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FACTORS AFFECTING FINE ROOT DYNAMICS OF TREES

Perhaps the most important function of the fine root system of forest trees is in the uptake of water and mineral nutrients. To perform this function adequately, the root system must be extensive and active enough to meet the needs of the canopy. Literature indicates that fine root production is substantial and that the seasonal pattern of fine root production is different from that of foliage production. Carbon incorporation into the soil in the form of dead roots is an important pathway in the total carbon flow through forest ecosystems. Root growth is sensitive to various climatic factors which are often imposed or strengthened by human activities. Factors that lead to growth suspension may or may not be the same as those that result in root shedding or senescence. The use of minirhizotrons to study fine root dynamics means that ecologists are no longer justified in claiming that below-ground production is impossible to quantify in forest ecosystems.

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INTRODUCTION

The need to understand functional mechanisms behind ecological observations is evident. Forest research workers studying tree growth often over-emphasize the importance of long-lived and therefore more accessible plant parts. Studies of the growth of supporting structures in a forest tree — branches, stems, large diameter roots, etc. — are prerequisites for an understanding of how a tree allocates its resources with age, while studies of the growth of leaves (or needles) and fine roots are of immediate vital functional importance. Most large diameter roots in forest trees die with the tree itself, while the fine roots have been shown to be in a constant flux, often with a high rate of death and renewal (Persson 1979). The physiological cost of maintaining a fine root system for a single tree may be up to 70% of the available carbon flow (Ågren et al. 1980). Although the importance of fine roots as a pathway for organic matter and mineral nutrients into the soil has been demonstrated in many forest ecosys-

tems, data on fine root growth and turnover in relation to climatic factors are still very limited.

The root system supplies a tree with almost all water and mineral nutrients that it needs for growth and survival, but we do not yet know how an optimal root system of any tree species is built-up. Questions to be addressed are: — What determines how much of a stand's net primary production will be utilized by fine roots? — Can some of the production that is used for fine root growth be redirected to production of other tree components, like stem wood? Although, no one would refute the important role played by roots in water and nutrient uptake, species that minimize the investment of energy into those functions seem to be at an advantage for silvicultural practices.

The absorptive surface area is a function of root length and diameter and degree of penetration by the individual root tips, but the efficiency of rooting depends on soil conditions as well as the degree of suberization and mycorrhizal infection.

The complex interactions of tree roots and mycorrhizal fungi and other soil micro-organisms are still poorly understood. The objective of the present paper is to review the factors influencing the growth dynamics of the fine roots and to discuss the problems associated with their quantification.

FINE ROOTS — DEFINITION

The most widely used approach to estimate fine root production and mortality has been to calculate time differences in the dry weight of live and dead roots less than 1 or 2 mm in diameter. Researchers have sometimes arbitrarily chosen root diameter size classes varying from <1 to 10 mm (Vogt & Persson 1991) to encompass fine roots. In most cases, there is no functional reason for the diameter class chosen. However, for most tree species, subdividing and separating roots into <1 and >1 mm in diameter has a sound morphological basis. Roots <1 mm in diameter consist of fine ramifications with mycorrhizal root tips that are morphologically very distinctive from the rest of the root system (Vogt & Persson 1991). The fine root fraction may account for a high proportion of total root length. For example, for Scots pine, the <1 mm root fraction has been shown to constitute as much as 80% of total root length (Persson 1980a). The mean diameter of the fine roots (<1 mm in diameter) for Scots pine was shown to be clearly concentrated to diameters <0.5 mm (cf. Fig. 1). Average fine root diameter varys with tree type (deciduous or evergreen), location and

soil type. Therefore, root diameter size classes must be established for each site and for each species. For instance, the average fine root diameter is about 1 mm in many American coniferous forests but about 0.5 mm in similar Scandinavian forests. Lyford (1975) estimated that most hardwood fine roots ranged from 0.2 to 0.5 mm in diameter, with root tips of 0.1 to 0.2 mm diameter. In hardwood sites, it may be necessary to use more detailed root diameter classes, such as <0.5 mm and 0.5 to 1.0 mm instead of just <1 mm.

Roots >1 mm in diameter tend to be secondary roots in which the epidermis and cortex have sloughed off and the xylem has become enclosed by a cylinder of phloem with an outside layer of suberized tissue. Organic matter returned to the soil by sloughing of the epidermis and cortex may represent approximately half of the dry matter of a young root (Vogt & Persson 1991). Tree roots also increase in diameter by cambial growth. However, the growth patterns of the fine root biomass in terms of weight, surface area and volume is closely connected with changes in root length (Persson 1980a). Fine roots <1 mm in diameter include both mycorrhizal host and fungal mantle tissues.

Coarse tree roots stay alive for many years and may sometimes be as old as the tree itself. However, only a few fine roots survive for many years. Minirhizotron data (Hendrik & Pregitzer 1992) confirm the limited longevity of fine roots — a life around 0.65 years at <30 cm and 0.46 years at >30 cm depth for a deciduous forest dominated by *Acer saccharum*. As a result of frequent branching, the fine roots form dense networks which are constantly invading new areas of the soil. These areas are continuously replaced as new areas of the soil are explored. The root systems of trees extent into new areas of the soil or reoccupy areas earlier explored, by means of thick fast-growing root tips, e.g. long root tips. The age and growth of long roots are very variable. Repeated branching occurs in soils rich in organic matter and this leads to a dense formation of a network of the fine roots often in connection with mycorrhizal infection.
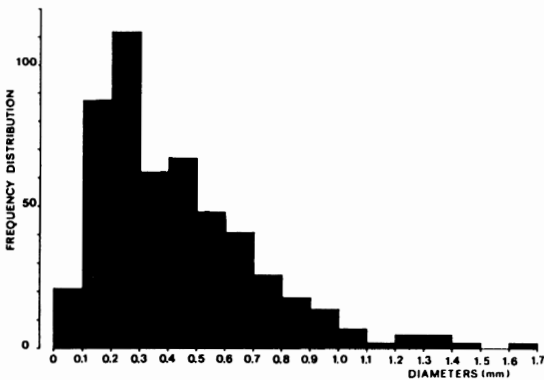

Fig. 1. Frequency distribution of *Pinus sylvestris* fine roots in the <1 mm diameter class (Persson 1980a). Because the diameter measurements were carried out in the middle of each fragment, parts of the roots can be thicker than 1 mm.

FINE ROOT GROWTH DYNAMICS

Fine roots of forest trees in temperate forests grow frequently at the humus-soil interface, in the uppermost 10 cm of the soil (Persson 1980a). Growth dynamics of fine roots may differ considerably between different sites, different tree

species and from one year to another (Persson 1980a, Vogt et al. 1980, 1991, Santantonio & Hermann 1985). There is a general assumption among foresters used to viewing the easily observable above-ground parts of the forest trees (e.g. leaves or needles) that fine roots may stay alive for at least one growing season. Although there are few data on the longevity of fine roots, there is no support for this assumption. On the contrary, most studies on the temporal pattern of fine root growth indicate a considerable variation in the fine roots during the growing season, indicating a high turnover rate (cf. literature in Persson 1980a). These turnover rates constitute the background to the long-term fluctuations in the soil organic matter during the life of a forest since the dead root material constitutes one important source of organic input into the soil environment.

FACTORS AFFECTING ROOT GROWTH

Roots — specialized organs

The tree root system may be regarded as an auxiliary organ providing mechanical fastening in the soil and absorbing water and mineral nutrients. These functions are indeed important, but we should remember that roots are highly specialized organs in which numerous syntheses may take place. From practical experience we know that vigorous root growth is necessary for good growth in above-ground tree structures. Water and mineral uptake are closely related to the total metabolic activity of the tree, including the degree of penetration of the fine roots. The influence of environmental factors on root growth is still rather obscure. The main factors that may influence root growth of forest trees are: age and type of tree species, carbon economy, nutrient and water supply, other abiotic factors such as soil temperature, soil strength and aeration, and finally chemical toxicity and allelopathy. Besides local climatic and edaphic factors, silvicultural practice may complicate the picture considerably.

Age and type of tree species

Studies of photosynthesis in different forest stands and for different species have shown the potential importance of fine roots in the cycling of carbon (Hermann 1977). Greater understanding of how genotype and site factors affect the amount of fine roots and their distribution and the quantity of total stand production is needed in order to evaluate how biological factors such as age of the trees and species affect the potential production. In most studies, the effects of soil water, nutrient status, stand composition, etc., have not been controlled experimentally, and have been confounded with the site conditions.

Site quality may significantly affect the relationship between the amount of fine roots and foliage produced annually (Santantonio et al. 1977). In closed canopy stands there is a consistent, strong negative relationship in dry matter partitioning between fine roots and stems (Santantonio & Grace 1987). This relationship incorporates differences in site, stand age and a range of species. In contrast to foliage, it may not be necessary for fine roots to completely occupy their environment at a given time. In closed forest stands, the carbon cost necessary for the uptake of water and nutrients by the fine roots appears to be in balance with the carbon partitioning to the foliage (Santantonio & Grace 1987).

The annual turnover of fine roots in a young Scots pine stand may be at least twice the average fine root biomass; in a mature stand, the turnover may be equal to the average fine root biomass (Persson 1979). Available data (Fig. 2 and Table 1) suggest that the fine root production (and fluctuations) are higher in a young Scots pine stand than in a mature one. Furthermore, the respiration costs increase considerably with the age of the tree. The mechanisms resulting in the rapid disappearance of roots upon death are of great interest since a high amount of carbon is involved. Apart from natural losses of root material from healthy trees as a result of replacement of the fine root system, severe losses may occur as a result of unfavourable soil conditions, soil toxicity, root decease or activities of soil animals or bacteria feeding directly on roots (see below).

Carbon economy

An indication of the importance of root production in the total carbon flow may be obtained from a carbon budget. If growth, respiration and the net photosynthesis are measured, the root production can then be calculated as the difference. Such a carbon budget reveals that, depending on tree age, 11–57% of the carbon that is assimilated annually by Scots pine trees is used for the growth of root systems; the corresponding respiration cost is 5–21% (Table 1). Investigations by Raich and Nadelhoffer (1989) show that live root respiration can be a major contributor to the total soil respira-
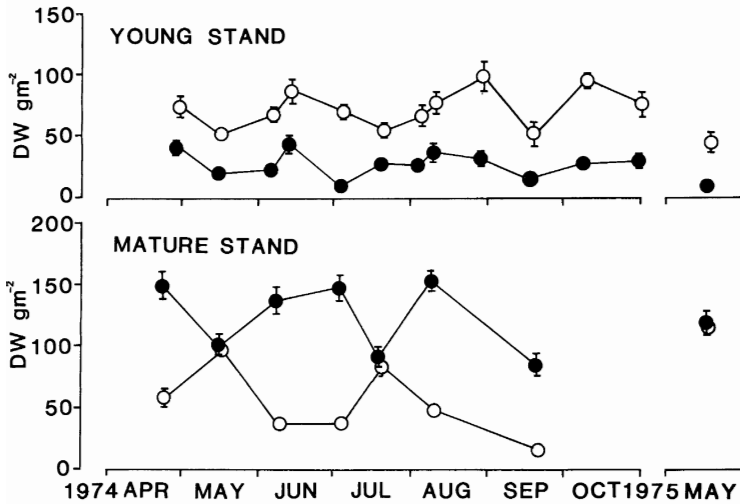
Fig. 2. Variability in the live and dead fine root biomass (<2 mm in diameter) in a young and mature Scots pine stand (Puhe et al. 1986). ○ = biomass; ● = necromass. Estimates are given as mean ± S.E.

tion, from 33% to 66% of the annual carbon release from the forest soil.

The carbohydrate storage in tree roots is generally fairly high (as much as 5–25% of the dry mass consists of starch; Wargo 1976, Ericsson & Persson 1980, Persson 1988). The starch content of fine roots varies considerably, part of which is related to diameter (Wargo 1976). The starch reserves are used for the growth as well as maintenance of the fine root system. It may be concluded that fine root growth leads to a reduction in starch concentration (Ford & Deans 1977, Ericsson & Persson 1980). Marshall and Waring (1985) developed a model to predict fine root production and turnover from soil temperature and starch depletion of the fine roots. The following hypotheses were tested: (i) that the growth of fine roots is accompanied by starch accumulation rather than depletion; (ii) that a fully developed fine root meets its maintenance requirements wholly from its starch and sugar reserves,

and (iii) that the root dies when its starch and sugar reserves are exhausted. From their results, it may be concluded that the initial starch concentration and soil temperature are key variables determining fine root turnover and fine root biomass.

Evidence from varying forest ecosystems demonstrates the importance of the root processes for the vitality of the forest tree (Persson 1988). In forests, damage often occurs above ground as needle loss (due to corrosion, drought, the effect of ozone, etc.) and below-ground in the root systems as fine root loss. In an area in SW Sweden, a needle loss of 20% was associated with a fine root loss of 10% (Puhe et al. 1986). However, there was no evidence that the reduced fine root growth was caused by a decreased translocation of carbohydrates from the shoots damaged by pollution. The evidence against the hypothesis of a gradual strangulation of the life processes due to a reduced photosynthesis, was — among other things — the fact that starch concentration was

Table 1. Annual carbon budget for an average tree in eight forest stands in Jädraås, Central Sweden (Ågren & Axelsson 1979). Estimates are given as $g\ C\ a^{-1}$.

Stand age	17	32	40	56	83	90	106	122
Net photosynthesis	1551	2738	6315	3348	7914	9880	10695	11653
Roots <5 mm	885 (57%)	307 (11%)	790 (13%)	1075 (32%)	4300 (54%)	4619 (47%)	4276 (40%)	6479 (56%)
Growth	592 (38%)	1861 (68%)	4186 (66%)	1768 (53%)	2848 (36%)	4067 (41%)	4992 (47%)	4115 (35%)
Respiration	74 (5%)	570 (21%)	1338 (21%)	504 (15%)	765 (10%)	1194 (12%)	1427 (13%)	1059 (9%)

almost the same (about 10% of the dry mass) in undamaged trees (with <10% needle loss) as in damaged trees (with more than 61% needle loss). The high starch levels in living fine roots may be the reason for them being able to stay alive in the forest soil for more than one year after clear cutting.

The general lack of an insight into the relationship between above- and below-ground production in forests results from the scarcity of reliable measurements of below-ground production (cf. reviews in Santantonio et al. 1977, Persson 1980a, Santantonio & Hermann 1985). Fine root production and mortality occurs simultaneously (Persson 1978, Santantonio & Grace 1987) and it is therefore difficult to separate them in time or space. Only limited attempts have been made to determine the precision of such estimates (Persson 1979). Changes in fibrous and mycorrhizal root biomass generally do not occur at the same time. Vogt et al. (1980) have shown that when less carbon is translocated to the root systems because of shoot growth, there is a decline in the proportion of the fine roots that are composed of mycorrhizal root biomass.

Nutrient status

There is always a much greater proliferation of roots in the LFH layer than in the mineral soil (Fig. 3). In the LHF layer, it would appear that there is a fairly low turnover of *Pinus sylvestris* fine roots and a large number of root tips per unit length having a heavy, ramified network of mycorrhiza (Persson 1980b). This vigorous proliferation is the result of better moisture and nutri-

tion conditions. Fine roots in the mineral soil, on the other hand, are characterized by a high turnover, fewer root tips per unit length, and the formation and elongation of fast growing long roots.

Estimations of fine root production have usually been carried out as part of total stand production studies in plantations and natural forests. Although most studies have been comparative, e.g. good versus poor sites (Keyes & Grier 1981), quantity and form of available nitrogen (Persson 1978, Nadelhoffer et al. 1985, Helmisaari 1990, Finér 1992), few studies have been experimental. Although it is often not possible to define from these studies which specific factors were most important, it is clear that a greater amount or proportion of the total net primary production goes to the fine roots when site conditions are less favourable for growth.

Data on fine root growth in response to the presence of plant nutrients in the vicinity of the tree roots are available from many field experiments in Sweden (e.g. Persson 1978, 1979, Ahlström et al. 1988, Persson & Ahlström 1990, Wallander et al. 1991). From these experiments it has been shown that an increased needle mass in stands with a high nitrogen supply often corresponds to a reduced amount of fine roots and mycorrhizal frequency (Fig. 4). Liquid fertilization using drop tubes indicates a positive effect on fine root growth in the area nearest the drop tube (Fig. 5). Other treatments, such as liming and compensatory fertilization (Fig. 6), may result in both negative and positive effects on the growth and development of fine roots, depending on soil type and dosage.
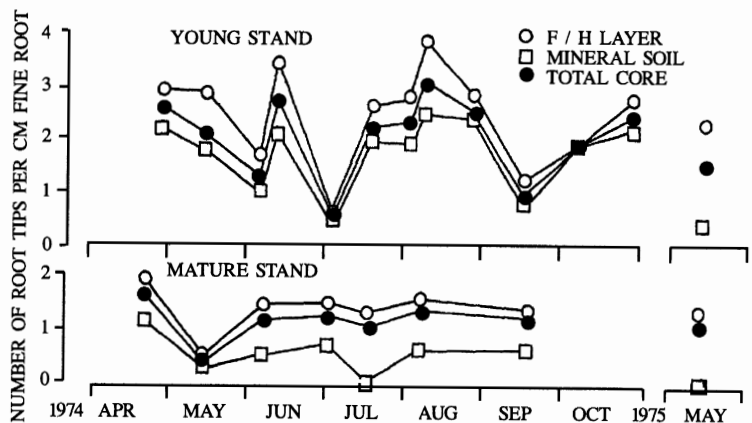

Fig. 3. Seasonal fluctuations in the number of root tips per cm fine root in a young and a mature Scots pine stand (Persson 1984).
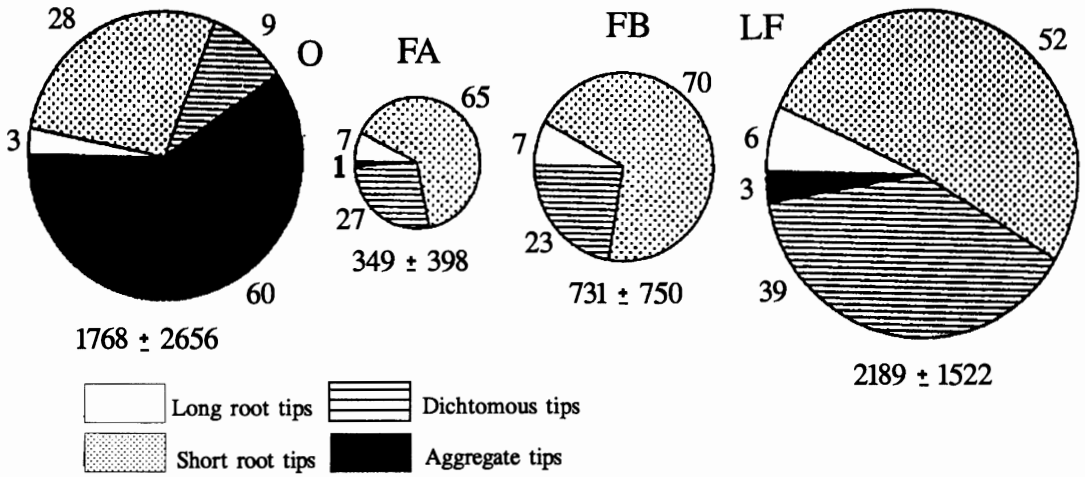
Fig. 4. The effect of fertilization on mycorrhizal formation studied with ingrowth technique. The data (0 = control plot) are from a mature Scots pine stand which had been fertilized with solid fertilizers at different application rates (FA and FB) and liquid fertilizers (LF) during the growth period. The size of circle is proportional to the total number of root tips, which is given below the circle ($\times \pm$ S.E.; 1 000 m^2/yr). The segments correspond to varying types of root tips — their percentage distribution is indicated by numbers outside each segment. 1 dichotomous root tip = 2 root tips; 1 aggregate tip = 30 root tips. Data from Ahlström et al. (1988).

Investigations into the long-term effects of forest liming on fine root growth dynamics show a tendency to increased specific root length and slightly thinner roots (Clemensson–Lindell & Persson 1993). Similar effects have also been shown using liquid fertilization (Persson 1978). Liming does not seem to have a persistent long-term effect on the fine root development. However, N-fertilization (Fig. 6) will cause persistent negative effects on both fine root and mycorrhizal development in most cases (Ahlström et al. 1988, Persson & Ahlström 1990/91).

Water status

Because of the unequal penetration of the precipitation through soil fissures, old root channels and differences in the permeability of soil layers, and because of the unequal uptake by root tips, moisture conditions in the soil is often very hetero-
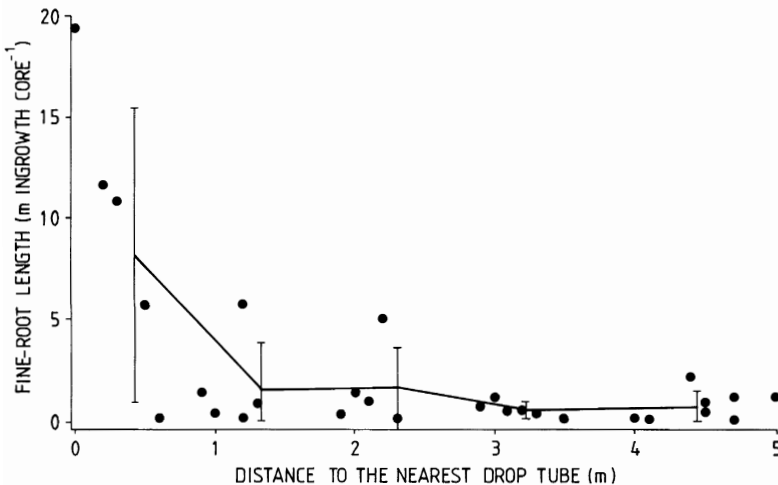

Fig. 5. The effect of distance to the nearest drop tube used for liquid fertilization in a 40-year-old Norway spruce stand (Persson 1988). Two series of ingrowth cores were implanted — one in May 1983 and one in May 1985. All ingrowth cores were resampled in October at the end of the 1983 and 1985 growing season. The distance to the nearest drop tube was measured at the same time as the ingrowth cores were taken up.
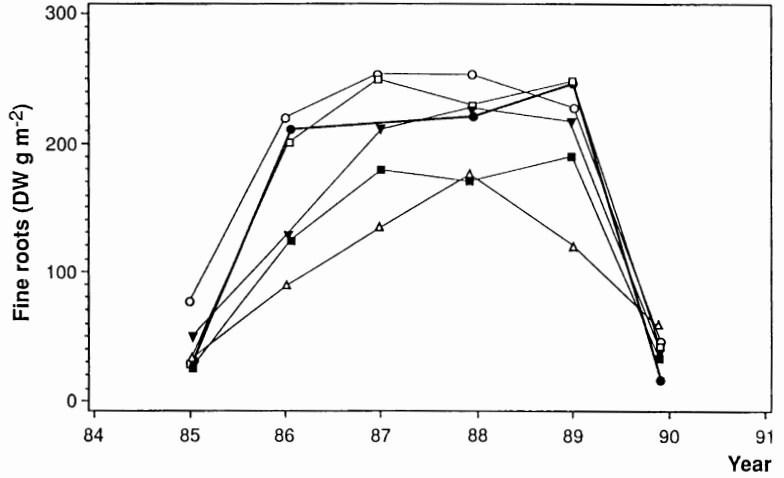
Fig. 6. The amount of living fine roots (<1 mm in diameter) in ingrowth cores in one 23-year-old Norway spruce stand in S. Sweden subjected to different experimental treatments (liming and compensatory fertilization, cf. Persson & Ahlström 1990/91). Control = ●, carbonate lime in increasing doses = ☐ and ■, dolomite lime = ○, peat-ash = △ and wood-ash = ▼.

geneous. New water and mineral nutrient resources must be found by the actively penetrating root tips. A high growth rate means that a large soil volume is penetrated, which contributes to the maintenance of a stable water regime. Data from one field experiment, indicates negative impacts from drought, particularly in the LFH-40 cm mineral soil layer (Fig. 7). In contrast to the ammonium sulphate treatment, which caused a superficial fine root distribution, the fine roots in the drought treatment were distributed most intensively in the deeper soil horizons.

Efficient water uptake by some part of the root system can provide the necessary water for the whole tree. Some roots may grow through dry zones when the water uptake and supply is guaranteed by other roots. In dry soils, as in the case of the drought experiment mentioned above (Fig. 7), roots have a tendency to grow towards more humid zones and are therefore generally found at greater depth than in moist soils (Lyr & Hoffmann 1967). The whole soil profile may

appear to be more occupied by fine roots in dry sites than in wet sites, even though the total fine root production may not differ significantly (Santantonio 1979, Puhe et al. 1986).

Other biotic factors

Root growth is the result of metabolic processes and is therefore regulated by soil temperature. Investigations of the effect of soil temperature on root growth are complicated since the growth rate also depends on soil moisture and shoot development. Most authors agree that optimal temperatures for root growth are lower than those for shoot growth of the same species (Lyr & Hoffmann 1967). In general increases in soil temperature stimulate the growth rates of roots and accelerate their maturation (Marshal & Waring 1985). Compacted soil leads to an increase in soil temperature, since heat can more easily be transported through it (Voorheess 1977).

Fig. 7. The vertical distribution of fine root biomass (black), necromass (white) and the total amount of fine roots (<1 mm in diameter) at the Skogaby investigation area in the control (C), the drought (D; two thirds of precipitation during the growing season excluded by a roof) and the ammonium sulphate addition (NS) treatment. (Persson, unpublished data).
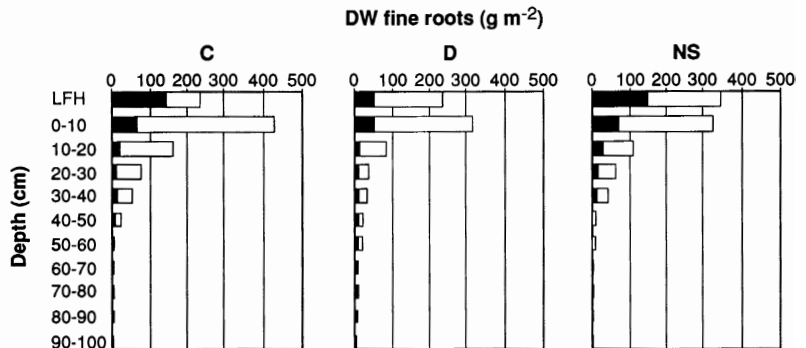
Roots are forced to penetrate large soil volumes, often against mechanical resistance of densely packed soil layers (Clemensson–Lindell et al. 1992). Tree roots often follow old root channels because of the lower resistance. In a mixed forest stand the root system overcomes soil resistance better and grows deeper than in monocultural forests (Hoffmann 1966). The ability of roots to overcome soil pore resistance is often related to soil oxygen content (Zahner 1968). Excess soil water can influence root growth adversely if the water has a low oxygen content. However, if the water is moving and contains enough of oxygen, roots can survive. For example, the roots of Norway spruce, known for their intolerance of anaerobic condition, can survive for many years below the water table (Paavilainen 1966).

Soil toxicity

Chemical toxicity in the forest soil often occurs as a result of human activities (Majdi & Persson 1989, 1992, Gobran et al. 1991, Clemensson–Lindell et al. 1992). For example, destabilization of the root systems as a consequence of soil acidification has been observed (Persson 1985, Puhe et al. 1986, Majdi & Persson 1993). Root damage is often observed as a decline in the amount of living fine roots, an increase in the amount of dead *versus* live fine roots and an increase in the amount of dead medium and coarse roots. The most important factors which may cause a reduction in fine root growth and mycorrhizal development are: (i) ion-imbalances, viz. a reduction in base saturation with subsequent losses of Ca and Mg by leaching and an increased concentrations of Al, Fe and H ions and also, in many cases, of heavy metals in the rhizosphere; and (ii) high N deposition leading to a disturbed mycorrhizal frequency and a root system more sensitive to disturbances (drought, wind-break, nutrient shortage, etc.).

The chemistry and acidity of the soil are most important in root–rhizosphere relationships. The processes of ion uptake are dependent of the degree of penetration of fine roots and mycorrhizas into the soil. If the uptake process is hampered, the growth of the whole tree may be affected. Root damage, in this context, may underline a predisposing stress, thus reducing water and mineral nutrient uptake. Root damage often seems to be related to poor soil conditions with generally low nutrient availability (Ulrich 1990).

Allelopathy

This term refers to the production of toxic substances by roots or plant residues that inhibit root growth.

It is a well-established fact that tree species frequently fail to develop when heather, *Calluna vulgaris*, is dominating in the ground vegetation (Handley 1963, Robinson 1972). A fungal toxin secreted by the roots of *C. vulgaris* is thought to be the reason. Water soluble substances from reindeer lichens (*Cladonia alpestris* (L). Rabenh.) have also been shown to inhibit the growth of mycorrhizal fungi by Scots pine (Brown & Mikola 1974).

These observations serve to emphasize the potential effects of allelopathic agents at an intraspecific level in forest ecosystems. Identification of allelopathic agents and the duration of their effects still have to be determined.

FUTURE ROOT INVESTIGATIONS

Methods for quantifying root production are still poorly developed (Vogt & Persson 1991). As a result, roots have rarely been included in field physiological studies of trees. However, during recent years, it has been possible to observe roots directly in the soil using minirhizotrons and television cameras. A new aspect of this technique is the ability to digitize the video images and to use the images to assess root growth (Taylor 1977, Hendrik & Pregitzer 1992, Majdi et al. 1992). It is therefore no longer possible for ecologists to claim that fine root production is impossible to quantify in terrestrial ecosystems.

Many major environmental problems result from the lack of information about the part played by tree roots in the cycling of carbon in forest ecosystems (Persson 1991). Some important areas for future root investigations in forest ecosystems are: (i) carbon and mineral nutrient allocation pattern in trees, ii) determine how long the nutrients remain in the below ground biomass compartments (i.e. resistence times), (iii) establish the physiological differences between young and old trees in the growth dynamics of fine roots, (iv) the linkage between soil, rhizosphere and fine root chemistry, (v) exudation from tree roots, (vi) uptake by mycorrhizal roots, (vii) patterns of distribution and movement of water in forest soils and the rhizosphere, and (viii) vitality criterias of fine roots.

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