

# **Tree fine root dynamics in cool temperate and boreal forest – a review with particular reference to Swedish research.**

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The amount of carbon and nitrogen cycled via fine root production and decomposition can be as large as, or larger than that circulated with above-ground litterfall (Nadelhoffer and Raich 1992; Fahey and Hughes 1994). There has previously been a lack of appreciation of the magnitude of the fine root contribution to the total tree carbon turnover. The development of field methods for studying the growth dynamics of fine roots has always been hampered by the fact that they are not readily visible. This has resulted in root growth phenomena being mainly interpreted from excavated core samples. Since root research workers nowadays can use miniature colour TV cameras, which are able to produce high-resolution images that can be digitised and stored in database files for processing, it is no longer justified to claim that fine-root growth dynamics is impossible to describe quantitatively. No long-term characterisation of mycorrhizal short root development besides the basic observations of Orlov (1957, 1960) had been made before the advent of minirhizotron studies (Majdi and Nylund 1996).

Fine roots of trees have above all been noticed in their function of basic constituents of mycorrhiza, those in cool temperate and boreal forest above all ectomycorrhiza. There has been a strong tradition of research in this field in the Nordic countries; however, these studies have focussed on function and identity of the fungal component (cf. Nylund 1988). Quantitative aspects of mycorrhiza dynamics under natural conditions have been few if any.

## **Development of research on fine root dynamics**

The fine root contribution to the carbon cycle started to be noticed in the large-scale integrated programmes set up in the 1970's, in Sweden Barrskogslanskapets ekologi /Swedish Coniferous Forest Project (SWECOM?)t, with a main forest research site at Jädraås ; 16° 12 N', 60° 00 E' 315; m a.s.l). Considering the difficulties in generalising previous, mainly qualitative reports, the approach was that of system ecology, aiming at quantifying pools and fluxes. A large and fundamental contribution to this work was done by Hans Persson (Persson, 1978, Persson, 1980), using soil coring and ingrowth cores as their main tool. A synthesis of the Jädraås findings was published in Persson (1978). That report was followed by a study by Linder and Axelsson (1982), focusing on a single tree rather than a stand, but estimating the fine root contribution using a total carbon budget rather than direct observations. In a carbon budget study based on Parsson's fine root turnover estimates, et al, (1980) claimed that root growth obtained by sequential soil coring accounted for 90% of total carbon allocated to roots while only 10% of that was used by root respiration. Total soil respiration was studied in a wide range of studies by Anders Nordgren, while root respiration

was examined i.e. by Widén and Majdi (2001). The issue of root vs. heterotrophic respiration continued to be debated (cf. Bowden et al 1993; the review by Hansson et al 2000). A most convincing case of quantification was recently provided by Högberg et al (2001) through girdling of an entire stand, confirming the median values reached at by Hanson et al in their extensive compilation of existing data. These girdling studies are currently being extended to various stand treatments (Linder, pers. comm.). Moreover Högberg et al, (2002) refuted the previous findings by Ågren et al, (1980) and concluded that 75% of carbon allocated to roots was respired and 25% was used for root growth.

After a phase when the main interest was focused on establishing basic patterns of element cycling through trees and stands, both large and small-scale experiments during the 1980's and 90' strived at assessing the impact of environmental strain in forest ecosystems. The largest one was the Skogaby programme, where the effects of combined acidification and nitrogen deposition were studied and compared with possible mitigation treatments (Synthesis report by Persson & Nilsson 2001). The principal consequence of this shift in interest was that qualitative comparisons and relative impacts came to emphasised, rather than establishing quantitative estimates of stand parameters regarding pools and fluxes.

While at the end of the period, satisfactory information had been obtained above all regarding the effect of acid deposition, another major environmental concern has received steadily increased attention: the consequences of the steadily increasing CO<sub>2</sub> level in the atmosphere and its assumed consequence, global change. Particularly by means of open-top chamber experiments, direct effects on fine root and mycorrhiza development have been described (Fransson, 2000)) and found to be less alarming in the magnitude of impact than was, above all, unbalanced eutrophication in connection with acid deposition. Yet, both scientific interest as such, as well as the demands for reliable information raised by the round of international negotiations on means and commitments to mitigate the increase in atmospheric CO<sub>2</sub>, brought forward the need for large-scale modelling of carbon cycling through various types of ecosystems. In the light of this development, the previous emphasis on establishing relative effects of pollutants and remedies was unfortunate: The new focus of research demanded quantitative data on carbon cycling through the ecosystem.

During the later part of the 1980's and all 90's a low-key debate had been going on regarding the reliability of methods estimating fine root standing biomass and turnover (reviewed by Vogt et al 1998). Assessing standing biomass seemed to offer no major problems except the hard work involved, and the difficulty in separating live from dead root material. The turnover, however, seemed to present major problems using traditional coring techniques. Alternative methods were looked for; including the N-budget (Aber et al 1985) and the <sup>14</sup>C abundance caused by nuclear weapons testing (Gaudinski, 2002, Tierney and Fahey 2002). The <sup>14</sup>C method however, is base on some assumptions i.e. the rate of root mortality is constant during the year and all carbon allocated to roots is from the current year assimilates. Because of both laboriousness and lacking reliability of methods, efforts were also made to track errors or even estimate the elusive fine root production or turnover rates by calculations and modelling more handy parameters (Singh et al 1984; Kurz and Kimmings 1986; Publicover and Vogt 1992; Mäkelä and Vanninen 2000). In particular, the Mäkelä and Vanninen model shows promise of being useful, being based on the parameters standing biomass and necromass and decomposition rate.

A particularly illustrating case of the shortcomings of coring methods is given by the reassessment of the fundamental paper by Ågren et al (1980) on the carbon budget of a single

pine tree. Based on seemingly solid data Persson (1978) estimated fine root turnover to take place several times a year, leading to a partitioning of carbohydrate allocated to the roots of 90% to growth, 10% to respiration, as mentioned above. The quoted findings of Högberg et al. (2001), that a more likely ratio would have been 50:50 motivated a critical re-examination of the previous work (Högberg et al 2002). The necessary consequence of this recalculation was that root turnover rates rather ought to have been about  $1 \text{ year}^{-1}$ . This kind of systematic error was identified as likely to be expected on poor sites by Hendricks et al (1993), who emphasised the general difficulty of finding a universally valid reference method for determining fine root turnover, writing at the point when the minirhizotron technique was being introduced.

## The minirhizotron

The minirhizotron technique can be used to obtain (i) quantitative information on root length, root density and root dynamics (production, mortality and longevity), and (ii) qualitative information on root colour, suberisation, branching characteristics, patterns of senescence and decomposition rate (Hendrick and Pregitzer 1992; 1993). This method has been used to monitor the effects of experimental manipulations (e.g., addition of water and nutrients) in different forest ecosystems. Fixed windows in subterranean observation chambers have been used for along time, but are rarely used in field studies because of the large-scale soil disturbance caused by their installation. The advent of proper video technique in the beginnings of the 1990's made it possible to replace the chambers by transparent tubes buried in the soil, capable of holding specially developed cameras for repeated or even continuous observation of fine roots. Constraints and now opportunities offered by the method were penetrated in a workshop in Swedish Båstad in 1996, and are discussed in a context of northern forest fine root research by Majdi (1996).

This is the only available method whereby individual roots, or root cohorts (groups of roots emerging in defined periods of time) can be followed from emergence to death and disappearance. While there is little doubt about the validity of the information on the developments of single fine roots, there has been a lot of discussion and critical examination regarding the reliability of minirhizotron observations of quantitative estimations of root turnover, but above all of standing fine root biomass. Repeated comparisons with soil coring and biomass estimations through minirhizotrons having achieved steady-state after insertion have shown the latter to correlated well with core data. Yet, the strength of the method consists in the possibility it offers to follow processes where time is a basic variable; in the study of fine root production and demography, minirhizotron observation is rapidly becoming the reference method (Fahey et al 200x). An outline of calculation methods for minirhizotron data is provided by Tierney and Fahey (2001).

The position of the LUSTRA root research team regarding the key input parameters in the overall modelling work is that soil cores are indispensable for establishing basic data on *standing root biomass*, while minirhizotron observations are the only reliable method of getting information on *production and turnover*, and can provide important information on fine root decomposition; litter bags are, however, as yet indispensable in getting firm *decomposition* data.

## Standing fine root biomass estimates in Sweden and under comparable conditions

There are several studies in which standing biomass ( $\text{g m}^{-2}$ ) of fine roots (diameter  $<2\text{mm}$  unless indicated otherwise) has been estimated in Swedish natural forest ecosystems or those that being undertaken experimental manipulations. Persson (1982) compared two mature *Pinus sylvestris* stands in Central Sweden, estimating biomass as 2200 and 1900  $\text{kg ha}^{-1}$ . Majdi and Persson (1995) estimated biomass in a 26 years old *Picea abies* stand to 4920  $\text{kg ha}^{-1}$ . Person et al., 1995 estimated biomass in a 100 years old as 1450-2560  $\text{kg ha}^{-1}$ , while in 20 years old stand the corresponding value was 260  $\text{kg ha}^{-1}$  (Person, 1983). In manipulated stands (induced drought and nitrogen fertilisation) the biomass in *Picea abies* (28 years old) in control, drought and ammonium sulphate plots was 2730, 1420 and 2650  $\text{kg ha}^{-1}$ , respectively (Persson et al, 1995). Majdi and Persson (1995) estimated two years later standing biomass from the same site manipulated with NS and found varying values in both control and NS plots (see Table 1).

Clemensson and Persson, 1993) studied effects of liming in a *Picea abies* (31 years old) on biomass ( $<1\text{ mm}$  in diameter). The biomass in C and limed plots was 1680 and 2880  $\text{kg ha}^{-1}$ , respectively. The standing biomass in a 69 years old *Picea abies* stand was 2570 and 2500  $\text{kg ha}^{-1}$ .

**Table 1.** Fine root standing biomass ( DW ton  $\text{ha}^{-1}$ ) in spruce and pine forests of different age in natural forest stands or in those manipulated with water nitrogen or liming .

Site/Treatment	Species	Age	Diameter (mm)	Biomass ( $\text{kg ha}^{-1}$ )	Reference
<b>Southern Sweden</b>					
Natural stands	<i>Picea abies</i>	26	$<2\text{ mm}$	4920	Majdi and Persson, 1993
	<i>Picea abies</i>	28	$<2\text{ mm}$	6562	Majdi and Persson, 1995
	<i>Picea abies</i>	30	$<2\text{ mm}$	5241	Majdi and Persson, 1995
N-fertilization	<i>Picea abies</i>	28	$<2\text{mm}$	7633	Majdi and Persson, 1995
	<i>Picea abies</i>	30	$<2\text{mm}$	1295	Majdi and Persson, 1995
<b>Northern Sweden</b>					
Natural stands	<i>Picea abies</i>	33	$<2\text{ mm}$	4000	Majdi, 2001
N-fertilization	<i>Picea abies</i>	33	$<2\text{ mm}$	6960	Majdi, 2001

## Estimating fine root turnover in Sweden and under comparable conditions

The first minirhizotron observations in Sweden were done in the Skogaby experiment, where the technique was used in a major study of eutrophication-acidification on forest soil. Observations, including unpublished data, covered a total of five years, plus one for equilibration avert installation of the observation tubes. During preceding work (Majdi and Persson 1995, Persson, et al 1995), soil cores and monoliths had been analysed for biomass and nutrient element distribution; now, in two papers, long root dynamics (Majdi and Kangas 1996) and mycorrhiza development (Majdi and Nylund 1996) were described. Using the same material, a more profound analysis of mycorrhizal root dynamics was published by Majdi et al (2001), and a synthesis report was included in the end report from the Skogaby project (Majdi and Nylund 2001). A major surprise waited. While treatment effects certainly were

forthcoming, the remained within expected ranges. But the overall picture of fine root longevity and turnover was dramatically longer than the Jädraås soil coring studies had indicated: the average long root lifetime proved to be in the range of a year, rather than the two-three month indicated by indirect methods. And a notable proportion of the roots remained viable for many years, and that group included even the supposedly short-lived mycorrhizal root tips. And meanwhile, similar information was supplied by minirhizotron research in cool climates abroad (Wisconsin pine 291 days, Coleman et al 2000; New Hampshire broadleaf forest 314 days, Tierney and Fahey 2001; more than 2 years, Tierney and Fahey 2003).

As Skogaby represented a maritime site and a vegetation zone of mixed coniferous-broadleaf forest, a second set of minirhizotrons was installed in the Flakaliden experimental area in northern Sweden, in a distinctly boreal climate with a vegetation period of only four months. In a first study (Majdi 2001), effects of irrigation and optimum fertilization were described. In spite of the radically different climatic conditions, fine root longevity turned out to be approximately the same as in Skogaby, slightly over a year in the control plot. In a following paper (Majdi and Andersson, 2003) both tree and ground vegetation fine roots were observed and quantified; the two components turned out to be of approximately the same size in that particular stand. In two further studies under publication, the influence of the 8 month winter and the effects of soil warming are discussed (Andersson and Majdi, under review; Majdi and Öhrvik, submitted). These reports further confirm the longevity of approximately one year, and the necessary conclusion, that standing biomass and new root production under near steady-state conditions are of similar size.

Similar turnover rates had also been reported from studies using other methods. Thus, Burke and Raynal (1994) reported rates of 0.8 to 1.2 year<sup>-1</sup>. On the other hand, much higher estimates were provided by Makkonen and Helmisaari (2001), ranging from 2 to 4 year<sup>-1</sup>. Using biomass to necromass ratios and decomposition rates as input data, Mäkela and Vanninen(2000) found turnover to range from 0.5 to 2 year<sup>-1</sup>. The noted not surprisingly that their model was most sensitive to changes in decomposition rate.

**Table 2** Root turnover (yr<sup>-1</sup>) in forest floor and mineral soil layers of spruce roots. Root turnover was calculated as inverse of median root longevity obtained from minirhizotron technique.

Soil layer	Treatment		
	Control	Irrigation	Nitrogen addition
<b>Northern Sweden</b>			
Forest floor	n.d	0.44	1.1
Mineral soil	1	0.93	0.9
<b>Southern Sweden</b>			
Mineral soil	1	n.d	0.9

## Estimating fine root biomass and production from above-ground data

Determining the standing biomass of fine roots through coring is reliable but labour intensive. As stated above, it is the firm opinion of the authors of this report that no calculation of fine

root production using differences in biomass data, ingrowth cores, or biomass/necromass ratios are fully reliable. The main reason for this position is not the lack of fulfilment of the basic assumptions underlying the analyses, nor the difficulties in precision, but the lack of calibration against an objective method. With the minirhizotron, we now have such a method, but when this is to be used for reference purposes, which would have to be used at each site anew, there is no reason not to expand the minirhizotron or with other kinds of observations or calculations.

In a major effort to model fine root production, Canadian researchers and colleagues elsewhere have examined a large number of parameters possibly correlated with root growth. In the latest report (Chen et al 2003/under publication), single-tree ground surface and fine root biomass were found to be well correlated. Turnover rates were estimated as functions of standing fine root biomass, stand age and mean annual temperature. Unfortunately, the predictions were not compared with minirhizotron measurements, but with other, conventional ways of estimating fine root production.

### **Fine root production and turnover- the requirements by LUSTRA**

Based on information above we have knowledge on fine root production and turnover in a limited number of spruce stands on in South at Skogaby site and another in north at Flakaliden site (See Majdi and Nylund, Majdi and Kangas and Majdi, 2000). To our knowledge, most studies of root dynamics in forest ecosystems are focused on tree roots only, whereas data on turnover and production of both spruce roots and understorey vegetation roots are limited (compare John and others 2001; Makkonen and Helmisaari 2001). However, these studies show that understorey vegetation may contribute significantly to the below-ground carbon budgets, and the root production and root N turnover in forest ecosystems might thus be underestimated when only tree roots are taken into account. Thus we do need data on turnover of understorey vegetation roots to our carbon budget within LUSTRA. Furthermore we have no data on production, mortality and turnover of fine roots for birch and pine. The third source of data we do not access to is fine root turnover in drained forest in Sweden.

### **Fine root standing biomass and turnover in the COUP model**

The LUSTRA project is using the COUP model (Jansson et al ....) as a major tool in modelling carbon flow and retention through the ecosystem. We have therefore examined the way the current version of COUP (ref) handles fine root parameters. In the current version, root growth is treated as a fraction of the net photosynthetic assimilation. Trees are taken as the standard of discussion, while field layer plants, in our ecosystems woody shrubs on one hand, grasses on the other, certainly have to be included in the comprehensive model. The starting point for the COUP calculations is net photosynthesis, and algorithms have to developed determining the fraction allocated to the below- ground parts of the tree/plant. Net photosynthesis can be estimated fairly accurately (ref, comment?) using seasonal, meteorological and stand parameters. The issue is, then, to find out what allometric relationships best describe this fraction.

The assumption underlying the following argument is that carbohydrate allocation to the root is related to the N, and possibly P requirement. Also, there is a cost-benefit function; in case

additional carbohydrate does not bring back more N (or P), the flow is reduced. Most likely, there is a sink-type feedback regulation. What complicates the matter is that not fine roots, but and above all mycorrhizal mycelia are responsible for the mineral nutrient uptake. Examining the major carbon sinks below ground, we thus have to count with

- production of new roots
- maintenance respiration of roots
- rhizospheric leakage from roots
- production of mycorrhiza
- production of mycorrhizal soil mycelium
- maintenance respiration of fungal tissue
- build-up of storage carbohydrate

Furthermore, there are three basic patterns in the carbohydrate allocation to the below-ground part of the tree:

1. *The annual pattern*, where carbohydrate is first directed to shoot expansion, then to fine roots, then to carbohydrate storage in the coarser roots – this being a very simplistic scheme.
2. *The stand rotation pattern* (directing the attention to the predominant forest land use in Sweden), where an initially small biomass of trees gradually occupies the soil resources of the site, exhibiting a net increase of below-ground biomass as well), but at some stage, presumably coinciding with canopy closure, the soil space occupation has reached 100%, nutrient uptake is small compared to internal nutrient circulation (including recovery of litter nutrients). At this point, root production is supposed to be limited to replacement of mortality. No net production is taking place.
3. *The site and species depending pattern*, where above all fertility, but also hydrology and soil texture interact with species-related patterns in determining overall above to below ground biomass relationships

For the modelling work, we propose that

- the annual pattern be ignored at this stage of model development, and as the annual variation in root litter supply to the decomposition process cannot be assumed to influence the output to the carbon pool in the long run. All the following applies to annual means.
- the next phase of root studies be dedicated to establishing relationships between stand parameters and fine root biomass (standing and/or production) in closed stands of varying age and on different sites. The immediate objectives of the work would be to establish whether fine root biomass remains constant with age, is correlated to green mass, total above-ground biomass, or to basal area. Also, the net N uptake should if possible be monitored.
- to explore the site-dependent variation in the relation between fine-root and total above ground, stem biomass, and surface area.
- Then, a simplified fine root standing biomass build-up model should be developed for younger stands, with the assumed steady state level of item 2. as an end point
- Meanwhile, the root turnover studies using minirhizotron technique should continue and be expanded to key sites covered by the studies described above
- Immediate matters to settle would be whether turnover varies with stand age, with site fertility, and if possible with the degree of internal circulation of mineral nutrients (N), and also with annual net photosynthesis
- Finally, the sensitivity of the soil carbon processes modelling of COUP to variations in fine root production (or more immediately, to variation in the root turnover rate) should be examined, in order to avoid unnecessary and very expensive exactness in their

determination, this measurement probably being the most demanding in terms of time and labour.

## References:

- ABER JD, MELILLO JM, NADELHOFFER KJ, MCCLAUGHERTY CA, PASTOR J 1985 Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecol.* (Berlin) 66, 317-321
- ANDERSSON P, MAJDI H ( ) Estimating root longevity at sites with long periods of low mortality. (Submitted to *New Phytologist*)
- BOWDEN RD, NADELHOFFER KJ, BOODE RD, MELILLO JM, GARRISON JB 1993 Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can J For Res* 23, 1402-1407
- BURKE MK, RAYNAL DJ 1994 Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil* 162, 135-146
- CHEN W, ZHANG Q, CIHLAR J, BAUHUS J, PRICE DT (under publ) Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: a new approach. *Plant and Soil*, under review.
- COLEMAN MD; DICKSON RE; ISEBRANDS JG 2000 Contrasting fine-root production, survival and soil CO<sub>2</sub> efflux in pine and poplar plantations. *Plant and Soil* 225, 129-139.
- FAHEY TJ, BLEDSOE CS, DAY FP, RUESS R, SMUCKER AJM (20xx) Fine root production and demography. (preprint)
- FRANSSON, PETRA, M.A. ANDY, F.S. TAYLOR AND R.D. FINLAY. 2000. Effects of continuous optimal fertilization on belowground ectomycorrhizal community structure in a Norway spruce *Forest. Tree Physiology* 20:599–606.
- HANSON PJ, EDWARDS NT, GARTEN CT, ANDREWS JA 2000 Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115-146
- HENDRICKS JJ, NADELHOFFER KJ, ABER, JD. 1993 Assessing the role of fine roots in carbon and nutrient cycling. *Tree* 8,174-178
- HÖGBERG P, NORDGREN A, BUCHMANN N, TAYLOR AFS, EKBLAD A, HÖGBERG MN, NYBERG G, OTTOSSON-LÖFVENIUS M, READ DJ 2001 Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 4 June: 789-792
- HÖGBERG P, NORDGREN A, ÅGREN GI 2002 Carbon allocation between tree root growth and root respiration in boreal pine forest. *Oecologia* 132:579-581
- KURZ WA, KIMMINS JP 1987 Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach. *Can J For Res* 17, 909-912
- LINDER S, AXELSSON B 1982 Changes in carbon uptake and allocation patters as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. In: *Carbon uptake and allocation in subalpine ecosystems as a key to management*. Proc. IUFRO workshop P.1.07-00; Corvallis, Oregon. Ed. By RH Waring.
- MAJDI H 1996 Root sampling methods – applications and limitations of the minirhizotron technique. *Plant and Soil* 185, 255-258.
- MAJDI H 2001 Changes in fine root production and longevity in relation to water and nutrient availability in a Norway spruce stand in northern Sweden. *Tree Physiology* 21, 1057-1061
- MAJDI H, ANDERSSON P 2003. production, longevity and nitrogen turnover of field layer vegetation and spruce roots in response to nutrient availability in northern Sweden. *Ecosystems*, in press
- MAJDI H, DAMM E, NYLUND J-E 2001 Longevity of mycorrhizal roots depends on branching order and nutrient availability. *New Phytologist* 150, 195-202
- MAJDI H, KANGAS P 1997 Demography of fine roots in response to nutrient applications in a Norway spruce stand in southwestern Sweden. *Ecoscience* 4, 199-205.
- MAJDI H, NYLUND J-E 1996 Does liquid fertilization affect life span of mycorrhizal fine roots and fine root dynamics? *Plant and Soil* 185, 305-309.
- MAJDI H, NYLUND J-E 2001 Skogaby – hur påverkades träden under mark? In: *Skogabyförsöket – Effekter av långvarig kväve- och svaveltillförsel till ett skogsekosystem*, Eds Persson T, Nilsson L-O. Naturvårdsverket, rapport 5173, Stockholm
- MAJDI H, PERSSON H 1995 Effects of ammonium sulphate application on the chemistry of bulk soil, rhizosphere, fine roots and fine-root distribution in a *Pice abies* (L.)Karst. Stand. *Plant and Soil* 168-169,151-160.
- MAJDI H, ÖHRVIK J ( ) Experimental soil warming extends the growing season – effects of nutrient availability on root production and mortality in a boreal forest in northern Sweden. (Under review by *Oecologia*)
- MAKKONEN K, HELMISAARI HS 2001 Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiology* 21, 193-198
- MÄKELÄ A, VANNINEN P 2000 Estimation of fine root mortality and growth from simple measurements: a method based on system dynamics. *Trees* 14, 316-323

- PERSSON, H., 1980 Fine root dynamics in a Scots pine stand with and without near optimum nutrient and water regimes. *Acta Phytogeogr. Suec* 68, 101-110.
- PERSSON, H. 1978. Root dynamics in a Young pine stand in central Sweden. *Oikos*, 30: 508-519.
- PERSSON, H. 1980. Death and replacement of fine roots in a mature Scots pine stand. *Ecol. Bull. (Stockholm)*, 32:251-260.
- ORLOV AY 1957 Observations on absorbing roots of spruce (*Picea excelsa* Link) under natural conditions. *Bot Z* 42, 1172-1180.
- ORLOV AY 1960 Growth and modification with age of the absorbing roots of spruce (*Picea excelsa* Link.). *Bot Z* 45, 888-896.
- PERSSON H 1978 Root dynamics in a young Scots pine stand in Central Sweden. *Oikos* 30:508-519
- PERSSON T, NILSSON L-O (eds.) 2001 *Skogabyförsöket – Effekter av långvarig kväve- och svaveltillförsel till ett skogsekosystem*. Naturvårdsverkets rapport 5173, Stockholm
- PERSSON H, VONFIRCKS Y, MAJDI H, NILSSON L-O 1995 Root distribution in a Norway spruce (*Picea abies* (L.)Karst) stand subjected to drought and ammonium-sulphate application. *Plant and Soil* 168-169,161-165.
- PUBLICOVER DA, VOGT KA 1993 A comparison of methods for estimating forest fine root production with respect to sources of error. *Can J For Res* 23: 1179-1186
- SINGH JS, LAUENROTH WK, HUNT HW, SWIFT DM 1984 Bias and random errors in estimators of net root production: a simulation approach. *Ecology* 65, 1760-1764
- STEELE SJ, GOWER ST, VOGEL JG, NORMAN JM, RYAN MG 1997 Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. In:*Biosphere-atmosphere interactions in the boreal forest* Margolis-HA (ed.); *Tree Physiology* 17, 8-9, 577-587
- TIERNEY GL, FAHEY TJ 2001 Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. *Plant and Soil* 229, 167-176
- TIERNEY GL, FAHEY TJ 2002 Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Can J For Res* 32: 1692-1697
- VOGT KA, VOGT DJ, BLOOMFIELD J 1998 Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil* 200, 71-89
- WIDÉN B, MAJDI H 2001 Soil CO<sub>2</sub> efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Can J For Res* 31, 786-796