Dissertationes Forestales 121

Root system traits of Norway spruce, Scots pine, and silver birch in mixed boreal forests: an analysis of root architecture, morphology, and anatomy

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Academic dissertation

To be presented with the permission of the Faculty of Agriculture and Forestry of the
University of Helsinki, for public examination in Lecture Hall 2 of Info Building,
Viikinkaari 11 on June 17th 2011 at 12 o'clock noon

Title of dissertation: Root system traits of Norway spruce, Scots pine, and silver birch in mixed boreal forests: analysis of root architecture, morphology and anatomy.

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Dissertationes Forestales 121

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ISSN 1795-7389
ISBN 978-951-651-329-7 (PDF)

(2011)

Publishers:
Finnish Society of Forest Science
Finnish Forest Research Institute
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
Finnish Society of Forest Science
P.O. Box 18, FI-10301 Vantaa, Finland
http://www.metla.fi/dissertationes

Kalliokoski, T. 2011. Root system traits of Norway spruce, Scots pine, and silver birch in mixed boreal forests: an analysis of root architecture, morphology and anatomy. Dissertationes Forestales 121. 67 p. Available at http://www.metla.fi/dissertationes/df121.htm.

ABSTRACT

The aim of this thesis was to unravel the functional-structural characteristics of root systems of *Betula pendula* Roth., *Picea abies* (L.) Karst., and *Pinus sylvestris* L. in mixed boreal forest stands differing in their developmental stage and site fertility.

The root systems of these species had similar structural regularities: horizontally-oriented shallow roots defined the horizontal area of influence, and within this area, each species placed fine roots in the uppermost soil layers, while sinker roots defined the maximum rooting depth.

Large radial spread and high ramification of coarse roots, and the high specific root length (SRL) and root length density (RLD) of fine roots indicated the high belowground competitiveness and root plasticity of *B. pendula*. Smaller radial root spread and sparser branching of coarse roots, and low SRL and RLD of fine roots of the conifers could indicate their more conservative resource use and high association with and dependence on ectomycorrhiza-forming fungi. The vertical fine root distributions of the species were mostly overlapping, implying the possibility for intense belowground competition for nutrients. In each species, conduits tapered and their frequency increased from distal roots to the stem, from the stem to the branches, and to leaf petioles in *B. pendula*. Conduit tapering was organ-specific in each species violating the assumptions of the general vascular scaling model (WBE). This reflects the hierarchical organization of a tree and differences between organs in the relative importance of transport, safety, and mechanical demands.

The applied root model was capable of depicting the mass, length and spread of coarse roots of *B. pendula* and *P. abies*, and to the lesser extent in *P. sylvestris*. The roots did not follow self-similar fractal branching, because the parameter values varied within the root systems. Model parameters indicate differences in rooting behavior, and therefore different ecophysiological adaptations between species.

Keywords: niche sharing, root plasticity, ectomycorrhiza, *Betula pendula*, *Picea abies*, *Pinus sylvestris*

ACKNOWLEDGEMENTS

As a carpenter, I learnt what hard physical work is. In that time, I never imagined that mental work could be even harder - to my backbone. However, long hours in front of my study desk strained my physical backbone more than physical work and, in same time, scientific writing routines strained my mental backbone.

Steady flow of money and good facilitates greatly eased the pain of my backbones - I kindly acknowledge Academy of Finland, Graduate School in Forest Sciences and Finnish Forest Research Institute, Vantaa Research Unit for provided funding and support for this study.

Numerous people have strengthened my backbones during this study. I would have not been able to perform this study without my supervisors, Dr. Risto Sievänen in Finnish Forest Research Institute and Dr. Pekka Nygren in University of Helsinki. Risto and Pekka, your hard work, guidance, encouragement and sheer stubbornness kept me going. I express my gratitude to you for your constant support.

I warmly thank Professor Annikki Mäkelä for support throughout the study. I am grateful to all other members of SCSS-project, inner and outer ones, Eero Nikinmaa, Jari Perttunen, Pekka Kaitaniemi and Anna Lintunen. You all provided good advice and discussions in our meetings. Anna, special thanks for you for being my peer group. Your optimism, ideas and our, sometimes heated, discussions have pushed me always forward.

I am grateful for my other co-authors, Heljä-Sisko Helmisaari and Taina Pennanen, for collaboration and comments. Without your expertise of fine roots and mycorrhiza the third article would have not been possible. I thank Harri Mäkinen for giving me the possibility to finalize my thesis within his project. The pre-examiners Professor Leena Finér and Dr. Harry Ozier-LaFontaine are gratefully acknowledged for their helpful and constructive comments on the thesis.

I am indebted to all those people who helped me in tedious field and laboratory work, or in data analysis. Without you I would still be in forest excavating roots, or in laboratory separating fine roots and cutting sections with microtome, or lost within SAS-code. In addition, my sincere thanks to my workmates in Metla who shared the coffee and lunch breaks with me.

Finally, I want to express my warmest thanks to my dearest ones, my wife Johanna and all my kids. Kids, thank you for giving me the opportunity to forget all work-related things. Johanna, your everlasting patience gave me strength to carry on.

Tikkurila, May 2011
Tuomo Kalliokoski

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by four research articles, which are referred to by their Roman numerals. The articles are reprinted with the kind permission of the publishers.

I Kalliokoski, T., Nygren, P. and Sievänen, R. 2008. Coarse root architecture of three boreal tree species growing in mixed stands. Silva Fennica 42: 189–210. http://www.metla.fi/silvafennica/full/sf42/sf422189.pdf

II Kalliokoski, T., Sievänen, R. and Nygren P. 2010. Tree roots as self-similar branching structures; axis differentiation and segment tapering in coarse roots of three boreal forest tree species. Trees 24:219–236.
DOI 10.1007/s00468-009-0393-1

III Kalliokoski, T., Pennanen, T., Nygren, P., Sievänen, R. and Helmisaari, H.-S. 2010. Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant and Soil 330:73–89.
DOI 10.1007/s11104-009-0177-9

IV Lintunen, A. and Kalliokoski T. 2010. The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in *Betula pendula*, *Picea abies* and *Pinus sylvestris*. Tree Physiology 30: 1433–1447.
DOI 10.1093/treephys/tpq085

AUTHOR'S CONTRIBUTION

I compiled the summary part of this doctoral thesis. I participated the planning of the study design and was responsible for the field measurements of belowground compartments in all studies. I carried out the data analyses in studies I and II and most of the writing. In studies III and IV, I analyzed and interpreted the data concerning fine and coarse roots and participated in the analysis and writing of results on ectomycorrhizae and aboveground data. In study II, Risto Sievänen carried out the actual programming; I participated in the planning of the model structure and model parameterization.

CONTENTS

ABBREVIATIONS

A		Altitude, number of coarse root segments in the longest path from any root tip to the first segment attached to the stump
a	µm	Conduit radius
BG		Branching generation; the developmental sequence of root segments. The segment attached to stump is assigned the branching generation 1, and so on
CRB	kg	Coarse root biomass
CSA	cm^2	Cross-sectional area of root, stem, or branch
D^{prox}	cm	Proximal diameter of the root segment
D^{dist}	cm	Distal diameter of root segment
DBH	cm	Tree diameter at breast height
D_0	cm	Tree diameter at root collar
DGGE		Denaturing gradient gel electrophoresis
ECM		Ectomycorrhiza-forming fungi
FRB	g	Fine root biomass
G	m^2 ha^{-1}	Basal area
GO		Gravelius order; Assigns the same order number to root segments belonging to the same axis and one higher to lateral segments. The root main axis has order 2 (stem is order 1) and the thickest root segment in each branching event continues the axis
K_{dist}/K_{prox}		Conductivity ratio of adjacent segments
l	m	Distance from the axis apex
M		Magnitude, number of external root segments in a root
p		Specifies the ratio of the proximal CSA of the parent segment to the sum of proximal CSAs of the child segments
PCR		Polymerase chain reaction
Q	m^3 s^{-1}	Volume flow rate
q		Determines the share of the sum of squared diameters of the child segments that is allocated to the thickest child segment
RLD	cm cm^{-3}	Root length density (root length divided by soil volume occupied)
SRL	m g^{-1}	Specific root length (root length divided by root dry mass)
T		Relative conduit tapering
WBE		Scaling model by West, Brown and Enquist (1999) proposing that the size of conduits increases with increasing distance from the stem or branch apex
ZRT	m	Zone of rapid root tapering

1 INTRODUCTION

1.1 The tree as a functional-structural entity

1.1.1 Interaction between structure and function

Trees are large, long-living and sessile organisms. During their life, the size of trees increases by several orders of magnitude (Thomas 2000), and they face many different environments with different external constraints. A tree's structure creates the physical framework for different functions; the design of a tree has to ensure resource capture and transport, and mechanical stability continuously during its life span (Niklas 1994, Nikinmaa et al. 2008). In order to manage this, trees adjust their structure and functions according to the surrounding environment. Consequently, tree species have different structural solutions for their functions, and the optimal shape of a tree differs according to the conditions (Niklas 1994). These functional and structural differences enable species to occupy different ecological niches (Hutchinson 1957, Arthur 1987), which ensures the coexistence of different species in the same habitats (Gause 1934). In the description of an ecological niche, the environmental conditions or resources required by the species create an imaginary space with multiple dimensions. Each dimension represents a specific environmental variable, e.g. air temperature, soil fertility, or solar radiation. Each species has a specific range of these variables that it may tolerate, referred to as the fundamental niche of a species (Hutchinson 1957). Species may separate their niches, for instance through spatial differences in the root system architecture, temporal partitioning of root activity, and functional differences in tree hydraulic architecture (Cody 1986, McKane et al. 2002, Silvertown 2004, Stubbs and Wilson 2004, Polechová and Storch 2008). Species specificity in the association with ectomycorrhiza-forming fungi (ECM) could also cause functional niche separation. For example, some ECM species are able to tap organic nitrogen, while others are not (Näsholm et al. 1998). However, the fundamental niches of many plant species overlap, because plants have a limited number of options for partitioning their fundamental niches. This implies that many plant species operate in suboptimal parts of their fundamental niches (Schenk 2006).

The interplay of the function and structure of a tree has long been understood (Shinozaki 1964). There have been a number of both experimental (Givnish 1988, Nikinmaa 1992) and modeling studies (Mäkelä 1985, Hari et al. 1990, Kellomäki and Strandman 1995, Perttunen et al. 1996, Sievänen et al. 2008) on the different aspects of this question in the aerial parts of trees. The development of functional-structural plant models has clarified many complex questions difficult to study under field conditions (Sievänen et al. 2000, Fourcaud et al. 2008). The roots and root systems of trees are more difficult to study than tree shoots. This reflects in the restricted number of experimental studies on belowground structural and functional features, and root models are not therefore as advanced as their aboveground counterparts (Blaise et al. 1999, Drouet and Pagès 2007, Tobin et al. 2007). Fundamental questions such as the role of sink and source activity in plant growth and development, or how the belowground competition between trees, and between trees and other plants affects tree performance, largely await clarification (Schenk 2006, Fourcaud et al. 2008). Progress in answering these questions is only possible through studies applying a whole-tree approach, in which both shoots and roots and their specific structural and functional features are adequately addressed (Marks and Lechowicz 2006).

In Finland, the main forest tree species are *Betula pendula* Roth, *Picea abies* (L.) H. Karst, and *Pinus sylvestris* L. Together, these conifers and *Betula* spp. account for over 95% of Finnish forest growing stock volumes. Of all forest stands of Finland, ca. 65% are dominated by *P. sylvestris*, ca. 25% by *P. abies*, and ca. 10% by deciduous tree species. (Finnish Statistical Yearbook of Forestry 2009). The natural growing sites of these species create a gradient from fertile to more infertile sites, *B. pendula* occupying the fertile, *P. abies* the medium fertile and *P. sylvestris* the infertile sites. Especially *B. pendula*, but also *P. sylvestris*, is a light-demanding pioneer species rapidly occupying gaps formed in the stand canopy layer, whereas *P. abies* is a shade-tolerant late-successional species establishing the secondary tree generation under both *B. pendula* and *P. sylvestris* canopies under natural conditions. These species thus form interesting contrasts in terms of site demands, stand development, and functional characteristics. In Fennoscandian boreal forest stands, mixtures composed of these species are common. However, in fertile sites, *P. abies* will eventually overgrow other species if disturbances do not create regeneration possibilities for *B. pendula* and *P. sylvestris* (Kalela 1946, Kellomäki 1991). A mixed forest stand of these species does not therefore represent a stable coexistence of the species, but a defined location on a time axis. This indicates the overlap of the ecological niches of these species (Gause 1934, Hutchinson 1957). The strong competitive potential of *P. abies* has mainly been accounted for by its higher shade tolerance compared to *B. pendula* and *P. sylvestris* (Kuusela 1990, Kellomäki 1991). However, a review of several species (Coomes and Grubb 2000) suggested that light may be a limiting factor in forests on moist, nutrient-rich soils, but the importance of belowground resource competition increases in more infertile soils. There have only been a few experimental studies that have also accounted for the structural-functional traits of root systems of *B. pendula*, *P. abies*, and *P. sylvestris* (Heikinheimo 1920, Laitakari 1927, 1935, Kalela 1937, 1950, 1954, Ylivakkuri 1954, Paavilainen 1966, Finér 1989, Laiho and Finér 1996, Helmisaari et al. 2007, Mäkelä et al. 2008). From the viewpoint of this thesis, interesting questions include whether the root traits of these species somehow indicate belowground niche differentiation, the competitive potential of the species, or whether trade-offs in root traits that affect the species' adaptive capacity could be defined.

1.1.2 General traits of tree roots

The main functions of tree root systems are to supply soil resources and anchor trees to the ground. Roots also contain carbohydrate and nutrient reserves and synthesize growth hormones (Kozlowski and Pallardy 1997). Recently, the effect of root exudates on tree growth through alteration of the soil around trees, thus either inhibiting or accelerating the function of soil micro-organisms, has been acknowledged (Schenk 2006). An equally important aspect of root systems is that root tips behave as actual sites for mutualistic interactions between trees and soil micro-organisms. In nutrient-poor boreal forest soil, trees are heavily dependent on improved nutrition provided by different ECM (van der Heijden and Sanders 2003). Accordingly, in boreal forests, ca. 95% of short root tips are colonized by ECM (Taylor et al. 2000).

In roots and root systems, different parts can be recognized and multiple classifications have been used (e.g. Cannon 1949, Sutton and Tinus 1983). Root branches are usually classified as coarse or fine roots based on the root diameter; most typically, roots with a diameter ≥ 2 mm are defined as coarse roots and thinner root branches as fine roots (Persson 1983, Sutton and Tinus 1983). This division according to diameter is, however, somewhat arbitrary, since root diameter does not indicate a particular functionality (Kramer 1946, Kramer and Bullock 1966, van Rees and Comerford 1990, Comenford et al. 1994, Lindenmair et al. 2004, Cermak et al. 2006), the diameter-function relationship is species dependent, and within the below-2-mm class, separate functional groups may also be defined (Eissenstat et al. 2000, Pregitzer 2002, Guo et al 2008). The justification for this classification comes from the view that it aids in obtaining information on the complex system (Danjon and Reubens 2008).

Coarse root axes within the root system can be also divided into different types (Cannon 1949, Sutton and Tinus 1983, Collet et al. 2006). The two most distinctive groups are shallow and sinker roots (Sutton and Tinus 1983, Danjon and Reubens 2008). Shallow root axes of mature trees spread several meters horizontally in the uppermost soil layers, determining the limits of the horizontal influence area of the root system. Sinker roots extend obliquely or vertically in soil determining the vertical influence area of the root system. They usually reach a depth of a couple of meters in boreal soils (Stone and Kalisz 1991), but up to tens of meters depth for some tree species in other regions (Cannon 1960, McElrone et al. 2004).

1.1.3 The concept of root system architecture

Tree architecture (Barthélémy and Caraglio 2007) describes the spatial configuration of a tree, i.e. the geometric dimensions, shapes, and explicit locations of botanical units in 3D space. Aboveground, the basic botanical unit consists of the internode, i.e. the segment between two branching events, a node attached with leaves, and axillary buds. Trees grow and develop by the repetition of these basic botanical units forming what is nowadays commonly acknowledged to be the modular structure of the tree. The production of basic units is controlled by species-specific "growth rules", i.e. ontogenetic development, resulting in the architecture typical for each tree species (Barthélémy and Caraglio 2007). The foundation of plant architectural studies lies in the seminal work of Hallé and Oldeman (1970) and Hallé et al. (1978), in which they classified the vast number of different tropical tree species into 23 architectural types.

Quantitative methods for studying plant and tree architecture were mostly developed from the perspective of tree shoots (Godin et al. 1999, Danjon and Reubens 2008). Both shoots and roots form a dynamic branched “system”, the components of which are connected in an organized network (Pagès 1999). The functioning of both shoots and roots depends on the entire structure or architecture of the system, including both the topological arrangement of components and their geometric characteristics. However, roots deviate from shoots in many ways: they are functionally less differentiated, do not have similar kinds of morphological markers (no leaves, leaf petioles, branches or stem, as in shoots) and have more irregular, opportunistic growth as a response to soil heterogeneity (Danjon and Reubens 2008). Due to these differences between shoots and roots, a specific architectural approach for root systems is needed (Danjon and Reubens 2008).

The architecture of a root system can be described with the aid of multiple variables such as the branching frequency of the segments, length of segments, branching angles with respect to the previous segment, the mortality of apices and axes, and topology, i.e. how the different parts of the root system are related to each other irrespective of their dimensions (Deo 1974, Fitter 1991, Harper et al.1991, Lynch 1995, Hodge 2004). Belowground, the basic unit could be determined to comprise a coarse woody root segment with fine roots, root hairs and possible nodules (Sievänen et al. 2000). ECM could also be included in belowground basic unit, since fungal hyphae of ECM form a sheath or mantle around the root, essentially replacing the root hairs. This effectively means that nutrients are taken up primarily via the fungus (Smith and Read 1997).

In this thesis, root architecture refers only to the characteristics of the coarse part of the root system, and finer structural elements are not included. This is based on the idea that coarse roots form the skeleton and determine the spatial limits (maximum horizontal spread and rooting depth) of the entire root system.

The characterization of the architectural properties of root systems of different species gives insights into the growth strategies of plants (Grime 2002), water and nutrient uptake (Ho et al. 2004) and transport (Clausnitzer and Hopmans 1994, Cortina et al. 2008), resource-use efficiency (Fitter 1991, Fitter et al. 1991, Fitter and Stickland 1991, Fitter and Stickland 1992), plant plastic responses to soil heterogeneity (Hodge 2004), and interactions between plants (Biondini 2001, Schenk 2006). Among the earliest root architectural analyses were the studies of Laitakari (1927, 1935), in which he characterized the spatial dimensions and branching patterns of *B. pendula*, *P. sylvestris* and *P. abies*; however, he did not consider the root system topology. Fitter (1987) modeled the topological forms of root systems and proposed that the two theoretical extremes in the root branching patterns are the herringbone pattern, which comprises a main axis and non-branching laterals (external segments), and dichotomous branching, in which branching occurs with equal probability on all segments. Using a cost-benefit analysis, i.e. the carbon cost of root construction for a given unit of obtained resource, Fitter (1991) found that roots following the herringbone topology are the most efficient under resource-poor conditions. The latest developments in the field of root system architecture are an experimental study, in which the effect of stem mechanical stimulation on root architectural characteristics was investigated (Reubens et al. 2009), and the modeling study of Drouet and Pagés (2007), in which they presented a tree model that accounted for both above- and belowground structural and functional characteristics.

1.1.4 The anatomical characteristics of the water pathway

A specific question related to tree architecture is water transport within a tree. The xylem anatomy and the architectural organization of the tree together determine the efficiency with which water and solutes can be conveyed from roots to shoots, and further to leaves. The size of xylem conducting elements has a fundamental effect on water flow within a tree, since according to the Hagen-Poiseuille equation, the flow rate is proportional to the fourth power of the radius of conducting cells (Tyree and Zimmermann 2002). The studied tree species exhibit clear differences in the structure of the basic conducting elements, i.e. conifers have narrow tracheids, while much wider vessels are the primary conducting elements of the angiosperm *B. pendula*. The architecture of a tree determines the macroscopic characteristics of the water pathway, e.g. the number of branch junctions and the manner in which the conductive tree segments are arranged with respect to each other (Fitter 1991, Rundel and Nobel 1991, Tyree and Zimmermann 2002).

A generally accepted theory for water movement in vascular plants is known as the cohesion-tension theory (Dixon and Joly 1894, Tyree and Zimmermann 2002). According to this theory, the driving force in the ascent of water in vascular plants is the pressure difference between evaporating leaf surfaces and water-supplying root elements. Surface tension in the leaves is transmitted through a continuous water column to the branch, stem and from thereon to the absorbing roots. Water is under metastable conditions when moving in xylem conduits, i.e. the xylem pressure is under the pressure of a vacuum. Metastable conditions are maintained through the hydrogen bonds in water molecules, which enable the cohesive and adhesive forces between water molecules and water and xylem conduit walls, respectively (Tyree 1997, Tyree and Zimmermann 2002).

The difference in xylem anatomy between different tree organs has long been known (see Tyree and Zimmermann 2002 and references therein). The mean conduit size decreases from the roots to the stem and further to the branches. In roots, water-conducting cells are usually also longer, have thinner cell walls, and larger pits than in the stem. In addition, number of conduits per unit of area is smaller, the annual rings contain fewer cells and the boundaries between rings are less defined, and the size of conduits increases as a function of distance from the tree base, root wood thus becoming increasingly less stem-like.

A new concept was introduced by West et al. (1999; hereafter referred to as the WBE model); an increase in conduit size with distance from stem apex minimizes the hydraulic resistance with a specific minimum value 1/6 of the scaling parameter in order to minimize the energy dissipated in fluid flow (West et al. 1999, West et al. 2000, Enquist and Niklas 2001, Enquist 2002, 2003;). West at al. also asserted that their model should be applicable when accounting for roots with minor modifications.

Another scaling theory states, based on the Hagen-Poiseuille values, that to maximize hydraulic conductance with a given investment, trees should have a constant relationship between the volume flow rate (Q) and the sum of the conduit radius cubed (Murray 1926, McCulloh et al. 2003, McCulloh and Sperry 2005; hereafter referred to as Murray's law). The assumptions of Murray's law lead to a hydraulic architecture where conduits should taper from the roots to the stem and thereafter to the branches, and the ratio of the conduit radius of adjacent segments equals their conductivity ratio (McCulloh and Sperry 2005). Murray’s law does not assume the number of conduits to be fixed at each level of the branching generation (BG), as the WBE model does, and thus the maximum conductance also depends on how the number of conduits changes between adjacent segments (McCulloh et al. 2004).

Studies concerning the assumptions and predictions of these scaling theories have produced controversial results (Enquist et al. 1999, Anfodillo et al. 2006, Kozlowski and Konarzewski 2004, Robinson 2004, Mäkelä and Valentine 2006, Mencuccini et al. 2007, Nygren and Pallardy 2008, Coomes and Allen 2009, Fan et al. 2009). It seems that while the WBE model has gained considerable support in a general sense, 'testing' it on a real tree presents a challenge (Niklas 2006). However, only in a few recent studies has the whole tree, including side branches (Atala and Lusk 2008, Sellin et al. 2008) and root systems (Nygren and Pallardy 2008), been accounted for. Therefore, most of the conclusions concerning scaling parameter values of the WBE model and hydraulic resistance of the "total path length" of the transport pathway only apply to the stem of trees. Murray’s law has been found to apply to those tree parts that have no role in mechanical support, whereas xylem conduits in compartments under mechanical constraints seem to deviate from the law, the greatest deviation being in the tracheids of coniferous trees (McCulloh et al. 2003, 2004, McCulloh and Sperry 2005).

The studies concerning the long-distance transport process in trees and also accounting for roots are scarce, and the scaling of anatomical characteristics from leaf petioles and distal branches to distal roots has not been examined in mature trees. The scaling relations in a mixed forest may differ from those of monoculture. The species-specific tapering patterns in the framework of tree architecture, or differences between species growing on the same site, are also largely unknown (Enquist 2003).

1.2 Role of coarse roots, fine roots and ectomycorrhizae in tree growth

1.2.1 Coarse roots

Tree growth in boreal forests is generally limited by the availability of nutrients, especially nitrogen (Tamm 1991, Jarvis and Linder 2000, Näsholm and Persson 2001). Therefore, the belowground compartments responsible for the detection, acquisition and transport of scarce soil resources play an important role in the growth and development of the tree.

Soil resources are unevenly distributed, or are subject to localized depletion, and thus coarse roots (diameter ≥ 2 mm) are the organs that mainly determine a tree's ability to exploit these resources; they define the spatial dimensions of the potential influence area of the root system, both in a horizontal and a vertical direction, and through differences in architecture they account for the exploration and exploitation efficiency of patchy soil resources (Fitter 1991, Fitter et al. 1991, Lynch 1995, Casper et al 2003, Hodge 2004, Hodge 2009, Hodge et al. 2009). They also determine the actual extent of segregation, or overlap of the belowground influence areas of different trees (Kajimoto et al. 2007). The configuration of parts of the root system within the influence area may deviate greatly between tree species and during the ontogeny of an individual (Fitter 1991, Hodge 2004, Hodge et al. 2009). The life span of the largest woody roots approaches the life span of the tree.

From the viewpoint of mechanical stability, a tree has to resist the bending and pushing forces of prevailing winds. Trees do this through adaptations to the characteristics of the crown, but also through the root characteristics; a tree may have a specialized taproot for improving anchorage, pronounced secondary thickening of roots beside the stump, creating a zone of rapid root tapering (ZRT), or a large number of roots to increase cohesion between the roots and soil (Eis 1974, Coutts 1986, Danjon et al. 2005, Nicoll et al. 2006).

Although interdependence between characteristics of the tree crown and root system are likely to be found (Grime 2002), the crown area projected to the soil surface (Assman 1970, Sterba and Amateis 1998, Webster and Lorimer 2003, Pretzsch and Schütze 2005) is not enough to grasp the essential area of a tree’s influence, since horizontal root spread greatly exceeds the crown width (reviewed by Stone and Kalisz 1991). Shallow lateral roots give rise to nutrient-foraging fine root elements. The role of sinker roots is to tap water reservoirs deep in the soil and increase the mechanical stability of the tree (Dawson and Pate 1996, Farrington et al. 1996, Reubens 2007).

Based on the available literature, no valid comparison of coarse root spread can be made between *B. pendula, P. abies,* and *P. sylvestris*; there is too much variation in study design, sampling techniques, and other factors (Stone and Kalisz 1991). However, Laitakari (1927, 1935) presented qualitative conclusions concerning the architectural differences between these species. The radial spread of the coarse root system of *B. pendula* was reported to be usually larger than in *P. sylvestris,* while there was no clear difference between *B. pendula* and *P. abies*. The coarse roots of these species mostly occupied different soil layers: *P. abies* exploited the topsoil, whereas *P. sylvestris* primarily occupied the elluvial and *B. pendula* the illuvial layer. The branching pattern of these species was also different: *B. pendula* had much more root branches along a given root length, i.e. a higher branching intensity and/or higher branching frequency, than *P. abies* and *P. sylvestris*. The differences between these species were greatest at infertile sites and decreased as a function of higher fertility.

1.2.2. Fine roots

The main function of the fine roots (diameter < 2 mm) together with ECM is to take up water and mineral nutrients from the soil. The relevance of coarse woody roots in the uptake of water and nutrients depends on their amounts and distribution in the soil profile (Comenford et al. 1994), e.g. 6–16% of water acquisition in *P. abies* (Lindenmair et al. 2004).

Root systems account for 10–45% of the total tree carbon pool of a stand (Sanantonio et al. 1977, Fogel 1983, Helmisaari 2002). Although fine roots account for a relatively small proportion of the total root biomass (< 5%, Vogt et al. 1996), they may account for 10–60% of the net primary production (NPP) of forest ecosystems (Vogt et al. 1996, Gower et al. 1997, Jackson 1997). Fine roots are thought to be major contributors to the soil carbon input due to their short turnover time (Norby and Jackson 2000). On the other hand, considerably longer turnover times for fine roots have been recorded, mainly from the labeling studies (see references in Högberg et al. 2006). These studies have argued that the rate of fine root production is over-estimated and up to 75% of carbon allocated to belowground biomass is used to support autotrophic respiration. This has led to the estimation that half of soil respiration could originate from living plant roots, their mycorrhizal fungi and other root-associated microbes driven by recent photosynthates. Accurate estimates of fine root biomass (FRB), production and turnover are needed for the estimation of soil carbon budgets (Lehtonen 2004). In any case, fine roots play an important role in the water, nutrient and carbon dynamics of a tree.

The question of how the aboveground abundance, e.g. number of stems ha^{-1} or basal area (G), of *B. pendula*, *P. abies*, and *P. sylvestris* is reflected belowground in mixed forest conditions is unresolved. The fine root biomass and length of deciduous trees are generally found to be greater than those of conifers in relation to their aboveground biomass (Finer et al. 1997).

The fine root morphological parameters, e.g. specific root length (SRL, root length divided by root dry mass, m g^{-1}), have been interpreted to be an indication of the cost-benefit ratio of roots. The cost is the root mass and the benefit is the obtained soil resources, which should be proportional to the root length (Fitter 1976, Lõhmus et al.1989, Eissenstat and Yanai 1997, Pregitzer et al. 2002). In general terms, deciduous trees have a higher SRL than coniferous trees (Ostonen et al. 2007a), and this difference was also found between the short roots of *B. pendula*, *P. abies* and *P. sylvestris* (Ostonen et al. 2007b). The vertical distributions of fine roots have additionally been found to differ between the studied conifers, *P. abies* having a larger proportion of fine roots in the topsoil than *P. sylvestris* (Kalela 1950, Helmisaari et al. 2007).

1.2.3 Ectomycorrhiza

Mycorrhizal associations improve tree growth through both nutritional and non-nutritional effects. The increase in nutrient and water uptake is primarily caused by an increased absorptive surface; the mycelia of ECM can reach much smaller soil pores than root hairs, and length of an ECM mycelium greatly exceeds the length of fine roots. It has been estimated that external ECM mycelia produce an increase of up to 60-fold in the surface area (Simard et al. 2002). Possibly the highest estimate is that a tree root with extending ECM mycelia can exploit up to a 1000-fold larger soil volume than a non-mycorrhizal root (Rousseau et al. 1994). Mycorrhiza can also alter the chemistry of the mycorrhizosphere by increasing the rate of weathering of soil minerals or access soil nutrients through the production of enzymes that degrade complex organic compounds inaccessible to plant roots (Lindahl et al. 2002). Moreover, mycorrhizae can improve plant nutrition by influencing the functioning of the soil bacteria (Simard et al. 2002). Examples of non-nutritional effects include the production of auxins or stimulation of the expression of auxin-regulated plant genes.

The host specificity of ECM can alter the competitive position of plants in a community (Newton and Haigh 1998, Nara 2006). In particular, the mycorrhiza-mediated uptake of organic nitrogen may be an important mechanism in competition between plants (Näsholm et al. 1998, Aerts 2002). Regarding the belowground competition between trees, the most important aspect of ECM may, however, to be the existence of a common mycorrhizal network (CMN; Newman 1988, Simard et al 1997). Although it has been established that materials can move between mycorrhizal plants, there are still many open questions, perhaps most importantly whether the net transfer of nutrients or carbon is extensive enough to affect plant physiology and ecology (Simard et al. 2002, Simard and Durall 2004). If proven to be so, it could change the fundamental concept of competition between trees.

1.3 Variability in root and root system traits

1.3.1 The concept of root plasticity

The heterogeneity of soil imposes specific demands on the root systems of a tree. This heterogeneity occurs both in space and time; nutrient availability can deviate by an order of magnitude between the locations occupied by different roots of single plant (Jackson and Caldwell 1993, Gross et al. 1995, Farley and Fitter 1999), and the rate of nutrient mineralization varies, e.g. due to weather seasons (Grime 1991, Grime 2002). The mixture of species further increases the heterogeneity of the surrounding environment of a single tree (Oliver and Larson 1996). The key element in successful soil foraging by a tree is the morphological and physiological plasticity of root characteristics (Caldwell and Pearcy 1994, Hutchings and John 2004). Plasticity can be described as a flexible strategy, which increases the fitness of a single tree in a given environment. This plasticity ultimately makes it possible to have different phenotypes of the same genotype, depending on the environmental conditions in which a plant grows (Bradshaw 1965, Weiner 2004).

The plastic responses of plants cover a wide range of phenomena, including both morphological and physiological changes, for instance in leaf number, the shoot-root ratio, root morphology, uptake kinetics and changes in root longevity (Weiner 2004). Plastic foraging responses can be described as morphological or physiological alterations that directly or indirectly enhance the capture of air- or soil-borne resources (de Kroon et al. 2009). Belowground, the most distinct appearance of morphological plasticity is the root proliferation in local nutrient patches through an increased branching frequency or higher branching intensity (Nobbe 1862 in Lynch 1995, Drew et al. 1973, Drew 1975, Drew and Saker 1975, 1978, Jackson and Caldwell 1991, Fitter 1994, Lynch 1995, Hodge et al. 1999, 2000, Wang et al. 2006, Zhang and George 2009). The modular structure of roots enables this architectural flexibility and makes the more or less precise deployment of root segments possible (Fitter 1994, Hodge et al. 2004, 2009). In the finest belowground compartments, i.e. root hairs and mycorrhizal hyphae, distinct proliferation responses to elevated nutrient conditions have also been observed (St. John et al. 1983, Robinson and

Rorison 1987). An equally important aspect of plasticity is the adaptation of physiological characteristics of the acquisition organs. Considerable changes of up to 80% have been observed in the physiological nutrient uptake capacity, i.e. uptake kinetics, per unit of root length due to elevated nutrient concentrations (Jackson et al. 1990, Jackson and Caldwell 1991).

Most studies concerning root plasticity have been performed with crop plants showing rapid growth and strong responses to increased soil resources. For plants of this kind, a high phenotypic plasticity ensures the efficient exploitation of brief pulses and patches of high resource availability. This is one reason why they have been selected for agricultural use (Fitter 1996). However, based on the studies performed so far, no broad distinction coud be made between herbaceous and woody species in the level of plasticity (Grime 2002).

1.3.2 Effect of site fertility

The accumulated observations indicate that under nutrient-poor conditions, plants generally shift allocation from shoot to roots, i.e. follow an extensive strategy (Keyes and Grier 1981, Vogt et al. 1987, Hodge 2009; however, see Grime 1994). In monocultures of *P. abies* and *P. sylvestris*, the allocation to the belowground compartments also increased from fertile to infertile sites, in terms of the ratio of foliage to fine roots (Helmisaari et al. 2007). It is not known whether the same trend could also be found in mixed forest comprised of the species used in this study. However, with same relative allocation to the roots, the allocation within root systems can vary from one plant species to another (Fitter 1991, Campbell et al. 1991). Especially in productive habitats, this plasticity occurring within both the root and shoot systems may be even more important for plant fitness than modifications to the root-shoot ratio (Grime 1994). However, studies on fine root morphology have yielded contradictory results, since SRL values have been reported to increase, remain constant, or decrease in response to site fertility (reviewed in Ostonen et al. 2007a).

The radial root spread of trees may be assumed to increase with decreasing site fertility, since trees have to explore a larger soil volume to gather the same amount of soil resources. This hypothesis was supported by the results of Laitakari (1927, 1935), since the radial spread of root systems of *B. pendula*, *P. abies*, and *P. sylvestris* increased along a gradient from fertile to infertile sites. However, root spreads may be similar or even larger in more fertile sites, since tree shoots are often bigger there. The observation that non-fertilized small trees had a similar root spread to much bigger fertilized trees (Johnsen et al. 2005) supports this view.

Globally, at least 50% of all roots are located in the upper 0.3 m of the soil profile, and 95% in the upper 2 m (Schenk and Jackson 2002), since soil resources are most abundant in the uppermost soil layers. However, the systematic exclusion of deeper soil layers in sampling may have overemphasized the importance of the upper soil layers for tree growth (Stone and Kalisz 1991). In boreal soils, the nitrogen content is much higher in the organic soil layer than in mineral soil (Mustajärvi et al. 2008), and consequently the quantity of fine roots of *P. abies* and *P. sylvestris* rapidly declines with depth in both fertile and infertile sites (Helmisaari et al. 2007). The topmost soil layers rapidly dry in poor sandy soils, and this forces trees to seek water from deeper layers through the secondary proliferation of sinker roots (Danjon et al. 2005). In the case of *B. pendula*, *P. abies*, and *P. sylvestris*, however, the mean depth of coarse roots was the highest in moraine soils, decreasing towards sandy soils, and no clear differences between fertile and infertile sites were observed (Laitakari 1927, 1935).

Studies considering the local root proliferation in tree seedlings (George et al. 1997, van Vuuren et al. 2003, Zhang and George 2009) have demonstrated that root dry matter and total root length increase more in species from more fertile habitats due to artificial nutrient "hot spots" than in species from more infertile habitats, i.e. *Betula populifolia* Marsh. > *Acer rubrum* L., and *P. abies* > *P. sylvestris*. These observations support the deductions that high morphological plasticity and active foraging, which imply a high carbon cost for plants, could only be a selective advantage in habitats where they ensure access to abundant soil resources. In infertile sites, plants fitness can be increased by long-lasting roots remaining viable under chronic mineral nutrient stress and thus absorbing brief temporary pulses of nutrients (Grime 2002). The natural growing sites of *B. pendula* are more fertile than those of *P. sylvestris*. Thus, the root characteristics may show higher plasticity in *B. pendula* than in *P. sylvestris*. However, studies on older forest-grown trees are scarce (St. John et al. 1983, Raich et al. 1994), and the interaction of tree roots and ECM may alter the response of roots. Several studies have outlined the decreasing importance of ECM for trees as a function of improving site fertility (Arnebrant 1994, Pennanen et al. 1994, Högberg et al. 2003, Nilsson et al. 2005).

1.3.3 Effect of stand developmental stage

The growth of tree woody coarse roots follows the general development of the tree. Thus, radial root spread could also be presumed to increase with tree age and size. However, in *Tournefortia argentea* L.f., roots already extended up to 18 m by the age of 3 years, while in *Pinus elliottii* Engelm. root spread was ca. 10 m at the age of 5 years (Stone and Kalisz 1991), and in *Pinus resinosa* Ait. root spread was completed between 15 to 20 years of age (Fayle 1975). In the studies of Laitakari (1927, 1935), the radial spreads of *B. pendula*, *P. abies*, and *P. sylvestris* increased with tree age and size in all three species. However, values close to the observed maximum spreads were also found from fairly small trees at the age of 40–50 years.

Corresponding with the trend in radial root spread, the mean rooting depth of shallow coarse roots also increased with tree age and size in *B. pendula*, *P. abies*, and *P. sylvestris* (Laitakari 1927, 1935). However, the maximum rooting depth of a tree is determined by the sinker roots, and they may already reach the maximum depth within the first ten years (Fayle 1975). In a study on mature hardwood forest trees (40–60 years old), no relationship was found between stand age and rooting depth (Kochenderfer 1973). This observation lends indirect support to the hypothesis that the maximum rooting depth may be reached at a fairly early stage of stand development.

The branching pattern of coarse roots clearly changed with stand age in *B. pendula*, *P. abies*, and *P. sylvestris*, i.e. the frequency of coarse root branches per unit area increased during stand development (Laitakari 1927, 1935).

In most of tree species, including *P. abies* and *P. sylvestris*, the stand total FRB has been found to increase only until canopy closure, and thereafter remain more or less constant (Vogt et al. 1983, Vanninen et al. 1996, Vanninen and Mäkelä 1999, Helmisaari et al. 2002). Mature trees had lower mean SRL values than younger trees in the study of Claus and George (2005). This difference in fine root morphology may be related to the branching of fine roots, since younger trees may have a higher proportion of first-order roots with high SRL values (Pregitzer et al. 2002). On the other hand, lower SRL values may indicate extended fine root longevity in mature trees.

The relationship between stand development and ECM has mainly been examined on the basis of the ECM fruiting body production. These studies have produced contradictory results; some of them found the highest production in the young stages (Chisilov and Demidova 1998, Hintikka 1988), while others have detected no differences between stands of different ages (Bonet et al. 2004). Using fungal ingrowth bags, Wallander et al. (2010) found that the biomass production of ECM was highest in young *P. abies* stands (10–30 yrs), coinciding with canopy closure. They related this result to the overall developmental phase of a tree, i.e. tree growth in this phase is rapid and the leaf area maximal.

1.3.4 Interactions in mixed stands

The structural and functional regularities, e.g. the spatial dimensions of root systems, topology, and mycorrhizal associations, of trees in mixed forests may differ from those of monocultures and may be specific to a particular species combination, determining its development as the output of the interactions between species. Natural mixed forests usually also have multiple tree cohorts, thus increasing the complexity of the community compared with even-aged stands (Oliver and Larson 1996, Grime 2002). The social status of plants may also affect the allocation pattern. Campbell et al. (1991) found that dominant plants exploited nutrient-rich patches to a greater extent than other plants due to higher growth rates. Meanwhile, suppressed plants allocated their new root growth more precisely, i.e. a larger proportion of their new root growth occurred in nutrient-rich zones. In contrast to pure, even-aged stands, easily measurable stand factors, e.g. basal area or stand volume, are not sufficient to describe the growth processes in mixed stands.

Interactions between species can be facilitative (Hauggaard-Nielsen and Jensen 2005), neutral (Venn et al. 2009), or competitive (Schenk 2006). The positive effects of other species could occur, for instance, by making otherwise unavailable soil resources available. Competition occurs between individuals of both the same and different species. Intraspecific interaction leads to decreased resource uptake per individual, and thus to a decline in growth. Competition between different species with identical growth characteristics is equivalent to the intraspecific competition in monoculture (Kelty 2006), yet in the long term this leads to the exclusion of one or another species from the habitat (Gause 1934). Interspecific competition between species that have complementary characteristics, such as different shade tolerances or rooting depths, is lower than intraspecific competition (Kelty 2006).

In studies on temperate mixed forests of *Fagus sylvatica* L. and *Picea abies*, clear vertical stratification of the rooting space was observed (Schmid and Kazda 2001, Schmid 2002, Bolte and Villanueva 2006), while in a mixed *F. sylvatica* - *Pinus sylvestris* stand, fine root vertical distributions were found to overlap (Curt and Prévosto 2003). Based on the studies of Laitakari (1927, 1935), *B. pendula* may open up passages for conifers down to the deeper mineral soil layers. *Betula pendula* may also improve soil quality by acquiring base cations from below the rooting zone of *P. abies* and *P. sylvestris* and through the deciduous litter input (Brandtberg et al. 2000). However, although changes in soil chemistry due to a deciduous admixture have been reported in many studies, little evidence of improved tree nutrition has been presented (reviewed by Rothe and Binkley 2001). On the other hand, *B. pendula* may have a larger belowground area of influence (Laitakari 1927, 1935) and higher FRB than the studied conifers (Finer et al. 1997), and thus suppress the development of the root systems of conifers in mixed forest conditions.

1.4 Modeling of the architecture of tree coarse roots

Root models can be roughly divided into ecosystem-level and single-tree models. Ecosystem-level models deal with the question of how roots affect the rhizosphere, e.g. in the form of carbon input, or the concentrations of oxygen or carbon dioxide (Darrah et al. 2006). With single-tree models, a variety of issues can be investigated, e.g. biomass partitioning between shoots and roots (Wirth et al. 2004), the uptake and transport of different substrates (Wang and Smith 2004), and biomechanics (Dupuy et al. 2005). In the simplest modeling approach, stem diameter has been used to predict the biomass of the root system (Marklund 1988, Petersson and Ståhl 2006). Empirical models of this kind cannot, however, be easily applied for different growing conditions or for mixed stands, and a similar root system biomass can be reached with multiple root system architectures leading to differences in uptake and transport efficiencies.

Modeling of root system architectural traits provides spatial and structural information on root systems, which is needed in studies of, for example, plant-medium exchanges or plant-plant interactions (Drouet and Pagès 2007). Developmental and fractal modeling are the main approaches applied in the modeling of coarse root architecture (Tobin et al. 2007).

Developmental modeling aims at predicting the 3D dynamics of the coarse roots (e.g. Jourdan and Rey 1997; Pagès et al. 2004, Drouet and Pagès 2007). Roots and root systems are characterized as a composition of the different types of root axes consisting of different morphotypes. Their relative layout along with their hierarchical relationships and their sequence of development is determined through the morphogenetic rules and local soil conditions.

In fractal modeling, the architecture of the coarse roots is produced by repeating self-similar substructures (Mandelbrot 1983, van Noordwijk et al. 1994; Ozier-Lafontaine et al. 1999; Smith 2001; van Noordwijk and Mulia 2002; Richardson and zu Dohna 2003). Self-similarity means in this framework that the characteristics of the branching event, relative to the diameter of the branches, do not change from the first to the last branching in the root (van Noordwijk and Mulia 2002). The root system is formulated as a composition of root segments. The organization and geometric dimensions of root segments within a root system are derived by self-similar branching rules, in which the dimensions of child root segments are derived recursively on the basis of the dimensions of the parent segments (van Noordwijk et al. 1994, van Noordwijk and Mulia 2002). For simulation of the root system, specifications are also needed for segment termination, branching angles and the number of child segments produced in each branching event (Ozier-Lafontaine et al. 1999).

The applicability of the fractal approach to modeling the characteristics of coarse roots has been tested with tropical (van Noordwijk and Purnomosidhi 1995, Ozier-Lafontaine et al. 1999, Salas et al. 2004) and temperate tree species (Richardson and zu Dohna 2003, Nygren et al. 2009) with satisfactory accuracy. The trees in these studies have been young and quite small, their root system traits thus probably mostly reflecting their water transport function. With increasing tree age and size, the effect of mechanical constraints on the root system traits presumably increase and the divergence of root system traits from a self-similar fractal could be presumed to increase. Thus, the ability of the fractal modeling approach to produce the coarse root architecture of mature boreal tree species has yet to be tested. Knowledge of the variability in model parameters in relation to different site fertilities and stand developmental stages, or the variability in model parameters within one root system (Richardson and du Zohna 2003, Soethe et al. 2007) also does not exist.

1.5 Aims of the study and research hypotheses

The studied species differ in their growth and development in many ways. *Betula pendula* and *P. sylvestris* are early-successional, light-demanding pioneer species, whereas *P. abies* is late-successional and shade-tolerant. Both of the conifers have a higher yield per obtained soil resource unit than *B. pendula*, and *P. sylvestris* has a higher nutrient use efficiency than *P. abies* (Kellomäki 1991). These differences presumably generate differences in specific belowground growth strategies.

Active resource foraging ensures the rapid establishment and high use of resources of *B. pendula*. I assumed that in root traits this means the need for a large root surface area, which leads to a large belowground area of influence as well as a high coarse and fine root length and mass. The dichotomous arrangement of root segments in topological terms is hypothetically appropriate for active foraging. Another property of this competitive growth strategy is the high morphological plasticity of roots i.e. relative continuous readjustment of the spatial distribution of adsorptive surfaces. I hypothesized that the high root plasticity of *B. pendula* could especially be seen in fine root morphology, i.e. in high SRL and root length density (RLD, cm cm^{-3}) values, due to changes in site fertility. I also hypothesized that in all tree species, the xylem anatomy differs between roots, stems and branches, and the conduit size increases from the stem apex toward the distal roots. The change in conduit size may, however, be non-continuous, and scaling parameter values may thus be compartment-specific. In *B. pendula*, the high use of soil resources is compensated by large vessels and a steep tapering of them in order to ensure the effective transport of soil-borne resources.

The high resource-use efficiency of *P. sylvestris* coupled with adaptation to relatively infertile sites leads to the assumption of generally less extensive root systems and lower morphological plasticity of the roots than in *B. pendula*. I assumed that a root system with a small area of influence, a small number of root branches and a low turnover rate may be more cost-efficient for the exploitation of temporary pulses of higher resource availability in infertile sites. The topology of the root system resembles the herringbone pattern more than the dichotomous pattern. Tracheids as conductive elements of *P. sylvestris* indicate the optimization between efficient transport and the avoidance of cavitation in dry habitats, and thus less steep scaling of conduit diameters could be presumed than in *B. pendula*.

I presumed that the belowground traits of *P. abies* are intermediate between *B. pendula* and *P. sylvestris*. The area of influence of root systems, number of root branches, and topology of roots may be closer to *B. pendula* than *P. sylvestris*. Lower morphological plasticity of roots due to higher resource-use efficiency than in *B. pendula* may especially be seen in the fine root characteristics, which may thus be close to the values of *P. sylvestris*. I assumed that the late-successional status of *P. abies* is not clearly illuminated in root traits.

Thus, the aim of my research was to examine the structural and functional characteristics of root systems of these three tree species in mixed boreal forests. The specific objectives were to:

1. determine the effect of site fertility and stand developmental stage of a mixed boreal forest stand on the root traits of *B. pendula*, *P. abies*, and *P. sylvestris*, and on the biomass production and diversity of ECM (I, III);
2. test applicability of the fractal branching approach for modeling the coarse root architecture of the studied species (II); and
3. investigate the effect of tree architecture on xylem anatomy at the whole-tree level, and empirically test the proposals of the theoretical scaling models (IV).

2 MATERIAL AND METHODS

2.1 Study sites

The fieldwork was carried out in the vicinity of the Hyytiälä Forestry Field Station of the University of Helsinki in southern Finland (61°50'N and 24°18'E, 160 m a.s.l.) during 2005 and 2006. Five study sites were selected (I) in mixed *Betula pendula*, *Picea abies*, and *Pinus sylvestris* stands (Table 1). The stands also contained other tree species, such as *Alnus incana* (L.) Moench, *Sorbus aucuparia* L., *Salix caprea* L., and *Juniperus communis* L. The forest type was classified according to Cajander’s (1949) system, in which stand fertility is assessed on the basis of the understorey vegetation.

Table 1. Characteristics of the mixed study stands comprised of *B. pendula*, *P. abies*, and *P. sylvestris*.

Development stage	Forest site type	Species	Regeneration type	Number of trees hectare^{-1}	G (m^2 ha^{-1})	Mean of stand Height (m)	Mean of stand DBH[d] (cm)
Sapling (15 yrs)	MT	*B. pendula*	Natural	2920	4.6	4.6	3.1
	MT	*P. abies*	Planted	6480	2.5	2.7	2.4
	MT	*P. sylvestris*	Natural	180	0.1	3.0	3.7
	MT	Others	Natural	3900	0.5	2.7	1.2
		Total		13480	8.0	3.2	2.3
Pole (30 yrs)	OMT[a]	*B. pendula*	Natural	530	6.2	14.0	12.6
	OMT	*P. abies*	Planted	3150	6.5	5.8	6.0
	OMT	*P. sylvestris*	Natural	270	4.7	14.4	14.4
	OMT	Others	Natural	430	1.9	9.8	8.1
		Total		4380	19.0	8.8	8.4
	MT[b]	*B. pendula*	Natural	480	5.0	12.9	11.5
	MT	*P. abies*	Natural	3450	3.0	4.3	4.1
	MT	*P. sylvestris*	Planted	830	10.7	11.5	12.2
	MT	Others	Natural	930	0.2	3.0	1.3
		Total		5690	19.0	8.2	8.0
	VT[c]	*B. pendula*	Natural	480	1.6	8.8	7.9
	VT	*P. abies*	Natural	920	4.8	7.9	8.7
	VT	*P. sylvestris*	Natural	390	3.3	8.7	10.4
	VT	Others	Natural	110	0.2	5.9	5.7
		Total		1900	10.0	8.2	8.8
Mature (50 yrs)	MT	*B. pendula*	Natural	70	1.1	14.4	13.0
	MT	*P. abies*	Planted	530	10.3	13.1	14.5
	MT	*P. sylvestris*	Planted	270	9.8	17.3	20.8
	MT	Others	Natural	10	0.1	11.0	8.5
		Total		880	21.0	14.5	16.2

[a] OMT = *Oxalis-Myrtillus* type
[b] MT = *Myrtillus* type
[c] VT = *Vaccinium* type
[d] DBH = Diameter at breast height, i.e. at 1.3 m from ground surface.

Among the stands of this study, the Oxalis-Myrtillus site type (OMT) represents the highest fertility, the Myrtillus type (MT) the medium, and the Vaccinium type (VT) the least fertile. The stands formed gradients of both stand developmental stage (15-, 30-, and 50-year-old MT stands) and site fertility (30-year-old OMT, MT, and VT stands). The aboveground stand characteristics were measured in two circular subplots located around each sample tree (Fig. 1). The soil samples were taken from each plot in order to determine the soil fertility. One soil core sample (max. 50 cm depth) was taken next to each sample tree, totalling 12 soil cores per stand. According to the USDA soil taxonomy, the most common soil type in the Hyytiälä area is Typic Haplocryod (Mokma et al. 2004). Mean soil profiles are presented in Figure 2 (other soil characteristics in Table 2 in I; and in Table 4 in III).

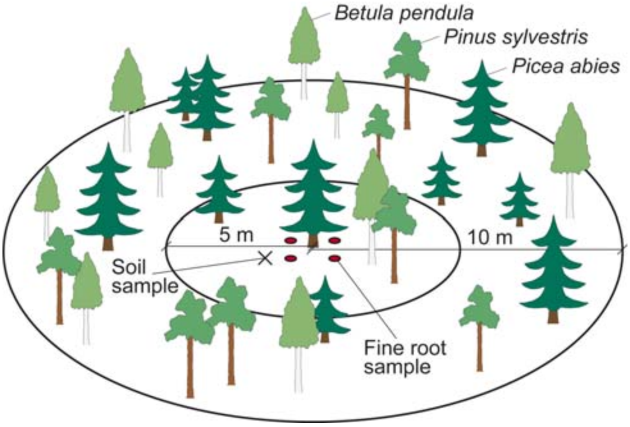


Figure 1. Scheme representing the above- and belowground sampling. Aboveground characteristics of trees were measured in two circular subplots (radius 5 and 10 m in sapling and pole stage stands; 10 and 20 m in the mature stand), which were placed around sample trees. All trees taller than 1.3 m and all trees with a diameter > 5 cm at 1.3 m aboveground were measured in the small and the wide circle, respectively. Fine root and soil sampling points are marked in the figure.

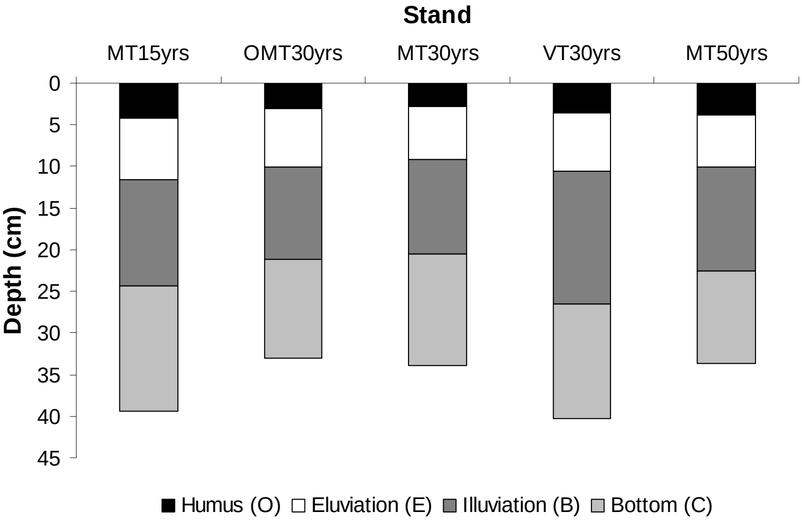


Figure 2. Mean soil profile of each study stand. Soil characteristics were determined from 12 soil cores per stand. The maximum sampling depth was 50 cm.

2.2. Material and methods

2.2.1 Field measurements

In order to study the root system architecture (I) and tree xylem anatomy (IV), and model the coarse root architecture (II), twelve sample trees were selected in each stand, four per species, among the dominant and co-dominant trees (Table 2). The selection of the sample trees was based on their crown characteristics, i.e. healthy trees with a long, living crown were selected. For each sample tree, all the roots attached to the root collar were excavated up to the first branching event and, thereafter, all coarse woody root segments (diameter > 2 mm) were exposed from one to three sample roots per tree. The orientation and geometric dimensions of each segment were measured, both in the exposed roots and in the shoots of the sample trees (Fig. 3). The variables used in this summary part, either measured or estimated in different compartments, are presented in Table 3.

Table 2. The mean values for the aboveground characteristics of the selected sample trees growing in the study stands. The values in parentheses are standard deviations.

Development stage	Forest site type	Species	Age (a)	D_0[a] (cm)	DBH (cm)	Height (m)
Sapling	MT	*B. pendula*	13 (1.3)	8.1 (2.72)	4.9 (2.17)	4.9 (1.17)
	MT	*P. abies*	15 (0.8)	7.9 (0.41)	4.7 (0.33)	4.1 (0.53)
	MT	*P. sylvestris*	13 (2.0)	7.9 (0.61)	4.8 (0.49)	4.4 (0.49)
Pole	OMT	*B. pendula*	36 (4.8)	26.4 (4.91)	19.5 (3.93)	19.0 (1.40)
	OMT	*P. abies*	34 (3.3)	18.2 (3.06)	13.0 (2.45)	13.5 (1.74)
	OMT	*P. sylvestris*	36 (0.6)	20.2 (3.22)	14.5 (2.58)	15.4 (0.59)
	MT	*B. pendula*	29 (1.7)	16.1 (4.61)	11.3 (3.69)	12.5 (0.70)
	MT	*P. abies*	28 (3.5)	11.7 (2.07)	7.8 (1.65)	10.2 (2.37)
	MT	*P. sylvestris*	30 (2.2)	14.5 (2.95)	10.0 (2.36)	12.2 (1.47)
	VT	*B. pendula*	32 (3.3)	19.1 (4.24)	13.7 (3.39)	11.9 (1.04)
	VT	*P. abies*	41 (3.7)	14.7 (2.64)	10.2 (2.11)	9.5 (1.25)
	VT	*P. sylvestris*	31 (3.1)	18.8 (2.50)	13.4 (2.00)	10.7 (0.41)
Mature	MT	*B. pendula*	48 (2.6)	30.0 (4.95)	22.4 (3.96)	20.9 (2.95)
	MT	*P. abies*	55 (0.6)	29.2 (1.40)	21.8 (1.12)	21.3 (2.14)
	MT	*P. sylvestris*	51 (3.3)	29.3 (4.34)	21.9 (3.47)	20.5 (1.68)

[a] D_0 = Diameter of the stump; height was determined from the highest point of the root collar or, when the root collar was completely belowground, from the ground level.

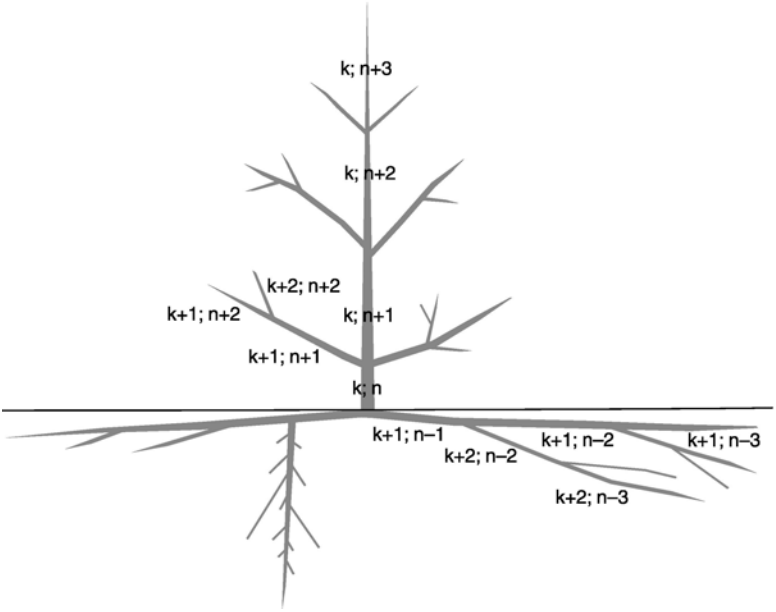


Figure 3. Schematic figure of the architectural hierarchy used in this thesis. The Gravelius order (GO) assigns the same order number (*k*) to segments belonging to the same axis and one order number higher to lateral segments (*k*+1, *k*+2, etc.). The stem is the main axis of the order 1 (*k*); lateral branches attached to stems are assigned the order 2 (*k*+1) etc. Similarly, in the root system, the main axis of a root is assigned the order 2 (*k*+1), lateral branches are assigned one order higher (*k*+2), and so on. The branching generation (BG) of a segment, in turn, follows the developmental sequence starting with proximal segment at stem base as generation 1 (*n*), its children as generation 2 (*n*+1), and so on. Branching generations have negative values belowground. Root branches for which the main axis had a vertical angle larger than 45° were denoted as sinker roots.

2.2.2 Root system architecture and modeling of coarse roots

The root architecture (I) was reproduced and variables calculated using a computer program constructed on the basis of the LIGNUM model (Perttunen et al. 1996). In this thesis, the representation of the tree follows the convention of the LIGNUM model. A tree is a composition of four structural units: tree segments, buds, branching points, and axes. A tree segment is a section of woody material between two branching points. A branching point is the position where one or more tree segments are attached to each other. An axis is a sequence of segments, branching points, and the terminal bud. The main axis of a root is formed by the thickest segment attached to a proximal root and is always continued by the thickest segment in a branching point. The proximal root is a segment directly attached to the root collar. The concept of a root refers to the main axis starting from a proximal root and all laterals attached to it. The root system refers to the all the roots of a tree.

Table 3. The measured or estimated variables used in the summary part. Estimated variables were predicted with a model.

Compartment and variable		
Shoot		
Biomass	kg	Estimated
Basal area	m^2 ha^{-1}	Measured
Cross sectional area of stump	cm^2	Measured
Transport distance	m	Estimated
Conduit diameter	µm	Measured
Conduit frequency	n mm^{-2}	Measured
Coarse roots		
Biomass	kg	Estimated
Radial spread	m	Estimated
Rooting depth	m	Estimated
Vertical distribution	m	Estimated
Branching angle	deg	Measured
Number of child segments		Measured
Root segment length	cm	Measured
Topological index	-	Estimated
Transport distance	m	Estimated
Conduit diameter	µm	Measured
Conduit frequency	n mm^{-2}	Measured
Fine roots		
Biomass	g m^{-2}	Measured
Vertical distribution	cm	Measured
Specific root length	m g^{-1}	Measured
Root length density	cm cm^{-3}	Measured
Ectomycorrhiza		
Biomass production	g m^{-2}	Measured
Taxonomic diversity	number of species	Estimated

The program was used to estimate the total length, biomass, and horizontal and vertical spreads of the excavated roots and to produce a visual depiction of the roots. The topological structure of the coarse roots was described with topological indices (Fitter 1996). The index was defined as the regression slope (β_1) between the number of external root segments in a root (magnitude, M) and the number of coarse root segments in the longest path from any root tip to the first segment attached to the stump (altitude, A):

$$\log A = \beta_0 + \beta_1 \log M \tag{1}$$

The total coarse root length and mass, and the horizontal and vertical spread of coarse roots were compared with roots simulated with a fractal root model (II). We modified the fractal model FracRoot from previous applications (Ozier-Lafontaine et al. 1999; Salas et al. 2004; Nygren et al. 2009). We characterized the 3D root architecture with the geometric dimensions of each segment, branching angles, branching intensity, and with the Gravelius order (GO) and BG. The modified root structure in the FracRoot model is illustrated in

Figure 4. We accounted for the ZRT and the tapering of individual segments, i.e. the difference between the proximal diameter (D^{prox}) and distal diameter (D^{dist}) of a root segment. We also considered the case in which a root terminates before reaching the preset minimum diameter, e.g. 2 mm, and allowed some parameters of the model to vary within roots.

In the FracRoot model, the thickest child segment (k, n+1) continues the axis of the parent segment (k, n), and all other child segments (k+1, n+1) are laterals having the same diameter. The parameter p specifies the ratio of the proximal cross-sectional area (CSA) of the parent segment to the sum of proximal CSAs of the child segments

$$p = \frac{\left(D_{k,n}^{prox}\right)^2}{\left(D_{k,n+1}^{prox}\right)^2 + (N-1)\left(D_{k+1,n+1}^{prox}\right)^2} \tag{2}$$

If $p = 1$ the CSA does not change across a branching point, while if $p > 1$ the CSA decreases from the parent to children, and if $p < 1$ it increases. The parameter q determines the share of the sum of squared diameters of the child segments that is allocated to the thickest segment

$$q = \frac{\left(D_{k,n+1}^{prox}\right)^2}{\left(D_{k,n+1}^{prox}\right)^2 + (N-1)\left(D_{k+1,n+1}^{prox}\right)^2} \tag{3}$$

The distal diameter of the parent segment was set so that the distal CSA was equal to the sum of the proximal CSAs of the child segments

$$D_{k,n}^{dist} = \frac{D_{k,n}^{prox}}{\sqrt{p}} \tag{4}$$

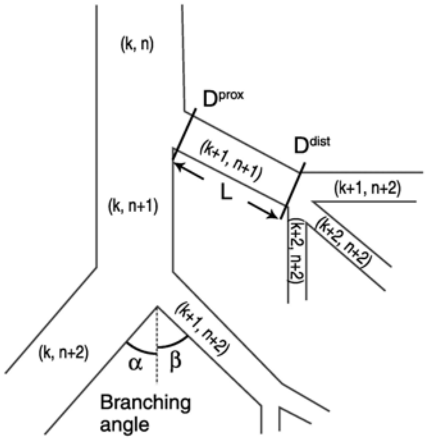


Figure 4. The FracRoot model considers a root as a collection of root segments. They are identified by their Gravelius order *k* and segment generation *n (k, n)*. The proximal segment of the root is assigned with the branching generation (BG) 1. D^{prox}, D^{dist}, and *L* are proximal and distal diameter and length of the segment. The branching angles (*α* and *β*) are measured relative to the direction of the parent segment.

We distinguished five different possibilities for the production of child segments, P0 – P4. In cases P0 and P1, no child segments are produced, i.e. the parent segment becomes external. Case P0 corresponds to the situation in which the child segment is not produced and the root terminates well above the minimum diameter, e.g. due to a trauma or other reason. Case P1 corresponds to the situation encountered in the field work when the parent segment reached the minimum diameter at which measurement was stopped (2 mm). In cases P2 – P4, two, three, and four child segments are produced, respectively, i.e. the parent segment becomes internal. In each branching event, the number of child segments was chosen randomly with estimated probabilities P0 – P4 that sum up to one. The length and branching angles of root segments were generated from the observed distributions formed by tree species, stand, and GO.

2.2.3 Fine root characteristics

To determine the fine root characteristics of the stands (III), four fine root cores were taken around each sample tree (one in each cardinal direction from the sample tree) with a soil corer (max. sampling depth 50 cm) once during the growing season in each plot. The fine root samples were divided into sections comprising the humus layer and the 0–10, 10–20, and 20–30 cm mineral soil layers. Soil was removed from the roots by washing and root fragments were sorted into different diameter classes of living and dead roots of *B. pendula*, *P. abies*, and *P. sylvestris* (Persson 1983; Makkonen and Helmisaari 1998). After separation, the roots were placed in a transparent water-filled tray and scanned. From the scanned images, the fine root length was determined with the program WinRhizo 2003b Basic (Regent Instruments lnc., Québec, QC, Canada), and the dried root samples were weighed. The fine root biomass (FRB, g m^{-2}), root length density (RLD, cm roots in cm^{-3} soil) and specific root length (SRL, m g^{-1}) were calculated for each sample. The mean values were then calculated for each species, stand, and soil layer.

2.2.4 Ectomycorrhiza

The fungal in-growth bag method (Wallander et al. 2001) was used to estimate the production of external ECM mycelia in each stand (III). Fifteen to nineteen in-growth bags (with 50-µm mesh) per stand were filled with 125 g acid-washed quartz sand and inserted horizontally between the humus and mineral soil layers. The bags were inserted in mid-June and harvested in mid-October. External mycelia of ECM grown in quartz sand-filled mesh bags were separated by shaking in water and thereafter the dry mass of mycelia was measured. From small sub-samples, the fungal community structure was analyzed by molecular methods: DNA extraction coupled with the polymerase chain reaction (PCR), denaturing gradient gel electrophoresis (DGGE), cloning, and sequencing (Vainio 1998, Pennanen et al. 2004, Korkama et al. 2006). Partial ITS sequences of good quality were manually checked, computer aligned and identified by comparing them with sequences retrieved from the GenBank and UNITE databases (Kõljalg et al. 2005). The sequences were submitted to GenBank under accession numbers FJ764974-FJ764993.

2.2.5 Xylem anatomy

To determine the anatomic characteristics of tree xylem within different tree organs (IV), vascular samples were taken from nine ca. 30-year-old trees, three of each species, growing on OMT, VT, and MT stands (Table 2 in IV). Sampling was carried out on the whole water pathway, fine roots and leaves excluded, i.e. from the 2-mm lower limit in roots to the final segment in branches (leaf petioles in *B. pendula*, distal shoots in the conifers). Six stem discs were collected, the first just above the root collar and thereafter one below each sample branch. Analogously, from the sample roots, 5–6 discs were collected along the main axis. From the lateral sample branches, three discs were sampled from each existing Gravelius order (GO) both in the shoots and roots (Fig. 1 in IV).

The anatomy of collected vascular samples was determined from microscopic transverse sections of samples of different tree organs. Xylem conduit diameters and frequencies were measured from the images captured with a digital camera mounted on the microscope. The petiole samples were imaged as a whole. In other compartments, the path of successive images from pith to bark was taken from the transverse sections (Table 3 in IV). From the images, the diameters of the conduit lumens were measured, and conduit frequencies were determined by calculating the number of conduits in a known area in the image with aid of a written macro. Total number of measured conduits in the study was over 100 000.

From the WBE theory, assuming a volume filling network, it can be derived that the conduit radius scales with distance from the apex as follows (Anfodillo et al. 2006):

$$a_k \propto l^{\frac{b}{\alpha}} \tag{5}$$

where a_k is conduit radius, l is the distance from the apex, b is a scaling parameter, and α can be derived from the relationship between the distance and tree diameter, D:

$$l = D^{\alpha} \tag{6}$$

and should have a value of 2/3 based on the elastic similarity model (Greenhill 1881, McMahon 1973, West et al. 1999a). Since theoretical values of b and α are 1/6 and 2/3, respectively, the theoretical scaling exponent b/α in eq. 5 is 1/4. Due to the approximation of tree height in the WBE model, an empirical correction factor of 0.84 is needed when tapering of the conduit diameter is predicted according to distance from the apex instead of segment number (Anfodillo et al. 2006).

$$a_k \propto l^{0.84\frac{b}{\alpha}} \tag{7}$$

The exponent in eq. 7 can be used to compare empirical results with the WBE exponent (Anfodillo et al. 2006).

Another scaling model, Murray's law, states that the volume flow rate, *Q*, and conduit radius, *a,* are related as (Murray 1926, McCulloh and Sperry 2005):

$$Q = \sum a^3 \tag{8}$$

The hydraulic architecture of a tree that conforms to eq. 8 leads to a xylem anatomy where the conductivity ratio of adjacent segments, K_{dist}/K_{prox}, equals the relative conduit tapering, T, between these segments

$$K_{dist} / K_{prox} = T \tag{9}$$

To examine whether our results corresponded with Murray's predictions in different species and tree compartments, we calculated the potential conductivity K for each segment in measured branching points using the Hagen-Poiseuille equation (Tyree and Zimmermann 2002):

$$K = \frac{a^4 \pi}{8\eta} \tag{10}$$

where η is the viscosity of xylem sap. We then compared K_{dist}/K_{prox}, from distal roots towards the stem apex, in a branching point with T. In the analyses, we used the diameter and number of conduits obtained from the proximal end of each segment to calculate K and the ratio of K_{dist} and K_{prox}, and thus accounted for the tapering taking place within a segment (Soethe et al. 2007).

2.2.6 Aboveground stand characteristics

In order to be able to explore the relationships between shoots and roots (III), the aboveground characteristics of the stands were measured in two circular subplots, located around a sample tree (Fig. 1). The measured variables were stem position, stem diameter at breast height, tree height, height to the first living branch, and crown projection in two opposite directions.

The foliage biomass of each tree on the subplots was estimated as a function of tree diameter at breast height, tree height, and the length of the living crown (Repola et al. 2007). The foliage mass was summed for each species on each subplot, and calculated per unit surface area (kg ha^{-1}). In addition, the canopy cover was calculated for each subplot using the measured positions and crown characteristics of the trees on the subplots. The canopy cover was calculated for each subplot using a Monte Carlo method. The positions of the trees on the subplots were marked on a stand map, and the horizontal crown projection of each tree was drawn on the basis of the field measurements. Ten thousand random points were produced in each subplot and the number of points in the area of the crown projection of any tree was recorded (Table 3 in III). The crown coverage was taken as the proportion of points within the crown projection area of the trees.

2.2.7 Statistical analyses

The data were analyzed using SAS Statistical Software v.9.1 (SAS Institute Inc., Cary, NC, USA). Both in coarse and fine root analysis, differences between tree species and stands were tested by analysis of variance followed by the Tukey-Kramer paired comparisons method for multiple comparisons. In linear curve fitting, statistical significance was defined by the F-test. Logarithmic transformations were used to normalize variables and remove the heteroskedasticity of residuals when necessary. In the test of coarse root tapering, the Gauss-Newton iterative method was used in non-linear curve fitting to define the partial derivatives of the model with respect to the parameters until the estimates converged. The differences in FracRoot parameter values were tested using the non-parametric Mann–Whitney U-test. Kolmogorov–Smirnov and Pearson's chi-square tests were used in the distribution analysis. Differences in xylem anatomy between compartments were defined with a linear hierarchical mixed model with a nested structure.

3 RESULTS

3.1 Architecture of coarse roots and fine root morphology

3.1.1 Horizontal belowground area of individual trees (I, II)

Betula pendula had a more extensive coarse root system than the conifers in each study stand, and the observed maximum spreads were generally bigger in *P. abies* than in *P. sylvestris* (Table 4 in I). The radial root spread in each species increased with stand development and from the most to the least fertile site. The maximum values were observed in the mature stand and were 20.5, 10.1, and 9.5 m for *B. pendula*, *P. abies*, and *P. sylvestris*, respectively. However, the belowground area of influence of a root system most frequently overlapped with other trees in the sapling stage; assuming a circular area of influence, the maximum number of other trees stems in the influence area of the excavated root system were 166, 117, and 90 in *B. pendula*, *P. abies*, and *P. sylvestris*, respectively. A circular influence area estimated using the observed maximum radial root spread leads, however, to the systematic overestimation of the belowground interactions, mostly due to the highly asymmetric spread of root systems (Fig. 5).

3.1.2 Vertical distribution of roots (I, II)

When stands were pooled, both conifers had 80% of the coarse root biomass (CRB) in the 30 cm soil layer, whereas in case of *B. pendula* the corresponding soil layer thickness was 50 cm (Fig. 6 a). The observed maximum values of rooting depth were 2.91, 2.65 and 1.62 m for *P. sylvestris*, *B. pendula*, and *P. abies*, respectively (Table 4 in I). Deep soil layers were reached with sinker roots in each species, i.e. root branches that extended vertically downwards. The proportion of all root branches belonging to sinker roots was 13% (II). The main axes of the coarse roots of the studied species mostly occupied different soil layers: *P. abies* exploited the topsoil, *B. pendula* primarily occupied the illuvial and *P. sylvestris* the elluvial layer. Each species had ca. 70% of its FRB in the humus and uppermost 10-cm mineral soil layers (Fig. 6 b).

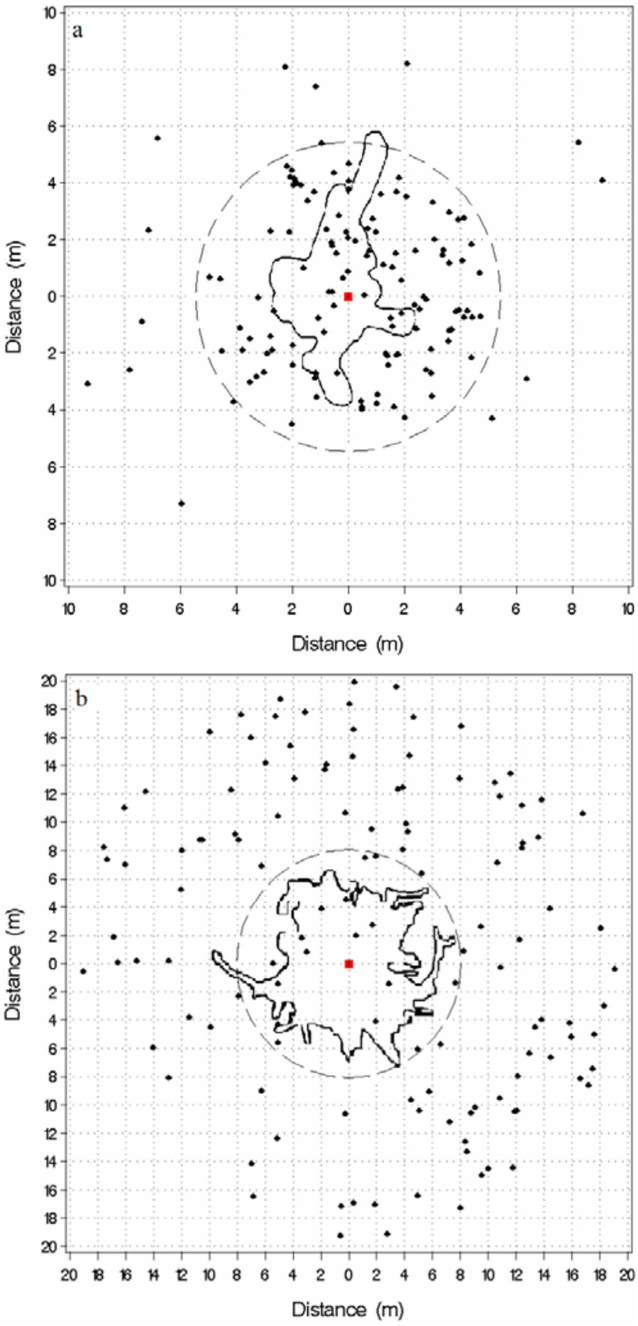


Figure 5. The area of influence of the root systems of *P. abies* trees. The stem of the sample tree is denoted with a red square, and the positions of other tree stems with dots. a) Sapling (age 16 yrs, height 4.5 m, D_0 7.8 cm). Within the influence area estimated from the observed maximum root spread (dashed circle; I) and modeled with FracRoot (solid line; parameter set 4 in Table 7 in II), there were 117 and 26 other tree stems, respectively. b) Mature tree (age 54 yrs, height, 22.6 m, D_0 30.8 cm). Number of other tree stems within circle and solid line were 15 and 9, respectively.

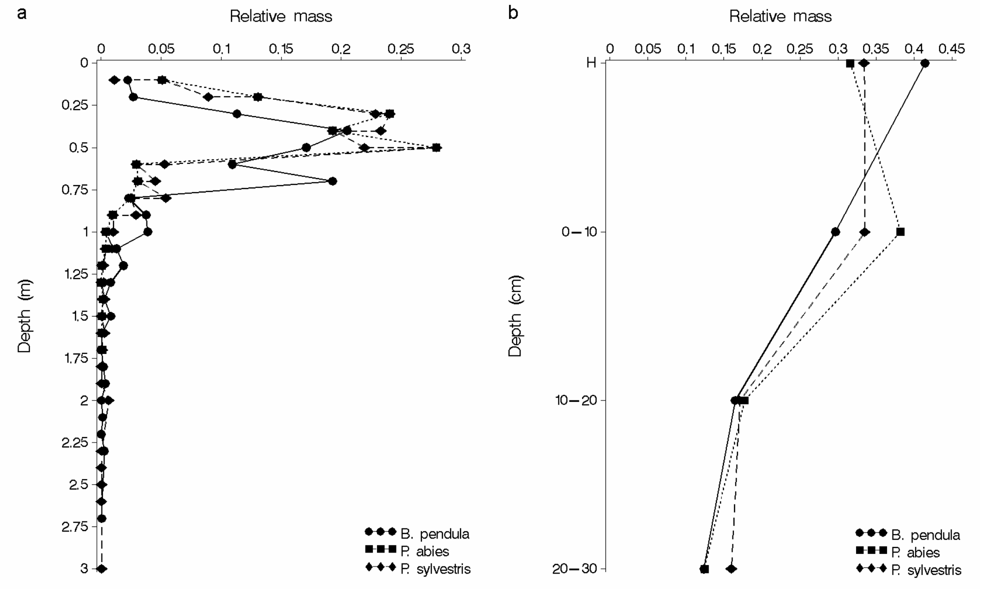


Figure 6. Relative root mass of *B. pendula*, *P. abies*, and *P. sylvestris* (stands pooled) as a function of soil depth. a) Coarse roots reconstructed from the excavated roots (number of roots = 94; I), b) fine roots (number of root cores = 167, H = Humus, i.e. organic layer; 0–30 cm represents mineral soil layers; III).

The rooting depth increased as a function of stand developmental stage in each species, both in terms of coarse and fine roots, while the effect of site fertility was to some extent species-specific: the proportion of *P. sylvestris* FRB was larger in the deepest layer of the most fertile stand than in the other stands; the FRB of P. *abies* clearly shifted from the humus layer to the uppermost 10-cm mineral soil layer with decreasing fertility; in *B. pendula*, the vertical distribution of the FRB remained the same along the fertility gradient. The vertical distribution of coarse roots clearly only changed in *B. pendula*, in which the coarse roots were deepest in the least fertile site (III).

3.1.3 Branching pattern of coarse roots (I, II)

The overall observation obtained from the excavated roots was that the branching pattern of the coarse roots was strongly species-specific (Fig. 7). Topologically, the roots of *P. sylvestris* resembled more the herringbone pattern than the roots of other species. *Betula pendula* had more irregular branching, and side branches extended further than in the other species. It also had a generally larger number of woody root branches, higher branching intensity, and thinner root segments than the conifers. Branching angles varied greatly, i.e. the values seemed to include considerable randomness; however, *P. sylvestris* had both larger horizontal and vertical branching angles than the other species (I, II).

The trees seemed to have a hierarchical organization within root systems; the number of produced child segments in a branching event was axis-specific in each species, the length of internal segments in *B. pendula* and external segments in *P. sylvestris* decreased with increasing segment order, and branching angles were larger in higher orders in *P. sylvestris* (Figs 4 and 5 in II). The effect of the stand development or site fertility was difficult to determine due to the high variability between individuals within each stand. Especially in *P. sylvestris*, the species specificity in root branching patterns seemed to overrule, at least to some extent, the effect of the differences between growing sites. In *B. pendula*, the proliferation of coarse roots was observed in specific spots in the fertile site (Fig. 8). Soil analysis confirmed the high nutrient contents of these spots. However, as a general trend, topological indices, i.e. the regression slopes between M and A (eq. 1), were higher and branching angles larger in the sapling than in the mature stage. Increasing site fertility, i.e. the transition from the least fertile VT site to the most fertile OMT site, had the largest effect on the segment length. Uniformly in all species, the mean segment length was the shortest in the most fertile site. Branching events with three or more new child segments were also more common on the most fertile site than on the other sites. This effect was the most pronounced in *B. pendula*.

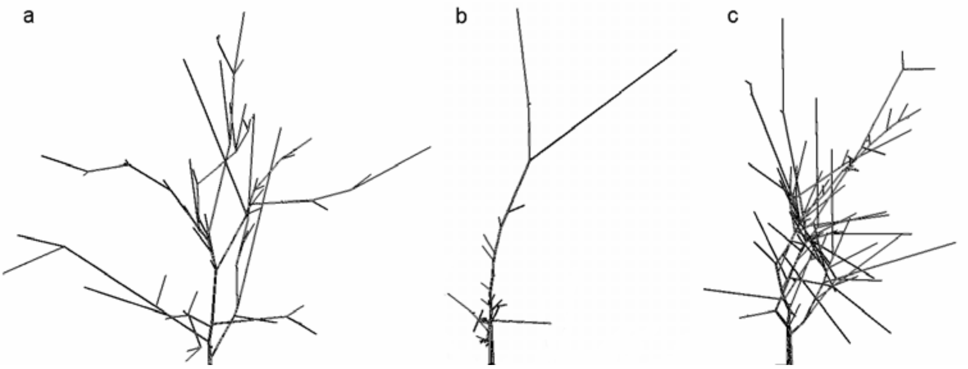


Figure 7. An example of the branching pattern in one excavated coarse root of each studied species growing on the least fertile VT site. a) *B. pendula*, proximal diameter of the root 52 mm, b) *P. sylvestris*, proximal diameter of the root 109 mm c) *P. abies,* proximal diameter of the root 76 mm. The maximum horizontal spread of each root was ca. 6 m.

Figure 8. A coarse root of *B. pendula* in the fertile OMT site showing the proliferation of roots a the spot with high soil fertility (humus layer C/N ratio 19, cation exchange capacity 36.60 cmol kg^{-1}, and base saturation 70%). The proximal diameter of the root was 51 mm and the maximum spread 0.93 m. Compare with Fig. 7 a.

3.1.4 Fine root morphology (III)

Fine root morphology was illustrated with the values of SRL. The SRL values were generally higher in *B. pendula* than in the conifers, but *P. abies* and *P. sylvestris* did not deviate from each other. The morphology of fine roots seemed to be more plastic in *B. pendula* than the other species (Fig. 9); there was an over two-fold increase in the SRL of the thinnest root diameter class (roots with diameter < 1 mm) with decreasing fertility, and the relative share of roots with a diameter < 1 mm of RLD also clearly increased in the humus layer with decreasing site fertility (Table 5 in III). Such changes in fine root characteristics along the site fertility gradient were not observed in the conifers (III).

3.2 Root biomass and length, and ECM characteristics

3.2.1 Root biomass and length (I, III)

The species did not differ from each other in the ratio between the stump cross-sectional area (CSA) and the total CSA of summed proximal roots. However, CRB and length per unit CSA of the proximal roots was higher in *B. pendula* than in the conifers (I). This type of difference between species also appeared to apply to fine roots, since *B. pendula* had generally the highest FRB and RLD independent of its relative aboveground abundance in the stand (III). Consequently, *B. pendula* produced more FRB and length per unit CSA of the proximal roots than the conifers. The biomass and length of both coarse and fine roots did not change much between developmental stages in any of the species, while site fertility had a clear effect on each species. For *B. pendula*, the maximum values of CRB and length were observed in the least fertile site. The coarse root mass per unit CSA was also higher for *P. abies* in the least fertile site than in other sites, while no such changes were observed for *P. sylvestris*.

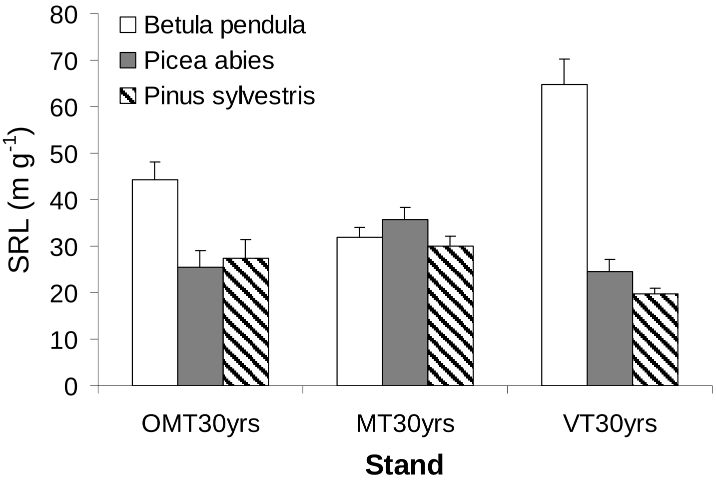


Figure 9. Mean specific root length (SRL, m g^{-1}) of fine roots (diameter < 2 mm) along the gradient of site fertility. Error bars are the standard error of the mean.

The most pronounced difference between species in terms of the response to the decreasing site fertility was observed in the FRB. The conifers had the clearly highest FRB in the least fertile site, while there was no difference according to site fertility in the FRB of *B. pendula* (Fig. 1b in III). *Betula pendula* accounted for the lowest relative share of the stand basal area in the least fertile site. Thus, in *B. pendula*, the relative allocation to belowground biomass was also higher in least fertile site than in other sites, although to a lesser extent than in the conifers. The relative proportion of roots with a diameter of < 1 mm of RLD was also highest in the least fertile site for *B. pendula*.

3.2.2 ECM characteristics (III)

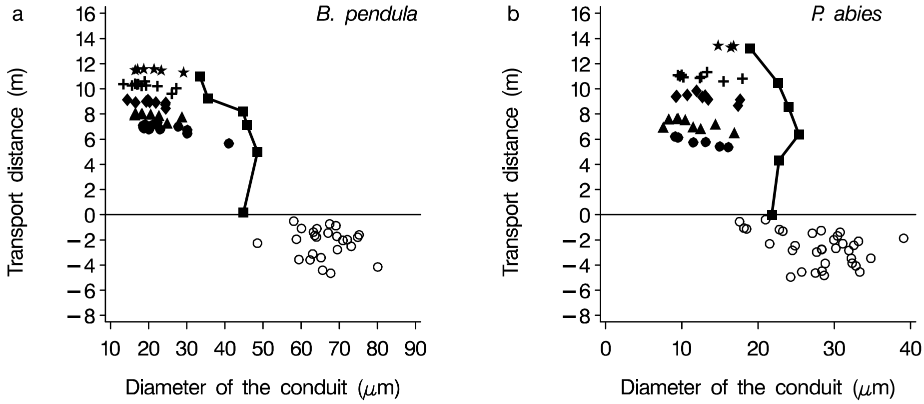
We examined the characteristics of the external ECM mycelium on the stand level (III). The biomass production of external hyphae was highest in the sapling stage of the developmental gradient and in the fertile site along the fertility gradient (Fig. 5a and b in III). If fungal biomass production was calculated as a proportion of the aboveground biomass of the stand, i.e. shoot biomass divided by ECM biomass, there was no difference in relation to site fertility.

In general, in-growth bags with a high mycelial biomass had the lowest taxonomic diversity of ECM. The number of ECM taxa tended to be higher in the least fertile site than in the most fertile site. The ECM community structure of the least fertile site also deviated from the other sites; sequences identified as *Tylospora fibrillus*, *Paxillus involutus* and uncultured Corticiales were more common in the least fertile site, while the sequences identified as *Tylospora* sp. and *Tomentella badia* occurred more frequently in the more fertile sites. No differences were observed between developmental stages in the ECM community structure.

Most notably, these results indicated that ECM biomass production was not directly related to the FRB; the least fertile site had the highest total FRB, but the lowest biomass production of external ECM hyphae.

3.3 The xylem characteristics of roots, stems and branches in the studied trees (IV)

Xylem anatomy (IV) differed between species and compartments (Fig. 10); the conduit diameter decreased and conduit frequency increased from the roots to the stem and from the stem to the branches in each species, and further to the leaf petioles in *B. pendula*. The tapering pattern also differed between compartments. In horizontally oriented shallow roots, conduits tapered along the transport distance from the root tip towards the stem base. In the stem, the conduit size most often increased upwards from the root collar, reached the maximum at an intermediate height, and then became smaller again. In branches, conduits tapered from the branch base towards the branch tip (Fig. 10). Regarding the effect of the tree architecture, conduit size diminished and frequency increased along the GO within the tree crowns of each species. Belowground, the root main axis had a slightly higher mean conduit diameter than laterals in *B. pendula*. Xylem characteristics seemed to differ between root types; conduits tended to be larger and less numerous in shallow than in sinker roots (Fig. 11).



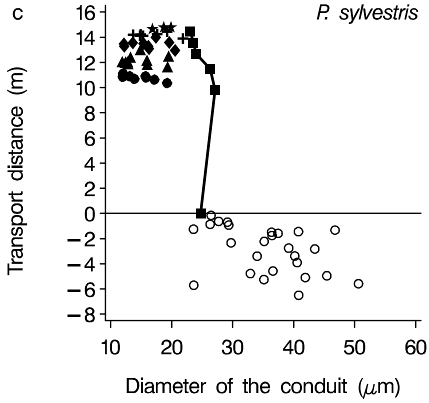


Figure 10. The relationship between the transport distance and xylem conduit diameter in a) *B. pendula*, b) *P. abies* and c) *P. sylvestris.* Each figure represents one sample tree. The stem base is used as a reference point from which the transport distance to the root, stem or branch segment is calculated. Negative values denote roots. The stem and each sample branch are denoted with different filled symbols, and roots are denoted with empty circles.

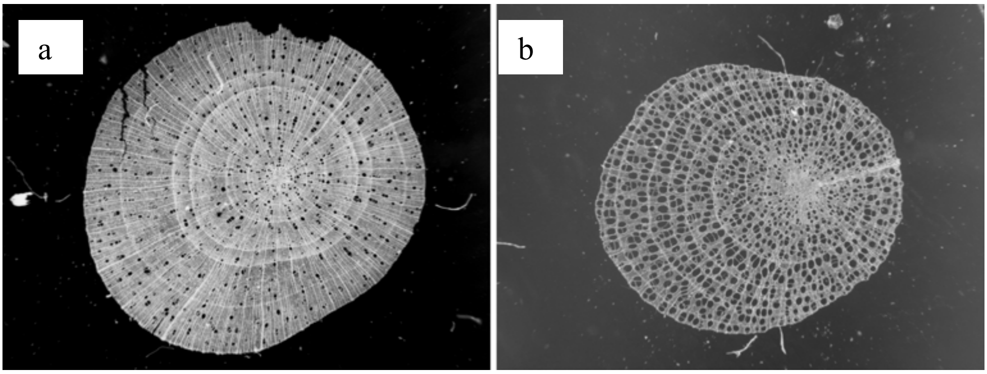


Figure 11. An example of the difference between root types in *B. pendula*. Transverse sections of a) a sinker root (diameter of root = 4.5 mm; path length from the stem = 0.5 m; depth of the sampling point = 0.5 m), and b) a shallow root (diameter of root = 7.2 mm, path length from the stem = 2.9 m, depth of sampling point = 0.40 m). 100X magnification in both images.

In coarse root segments, the mean diameter and frequency of conduits was 63 µm and 78 conduits per mm^{-2} in *B. pendula*, 33 µm and 815 conduits per mm^{-2} in *P. sylvestris*, and 28 µm and 1125 conduits per mm^{-2} in *P. abies* (earlywood conduits in the conifers). By applying the calculated mean values of conduit radius in the Hagen-Poiseuille equation (eq. 10) and multiplying this result with the mean conduit frequency, the conductivity of root segments of *P. abies* is ca. 55% and *P. sylvestris* ca. 80% of the value for *B. pendula.*

The conduit diameter increased along the radial distance from the pith, i.e. as a function of the cambium age, in the stem and branches in each species. In roots, this pattern was found in *B. pendula* and *P. abies*; in *P. sylvestris*, the conduit diameter decreased with radial distance. However, the variation in the root xylem anatomy pattern from the pith outwards was large and the proportion of explained variation was extremely low in each species. The coefficient of determination ranged from 0.01 to 0.08 for conduit diameter, and from 0.33 to 0.01 for conduit frequency. In many root samples, the conduits were larger and less numerous in some growth rings around the protoxylem, but size then abruptly diminished and subsequently remained constant (Fig. 4 in IV).

Our results supported the predictions of the WBE model in the sense that the size of conduits increased from branches to the stem and thereafter to the roots (Fig. 12), and the values of scaling exponents (Table 4 in IV) were higher than the proposed theoretical value of 1/6 corresponding to the WBE model. The mean conduit diameter also increased as a function of increasing distance from the apex on the whole-tree level. However, the tapering pattern of the conduits differed between compartments, and continuous tapering with a single scaling parameter value along the entire distance on the whole-tree level did not therefore apply in our data (Table 4 in IV).

Murray's law applied quite well to the shoots, while in the roots the observed relationship between relative conduit tapering and the conductivity ratio clearly deviated from the predicted one in each species, especially in *P. sylvestris* (Fig. 9 in IV). The observed values in roots include considerable uncertainty due to the small number of root observations included in this analysis (N = 37).

3.4 Modeling of coarse root architecture (II)

We tested the applicability of the fractal branching model for estimating the characteristics of coarse roots and root systems of *B. pendula*, *P. abies*, and *P. sylvestris* (II). With parameter values derived from the data, we estimated the spatial dimensions, branching pattern and root biomass and length of coarse roots of the studied species.

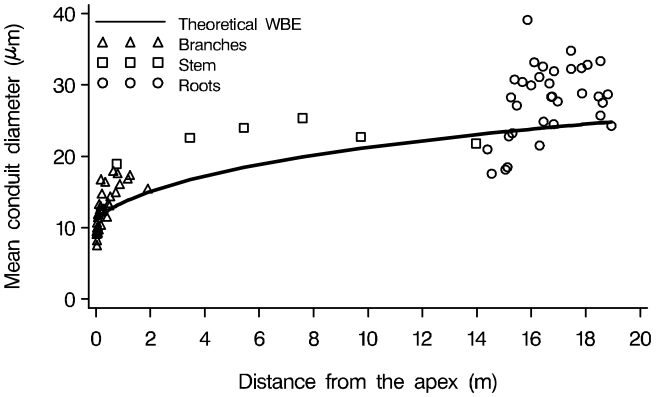


Figure 12. The change in the conduit diameter along the distance from the apex in roots to the stem and branches of one *P. abies* tree growing on the fertile OMT site. The solid curve represents the change in conduit diameter predicted by the WBE model (eq. 7, *b* = 1/6).

Our results indicated that roots of the studied tree species were not self-similar structures and, thus, it was not possible to model them with species-specific constant parameters; model parameters, p, q, and branching angles mostly depended on the GO and BG (Figs 2, 4 and 5 in II). Our results also demonstrated that tapering of the individual root segments and the ZRT could be accounted for by the parameter p (the ratio of the proximal CSA of the parent segment to the sum of proximal CSAs of the child segments), and by the relationship between BG and p, respectively (Fig. 2 in II). In terms of the model parameters, the effect of the stand developmental stage was mostly seen in the parameter p. Values decreased from saplings to mature trees in each species, whereas with increasing site fertility, each species had shorter and more numerous root segments. As an overall result, we conclude that the model was capable of accounting for the main coarse root characteristics in *B. pendula* and *P. abies*, and moderately capable of describing the root system of *P. sylvestris* (Table 4). In terms of the mean values, observed and predicted horizontal root spread corresponded each others quite closely, while the model overestimated the maximum rooting depth (Table 4). Moreover, the accuracy of the length and biomass estimates of the biggest roots was quite low, especially in *B. pendula* and *P. abies*. Branching angles have a large influence on the root appearance. We generated both the horizontal and vertical branching angle of root segments independently from the observed distributions, since no joint distribution was found. We did not separate the sinker and shallow roots in our model. Due to these facts, the simulated roots had a more irregular appearance than the observed roots (Fig. 13).

Table 4. Observed versus. modeled characteristics of coarse roots of *B. pendula*, *P. abies*, and *P. sylvestris* (stands pooled). Values presented in parentheses are the standard deviation. Different letters denote significant differences ($p < 0.05$) between observations and simulations within each tree species.

Tree species	N	Root length (m)	Root mass (kg)	Root spread (m)[a]	Root depth (m)[b]
B. pendula					
Observed	26	32.34 (41.17) a	1.10 (1.70) a	4.82 (3.93) a	0.72 (0.50) a
Modeled	26	34.31 (21.37) a	1.07 (1.32) a	4.80 (2.55) a	2.35 (1.16) b
P. abies					
Observed	28	27.31 (25.66) a	1.08 (1.31) a	3.72 (1.98) a	0.49 (0.32) a
Modeled	28	27.07 (17.28) a	1.02 (1.48) a	3.71 (1.72) a	1.86 (1.05) b
P. sylvestris					
Observed	40	14.37 (15.32) a	0.77 (1.11) a	3.03 (1.90) a	0.54 (0.48) a
Modeled	40	20.29 (11.80) a	0.75 (1.00) a	3.48 (1.68) a	1.95 (0.98) b

[a] Root spread = the horizontal spread, defined as the mean length of the side of the box containing the root projected to the soil surface.

[b] Root depth = the maximum depth evaluated as the vertical distance from the insertion point of the root in the root collar to the bottom of the box containing the root.

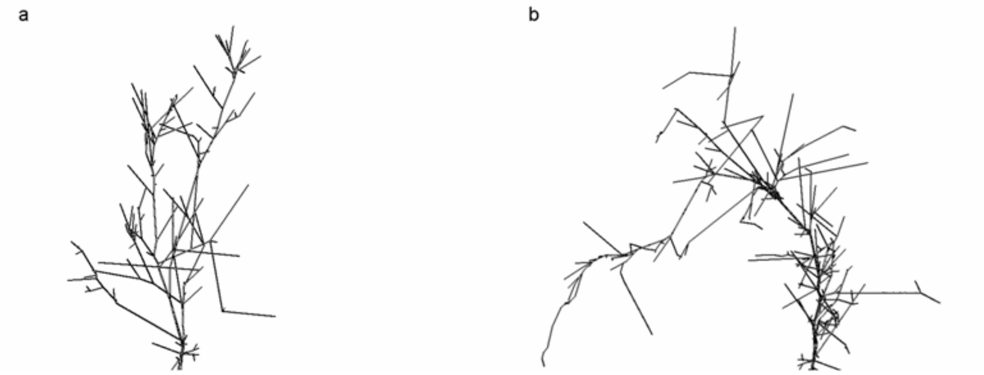


Figure 13. Top view of a) an observed sample root and b) an example of a simulated root in *Picea abies*. The diameter of the proximal root segment in the simulated root was the same as in the observed root. The total length and biomass of the observed sample root was 92.6 m and 3.85 kg. The respective values for the simulated root were 75.6 m and 4.39 kg.

4 DISCUSSION

4.1 Root traits of three boreal tree species in mixed forest stands

Our results revealed that both the coarse and fine root characteristics of the studied boreal tree species differed considerably between species. Table 5 synthesizes the central results in both a quantitative and qualitative form. The horizontal area of influence of the coarse root system of *B. pendula* was the largest in all stands, and it had the highest number of coarse root branches, creating a dense, highly ramified root mat within the influence area. As a result, the total CRB and coarse root length of *B. pendula* was generally higher than that of the conifers. Especially in comparison with the clearly shorter coarse root spreads and sparse branching of coarse roots in *P. sylvestris*, the coarse root systems of *B. pendula* exploited rooting space both more extensively and intensively.

The results concerning the characteristics of the coarse roots are in line with earlier qualitative observations on the root characteristics of these species (Laitakari 1927, 1935). In addition, *Betula pendula* had a generally higher FRB, RLD and SRL than the conifers. These results indicate that in terms of fine root characteristics, *B. pendula* also had more extensive root systems than the conifers. The high FRB and SRL values of *B. pendula* have likewise been observed in several other studies (Curt and Prévosto 2003, Ostonen et al. 2007a, Ostonen et al. 2007b).

We examined the characteristics of ECM on the stand level, and could not therefore relate them to a specific tree species. However, the lower observed SRL and RLD values of the conifers may indicate a stronger dependence on ECM associations (Sohn 1981, Bauhus and Messier 1999).There have been few studies on the characteristics of external hyphae of ECM under field conditions, and their effect on root traits and belowground competition between trees is consequently poorly known (Wallander 2006).

Table 5. The selected root characteristics of the studied species showing the qualitative and quantitative differences between species and the effect of stand developmental stage or site fertility on the given characteristics.

Root characteristic	*B. pendula*	*P. abies*	*P. sylvestris*
Coarse roots (D ≥ 2 mm)			
Horizontal spread (m)[a]	13.0	10.0	8.0
Change with increasing site fertility	Decreases	Decreases	Decreases
Change with stand developmental stage	Increases	Increases	Increases
Rooting depth	Illuvial	Topsoil	Elluvial
Change with increasing site fertility	Decreases	No effect	Increases
Change with stand developmental stage	Increases	Increases	Increases
Topology	Dichotomous	Dichotomous	Herringbone
ZRT in 50-yr-old trees	> 2 m	≤ 2 m	< 2 m
Number of root segments	High	Medium	Low
Change with increasing site fertility	Decreases	Decreases	No effect
Change with stand developmental stage	No effect	No effect	No effect
Branching intensity	High	Medium	Low
Change with increasing site fertility	Increases	Increases	Increases
Change with stand developmental stage	Decreases	No effect	No effect
Root mass	High	Medium	Low
Change with increasing site fertility	Decreases	Decreases	No effect
Change with stand developmental stage	No effect	No effect	Increases
Root length	High	Medium	Low
Change with increasing site fertility	Decreases	Decreases	No effect
Change with stand developmental stage	No effect	No effect	No effect
Conduit diameter[b] (µm)	63	28	33
Conduit frequency[b] (n mm^{-2})	78	1125	815
Parameter p	1.53	1.80	2.63
Parameter q	0.70	0.72	0.74
Fine roots (D < 2 mm)			
Biomass (g m^{-2})	75	38	43
Change with increasing site fertility	Decreases	Decreases	Decreases
Change with stand developmental stage	Increases	No effect	No effect
RLD (cm root in cm^{-3} soil)	4.14	1.70	1.64
Change with increasing site fertility	Decreases	No effect	No effect
Change with stand developmental stage	No effect	No effect	No effect
SRL (m g^{-1})	39	28	24
Change with increasing site fertility	Decreases	No effect	No effect
Change with stand developmental stage	Increases	No effect	Increases

[a] The average spread of roots with a diameter of 10 cm.

[b] Earlywood conduits in the conifers

However, there is accumulating evidence that the selection of ECM fungi and the quantity of external mycelia varies between tree individuals and could be controlled by the properties of the host tree (Rajala 2008), resulting in variation in ECM communities between different tree individuals.

Of the studied species, *B. pendula* has the highest rate of dispersal and the most rapid height growth in the early stages of development (Kellomäki 1991). Plants species with this type of growth strategy are often regarded as competitively inferior, and their long-term coexistence with competitively superior species in the same habitat is thought to be ensured by the occurrence of regenerative niches (Polechová and Storch 2008), i.e. by the rapid occupation of canopy gaps that eventually form. However, due to a low resource use-efficiency (Kellomäki 1991, Meinzer et al. 2005), *B. pendula* must have belowground structures that enable both ample resource uptake and rapid transport. The observed root traits of *B. pendula* seem to support this view and indicate its high foraging capacity and belowground competitiveness. Extensive root systems such as those observed in *B. pendula* are proposed to have a higher water and nutrient uptake efficiency (van Noordwijk and de Willigen 1991), and the foraging precision has also been observed to be greater in species with larger root systems (Einsmann et al. 1999, Farley and Fitter 1999). However, Campbell et al. (1991) observed a trade-off between scale and precision in resource foraging in heterogenic soils, i.e. larger plants exploited nutrient patches to a greater extent because they had greater growth rates, whereas as smaller plants allocated more of their new root growth to nutrient-rich areas.

The occurrence of size-asymmetric competition, i.e. where larger organism acquire disproportionately more resources than expected from the size difference between competitors (Schenk 2006), is not clear in belowground competition (Schwinning and Weiner 1998). However, depending on the scale of nutrient heterogeneity, the size and shape of the area of influence may be as important as precision in enabling plants to access nutrient patches. Plants with many short lateral roots may be strong belowground competitors with the nearest neighbors, while more sparse systems with longer lateral root spread may enable plants to search over longer distances and locate pockets where nutrients are abundant or competing roots are absent (Casper et al. 2003). *Betula pendula* had, however, both more roots and a larger influence area than the conifers.

To compete effectively with other plants, efficient transport of soil-derived resources is needed for assimilating or synthesizing tissue. The architecture of a plant, and not only the geometrical dimensions, or absolute root mass and length, determines its competitive potential. Architecture influences factors such as the efficiency with which water and solutes can be conveyed from roots to shoots, and further to leaves (Rundel and Nobel 1991). Topology determines the manner in which the conducting elements are arranged (Fitter 1991).

Determination of the topological characteristics of the coarse roots indicated that in terms of the two extremes, the branching pattern of *P. sylvestris* coarse roots approached the herringbone pattern, while the branching of roots in the other species more closely resembled the dichotomous pattern. The herringbone pattern has been proposed to be superior for resource uptake under nutrient-poor conditions. This is mostly due to the larger number of exterior root segments on low GOs and BGs. These segments extend rapidly out of the depletion zone of their parent segment, thus enabling efficient acquisition of the mobile soil resources (Fitter 1991). Root activity may consume more than half of the available photosynthates in mature plants (Fogel 1985), and evolutionary pressure has therefore most probably favored plants that exploit soil resources with an efficient strategy, i.e. the minimum investment cost for the acquired unit of resource (Lynch 1995). The root topology of *P. sylvestris*, in addition to the larger branching angles than in other species, may thus illustrate its greater adaptation to poor habitats. On the other hand, in terms of potential xylem conductivity (eq. 10), the transport efficiency of *B. pendula* root segments was higher than that of the conifers. Of course, the analysis of potential conductivity does not account for the proportion of functional conduits, and the share of functional xylem out of the whole CSA of a tree that may therefore differ between tree species. The bordered pits in the interface between tracheids also restrict water flow in the conifers, thus further reducing their transport efficiency (Tyree and Ewers 1991, Choat et al. 2008). However, Becker et al. (1999) observed no differences in xylem conductivities between conifers and angiosperms.

There is a trade-off between the hydraulic efficiency of the xylem and safety (cavitation vulnerability, Hacke et al. 2006). The xylem structure of species common in drought-prone habitats may thus be an outcome of the need to favor safety over efficiency. Conifer xylem has been found to exhibit lower levels of embolism and a higher resistance to cavitation than in associated angiosperms (Sperry et al. 1994, Tyree et al. 1998). This may contribute to the distribution patterns of the studied species in natural ecosystems, i.e. *P. sylvestris* with small tracheids on dry sites, *B. pendula* with large vessels in moister, more productive habitats (Shumway et al. 1993, Tissier et al. 2004). However, our observation that *P. abies* had smaller xylem conduits than *P. sylvestris* does not support this view.

In addition to the demands for efficient foraging and transport of soil-borne resources, trees must adapt to mechanical stability demands, implying resistance against wind, water, and gravitational forces (Reubens et al. 2007). The zone of rapid root tapering mostly highlights the area in which mechanical forces have the largest effect on the root system (Eis 1974, Coutts 1987, Danjon et al. 2005). This area was quite limited in all species, reaching a couple of meters in 50-yr-old trees. The extension of the ZRT tended to be the largest in *B. pendula*, probably because of the large crowns, i.e. due to the larger wind load. Small ZRT extensions in *P. sylvestris* indicate the effect of the taproot. The observed abrupt decrease in conduit size in a radial direction for some root segments (Fig. 4 in IV) could also be interpreted as a result of the mechanical forces being transmitted over a greater distance from the stem base as the size of the tree increases, i.e. a ‘non-supporting root’ with large conduits has become a ‘supporting root’ with small conduits (Fayle 1968).

The overall characteristics of the root systems of the conifers, i.e. a small to medium area of influence, small number of root branches, and small SRL values, especially in *P. sylvestris*, gave the impression that their growth strategy was related more to resource conservation than efficient foraging. We did not, however, measure actual physiological activity, e.g. nutrient uptake rate, and species may differ in resource acquisition efficiencies (Göransson et al. 2008). The more conservative growth strategy, lower morphological plasticity, and lower turnover rates in the conifers than in *B. pendula* may also indicate that their fine roots have a higher ability for physiological adaptation of their uptake kinetics (Grime 2002). Thus, our interpretation of species differences in foraging capacities probably is too simple.

We observed vertical stratification of the soil space between the studied species in terms of the coarse roots, but not in terms of the fine roots. The main axis of the excavated coarse roots of *P. abies* exploited the topsoil, in *P. sylvestris* the elluvial, and *B. pendula* primarily occupied the illuvial soil layer, corresponding to earlier observations (Laitakari 1927, 1935), while each species clearly had the highest proportion of fine roots in the humus layer. The vertical rooting pattern again indicates the efficient scavenging of scarce soil resources by *B. pendula*, since it exploited vertically the largest soil volume. It presumably had coarse roots in deeper soil layers for water and fine roots in the topmost layer for nutrients. Some studies have deduced that the high proportion of roots in the uppermost soil layers indicates an advantage in the competitive ability of a species due to good access to nutrient rich soil layers (e.g. Genney et al. 2002). This interpretation suggests a high belowground competitive ability in *P. abies*. However, the topmost layers are also the most drought-prone, and superficial rooting increases susceptibility to wind damage (Schmid and Kazda 2001, Schmid 2002).

The observed differences in the vertical distributions of coarse and fine roots correspond to the observation in *Quercus rubra* that most of the fine roots were attached to the small woody roots returning to the forest floor from the major lateral roots in deeper soil layers, forming "root fans" in the organic soil layer (Lyford 1980). In the mixture of *F. sylvatica* and *Q. petrea*, coarse roots of *Q. petrea* also occurred at moderate to high densities up to a soil depth of 80 cm, while its fine root system was extremely superficial (Leuschner et al. 2001). This type of difference in vertical distribution between coarse and fine roots may indicate that species can reduce competition for water by vertically partitioning the soil space with coarse roots (Casper et al. 2003), but this option may be less available in the competition for nutrients (McKane et al. 2002, Hodge 2004). In our study stands, the nutrient concentrations were much higher in the humus layer than in the deeper layers of the soil profile (Table 2 in I and Table 4 in III). The observed fine root distributions may thus indicate a high level of competition for nutrients, especially nitrogen, in the topsoil of the mixed stands of the studied species. On the other hand, temporal and functional niche separation between species may occur, such as temporal differences in nitrogen uptake activity (Gebauer and Ehleringer 2000), or the uptake of different forms of nutrients (Miller 2007), and this may reduce competitive interactions. Species-specific mycorrhizal associations may play a significant role in the functional niche separation of trees by allowing the uptake of otherwise inaccessible forms of nutrients (van der Hejden and Sanders 2003). Since we examined the characteristics of ECM on the stand level, we could not relate these to a specific tree species.

We did not account for the fine roots of understorey vegetation in our analysis. Earlier studies have demonstrated that removing either tree (Riegel and Miller 1992) or understorey roots (Grime 2002) from the belowground competition increases the biomass of the other competitor. Thus, competition for soil resources may be higher than assumed on the basis of tree fine roots only, especially in the topmost soil layers (e.g. Kochenderfer 1973). However, we sampled fine roots only in the uppermost 30 cm soil layer, and possible secondary proliferation of tree fine roots in deeper soil layers could not therefore be ruled out.

The observation that the conifers, especially *P. abies*, had more fine roots in deeper soil layers than usually observed in monoculture (Helmisaari et al. 2007) gives the impression that *B. pendula* behaves as a ‘soil improver’ by opening up passages for conifer roots to deeper soil layers and increasing the amount of more rapidly decaying deciduous litter. Our observation is consistent with earlier studies showing that the ability to acquire nutrients at depth can vary depending on which species are present, and are therefore affecting the soil characteristics, e.g. in the form of litter input, and competing for resources (Berendse 1981, 1982, D'Antonio and Mahall 1991, Genney et al. 2002, Jumpponen et al. 2002).

We also observed sinker roots in all species. The sinker roots usually extended the vertical influence area of the root systems of the studied species down to the depth of 2–3 m. The sinker roots typically ended at a branching point with multiple short, rapidly tapering child segments (‘root brush’). Under humid conditions, sinker roots may have a more important role in anchoring the tree firmly to the soil (Reubens et al. 2007) than in water acquisition. Under arid conditions or during seasonal drought spells, however, sinker roots may have important role in the acquisition of water from the deep soil layers (Dawson and Pate 1996, Farrington et al. 1996, Danjon et al. 2005), but their role in nutrient dynamics is probably quite limited.

Our results concerning ECM biomass production differed from those of Nilsson et al. (2005), who observed a direct relationship between the mycorrhizal biomass and the stand FRB. The ECM may be a component in nutrient uptake that is not directly proportional, at least in the short term, to the number of roots (Koide et al. 2007), but rather to other factors such as the competitive status of the tree. Such interesting questions as how mycorrhizal colonization affects the root architecture, or whether the studied species differ in terms of the benefit from the mycorrhizal symbiosis, e.g. carbon investment in mycorrhiza per unit of acquired nitrogen, were not within our scope. The influence of ECM species on host tree performance varies, because they differ with respect to the amount and exploration type of the external mycelia (Agerer 2001) and the nutrient retrieval efficiency of the mycelia (Bending and Read 1995). We did not examine the understorey vegetation, but it is well known that grasses, herbaceous plants and shrubs also have mycorrhizal associations (Smith and Read 1997), and may thus have either direct or indirect effects on the ECM biomass production or community structure (Leake et al. 2004). These effects were not accounted for in this study. Our study period may also have been too short (one growing season) to accurately describe variations between sites, since a period longer than a year may be needed to colonize the whole mesh bag (Potila et al. 2009).

We collected the material of this study from five stands and we did not have replicate stands for developmental stages and fertility classes. This naturally restricts the generalization of our results. Another restriction in our study is the lack of monocultures as reference stands for each species. The effect of interspecific competition on the root traits was only possible to determine indirectly.

4.2. Plasticity of root traits

4.2.1 Effect of site fertility

For any given set of soil conditions and plant demands, an optimum distribution of roots in soil exists, and this distribution will be achieved by a particular architectural configuration (Fitter 1991). A specific configuration is reached through the plastic responses of root systems. Roots are able to locate patches of nutrient sources in the soil, proliferate in them and, on the other hand, to grow without branching in zones of low fertility (Nobbe 1862 in Lynch 1995, Hodge 2004). Root morphological responses were not, however, uniform across the studied species, corresponding to observed species specificity in the plastic responses of non-woody plants (Hodge 2004). In *B. pendula*, the peaks in the number of coarse root segments, coarse root length and mass were observed in the least fertile site, i.e. in nutrient-poor conditions a larger soil volume was explored for the gained unit of soil resources. The coarse root characteristics of *P. sylvestris* did not essentially differ according to site fertility and the change in *P. abies* was moderate. The proliferation of coarse root segments in nutrient-rich soil patches was only observed in *B. pendula*. The morphological characteristics of the fine roots, i.e. SRL and RLD, also changed more along the site fertility gradient in *B. pendula* than in the conifers. Both the SRL and the proportion of roots with the highest uptake efficiency, i.e. roots with diameter < 1 mm, peaked in *B. pendula* in the least fertile site.

We interpret the large variation in *B. pendula* root traits in relation to site fertility as an indication of higher root plasticity than that of the conifer roots. These observations are in line with the hypothesis that fast-growing species from fertile habitats show more morphological plasticity (Grime 2002), since the natural habitats of *B. pendula* are more fertile than those of *P. sylvestris*. The difference between *B. pendula* and *P. abies* may be related to their successional status; *B. pendula* is a pioneer species, for which rapid establishment and active resource foraging are important, while a more conservative growth strategy better fits the late-successional *P. abies*. The changes in fine root morphology may indicate that *B. pendula* has a greater potential for effective occupation of nutrient patches created by irregular litter input, minor-scale activities of soil animals and root activities themselves (Eissenstat 1992, Lynch 1995, Eissenstat et al. 2000). On the other hand, in terms of FRB, the plastic response of the conifers to decreasing site fertility was more pronounced than in *B. pendula*. Thus, the increased SRL and RLD of *B. pendula* may not imply the superior competitive ability of this species, but rather the effect of soil resource depletion by the other species (Bauhus et al. 2000). It could be asked whether the species differ in their primary strategy for mineral nutrition in low fertility sites, i.e. the extensive strategy of the conifers (increased FRB) as compared to the intensive strategy of *B. pendula* (adjustment of the morphological characteristics of the fine roots).

Traditionally, a high soil nitrogen content has been thought to reduce ECM growth (Wallenda and Kottke 1998), and more recent studies have shown reductions in the growth of external mycelia in response to elevated nitrogen availability (Nilsson and Wallander 2003, Nilsson et al. 2005, Hendricks et al. 2006). In this study, site fertility did not have an impact on ECM biomass production after the differences between stands in shoot biomass were removed. This result could indicate that within this range of site fertilities, trees are equally dependent on the improved nutrition provided by ECM, thus indirectly supporting the proposal of Lindahl et al. (2002) of a less phytocentric model of nutrient cycling in boreal soils. On the other hand, this result may support the view that the supply of carbon may have large effect on the biological activity of soils, e.g. on ECM mycelium production (Lindahl et al. 2002).

The community structure of mycorrhizal species seemed to differ slightly between the least fertile site and the other sites. The differences could be explained by the observed increase in the C/N ratio and decrease in base saturation as a function of decreasing site fertility (Table 4 in III), since the structure of the ECM community has been observed to correlate with the extractable ammonium concentration and base saturation of the soil (Toljander et al. 2006).

4.2.2 Effect of the stand developmental stage

The effect of the stand developmental stage on the root traits was mostly seen in the increment of both the horizontal and vertical area of influence of root systems in each species. Observed maximum values for *B. pendula* in a 50-yr-old stand correspond quite well with the maximum values presented in the literature, while for the conifers the values were clearly smaller (Stone and Kalisz 1991). Thus, the horizontal root spreads of *B. pendula* would presumably no longer increase as a function of stand age, whereas the horizontal area of influence of the conifers would probably still increase after the first 50 years. This difference between species quite probably reflects the more rapid overall development of *B. pendula*. The mean rooting depth increased along with the stand developmental stage, i.e. older trees generally exploited greater soil volumes than younger trees. However, at the maximum rooting depth determined by sinker roots, no such clear trend was observed. In other studies, much larger rooting depths for *P. abies* and *P. sylvestris* have been reported (Stone and Kalisz 1991) than what we observed. This indicates that the rooting depth of these species is determined more by environmental conditions than species-specific intrinsic properties.

In other coarse root traits, the variation between tree individuals was mostly larger than the difference between developmental stages. Laitakari (1935) observed a larger number of coarse root segments and root length in later stages of development of *B. pendula*, i.e. root systems were denser per unit area. Our results did not demonstrate this kind of effect of stand development on the root architecture of *B. pendula*. Our mature trees were much younger than the oldest trees in the study of Laitakari (50 and 150 years, respectively), which may explain the difference.

Our fine root results are in line with earlier studies in a sense that after canopy closure, FRB has been observed to be quite stable (Vogt et al. 1983, Vanninen et al. 1996, Vanninen and Mäkelä 1999, Helmisaari et al. 2002). This may indicate that the belowground growing space was already closed at the age of 15 years. Higher SRL values in younger stages could be a sign of ongoing branching of fine root systems, since SRL has been found to depend on BG (Pregitzer et al. 2002). As we did not analyze BGs fine roots that could not be confirmed, and the possible difference in fine root longevity between developmental stages cannot be ruled out.

We found that ECM biomass production peaked in the sapling stage of 15-yr-old trees. This result is supported by the observation of the highest ECM biomass production in young stages (10–30 yrs old) in the chronosequence of *P. abies* (Wallander et al. 2010). The interpretation was that a high ECM biomass production coincides with high fine root activity and the rapid overall development of trees before canopy closure. However, although we used ingrowth bags, as did Wallander et al. (2010), the clearest difference between the studies was that we used quartz sand, while they used incubated forest soil. It is interesting that despite the different growing media, similar results were obtained. On the other hand, a bigger problem in both studies may be that ingrowth bags could favor fungal species characterized by fast colonization and growth (Hendricks et al. 2006).

4.3 Modeling of coarse root architecture and tree hydraulic architecture

4.3.1 FracRoot

Fractal geometry has been regarded as a promising approach for providing quantitative summaries and functional insights into tree and root architecture (Lynch 1995, Berntson 1996). In this study, we tested FracRoot and WBE models, the original versions both of which are based on the fractal assumption of self-similar area-preserving branching (Ozier-LaFontaine et al. 1999, West et al. 1999)

Root characteristics such as root length are needed for interpreting root system functions. The original version of FracRoot (Ozier-Lafontaine et al. 1999) produced root systems by repeating self-similar sub-structures, branching events and root segments, with species-specific constant parameters. If similar scale-independent branching rules were applied to the roots of trees, the interesting root characteristics could be derived with an easily measurable variable, such as the diameter of the first root segment (van Noordwijk et al 1994). However, we observed a pattern of variation in the parameter values within roots of the studied species, which illustrates that root systems of the studied tree species are not self-similar fractals, and species-specific parameters could not therefore be used in the simulations (Richardson and zu Dohna 2003, 2005). Most importantly, root axes tapered, constituting the zone of rapid tapering (ZRT) as a response to the need for mechanical stability, and the proximal and distal ends of the roots were thus differentiated (Fig. 4 in I and Fig. 2 in II). Tapering was also observed within single root segments, corresponding to the results of Soethe et al. (2007). Tapering of the root segments and axes has a major effect on the output of the fractal root model, especially in terms of root biomass. The results of our simulations showed that tapering can be accounted for with the relationship between the root segment branching generation and parameter *p* (Fig. 2 in II). In addition, we could not establish a relationship between root diameter and segment length or branching angles, and the number of child segments in a branching event was not uniform within a root (Ozier-LaFontaine et al. 1999), but these parameter values were largely axis-specific. These patterns of variability thus indicate that axis-specific morphogenetic rules may override the micro-scale heterogeneity of the soil (Pagès et al. 2004). On the other hand, our results may indicate that the genetically determined development of tree roots would follow self-similarity quite closely, without environmental constraints. The multifractal description used for model parameters in our study provides at least a partial solution to this problem.

Thus, our results differ from those of earlier studies, in which satisfactory accuracy in the prediction of the root system biomass and length has been obtained with species-specific constant parameters (Ozier-Lafontaine et al. 1999, Smith and Roberts 2003, Salas et al. 2004, Nygren et al. 2009). Notably, the trees were much younger and also smaller in the above-cited studies than in ours. The functional adaptation of root traits, for instance to mechanical constraints, may change with tree size, which may partly explain why the earlier studies observed less variability in parameters within roots. On the other hand, those studies did not account for the tapering of root segments or root axes, which, if present, may at least partly mask the variability in parameter values.

Regarding the differences between species, it seems that the root system structure of *B. pendula* and *P. abies* resembles more the structure obtained by repeating self-similar substructures than the root system of *P. sylvestris*. This was indicated by the better estimates for *B. pendula* and *P. abies* than for *P. sylvestris*. The accuracy of the applied fractal branching model was moderate; the R^2 values ranged between 0.44–0.64 for the estimation of the root length and between 0.73–0.85 for root mass (Table 8 in II). However, Table 4 shows that, apart from the estimates of root length in *P. sylvestris* and rooting depth in all species, the predictions of the model were acceptable in terms of the mean values for several simulated roots. The root mass estimates were more accurate in all species than root length estimates. Less accurate length estimations may be partly accounted for the fact that the first segment of root measured in the field forms a considerable proportion of the total root biomass, while its effect on the total root length is largely negligible, as Nygren et al. (2009) have pointed out.

The plasticity in root growth makes the modeling of a root system's spatial dimension a challenging task. The maximum lateral root spread was quite accurate in *P. abies* and moderate in *B. pendula*, while in *P. sylvestris* the predictions did not correspond to the observations. The maximum rooting depth was generally poorly predicted in all species. One reason for the poor simulation estimates of spatial dimensions of *P. sylvestris* may be observed several-meters-long root axes without any side branches with a diameter > 2 mm (Fig. 7b). Another important aspect is the available soil growing space and the effect of soil horizons. The quantity of stones and other obstacles affects the available soil space and thus restricts and randomizes the directions in which roots can grow from a branching event. This may partly explain the poor predictions of maximum rooting depth. Another explanation could be the independent generation of vertical and horizontal branching angles from their distributions. In reality, the branching angles may be dependent on the depth at which branching takes place due to the vertical soil horizons of podzolic soils. However, we could not relate the angle distribution classes and soil horizons based on field measurements. The incorporation of specific parameter values for the shallow and sinker root types could also improve the rooting depth estimates.

4.3.2. WBE model

When theoretical scaling models, the WBE model and Murray's law, were fitted to our data, it appeared that these models did not provide practical tools to investigate the scaling of the xylem anatomical traits in a tree species. However, they are valuable for summarizing general concepts on the hydraulic architecture of trees.

The values of the scaling parameter in the WBE model were higher on the whole-tree level than the proposed figure of 1/6, and the smallest conduit diameters were found in leaf petioles of *B. pendula*, thus supporting some of the central predictions of the WBE model. However, we found that although the conduits were the largest in the roots and tapered to the stem and thereon to the branches, as proposed (West et al. 1999), the assumptions of a constant conductivity ratio, constant tapering, and an unchanged total number of conduits were not fulfilled. Variation in the within-tree tapering pattern with distance from the tree apex was also observed by Mencuccini et al. (2007). The observed deviations from the proposed theoretical scaling could partly be explained by architectural differences in the studied trees compared to the theoretical architecture of the WBE model (McCulloh and Sperry 2005). The main differences are that in the studied species the leaves are not situated at terminal units but can be encountered in almost any BG, xylem anatomy depends on GO, and the branching of the segments is closer to the proportionate allotomous branching pattern, i.e. the CSA of a parent segment is divided unequally between child segments (van Noodwijk et al. 1994), than the dichotomous one used in the WBE model. The dependence of scaling and the tree's carbon balance, i.e. photosynthetic gain versus conduit wall construction costs, was also proposed as a possible explanation for the observations on different scaling from that proposed by the WBE model (Mencuccini et al. 2007). However, our interpretation is that the WBE model does not properly take into account the hierarchical organization of the different organs within a tree.

The conductivity predicted by Murray's law was too low in roots at a given conduit tapering rate, whereas in shoot observations it corresponded with the predictions quite well. This result was against our hypothesis, since stem conduits are under larger mechanical constraints than root conduits and should therefore deviate more from Murray's optimum. In our dataset, the conduits of distal roots are the closest to the "free of mechanical constraints"-assumption, although even they are not fully free of mechanical demands, since their walls have to be thick enough to resist implosion. Due to the small number of root observations used in the analysis of Murray's law, definitive conclusions on the observed within-tree pattern and the applicability of Murray's law for predictive use could not be made.

The overall problem with both models is that they do not take into account the fact that trees cannot freely maximize their water transport, but a tree's hydraulic architecture is rather a result of the interplay between efficient water transport, embolism, and mechanical stability. The observed steeper scaling in *B. pendula* than in the conifers may be a result of the possibility for freer optimization of the conduit diameter for the water transport demand, since it has fibers providing mechanical strength to the wood. On the other hand, in the conifers, the torus-margo structure in the bordered pits is a direct adaptation to prevent embolism, but it essentially halves the efficiency of water transport (Choat et al. 2008). *Betula pendula* does not have this type of structure, and the observed steeper scaling than in the conifers could therefore be presumed due to the larger need for the avoidance of cavitation. Embolism may also have a positive role in the functional water storage of a tree (Tyree and Zimmermann 2002). The intriguing proposal of McCulloh and Sperry (2005) that biomechanics have an effect on anatomical scaling only receives indirect support from our results, since our analyses do not provide a possibility for establishing direct causal relationships between scaling and biomechanics. The absolute size of conduits is known to reduce due to the effect of mechanical constraint (e.g. Kern et al. 2005).

We excluded fine roots and leaves from our analysis. Their function is more to act as resource-exchange surfaces than participate in the long-distance transport of water and solutes. Thus, different scaling of conduits could be presumed in them than in the water-conducting pathway analyzed in this study. However, this is a simplified view, since e.g. term 'fine roots' includes a functionally and morphologically heterogeneous group of organs loosely tied together with the diameter definition (Eissenstat et al. 2000, Pregitzer 2002, Guo et al. 2008).

5 CONCLUSIONS AND FUTURE PROSPECTS

This study demonstrated that the root system architecture and belowground responses to the developmental stage of a stand and site fertility may differ considerably between the studied boreal tree species, *B. pendula*, *P. abies*, and *P. sylvestris*. Many structural features have more than a single function, and many functions depend on several factors. Simple root:shoot ratios, or the idea of functional balance between root and foliage mass, are not enough to properly describe the differences between species in the plasticity of root growth, and thus the belowground competition between these species. With a similar allocation to the belowground structures, multiple root architectures could be created, leading to the large differences between species in resource acquisition efficiency. Hence, more studies on the structural and functional characteristics of roots and root systems of these species are needed in order to better understand their belowground interactions in mixed boreal forests.

We did not study actual physiological functions in the roots, such as water and nutrient uptake. The observed spatial and structural differences between the species in root traits may reflect the belowground competitive potential of these species. However, species may differ greatly, for instance, in resource use efficiency, how much carbon is invested belowground in order to gain a unit of nitrogen, or in their competitive responsiveness. Within coexisting plant communities, competition strategies of trees may vary from avoidance to tolerance, or even to confrontation (Novoplansky 2009). Therefore, studies measuring the real belowground functionality are needed. Moreover, the physiological basis of the root architecture should be firmly established in order to understand how individual traits of root axes are integrated into overall root system architecture, or how root architectural characteristics respond to environmental conditions. From the functional viewpoint, especially the linkage of fine and coarse roots should be better established; we still do not understand why a root branch starts to grow from a fine to a coarse root. In our study, the problem of classifying the roots on the basis of diameter was already encountered during the field work, since roots with diameter equaling 2 mm were mostly woody coarse roots. Morphological variation within each ‘fine root’ class was also considerable. A study illuminating the mechanism of this specific question should be performed under controlled laboratory conditions.

The role of ECM in nutrient uptake is widely acknowledged. However, our results demonstrate that the relationship between trees and ECM is still poorly understood. According to traditional thinking, the importance of ECM to tree nutrition diminishes with increasing site fertility. However, in our study we observed no difference in ECM biomass production in relation to site fertility; moreover, it was not directly related to the stand total FRB. Both this and results concerning the relationship between aboveground and fine-root characteristics indicate the need for methodological development in order to be able to study these issues on the single tree level under field conditions.

Better accounting for the structure and functions of the roots, and belowground competition between trees is needed to take a step forward in the modeling of plant development and ecosystem functioning. The results of this thesis provide tools for improving the existing single-tree and stand-level models. Our results demonstrate that parameters in the fractal branching model could be used as indicators of differences in rooting behavior and, therefore, of differences in ecophysiological adaptations between species. With the fractal branching approach, the essential elements of root systems of the studied species could be partly described as a static ‘snapshot’. However, to incorporate the real dynamics of root growth into a model, several questions should be addressed: how much roots grow during a time step, how branching is regulated (uniform growth media vs. heterogeneous natural soils), within-root system regulation (root branches are not autonomous, but how are their characteristics controlled?), or how interspecific competition affects the model parameters. More studies investigating the whole continuum from mycorrhiza to roots and to branches and leaf petioles simultaneously in same stands are also needed to shed light on complex interactions between different organs. From viewpoint of modeling, this information is especially needed if models describing both the function and structure of trees are to be further developed.

REFERENCES

Aerts, R. 2002. The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: Van der Heijden, M.G.A. & Sanders, I. (eds.). Mycorrhizal Ecology, Ecological studies, vol.157. Springer-Verlag, pp.117–134.

Agerer, R. 2001. Exploration types of ectomycorrhizae. A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. Mycorrhiza 11: 107–114.

Anfodillo, T., Carraro, V., Carrer, M., Fior, C., & Rossi, S. 2006. Convergent tapering of xylem conduits in different woody species. New Phytologist 169: 279–290.

Arnebrant, K. 1994. Nitrogen amendments reduce the growth of extramatrical ectomycorrhizal mycelium. Mycorrhiza 5:7–15.

Arthur, W. 1987. The niche in competition and evolution. John Wiley & Sons, Chichester. 175 p.

Assmann, E. 1970. The principles of forest yield study. Pergamon Press Ltd., Oxford. 506 p.

Atala, C. & Lusk, C.H. 2008. Xylem anatomy of *Betula pendula* Roth saplings: Relationship to physical vascular models. Gayana Botanica 65: 18–27.

Barthélémy, D. & Caraglio, Y. 2007. Plant architecture: A dynamic, multilevel, and comprehensive approach to plant form, structure and ontogeny. Annals of Botany 99: 375–407.

Bauhus, J. & Messier, C. 1999. Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. Canadian Journal of Forest Research 29: 260–273.

—, Khanna, P.K. & Menden, N. 2000. Aboveground and belowground interactions in mixed plantations of Eucalyptus globulus and Acacia mearnsii. Canadian Journal of Forest Research 30: 1886–1894.

Becker, P., Tyree, M.T. & Tsuda, M. 1999. Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. Tree Physiology 19: 445–452.

Bending, G.D. & Read, D.J. 1995. The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. Foraging behaviour and translocation of nutrients from exploited litter. New Phytologist 130: 401–409.

Berendse, F. 1981. Competition between plant populations with different rooting depths II. Pot experiments. Oecologia 48: 334–341.

— 1982. Competition between plant populations with different rooting depths III. Field experiments. Oecologia 53: 50–55.

Berntson, G.M. 1996. Fractal geometry, scaling, and the description of plant root architecture. In: Waisel, Y., Eshel, A., Kafkafi, U. (eds.). Plant roots—the hidden half, 2nd edn. MDI Dekker, New York, pp. 259–272.

Biondini, M. 2001. A three-dimensional spatial model for plant competition in an heterogeneous soil environment. Ecological Modelling. 142: 189–225.

Blaise, F., Fourcaud, T., Stokes, A. & De Reffye, P. 1999. A model simulating interactions between plant shoot and root architecture in a non-homogeneous environment. In: Stokes, A. (ed.). The supporting roots of trees and woody plants: form, function and physiology. Series: 'Developments in Plant and Soil Sciences', Vol. 87. Dordrecht: Kluwer Academic Publishers. pp 195–207.

Bolte, A. & Villanueva, I. 2006. Interspecific competition impacts on the morphology and distribution of fine roots in European beech (Fagus Sylvatica L.) and Norway spruce (Picea abies (L.) Karst.). European Journal of Forest Research 125: 15–26.

Bonet, J.A., Fisher, C.R. & Colinas C. 2004. The relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi in Pinus sylvestris forests of the central Pyrenees. Forest Ecology and Management 203: 157–175.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13: 115–155.

Brandtberg, P.O., Lundkvist, H. & Bengtsson, J. 2000. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. Forest Ecology and Management 130:253–264

Cajander, A.K. 1949. Forest types and their significance. Acta Forest Fennica 56: 1–71.

Caldwell, M.M. & Pearcy, R.W (eds.). 1994. Exploitation of environmental heterogeneity by plants - Ecophysiological processes - Above- and belowground. Academic Press, lnc, San Diego, California, 429 p.

Campbell, B.D., Grime, J.P. & Mackey, J.M.L. 1991. A trade-off between scale and precision in resource foraging. Oecologia 87: 532–538.

Cannon, W.A.1949. A tentative classification of root systems. Ecology 30: 542–548.

Cannon, H.L. 1960. The development of botanical methods of prospecting for uranium on the Colorado Plateau. US Geological Survey Bulletin 1085-A. pp. 1–50.

Casper, B.B., Schenk, H.J. & Jackson, R.B. 2003. Defining a plant's belowground zone of influence. Ecology 84: 2313–2321.

Čermák, J., Ulrich, R., Staněk, Z., Koller, J. & Aubrecht, L. 2006. Electrical measurement of tree root absorbing surfaces by the earth impedance method: 2. Verification based on allometric relationships and root severing experiments. Tree Physiology 26: 1113–1121.

Chisilov, G. & Demidova, N. 1998. Non-wood forest products and their research in Arkhangelsk, Russia. In: Lund, G., Pajari, B. & Korhonen, M. (eds.). European Forestry Institute Proceedings 23: 147–153.

Choat, B., Cobb, A. & Jansen, S. 2008. Structure and function of bordered pits: New discoveries and impacts on whole plant hydraulic function. New Phytologist 177:608–626.

Claus, A. & George, E. 2005. Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Canadian Journal of Forest Research 35:1617–1625.

Clausnitzer, V. & Hopmans, J.W. 1994. Simultaneous modeling of transient three-dimensional root growth and soil water flow. Plant and Soil 164: 299–314.

Cody, M.L. 1986. Structural niches in plant communities. In: Diamond, J. & Case, T.J. (eds.). Community Ecology, Harper & Row Publishers, New York, pp. 381–405.

Collet, C., Löf, M. & Pagès, L. 2006. Root system development of oak seedlings analysed using and architectural model. Effects of competition with grass. Plant Soil 279: 367–383.

Comenford, N.B., Semthurst, P.J. & Escamilla, J.A. 1994. Nutrient uptake by woody root systems. New Zealand Journal of Forest Science 24: 195–212.

Coomes, D.A. & Allen, R.B. 2009. Testing the Metabolic Scaling Theory of tree growth. Journal of Ecology 97: 1369–1373.

— & Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecological Monographs 70: 171–207.

Cortina, J., Green, J.J., Baddeley, J.A. & Watson, C.A. 2008. Root morphology and water transport of *Pistacia lentiscus* seedlings under contrasting water supply: A test of the pipe stem theory. Environmental and Experimental Botany 62: 343–350.

Coutts, M.P. 1986. Components of tree stability in Sitka spruce on peaty gley soil. Forestry 59: 173–197.

— 1987. Developmental processes in tree root systems. Canadian Journal of Forest Research 17: 761–767.

Curt, T. & Prévosto, B. 2003. Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. Plant and Soil 255: 265–279.

Danjon, F. & Reubens, B. 2008. Assessing and analyzing 3D architecture of woody root systems, a review of methods and applications in tree and soil stability, resource acquisition and allocation. Plant and Soil 303: 1–34.

—, Fourcaud, T. & Bert, D. 2005. Root architecture and wind-firmness of mature *Pinus pinaster*. New Phytologist 168: 387–400.

D'Antonio, C.M. & Mahall, B.E. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. American Journal of Botany 78: 885–894.

Darrah, P.R., Jones, D.L., Kirk, G.J.D. & Roose, T. 2006. Modelling the rhizosphere: a review of methods for 'upscaling' to the whole-plant scale. European Journal of Soil Science 57: 13–25.

Dawson, T.E. & Pate, J.S. 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: A stable isotope investigation. Oecologia 107: 13–20.

de Kroon, H., Visser, E.J.W., Huber, H., Mommer, L. & Hutchings, M.J. 2009. A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. Plant, Cell and Environment 32: 704–712.

Deo, N. 1974. Graph theory with applications to engineering and computer science. Prentice-Hall, Englewood Cliffs NJ. 478 p.

Dixon, H.H. & Joly, J. 1894. On the ascent of sap. Philosophical Transactions of the Royal Society London, Series B 86, pp. 563–576.

Drew, M.C. 1975. Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytologist 75: 479–490.

— & Saker, L.R. 1978. Nutrient supply and the growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake in response to a localised supply of phosphate. Journal of Experimental Botany 29: 435–451.

— & Saker, L.R. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. Journal of Experimental Botany 26: 79–90.

—, Saker, L.R. & Ashley, T.W. 1973. Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. Journal of Experimental Botany 24: 1189–1202.

Drouet, J.-L. & Pagès, L. 2007. GRAAL-CN: A model of GRowth, Architecture and ALlocation for Carbon and Nitrogen dynamics within whole plants formalised at the organ level. Ecological Modelling 206: 231–249.

Dupuy, L., Fourcaud, T. & Stokes, A. 2005. A numerical investigation into the influence of soil type and root architecture on tree anchorage. Plant Soil 278: 119–134.

Einsmann, J.C., Jones, R.H., Pu, M. & Mitchell, R.J. 1999. Nutrient foraging traits in 10 co-occurring plant species of contrasting life forms. Journal of Ecology 87: 609–619.

Eis, S. 1974. Root system morphology of western hemlock, western red cedar, and douglas-fir. Canadian Journal of Forest Research 4: 28–38.

Eissenstat, D.M. 1992. Costs and benefits of constructing roots of small diameter. Journal of Plant Nutrition 15: 763–782.

— & Yanai, R.D. 1997. The ecology of root life span. Advances in Ecological Research 27: 1–62.

—, Wells, C.E., Yanai, R.D. & Whitbeck, J.L. 2000. Building roots in a changing environment: implications for root longevity. New Phytologist 147: 33–42.

Enquist, B.J. 2002. Universal scaling in tree and vascular plant allometry: Toward a general quantitative theory linking plant form and function from cells to ecosystems. Tree Physiology 22: 1045–1064.

— 2003. Cope's rule and the evolution of long-distance transport in vascular plants: allometric scaling, biomass partitioning and optimization. Plant, Cell and Environment 26: 151–161.

— & Niklas, K.J. 2001. Invariant scaling relations across tree-dominated communities. Nature 410: 655–660.

—, West, G.B., Charnov, E.L. & Brown, J.H. 1999. Allometric scaling of production and life-history variation in vascular plants. Nature 401: 907–911.

Fan, Z.X., Cao, K.F. & Becker, P. 2009. Axial and radial variations in xylem anatomy of angiosperm and conifer trees in Yunnan, China. Iawa Journal 30: 1–13

Farley, R.A. & Fitter, A.H. 1999. The responses of seven co-occurring woodland herbaceous perennials to localized nutrient-rich patches. Journal of Ecology 87: 849–859.

Farrington, T., Turner, J.V. & Gailitis, V. 1996. Tracing water uptake by jarrah (*Eucalyptus marginata*) trees using natural abundances of deuterium. Trees 11: 9–15.

Fayle, D.C.F. 1968. Radial growth in tree roots; distribution, timing, anatomy. Technical report no. 9. Faculty of Forestry, University of Toronto, Canada, 183 p.

— 1975. Distribution of radial growth during the development of Red pine root systems. Canadian Journal of Forest Research 5: 608–625.

Finér, L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208: 1–63.

—, Messier, C. & De Grandpré, L. 1997. Fine-root dynamics in mixed boreal conifer-broad-leafed forest stands at different successional stages after fire. Canadian Journal of Forest Research 27: 304–314.

Finnish Statistical Yearbook of Forestry. 2009. Finnish Forest Research Institute. 452 p.

Fitter, A.H. 1976. Effects of nutrient supply and competition from other species on root growth of Lolium perenne in soil. Plant and Soil 45: 177–189.

— 1987. An architectural approach to the comparative ecology of plant root systems. New Phytologist 106(suppl.): 61–77.

— 1991. The ecological significance of root system architecture: an economic approach. In: Atkinson, D. (ed.). Plant root growth. An ecological perspective. Blackwell Scientific Publications, Oxford. p. 229–243.

— 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell, M.M. & Pearcy, R.W (eds.). Exploitation of environmental heterogeneity by plants - Ecophysiological processes - Above- and belowground. p. 305–323.

— 1996. Characteristics and functions of root systems. In: Waisel, Y., Eshel, A. & Kafkafi, U. (eds.). Plant roots. The hidden half. Marcel Dekker, lnc., New York. p. 1–20.

— & Stickland, T.R. 1991, Architectural analysis of plant-root systems. 2. Influence of nutrient supply on architecture in contrasting plant-species. New Phytologist 118: 383–389.

— & Stickland, T.R. 1992. Architectural analysis of plant root systems 3. Studies on plants under field conditions. New Phytologist 121: 243–248.

—, Stickland, T.R., Harvey, M.L. & Wilson, G.W. 1991. Architectural analysis of plant-root systems. 1. Architectural correlates of exploitation efficiency. New Phytologist 118: 375–382.

Fogel, R. 1983. Root turnover and productivity of coniferous forest. Plant Soil 71: 75–85.

— 1985. Root as primary producers in below ground ecosystems. In: Fitter, A.H., Atkinson, D., Read, D.J., Usher, M.B. (eds.). Ecological interactions in soil. Blackwell, Oxford London, pp. 23–26.

Fourcaud, T., Zhang, X., Stokes, A., Lambers, H., & Körner, C. 2008. Plant growth modelling and applications: The increasing importance of plant architecture in growth models. Annals of Botany 101: 1053–1063.

Gause, G.F. 1934. The struggle for existence. [Online book]. Available at: http://www.ggause.com/Contgau.htm.

Gebauer, R.L.E. & Ehleringer, J.R. 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81: 1415–1424.

Genney, D.R., Alexander, I.J. & Hartley, S.E. 2002. Soil organic matter distribution and below-ground competition between *Calluna vulgaris* and *Nardus stricta*. Functional Ecology 16: 664–670.

George, E., Seith, B., Schaeffer, C. & Marschner, H. 1997. Responses of *Picea*, *Pinus*, and *Pseudotsuga* roots to heterogeneous nutrient distribution in soil. Tree Physiology 17:39–45.

Givnish, T.J. 1988. Adaptation to sun vs. shade: A whole-plant perspective, Australian. Journal of Plant Physiology 15: 63–92.

Godin, C., Costes, E. & Sinoquet, H. 1999. A method for describing plant architecture which integrates topology and geometry. Annals of Botany 84: 343–357.

Göransson, H., Ingerslev, M. & Wallender, H. 2008. The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature *Quercus robur*, *Fagus sylvatica* and *Picea abies* stands. Plant and Soil 306: 129–137.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. & Stow, T.K. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Research 102: 29029–29041.

Greenhill, A.G. 1881. Determination of the greatest height consistent with stability that a vertical pole or mast can be made, andof the greatest height to which a tree of given proportions can grow. Proceedings of the Cambridge Philological Society 4: 65–73.

Grime, J.P. 2002. Plant strategies, vegetation processes, and ecosystem properties. 2. ed. John Wiley & Sons, Ltd, Chichester, 417 p.

—, Campbell, B.D., Mackey, J.M.L. & Crick, J.C. 1991. Root plasticity, nitrogen capture and competitive ability. In: Atkinson, D. (ed.). Plant root growth. An ecological perspective. Blackwell Scientific Publications, Oxford. p. 381–397.

Gross, K.L., Pregitzer, K.S. & Burton, A.J. 1995. Spatial variation in nitrogen availability in three successional plant communities. Journal of Ecology 83: 357–367.

Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y. & Wang, Z. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. New Phytologist 180: 673–683.

Hacke, U.G., Sperry, J.S., Wheeler, J.K. & Castro, L. 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiology 26: 689–701.

Hallé, F. & Oldeman, R.A.A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Masson, Paris, 178 p.

—, F., Oldeman, R.A.A. & Tomlinson, P.B. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin, 441 p.

Hari, P., Nikinmaa, E. & Holmberg, M. 1990. Photosynthesis, transpiration and nutrient uptake in relation to tree structure. In: Dixon, R.K., Meldahl, R.S., Greogory R.A. & Warren, W.G. (eds.). Process Modelling of Forest Growth Responses to Environmental Stress. Timber Press, Portland, Oregon, Ch. 4, pp. 50–57.

Harper, J.L., Jones, M. & Sackville-Hamilton, N.R. 1991. The evolution of roots and the problems of analysing their behaviour. In: Atkinson, D. (ed.). Plant root growth. An ecological perspective. Blackwell Scientific Publications, Oxford. p. 3–22.

Hauggaard-Nielsen, H. & Jensen, E.S. 2005. Facilitative root interactions in intercrops. Plant and Soil 274: 237–250.

Heikinheimo, O. 1920. Kuusen iän määräämisestä ja kuusen myöhäisjuurista. Communicationes Instituti Forestalis Fenniae 2: 1–29.

Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E. & Mälkönen E. 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. Forest Ecology and Management 165: 317–326.

—, Derome, J., Nöjd, P. & Kukkola, M. 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiology 27: 1493–1504.

Hendricks, J.J., Mitchell, R.J., Kuehn, K.A., Pecot, S.D. & Sims, S.E. 2006. Measuring external mycelia production of ectomycorrhizal fungi in the field: the soil matrix matters. New Phytologist 171: 179–186.

Hintikka, V. 1988. On the macromycete flora on oligotrophic pine forest of different ages in South Finland. Acta Botanica Fennica 136: 95–98.

Ho, M.D., McCannon, B.C. & Lynch, J.P. 2004. Optimization modeling of plant root architecture for water and phosphorus acquisition. Journal of Theoretical Biology 226: 331–340.

Hodge, A. 2004. The plastic plant: root responses to heterogenous supplies of nutrients. New Phytologist 162: 9–24.

— 2009. Root decisions. Plant, Cell and Environment 32: 628–60.

—, Robinson, D., Griffiths, B.S. & Fitter, A.H. 1999. Nitrogen capture by plants grown in N-rich organic patches of contrasting size and strength. Journal of Experimental Botany 50: 1243–1252.

—, Robinson, D. & Fitter, A.H. 2000. An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from, nutrient-rich patches in soil. New Phytologist 145: 575–584.

—, Berta, G., Doussan, C., Merchan, F. & Crespi, M. 2009. Plant root growth, architecture and function. Plant and Soil 321: 153–187.

Högberg, M.N. & Read, D.J. 2006. Towards a more plant physiological perspective on soil ecology. TRENDS in Ecology and Evolution 21: 548–554.

—, Bååth, E., Nordgren, A., Arnebrant, K. & Högberg, P. 2003. Contrasting effects of nitrogen availability on plant carbon supply to mycorrhizal fungi and saprotrophs - a hypothesis based on field observations in boreal forest. New Phytologist 160: 225–238.

Hutchings, M.J. & John, E.A. 2004. The effects of environmental heterogeneity on root growth and root/shoot partitioning. Annals of Botany 94: 1–8.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22: 415–427.

Jackson, R.B. & Caldwell, M.M. 1991. Kinetic responses of Pseudoroegneria roots to localized soil enrichment. Plant and Soil 138: 231–238.

— & Caldwell, M. M. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. Journal of Ecology. 81: 683–692.

—, Manwaring, J.H. & Caldwell, M.M. 1990. Rapid physiological adjustment of roots to localized soil enrichment. Nature 344: 58–60.

—, Mooney, H.A. & Schulze, E.-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of National Academy of Sciences, USA 94: 7362–7366.

Jarvis, P. & Linder, S. 2000. Constraints to growth of boreal forests. Nature 405: 904–905.

Johnsen, K., Maier, C. & Kress, L. 2005. Quantifying root lateral distribution and turnover using pine trees with a distinct stable carbon isotope signature. Functional Ecology 19: 81–87.

Jourdan, C. & Rey, H. 1997. Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system 1. The model. Plant Soil 190: 217–233

Jumpponen, A., Högberg, P., Huss-Danell, K. & Mulder, C.P.H. 2002. Interspecific and spatial differences in nitrogen uptake in monocultures and two-species mixtures in north European grasslands. Functional Ecology 16: 454–461.

Kalela, E.K.1937. Tutkimuksia kuusi-harmaaleppä-sekametsi-köiden kehityksestä. Acta Forestalia Fennica 44: 1–179.

— 1946. Metsät ja metsien hoito. Werner Söderström Oy. 367 p.

— 1950. Männiköiden ja kuusikoiden juurisuhteista. Summary: On the horizontal roots in pine and spruce stand. Acta Forestalia Fennica 57: 69–79.

— 1954. Mäntysiemenpuiden ja -puustojen juurisuhteista. Suppl. Acta Forestalia Fennica 61. 16 p.

Kajimoto, T., Osawa, A., Matsuura, Y., Abaimov, A.P., Zyryanova, O.A., Kondo, K., Tokuchi, N., Hirobe, M. 2007. Individual-based measurement and analysis of root system development: case studies for Larix gmelinii trees growing on the permafrost region in Siberia. Journal of Forest Research 12: 103–112.

Kellomäki, S. 1991. Metsäekologia. Silva Carelica 7. 391 p.

— & Strandman, H. 1995. A model for the structural growth of young Scots pine crowns based on light interception by shoots. Ecological Modelling 80: 237–250.

Kelty, M.J. 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233: 195–204.

Kern, K.A., Ewers, F.W., Telewski, F.W. & Koehler, L. 2005. Mechanical perturbation affects conductivity, mechanical properties and aboveground biomass of hybrid poplars. Tree Physiology 25: 1243–1251.

Keyes, M.R. & Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research 11: 599–605.

King, J.S., Giardina, C.P., Pregitzer, K.S. & Friend, A.L. 2007. Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. Canadian Journal of Forest Research 37: 93–102.

Kochenderfer, J.N. 1973. Root distribution under some forest types native to west Virginia. Ecology 54: 445–448.

Koide, R.T., Shumway, D.L., Xu, B. & Sharda, J.N. 2007. On temporal partitioning of a community of ectomycorrhizal fungi. New Phytologist 174: 420–429

Kõljalg, U., Larsson, K.-L., Abarenkov, K., Nilsson, R.H., Alexander, I.J., Eberhardt, U., Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A.F.S., Tedersoo, L., Vrålstad, T. & Ursing, B.M. 2005. UNITE: a database providing web-based methods for the molecular identification of ectomycorrhizal fungi. New Phytologist 166: 1063–1068.

Korkama, T., Pakkanen, A. & Pennanen, T. 2006. Ectomycorrhizal community structure varies among Norway spruce (*Picea abies*) clones. New Phytologist 171: 815–824.

Kozlowski, T.T. & Pallardy, S.G. 1997. Physiology of woody plants. Academic press, San Diego, 411 p.

Kozlowski, J. & Konarzewski, M. 2004. Is West, Brown, and Enquist's model of allometric scaling mathematically correct and biologically relevant? Functional Ecology 18: 283–289.

Kramer, P.J. 1946. Absorption of water through suberized roots of trees. Plant Physiology 21: 37–41.

—, Bullock, H.C. 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. American Journal of Botany 53: 200–204.

Kuusela, K. 1990. The dynamics of boreal coniferous forests. SITRA, Helsinki, 168 pp.

Laiho, R. & Finér, L. 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland. Scandinavian Journal of Forest Research 11: 251–260.

Laitakari, E. 1927. Männyn juuristo. Morfologinen tutkimus. Summary: The root system of pine (*Pinus sylvestris*). A morphological investigation. Acta Forestalia Fennica 33. 379p.

— 1935. Koivun juuristo. Summary: The root system of birch (*Betula verrucosa* and *odorata*). Acta Forestalia Fennica 41. 168 p.

Leake, J.R. 2004. Myco-heterotroph/epiparasitic plant interactions with ectomycorrhizal and arbuscular mycorrhizal fungi. Current Opinion in Plant Biology 7: 422–428.

Lehtonen, A., Mäkipää, R., Heikkinen, J., Sievänen, R. & Liski, J. 2004. Biomass expansion factors (BEF) for Scots pine, Norway spruce and birch according to stand age for boreal forests. Forest Ecology and Management 188: 211–224.

Leuschner, C., Hertel, D., Coners, H. & Büttner, V. 2001. Root competition between beech and oak: a hypothesis. Oecologia 126: 276–284.

Lindahl, B.O., Taylor, A.F.S. & Finlay, R.D. 2002. Defining nutritional constraints on carbon cycling in boreal forests - towards a less 'phytocentric' perspective. Plant and Soil 242: 123–135.

Lindenmair, J., Matzner, E. & Zimmermann, R. 2004. The role of woody roots in water uptake of mature spruce, beech, and oak trees. In:Matzner, E. (ed.). Biogeochemistry of forested catchments in a changing environment; a German case study. Ecological Studies 172, Springer, Berlin, 498 p.

Lõhmus, K., Oja, T. & Lasn, R. 1989. Specific root area: a soil characteristic. Plant Soil 119: 245–249.

Lyford, W.H. 1980. Development of the root system of northern red oak (*Quercus rubra* L.). Harvard Forest Paper 21. 31 p.

Lynch, J. 1995. Root architecture and plant productivity. Plant Physiology 109: 7–13.

Mäkelä, A. 1985. Differential games in evolutionary theory: Evolutionary stable height growth strategies of trees. Theoretical Population Biology 27: 239–267.

—, Valentine, H.T. 2006. The quarter-power scaling model does not imply size-invariant hydraulic resistance in plants. Journal of Theoretical Biology 243: 283–285.

—, Valentine, H.T. & Helmisaari, H.-S. 2008. Optimal co-allocation of carbon and nitrogen in a forest stand at steady state. New Phytologist 180: 114–123.

Makkonen, K. & Helmisaari, H.-S. 1998. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. Forest Ecology and Management 102: 283–290.

Mandelbrot, B.B. 1983. The fractal geometry of nature. W.H.Freeman, New York, 468 p.

Marklund, L.G. 1988. Biomassafunktioner för tall, gran och björk i Sverige. Summary: biomass functions for pine, spruce and birch in Sweden. Sveriges lantbruksuniversitetet, institutionen för skogstaxering, Rapport 45. Umeå. 73 p.

Marks, C.O. & Lechowicz, M.J. 2006. A holistic tree seedling model for the investigation of functional trait diversity. Ecological Modelling 193: 141–181.

McCulloh, K., Sperry, J.S. & Adler, F.R. 2003. Water transport in plants obeys Murray's law. Nature 42: 939–942.

— & Sperry, J. 2005. Patterns of hydraulic architecture and their implications for transport efficiency. Tree Physiology 25: 257–267.

—, Sperry, J.S. & Adler, F.R. 2004. Murray's law and the hydraulic *vs* mechanical functioning of wood. Functional Ecology 18: 931–938.

McElrone, A.J., Pockman, W.T., Martínez-Vilalta, J. & Jackson, R.B. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. New Phytologist 163: 507–517.

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kiellandk, K., Kwiatkowski, B.L., Laundre, J.A. & Murray, G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature: 68–71.

McMahon, T.A. 1973. Size and shape in biology. Science 179: 1201–1204.

Meinzer, F.C., Bond, B.J., Warren, J.M. & Woodruff, D.R. Does water transport scale universally with tree size? Functional Ecology 19: 558–565.

Mencuccini, M., Hölttä, T., Petit, G. & Magnani, F. 2007. Sanio's laws revisited. Size-dependent changes in the xylem architecture of trees. Ecology Letters 10: 1084–1093.

Miller, A.E., Bowman, W.D. & Suding, K.N. 2007. Plant uptake of inorganic and organic nitrogen: neighbor identity matters. Ecology 88: 1832–1840.

Mokma, D.L., Yli-Halla, M. & Lindqvist, K. 2004. Podzol formation in sandy soils of Finland. Geoderma 120: 259–272.

Murray, C.D. 1926. The physiological principle of minimum work. I. The vascular system and the cost of blood volume. Proceedings of National Academy of Sciences, USA 12: 207–214.

Mustajärvi, K., Merilä, P., Derome, J., Lindroos, A.-J., Helmisaari, H.-S., Nöjd, P. & Ukonmaanaho, L. 2008. Fluxes of dissolved organic and inorganic nitrogen in relation to stand characters and latitude in Scots pine and Norway spruce stands in Finland. Boreal Environment Research 13(Suppl. B): 3–21.

Nara, K. 2006. Pioneer dwarf willow may facilitate tree succession by providing late colonizers with compatible ectomycorrhizal fungi in a primary successional volcanic desert. New Phytologist 171: 187–198.

Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M. & Högberg, P. 1998. Boreal forest plants take up organic nitrogen. Nature 392: 914–916.

Näsholm, T. & Persson, J. 2001. Plant acquisition of organic nitrogen in boreal forests. Physiologia Plantarum 111: 419–426.

Newman, E.I. 1988. Mycorrhizal links between plants: their functioning and ecological significance. Advances in ecological research 18: 243–270.

Newton, A.C., Haigh, J.M. 1998. Diversity of ectomycorrhizal fungi in Britain: a test of the species-area relationship, and the role of host specificity. New Phytologist 138: 619–627.

Nicoll, B.C., Gardiner, B.A., Rayner, B. & Peace, A.J. 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. Canadian Journal of Forest Research 36: 1871–1883.

Nikinmaa E. 1992. Analyses of the growth of Scots Pine; matching structure with function. Acta Forestalia Fennica 235. 68 p.

—, Hari, P. & Mäkelä, A. 2008. Connections between processes, transport and structure. In: Hari, P. and Kulmala, L. (eds.) Boreal forest and climate change. Advances in global change research 34: 425–432.

Niklas, K.J., 1994. Plant Allometry, the Scaling of Form and Process. University of Chicago Press, Chicago, London, 365 p..

— 2006. Scaling the paths of resistance. New Phytologist 169: 219–222.

Nilsson, L.O. & Wallander, H. 2003. The production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. New Phytologist 158: 409–416.

—, Giesler, R., Bååth, E., Wallander, H. 2005. Growth and biomass of mycorrhizal mycelia in coniferous forests along short natural nutrient gradients. New Phytologist 165: 613–622.

Norby, R.J. & Jackson, R.B. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytologist 147: 3–12.

Novoplansky, A. 2009. Picking battles wisely: plant behaviour under competition. Plant, Cell and Environment 32: 726–741.

Nygren, P. & Pallardy, S.G. 2008. Applying a universal scaling model to vascular allometry in a single-stemmed, monopodially branching deciduous tree (Attim's model). Tree Physiology 28: 1–10.

—, Lu, M. & Ozier-Lafontaine, H. 2009. Effects of turnover and internal variability of tree root systems on modelling coarse root architecture: comparing simulations for young *Populus deltoides* with field data. Canadian Journal of Forest Research 39: 97–108.

Oliver, C.D. & Larson, B.C. 1996. Forest Stand Dynamics. Update edition. New York, John Wiley. 520 p.

Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M.R., Lõhmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M. & Brunner, I. 2007a. Specific root length as an indicator of environmental change. Plant Biosystems 141: 426–442.

—, Lõhmus, K., Helmisaari, H.-S., Truu, J. & Meel, S. 2007b. Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. Tree Physiology 27: 1627–1634.

Ozier-Lafontaine, H., Lecompte, F. & Sillon, J.F. 1999. Fractal analysis of the root architecture of *Gliricidia sepium* for the spatial prediction of root branching, size and mass: model development and evaluation in agroforestry. Plant and Soil 209: 167–180.

Paavilainen, E. 1966. Maan vesitalouden järjestelyn vaikutuksesta rämemännikön juurisuhteisiin. Summary: On the effect of drainage on root systems of Scots pine on peat soils. Communicationes Instituti Forestalis Fenniae 61: 1–110.

Pagès, L. 1999. Why model root system architecture? In: Stokes, A. (ed.) The supporting roots of trees and woody plants: form, function and physiology. Developments in plant and soil sciences 87. Kluwer, Dordrecht, pp. 187–194

—, Vercambre, G., Drouet, J.L., Lecompte, F., Collet, C. & Le Bot, J. 2004. Root type: a generic model to depict and analyse the root system architecture. Plant and Soil 258: 103–119.

Pennanen, T., Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J. & Fritze, H. 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. Microbial Ecology 38: 168–179.

—, Caul, S., Daniell, T.J., Griffiths, B.S., Ritz, K., Wheatley, R.E. 2004. Community-level responses of metabolically-active soil microorganisms to the quantity and quality of substrate inputs. Soil Biology and Biochemistry 36: 841–848.

Persson, H.A. 1983. The distribution and productivity of fine roots in boreal forests. Plant and Soil 71: 87–101.

Petersson, H. & Ståhl, G. 2006. Functions for belowground biomass of *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens* in Sweden. Scandinavian Journal of Forest Research 21: 84–93.

Perttunen, J., Sievänen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H. & Väkevä, J. 1996. LIGNUM: A tree model based on simple structural units. Annals of Botany 77: 87–98.

Polechová, J. & Storch, D. Ecological niche. In: Jørgensen, S.E. & Fath, B.D. (eds.). Evolutionary Ecology. Encyclopedia of Ecology 2: 1088–1097.

Potila, H.M., Wallander, H. & Sarjala, T. 2009. Growth of ectomycorrhizal fungi in drained peatland forests with variable P and K availability. Plant and Soil 316: 139–150.

Pregitzer, K. S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L. 2002. Fine root architecture of nine North American trees. Eclogical Monographs 72: 293–309.

Pretzsch, H. & Schütze, G. 2005. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed Stands. Plant Biology 7: 628–639.

Raich, J.W., Riley, R.H. & Vitousek, P.M. 1994. Use of root-ingrowth cores to assess nutrient limitations in forest ecosystems. Canadian Journal of Forest Research 24: 2135–2138.

Rajala, T. 2008. Responses of soil microbial communities to clonal variation of Norway spruce. Dissertationes Forestales 58. 50 p.

Repola, J., Ojansuu, R., Kukkola, M. 2007. Biomass functions for Scots pine, Norway spruce and birch in Finland. Working papers of the Finnish Forest Research Institute 53. p 28.

Reubens, B., Poesen, J., Danjon, F., Geudens, G. & Muys, B. 2007. The role of fine and coarse roots in shallow slope stability and soil erosion control with focus on root system architecture: a review. Trees 21: 385–402.

—, Pannemans, B., Danjon, F., De Proft, M., De Baets, S., De Baerdemaeker, J., Poesen, J. & Muys, B. 2009. The effect of mechanical stimulation on root and shoot development of young containerised *Quercus robur* and *Robinia pseudoacacia* trees. Trees 23: 1213–1228.

Richardson, A.D. & zu Dohna, H.Z. 2003. Predicting root biomass from branching patterns of Douglas-fir root systems. Oikos 100: 96–104.

— & zu Dohna, H.Z. 2005. Predicting root biomass from branching patterns of Douglas-fir root systems. Oikos 108: 648–648 (vol 100, pg 96, 2003).

Riegel, G.M., Miller, R.F. & Krueger, W.C. 1992. Competition for resources between understorey vegetation and overstorey *Pinus ponderosa* in Northeastern Oregon. Ecological Applications 2: 71–85.

Robinson, D. 2004. Scaling depths: below-ground allocation in plants, forests and biomes. Functional Ecology 18: 290–295.

— & Rorison, I.H. 1987. Root hairs and plant growth at low nitrogen availabilities. New Phytologist 107: 681–693.

Rothe, A. & Binkley, D. 2001. Nutritional interactions in mixed species forests: a synthesis. Canadian Journal Forest Research 31: 1855–1870.

Rousseau, J.V., Sylvia, D.M. & Fox, A.J. 1994. Contribution of ectomycorrhiza to the potential nutrient-absorbing surface of pine. New Phytologist 128:639–644.

Rundel, P.W. & Nobel, P.S. 1991. Structure and function in desert root systems. In: Atkinson, D. (ed.). Plant root growth: An ecological perspective. Blackwell Scientific Publications, Oxford. pp. 349–378.

Salas, E., Ozier-Lafontaine, H. & Nygren, P. 2004. A fractal root model applied for estimating the root biomass and architecture in two tropical legume tree species. Annals of Forest Science 61: 337–345.

Santantonio, D., Hermann, R.K. & Overton, W.S. 1977. Root biomass studies in forest ecosystems. Pedobiologia 17: 1–31.

Schenk, H.J. 2006. Root competition: beyond resource depletion. Journal of Ecology 94: 725–739.

— & Jackson, R.B. 2002. Rooting depths, lateral root spreads and belowground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90: 480–494.

Schmid, I. 2002. The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. Basic and Applied Ecology 3: 339–346.

— & Kazda, M. 2001. Root distribution of Norway spruce in monospecific and mixed stands on different soils. Forerst Ecology and Management 159: 37–47.

Schwinning, S. & Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113: 447–455.

Sellin, A., Rohejärv, A. & Rahi, M. 2008. Distribution of vessel size, vessel density and xylem conducting efficiency within a crown of silver birch (*Betula pendula*). Trees 22: 205–216.

Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. Japanese Journal of Ecology 14: 97–105.

Shumway, D.L., Steiner, K.C. & Kolb, T.E. 1993. Variation in seedling hydraulic architecture as a function of species and environment. Tree Physiology 12: 41–54.

Sievänen, R., Nikinmaa, E., Nygren, P., Ozier-Lafontaine, H., Perttunen, J. & Hakula, H. 2000. Components of functional-structural models. Annals of Forest Science 57: 399–412.

—, Perttunen, J., Nikinmaa, E. & Kaitaniemi, P. 2008. Toward extension of a single tree functional-structural model of Scots pine to stand level: effect of the canopy of randomly distributed, identical trees on development of tree structure. Functional Plant Biology 35: 964–975.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19: 605–611.

Simard, S.W. & Durall, D.M. 2004. Mycorrhizal networks: a review of their extent, function and importance. Canadian Journal of Botany 82: 1140–1165.

—, Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M. & Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388: 579–582.

—, Durall, D. & Jones, M. 2002. Carbon and nutrient fluxes within and between mycorrhizal plants. In: van der Heijden, M.G.A. and Sanders, R. (eds.). Mycorrhizal ecology. pp. 33–61.

Smith, D.M. 2001. Estimation of tree root lengths using fractal branching rules: a comparison with soil coring for *Grevillea robusta*. Plant and Soil 229: 295–304.

— & Roberts, J.M. 2003. Hydraulic conductivities of competing root systems of *Grevillea robusta* and maize in agroforestry. Plant and Soil 251: 343–349.

Smith, S.E. & Read, D.J. 1997. Mycorrhizal symbiosis. Academic Press, San Diego. 605 p.

Soethe, N., Lehmann, J. & Engels, C. 2007. Root tapering between branching points should be included in fractal root system analysis. Ecological Modelling 207: 363–366.

Sohn, R.F. 1981. *Pisolithus tinctorius* forms long ectomycorrhizae and alters root development in seedlings of *Pinus resinosa*. Canadian Journal of Botany 59: 2129–2134.

Sperry, J.S., Nichols, K.L., Sullivan, J.E.M. & Eastlack, S.E. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75: 1736–1752.

Sterba, H. and Amateis, R. L. 1998. Crown efficiency in a loblolly pine (*Pinus taeda*) spacing experiment. Canadian Journal of Forest Research 28: 1344–1351.

St. John, T.V., Coleman, D.C. & Reid, C.P.P. 1983. Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. Plant and Soil 71: 487–493.

Stone, E.L. & Kalisz, P.J. 1991. On the maximum extent of tree roots. Forest Ecology and Management 46: 59–102.

Stubbs, W.J. & Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. Journal of Ecology 92: 557–567.

Sutton, R.F. & Tinus, R.W. 1983. Root and root system terminology. Forest Science 24. 137 p.

Tamm, C.O. 1991. Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability. Ecological Studies 81. Springer-Verlag, Berlin, 115 p.

Taylor, A.F.S., Martin, F. & Read, D.J. 2000. Fungal diversity in ectomycorrhizal communities of Norway spruce (*Picea abies* (L.) Karst.) and beach (*Fagus sylvatica* L.) along north-south transects in Europe. In: Schulze, E-D. (ed.). Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies. Springer-Verlag, Berlin. p. 343−365.

Thomas, P. 2000. Trees: Their Natural History. Cambridge University Press, Cambridge, UK, p. 286.

Tissier, J., Lambs, L., Peltier, J.-P. & Marigo, G. 2004. Relationships between hydraulic traits and habitat preference for six Acer species occurring in the French Alps. Annals of Forest Science 61: 81–86.

Tobin, B., Cermak, J., Chiatante, D., Danjon, F., Di Iorio, A., Dupuy, L., Eshel, A., Jourdan, C., Kalliokoski, T., Laiho, R., Nadezhdina, N., Nicoll, B., Pagès, L., Sande-Silva, J., Spannos, I. 2007. Towards developmental modelling of tree root systems. Plant Biosystems 141: 481–501.

Toljander, J.F., Eberhardt, U., Toljander, Y.K., Leslie, R.P. & Taylor, A.F.S. 2006. Species composition of an ectomycorrhizal fungal community along a local nutrient gradient in boreal forest. New Phytologist 170: 873–884.

Tyree, M.T. 1997. The Cohesion-Tension theory of sap ascent: current controversies. Journal of Experimental Botany 48: 1753–1765.

— & Ewers, F.W. 1991. The hydraulic architecture of trees and other woody plants. New Phytologist 119: 345–360.

— & Zimmermann, M.H.Z. 2002. Xylem strucutre and the ascent of sap. Springer Series in Wood Science, Springer, Berlin, 278 p.

—, Patino, S. & Becker, P. 1998. Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. Tree Physiology 18: 583–588.

Vainio, J., Korhonen, K. & Hantula, J. 1998. Genetic variation in *Phlebia gigantea* as detected with random amplified microsatellite (RAMS) markers. Mycological Research 102: 187–192.

van der Heijden, M.G.A & Sanders, I.R. 2003. Mycorrhizal ecology. Springer, Berling, 469 p.

Vanninen, P. & Mäkelä, A. 1999. Fine root biomass of Scots pine stands differing in age and site fertility in southern Finland. Tree Physiology 12: 823–830.

—, Ylitalo, H., Sievänen, R., Mäkelä, A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees 10: 231–238.

van Noordwijk, M. & De Willigen, P. 1991. Root functions in agricultural systems. In: Persson, H.& McMichael, B.L. (eds.). Plant roots and their environment. Elsevier, Amsterdam. pp. 381–395.

— & Purnomosidhi. 1995. Root architecture in relation to tree-soil-crop interactions and shoot pruning in agroforestry. Agroforestry Systems 30: 161–173.

— & Mulia, R. 2002. Functional branch analysis as tool for fractal scaling above- and belowground trees for their additive and non-additive properties. Ecological Modelling 149: 41–51.

—, Spek, L.Y. & Dewilligen, P. 1994. Proximal root diameter as predictor of total root size for fractal branching models. 1. Theory. Plant and Soil 164: 107–117.

van Rees, K.C.J. & Comerford N.B. 1990. The role of woody roots of slash pine seedlings in water and potassium absorbtion. Canadian Journal of Forest Research 20: 1183–1191.

van Vuuren, M.M.I., Muir, A.A. & Orians, C.M. 2003. Growth and nutrient uptake by birch and maple seedlings on soil with patchy or homogeneous distribution of organic matter. Canadian Journal of Forest Research 33: 2019–2026.

Venn, S.E., Morgan, J.W. & Green, P.T. 2009. Do facilitative interactions with neighboring plants assist the growth of seedlings at high altitudes in alpine Australia? Arctic, Antarctic, and Alpine Research 41: 381–387.

Vogt, K.A., Grier, C.C., Meier, C.E. & Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in Western Washington, as suggested by fine-root input. Ecological Monographs 53: 139–157.

—, Vogt, D.J., Moore, E.E., Fataga, B.A., Redlin, M.R. & Edmonds, R.L. 1987. Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. Journal of Ecology 75: 857–870.

—, Vogt, D.J., Palmiotto, P.A., Boon, P., O´Hara, J. & Asbjornsen, H. 1996. Review of root dynamics grouped by climate, climatic forest type and species. Plant and Soil 187: 159–219.

Wallander, H. 2006. External mycorrhizal mycelia—the importance of quantification in natural ecosystems. New Phytologist 171: 240–242.

—, Nilsson, L.O., Hagerberg, D. & Bååth, E. 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. New Phytologist 151: 753–760.

—, Johansson, U., Sterkenburg, E., Durling, M.B. & Lindahl, B.D. 2010. Production of ectomycorrhizal mycelium peaks during canopy closure in Norway spruce forests. New Phytologist 187: 1124–1134.

Wallenda, T. & Kottke, I. 1998. Nitrogen deposition and ectomycorrhizas. New Phytologist 139: 169–187.

Wang, E. & Smith, C.J. 2004. Modelling the growth and water uptake function of plant root systems: a review. Australian Journal of Agricultural Research 55: 201–523.

Wang, L.X., Mou, P.P. & Jones, R.H. 2006. Nutrient foraging via physiological and morphological plasticity in three plant species. Canadian Journal of Forest Research 36: 164–173.

Webster, C.R. & Lorimer, C.G. 2003. Comparative growing-space efficiency of four tree species in mixed conifer-hardwood forests. Forest Ecology and Management 177: 361–377.

Weiner, J. 2004. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology, Evolution and Systematics 6: 207–215.

West, G.B., Brown, J.H. & Enquist, B.J. 1999. A general model for the structure and allometry of plant vascular systems. Nature 400: 664–667.

—, Brown, J.H. & Enquist, B.J. 2000. The origin of universal scaling laws in biology. In: Brown, J.H. & West, G.B. (eds.). Scaling in Biology. Oxford University Press, Oxford, pp. 87–112.

Wirth, C., Schumacher, J. & Schulze, E.-D. 2004. Generic biomass functions for Norway spruce in Central Europe – a metaanalysis approach toward prediction and encertainty estimation. Tree Physiology 24: 121–139.

Yli-Vakkuri, P. 1954. Tutkimuksia puiden välisistä elimillisistä juuriyhteyksistä männiköissä. Acta Forestalia Fennica 60: 1–102.

Zhang, J. & George, E. 2009. Root proliferation of Norway spruce and Scots pine in response to local magnesium supply in soil. Tree Physiology 29: 199–206.