

Coarse Root Architecture of Three Boreal Tree Species Growing in Mixed Stands

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Root system architecture determines many of the vital functions of a tree, e.g. stability of anchorage and resource uptake. The shoot:root ratio is determined through the allocation of resources. Studies on below-ground architectural elements in boreal mixed forests are relatively scarce despite the fact that knowledge on below-ground interactions and allocation changes in relation to stand developmental stage and soil fertility is needed both in ecological and silvicultural research. In this study, sixty tree root systems of three different tree species, *Betula pendula*, *Picea abies* and *Pinus sylvestris*, were excavated in five mixed forest stands in order to quantify differences between the species and sites in terms of rooting behaviour. Root architecture differed greatly between the species, implying different solutions for the functions of root systems. Half of the *P. sylvestris* had developed a taproot as a response to anchorage needs, while *P. abies* correspondingly had pronounced secondary growth of proximal roots. *Betula pendula* had the most extensive root system, illustrating the greater demand of deciduous trees for water. *Betula pendula* was also the most sensitive to soil fertility: it favoured exploration on the poorest site, as illustrated by the high total root length, whereas on the most fertile site its strategy was to efficiently exploit soil resources through increased branching intensity. The results obtained in this study provide basic knowledge on the architectural characteristics of boreal tree root systems for use by forestry professionals and modellers.

Keywords *Betula pendula*, *Picea abies*, *Pinus sylvestris*, branching pattern, influence area, developmental stage, site type

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1 Introduction

In the ecological literature, studies on the structural and architectural elements of the below-ground parts of trees are relatively scarce, although the importance of root architecture for the growth of individual trees has long been understood (Nobbe 1862 in Lynch 1995, Cannon 1911, Laitakari 1927, 1935, Ylivakkuri 1954). Root architecture usually refers to the spatial configuration of the root system, i.e. the size and explicit location of the woody parts. Finer structural elements like root hairs and mycorrhizal hyphae are not normally included (Lynch 1995). The architecture of a root system can be described with the aid of multiple variables like branching frequency of the nodes, length of internodes, branching angle, 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). The functions of a root system are the acquisition of soil-based resources, anchorage, and secondary functions like resource storage. These functions presumably set requirements on the constitution of the root system and thus affect its architecture (Fitter 1991).

Fitter (1996) presented simple topological indices, by which it is possible to characterize branching structure of root system. One definition for such topological index is the regression slope (β_1) between the number of internodes in the longest path from any root tip to the first internode connected to the stump (altitude, *Alt*) and the number of exterior internodes in a root (magnitude, *Mag*)

$$\log Alt = \beta_0 + \beta_1 \log Mag \quad (1)$$

Using this index, branching of root systems is possible to describe as a herringbone- (main axis is the longest and thickest branch, and there are few non-branching side branches, theoretical maximum index value 1) or dichotomous-type (all branches of the same order are of the same size and the number of root tips is high, index value approaches zero), or between these two extremes, and thus relate growth strategy of a root system – i.e. exploration versus exploitation

– to the explicit value. However, these indices were applied originally for herbaceous plants and therefore their applicability for large woody root systems has to be tested.

Improved modelling techniques, like process-based and functional-structural growth models, have enabled the generation of realistic simulations of the growth and development of single tree or whole stand (e.g. Perttunen et al 1996, Mäkelä et al. 2002). In tree-level models, the next step would be the explicit description of resource allocation and nutrient acquisition. The ability of a plant to exploit unevenly distributed forest soil resources is mainly dependent on the spatial deployment of its root system (Lynch 1995), i.e. the coarse root architecture, since the influence area of finer below-ground parts is limited. On the other hand, it has been reported that the architecture and allocation pattern of root systems differ between species, site conditions, and developmental stage (Fitter et al. 1991, Fitter and Stickland 1991, 1992, Stone and Kalisz 1991, Lynch 1995, Schenk and Jackson 2002). Therefore, research dedicated to these processes in defined conditions with specific species is needed. Moreover, the competition between trees in many models of forest stand development, e.g. Pipe Qual (Mäkelä 2002) or MOTTI (Hynynen et al. 2002), is based on the influence area or other characteristics of the crown. Lateral root spread has been shown to exceed the crown width in many studies (reviewed by Stone and Kalisz 1991) and, therefore, the below-ground interactions between trees may be different from that of the above-ground parts.

The aim of this study was to describe the coarse root architecture of the main Finnish forest tree species, *B. pendula*, *P. abies* and *P. sylvestris*, in different developmental stages and forest types in mixed boreal forests in order to gain ecological insight to the questions related to the topics discussed above. The first specific objective was to quantify the differences between species and sites in terms of rooting behaviour based on field data and 3-D root system reconstruction by a computer model. These data made it possible to determine variables describing the total size of coarse root systems like total length and total number of internodes and, on the other hand, more detailed architectural variables like branching pattern, mean length of internodes and tapering of root

Table 1. Selected characteristics of the mixed boreal study stands situated in Southern Finland

Devel. stage	Forest type	Species	Regener. type	No of trees per hectare m ² ha ⁻¹	Basal area m	Mean on stand		Sample trees		
						Height cm	D _{1.3} yrs.	Age cm	D ₀ m	Height
Sapling	MT	<i>B. pendula</i>	Natural	2920	4.6	4.6	3.1	13	8.1	4.9
	MT	<i>P. abies</i>	Planted	6480	2.5	2.7	2.4	15	7.9	4.1
	MT	<i>P. sylvestris</i>	Natural	180	0.1	3.0	3.7	13	7.9	4.4
	MT	Others	Natural	3900	0.5	2.7	1.2			
		Total		13480	8.0	3.2	2.3			
Pole	MT	<i>B. pendula</i>	Natural	480	5.0	12.9	11.5	29	16.1	12.5
	MT	<i>P. abies</i>	Natural	3450	3.0	4.3	4.1	28	11.7	10.2
	MT	<i>P. sylvestris</i>	Planted	830	10.7	11.5	12.2	30	14.5	12.2
	MT	Others	Natural	930	0.2	3.0	1.3			
		Total		5690	19.0	8.2	8.0			
Mature	MT	<i>B. pendula</i>	Natural	70	1.1	14.4	13.0	48	30.0	20.9
	MT	<i>P. abies</i>	Planted	530	10.3	13.1	14.5	55	29.2	21.3
	MT	<i>P. sylvestris</i>	Planted	270	9.8	17.3	20.8	51	29.3	20.5
	MT	Others	Natural	10	0.1	11.0	8.5			
		Total		880	21.0	14.5	16.2			
Pole	OMT	<i>B. pendula</i>	Natural	530	6.2	14.0	12.6	36	26.4	19.0
	OMT	<i>P. abies</i>	Planted	3150	6.5	5.8	6.0	34	18.2	13.5
	OMT	<i>P. sylvestris</i>	Natural	270	4.7	14.4	14.4	36	20.2	15.4
	OMT	Others	Natural	430	1.9	9.8	8.1			
		Total		4380	19.0	8.8	8.4			
Pole	VT	<i>B. pendula</i>	Natural	480	1.6	8.8	7.9	32	19.1	11.9
	VT	<i>P. abies</i>	Natural	920	4.8	7.9	8.7	41	14.7	9.5
	VT	<i>P. sylvestris</i>	Natural	390	3.3	8.7	10.4	31	18.8	10.7
	VT	Others	Natural	110	0.2	5.9	5.7			
		Total		1900	10.0	8.2	8.8			

OMT = *Oxalis-Myrtillus* typeMT = *Myrtillus* typeVT = *Vaccinium* type

axes. As a second specific object, characterization of the branching pattern of root systems by means of topological indices was tested in order to determine whether the indices used with herbaceous plants also apply to the root systems of boreal tree species.

2 Materials and Methods

2.1 Site Description

The study 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. According to weather data collected during the past 48 years at the Forestry Station's meteorological station, the monthly average temperature maxima from June to August vary from 13 to 19°C and minima from November to March from -21°C to -4°C. Annual precipitation varies from 500 to 1000 mm. Precipitation is divided relatively evenly throughout the year, although the heaviest precipitation usually occurs during the summer (June to September). From late October to April precipitation usually falls as snow and the depth of the snow cover may reach one meter. According to the USDA soil taxonomy, the most common soil type in the Hyytiälä area is Typic Haplocryod (Mokma et al. 2004).

Five study sites were selected in mixed *Betula pendula* Roth., *Picea abies* (L.) Karst., and *Pinus sylvestris* L. stands. Site description can be found in Table 1. According to the Finnish forest type system (Cajander 1949), forests are classified into forest site types based on the understorey vegeta-

tion, and these types are assumed to illustrate the site productivity. According to this system, the forests around the Hyytiälä Forestry Field Station mainly belong to *Myrtillus* type (MT). The *Myrtillus* type is mesic, intermediate in fertility and yield capacity ($6.7 \text{ m}^{-3}\text{ha}^{-1}\text{a}^{-1}$ pure Scots pine stand in South Finland, Vuokila and Väliaho 1980). The natural main tree species is *P. abies*, and the ground vegetation is characterised by dwarf shrubs, forbs, and mosses. Three MT stands were selected on the basis of the developmental stage of the stand, i.e. mature, pole, and sapling stage. In addition, one pole stage stand of the *Vaccinium* type (VT) and one of the *Oxalis-myrtillus* type (OMT) were selected to form a pole stage fertility gradient. The *Vaccinium* type is drier and less fertile than MT, whereas OMT represents a higher fertility class. In natural conditions, VT forests are dominated by *P. sylvestris* and the ground vegetation consists mainly of dwarf shrubs, mosses, and lichens. The OMT type has the highest yield capacity of the three selected types. The natural main tree species is *P. abies* and different grasses, forbs, and ferns are abundant in the ground vegetation, while the proportions of dwarf shrubs and mosses are lower than that in MT. Selected sites differed from each other in terms of silvicultural operations e.g. VT was naturally regenerated, whereas in other sites at least one tree species was planted. Moreover, mature MT and VT had undergone thinning, whereas others had not. Yet, differences in silvicultural operations was considered to have smaller effect on studied variables than stretching study area to a wider geographical area, in order to have sites which would have undergone exactly similar operations. Twelve trees on each plot, four per species, were selected primarily from the dominant tree layer for the measurement of root system architecture.

2.2 Excavation and Architectural Measurements

Each tree selected for measurements of root system architecture was cut and the age of the tree was determined by counting the annual rings. Crown characteristics were analyzed in a related study. All the roots attached to the root collar were

excavated up to the first node. Node is used here to describe the point of origin of a branch in a root system. Internode is a segment between two nodes (branching internode) or between node and segments end (non-branching internode). Both primary roots (derived from the embryo root of the seed) and adventitious roots (in this study considered as roots formed after germination from the stem, old roots etc.; Cannon 1949, Sutton and Tinus 1983) were exposed. This part of the root system is hereafter called the proximal root system, and non-adventitious roots attached to the root collar are called proximal roots. The definition of adventitious roots was based on their different morphology: bark deformation in the insertion point of the root branch, more rapid tapering, and different branching pattern. The excavation was carried out carefully with small hand tools in 2005, and by a pneumatic Soil-Pick tool (MBW SP125; M-B-W, Ltd., Bolton, UK) in 2006. The Soil-Pick tool produces a super-sonic jet of air and exposes root branches down to 2 mm without damaging them. After exposure of the proximal root system, one to three roots per tree were selected as sample roots. In selection of the sample roots semi-random procedure was used i.e. the only restriction was the aim to cover the diameter range of proximal roots in each species in each site. The number of sample roots was set so that about 200 nodes per species were analysed in each stand, and at least one root of each sample tree was completely excavated. Sample roots were exposed completely, i.e. all the root branches were excavated until a minimum diameter of 2 mm, which was set as the lower limit for the coarse root system.

Proximal roots were numbered and their characteristics and, in the case of sample roots, subsequent internodes were measured. The measured variables were azimuth with a hand-bearing compass; inclination angle with a clinometer in 2005 and with a Vertex device (Vertex III, Haglöf Sweden AB, Långsele, Sweden) in 2006; depth and length of proximal roots and length of the internodes with a measuring tape. In addition, the diameter of each internode was measured next to the root collar, in each node before bifurcation, and immediately after bifurcation with a calliper.

2.3 Basic Density

Samples for the determination of basic wood density (dry mass divided by fresh-volume) were taken from one root system per tree species on each plot. Small sections were taken in such a way that the whole range of internode diameters from 2 mm to the stump was included. Fresh volume (with bark) of the samples was determined in the field immediately after cutting by measuring the length of the sample and calculating the mean of two diameters at 90° angles in the middle of the sample. The samples were weighed after drying in an oven for 72 h at 70°C.

2.4 Soil Characteristics

Soil samples were also taken from each plot in order to confirm differences in soil fertility between sites. One soil core sample was taken next to each sample tree to cover the whole study area, totalling 12 soil cores per stand. Wherever possible, the soil horizons were identified and their thickness measured. The humus layer was separated from the mineral soil before the analyses, and the mineral soil was divided into 10 cm sections. All the soil samples were dried for 48 h at 60°C. After drying samples were sieved through the 2 mm sieve and their pH measured in water. Total C, N and H were analyzed by LECO CHN-1000 -analyzer (LECO Corporation, St. Joseph, MI, USA) according to ISO 10694:1995 and ISO 13878:1998 standards. Exchangeable basic and acidic cations were determined, after extraction with BaCl₂, on an ICP/AES instrument (TJA Iris Advantage, Thermo Jarrell Ash Corporation, Franklin, MA, USA; Hendeshot et al. 1993). The soil moisture content was determined on a LECO TGA-601 Thermogravimetric Analyzer (LECO Corporation, St. Joseph, MI, USA). Soil stoniness was measured according to the procedure of Viro (1958) as modified by Tamminen (1991).

2.5 Data Analyses

The excavation data were analysed using a computer programme constructed on the basis of the LIGNUM model (Perttunen et al. 1996). The

programme calculated a number of characteristics of the excavated roots (total length and extension, biomass etc.) and produced a visual depiction of the roots.

The data were analyzed using SAS Statistical Software v.9.1 (SAS Institute Inc., Cary, NC, USA). Differences between tree species and stands were tested by ANOVA (GLM procedure). Tukey-Kramer paired comparisons method was used for multiple comparisons. Linear curve fitting was performed using the REG procedure and non-linear fitting by the NLIN procedure. Logarithmic transformations were used to normalize variables and remove heteroscedasticity of residuals when necessary. The normal and theoretical distributions were fitted to the data using the UNIVARIATE procedure and difference between the two empirical distributions was tested using NPAR1WAY procedure.

3 Results

3.1 Soil Properties

Site classification made on the basis of the understorey vegetation was mainly reflected in the pH, C/N ratio, and exchangeable Ca and Mg concentrations in the humus layer. In the mineral soil, only the C/N ratio in VT deviated from MT and OMT ($p=0.0014$ and $p<0.0001$, respectively), and there were no statistically significant differences in any measured variable between mineral soil sections defined by depth. Therefore, only the mean values for the whole mineral soil layer are presented in Table 2. No significant differences were found in the pH values between the developmental stages on the MT sites, whereas the forest type had a clear effect; humus pH was higher on the OMT and MT than on the VT site ($p<0.0001$), while no significant differences were found between the OMT and MT sites. The C/N ratio in the humus on the mature MT site was higher than on the pole stage MT site ($p=0.0017$). The largest difference in the C/N ratio was between the forest types (OMT and VT sites $p<0.0001$). The exchangeable Ca and Mg concentrations in the humus layer were higher on the OMT than on the VT site ($p<0.0001$ and

Table 2. Selected soil characteristics of the studied mixed boreal forests situated in Southern Finland. Sum of humus and mineral soil layers depth determines the depth of sampling. Abbreviations as in Table 1.

Devel. stage	Forest type	Layer	Layer depth mm	Stone %	pH in water	C/N ratio	C % Dw	N % Dw	Ca mg kg ⁻¹	Mg mg kg ⁻¹	P mg kg ⁻¹
Sapling	MT	Humus	40	34	4.2	27	19.0	0.69	1224	190	32
		Mineral	350		4.7	19	1.7	0.09	75	19	0.57
Pole	MT	Humus	30	10	4.5	23	20.6	0.88	–	–	–
		Mineral	310		5.0	19	1.3	0.07	70	9	0.52
Mature	MT	Humus	40	38	4.1	29	20.3	0.69	1413	158	31
		Mineral	300		4.8	19	1.9	0.10	45	8	0.60
Pole	OMT	Humus	30	24	4.7	19	16.5	0.85	2171	248	16
		Mineral	300		5.9	18	2.3	0.13	319	49	0.76
Pole	VT	Humus	35	6	3.7	30	23.9	0.79	550	108	39
		Mineral	370		4.8	22	1.4	0.06	22	4	0.51

Stone % = percentage of stones in 30 cm deep soil layer

$p=0.0130$), but the Ca and Mg concentration in the MT humus did not differ significantly from either the OMT or VT humus. There were considerable differences in the stoniness of the sites: on the VT site it was only 6%, and on the mature MT site it was almost 40%.

3.2 Coarse Root Architecture of the Root Systems

3.2.1 Differences Between the Tree Species

The overall pattern of the root system was relatively different in the three species (Fig. 1 A–F). *Picea abies* usually had less than ten large, horizontally-oriented proximal roots near the soil surface. *Betula pendula* usually had ca. 20 smaller proximal roots located both near the soil surface and in deeper layers. The proximal root system of *B. pendula* was deeper than that of *P. abies* on the pole stage MT ($p<0.0001$), OMT ($p<0.0001$) and VT sites ($p=0.0265$). Inclination angle 45° was considered as the limit between horizontal and vertical roots. A higher proportion of proximal roots was vertically-oriented in *B. pendula* (mean of all sites 28%) than in *P. abies* or *P. sylvestris* (both 10%; taproots in *P. sylvestris* excluded). Also the mean inclination angle was bigger in *B. pendula* (26°) than in the conifers (*P. sylvestris* 17° $p<0.0001$ and *P. abies* 18° $p<0.0001$). Half of the *P. sylvestris* trees had a pronounced tap-

root. In other respects, the typical pattern of the *P. sylvestris* proximal root system was between the two other species. However, in most variables such as the relative sum of the squared diameters of proximal roots (RelSumD²), i.e. the ratio between the sum of the squared diameters of proximal roots and the squared diameter of the stump, statistically significant differences were not detected between the species in any developmental stage or forest type (Table 3). There was a larger difference between the species in the number of roots attached to the root collar than in RelSumD². However, in this variable the only significant deviation was that between *B. pendula* and *P. abies* on the OMT site ($p=0.0178$). All three species also had a considerable number of adventitious roots, which were located both on the root collar and in all the branching levels.

The characteristics of the whole root systems of each species were illustrated using variables obtained from completely excavated sample roots. The roots of *B. pendula* seemed to occupy horizontally the greatest area in each stand (Table 4), yet the difference was significant only between *B. pendula* and *P. sylvestris* ($p=0.0308$). In a vertical direction the species occupied different layers (Fig. 2, Table 4). *Picea abies* had shallow root systems in terms of mean depth compared to the other species ($p<0.0001$ with *B. pendula* in all sites apart of sapling stand; $p<0.0001$ with *P. sylvestris* in mature and pole stage MT, and in sapling site $p=0.0772$). *B. pendula* occupied pri-

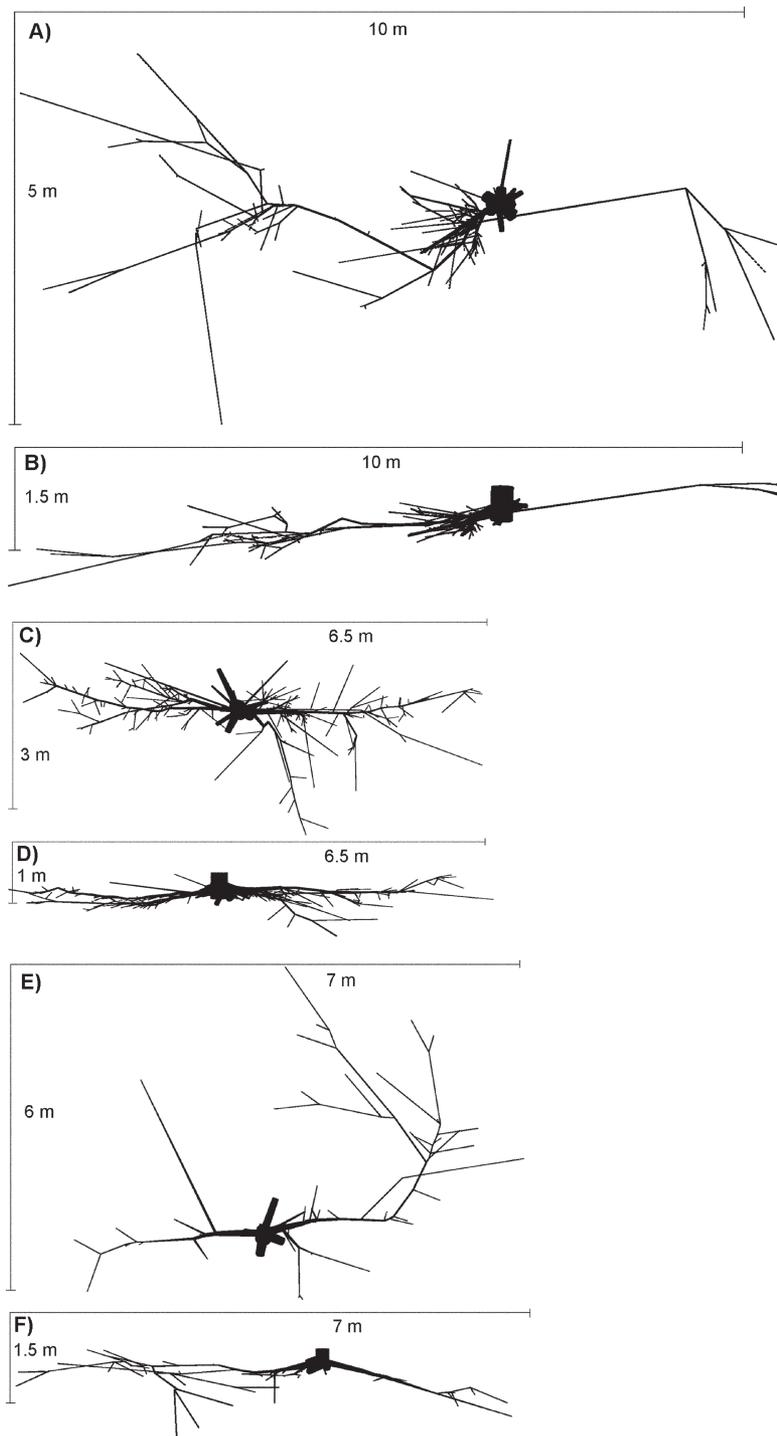


Fig 1. Visual depictions of the excavated and virtually reconstructed root systems of the 30-year-old trees growing on OMT site. Top and side views. A–B *Betula pendula*; C–D *Picea abies*; E–F *Pinus sylvestris*.

Table 3. Mean characteristics of proximal root system of *Betula pendula*, *Picea abies* and *Pinus sylvestris* in different developmental stages and site types of the study situated in Southern Finland.

Species and Devel. stage	Forest type	Rel		N	SD	D	Proximal roots				Adventitious roots				
		SumD ²	SD				SD	L	SD	Dh	SD	N	SD	D	SD
<i>Betula pendula</i>															
Sapling	MT	0.86	0.33	11	4.2	2.0	0.9	33	45	12	4	6	5	0.6	0.3
Pole	MT	1.02	0.42	20	7.7	3.1	1.8	34	45	30	8	12	9	0.7	0.4
Mature	MT	0.88	0.08	25	7.8	5.0	2.9	48	57	35	12	21	12	1.1	0.7
Pole	OMT	1.75	0.35	28	11.0	5.3	3.9	31	30	30	8	14	12	1.0	0.7
Pole	VT	1.29	0.25	16	6.0	4.7	2.4	38	64	25	7	4	2	1.2	1.1
<i>Picea abies</i>															
Sapling	MT	1.02	0.24	10	1.4	2.3	1.0	69	58	11	4	5	2	0.5	0.3
Pole	MT	0.96	0.31	11	2.6	3.1	2.0	40	39	16	6	7	4	0.7	0.4
Mature	MT	1.31	0.50	21	6.2	6.4	3.7	51	49	35	11	18	7	1.1	0.6
Pole	OMT	1.87	0.35	12	4.0	6.8	3.0	42	50	21	5	5	5	1.2	1.0
Pole	VT	1.87	0.23	8	2.2	6.4	3.3	42	39	18	6	6	1	1.0	0.6
<i>Pinus sylvestris</i>															
Sapling	MT	1.11	0.44	9	3.4	2.6	1.2	52	52	12	7	5	3	0.8	0.3
Pole	MT	1.21	0.21	13	4.3	4.2	1.9	58	76	23	11	11	6	0.6	0.6
Mature	MT	1.05	0.47	22	6.9	5.4	3.5	42	42	36	11	24	9	1.3	1.3
Pole	OMT	1.68	0.18	15	5.9	5.6	3.7	42	54	30	10	4	3	1.5	0.6
Pole	VT	1.35	0.15	15	3.3	4.9	2.3	31	35	20	7	5	3	1.3	0.7

RelSumD² = Ratio between the sum of squared basal diameters of proximal roots and squared stump diameter

D = Mean diameter (cm)

N = Mean number

L = Mean length (cm)

Dh = Mean depth of insertion to root collar (cm)

SD = Standard deviation

Other abbreviations as in Table 1.

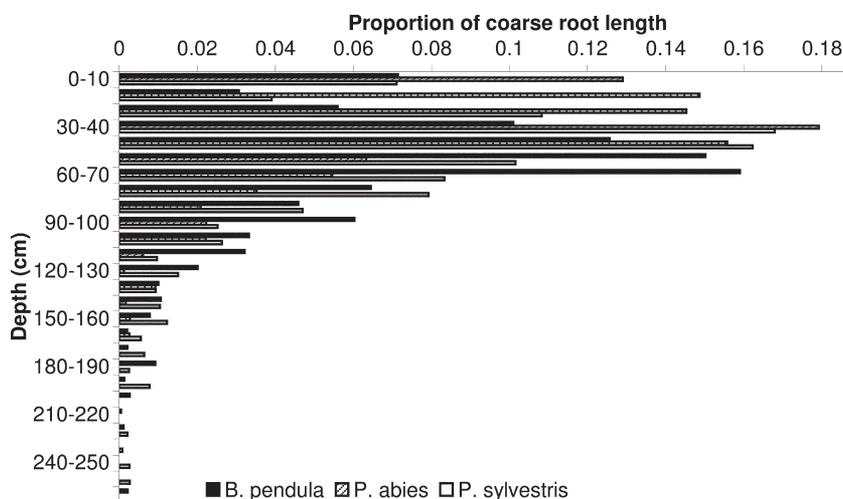


Fig 2. Vertical distribution of the coarse roots of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* averaged over different developmental stages and site types.

Table 4. Spatial dimensions of excavated root systems of *Betula pendula*, *Picea abies* and *Pinus sylvestris* in different developmental stages and site types illustrated by sample roots. Distances were defined from root systems virtually reconstructed using LIGNUM. Mean radial extension was calculated as the average of observed maximum radial extensions of completely exposed roots in each species and site.

Species and Devel. stage	Forest type	Radial extension (m)			Depth (m)		
		max	mean	SD	max	mean	SD
<i>Betula pendula</i>							
Sapling	MT	5.7	3.2	1.8	0.76	0.25	0.17
Pole	MT	8.1	5.2	2.1	1.08	0.43	0.21
Mature	MT	20.5	11.6	6.7	2.65	0.74	0.47
Pole	OMT	10.2	6.6	3.9	1.57	0.47	0.20
Pole	VT	10.6	8.1	1.9	1.70	0.55	0.16
<i>Picea abies</i>							
Sapling	MT	5.4	3.8	1.4	0.64	0.16	0.18
Pole	MT	4.4	3.2	0.8	0.83	0.21	0.14
Mature	MT	10.1	8.7	1.4	1.61	0.56	0.37
Pole	OMT	5.6	3.9	1.1	0.80	0.37	0.12
Pole	VT	10.1	6.7	2.3	1.62	0.36	0.20
<i>Pinus sylvestris</i>							
Sapling	MT	4.7	2.5	1.1	0.80	0.26	0.24
Pole	MT	7.6	4.5	2.0	1.05	0.43	0.17
Mature	MT	9.5	6.0	2.3	2.91	0.81	0.43
Pole	OMT	8.3	4.9	2.2	1.05	0.42	0.18
Pole	VT	6.9	5.3	1.8	0.86	0.33	0.17

SD = Standard deviation

marily the illuvial layer (the B horizon), whereas *P. sylvestris* occupied the elluvial layer (the E horizon).

The root systems in most cases branched dichotomously since, only one new internode emerged in 90% or more of the nodes in each species. Topologically, most of the root systems resembled a proportionate allotomous branching pattern (van Noordwijk et al. 1994), although in the reconstructed 3-D pictures many of the root systems of *P. sylvestris* had a more herringbone branching pattern. The topological indices (Eq. 1, Table 5) indicated that the branching patterns differed between the species (slope values highly significant in the regressions for each species), and *P. sylvestris* tended to have the highest, *B. pendula* the second and *P. abies* the lowest index value.

The species differed in terms of their branching intensity, as depicted by the mean length of the internodes (Table 6). When only the species were separated, the mean length of the internodes was strikingly similar between the conifers, whereas internodes of *B. pendula* deviated from those of the conifers ($p=0.0027$ with *P. sylvestris* and

$p=0.0055$ with *P. abies*). *P. sylvestris* had lower basic density than the other species ($p<0.0001$). Basic density in *P. sylvestris* and *B. pendula* density seemed to have a decreasing pattern from the stump towards the root tip, while in *P. abies* showed an opposite trend. However, the trends were so irregular that only mean values of each species in each plot are presented in Table 6.

The branching angle also had a strong effect on the overall shape of the root systems. Both horizontal and vertical angle distributions were calculated as the relative deviation of polar and azimuth angles of an internode from the same angles of the previous ("mother") internode in each node (Fig. 3A and B). The distributions were quite symmetrical, yet highly peaked, and therefore they did not fit either the normal or skewed theoretical distributions (e.g. lognormal, Weibull). Subsequent internodes in *P. sylvestris* deviated more from the "mother" internode than in the other species (Kolmogorov-Smirnov test; vertical angle distribution $p\leq 0.0003$ between *P. sylvestris* and *B. pendula*; horizontal angle distribution $p<0.0001$ between *P. sylvestris* and others).

Table 5. Topological indices of root systems of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* calculated according to the procedure of Fitter (1996) in different developmental stages and site types (Eq. 1). Slope used as an index value. SE = standard error. Other abbreviations as in Table 1.

Species and Devel. stage	Forest type	Slope β_1	SE	p	R ²
<i>Betula pendula</i>					
Sapling	MT	0.678	0.166	0.0066	0.73
Pole	MT	0.386	0.290	0.2535	0.31
Mature	MT	0.490	0.118	0.0529	0.90
Pole	OMT	0.000	0.000	< 0.0001	–
Pole	VT	0.000	0.000	< 0.0001	–
<i>Picea abies</i>					
Sapling	MT	0.378	0.148	0.0432	0.52
Pole	MT	0.627	0.089	0.0009	0.91
Mature	MT	0.066	0.038	0.2249	0.60
Pole	OMT	0.199	0.080	0.0903	0.67
Pole	VT	0.000	0.000	< 0.0001	–
<i>Pinus sylvestris</i>					
Sapling	MT	0.910	0.114	< 0.0001	0.86
Pole	MT	0.844	0.138	0.0002	0.81
Mature	MT	0.150	0.248	0.5894	0.11
Pole	OMT	0.161	0.084	0.1277	0.48
Pole	VT	0.416	0.097	0.0128	0.82

Table 6. Mean number, length, and basic density of root internodes of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* in different developmental stages and site types. Abbreviations as in Table 1.

Species and Devel. stage	Forest type	Number	SD	Length (cm)	SD	Density (g cm ⁻³)	SD
<i>Betula pendula</i>							
Sapling	MT	17	8	44	49	0.449	0.06
Pole	MT	46	25	43	43	0.385	0.03
Mature	MT	121	106	73	84	0.394	0.05
Pole	OMT	130	27	28	42	0.413	0.07
Pole	VT	75	13	56	61	0.411	0.05
<i>Picea abies</i>							
Sapling	MT	22	10	54	53	0.406	0.04
Pole	MT	27	16	49	49	0.408	0.06
Mature	MT	94	54	57	64	0.371	0.03
Pole	OMT	103	55	25	33	0.387	0.03
Pole	VT	131	40	40	46	0.499	0.05
<i>Pinus sylvestris</i>							
Sapling	MT	9	5	54	56	0.320	0.03
Pole	MT	19	13	59	74	0.341	0.04
Mature	MT	77	48	47	65	0.301	0.03
Pole	OMT	73	68	26	35	0.330	0.05
Pole	VT	37	23	39	54	0.333	0.06

SD = Standard deviation

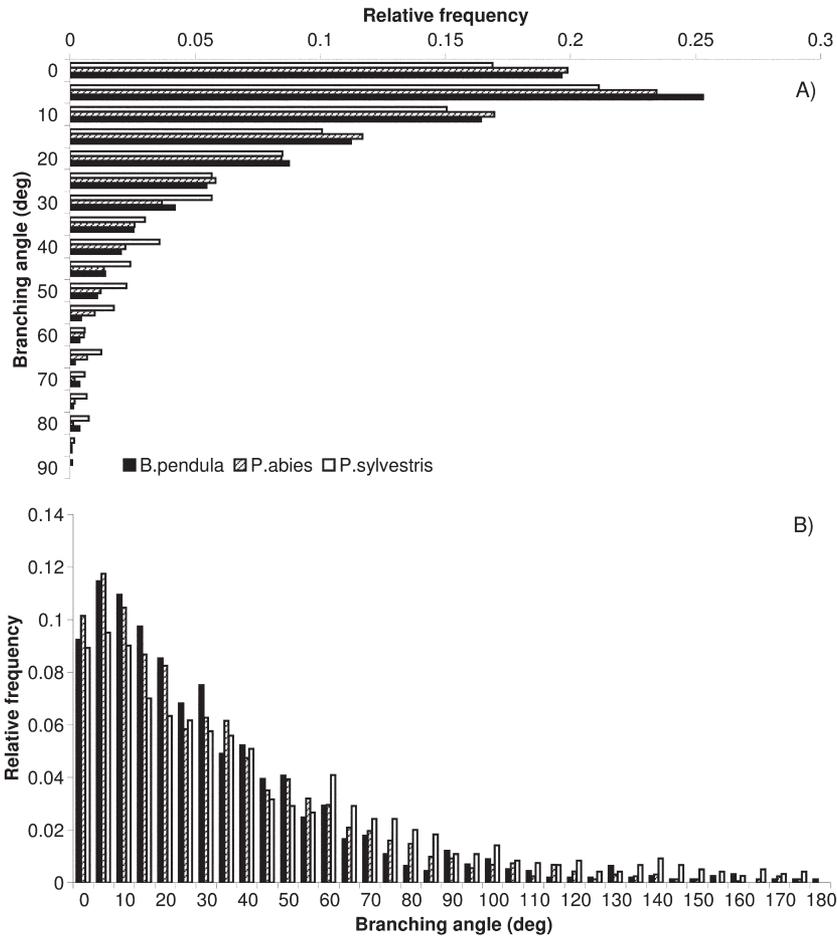


Fig. 3. Vertical (A) and horizontal (B) branching angles in the excavated root systems of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* averaged over different developmental stages and site types. Angles were calculated as the relative deviation of polar and azimuth angles of an internode from the same angles of the previous (“mother”) internode in each node.

Tapering of the root axes (*T*) could be described using the non-linear regression:

$$T = (1 + aD + bD^2)^{-1} \tag{2}$$

The models were statistically significant for each species and site at $p < 0.0001$. The main axis of a root, defined as a chain, consisted of the thickest internodes in a root, and other (secondary) root axes were separated. The secondary axes were further divided into two groups; the first group consisted of branches that led off from the main axis at a distance of less than 1.5 m from the root collar, and the second of all the other branches.

In each case, tapering was calculated as the ratio of the diameter at the beginning of a root axis to the diameter immediately before each node (Fig. 4A and B). Tapering was more regular along the main axis than in secondary axis in each species. However, the regressions for the secondary axes also produced reliable estimates in most cases. The RMSE values were larger along the secondary than along the main axes (Table 7). Estimates of tapering showed that the main root axis of *B. pendula* tapered at the slowest rate at every site and, in most cases, the main root axis of *P. sylvestris* tapered the most rapidly. The clearest difference in this variable was observed in the

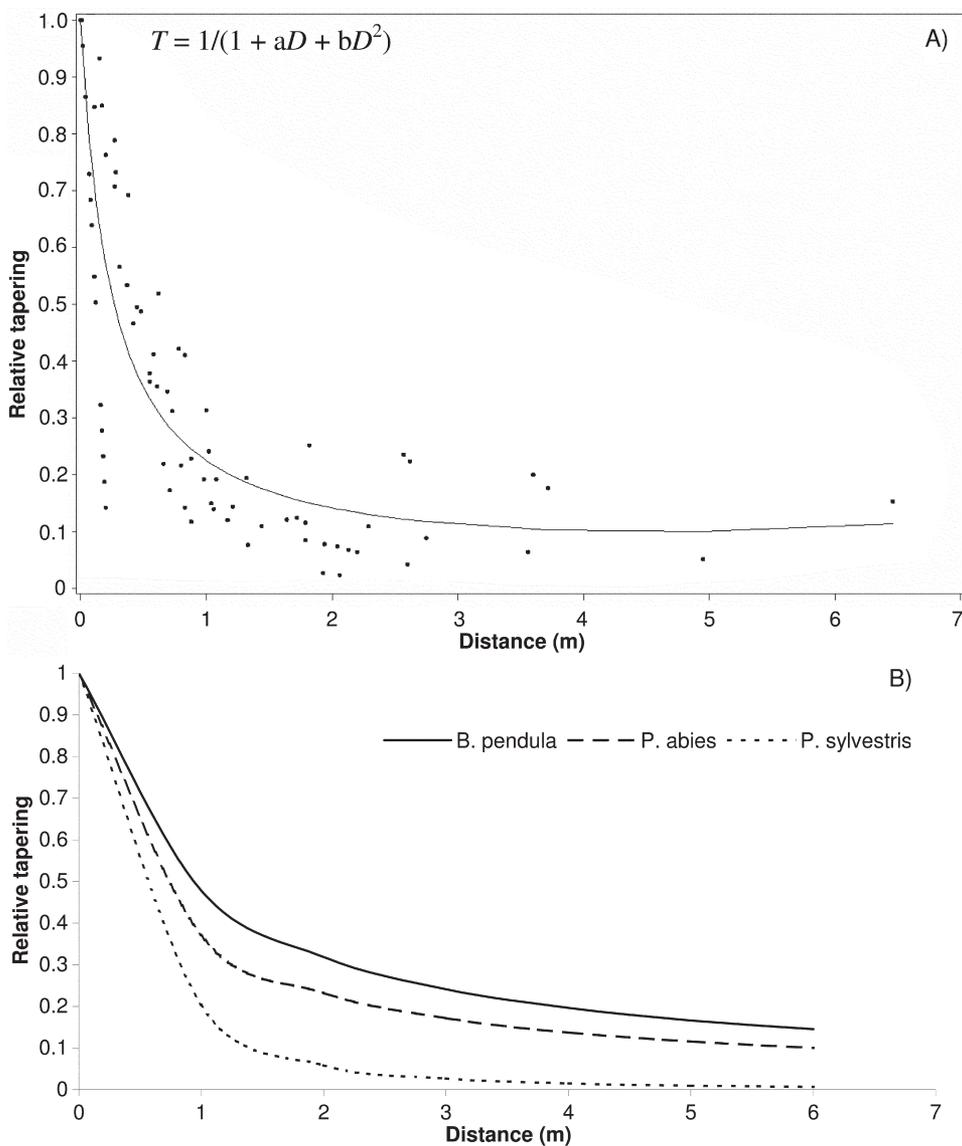


Fig. 4. A) Relative tapering of the main root axes of *P. sylvestris* on an OMT site as a function of distance from the root base. T = Tapering of root axes. D = Distance from the root base. Parameters $a = 2.026$ and $b = 0.878$. B) Tapering of the main root axes of mature *Betula pendula*, *Picea abies*, and *Pinus sylvestris* on an MT site. Curves were drawn using the parameter values obtained from non-linear regressions.

mature MT site and the pole stage VT site.

Variables that describe the total size of a root system, like the number of internodes, total length, and total mass of a root, seemed to be species-specific. Because the diameters of the selected sample roots differed between the species, the total variables were standardised by

dividing them by the squared basal diameter of the proximal root. In addition, logarithmic transformation was used to normalize standardised variables. As a result of this procedure, clear differences were observed in the mean values between the species (Table 8). *Betula pendula* produced the highest and *P. sylvestris* the lowest

Table 7. Values of parameters a and b and RMSE obtained from non-linear regression for tapering of root axes (Eq 2) of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* in different developmental stages and site types. Abbreviations as in Table 1.

Species and Devel. stage	Forest type	Main axes			Secondary axes		
		a	b	RMSE	a	b	RMSE
<i>Betula pendula</i>							
Sapling	MT	2.860	-0.458	0.117	2.991	-1.332	0.108
Pole	MT	2.332	-0.287	0.088	1.883	-0.373	0.173
Mature	MT	1.112	-0.022	0.067	1.801	-0.462	0.145
Pole	OMT	2.701	-0.169	0.130	4.863	-1.144	0.187
Pole	VT	1.340	-0.039	0.145	1.545	-0.243	0.203
<i>Picea abies</i>							
Sapling	MT	3.359	-0.433	0.083	1.645	-0.423	0.167
Pole	MT	2.884	1.011	0.090	2.896	-0.848	0.164
Mature	MT	1.739	-0.043	0.074	1.409	-0.095	0.154
Pole	OMT	2.026	0.878	0.102	3.590	-0.836	0.183
Pole	VT	2.141	0.005	0.063	1.962	-0.372	0.182
<i>Pinus sylvestris</i>							
Sapling	MT	5.067	-0.305	0.078	3.923	-1.091	0.173
Pole	MT	3.425	0.309	0.093	1.638	-0.333	0.143
Mature	MT	-0.170	4.084	0.079	2.582	-0.268	0.161
Pole	OMT	3.865	-0.410	0.143	4.970	-1.118	0.137
Pole	VT	1.216	1.990	0.096	1.790	-0.356	0.175

Table 8. Logarithmic values of standardised total size variables of excavated sample roots of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* in different developmental stages and site types; calculated as total number, length or mass of single root divided by squared basal diameter of proximal root. Abbreviations as in Table 1.

Species and Devel. stage	Forest type	Logarithm of standardised total		
		Number	Length (cm cm ⁻²)	Mass (g cm ⁻²)
<i>Betula pendula</i>				
Sapling	MT	1.08	4.23	3.20
Pole	MT	1.16	4.56	3.20
Mature	MT	1.10	4.81	3.94
Pole	OMT	1.28	4.17	3.17
Pole	VT	1.53	5.29	3.75
<i>Picea abies</i>				
Sapling	MT	1.19	4.71	3.03
Pole	MT	0.98	4.43	2.92
Mature	MT	0.92	4.36	3.42
Pole	OMT	0.87	3.48	2.91
Pole	VT	1.25	4.48	3.70
<i>Pinus sylvestris</i>				
Sapling	MT	0.71	3.90	2.30
Pole	MT	0.45	3.39	2.60
Mature	MT	0.64	3.71	3.04
Pole	OMT	0.51	3.09	2.81
Pole	VT	0.72	3.55	2.77

standardised number of internodes, total length, and total mass. Difference in all transformed standardised variables between *P. sylvestris* and other species was statistically significant (total number $p < 0.0001$, total length $p < 0.0001$, total mass $p < 0.0001$ and $p = 0.0004$ with *B. pendula* and *P. abies*, respectively), whereas *B. pendula* and *P. abies* did not deviate significantly from each other in standardised variables.

3.2.2 Differences Between Developmental Stages within Each Species

The effect of developmental stage on the characteristics of the root systems was studied by comparing the sapling, pole, and mature stages on the MT site. Both the mean proximal root diameter and the number of proximal roots increased within a species from the sapling to the mature developmental stage. These changes corresponded to the diameter growth of the stump. Consequently, no significant differences were found between the developmental stages in the RelSumD² (Table 3).

The maximum radii of the root systems clearly increased from the sapling to the mature stage in all three species (Table 4). The mean values of the observed maximum extensions in 50-year-old mature trees were over twice as large as in the 15-year-old saplings of *P. abies* and *P. sylvestris* ($p < 0.01$), and over three times larger than in *B. pendula* saplings ($p < 0.01$). However, only in *P. sylvestris* radius was significantly bigger also in 30-year-old stand than in sapling stand ($p = 0.0304$). The conifers reached similar peak values, but the mean of the maximum radii of *P. abies* root systems was notably larger in the mature stage. Also rooting depth increased along the developmental stage from the sapling to the mature stand (trend significant in each species $p < 0.05$).

According to the index values (Eq. 1), the topology of the root systems changed with developmental stage in a similar way in the conifer species, i.e. the indices were higher on the sapling and pole stage MT sites and very low on the mature MT site in both species. *Betula pendula* deviated from the conifers by having quite similar index values on all MT sites, which implies that developmental stage did not affect topology of its root system (Table 5).

Basic density changed between developmental stages in *B. pendula* and *P. abies* (Table 6). However, direction of change was opposite in these two species i.e. saplings of *B. pendula* had lighter wood than trees in pole ($p = 0.0029$) and mature stage ($p = 0.0133$), whereas in *P. abies*, trees in mature stage site had lighter wood than saplings ($p = 0.0444$) and there seemed to be slight difference also with pole stage ($p = 0.0777$). In *P. sylvestris*, no statistically significant difference was detected between developmental stages.

Tapering of the main root axis was quite similar between the developmental stages in *P. sylvestris*, whereas the main axes of *B. pendula* tapered more slowly in the older developmental stages. In *P. abies*, there was almost no difference between the sapling and pole stages, but in the mature stage the main axes tapered much more slowly (Table 7). Tapering of the secondary axes was more irregular and no clear trend was found between the developmental stages.

The developmental stage of a stand had significant effect only on the standardised mass in *P.*

sylvestris, in which mature trees had significantly higher root mass than saplings ($p = 0.0287$). In standardised number or length no significant differences were detected between stages, although saplings of *P. sylvestris* seemed to have slightly higher number and length than pole stage trees ($p = 0.0593$ in number, and $p = 0.0993$ in length) (Table 8). Mean length of internodes increased in *B. pendula* from younger stages to mature stage ($p < 0.001$), whereas in the conifers, developmental stage had no effect on the mean length of internodes.

3.2.3 Differences Between Forest Site Types within Each Species

The effect of site type was studied by comparing the root system characteristics between the pole stage VT, MT and OMT sites. The effect of forest site type was parallel in the most variables for all species, but the effect was generally stronger for *B. pendula* than for the conifers.

In all species, the highest mean value of RelSumD² was observed on the OMT site, and in each species difference between OMT and YF sites was significant ($p = 0.0357$ in *B. pendula*, $p = 0.0050$ in *P. abies* and $p = 0.0142$ in *P. sylvestris*). However, OMT and VT was more similar in terms of RelSumD², since only in *P. sylvestris* RelSumD² seemed to deviate also between OMT and VT ($p = 0.0729$). The reason for the difference in RelSum² between the VT and MT sites was clearly the larger mean diameter of proximal roots on the VT than on the MT site in all three species (significant in *P. abies* $p = 0.0001$). An increasing trend ($p = 0.20$) with productivity of the site was observed in the number of proximal roots of *B. pendula*, but not in the conifers. The adventitious rooting of *B. pendula* increased with increasing site productivity (Table 3).

Between forest types, the mean of the maximum root system radius was the largest on the VT site in all species, but variation within all site types was high (Table 4). The effect of site productivity on rooting depth varied among the species. The mean depth of the roots of *B. pendula* was the biggest on the VT site ($p < 0.01$), while the roots of *P. sylvestris* were the most superficial on the VT ($p < 0.05$). The rooting depth of *P. abies*

was similar on the VT and OMT sites, and the shallowest on MT ($p < 0.0001$). However, both *B. pendula* and *P. abies* reached their maximum depth on the VT.

The change in topological indices with forest type was almost parallel for all the species, i.e. the index values increased considerably from OMT to MT, and decreased from MT to VT. However, the index value for *P. sylvestris* was higher on VT than on OMT; there was no difference between VT and OMT in *B. pendula*, and the index value for *P. abies* was even lower on VT than on OMT (Table 5).

The clearest effect of forest site type was in the mean length of the internodes, which was the shortest on the OMT site in all species. Further, the mean values were surprisingly similar between the species on OMT (Table 6). In *B. pendula*, internode length decreased linearly with increasing productivity ($p < 0.01$), whereas the internode length of *P. sylvestris* increased clearly ($p = 0.0028$) and in *P. abies* only slightly ($p = 0.1913$) from VT to MT and then decreased sharply from MT to OMT ($p < 0.0001$ in both).

No statistically significant difference was observed between forest types in basic density of *B. pendula* and *P. sylvestris*. *Picea abies* had heavier wood in VT than in the other sites ($p < 0.0001$, Table 6). Spruce trees in VT were established in understorey and therefore their growth was suppressed about twenty years until opening the dominating canopy.

The site type did not have any effect on tapering of the main root axis of *P. sylvestris*, whereas the main root axis of *B. pendula* and *P. abies* tapered clearly less on VT than on OMT. The secondary axes tapered more on the OMT site than on VT in all three species (Fig. 3 A, Table 7).

All the standardised total variables of *B. pendula* reached their maxima on the VT site, but only the total length was significantly different ($p = 0.05$) between the VT and OMT sites. The effect of forest site type on the coniferous species was much smaller also in terms of these variables (Table 8). Similar values of the standardised total variables in all forest site types were found in *P. sylvestris*. In *P. abies*, the total number was quite similar between forest types, yet the standardised total length was the lowest in OMT ($p = 0.0267$ with MT and $p = 0.0417$ with VT) and as the result

of this, together with observed increment in the basic density from VT to other sites, the highest total mass was observed in VT ($p = 0.0141$ with MT and $p = 0.0192$ with OMT).

3.3 Proximal Root Diameter as a Predictor of Total Root Size

The species-specificity of the total variables was illustrated by means of simple linear regressions, in which only the species were separated and stand adjustments were not used (Fig. 5). Despite this, reasonably reliable estimates were obtained. The squared proximal root basal diameter was used as the independent variable. Dependent variables were total length, total number of internodes, and total mass of a single root. The models were forced through the origin, since a root cannot have any dimensions if the diameter at starting point is zero. The indicator variables (dummy) were used to separate the individual species. *Betula pendula* produced considerably more root biomass per cross sectional area (Fig. 5 A) than *P. sylvestris* and *P. abies*, which was a result of the higher number of internodes and total length in *B. pendula* (Fig. 5 B and C).

4 Discussion

4.1 Proximal Root System

Root architecture is a result of genotype-environment interactions (van Noordwijk et al. 1996). The rooting behaviour of the species studied was different. The characteristics of the root systems also seemed to be more species-specific, and were relatively independent of the stand developmental stage or forest type. As far as the two main functions of the root system are concerned, i.e. anchorage and resource acquisition, the characteristics of the proximal root system seem to be primarily related to their anchorage function. However, the species differed in terms of how they have solved this problem. *Betula pendula* had the highest number of proximal roots on each site, thus increasing cohesion between the soil and root system (Coutts 1986). Half of the

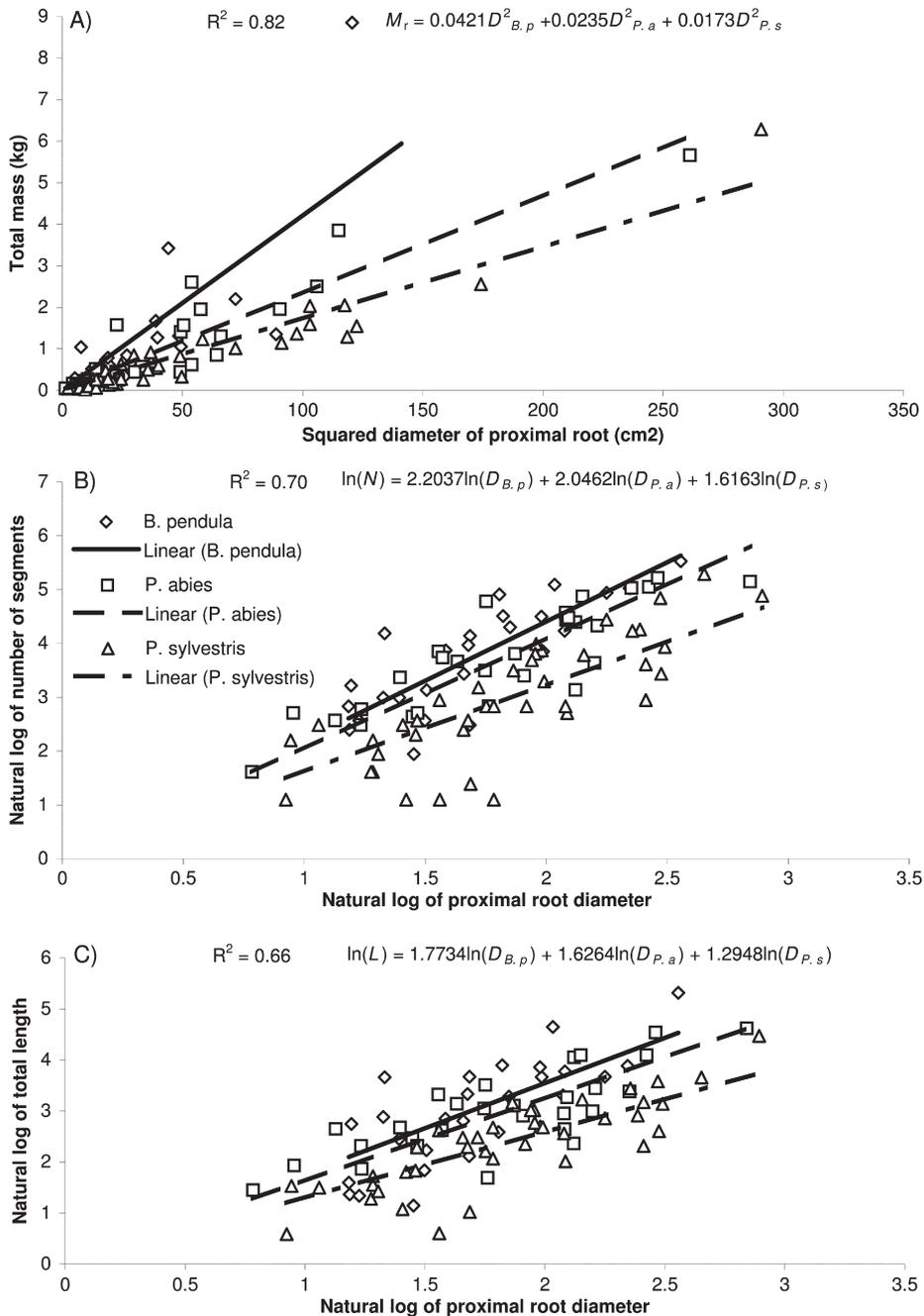


Fig 5 A–C. Total size of a root (main axis and all lateral axes combined) of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* in different developmental stages and site types as a function of the squared basal diameter of the proximal root. M_r = Total mass of a root. N_r = Total number of internodes in a root. L_r = Total length of all internodes in a root. $D_{B,p}$ = Basal diameter of a *B. pendula* proximal root. $D_{P,a}$ = Basal diameter of a *P. abies* proximal root. $D_{P,s}$ = Basal diameter of a *P. sylvestris* proximal root.

P. sylvestris trees had a taproot, whereas secondary diameter growth of the proximal roots was the most pronounced in *P. abies*, indicating that more prominent thigmomorphogenetic development in the roots is a complementary means to react to mechanical stress (Coutts et al. 1999). Although the lack of a taproot in *P. sylvestris* in some studies (Laitakari 1927) has been related to soil properties, in our study trees growing in close proximity to each other on the most homogeneous VT site were different; some having and others lacking a taproot. Thus, it may be hypothesised that the existence of a taproot is genetically determined at the tree level.

4.2 Influence Area of a Single Tree

The other main function of root systems, resource acquisition, is reflected in the spatial dimensions (influence area), branching pattern, and total size variables of a root system. The differences in the spatial dimensions of root systems between species, found in our study may be a result of differences in growth strategy. In general, for a given size of a tree, angiosperm deciduous trees transport daily much more water than the slower growing gymnosperm conifers (Meinzer et al. 2005), and therefore we can most probably assume that the same differences exist between the deciduous *B. pendula* and the conifers *P. sylvestris* and *P. abies*. *Betula pendula* had solved this problem by producing an extensive root system in all dimensions. This observation is consistent with hypotheses concerning the higher water and nutrient uptake efficiency of more extensive root systems (van Noordwijk and de Willigen 1991).

The observed different patterns between the species in vertical distribution of their roots, i.e. *P. abies* exploited the topsoil, whereas other species had a large number of roots in the deeper mineral soil layers, and that *B. pendula* occupied primarily the illuvial and *P. sylvestris* elluvial layer, are in good agreement with the studies of Laitakari (1927, 1935). However, both the horizontal and vertical extension was slightly overestimated, because the distances were determined according to the assumption that the internodes are straight. However, the depth estimate is more affected by the fact that the vertical variation in the soil

surface – e.g. old stumps, rocks, depressions etc. – was not taken into account. This may have an important effect on individual roots, but it should have negligible effect on the distributions at the species level. Another problem is the accumulation of litter around the bottom of the tree stem, which may be the reason for the increase in the mean depth of the root systems with age because the cutting height was determined as immediately above the soil surface or just above the first proximal root. Owing to these reservations, the absolute depth values may be slight overestimations, especially in old stands. However, the differences between the species are valid.

Determination of the influence area on the basis of the horizontal and vertical extension includes a strong assumption concerning the symmetrical dimensions of root systems. However, root systems can be highly asymmetric owing to the effect of non-symmetric mechanical stress (Coutts 1986, Coutts et al. 1999) and patchy nutrient availability in the soil (Lynch 1995, Casper et al. 2003). In controlled-environment studies on fast-growing grasses, it is relatively easy to determine the influence area and to obtain data for model parameterization. However, interpretation of the results in field studies with long-living trees is more complicated, and knowledge on many below-ground processes, e.g. how plants detect nutrient “hot-spots”, is currently lacking. In addition, resource transfer between trees through root grafts (Yli-Vakkuri 1954, Bormann 1966, Keeley 1988, Külla and Löhmus 1999) or via common mycorrhizal networks (Newman 1988, Simard et al. 1997, Robinson and Fitter 1999) may be just as important as an asymmetric root system for regulating the influence area of a single tree. However, the extent and importance of these factors is still under discussion.

Interestingly, only one root graft between two *B. pendula* individuals was found in this study even though in 60 trees all roots attached to root collar (929 roots) were exposed to their first branching event and additional 92 roots were exposed completely, totalling 6300 internodes. Yli-Vakkuri (1954) found that root grafting is usual phenomenon in *P. sylvestris* stands over 40-year-old i.e. over 20% of trees had grafts. In younger stands grafts were much rarer e.g. no grafts were observed in stands under 20 yrs.

and only 2% of trees 20–40-year-old had grafts. However, in this study, no root grafts were found even in 50-year-old stand, although almost 1500 root segments were exposed there. One explanation could be that Yli-Vakkuri studied root grafts in pure, naturally regenerated *P. sylvestris* stands, whereas in our study, apart of VT site, at least one tree species was planted. Genetic dissimilarity is bigger between trees in artificially than in naturally regenerated stand, which could inhibit root graft formation (Loehle and Jones 1990). Question how common root grafts are is important, since they are thought to be pathways for root rot (*Heterobasidion annosum* (Fr.) Bref.) to spread from diseased tree to healthy trees (e.g. Kùlla and Löhmus 1999). If root grafts are much more uncommon than thought, then another mechanism for root rot spread may exist.

4.3 Branching Patterns

Each species seemed to have its own characteristic root branching pattern, although the trends related to the developmental stage and forest site type were mostly parallel for all three species. Fitter et al. (1991) showed, on the basis of correlation calculations between exploitation efficiency and architectural variables obtained from modelled root systems, that internode length is the dominant factor from the efficiency viewpoint. Their model considered only one aspect, the exploitation efficiency, and they assumed that the roots grew in homogeneous soil. Despite this, the results obtained in our study in heterogeneous boreal mixed forest are consistent with their predictions, because all the species mainly adjusted their internode length according to the forest site type.

It appeared to be possible to describe the topology of the root systems to some extent on the basis of simple topological indices (Fitter 1996). The slope values of the regressions were significant, indicating that the species differed from each other. The slope value was very high for *P. sylvestris* in the sapling and pole stages (0.910 and 0.844, relatively; theoretical maximum is 1), indicating strongly root system branching in a herringbone manner; hence favouring exploration over exploitation in the early phases of development.

Betula pendula and *P. abies* also had their highest indices on the sapling and pole stage MT site, although the indices were clearly lower than in *P. sylvestris*. Consistently in all three species, the root systems on the mature MT and more fertile OMT sites approached dichotomous branching, as indicated by the low index value. This implies preference of exploitation over exploration, or that there is no need for extensive exploration if the skeleton of the root system has already been formed or if soil resources are abundant.

However, the observation that all the species had lower indices on the VT than on the MT site (*P. abies* even lower than on OMT) is difficult to interpret and also contradicts the predictions of Fitter and Stickland (1991). The difference in the indices between VT and MT was mainly the result of a notably larger number of exterior internodes on the VT site. A possible explanation could be that the simple indices used here are not able to depict the essential functionality of the root systems of long-living forest trees in respect to varying soil fertility. A more speculative explanation for the conflicting observation could be the effect of mycorrhizal associations. The structure of the mycorrhizal community has been shown to alter with changes in soil fertility (Pennanen et al. 1999). Moreover, Nilsson et al. (2005) reported the highest fungal biomass on a site with the lowest productivity. Therefore one could speculate that the more extensive mycorrhizal hyphae on VT sites could have greater importance for the exploration of soil resources than on MT sites, leading to differences in the root system architecture. However, to the authors' knowledge, no studies have been carried out on this question.

Tapering of the root axes could be described using a simple non-linear regression. The results imply that the tapering of the root axis is the result of the two combined objectives; the anchorage stability and uptake of the soil resources. First, species-specific traits were found, especially in tapering of the main axis; main axis of *P. sylvestris* tapered similar way in the different developmental stages and site types, while secondary growth of structural roots of both *P. abies* and *B. pendula*, which do not have a taproot, was more pronounced in mature MT and OMT sites, in order to support the increasing stem mass and resist the

wind forces affecting the larger crown. Second, site type affected the tapering of secondary axes more than the developmental stage i.e. root axes tapered slowly in VT compared with OMT, while tapering was more similar even between mature and sapling stages on same forest type. That could illustrate importance of the secondary axes in the exploration of the scarce soil resources in the case of the low soil fertility.

4.4 Total Size of the Root Systems

4.4.1 Trends in the Standardised Total Size Variables of Individual Roots

The total size of the root systems, determined on the basis of sample roots, i.e. total number of internodes, total length and total mass, seemed to be a strongly species-specific characteristic. *Pinus sylvestris* had small and simple root systems, especially in comparison with *B. pendula*. Differences in the absolute values of the total size variables were obvious between the developmental stages. When secondary growth of the proximal roots was taken into account, only root mass in *P. sylvestris* changed significantly from saplings to mature stage, as a result of slight trends between in the standardised number and length.

Interpretation of trends related to the forest site type is more difficult. The roots of *P. sylvestris* did not appear to respond to soil fertility, whereas *B. pendula* showed a high sensitivity to soil fertility by adjusting the characteristics of its root systems to different environmental conditions. *Betula pendula* reacted to a higher fertility by intensifying branching and producing more branches in each node, thus favouring exploitation as a rooting strategy. In dry, nutrient-poor conditions, total length of the roots was notably larger, illustrating the importance of exploration. *Picea abies* on the VT site had been suppressed (illustrated in higher wood density in VT) and its mean age was higher than that in the other pole stage sites. Therefore, the effects of forest site type on the roots of *P. abies* should be treated with caution. The observed differences between the species in terms of how strongly they adjusted the characteristics of their root system according to soil fertility, agrees with the predictions of

Grime (2001), i.e. *P. sylvestris* can be regarded as a “stress-tolerator”, whose growth strategy is the conservation of captured resources and, therefore, it does not need to adjust the characteristics of its root systems as much as *B. pendula*, which follows the growth strategy of a “competitor” trying to maximise capture of the resources. However, our finding is contradictory to the conclusion of Putz and Canham (1992), who concluded that plants typically growing under resource-poor conditions need to have higher root plasticity because of a higher spatial heterogeneity of soil resources. However, although the most typical growing sites in natural conditions are different for these species, i.e. *P. sylvestris* dominates in the least fertile and the other two species growing on more fertile sites, the difference may be so small that it explains our conflicting result.

In addition, both developmental and fertility trends are affected by silvicultural operations like thinning, which stimulate the diameter growth of structural roots (proximal roots) in order to increase the mechanical stability of trees (Wilson 1975, Fayle 1983, Urban et al. 1994, Nicoll et al. 2006). This effect was obvious when comparing the 30-year-old MT and VT sites. The more fertile MT site had much more trees per hectare than the less-fertile VT site, which was thinned once. The mean diameter of the proximal roots was much smaller on the MT site for each species. The squared basal diameter of the proximal roots was the best predictor over the stands for the total size of individual roots. Therefore, interpretation of a single effect on the properties of root systems is difficult.

4.4.2 Total Size of Single Roots and the Root System through the Simple Linear Regressions

Van Noordwijk et al. (1994) used the diameter of a proximal root to derive the theoretical total root size. However, they did not seek empirical confirmation from field observations for their deductions. Oppelt et al. (2001) related root collar diameter to the total size of root systems in tropical trees. They operated at the whole root system level and predicted variables like the number of internodes and total length on the basis of

linear regressions. In our study, similar regressions were used to estimate total size variables of individual roots. However, the slope values, e.g. for total length (1.29–1.77), were clearly lower than the allometric exponent 2 proposed by van Noordwijk et al (1994), and also lower than Oppelt et al. (2001) reported (1.95) in their study. Estimates obtained from single roots were statistically reasonably accurate and, consequently, the same regularities could be assumed to exist at the whole root system level. It is possible to estimate the total size of the whole root system using the equations presented in this paper. However, even better estimates might have been obtained by taking into account the variation between the stands through stand adjustments for intercept and slope, as applied by Nielsen and Hansen (2006). Unfortunately, because of the small number of observations per stand, it was not reasonable to construct regression models based on different stands.

5 Conclusions

The overall finding was that the main feature of the studied root systems was plasticity. This was illustrated by the large variation in all the observed variables between tree individuals and even within the same root system. As a consequence, statistically significant differences between species or stands were scarce. However, species-specific traits of root system architecture, like spatial dimensions, branching patterns, tapering of root axes, and total number of internodes and total length, appeared to be more important than the site effects. Simple regressions, in which only the species were separated, produced relatively reliable estimates of root system characteristics. Therefore, the results obtained in this study provide ecological information about the roots and root systems of three boreal tree species, e.g. the approximate influence area of the root system of an individual tree that forestry professionals need to take into account in silvicultural operations. More detailed architectural variables like tapering of the root axes and internode length on the different types of site presented in this paper may be useful for modelling purposes.

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Total of 52 references