Root length and distribution in the mineral soil of a mixed deciduous forest (experimental forest aelmoeseneie)

VANDE WALLE, I., WILLEMS, S. & LEMEUR, R.

Laboratory of Plant Ecology
Coupure Links 653, B - 9000 Gent
e-mail : inge.vandewalle@rug.ac.be

Abstract

Root length and root mass were studied in two different forest stands : an oak-beech and an ash stand, both in the 'Aelmoeseneie' experimental forest at Gontrode, Belgium. In the oak-beech stand, the length of the finest roots (< 1 mm) was significantly higher than the length of the other diameter classes (1-2 and 2-5 mm) in the upper 60 cm of the mineral soil. Because of large variances, this significance could not be found in the ash forest. In this ash forest type, the length of the finest roots in the upper mineral soil layer (0-15 cm) was higher than all the other lengths, both considering the vertical root length distribution within the ash plot, and comparing the ash plot to the oak-beech stand. For the root mass, only the amount of roots with a diameter between 2 and 5 mm in the upper mineral soil layer of the ash plot was significantly higher than the others. Specific root length (m root/g D.M.) is calculated for both the oak-beech and the ash plot. These values can be used to convert biomass data into root length data, which gives a better indication of the water uptake capacity of the forest stand.

Key words : *Quercus robur, Fagus sylvatica, Fraxinus excelsior, deciduous forest, root length, root mass, root distribution, specific root length*

1. Introduction

Water is an essential plant component, and as such, inevitable for plant life. Because of its unique properties, water is the basis of much environmental physiology. It is a strong solvent, thus providing a good medium for biochemical reactions and for transport. Water is also involved as a reactant in processes such as photosynthesis and hydrolysis. Its thermal properties are important in temperature regulation of the plant and its incompressibility is important in support and growth (Jones, 1992).

Root systems support the plant and provide the means for absorbing water and nutrients from the soil. To be efficient absorbers of water and nutrients, roots need large absorbing surfaces. As such, root length gives a better indication of the water uptake capacity of a crop than root biomass.

Fine roots (diameter < 1 mm) are the most active part of the root system, as far as water uptake is concerned (Landsberg, 1986; Van Den Burg, 1996; Lambers *et al.*, 1998).

The way of development of a root system depends on different environmental factors (Hendriks & Bianchi, 1995). A number of factors are reported to explain the large variability in the results of root system investigation programmes performed in forest ecosystems. Soil water content, soil temperature and the degree by which the soil is compacted (Persson, 1979; Landsberg, 1986; Van Den Burg, 1987; Van Praag *et al.*, 1988; Hendrick & Pregitzer, 1993; Lambers *et al.*, 1998), the nutrient status of the soil (Ehrenfeld *et al.*, 1992; Arnone, 1997; Egli & Körner, 1997; Majdi & Kangas, 1997; Mou *et al.*, 1997) and stand age (Ehrenfeld *et al.*, 1992; Hendriks & Bianchi, 1995), are all referred to as influencing the root length and the root length variability. The influence of external factors as distance to the stem of the trees, throughfall and stem flow, thickness of the humus layer is not unambiguous. Büttner & Leuschner (1994) mention a strong positive correlation between biomass and distance to the stem for beech, in contrast to what is found for oak. Pieters & Segers (1992) state that a huge stem flow favours the growth of fine roots (< 1 mm) near to the stem.

Knowledge of the rooting depth, the root length and the vertical root distribution is necessary to come to a realistic simulation of the water balance of a forest ecosystem. The objective of the experiment introduced here was to examine the root distribution in a mixed deciduous forest : the 'Aelmoeseneie' experimental forest at Gontrode. As this experimental forest exists of two different forest types, the question was if there exists a difference in vertical root distribution between those two forest types.

2. Material and methods

2.1. Site description

Measurements are performed in the 'Aelmoeseneie' experimental forest. This forest is situated in Gontrode (50°58'N, 3°48'E), near to the city of Gent. This mixed deciduous forest covers a total area of 28 ha. The experimental zone (1.827 ha), which has been closed for the public since 1994, exists of two plots : an oak-beech stand with *Quercus robur* and *Fagus sylvatica* as main tree species, and an ash stand with *Fraxinus excelsior* as dominant species. Information about stem number, basal area, stem volume, stem mass and tree height can be found in Vande Walle *et al.* (1998). The soil of the oak-beech stand is a typical thin quaternary layer of sand loam with a spotted texture B horizon on a shallow impermeable clay and sand complex of tertiary origin (uLdb-uLub). In the ash forest type, the impermeable layer ceases, but this alluvial part of the experimental zone is obvious ground water dependent (soil type Ldp-Lhp). In the experimental area, an extended set of information about the water, carbon and nutrient cycle is collected. A description of the experimental set-up for the biogeochemical research is given in Samson *et al.* (1996).

2.2. Sampling method

Different methods to study root systems are described in the literature. Each of them can be used in specific circumstances. The most important methods for tree root study are (Persson, 1979; Kienhuis, 1987; Olsthoorn, 1988; Nadelhoffer & Raich, 1992; Pieters & Segers, 1992; Cermák *et al.*, 1998) :

a) The entire root system can be excavated. This method gives an excellent view on the root system, but is very labour intensive, time-consuming and destructive.
b) The root system can be subdivided in 'soil blocks' of fixed dimensions (monoliths), which can be studied in the laboratory afterwards. Besides root distribution, root growth can be determined. Therefore, roots are removed from the soil blocks, which are placed back in the soil. This monolith-method is labour-intensive, and can't be used when thick roots are present in the soil. Also, when the soil is too sandy, soil particles don't stick together very well, and this method can't be used.
c) Samples can be taken by using a root auger with a special indented head. This method can be used to give an idea of the spatial variability of the rooting system and is not destructive. However, it is difficult to use if thick and woody roots are present.
d) Profile walls can be dug horizontally or vertically. Information can be saved as drawings or photographs. This method gives a clear two-dimensional image of the root system, but is destructive and labour-intensive. Another negative aspect of this method is the fact that some roots are overlooked, and as such, not taken into account.
e) A method which doesn't disturb the soil uses 'mini-rhizotrons'. Transparent tubes are brought into the soil. Pictures can be taken by using an endoscope. Comparison of photographs taken at different times, gives an indication of the evolution of the root system. Mini-rhizotrons are easy to install, and give a good spatial integration. However, the technique is expensive, and has the disadvantage that only the roots growing against the transparent wall are observed. By using this technique, only the evolution of the root length can be examined, and the determination of root mass is impossible (Olsthoorn, 1988; Hendrick & Pregitzer, 1993; Majdi & Kangas, 1997).

In the study presented here, the third method (root auger) was chosen. This is a relative cheap method, which doesn't disturb the forest soil too much, and which makes it possible to take samples at different places in the forest. As such, horizontal variability could be studied. This method is developed by Goedewaagen (Kienhuis, 1987). The brace head existed of a metal cylinder, which had saw teeth. The diameter was 8 cm, and the length was 14.5 cm, and as such, the volume of each sample was equal to 729 cm^3.

Samples were taken in July and August 1997, in the oak-beech plot as well as in the ash plot (Figure 1). As other experiments are going on in the experimental zone, the choice of sampling places was somewhat limited. At each sampling place, 5 samples of the mineral soil were taken :

0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm and 60-75 cm. As 12 places were sampled, 60 soil samples had to be examined.

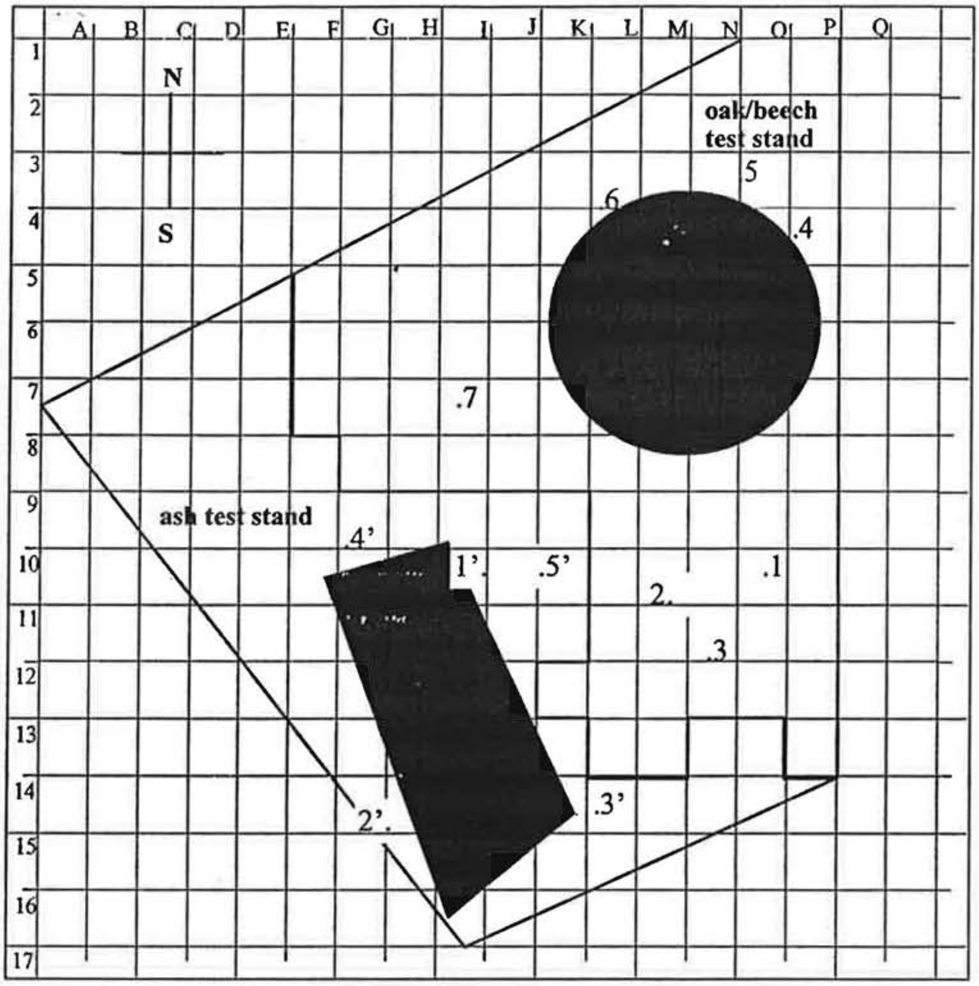

Figure 1. Experimental zone in the 'Aelmoeseneie' forest with indication of the sampling places (1,2,3,4,5,6,7 : samples in the oak-beech plot; 1',2',3',4',5' : samples in the ash plot). The black areas are the level II plots.

2.3. Treatment of the soil samples

The soil samples were washed to separate the roots from the soil material. Each soil sample was brought in a bucket. Water and $Na(PO_4)_6$ were added. After mixing, the product needed 48 hours to disperse the clay complexes. Afterwards, the content of the bucket was poured over a sieve with a mesh width of 0.5 mm. The roots could be separated from the organic material particles manually. The roots were divided in different diameter classes. In accordance to the literature (Landsberg, 1986; Kienhuis, 1987; Van Praag *et al.*, 1988; Ehrenfeld *et al.*, 1992; Büttner & Leuschner, 1994; Hendriks & Bianchi, 1995; Van Den Burg, 1996; Mou *et al.*, 1997), diameter classes considered are :

a) < 1 mm
b) 1-2 mm
c) 2-5 mm
d) > 5 mm.

Fine roots (< 1 mm) play the most important role in the water uptake by the trees. A sliding compass was used to measure the root diameters.

Living and dead roots were separated on the base of morphological characteristics. Living roots have a white, elastic heart, while dead roots are mostly darkly coloured and less flexible (Pieters & Segers, 1992; Büttner & Leuschner, 1994). The roots were dried at 60 °C, for 2 days.

2.4. Root length and root biomass

The capacity of water and nutrient uptake is strongly related to the water absorbing surface. As such, it is interesting to determine the length of the roots of the different diameter classes. Biomass doesn't give an adequate indication of the water uptake capacity, but is measurable easier than root length.

Roots are not always straight. This makes direct measurement of the root length difficult. Sometimes, an enormous root length has to be determined, which makes the direct method time-consuming. Indirect methods study the root length of a part of the soil sample. The total root length is then recalculated by the use of the ratio [root biomass of the sample / root biomass of the studied subsample]. These methods give no exact results, as large variations can occur in the ratio mass/length.

In this study, the root length of the entire sample was measured. The CI-203 Portable Laser Area Meter was used (CID, instruction manual). This system consists of an optical scanner and a little tray (the CI-203RT Root Tray) where the roots are put. These roots are spread as much as possible over the surface of the tray. A rotating mirror causes a laser beam to scan the roots 400 times per second. This beam is reflected by the special surface of the tray, and the reflected part is detected by a light sensor. The microcomputer calculates the total length of the roots in the tray on the base of this reflected signal and the speed of the moving scanning system.
The roots were weighed with a balance. type AG204 DELTARANGE (precision 0.1 mg).

3. Results

Statistical analysis of root length, root mass and specific root length was carried out with the statistical package SPSS. In this analysis, only data of roots less than 5 mm in diameter were involved. Roots more than 5 mm in diameter didn't appear frequently in the samples, and are not that important in the water uptake by the trees. One-Way ANOVA was conducted to analyse differences in both root length and root mass. In the first place, the different diameter classes were compared within each soil layer. Afterwards, the vertical distribution within each diameter class was examined. At last, the root length and mass in the two forest types were compared. Significant results ($p < 0.05$) are mentioned in the text below.

3.1. Root length

3.1.1. Vertical distribution of the living roots

Figure 2 and Figure 3 exhibit the root length in the successive layers of the soil profile for the oak-beech and the ash stand respectively.

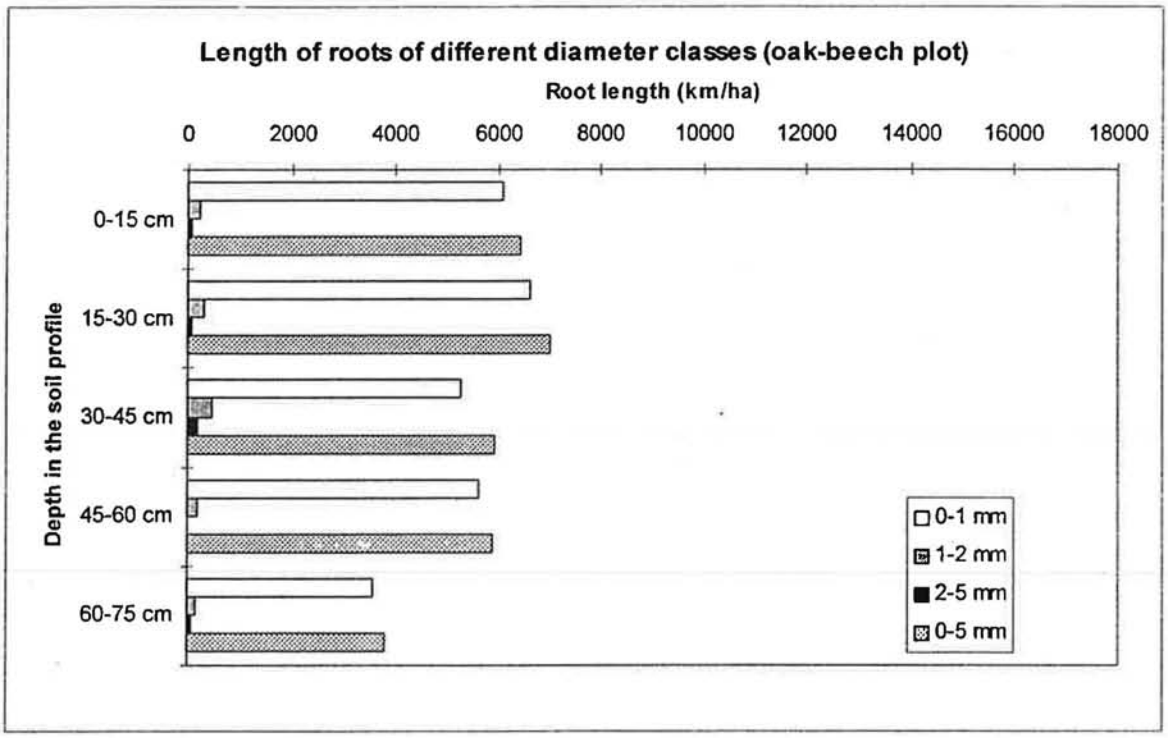

Figure 2. Living root length for the different soil layers of the oak-beech stand (root length expressed in km/ha over a depth of 15 cm)

In the oak-beech stand, the length of the roots < 1 mm was always significantly higher than the length of the other diameter classes, except for the lower soil layer (60-75 cm). For the ash plot, it is obvious that the length of the finest roots was always higher than the length of the other roots (Figure 3). However, mean root length differed only significantly in the upper soil layer of the ash plot.

A second statistical test was used to study the vertical distribution of the root length. This analysis made clear that there was neither a significant increase nor a decrease in the length of the roots of different diameter classes with increasing depth in the soil profile of the oak-beech plot. For the ash plot however, the length of the finest roots in the upper soil layer was significantly higher than the length in the other layers. For the other diameter classes, no significant differences in root length were found.

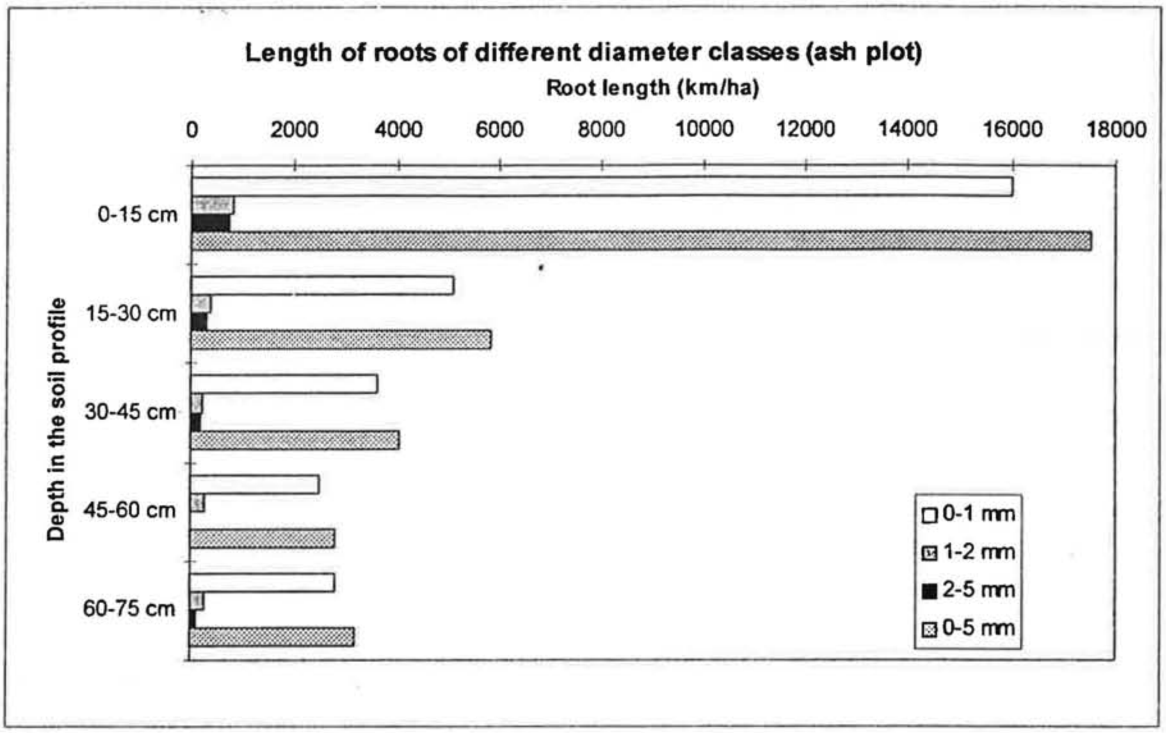

Figure 3. Living root length for the different soil layers of the ash stand (root length expressed in km/ha over a depth of 15 cm)

3.1.2. Comparison of the root density in the oak-beech and the ash stand

In Table 1, 2 and 3, a comparison is made between the root length of the living roots of different diameter classes in the five observed soil layers of the two plots. In these tables, root length is expressed as root density, which is the length of the roots (in cm) per cubic cm of soil.
Statistical analysis proved here that only the means of the length of the finest roots differed significantly for the upper layer of the oak-beech and the ash stand. Because of the large variances on the calculated means, no other significant differences could be indicated.

*Table 1. Root density (and standard deviation) of the living roots with a diameter < 1 mm (cm root/cm³ soil); significant differences are indicated with an **

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.4073 (0.2091) *	1.0666 (0.1791)*
15 - 30	0.4415 (0.2049)	0.3409 (0.1476)
30 - 45	0.3507 (0.2196)	0.2404 (0.1580)
45 - 60	0.3756 (0.5669)	0.1674 (0.1307)
60 - 75	0.2377 (0.1641)	0.1877 (0.1140)

Table 2. Root density (and standard deviation) of the living roots with a diameter between 1 and 2 mm (cm root/cm³ soil)

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.0158 (0.0104)	0.0539 (0.0390)
15 - 30	0.0209 (0.0205)	0.0269 (0.0150)
30 - 45	0.0312 (0.0237)	0.0167 (0.0133)
45 - 60	0.0135 (0.0122)	0.0180 (0.0132)
60 - 75	0.0098 (0.0117)	0.0185 (0.0182)

Table 3. Root density (and standard deviation) of the living roots with a diameter between 2 and 5 mm (cm root/cm³ soil)

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.0054 (0.0093)	0.0482 (0.0374)
15 - 30	0.0057 (0.0098)	0.0207 (0.0213)
30 - 45	0.0134 (0.0195)	0.0129 (0.0133)
45 - 60	0.0036 (0.0061)	0.0021 (0.0030)
60 - 75	0.0055 (0.0096)	0.0075 (0.0103)

From the data in the Tables 1, 2 and 3, it was calculated that in the upper 30 cm of the oak-beech stand, 47 % of the finest roots appeared. For the medium fine roots (1-2 mm) and the 'thicker' roots (2-5 mm), this percentage was 40 and 33 respectively. When the diameter classes are considered together, 46 % of the roots appeared in the upper 30 cm. For the ash stand, this was 70 % (70 % for diameter class 0-1 mm, 60 % for the class 1-2 mm and 75 % for the class 2-5 mm).

3.1.3. Ratio living/dead roots

The root length of the living and the dead roots of the 0-1 mm diameter class is presented in Table 4. The ratio living to dead roots was calculated and presented in Table 5.

Table 4. Length (cm root/cm³ soil) of the living and the dead roots of the 0-1 mm diameter class for the oak-beech and the ash plot

Depth	Oak-beech plot		Ash plot	
(cm)	Living	Dead	Living	Dead
0 - 15	0.4073 (0.2091)	0.0491 (0.0140)	1.0666 (0.1791)	0.1297 (0.0667)
15 - 30	0.4415 (0.2049)	0.0481 (0.0191)	0.3409 (0.1476)	0.0557 (0.0339)
30 - 45	0.3507 (0.2196)	0.0560 (0.0574)	0.2404 (0.1580)	0.0200 (0.0078)
45 - 60	0.3756 (0.5669)	0.0366 (0.0386)	0.1674 (0.1307)	0.0221 (0.0027)
60 - 75	0.2377 (0.1641)	0.0353 (0.0225)	0.1877 (0.1140)	0.0249 (0.0152

Table 5. Ratio living/dead roots for the oak-beech and the ash plot (diameter of the roots < 1 mm)

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	8.29	8.22
15 - 30	9.18	6.12
30 - 45	6.26	12.04
45 - 60	10.25	7.59
60 - 75	6.74	7.55

For the ratio living/dead roots, no significant differences were found, neither between the two plots, nor vertically within one plot.

3.2. Root mass

3.2.1. Vertical distribution of the living roots

Figure 4 and Figure 5 show the root mass in the upper soil layer and in the upper 75 cm of the mineral soil of both the oak-beech and the ash plot. Comparison of the root mass of the different diameter classes within each soil layer, delivered no significant differences for the oak-beech plot. In the ash plot, the mass of the roots with a diameter between 2 and 5 mm was significantly higher ($p < 0.05$) than the mass of the other roots for the upper layer. From Table 8 it is clear that the mass of these roots (2-5 mm) was also higher in the second (15-30 cm) and the third (30-45 cm) soil layer of the ash plot. However, because of high variances, these differences could not be seen as being significant.

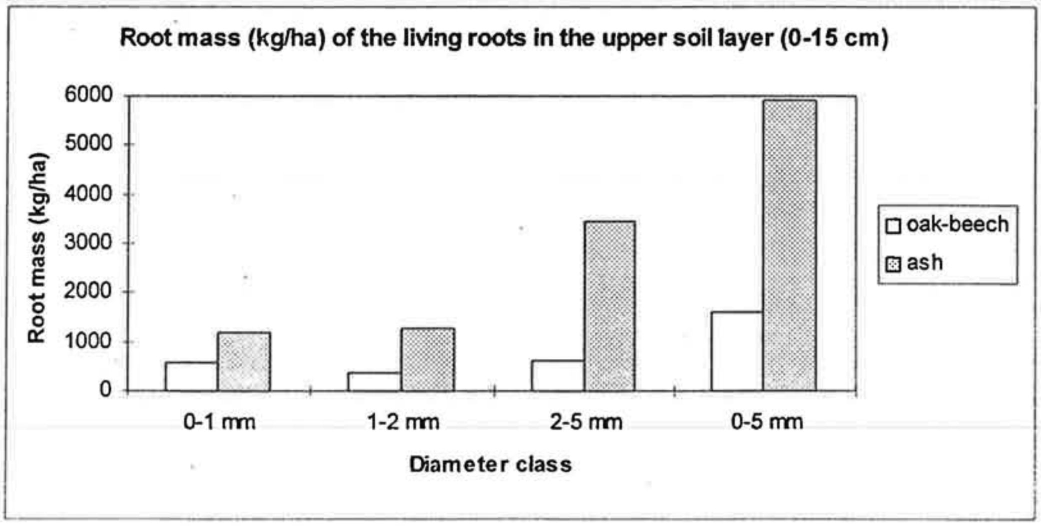

Figure 4. Root mass (kg/ha) of the living roots in the upper soil layer of the oak-beech and the ash stand.

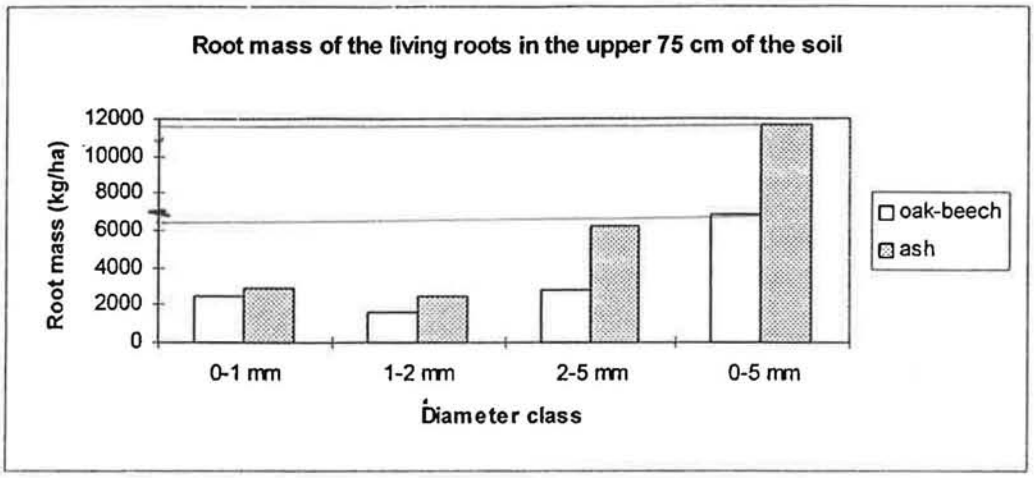

Figure 5. Root mass (kg/ha) of the living roots in the upper 75 cm of the mineral soil in the oak-beech and the ash plot.

3.1.2. Comparison of the root mass in the oak-beech and the ash stand

Table 6, 7 and 8 compare the root mass of the roots of different diameter classes of both forest types. Only one significant difference was detected. It concerned the mass of the roots with a diameter between 2 and 5 mm. In the upper mineral soil layer of the ash plot, the mass of these "thicker" roots was significantly higher than in the oak-beech plot. The mass of the other diameter classes is twice (0-1 mm) to threefold (1-2 mm) as much as in the oak-beech plot, but because of large variances, these differences might not be considered as being significant.

Table 6. Root mass (and standard deviation) of the living roots < 1 mm (mg D.M./cm³ soil)

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.386 (0.267)	0.820 (0.148)
15 - 30	0.471 (0.275)	0.320 (0.130)
30 - 45	0.357 (0.190)	0.360 (0.195)
45 - 60	0.271 (0.236)	0.200 (0.122)
60 - 75	0.200 (0.153)	0.220 (0.130)

Table 7. Root mass (and standard deviation) of the living roots with a diameter between 1 and 2 mm (mg D.M./cm³ soil)

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.271 (0.457)	0.840 (0.994)
15 - 30	0.271 (0.468)	0.280 (0.205)
30 - 45	0.286 (0.234)	0.200 (0.245)
45 - 60	0.129 (0.150)	0.140 (0.090)
60 - 75	0.086 (0.146)	0.180 (0.217)

*Table 8. Root mass (and standard deviation) of the living roots with a diameter between 2 and 5 mm (mg D.M./cm³ soil); significant differences are indicated with an * ($p < 0.05$)*

Depth (cm)	Oak-beech plot	Ash plot
0 - 15	0.429 (0.810)*	2.300 (1.860)*
15 - 30	0.229 (0.390)	1.060 (1.190)
30 - 45	0.657 (1.100)	0.500 (0.400)
45 - 60	0.186 (0.348)	0.160 (0.207)
60 - 75	0.386 (0.758)	0.140 (0.195)

3.2.3. Ratio living / dead roots

As was done for the root length, the ratio root mass of the living roots to root mass of the dead roots was calculated. These values are shown in Table 9. No significant differences were found for this ratio, neither in depth, nor between the plots.

Table 9. Mass (mg D.M. /cm³ soil) of the living and the dead roots of the 0 - 1 mm diameter class for the oak-beech and the ash plot

Depth	Oak-beech plot			Ash plot		
(cm)	living	dead	ratio	living	dead	ratio
0 - 15	0.386	0.057	6.52	0.820	0.260	3.82
	(0.267)	(0.054)		(0.148)	(0.152)	
15 - 30	0.471	0.043	10.08	0.320	0.200	3.10
	(0.275)	(0.054)		(0.130)	(0.187)	
30 - 45	0.357	0.029	10.98	0.360	0.080	6.70
	(0.190)	(0.049)		(0.195)	(0.045)	
45 - 60	0.271	0.057	6.81	0.200	0.020	19.92
	(0.236)	(0.079)		(0.122)	(0.045)	
60 - 75	0.200	0.043	6.13	0.220	0.080	8.86
	(0.153)	(0.054)		(0.130)	(0.130)	

3.3. Specific root length

The specific root length is the root length per unit of root mass. This value gives an idea of the fineness of the root system. A high value of the specific root length indicates a dominance of small diameters and vice versa (Pieters & Segers, 1992). As was told before, the root length gives a better idea of the water uptake capacity of a crop than the root mass. However, as it is much easier to measure root mass, it is interesting to know the ratio root length to root mass. This value could be used to convert root mass data into root length information. As such, one can obtain a better insight in the water uptake capacity of the studied crop. The specific root lengths of the different diameter classes are shown in Table 10.

*Table 10. Specific root length (m/g D.M.) for the oak-beech and the ash plot; significant differences between plots are indicated with an *; significant differences within one plot are indicated with letters (same letter means no significant difference)*

Root class	Oak-beech plot	Ash plot
Dead, 0-1 mm	9.45 * a	5.14 * a
Living, 0-1 mm	11.57 a	9.11 b
Living, 1-2 mm	1.44 b	1.16 c
Living, 2-5 mm	0.22 b	0.32 c

The specific root length didn't differ significantly between the two plots, except for the dead roots (diameter 0-1 mm). For both plots, the specific root length was comparable for the roots more than 1 mm in diameter. For the finest roots, significant differences were found. Those are indicated in Table 10.

4. Discussion

As could be expected, the length of the finest roots (< 1 mm) is far more greater than the length of the other diameter classes. Because of large variances, however, this length could not always be indicated as being significantly higher. These large variances are an indication that roots are not uniformly distributed in the horizontal direction in the studied areas. It is remarkable that the length of the finest roots is much larger in the upper layer of the ash plot compared with the oak-beech stand. This can possibly be explained by the fact that in the study presented here, only the mineral soil was observed. The ash stand has a very thin organic layer, in contrast to the oak-beech plot. As such, one can expect that the trees in the ash stand need to develop their root system in the mineral soil, while the trees in the other stand also use the relative thick organic layer to develop their root system. Results found by Hendriks & Bianchi (1995) indicate that the vertical root distribution becomes more homogeneous with increasing stand age. As our study was performed in a 70-years-aged forest, our results seem to confirm the Dutch investigation.

Hendriks & Bianchi (1995) also mention that the root development in the deeper soil is higher in a mixed stand than in pure stands, as there is more competition between the different (tree) species. In our investigation, two mixed forest stands are studied, and this can be the reason why no significant difference is observed between the two forest types.

The values of root length found in the 'Aelmoeseneie' forest are in the lower range of values reported by other authors (Hendriks & Bianchi, 1995; Arnone, 1997). An important remark must be noted here. When using a sieve with a mesh width of 0.5 mm, it is inevitable that part of the finest roots are washed away. Hendriks & Bianchi (1995) estimate that far less than 5 % of the root length was lost by the washing procedure. We suppose that this is an underestimation of the real loss in our study. Hendrick & Pregitzer (1993) used minirhizotron images to study root evolution.

Those images indicated that more than 80 % of all roots were < 0.5 mm in diameter. According to these authors, washing soil samples through sieves with mesh openings equal to or greater than 0.5 mm causes a loss of part of these very fine roots. Unfortunately, it is nearly impossible to estimate the percentage of roots missed in this way.

Values of root density found by Hendriks and Bianchi (1995) are an order of magnitude higher than results in the 'Aelmoeseneie' forest, especially for the upper soil layers (0-15 and 15-30 cm). Hendriks & Bianchi (1995) used an indirect method to determine the root length in these upper soil layers, which can be a possible explanation of the higher root lengths they found. Olsthoorn (1991) found root densities between 0.26 cm/cm^3 and 1.87 cm/cm^3, which is comparable to values found here. Mitscherlich (1969) mentions a root length of 2500 km/ha for a 63-years-old beech stand, and 13600 km/ha for a 35-year old Scots pine stand. Differences between results of root studies can also be explained by factors as differences in ground water depth, in meteorological circumstances or nutrient status of the soil.

As for the root length, values of the root mass are in the range of values found in literature (Persson, 1979; Van Praag *et al.*, 1988; Olsthoorn, 1991; Ehrenfeld *et al.*, 1992; Hendrick & Pregitzer, 1993; Büttner & Leuschner, 1994; Hendriks & Bianchi, 1995; Ehrenfeld *et al.*, 1997). Values of root mass are more similar in the different studies than values of the root length. This can be a consequence of the fact that root mass is much simpler to measure than root length or root density. In our study, the fact that some roots have been washed out will be of less importance. It concerns the finest roots, which are very light. Therefore, the loss in biomass will be smaller than the loss in root length, compared to the biomass and root length of all roots less than 5 mm in diameter.

In both the oak-beech and the ash plot, the ratio living to dead roots is approximately 8. This value is more or less equal when calculated on base of the root length or on base of the root mass. This is a relative high value compared to what Pieters & Segers (1992) found (value of 3 to 4, for roots in the upper 15 cm). In our study however, samples were taken only at one moment in the growing season. It is possible that this value would change if samples were taken at another moment. Research by Hendrick & Pregitzer (1993) showed a period of fine root production in spring, and a dominance of root mortality in fall and winter. Especially the finest roots are subject to this seasonal dynamics.

Values for the specific root length are comparable to values reported by other researchers (Pieters & Segers, 1992; Hendricks & Bianchi, 1995). As it is much more labour-intensive to measure root length accurately, and as the values found for the specific root length are comparable to those found in literature, we would suggest to use these specific root lengths to convert root mass into root length.

5. Acknowledgements

Research in the experimental forest is funded by the Federal Office for Scientific, Technical and Cultural Affairs (contract CG/DD/05a), the Flemish Community (contract IBW/1/1999) and the University of Gent (project 011B5997).

6. References

Arnone III, J.A. (1997). Temporal responses of community fine root populations to long-term elevated atmospheric CO_2 and soil nutrient patches in model tropical ecosystems. *Acta Oecologia*, 18, 367-376.

Büttner, V. & Leuschner, C. (1994). Spatial and temporal patterns of fine root abundance in a mixed oak-beech forest. *Forest Ecology and Management*, 70, 11-21.

Cermák, J., Riguzzi, F. & Ceulemans, R. (1998). Scaling up from the individual tree to the stand level in Scots pine. I. Needle distribution, overall crown and root geometry. *Ann. Sci. For.*, 55, 63-88.

Egli, P. & Körner, C. (1997). Growth responses to elevated CO_2 and soil quality in beech-spruce model ecosystems. *Acta Oecologia*, 18, 343-349.

Ehrenfeld, J.G., Kaldor, E. & Parmelee, R.W. (1992). Vertical distribution of roots along a soil toposequence in the New Jersey Pinelands. *Can. J. For. Res.*, 22, 1929-1936.

Ehrenfeld, J.G., Parsons, W.F.J., Han, X., Parmelee, R.W. & Zhu, W. (1997). Live and dead roots in forest soil horizons : contrasting effects on nitrogen dynamics. *Ecology*, 78, 348-362.

Hendrick, R.L. & Pregitzer, K.S. (1993). The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can. J. For. Res.*, 23, 2507-2520.

Hendriks, C.M.A. & Bianchi, F.J.J.A. (1995). Root density and root biomass in pure and mixed forest stands of Douglas-fir and Beech. *Dutch Journal of Agricultural Science*, 43, 321-331.

Jones, G.H. (1992). Plants and microclimate. A quantitative approach to environmental plant physiology. Cambridge, University Press, 428 p.

Kienhuis, A.J.M. (1987). Bewortelingsonderzoek bij bomen : theorie en praktijk. Wageningen, Rijksinstituut voor Onderzoek in de Bos- en Landschapsbouw "De Dorschkamp", 51 p.

Lambers, H., Chapin III, F.S. & Pons, T.L. (1998). Plant Physiological Ecology. New York, Springer-Verlag, 540 p.

Landsberg, J.J. (1986). Physiological Ecology of Forest Production. London, Academic Press, 198 p.

Laser Area Meter CI-203. (1995). Instruction manual. Vancouver, CID Inc., 20 p.

Majdi, H. & Kangas, P. (1997). Demography of fine roots in response to nutrient applications in a Norway spruce stand in southwestern Sweden. *Ecoscience*, 4, 199-205.

Mitscherlich, G. (1969). Wald, Wachstum und Umwelt. 1. Band Form und Wachstum von Baum und Bestand. J.D. Sauerländer's Verlag, Frankfurt am Main. Chap. 2 : Die Wurzeln, 45-56. Source : Hendriks & Bianchi (1995).

Mou, P., Mitchell, R.J. & Jones, R.H. (1997). Root distribution of two tree species under a heterogeneous nutrient environment. *J. Appl. Ecol.*, 34, 645-656.

Nadelhoffer, K.J. & Raich, J.W. (1992). Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology*, 73, 1139-1147.

Olsthoorn, A.F.M. (1988). Wortelonderzoek aan bomen als onderdeel van het Nederlandse verzuringsonderzoek in Douglasbossen. *NBT*, 60, 222-224.

Olsthoorn, A.F.M. (1991). Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. I. Root biomass in early summer. *Dutch Journal of Agricultural Science*, 39, 49-60.

Persson, H. (1979). Fine-root production, mortality and decomposition in forest ecosystems. *Vegetatio*, 2, 101-109.

Pieters, A. & Segers, R. (1992). Wortelparameters, ectomycorrhiza's en boomvitaliteit. Eindverslag Project bodemmeetnet in de bossen van het Vlaamse Gewest, LI/BODEM/5/1991. KULeuven, Afdeling Land- en Bosbeheer, Laboratorium voor Bosbouw en Ministerie van de Vlaamse Gemeenschap, AMINAL, Dienst Waters en Bossen, 68 p.

Samson, R., Nachtergale, L., Schauvliege, M., Lemeur, R. & Lust, N. (1996). Experimental set-up for biogeochemical research in the mixed deciduous forest Aelmoeseneie (East-Flanders). *Silva gandavensis*, 61, 1-14.

Van Den Burg, J. (1987). Relaties tussen het vochtleverend vermogen van de grond, het waterverbruik en de groei van een aantal boomsoorten : een literatuurstudie. Wageningen, Rijksinstituut voor Onderzoek in de Bos- en Landschapsbouw "De Dorschkamp", 77 p.

Van Den Burg, J. (1996) (ed.). Methoden. In : De betekenis van bodem en klimaat voor het Nederlandse bos. Wageningen, DLO Institute for Forestry and Nature Research, 17-35. IBN Scientific Contributions : 4.

Vande Walle, I., Mussche, S., Schauvliege, M., Lemeur, R. & Lust, N. (1998). Inventaris proefbos Aelmoeseneie (Gontrode). Gent, Universiteit Gent, Laboratorium voor Plantecologie en Laboratorium voor Bosbouw, interne publicatie, 33 p.

Van Praag, H.J., Sougnez-Remy, S., Weissen, F. & Carletti, G. (1988). Root turnover in a beech and a spruce stand of the Belgian Ardennes. *Plant and Soil*, 105, 87-103.