*Populus simonii*	F	Strong	0.3
Bougainvillea	*Bougainvillea spectabilis*	F	Strong	0.3
Persian lilac	*Melia azedarach*	F	Strong	0.3
Palberg	*Palbergia hypeana*	F&BA	Relatively strong	0.7
Chinese catalpa	*Catalpa ovata*	F&BA	Relatively strong	0.7
Szechuan jasmine	*Gardenia szechuanensis*	F&BA	Relatively strong	0.7
Jasmin	*Gardenia jasminoides*	F&BA	Relatively strong	0.7
Magnolia, yulan	*Magnolia denudata*	F	Relatively strong	0.7
Eucalyptus	*Eucalyptus tereticornis*	F&BA	Relatively strong	0.7
Olive tree	*Olea europaea*	F&BA	Relatively strong	0.7
Pomegranate	*Punica granatum*	F&BA	Relatively strong	0.7
Windmill palm	*Trachycarpus fortunei*	F&BA	Relatively strong	0.7
Snowball elder	*Viburnum awabuki*	F&BA	Relatively strong	0.7
	Rhapis excelsa	F&BA	Relatively strong	0.7
Oleander	*Nerium indicum*	F&BA	Relatively strong	0.7
Oriental berryelm	*Celtis orientalis*	F	Relatively strong	0.7
Chinese sassafras	*Sassafras tzuma*	F	Relatively strong	0.7
Indian erythrina	*Erythrina indica*	F	Relatively strong	0.7
Camphotec tree	*Camphtotheca acuminata*	F	Relatively strong	0.7
Cyca	*Cycas revoluta*	F	Relatively strong	0.7

Table 23: Relative tolerance of decideous trees to acid deposition as screened in Chinese bioassays (BA) and as derived from field surveys (F), part 1. * represents values estimated in accurate laboratory surveys.

One problem arose in connecting the Chinese relative sensitivity classifications into numerical BC/Al limit values. Some of the plants on the Chinese lists ocurred on both lists. These were however too few for a calibration of the Chinese list, but could be used for back-checking. Cumulative distributions of BC/Al limit values were made from the numerical lists available. Tab. 25 show the maximum value of local maxima of the critical BC/Al limit within each vetation group. Connection between the Chinese sensitivity classification and the numerical values of BC/Al ratios was established by pairing the maxima with the Chinese classes.

English name	Latin name	Method	Sensitivity class	Estimated BC/Al(crit)
Winter sweet	*Chimonanthus praecox*	F	Slightly sensitive	1.4
Camphor tree	*Cinnamomum camphora*	F	Slightly sensitive	1.4
Japanese cinnamon	*Cinnamomum japonica*	F	Slightly sensitive	1.4
Persian cinnamon	*Cinnamomum parthenoxylum*	F	Slightly sensitive	1.4
Liguster	*Ligustrum quihoui*	F	Slightly sensitive	1.4
Chinese locust	*Gleditsia sinensis*	F	Slightly sensitive	1.4
Confederate rose	*Hibiscus mutabilis*	F	Slightly sensitive	1.4
Loqat	*Eriobotrya japonica*	F	Slightly sensitive	1.4
Emperor tree	*Paulownia catalpifolia*	F	Slightly sensitive	1.4
	Bauhinia variegata	F	Slightly sensitive	1.4
Paper mullberry	*Broussonetia papyrifera*	F	Slightly sensitive	1.4
	Grevillea robusta	F	Sensitive	1.4
White jasmin	*Jasminum nudiflorum*	F	Slightly sensitive	1.4
Oriental mahogany	*Melia toosendan*	F	Slightly sensitive	1.4
Chinese mahogany	*Toona sinensis*	F	Sensitive	2
Formosan sweet gum	*Liquidambar formosana*	F	Sensitive	2
Peach	*Prunus persica*	F	Sensitive	1.4*
Oriental plane	*Platanus orientalis*	F	Sensitive	2
Heavenly bamboo	*Nandina domestica*	F	Sensitive	2
Chinese fig	*Ficus sublanceolata*	F	Sensitive	2
Corkscrew willow	*Salix matsudana*	F	Sensitive	2
Pagoda tree	*Sophora japonica*	F	Sensitive	2
Alibizza	*Alibizza julibrissin*	F	Sensitive	2
Chinese wingnut	*Pterocarya stenoptera*	F	Sensitive	2
Eucalyptus mahogany	*Eucalyptus robusta*	F	Sensitive	3*
False acacia	*Robinia pseoudoacacia*	F	Very sensitive	6
Worm willow	*Salix tortuosa*	F	Very sensitive	6
	Ormosia nosiei	F	Very sensitive	6
White mullberry	*Morus alba*	F	Very sensitive	6
Chinese maple	*Acer buergerianum*	F	Very sensitive	6
Chinese elm	*Ulmus parvifolia*	F	Very sensitive	6
Chinese redbud	*Cercis chinensis*	F	Very sensitive	6

Table 24: Relative tolerance of trees to acid deposition as screened in Chinese bioassays (BA) and as derived from field surveys (F), part 2. * represents values estimated in accurate laboratory experiments.

Vegetation type	n	I	II	III	IV	V	VI	VII	VIII
Conifers	35	0.3	0.5	1.2	2	10			
Deciduous	36		0.6	1.4	2	6		75	
Grasses	39		0.5	1.0		10	45		300
Herbs	25	0.3		1.0	3	5	50	100	800
Crop plants	17				2	6	50	80	400
Average		0.3	0.5	1.1	2.2	9	50	90	500
Chinese tolerance		Strong	Rel. strong	Sl. sens.	Sens.	Very sens.	Very sens.	Very sens.	Very sens.

Table 25: The table show the BC/Al value at local maxima in the frequency distribution of the critical BC/Al limit within each vegtation group listed. Connection between the Chinese sensitivity classification and the numerical values of BC/Al ratios was established by matching the average maxima BC/Al limits with the Chinese sensitivity classes.

Chinese tolerance	Strong	Rel. strong	Sl. sens.	Sens.	Very sens.
Conifers	0.3	0.5	1.2	2	10
Deciduous	0.6	1.4	2	6	75

Table 26: The table show possible BC/Al-limits for the Chinese sensitivity classification. The numerical values of BC/Al ratios was established by pairing the maxima for each plant class with the Chinese classes.

10   Field response for trees

Data for field response yielding unique and clear connections between soil
acidity and tree decline is not possible to find. The reason for this are many.
If Fig. 1 is studies, it becomes evident that many factors will affect growth
or decline of growth. Under laboratory experimental conditions, these factors
can be controlled, and the factors not studied can be eliminated by clever
experimental design. Then a clear connection between say soil pH and growth
can be produced, as the "noise" from other factors in the experiment will be
low.

Under field conditions, several of these factors cannot be controlled and
eliminated for practical reasons. This often leads a systenm "noise" of the same
magnitude as the signal sought for. Thus variations in growth due to water
availability during one decade may be larger than the impact on growth by
progessing soil acidification under the same decade. The effect of acidification
may thus be significant, but invisible due to the inability of the desing to
separate it from the "noise".

When we find a field response, it is no certain way we can make sure that
the trend is due to soil acidification, as other factors can never be excluded.
This is further enhanced by the fact that some of the different factors may
have synergetic effects.

10.1   Data sources for field response

Data on field observations of growth decline coupled to soil chemistry is diffi-
cult to find, often the growth data is semi-quantitative. Often data collected
not for this purpose was brought together from different sources to yield in-
formation enough to generate an overview picture and connections. Several
studies from North America, France, Germany, Poland, Africa and China
were found. Where data from individual studies came from and how they
have been combined, has been listed in Tab. 27-41. The data concerning
Norway spruce, silver fir, scots pine, armand pine, masson pine, red spruce,
European beech, orange and teak. Data of a more general nature was ex-
tracted from Falkengren-Grerup and Eriksson, 1990, Papke and Krahl-Urban,
1988; Rehfuss, 1988, Ulrich and Matzner, 1988; Ulrich et al., 1984, 1988; Zöttl,
1988.

Several of the references cited do not contain any relation on growth related
to soil chemistry, but further evaluation would lead to such a correlation.
Sometimes only growth data alone or soil chemistry alone is available for a
certain site. Then the lacking soil chemistry or growth data for the same site
was sometimes found in another reference.

Tab. 27 lists where we found different components needed to assess the

growth rate response under field conditions. It must be stated that the re-
sponse can be determined with good accuracy in a number of laboratory as-
says, but that the same degree of exactness is not possible with the field data.
The sensitivity of several other species could be approximated by combin-
ing quantitative data with semi-quantitative and qualitative determinations
(Kowallowski, 1991; Cronan et al, 1989).

A study on Armand and Masson Pine in China was found (Ma, 1991),
where the Armand Pine stand was healthy in 1960 with a high BC/Al ratio
of 8.8 and dying in 1984 when the BC/Al-ratio was 0.04. The growth rate
was set at 100% for 1960 and 20% for the dying stand. Other studies were
found in results reported from France, with tree ring analysis of growth in
one reference and accurate soil chemistry for three spruce sites (one healthy,
two declining) and two silver fir sites (one healthy, one declining) in other
references. The data could be brought together to give a quantitative relation.
Data for soil chemistry at mountain sites in New Hampshire, New York and
Vermont, USA, was compared with tree ring analysis of tree growth from
the same mountain along transects up the mountain. Soil data for the sites
were found in separate references. Almost all sites leave some or much room
for interpretation of the data. Several of the studies cited above, compare
growth and growth reductions to Al soil solution concentrations only. When
one investigator reports significant growth changes at 2.5 mg Al/l, whereas
another reports no change until 15 mg Al/l or more, then this difference can
often be traced back to differences in Ca and Mg concentrations of the soil
solution. The growth effect expressed as a function of (Ca+Mg+K)/Al ratio
instead of Al concentration alone will generally remove most of the difference
between such studies on the same plant species.

Reference	Site	Parameter	Tree species
Matzner et al., 1987	Sollingen	Damaged, needle loss, BC, Al	Norway spruce
Matzner and Ulrich, 1984	Sollingen	BC/Al	Norway spruce
Ulrich 1983,1985	Sollingen	Damaged/Healthy, uptake, BC/Al	Norway spruce
Matzner and Bredemeier, 1985	Sollingen	Damaged/Healthy, uptake, BC/Al	Norway spruce, Beech
Kreutzer, 1990	Sollingen	BC, Al	Norway Spruce, Beech
Cronan et al., 1987	Sollingen	BC, Al	Norway spruce
Matzner et al., 1987	Egge Mountains	Healthy, growth, BC, Al	Norway spruce
Ulrich 1983,1985	Lüneburger heide	Damaged/Healthy, uptake, BC/Al	Norway spruce
Matzner and Bredemeier, 1985	Lüneburger heide	Damaged/Healthy, uptake, BC/Al	Norway spruce, Beech
Haus, 1985	Lange Bramke	Uptake change, BC, Al	Norway spruce
Cronan et al., 1987	Lange Bramke	BC, Al	Norway spruce
Ulrich et al., 1988	Hils	Growth	Norway spruce
Raben, 1988	Hils	BC, Al	Norway spruce
Spiecker, 1990	N. Black Forest	Growth	Norway spruce
Zöttl (pers comm), 1990	Schluchsee, Black Forest	BC/Al	Norway spruce
Feger, 1992	Schluchsee	Growth	Norway spruce
Kreutzer, 1990	Schluchsee, N. Black Forest	BC, Al	Norway spruce, Beech
Zöttl and Aldinger, 1988	S. Black Forest	Growth, BC/Al	Norway spruce
Zöttl (pers comm), 1990	Villingen, Black Forest	BC/Al	Norway spruce
Feger et al., 1990	Villingen	Growth	Norway spruce
Kreutzer, 1990	Villingen, S. Black Forest	BC, Al	Norway spruce, Beech
Kreutzer, 1990	Oberswarmsteinach	BC, Al	N. Spruce, Silver fir
Zech et al., 1988	Oberswarmsteinach	Uptake change, BC/Al	N. spruce, Silver fir
Werner, 1990	Oberswarmsteinach	Uptake, BC/Al	Norway spruce
Schulze, 1985	Fichtelgebirge	Root growth, BC/Al	Norway spruce
Kreutzer, 1990	Wulfersreuth	BC, Al	N. Spruce, Silver fir
Zech et al., 1988	Wulfersreuth	Uptake change, BC/Al	N. spruce, Silver fir
Werner, 1990	Wulfersreuth	Uptake, BC/Al	Norway spruce
Zech et al., 1988	Selb, Fichtelgeb.	Uptake change, BC/Al	N. spruce, Silver fir
Werner, 199 0	Selb, Fichtelgeb.	Uptake, BC/Al	Norway spruce
Becker et al., 1989	Vosges mountains	Tree-ring analysis	Silver fir
Becker 1991	Vosges mountains	Tree-ring analysis	Silver fir
Landmann, 1991	Vosges mountains	Defoliation, growth	Silver fir
Landmann, 1991	Vosges mountains	Defoliation, growth	Norway spruce
Landmann, 1991	Vosges mountains	Defoliation, growth	Beech
Landmann, 1991	Vosges mountains	Defoliation, growth	Oak
Bonneau, 1991	Aubure, Alsace	Healthy/Damaged, growth, BC/Al	Norway spruce
Bonneau, 1991	Mont Louziere, Alsace	Healthy/Damaged, growth, BC/Al	Norway spruce
Bonneau, 1991	Louchbach, Alsace	Damaged, growth, BC/Al	Norway spruce
Bonneau, 1991	Germaingoutte, Alsace	Healthy, growth, BC/Al	Norway spruce
Bonneau, 1991, Becker 1991	Grande Montagne, Alsace	Damaged, growth, BC/Al	Silver fir
Bonneau, 1991, Becker 1991	Ste. B. de Chipotte, Alsace	Healthy, growth, BC/Al	Silver fir
Dambrinne et al., 1992	Strengbach, Alsace	Uptake, defoliation	N. spruce, Silver fir
Dambrinne (per. com.)	Strengbach, Alsace	BC/Al, growth	N. spruce, Silver fir
Rasmussen 1986	Klosterhede	Uptake, BC/Al	Norway spruce
Rasmussen et al., 1992	Klosterhede	Growth	Norway spruce
Rasmussen 1986	Strödam	Uptake, BC/Al	Norway spruce
Rasmussen et al., 1992	Strödam	Growth	Norway spruce
Rasmussen 1986	Tange	Uptake, BC/Al	Norway spruce
Rasmussen et al., 1992	Tange	Growth	Norway spruce

Table 27: Data sources for field response of tree growth to soil acidification in Europe.

Reference	Site	Parameter	Tree species
Ma 1991	Wushan mountain, Sichuan	Relative growth, BC/Al	Armand pine
Ma 1991	Nanshan, Chongqing	Relative growth, BC/Al	Masson pine
Ma 1991	Emei mountain, Chongqing	Relative growth, BC/Al	Faber fir
Bruck, 1989	Mt. Michel	Tree-ring analysis	Fraser fir, Red spruce
Barnard et al., 1989	Camels Hump VE	Tree-ring analysis	Red spruce
Johnson et al., 1985	Camels Hump, VE	Growth, BC, Al	Red spruce
Vogelmann et al., 1985	Camels Hump, VE	Mortality	Spruce, fir, beech, maple
Barnard et al., 1989	Whiteface mountain NY	Tree-ring analysis	Red spruce
Cronan et al., 1987	Whiteface mountains	BC, Al	Red spruce
Shortle and Smith, 1988	Whiteface mountains	BC, Al	Red spruce
Barnard et al., 1989	White mountain. NH	Tree-ring analysis	Red spruce
Driscoll et al., 1987	White mountain, NH	BC, Al	Red spruce
Barnard et al., 1989	Adirondack park NY	Tree-ring analysis	Red spruce
Cronan et al., 1987	Adirondack park NY	BC, Al	Red spruce
Chen et al., 1983	Adirondack park	BC, Al	Red spruce
Barnard et al., 1998	Huntington forest NY	Tree-ring analysis	Red spruce
Cronan et al., 1987	Huntington forest NY	BC, Al	Red spruce
Johnson et al., 1985	Appalachians, PA, VW	Growth, BC, Al	American Beech
Cronan et al., 1987	Coweeta	Uptake, BC, Al	Red spruce
Driscoll et al., 1992	Hubbard Brook, NH	Tree-ring analysis, BC, Al	Red spruce
Johnson l et al., 1992	Hubbard Brook, NH	Soil chemistry	Red spruce
Lin and Myhre, 1990	Florida	Growth, BC, Al	Orange
Yokomizu and Ishihara, 1973	Japan	Growth, BC, Al	Orange
Drechsel et al., 1990	Benin	Relative growth, BC, Al	Teak

Table 28: Data sources for field response of tree growth to soil acidification in Asia, Africa and America.

10.2 Results

There are virtually no results readily available in the literaturte on tree growth response to soil solution Al in a form that is free of critisism. Much was gained in understanding by synthesizing the available information for very diverse sources, even if such transdisiplinary work sometimes are not wanted by all parts of the science. It sometimes meant combining results, experiences and opinions of researchers which amongst themselves would not always be on very good terms, something that prevents constructive discussion on how the synthesis is best made. Figure 40 show the results for Red Spruce (*Picea rubens*), Norway Spruce (*Picea abies*) and Silver Fir (*Abies alba*) using data from the New York Adirondack mountains, the White mountains in New Hampshire and Camels Hump Vermont together with data from the German Harz, Fichtelgebirge and Schwarzwald and the French Vosges mountains. Fig. 41 show similar results for deciduous trees in Central Europe and Japan. The field data show the same shape as the laboratory data for the same species, but shifted towards higher Al tolerance. The drawn line represents the valence

unspecific model, k=0.15.

Data for forest decline on the Green Mountains in New Hampshire and Camels Hump in Vermont indicate that Fraser Fir closely follow Red Spruce response under field conditions (Krahl-Urban et al., 1988; Johnson, 1988).

The field growth response data is based on observation of growth of large mature trees in natural forests using tree ring analysis or yearly stem width increment combined with soil and soil water analysis data. Data were derived from an evaluation of results presented in American, French, and Canadian studies (Becker, 1991; Bonneau, 1991; Driscoll et al., 1987; Barnard et al., 1989.
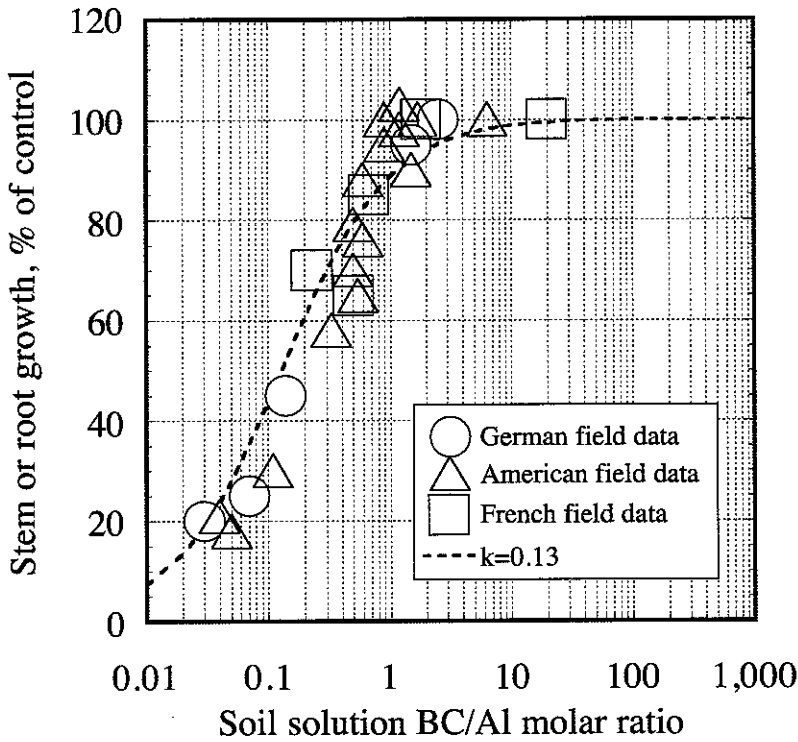
Figure 40: The relation between field observations of growth decline for Red Spruce (*Picea rubens*) taken from American data, Norway Spruce (*Picea abies*) and Silver Fir (*Abies alba*) taken from French and German data. Data used to construct the values for the diagram were taken from Becker, 1991; Bonneau, 1991; Driscoll et al., 1987; Barnard et al., 1989; Krahl-Urban et al., 1990; Werner, 1990.
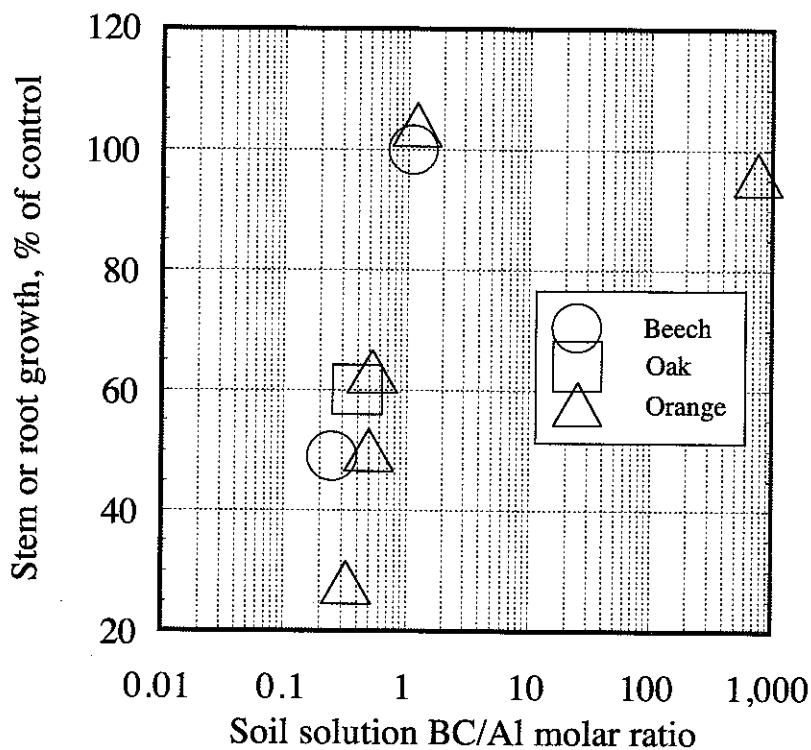
Figure 41: The relation between field observations of growth decline for some deciduous trees. Data used to construct the values for the diagram were taken from Bonneau, 1991; Driscoll et al., 1987; Barnard et al., 1989; Krahl-Urban et al., 1990; Werner, 1990; Ulrich (1985), Worku (1982) and Vogelmann et al., 1985.
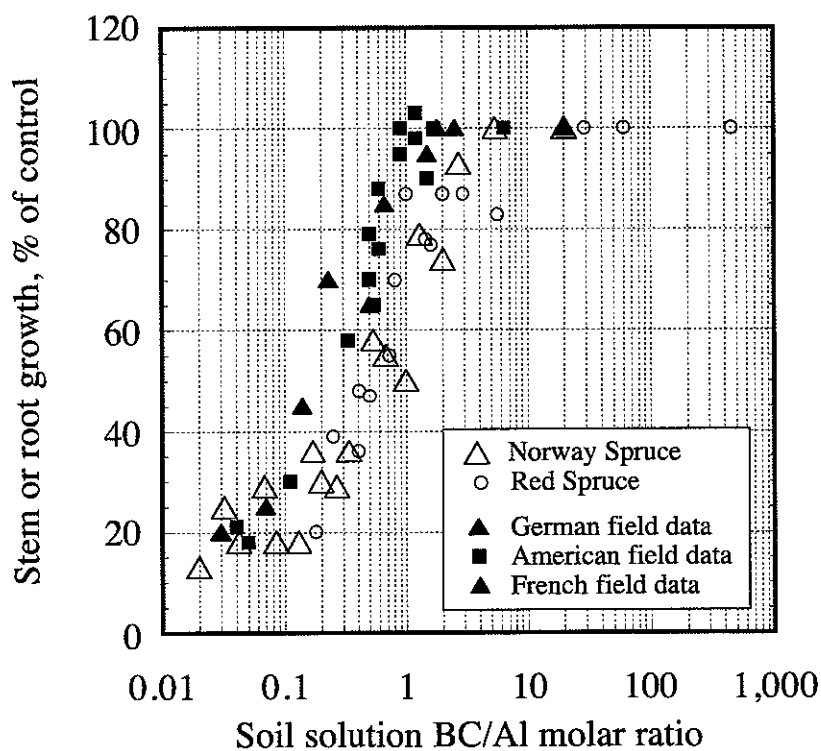
Figure 42: The response data for norway spruce (*Picea abies*) and red spruce (*Picea rubens*) as compared to field response data for the same tree species. Trees appear to be more tolerant to Al under field conditions than in laboratory bioassays. Explanations for the difference can be found in the text.
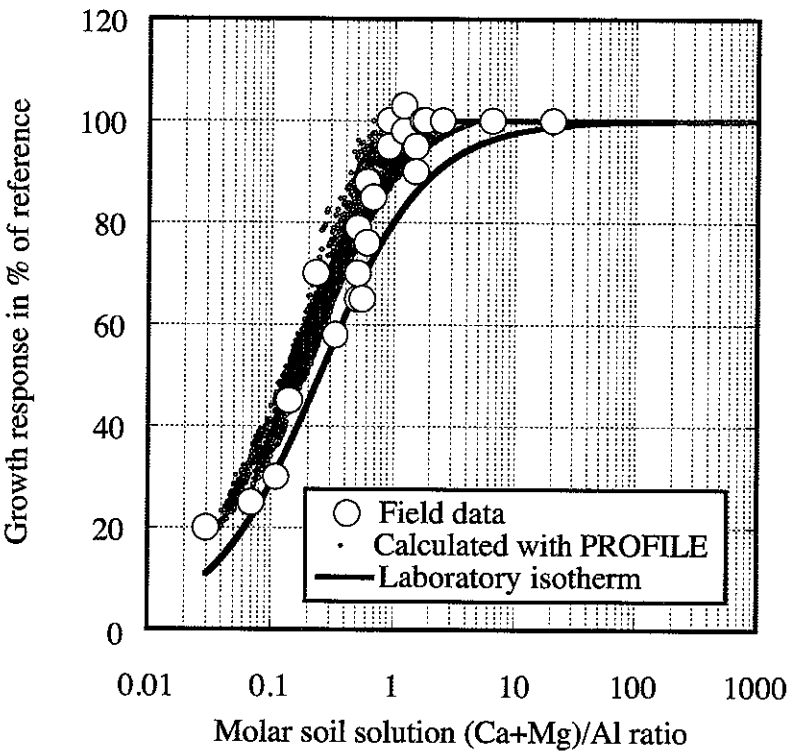
Figure 43: The relation between field growth and soil solution BC/Al ratio. The diagram show how the laboratory isotherm will result in a calculated growth response corresponding to the field isotherm and data. The laboratory bioassay isotherm was incorporated in the soil chemistry model PROFILE and the tree was allowed to optimize its uptake.
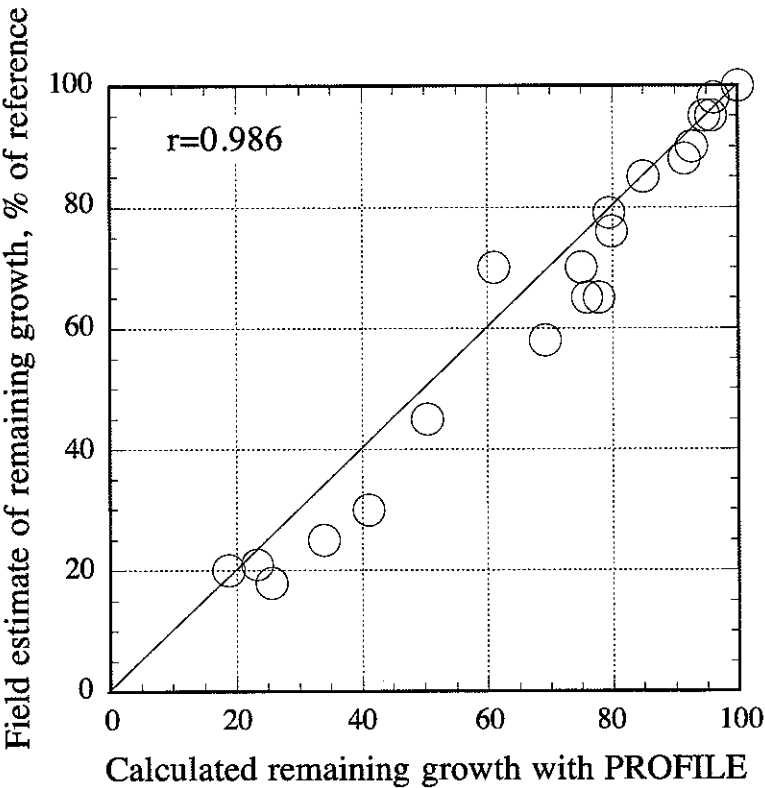
Figure 44: Testing the predicted growth changes versus observed field growth change. The correlation between observed values and calculated is good. The model slightly overpredict the response in the field when k=0.4. There is no overprediction if k=0.33.
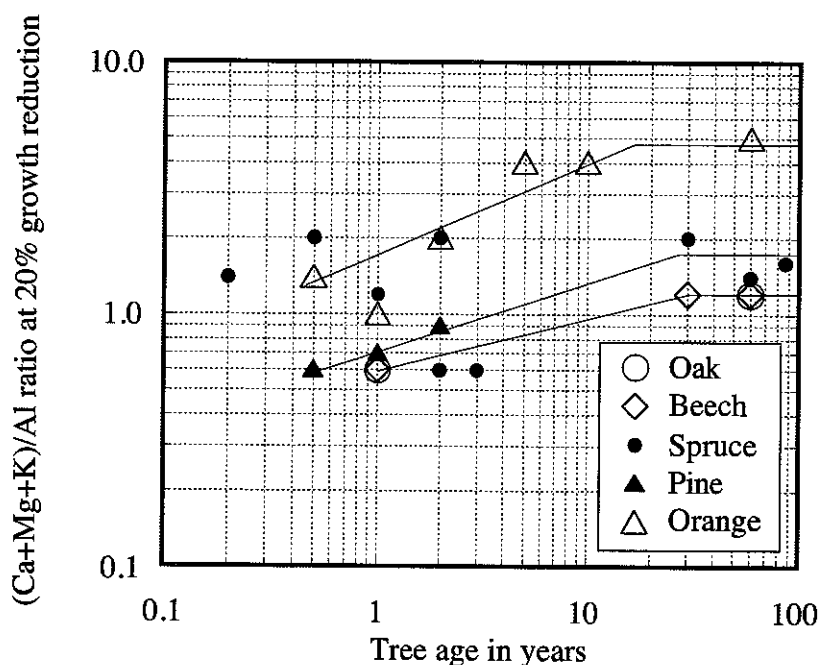
Figure 45: It can be seen from the data that the sensitivity may change over time as the plant gets older. Orange, beech, oak and pine all seem to follow the same pattern, whereas spruce possibly show a significantly different behaviour. All trees become more sensitive with age. A guess would be that spruce in reality have the same increase in sensitivity with age as is suggested by field surveys.

The relevance of using seedlings and juvenile trees as representatives for mature trees can be analysed with the data presented in Fig. 45. The available information indicate that the sensitivity of beech, oak, orange and pine increase with time.

10.3   Differences between field and laboratory conditions

The consistency of the difference observed between field results and laboratory assays, may possibly allow for extrapolation to other plants with similar root functioning, using laboratory bioassay values. The difference may be explained by the following factors. It can be seen how the slope of the response-function change with response mechanism. It can be seen that trees will tolerate more

Al under field conditions as compared to laboratory conditions, if the response is related to the BC/Al value of the B-horizon. This could possibly be the effect of mycorrizza fungi and local phenomena around the roots, not captured in a laboratory experiment. More likely is however, is the effect of different BC/Al values in different parts of the soil, making the B-horizon value a low estimate.

In the field data, growth was related to the BC/Al ratio of the soil solution in the B-horizon, where it is usually lowest in many soils. In the O- and E-layer the ratio may sometimes be significantly higher. This implies that growth and nutrient uptake may be affected in the B-layer, but less or unaffected in other soil layers under mild to moderate soil acidification conditions. Some trees may reallocate uptake to less affected layers, to compensate for the loss. In laboratory experiments, the conditions have been controlled in such a way that all roots experienced the designed BC/Al ratio. Under severe soil acidification, the whole soil profile will be affected, and a low BC/Al ratio throughout prevail. Accordingly, the two curves should converge at low BC/Al rations, which they also appear to do. The response data for norway spruce (*Picea abies*) and red spruce (*Picea rubens*) as compared to field response data for the same tree species is shown in Fig. 42. Trees appear to be more tolerant to Al under field conditions than in laboratory bioassays. Thus the laboratory experiments represents the effect of BC/Al the plant roots in a particular soil layer would experience, but this must be weighted together for all layers to estimate what the plant as a whole would experience. This implies that in soil modeling, the laboratory values should be used in multi-layered models.

10.4   Testing against German regional data

This was tested in the PROFILE model (Sverdrup and Warfvinge, 1988; Warfvinge and Sverdrup, 1992). For each layer the laboratory assay isotherm was applied. If uptake in one layer was restricted by the effect of the BC/Al ratio, then the tree was allowed to reallocate its uptake to another soil layer, only limited by availability. This will delay growth response until there is a breakthrough of low BC/Al ratios in a larger part of the soil profile. The PROFILE model, configured in this way, was applied to an input dataset for 13,898 forest sites evenly distributed over the complete forested area of Germany. The calculated growth reduction was plotted against the calculated BC/Al ratio and compared to field data on stem growth response and the laboratory isotherm applied inside the model. The result are shown in Fig. 43 using all the German sites.

The results are also shown in Fig. 44 using the critical loads data base point closest to the actual site. The distance from the calculation point where soil data was gathered to the point where needle loss and growth change was

measured vary from 20 to 1780 meter. The correlation between observed and field estimated growth change is $r^2=0.97$, the standard deviation less than 7%-points.

The relation between root biomass and stem biomass for a number of trees indicate that the tree re-allocates important nutrients to leaves and puts less priorities on new root biomass production, when they are stressed by soil acidity. This implies that the tree would become more sensitive to water stress and more susceptible to damage by wind as its root mass becomes less in relation to crown mass, and as the roots penetrate the ground less well.

11 Further acidification effects on trees

11.1 Needle yellowing

The data for yellowing and defoliation was derived by assigning the mean value for each defoliation or yellowing class used. There is a relation between yellowing and defoliation to be seen in the data, a conclusion contradictory to the conclusion made earlier by the French research team (Landmann, 1991). There is possibly large margins of error involved in these relations, but the general trend is believed to be correct.

11.2 Defoliation and growth

There are a few reports of studies available that yield a relation between growth rate and needle loss for conifers in Sweden (Söderberg, 1993), in North America (Barnard et al., 1990) and in the Vosges Mountains in Northeastern France (Becker, 1990). The Swedish study is based on coring and needle loss estimation at 16,650 Norway spruce trees and 15,600 scots pine trees at equally many sites randomly distributed over Swedens forested area. The same correlation was found for the 5 different region in Sweden, despite a large climatic variation over the area surveyed. This seem to exclude bias due to climatic influences, and point to a basic coupling between growth and needle loss. In North America, less trees were surveyed, the sample is estimated at approximately 2,000 red spruce trees in New England (Krahl-Urban et al., 1988). Apparently, fraser fir show the same type of response (Krahl-Urban et al., 1988). The French survey involved a number of stands in small regions of Northeastern France. Sample size for silver fir is 1,000 trees distributed among approximately 275 sites. The obtained relations have been displayed in Fig. 47, 48 and compared in Fig. 46.

The following empirical relations can be derived to describe the correlations between needle loss (BF) in % and stem growth (G) in % for Norway spruce, scots pine, Red spruce and Silver fir.

$$Growth(Norway) = 101.9 - 0.5748 \cdot r_{BF} - 0.004531 \cdot r_{BF}^2 \qquad (93)$$

$$Growth(scots\ pine) = 99.51 - 0.03194 \cdot r_{BF} - 0.009566 \cdot r_{BF}^2 \qquad (94)$$

$$Growth(red\ spruce) = 99.94 - 1.667 \cdot r_{BF} - 0.0067 \cdot r_{BF}^2 \qquad (95)$$

$$Growth(silver\ fir) = 100.6 - 1.6138 \cdot r_{BF} - 0.00607 \cdot r_{BF}^2 \qquad (96)$$

The set of equations can be inverted to give the relation between needle loss and growth:

$$Defoliation(Norway) = 98.9 - 0.5767 \cdot r_G - 0.003608 \cdot r_G^2 \qquad (97)$$

$$Defoliation(scots\ pine) = 98.76 - 0.25229 \cdot r_G - 0.0063159 \cdot r_G^2 \qquad (98)$$
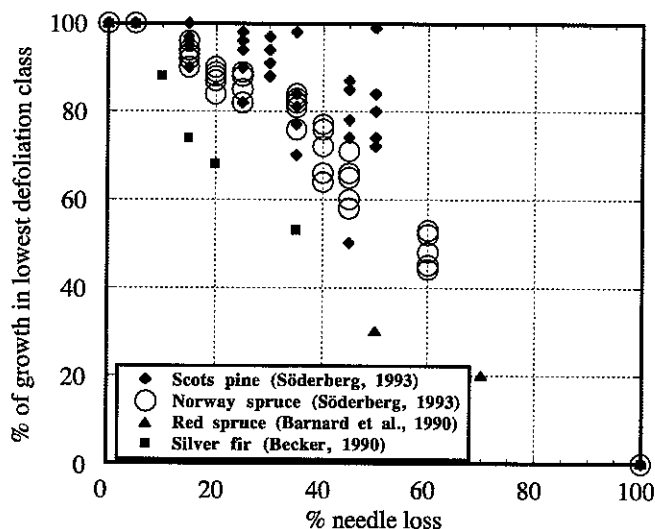
Figure 46: The relation between observed defoliation and stem growth for Norway spruce (*Picea abies*), scots pine (*Pinus sylvestris*), red spruce (*Picea rubens*) and silver fir (*Abies alba*). Data from Barnard et al., (1989); Becker (1991) and Söderberg (1993).

$$Defoliation(red\ spruce) = 100.18 - 1.84 \cdot r_G + 0.00839 \cdot r_G^2 \qquad (99)$$

$$Defoliation(silver\ fir) = 100 - 1.51891 \cdot r_G + 0.0052584 \cdot r_G^2 \quad (100)$$

The equations can be used to convert growth to needle loss or vice versa.

11.3   Tree mortality and root decline

The available information (Abrahamsen, 1984; Ryan et al., 1986a,b; Keltjens and van Loenen, 1989) indicates that there is a coupling between plant survival rate and root growth reductions. The available data for conifers have been plotted in Figs. 49. It can be seen in Fig. 49 that the pattern is the same for Norway spruce, douglas fir and western hemlock. The data indicate that the Norway spruce will have 50% survival at 55% root growth reduction, and that 30-35% root growth reduction will lead to 100% mortality in the long term perspective. The equation given in Fig 49 is an empirical relation not based in any process, as root processes coupled with internal plant processes are responsible for the shape of the curve. The picture appear to be similar for western hemlock and douglas fir.

The data presently available indicate an empirical relation for tree survival in %:

$$Survival = -104 + 3.638 \cdot r_G - 0.0163 \cdot r_G^2 \tag{101}$$

where r_G is the root growth as percent of control. The relation apply to the survival of relatively young trees, and experimental data of the same kind is not available for older trees. It is possible that the increased mortality may persist into higher year classes. Support for this is found in the fact that older trees seem to suffer more than younger from acid rain and its effects in regional forest damage surveys.
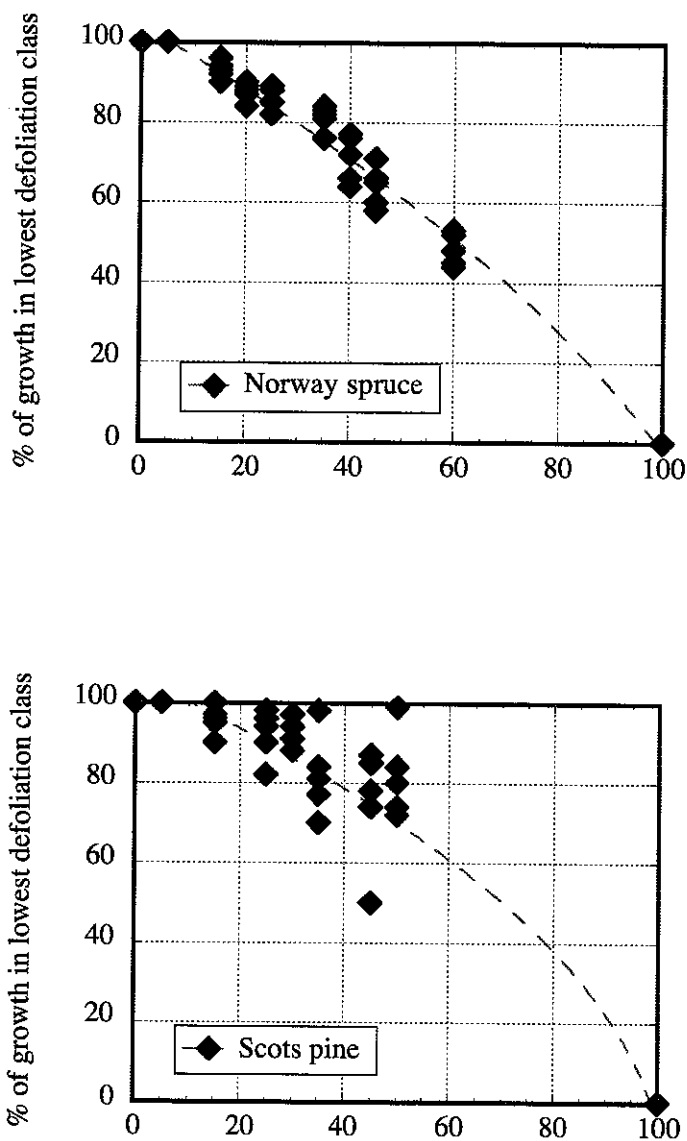
Figure 47: The relation between observed defoliation and stem growth for Norway spruce (*Picea abies*) and scots pine (*Pinus sylvestris*), data from Söderberg (1993)
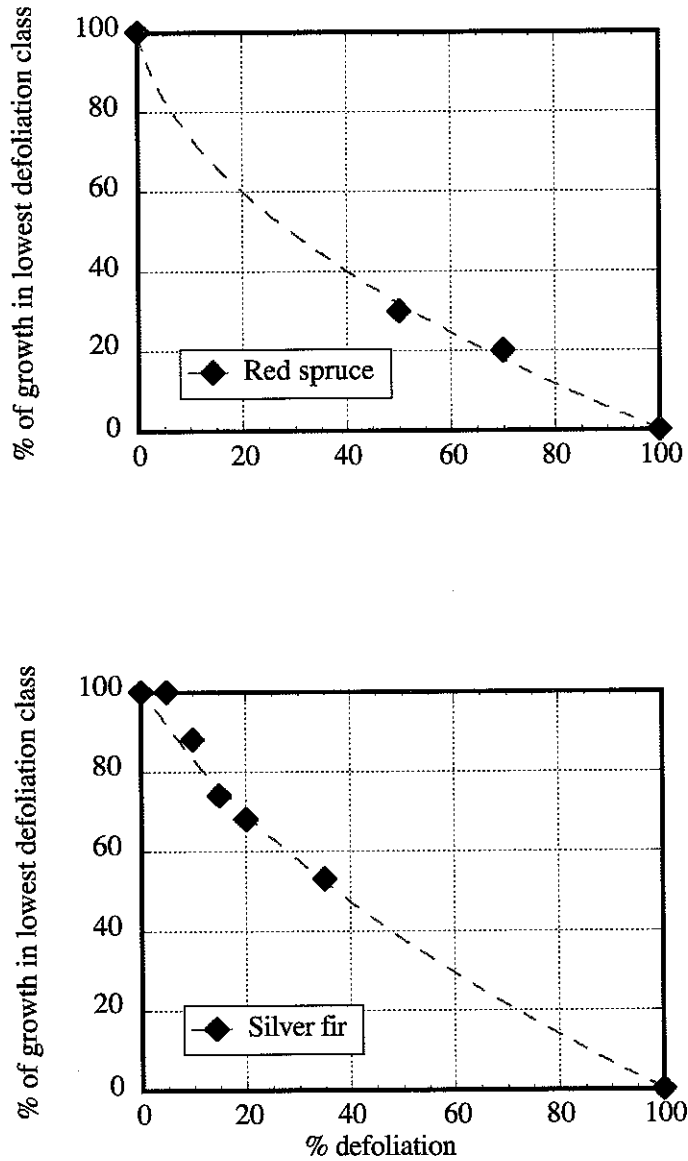
Figure 48: The relation between observed defoliation and stem growth for red spruce (*Picea rubens*), data from Barnard et al., (1989) and Silver fir (*Abies alba*), data from Becker (1991).
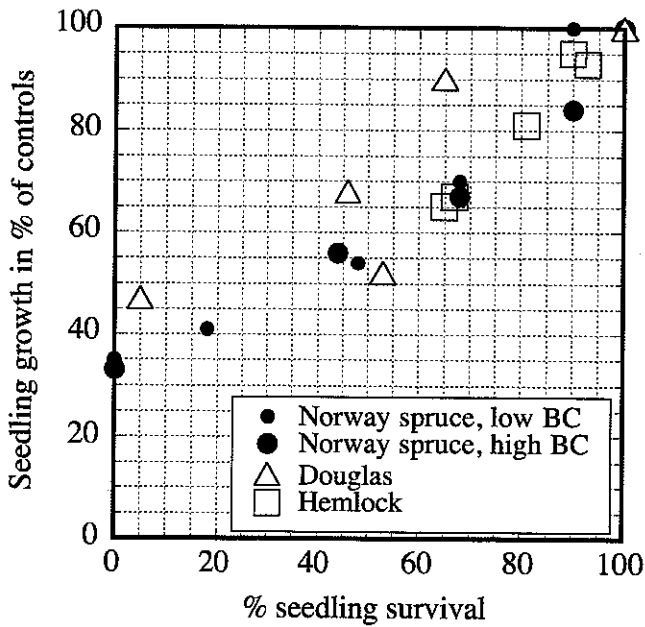
Figure 49: The relation between survival rate and root growth for Norway spruce in the experiments of Abrahamsen (1984), for douglas fir in the experiments of Ryan et al., (1986a,b) and Keltjens and van Loenen (1989), for western hemlock in the experiments of Ryan et al., (1986a,b) and Keltjens and van Loenen (1989).

12 Laboratory results for ground vegetation

12.1 Weeds, herbs and grasses

Fig. 50 show the response data for different types of grass such as *Carex remota, Brachypodium sylvaticum, Deschampsia flexuosa, Holcus lanatus, Bromus erectus* and *Juncus squarrosus*.

Data found for *Deschampsia flexuosa* are shown in Fig. 51. Response data was taken from Pegtel (1987), Rorison (1985), Hackett (1987), Runge (1986) and Rode (1988).

Hackett (1987) performed experiments on *Deschampsia flexuosa*, and compared the results to experiments with *Alopecurus pratensis, Festuca pratensis* and *Lolium perenne*, the results are shown in Fig. 52. The different datasets for *Deschampsia flexuosa* are consistent.

Andersson and Brunett and Andersson 1993a,b conducted as series of experiments on (*Bromus benekenii*), a grass of typical for Swedish beech forests, further the herbs *Allium ursinum*, and *Galium odoratum*. The results are particularly interesting since the study allow the separation of the effect of Al from that of H. The results have been displayed in Fig. 53 and 56 for Boklosta. The results show that there is a small shift in the curve, depending upon whether root elongination or root weight is used. The most interesting results are shown in Fig. 56. Those diagrams show that the response line related to BC/Al in relation the the response line related to BC/H are shifted by a factor of 3. This implies that in the response expression Al and H are additive on an equivalent basis. This is also a very strong indication that the valence of the adverse ion is a measure of its adverse strength. For boklosta at least, the response expression may be written:

$$f(BC/Al) = \frac{[BC^{2+}]^{n-m} \cdot (BC/(Al + n \cdot H))^m}{[BC^{2+}]^{n-m} \cdot (BC/(Al + n \cdot H))^m + K_{Exp}} \qquad (102)$$

It could probably be assumed that this is valid in general for most plants, considering that such a relationship are hinted at in many other studies, even if it is not always quantifiable in terms of response coefficients. Some of the data for spruce hint at a similar relationship for Norway spruce where:

$$K_{Exp}(Al + n \cdot H) = \frac{1}{n} \cdot K_{Exp}(Al) \qquad (103)$$

Fig. 57 show the bioassay response of heather (*Calluna vulgaris*) and American cranberry (*Vaccinium macrocarpon*). The data was taken from Rode 1988 and Medappa and Dana 1970.

Fig. 58 show some herbs of the meadow and forest clearings such as *Galium saxatile* and *Digitalis purpurea*. They are both Al tolerant and

seem to increase in areas with soil acidification in Sweden. Fig. 58 also show some Al intolerant plants such as *Geum urbanum*, *Origanum vulgare* and *Mycelis muralis*.

The results for *Allium ursinum* and *Galium odoratum* are shown in Fig. 59. For *Galium odoratum*, not as many datapoints are available as for *Bromus benekenii*, but the results indicate the same additivity of Al and H in the response mechanism as was the case for *Bromus benekenii*.

Response data for *Arnica montana* is shown in Fig. 60. The data was taken from Pegtel (1987). Note that the response is to the Ca+Mg/Al ratio excluding K. K does not seem to have any antagonistic effect on Al with arnika.
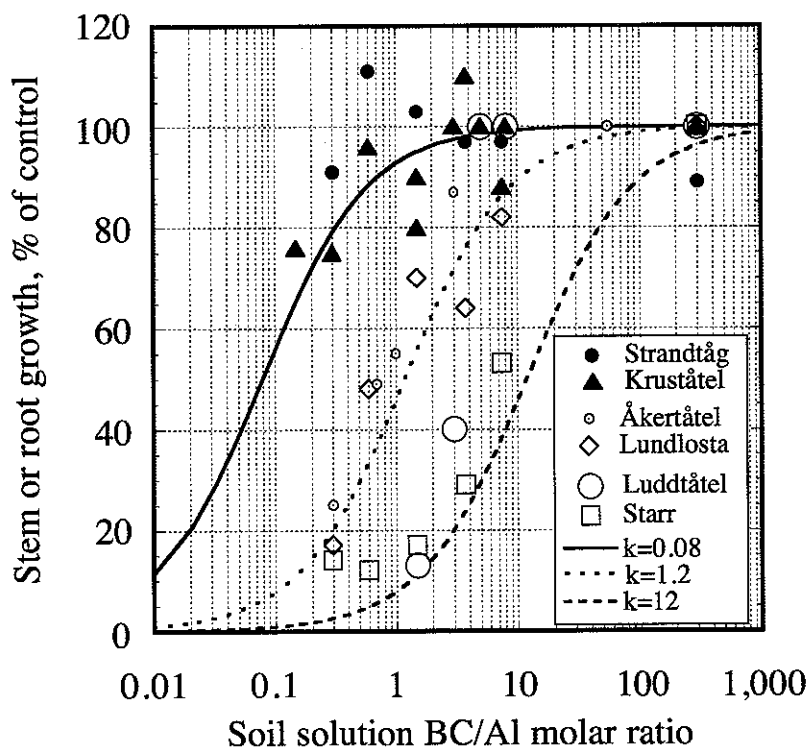
Figure 50: Response data for *Carex remota, Brachypodium sylvaticum, Holcus lanatus, Bromus erectus, Deschampsia flexuosa,* and *Juncus squarrosus*. All the grasses shown above appear to follow the unspecific mechanism.
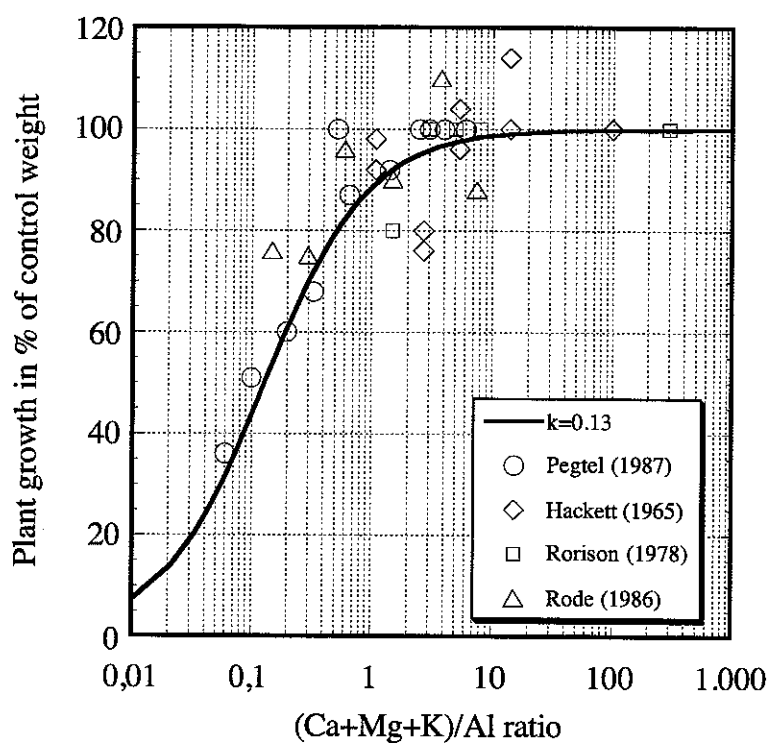
Figure 51: Response data for *Deschampsia flexuosa* according to different studies.
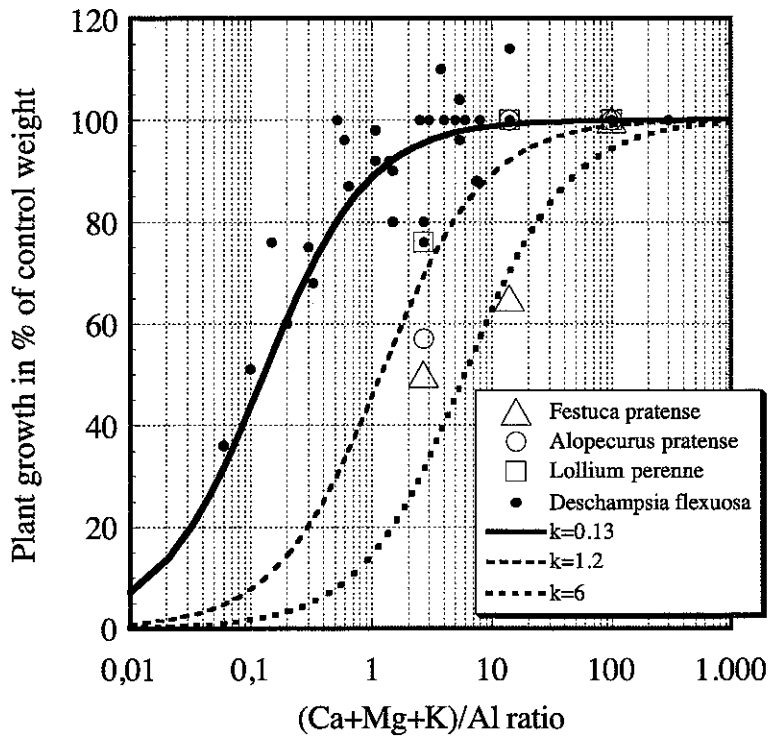
Figure 52:   Response data for *Deschampsia flexuosa* as compared to *Alopecurus pratensis*, *Festuca pratensis* and *Lolium perenne*.
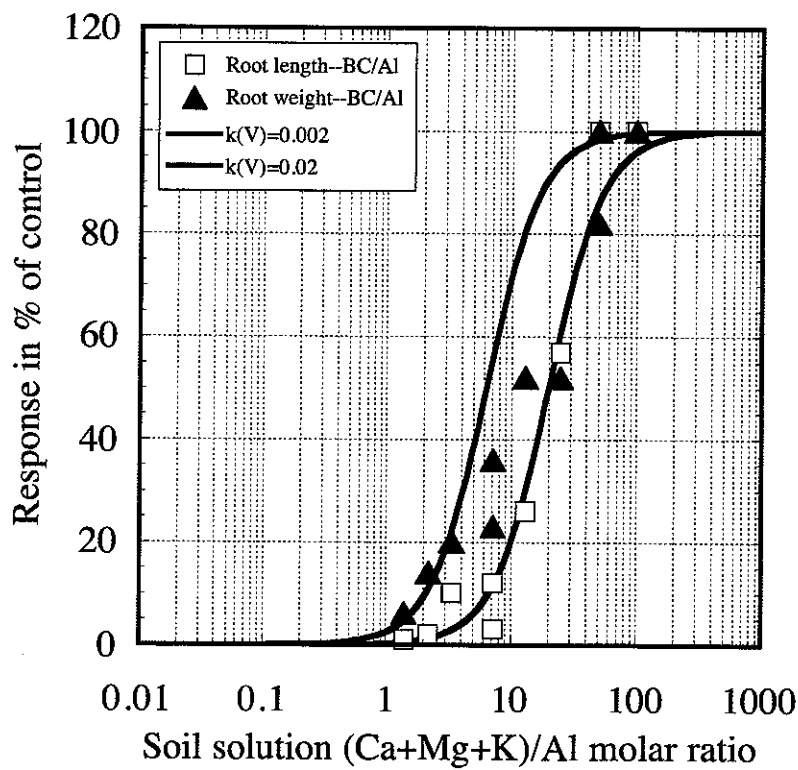
Figure 53: The response data for *Bromus benekenii* in terms of response to the BC/Al ratio and expressed in terms of root weights or root elongination. The two re systematically shifted in comparison to each other.
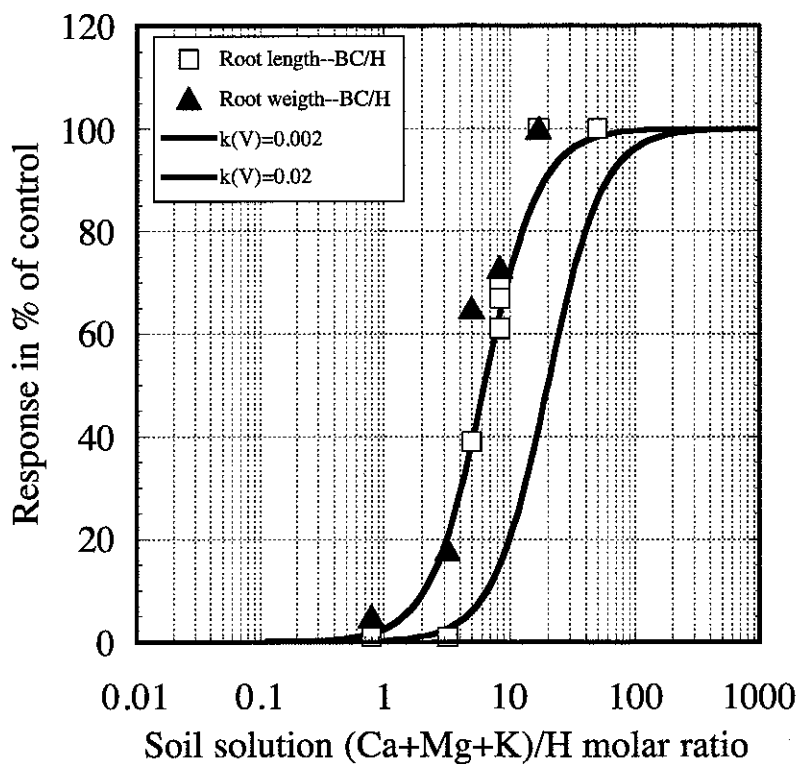
Figure 54: The response data for (*Bromus benekenii*) in terms of response to the BC/H ratio and expressed in terms of root weights or root elongination.
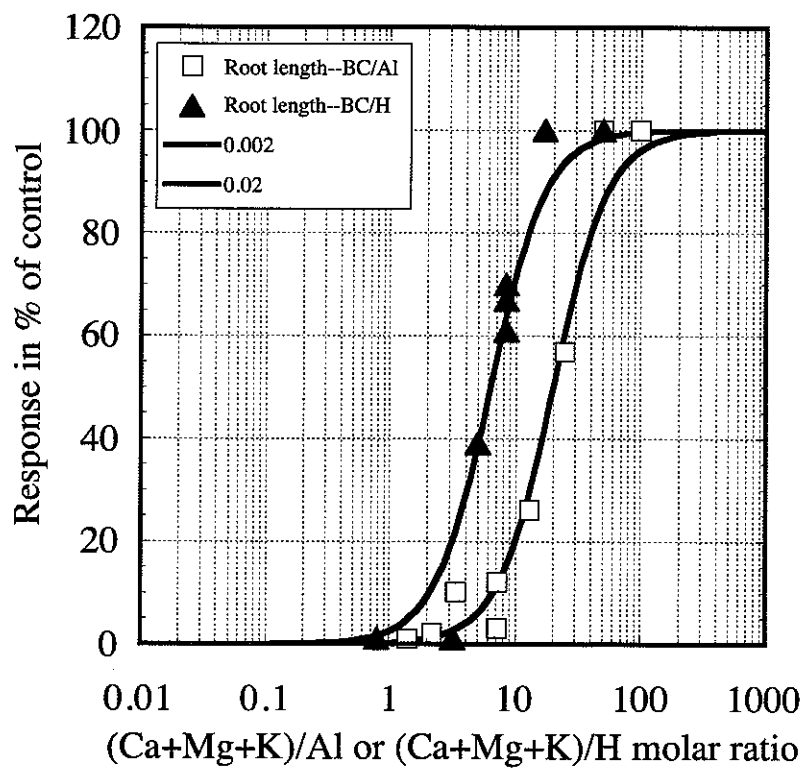
Figure 55: The response data for (*Bromus benekenii*) in terms of root elongination as related to the BC/Al and BC/H ratios.
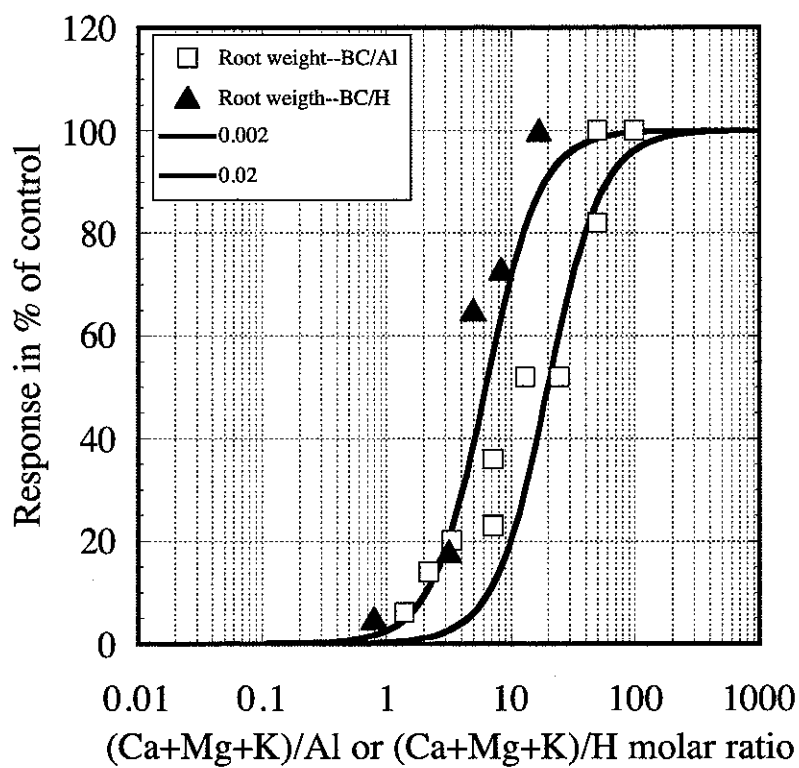
Figure 56: The response data for (*Bromus benekenii*) in terms of root elong-ination as related to the BC/Al and BC/H ratios.
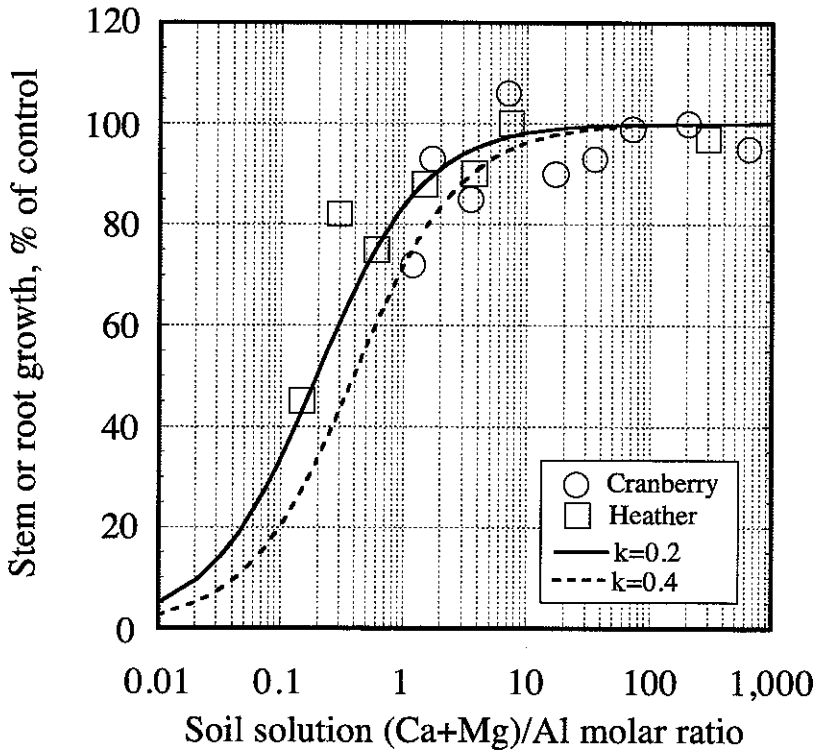
Figure 57: The response data for heather (*Calluna vulgaris*) and American cranberry (*Vaccinium macrocarpon*). They follow the unspecific mechanism.
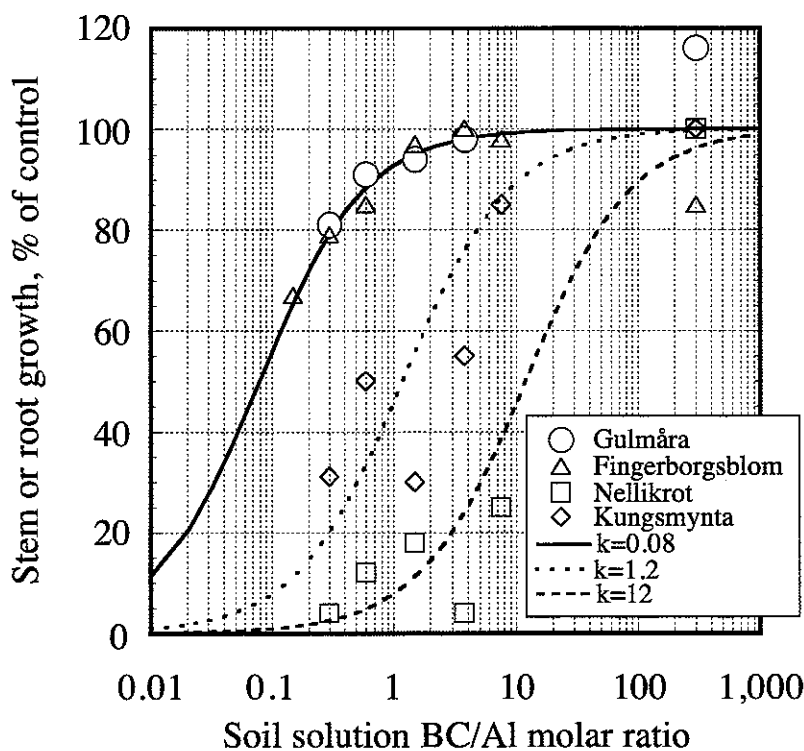
Figure 58: Response data for *Galium saxatile, Digitalis purpurea, Geum urbanum, Origanum vulgare* and *Mycelis muralis*. All the herbs shown above appear to follow the valence unspecific mechanism.

Figure 59: Response data for *Galium odoratum* and *Allium ursinum*.

Figure 60: Response data for *Arnica montana*. The data was taken from Pegtel (1987). Note that the response is to the Ca+Mg/Al ratio excluding K. K does not seem to have any antagonistic effect on Al with arnika.

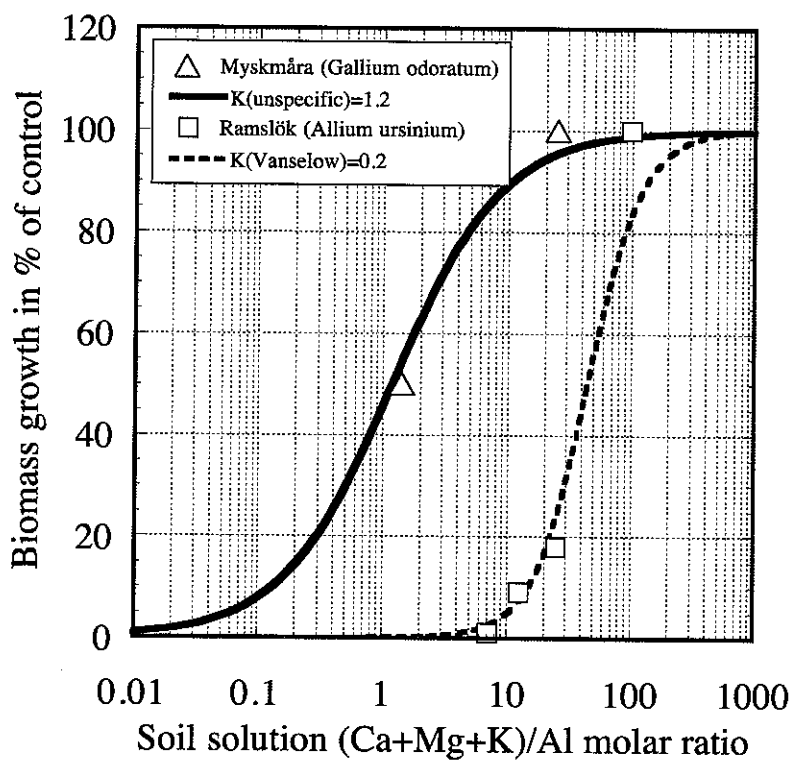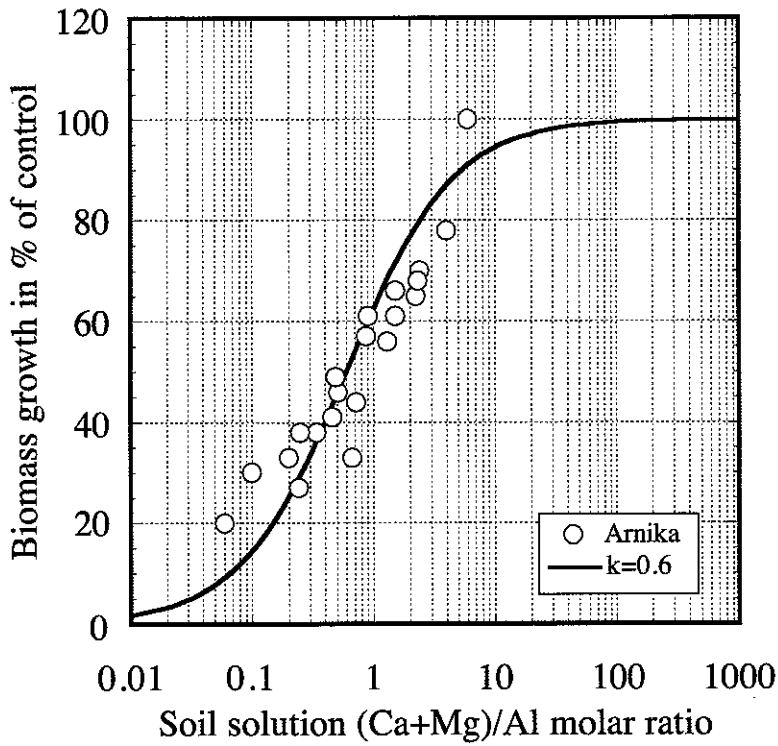| Plant species	Latin name	Reaction type	K-value	BC/Al(crit)
May lily	*Maianthemum bifolium*	n.d.	n.d.	0.3
Wood sorrel	*Oxalis acetosella*	n.d.	n.d.	0.3
Heath bedstraw	*Galium saxatile*	Unspecific	K=0.08	0.3
Foxglove	*Digitalis purpurea*	Unspecific	K=0.08	0.3
Blueberry	*Vaccinium myrtillus*	n.d.	n.d.	0.4
Erica	*Erica*	n.d.	n.d.	0.6
Chichweed wintergreen	*Trientalis europaea*	n.d.	n.d.	0.8
Heather	*Calluna vulgaris*	Unspecific	K=0.2	0.8
Lingon-berry	*Vaccinium vitis-idaea*	n.d.	n.d.	1.2
American cranberry	*Vaccinium macrocarpon*	unspecific	K=0.4	1.5
Black medic	*Medicago lupulina*	n.d.	n.d.	1.5
Arnika	*Arnica montana*	Unspecific	K=0.6	2.5
Yellow wood anemone	*Anemone ranunculoides*	n.d.	n.d.	3
Lily-of-the-valley	*Convallaria majalis*	n.d.	n.d.	3
Black pea	*Lathyrus migra*	n.d.	n.d.	3
Sweet wodruff	*Galium odoratum*	Unspecific	K=1.2	4.5
Bush vetch	*Vicia sepium*	Unspecific	K=1.2	4.5
Yellow lupin	*Lupinus luteus*	Unspecific	K=1.2	4.5
Majoram	*Origanum vulgare*	Unspecific	K=1.2	4.5
Alfalfa	*Medicago sativa* var. falcata	n.d.	n.d.	5
Wood anemone	*Anemone nemorosa*	n.d.	n.d.	5
Crocus	*Crocus spp*	n.d.	n.d.	5
Smultron	*Fragaria vesca*	n.d.	n.d.	5
Zigzag clover	*Trifolium medium*	n.d.	n.d.	5
Cowslip	*Primula veris*	n.d.	n.d.	15
Wood avens	*Geum urbanum*	Unspecific	K=12	45
Columbine	*Aquilegia vulgaris*	n.d.	n.d.	50
Bellflower	*Campanula persicifolia*	n.d.	n.d.	50
Sand leek	*Allium scorodoprasum*	n.d.	n.d.	50
Autumnal kawkbit	*Leontodon autumnalis*	Unspecific	K=12	80
Ramsons	*Allium ursinum*	Vanselow	K=0.2	100
Ranunclaceous plants	*Ranunculus spp*	n.d.	n.d.	100
Wall lettuce	*Mycelis muralis*	Unspecific	K=40	120
Common chickweed	*Stellaria media*	Unspecific	K=40	120
Common valerian	*Valeriana officinalis*	n.d.	n.d.	150
Mouse-ear chickweed	*Cerastium fontanum*	Unspecific	K=70	300
Selfheal	*Prunella vulgaris*	Unspecific	K=200	800
Common dandelion	*Taraxacum officinale*	Unspecific	K=200	800

Table 29: Response type and estimated aluminium response coefficients for different species of herbs and legumes. The limiting BC/Al-value represents root growth for laboratory results reduced to 80% of normal. n.d. represents values derived from a combination of the quantitative data in this study, semi-quantitative data, as well as unpublished data.

Plant species	Latin name	Reaction type	K-value	BC/Al(crit)
Heath rush	*Juncus squarrosus*	Unspecific	K=0.08	0.3
Wavy hair-grass	*Deschampsia flexuosa*	Unspecific	K=0.13	0.5
Perennial rye-grass	*Lolium perenne*	Unspecific	K=0.13	0.5
Redtop	*Agrostis stolonifera*	Unspecific	K=0.2	1
Common bent	*Agrostis capillaris*	Unspecific	K=0.2	1
Rough crabgrass	*Digitaria sanguinalis*	Unspecific	K=0.2	1
Tuften hair-grass	*Deschampsia cespitosa*	n.d.	n.d.	2
False brome	*Brachypodium sylvaticum*	Unspecific	K=1.2	6
Upright brome	*Bromus erectus*	Unspecific	K=1.2	6
Meadow foxtail	*Alopecurus pratensis*	Unspecific	K=1.2	6
Yorkshire fog	*Holcus lanatus*	Unspecific	K=1.5	8
Steppe-grass	*Stipa capillata*	n.d.	n.d.	10
Large meadow-grass	*Poa remota*	n.d.	n.d.	10
Meadow-grass	*Poa supina*	n.d.	n.d.	10
Brown bent	*Agrostis vinealis*	n.d.	n.d.	10
Mat-grass	*Nardus stricta*	n.d.	n.d.	10
Red millet	*Digitaria ischaemum*	Unspecific	K=8	15
Meadow fecue	*Festuca pratensis*	Unspecific	K=8	20
Lesser hairy brome	*Bromus benekenii*	unspecific	k=12	30
Remote sedge	*Carex remota*	Unspecific	K=12	45
Tawny sedge	*Carex hostiana*	n.d.	n.d.	45
Wood sedge	*Carex sylvatica*	n.d.	n.d.	45
Trembling sedge	*Carex aigilata*	n.d.	n.d.	45
Smooth meadow-grass	*Poa pratensis*	Unspecific	K=50	250
Annual meadow-grass	*Poa annua*	Unspecific	K=70	300
Wood meadow-grass	*Poa nemoralis*	n.d.	n.d.	300

Table 30: Response type and estimated aluminium response coefficients for different species of grasses. The limiting BC/Al-value represents root growth for laboratory results reduced to 80% of normal. n.d. represents values derived from a combination of the quantitative data in this study and semi-quantitative data.

12.2   Domesticated ground vegetation

Fig. 61 show different cultivated grain cereals, wheat (*Triticum aestivum*), barley (*Hordeum vulgare*, rye (*Secale cereale*), they seem to follow the Vanselow mechanism. A whole range of sensitivities is represented for wheat of different origins. Field data with North American Hart wheat fall on the same line as Polish Atlas wheat.

Fig. 62 show further cereal crop plants, 4 different strains of sorghum (*Sorghum sativa*) and 4 different strains of rice (*Oryza sativa*). These also follow the Vanselow mechanism, but sorghum is very sensitive to Al.

Fig. 63 show bush vetch (*Vicia sepium*), yellow lupin (*Lupinus luteus*), horse bean (*Vicia fabia*), cowpea (*Vignia unguiculata*) and sweet corn or maize (*Zea mays*). Horse bean and cowpea follow the Vanselow mechanism, Yellow lupin and alfalfa the unspecific mechanism.

Experiments such as those reported by Skeen (1928) show very clearly that there can be no question of the antagonistic effect of Ca for Fe and Al on the growth of lupins (*Lupinus albus, Lupinus phaseolus*). But it is also apparent that the toxic effect of these ions are not completely antagonized.

Fig. 64 show subterranean clover (*Trifolium subterranum*), soya bean (*Glycine max*) and alfalfa (*Medicago sativa*). Soya bean follow the unspecific mechanism, clover and alfalfa the Vanselow mechanism. Very much data is available for soya bean, only a small selection is shown here (Noble et al., 1988; Alva et al., 1988).

12.3   Response functions and critical limits

Plant species, latin name, type of Al response type, coefficient of the response function, and BC/Al ratio at which growth has been reduced to 80% of normal is listed for different types of plants in Tabs. 29-31. It approximates the BC/Al-limit for reduction to 90% of normal growth under field conditions.
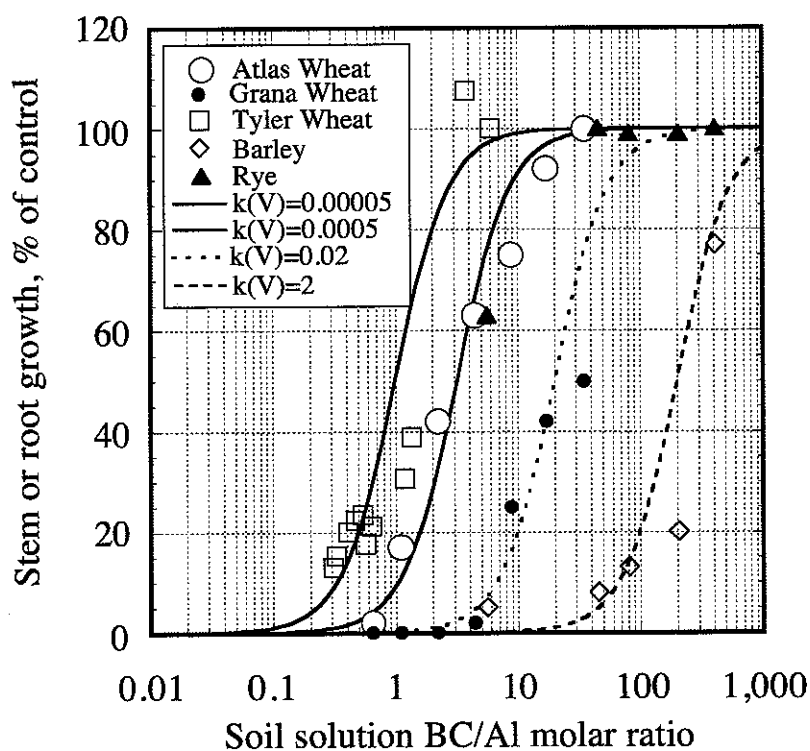
Figure 61: Response data for wheat (*Triticum aestivum*), barley (*Hordeum vulgare*, rye (*Secale cereale*).
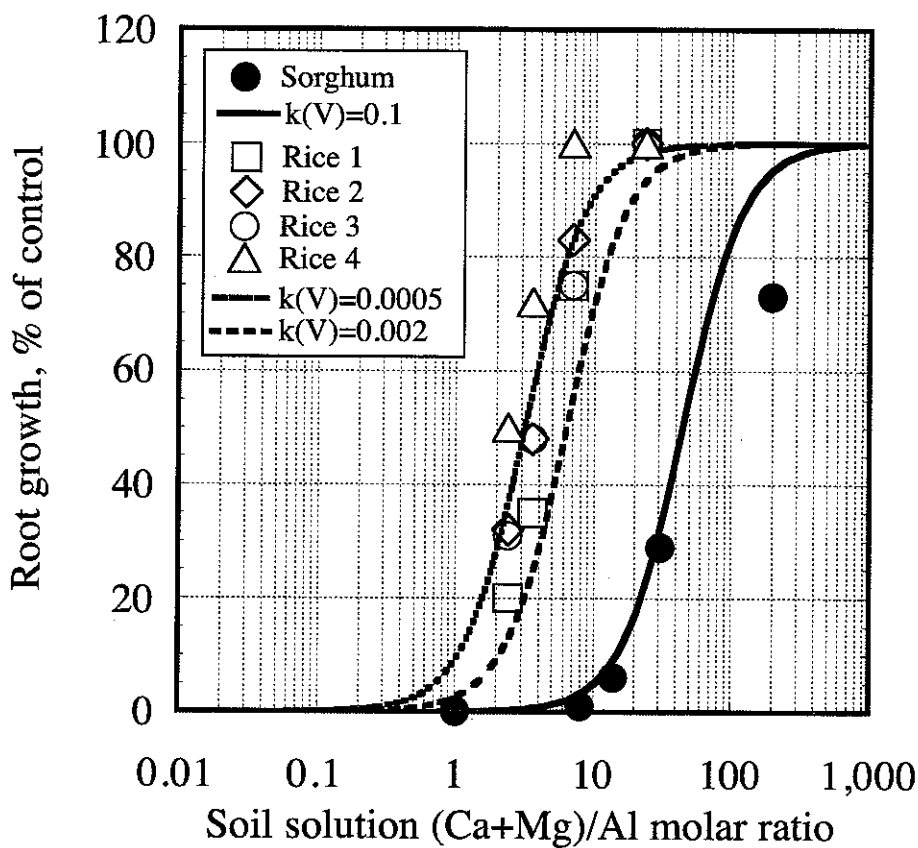
Figure 62: Response data for sorghum (*Sorghum sativa*) and 4 different strains of rice (*Oryza sativa*).
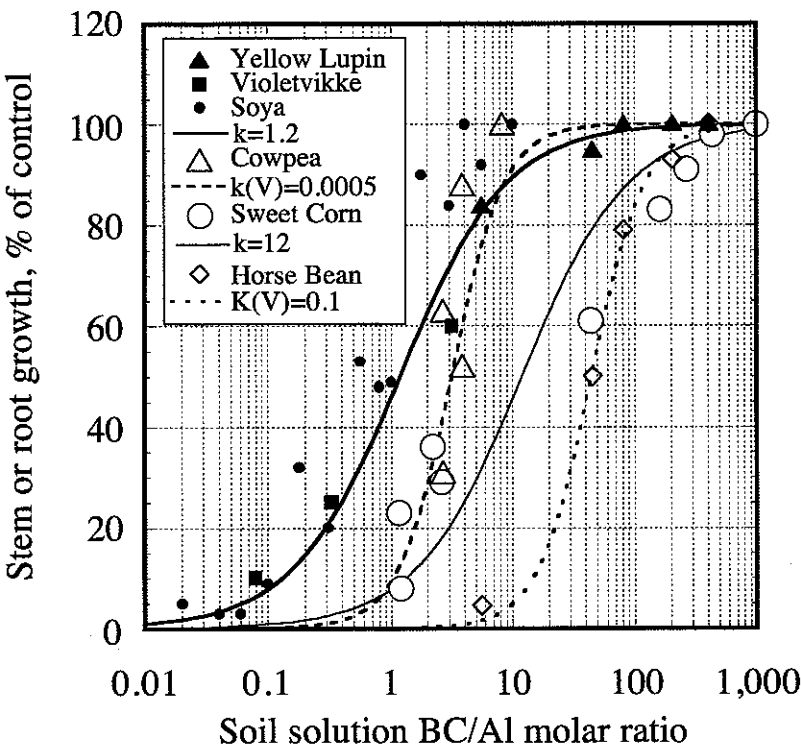
Figure 63: Response data for bush vetch (*Vicia sepium*), yellow lupin (*Lupinus luteus*), cowpea (*Vignia unguiculata*), horse bean (*Vicia faba*), soya bean (*Glycine max*) and maize (*Zea mays*).
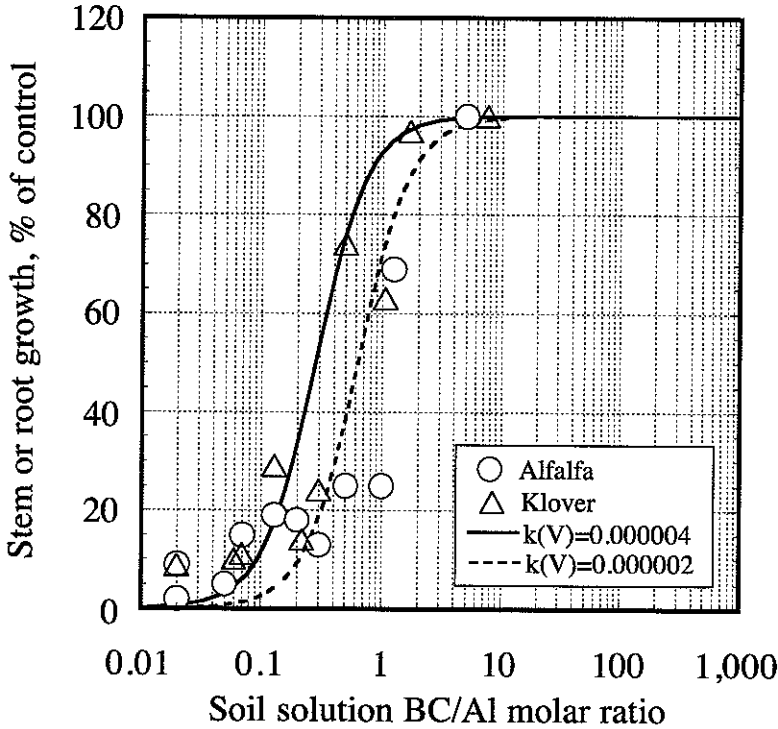
Figure 64: Response data for subterranean clover (*Trifolium subterranum*) and alfalfa (*Medicago sativa*). The tolerance of these plants to Al is intermediate, and comparable to the tolerance of Norway spruce. White clover (*Trifolium repens*), not included in the diagram, was much more sensitive with a k=0.01.

Plant species	Latin name	Reaction type	K-value	BC/Al(crit)
Subterranean clover	*Trifolium subterraneum*	Vanselow	K=0.000004	0.6
Alfalfa	*Medicago sativa*	Vanselow	K=0.000002	1.2
Soya bean	*Glycine max*	Unspecific	K=0.4	1.5
Tyler wheat	*Triticum aestivum*	Vanselow	K=0.00005	2
Potato	*Solanum tuberosum*	Vanselow	K=0.00002	2
Tomato	*Lycopersicon esculertum*	n.d.	n.d.	2.5
Rye	*Secale cereale*	Vanselow	K=0.0005	6
Atlas wheat	*Triticum aestivum*	Vanselow	K=0.0005	6
Rice	*Oryza sativa*	Vanselow	K=0.0005	6
Cowpea	*Vignia unguiculata*	Vanselow	K=0.0005	6
White clover	*Trifolium repens*	Vanselow	K=0.0.01	20
Grana wheat	*Triticum aestivum*	Vanselow	K=0.02	40
Lettuce	*Latuca sativa*	Vanselow	K=0.001	40
Sweet Corn, Maize	*Zea mays*	Unspecific	K=12	45
Horse Bean	*Vicia faba*	Vanselow	K=0.1	80
Sorghum	*Sorghum sativa*	Vanselow	K=0.1	80
Barley	*Hordeum vulgare*	Vanselow	K=2.0	400

Table 31: Response type and estimated aluminium response coefficients for different species of crop plants. The limiting BC/Al-value represents root growth for laboratory results reduced to 80% of normal. n.d. represents values derived from semi-quantitative data.

13   Discussion

13.1   The effect of H^+-ions

The response model indicates that H^+ also may have an adverse effect, but that this generally occurs under more acid conditions than the effect of Al, thereby masking the effect of H^+. The effect of H^+ ought only to be pronounced in very acid organic soils with much dissolved organic matter, or quartz soils without significant Al in solution. This is consistent with the observation that as soils acidify, the ion exchange positions become filled with Al as a replacement for base cations, but at a later stage, when either the Al source has become exhausted or the soils have become extremely acidified, Al will be replaced by H^+ as the adverse agent.

Tab. ?? contains a limiting pH, corresponding to the H^+-concentration required cause the same effect as Al is soils without dissolved free ionic Al in the soil solution. The values were derived by using equation 15 to estimate the $[H^+]$ which would give the same effect as Al. The values were based on a soil BC concentration of 3 mg/l. The limiting pH is based on assuming an operational aluminium equilibrium gibbsite coefficient of -pK=8.4. The critical pH has significance for vegetation response to acid deposition on moors, bogs, peats and very humic soils, where the Al soil solution concentration is very low.

As was seen earlier, data by Andersson and Brunett (1993) in particular show that H^+ is involved in the mechanism for grasses. For bacteria and fungi, Jönsson et al., (1994) extracted data that clearly show that three H^+ must be added to Al (n=3) if the response in of the Vanselow type and one H^+ must be added to Al (n=1) if the response is of the unspecific type. Other data hint a a similar thing for the root growth of Norway spruce, but the root growth data do not allow any exact determinations.

These observation suggests that the key issue is the competition of wanted ions with unwanted ions at the surface. This implied that Cu, Mn or any other unwanted ion would be able to act in a similar way as Al, provided it is present in similar concentrations, and has a similar affinity for the organic surface material.

pH limits for growth rate effects on different plant species can be given;

pH=3.0-3.2 western red cedar, Digitalis, Deschampsia, Galium saxatile, Juncus, Vaccinium myrtillus, Erica, feather mosses

pH=3.2-3.4 sitka-, white- and black spruce

pH=3.4-3.6 douglas fir, hemlock spruce, cedar, white-, monterrey-, sand-, and slash pine, rhododendron, Trifolium, Calluna, Agrostis, Digitaria, Medicago, Vaccinium vitis-idea, Vaccinium macrocarpon, Cladina

pH=3.6-3.8 longleaf- and aleppo pine, scots-, armand-, virginia-, pitch-, cembra-
, loblolly- and jack pine, larch, cotton, Brachyopodium, Triticum, Vicia,
Origanum, Arnika montana, Anemone nemorosa, Convallaria

pH=3.8-4.0 Norway- and red spruce, balsam-, faber and silver fir, orange,
maples, beeches, oaks, birch, honeylocust, teak, peach, rowan, horn-
beam, lime, paper birch, alder, ash, Geum, Carex, Bromus, Holcus,
Campanula, Secale, Oryza

pH=4.0-4.3 fraser fir, black spruce, masson pine, coffee, aspen

pH=4.3-4.5 Poa, Nardus, Hordeum

pH=4.5-4.7 Mandarin fir, Chinese fir, Galium odoratum, Bromus benekenii,
Prunella, Taraxacum

The values represent critical pH in the absence of aluminium. The values
take the effects of different rooting depths into account. The values are ap-
proximate, except for Bromus benekenii and Galium saxatile which have pH
4.7.

13.2 Molecular mechanisms

It is somewhat disturbing that spruce trees (*Picea* and *Abies*) seem to follow
an isotherm implying a valence unspecific mechanism we cannot fully explain
in terms of molecular mechanisms (See Table 1). Either the plant is able to
float excess charges around on the surfaces, maybe the surface acts like a con-
tinuum of receptor sites where the imbalance of charge is compensated for by
some type of exudation of organic acids or protons (Cronan, 1991 suggests ion
exchange as the driving mechanism, and Marschner, 1991 suggests something
that could be twisted to support such an idea). Maybe proper ion exchange
do not occur at all, but rather some type of charge-driven physical adhesion
to the surface prior to uptake. For red spruce, different Ca and Mg concentra-
tions at constant BC/Al ratio did not change the response significantly. For
red spruce the Ca and Mg concentration varied from at total BC concentrtion
of 0.2 mol/l (Hutchinson et al., 1985) to 1.8 mol/l (Schier, 1985).

For pines and deciduous trees, some peculiarities also appear. The response
follow the Vanselow type of response, but the on the BC concentration in
addition to the dependence on the BC/Al ratio may not be as strong as implied
by Eq. 17. Some experiments indicate that the exponent n on the base cation
concentration as defined in the empirical expression, may be closer to 0.5 than
1.0, and that the exponent m=2. For example Hutchinson et al., 1985 did
experiments at 4 and 16 mg/l of Ca and Mg. If n=0 for the Vanselow type of
response, then that could be interpreted as a valence unspecific second order

responce, that BC ions would somehow exchange in twos with Al at the root surface.

13.3 Forest decline pathways

Soil acidification will make trees more susceptible to drought and wind damage. In nature, the soil moisture saturation of a normal forest vary in the range 0.15-0.30 m^3 of water per m^3 of soil. Tree growth shows the strongest dependence on soil moisture in the range 0.05-0.20 m^3 of water per m^3 of soil (Sverdrup et al., 1992). During dry periods, moisture saturation may drop to 0.05 m^3 of water per m^3 of soil. The growth rate is much influenced by changes in the range 0.05-0.20 m^3 of water per m^3 of soil, and additional stress on the tree by Al during dry periods when growth is already significantly reduced by this factor, may push the tree below the minimum uptake limit required to sustain life. The BC/Al ratio vary down through the soil profile, from high values at the top due to much Ca and Mg and little Al to very low in the E and B horizon of acidified soils, generally it increases again towards the C layer (Sverdrup and Warfvinge, 1988). Under soil acidification, conditions can get very unfavorable through low BC/Al ratio in the lower part of the rooting zone, causing trees to locate most of their roots to the top layers. Thus the tree will become less well anchored in the ground, and may easier suffer from windfall.

In acidification other factors than soil acidification may lead to vegetation changes. Direct effects by fumigation may cause foliar damage, and nitrogen deposition may alter competition for nutrients between plant species. In this sense, several types of ground vegetation can be listed in order of increasing N tolerance, such as the very sensitive lichens, heather, Lingon, over more tolerant like blueberry to N promoted species like grasses and herbs. The picture is further complicated by the fact that N deposition and acid deposition follow each other and N deposition often contributes significantly to the total acid load. Climate changes, natural or anthopogenically induced may lead to vegetation change. Finally, many vegetation ecosystems are not totally stable, but may shift between several simultaneous stable states after minor system disturbances or as a part of ecosystem aging and evolution.

13.4 Effect of temperature

Aniol (1983) studied the effect of temperature on the critical Al concentration, and found a strong correlation for two species of wheat. The plant was affected by lower concentrations of Al at higher temperature. The effect was quite strong, corresponding to an Arrhenius factor A=6310 corresponding to an activation energy of 52.4 kJ/mol. The reason for this is not explained by

Aniol, but we can think of some possible explanations. First, the effect may be connected to the fact that the plant grows faster when the temperature increases. The observed effect is however stronger than the growth increase with temperature increase (A=5200, Sverdrup et al., 1992). An alternative explanation would be that the change in temperature changes chemical reactions like ion exchange at the root surface. The increase in Al toxicity with temperature, was accompanied by an increase in root Al content. The activation energy is indicative of a chemical process, and large enough to exclude diffusion processes.

13.5 P/Al-ratio

Some of the studies on trees, cereals and legumes revealed that the P/Al ratio may also be an important factor for growth, especially in soils with no or little excess production of P over growth demand (Alva et al., 1986; Asp and Berggren, 1990). Since P is an essential element and growth rate regulating, similar effects can be expected for trees as well. How this can be worked into the damage function will be the subject of future studies. Some data is available for tea (Fig. 38) and that data may indicate the effect of P supply and the P/Al ratio on growth together with the $(Ca+Mg+K)/Al$. However, at present there is not enough data available to get a good overview picture. Data on the effect of P/Al ratio on the effect of the BC/Al ratio on growth is needed. Data available for such studies would include Varco and Sartain (1966); Andrew et al. (1973); Rode (1988); Alva et al. (1988); Asp and Berggren (1990).

13.6 Nitrogen

Data may be interpreted to indicate that the source of nitrogen may be important. The effect of nitrogen source may however be an effect of several independent and different mechanisms, such as:

- The soil chemistry effect of acidity produced by nitrification of NH_4 prior to uptake

- The effect of ANC production by nitrate uptake by plants in contrast to the acidity produced by ammonium uptake

- A physiological effect on the plant, arising from the form of N taken up. Theoretically, the plant will have to spend less energy if NH_4 is taken up.

In several studies reporting the effect of type of N source on the Al-tolerance, the general impression we get is that the effect on soil ANC seems to be the important mechanism, rather than plant physiological mechanisms.

13.7   Generality and exceptions from the rule

We do not doubt that the sceptical reader can find contradictions to our results and the data presented here. The diversity of nature and genetics of plants make this very likely. Still, we think this study compiles and evaluates the data systematically in relation to a consistent methodology, based in an analogy to surface ion exchange, as suggested by Cronan (1991) and others. Even if the reader rejects our theoretical considerations and hypothesises conserning molecular mechanisms, an irrefutable empirical pattern remains. This work synthesizes a large amount of the information available in the literature, and points out a pattern of relative sensitivities to aluminium and soil acidification, which we think is basically correct. It should be recognized that there is substantial uncertainties connected to much of the data, setting limits to some of the interpretations made.

Vegetation type	Ocurring tree type	BC/Al limit	Occurring plant type	BC/Al limit	Suggested limit
Polar or rock desert	Betula	0.7	Nardus stricta	10	6
	Calluna	0.8	Carex remota	45	
			Agrostis capillaris	1	
			Ranunculus	3	
Tundra	Salix	5	Agrostis capillaris	1	2
	Pinus	1	Carex remota	45	
	Betula spp	0.7	Vaccinium myrt.	0.6	
			Caluna	0.8	
Cool semi-desert scrub	Pinus mugo	1.2	Nardus spp	5	2
Montane cold scrub grass	Rhododendron	5	Agrostis spp	1	
Cool scrub/Grassland	Caluna	0.8	Deschampsia	2	
	Pinus	1	Vaccinium idea	1.2	
			Caluna	0.8	
			Empetrum	1.2	
			Stipa capillata	10	
Main taiga	Picea abies	1.2	Deschampsia	1	1
Southern taiga	Pinus sylvestris	1.2	Carex	100	
	Betula pendula	0.8	Vaccinium myrt.	0.6	
	Pinus cembra	1.0	Agrostis	1	
	Larix decidua	2	Juncus	0.5	
Coniferous forest	Picea abies	1.2	Vaccinium	0.3	1
	Pinus sylvestris	1.2	Agrostis	1	
	Pinus cembra	1.0			
	Larix decidua	2			
Mixed forest	Picea abies	1.2	Poa	10	1.5
	Pinus sylvestris	1.2	Trifolium	5	
	Betula pendula	0.8			
	Larix decidua	2			
	Acer platanoides	0.6			
Temperate broadleaf	Abies alba	1.2	Poa	10	0.6
	Fagus sylvatica	0.6	Nardus stricta	10	
	Quercus robur	0.6	Convallaria majalis	3	
	Betula populifolia	2	Trifolium	5	
	Acer platanoides	0.6	Allium	50	
Interrupted temperate woods	Betula papyrifera	2	Digitaria	1	1
	Pinus silvestris	1.2	Lolium	0.5	
	Fagus	0.6	Origanum	4.5	

Table 32: 1–Suggested indicator species and their BC/Al limits for ecosystem classes in Asia.

Vegetation type	Ocurring tree type	BC/Al limit	Occurring plant type	BC/Al limit	Suggested limit
Mediterranean woodland	Pinus radiata	0.8	Taraxacum	80	1
	Pinus taeda	1.5	Poa	10	
	Pinus halepensis	0.5	Digitaria1	10	
	Robinia pseudoacacia	1.4	Lolium	0.5	
	Ouercus palustris	0.6			
Dry/highland woods	Pinus sylvestris	1.4	Poa	10	2
	Pinus taeda	1.5	Nardus stricta	10	
	Pinus ponderosa	2	Agrostis	1	
	Pinus armandii	1	Digitaria	10	
Interrupted tropical woods	Eucalyptus gummifera	3	Stipa	10	2
	Robinia pseudoacacia	1.4			
	Citrus aurantium	2			
	Poa	10			
	Vitis vinifera	0.5			
Subtropical dry forest	Pinus palustris	2	Poa	10	2
	Pinus clausa	0.6			
	Schima superba	10			
	Cunninghamia lanceolata	20			
	Pinus massonii	4			
	Camillia sinensis	1.4			
Subtropical wet forest	Tuja plicata	0.1			1
	Pseudotuga menziesii	0.3			
Tropical dry forest	Citrus	2	Calcicole grasses	1	1
	Coffea arabica	75	Zea mays	45	
	Eucalyptus	3			
	Acacia	2			
Tropical wet forest	Tectona grandis	0.6	Legumes	10	0.6
	Guapira olfersiana	1.4	Tropical orcids	100	
	Citrus	2			
Tropical savannah	Acacia	2	Poa	10	10
			Bromus	10-100	

Table 33: 2–Suggested indicator species and their BC/Al limits for ecosystem classes in Asia.

Vegetation type	Ocurring tree type	BC/Al limit	Occurring plant type	BC/Al limit	Suggested limit
General farmlands	Acer	0.6	Triticum aestivum	6	10
	Castaneda	0.6	Secale cereale	6	
	Quercus	0.7	Latuca sativa	40	
			Glycine max	1.5	
			Zea mays	45	
			Sorgum sativa	80	
Irrigated paddyland	Populus	6	Oryza sativa	6	10
	Alnus	5			
	Salix	5			
Irrigated other farmland	Acer	0.6	Triticum aestivum	6	10
	Castaneda	0.6	Secale cereale	6	
	Quercus	0.7	Lettuca sativa	40	
			Glycine max	1.5	
			Zea mays	45	
			Sorgum sativa	80	
Coastal wetland, cold	Populus	6	Carex	10-250	10
Coastal wetland, mangrove	Salix	5	Poa	100	
Coastal wetland and hinterland	Pinus	0.8	Allium	50	
			Stellaria	120	
			Taraxacum	800	
Hotscrub/Grassland	Acacia	2	Poa	250	10
Succulent and thorn dry woods	Pinus	2	Bromus benekenii	30	
Semi-arid forest	Pinus halepensis	0.5	Succulents	1000	
	Cotton	1.2			
Non-polar rocky vegetation	Pinus	1.5	Poa	100	10
Sand desert			Calcicole plants	10	
Semidesert			Triticum	6	
Steppe			Stipa capillata	10	

Table 34: 3–Suggested indicator species and their BC/Al limits for ecosystem classes in Asia.

Vegetation type	Rooting depth, meter	Gibbsite koefficient	pK_{gibb}
Polar or rock desert	0-0.1	100	8.0
Tundra	0-0.2	150	8.1
Cool semi-desert scrub	0-0.3	200	8.3
Montane cold scrub grass	0-0.3	200	8.3
Cool scrub/Grassland	0-0.3	200	8.3
Main taiga	0-0.5	300	8.5
Southern taiga	0-0.5	300	8.5
Coniferous forest	0-0.5	300	8.5
Mixed forest	0-0.8	500	8.7
Temperate broadleaf	0-0.8	500	8.7
Interrupted temperate woods	0-0.5	300	8.5
Dry/highland woods	0-0.5	300	8.5
Mediterranean woodland	0-0.5	300	8.5
Interrupted tropical woods	0-0.5	300	8.5
Subtropical dry forest	0-0.5	300	8.5
Subtropical wet forest	0-0.2	150	8.1
Tropical dry forest	0-0.5	300	8.5
Tropical wet forest	0-0.2	150	8.1
Tropical savannah	0-0.5	300	8.5
General farmlands	0-0.3	200	8.3
Irrigated paddyland	0-0.3	200	8.3
Irrigated other farmland	0-0.3	200	8.3
Coastal wetland, cold	0-0.5	300	8.5
Coastal wetland, mangrove	0-0.5	300	8.5
Coastal wetland and hinterland	0-0.5	300	8.5
Hotscrub/Grassland	0-0.3	200	8.3
Succulent and thorn dry woods	0-0.3	200	8.3
Semi-arid forest	0-0.5	300	8.5
Non-polar rocky vegetation	0-0.2	150	8.1
Sand desert	0-0.5	300	8.5
Semidesert	0-0.5	300	8.5

Table 35: Suggested model entry values for calculation of critical loads using the SMB in Asia in the RAINS-ASIA Project.

Vegetation type	BC/Al-limit
Polar or rock desert	6
Tundra	2
Cool semi-desert scrub	2
Montane cold scrub grass	2
Cool scrub/Grassland	2
Main taiga	1
Southern taiga	1
Coniferous forest	1.5
Mixed forest	1
Temperate broadleaf	0.6
Interrupted temperate woods	1
Dry/highland woods	2
Mediterranean woodland	1
Interrupted tropical woods	2
Subtropical dry forest	2
Subtropical wet forest	1
Tropical dry forest	1
Tropical wet forest	0.6
Tropical savannah	10
General farmlands	10
Irrigated paddyland	10
Irrigated other farmland	10
Coastal wetland, cold	10
Coastal wetland, mangrove	10
Coastal wetland and hinterland	10
Hotscrub/Grassland	10
Succulent and thorn dry woods	10
Semi-arid forest	10
Non-polar rocky vegetation	10
Sand desert	10
Semidesert	10

Table 36: Suggested model entry values for calculation of critical loads in Asia in the RAINS-ASIA Project, based on FAO classified landscape types.

14   Conclusions

The results suggests that soil chemistry can affect the growth of all trees and ground vegetation species. A particular plant species is affected by soil acidification when acidification change the soil chemistry beyound the chemical change. The effect is manifested as decline in growth and increased mortality. The correlation between low BC/Al values and growth decline in laboratory assays and field studies, are supported by a large number of observations. Under acid conditions, plants react to soil solution Al according to patterns that can be interpreted as three distinct ion exchange responses. The distribution of different trees and ground vegetation species among these response types are:

- Vanselow response, little elasticity

    - Pine, larch, hemlock, cedars and douglas
    - Deciduous trees

- Valence unspecific response, intermediate elasticity

    - Spruce and fir
    - Herbs and grasses

- Gapon response, much elasticity

    - Willow and coffee

The differences in response arise from differences in how the different plants actually take up nutrients from the soil solution. Bioassay experiments on plant tolerance to Al can be related to field conditions for different types of spruce and fir as is indicated in Figs. 2-4. For laboratory conditions, the data for spruce and fir can be fitted to an expression of the valence unspecific type. All grasses, herbs and flowers studied, fitted the valence unspecific response best.

The laboratory values for plants where field data is also available (Norway spruce, red spruce, European beech, red oak) seem to indicate that B-horizon BC/Al values to apply to critical load calculations for field conditions, are one half of the laboratory values (Table 2). In relation to calculations of critical loads of acidity, sulphur and nitrogen deposition to forest ecosystems, a general value of BC/Al$\geq$1.0 seems well chosen for European forests. For the calculation of critical loads, the laboratory values should be used if a multilayer model is utilized.

Teak, guapira, orange and cotton are all more tolerant to Al than trees of the temperate zone. They are possibly accostumed by evolution to tolerate

more Al from growing on Al-oxide-rich, non-glaciated old soils. Most of the commercially important tree species in Europe like spruce, fir, pine, birch, oak and beech seem to have a critical field BC/Al-ratio in the range of 0.6-1.0. This would put a small safety margin into the critical loads applied in Europe.

15 Acknowledgment

References

Abrahamsen, G.: 1984, Effects of acidic deposition on forest soil and vegetation, *Phil. Trans. R. Soc. Lond.* **B 305**, 369–382.

Adams, F. and Lund, Z. F.: 1966, Effect of chemical activity of soil solution aluminium on cotton root penetration of acid subsoils, *Soil Science* **101**, 193–198.

Ahmad, F. and Tan, K. H.: 186, Effect of lime and organic matter on soybean seedlings grown in aluminium toxic soil, *Soil Science Society of America Journal* **50**, 656–661.

Alcamo, J. e. a.: 1987, Acidification in europe, a simulation model for evaluating control strategies., *Ambio* **16**, 232–244.

Alva, A. K., Edwards, D. G. and Blamey, F. P. C.: 1986a, Relationships between root length of soybean and calculated activities of aluminium monomers in nutrient solution, *Soil Science Society of America Journal* **50**, 959–962.

Alva, A. K., Edwards, D. G., Asher, C. J. and Blamey, F. P. C.: 1986b, Effects of phosphorus/aluminium molar ratio and calcium concentration on plant responce to aluminium toxicity, *Soil Science Society of America Journal* **50**, 133–137.

Anderson, M.: 1992, The effects of pH and aluminium on growth of Galium odoratum (L) Scop. in flowing solution culture, *Environmental and experimental botany* **32**, 497–504.

Anderson, M. E.: 1993, Aluminium toxicity as a factor limiting the distribution of Allium ursinium (L)., *Annals of Botany* **72**, xx–yy.

Anderson, M. E. and Brunet, J.: 1993, Sensitivity to H and Al ions limiting growth and distribution of the woodland grass Bromus benekenii, *Plant and Soil* **153**, 243–254.

Andrew, C. S., Johnson, A. D. and Sandland, R. L.: 1973, Effect of aluminiumon the growth and chemical composition of some tropical and temperate pasture legumes, *Aust. J. Agric. Res.* **24**, 325–339.

Aniol, A.: 1983, Aluminiumuptake by roots of two winter wheat varieties of different tolerance to aluminium, *Biochem. Physiol. Pflanzen* **178**, 11–20.

Arovaara, H. and Ilvesniemi, H.: 1990, The effect of soluble inorganic aluminium and nutrient imbalances on *pinus sylvestris* and *picea abies*

seedlings, in P. Kauppi (ed.), *Acidification in Finland*, Springer.Verlag, Berlin, pp. 715–733.

Arp, P. and Quimet, R.: 1986, Uptake of Al, C, and P in black spruce seedlings; effect of organic versus inorganic Al in nutrient solutions, *Water, Air and Soil Pollution* **31**, 367–375.

Asher, C. J.: 1987, Effects of nutrient concentration in the rhizosphere on plant growth, in D. Hintze (ed.), *Transactions of the XII congress of the International Society of Soil Science*, Int. Soil Sci. Soc., pp. 209–216.

Asp, H. and Berggren, D.: 1990, Phosphate and calcium uptake in beech (Fagus Sylvatica L) in the presence of aluminium and natural fulvic acids., *Physiol. Plant.* **80**, 307–314.

Asp, H., Bengtsson, B. and Jensen, P.: 1988, Growth and uptake in spruce (*picea abies*) grown in sand culture with various aluminum contents, *Plant and Soil* **111**, 127–133.

Aune, E. I., Dahl, E. and Löes, A.-K.: 1989, Comparison of forest soils in relation to acid precipitation in central Norway, south Norway and Schwarzwald in West Germany, *Medd. Nor. Inst. skogforsk.* **42**, 133–146.

Barnard, J. E. and Lucier, A. A.: 1991, Changes in forest health and productivity in the United States and Canada, in P. Irving (ed.), *Acidic deposition; State of science and technology. Summary report of the U S national acid precipitation assessment program*, National Acid Precipitation Assessment Program, pp. 135–138.

Baynard, J. E. (ed.): 1990, National Acid Precipitation Assessment Program.

Becker, M.: 1991, Impacts of climate, soil and silviculture on forest growth and health, in G. Landmann (ed.), *French research into forest decline– DEFORPA programme, 2nd report*, Ecole Nationale du genie rural, des euax et des forets, pp. 23–38.

Becker, M., Landmann, G. and Levy, G.: 1989, Silver fir decline in the Vosges mountains(France): Role of climate and silviculture, *Water, Air and Soil Pollution* **48**, 77–86.

Berggren, D.: 1990, Species of Al, Cd, and Cu in forest soil solutions: Analytical methods, mobilization mechanisms and toxicity to plants, *Technical report*. PhD Thesis.

Bingham, F. T., Page, A. L., Mitchell, G. A. and Strong, J. E.: 1979, Effects of liming an acid soil amended with sewage sludge enriched with Cd, Cu, Ni

and Zn on yield and Cd content of wheat grain, *Journal of Environmental Quality* **8**, 202–207.

Bolt, G. H. and Riemdijk, W. H. v.: 1982, *Ion adsorption on inorganic variable charge constituents*, Elsevier Scientific Publishing Company.

Bonneau, M.: 1991, Effects of atmospheric pollution via the soil, in G. Landmann (ed.), *French research into forest decline–DEFORPA programme, 2nd report*, Ecole Nationale du genie rural, des euax et des forets, pp. 87–100.

Bossel, H., Metzler, W. and Schäfer, H.: 1985, *Dynamik des Waldsterbens*, Springer–Verlag.

Brown, D.: 1982, The effect of pH and calcium on fish and fisheries., *Water Air and Soil Pollution* **16**, 343–351.

Bruck, R. J.: 1988, Research site; Mount Mitchell (Southern Appalachians); decline of Red Spruce and Fraser Fir, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 108–11.

Cambraia, J., Galvani, F. R. and Estevao, M. M.: 1983, Effects of aluminium on organic acid, sugar and amino acid composition of the root system of sorghum, *J. Plant Nutrition* **6**, 313–322.

Chen, C., Gherini, S., Hudson, R. and Dean, S.: 1983, The Integrated Lake-Watershed Acidification Study, *Final Report EPRI EA-3221*, Electrical Power Research Institute, Palo alto, California.

Chenery, E. M.: 1955, A preliminary study of aluminium and the tea bush, *Plant and soil* **6**, 174–200.

Christensen, T.: 1984, Cadmium soil sorption at low concentrations: I. Effect of time cadmium load, ph and calcium, *Water, Air and Soil Pollution* **21**, 105–114.

Cronan, C. e. a.: 1989, Aluminium toxicity in forests exposed to acidic deposition; The Albios results, *Water, Air and Soil Pollution* **48**, 181–192.

Cronan, C., Kelly, J. M., Schofield, C. and Goldstein, R. A.: 1987, Aluminium geochemistry and tree toxicity in forests exposed to acidic deposition, Selper Ltd, London, pp. 649–656.

Cronan, C. S.: 1991, Differential adsorption of Al, Ca and Mg by roots of red spruce (*Picea rubens* sarg.), *Tree physiology* **8**, 227–237.

Daziel, T., Morris, R. and Brown, D.: 1985, The effects of low pH, low calcium concentrations and elevated aluminium concentrations on sodium fluxes in brown trout, Salmo Trutta L., *Water Air and Soil Pollution* **31**, 569–577.

de Vries, W. and Breeuwsma, A.: 1987, The relation between soil acidification and elemental cycling, *Water, Air and Soil Pollution* **35**, 293–310.

de Vries, W. and Kros, J.: 1989, The long term impact of acid deposition on the aluminium chemistry of an acid forest soil, in J. Kämäri, A. Jenkins, D. F. Brakke, R. F. Wright and S. A. Norton (eds), *Regional Acidification Models*, pp. 231–255.

DeWald, L. E., Sucoff, E., Ohno, T. and Buschena, C.: 1990, Responce of northern red oak (quercus rubra) seedlings to soil solution aluminium, *Can. J. For. Res.* **20**, 331–336.

Drechsel, P., Schmall, S. and Zech, W.: 1991, Relationships between growth, mineral nutrition and soils in young teak plantations in Benin and Liberia, *Water, Air and Soil Pollution* **54**, 651–656.

Driscoll, C., Fuller, R., Santore, R. and Lawrence, G.: 1986, The speciation of ions in acidic soil solutions, *Transaction of the XIII congress of the international society of soil science* **V**, 59–62.

Edwards, J. H., Horton, B. D. and Kirkpatrick, H. C.: 1976, Aluminium toxicity symptoms in peach seedlings, *J. Am. Soc. Hort. Science* **10**, 139–142.

Eldhuset, T. D.: 1988, Virkninger av aluminium på höyere planter ved lav ph; en litteraturoversikt., *Medd. Nor. Inst. Skogforsk.* **40**, 1–19.

Enyedi, A. and Kuja, A.: 1986, Assessment of relative sensitivities during early growth stages of selected crop species subjected to simulated acidic rain, *Water, Air and Soil Pollution* **31**, 325–335.

Evers, F. H.: 1983, Ein versuch zur aluminium toxizität bei fichte, *Der Forst und Holzwirt* **12**, 305–307.

Falkengren-Grerup, U.: 1987, Long–term changes in pH of forest soils in southern Sweden, *Environmental Pollution* **43**, 79–90.

Falkengren-Grerup, U. and Eriksson, H.: 1990, Changes in soil, vegetation and forest yield between 1947 and 1988 in beech and oak sites of southern sweden., *Forest Ecology and Management* **38**, 37–53.

Forsline, P., Musselman, R. C., Dee, R. and Kender, W.: 1983, Effects of acid rain on grapewines, *Am. Jour. Enol. Vitic.* **34**, 17–22.

G., K. W. and van Loenen, E.: 1989, Effects of aluminium and mineral nutrition on growth and chemical composition of hydroponically grown seedlings of five different forest tree species, *Plant and Soil* **119**, 39–50.

Gobran, G., Bergholm, J., Clegg, S. and Nilsson, L. O.: 1991, The relationship between rhizosphere and needle chemistry in skogaby, *Technical report*. Project 2.2, Results 9.

Godbold, D. L. and Huettermann, A.: 1986, The uptake and toxicity of mercury and lead to spruce (Picea abies karst) seedlings., *Water, Air and Soil Pollution* **31**, 509–515.

Goyer, R. A.: 1988, *Toxic effects of metals*, Collier Macmillan Publishers.

Grauer, U. E. and Horst, W. J.: 1990, Effect of pH and nitrogen source on aluminium tolerance of rye (*secale cereale*) and yellow lupin (*lupinus lutetus*), *Plant and Soil* **127**, 13–21.

Guerrier, G.: 1982, Relation between sorghum root system and aluminium toxicity, *J. Plant Nutrition* **5**, 123–136.

Göransson, A. and Eldhuset, T. D.: 1987, Effects of aluminium on growth and nutrient uptake of betula pendula seedlings, *Physiol. Plantarium* **69**, 193–199.

Haas, A. R. C.: 1936, Phosphorus nutrition of citrus and the beneficial effect of aluminium, *Soil Sci.* **42**, 187–201.

Hackett, C.: 1965, Ecological aspects of the nutrition of *deschampsia flexuosa*, *Ecology* **53**, 315–333.

Hahs, M. and Ulrich, B.: 1988, Research site, Lange Bramke catchment, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 60–63.

Helyar, K. R. and Anderson, A.: 1971, Effects of lime on the growth of five grass species, on aluminium toxicity and on phosphorus availability, *Austr. J. Agric. Res.* **22**, 707–721.

Horst, W. J. and Göppel, H.: 1986, Aluminium toleranz von ackerbohne (*vicia faba*), lupine (*lupinus luteus*), gerste (*hordeum vulgare*) und roggen (*secale cereale*). 1; spross und wurzelwachstum in abhengigkeit vom aluminium angebot, *Z. Pflanzenernähr. Bodenk.* **149**, 83–93.

Horst, W., Wagner, A. and Marsschner, H.: 1983, Effects of aluminium on root growth, cell division rate and mineral element contents in roots of *vigna unguiculata* genotypes, *Z. Pflanzenphysiol. Bd.* **109**, 95–103.

Howeler, R. H. and Cadavid, L. F.: 1976, Screening of rice cultivars for tolerance to Al-toxicity in nutrient solutions as compared with a field screening method, *Agronomy Journal* **68**, 551–555.

Hue, N. V., Craddock, G. R. and Adams, F.: 1986, Effect of organicv acids on aluminium toxicity in subsoils, *Soil Science Society of America Journal* **50**, 28–34.

Huetterman, A. and Ulrich, B.: 1984, Solid phase-solution-root interaction in soils subjected to acid deposition, *Phil. Trans. R. Lond.* **B 305**, 352–368.

Hutchinson, T. C., Bozic, L. and Munoz-Vega, G.: 1986, Responces of five species of conifer seedlings to to aluminium stress, *Water, Air and Soil Pollution* **31**, 283–294.

Ilvesniemi, H.: 1992, The combined effect of mineral nutrition and soluble aluminium on *pinus sylvestris* and *picea abies* seedlings, *Forest ecology and management* **51**, 227–238.

Jarvis, S. and Hatch, D.: 1986, The effects of low concentrations of aluminium on the growth and uptake of nitrate-N by white clover, *Plant and Soil* **95**, 43–55.

Johnson, A.: 1988a, Research site; Camels Hump; Red Spruce damage, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 100–103.

Johnson, A.: 1988b, Research site; Whiteface Mountain; Red Spruce damage, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 104–105.

Johnson, D. and Taylor, G.: 1989, Role of air pollution in forest decline in eastern North America, *Water, Air and Soil Pollution* **48**, 21–43.

Johnston, A., Goulding, K. and Poulton, P.: 1986, Soil acidification during more than 100 years under permanent grassland and woodland at Rothamsted, *Soil Use and Management* **2**(1), 3–10.

Joslin, J. D. and Wolfe, M. H.: 1988, Responses of red spruce seedlings to changes in soil aluminium in six amended forest soil horizons, *Can. J. For. Res.* **18**, 1614–1623.

Joslin, J. D. and Wolfe, M. H.: 1989a, Aluminium effects on northern red oak seedling growth in six forest soil horizons, *Soil Sci. Soc. Am. J.* **53**, 274–281.

Joslin, J. D. and Wolfe, M. H.: 1989b, Responses of red spruce seedlings to changes in soil aluminium in six amended forest soil horizons, *Soil Sci. Soc. Am. J.* **53**, 274–281.

Kelly, J. M., Schädele, M., Thornton, F. C. and Joslin, J. D.: 1990, Sensitivity of tree seedlings to aluminium; lll; red oak, sugar maple and European beech, *J. Environ. QWual.* **19**, 172–179.

Kentatämies, K.: 1991, The effects of atmospheric pollutants on soils and terrestial ecosystems, in K. Kenttämies (ed.), *Acidification Reseach in Finland*, Ministry of the Environment, Helsinki, pp. 15–23.

Kimmins, J. P. and Hawkes, B. C.: 1978, Distribution and chemistry of fine roots in a white spruce-subalpine fir stands in British Columbia, *Can. J. For. Res.* **8**, 265–279.

Kirkpatrick, H. C., Thompson, J. M. and Edwards, J. H.: 1975, Effects of aluminium concentration on growth and chemical composition of peach seedlings, *J. Am. Soc. Hort. Science* **10**, 132–134.

Konishi, S., Miyamoto, S. and Taki, T.: 1985, Stimulatory effect of aluminium on tea plants grown under low and high phosphorus supply, *Soil Sci. Plant Nutr.* **31**, 361–368.

Kowalkowski, A.: 1991, Survival rate of tree and shrub seedlings under extreme environmental nitrogen pollution, *Water, Air and Soil Pollution* **54**, 51–59.

Kreutzer, K.: 1988, Calcareous alps, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 82–83.

Kreuzer, K.: 1988, Bavarian forest, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 70–71.

Landmann, G.: 1991, Ground monitoring of forest vitality, in G. Landmann (ed.), *French research into forest decline–DEFORPA programme, 2nd report*, Ecole Nationale du genie rural, des euax et des forets, pp. 7–22.

Lee, J. and Pritchard, M. W.: 1984, Aluminium toxicity expression on nutrient uptake, growth and root morphology of *trifolium repens* cv. grasslands huia, *Plant and Soil* **82**, 101–116.

Liao, L. and Chen, C.: 1991, Effects of simulated acid rain on root growth of *cunninghamia lanceolata* and *schima superba* saplings in acidified soil, *Journal of Environmental Sciences (China)* **3**, 45–52.

Liebig, G., Vanselow, A. and Chapman, H.: 1942, Effects of aluminium on copper toxicity, as revealed by solution culture and spectrographic studies of citrus, *Soil Science* **53**, 341–351.

Lin, Z. and Myhre, D. L.: 1990, Citrus root growth as affected by soil aluminium level under field conditions, *Soil Science Society of America Journal* **54**, 1340–1344.

Ma, G.: 1991, Nutritional disturbances and declining armand pine in southwestern China, *Water, Air and Soil Pollution* **54**, 91–96.

MacDonald, N. W., Hart, J. B. and Nguyen, P. N.: 1986, Simulated acid rain effects on jack pine seedling establishment and nutrition, *Soil Science Society of America Journal* **50**, 219–225.

Makkonen-Spiecker, K.: 1985, Auswirkungen des aluminiums af junge fichten (*picea abies* karst) verschiedener provennienzen, *Forstwissenschaftliche Centralblatt* **104**, 341–353.

Marschner, H.: 1991, Mechanisms of adaption of plants to acid soils, *Plant and Soil* **134**, 1–20.

Matsumoto, H. and Yamaya, T.: 1989, Inhibition of potassium uptake and regulation of membrane-associated Mg2+-ATPase activity of pea roots by aluminium, *Soil SCi. Palnt Nutr.* **32**, 179–188.

Matziris, D. and Nakos, G.: 1978, Effects of simulated acid rain on juvenile characteristics of aleppo pine (*pinus halepensis*), *Forest Ecology and Management* **1**, 267–272.

Matzner, E. and Ulrich, B.: 1984, Raten der deposition, der internen production und des umsatses von protonen in zwei waldökosystemen, *Zeitschrift Pflansennärhrung und Bodenkunde* **147**, 290–308.

Matzner, E., Murach, D. and Fortmann, H.: 1987, Soil acidity and its relationship to root growth in declining forest stands in Germany, in P. Mathy (ed.), *Air pollution and ecosystems*, D. Reidel, Amsterdam, pp. 273–282. Conference proceedings of CEC International Symposium, Grenoble, 18-22 May, 1987.

McCormack, L. H. and Steiner, K. C.: 1978, Variation in aluminium tolerance among six genera of trees, *For. Sci.* **24**, 565–568.

McCormick, L. H. and Amendola, A.: 1983, Soil pH, extractable aluminium and tree growth on acid minesoils, *Comun. Soil Sci. Plant Anal.* 14, 249–262.

McLaughlin, D., Linzon, S., Dimma, D. and McIlveen, W.: 1987, Sugar maple decline in Ontario, in T. Hutchinson and K. Meema (eds), *Effects of atmospheric pollutants on forests, wetlands and agricultural ecosystems*, Springer-Verlag, Berlin, pp. 101–116.

McQuattie, C. J. and Schier, G. A.: 1990, Responce of red spruce seedlings to aluminium toxicity in nutrient solution; alterations in root anatomy, *Can. J. For. Res.* 20, 1001–1011.

Medappa, K. C. and Dana, M. N.: 1970, Tolerance of cranberry plants to manganese, iron and aluminium, *J. Amer. Hort. Sci* 95, 107–110.

Moore, P. A. and Patrick, W. H.: 1989, Calcium and magnesium availability and uptake by rice in acid sulfate soils, *Soil Science Society of America Journal* 53, 816–822.

Moore, P. A., Attanandana, T. and Patrick, W. H.: 1990, Factors affecting rice growth on acid sulfate soils, *Soil Science Society of America Journal* 54, 1651–1656.

Morris, R., Taylor, E. W., Brown, D. J. A. and Brown, J. A.: 1989, *Acid toxicity and aquatic animals*, Cambridge University Press, Cambridge. Society for experimental biology seminar series nr: 34.

Mulder, J., van Grinsven, J. and van Breemen, N.: 1987, Impacts of acid atmospheric deposition on woodland soils in the netherlands; III Aluminium chemistry, *Soil Sci. Soc. Am.* 51, 1640–1646.

Mullette, K. J.: 1975, Stimulation of growth in eucalyptus due to aluminium, *Plant and Soil* 42, 495–499.

Neitzke, M. and Runge, M.: 1985, Keimlings und jungpflanzenentwicklung der buche (*fagus sylvatica*) in abhängigkeit vom Al/Ca verhältnis des bodenextraktes, *Flora* 177, 237–249.

Nilsson, J. and Grennfelt, P.: 1988, *Critical loads for sulphur and nitrogen*, Nordic Council of Ministers. Nord 1988:15.

Nilsson, S. I. and Bergkvist, B.: 1983, Aluminium chemistry and acidification processes in a shallow podsol on the swedish wset coast, *Water, Air and Soil Pollution* 20, 311–329.

Noble, A. D., Fey, M. V. and Sumner, M. E.: 1988a, Calcium-aluminium balance and the growth of soybean roots in nutrient solutions, *Soil Science Society of America Journal* **52**, 1651–1656.

Noble, A. D., Sumner, M. V. and Alva, A. K.: 1988b, The pH dependency of aluminium phytotoxicity alleviation by calcium sulfate, *Soil Science Society of America Journal* **52**, 1398–1402.

Nosko, P., Brassard, P., Kramer, J. and Hershaw, K. A.: 1988, The effect of aluminium on seed germination and early seedling establishment, growth and respiration of white spruce (*picea glaca*), *Can. J. Bot.* **66**, 2305–2310.

Ohno, T., Sucoff, E., Erich, M. S., Blomm, P., Buschena, C. A. and Dixon, R. K.: 1988, Growth and nutrient content of red spruce seedlings in soil amended with aluminium, *J. Environ. Qual.* **17**, 666–672.

Olsthoorn, T. N. a.: 1990, Integrated modelling in the Netherlands, in J. Ferhann (ed.), *Environmental models, emissions and consequences*, pp. 461–479.

Ownby, J. D. and Popham, H. R.: 1989, Citrate reverses the inhibition of wheat root growth caused by aluminium, *J. Plant Physiol.* **135**, 588–591.

Paoletti, E. and Bellani, L. M.: 1990, The in-vitro response of pollen germination and tube length to different types of acidity, *Environmental pollution* **67**, 279–286.

Papke, H. E. and Krahl-Urban, B.: 1988, The forest, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 16–35.

Parker, D. R., Kinraide, T. B. and Zelasny, L. W.: 1988, Aluminium speciation and phytotoxicity in dilute hydroxy-aluminium solutions, *Soil Science Society of America Journal* **52**, 438–444.

Parker, D. R., Kinraide, T. B. and Zelasny, L. W.: 1989a, On the phytotoxicity of polynuclar hydoxy-aluminium complexes, *Soil Science Society of America Journal* **53**, 789–796.

Parker, D. R., Zelasny, L. W. and Kinraide, T. B.: 1989b, Chemical speciation and plant toxicity of aqueous aluminium, in L. E. Lewis (ed.), *Environmental chemistry and toxicology of aluminium*, American Chemical Society, pp. 117–145.

Pavan, M. and Bingham, F. T.: 1982, Toxicity of aluminiumto coffee seedlings growth in nutrient solution, *Soil Science Society of America Journal* **46**, 993–997.

Pavan, M., Bingham, F. and Pratt, P.: 1982, Toxicity of aluminium to coffe in ltisols and oxisols amended with $caco_3$, $mgco_3$ and $caso_4 \cdot h_2o$, *Soil Science Society of America Journal* **46**, 1201–1207.

Pegtel, D. M.: 1986, Responces of plants to Al, Mn and Fe with particular reference to succisa pratensis moench, *Palnt and Soil* **93**, 43–55.

Pegtel, D. M.: 1987, Effect of ionic Al in culture solutions on the growth of *arnika montana* and *deschampsia flexuosa*, *Plant and Soil* **102**, 85–92.

Persson, H. and Majdi, H.: 1991, What happend to roots ?, *Technical report*. Project 2.1, Results 8.

Praag, v. H. J. and Weissen, F.: 1985, Aluminium efects on spruce and beech seedlings, *Plant and Soil* **83**, 331–338.

Praag, v. H. J., Weissen, F., Sougnez-Remy, S. and Carletti, G.: 1985, Aluminium effects on spruce and beech seedlings, *Plant and Soil* **83**, 339–356.

Raben, G.: 1988, *Untersuchungen zur raumeitlichen Entwicklung boden– und wurtzelchemischer Stressparameter und deren Einfluss auf die Feinwurzelentwicklung in bodensauren Waldgesellchaften des Hils*, Vol. Reihe A, Bd. 38 of *Berichte des Forschungszentrums Waldökosysteme/Waldsterben*, Göttingen, Germany.

Ragland, J. L. and Coleman, N. T.: 1959, The effect of soil solution aluminium and calcium on root growth, *Soil Science Soc. Proc.* **111**, 355–357.

Rasmussen, L.: 1986, Potential leaching of elements in three Danish spruce forest soils, *Water, Air and Soil Pollution* **31**, 377–383.

Raynal, D. J., Joslin, J. D., Thornton, F. C., Schädele, M. and Henderson, G. S.: 1990, Sensitivity of tree seedlings to aluminium; lll; red spruce and loblolly pine, *J. Environ. Qual.* **19**, 180–187.

Rehfuss, K. E.: 1988, Research site; Luchsplatzl; damage to Norway Spruce, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 72–76.

Rengel, Z. and Robinson, D. L.: 1990, Modeling magnesium uptake from an acid soil; l; Nutrient relationships at the soil-root interface, *Soil Science Society of America Journal* **54**, 785–791.

Rorison, I. H.: 1978, The effects of soil acidity on nutrient avalability and plant response, in T. Hutchinson and M. Havaas (eds), *Effects of acid precipitation on forest ecosystems*, Plenum Press, New York, pp. 283–304.

Rorison, I. H.: 1985, Nitrogen source and the tolerance of *deschampsia flexuosa, holcus lanatus* and *bromus erectus* to aluminium during seedling growth, *Journal of Ecology* **73**, 83–90.

Runge, M.: 1986, Wirkungen der bodenazidität auf pflanzengesellschaft, *Transaction of the XIII congress of the international society of soil science* **V**, 110–118.

Ryan, P. J., Gessel, S. P. and Zanoski, R. J.: 1985, Acid tolerance of pacific northwest conifers in solution culture; II: Effects of varying aluminium concentration at constant pH, *Plant and Soil* **96**, 259–272.

Ryan, P. J., Gessel, S. P. and Zanoski, R. J.: 1986, Acid tolerance of pacific northwest conifers in solution culture; I: Effects of high aluminium concentration and solution acidity, *Plant and Soil* **96**, 239–257.

Sanhueza, E. e. a.: 1988, Characterization of the Venezuelan environment and its potential for acidification, in H. Rodhe and R. Herrera (eds), *Acidification in tropical countries*, Scope, J. Wiley and sons, Ltd., pp. 197–255.

Schier, G.: 1985, Responce of red spruce and balsam fir seedlings to aluminium toxicity in nutrient solutions, *Canadian Journal of Forest Research* **15**, 29–33.

Schriner, D. S.: 1991, Response of vegetation to atmospheric deposition and air pollution, in P. Irving (ed.), *Acidic deposition; State of science and technology. Summary report of the U S national acid precipitation assessment program*, National Acid Precipitation Assessment Program, pp. 143–151.

Schulze, E.-D.: 1987, Tree response to acid deposition into the soil, a summary of the COST workshop at Juelich 1985, in P. Mathy (ed.), *Air pollution and ecosystems*, D. Reidel Publishing Company, pp. 225–241.

Schädele, M., Thornton, F. and Raynal, D.: 1986, Non-metabolic binding of aluminium to roots of loblolly pine and honeylocust, *J. Plant Nutrition* **9**, 1227–1238.

Skeen, J.: 1929, The tolerance limit of seedlings for aluminium and iron and the antagonism of calcium, *Soil Science* **27**, 69–80.

Smit, H. P., Keltjens, W. G. and van Breemen, N.: 1987, Effects of soil acidity on Douglas fir seedlings. 2; The role of pH, aluminiumconcentration and nitrogen nutrition., *Neth. J. Agri. Sci.* **35**, 537–540.

Spiecker, H.: 1991, Growth variation and emvironmental stresses; lang-term observations on permanent research plots in southwestern Germany, *Water, Air and Soil Pollution* **54**, 247–256.

Steiner, K. C., Barbour, J. R. and McCormick, L. H.: 1984, Responce of populus hybrids to aluminium toxicity, *Forest Science* **30**, 404–410.

Steiner, K. C., McCormack, L. H. and Canavera, D. S.: 1980a, Differences in response of paper birch provenances to aluminium in solution culture, *Can. J. For. Res.* **10**, 25–29.

Steiner, K. C., McCormick, L. H. and Canavera, D. S.: 1980b, Differential responce of paper birch provenances to aluminium in solution culture, *Can. J. For. Res.* **10**, 25–29.

Stienen, H. and Bauch, J.: 1988, Elment content in tissues of spruce seedlings from hydroponic cultures simulating acidification and deacidification, *Plant and Soil* **106**, 231–238.

Sucoff, E., Buschena, C. and Bloom, P.: 1989, Responce of honeylocust (gleditsia tracanthos) to soil solution aluminium, *Plant and Soil* **113**, 93–99.

Sucoff, E., Thornton, F. C. and Joslin, J. D.: 1990, Sensitivity of tree seedlings to aluminium; l; honeylocust, *J. Environ. Qual.* **19**, 163–171.

Suhayda, C. G. and Haug, A.: 1986, Organic acids reduce aluminium toxicity in maize root membranes, *Physiol. Plantarium* **68**, 189–195.

Sverdrup, H.: 1990, *The kinetics of chemical weathering*, Lund University Press .

Sverdrup, H. and Warfvinge, P.: 1988, Assesment of critical loads of acid deposition on forest soils, in J. Nilsson (ed.), *Critical loads for sulphur and nitrogen*, Nordic Council of Ministers and The United Nations Economic Comission for Europe (ECE)., pp. 81–130.

Sverdrup, H. and Warfvinge, P.: 1990, The role of forest growth and weathering in soil acidification, *Water, Air and Soil Pollution* **52**, 71–78.

Sverdrup, H. and Warfvinge, P.: 1993, Calculating field weathering rates using a mechanistic geochemical model–PROFILE, *Journal of Applied Geochemistry* **8**, 273–283.

Sverdrup, H. U., de Vries, W. and Henriksen, A.: 1990, *Mapping critical loads*, Nordic Council of Ministers, Geneva. Miljörapport 1990:15, Nord 1990:98.

Sverdrup, H., Warfvinge, P. and Jönsson, C.: 1993, Critical loads of acidity and nitrogen for forest soils, groundwater and first order streams in sweden, in M. Hornung, J. Delve and R. Skeffington (eds), *Proceedings from*

the British Critical Loads Conference, Her Majesty's Service Organization Publications, pp. pp–bb.

Tamm, C. and Hallbäcken, L.: 1985, Changes in soil pH over a 50-year period under different canopies in SW Sweden, in H. C. Martin (ed.), *International Conference on Acid Precipitation, Muskoka, Canada, Part 2*, Riedel Publishing Company, pp. 337–341.

Tepper, H. B., Yang, C. S. and Schädele, M.: 1989, Effect of aluminium on growth of root tips of honey locust and loblolly pine, *Environmental and Experimental Botany* **29**, 165–173.

Thornton, F. C., Schädele, M. and Raynal, D. J.: 1989, Tolerance of red oak and american beech seedlings to aluminium, *J. Environ. Qual.* **18**, 541–545.

Thornton, F., Schädele, M. and Raynal, D. J.: 1986a, Effect of aluminium on the growth of sugar maple in solution culture, *Can. J. For. Res.* **16**, 892–896.

Thornton, F., Schädele, M., Raynal, D. J. and Zipperer, C.: 1986b, Effects of aluminium on honeylocust (gleditsia triacanthos) seedlings in solution culture, *J. Exp. Bot.* **37**, 775–785.

Tischner, T., Kaiser, U. and Huettermann, A.: 1985, Untersuchungen zum einfluss von aluminium-ionen auf das wachstum von fichtenkeimlingen in abhengigkeit vom ph-wert, *Forstwissenschaftliche Centralblatt* **104**, 329–336.

Tomlinson II, G. H.: 1983, Die-back of red spruce, acid deposition and changes in soil nutrient status-A review, in B. Ulrich and J. Pankrath (eds), *Effects of accumulation of air pollutants in forest ecosystems*, D. Reidel Publishing Company, pp. 331–342.

Truman, R. A., R., H. F. and Ryan, P. J.: 1986, Effect of varying solution ratios of Al to Ca and Mg on the uptake of phosphorus by *pinus radiata*, *Plant and Soil* **96**, 109–123.

Tyler, G.: 1983, *Does acidification increase metal availability and thereby inhibit decomposition and mineralization processes in forest soils?*, National Swedish Environmental Protection Board. Report, SNV PM 1636.

Tyler, G.: 1987, Acidification and chemical properties of *fagus sylvatica* forest soils, *Scand. J. For. Res.* **2**, 263–271.

Ulrich, B.: 1983, An ecosystem oriented hypothesis on the effect of air pollution on forest ecosystems, in G. Persson and A. Jernelöv (eds), *Ecological effects of acid deposition*, Swedish Environmental Protection Board, pp. 221–231. SNV-PM 1636, Stockholm.

Ulrich, B.: 1985a, Interaction of indirect and direct effects of air pollutants in forests, in C. Troyanowsky (ed.), *Air pollution and plants*, Gesellschaft Deutsche Chemiker, VCH Verlagsgesellschaft, WEinheim, pp. 149–181.

Ulrich, B.: 1985b, Stability and destabilization of central European forest ecosystems, a theoretical data based approach, in J. Cooley and F. Golley (eds), *Trends in ecological research for the 1980s*, Nato conference series, pp. 217–237.

Ulrich, B. and Matzner, E.: 1983, Abiotische folgewirkungen der weitraumigen ausbreitung von luftverunreinig. Forschungsbericht 104 02 615.

Ulrich, B. and Matzner, E.: 1988a, Research sites in the Solling area-changes in the ecosystem, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 44–49.

Ulrich, B. and Matzner, E.: 1988b, Solling, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 42–43.

Ulrich, B., Wiedey, G. and Gehrmann, J.: 1988, Research in the Hils mountains–comparative studies of spruce stands exposed to different pollution levels, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 50–55.

Varco, J. J. and Sartain, J. B.: 1966, Effects of phosphorus, sulfur, calcium hydroxide and pH on growth of annual bluegrass, *Soil Science Society of America Journal* **50**, 128–132.

Vogelmann, H. W., Badger, G. J., Bliss, M. and Klein, R. M.: 1985, Forest decline on Camels Hump, Vermont, *Bulletin of the Torrey Botanical Club* **112**, 274–287.

Warfvinge, P. and Sverdrup, H.: 1992, Calculating critical loads of acid deposition with PROFILE – a steady-state soil chemistry model, *Water, Air and Soil Pollution* **63**, 119–143.

Warfvinge, P., Falkengren-Grerup, U. and Sverdrup, H.: 1993, Modeling long-term base supply to acidified forest stands, *Environmental Pollution* **80**, 1–13.

Wittig, R.: 1986, Acidification phenomena in beech (fagus sylvatica) forests of Europe, *Water, Air and Soil Pollution* **31**, 317–323.

Wolfe, M. H. and Joslin, J. D.: 1989, Honeylocust (gleditsia triacanthos) root responce to aluminium and calcium, *Plant and Soil* **119**, 181–185.

Worku, Z., Warber, R. M. and Fox, R. L.: 1982, Comparative tolerance of three citrus rootstocks to soil aluminiumand manganese, *Hawaiian Institute of Tropical Agriculture and Human Resources Research Series* **17**, 2–16.

Wright, R. J., Baligar, V. C. and Ahlrichs, J. L.: 1989, The influence of extractable and soil solution aluminium on root growth of wheat seedlings, *Soil Science* **148**, 293–302.

Yokomizo, H. and Ishihara, M.: 1973, Studies of mineral nutrition of fruit trees by sand and water culture., *Kaju Shikenjo Hokoku A* **12**, 29–77.

Zech, W., Horn, R., Kaupenjohann, M. and Hantschel, R.: 1988, Research sites–Oberschwarmsteinach, Wulfersreuth and Selb (Fichtelgebirge); site specific damage to Norway Spruce, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 66–69.

Zöttl, H. and Aldinger, E.: 1988a, Research site; Freudenstadt (Northern Black Forest); damage to Norway Spruce, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 93–94.

Zöttl, H. and Aldinger, E.: 1988b, Research site; Rossberg (Northern Black Forest); damage to Silver Fir, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 95–97.

Zöttl, H. W.: 1988, Black forest, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 88–89.

Zöttl, H. W. and Mies, E.: 1988, Research site; Kälbelescheuer (Southern Black Forest); damage to Norway Spruce and Silver Fir, in B. Krahl-Urban, H. E. Papke, K. Peters and C. Schimansky (eds), *Forest decline*, Juelich Research Center, Germany and U S Environmental Protection Agency, Washington D. C., pp. 90–92.