Soil acidification effects on fine root growth of Douglas-fir on sandy soils

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NN08201, 2421

Soil acidification effects on fine root growth of Douglas-fir on sandy soils

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PROEFSCHRIFT
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 24 april 1998
des namiddags te half twee in de Aula.

Wn 954052

BIBLIOTHEEK DER
LANDBOUWHOGESCHOOL
WAGENINGEN

NN08201, 2421

Stellingen

1. Bodemverzuring vergroot de wortelsterfte van bomen in perioden van droogte en verlengt de groeivertraging van het bos na extreme droogte.

2. De verschijnselen van het 'Tannensterben' rond het begin van deze eeuw zijn verklaarbaar via de effecten van aluminium op worteldichtheid.

   G. Wiedemann 1927. Untersuchungen über das Tannensterben. Forstwissenschaftliches Centralblatt 49: 759-780, 815-827, en 845-853.

3. Over ongeveer 200 jaar - een relatief korte tijd voor bodemvormende processen - worden de omstandigheden voor bosgroei riskant op de meeste Nederlandse bosbodems bij voortgaande depositie van verzurende stoffen, omdat de buffervoorraden van aluminium in de bodem dan sterk zijn afgenomen, waarna de pH naar alle waarschijnlijkheid sterk zal dalen.

   J. Mulder, N. van Breemen, L. Rasmussen & C.T. Driscoll 1989. Aluminum chemistry of acidic sandy soils with various inputs of acidic deposition in The Netherlands and in Denmark. In: T.E. Lewis (ed.), Environmental chemistry and toxicity of aluminum. 194th Annual Meeting of the American Chemical Society, New Orleans, August 1987. Lewis Publishers, Baton Rouge, Michigan; 171-194.

4. De methoden en berekeningen van wortelproductie, levensduur van wortels en wortelmortaliteit - vaak ongenuanceerd samengevat met de Engelse term 'fine root turnover' - worden vooral geaccepteerd omdat ze acceptabele waarden opleveren.

5. De hydraulische geleidbaarheid van hyfen van mycorrhiza is zeer laag, anders zou een boom juist op arme groeiplaatsen met een betere mycorrhizabezetting overgaan op een 'verspillingsstrategie', met een gemakkelijke wateropname en een snel waterverbruik.

6. Bodemverzuring heeft de concurrentieverhoudingen tussen een aantal plantensoorten in het Nederlandse bos beïnvloed; mede daarom blokkeren bochtige smele en Amerikaanse vogelkers op dit moment in grote delen van het Nederlandse bos de natuurlijke bosontwikkeling.

   H. Sverdrup & P. Warfvinge 1993. The effect of soil acidification on the growth of trees, grass and herbs as expressed by the (Ca+Mg+K)/Al ratio. Reports in Ecology and Environmental Engineering 1993-2, Lund University, Sweden. 109 p.

Stellingen behorend bij het proefschrift van A.F.M. Olsthoorn: Soil acidification effects on fine root growth of Douglas-fir on sandy soils. Wageningen, 24 april 1998.

7. De Perforon-methode leent zich goed voor tijdserieonderzoek aan wortels en bodemecologie, en leidt bovendien tot ideeënvorming over hypothesen die daarna kwantitatief onderzocht kunnen worden met eventueel andere methoden.

8. In een bos vormt het einde van het voorjaar het beste ijkpunt voor de vaststelling van de optimale worteldichtheid aangepast aan de bodemkwaliteit; naar analogie van het algemeen aanvaarde beste ijkpunt voor de waterpotentiaal van planten rond het ochtendgloren.

9. De verschillen in wortelmortaliteit gedurende een droogte zijn een wezenlijke factor in de concurrentieverhoudingen in een gemengd bos.

   H.H. Bartelink 1998. Simulation of growth and competition in mixed stands of Douglas-fir and beech. Ph.D. Thesis, Wageningen Agricultural University. 219 p.

10. De populatiedynamica van de roodzwarte dennencicade zou de ontwikkeling van de vitaliteitskenmerken van grove den na een droogte kunnen verklaren.

    L.G. Moraal 1996. Bionomics of Haematoloma dorsatum (Hom., Cercopidae) in relation to needle damage in pine forests. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 69: 114-118.

11. Op grond van de huidige opbouw van het Nederlandse bos leveren fouten in het beheer pas over een jaar of twintig knelpunten op in de houtvoorziening of financiële opbrengst.

12. Zolang de beheersdoelstellingen voor een bos niet voldoende expliciet geformuleerd zijn, heeft het opstellen van blesinstructies geen enkele zin.

13. Het opdelen in jaarlijkse aanbestedingen van de vierjarige LNV-onderzoekprogramma's - de huidige langetermijnplanning binnen het landbouwkundig onderzoek - leidt tot beperkingen in de onderzoekmethodiek, en heeft dus grote nadelen voor de belanghebbenden van dit onderzoek en het Ministerie zelf.

14. Nieuwe genetische technieken (geslachtsbepaling, klonen, etc.) zijn met name riskant omdat de wensen van mensen zo onnatuurlijk zijn.

15. Dat de ideeën uit de jaren zeventig nu algemeen als ouderwets worden gezien, zegt vooral iets over de jaren negentig.

Stellingen behorend bij het proefschrift van A.F.M. Olsthoorn: Soil acidification effects on fine root growth of Douglas-fir on sandy soils. Wageningen, 24 april 1998.

Contents

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The work between 1985 and 1990 was largely financed by the Dutch Priority Programme on Acidification (APV) initiated by several Ministries and other parties. The IBN-DLO offered facilities during the preparation of this thesis.

The publishers of Netherlands Journal of Agricultural Science and Plant and Soil are acknowledged for their permission to include papers and figures in this thesis.

ISBN 90-5485-840-0 (Ph.D. Thesis)
ISBN 90-76095-05-1 (IBN Scientific Contributions 12)

Abstract

Olsthoorn, A.F.M. 1998 Soil acidification effects on fine root growth of Douglas-fir on sandy soils. *Ph.D. Thesis, Wageningen Agricultural University, Wageningen, The Netherlands.*

The ammonium sulphate deposited in forest ecosystems in The Netherlands as a result of air pollution currently exceeds 80 kg N ha^{-1} yr^{-1} locally. To study the influence of this air pollution on fine root density and its dynamics, fine root growth was monitored for three years in two young mature stands of Douglas-fir on sandy soils in the central part of The Netherlands in the ACIFORN project (ACIdification of FORests in The Netherlands). In the drier site the fine root density in early summer was higher and more strongly reduced after a dry spring than at the more favourable site. The fine root density appeared to depend on the proximity of the tree stems in the stand. In normal years, the main peak of fine root growth occurred in spring, with less growth during summer. After a dry spring, fine root growth on the drier site reacted strongly to periods with rain in summer. In a greenhouse trial with one-year-old seedlings of Douglas-fir in sand, ammonium sulphate was added to simulate the present acidic deposition. Part of the ammonium was nitrified into nitrate. This resulted in different ammonium, nitrate, aluminium levels and pH in the different treatments. In the treatments with the highest applications, fine root length was reduced by 50 % compared to the control, and the specific root length was reduced by 40 %.

A critical review of the results reported in the literature, to ascertain the total effect of the soil chemical changes since the start of the industrial revolution on the fine root density, revealed that aluminium is the main factor reducing fine root growth, even at sub-lethal concentrations in the soil solution. The fine root length is probably reduced by 50 % in the topsoil, and by 75 % in the subsoil. Excessive nitrogen availability reduces the total fine root biomass by 30 %. The net result is that the fine root system is less dense and more shallow than it would be without acidic deposition. This reduces the potential for water uptake on coarse sandy soils, and increases fine root mortality in long dry periods, especially on poor sites. An elementary model to describe fluctuations in the fine root density during and after a drought is used to illustrate the effects of soil acidification and nitrogen enrichment on drought susceptibility. Accumulated deposition has enhanced the risks of tree mortality or forest dieback induced by severe drought.

Aan mijn vader

MOTTO

Watch out for the undertoad!

John Irving 1976. The world according to Garp. Corgi Books, London. 570 p.

Iedere jongen hunkerde naar het ogenblik waarop hij van een kind in een bramzijgertje zou veranderen.

The Zuiderzee according to Jan de Hartog: Het boekenweekgeschenk uit 1967 is de meest fantastische beschrijving van de kinderziel, het vissermansleven op houten zeilschepen en gereformeerde gewoonten rond de Zuiderzee.
Jan de Hartog 1967. Herinneringen van een bramzijgertje. Vereniging ter Bevordering van de Belangen des Boekhandels, Commissie voor de Collectieve Propaganda van het Nederlandse boek, Amsterdam. 158 p.

1. Introduction

1.1 Background

In the early eighties, much media attention was paid to the risks to forest vitality and growth, posed by the effects of air pollution. It was predicted that air pollution would cause large scale forest decline ("Waldsterben"), or tree mortality - even within one decade - in large parts of Europe and other industrial areas. In many countries, large research programmes were established to monitor changes in detail, and to identify the mechanisms responsible for forest decline. In The Netherlands, the Priority Programme on Acidification was set up. It consisted of a large number of research projects comprising laboratory and field studies focusing on air pollution effects on forests and other ecosystems. One of the central questions was how air pollution affects forest growth. The ACIFORN (ACIdification of FORests in The Netherlands) project was a major field study in the programme. It entailed monitoring forest growth and the main factors influencing growth, including air pollution, in detail for several years in two young mature Douglas-fir plantations on sandy soils in the central part of The Netherlands. Sandy soils were chosen, as most forests in The Netherlands are located on such soils. Douglas-fir, an exotic in The Netherlands, was selected as tree species, because its physiology has been relatively well studied in its native area, and the vitality characteristics (needle retention and needle colour) in The Netherlands are far from ideal at present. This thesis describes the root research conducted within the ACIFORN project.

Roots have two functions for plants: a) stability, and b) the uptake of water and nutrients. For trees, the stability is provided by the coarse roots (with a diameter larger than 2 mm), anchored in a large volume of soil by fine roots (with a diameter smaller than 2 mm). The uptake of water and nutrients occurs mainly via the fine roots. Water and nutrients are essential for normal plant functioning, enabling growth, both above and below the soil surface. The fine root system forms the main interface between the tree and the soil solution, and is of crucial importance for tree functioning. Moreover, production and mortality of fine roots account for a significant part of the carbon balance of the entire forest ecosystem. Mycorrhizal fungi and rhizosphere fungi and bacteria are part of this interface, but were not investigated in detail in this study. Their functioning and dynamics were investigated in other studies within the Priority Programme on Acidification.

The relation between air pollution and forest vitality is complex, as forest vitality is a result of many natural and anthropogenic processes, and air pollution itself is very diverse in composition and concentration, depending on regional emissions of air pollutants, topography and local climate. Since the beginning of the industrial revolution, about two centuries ago, sulphur dioxide has damaged foliage locally around factories, and, on a much larger scale, the buffer capacity of the soil has decreased due to cumulative deposition. In recent decades, ammonia originating from intensive animal husbandry has become one of the main components of deposition in The Netherlands. In the air, the ammonia reacts with sulphur dioxide to form ammonium sulphate. The ammonium ion takes over the acid load of the sulphur dioxide; the sulphate ion itself is not reactive with respect to soil acidification. Ammonium sulphate can be precipitated in forests or other ecosystems through rain or as dust, in respectively wet and dry deposition.

Ammonium can have a fertilising effect on forest ecosystems when nitrogen availability limits growth. Shoot growth is usually stimulated by nitrogen, resulting in an increased transpiration demand by the canopy. However, excess nitrogen influx to forests disrupts the nutrient supply to trees and may induce deficiencies of other nutrients such as phosphorus, potassium, and magnesium, especially when the soil quality is limited, as is the case on most sandy soils.

In the soil, ammonium can be oxidised to nitrate by bacteria, in the nitrification process. When nitrate is produced, protons (H+ ions) are also formed, resulting in soil acidification. At present, sandy soils in The Netherlands are usually in the buffering range of aluminium, which means that acidification results in larger amounts of dissolved aluminium. Ammonium can also be taken up directly by the roots as their main nitrogen source. Nitrogen is the most important macro-nutrient, consequently, the ionic form (NH_4^+ or NO_3^-) strongly affects the cation-anion balance in the total nutrient uptake. Ammonium uptake usually leads to acidification of the rhizosphere by a proton efflux, necessary for maintenance of electrical neutrality of the soil-plant system. Both the nitrification and the root proton efflux, acidify the root environment, accompanied by an increase of soluble aluminium. The ammonium and aluminium may accumulate in the soil solution, reaching toxic levels, reducing root tip elongation and decreasing fine root densities.

Root density and root functioning are very important in sandy forest soils that are usually limited in water and nutrient availability. It seems likely that a reduced fine root density might result in a reduction of water uptake and an increased drought susceptibility. This led to the main question in this study: *How does the acidification of sandy soils, mostly combined with nitrogen enrichment, affect the fine root system, and what are the consequences for tree functioning?* This question is broken down into more detailed separate questions in the section below.

1.2 Aims

Various studies were performed to evaluate how soil acidification and nitrogen enrichment have influenced fine root growth of Douglas-fir on sandy soils, and to ascertain the consequences of this for tree functioning. The following questions were addressed:

- What is the fine root density of Douglas-fir plantations in early summer and what are its dynamics, e.g. through shortage of water in dry periods, on acid sandy soils differing in site quality and under the present levels of acidification?

- What is the cumulative effect of two centuries of soil acidification and how is this currently affecting fine root growth in sandy soils?

- What are the consequences of a reduced fine root density for water uptake and drought susceptibility?

The fine root density was studied in the field in early summer, to ascertain the potential for uptake of water and nutrients on these sites in an important part of the growing season. Fine roots are important in the total yearly belowground carbon allocation in forests. The effects of soil acidification and nitrogen enrichment were studied in a greenhouse trial with seedlings under controlled conditions, that mimicked acidic deposition on sandy soils. In addition, conclusions were derived from the results of comparable projects in other countries, where mature forest stands had been subjected to manipulations of e.g. nutrients for periods of several years.

1.3 Synopsis

In this thesis, Chapters 2 and 3 present field data on fine root biomass and fine root dynamics and estimates of the belowground carbon allocation in two plantations differing in site quality. Chapter 4 evaluates the sampling methods used in chapter 2, because if there were a relation between fine root density and proximity of tree stems in a closed forest, the sampling methods would have to take this into account. The large data set available from the first year of sampling was used to verify field methods. Chapter 5 presents data from a greenhouse experiment on one-year-old seedlings to simulate the effects of soil acidification and nitrogen enrichment under controlled conditions. In the ACIFORN forest sites, no field manipulation with ammonium sulphate was performed. Chapter 6 evaluates the effects on fine root density resulting from the changes in soil chemistry during the last two centuries brought about by the accumulated deposition of air pollutants. Results, mostly collected from other studies, are used in a critical review to quantify the effects for mature Douglas-fir forest on acid sandy soils. Chapter 7 discusses the total effect of reduced fine root densities on water uptake and drought susceptibility. The potential for water uptake is assessed with an existing simulation model for water uptake. Data from the two ACIFORN sites on litter fall and fine root activity during and after a drought are used to elucidate the consequences of a reduced fine root density for drought susceptibility. Finally, a hypothesis is presented for changes in annual fluctuations in fine root biomass under the present levels of deposition of air pollutants, illustrated with an elementary root growth model for fine roots during and after a drought. The epilogue (Chapter 8) presents the conclusions about the scientific, practical and methodological achievements, raises some unanswered questions and anticipates future developments. Finally, summaries in English and Dutch are presented.

2. Fine root density and root biomass of two Douglas-fir stands on sandy soils in The Netherlands: 1. Root biomass in early summer

Abstract

In two fully stocked, fast growing Douglas-fir plantations of the Dutch ACIFORN project, detailed studies were carried out on fine root biomass and fine root length to obtain information on fine root densities. For three consecutive years, fine roots were sampled with a root corer in the early part of the growing season. The coarse root biomass was calculated from aboveground stand parameters. The vertical distribution of fine roots in these sites was similar. In the stand with less aboveground biomass the dry weight and density of the fine roots were higher. The fine root biomass agreed with values found in Douglas-fir stands in the Pacific Northwest of the USA. Up to 80 cm depth the fine root biomass varied from 3900 kg ha^{-1} in moist conditions to 900 kg ha^{-1} after dry periods. The fine root length varied accordingly, with a maximum of 27.10^6 m ha^{-1} and a minimum of 3.10^6 m ha^{-1}. The fine root density in the mineral topsoil varied between 0.6 and 0.05 cm cm^{-3}; in the subsoil it varied between 0.3 and 0.04 cm cm^{-3}. In 1989 there was some sudden root death during a dry period.

Keywords: coarse root biomass, fine root biomass, fine root density, fine root length, *Pseudotsuga menziesii*, shoot:root ratio

Introduction

In the ACIFORN project (ACIdification of FORests in The Netherlands) growth parameters and the main factors influencing growth were monitored in detail in two Douglas-fir stands in the central part of The Netherlands for several years, to study the impact of air pollution on forest growth (Evers et al. 1987). Fine root density was assessed because it is one of the stand characteristics linking soil hydrology and soil chemistry to forest growth. Furthermore, the growth and mortality of fine roots account for a significant part of the carbon balance of the entire stand. The main emphasis was on fine roots (roots with a diameter of less than 2 mm, including all root tips) because they control the tree's capacity to take up water and nutrients, and constitute the main interface with the soil solution. Mycorrhizal fungi are part of this interface, but were not studied separately. This chapter presents data on fine root density, root biomass, and elementary root morphology. The data on fine roots were collected in the field in three consecutive years (1987, 1988, and 1989). Coarse root biomass (roots with a diameter of more than 2 mm, excluding all root tips) was estimated from aboveground stand parameters according to Santantonio et al. (1977) using an allometric relation between diameter breast height of the stem and coarse root dry weight that Kuiper & Coutts (1992) established for Douglas-fir in The Netherlands.

To collect basic information on the fine root density and fine root biomass (dry matter), a root sampling programme was carried out in the first half of the growing season in the three consecutive years. In 1989 a dry period preceded the sampling. The effect of this dry period on root density will be described. The survey of fine roots was intended to provide estimates per plot or stand, because fine roots cannot be attributed to a single tree (McMinn 1963; Kuiper & Coutts 1992).

In the third chapter (Olsthoorn & Tiktak 1991) data are presented to show how the periodicity of fine root growth depends on weather conditions and soil moisture, and the total carbon allocation to the root system is estimated.

Site description

The two ACIFORN stands were planted on clear-cut areas with a coastal provenance of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and are located 10 km apart in the 'Veluwe' area in The Netherlands (Fig. 2.1). The stands are even-aged and have been repeatedly thinned. They were last thinned more than three years before the ACIFORN project started; at the time of sampling the canopy was completely closed. There was no ground vegetation, hence all living roots were assumed to be Douglas-fir.

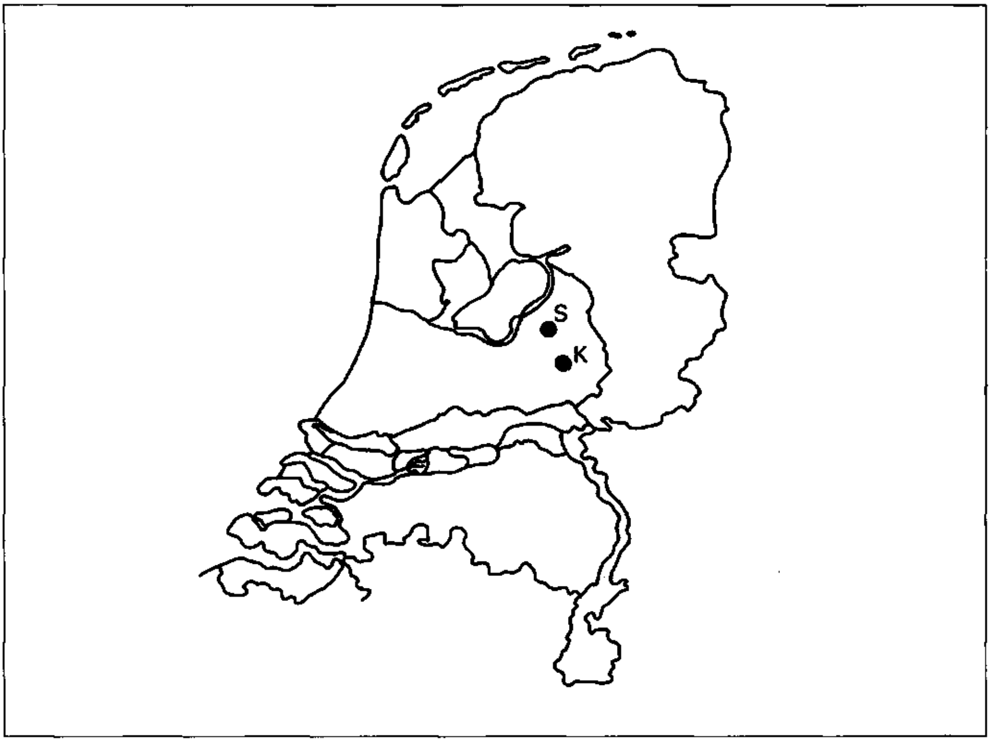

Figure 2.1.
Location of the two ACIFORN Douglas-fir stands in The Netherlands: K = Kootwijk and S = Speuld.

The soils in both stands are sandy and well drained. The water table is very deep and the soil contains very little gravel. One of the stands ('Kootwijk', 52°11'N, 5°46'E) is located on eolian sands which have been farmed in previous ages before forest stands were established. The soil is horizontally homogeneous, and consists of a Leptic podzol (FAO/UNESCO 1974). The Ap is 40 cm thick. The C horizon starts at 90 cm depth. The pH-KCl of the thin and discontinuous humus layer in the organic horizon is 2.9; the pH-KCl at 80 cm depth is 4.6. The other stand ('Speuld', 52°15'N, 5°41'E) is located on preglacial sand deposits, which are very heterogeneous, especially in the subsoil below 40 cm depth. The soil profile consists of an Orthic podzol or Luvisol (FAO/UNESCO 1974). The A horizon is very thin (7 cm) and the C horizon starts at 60 cm depth. The pH-KCl in the thin and discontinuous humus layer of the organic horizon is 3.1; the pH-KCl at 80 cm depth is 4.3. The Speuld soil contains more loam than the Kootwijk soil. A detailed soil survey was done to identify the area with the most homogeneous soil, and the root sampling was done in that area. The soil surface is level in both stands.

The stand descriptions are presented in Table 2.1a. Tree age and number of trees per hectare are similar. In Table 2.1b the basal area increment and stem volume increment is presented for 1987, 1988 and 1989. In Kootwijk the productivity is lower than in Speuld. In each stand a single small subplot of 10 x 11 m was established to sample fine roots.

Table 2.1.

Stand description (a) of the subplots used for root measurements in both ACIFORN plots in forestry districts Kootwijk and Speuld and stand growth (b) in 1987, 1988 and 1989.

FORESTRY DISTRICT:	KOOTWIJK	SPEULD
a) Stand description (per January 1 1987):		
Tree age:	36 years	28 years
Stems per hectare:	992	886
Average height of dominant trees:	19.0 m	20.3 m
Diameter of tree with mean basal area (d_g):	18.7 cm	21.3 cm
b) Stand growth:		
Basal area , current annual increment:		
1987	1.40 m^2 ha^{-1}	2.21 m^2 ha^{-1}
1988	1.57	2.41
1989	1.75	2.31
Volume, current annual increment:		
1987[1)]	13.1 m^3 ha^{-1}	21.2 m^3 ha^{-1}
1988	19.2	31.6
1989	24.6	30.8

[1)] Tree heights were not measured at the beginning of 1987. The height/diameter relation of the winter '87/'88 was used to calculate stem volumes for that period. Therefore the volume increment in 1987 for both Kootwijk and Speuld may have been underestimated.

Methods

In 1987, 1988 and 1989 a root corer sampling programme was used to assess the root density at different depths, the spatial variability of fine root density and the fine root biomass. In Kootwijk the samples were taken from July 6 to 13 in 1987, and again on May 26 in 1988 and June 18 in 1989. In Speuld samples were taken from June 15 to July 3 in 1987, May 16 to 20 in 1988 and also June 13 to 15 in 1989. In 1987 37 sampling points per plot were chosen in Kootwijk and 55 in Speuld, to find the statistically acceptable minimum numbers of samples for the subsequent years. In Speuld a second plot (henceforth referred to as Speuld west) was selected in 1988 on a more sandy part of the stand to take account of the spatial variability of the soil. In 1988 and 1989 only 12 sampling points were chosen per plot. They were distributed systematically in the plots and were at different distances from the tree stems, because the trees are spaced irregularly. It was assumed that the spatial variability of the fine root density is independent of distance from the tree (Reynolds 1970; Kummerow et al. 1990).

The root corer used in the study was designed by Goedewaagen (Böhm 1979). It is a cylindrical soil coring sampling tube, 8 cm in diameter and 15 cm long and has a sharp serrated edge to cut small roots. It was driven into the soil with a 2 kg hammer. The sample was divided into different subsamples if it was necessary to account for different soil horizons. The soil was sampled to a depth of 80 cm. The roots below 80 cm depth were not sampled. Samples were stored in a freezer at -20 °C until processing.

Before measuring root length and root biomass the sand and loam were washed off the roots with tap water above a 2 mm mesh sieve. Only living roots were taken into account. They were separated by hand from organic matter and dead roots, on the basis of colour, brittleness, structure of cortex or bark and colour of stele or xylem, as described by Santantonio & Hermann (1985) and Vogt et al. (1981 and 1983). It was assumed that it is possible to recognise dead roots in a corer sample one week after their death. The total length of living fine roots was estimated using the line intersect method (Tennant 1975). Intersections were counted by eye on fresh samples. Finally, the roots were oven-dried at 70 °C for at least 16 hours to determine the dry weight (biomass) of the samples. The data presented on fine root dry weight have not been corrected for the weight of soil particles that might still be attached to the roots. The values for each sampling point were recalculated to 10 cm intervals so that the averages and standard deviations could be calculated for each 10 cm soil layer.

In the 1988 sampling the fine roots in the organic horizon were not determined separately, but were added to the first sample in the mineral soil. They were subsequently estimated, on the assumption that the relation between the amount of fine roots in the organic horizon in 1988 and the total amount up to 80 cm depth was the same as in 1987.

When processing the roots from the 1989 sampling, an attempt was made to distinguish roots that had recently died from those that already had died before the dry period, so that the fine root densities before the dry period could be estimated. However, this could not be done with great accuracy.

Coarse root biomass was not measured directly in the ACIFORN research sites. It was estimated from aboveground stem diameters, using allometric equations from Santantonio et al. (1977) and Kuiper & Coutts (1992). Kuiper & Coutts (1992) established the relation

$$W_{cr} = 0.01\ d^{2.63} \tag{1}$$

between dry weight of the coarse roots (W_{cr}, in kg) and tree diameter (d, in cm) at breast height (1.30 m) for Douglas-fir of similar ages and comparable sites in The Netherlands with a correlation coefficient (r^2) of 0.96.

Results

NUMBER OF SAMPLING POINTS

The average fine root length up to 80 cm depth in Kootwijk in 1987 was 25.10^6 m ha^{-1} with a 95 % confidence interval ranging from 22.10^6 to 28.10^6 m ha^{-1}, based on 37 sampling points. In Speuld the average was 19.10^6 m ha^{-1} with a 95 % confidence interval ranging from 17.10^6 to 21.10^6 m ha^{-1}, based on 55 sampling points. Figure 2.2 shows the standard error of the mean at different numbers of sampling

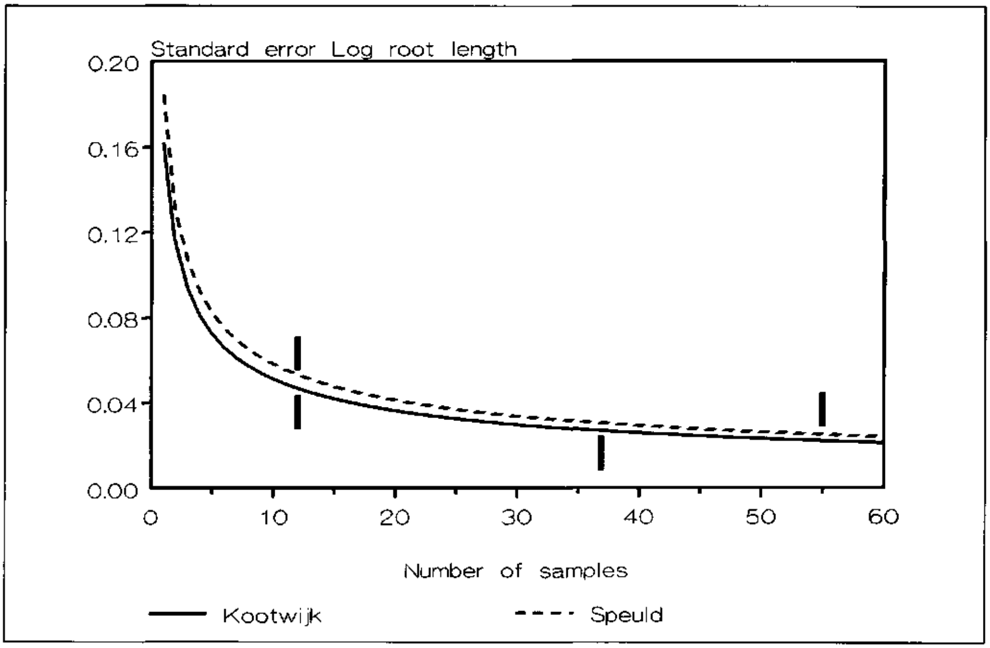

Figure 2.2.

Estimated standard error in relation to number of sampling points. Standard error was calculated from data on total fine root length per hectare from each sampling point after logarithmic transformation. Bars on the right indicate the number of sampling points in 1987 for both sites. Bars on the left indicate number of sampling points in each subplot in 1988 and 1989.

points for logarithmically transformed data on total fine root length up to 80 cm depth from both Kootwijk and Speuld. Below 10 samples the standard error increases fairly sharply. Therefore, in 1988 and 1989 12 sampling points per sub-plot were considered to present reliable data on the distribution of fine root biomass and fine root density in the soil profile. The estimated 95 % confidence interval for 12 sampling points in 1987 ranged from 20.10^6 to 31.10^6 m ha^{-1} in Kootwijk and from 15.10^6 to 24.10^6 m ha^{-1} in Speuld.

FINE ROOTS

The results of the root corer sampling programme in both ACIFORN stands in 1987, 1988 and 1989 are presented in Tables 2.2 and 2.3, up to a depth of 80 cm, for each 10 cm soil layer. The vertical root length distribution of both sites up to 80 cm depth was similar in all years. The results for 1987 and 1988 were almost identical. The total fine root biomass in Kootwijk was 3900 kg ha^{-1} in 1987 and 4300 kg ha^{-1} in 1988. The corresponding figures for Speuld east were 2800 and 3200 kg ha^{-1} respectively. In the second subplot in Speuld (Speuld west) there were nearly 2800 kg ha^{-1} fine roots in 1988; the differences between Kootwijk and Speuld west were somewhat greater than those between Kootwijk and Speuld east. Both subplots have to be used in a 1:1 ratio to calculate stand averages for Speuld.

The fine root density in Kootwijk in the top 40 cm of the mineral soil ranged from 0.3 to 0.7 cm cm^{-3} in both 1987 and 1988. At 40 cm depth the fine root density was about 0.3 cm cm^{-3} and decreased to nearly zero at 80 cm depth. The total thickness of the organic horizon in both stands was 4 cm. Based on the assumption that the fine roots in the bottom part of the organic horizon were confined to a layer 2 cm thick, the fine root density in Kootwijk was nearly 2 cm cm^{-3} in both 1987 and 1988. The specific root length (SRL) of the fine roots in Kootwijk was around 10 m g^{-1} in the organic horizon and decreased to 3 or 4 m g^{-1} at 80 cm depth with a steep decline at 40 cm depth where the bottom of the Ap horizon is located.

In Speuld the fine root density was somewhat lower than in Kootwijk. In the top 40 cm of the mineral soil in Speuld it ranged from 0.2 to 0.5 cm cm^{-3} in 1987 and 1988. Below 40 cm depth it ranged from 0.1 to 0.2 cm cm^{-3}. The fine roots in Speuld extended further down in the soil profile. Using the same assumptions as for Kootwijk, the fine root density in the bottom 2 cm of the organic horizon in Speuld was less than 1.4 cm cm^{-3} in 1987 and 1988. The SRL in Speuld was greater than in Kootwijk in the whole soil profile in 1987 and 1988 and the decline of the SRL with increasing depth was more gradual.

In June 1989, root densities and fine root dry weights were very small at both sites, because of a dry period in May (see also Olsthoorn & Tiktak 1991). In both Kootwijk and Speuld the fine root biomass was one-third to one-quarter that of the two previous years. The decrease in fine root density was even more pronounced because the average SRL in 1989 was a third less than in the two preceding years. In both plots, the fine root density in the upper 40 cm of the mineral soil ranged from 0.03 to 0.1 cm cm^{-3}; below 40 cm depth it ranged from 0.03 cm cm^{-3} to zero. In the bottom part of the organic horizon the fine root density was less than 0.4 cm cm^{-3} in 1989 in both Kootwijk and Speuld. In 1989 the SRL was much smaller in both Kootwijk and Speuld. During a dry period the thicker fraction of the fine roots appear to have a greater chance of surviving, hence the smaller value of the SRL.

In Table 2.3, the coefficients of variation of fine root biomass, fine root density and SRL for both sites and in all three years are presented. The coefficients of variation increased as the amount of fine roots decreased, as can be seen at greater depth in the soil profile and in the results of the 1989 sampling. The standard deviations in Speuld were larger than in Kootwijk, reflecting soil heterogeneity. For each 10 cm layer the standard deviations were larger than the standard deviation of the totals up to 80 cm depth. In 1987 at both sites, the total fine root length per sampling point (50 cm^2 soil surface) varied between 2 m and 40 m (average around 10 m). High root densities were found in old decayed coarse roots from the previous forest stand (see also Van Noordwijk et al. 1991).

COARSE ROOTS

The estimates of the coarse root biomass presented in Table 2.4 are based on diameter at breast height of a tree with a mean basal area (d_g, see Table 2.1). The coarse root biomass was estimated for four winter periods. The growth could thus be estimated for three growing seasons. Coarse root biomass gradually accumulated over the years, because stem diameters increased; the stands were not thinned in that period. The turnover of coarse roots was assumed to be accounted for by the use of an allometric relationship. Since the stem growth did not fluctuate much over the three years, the estimated growth of coarse roots was nearly constant. In Kootwijk the total amount of coarse roots, and their growth was less than in Speuld, as could be expected from the data on aboveground growth of the stand.

Discussion

The fine root densities in these two Douglas-fir stands on sandy soils in The Netherlands are low compared to agricultural crops (De Willigen & Van Noordwijk 1987): the maximum was 0.7 cm cm^{-3} in the topsoil in 1987 and 1988 and the minimum was 0.08 cm cm^{-3} following the dry period in 1989 (Table 2.2). The roots with a diameter between 2 and 5 mm were not determined in this study but might also contribute to uptake of water and nutrients. However, according to Eis (1987) the roots in this fraction only add around 2 % to the total length of Douglas-fir roots that are less than 2 mm in diameter. This is well within the range of variation of the data presented in this chapter. The coefficients of variation of fine root densities and fine root biomass (Table 2.3) are in the same order of magnitude as Van Noordwijk et al. (1985) found for grassland.

The data on fine root biomass for Douglas-fir stands in the Pacific Northwest of North America are in agreement with these data. Instead of dry weight alone, length and densities of fine roots better express the potential to take up water and nutrients (De Willigen & Van Noordwijk 1987). Assuming an SRL of 10 m g^{-1} dry matter, the fine root length in these North American studies varies from 20.10^6 m ha^{-1} to 60.10^6 m ha^{-1} in the whole rooted profile (Santantonio & Hermann 1985; Eis 1987; Vogt et al. 1983). Vogt et al. (1983) recorded some smaller values in October: from 2.10^6 m ha^{-1} in very productive sites to 35.10^6 m ha^{-1} in poorly productive sites. Bowen (1985) found that the values of fine root densities of trees in general are much smaller than those of grasses or cereals; the greatest fine root

Table 2.2.

Average fine root biomass (dry weight) per hectare, fine root density and specific root length (SRL) in all subplots of the ACIFORN sites in 10 cm layers (H = humus layer of the organic horizon) in three consecutive years.

Depth (cm)	Biomass (kg ha^{-1})	Density (cm cm^{-3})	SRL (m g^{-1})	Biomass (kg ha^{-1})	Density (cm cm^{-3})	SRL (m g^{-1})	Biomass (kg ha^{-1})	Density (cm cm^{-3})	SRL (m g^{-1})
Kootwijk	*1987*			*1988*			*1989*		
H	322	1.87	11.64	379	1.97	10.40	145	0.37	5.13
0-10	813	0.74	9.12	691	0.55	8.01	114	0.06	5.42
10-20	674	0.54	8.08	710	0.51	7.23	170	0.05	3.23
20-30	661	0.41	6.17	691	0.43	6.24	257	0.06	2.19
30-40	575	0.26	4.53	615	0.34	5.53	187	0.03	1.64
40-50	463	0.20	4.37	656	0.24	3.73	63	0.02	3.08
50-60	291	0.12	4.20	390	0.12	3.03	92	0.02	2.36
60-70	110	0.04	3.57	126	0.04	2.88	28	0.007	2.39
70-80	35	0.01	3.98	70	0.02	3.00	10	0.003	3.23
Total:	3944			4327			1066		
Arithmetical average:			6.19			5.56			3.18
Speuld east	*1987*			*1988*			*1989*		
H	186	1.01	10.86	215	1.34	12.48	90	0.34	7.56
0-10	582	0.55	9.46	510	0.45	8.83	190	0.09	4.52
10-20	535	0.45	8.36	496	0.37	7.5	136	0.06	4.43
20-30	432	0.32	7.43	552	0.37	6.79	289	0.07	2.58
30-40	292	0.18	6.00	410	0.27	6.67	115	0.03	2.57
40-50	250	0.14	5.62	366	0.20	5.35	44	0.02	5.07
50-60	205	0.11	5.38	239	0.13	5.25	38	0.01	3.00
60-70	149	0.07	4.77	203	0.11	5.60	26	0.006	2.36
70-80	139	0.06	4.26	228	0.10	4.27	1	0.001	5.00
Total:	2769			3219			929		
Arithmetical average:			6.90			6.97			4.12
Speuld west				*1988*			*1989*		
H				185	1.06	11.44	85	0.26	5.98
0-10				389	0.33	8.36	201	0.12	5.81
10-20				576	0.45	7.74	179	0.07	3.89
20-30				439	0.35	7.96	266	0.08	3.10
30-40				296	0.20	6.65	131	0.04	3.24
40-50				183	0.11	5.78	87	0.02	2.79
50-60				218	0.09	4.26	84	0.02	2.33
60-70				236	0.09	3.75	18	0.01	4.30
70-80				237	0.09	3.73	0	0.00	-
Total:				2759			1051		
Arithmetical average:						6.63			3.93

Table 2.3.
Coefficient of variation as percentage of average fine root biomass (dry weight) per hectare, fine root density and specific root length (SRL) in all subplots of the ACIFORN sites in 10 cm layers (H = humus layer of the organic horizon) in three consecutive years. The coefficients of variation were calculated after logarithmically transforming of the data to correct for skewed frequency distribution of the fine root parameters.

Depth (cm)	Biomass (%)	Density (%)	SRL (%)	Biomass (%)	Density (%)	SRL (%)	Biomass (%)	Density (%)	SRL (%)
Kootwijk	*1987*			*1988*			*1989*		
H	81	84	38	41	42	27	113	126	11
0-10	44	48	27	54	48	25	116	87	58
10-20	41	48	26	73	58	23	105	98	61
20-30	55	59	32	68	61	22	101	100	88
30-40	80	89	39	56	57	30	130	93	95
40-50	67	75	42	87	48	27	109	118	91
50-60	82	109	52	111	73	49	170	136	146
60-70	142	111	137	129	99	77	225	204	158
70-80	176	161	137	194	186	113	330	304	277
Total:	38			40			62		
Arithmetical average:			22			17			30
Speuld east	*1987*			*1988*			*1989*		
H	103	10	42	52	58	29	118	145	107
0-10	64	57	31	72	71	43	117	107	118
10-20	63	52	33	46	54	23	112	184	109
20-30	70	66	72	63	65	23	149	210	151
30-40	81	64	42	87	81	27	221	254	155
40-50	86	75	41	102	97	36	272	223	134
50-60	104	121	64	84	100	57	189	137	178
60-70	128	133	77	89	108	54	200	167	127
70-80	197	166	101	203	162	59	200	292	279
Total:	54			52			103		
Arithmetical average:			26			16			71
Speuld west				*1988*			*1989*		
H				51	69	26	169	115	126
0-10				97	123	42	111	91	58
10-20				79	87	55	84	104	66
20-30				65	55	28	114	101	74
30-40				81	84	41	83	130	102
40-50				98	92	45	116	113	101
50-60				179	128	72	188	161	124
60-70				208	166	75	176	195	131
70-80				261	187	92	-	-	-
Total:				69			70		
Arithmetical average:						21			42

Table 2.4.

Estimation of dry weight of coarse roots (W_{cr}, roots > 2 mm diameter) per tree and per hectare via diameter breast height of a tree of mean basal area (dg; measured in winter). In formula: W_{cr} = 0.01 dg2.63, with r^2 = 0.96, from Kuiper & Coutts 1992.

SITE	YEAR[1]	d_g (cm)	W_{cr} TREE^{-1} (kg tree^{-1})	W_{cr} ha^{-1} (tons ha^{-1})	GROWTH OF W_{cr} (tons ha^{-1} yr^{-1})
Kootwijk	*(992 trees ha^{-1})*				
	86/87	18.7	24	23.8	
	87/88	19.2	25	24.8	1.0
	88/89	19.7	27	26.8	2.0
	89/90	20.3	29	28.8	2.0
Speuld	*(886 trees ha^{-1})*				
	86/87	21.3	32	28.4	
	87/88	22.1	35	31.0	2.6
	88/89	22.8	38	33.7	2.7
	89/90	23.5	41	36.3	2.6

densities he recorded for trees in the topsoil were 3 cm cm^{-3} for *Pinus radiata* and 5 cm cm^{-3} for *Pinus sylvestris.*

After a dry period the SRL is almost halved, showing that the finest roots in the fine root fraction are very sensitive to drought stress. This study suggests that in the surviving fine root fraction, runner roots with secondary thickening as described by Sutton & Tinus (1983) play a major role. This means that the situation is relatively favourable for a completely new system of fine roots to develop quickly when more moisture becomes available after rain, because roots with secondary thickening are capable of forming extra root tips during branching. Hence, the number of growing root tips can increase quickly under such circumstances.

Each year there were more fine roots in Kootwijk than in Speuld. The aboveground growth in Kootwijk is slower than in Speuld. Thus there were more fine roots at the site with the poorest soil quality. Keyes & Grier (1981) also found larger amounts of fine root biomass in poorly productive sites. When the physical and chemical conditions of the soil are good, trees can take up enough water and nutrients with lower root densities. In combination with root density, the soil hydraulic conductivity plays an important role in the ability of root systems to take up water (De Willigen & Van Noordwijk 1987). The unsaturated hydraulic conductivity is usually greater in soil with a larger loam or organic matter content.

Trees on very productive sites need a relatively large coarse root system to support the aboveground biomass and to guarantee transport capacity for water and nutrients. It seems logical for the coarse root fraction to be directly proportional to the aboveground biomass. In studies on the relationship between shoots and roots it is certainly appropriate to separate the fine and the coarse root fractions, even in seedling trials. The estimated weight of the coarse roots in these two Dutch Douglas-fir plantations is 6 (Kootwijk) or 10 (Speuld) times the weight of the fine roots, even when fine root density is high. To analyse the functional equilibrium (Brouwer 1983) between aboveground and belowground plant parts in woody plants, it is logical to only sample tissue that is in exchange with its environment: i.e. leaves and fine roots. The ratio of leaf area index (LAI) over root area index (RAI) would be a good indicator for the functional equilibrium between shoots and roots. The relative large weight of the supportive coarse roots makes it difficult to detect any shifts in belowground uptake capacity in relation to the assimilating leaf surface. If for example changes induced by atmospheric deposition of nitrogen are to be detected, careful attention should be paid to fine root density.

Acknowledgements

This project was supported by the Dutch Priority Programme on Acidification. Roots and data were processed by G.M.J.H. Ackermans, A. Verdoes, J.M. Klap, C. van der Haar, M. Stempher, W. de Bruijn, and W.H.K. Post. 'De Dorschkamp' Research Institute for Forestry and Urban Ecology offered facilities during the preparation of this chapter. G.M.J. Mohren, W.G. Keltjens, R. Rabbinge, R.A.A. Oldeman and G.F. Weetman made valuable comments on the manuscript.

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3. Fine root density and root biomass of two Douglas-fir stands on sandy soils in The Netherlands: 2. Periodicity of fine root growth and estimation of belowground carbon allocation

Abstract

Detailed studies on the periodicity of fine root growth were carried out in the two Douglas-fir stands of the Dutch ACIFORN project over a two year period. The perforon method allows the direct, in situ observation of root tips growing in long horizontal tubular channels in the soil. The number of white root tips was used as an indication of periodicity of fine root growth. In the first year the number of white root tips peaked just before budbreak, and then declined gradually towards autumn. Despite a fairly high soil temperature in the winter few white root tips developed between October and April. In both stands most of the fine roots died during the dry spring of the second year. There is some evidence that many fine roots died at bulk soil water pressure heads of around -0.08 MPa. Due to dry periods in the second year of observation, the periodicity of fine root growth showed a different pattern, especially in the stand with lower water holding capacity in the soil. Based on certain assumptions, the belowground carbon allocation in both stands was estimated from the biomass of fine and coarse roots. In the less productive stand more carbon per surface area is allocated to the fine roots than in the more productive stand, but the carbon allocation to the coarse roots is greater in the more productive stand. The effect of recent nitrogen deposition from the atmosphere on belowground carbon allocation is discussed briefly.

Keywords: atmospheric nitrogen deposition, belowground carbon allocation, fine root periodicity, mortality, *Pseudotsuga menziesii*, soil water potential, turnover of fine roots, water relations

Introduction

The periodicity of tree root growth is understood less well than the periodicity of aboveground growth. Since the total amount of carbon allocated to the root system largely depends on the growth of fine roots (McClaugherty et al. 1982; Linder & Axelsson 1982), data on fine root biomass, including information on death and replacement, are essential to be able to estimate of the amount of assimilates necessary for belowground growth. In Chapter 2, Olsthoorn (1991) presented data on fine root density and root biomass in two Douglas-fir plantations of the ACIFORN-project (ACIdification of FORests in The Netherlands) on sites of different quality in The Netherlands over three consecutive years.

The 'average turnover' of fine roots per year can be defined as the quotient of the mean annual fine root biomass divided by the annual fine root production. Santantonio & Hermann (1985) used this as a definition of 'turnover rate'. In the ACIFORN stands, only the fine root biomass in the early summer in three consecutive years is known (Olsthoorn 1991). Both Santantonio & Hermann (1985) and Kurz & Kimmins (1987a) found that in early summer the fine root biomass in the stands they studied in the Pacific Northwest of America was much larger than the yearly mean. Kurz & Kimmins found the annual fine root production to be equal to the fine root biomass in May. Considering the differences in definition, this is in agreement with the findings of Santantonio & Hermann (1985).

In the present study use was made of the fine root biomass in early summer, together with data on coarse roots, to estimate the total belowground carbon allocation in the two stands. With some assumptions, the total yearly carbon allocation (in tons of carbohydrates per hectare per year) to the root system of trees can be expressed as:

$$C_b = (W_{fr} \times M_{fr} + P_{fr} / G) + (W_{cr} \times M_{cr} + P_{cr} / G) \qquad (1)$$

where

C_b = belowground carbon allocation (t CH_2O ha^{-1} yr^{-1})

W_{fr} = weight of fine roots (t ha^{-1})

M_{fr} = maintenance respiration fine roots (t CH_2O t^{-1} yr^{-1})

P_{fr} = production of fine roots (t ha^{-1} yr^{-1})

G = growth efficiency (t t^{-1} CH_2O)

W_{cr} = weight of coarse roots (t ha^{-1})

M_{cr} = maintenance respiration coarse roots (t CH_2O t^{-1} yr^{-1})

P_{cr} = production of coarse roots (t ha^{-1} yr^{-1})

As the soil fertility of these stands is different, the results of these calculations could be indicative of the effects of increased nitrogen supply due to recent atmospheric input on the total belowground allocation of carbon and on fine root densities in forested areas and could partly explain the reported nutrient imbalances in European forests as a result of nitrogen saturation (Mohren et al. 1986; Hüttl 1990; Kazda 1990; Van den Burg 1990). The present Chapter deals with the periodicity of fine root growth in relation to weather and soil moisture conditions in the same stands to be able to make an estimate of the belowground carbon allocation per year.

Methods

FIELD MEASUREMENTS

The studies on periodicity of root growth were carried out in two fully stocked, fast growing Douglas-fir plantations of the ACIFORN-project, which were used to study the influence of air pollution on forest growth (Evers et al. 1987). For a description of sites and stands see Chapter 2 (Olsthoorn 1991).

Use was made of the Perforon method (or perforated soil system), originally developed by Van den Tweel & Schalk (1981) and Bosch (1984) for greenhouse trials, to study the periodicity of root growth of Douglas-fir. Roots inside the tubular channels made by this method behave as if encountering natural open spaces or cracks in the soil (Whiteley & Dexter 1984) and can be observed.

In each stand three dominant or co-dominant trees were selected for the root studies. Details of the perforon root cellar are given in Figure 3.1. A pit was dug 1.3 m away from the stem. A 3 mm thick stainless steel plate, with perforations 14 mm in diameter, was positioned at the wall closest to the tree. The perforations in the steel plate were arranged in 23 horizontal rows and 36 alternating vertical columns. The other walls were covered with insulated boards to support the soil and to hold the steel plate exactly in position. The pit was covered when no observations were being made.

In March 1987 horizontal tubular channels 12 mm in diameter and 32 cm long were made by inserting a small corer through the perforations in the steel plate, in a 15 cm vertical zone, and removing the soil cores. In sandy material the channels remained open for over three years, even during periods of severe frost or drought. After the initial disturbance the roots were able to grow freely within and across the channels. Observations on root tips were made with a small medical endoscope 4 mm in diameter and 30 cm long (uroscope), mounted on a small CCD camera with a camera support. The images of the roots were displayed on a TV screen. At the end of the 1987 growing season a balance was achieved between the number of new roots growing into the channels and the number of roots growing across the channels back into the soil. In this Chapter only the data on numbers of root tips in 1988 and 1989 are presented. In the tree perforon root cellars per site, the total length of the observation channels was 53 m.

Root tips inside the channels were observed monthly so that the current activity of the roots could be recorded. Mycorrhizal root tips could be distinguished from non-mycorrhizal brown root tips by colour or structure of the fungal mantle at the root tips (Fig. 3.1c). Living root tips were classified as mycorrhizal, brown or white. Mycorrhiza were recorded separately, because the periodicity of the growth of the mycorrhizal root tips was difficult to see since there were only minor changes in colour during active growth. Non-mycorrhizal roots were considered to be actively growing when the root tips were white (Krueger & Trappe 1967). Root tips that were black, shrivelled or mouldy were considered dead and were not counted.

The monthly increase in stem diameter during the growing season was measured with permanent increment bands (PVC) on the trees being monitored by the perforon system.

Soil water pressure heads (water potentials) were monitored twice daily on a nearby subplot with tensiometers at depths ranging from 10 to 200 cm (Burt 1978). Soil water contents at 50 to 150 cm depth were measured with the neutron scattering technique (Gardner & Kirkham 1952) in three access tubes per site. The soil water contents of the upper 70 cm of the soil were measured weekly by Time Domain Reflectometry (Topp et al. 1980). To obtain a continuous time series of soil water pressure heads and water contents, the SWIF model (Soil Water In Forested ecosystems; Tiktak et al. 1990) was calibrated with data on water contents and pressure heads. However, because tensiometer readings are not accurate when the soil is dry, preference was given to the data on water contents.

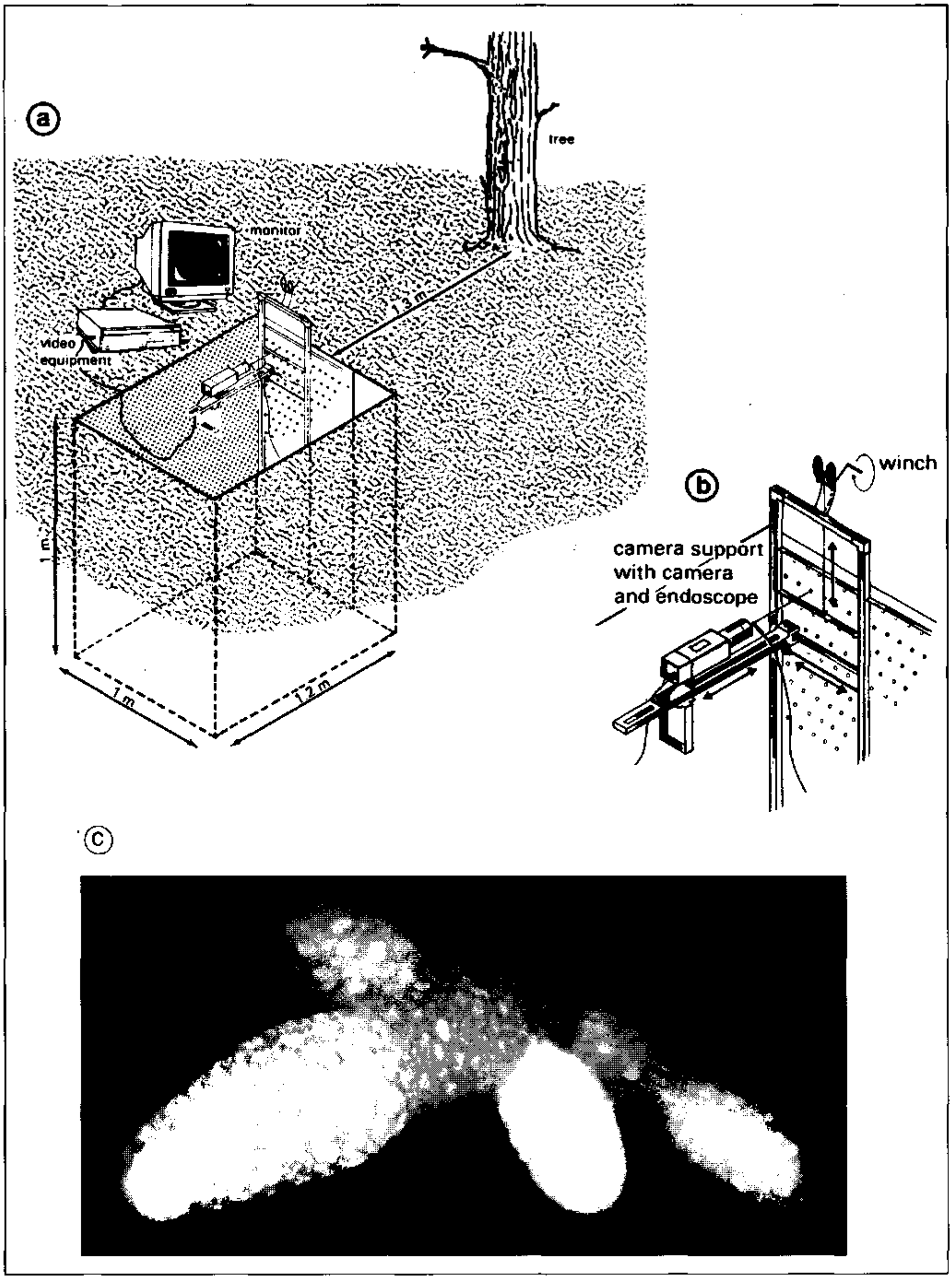

Figure 3.1.
Schematic illustration of a) perforon root cellar with video equipment near a mature tree in a forest stand, b) camera stand with endoscope and CCD video camera and c) example of *Russula ochroleuca* mycorrhiza (diameter 1 mm) as visible in the perforon root cellar during development (endoscope photograph by G.M.J.H Ackermans).

Rainfall was measured continuously in clearings near the ACIFORN stands. Soil temperature was continuously measured with diodes. The air temperature was continuously measured above the canopy.

CALCULATION OF BELOWGROUND CARBON ALLOCATION

To estimate the amount of carbohydrates needed for the root system to perform as observed (see also Chapter 2; Olsthoorn 1991), we assumed that:

- The fine root biomass found in the corer sampling in early summer 1987 and 1988 (Olsthoorn 1991) was at its maximum level at both sites. Both preceding winters were very mild and springs were moist, so high fine root mortality in that period is unlikely.
- In both stands the annual production of fine roots is equal to the maximum fine root biomass in early summer (Kurz & Kimmins 1987a).
- Coarse root growth can be estimated with the allometric relation developed by Kuiper & Van Dijk (1988) using diameter increment of the stems, as presented by Olsthoorn (1991).
- 50 % of the biomass of the coarse roots consists of heartwood, with no respiratory demands (Böttcher & Liese 1975).
- It is justifiable to exclude respiration by mycorrhizal root tips from the calculation of carbon allocation, because the frequency of mycorrhizal root tips on the ACIFORN sites was below 10 % (Jansen & De Nie 1988).

Our calculations of growth and maintenance respiration with Equation 1 were based on parameters used in a simulation model of Douglas-fir growth developed by Mohren (1987). The relative maintenance respiration depends on the nitrogen and mineral content of the biomass, according to the following equation (Penning de Vries 1975; De Wit et al. 1978):

$$M = 0.25 * F_N + 0.08 * F_M \qquad \text{(at 25 °C)} \qquad (2)$$

where

M = respiratory demand in g CH_2O g^{-1} d^{-1}

F_N = nitrogen fraction of the dry matter

F_M = mineral fraction of the dry matter.

The average nitrogen fraction of the fine roots from both sites in the 1988 sampling programme was 0.013; the average mineral fraction was 0.006 (see Appendix 2). Assuming an aboveground growing season of 200 days at 15 °C with a Q_{10} of 2 (if the temperature is 10 °C lower, the relative maintenance respiration is halved) results in the yearly maintenance respiration (M_{fr}) for fine roots being 0.38 g CH_2O g^{-1} yr^{-1}. The respiration characteristics for the maintenance of the living coarse root biomass (M_{cr}) are taken the same as those calculated by Mohren (1987) with Equation 2 for the sapwood in the stem, with very small nitrogen and mineral fractions, resulting in 0.021 g CH_2O g^{-1} yr^{-1} for coarse root sapwood in a 200 day season.

The carbohydrates actually transported to the root system were derived from the estimated annual growth of fine and coarse roots using a conversion efficiency

(G) of 0.65 g of dry matter produced per gram carbohydrates (from Mohren 1987, based on Penning de Vries & Van Laar 1982).

Results

SOIL MOISTURE AND SOIL TEMPERATURE

Figure 3.2 presents data on rain and soil water pressure heads for 1988 and 1989. In 1988 only a few short rain-free periods occurred. In 1989, there was a dry period in May and June, followed by other dry periods, interrupted by some heavy showers. Kootwijk and Speuld are 10 km apart and have the same rainfall pattern. This was reflected in the pattern of the soil water pressure heads in both years. In Kootwijk the soil water pressure heads were less and decreased earlier in spring than Speuld in both years, because the soil had a smaller water holding capacity. In Speuld the water pressure heads rarely fell below -0.1 MPa (pF 3), even in 1989. In Kootwijk the soil at a depth of 80 cm was relatively dry for long periods, especially in 1989. In the upper 50 cm of the soil, soil water pressure heads in Kootwijk were as low as -0.1 MPa (pF 3) in May 1989, whereas in Speuld this value was not reached until July 15 in 1989. Because of heavy showers during the summer of 1989 the water pressure heads at 15 cm depth were very variable. The water pressure heads at greater depth showed a more steady pattern.

Figure 3.3 presents air temperature for Speuld and soil temperature for Kootwijk. The winters were mild for The Netherlands; hardly any frost occurred and the soil was never frozen.

PERIODICITY OF ROOT GROWTH

The individual trees varied little in growth behaviour. As the patterns in the active growth period were comparable, the results of the individual perforons for one site were combined to give a general impression of the interaction with soil conditions. The numbers of mycorrhizal, brown and white root tips in the winter period were estimated from observations in only one perforon per site. The number of white root tips is used as an indication of the periodicity of root growth, but the numbers of root tips cannot be extrapolated to a hectare, because the physical conditions for root growth are different from soil and the soil volume sampled was small.

Figure 3.4 shows the total number of visible living root tips per soil layer of 20 cm. At both sites the root tips were most numerous in the topsoil, in accordance with the vertical distribution of fine root density observed in root core samples (Olsthoorn 1991). In spring the total number increased somewhat and in Speuld the number varied, especially in 1989. In the late summer of 1989 the total number of root tips in Kootwijk increased in the two deepest soil layers, but there was a decrease in the two uppermost soil layers in Speuld in that period. In autumn numbers declined in both sites at all depths.

Figure 3.5 shows that the occurrence of white root tips was almost completely restricted to the period between the beginning of April and the end of September, with hardly any white root tips between October and March, while soil temperature was over 5 °C for much of the winter season (Fig. 3.3). The root tips resumed growth fairly late in spring. The stem diameter growth started later in spring, associated

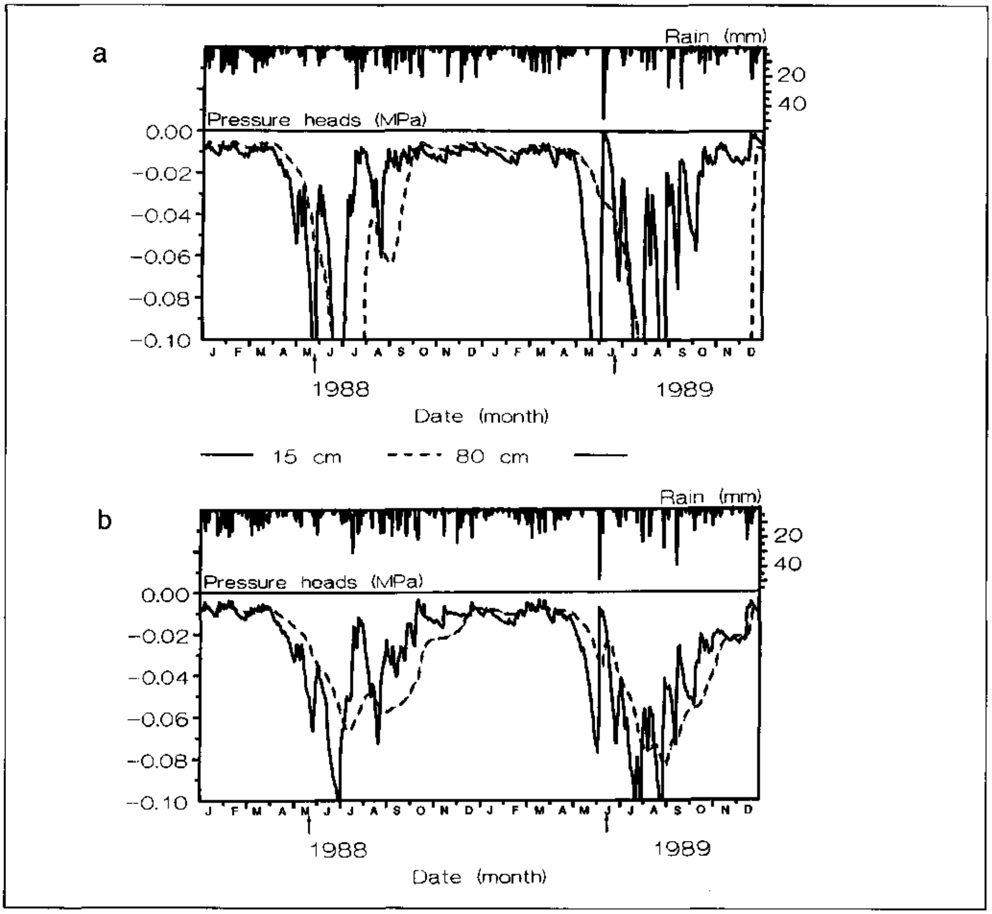

Figure 3.2.

Amounts of rain and estimates of soil water pressure heads during 1988 and 1989 for a) Kootwijk and b) Speuld. The estimates of soil water pressure heads are calculated with the simulation model SWIF, calibrated with tensiometer and neutron probe measurements (Tiktak et al. 1990). Arrows indicate root corer sampling date (Olsthoorn 1991).

with budbreak (May). In 1988 the white root tips at both sites were especially numerous in late spring, when budbreak occurred, and declined slowly toward the autumn. In 1989, the pattern in Speuld was nearly the same as in 1988, but in Kootwijk the pattern in both years was very different: there were relatively few white root tips in spring 1989, but many white root tips at all depths during the whole summer. Furthermore, in Kootwijk the number of white root tips in the lowest soil layer declined the latest. In Speuld the number of white root tips showed the same pattern in all soil layers.

In Speuld the development of the stem diameter increment in 1989 was the same as in 1988. In Kootwijk the diameter increment was interrupted at the end of the summer of 1989, possibly because of low water pressure heads in the soil.

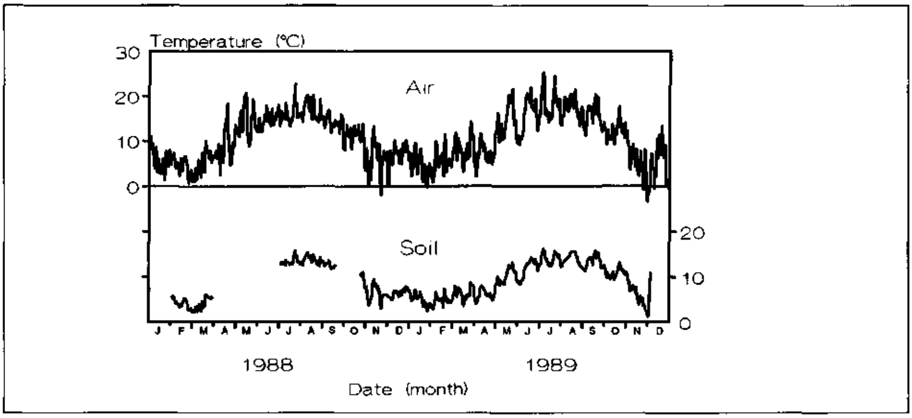

Figure 3.3.
Air temperatures above the forest canopy (Speuld) and soil temperatures at 15 cm depth (Kootwijk) during 1988 and 1989.

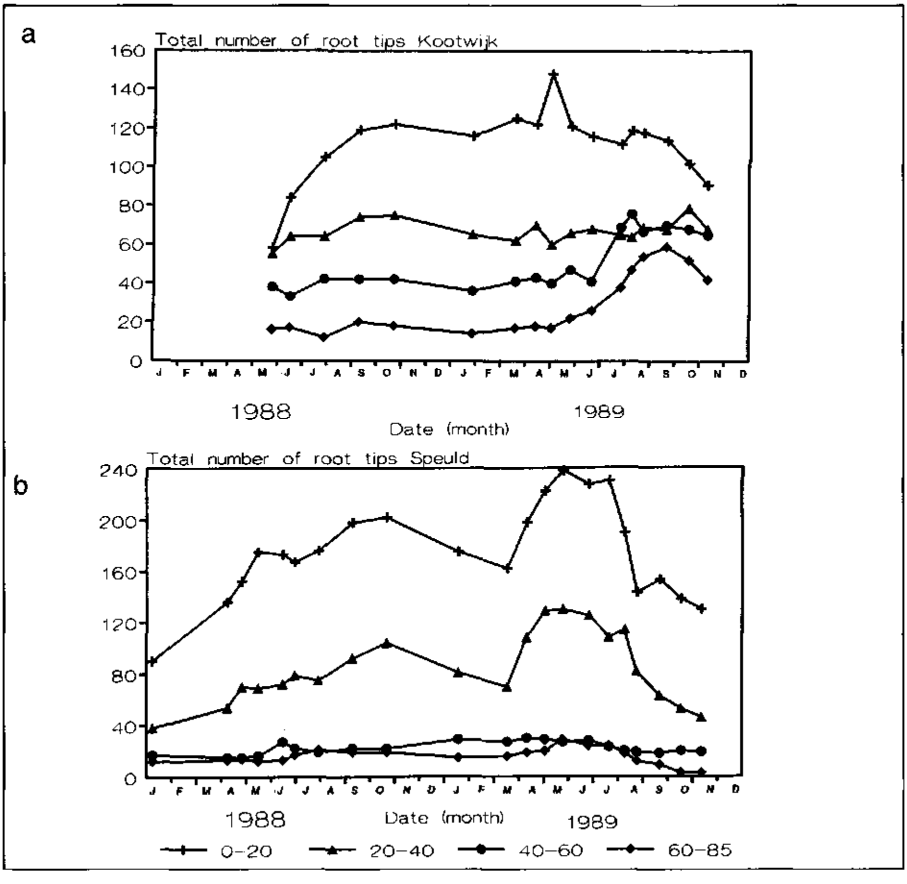

Figure 3.4.
Total number of visible living root tips (mycorrhizal and non-mycorrhizal white and brown root tips) of Douglas-fir in three perforon root cellars during 1988 and 1989 in a) Kootwijk and b) Speuld (legend: depth indicated in cm).

In periods with many white root tips there were usually few brown root tips, but the numbers increased later (Fig. 3.6). In Speuld there was an increase in the springs of 1988 and 1989, as there was in Kootwijk in 1988. But in spring 1989 there was relatively little growth in Kootwijk (Fig. 3.5) and therefore the number of brown root tips did not start to increase until summer and then mainly in the two deepest soil layers (see Fig. 3.4). In the summer of 1989, there was a decrease in the number of brown root tips in Speuld when there was little root growth activity, and many roots died in the dry soil. The decrease was observed in the two uppermost soil layers (see Fig. 3.4).

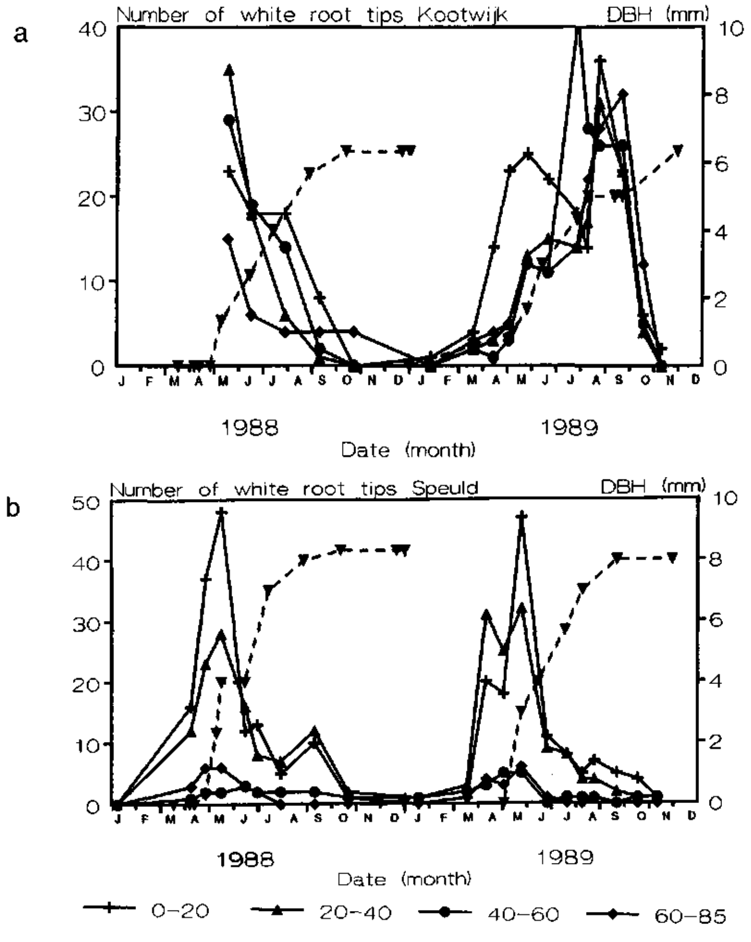

Figure 3.5.
Number of visible white root tips of Douglas-fir in three perforon root cellars and average diameter increment at breast height (DBH) of the three observed trees (cumulative per year) during 1988 and 1989 per soil layer in a) Kootwijk and b) Speuld (legend: depth indicated in cm; dashed line is DBH increment).

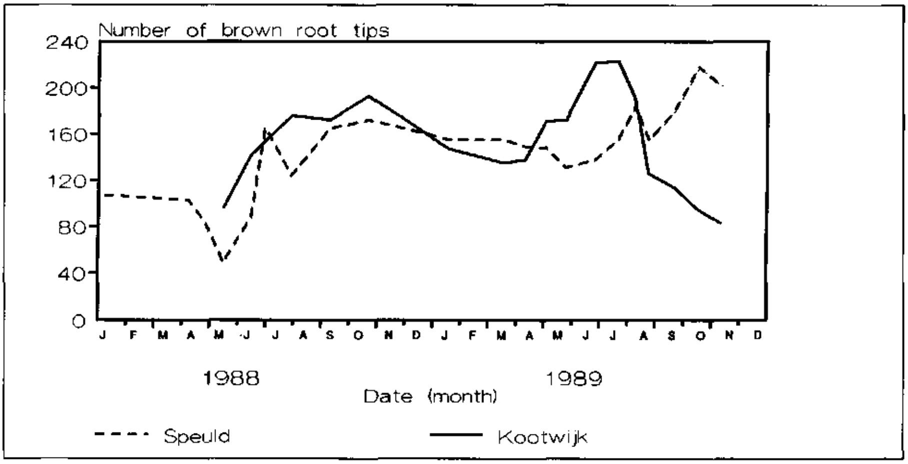

Figure 3.6.
Number of visible brown non-mycorrhizal root tips of Douglas-fir in three perforon root cellars during 1988 and 1989 in Kootwijk and Speuld (legend: depth indicated in cm).

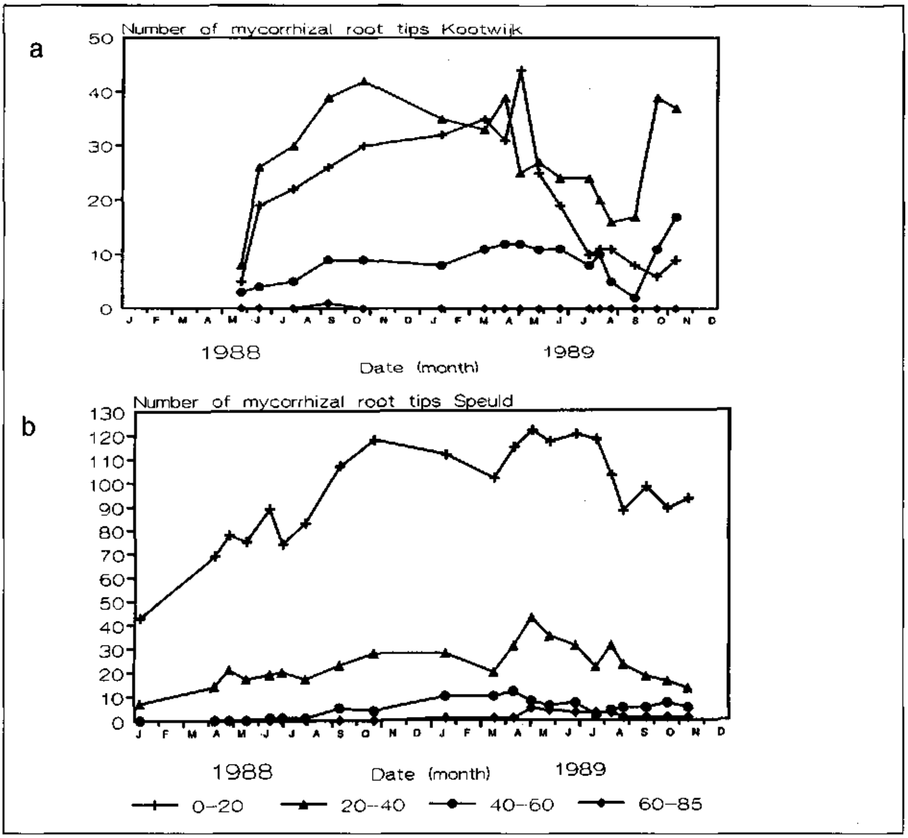

Figure 3.7.
Number of visible mycorrhizal root tips of Douglas-fir in three perforon root cellars during 1988 and 1989 in a) Kootwijk and b) Speuld (legend: depth indicated in cm).

The dynamics in the numbers of mycorrhizae are shown in Figure 3.7. Some of the mycorrhizae may have been growing at the time of observation; this is not detectable from these data. The longitudinal growth of the mycorrhizal root tips was much slower than that of non-mycorrhizal white root tips. The fluctuation in number of mycorrhizae is caused either by mycorrhizal roots growing into or out of the channels, or by the death of visible mycorrhizae. Each spring, longitudinal growth of mycorrhizae could be seen in the development of new 'sprouts' at the mycorrhizal root tips (Fig. 3.1c). Not only the absolute number of mycorrhizae, but also the frequency of mycorrhizal root tips decreased with depth, as can be seen from Figures 3.4 and 3.7. However, mycorrhizae were found at all observed depths. In Kootwijk the numbers of mycorrhizal root tips started to increase from the spring of 1988 (Fig. 3.7). In the two uppermost soil layers the number of mycorrhizal root tips remained fairly constant until the summer of 1989 when they declined drastically, before increasing rapidly again in the autumn. In the two deeper soil layers there were no changes in the number of mycorrhizal root tips. The results from Speuld suggest that during the winter, roots with a mycorrhizal mantle can continue to grow at lower temperatures than roots without such a fungal mantle. In the mild winter of '87/'88 the number of brown root tips remained the same (Fig. 3.6), but the number of mycorrhizal root tips rose as new tips continued to grow into the channels. During the summer of 1989 the numbers of mycorrhizae in Speuld declined more slowly than the numbers of brown root tips (see also Appendix 1).

Table 3.1.

Estimated belowground carbon allocation in both ACIFORN Douglas-fir stands in 1988. Fine and coarse root biomass data from Olsthoorn (1991). Symbols, calculation methods and assumptions are explained in the text.

	Coarse roots (sapwood)	Fine roots	Total
Kootwijk:			
Biomass (t ha^{-1})	12.4 (= W_{cr})	4.3 (= W_{fr})	
Growth (t ha^{-1} yr^{-1})	1.0 (= P_{cr})	4.3 (= P_{fr})	
Requirements for:			
- maintenance respiration *)	0.3	1.6	1.9
- growth *)	1.5	6.6	8.1
Total carbon requirements *)	1.8	8.2	10.0 (= C_b)
Speuld:			
Biomass (t ha^{-1})	15.5 (= W_{cr})	3.0 (= W_{fr})	
Growth (t ha-1 yr^{-1})	2.6 (= P_{cr})	3.0 (= P_{fr})	
Requirements for:			
- maintenance respiration *)	0.3	1.1	1.4
- growth *)	4.0	4.6	8.6
Total carbon requirements *)	4.3	5.7	10.0 (= C_b)

*) in t CH_2O ha^{-1} yr^{-1}

ESTIMATION OF BELOWGROUND CARBON ALLOCATION

The calculations in Table 3.1 were made only for 1988, using Equation 1, in order to give an impression of the carbon allocation to the belowground part of the forest stand, based on data from Olsthoorn (1991). Because of the greater nitrogen and mineral content, the estimated maintenance respiration of fine roots in both sites was greater than that of the coarse root biomass, even though their dry weight was much less. In 1988 the total amount of assimilates needed for the performance of the root system in both Kootwijk and Speuld was just over 10 ton CH_2O ha^{-1} yr^{-1}. However, in Kootwijk the total requirements of the fine roots (8.2 ton CH_2O ha^{-1} yr^{-1}) were greater than in Speuld (5.8 ton CH_2O ha^{-1} yr^{-1}), and the total requirements of the coarse roots were less. The total requirements for growth of the root system in Kootwijk and in Speuld were respectively 4.3 and 5.9 times more than total maintenance respiration.

Discussion

FINE ROOT MORTALITY AND SOIL WATER PRESSURE HEADS

In the perforon root cellars it was observed that during the summer 1989 sometimes white root tips had already died within four weeks. The 1989 root sampling programme (Olsthoorn 1991), revealed that early in the summer of 1989 the fine root biomass in Kootwijk was only 24 % of the fine root biomass in the same period in 1987 and 1988; the corresponding value for Speuld was 34 %. Kurz & Kimmins (1987a) also found less fine root biomass after a dry period in summer.

Kuhns & Gjerstad (1988) state that the transport of assimilates to the root system decreases in dry periods. This may cause a temporary reduction in root growth. Extreme drought can cause fine roots to die, as is described in Parker & Pallardy (1988), Marshall (1986) and Deans (1979). Parker & Pallardy (1988) state that roots lose relatively more water at the wilting point than leaves, because of the collapse of the cortical tissue. However, the roots do not always die under these conditions. Drought can greatly reduce the biomass of fine roots when insufficient carbohydrates (starch and sugars) are available in those roots (Marshall 1986). Krueger & Trappe (1967) found that starch and sugar concentrations in fine roots of Douglas-fir seedlings peaked just before budbreak and were at a minimum in June. Singh & Srivastava (1986) also found a declining carbohydrate content just after budbreak. This would imply that fine roots are especially sensitive to water shortage in early summer. Deans (1979) found that in some situations fine roots of spruce die when soil pF values are less than 3.

Based on the assumption that it is possible to recognise dead roots in a corer sample as soon as one week after their death, it was possible to relate the amount of fine roots in both years to the soil water potential conditions one week before sampling. In Figure 3.2, the date of the root corer sampling is indicated for both sites in 1988 and 1989. In 1988 the soil water pressure heads in both sites did not decrease below -0.05 MPa (= pF 2.7) in that period. In 1989 however, there was a period in both Speuld and Kootwijk during which soil water pressure heads were below -0.08 MPa (= pF 2.9) at 15 cm depth. This means that in sandy soils some of the fine roots had already died at soil water pressure heads of around -0.08 MPa

(= pF 2.9). At 80 cm depth the soil water pressure heads at Speuld were still more than -0.03 MPa (= pF 2.5) whereas in Kootwijk it was more than -0.05 MPa (= pF 2.7) in that period.

If many roots in the topsoil die, the demand for uptake of water per unit of root length in the subsoil increases. According to De Willigen & Van Noordwijk (1987) this implies that the gradients of water content in the rhizosphere become steeper in a soil with a poor hydraulic conductance, as in Kootwijk. At rapid water uptake rates, roots in the subsoil must have died at water pressure heads of -0.03 MPa (= pF 2.5) in the bulk soil, because water pressure heads in Speuld at 80 cm depth were more than that just before sampling in 1989 (Fig. 3.2). Water pressure heads in the rhizosphere were not determined. The water pressure heads at the root surface may fall to a lethal level even though the bulk soil still contains a reasonable amount of water. This situation associated with differing physical soil conditions could explain the large differences that are found in literature for soil moisture conditions that result in fine root death (Deans 1979; Parker & Pallardy 1988). Both transpiration and soil hydraulic conductivity influence the difference between water pressure heads at the root surface and in the bulk soil (De Willigen & Van Noordwijk 1987). Therefore, the values that were found for these sites in the early part of the growing season may not be valid in other conditions.

PERIODICITY OF ROOT GROWTH

The soil temperatures at 15 cm depth in winter were around 5 °C, and the fine root growth activity was limited, though Kuhns et al. (1985) found that root growth can occur when the soil temperature is above 4 °C and Teskey & Hinckley (1981) found root growth all year around. Root growth was not intensively monitored during the winter periods, but occasionally a white root tip was found. Krueger & Trappe (1967) also found occasional white root tips in Douglas-fir seedlings in a nursery in winter, even in periods with frost. They found for Douglas-fir seedlings in Oregon, USA that many active root tips occurred just before budbreak, few during shoot elongation, but thereafter numbers slowly increased to moderate levels until mid autumn. Ladefoged (1939) and Lyr & Hofmann (1967) found that root growth activity in most tree species peaked in June or July. Santantonio & Hermann (1985) found a less distinct seasonal pattern in the number of new root tips of Douglas-fir in Oregon. They found that the number of new root tips fluctuated much more on the dry site than on the wetter sites. This agrees with our findings in Kootwijk (dry) and Speuld (wet). On drier sites fine roots take a greater part of the carbon budget of the stand (Table 3.1).

During the actual period of longitudinal growth of the root tips in Kootwijk in the summer of 1989, the mycorrhizal fungus did not inoculate the roots, but apparently the fresh root tips were easy to colonise as soon as the longitudinal growth stopped, as can be seen in the quick increase in number of mycorrhizae in Kootwijk in the autumn of 1989 (Fig. 3.7).

We did not measure the average turnover of fine roots, but the intense root tip activity in 1989 (especially in Kootwijk after the dry periods) suggests it was greater in 1989 than in 1988. However, in 1989 the average stem increment of the trees observed at both sites did not decrease as a result of the necessarily greater demand for assimilates in the root system.

BELOWGROUND CARBON ALLOCATION

Few data are available on heartwood formation in coarse roots. Böttcher & Liese (1975) presented data for Larch, where a substantial part of the coarse roots consists of heartwood. In our calculations (Table 3.1), the carbon allocation patterns will not change drastically if the assumption on sapwood:heartwood ratio is changed.

Chakravarty & Chatarpaul (1990) have shown that the shoot:root ratios of seedlings of *Larix laricina* decreased as mycorrhizal infection increased. Baas et al. (1989) found that in fungal tissue of vesicular-arbuscular mycorrhizal plants the respiration rates were faster than in sterile root tissue, and more energy was needed to take up nutrients. Mycorrhizae thus play a role in the carbon allocation patterns and the functional equilibrium in plants. Considering the few mycorrhizae in our stands (Jansen & De Nie 1988) and the nature of our calculations, inclusion of fungal respiration would not make the results more accurate.

In the carbon allocation to the total root system the amount of carbohydrates needed for fine root growth is especially large. This means that the assumed annual fine root production strongly influences the estimate of the total belowground carbon allocation. It is difficult to measure fine root production in the field. Estimates are usually based on sampling with a root corer at intervals of one month. The production and mortality of fine roots is then calculated from differences in the amount of biomass and necromass in these samples. Singh et al. (1984) and Kurz & Kimmins (1987b) have shown that this can cause over- or underestimation of the actual productivity.

Santantonio (1989) proposed using aboveground stand performance to calculate the total carbon allocation to the root system. In his approach, which is based on literature data, the percentage of the total primary production in a stand allocated to the root system depends on the amount allocated to the stem. This relation is estimated in a simple regression model, and it describes changes to the shoot:root ratio induced by site quality.

From the approach of Santantonio (1989) and calculations according to this principle with data from the ACIFORN Douglas-fir stands (results not shown), the conclusion is that the average annual turnover of fine roots in this study does indeed agree with our assumption that the annual production of fine roots is equal to the fine root biomass in early summer.

Usually, there are fewer fine roots at more productive sites. (Kurz & Kimmins 1987a; Vogt et al. 1987; Walters & Reich 1989). Irrigation and fertilization also result in fewer fine roots (Linder & Axelsson 1982). This conclusion could also be drawn in these two study sites (Olsthoorn 1991). This means that the total carbon allocation to the fine roots in Kootwijk is larger than in Speuld, even if there is some uncertainty in our estimation of the annual production of fine roots. The carbon allocation to the coarse roots shows the opposite picture: smaller in Kootwijk than in Speuld, because of its relation to aboveground growth rates. This is to be expected, because the coarse root system has the same function as the stem: support and transport of solutes, whereas the fine roots serve as an interface for the uptake of water and nutrients.

According to Brouwer (1983), the shoot:root ratio in herbaceous plants is fairly stable if the growing conditions remain constant. In forest soils in The Netherlands however, nitrogen availability has changed because of atmospheric deposition and instead of being limiting it is now excessive (Van Breemen et al. 1982; Mohren et al. 1986; Hüttl 1990; Kazda 1990; Van den Burg 1990). This means that shoot growth is stimulated, whereas the allocation to the fine roots is decreased (Linder & Axelsson 1982). As a result of nitrogen deposition, the coarse root biomass has increased concomitantly with stem biomass. However, because the fine root biomass is the major destination for the carbohydrates, it is concluded that nowadays the carbon allocation to the root system is less than it was before nitrogen availability increased because of intensified factory farming in The Netherlands (Van den Burg & Kiewiet 1989). This partially explains why nitrogen fertilization results in increases in aboveground tree growth.

When fine root biomass decreases, the fine root density also decreases. As a result, functional equilibrium of the shoot:root ratio (the ratio of needle biomass to fine root biomass) shifts considerably. The stimulated aboveground growth does have a drawback: the capacity for uptake is reduced whereas the demand for water and nutrients of the aboveground biomass has increased. This may enhance the stands susceptibility to drought and deficiencies of nutrients other than nitrogen.

Acknowledgements

This project was supported by the Dutch Priority Programme on Acidification. The perforon root cellars were installed with help from E.A.P. de Bruijn, J. Post and J. Laurens. A.W.M. Vermetten provided air temperature data. 'De Dorschkamp' Research institute of Forestry and Urban Ecology offered facilities during the preparation of this Chapter. G.M.J. Mohren, W.G. Keltjens, R. Rabbinge and G.F. Weetman deserve special mention for valuable comments on the manuscript. Figures were prepared by J. Tahitu.

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4. The relation between fine root density and proximity of stems in closed Douglas-fir plantations: implications for sampling design

Abstract

Detailed studies were carried out in two fully stocked, fast growing Douglas-fir plantations of the Dutch ACIFORN project in three consecutive years, to obtain information on fine root densities (Olsthoorn 1991). Data collected in early summer 1987 were used to study the relation of fine root density and proximity to the nearest tree or the dominant tree. A large number of samples (37 in one site and 55 in another) was collected in a small area (10 x 11 m). Two distances were measured at each sampling point: the distance to the nearest tree and the distance to the tree with a dominant crown above that point. There was large variability in fine root density in the samples. Tests with different regression models showed a distinct rooting pattern for one of the two locations. It is concluded that systematic errors in the assessment of fine root density can arise when sampling points are chosen at a constant distance from trees. For Douglas-fir, this systematic error could have been an overestimation of the fine root density by up to 10 %. Therefore, to avoid systematic errors, a stratified random design or a random sampling design should be used. When trees are spaced irregularly, a grid sampling design is also appropriate.

Keywords: fine root distribution, methods, *Pseudotsuga menziesii*, sampling design, spatial variability, closed forest

Introduction

The fine root density in a closed forest is usually considered to be independent of distance from the tree (McMinn 1963; Moir & Bachelard 1969; Reynolds 1970, 1975; Kummerow et al. 1990). The density of the fine roots belonging to individual trees will decrease with increasing distance from the tree base. In a closed stand, the root systems intermesh (Kuiper & Coutts 1992; Büttner & Leuschner 1994). In such cases, the total fine root density is the cumulative total of the fine roots of individual trees in the vicinity of the sampling point and need not necessarily show a strong correlation with distance from a tree. If this is so, different sampling strategies would lead to estimates of root density without systematic error (e.g. sampling at fixed distance from the trees). However, if there is a general pattern in the fine root density in a stand, this has implications for sampling methods.

The distribution of the throughfall water in the stand, and the subsequent horizontal heterogeneity of the water content and the chemical condition of the soil have potential influence on the fine root density in relation to the tree positions. Douglas-fir has hardly any or no stem flow, and throughfall water is led to the outside of the tree crown (Bouten et al. 1992). The resulting drier conditions under the tree base might cause a lower fine root density.

This chapter reports on a study investigating the relationship between fine root density and tree distance. The study used data from the ACIFORN project (ACIdification of FORests in The Netherlands), in which growth parameters and the factors influencing growth were monitored in detail in two Douglas-fir stands in the centre of The Netherlands for several years to study the impact of air pollution on forest growth (Mohren, 1991). The fine root density was assessed up to a depth of 80 cm. In a small sampling area, many samples were taken in the first sampling year (1989), at varying distances from the tree bases. The resulting data were statistically analysed in the present study, to ascertain the implications for sampling design.

Methods

SITE DESCRIPTION

The two ACIFORN stands, which are located 10 km apart in the 'Veluwe' area in The Netherlands, are young mature plantations of a coastal provenance of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on former clear-cut areas. The soils in both stands are sandy and well drained. The water table is very deep and the soil contains very little gravel. The stand in Kootwijk is located on horizontally homogenous eolian sands; the stand in Speuld is located on preglacial sand deposits containing some loam, which are slightly less homogenous, especially in the sub-soil. The ground is level in both stands. The number of trees per hectare is about 1000 in Kootwijk and about 900 in Speuld, so the average distance between trees is 3.4 m and 3.6 m, respectively. Site descriptions can be found in detail in Olsthoorn (1991).

FINE ROOT LENGTH

In Kootwijk, samples from 37 sampling points were taken in early July in 1987. In Speuld East, samples from 55 sampling points were taken in the second half of June in 1987. In 1988 and 1989 only 12 samples were taken, to be able to calculate the average fine root density (Olsthoorn 1991). The sampling points were located systematically on a grid in the plots and were at different distances from the tree bases, because the trees were spaced irregularly. In Speuld, a second plot was sampled in 1988 and 1989 (Speuld West). In both sites, samples were collected at the end of May 1988 and mid June 1989. The root corer used in the study was designed by Goedewaagen (Böhm 1979); it takes a soil core of 50 cm^2 in cross section and 15 cm long. The soil was sampled to a depth of 80 cm. Only living fine roots were taken into account (roots with a diameter of less than 2 mm, including all root tips). The total length of living fine roots in the samples was estimated using the line intersect method (Tennant 1975). The values for each sampling point were recalculated to 10 cm soil depth intervals. Methods of estimation of fine root length are described in detail in Olsthoorn (1991).

TREE DISTANCE

The distance to the centre of the nearest tree was measured with a measuring stick from the centre of each sampling point. The position of the centre of the tree was estimated. The distance to the tree with a dominant crown at the position of the sampling point was also measured. A tree was considered dominant if its crown

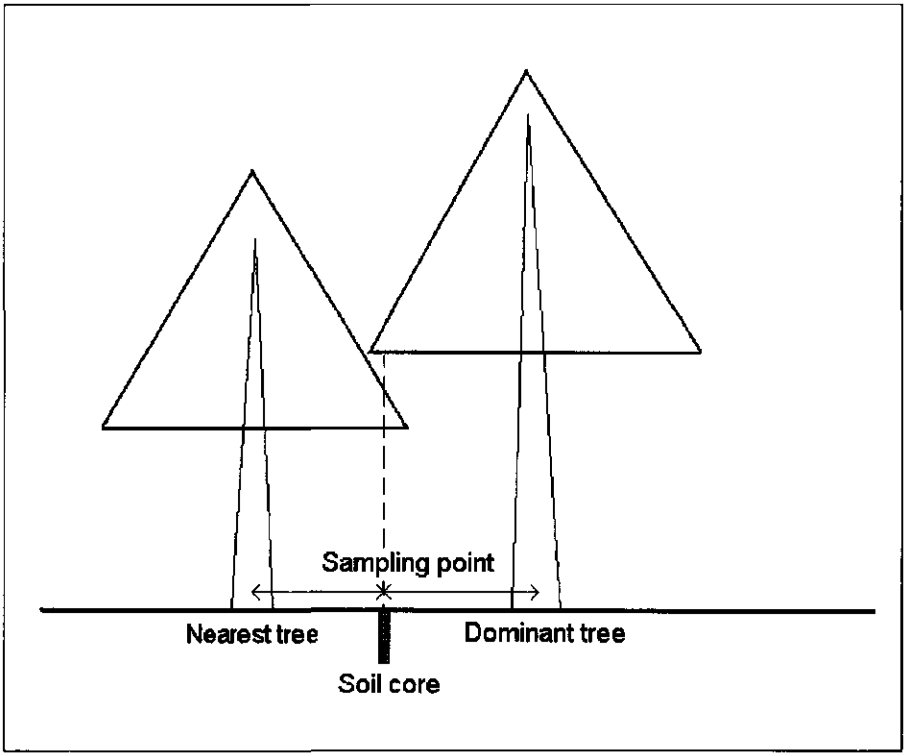

Figure 4.1.
Measurement of distance to nearest tree and dominant tree, if the crown of a tree other than the nearest was located above the sampling point.

overhung the sampling point and/or if its branches were higher than those of other surrounding trees at that point (Fig. 4.1). In most cases the nearest tree also was the dominant tree. As roots could not be sampled with the auger below the tree base, there are no data on fine root length within 25 cm (Kootwijk) and 35 cm (Speuld) from the tree centre (the average tree diameter was about 20 cm in both stands). When large roots were encountered in the sampling positions selected near a tree base, a point 10 cm from that point was chosen where the root corer could enter the soil.

STATISTICAL PROCEDURE

The data from 1987, 1988 and 1989 for both sites were used, with emphasis on the larger data sets of 1987. The total fine root length per sampling point up to 80 cm depth and the fine root length per 10 cm soil depth and the litter layer were analysed. Different statistical models were tested, usually with a log transformation of the fine root length (to ensure positive values for the expected root length). We tested different statistical models: linear, parabolic, third power, exponential, log-linear, Gompertz, inverse polynomous (see Genstat 1993; Oude Voshaar 1995), and the function $f(x) = a + bx + c/x$. The last function was attractive as it gave a realistic description: an increasing - decreasing function that is asymmetric at around its optimum. In addition to these parametric functions, the more flexible spline functions were fitted (Genstat 1993) to study further improvement of the parametric function. A spline function is a complicated function that is derived from a cubic smoothing procedure and contains segments of cubic polynomial functions and has a complicated parametrization in an additive model (Genstat 1993, 1995). Spline functions cannot be used for direct interpretation or extrapolation. The number of degrees of freedom in spline functions should be kept low, compared with the number of data points.

The following statistical tests were carried out:

1. Investigation of the best fitting statistical model (see above) for the total fine root length in relation to the distance to the nearest or the dominant tree for the whole root depth (up to 80 cm). All eight data sets were analysed separately (2 sites, three years, Speuld one plot extra in 1988 and 1989).
2. Analysis of litter layer and each 10 cm soil depth up to 80 cm separately.
3. Analysis of the pooled soil depths, assuming similar patterns for the different depths, and also an analysis including interactions with depth.

Only the results demonstrating the relationships are shown. The focus is on the large 1987 data set.

Results

TEST 1

In Kootwijk in 1987, the average fine root length per sampling point of 50 cm^2 surface area up to a depth of 80 cm was 13.4 m, with a maximum of 27.4 m and a minimum of 6.5 m. Figure 4.2a shows all data plotted against the distance to the nearest tree and Figure 4.2b shows the data plotted against the distance to the dominant tree. The maximum distance was 2.36 m to the nearest tree and 2.42 to the dominant tree. In Speuld in 1987, the average fine root length per sampling point of 50 cm2 surface area up to a depth of 80 cm was 10.2 m, with a maximum of 19.8 m and a minimum of 2.3 m. See Figures 4.3a and 4.3b for plots of data versus distance to trees. The maximum distance was 2.84 m to the nearest tree and 4.40 to the dominant tree.

Various regression functions were fitted to test the relation between fine root density and tree distance in both sites. Significant models are summarised in Table 4.1. In Speuld no significant relation was found between fine root density and distance to nearest or dominant tree, even for the 55 samples available for 1987. For Kootwijk in 1987 a significant relation was found ($p = 0.008$ to the nearest tree and $p = 0.004$ to the dominant tree; $n = 37$). The model $f(x) = a + bx + c/x$ may be regarded as a suitable description, as the spline functions do not fit better. This means that in Kootwijk in 1987 there was a lower fine root density close to the tree base, a maximum density at about 70 cm from the tree centre, and the density decreased slightly at greater distances. In Figures 4.2 and 4.3, both the spline model with three degrees of freedom and the model $f(x) = a + bx + c/x$ are plotted for the 1987 data. None of the models proved significant for the data in 1988 and 1989 for the same plot, when only 12 samples were available per plot.

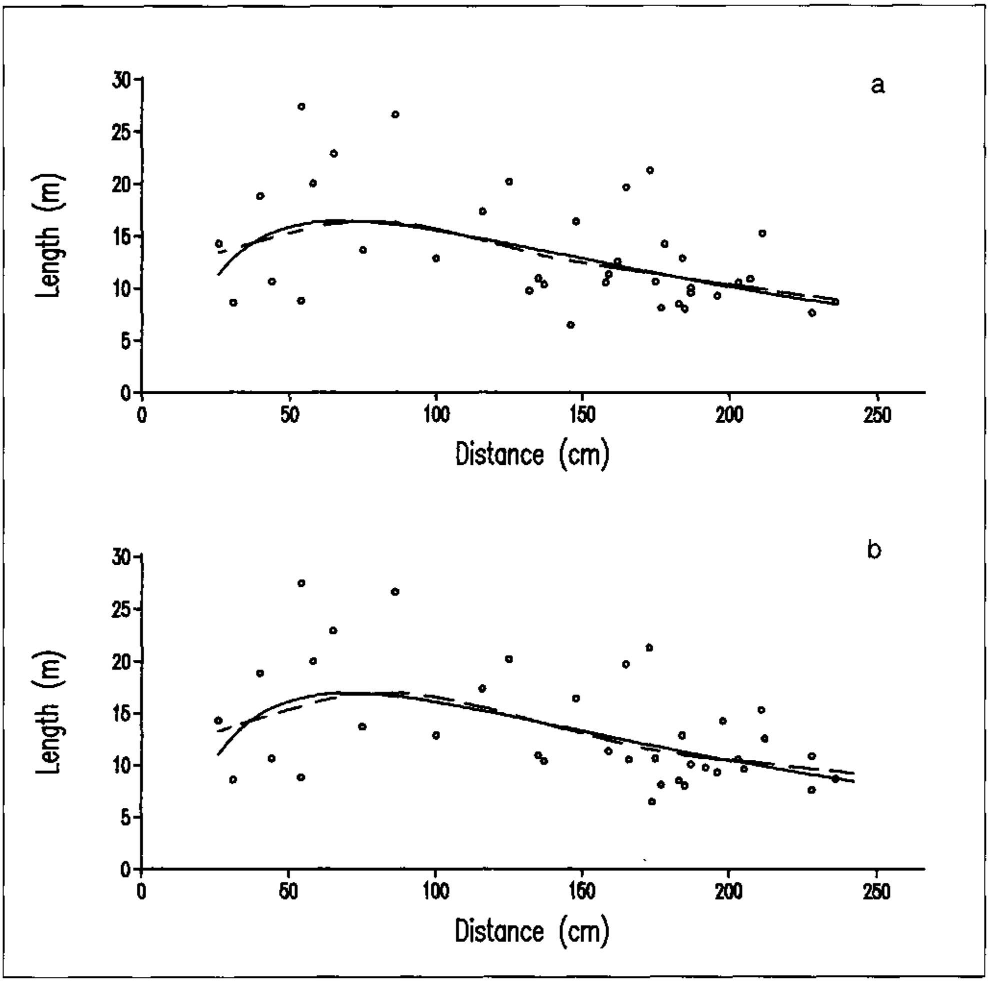

Figure 4.2.

Total fine root length (m) per sampling point of 50 cm^2 surface area up to a depth of 80 cm in Kootwijk, plotted against the distance to the nearest tree (a) and to the dominant tree (b). The lines indicate the relationships according to the spline function (dotted line) with three degrees of freedom (p = 0.019; significant) and the function f(x) = a + bx + c/x (p = 0.008; significant).

TESTS 2 AND 3

The regression tests were also performed for the fine root data per 10 cm soil depth. Like the data for the total rooting depth up to 80 cm in Figures 4.2 and 4.3, the fine root length data per 10 cm soil depth also showed a large variation (data not shown) in graphs and in regression tests. No significant relation was found for most of the tests, except for the depths between 30 and 60 cm in Kootwijk in 1987 (n = 37), where the same models were found to be significant, with a maximum fine root density 70 to 80 cm from the tree centre (graphs not shown). The spline function for

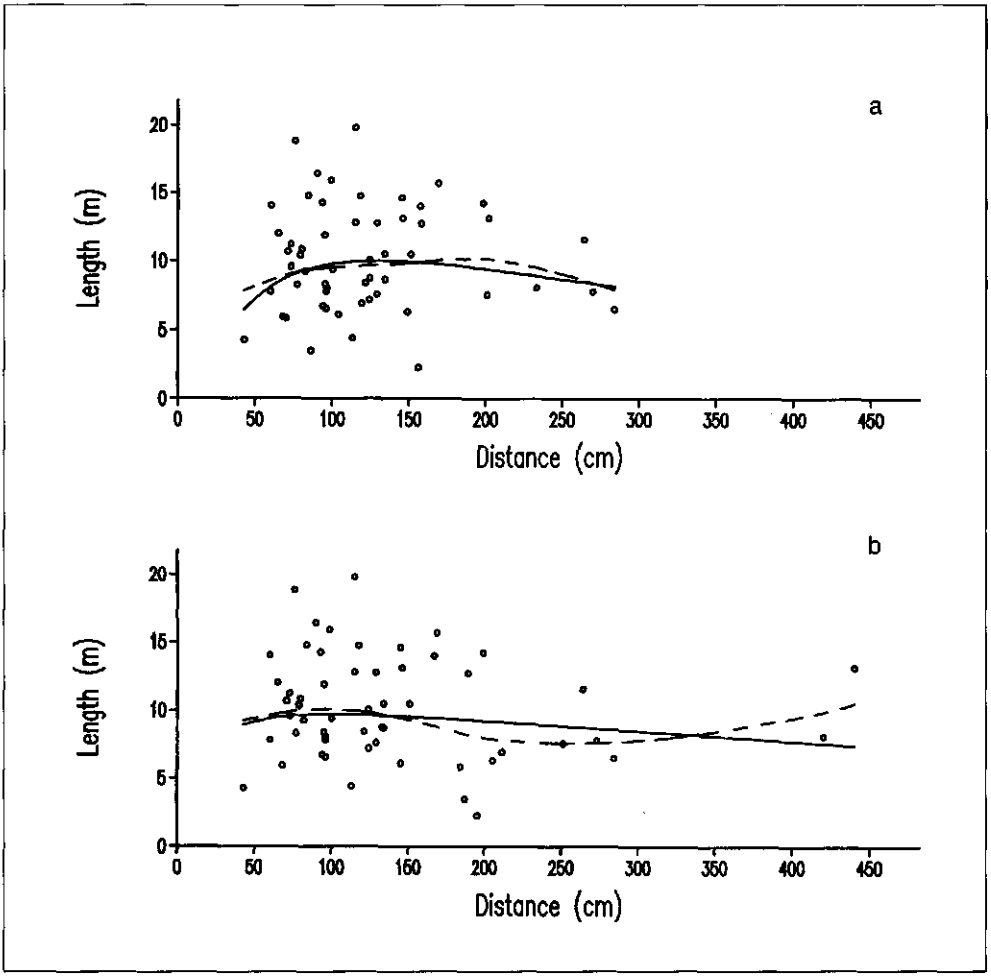

Figure 4.3.
Total fine root length (m) per sampling point of 50 cm^2 surface area up to a depth of 80 cm in Speuld, plotted against the distance to the nearest tree (a) and to the dominant tree (b). The lines indicate the relationships according to the spline function (dotted line) with three degrees of freedom ($p = 0.629$; not significant) and the function $f(x) = a + bx + c/x$ ($p = 0.401$; not significant).

each 10 cm soil depth indicated that the pattern can vary per unit depth, but because of the large overall variation, no significant model could be found. No significant relations were found in the data for 1988 and 1989, for which there were only 12 samples per plot.

Table 4.1.
Explained variance of the root density (cumulative root length over the entire rooting depth up to 80 cm) in two sites by various explanatory models based on the distance A) to the nearest tree or B) to the dominant tree, using the data from 1987. SPL [..] is a spline function with the number of degrees of freedom.

SITE:		KOOTWIJK		SPEULD EAST	
A) Distance (x) to the nearest tree:					
MODEL:	SIGNIFICANCE:	$R^2_{adj.}$	P	$R^2_{adj.}$	P
ax		0.15	0.011	0.0	0.917
a + bx + c/x		0.20	*0.008*	0.0	0.401
SPL[2] (x)		0.17	0.016	0.0	0.603
SPL[3] (x)		0.19	0.019	0.0	0.629
SPL[4] (x)		0.20	0.024	0.0	0.634
B) Distance to the 'dominant tree':					
MODEL:	SIGNIFICANCE:	$R^2_{adj.}$	P	$R^2_{adj.}$	P
ax		0.17	0.007	0.0	0.417
a + bx + c/x		0.24	*0.004*	0.0	0.656
SPL[2] (x)		0.21	0.007	0.02	0.246
SPL[3] (x)		0.23	0.008	0.04	0.185
SPL[4] (x)		0.23	0.013	0.05	0.164

Discussion

The results show a large variation in fine root density at all distances from the tree base in all data sets from the two sites with Douglas-fir. It is known that there is considerable small scale variability in soil conditions in a forest soil (Wilding 1985). This variation can sometimes be explained by the heterogeneity of the soil physical characteristics (Gerard et al. 1982; Strong & la Roi 1985) or of the soil chemistry (Beese 1986; Blanck et al. 1993). Fine roots react strongly to this (see e.g. Meyer 1967; Göttsche 1972; Ford & Deans 1977; Farrish 1991), resulting in growth at favourable places and dormant roots at less favourable places (Wilcox 1954; St. John et al. 1983). Hairiah et al. (1991) showed that fine roots avoid acid soil conditions, with elevated aluminium toxicity. Detailed studies are necessary to demonstrate this small scale heterogeneity for different situations.

On a somewhat larger scale, the tree positions can influence soil heterogeneity via the effects of throughfall water. Throughfall water is usually not distributed regularly. Bouten et al. (1992) found that in Douglas-fir in the ACIFORN stands, the rainwater is led to the outside of each tree crown, so there is little or no stem flow. They found this while assessing the horizontal variability of the water content in the soil. Rampazzo & Blum (1992) found that in beech, the large quantity of stem flow and the acidic deposition load concentrated in the throughfall water can greatly affect the soil chemistry. They found that the soil pH could be several units lower near trees than halfway between the trees, depending on soil type. This may greatly affect rooting patterns around the trees. In a mixed stand, Büttner & Leuschner (1994) found more fine roots of beech than of oak directly around oak stems, an indication of a heterogeneous distribution of fine roots.

The present results are based on only one tree species, for two sandy sites, and only one year with enough sampling points to enable a systematic pattern in the fine root density to be found. In one site, a significant relation could be determined for a specific rooting pattern. In the other, the small scale variation was too large to find a significant relation. The present analysis suggests that the fine root density in a Douglas-fir stand might be slightly lower close to the stem and at the remotest points from a tree stem. It might be possible to demonstrate this relation for this tree species without stemflow by collecting samples directly at the base of the tree. These results for Douglas-fir demonstrate that a systematic error of up to 10 % could be incurred if the fine root density are sampled 1 m from the tree only. Even though many authors have found that the fine root density is independent of tree positions (McMinn 1963; Moir & Bachelard 1969; Reynolds 1970, 1975; Kummerow et al. 1990), it is easy to avoid incurring systematic errors of this type by using a random sampling design in a forest plot.

The results show that large numbers of samples are needed to find a distinct pattern in the fine root density in relation to the tree positions. In 1988 and 1989 no pattern could be found when only 12 samples were collected to estimate the average fine root density. Gilman (1989) and Nielsen & Mackenthun (1991) related the fine root density to crown parameters or to stem density in a stand. Nielsen & Mackenthun (1991) fitted a logistic model of fine root distribution around trees of certain diameters. However, as they had no root samples within a 2 m radius from the tree and fairly low numbers of sampling points, their model could not be validated. Their model might be easier to prove in open forest, or around single trees in short vegetation (e.g. savannah), with relatively low numbers of samples.

Conclusions

1) The results show that there is considerable variation in the amount of fine roots in a fully stocked Douglas-fir plantation on sandy soils, at all depths within a small plot of one soil type. Because of this large variation, a large number of sampling points is needed to determine mean fine root density (> 10 or 20).
2) The location of these sampling points is also important, as the fine root density may depend on the distance to the nearest or dominant tree. A random selection of points in the research plot will give an unbiased estimation of the root density. A stratified random sampling design with sampling points stratified according to tree distance is more accurate. The number of points in each distance range should be related to the distances that are actually present in the forest stand. If trees are irregularly spaced, a systematic sampling design (e.g. a grid) meets these requirements in the simplest way. If trees are regularly spaced, e.g. in young plantations, grid sampling can lead to systematic errors.
3) If the rooting pattern itself is to be investigated, e.g. for different soil types or tree species, then even larger numbers of samples are needed, based on samples at different distances from trees, also depending on local forest structure.

Acknowledgements

This project was supported by the Dutch Priority Programme on Acidification. Roots were processed by G.M.J.H. Ackermans, A. Verdoes, and C. van der Haar. IBN-DLO and SC-DLO offered facilities during the preparation of this Chapter. G.M.J. Mohren, W.G. Keltjens, and R. Rabbinge made valuable comments on the manuscript and Ms. J. Burrough-Boenisch gave advice on the English.

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5. Influence of ammonium on fine root development and rhizosphere pH of Douglas-fir seedlings in sand

Abstract

Ammonium sulphate is a major component of the air pollutants deposited on forests in The Netherlands. Different amounts of NH_4^+ were added to Douglas-fir seedlings grown in tall containers of sand, to study the influence of high concentrations of NH_4^+ in the soil on the development of fine roots and the effects of nitrogen uptake on rhizosphere pH. At the end of this eight-month experiment part of the ammonium appeared to have nitrified into nitrate. High doses of ammonium negatively affected root length and root length per unit of dry matter (specific root length). Although Douglas-fir shows a preferential ammonium uptake in nutrient solutions the increases in the pH of the rhizosphere in this experiment indicate that nitrogen was mostly taken up as nitrate. When the ammonium concentration in the soil is low, it cannot be taken up readily because of its low mobility in soil. Shoot growth was stimulated by high availability of nitrogen. The possible effects of high doses of ammonium on long term forest vitality are discussed.

Keywords: ammonium, nitrogen, *Pseudotsuga menziesii*, rhizosphere pH, sand culture, shoot/root ratio, specific root length (SRL), toxicity.

Introduction

Ammonium originating from manure produced by intensive livestock farming is a major component of the total deposition of air pollutants in The Netherlands, where the annual deposition of NH_4^+ can exceed 100 kg nitrogen per hectare. When ammonium (NH_4^+) is converted into nitrate (NO_3^-) by nitrification, the soil acidifies (Van Breemen et al. 1982). The acidification of forest soils causes cations (K^+, Ca^{2+} and Mg^{2+}) to leach out and aluminium to go into solution (Mulder et al. 1987). Large amounts of aluminium ions (Al^{3+}) in the soil solution, particularly in combination with small concentrations of Ca^{2+} and Mg^{2+}, have been shown to be toxic to several forest tree species (Eldhuset et al. 1987).

Ammonium can have a fertilising effect on forest stands when nitrogen availability limits growth. However, excess nitrogen influx to forests on infertile sandy soils causes an imbalance in the nutrient supply to trees and may induce deficiencies of other nutrients such as P, K and Mg. Moreover, the NH_4^+ may accumulate in the rooting medium, reaching toxic levels and impairing root development and plant functioning (Keltjens & Van Ulden 1987).

Since plants require much more nitrogen than other nutrients, the form (NH_4^+ or NO_3^-) in which nitrogen is taken up by the roots largely determines the ionic uptake balance and rhizosphere pH. Uptake of N in the form of NH_4^+ results in a cation/anion uptake ratio > 1 and electrical neutrality will thus be maintained by a net efflux of protons from the roots. This will cause rhizosphere pH to fall. The uptake of NO_3^- mostly results in a cation/anion ratio < 1, with a corresponding increase in the rhizosphere pH (Gijsman 1990; Rygiewycz et al. 1984a, b). As the Al activity increases with decreasing pH, NH_4^+ uptake may result in more pronounced effects of Al toxicity.

In our experiment we added NH_4^+ directly to the soil and examined the effects on the root development and rhizosphere pH of Douglas-fir seedlings in a greenhouse. We assessed the chemical composition of the soil and shoot and root parameters of the Douglas-fir seedlings at the end of an eight-month growing period.

Material and methods

In May 1986, one-year-old nursery grown Douglas-fir seedlings (*Pseudotsuga menziesii* (Mirb.) Franco; provenance Arlington 202) were planted in 25-litre stainless steel containers. The containers were filled with inland dune sand (CEC around 2 mmol(+) kg^{-1} soil; organic matter 0.5 % ; pH H_2O 4.7), covered with 2 cm of fine gravel to reduce evaporation. A single plant was grown in each container and there were four containers per treatment. All seedlings were supplied with nutrients sufficient for a dry matter production of 10 g per plant, calculated according to Fiedler et al. (1985) and Larsen (1976), and including 1.5 mmol NH_4^+ per plant. The 4 treatments were as follows (the treatment code in brackets refers to the corresponding nitrogen deposition, in kg N per hectare): (N0) no NH_4^+ added, (N17) 6 mmol NH_4^+/plant, (N140) 48 mmol NH_4^+/plant, (N340) 120 mmol NH_4^+/plant. The NH_4^+ was supplied as ammonium sulphate in five equal portions at weekly intervals during July and August. The moisture content in all containers was monitored with small tensiometers and kept at pF 1.6. When necessary, demineralised water was added to compensate for evapotranspiration. No water leaked from the containers, although measurements at the end of the experiment showed that the moisture contents were slightly larger at the bottom. From September onwards artificial lighting was used to maintain day length at 14 hours. Greenhouse temperature was kept at 20 °C.

All plants were harvested in January 1987. The dry weight of the woody parts of the shoots and of the needles were measured. The pots were then frozen for 14 h at -20 °C, and the resulting solid soil/root mass was tipped out and sawed into four layers 14, 10, 10 and 14 cm thick. Per layer, the soil was sampled for chemical analysis and estimation of the moisture content. The roots from each soil layer were collected directly after thawing for 2 h, to ensure that the uptake behaviour was still reflected in the rhizosphere pH. The roots were dried at room temperature for 30 minutes and then the rhizosphere soil was collected by shaking the roots over a tray. All roots were then washed over a sieve and their length and dry weight were recorded. The pH of the bulk soil was measured in a mixed soil sample from each layer. Rhizosphere soil pH and bulk soil pH were both measured using a 1:5 ratio of air-dry soil to water. Total root length was estimated by the line intersect method (Newman 1966; Tennant 1975). Plant dry weight was measured after drying at 70 °C for 16 hours. Moist soil samples were extracted with 1 M KCl to find the NO_3^-, NH_4^+, Al^{3+}, Ca^{2+} and Mg^{2+} contents. Chemical analyses were performed as described by Keltjens & Van Ulden (1987).

Results

SOIL CHEMISTRY

In the control and the lowest ammonium treatment (N0 and N17) almost no ammonium was present in the soil at the end of the experiment (Fig. 5.1a), but nitrate was present in considerable amounts (Fig. 5.1b). In the N140 and N340 treatments more NH_4^+ and NO_3^- had accumulated in the soil. In treatment N340 the NH_4^+ concentrations in the soil were much higher than in treatment N140, but the concentrations of NO_3^- were the same with both treatments. At all four levels of NH_4^+ application the more mobile NO_3^- was found mainly in the lower part of the containers, where it had moved with the net downward movement of water.

The pattern of the NH_4^+ and NO_3^- concentrations in the soil in the four treatments suggests that the soil has a maximum nitrification capacity. At low levels

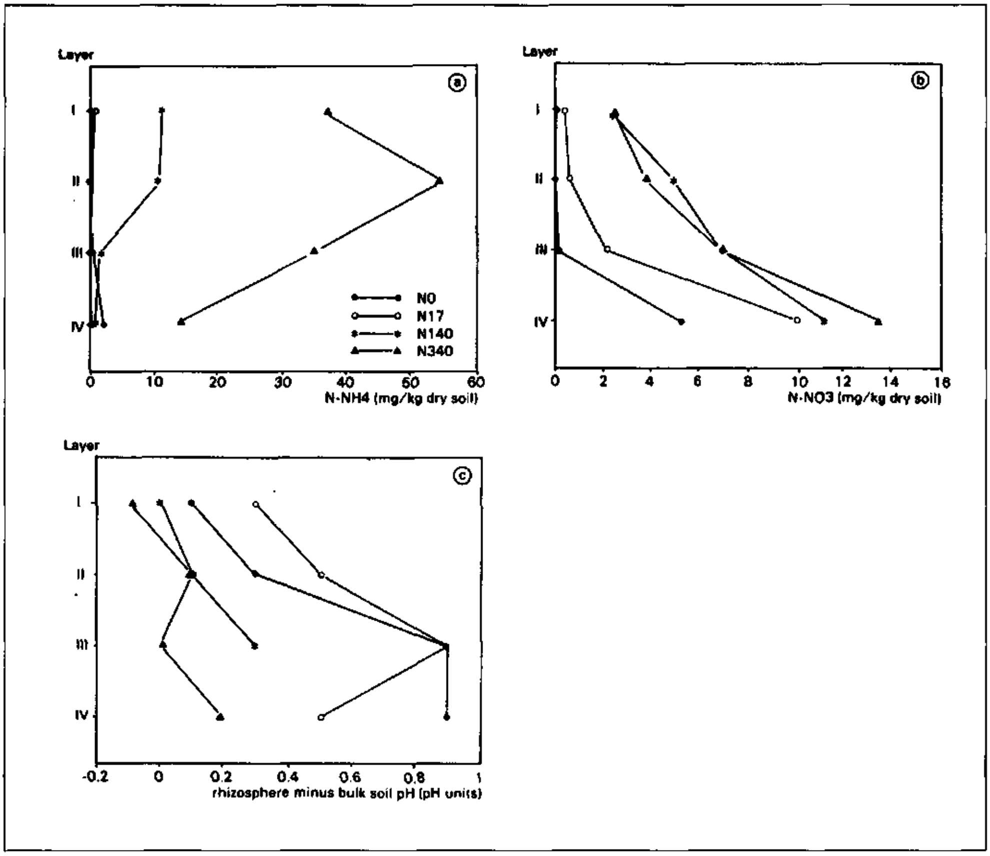

Figure 5.1.
Concentrations of ammonium (a) and nitrate (b) in four layers in containers (50 cm tall) of dune sand. Difference between rhizosphere pH and bulk soil pH in the same layers (c). Each point is an average of four containers. Measurements at the end of an eight-month growing period.

of NH_4^+ supply (N0 and N17) all NH_4^+ is nitrified or taken up, but the NO_3^- accumulates. Maximum nitrification capacity is attained at a level between N17 and N140. At higher NH_4^+ supply, nitrate concentrations in the soil remain constant, while NH_4^+ concentrations increase.

In almost all rhizosphere soil samples the pH was higher than that of the bulk soil, even at high levels of NH_4^+ supply (Fig. 5.1c; Table 5.1). In treatments N0 and N17, the pH increase in the root zone was large, especially near the bottom of the containers, where ample NO_3^- and little NH_4^+ were present. The rise in rhizosphere pH was smallest in the uppermost layer of treatments N140 and N340, where large quantities of NH_4^+ were present.

No significant differences between the four treatments developed in the pH of the bulk soil (Table 5.1), or between layers within the containers. At high NH_4^+ supply more Al_3^+ is adsorbed and adsorbed Ca^{2+} tends to decrease (Table 5.1); therefore the Al_3^+/Ca^{2+} ratio in the soil increases with increasing NH_4^+ supply. In the two highest NH_4^+ treatments this ratio reached such high levels that damage to the fine roots can be expected (Meiwes et al. 1986). The NH_4^+/Ca^{2+} ratio was especially high in treatment N340 (Table 5.1).

PLANT GROWTH

The total root length and root distribution in treatments N0, N17 and N140 was similar (Table 5.2; Fig. 5.2a). In treatment N340, the root length was depressed,

Table 5.1.

Chemical parameters of the soil, supplied with four different levels of ammonium sulphate. Data are averaged over four layers per pot, and determined at the end of the experiment. Treatment names refer to the equivalent nitrogen supply in kg N per hectare. (n = 4; standard deviations in brackets)

TREATMENT	N0	N17	N140	N340
NH_4^+ added: (mmol/container)	1.5	7.5	49.5	121.5
SOIL PARAMETERS				
Bulk pH-H_2O	4.1 (0.1)	4.0 (0.0)	3.9 (0.1)	4.0 (0.1)
Rhizosphere pH-H_2O	4.7 (0.4)	4.6 (0.3)	4.1 (0.2)	4.1 (0.1)
Rhiz. pH minus bulk pH	0.6 (0.4)	0.6 (0.3)	0.2 (0.2)	0.1 (0.2)
NO_3^- (mg N kg^{-1} dry soil)	1.6 (1.2)	3.6 (0.7)	6.4 (1.1)	6.9 (1.6)
NH_4^+ (mg N kg^{-1} dry soil)	0.7 (1.1)	0.2 (0. 4)	6.3 (1.3)	33.4 (4.3)
Al^{3+} (mg kg^{-1} dry soil)	25.0 (1.3)	27.9 (0.8)	33.4 (1.3)	33.1 (2.5)
Ca^{2+} (mg kg^{-1} dry soil)	14.9 (8.6)	12.5 (5.6)	11.1 (3.7)	11.1(10.6)
$Al^{3+}:Ca^{2+}$ ratio (mol mol^{-1})	2.4	3.3	5.0	5.0
$NH_4^+:Ca^{2+}$ ratio (mol mol^{-1})	0.13	0.05	1.62	8.61

especially in layers I and II, where levels of NH_4^+ were high (see also Fig. 5.1a). The specific root length (SRL; ratio of root length to root dry weight) decreased from 14.1 m/g dry matter in treatment N0 to 8.3 m/g dry matter in treatment N340, mainly because of the reduced root length, whereas root dry weight was decreased only slightly by high additions of NH_4^+ (N340). Figure 5.2b shows the SRL in the different layers of the treatments. The lower SRL in layer I of each treatment is a result of the higher number of structural roots in the fraction of fine roots (< 2 mm diameter). In layer IV, the lower SRL might be the result of slight soil compaction. The specific root length was smallest in the layers with the highest concentrations of NH_4^+.

Greater shoot dry weights at higher nitrogen levels (Table 5.2), point to the fertilising effect of NH_4^+ in the experiment. The stimulated shoot growth caused the shoot/root ratio in the highest treatment (N340) to be nearly double that of the control plants (N0).

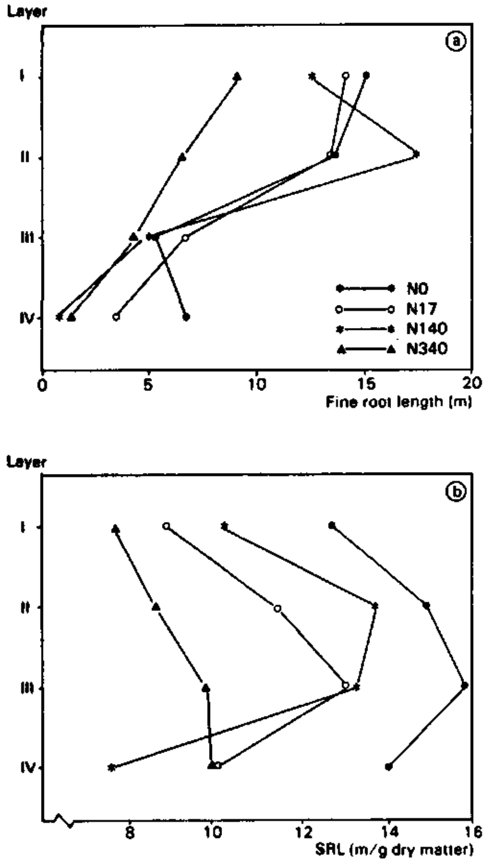

Figure 5.2.
Total root length (a) and specific root length (SRL) (b) of 1-year old Douglas-fir seedlings, in four layers in containers. Each point is an average of four containers. Measurements at the end of an eight-month growing period.

Table 5.2.
Root and shoot characteristics of Douglas-fir seedlings grown for eight months in sand with different additions of ammonium sulphate. For description of treatments see Table 5.1. (n = 4; standard deviations in brackets)

TREATMENT	N0	N17	N140	N340
PLANT PARAMETERS				
Total root length (m plant^{-1})	40.7 (13.7)	37.6 (16.1)	35.4 (7.3)	20.4 (2.8)
Root dry weight (g plant^{-1})	3.3 (0.8)	3.9 (1.1)	3.4 (0.8)	2.9 (0.8)
SRL*) (m g^{-1})	4.1 (2.4)	10.4 (2.1)	12.1 (2.6)	8.3 (1.0)
Shoot dry weight (g plant^{-1})	2.7 (0.8)	3.4 (0.7)	3.5 (1.5)	3.7 (1.2)
Shoot:root ratio	0.8 (0.1)	0.9 (0.2)	1.0 (0.2)	1.3 (0.1)

*) *Specific root length of roots < 2 mm diameter*

Discussion

NITRIFICATION AND SOIL CHEMISTRY

In treatments N0 and N17, almost all NH_4^+ was nitrified or taken up during the experimental period, resulting in NO_3^- being the main nitrogen source at the end of the experiment. The maximum nitrification rate was found in treatments N140 and N340. Here there was a mixture of NH_4^+ and NO_3^- in the soil at the end of the experiment. Figures 5.1a and 5.1b illustrate the differences in mobility between NH_4^+ and NO_3^- in the soil. Although all NH_4^+ was applied at the start of the experiment, at the end of the experiment most was still found in the two top layers. The net water movement in the soil was downward, although no water drained from the container. This was reflected by the high concentrations of NO_3^- in the deeper soil layers.

Initially the pH of the soil was 4.7, but by the end of the experiment it was around 4.0 in all treatments. During nitrification H^+ ions are produced and therefore the pH in all treatments should have fallen considerably. In treatments N140 and N340 more H^+ was produced than necessary for this drop in pH; this was found from a titration curve made for this soil. The surplus H^+ generated in treatments N140 and N340 was buffered by Al^{3+} going into solution. In these cases, the Al^{3+} concentration was indeed significantly higher than in the two lowest treatments (Table 5.1). Calcium concentrations in the soil declined as NH_4^+ supply increased. As a result the Al^{3+} /Ca^{2+} ratios in treatments N140 and N340 reached levels at which root damage may occur. According to Meiwes et al. (1986) a molar Al^{3+} /Ca^{2+} ratio of > 5 in a solution culture can damage fine roots of Norway spruce.

NITROGEN UPTAKE

In solution culture, Douglas-fir shows a preference for NH_4^+ rather than NO_3^-. The results obtained by Keltjens & Van Loenen (1989) show that in an equimolar NH_4NO_3 solution, 65 % of the nitrogen is taken up as NH_4^+ (at pH 3.8). In our experiment, the pH of the rhizosphere was mostly higher than that of the bulk soil. This indicates that uptake of NO_3^- was dominant. Nitrification and the differing mobility in soil resulted in different ratios between NO_3^- and NH_4^+ in each treatment, as well as between the soil layers in the containers. In treatments N0 and N17 the main nitrogen source was NO_3^-. This is why the pH in the rhizosphere was higher. Moreover, in treatments N140 and N340 the rhizosphere pH was often higher than the bulk soil pH, despite the presence of a mixture of NH_4^+ and NO_3^-. This implies that the supply of NH_4^+ to the roots was limited by the lower mobility of NH_4^+. Where NH_4^+ is present in large concentrations its transport to the root surface is not limited. NH_4^+ is then taken up in sufficient quantities to keep the rhizosphere pH close to the pH of the bulk soil (Fig. 5.1a and 5.1c). In all treatments the difference between rhizosphere pH and bulk soil pH was greater in the deeper layers of the container, where NH_4^+ was in short supply.

EFFECTS ON ROOT GROWTH

Root development was severely inhibited at the highest ammonium supply. In treatment N340 the Al^{3+} /Ca^{2+} ratio in the soil was the same as in treatment N140, but the NH_4^+/Ca^{2+} ratio was much higher. At high levels of ammonium (layers I, II and III in treatment N340) the specific root length was very low compared with the control (N0). Van den Driessche (1978) also found that when growing Douglas-fir seedlings at pH 4 in a sand culture, the SRL was higher with NO_3^- nutrition than with NH_4^+ nutrition. However, the reduced root development we found at the highest treatment cannot be attributed to NH_4^+ only, because the direct effects of NH_4^+ are confounded by the influence of NH_4^+ on the rhizosphere pH and the Al activity in the rhizosphere. These primary and secondary effects of NH_4^+ on root growth cannot be distinguished in our experiment.

Given the preferential uptake of NH_4^+ and its effect on the pH in the rhizosphere, some conclusions can be drawn about rhizosphere changes during root growth in a soil containing both NO_3^- and NH_4^+. When a root tip enters a volume of fresh soil it will take up the available NH_4^+. As a result, the rhizosphere pH will decrease, with negative effects on growth, as described above. This implies that root growth is reduced until the NH_4^+ in the rhizosphere is depleted, and rhizosphere pH increases because of uptake of NO_3^-. If this process continued, the net result would be a severely restricted root growth in soils having a low pH and much ammonium available. Recently, Gijsman (1990) found that the pH of the rhizosphere at the root tip of Douglas-fir is usually higher than that of the rhizosphere further back. If uptake behaviour is different at the root tip, this may favour root growth under these conditions. However, if NH_4^+ uptake starts in the zone of root elongation this may still imply that root tip growth is slowed down by high levels of ammonium in acid soils. Pursuing this argument, Gijsman (1990) concludes that the presence of nitrate is essential for the normal functioning of Douglas-fir roots in acid soils.

LONG-TERM EFFECTS OF AMMONIUM DEPOSITION ON FOREST VITALITY

High rates of ammonium deposition lead to acidification of forest soils (Van Breemen et al. 1982) and may result in nutrient imbalances of forest stands (Van den Burg & Kiewiet 1989). Excessive nitrogen nutrition may make trees more susceptible to disease (De Kam et al. 1989) and to frost (Aronsson 1980). Our experiment shows that high levels of ammonium deposition may have strong negative effects on root growth under field conditions: root densities will decrease and root uptake capacity will be reduced. At the same time, shoot growth may be stimulated by the increased nitrogen availability, especially on formerly nitrogen-deficient sites. The transpiration of the forest stand may increase, and on dry soils this will lead to larger water deficits.

Linder et al. (1987) reported the effects of drought on the survival of *Pinus radiata* after heavy fertilization in the Australian 'Biology of Forest Growth' project. Although they did not present data on root growth it is clear that the shift in shoot/root ratio caused by fertilization (see also Linder & Axelsson 1982) decreased the chances of survival. In their control treatment no trees died from drought, although there was severe needle loss. But in the fertilised stand 7 % of the trees died. Drought periods in The Netherlands might not be as severe as in Australia, but this example shows that the risks of tree mortality may increase under Dutch levels of atmospheric deposition of pollutants, especially of nitrogen compounds.

Acknowledgements

This project was supported by the Dutch Priority Programme on Acidification. The Research Institute for Forestry and Urban Ecology 'De Dorschkamp' offered facilities during the preparation of this chapter. G.M.J. Mohren deserves special mention for his valuable comments on the manuscript.

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6. Effects of soil acidification and nitrogen enrichment on fine root density of Douglas-fir on sandy soils: 1. Critical review of literature data

Abstract

This chapter presents a compilation and critical evaluation of the literature on the effects of acidic deposition on sandy soils on fine root density, and gives a conservative estimate of these effects. Soils have been affected by anthropogenic acidic deposition since the start of the industrial revolution. Results of seedling studies conducted under controlled conditions have been used to formulate the mechanism of the changes, but the results of field studies were essential to establish the quantitative effect of the changes on fine root density under field conditions. Three steps have to be considered when calculating the total effects on fine root density for Douglas-fir.

1) Cumulative acidic deposition during the last two centuries has caused site conditions to change. This has triggered a large increase in the total aluminium concentration in the soil solution, by a factor of 30 to 50 in the topsoil (up to 20 or 30 cm depth), and by a factor of more than one hundred in the subsoil (below 20 or 30 cm depth). The nitrogen deposition has caused very high foliar nitrogen contents, high levels of arginine, accompanied by deficiencies of other nutrients. Almost all forest stands in The Netherlands are nitrogen saturated. 2) Aluminium is the main toxic factor affecting fine root growth in acid sandy soil. At sub-lethal levels aluminium toxicity reduces fine root length, but does not affect the fine root biomass of Douglas-fir, an aluminium-tolerant tree species. The fine root length of this species has been reduced by 50 %, and in the subsoil by as much as 75 % through aluminium toxicity. 3) An increasing nitrogen availability elevates the shoot:root ratio of plants. The nitrogen saturated situation prevailing in The Netherlands has probably decreased the fine root biomass by up to 30 % of what it would have been under natural nitrogen-deficient conditions.

The interpretation of literature data reveals that the fine root system of Douglas-fir in The Netherlands is shallower, and less dense than it would be without the effects of acidic deposition. The total accumulated anthropogenic deposition has reduced the fine root density of Douglas-fir on acid sandy soils in The Netherlands by over 50 % in the topsoil, and even more (probably over 75 %) in the subsoil. The same effects might have taken place in forests on sandy soils elsewhere in NW-Europe, especially those with tree species that are more sensitive to Al toxicity than Douglas-fir.

Keywords: fine root biomass, fine root length, specific root length, nitrogen saturation, shoot:root ratio, long-term soil acidification, ammonium, aluminium toxicity, Douglas-fir, *Pseudotsuga menziesii*, Netherlands, background deposition

Introduction

Anthropogenic acidic deposition during the last two centuries has had consequences for the functioning of trees in forest ecosystems. It affects both the aboveground and the belowground biomass of the trees. Ulrich (1983a), Tamm (1991), Marschner (1991) and Matzner & Murach (1995) have speculated that soil acidification has caused the fine root density of trees in forest ecosystems to decrease, and the fine root system to become shallower. This 'Ulrich hypothesis' cannot be verified because of lack of long time series of data on fine root density in forest soils. In the 1960s in the Solling project near Göttingen in Germany, root research focusing on site differences was done (e.g. Meyer 1967; Röhrig 1966), to be followed in the 1980s by Ulrich's group focusing on effects of acidification (e.g. Murach & Wiedemann 1988). Even when roots were studied in the same stands, any effect of soil acidification would have been hard to discern, because of the short time interval between the studies, differences in root research methods, and natural processes due to ageing of the stand (Göttsche 1972; Murach 1984; Ulrich 1995).

Uptake of water and nutrients by trees is mostly restricted to the fine roots (diameter < 2 mm), which form the main contact between the soil and the tree (e.g. Eis 1987). At present, the fine root density of Douglas-fir in The Netherlands is low (Olsthoorn 1991), compared to that of agricultural crops (De Willigen & Van Noordwijk 1987). Therefore, it seems likely that small changes in the fine root density may have a large effect on uptake of water and nutrients (De Willigen & Van Noordwijk 1987). The deposition of acidifying substances in The Netherlands is somewhat different from other areas in Europe, as more ammonium sulphate is deposited from intensive livestock farming, whereas the direct effects of SO_2 and acid mist are smaller than in the central European hills (Heij & Schneider 1991). Our study was limited to the effects of anthropogenic deposition on poor acid sandy soils. Most Dutch forests are situated on such soils. On alkaline soils, acid deposition and natural acidifying processes lead to totally different rooting conditions, as the pH buffering range is of a different order (Ulrich 1983a; De Vries & Breeuwsma 1986), and the consequences for root growth under such conditions may be negligible.

In the present study, data in the literature were analysed to determine the influence of long-term soil acidification and nitrogen enrichment on fine root density in Douglas-fir plantations on acid sandy soils in The Netherlands. The central questions were:

1) How have site conditions in sandy soils changed through cumulative soil acidification in the last two centuries, in terms of aluminium chemistry and nitrogen availability?
2) How has the aluminium chemistry affected the fine root density in different soil horizons and what have been the effects on vertical fine root distribution in the soil?
3) How has the nitrogen accumulation affected the fine root biomass in relation to biomass of foliage and secondary tissue?

The answers to these questions were used to derive conclusions about the order of magnitude of the total changes in fine root density of Douglas-fir in The Netherlands brought about by anthropogenic acidic deposition. In other words: to quantify the Ulrich hypothesis for Douglas-fir on sandy soils in The Netherlands. The implications for water uptake and biomass dynamics in periods of drought will be evaluated in a subsequent chapter (Olsthoorn et al. 1998).

Basic assumptions

This study compiles and analyses data from literature. Most data were found by standard literature searching procedures, using keywords and author names, and by following up references mentioned in recent papers. In addition, the recent volumes of some international journals on (tree) physiology, forestry and soil science were screened completely.

The results of laboratory studies were used to generate hypotheses on the type of effects of soil acidification and nitrogen enrichment on fine root development. The results of field studies were used to quantify the changes in the fine root density in forests on sandy soils. The literature had to be screened carefully, as some references seemed to lead to conflicting conclusions. Sometimes, this was due to differences in plant species, fertiliser combinations, treatment levels, method, sampling period or goal. In order to be able to apply the results for forests on acid sandy soils, particularly focusing on the Dutch situation, it was necessary to make the following assumptions.

- The biomass of coarse roots is of minor importance for the uptake of water and minerals. For Douglas-fir, Eis (1987) found that coarse roots comprise only 5 % of the total root length, probably with poor uptake abilities (Kramer & Bullock 1966).
- The belowground biomass primarily reacts to changing conditions in terms of the effects on the fine root fraction. The coarse roots usually behave the same way as the aboveground secondary tissue (branches and stem) in the functional balance of the tree, as they have the same function: support and transport of water and solutes (Santantonio et al. 1977; Santantonio 1989; Van Dijk et al. 1990; Kuiper & Coutts 1992; Fabião et al. 1995).
- The fine root density is comparable with a full grown stand when the LAI of young trees has reached a final value, e.g. when a plantation is closed (see e.g. Fahey & Hughes 1994; Dye 1996). Therefore, data on fine root density from young stands over age ten are considered to be comparable with mature stands.
- The aluminium concentration of the soil solution is the main toxic factor impairing root growth at pH-$H_2O < 4.2$ (Ulrich 1983b), which is the pH range of the Dutch acid forest soils. Dissolved Al in Dutch forest soils consists mainly of monomeric forms. Noble et al. (1988) showed that Al^{3+} in particular, but also soluble monomeric Al hydroxides limit root length (see also Pan et al. 1988; Wagatsuma et al. 1987; Dahlgren et al. 1991; Kinraide 1991). In this chapter, the Al effect on fine roots is described in relation to the total Al concentration in the soil solution, and it will be indicated when other nutrients are added in experiments.
- At sub-lethal levels, aluminium has no direct effect on the aboveground growth, i.e. does not affect the shoot:root ratio of the biomass (Keltjens & Van Loenen

1989). At such levels, aluminium particularly affects fine root functioning, which results in disturbed nutrient uptake, changing nutrient concentrations in all plant parts and a different fine root morphology (e.g. Ren & Sucoff 1990; McQuattie & Schier 1990; Vogelei & Rothe 1988; and most references in Table 6.4).

The effect of heavy metals (Hg, Cu, Pb, Cd, V, Tl) was not assessed in this study, although they may affect root functioning more strongly than Al. Heavy metal concentrations in forest soils are usually far below toxic levels (Godbold 1994).

Critical appraisal of the literature

1) CHANGES IN SITE CONDITIONS

a) Soil acidification and aluminium chemistry

Since the start of the industrial revolution at the beginning of the nineteenth century, the SO_2 concentrations in the air have increased, leading to deposition of wet and dry acidifying substances (Galloway et al. 1982, 1984). From a study of glacier corings in Switzerland, Döscher et al. (1995) showed that in 1980 the deposition of S was 6 times greater and the deposition of nitrogen 2.3 times greater than in 1850. From the old fertiliser trial in Rothamstead, Johnston et al. (1986) calculated that the total annual SO_2 deposition in unfertilised woodlands in the period 1850 to 1890 was less than in the year 1985. Johnson et al. (1994) showed that acidic deposition and natural leaching had caused the pH in the top mineral layers in soils of the Adirondack Mountains, New York, to decrease by 0.3 to 0.5 units during the previous 50 years, and the Ca-saturation to decrease. This suggests that Al buffering started to play a role in the eastern USA 50 years ago. The implementation of environmental legislation has recently caused SO_2 emissions to fall in western Europe. Downing et al. (1995) have stated that the SO_2 deposition started to decline in England in 1973 in the same way as Ulrich (1989) described for the SO_2 emission in Germany during the 1980s.

Ulrich & Meyer (1987) cited a large number of old references on soil acidification through industrial activity during the first half of this century in eastern Germany (Ore mountains; see also Ulrich et al. 1984). They concluded that as long ago as 1930, the pH of various soil types had fallen below the basic cation buffering range. In some areas of Germany (e.g. Black Forest) the deposition rates during that period did not seem to be as high, though acid soils occurred at higher altitudes. Ulrich (1995) estimated that the base saturation at a depth of 30 - 60 cm in German forest soils was always over 30 % before 1800, while at present this is less than 15 % in 67 % of the German forest sites. Using comparable methodology to old studies (saturation extracts) Ulrich et al. (1980) showed that the Al concentration in the soil was still increasing between 1966 and 1979 in the Solling area. Ellenberg et al. (1986) found Al leaching from the soil profile, as a sign of decreasing buffering capacity.

Hallbäcken & Tamm (1986) described a general decrease of the pH by between 0.3 and 0.9 units at depths of up to 70 cm in Swedish forest soils in the last 50 years. In the topsoil (up to the A_2-horizon) the pH was over 4.4 in 1927. The pH decreases were smaller in the north of Sweden, where there was less deposition (Tamm &

Hallbäcken 1988). Billet et al. (1988) also found little evidence of anthropogenic acidification in the north of Scotland since 1949. Tyler et al. (1987) showed that pH changes in the acid topsoil of Swedish podzols (pH-KCl around 3.2) were smaller than in the subsoil (respectively 0.2 and 0.7 pH unit). In brown forest soils with a pH-KCl of around 5, the pH changes were about the same at all depths (0.7 pH unit). Tyler et al. (1987) found a good relationship between pH and Al concentration in the soil solution, associated with a sharp decrease in the base saturation with decreasing pH (see also Rendig & Taylor 1989; Farrell et al. 1994). For Swedish soils, Falkengren-Grerup et al. (1987) found that between 1949 and 1985 the loss of basic cations was large from all soil horizons. Most of the 10 sites studied had entered the Al buffering range in the topsoil. Falkengren-Grerup & Ericsson (1990) found that 70 % of the basic cations disappeared from the top of the C-horizon between 1947 and 1988 and that exchangeable Al had doubled.

As long ago as 1954, Van Goor (1954) found the largest concentrations of extractable Al around 20 cm depth in sandy soils in The Netherlands (Morgan-Venema extraction; see also Van der Salm 1985). Since the 1960s, ammonium originating from manure produced by intensive livestock farming, has become one of the main components in the deposition of air pollutants in The Netherlands (Heij & Schneider 1991). When the ammonium is nitrified (De Boer et al. 1989), protons are produced, leading to soil acidification (Van Breemen et al. 1982), while the soil solution contains relatively high concentrations of both ammonium and nitrate. Rapp (1991) found more Al in the soil solution in NH_4^+ treated forest plots, compared to the control. The uptake of NH_4^+ by roots results in a release of protons in the rhizosphere (Gijsman 1990), and depressed uptake of other cations (Boxman et al. 1986) elevating nutrient imbalances. At present, acid forest soils in The Netherlands usually have a pH-H_2O below 4.2. Therefore, they are in the buffering range of aluminium (Ulrich 1983b). The proton release during nitrification and nutrient uptake affects the buffering capacity of the soil, and reduces the acid-neutralising capacity (ANC; see Van Breemen 1987). Even if the pH does not decrease, the concentration of soluble aluminium may rise and mineral cations may leach from the rooting zone (Mulder et al. 1987). They also found that in Dutch acid forest soils the Al concentration in the soil solution increases with depth. Mulder et al. (1989a) even predicted a possible depletion of organic solid-phase Al within several decades (see also Wesselink 1994). This would cause a further decrease of soil pH and result in extremely poor growing conditions.

The lack of time series of soil chemical monitoring longer than two decades (Wesselink 1994) makes it complicated to validate the models describing soil responses to different acid deposition scenarios (De Vries et al. 1989; De Vries 1994; Wesselink 1994). However, several soil acidification models have been developed in the acidification research in The Netherlands, and have been calibrated thoroughly for the present conditions (see e.g. Van Breemen & Verstraten 1991; De Vries 1994). Some of these models have been used to calculate the soil chemical conditions for a natural or background deposition scenario (Table 6.1A), with deposition levels of SO_x, NO_x and NH_x a factor 10 to 20 lower (Galloway et al. 1982 and 1984). With the weathering and buffering processes that take place in the different soil horizons, the models reach a steady state after a number of years. This calculated steady state can be considered as a good estimate for soil chemical conditions before the start of the industrial revolution, around the year 1800. Calculations with the RESAM model are described in Table 6.1 (J. Kros, pers. comm.). The calculations for the present deposition rates are in accordance with field data on the soil solution (Van Breemen & Verstraten 1991). With the background deposition scenario, a soil profile comparable to the sites used in this study (Olsthoorn 1991) would be in the cation buffering range at all depths. This results in total Al concentrations in the soil solution of the top 20 cm of the soil profile that are lower than with present deposition levels by a factor 30 to 50 (Table 6.1B). Below 20 cm depth, the factor of increase is over 100. The results of this model calculation agree with the other references cited above for shorter periods, and with the simulation results of Sverdrup & Warfvinge (1995) for a period between 1850 and 2000.

However, Al in the soil solution can be detoxified by complexing with dissolved organic carbon (DOC; Driscoll et al. 1985; Nätscher & Schwertmann 1993; Cronan 1994; Wesselink 1994).

Mulder et al. (1989b; see also Van Breemen et al. 1988; Van Dobben et al. 1992) found that between 25 and 100 % of the soluble Al in the organic and E horizons in sandy soil, was organically chelated, as Adams & Moore (1983) had predicted. Deeper in the soil (B horizon and below) the percentage of complexation is very small, around 1 % of the Al in the soil solution (Table 6.2). This results in free Al concentrations (active, non-chelated) of over 1.5 $mol_c\ m^{-3}$ in the soil solution of the subsoil and below 1 $mol_c\ m^{-3}$ in the topsoil (up to 20 cm depth).

b) Nitrogen availability

Nitrogen is a growth limiting factor in most temperate forest ecosystems (Tamm 1991). Bobbink & Roelofs (1995) estimated that the critical nitrogen deposition for nutrient imbalances for forest on poor soils is 10 to 15 kg N $ha^{-1}\ yr^{-1}$ compared with 20 to 50 kg N $ha^{-1}\ yr^{-1}$ for forests on better soils. Pardo & Driscoll (1996) found a critical deposition of 7 kg N $ha^{-1}\ yr^{-1}$ for acidification and 20 kg N $ha^{-1}\ yr^{-1}$ for eutrophication effects on a shallow soil in the USA.

Nitrogen used to be deficient in forest on sandy soils in The Netherlands, but this has changed because of the increase in anthropogenic deposition from intensive livestock farming, industry and vehicular transport. Using deposition models, Erisman & Heij (1991) determined that the average deposition rate of nitrogen was 48 kg N per hectare per year in The Netherlands, the highest in Europe. It was slightly higher in forests due to the roughness of the canopy: 53 kg, with regionally average deposition rates of over 80 kg nitrogen per hectare per year (three quarters from dry deposition). Van Breemen & Verstraten (1991) recorded similar values in throughfall water in forest stands in different regions in The Netherlands, which resulted in high levels of nitrogen in the soil solution of sandy soils. Most forest plots used for acidification studies in The Netherlands have been in areas with high nitrogen deposition (Mohren 1991).

Rehfuess et al. (1991) found P and Mg deficiencies 20 years after repeated nitrogen fertilisation on podzolic soils. Mohren et al. (1986) found that all the Douglas-fir stands analysed in 1984 were very high in nitrogen and low in phosphorus, resulting in very high (over 30) nitrogen:phosphorus ratios. In 1960 however, the same stands still had low nitrogen contents, and showed a positive stem growth response to both nitrogen and phosphorus fertilisation, applied

Table 6.1.
Results of the RESAM model (REgional Soil Acidification Model, J. Kros, pers. comm., DLO-Winand Staring Centre, Wageningen) for a cambic podzol (comparable to the Speuld site, used for root research, see Olsthoorn 1991). See De Vries et *al.* 1995 for a description of the model. A comparison is made between normal deposition levels for Douglas-fir forest in The Netherlands in 1990 (Heij & Schneider 1991) and the natural, background deposition level (Galloway et al. 1984). Data for 1990 are in agreement with field measurements (Van Breemen & Verstraten 1991).

A) Deposition levels (in $mol_c\ ha^{-1}\ yr^{-1}$*)*

DEPOSITION COMPOUND	1990 LEVEL	BACKGROUND LEVEL	RATIO OF INCREASE
SO_x	1790	200	8.9
NO_x	1425	100	14.3
NH_x	3200	200	16.0

B) Calculated total aluminium concentration ($mol_c\ m^{-3}$*) in the soil solution at different soil depths*

DEPOSITION	1990 LEVEL	BACKGROUND LEVEL	RATIO OF INCREASE
SOIL DEPTH			
0-10 cm	1.0	0.03	33
10-20	1.9	0.04	48
20-30	2.4	0.02	120
30-40	3.4	0.02	170
40-60	4.1	0.04	103

C) Calculated pH of the soil solution (pH-H_2O*)*

DEPOSITION	1990 LEVEL	BACKGROUND LEVEL
SOIL DEPTH		
0-10 cm	3.50	4.30
10-20	3.60	4.30
20-30	3.65	4.47
30-40	3.70	4.47
40-60	3.62	4.25

separately or combined (Blok et al. 1975). At present, the nitrogen concentrations in older needles are even higher than in first year needles (Evers et al. 1992). In a comprehensive summary, Van den Burg (1990) described the changes in forest nutrition brought about by the deposition of air pollutants in The Netherlands. He showed that the nitrogen concentration in six-month-old needles of Douglas-fir had risen from deficient in the 1960s (below 14 g N kg^{-1} DM) to supra-optimal levels (over 25 g N kg^{-1} DM) in the 1980s. Van Tol et al. (1993) showed supra-optimal nitrogen concentrations in foliage of 7 tree species in almost all of the 2000 stands that were assessed in The Netherlands. Usually this was accompanied by deficiencies of other nutrients, especially P and Mg (see also Van den Burg 1991a).

The research cited above confirms that the trees have attained very high nitrogen contents, leading to high concentrations of nitrogen-storing amino acids like arginine (Van Dijk & Roelofs 1988; Gao & Cahoon 1990; Pérez-Soba & De Visser 1994), and leading to the leaching of nitrogen to the subsoil (Van Breemen et al.

Table 6.2.
Calculation of free Al (active, non-chelated monomeric Al) in the soil solution for two sites on sandy soils in The Netherlands, based on maximum binding capacity of dissolved organic carbon (DOC; data from Mulder et al. 1989b: averages of 100 samples between 1982 and 1987 for each sampling point; soil samples were collected below each soil horizon; Gerritsfles is a drift sand without a developed soil profile).

SITE[a]	DEPTH[a] (cm)	pH[a] (H_2O)	DOC[a] ←	Al (CHELATION[b]) CAPACITY ($\text{mol}_c\ \text{m}^{-3}$)	TOTAL[a] Al PRESENT	FREE[b] Al →
Gerritsfles						
	0	4.17	6.5	0.07	0.04	0
	10	3.98	7.8	0.08	0.8	0.72
	40	4.00	2.5	0.02	2.1	2.1
	100	4.17	1.1	0.01	1.7	1.7
Tongbersven						
	0	4.1	5.0	0.06	0.03	0
	12	3.4	6.8	0.07	0.1	0.03
	35	4.0	1.8	0.02	1.5	1.5
	57	4.1	1.9	0.02	2.1	2.1
	100	4.1	2.8	0.03	1.8	1.8

a) Data from Mulder et al. 1989b
b) Calculated according to Mulder et al. (1989a), with 11 mmol Al for each mol DOC, at pH 4.0

1987; Ågren & Bosatta 1988; Kölling 1991; Feger 1992; Tietema et al. 1995). This is the case in many Douglas-fir stands in The Netherlands (Van Breemen & Verstraten 1991; Van Dijk & Roelofs 1988).

2) ALUMINIUM AND FINE ROOT LENGTH

A great number of authors have described toxic conditions for root growth of forest trees (e.g. Rost-Siebert 1983; Hüttermann 1985; Schaedle et al. 1989; Schier & McQuattie 1995). Göransson & Eldhuset (1991) also described lethal aluminium concentrations in solution cultures for different tree species. In the field, soluble monomeric aluminium concentrations are usually below lethal levels, even in very acid soils (e.g. Joslin & Wolfe 1989; Göransson & Eldhuset 1987). Therefore in the present study, disturbances of fine root growth at sub-lethal Al levels are more interesting (see also Tischner et al. 1983). Al can have effects on plant functioning even at low concentrations, $0.2\ \text{mol}_c\ \text{m}^{-3}$, especially when the availability of P is limited (Clegg & Gobran 1995). Foy (1984) stated that short stubby fine roots are a typical symptom of Al toxicity. McQuattie & Schier (1990) noted that increasing the Al in the solution caused the number of cell layers in the root tip of red spruce seedlings to increase, accompanied by distinct anatomical changes in the cells, especially if no ectomycorrhizal fungi were present (see also Schier & McQuattie 1995). There is substantial evidence that there are interactions with nutrients like Ca and Mg (Ebben 1991; Tan et al. 1992; Hecht-Buchholz & Schuster 1987; Schlegel et al. 1992; Boudot et al. 1995). Generally, a better availability of these nutrient cations can alleviate the toxic effects of Al on root functioning (Henriksen et al. 1992; Göransson & Eldhuset 1995; Cronan & Grigal 1995).

Root length is especially likely to be reduced by Al toxicity, even when fine root dry weight is only slightly affected (Keltjens & Van Loenen 1989; Olsthoorn et al. 1991; Gorissen et al. 1993). Assuming a constant biomass of fine roots, a reduction of root length results in a decrease in the fine root density. It is for this reason that the Specific Root Length (SRL: fine root length per gram dry matter) is an important indicator of possible physical and chemical limitations in the soil to the root uptake capacity (Heath 1990; Korotaev 1992; Keltjens & Van Loenen 1989; Olsthoorn et al. 1991; Godbold et al. 1988; Schaedle et al. 1989). In this thesis, the SRL is defined as the number of metres per gram of root dry matter in the fine root fraction (root diameter < 2 mm). The SRL declines concomitantly with the decrease in cell elongation in the root tip at low pH, if cell division is still possible (Marschner 1991; Smith & Krikorian 1992; Parker 1995) or at high mechanical impedance (Taylor & Rattliff 1969) e.g. deeper in the soil where the bulk density is higher (Taylor 1974; Heilman 1981). The SRL can be included as a simple morphological indicator in simulation models that describe fine root density and uptake processes (e.g. Mohren 1991).

If the soil chemical changes differ per horizon, the vertical distribution of fine roots in the soil can be affected, leading to changes in the ability to take up water and nutrients from different parts of the soil profile. Aluminium may also influence the hydraulic conductivity of the fine roots (Kruger & Sucoff 1989b; Chen et al. 1991; Ren & Sucoff 1990).

Plant species vary in their susceptibility to aluminium toxicity (McCormick & Steiner 1978; Raynal et al. 1990; Ebben 1991; Huang & Bachelard 1993). Ebben (1991) has ranked tree species, following Rost-Siebert (1985), according to a Ca:Al threshold for damage to the fine roots (see also Sverdrup & Warfvinge 1993). Rode (1988) and Rode & Runge (1991) stated that the severe susceptibility of calcicoles (plant species of calcareous soils) to Al is related to the decrease in the rhizosphere pH at the root tip, when NH_4^+ is present in the soil solution (see also Adams 1966); because then the calcium requirement of the plasmalemma cannot be met. Calcifuges (plant species of acid soils) are able to raise the rhizosphere pH at the root tip, to prevent damage by Al. Gijsman (1990) found that Douglas-fir is able to do so, even when NH_4^+ is the only nitrogen source. Keltjens & Van Loenen (1989) found that oak and birch were more sensitive to Al than Douglas-fir, suggesting that this was probably related to their greater preference for NH_4^+ rather than NO_3^-. Therefore, Douglas-fir can be listed among the more acid-tolerant species, like Scots pine (Keltjens & Van Loenen 1989), Sitka spruce and western hemlock (Ebben 1991; Ryan et al. 1986; Van den Burg 1981). However, Douglas-fir is not as Al tolerant as white brittle gum (*Eucalyptus mannifera*) which is well adapted to the old lateritic acid soils of Australia (Huang & Bachelard 1993). Table 6.3 summarises a review by Schaedle et al. (1989) presenting the concentration ranges of Al in the soil solution for groups of tree species of different susceptibility, based on the effects of Al on the plant nutritional status and biomass production. In intermediate and tolerant trees, nutrient effects become visible at lower Al concentrations than biomass effects. Göransson & Eldhuset (1987) found lethal effects of Al at a concentration of 15 $mol_c\ m^{-3}$

(under optimal nutrition conditions), but effects on the Ca and Mg contents of the seedlings at much lower Al concentrations (1 mol_c m^{-3}). Göransson & Eldhuset (1991) found nutrition effects for Norway spruce at 0.3 mol_c m^{-3} and for Scots pine at 1 mol_c m^{-3}. Tischner et al. (1983) and Schier & McQuattie (1996) found effects on shoot:root ratio below Al concentrations of 1 mol_c m^{-3}, especially in non-mycorrhizal seedlings. The lower Al concentration inducing changes in nutrient status, is probably also the level at which changes in root morphology start. Adverse effects on biomass growth and changes in shoot:root ratio start at higher Al concentrations, particularly in the tolerant species.

The results from a number of trials, seedlings and mature stands, on the effect of aluminium on fine root length and SRL are summarised in Table 6.4. The data are presented according to the trial conditions: A) solution culture; B) sand culture; C) soil mixtures or soil monolith trials in the laboratory, or D) field manipulations with mature trees. Laboratory studies are difficult to translate to field conditions (Kreutzer 1994; Clegg & Gobran 1995), therefore the field studies are extremely valuable. Some references with seedling studies are not mentioned in Table 6.4, as the highest Al concentration described was unrealistically high, up to 84 mol_c m^{-3} (e.g. McCormick & Steiner 1978). In those cases, the Al that was added to the nutrient solutions cannot totally have been present in soluble form, especially when the pH was over 4.2 (Sainju & Good 1993). In Table 6.4, the changes in fine root morphology (e.g. SRL, fine root length, root tip elongation, or fine root diameter) are presented in combination with the corresponding Al concentration (and pH, as a description of the trial conditions). The total Al concentration is given in mol_c m^{-3} in the (soil) solution, to standardise the relations. The reduction in fine root length was calculated as the percentage of reduction between the control and the highest Al treatment. A reduction of e.g. 90 % means that only 10 % of the root length in the control is present in the highest Al treatment (or at the lowest pH if the Al concentration is unknown).

Table 6.3.

Response of tree seedlings to aluminium as expressed by changes in nutrient status (A) or growth impairment (B), grouped according to their sensitivity. Data summarised from a review by Schaedle et al. (1989).

	TOXIC SOLUBLE ALUMINIUM CONCENTRATION (mol_c m^{-3})	
	NUTRIENT EFFECT (A)	GROWTH EFFECT (B)
Sensitivity		
Sensitive species[a)]	0.04 - 0.10	0.04 - 0.10
Intermediate species[b)]	0.18 - 0.50	0.18 - 1.00
Tolerant species[c)]	0.50 - 1.10	1.10 - 3.50 (- 7.00[d)])

a) *Populus sp.*, Norway spruce, honey locust, white spruce, peach
b) sugar maple, red spruce (may be sensitive), black spruce, Eur. beech, loblolly pine
c) Douglas-fir, western hemlock, western red cedar, Sitka spruce, Am. Beech, red oak, balsam fir
d) fewer data: birch (several species), pin oak, white ash, black cherry, pine (several species)

In many cases the references of Table 6.4 did not give a threshold value for the Al concentration above which marked changes occur in the fine root morphology features. Therefore, we derived the threshold value from data in tabular or graphic form, if sufficient levels of Al had been tested. Usually, only the order of magnitude of this Al threshold value can be given. The threshold values are only valid under the experimental conditions, but give a general indication of the sensitivity of the tree species. The lethal Al concentrations as presented are very high, especially for tolerant tree species, and much higher than Al concentrations found in acid forest soils in practice.

In the solution cultures (Table 6.4A), the root length reduction ranges between 0 and 90 % relative to the control. The reduction is usually small when all treatments are below the threshold value for morphological changes, e.g. if the highest Al concentrations are very low. In the latter case we can even see a stimulating effect caused by Al (reference 6 in Table 6.4: Ren & Sucoff 1990). Bengtsson et al. (1994) also described positive effects of low Al concentrations, around 0.1 $mol_c\ m^{-3}$. The solution culture experiments usually entailed adding a complete set of nutrients. This makes the comparison with the Dutch sandy forest soils more difficult, as these soils usually are nutrient-poor. However, when Al concentrations (Table 6.1B) in the solution cultures are in the range between 1.0 and 2.5 $mol_c\ m^{-3}$, the root length is often reduced by between 24 and 90 % of the control.

In the sand cultures (Table 6.4B), the reduction in root length varies between 50 and 78 % of the control, in situations that are comparable to Dutch forest conditions, with low levels of Ca and Mg. In the soil mixture experiments with seedlings (Table 6.4C), the range of the reduction in root length varies between 10 and 83 %, and often shows values around 50 %. The influence of NH_4^+ in the experiments with Al is noteworthy. In some experiments, the data range for pH or Al concentrations was smaller when NH_4^+ was the N source, as plants died under the more extreme situations. This means that no data could be shown, or there is a reduction of 100 %, e.g. Smit et al. 1987b; Rode & Runge 1991; De Visser & Keltjens 1993). In experiments with soils, this phenomenon must have been the result of the extremely acid conditions in the rhizosphere (see also Olsthoorn et al. 1991). This effect of ammonium nutrition might prevent the establishment of natural regeneration in forests to a large extent, as the formation of a taproot could be greatly hindered, as Smit et al. (1987a) and Hüttermann (1985) described.

The difficulty in the field experiments (Table 6.4D) is that the controls often had a relatively high Al concentration that may already have exceeded the Al threshold value for morphological changes. The range of conditions was usually small, with the Al concentration mostly high, and data on the actual Al concentrations in the soil solution were too scarce to be able to derive conclusions about the threshold Al concentration for morphological changes.

Table 6.4.

Effects of the aluminium concentration in the rooting medium on fine root length of different tree species, often observed in seedlings grown under different conditions. Diameter of fine roots in most studies < 2 mm, sometimes < 1 mm. If soil chemical data from the rhizosphere were available, these are shown. In experiments in sand or soil, there are usually soil chemical changes during the trial. The conditions at the end of the experiment are specified. The duration of seedling studies varies from several days to several years. The control treatments in this table consist of very low Al concentrations (see Table 6.1) or a pH of the (soil) solution of at least 4.25. If possible, a threshold value is given for Al effects on large changes in the SRL or fine root length. If the study examined the sensitivity of several species, an Al sensitive and an Al tolerant species have usually been chosen. Uncertain effects are given between brackets. Unknown parameters are indicated by '?'.

EXPERIMENTAL CONDITIONS							RESULTS	
TREE SPECIES	CONTROL TREATMENT			HIGHEST ALUMINIUM TREATMENT			LENGTH CHANGE (%)	THRESHOLD[b] AL CONC. ($mol_c\ m^{-3}$)
	pH	ALUMINIUM ($mol_c\ m^{-3}$)	FINE ROOT Length[a]	pH	ALUMINIUM ($mol_c\ m^{-3}$)	FINE ROOT Length[a]		
	a) Solution cultures:							
5 herb species (calcifuges)[1]	3.8	0	100[1]	3.8	1.0	100[1]	0	(>1)
5 herb species (calcicoles)[1]	,,	,,	,,	,,	,,	75-100	0 / - 25	(~0.1)
honey locust[2]	5.0	0	175	4.0	1.5	25	-85	>0.6
loblolly pine[3]	4.0	0.01	var.[c]	4.0	(4.4)	var.[c]	-29 / - 65	-
slash pine[3]	,,	,,	,,	,,	,,	,,	-33 / - 50	-
northern red oak[5]	3.8	0	30	3.8	2.0	19	-37	<0.75
,, ,,[5]	,,	,,	41	,,	,,	19	-54	,,
honey locust[6]	3.8	0	44	3.8	0.45	46	4	-
western hemlock[8]	3.5	0	50	3.5	3.3	37	-24	(2.5)
Douglas-fir[8]	,,	,,	46	,,	,,	38	-16	(3.3)
western red cedar[8]	,,	,,	49	,,	,,	47	-3	(>3.3)
Sitka spruce[8]	,,	,,	50	,,	,,	37	-25	(3.3)
red spruce[9]	3.8	0	0.57[9]	3.8	7	1.14[9]	-50	1.7 - 3.5
Norway spruce (- LT)[11]	4.0	0	26.8	4.0	0.8	13.6	-49	<0.8
Norway spruce[13]	3.8	0	90	3.8	0.5	50	-45	<0.5
Norway spruce[16]	4.0	0	24	4.0	1.2	2	-91	0.8
Eur. beech[17]	4.2	0	9.3[17]	4.2	1.0	1.66[17]	(-92)	0.1 - 1.0
,, ,,[18]	,,	,,	4.2[18]	,,	,,	0.67[18]	(-84)	0.1 - 1.0
Douglas-fir[26]	3.5	0	1.84	3.5	(11.8)	1.61	-13	<1.5
Eucalyptus mannifera[29]	3.7	0	51	3.7	2.2	78	51	>2.2
Pinus radiata[29]	,,	,,	26	,,	,,	30	15	~0.37
	b) Sand cultures:							
eastern white pine - PT[10]	3.8	0	113	3.8	3.7	25	-78	(1 - 1.8)
,, ,, ,, + PT[10]	,,	,,	102	,,	,,	34	-67	(2.7 - 3.7)
Douglas-fir[14]	4.7	?	41	4.1	?	20	-51	(pH 4.1)
	c) Soil mixtures / soil monoliths:							
cotton[4]	4.5	0.07	7.1[4]	4.0	1.1	3.4[4]	-52	0.33
honey locust[7]	5.0	?	6.3	4.0	?	5.7	-10	-
Scots pine[12]	5.9	?	7.5	3.8	?	6.5	-13	-
Norway spruce[12]	,,	,,	2.0	,,	,,	1.0	-50	-
Douglas-fir[25]	3.4	0.4	13.7	3.0	7.0	8.0	-42	-
Douglas-fir[27]	5.5	?	134	3.3	?	23	-83	-
,, ,,[28]	5.5	?	158	4.0	?	65	-49	
	d) Mature trees (field manipulation):							
Norway spruce[15]	3.9	3.7	12	3.3	7.7	15	25	-
,, ,,[15]	,,	0.26	13	,,	0.77	9	-31	(0.77-3.3)
Norway spruce[19]	4.3	(4.2)	17.8	4.0	2.6	14.5	-19	-
Norway spruce[20]	6.5	?	19	4.1	?	18	-5	-
,, ,,[21]	6.0	?	15	4.2	?	14	-7	-
Norway spruce[22]	(4.3)	?	15	(4.0)	?	13	-13	-
Norway spruce[23]	,,	?	0.7[23]	,,	?	0.9[23]	-22	-
Norway spruce[24]	,,	?	14.3	,,	?	12.8	-11	-

a) Length in mm or cm, SRL in $m\ g^{-1}$, unless otherwise indicated in the notes below

b) Critical concentration with sudden change in SRL or root length development

c) Genetic trial: various reactions within tree species

References and additional information

1) Rode & Runge (1991): 6 levels of Al and different forms of N (NO_3^- and NO_3^-/NH_4^+), fine root length in % of control, strong effects of N form (see also Rode 1988)
2) Thornton et al. (1986): 5 levels of Al
3) Nowak & Friend (1995): 2 levels of Al, 6 genotypes tested of both species
4) Adams & Lund (1966): 'Dickson' soil results used, 4 $Ca(OH)_2$ levels, split root experiment, root penetration measured, also $Ca(OH)_2$ added
5) Kruger & Sucoff (1989a): 3 levels of Al with 2 levels of Ca, respectively with and without Ca addition
6) Ren & Sucoff (1990): 6 levels of Al, optimal root length at 0.14 $mol_c\ m^{-3}$
7) Schindelbeck & Riha (1988): silt loam, 3 lime levels, with addition of P, SRL data
8) Ryan et al. (1986): 6 levels of Al
9) McQuattie & Schier (1990): 4 levels of Al, root tip diameter data, reacts as inverse of SRL (root biomass unaffected)
10) Schier & McQuattie (1995): 6 levels of Al, test with or without Pisolithus tinctorius mycorrhiza (PT)
11) Godbold & Jentschke (1990): 2 levels of Al, test without Lactarius theiogalus (LT) (see also Godbold 1994)
12) Bartsch (1987): 2 levels of liming in sandy loamy soil, Al was originally 76 % of CEC, pH-H_2O respectively 3.8 and 5.9, length growth data from moist phase used
13) Godbold et al. (1988): 2 levels of Al
14) Olsthoorn et al. (1991): 4 levels of rhizosphere pH (different ratios of NO_3^- and NH_4^+)
15) Häussling et al. (1991): 2 mature stands, one treated with acid rainwater (pH 2.7), then soil solution also contains more Ca and Mg, data for mineral soil
16) Godbold & Kettner (1991): 4 levels of Al, 8 days exposure to Al
17) Bengtsson et al. (1994): 3 levels of Al, Al concentration of 0.1 $mol_c\ m^{-3}$ gave beneficial effects on uptake, Ca uptake data for root tips, in mmol $g^{-1}\ h^{-1}$
18) Same reference as 17: data for whole root system
19) Majdi & Persson (1995b): control stand and $(NH_4)_2SO_4$ treated stand (100 kg N $ha^{-1}\ yr^{-1}$), data 0 - 10 cm presented, pH-rhizosphere + Al concentration rhizosphere (water extract), stand age ~30 yrs
20) Clemensson-Lindell & Persson (1993): SRL data for LFH layer in Farabol, limed (6000 kg ha^{-1} between '76 and '87) and unlimed control (='high Al' in this table), stand age 57 yrs
21) Same reference as 20: SRL data for LFH layer in Fäxboda, limed (412 kg Dolomite per ha in 1980) and unlimed control (='high Al'), stand age 40-50 yrs
22) Clemensson-Lindell & Persson (1995): same stand as reference 19, SRL data for 0 - 30 cm, live root vitality class 2 (dominant in live root fraction), indication of pH from ref. 19, stand age ~30 yrs
23) Majdi & Persson (1995a): same stands as reference 19 and 23, diameter increase is interpreted as SRL reduction, indication of pH from ref. 19, stand age ~30 yrs
24) Clemensson-Lindell & Åsp (1995): same stands as reference 19, 23 and 24, SRL data for humus layer, live root vitality class 2 (dominant in live root fraction), indication of pH from ref. 19, stand age ~30 yrs
25) De Visser & Keltjens (1993): 4 levels of NH_4^+, resulting in pH ranging from 3 to 3.5 in the soil solution, SRL data from experiment I
26) Keltjens (1990): 5 levels of Al, SRL data for low availability of Ca and Mg
27) Smit et al. (1987b): 4 soil pH-H_2O levels, SRL data for NO_3^- nutrition
28) Same reference as 27: SRL data for NH_4^+ nutrition, no survival at pH-H_2O 3.3
29) Huang & Bachelard (1993): 4 levels of Al

Table 6.5.
Effects of 'low' and 'high' nutrient availability on fine root biomass in forest ecosystems. Diameter of fine roots < 2 mm, unless otherwise indicated. A: comparisons of low and high site quality of unfertilised locations, B: fertiliser trials. In A), site comparisons, usually the average of different years in the period May/June are presented. In B), only data of unirrigated fertilised plots are listed, usually the control is compared with the highest N-treatment, the addition of other nutrients is indicated. In fine root data from time series, the data in the period May/June are preferred (often derived from graphs), in fertiliser trials usually the last year of the measurements is used, for the largest effect of the treatment. Units of fine root data are indicated. Uncertain effects are given between brackets.

EXPERIMENTAL CONDITIONS				RESULTS		
TREE SPECIES	AGE	TREATMENT (ELEMENTS)	NITROGEN FERTILISATION (kg N ha^{-1})	AMOUNT OF FINE ROOTS AT LOW AND HIGH *) NUTRIENT LEVEL		ROOT BIOMASS CHANGE (%)
		A) Unfertilised site quality:		low	high	
Douglas-fir[1]	40	-	0	8.3	2.7	-67
Pinus radiata[2]	8	-	0	39.5	129.2	228
Douglas-fir[3]	30/35	-	0	4.1	3.0	-26
Douglas-fir[4]	40/70	-	0	3.2	1.8	-43
Douglas-fir[5]	70/170	-	0	3.0	3.4	13
Norway spruce[6]	mature	-	0	2341	485	-79
beech[6]	mature	-	0	8500	360	-95
Douglas-fir[7]	70	-	0	2.5	0.6	-76
Scots pine[22]	*mature*	-	0	0.8	0.6	-25
Eucalyptus globulus[24]	11 - 16	-	0	210	364	73
		B) Fertiliser trials:		Control	Fertilised	
Pinus radiata[2]	8	complete	230	39.5	82.8	109
,, ,,	,,	complete	230	129.2	157.8	22
mixed stand[8]	30-200	N	200	2.60	0.75	-71
,, ,,	,,	,,	,,	0.75	0.35	-53
,, ,, ,,	,,	,,	3.35	1.10	-67	
Norway spruce[9]	60	N.P.Ca.Mg	200	8.3	10.7	29
,, ,,	60	,,	,,	6.7	6.3	-6
,, ,,	60	,,	,,	6.1	5.8	-5
,, ,,	60	,,	,,	5.4	4.3	-20
Scots pine[10]	35/40	N-gradient	-	0.5	0.3/0.5	0 / - 40
mixed stand[11]	-	N,P,K,lime	1000	12.5	27.0	116
European beech[12]	140	N	140	7.3	6.2	-15
Scots pine[13]	130	N,P,K,B	460	3.4	2.2	-35
Scots pine[14]	74	N	150	0.9	0.5	-44
Norway spruce[14]	46	,,	,,	0.7	1.3	85
Norway spruce[14]	84	,,	225	1.6	1.4	-13
Norway spruce[14]	18	,,	120	1.1	1.4	27
Norway spruce[14]	36	,,	150	1.1	1.1	0
Sitka spruce[15]	35	N	300	0.12	0.12	0
western hemlock[16]	40	N	225	1600	1500	-6
,, ,,	25	,,	,,	1000	1000	0
,, ,,	45	,,	,,	1900	1400	-26
,, ,,	40	,,	,,	1000	1000	0
,, ,,	35	,,	,,	2500	2700	8
,, ,,	20	,,	,,	5600	5700	2
Scots pine[17]	35	N	2000	100	75	-25
Douglas-fir[18]	~14	N	670	5.6	1.4	-75
Scots pine[19]	15	N	480	27.6	38.6	40
,, ,,	85	,,	,,	36.1	44.6	23
Norway spruce[20]	40/60	N	700	0.85	1.43	68
Norway spruce[21]	29	N	600	12.2	7.7	-36
Eucalyptus globulus[23]	6	N, K, P, (Mg)	?	0.06	0.04	-33
Norway spruce[25]	28	$(NH_4)_2SO_4$	100	273	265	-3
,, ,, [26]	29	,,	200	524	532	2
,, ,, [27]	31	,,	400	9.2	4.7	-49
Pinus radiata[28]	20	balanced	2100	3.3	1.8	-45

*) *Data in different units, see references next page; value between brackets if 'low' productivity is relatively*

References and additional information

1) Keyes & Grier (1981): Washington, USA, loamy sand/silty loam, method: coring (-45 cm, in April/May), 20 samples/plot, data in t ha^{-1}
2) Squire et al. (1978): Victoria, Australia, sandy clay loam, method: coring (-23 cm, in March/April, = autumn in southern hemisphere), 8 samples/plot, fertilisation with macro and micro nutrients, data in cm 100 ml^{-1} soil, root diameter < 0.5 mm
3) Olsthoorn (1991): Netherlands, podzolic sands, method: coring (-80 cm in May/June), 12 samples/plot; 'low' fertility also high N deposition, data in t ha^{-1}
4) Kurz & Kimmins (1987): British Columbia, Canada, moraine podzolic soils, method coring (-50 cm, in May), 10 samples/plot, data in t ha^{-1}
5) Santantonio & Hermann (1985): Oregon, USA, clay loam soils, method: coring (-75 cm, in May/June), 9 samples/plot, data in t ha^{-1}, root diameter < 1 mm
6) Meyer (1967): north Germany, mature stands, sandy podzol/loamy brown earth, method: coring (-50 cm, in October), 8 (4) samples/plot, data in tips 100 ml^{-1} soil
7) Vogt et al. (1987): Washington, USA, different soils (Vogt et al. 1983), method: coring (-15 cm, in March), 10 samples/plot, data in t ha^{-1}
8) Gower & Vitousek (1989): Hawaii (Metrosideros polimorpha + ferns), young volcanic soils, method: coring (-30 cm, probably in March), 4 samples/plot, 4 replicates, data in t ha^{-1}, root diameter respectively < 1 mm, 1-2 mm and < 2 mm
9) Zöttl (1964): south-west Germany, pseudogley and podzolic brown earth soils, method: coring (-60 cm, sampling month unknown), 10 samples/plot, data in t ha^{-1}
10) Ritter (1990): east Germany, brown podzolic soil, method: coring (-5 cm, in September/November), (4) samples/plot, transect 0 to 3 km from large farm, data in t ha^{-1}
11) Safford (1974): New Hampshire, USA, (beech, birch, maple), coarse loamy soil, method: coring (-60 cm, in June/July), 10 samples/plot, data in t ha^{-1}, root diameter < 3 mm
12) Rapp (1991): Solling, Germany, podzolic brown earth (with pseudogley), method: coring (-40 cm, in May), 10 samples/plot, data in t ha^{-1}
13) Ahlström et al. (1988): central Sweden, glaciofluvial podzolic sands, method: ingrowth cores (-30 cm, in October/November), 10 samples/plot, data in t ha^{-1}
14) Persson & Ahlström (1990): south and central Sweden, different soils, method: ingrowth cores (-30 cm, in October), (10) samples/plot, data in t ha^{-1}, root diameter < 1 mm
15) Alexander & Fairley (1983): Scotland, UK, method: coring (-10 cm, in May), 15 samples/plot, 3 replicates, data in t ha^{-1}, root diameter < 1 mm
16) Gill & Lavender (1983): Washington, USA, silt loams, method: coring (-20 cm, in January - September), 12 samples/plot/date (average of 6 sampling periods) , data in number of root tips
17) Ritter & Tölle (1978): east Germany, sandy podzolic soils, method : coring (-5 cm, in October), 4 samples/plot; 'low' fertility site also high N deposition, data in percentage of control
18) Vogt et al. (1990): Washington, USA, methods unknown (see Vogt et al., 1985), data in t ha^{-1}
19) Heinsdorf (1976): east Germany, sandy podzolic soils, method: profile wall (-100 cm, in December), data in number of roots per dm^{2} wall
20) Raspe & Feger (1992): south-west Germany, sandy acid soils, method: coring (-40 cm, in October), 12 samples/plot, data in mineral soil, data in g dm^{-3}
21) Nilsson & Wiklund (1995): Clemensson-Lindell & Asp (1995) and Clemensson-Lindell & Persson (1995), Sweden, podzolic soil, method: coring (-30 cm, in August), 4 samples/plot, 4 replicates, data in g dm^{-3}
22) Anders (1996): east Germany, sandy soils, method: coring (-50 cm, sampling month unknown), 4 samples/plot; 'low' fertility site also high N deposition, data in g 100 cm-2, root diameter < 1 mm
23) Fabião et al. (1995): Portugal, sandy soil, method: monolith 0.5 x 0.5 m around stem base (-60 cm, in February), 6 replicates, data in kg tree^{-1}
24) Fabião et al. (1985): Portugal, sandy and clayey soil, method: ingrowth cores (-40 cm, in March), harvest after one year, 9 or 14 samples/plot, ingrowth in clay is slower, data in g m^{-2}
25) Persson et al. (1995): Sweden, loamy sandy podzol, method: monolith (-100 cm, in June), 4 samples/plot, 4 replicates, data for 1989, data in g m^{-2}
26) Majdi & Persson (1995b): same site, data for 1990, method: coring (-30 cm, in September), 10 samples/plot, 4 replicates, data in g m^{-2}, root diameter < 1 mm
27) Clemensson-Lindell & Persson (1995): same site, data for 1992, method: coring (in LFH-layer, in September): 8 samples/plot, 4 replicates, data for LFH layer, no differences in mineral soil, data in g dm^{-3}, root diameter < 1 mm
28) Ryan et al. (1996): Australian Biology of Forest Growth project, Canberra, method: digging (-40 cm, in March, = autumn in southern hemisphere), 15 samples/plot , both plots irrigated, one fertilised, data in t ha^{-1}

In the field studies - with liming, artificial acidification, or the addition of $(NH_4)_2SO_4$ - the root length is positively influenced if the control also has a high Al concentration, and further acidification results in improved availability of Ca and Mg (e.g. reference 15 in Table 6.4: Häussling et al. 1991). Clemensson-Lindell & Persson (1993) found that liming continued to have a positive effect on the SRL 5 to 18 years after the treatment (see also Meiwes 1995). Bearing these considerations in mind, we can see a reduction in the fine root length with increasing soil acidity, ranging between 5 and 30 % of the 'control'.

Most references in Table 6.4 only present data on the total Al concentration in the (soil) solution. No data are available to calculate the concentration of free Al that is actually toxic, in the total amount of soluble Al. This means that it might be difficult to use the uncorrected data to find a single threshold value for Al effects on fine root morphology for the field situation for Douglas-fir (see also Innes 1993; Løkke et al. 1996). The complexation of Al with DOC (see above) explains the large differences found for critical values for another tree species, Norway spruce, where effects of Al begin between 0.3 mol_c m^{-3} and 3 mol_c m^{-3} (see Innes 1993 and Kreutzer et al. 1989). The clearest values for a threshold value for Al are found in the solution cultures (Table 6.3A). There, DOC is absent, and all Al is present in toxic monomeric forms, as is probably also the case in the sand cultures. In the soil mixtures and in the field experiments, DOC is present in the top mineral soil layers and in the litter layer (e.g. Mulder et al. 1989b). Therefore, the threshold value for morphological changes from the solution cultures, needs to be corrected to be of use in the data for total Al concentration in the soil solutions in Table 6.4. Unfortunately, the references gave no data on DOC concentration. If the DOC concentration were known, the toxic Al concentration could have been calculated, using the binding capacity of DOC of 11 mmol Al per mol DOC at pH 4.0 found by Mulder et al. (1989a; see also Berggren 1992; Dietze 1987).

The complexation mechanism with DOC can also account for the difference in level of the Al/BC ratio (aluminium to basic cation ratio) in experiments in real soil compared with the level of this ratio found in solution cultures for Al damage to fine roots that Sverdrup & Warfvinge (1993) found in their extensive literature search. On average they found that the total Al concentration in the field situation had to be twice as high as in solution cultures, to achieve the same effects on fine roots. This implies that on average the total Al concentration in the soil solution in soil mixtures (Table 6.4C) and in mature forest (Table 6.4D) must be twice as high as in solution culture studies to have the same effect on the length development of fine roots.

From the data in Table 6.4, it can be deduced that the reduction in fine root length can be up to 50 to 90 % of the control, when the threshold value for the total Al concentration is within the range of the treatment conditions. If the threshold value is not within the range of the treatment conditions, then the reduction in fine root length is often less than 50 %. The threshold values vary greatly between tree species, as is the case for agricultural crops, where there are often large genotypical differences within species (Marschner 1995). For Al tolerant tree species, like Douglas-fir (see Table 6.3), the Al threshold for morphological changes is sometimes, though not always, below 1.5 mol_c m^{-3}. Keltjens (1990) also found an Al threshold value of below 1.5 mol_c m^{-3}, based on changes in fine root diameter, and Ca uptake

(Keltjens & Van Loenen 1989). Some references (e.g. Smit et al. 1987b) stated that at a pH around 4.1 large changes occur in the fine root length of Douglas-fir trees. In forest soils, this is the pH where the Al buffering range starts in the acidifying process.

In this study, the mycorrhizal mediated effects of Al on fine root length are not taken into account. Al has an effect on growth of mycorrhiza (see e.g. Schier & McQuattie 1995; Godbold & Jentschke 1990), but there are no major effects in the physiological response of tree seedlings at sub-lethal Al levels (Jentschke et al. 1991). The mycorrhizal frequency is currently very low for Douglas-fir in The Netherlands (Jansen & De Nie 1988).

The conclusion from the data summarised in Table 6.4 is that the largest changes in the fine root length of Al-tolerant tree species take place between 1.0 and 2.0 $mol_c\ m^{-3}$ of free monomeric Al in the soil solution. Schaedle et al. (1989) gave a range in the same order of magnitude (Table 6.3). The long-term accumulation of acidifying compounds in forest soils in The Netherlands has resulted in toxic but sub-lethal concentrations of Al (Tables 6.1 and 6.2) above the threshold for morphological changes for Douglas-fir. The following conclusions can be drawn about the effects on fine root length:

- Al has a large effect on the fine root length. This results in the fine root density of Douglas-fir in The Netherlands being decreased by a factor of presumably 50 % in the topsoil, as a conservative estimate (see references from Table 6.4), compared to a situation with low levels of Al in the soil solution.
- In the subsoil (in Table 6.1 below 20 cm, see also Table 6.2), the Al concentrations of between 2.4 and 4.1 $mol_c\ m^{-3}$ are far above the threshold value for morphological changes in the fine root fraction, even for an Al-tolerant tree species like Douglas-fir. Therefore, the fine root length is more severely affected. The reduction of the fine root density in the subsoil might be as much as 75 %. This will have resulted in a fine root system that on average is more shallow than in sandy soils unaffected by acidic deposition.

3) NITROGEN AND FINE ROOT BIOMASS

Results of seedling studies cannot be used to derive the influence of the nitrogen status of the soil-plant system on the fine root biomass in a forest, as these cannot be translated to the field situation on a quantitative basis. Therefore, fine root studies from a great number of field studies in mature stands are summarised in Table 6.5, in which the fine root biomass in stands with low nitrogen availability is compared with stands with high availability.

The site comparisons without N fertilisation (Table 6.5A.) show that the fine root biomass is usually larger in poorer quality sites (see also Fabião et al. 1985). Data from Squire et al. (1978; reference 2 in Table 6.5) seem to contradict this. However, the fine roots in that study were sampled in autumn, after large numbers of fine roots had probably died during the preceding dry summer (see e.g. Vogt et al. 1985; Olsthoorn & Tiktak 1991). Therefore, the best representation of the site quality on fine root biomass can be found in early summer - after the root growth flush in spring and before possible fine root mortality during dry periods. Data obtained in autumn run the risk of being influenced by the local weather conditions. In some years and in some climate zones, the results in autumn will not be greatly different from the results in early summer. For *Pinus radiata* in Australia in March (comparable with September in the Northern hemisphere), Ryan et al. (1996) showed that after the summer fewer fine roots were present in the control, than in an irrigated treatment. But in irrigated stands without drought effects in both situations, fertiliser application reduced the amount of fine roots.

In studies on the effect of site quality it is impossible to separate the effects of water and nutrient availability (Vogt et al. 1990; De Visser et al. 1994). Therefore, in Table 6.5B, data from trials with solid fertilisers are listed. The plots in one study have similar soil physical properties, so availability of water cannot interfere with the results. Studies with a large nitrogen supply and without other nutrients are especially valuable for comparison with the present Dutch conditions. In most studies however, relatively low amounts of nitrogen were added, sometimes in combination with other nutrients, and sometimes with lime. Lime varies in its effect on pH depending on how it is applied, and depending on the concentration of cations like Mg, K, and Ca in the soil solution (Ponette et al. 1996). The effects of nutrients other than nitrogen make the results of additional fertilisation or liming treatments less valuable for our purpose, as indicated in the last column. In 23 cases the fine root biomass at the lowest nutritional level, usually the control treatment, was larger than at the highest nutritional level, as Vogt et al. (1985) also showed for other periods in the year (see also Walters & Reich 1997). In 11 cases the fine root biomass was approximately the same (< 10 % difference), and in 12 cases the biomass was larger in the highest nutritional level. Clemensson-Lindell & Persson (1995) found the greatest effects in the humus layer. They also found 30 % more aboveground growth at an application of ammonium sulphate (100 kg N ha^{-1} yr^{-1}). To derive a general picture, we must take a closer look at factors that affect the shoot:root ratio in plants.

Based on earlier studies (e.g. Brouwer 1962; De Wit et al. 1978), Schuurman (1983) described a general concept to understand the shift in shoot:root balance through changes in the availability of nutrients (Fig. 6.1). With increasing nutrient availability, there is a continuous increase in shoot:root ratio. Shoot dry weight increases more quickly than root dry weight. Root biomass attains its optimal value at lower nutrient levels than shoot biomass. Shoot dry weight declines only at very high nutrient levels. In a review of different models that describe the shoot:root balance, Bastow Wilson (1988) even labelled nutritional elements in excess as toxic, and argued that few authors provide root biomass figures at these high levels of nutrients. In a fertilisation trial with maximum 1800 kg N per hectare, Ebell (1972) demonstrated that stem growth was optimal for 20-year old Douglas-fir when the needle nitrogen concentration was 2 %, and that growth declined at higher nitrogen concentrations. In a fertilisation trial with application rates of up to 1200 kg N supplied within four years, Kennel & Wehrman (1967) found optimum growth at 1.9 % N in needles of 40-year old Scots pine on poor soils, and declining growth at higher N contents.

Schuurman's general concept (1983) allows for a range of reactions to varia-

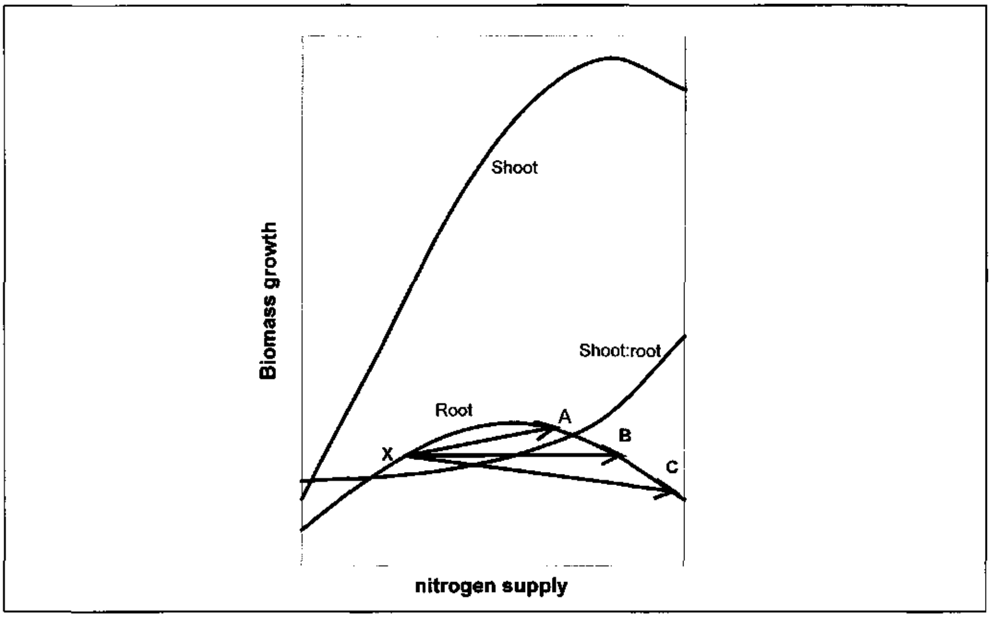

Figure 6.1
Schematic response of root and shoot growth of plants to varation in the supply of nitrogen (after Schuurman 1983), with three scenarios for net result of changes in nitrogen supply for biomass of fine roots: X = biomass at sub-optimal nitrogen supply: A = scenario to increasing biomass: B = scenario to equal biomass; C = scenario to decreasing biomass.

tion in the availability of various soil ecological parameters, like individual nutrients. The scenarios of the net effect on fine root biomass therefore vary depending on the rate of increase of nutrition level (Fig. 6.1, scenario A, B or C). Examples of these different scenarios have been shown in numerous studies on different plant species, where the shoot:root ratio can shift considerably (see e.g. Brouwer 1962, 1983; Brouwer & De Wit 1968; Lambers 1983; Robinson & Rorison 1988; Boot & Mensink 1990; Van der Werf 1993). For trees this has been demonstrated mainly with seedlings (e.g. Van den Driessche 1984; Ågren & Ingestad 1987; Ingestad & Lund 1979; Cromer & Jarvis 1989; Olsthoorn et al. 1991; De Visser & Keltjens 1993; Mackie-Dawson et al. 1995).

According to Tucker & Von Seelhorst (1898), increasing water availability affects the decrease of root biomass of seedlings much more than increasing nutrient availability does. Therefore, we need to look for field experiments in which there were no differences in water availability. At low nitrogen availability Tucker & Von Seelhorst (1898) found a small increase in root biomass with an increase of the level of nitrogen, when enough phosphorus and potassium were available. However, when the phosphorus availability was low, the decrease in quantity of root biomass when nitrogen was added was larger than with high levels of phosphorus. Hoffmann (1975) and Fiedler et al. (1985) also showed that there are interactions between different nutrients. Hoffmann (1975) found the greatest fine root biomass at higher nitrogen levels when the phosphorus nutrition was also improved. He clearly demonstrated that root biomass decreased at the highest nitrogen levels in a tree seedling trial (see also Cromer & Jarvis 1989; Beese & Matzner 1986; Olsthoorn et al. 1991). In a seedling trial with Douglas-fir, Van den Burg (1991b) showed that the largest fine root biomass was found in the control treatment (no nitrogen added), but only when the availability of other nutrients was poor. Dighton et al. (1993) showed that extra nitrogen increases the shoot:root ratio of *Eucalyptus grandis* more than extra phosphorus, as the shoot reacted more strongly to N fertilisation than the roots. Grove (1988) showed that aboveground growth reacted more strongly to N than to P. Ten Berge et al. (1994) found that for fast growing crops like rice at high nitrogen levels, the biomass of roots continued to increase with increasing nitrogen levels, whereas the shoot:root ratio remained nearly constant. Ericsson (1990 and 1994) showed that with increasing levels of nitrogen, phosphorus or sulphur in seedling trials, the shoot:root balance of the tree seedlings increased, until the optimum nutrition level was reached, while other nutrients (K, Mg, Mn) showed the opposite effect (see also Wikström & Ericsson 1995). Spiecker (1991) demonstrated that aboveground growth (stemwood) in mature Norway spruce forest increased quickly after N fertilisation, while changes were less with P fertilisation only. Additional P fertilisation prolonged the effect of N-fertilisation. In their model, Thornley & Cannell (1992) described that the foliage:fine-root balance, a good expression of a functional shoot:root balance in tree species, increases concomitantly with the soil organic matter content or the nitrogen content (see also Reynolds & Thornley 1982; Axelsson & Axelsson 1986; Grove et al. 1988).

In The Netherlands, the phosphorus availability can be considered to be low, as most forest stands are located on poor sandy soils (Mohren et al. 1986; Van Tol et al. 1993). Therefore, to estimate changes in fine root biomass in forest stands through increased nitrogen availability, we especially need to look at data on fine root biomass obtained from long-term fertiliser experiments in mature forest stands involving nitrogen application only. In fertiliser trials with low amounts of nitrogen only, the fine root biomass sometimes increases when nitrogen is added. This might correspond with the first range in the general model by Schuurman (1983; Fig. 6.1, scenario A). The conditions in the references of Table 6.5 with a large stimulus in the fine root biomass, are generally not comparable with the present Dutch situation, because either the amount of N is relatively small or other nutrients are added in the trials.

At present, forest trees in The Netherlands are nitrogen saturated (Van Breemen et al. 1987). Consequently, it is to be expected that the fine root biomass is decreasing with increasing nitrogen availability (according to Fig. 6.1, from B to C). While levels of nitrogen deposition were rising there might have been a positive effect on the fine root biomass in the lower range of nitrogen availability (Majdi & Persson 1995a and references in Table 6.5B), followed by a downturn when nitrogen levels continued to increase (Fig. 6.1, towards scenario C). Heinsdorf (1976) found the highest fine root density for Scots pine at all ages in stands ranging from 8 to 85 years at intermediate nitrogen fertilisation levels, with a small decrease at higher fertilisation levels. In many cases, when the N fertilisation is below a total of 1000 kg ha^{-1} the fine root biomass increases concomitantly with increasing N (Fig. 6.1, scenario A).

Reductions in the fine root biomass were sometimes found even then (Fig. 6.1, scenario C). In most studies, we do not know the nitrogen status of the unfertilised stands. This (and other differences between the experiments) could explain the differences in reaction. The average reduction in the fine root biomass in all experiments with over 500 kg nitrogen and no other nutrients is 22 % (six cases, see Table 6.5). In the two most extreme cases, when around 2000 kg of nitrogen is added, the average reduction is 35 %.

Considering the large amount of added nitrogen, the results of Ritter (1990), Ritter & Tölle (1978), and Ryan et al. (1996) - respectively references 10, 17, and 28 in Table 6.5 - are most comparable to the present conditions in The Netherlands, where at least 1000 kg N ha^{-1} has been deposited in forests in recent decades. In most forest stands in The Netherlands, the fine root biomass of Douglas-fir might be roughly at the same level as before nitrogen deposition started (Fig. 6.1, scenario B), but has most probably decreased slightly (Fig. 6.1, scenario C) as a net outcome of the accumulated nitrogen deposition. Judging from the data in Table 6.5B, the effect of rising nitrogen availability might be a reduction in the fine root biomass of up to 30 %, being in the same order of magnitude that Ritter (1990), Ritter & Tölle (1978), and Ryan et al. (1996) found at similar high levels of nitrogen supply. We want to present a conservative estimate, as there is no way of verifying this conclusion. Therefore, our estimate of this reduction might underestimate the real effects.

Conclusions: estimation of changes in fine root density induced by anthropogenic acidic deposition

1) Changed site conditions: Due to the accumulation of anthropogenic acidifying deposition and the resulting different buffering range from 200 years ago, the total Al concentration in the soil solution has probably increased by a factor of 30 to 50 in the topsoil, and by a factor of over one hundred in the subsoil of the Dutch acid forest soils (Table 6.1.). In the topsoil, more than 50 % of the Al can be chelated in non-toxic forms. But in the subsoil, nearly all Al is present in toxic monomeric forms. Based on the leaching of nitrate from the soil profile and the high nitrogen concentration in young and old needles of Douglas-fir, the nitrogen availability in the Douglas-fir plantations in The Netherlands is rated as high or over-optimal. The concentrations of P, K, and Mg are rated as rather low, especially if expressed in relation to nitrogen.

2) Al effect on fine root length: The fine root density is affected by the changes in the Al concentrations in the different soil horizons (Table 6.4). It is severely reduced, probably by about 50 %, compared with the fine root density in sandy soils in the cation buffering range. The fine root density in the subsoil is probably reduced even more (by 75 %), resulting in a shallower fine root system.

3) Nitrogen effect on fine root biomass: The fine root biomass has changed due to the changes in the nitrogen availability (Table 6.5). It seems most probable that the increased nitrogen availability has led to a small decrease (up to 30 %) in the fine root biomass in Dutch Douglas-fir plantations.

The nitrogen effect on fine root biomass and the Al effect on fine root length must be combined in a demonstration of the total effects on fine root density caused by the accumulation of acidic deposition during the last 200 years. The final result of the interpretation of literature data is that the total effect of anthropogenic deposition on the fine root density of Douglas-fir, an Al-tolerant tree species, is a reduction of over 50 % of the fine root density in the topsoil and an even larger reduction in the subsoil, probably over 75 %. This interpretation of the available data strongly supports Ulrich's hypothesis (Ulrich et al. 1979; Ulrich 1983a). The same effects might have taken place in other parts of NW-Europe in forests on sandy soils that would be in the cation buffering range without anthropogenic acidic deposition, especially if the tree species in question are more sensitive to Al toxicity. In areas with a smaller nitrogen deposition and mainly SO_x deposition, the aluminium effects alone can have a strong reducing effect on fine root density.

The changes in fine root density have to be weighed against changes in the aboveground biomass, as roots are a part of the pathway used by water and nutrients in the functioning of the total tree. The effects of decreased fine root densities and changes in fine root distribution in the soil profile for water uptake will be evaluated in a subsequent Chapter (Olsthoorn et al. 1998).

Acknowledgements

We are grateful to J. Kros for calculations with the RESAM model to determine soil chemical conditions with the background deposition levels, in comparison with the present deposition levels, W. de Vries for allowing to use the RESAM model for this purpose, G.M.J. Mohren, R. Rabbinge and N. van Breemen for comments on the manuscript, N. van Breemen, W. de Vries, P.H.B. de Visser, J. van den Burg and W. Vos for stimulating discussions, and to K. Redei for translation of Russian articles. Ms. J. Burrough-Boenisch gave advice on the English.

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7. Effects of soil acidification and nitrogen enrichment on fine root density of Douglas-fir on sandy soils: 2. Implications for drought susceptibility

Abstract

In maritime temperate climates the fine root growth of trees has seasonal periodicity; it generally peaks in spring, declines during summer and may upturn slightly in autumn if temperature and moisture conditions are favourable again. Precipitation has great influence on the periodicity of root growth, as dry conditions lead to cessation of growth and even to mortality. Soil acidification, mostly combined with nitrogen enrichment, is known to cause a decrease in fine root density. This research aimed to identify the effect this decrease has on fine root mortality of Douglas-fir on sandy soils in dry conditions, on regrowth of fine roots, and on tree functioning. A field study showed that both the fine root density and the needle biomass of Douglas-fir are more severely affected on drier sites in conditions of drought. A simulation study with simplified belowground conditions demonstrated that differences in fine root density do not have great consequences for water uptake in short dry periods (up to several days), unless the hydraulic conductivity of the soil is very low under dry conditions. It was hypothesised that differences in fine root density would have great consequences in longer drought periods, during which the rhizosphere is drier and more fine roots die. The elementary root growth model presented describes the changes in fine root density in a drought, and the regrowth after the drought period, when water becomes available again. The final conclusion is that fine root mortality in a drought period is enhanced by soil acidification, and that fine roots take longer to regrow after a drought. This means that the drought susceptibility of Douglas-fir is increased by the effects of soil acidification. Limitations in the tree's uptake capacity can explain why forest growth sometimes takes more than a year to recover from severe drought.

Keywords: fine root mortality, fine root growth, soil acidification, nitrogen deposition, drought, site quality, water uptake, needle loss, model

Introduction

The fine root growth of forest trees on sandy soils in a maritime temperate climate usually peaks in spring, with less fine root growth occurring during summer when soil moisture is often limiting (e.g. Wilcox 1968; Hoffmann 1972; Kurz & Kimmins 1987; Buwalda & Hutton 1988; Olsthoorn & Tiktak 1991; Hendrick & Pregitzer 1993a, b, 1996). Sometimes the fine root density increases in autumn, due to favourable growing conditions (temperature and moisture). In periods of prolonged drought, the mortality of fine roots is more pronounced in the topsoil (up to 20 or 30 cm depth) than in the subsoil (below 20 or 30 cm depth; see Hendrick & Pregitzer 1996; Kurz & Kimmins 1987). Fine root mortality under drought conditions has been demonstrated in roofed-over drought experiments in which part of the throughfall water was prevented from entering the soil profile (Lamersdorf & Blanck 1993; Murach et al. 1993; Holstener-Jorgensen & Holmsgaard 1994). A small reduction of the soil water potential to -0.03 MPa may stimulate fine root growth, but in a drier soil root growth stops, and eventually the fine roots die (Hoogenboom & Huck 1986; Hoogenboom et al. 1988; see also Bevington & Castle 1985; Rendig & Taylor 1989, p.52). In this chapter, a drought is defined as a spell of dry weather, when soil moisture becomes limiting for primary production for a prolonged period. In a maritime temperate climate, such conditions may be common on sandy soils, and prolonged drought may occur once every 20 years.

It seems probable that as a result of soil acidification and soil nitrogen enrichment during the last two centuries, the fine root density (roots with diameter < 2 mm) of Douglas-fir in The Netherlands is only able to achieve half of its potential (Olsthoorn & Keltjens 1998). The fine root system is much shallower as the fine root density in the subsoil attains less than 25% of its potential, mainly because of the strongly increased Al concentrations in the soil solution, as soils have reached the buffer range of Al, i.e. pH-H_2O < 4.2 due to soil acidification (Olsthoorn & Keltjens 1998). The consequence is that a much smaller fine root system is available to take up water and nutrients. Concomitantly, transpiration, and consequently water uptake, has probably increased in response to the stimulating effects of nitrogen on the aboveground tree parts. In an acidification field trial in 28-year old Norway spruce, Clemensson-Lindell & Persson (1995) found that a decrease in fine root density was accompanied by a 30 % increase of the needle biomass thanks to fertilisation with ammonium sulphate. This phenomenon was also demonstrated by Van Oene (1994) in a simulation approach (see also Matzner & Murach 1995; Prietzel et al. 1997). De Visser & Keltjens (1993) demonstrated that high levels of ammonium sulphate fertilisation can initially increase shoot growth of seedlings, but that this can increase the probability of seedling mortality (see also De Visser et al. 1996). Linder et al. (1987) have shown this in a field experiment, where drought conditions caused tree mortality in the fertilised treatment.

One consequence of a decrease in fine root density is the need to increase water uptake rate per unit of root length to maintain the same or a higher transpiration rate. This higher rate decreases water potentials in the rhizosphere, increasing the gradient from the bulk soil to the root surface (De Willigen & Van Noordwijk 1987, p. 147; Rendig & Taylor 1989, p. 123). Olsthoorn & Tiktak (1991) have given circumstantial evidence for lethal conditions for fine roots for defined inadequate moisture conditions in the bulk soil. The exact lethal water potential in the bulk soil cannot be given, as it also depends on the actual transpiration demand (related to LAI, and weather conditions, see Larson 1980) and fine root characteristics (thickness, suberization and mycorrhizal infection) and substrate (Deans 1979). Consequently, it seems feasible that decreased fine root density will hasten the conditions for fine root mortality in periods of drought. This may have a major effect on fine root dynamics and drought susceptibility, especially as trees cannot adapt their shoot-root ratio rapidly (Hinckley & Ceulemans 1989). In the present study, the effects of fine root mortality resulting from reduced transport of carbohydrates to the fine roots (Marshall 1986; Kuhns & Gjerstad 1988; Gorissen et al. 1994) were ignored, as it was assumed that the physical soil conditions in an extreme drought dominate fine root mortality during the drought.

To analyse the effects of soil acidification and nitrogen enrichment on fine root dynamics and drought susceptibility of trees, we pursued various lines of research: 1) In a field study, the effects of a difference in soil quality on fine root and needle dynamics in a dry year were investigated for two sites with Douglas-fir. 2) In a simulation study, the effects of reduced fine root densities on short-term water uptake were studied with a water uptake model. 3) This led to several hypotheses on changed biomass dynamics (fine roots and foliage) and their implications for long-term water uptake and for drought susceptibility under the conditions prevailing in The Netherlands (heavy anthropogenic acidic deposition). 4) The hypotheses were summarised in a simple model that describes fine root biomass dynamics both under drought conditions and under favourable growing conditions (moisture and temperature), exploring the effects of soil acidification on mortality during and regrowth after a drought period.

This chapter describes results of a field study and a simulation study. In the discussion, the results of both analyses are evaluated with regard to the central question in this research: *How does the acidification of sandy soils, mostly combined with nitrogen enrichment, affect the fine root system, and what are the consequences for tree functioning?*

Material and methods

SITE DESCRIPTION

Two stands, planted on clear-cut areas with a coastal provenance of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), located 10 km apart in the 'Veluwe' area in The Netherlands, were studied as part of the Dutch Priority Programme on Acidification in the ACIFORN project (ACIdification of FORests in The Netherlands). At the time of sampling the stands were completely closed. There was no ground vegetation, hence all the living roots could be assumed to be Douglas-fir. The soils in both stands are sandy and well drained. The water table is very deep (not within reach of the tree roots) and the soil contains very little gravel. One of the stands ('Kootwijk', 52°11'N, 5°46'E) is located on eolian sands, with previous agricultural influence. The soil consists of a Leptic podzol (FAO/UNESCO 1974). The A_p is 40 cm thick; the C horizon starts at 90 cm depth. The pH-KCl is about 2.9 in the humus layer and about 4.6 at 80 cm depth. The second stand ('Speuld', 52°15'N, 5°41'E) is located on preglacial sand deposits, which are less homogenous, especially in the subsoil (i.e. below 40 cm depth). The soil consists of an Orthic podzol or Luvisol (FAO/UNESCO 1974). The A horizon is very thin (7 cm) and the C horizon starts at 60 cm depth. The pH-KCl of the humus layer is 3.1 and 4.3 at 80 cm depth. The Speuld soil contains more loam than the Kootwijk soil, increasing the waterholding capacity. The hydraulic conductivity of the Speuld soil is slightly better than coarse sand according to Rijtema (1969; see Florax et al. 1990) and is better than that of the Kootwijk soil (Tiktak & Bouten 1990). The ground is level in both stands, and tree age and number of trees per hectare are similar. At Kootwijk, site productivity is about 60% lower than at Speuld. For detailed information on the sites see Olsthoorn (1991) or Mohren (1991).

FIELD STUDY: DETERMINATION OF FINE ROOT DENSITY AND NEEDLE LOSS IN RELATION TO SOIL MOISTURE

Soil water potential on both sites was monitored twice daily in a sub-plot with tensiometers at depths ranging from 10 to 200 cm (Burt 1978). To obtain a continuous time series of soil water potential, the SWIF model (Soil Water In Forested ecosystems, Tiktak et al. 1990) was calibrated with data from tensiometer readings, Time Domain Reflectometry (TDR), neutron probe and measurements of soil water contents. For details, see Olsthoorn & Tiktak (1991).

In each stand, a small sub-plot of 10 x 11 m was established to sample fine roots up to 80 cm depth with a root corer in the early summer of 1987, 1988 and 1989. Methods and basic results of fine root density were reported in Olsthoorn (1991). Here, a summary of the data is presented, to describe the drought effect in the spring of 1989. To assess fine root density in early summer, 12 fine root samples up to 80 cm depth were taken with a root auger, on July 6 to 13 1987, May 26 1988 , and June 18 1989 at Kootwijk, and June 15 to July 3 1987, May 16 to 20 1988 and June 13 to 15 1989 at Speuld (Olsthoorn 1991). In both stands, periodicity of root growth was measured with the Perforon method (or perforated soil system; Olsthoorn & Tiktak 1991), originally developed by Van den Tweel & Schalk (1981) and Bosch (1984) for greenhouse trials. Roots inside tubular channels made by this method behave as if encountering natural open spaces or cracks in the soil (Whiteley & Dexter 1984) and can be observed with an endoscope. The channels are accessible from an insulated soil pit, through a perforated stainless steel plate. Fine root tips can be counted and recorded on video. In each stand, three dominant or co-dominant trees were selected for the Perforon studies (for details see Olsthoorn & Tiktak 1991). Root tips were observed monthly, to record the current activity of the roots. White root tips of Douglas-fir were assumed to be actively growing (Krueger & Trappe 1967), as they became brown within two weeks when growth had ceased. The monthly increase in stem diameter during the growing season was measured, using permanent increment bands on the trees that were being monitored for fine root activity. Only average data for the number of white root tips on both sites are presented (see Olsthoorn & Tiktak 1991 for more details). For comparison with root dynamics, average needle loss in each period was taken from Van der Maas et al. (1991) who measured needle loss by positioning 12 trays of 1 m^2 surface area randomly in both stands. Needles and small branches were collected, separated and weighed every 28 days.

SIMULATION STUDY: DESCRIPTION OF THE MODEL OF WATER UPTAKE

Water uptake was calculated using a model derived from Kowalik & Eckersten (1984), that describes the water flow in the Soil - Vegetation - Atmosphere - Transfer model (SVAT) in an elementary way. Water uptake by roots (U, g m^{-2} s^{-1}) must replenish the amount of water in the tree (V, g m^{-2}) that is lost by transpiration. The model calculated total water uptake (U) by the roots using:

$$U = (\psi_s - \psi_l) / (r_r + r_p) \qquad (1)$$

This is the equation from Van den Honert (1948), where ψ_s is soil water potential in the root zone (MPa), ψ_l is leaf water potential (MPa), r_r is the resistance for water flowing in the soil to the root surface (MPa s m^2 g^{-1}), and r_p is the internal plant resistance for water transport to the leaves in the transpiration process (MPa s m^2 g^{-1}). See also Hinckley et al. (1978 and 1991). The transpiration (E_t, g m^{-2} s^{-1}) was calculated according to Monteith (1980). The influence of root density on water uptake was taken from Feddes & Rijtema (1972). Each root was attributed a cylindrical soil volume to calculate the distance between the roots (see also De Willigen & Van Noordwijk 1987, p. 173). The model had been adapted to Douglas-fir stands on sandy soils in The Netherlands by Florax et al. (1990), and their version of the model (PLAWAT: plant water status) was used here. Descriptions of water uptake into fine roots (equations 2 and 3) were taken from Feddes & Rijtema (1972) and Feddes (1981).

Soil hydraulic resistance for flow of liquid water in the soil and from the soil into the root surface, r_r (MPa s m^2 g^{-1}) is the sum of the series-linked resistances to flow of liquid water in the soil and from the soil into the root surface:

$$r_r = b / K(\psi_s) \qquad (2)$$

where $K(\psi_s)$ is the unsaturated soil hydraulic conductivity (g m^{-1} s^{-1} or cm s^{-1}) as determined by soil water potential. The empirical root density resistance factor b (MPa) takes into account the length and geometry of the root system (Feddes 1981):

$$b = \ln(r_2 / r_1) / (2 \times \pi \times L_v \times L) \qquad (3)$$

where r_1 is the root radius (cm); r_2 is half the mean distance between roots in the soil body (cm); L is the effective rooting depth in the soil profile (cm), L_v is the length of the roots per unit soil volume (cm cm^{-3}). According to Gardner & Ehlig (1963) and Feddes & Rijtema (1972) the value of b usually takes on a value around $4\ 10^{-6}$ MPa.

Input data for the model calculations for a hypothetical situation were: weather conditions, stand characteristics, physical soil characteristics (hydraulic conductivity), soil water potential and root density. The calculations were performed using data from three clear sunny days in September. The leaf area index was set to 6, based on Mohren (1991). The soil water potential in the model runs was set to -0.1 MPa or -1.0 MPa. The hydraulic conductivity was taken from Rijtema (1969) for two simplified soil profiles, roughly corresponding to the Kootwijk and Speuld field sites. No attempt was made to accurately describe the hydraulic characteristics of these sites, but instead a simplified approach was taken, taking only one layer into account. The soil water potential remained constant during the run, as only the short-term consequences of different fine root densities were assessed. The time step in the model is one minute. In the calculations, water uptake occurs in a soil layer of 75 cm depth with a root density (L_v) that is uniform in vertical direction. The root density in the model runs was varied from 0.01 to 5.0 cm cm^{-3}. At the highest root density, the capacity for uptake of water is near maximum (De Willigen & Van Noordwijk 1987, p. 150). For each run a different value of b was calculated, resulting in a different r_r, and subsequently different water uptake and transpiration rates. Each run of three days was preceded by three days with the same weather, soil moisture and fine root conditions, to initialise stored water in the tree (V).

Results

FIELD STUDY: SOIL MOISTURE

In 1988, precipitation was distributed fairly evenly over the year, as is common for Dutch climatic conditions, and thus, 1988 can be considered a normal year, without periods of drought. In 1989, a long dry period occurred in the spring, followed by a summer with some short warm dry periods, interspersed with some heavy showers. The soil water potential at both Kootwijk and Speuld was lower in 1989 than in 1988. The water potential in the topsoil (at 15 cm depth) fluctuated more than in the subsoil (at 80 cm depth). At Kootwijk, the water potential was much lower than at Speuld for prolonged periods in both years. In the summer of 1988, the soil water potential at Kootwijk only fell below -0.10 MPa for two short periods in June and July. In 1989, these periods were much longer; there were three periods between May and August when this occurred at 15 cm depth, and at 80 cm depth the soil water potential remained below -0.10 MPa from July up to December. At Speuld in 1988, the soil water potential did not fall below -0.10 MPa. In 1989, the periods with a water potential below -0.10 MPa were very short. The soil water potential at 80 cm depth did not fall below -0.08 MPa in both years. Conditions of soil moisture and precipitation for the years 1988 and 1989 were described in detail in Olsthoorn & Tiktak (1991).

FIELD STUDY: FINE ROOT DENSITY

Fine root density in early summer at Kootwijk was 0.29 cm cm^{-3} in 1987 and 0.28 cm cm^{-3} in 1988 (average fine root density in mineral soil 0 - 80 cm depth; Table 7.1; data from Olsthoorn 1991). The comparable figures for Speuld were 0.24 and 0.23 cm cm^{-3}. In 1989, after a dry spring, the average fine root density at Kootwijk was only 0.03 cm cm^{-3} and at Speuld 0.04 cm cm^{-3}. In the dry year, 1989, the fine root density was reduced by 89 % at Kootwijk and 83 % at Speuld. The specific root length (SRL: average length of fine roots per gram dry weight, in m g^{-1}) in 1987 and 1988 was between 5.5 and 6 m g^{-1} at Kootwijk and around 6.8 m g^{-1} at Speuld. In 1989, there was a reduction in the SRL, with the SRL being around 3 m g^{-1} at Kootwijk and around 4 m g^{-1} at Speuld. This implies that in the fine root fraction (< 2 mm) it was mainly the thicker roots that persisted under the dry conditions. This explains why the fine root biomass in 1989 in both sites was somewhat less affected than the fine root density.

The root tip activity in 1988 and 1989 is presented in Figure 7.1 (data from Olsthoorn & Tiktak 1991). In 1988, there was a peak in the fine root activity in early spring, which decreased after onset of diameter increment (Fig. 7.1). The number of growing root tips per unit of soil volume was less in the subsoil. Although

Table 7.1.

Summarised fine root data in early summer, up to 80 cm depth: average fine root density (in mineral soil), total fine root biomass (dry weight) per hectare, and average specific root length (SRL) in both stands of the ACIFORN project. Data are average of 12 samples (except in 1987: 37 and 55 samples at Kootwijk and Speuld respectively) with an 8 cm diameter root corer up to 80 cm depth. For Speuld, the average of two subplots are presented (details, coefficients of variation and additional data in Olsthoorn 1991). To compare 1989 with the preceding years, the decrease in fine root biomass and SRL is given from the average data for 1987 and 1988, as they were comparable in moisture conditions in winter, spring, and early summer.

Site	Year	Density ($cm\ cm^{-3}$)	Biomass ($kg\ ha^{-1}$)	SRL ($m\ g^{-1}$)
Kootwijk	1987	0.29	3944	6.19
	1988	0.28	4327	5.56
	1989	0.03	1066	3.18
Decrease in 1989:		89%	71%	46%
Speuld	1987	0.24	2768	6.90
	1988	0.23	2989	6.80
	1989	0.04	990	4.03
Decrease in 1989:		83 %	66 %	41 %

measurements at Kootwijk started at a later date in spring 1988, the general pattern for 1988 appeared to be the same at both sites. In 1989, the dry year, the pattern at Speuld was similar to 1988, but at Kootwijk, the fine root activity in summer was higher than in 1988, after the mortality of roots in spring (Table 7.1). At Kootwijk, the diameter increment stopped temporarily in the summer of 1989, and the final diameter for the year was achieved in September.

FIELD STUDY: NEEDLE LOSS

The effect of drought on annual needle loss was large (Table 7.2). In moist years, the annual needle loss at Kootwijk is smaller than at Speuld, as can be expected from the differences in site quality and the associated differences in LAI (Whitehead et al. 1984; Mohren 1991). The amount of needles lost on both sites was much larger in 1989 than in 1988, and the increase at Kootwijk (94 %), led to an annual needle loss in 1989 that exceeded the needle loss at Speuld (53 %). This can also be seen in Figure 7.2. In 1988, needle loss on both sites was largest in September and October. In 1989, the pattern in needle loss was completely different, as a result of the drier conditions. At Kootwijk, the amount of needles lost in July already exceeded the total needle loss in the year 1988; it peaked in August, with continuing high needle loss in October. At Speuld, the reaction to drought was more restrained, with a steady increase in the needle loss until October.

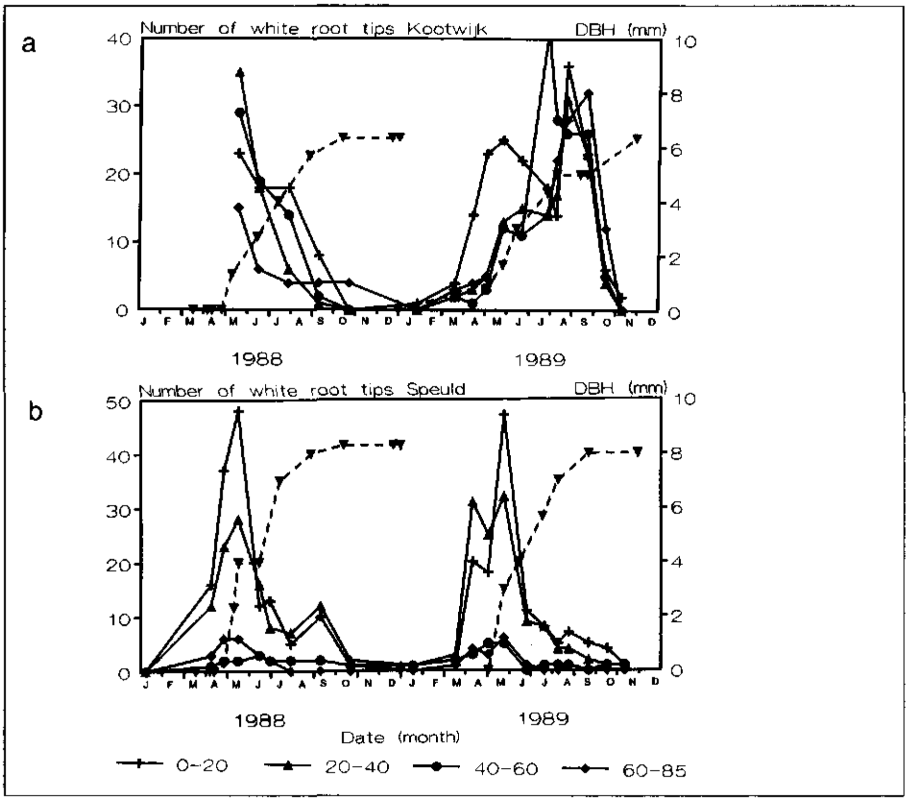


Figure 7.1.
Number of visible white root tips of Douglas-fir in three Perforon root cellars and average diameter increment at breast height (DBH) of the three observed trees (cumulative per year) during 1988 and 1989 per soil layer in a) Kootwijk and b) Speuld (legend: depth indicated in cm; dashed line is DBH increment).

Table 7.2.
Total needle loss in 1988 and 1989 at Kootwijk and Speuld. Data are the average of 12 sampling points of 1 m^2 each, collected every 28 days (data from the Department of Soil Science & Geology, Wageningen Agricultural University, published in Van der Maas et al. 1990; coefficients of variation not published).

Site:		Year:	Needle loss (g m^{-2})
Kootwijk		1988	177
		1989	344
	Extra loss in 1989:		94 %
Speuld		1988	219
		1989	335
	Extra loss in 1989:		53 %

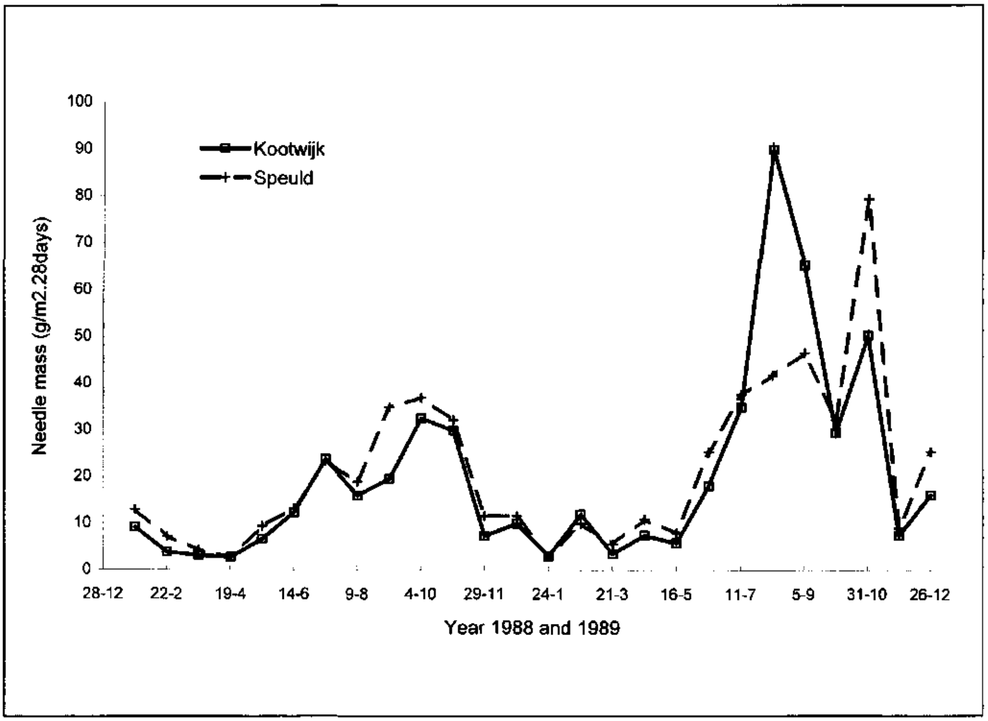


Figure 7.2.
Needle loss in 1988 and 1989 at Kootwijk and Speuld (in g m^{-2} $28d^{-1}$, n = 12). Data from the Department of Soil Science & Geology, Wageningen Agricultural University, published in Van der Maas et al. (1990).

SIMULATION STUDY: EFFECTS OF FINE ROOT DENSITY ON WATER UPTAKE

The calculated transpiration (E_t) at a soil water potential of -0.1 MPa (pF 3) on two simplified soil profiles differing in hydraulic conductivity is presented in Figures 7.3a and 7.3b. The hydraulic conductivity of the Speuld site lies between coarse sand and loamy sand. The hydraulic conductivity at the Kootwijk site is lower than coarse sand, especially in dry soil (Tiktak & Bouten 1990; see also Passioura 1988). The diurnal pattern in the transpiration is directly related to incoming solar radiation. The highest transpiration rates are found around noon, whereas at night the transpiration rate is very low. The highest fine root density is unrealistic for Douglas-fir, but represents the transpiration when the root resistance does not limit water uptake. In this case, the transpiration is driven by canopy structure and stomatal resistance. Therefore, the transpiration on coarse sand is equal to that on loamy sand when the root density is 5 cm cm^{-3}. When water uptake is not restricted by root density, the average transpiration under these conditions, as estimated by the model, amounts to 2 to 2.5 mm per day.

The actual fine root densities in Douglas-fir plantations are less than the high value in the calculations. The simulated influence of a decrease in fine root density on coarse sand can clearly be seen in Figure 7.3a. At root densities equal or below 1.0 cm cm^{-3} the stomata close during the second half of the day or earlier. At the lowest fine root density, the water volume (V) in the tree decreases, as during daytime water uptake is less than is transpired, and water uptake during the night, cannot balance the water deficit in the tree to regain full turgidity before sunrise. In coarse sand, the transpiration at a soil water potential of -0.1 MPa may be limited by 80% during the afternoon, due to low fine root densities. The average transpiration at a root density of 0.2 cm cm^{-3} in this period of the year, as calculated with the model, is only 0.56 mm day^{-1}.

On loamy sand (Figure 7.3b), the transpiration is not limited by the lower fine root densities. Even at a fine root density of 0.03 cm cm^{-3} the transpiration is still at the maximum induced by the evaporative demand, and stomata remain open. Only at the lowest fine root density in our model runs, 0.01 cm cm^{-3}, is the transpiration slightly limited during the afternoon hours. On days with comparable weather conditions, a transpiration of 2 to 3 mm per day was calculated from soil moisture changes at the Speuld site (Bouten 1992).

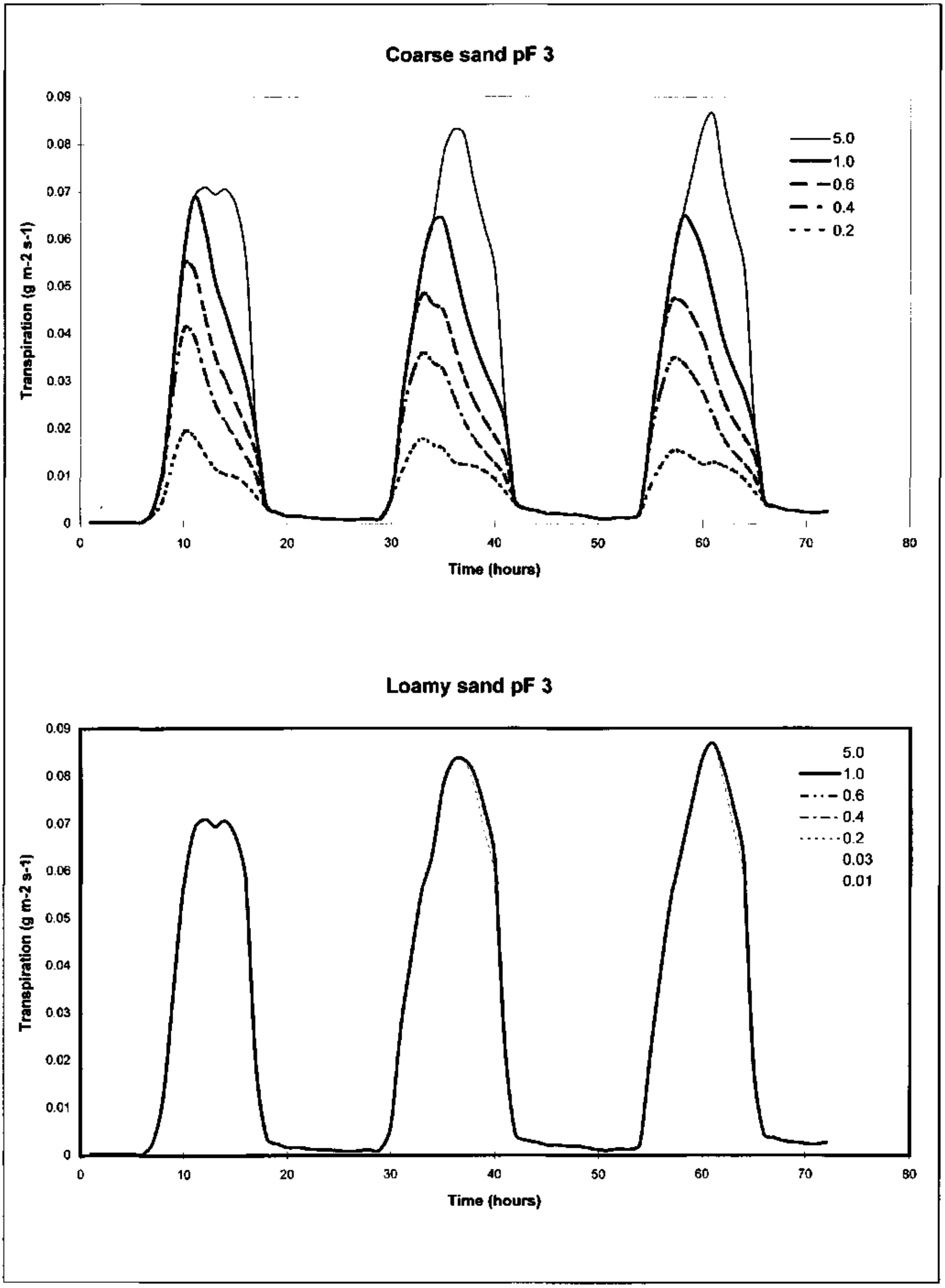
When the water potential of the soil is very low, -1.0 MPa (pF 4), the hydraulic conductivity in both soil types is lower (Rijtema 1969). The stomata close at 10 am, but the internal water deficits can be replenished during the night, so the next morning, the stomata can reopen for several hours (graphs not shown). On coarse sand at -1.0 MPa, with fine root densities ≤ 1 cm cm^{-3}, the transpiration is restricted to the minimum. On loamy sand at -1.0 MPa, the transpiration is also limited when the fine root densities are smaller (graphs not shown). For nearly all fine root densities ≤ 1 cm cm^{-3}, the stomata close already in the morning. The transpiration is further limited when fine root densities decrease further (0.03 and 0.01 cm cm^{-3}).

Discussion

1) SITE DIFFERENCES IN REACTION TO DROUGHT

The influence of site quality on fine root biomass is often described (see e.g. references in Olsthoorn & Keltjens 1998; Keyes & Grier 1981; Kurz & Kimmins 1987; Santantonio & Hermann 1985; Vogt et al. 1983 and 1987). On a more favourable site (Speuld), the amount of fine roots in early summer is usually less than on dry sandy sites (Kootwijk), as is shown in Table 7.1. This interdependence emerges in spring or early summer. In most cases, the relationship is reversed after a drought (see e.g. references in Olsthoorn & Keltjens 1998; Squire et al. 1978).

On dry sites, less water is available, therefore the water is depleted more quickly, and fine root mortality may occur under high evaporative demand. In a previous chapter (Olsthoorn 1991) it was shown that the finer fraction of the fine roots is more likely to die in a dry period. As a result, the Specific Root Length (SRL) decreases after a period of drought. In warm weather, fine root mortality may occur already when the bulk soil has a water potential between -0.05 and -0.08 MPa (Olsthoorn & Tiktak 1991). Under those conditions, the water potential at the root surface may be near to or below the wilting point. Under more favourable site conditions, the water potential at the root surface remains higher for a longer period, and there is less risk of fine root mortality, as the initial water availability in the soil



Coarse sand pF 3

Loamy sand pF 3

Figure 7.3.

Canopy transpiration (E_t, in g m^{-2} s^{-1}) calculated with the PLAWAT model for different fine root densities (in cm cm^{-3}) during three days (day 249 to 251 in 1988; time 0 is 0.00 hours of day 249), a) in coarse sand and b) in loamy sand. Soil water potential of the bulk soil at each model run was -0.1 MPa.

is higher, and the water is transported to the roots more quickly because of a greater hydraulic conductivity (see also De Willigen & Van Noordwijk 1987, p. 150).

Figure 7.1 shows that the reaction of the fine roots at Kootwijk to the rain events in 1989 was more pronounced than at Speuld. Despite the lower fine root densities in 1989 at both sites, the possibilities for water uptake were adequate at Speuld, as the soil did not dry out so much. At Kootwijk, large amounts of needles were shed at the beginning of summer in 1989 (Fig. 7.2). This is an adaptation to decrease evaporative demand (Tyree & Sperry 1988; Borchert 1991), and new fine root growth is possible only when water becomes available again. In an irrigation experiment in mature conifer forest, De Visser et al. (1994) found a clear relation between water availability and time of needle shedding: in the irrigated treatments, needle shedding occurred later in the autumn.

The net result of the processes described above is that the dynamics of both fine roots and needles are more pronounced at the site with the lowest water availability, in this case at Kootwijk (Table 7.2 and Fig. 7.2). Kootwijk normally has the lower LAI, and a higher risk of losing more needles during long dry periods. After rain events, there is substantial fine root activity at Kootwijk to restore the initial fine root density. If large amounts of foliage are shed (several age classes), it may take several years for conifers to reach their maximum LAI value. At the drier site, the fine roots show greater mortality and the canopy sheds more needles during a drought episode, whereas the initial fine root density is larger and the initial needle biomass is smaller than the more favourable site. If fine root mortality occurs during a longer drought period, the thicker and more persistent fine root fraction forms the remaining apparatus for water uptake (Olsthoorn 1991). When the conditions for a large transpiration demand persist, the rate of water uptake per unit of fine root length increases, and the water potential in the rhizosphere decreases further. This could endanger the remaining thicker fine root fraction.

2) SIMULATION OF ROOT DENSITY EFFECTS ON WATER UPTAKE

The model calculations demonstrate that in soils where the hydraulic conductivity is large enough even in dry conditions, e.g. in loamy sand, the direct effects of a reduced fine root density on water uptake and transpiration are limited. On coarse sandy soils where the hydraulic conductivity is small, especially under dry conditions, a reduced fine root density results in reduced water uptake and limited transpiration. This, together with the overall lower water availability, explains the great susceptibility to drought of Douglas-fir on dry sandy soils in The Netherlands.

A more detailed model would enable the additional effects of a shallower fine root system to be calculated. The present model would show that halving the average rooting depth will automatically limit the transpiration by half. Under field conditions, both fine root density and water capacity decrease with increasing soil depth, and a reduction of rooting depth has a less pronounced effect. Mohren & Van de Veen (1995) used the FORGRO model on a Norway spruce stand in Solling (Germany), with an estimation of transpiration similar to PLAWAT, but including information on fine root density at different depths in the soil. The stem growth in that case decreased by only 5 %, when fine root depth was restricted to 40 cm depth (with the same total fine root biomass). The effects of differences in fine root density on short-term water uptake in their model were limited, when the fine root density was in the range of densities found in mature Douglas-fir stands in The Netherlands.

3) INCREASED BIOMASS DYNAMICS INDUCED BY SOIL ACIDIFICATION AND NITROGEN ENRICHMENT

Soil acidification and nitrogen enrichment have probably limited fine root density by more than 50 % (Olsthoorn & Keltjens 1998). The same effect found on the drier sites with low hydraulic conductivity during periods of drought (see discussion point 1: increased fine root mortality in a drier rhizosphere under extreme conditions) probably results from the decrease in fine root length caused by soil acidification: water potential gradients in the rhizosphere will become steeper, and conditions bringing about fine root mortality will occur more often. In a field trial with applications of ammonium sulphate, Persson et al. (1995) demonstrated that the mortality of fine roots especially in the topsoil increases with increasing application rates. When enough fine roots have died, a tree may die from desiccation. Linder et al. (1987) have shown that high transpiration demands resulting from increased foliage area after fertilisation may indeed lead to tree mortality during severe drought (see also Benson et al. 1992). Landsberg (1986) reported from the same experiment that the lowest soil water potential occurred in the fertilised treatments in 20-year old *Pinus radiata*, as a result of increased transpiration as compared with the unfertilised control (see also Myers & Talsma 1992). The lowest pre-dawn water potentials in the foliage also occurred in the fertilised treatment: -1.5 MPa. Linder et al. (1987) already warned of the dangers accompanying high nitrogen fertilisation rates in areas with regular long dry periods. The effects of the drought in the Australian experiment might have been even larger if the nitrogen concentrations in the fertilised treatment had been supra-optimal, as is common in The Netherlands under present deposition levels (Van den Burg 1990).

4) AN ELEMENTARY MODEL TO DESCRIBE FINE ROOT DYNAMICS

Fine roots grow when carbohydrates are available to the root system, temperatures are above 5 °C and soil moisture is not limiting (Kuhns et al. 1985; Burke & Raynal 1994). They die when carbohydrates are inadequate to sustain maintenance requirements, or when the soil is too dry (Coutts 1982; Dambrine et al. 1995). In forests, transpiration often recovers very slowly when precipitation resumes after a prolonged drought (Lyr & Hoffmann 1967; Edwards & Dixon 1995; De Visser 1994). The dieback of fine roots under dry conditions increases the resistance for water uptake, and it takes time to restore the original fine root density. Shorter periods of dry conditions often lead to quick re-establishment of transpiration (Cermak et al. 1980). In the latter case, the fine roots can probably overcome the dry period, and no extra fine root mortality occurs.

In Figure 7.4, two curves indicate how fine root growth might take place. A tree starts with one growing root tip with a fixed growth rate in a homogenous volume of soil (1 m^3 in this example). One or two centimetres behind each growing root tip, the root branches, and the new root tip also grows at this rate. The ongoing branching and root growth lead to a fully developed fine root system exploring the entire soil volume within several years. Fahey & Hughes (1994) and Dye (1996) gave indications for the time needed for a tree root system to reach a full density: within 4 and 10 years from planting respectively. The curve representing the fastest growth in Figure 7.4 is based on an average growth rate per root tip of 5 cm per month, and a branching index of 1 cm^{-1}, implying that with each centimetre root growth, one branch will develop. This results in the establishment within 8 months of a full grown fine root system with a fine root density of 0.6 cm cm^{-3} that is commonly found in the mineral topsoil (0-30 cm) in Douglas-fir stands in The Netherlands (Olsthoorn 1991). The slower growth curve is based on an average growth rate of each root tip of 1 cm per month, and a branching index of 0.3 cm^{-1}. In this case, it takes 52 months of growth before an average root density of 0.6 cm cm^{-3} is achieved. The present model does not include differences in growth rate during the season, e.g. in different temperature or moisture conditions.

The curves in Figure 7.4 are only intended to demonstrate the effects of root growth rate and of the branching index. In reality, there will be a difference in growth rate of main fine roots and lateral fine roots (long and short roots, according to Sutton & Tinus 1983). In the Perforon root observation cellars (Olsthoorn & Tiktak 1991), the greatest observed growth rate was 5 cm per two weeks in an open space (with 100 % relative air humidity). Bartsch (1987) noted a maximum growth rate of 4.8 mm day^{-1} for Norway spruce seedlings and 12.3 mm day^{-1} for Scots pine. Kuhns et al. (1985) demonstrated that growth rate of root tips is not only related to

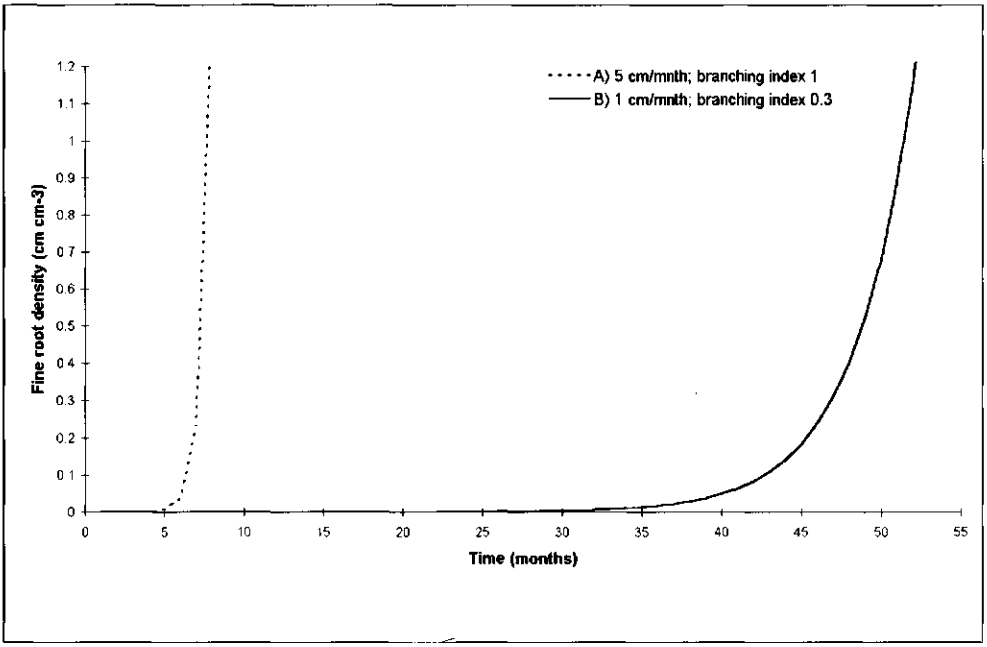


Figure 7.4.

Simple model for increase in fine root density with A) quick and B) slow growth rate, with respectively 5 and 1 cm elongation per month for each root tip, and branching index of respectively 1 and 0.3 cm^{-1}. All fine root tips are assumed to have the same constant elongation rate and branching index.

temperature (with a minimum of 4 °C and an optimum of 20 °C), but also to soil water potential. Teskey & Hinckley (1981) found a maximum growth rate of 5 mm day^{-1} at -0.1 MPa for *Quercus rubra*. Morrow (1950) showed varying growth rates for sugar maple through the year: from 0.6 to 1 mm day^{-1} between March and June, with a total of 78 mm yr^{-1} (0.6 cm $month^{-1}$). In red pine, Wilcox (1968) found an influence of the branching order: the primary root grew 5 mm day^{-1}, first order laterals grew 3 mm day^{-1}, and second order laterals 1.5 mm day^{-1} during the spring. Later in the year growth rate declined, or root tips became dormant. Lôhmus et al. (1991) showed that long roots (tender roots) grew 102 - 777 mm yr^{-1} (0.8 - 6.4 cm $month^{-1}$), while short roots (absorbing roots) only grew a maximum of 15 mm yr^{-1} (0.1 cm $month^{-1}$). The growth rates recorded for root tips of different tree species are usually of the long root type, while the total numbers of root tips of the higher order lateral short root type are much higher. The growth is usually recorded in favourable circumstances, early in the season and under moist conditions. Given the observations of Fahey & Hughes (1994) and Dye (1996) that a fine root system establishes itself within 4 to 10 years from planting, the extensive data of Lôhmus et al. (1991) seem most valid. Therefore, the slow growth curve seems the best approximation of fine root growth rates for Douglas-fir under Dutch climatic conditions.

The growth as described in Figure 7.4 can be made more complex by accounting for different growth rates during different parts of the year, for different branching orders of fine roots, and by accounting for different temperatures, and for fluctuations in soil moisture. In the example in Figure 7.4, no mortality has been included yet. Adding mortality, e.g. as resulting from a maximum root life span, would result in a slower increment of the curves after some time, and the establishment of a maximum density.

When a drought causes fine root mortality, the fine root density can decrease rather quickly, within several days or weeks (Olsthoorn 1991). Under the present acidification conditions, the fine root density at Kootwijk decreased to approximately 0.06 cm cm^{-3} in the top mineral soil (0 - 30 cm) after the dry spring in 1989, which is only 10 % of the initial fine root density in early summer. Based on data from Olsthoorn & Keltjens (1997), the fine root density in periods with only a background deposition, when Al was virtually absent in the soil solution, must have been at least twice as high in the mineral topsoil, i.e. approximately 1.2 cm cm^{-3}. When the fine root density is higher, moisture gradients in the rhizosphere are smaller, and the risk of fine root mortality during a drought is smaller. Hence, a drought comparable to the one in 1989 might have resulted in e.g. a 20 % survival of the roots after the drought, as a first assumption. This would lead to a totally different starting position for regrowth in periods with favourable growing conditions after drought. In Figure 7.5, this is illustrated with the slow growth model from Figure 7.4. In the background deposition scenario (no soil acidification), it would take some 6 months for the roots to regrow to the situation prior to the drought. With the same growth model, this regrowth would take approximately 9 months under present deposition conditions (with soil acidification). However, because of the adverse effects of Al on fine root growth, especially on the elongation process (Godbold 1994), SRL will be smaller (Olsthoorn & Keltjens 1998), and the fine root density will increase more slowly, even if the same amount of carbohydrates are available for fine root growth. Boxman et al. (1995) found increased root growth in mature conifer forest under soil conditions where only a background deposition is present in the throughfall water, compared to a control plot with ambient soil conditions (see also Van Dijk et al. 1990). Therefore, it is more likely that the growing rate per root tip will be reduced by some 50 % under current conditions, increasing the period of regrowth to 17 months. In practice, the period of regrowth will be spread out over an even longer period, as during winter temperatures are too low for root growth, and in summer the soil is periodically too dry (even in a maritime temperate climate).

In a study of the effects of long dry periods in NW Europe during the summers of 1947, 1952, 1964, 1976, 1983, Spiecker (1991a, b) found that the best prediction for forest growth was a drought index that included weather data from the five preceding years. He also noted that suppressed trees often died in the year after a severe drought, not during the drought period itself. In The Netherlands, Memelink (1951) and Sipkens (1952) found that it took Japanese larch 2 to 4 years to recuperate from the 1947 drought. Douglas-fir recuperated somewhat faster, but also suffered several years of increment loss. Grandjean (1960) found top-shoot mortality and individual tree mortality in 1960 as a result of the drought in 1959 in The Netherlands. Payette et al. (1996) found that periods of decline of sugar maple in North America, associated with dieback of individuals or large scale insect damage, usually lasted more than one year after dry summers. Using tree ring analysis in a

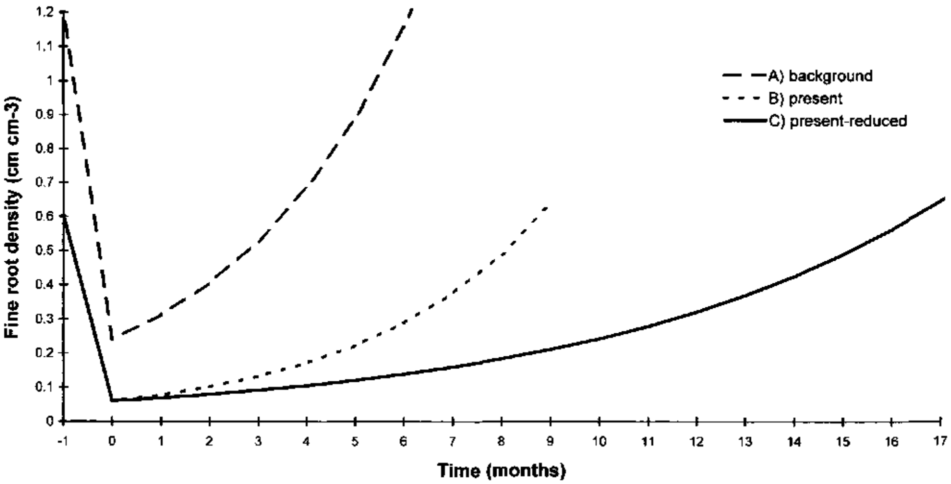


Figure 7.5.

Development of fine root density during and after a drought. Scenarios with soil conditions A) under background deposition, B) under present deposition, and C) under present deposition and reduced root growth rate. For assumptions see text.

mixed stand, Abrams et al. (1997) concluded that there had been substantial tree mortality after the drought in 1930 in Virginia (USA), with large effects on forest succession, as the least drought-tolerant tree species were particularly affected. Holstener-Jørgensen & Holmsgaard (1994) found that growth in a year following a severe drought (1976 in Denmark) was less than during the drought year itself (see also Holmsgaard 1955, for comparable data from earlier droughts). In a drought experiment during 1976, Holstener-Jørgensen & Holmsgaard (1994) found that the weather effect lasted for more than one year, even with abundant rain in 1977. In the UK, Power (1994) showed that apical growth in 1977 was less than in 1976. Peterken & Mountford (1996) even found a growth reaction up to eight years after the same drought period, while growth was normal before 1976. According to their measurements, the effects lasted longer on shallow soil profiles, where one would expect the dynamics in fine root density to be more pronounced. Lyr & Hoffmann (1967) showed that many fine roots die in a drought, and interpreted the resulting growth depression as a long-lasting limitation for photosynthesis.

As a result of soil acidification and nitrogen enrichment, trees are forced to operate at a lower fine root density, nearer to desiccation. As this desiccation level is largely unknown, no prediction can be given of conditions lethal to the tree or stand. The influence of soil acidification on this process cannot be quantified separately, but in principle the fine root density before a drought starts is already at a lower level (Olsthoorn & Keltjens 1998), and fine root mortality will increase. This is likely to result in a lower starting point for root density regrowth when growing conditions become favourable again, with the added disadvantage of a lower growth rate due to the adverse effects of Al on fine root growth. The risk of desiccation of individual trees will be higher than before the acidic deposition started, especially if an extreme drought event occurs after a period of several years in which growing conditions have been favourable, resulting in high LAI.

Conclusions

1) On dry sites the temporal fluctuations in Douglas-fir biomass, both for fine roots and for needles, are larger than on more favourable sites. This leads to different dynamics: greater mortality in a drought on drier sites, and more regrowth when conditions become favourable again, to re-establish the necessary level of fine root and needle biomass.

2) Differences in fine root density do not have large consequences for water uptake during short periods of drought (up to several days), unless the hydraulic conductivity of the soil is very low under dry conditions.

3) Differences in fine root density probably have major repercussions during longer drought periods. The decreased fine root densities induced by anthropogenic acidic deposition will therefore lead to greater mortality for fine roots and needles in a drought.

4) An elementary model describing fine root dynamics indicates that a reduction in

fine root density through accumulated acidic deposition means that a longer period is needed for the fine root system to recover to a normal level after a prolonged drought. Limitations in the uptake capacity after a severe drought explain why forest growth is sometimes restrained for more than one year.

As a result of the inferences stated above, the final conclusion is that the anthropogenic acidic deposition and the associated eutrophication has increased the biomass dynamics of Douglas-fir, comparable to the larger biomass dynamics on dry sites, relative to more favourable sites. Consequently, the susceptibility of Douglas-fir in The Netherlands to drought has increased. It cannot be predicted under which drought conditions Douglas-fir stands will suffer severe damage, but it is clear that soil requirements have to be taken more seriously when establishing a plantation in sandy soils affected by acidic deposition. The dry years in recent decades have not caused visible large scale tree mortality, although the needle retention of Douglas-fir in the Dutch annual vitality inventory has been decreasing since 1983 (Hilgen 1995; Reuver 1997). The same arguments appear to be valid for other tree species in The Netherlands with high water requirements, such as Norway spruce or Japanese larch, especially for those tree species whose aluminium tolerance is less than that of the relative Al-tolerant Douglas-fir.

Acknowledgements

We are grateful to N. van Breemen, C.J.M. Konsten en M.P. van der Maas, and E. Veldhorst (Wageningen Agricultural University, Dept. of Soil Science and Geology) for permission to use needle loss data; to G.M.J.H. Ackermans, A. Verdoes, J.M. Klap, C. van der Haar, M. Stempher, and W. de Bruijn (Wageningen Agricultural University, Dept. of Forestry) for processing roots; and to J. van den Burg for literature suggestions. Valuable comments on the manuscript were made by W.G. Keltjens. P.J. Kowalik from Gdansk, Poland provided the initial version of the original SVAT model and assisted with J.P.G.G.M. Florax in the use of the model. Ms. J. Burrough-Boenisch gave advice on the English.

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8. Epilogue

The field work for this study started in 1986 in two forest stands on sandy soils without groundwater influence, and many aspects of the forest ecosystem were monitored until the end of 1989. The first year was used to check the methods for root research, both in the field and in the greenhouse. In this chapter, the outcome of the project is presented under headings about scientific and methodological achievements, and the implications for forest management are discussed. Finally, some remaining ecological issues for root research are listed and future developments are anticipated.

Scientific achievements

SITE QUALITY AND EFFECTS OF DROUGHT ON FINE ROOT MORTALITY

The unusually dry spring of 1989 brought about a clear response in the fine root density in early summer. This difference with the preceding two monitoring years was very fortunate, as it led to hypotheses on fine root dynamics, especially about the mortality that may occur in dry periods. In normal or moist years, the fine root density in early summer is greater on dry sites than on more favourable sites (Chapter 2). This strategy probably minimises the risks of fine root mortality in a drought, as a greater root length enables the water potential in the rhizosphere to remain closer to that in the bulk soil (Chapter 7). On the dry site in particular, however, the long dry period in spring (1989) had major effects on the fine root density in early summer, despite this greater root density (Chapter 2). If the initial fine root density had been smaller, the proportion of fine root mortality might even have been larger. The net result is that on dry sites, the mortality of fine roots and needles alike is greater in periods of drought than on more favourable sites (Chapter 7).

ALUMINIUM AND NITROGEN EFFECTS ON FINE ROOT DENSITY

To mimic acidification of forest soils, different amounts of ammonium were added to containers filled with sand in a greenhouse trial with one-year-old Douglas-fir seedlings (Chapter 5). A gradient developed in the soil, with high levels of ammonium near the top of the containers, and high levels of nitrate near the bottom of the container, because of the difference in mobility in soils. The moisture condition was monitored closely, so all plants grew at exactly the same water potential, and no water left the containers. In the test period (8 months), buffering of acidification even took place, by aluminium dissolving. The conditions in the trial therefore were very similar to field conditions. Nitrate was the dominant nitrogen form in root uptake, unless large amounts of ammonium were readily available: near the top of the containers receiving the largest dose (Chapter 5). This trial and other literature sources have shown that ammonium and aluminium in a mixture reduce the fine root length of Douglas-fir (Chapters 5 and 6). Ammonium and aluminium are also present in a mixture in acid sandy soils in The Netherlands. The aluminium and the nitrogen effects in the trial cannot be separated, as ammonium uptake can lead to a lower pH in the rhizosphere, and aluminium might be present in more toxic forms or concentrations than in the bulk soil in which we measured the aluminium concentration.

Many authors have focused on the lethal effects of aluminium on fine roots, yet lethal concentrations are rare in forest soils, and therefore the effects of sub-lethal concentrations are more important. It is clear that aluminium at sub-lethal levels sharply reduces fine root length when the threshold concentration in the soil solution of forest soils is exceeded (Chapters 5 and 6). Fine root biomass is less affected. The concentration of toxic forms of aluminium is high, especially in the subsoil. In the topsoil, aluminium is partly buffered by dissolved organic carbon (DOC).

The availability of nitrogen mainly has an effect on fine root biomass (Chapter 7). However, the influence of nitrogen on the fine root biomass has to be treated carefully. The shoot:root ratio always increases with increasing nitrogen levels, but this does not mean that fine root biomass always decreases. There is a range of nitrogen availability where the fine root biomass increases with increasing nitrogen level to a maximum biomass (see Fig. 6.1: an optimum curve). This range was exceeded in The Netherlands many years ago (Chapter 6), and the biomass of fine roots is currently lower than before the start of large-scale intensive livestock farming in The Netherlands, when nitrogen levels were sub-optimal in forests on sandy soils.

Both aluminium and nitrogen work in the same direction towards a lower fine root density, but the aluminium effect on root length dominates the nitrogen effect on fine root biomass under present Dutch conditions (Chapter 6). The anthropogenic acidic deposition and the nitrogen enrichment have increased the biomass dynamics of Douglas-fir on sandy soils, both for fine roots and needle biomass, by analogy with the greater dynamics of dry sites relative to more favourable sites. The general conclusion of the thesis is that this has enhanced drought susceptibility and the probability of tree mortality in a drought.

MYCORRHIZAL FREQUENCY AND DEPTH OF ROOT TIPS

Though mycorrhizae were outside the scope of the study, some data about mycorrhizae are presented in Chapter 3. It was shown that the mycorrhizal frequency on root tips in the forest soil is constant at all soil depths for Douglas-fir in The Netherlands. Baar (1995) has shown the same for Scots pine in The Netherlands. This is an important observation, as many mycorrhizal studies only take samples of mycorrhizal roots in the litter layer and the mineral topsoil. Sampling of mycorrhiza should not be restricted to the topsoil or the litter layer, particularly if the species composition of the mycorrhizal fungi differs per soil horizon. Of course, there are fewer root tips in the subsoil (below 30 or 40 cm depth), but there too the occurrence of mycorrhiza is important for root functioning.

Appendix 1 lists some additional observations on the types of mycorrhiza, and the frequency of the different types in both field plots. The observations suggest that the tolerance of drought varies among mycorrhizal types, but there could be an interaction with site effects.

Methodological achievements

To observe fine roots, the soil ecosystem has to be disturbed: either by sampling roots destructively, or by installing a structure to gain access to the soil, with the risk of influencing the soil environment too much for undisturbed root growth. Each method of root research has its specific goal, and should cause no reaction of the roots for that feature. If other features are affected, the method can still be reliable. In this study, several methods were used, though not all were successful.

PERFORON METHOD

At the Department of Forestry of the Wageningen Agricultural University, a new method for root research, the Perforon method or perforated soil system, was available for research. We adapted this method to the field situation to study fine root growth of mature trees in the whole soil profile. The Perforon method is a very attractive method to study the belowground environment. It is described in Chapter 3 (see also Van den Tweel & Schalk 1981; Bosch 1984). Using an endoscope, root tips growing in horizontal channels in the soil can be observed very closely, to judge if they are alive or dead. Each few weeks, the ingrowth of new root tips can be counted. The data were used to study periodicity of root growth. The volume of soil that was perforated in the forest, was too small to be able to assess average fine root density, given the large variability in the fine root density (Chapters 2 and 4). In pot trials, the soil volume can be completely perforated in special containers, so enabling more quantitative data to be collected. Growth in the channels in the soil seems fairly normal, because branching occurs and fine roots sometimes survive for long periods (a few roots were alive throughout the monitoring period: three growing seasons). However, as the visible roots are not growing surrounded by soil, the method is considered to be unsuitable for studying fine root mortality. The Perforon method has proved to be suitable for direct and detailed observations of fine roots (see also Appendix 1), and for the collection of soil ecology data in time series, including in field situations.

Although the method was only used for data on root tips, it provided a splendid view of the belowground ecosystem. Different soil fungi and soil animals were often seen, in beautiful structures and movements, apparently undisturbed by the cold light. Very often, it was not immediately clear what process was taking place; sometimes sequential recordings on video tape gave more information, e.g. on the branching behaviour of fine roots or the development of fungal structures. Observations of soil fauna can be time consuming but often lead to hypotheses on ecological processes in the soil, e.g. root development or fungal and animal interactions, which can be confirmed qualitatively by the Perforon method. In some cases, simulation models may be available to test the meaning of the identified processes more quantitatively, especially if relevant data are available in the literature. In most cases, it will be necessary to quantify these processes with other methods, e.g. in a laboratory with known fungus species, or with known numbers of animals.

Implications for forest management

SITE REQUIREMENTS OF TREE SPECIES

Anthropogenic acidic deposition has considerably changed site conditions on sandy soils in The Netherlands during the last two centuries: the aluminium concentration in the soil solution has increased, and forest ecosystems have become nitrogen saturated (Chapter 6). For Douglas-fir in The Netherlands, the Ulrich hypothesis could be quantified: the fine root system is less dense and more shallow than it would be without acidic deposition. This increases the mortality risks for fine roots in dry conditions, leading to a greater drought susceptibility of Douglas-fir. Therefore, the risks of tree mortality during or after a prolonged drought period have increased. Foresters can apply this knowledge in practice when choosing a tree species (or a mixture) for a specific site. They should pay more attention to the soil fertility demands of tree species than indicated in handbooks.

LONG GROWTH DEPRESSION AFTER PERIODS OF DROUGHT

The insight obtained into the dynamics in the fine root density can also explain why some very dry years have a long-lasting effect on forest growth (Chapter 7). Substantial fine root mortality from a severe drought can cause forest growth depressions of several years, as it can take several years to re-establish a root system sufficiently dense for substantial water uptake. Long-term data on forest growth, or tree ring analysis often show that growth decreases for several years. Improving the root density model in Chapter 7 might further clarify the rate of fine root regeneration after a severe drought. Data series on fine root density before, during, and after dry periods will be essential to calibrate (and validate) the model.

LIMING AS A PRECAUTIONARY MEASURE

The merits of liming to alleviate soil acidification by reducing aluminium toxicity, are still being debated. Recently, Binkley & Högberg (1997) concluded that in Sweden, where nitrogen availability is low almost everywhere, liming would reduce forest growth and forest health. Spiecker (1995) found that liming produced a small growth increase. Liming has a delayed effect on the pH in the soil profile. After five years, pH effects are only to be found in the litter layer (Van den Burg & Olsthoorn 1996). It takes longer for the pH deeper in the soil to be affected. The effects of liming are twofold: the pH of the soil increases, and the amount of available calcium in the ecosystem is increased.

The beneficial effect of a pH increase is that aluminium will react to the changing pH, and toxic forms will be virtually absent above a pH of 4.2 in the soil solution (~pH-H_2O). However, large amounts of lime are necessary to change the pH (e.g. over 3000 kg ha-1). It takes a very long time to change the aluminium chemistry for root growth substantially. In the topsoil, aluminium is partly buffered by dissolved organic carbon (DOC) in the soil solution, and liming will mainly have a detoxifying effect in the subsoil, where DOC is mostly absent (Chapter 6).

Forests on poor sandy soils are often short of calcium (Van den Burg & Olsthoorn 1996). Calcium is phloem immobile: it cannot move towards the root tip with the assimilates that are necessary for root tip growth (Marschner 1995). Therefore, it must be taken up from the soil solution during root growth. Liming eventually makes calcium available for uptake by plant roots. Only low quantities of calcium are necessary to increase the amount of calcium in the soil solution. On poor soils, phosphate too is often short. Most commercial phosphate fertilisers contain sufficient calcium to boost calcium uptake (Van den Burg & Olsthoorn 1996). If foliar analysis of trees reveals an apparent shortage of calcium, liming is a complicated method to increase the calcium available for root uptake.

Liming also has risks to the ecosystem, as it adversely affects ground vegetation, carabid beetles, and soil mycoflora, even if nitrogen mineralisation rates do not increase dramatically (Van Tol 1995). Given that the beneficial effects of liming are not completely clear (Binkley & Högberg 1997) and that it can so dramatically affect the natural state of the forest ecosystem, liming cannot therefore be advised as a practical measure. The best method to avoid toxic aluminium effects on root growth is to stop further acidification of the soil, by reducing emissions of sulphur and nitrogen. The soil will then gradually return to its natural condition with low levels of toxic aluminium, as shown in the model calculations in Chapter 6 (Table 6.1.). With the background deposition scenario, this took approximately 50 years in the model calculations (J. Kros, pers. comm.), as a first indication of the time needed for the restoration process.

Remaining ecological issues in root research

METHODS TO ESTIMATE FINE ROOT PRODUCTION

Chapter 3 presents an estimate of the allocation of carbohydrates in the root system. The calculation is based on certain generally accepted assumptions. However, there are no sound methods to estimate the production of fine roots and mortality of fine roots in different periods and under different conditions. The longevity of fine roots varies greatly, as it depends on the conditions after the root is formed. Dry conditions can cause a quick death (Chapters 2 and 7). The life span observed in the Perforon root cellars was from three weeks (in a dry period) to over three growing seasons (Chapter 3). Therefore, it is difficult to give an average for life span of fine roots, and the term 'fine root turnover' only makes it less transparent which processes are actually taking place. The basic problem is that it is impossible to guess the age of a root in undisturbed situations. Sampling with a root auger provides accurate data on fine root density and biomass, but it is impossible to determine age of the sampled roots. Visible roots in e.g. the Perforon method or behind glass walls in rhizotrons might behave completely differently from roots in soil. In the mini-rhizotron studies we performed, there was always condensation water on the plastic sheets, even in dry periods. Probably, the mini-rhizotron was slightly cooler than the surrounding soil, thus causing water vapour in the soil to condense. The mortality of the roots might have been completely different than in real soil. Therefore, a major breakthrough for root research would be a method to assess production and mortality without the drawback of different kinds of experimental disturbance. Many persons have been working on this problem for a long time, but there are no signs of this breakthrough.

ROOT DYNAMICS IN MODELS SIMULATING FOREST GROWTH

The effects of a low fine root density on root dynamics and on forest growth after a severe drought (Chapter 7) point to the importance of proper descriptions of the dynamics in fine root density in models simulating forest growth. In the Australian Biology of Forest Growth project (BFG), the forest growth model BIOMASS described forest growth in irrigation and fertilization experiments in mature forest very well, except after severe drought (McMurtrie & Landsberg 1992). In that case, forest growth was overestimated in the year after the drought period. It seems that some physiological responses were incompletely or incorrectly incorporated in the model. This could be the malfunctioning of several plant parts after drought, with the slow recovery of the fine root density after drought periods as an important part of the explanation. Unfortunately, no data on fine root density were collected in the BFG experiment.

In the elementary model for fine root growth (Fig. 7.4), the description of growth could be made more realistic, by including different growth rates:

a) in different parts of the year (internal periodicity of the trees),
b) for different temperatures,
c) for fluctuations in soil moisture,
d) for different branching order of fine roots (long and short roots), and
e) for different soil depths or horizons.

In calculations of fine root production and mortality, Kurz & Kimmins (1987) treated fine roots in different soil horizons as separate populations with different dynamics, even when hydraulic lift (release of water from deeper horizons by roots in dry soil nearer the soil surface) could prevent fine root mortality in dry soil layers to a certain degree (Dawson 1996). It is especially difficult to describe the mortality of fine roots in simulation models, as only limited information is available on the conditions lethal for fine roots (Chapters 3 and 7). It has to be taken into account that there is probably a relation between risks of mortality and fine root diameter, as demonstrated from differences in specific root length (SRL) before and after a drought (Chapter 2).

MORTALITY RISKS FOR TREES IN DRY PERIODS

In Chapter 7, the increase in drought susceptibility through soil acidification is demonstrated. At present, it is impossible to indicate the threshold value for water potential in the bulk soil in different conditions for evapotranspiration, brought about by weather, Leaf Area Index, etc. How dry does it have to be, to be lethal for a substantial number of trees in a forest stand? So far, no large-scale tree mortality has occurred in The Netherlands, even in recent abnormally dry periods, e.g. 1976. A comparison can be made with areas with genuine large-scale forest dieback in Central Europe. There, although the soil is acidified throughout the whole area, usually only the trees near the timberline in the hills are actually dying in great numbers. These trees encounter the most extreme climatic influences, and acidification is the final blow. In The Netherlands, we do not have a timberline with extreme climatic conditions, which is why the exact lethal drought conditions are unknown for a given tree species on a given site.

INFLUENCE OF MYCORRHIZA

Mycorrhizae are generally thought to be beneficial for trees. The beneficial effects can vary greatly between species or even between forms within one species (dikaryon), see Dosskey et al. (1992) and Lamhamedi et al. (1992). Vogt et al. (1995) expected that mycorrhizae, and certainly the species or dikaryons with strands, might bridge the gap in water potential in the bulk soil and in the root itself. They claimed that the hyphae might take better advantage of the small-scale soil heterogeneity than roots. However, Hairiah et al. (1991) proved that roots can avoid parts of the soil with high levels of aluminium, and can grow preferentially in parts with lower aluminium concentrations, also taking advantage of small-scale heterogeneity. Each soil forms its own split-root system, both for roots and for hyphae.

The mycorrhizal frequency of Douglas-fir in The Netherlands is very low (Jansen & De Nie 1988), although normally mycorrhizae can have great influence on biomass allocation, as Dosskey et al. (1992) proved for tree seedlings. Given the low mycorrhizal frequency, the influence on functioning of Douglas-fir in The Netherlands cannot be large at present. It is difficult to assess the actual contribution of mycorrhizal fungi to uptake of nutrients and water (George & Marschner 1996), and therefore in an extensive review article Rapp & Jentschke (1994) concluded that not much is known yet of the ecological role of different mycorrhizal species. Some mycorrhizal fungi species appear to increase drought resistance of trees (Garbaye & Churin 1997), with possible influence on competitiveness of individual tree species.

Jung & Blaschke (1995) expected that a higher nitrogen availability in general would lead to lower mycorrhizal frequencies, and increase the probability of infection by pathological fungi, e.g. Phytophthora. However, the reaction to the availability of nitrogen differs per mycorrhizal species (Kernaghan et al. 1995; Termorshuizen & Schaffers 1987). Deficiency of magnesium and calcium do not seem to lead to higher mycorrhizal frequency, but phosphorus deficiency stimulates the formation of mycorrhiza (Rapp & Jentschke 1994). In general, Rapp & Jentschke (1994) expected that the reduction in mycorrhizal frequency in many European forests could be the result of soil acidification and/or nitrogen availability. It is not clear which mechanism dominates this effect.

Wolters & Schaefer (1994) stated that acidification also affects other aspects of soil ecology: the diversity in soil fungi and soil fauna decreases, while some species can benefit from the changes in soil chemistry. Some effects on soil ecology are known qualitatively, but to elucidate their ecological significance, much quantitative work has to be done in many situations (including tree species and fungal species). One interesting feature for research on mycorrhizae would be to study the influence on hydraulic conductivity of the root system. Some studies suggest that the hydraulic conductivity might decrease when mycorrhiza is present (Coleman et al. [1987]). This means that the tree does not readily take up water, as the resistance of the whole root system for water uptake is greater (Chapter 7), and more moisture is retained in the soil. This might have its advantages in long dry periods, but may also have competitive disadvantages if the water is taken up by roots of neighbouring plants without mycorrhizae.

Looking ahead to future developments and implications for forest policy

It will only be possible to restore the forest environment to pre-industrial conditions if the deposition rates for sulphur and nitrogen in forest ecosystems decrease. The soil solution chemistry will adapt rather quickly (Bredemeier et al. 1995; Wright et al. 1995; Boxman et al. 1995; Koopmans 1996), but the total amount of nitrogen that is stored in the ecosystem will decrease very slowly, or only after catastrophes like fire or a large harvest of biomass (Koopmans 1996). In a recent evaluation of the efficacy of Dutch government policy on deposition of air pollutants, Klein et al. (1996) concluded that the goal of reducing deposition by 70 % of the deposition in 1980 will not be reached. The reduction will only reach a maximum of 40 to 60 %, and after the year 2005 no further reduction is to be expected, as most measures for emission reduction will have achieved maximum efficacy. In that case, the deposition rate will still be too high for 75 % of the forest and nature reserves in The Netherlands (Klein et al. 1996). On a world scale, Galloway (1995) expected that emissions will even rise dramatically, mainly because of economic growth in developing countries, especially in Asia. In Sweden, Sverdrup & Warfvinge (1995) calculated that a reduction of at least 80 % of sulphur and 50 % of nitrogen emission is necessary to reach good conditions for tree growth, i.e. conditions with the same high base saturation in the soil as before the onset of anthropogenic acidic deposition. In The Netherlands too, soil acidification and nitrogen enrichment will still lead to low fine root densities and nutrient imbalances and this will affect the vitality characteristics of forest trees, as has been demonstrated in many studies (e.g. Van den Burg 1990; Bonneau et al. 1995; Dambrine et al. 1995; Van den Burg & Olsthoorn 1996; Olsthoorn & Maas 1994). The probability of droughts in The Netherlands, notably in the summer, is also expected to rise through climatic changes (Nabuurs et al. 1997, based on Houghton et al. 1996 and Kirschbaum et al. 1996). Nabuurs et al. (1997) have even advised forest managers to avoid planting Norway spruce and Douglas-fir in The Netherlands, and to use broad-leaved tree species instead, preferably from areas just south of The Netherlands.

Another potential hazard is that with ongoing deposition and depletion of the Al buffer (Mulder et al. 1989; Wesselink 1994), the soil pH might further decrease. Gijsman (1990) expected that the nitrification process would then stop. This will increase the problems for root growth, as ammonium would become virtually the only nitrogen source for root uptake, and rhizosphere pH would be even lower than soil pH, and iron and manganese toxicity might emerge (Foy et al. 1978).

The natural conditions in the forest are an important feature in Dutch forest policy plans (BBP 1994). Each year, the condition of the forest is assessed, to monitor changes in vitality characteristics (Reuver 1997). Given that both the natural processes and tree vitality are influenced by deposition of air pollutants, the plans for forest and nature conservation will not be realised unless environmental measures are taken. The conclusions of this study underline this need.

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Summary

In the early eighties, much media attention was paid to the risks to forest vitality and growth, posed by the effects of air pollution. It was predicted that air pollution would cause large-scale forest decline ('Waldsterben'), or tree mortality - even within one decade - in large parts of Europe and other industrial areas. In many countries, large research programmes were established to monitor changes in detail, and to identify the mechanisms responsible for forest decline. In The Netherlands, the ACIFORN project (ACIdification of FORests in The Netherlands) was part of the Priority Programme on Acidification set up to investigate how air pollution affects forest growth. It involved monitoring two young mature Douglas-fir plantations in detail for several years. This thesis describes the root research in the ACIFORN project. The focus was on fine root growth, as fine roots are essential for the uptake of water and nutrients, and form the main interface of the tree with the soil solution. The fine root density defines the potential for uptake, and roots account for a significant part of the carbon balance of the entire forest ecosystem. The main question addressed by the research was: *How does soil acidification of sandy soils, mostly combined with nitrogen enrichment, affect the fine root system, and what are the consequences for tree functioning?* Various studies were performed to answer more detailed questions.

METHODOLOGY FOR ASSESSING FINE ROOTS

A root corer was used to assess the fine root density and fine root biomass up to 80 cm depth for three years in the early part of the summer in the two research sites (Chapter 2). The extensive data set collected in early summer 1987, the first year of observation, was used to test the minimum number of samples required to obtain a reliable average of fine root density and fine root biomass (Chapter 2), and the relation between the fine root density and the proximity of tree stems in a closed forest (Chapter 4). At the Speuld site, 55 samples and at the Kootwijk site, 37 samples up to 80 cm depth were collected in a small area (10 x 11 m). For each sample point, the distance to the nearest tree was measured, and also the distance to the tree with a dominant crown above the sampling point. The variability in the fine root density in the samples was large, but regression models revealed a distinct rooting pattern in one case. From this it is concluded that to avoid systematic errors in the assessment of fine root data, a stratified random design should be used. When trees are spaced irregularly, a grid sampling design may be used, as in this study. If constant distances had been used in these young Douglas-fir stands, the systematic error could have been an up to 10 % overestimation of the fine root density. Very large numbers of samples are necessary to determine a horizontal pattern in fine root density in a forest. In the two consecutive years, 12 samples on each plot were taken in a systematic grid as the trees were irregularly spaced, in order to obtain reliable data on average fine root density and fine root biomass (Chapter 2).

FINE ROOT DENSITY AND FINE ROOT BIOMASS

Though the vertical distribution of the fine root density was similar in both stands (Chapter 2), the dry weight and density of fine roots were higher in the stand with less aboveground biomass (the drier site: Kootwijk). The fine root biomass on this site was around 4 t ha^{-1} in normal years (1987 and 1988), and around 1 t ha^{-1} after a dry spring (1989). The fine root biomass on the more favourable site, Speuld, was 3 t ha^{-1} in the normal years, but was also 1 t ha^{-1} after the dry spring. From this it is inferred that a long dry period in spring greatly affects the fine root system. After a dry spring, the fine root length was affected even more than the biomass, because of higher mortality in the finest root fraction, especially on the dry site, bringing about a 45% reduction in the specific root length (length per gram of dry matter of the fine roots). The fine root density in the mineral topsoil (i.e. < 30 cm depth) averaged 0.6 cm cm^{-3} in normal years and was 0.05 cm cm^{-3} after the dry spring. The corresponding figures for the subsoil (i.e. > 30 cm depth) were 0.3 and 0.04 cm cm^{-3}.

COARSE ROOT SYSTEM

The growth of coarse roots was estimated from aboveground stem growth, and was up to 2.0 t ha^{-1} yr^{-1} on the drier site and up to 2.7 t ha^{-1} yr^{-1} on the more favourable site (Chapter 2). The estimated amount of carbohydrates invested annually in the root system was 10 Mg ha^{-1} yr^{-1}, 80 % of which was allocated to the fine root fraction on the dry site, compared with only 55 % on the more favourable site (Chapter 3). The remainder is invested in the coarse root system. This demonstrates that coarse roots and fine roots differ diametrically in terms of the shoot:root ratios brought about by changes in nutrient or water availability. Coarse roots behave as shoots in this ratio.

FINE ROOT DYNAMICS

The periodicity in fine root growth was monitored during 1987, 1988, and 1989 (Chapter 3). The first two years were normal in terms of weather and soil moisture conditions in a maritime temperate climate. The third year was very dry in spring, with a hot summer interspersed with heavy showers. The periodicity of root growth was studied with the Perforon method, or Perforated Soil System, which enables roots to be observed in 12 mm diameter channels with a small endoscope. In normal years the fine root growth peaked in spring just before budbreak, and declined during summer. Few root tips grew during winter, despite the fairly warm soil. In both stands, most fine roots died during the dry spring in 1989. It appeared that many fine roots died at a water potential of -0.08 MPa in the soil. The water potential in the rhizosphere (a small soil layer directly around the fine roots) must have been substantially lower. On the drier site that initially had the highest fine root density, fine root growth reacted strongly during the summer after the dry spring, in the intermittent rainy periods.

EFFECTS OF ACIDIFICATION ON FINE ROOTS

The effects of large amounts of ammonium sulphate on the fine root growth of one-year-old seedlings of Douglas-fir were studied in a sand culture under controlled soil moisture conditions to simulate the present acidic deposition (Chapter 5). At the end of the eight-month experiment, part of the ammonium had nitrified into nitrate. This resulted in the different treatments having different ammonium, nitrate, and aluminium levels and rhizosphere pH. In the treatment with the largest amount of ammonium sulphate, fine root length of the seedlings was halved compared with the control, and the specific root length was reduced by 40 %. Shoot growth was increased through the extra nitrogen availability in this treatment, leading to a 60 % increase in the shoot:root ratio of the seedlings. Although Douglas-fir shows a preferential ammonium uptake in nutrient solutions, the increases in the pH of the rhizosphere in this experiment indicate that nitrogen was mostly taken up as nitrate, unless large amounts of ammonium were present. It was concluded that when the ammonium concentration in the soil is low, it cannot be taken up readily, because of its poor mobility in soil.

The effects of soil acidification on fine roots were further tested by reviewing literature data on the accumulated effects of the last two centuries of soil acidification on the fine root growth of Douglas-fir (Chapter 6). Data from seedling studies by various researchers were used to formulate the mechanism of the changes. However, field results were essential to produce a quantitative estimate of the changes in the fine root density under field conditions in mature forest. To calculate the total effects, conclusions about three aspects were distinguished: 1) Site conditions have been changed by the accumulation of acidic deposition, as the total aluminium concentration has increased 30 to 50 times in the soil solution of the topsoil, and over 100 times in the subsoil. Nitrogen deposition has caused almost all forest stands in The Netherlands to become nitrogen saturated. 2) Aluminium is the main toxic factor affecting fine root growth in acid sandy soils, even at sub-lethal levels. Aluminium toxicity decreases the fine root length by 50 % in the topsoil, and by as much as 75 % in the subsoil. However, the fine root biomass is affected little by Al, if at all, especially in Douglas-fir, which is aluminium tolerant. 3) Under conditions of nitrogen saturation, the fine root biomass is most probably reduced by 30 %.

From the literature data it was concluded that at present, the fine root system of Douglas-fir in The Netherlands is less dense and more shallow than it would be without acidic deposition. This review of the literature enabled the Ulrich hypothesis to be quantified for Douglas-fir on acidified sandy soils. It seems likely that the same effects might have taken place in forests on sandy soils in other parts of NW Europe, especially in tree species that are more sensitive to aluminium toxicity than Douglas-fir.

EFFECTS OF ACIDIFICATION EFFECTS ON DROUGHT SUSCEPTIBILITY

The effects of reduced fine root density on water uptake potential and drought susceptibility are assessed in Chapter 7. Data from Kootwijk and Speuld are used to demonstrate that drought causes a reduction in the biomass of fine roots and needles. This reduction is greater on a drier site. Calculations with a simulation model for water uptake showed that the reduced fine root density brought about by acidic deposition leads to a lower potential for water uptake on coarse sandy soils, but has no major direct effects on loamy sand. Soil acidification reduces the fine root density, causing a decrease of the water potential in the rhizosphere in a severe drought, and leads to increased fine root mortality in long dry periods, especially on the driest sites. The effects of soil acidification and nitrogen enrichment on drought susceptibility are illustrated with an elementary model to describe fluctuations in the fine root density during and after a drought. The model shows that the fine root density is more seriously affected in a drought through soil acidification, and that the root system recovers more slowly from the drought-induced mortality, especially when hampered by aluminium toxicity. Consequently the susceptibility of Douglas-fir to drought has increased. Substantial fine root mortality from a severe drought can depress forest growth for several years. The risks of tree mortality or forest dieback being induced in the future by severe droughts have increased as a result of the accumulated deposition.

EPILOGUE

Chapter 8 looks back on the scientific, practical and methodological achievements of the study, and looks forward to future developments. The scientific achievements are more insight into 1) the relation between the site quality and the dynamics of the fine root density and the needle biomass in a drought period; 2) the relation between soil acidification, nitrogen enrichment and drought susceptibility of Douglas-fir on sandy soils; and 3) the relation between mycorrhizal frequency and rooting depth. A methodological achievement is that the Perforon method has been made suitable for field research on mature trees, to study periodicity of fine root growth. The implications for forest management are 1) that as long as conditions of soil acidification persist, more care should be taken in satisfying the site requirements of tree species; 2) that fine root mortality in a drought can explain long growth depressions after drought; and 3) that liming is an undesirable and unnecessary precautionary measure against soil acidification, as reduction of the emission rates of air pollutants is preferable.

Some important ecological issues in root research remain unsolved. There is still no unbiased method to estimate fine root production and mortality. The subroutines describing the fine root dynamics in simulation models describing forest growth still need improvement, particularly with respect to the effects of a severe drought. The exact drought conditions for large-scale tree mortality in acidified sandy soils are still unknown. The quantification of the influence of mycorrhizae on hydraulic properties of the root system deserve special attention.

Under present government plans, deposition rates will not decrease sufficiently to bring about an improvement in the soil quality in forests and nature reserves on sandy soils. The increased drought susceptibility of Douglas-fir is an extra hazard if climatic conditions in The Netherlands change towards drier summers.

Samenvatting

In het begin van de jaren tachtig werd door de media veel aandacht besteed aan de gevaren van de gevolgen van luchtvervuiling voor bosvitaliteit en bosgroei. Er werd voorspeld dat luchtvervuiling - zelfs binnen tien jaar - in grote delen van Europa en andere industriegebieden grootschalige bossterfte ('Waldsterben') of sterfte van individuele bomen zou veroorzaken. In vele landen werden grote onderzoeksprogramma's opgezet om de veranderingen in detail te volgen, en om de werking te begrijpen van de processen die verantwoordelijk waren voor de achteruitgang in vitaliteit. In Nederland was het ACIFORN-project (ACIdification of FORests in The Netherlands) opgezet als onderdeel van het Additioneel Programma Verzuringsonderzoek (APV) om te onderzoeken hoe luchtvervuiling het bos beïnvloedt. In het project werden twee ongeveer 40 jaar oude Douglasopstanden gedurende enige jaren bestudeerd. Dit proefschrift beschrijft het wortelonderzoek in het ACIFORN-project. Vooral de groei van fijne wortels werd bekeken, omdat fijne wortels van groot belang zijn voor de opname van water en voedingsstoffen en omdat ze het meest direct in contact staan met de verzuurde bodem. De worteldichtheid bepaalt de mogelijkheden voor opname en fijne wortels gebruiken een aanzienlijk deel van de koolhydraten die een boom produceert. De hoofdvraag in dit onderzoek was: *Welk effect heeft bodemverzuring, vaak in combinatie met stikstofverrijking, op de fijne wortels en wat zijn de consequenties voor het functioneren van bomen?* Diverse onderzoeken zijn gedaan om deelvragen op te lossen.

METHODIEK VOOR WORTELONDERZOEK

Gedurende drie jaar werd een wortelboor gebruikt om de worteldichtheid en de wortelmassa tot 80 cm diepte te bepalen in het begin van de zomerperiode (Hoofdstuk 2). In 1987, het eerste jaar van het veldonderzoek, is een groot aantal monsters genomen om te bepalen hoeveel monsters minimaal nodig zijn om een betrouwbaar gemiddelde van de worteldichtheid en de wortelmassa te kunnen berekenen (Hoofdstuk 2) en om te zien of er een relatie is tussen de worteldichtheid en de afstand tot de boom (Hoofdstuk 4). Op de locatie Speuld zijn 55 monsters genomen en op de locatie Kootwijk 37 monsters, verspreid over een kleine oppervlakte (10 x 11 m). Van elk monsterpunt werd de afstand tot de dichtstbijzijnde boom bepaald en ook de afstand tot de boom waarvan de kroon boven het monsterpunt hing. De variatie in de worteldichtheid van de verschillende boormonsters was groot, maar met behulp van statistische modellen kon in een van de locaties een verband worden aangetoond tussen de worteldichtheid en de afstand tot de boom. Dit betekent dat wortelmonsters op verschillende afstanden tot de boom genomen moeten worden om fouten in de interpretatie te voorkomen (gestratificeerd volgens de in het bos voorkomende afstanden tot de boom). Als de bomen onregelmatig verspreid zijn, kan ook systematisch bemonsterd worden in een raster, zoals in dit onderzoek gedaan is. Als er op constante afstand tot de boom bemonsterd zou zijn, zou in dit type bos (maximaal) een fout van 10% overschatting van de worteldichtheid gemaakt kunnen zijn. Het blijkt dat grote aantallen wortelmonsters nodig zijn om een patroon te ontdekken in de worteldichtheid bij verschillende afstanden tot de boom (Hoofdstuk 4). In de twee volgende meetjaren, 1988 en 1989, zijn steeds 12 monsters per proefveld genomen om een betrouwbaar gemiddelde te verkrijgen voor worteldichtheid en wortelmassa (Hoofdstuk 2).

WORTELDICHTHEID EN WORTELMASSA VAN DE FIJNE WORTELS

De verticale verdeling van fijne wortels in de bodem was ongeveer gelijk in de beide onderzoekslocaties (Hoofdstuk 2). Een duidelijk verschil tussen de beide locaties was echter dat er meer fijne wortels aanwezig waren in de bodem van de locatie met minder vochtleverend vermogen van de bodem, Kootwijk, met daardoor de minste bovengrondse groei. In normale jaren (1987 en 1988) was de levende wortelmassa van de fijne wortels daar ongeveer 4 ton per hectare, terwijl na een droog voorjaar (1989) de levende wortelmassa slechts 1 ton per hectare was. De levende wortelmassa in de locatie met betere bodemomstandigheden, Speuld, was 3 ton per hectare in normale jaren en eveneens 1 ton per hectare na het droge voorjaar. Hieruit blijkt dat een droog voorjaar een groot effect heeft op de aanwezigheid van fijne wortels. De specifieke wortellengte (de lengte per gram droge stof van de fijne wortels) nam sterk af (met 45%). Daaruit blijkt dat de wortellengte nog meer was aangetast dan de wortelmassa, omdat vooral de allerfijnste wortels doodgingen. Gemiddeld over beide locaties lag de worteldichtheid in de minerale bovengrond (tot ongeveer 30 cm diepte) rond 0,6 cm cm^{-3} in normale jaren en slechts rond 0,05 cm cm^{-3} na een droog voorjaar. In de ondergrond (beneden 30 cm diepte) waren deze cijfers respectievelijk 0,3 en 0,04 cm cm^{-3}.

GROVE WORTELSTELSEL

De groei van het grove wortelstelsel werd afgeleid van de bovengrondse stamgroei, en deze bedroeg ongeveer 0,2 ton per hectare per jaar in de drogere locatie en tot 2,7 ton per hectare per jaar bij betere bodemomstandigheden (hoofdstuk 2). De benodigde hoeveelheid koolhydraten voor groei en onderhoud van het gehele wortelstelsel werd geschat op 10 ton per hectare per jaar voor beide locaties, waarbij op de drogere groeiplaats 80 % in de fijne wortels geïnvesteerd werd en op de betere groeiplaats slechts 55 % (hoofdstuk 3). De rest word gebruikt voor het grove wortelstelsel. Dit betekent dat grove en fijne wortels een tegenovergesteld beeld vertonen bij veranderingen in de spruit-wortelverhouding als gevolg van beschikbaarheid van water of voedingsstoffen. Grove wortels gedragen zich dan zoals de bovengrondse biomassa.

DYNAMIEK VAN DE FIJNE WORTELS

De dynamiek in de groei van de fijne wortels (periodiciteit) werd gevolgd gedurende 1987, 1988 en 1989 (Hoofdstuk 3). Het weer en dus de vochtvoorziening in de bodem in de eerste twee jaar waren vrij normaal voor een maritiem gematigd klimaat. Het derde jaar was erg droog in het voorjaar, met een warme zomer die werd onderbroken door een aantal zware buien. De periodiciteit van de wortelgroei werd gevolg met de Perforon-methode, of Perforated Soil System. Met deze methode kunnen wortels in gangen van 12 mm doorsnede worden geobserveerd met een kleine endoscoop. In normale jaren was er een piek in de wortelactiviteit in het voorjaar, juist voor het uitlopen van de knoppen, met een geleidelijke afname gedurende de zomer. In de winter was er nauwelijks wortelactiviteit, ondanks de relatief hoge bodemtemperaturen. In het droge voorjaar van 1989 trad in beide locaties grote wortelsterfte op. Veel wortels bleken al bij een waterpotentiaal in de bodem van -0,08 MPa (pF 2,9) af te sterven. De waterpotentiaal in de rhizosfeer (een dun bodemlaagje direct rond de fijne wortels) moet op dat moment nog veel lager zijn geweest. In de bodem van de drogere locatie, die in de eerste jaren de hoogste worteldichtheid had, vertoonden de wortelpunten veel groei in de neerslagperioden in de zomer na het droge voorjaar.

EFFECTEN VAN BODEMVERZURING OP FIJNE WORTELS

In een kasproef werden de gevolgen van bodemverzuring gesimuleerd door de toediening van verschillende hoeveelheden ammoniumsulfaat in een zandcultuur met eenjarige zaailingen van Douglas (Hoofdstuk 5). Aan het einde van het acht maanden durende experiment was een deel van de ammonium genitrificeerd. Daardoor waren er verschillende hoeveelheden ammonium, nitraat, aluminium aanwezig en verschilde de pH van de rhizosfeer bij de verschillende behandelingen. In de behandeling met de hoogste dosering ammonium was de wortellengte slechts de helft van die in de controlebehandeling. De specifieke wortellengte was gereduceerd met 40 %. Door de extra stikstofbeschikbaarheid werd de spruitgroei gestimuleerd in de behandeling met de hoogste dosering, waardoor de spruit-wortelverhouding steeg met 60 %. Hoewel Douglas in voedingsoplossingen bij voorkeur ammonium opneemt, bleek uit de stijging van de pH in de rhizosfeer in dit experiment, dat de stikstof meestal in de vorm van nitraat werd opgenomen, behalve als er grote hoeveelheden ammonium beschikbaar waren. Ammonium in lage concentratie kan niet in grote hoeveelheden door wortels worden opgenomen omdat de mobiliteit in de bodem vrij gering is.

De effecten van bodemverzuring op fijne wortels zijn in een groot literatuuronderzoek op een rij gezet om de gevolgen van twee eeuwen bodemverzuring in te kunnen schatten voor wortelgroei van Douglas (Hoofdstuk 6). Gegevens uit proeven met zaailingen zijn gebruikt om de richting van de veranderingen te bepalen. Veldgegevens waren echter essentieel om kwantitatieve schattingen van de veranderingen in volwassen bos te kunnen maken. Om het totale effect op de worteldichtheid te kunnen bepalen, zijn conclusies over drie aspecten onderscheiden: 1) De groeiplaatsomstandigheden zijn veranderd door de accumulatie van verzurende depositie van luchtverontreiniging, waardoor de aluminium concentratie in het bodemvocht 30 tot 50 keer zo hoog is geworden in de bovengrond, en zelfs meer dan 100 keer zo hoog in de ondergrond. Door stikstofdepositie zijn vrijwel alle bossen in Nederland stikstofverzadigd geworden. 2) Aluminium is de voornaamste toxische stof voor wortelgroei van bomen in zure zandgronden, zelfs als de concentraties niet hoog genoeg zijn om direct dodelijk te zijn. In totaal is bij Douglas de wortellengte in de bovengrond met 50 % gereduceerd en in de ondergrond zelfs met 75 % door aluminiumtoxiciteit. De wortelmassa wordt bij dergelijke concentraties echter niet of nauwelijks beïnvloed bij Douglas, die vrij tolerant is voor aluminium. 3) Door stikstofverzadiging is de wortelmassa van de fijne wortels zeer waarschijnlijk met ongeveer 30 % gereduceerd.

Door het combineren van de drie bovenstaande conclusies uit de literatuur blijkt dat het fijne wortelstelsel van Douglas in Nederland minder dicht en meer oppervlakkig is dan het zou zijn zonder de invloed van verzurende depositie. Door het literatuuroverzicht kon de hypothese van Ulrich gekwantificeerd worden voor

Douglas op verzuurde zandbodems. Het is vrij waarschijnlijk dat vergelijkbare effecten zijn opgetreden in bossen op zandige bodems in andere delen van Noordwest-Europa, vooral bij boomsoorten die gevoeliger zijn voor aluminiumtoxiciteit dan Douglas.

GEVOLGEN VAN BODEMVERZURING VOOR DROOGTEGEVOELIGHEID

De effecten van een verminderde worteldichtheid door bodemverzuring op de mogelijkheden voor wateropname worden besproken in Hoofdstuk 7. Uit de gegevens over Kootwijk en Speuld blijkt dat bij droogte de wortelmassa en de naaldhoeveelheid afneemt. Deze afname is groter op de locatie met slechtere bodemomstandigheden. Uit berekeningen met een simulatiemodel voor wateropname blijkt dat de mogelijkheden voor wateropname bij afnemende worteldichtheden minder groot worden indien de bodem bestaat uit grof zand. Als de bodemomstandigheden beter zijn, zoals in lemig zand, veroorzaakt afname in de worteldichtheid in korte droogteperioden nauwelijks een vermindering in de mogelijkheden voor wateropname. Omdat de worteldichtheid door verzuring is afgenomen, droogt de rhizosfeer sterker uit in droogteperioden en treedt er een sterkere wortelsterfte op, vooral op de slechtere groeiplaatsen. Dit treedt vooral op in langere droge perioden. De effecten van bodemverzuring en stikstofverrijking op droogtegevoeligheid kunnen geïllustreerd worden met een globaal wortelmodel dat de fluctuaties in worteldichtheid beschrijft tijdens en na een droogteperiode. Het wortelmodel toont aan dat bodemverzuring de afname in de worteldichtheid in een droogte versterkt en dat het wortelstelsel zich door aluminiumtoxiciteit langzamer herstelt na de sterftefase in een droogteperiode. Daardoor is de droogtegevoeligheid van Douglas toegenomen. Wortelsterfte door droogte kan ook verklaren waarom de groei van bomen soms enige jaren is geremd na een droogteperiode. Door de geaccumuleerde bodemverzuring is de kans op boom- of bossterfte in toekomstige droogteperioden toegenomen.

EPILOOG

Hoofdstuk 8 evalueert de wetenschappelijke, practische en methodologische resultaten van het onderzoek en geeft een blik op de toekomst. De wetenschappelijke resultaten zijn, dat er meer inzicht is ontstaan in 1) het verband tussen bodemkwaliteit en de dynamiek van de worteldichtheid en de naaldmassa tijdens droogteperioden; 2) het verband tussen bodemverzuring, stikstofverrijking en droogtegevoeligheid van Douglas op zandige bodems; en 3) de relatie tussen mycorrhizafrequentie en worteldiepte. Een methodologisch resultaat is dat de Perforon-methode geschikt gemaakt is voor veldstudies aan volwassen bomen. Praktische resultaten die uit het onderzoek voortvloeien zijn 1) dat de bodemeisen van boomsoorten meer serieus moeten worden genomen, zolang de bodemverzuring doorgaat; 2) dat de wortelsterfte tijdens een droogte kan verklaren waarom de groei zo lang onderdrukt blijft na een ernstige droogteperiode; en 3) dat bekalken een ongewenste en nadelige praktijkmaatregel is om de gevolgen van verzuring tegen te gaan. Terugdringen van de uitstoot van luchtverontreiniging verdient de voorkeur.

Er zijn nog een aantal ecologische vragen te beantwoorden met behulp van wortelonderzoek. Er zijn nog geen betrouwbare methoden om de precieze groei en mortaliteit van wortels vast te stellen. De beschrijving van de worteldynamiek in simulatiemodellen voor bosgroei moet nog verbeterd worden, vooral met betrekking tot de effecten van ernstige droogteperioden. De precieze omstandigheden waarbij door droogte grootschalige mortaliteit van bomen optreedt op verzuurde bodems zijn nog niet bekend. De kwantificering van de effecten van mycorrhiza op het watergeleidend vermogen van het wortelstelsel verdienen speciale aandacht.

Bij de huidige regeringsplannen zal de depositie van verzurende stoffen niet voldoende afnemen om een bodemverbetering tot stand te brengen in bossen en natuurgebieden op zandgronden. De toegenomen droogtegevoeligheid van Douglas is een extra groot risico als door klimaatverandering de zomers in Nederland droger zouden worden.

Appendix 1

Mycorrhiza types in the perforon root cellars

One type of mycorrhiza could be distinguished with certainty according to the table made by Jansen and De Vries (unpublished) for mycorrhizae on Douglas-fir in The Netherlands. A yellow-green warty mycorrhiza type in Speuld was identified as *Russula ochroleuca*. A white fluffy type with a pink mantle in Kootwijk might be some species of *Inocybe* and a snowy white type in Speuld has an appearance like *Hebeloma*. The growing speed of *R. ochroleuca* root tips in the perforations was approximately 5 mm per year. The white fluffy type could grow faster, but only with an intermittent phase without a fungal mantle.

The majority of the mycorrhizae consisted of two types in Speuld (*Russula ochroleuca* and a snowy white type) and one type in Kootwijk (white fluffy type). The root tips of some trees have a very high mycorrhizal frequency, whereas the root tips of other trees in the perforations were nearly all non-mycorrhizal. In Table 1 the numbers per perforon are shown for one date (20 September 1989) as an example. Several types of mycorrhiza were only found on roots of one tree. The white fluffy type was only found in Kootwijk, but apparently on a larger scale. In September 1989 in perforon S2, 71 % of the root tips was set with a fungal mantle (*R. ochroleuca*). As numbers of brown root tips have decreased more than mycorrhizal root tips in the dry summer (Chapter 3) this percentage was higher than other periods in this perforon. In Kootwijk the mycorrhizal frequency was lower than in other periods, as many white fluffy type mycorrhiza have died in the dry period (Chapter 3).

Table 1.

Different types of mycorrhiza on September 20 1989 in three perforon root cellars in Kootwijk (K) and Speuld (S). Rus = *Russula ochroleuca*, SW = snowy white type, WF = white fluffy type, OT = other types of mycorrhiza, TRT = total number of live root tips (white, brown and mycorrhizal) and %MRH = percentage mycorrhizal root tips in the total number of root tips (TRT).

	PERFORON	RUS	SW	WF	OT	TRT	%MRH
Kootwijk	K1	0	0	8	0	109	7
	K2	0	0	2	0	140	1
	K3	0	0	17	0	63	27
Speuld	S1	0	0	0	9	38	24
	S2	97	0	0	0	137	71
	S3	0	14	0	2	75	21

Appendix 2

Chemical composition of fine roots of douglas-fir

Composition of fine roots from two sites with Douglas-fir in The Netherlands, and in different soil horizons.

ELEMENT:	N	Al	P	K	Ca	Mg	Na
Speuld							
-1 to 7 cm depth	1227	2407	36	17	175	23	19
7 to 14	1045	3210	35	22	140	21	19
14 to 26	1083	5960	38	23	105	22	24
26 to 61	762	11500	27	33	45	20	21
61 to 85	671	13427	24	43	38	23	21
Kootwijk							
-1 to 6 cm depth	1095	3068	39	12	22	24	15
6 to 37	1034	8158	51	24	93	26	15
37 to 57	629	13347	31	17	29	16	14
57 to 85	667	12936	28	19	22	16	24

Contents in mmol kg^{-1}, except Al, in mg kg^{-1}.

SHORT COMMENTS:

The data are the average of a small number of samples in the 1988 sampling campaign (see Chapter 2); the root samples had to be combined per horizon to have enough dry matter for chemical analyses. The data for Speuld are an average of samples of two plots within one stand (east and west).

N: Total nitrogen content, decreases with increasing depth.
Al: Most of the aluminium is located at the outside of the roots, this is not physiologically active. It increases with increasing depth; in the sub-soil, the aluminium content is over 1 % of the dry weight.
P: Decreases slightly with increasing depth.
K: Increases with increasing depth in Speuld; might leach out partly during the washing procedure of roots, might be underestimated.
Ca: Decreases with increasing depth.
Mg: Decreases slightly with increasing depth, or remains constant.
Na: Data near detection limit: not reliable
S: Not measured.

Data from: J.M. Klap 1991. De gevolgen van bodemverzuring voor biomassa en chemische samenstelling van fijne wortels van Douglas. (Consequences of soil acidification for biomass and chemical composition of fine roots of Douglas-fir). M.Sc. Student thesis, Dept of Forestry Nr. 91-12, and Dept of Soil Science and Plant Nutrition, Wageningen Agricultural University. 66 p.

Apendix 3

List of associated papers/abstracts from the root research project with A.F.M. Olsthoorn as (co-)author:

PEER REVIEWED PAPERS

Gorissen, A., A.E. Jansen & A.F.M. Olsthoorn 1993. Influence of a two year application of ammonium sulphate on growth, nutrient uptake, and rhizosphere microflora of juvenile Douglas-fir. Plant and Soil 157: 41-50.

Olsthoorn, A.F.M. 1991. Fine root density and root biomass of two Douglas-fir stands on sandy soils in The Netherlands. 1. Root biomass in early summer. Netherlands Journal of Agricultural Science 39, 1: 49-60.

Olsthoorn, A.F.M., W.G. Keltjens, B. van Baren & M.C.G. Hopman 1991. Influence of ammonium on fine root development and rhizosphere pH of Douglas-fir seedlings in sand. Plant and Soil 133: 75-81.

Olsthoorn, A.F.M. & A. Tiktak 1991. Fine root density and root biomass of two Douglas-fir stands on sandy soils in The Netherlands. 2. Periodicity of fine root growth and estimation of belowground carbon allocation. Netherlands Journal of Agricultural Science 39, 1: 61-77.

Van de Veen, J.R., G.M.J. Mohren & A.F.M. Olsthoorn 1993. Simulation of integrated effects of air pollution and soil acidification on forest ecosystems. In: M.E.A. Broekmeyer, W. Vos & H. Koop (eds.), European forest reserves. Proceedings of the European Forest Reserves Workshop, May 1992, Wageningen. Pudoc, Wageningen; 281-285.

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Olsthoorn, A.F.M., J.M. Klap & J. Oude Voshaar (1998). The relation between fine root density and proximity of stems in closed Douglas-fir plantations: implications for sampling design. (Chapter 4 in this thesis).

Olsthoorn, A.F.M. & W.G. Keltjens (1998). Effects of soil acidification and nitrogen enrichment on fine root density of Douglas-fir in The Netherlands: 1. Critical review of literature data. (Chapter 6 in this thesis).

Olsthoorn, A.F.M., G.M.J. Mohren & R. Rabbinge (1998). Effects of soil acidification and nitrogen enrichment on fine root density of Douglas-fir on sandy soils: 2. Implications for drought susceptibility. (Chapter 7 in this thesis).

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Noppert, F., W. Bouten, F. Bosveld, A. Vermetten, A. Tiktak, E. Steingröver & A. Olsthoorn 1991. Detection of effects of meteorology, soil moisture and air pollution on the transpiration dynamics of a Douglas fir stand. In: P.W. Evers, W.Bouten, J.J.M. van Grinsven & E.G. Steingröver (eds.), CORRELACI. Identification of traditional and air pollution related stress factors in a douglas fir ecosystem: the ACIFORN stands. Report 623. Research Institute for Forestry and Urban Ecology 'De Dorschkamp', Wageningen; 193-202.

Olsthoorn, A.F.M. 1988. Root research on Douglas-fir with special attention to effects of acidification. In: A.E. Jansen, J. Dighton & A.H.M. Bresser (eds.), Ectomycorrhiza and acid rain. Proceedings Workshop on ectomycorrhiza/Expert meeting, December 10-11 1987, Berg en Dal, The Netherlands. Air Pollution Report 12, Commission of the European Communities, Brussels, Eur 11543; 77-78.

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Olsthoorn, A.F.M., B. van Baren A.L. & Bosch 1986. The perforated soil system or 'Perforon', a versatile root observation method. Proceedings 18th IUFRO World Congress, Sept. 1986, Vol 2, II, page 849, poster 254.

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Van der Maas, M.P., J.J.M. Belde, J. Klap & A.F.M. Olsthoorn 1989. Dynamics of the potassium status of two Douglas-fir stands. Poster Abstracts. International Congress on Forest Decline Reseach: State of Knowledge and Perspectives, Friedriechshafen, October 1989, Vol. 1: page 484, poster 227.

Dankwoord

In augustus 1985 ben ik begonnen aan het wortelonderzoek dat beschreven is in dit boekje, met als stevige basis een kort projectvoorstel èn een aantal uitgewerkte ideeën van Arjen Bosch die toen op de Vakgroep Bosteelt werkzaam was, en tevens gestimuleerd door het enthousiasme van Prof. Oldeman. Ik voelde mij zeer vereerd om met de methode van het geperforeerd bodemsysteem, de Perforon- methode, aan de gang te kunnen, ook in het bos zelf. Ik heb uiteindelijk 50 dagen doorgebracht met het kijken naar wortels in de bosbodem (en het slepen van een ongelofelijke hoeveelheid videoapparatuur). Dit biedt een fantastisch perspectief van een onbekende wereld: je zou er bijna fenomenoloog van worden. Een aantal vragen (en antwoorden) op het gebied van de worteldynamiek zijn zeker geïnspireerd door deze blik op het ondergrondse universum, met schimmels, mycorrhiza, en bodemdieren. De eerste wortelpunt die ik in het bos zag, groeide omhoog, stopte al meteen met groeien, waarschijnlijk omdat een deel van de top weggegeten was en toen ik na twee jaar net dacht dat hij ècht dood was, groeide hij door met een verse wortelpunt. Wortels kunnen alles! Maar niet altijd! In droge perioden gaan ze soms binnen drie weken dood, nadat ze gevormd zijn in een snelle groeiperiode, en zijn dan direct volledig beschimmeld. Ecologie is dynamiek.

Gestimuleerd door een (on)gezonde argwaan voor methoden van wortelonderzoek heb ik in de beginperiode met een groot aantal mensen gesproken over hoe een van de vragen opgelost kon worden: hoeveel wortels groeien er in een Douglasbos. In die beginperiode heb ik gesproken met o.a. Anton de Jager en Meine van Noordwijk van het toenmalige Instituut voor Bodemvruchtbaarheid, Co Groenwold, en Nico van Breemen. Daarom heb ik ook gekozen voor een combinatie met traditionele methoden van wortelonderzoek, o.a. met de wortelboor. Die beginperiode, waarbij een kaspoef werd opgezet met de ideeën en het beregeningssysteem van Arjen Bosch en in samenwerking met Beatrix van Baren, was van cruciaal belang voor de behaalde resultaten. Bij de opzet van de proeven was Willem Keltjens ook een essentiële factor. Hij gaf vanuit een jarenlange ervaring met aluminium toxiciteit voor tropische gewassen op een uiterst plezierige manier tips en adviezen. Zonder hem waren met name de interpretaties van de veldresultaten via de kasproeven en de literatuur niet mogelijk geweest. Ook de manier waarop hij studenten begeleidde en motiveerde is voor mij altijd een voorbeeld geweest. Ik ben hem voor dit alles zeer dankbaar.

De prikkel tot dit proefschrift is gegeven door Frits Mohren, reeds lang geleden, maar op een goed gekozen moment. Omdat hij ook steeds bereid geweest is om elk woord dat ik schreef weer door te strepen, indien noodzakelijk, of op zijn minst ter discussie te stellen was hij van zeer grote waarde voor mij. Ook stimuleerde hij steeds tot kwantitatieve interpretatie van de resultaten, o.a. via het gebruik van simulatiemodellen. De vergaderingen van de 'Werkgroep Wortelmodel' met Rudy Rabbinge, Willem Keltjens en Frits Mohren waren zeer stimulerend, ondanks dat er uiteindelijk geen uitgebreid simulatiemodel voor wortelgroei is ontwikkeld. Rudy Rabbinge ben ik zeer dankbaar voor zijn continue stimulans om door te gaan via korte en uiterst vriendelijke briefjes, juist op de momenten dat het steeds lastiger leek om het af te maken in de laatste jaren. Van zijn blik op de inleiding (van wat dan ook) heb ik veel geleerd.

Het vertrek van Prof. Oldeman bij de Vakgroep Bosbouw, en met name de redenen die hij daarvoor zelf aangaf, heb ik altijd zeer betreurd. Hij heeft mij de ruimte gegeven om het onderzoek op mijn eigen wijze op te zetten en was altijd enthousiast, vooral over de resultaten van de perforon-wortelkelders. Hij kan er dan ook trots op zijn dat de beelden het zelfs het TV programma 'Het Klokhuis' hebben gehaald en is verwerkt in de informatie in de wortelgang van het boomkronenpad bij het SBB bezoekerscentrum Houtvester Kuhnhuis in de Boswachterij Gieten-Borger in Drenthe. Ook daar weten ze dat het kronendak en wortels iets met elkaar te maken hebben. De sfeer op de vakgroep Bosteelt, later een sectie van de vakgroep Bosbouw, was zeer behulpzaam. Dit gold vooral voor de veel te vroeg overleden Bos Schalk, de inspirator voor de Perforon-methode door zijn grote nieuwsgierigheid. Zijn hulp was vooral bij de kasproef onmisbaar. Peter van den Tweel, Willie Smits en vooral Arjan Bosch hebben de perforon-methode daarna verder ontwikkeld tot een volwaardige methode van wortelonderzoek die letterlijk een andere, directe, blik op wortels en het wortelmilieu geeft. Joop Post en Albert Zweers hebben mij met name bij het veldwerk geholpen en Ed de Bruijn was o.a. behulpzaam was bij het ontwerp van de Perforon-wortelkelders in het bos en heeft ook veel koffie gezet. Later waren Jelle Hiemstra en Peter Leersnijder in de bovenkamer van Hinkeloord mijn kamergenoten, wat regelmatig tot spontaan overleg leidde over allerhande zaken.

Over de voorbereiding en de resultaten heb ik met een groot aantal mensen van gedachten gewisseld in de gehele periode tussen 1985 en nu. Een aantal wil ik hier speciaal noemen. Dat begint met de ACIFORN groep die tussen 1985 en 1990 bijna maandelijks in collegiale sfeer vergaderde over de voortgang van het project. Vooral de voorzitter Peter Hofschreuder wil ik bedanken voor zijn bindende rol bij een aantal praktische problemen die af en toe optraden. Daarnaast was het zeer plezierig op te trekken met Carla Konsten, Rien van der Maas, Aart Vermetten, Willem Bouten en Aaldrik Tiktak, Pieter de Visser, Peter Cortes en Peter Evers. Het werk van de ACIFORN groep werd nieuwsgierig gevolgd en gestimuleerd door Toni Schneider met assistentie van eerst Ton Bresser en later Bert-Jan Heij van het RIVM dat het Verzuringsonderzoek coördineerde. Tot bij de afronding van het proefschrift heb ik veel advies gekregen van o.a. Nico van Breemen, Jan Mulder, Hans van Grinsven, Wim de Vries, Hans Kros, Jan Renger van de Veen, Jan Oude Voshaar, Peter de Willigen en altijd Meine van Noordwijk, die steevast opmerkte dat mijn vraag van dat moment eigenlijk ook al in hun proefschrift beantwoord was. En dat klopte: daar staat alles al in over wortels en wortelopname van water en voedingsstoffen. Gelukkig bleef er nog wat werk aan boomwortels over. Jan van den Burg heeft, naast andere adviezen, een groot aantal literatuursuggesties gegeven. De samenwerking met Ton Gorissen, Nina Joosten, Arjan Gijsman, Annelies Jansen, Frits de Vries en Pieter de Visser via diverse gezamenlijke proeven was ook altijd een genoegen. Ik heb er een aantal vriendschappen aan overgehouden. A visit in 1987 to the group of Hans Persson in Uppsala provided insight in common and uncommon methods of root research, and proved very helpfull in later years. Ook aan de plaatselijke beheerders van het Staatsbosbeheer te Speuld (Dhr. Niezen) en Kootwijk (Dhr. Minnen) is grote dank verschuldigd voor het tolereren van een groepje eigenwijze onderzoekers met veel apparatuur binnen hekwerken op hun terreinen.

Naast de hier genoemde mensen zijn er een groot aantal die op de een of andere wijze hebben bijgedragen aan de resultaten. Ik kan ze niet allen noemen, omdat hier de ruimte ontbreekt. De aard en omvang van de bijdragen was uiteraard zeer verschillend, maar ze waren allen essentieel, en ik ben allen dankbaar, vooral om de plezierige wijze waarop ik steeds medewerking kreeg. Speciale vermelding verdienen de studenten en assistenten die mij geholpen hebben bij dit arbeidsintensieve onderzoek. Je kunt namelijk pas over gegevens nadenken als je deze tot je beschikking hebt. Guy Ackermans en Arie Verdoes gaven direct het eerste veldjaar het goede voorbeeld met een ongelooflijke hoeveelheid wortelmonsters. Dit is daarna door Cees van der Haar, Jaco Klap, Martin Stempher en Willeke de Bruijn goed doorgezet. Cees en Martin zijn als analist voor mij gedurende geruime tijd een grote steun geweest; hopelijk weten ze dit ook als paranimf vol te houden. Alles bij elkaar is er ruim anderhalve kubieke meter grond in zo'n 3000 monsterzakjes uit het bos naar Wageningen vervoerd, zijn de gaten weer zorgvuldig met evenveel, maar andere, gezeefde grond gevuld en is er voor de kasproef enige kuubs stuifzandgrond verzameld. Grote cellen in de vriesruimte van het Biotechnion zijn dan ook regelmatig bijna geheel gevuld geweest. De wortelmetingen voor elk monsterzakje kostte ongeveer een half uur inclusief uitspoelen en minutieus sorteren, en vaak zijn er nog aanvullende chemische analyses gedaan. Het is een wonder dat de zandvang in de afvoer bij de kas op Hinkeloord niet verstopt heeft gezeten. De statistische uitwerkingen van de vele veldgegevens door Wietse Post was voor mij zeer leerzaam, en het was een genoegen om samen met hem ruzie te hebben met het programma Lotus (versie Dinosaurus!) en er dan toch mooie dingen mee te doen in macro's. Marjan Hopman heeft veel bijgedragen aan de kasproef door haar grote enthousiasme en inzet. Met z'n tweeën hebben wij bevroren grond doorgezaagd, alle laboratoria van de vakgroep Bodemkunde en Plantenvoeding volgegooid met zand om te drogen en de metingen en analyses van de wortels gedaan. Joy Burrough-Boenisch gaf advies over het engels en haar vragen over onduidelijkheden in de tekst losten niet alleen taalproblemen op. Thom van Rossum, Gon van Laar en Mieke Pijfers gaven reliëf aan de afwerking van de tekst en figuren.

Ook wil een aantal mensen in mijn persoonlijke omgeving noemen die op geregelde tijden mijn opmerkingen konden bufferen, over soms details zoals regen terwijl ik met de videoapparatuur het bos in wilde, of juist geen regen terwijl er wel regen verwacht was, zodat ik achter mijn bureau zat, en niet met de videoapparatuur in het veld. Ook de werksituatie, bijvoorbeeld fusieperikelen op de vakgroep Bosbouw, moest worden opgevangen in de huissituatie van de woongroep op het Klaas Katerplein, vooral door Irma Noltes die er even lang gewoond heeft als ik, maar ook door andere huisgenoten zoals Eric Jansen, die o.a. mijn interesse voor electrische gitaren heeft gestimuleerd. Daan Noltes heeft mij zeer veel geleerd over het opvoeden van kinderen. Weekeinden in Friesland bij Menno Brandsma, eerst in Hallum en later in Balk, waren ook altijd prikkelend, al of niet gezamenlijk afgelegd met Edwin Kroese. Ik ben jarenlang benieuwd geweest naar hun optreden tijdens het feest na de promotie en het is vreselijk dat Menno dit niet meer mee kan maken. Ook Miek de Jong (met haar vader), Tia Hermans en Lijbert Brussaard leken altijd vertrouwen te hebben in de goede afloop. De morele hulp van Vocaal Ensemble "Dolce Espressivo" met Aart van den Berg, Jitze Kopinga, Leen Moraal en Sven de Vries gedurende de laatste jaren moet ook niet onderschat worden. De drank en het eten op maandagavond was een plezierige vorm van overmacht. Het zingen ook. Het werken aan het schip van Gotse van der Velde en het zeilen ermee, eerst de Eendracht en later de Elegant, heeft altijd veel ontspanning gegeven. Op het water kun je goed van de grond loskomen. Met Jef van Beckhoven kon ik de spanningen er goed uitlopen op zondag, en waarschijnlijk ben ik voor hem een aardige case van een proefschrift dat tot een eindeloos einde komt. Bij Wieger Schaap en Diane Blumenfeld heb ik een geweldige tijd doorgebracht tijdens mijn bezoek aan Oregon en Washington in de Verenigde Staten in 1987. Daar heb ik de ware Douglasbossen leren kennen en ook veel amerikaanse wortelonderzoekers. De laatste tijd ben ik veel mensen (bij o.a. het IBN, het IKC-Natuurbeheer en bij de KNBV) dankbaar dat zij mijn afwezigheid tolereerden, omdat 'andere' zaken voor gingen. Mijn buren Ger en An Nöllen ben ik zeer dankbaar voor hun goede zorgen en omdat An in de broodnodige vacanties en tijdens buitenlandse reizen steeds voor mijn huis en planten zorgde.

Het laatste jaar is Toos de Rijk, met Michiel en Jantine, een grote stimulans geweest, o.a. door ook eens andere dingen te organiseren: haar verhuizing, een zandbak omzetten in een volière, en vooral natuurlijk het wandelen. Daarnaast heeft ze verhelderend commentaar gegeven op de concluderende delen van het proefschrift. Bedankt! Michiel dank ik hartelijk voor de toestemming om een mooie tekening uit zijn kindertijd te gebruiken voor de omslag.

De diepste dank gaat uit naar mijn vader die, met mijn veel te vroeg overleden moeder en stiefmoeder, mij steeds heeft gestimuleerd om te doen wat ik wilde. Door hem wist ik al vanaf mijn vierde jaar dat ik naar Wageningen wilde. Ik had natuurlijk geen idee wat je daar kon doen, maar ik wist zeker dat het de moeite waard was. Ik kan nu zeggen dat ik mij daarin niet in vergist heb. De goede familiesfeer met Marijke, Rob en Marjolein en hun families (en recentelijk Corrie van Zundert) heeft zeker bijgedragen aan dit proefschrift. Ik ben mijn vader ook zeer erkentelijk voor de "Verhalen uit de Veen", die hij in 1996 ook heeft afgerond in een boekje. Daarin worden de "roots" van de familie op de boerderij duidelijk en zijn bewondering voor zijn ouders. Alles heeft toch weer te maken met wortels: bomen en familiestambomen. Daarom is het ook zo leuk dat mijn peetoom en peettante uit Australië zullen proberen om bij de promotie aanwezig te zijn.

Ad Olsthoorn
Bennekom
winter 1997/1998

Curriculum vitae

Adrianus Franciscus Maria Olsthoorn (Ad) is geboren op 10 oktober 1953 te Cuyk in noordoost Brabant. Na beëindiging van de lagere school aldaar in 1965, maakte hij in Boxmeer de HBS-B af in 1971. In Wageningen studeerde hij Bosbouw aan de Landbouwhogeschool. Hij bracht een praktijktijd van een jaar door in Australië, op de Australian National University te Canberra. De ecologie van de verspreiding van *Pinus radiata* in *Eucalyptus*-bos rond de plantages werd bestudeerd voor een Australische promotieassistent. Terug in Wageningen deed hij voor een gecombineerd vak Bosteelt en Meteorologie met Klaas van Dort en Harrie Raad onderzoek aan het effect van eiken en beuken op hun ondergroei. Tevens werd het concurrentiegedrag van eik en beuk in menging bestudeerd. Voor het vak Bodemkunde deed hij met Wilma Visser onderzoek aan de graafactiviteiten van driehoornmestkevers in zandbodems in het kader van het promotieonderzoek van Lijbert Brussaard. Ter afronding van de studie bestudeerde hij voor het vak Graslandcultuur hoe eenjarige planten zich handhaven in een permanente grasvegetatie. Hij studeerde in 1981 af met lof. Tijdens de studie was hij ruim anderhalf jaar actief als student-assistent voor practica in de houtanatomie, plantenanatomie en vegetatiekunde. Hij heeft drie maanden als vacantiekracht gewerkt bij de papierfabriek Van Gelder te Renkum, onder andere als opperpapierscheurder in het kwaliteitslaboratorium.

Na afloop van de studie deed hij vervangende dienst aan het toenmalige Instituut voor onderzoek in de Bos- en Landschapsbouw 'De Dorschkamp', met als onderwerp het inzaaien van visueel aantrekkelijke kruiden als alternatief voor bestrijdingsmiddelen in landschappelijke beplantingen. In 1983 werkte hij als vrijwilliger in Sneek aan een gemeentelijke Groennota die tot doel had het gebruik van bestrijdingsmiddelen in de openbare plantsoenen gefaseerd af te bouwen. Ondanks de daaropvolgende bezuinigingen in Sneek is dit meerjarenplan geslaagd door de grote inzet van de Plantsoenendienst. In 1984 en 1985 was hij anderhalf jaar werkzaam op het Consulentschap Stedelijk Groen te Boskoop.

In 1985 begon het werk aan dit proefschrift aan de Vakgroep Bosteelt van de Landbouwuniversiteit te Wageningen (later opgegaan in de vakgroep Bosbouw) in een van de vele onderzoeksprojecten op het gebied van effecten van luchtverontreiniging, betaald door het Additioneel Programma Verzuringsonderzoek. Het wortelonderzoek beschreven in dit proefschrift was deel van het onderzoek aan effecten op bossen in het ACIFORN-project (ACIdification of FORests in The Netherlands). In 1990 verwisselde hij dit dienstverband voor een aanstelling als onderzoeker bosbeheer aan het Instituut voor Bos- en Groenbeheer 'De Dorschkamp', later gefuseerd met het RIN tot het DLO Instituut voor Bos- en Natuuronderzoek. Naast voortgaand onderzoek aan vitaliteitsaspecten, trad onderzoek aan gemengd bos steeds meer op de voorgrond. Hij was tot 1997 coördinator van een driejarig Europees netwerk van 22 onderzoekers uit 13 landen aan gemengd bos (Concerted Action Mixed Forest). Als bestuurslid van de Koninklijke Nederlandse Bosbouw Vereniging is hij tevens lid van de Studiekringcommissie en de Activiteitencommissie. Daarnaast is hij lid van de werkgroep Pro Silva.

Ad Olsthoorn woont in Bennekom, heeft geen auto, gebruikt vreselijk veel papier en houdt van fietsen, wandelen, zeilen en muziek.