

Problems and options in modelling fine-root biomass of single mature Norway spruce trees at given points from stand data

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Abstract: In a 75-year-old Norway spruce (*Picea abies* (L.) Karst.) stand, three different single-tree models were tested to predict the fine-root biomass of root samples. This approach is based on the assumption that the fine-root biomass at a given point determines the availability of belowground resources as, for example, soil water. All models assume a monotonously decreasing function describing the distribution of the fine-root biomass of a subject tree depending on the distance to the trunk of the tree. To the contrary, the models differ in the maximum distance from the stem where roots can be found. There were high correlations between the observed and the predicted fine-root biomasses for all models in a part of the stand where the trees are distributed less uniformly and where root biomasses are most heterogeneous. In a section with medium stand density, the model of diameter at breast height dependent root spread yields higher correlation coefficients compared with the fixed-distance approach of the two other models. Significant correlations between model predictions of root distributions and measured soil water potential supported the validity of the models. The results of the model estimations imply differences in the maximum distance of lateral root spread dependent on stand density.

Résumé : Trois modèles différents d'arbre individuel ont été testés pour prédire la biomasse de racines fines dans des échantillons de racines provenant d'un peuplement d'épicéa commun (*Picea abies* (L.) Karst.) âgé de 75 ans. Cette approche est basée sur la prémisse que la biomasse de racines fines, à un moment donné, détermine la disponibilité des ressources édaphiques telles que l'eau du sol. Tous les modèles assument que la distribution de la biomasse de racines fines en fonction de la distance du tronc d'un arbre est décrite par une fonction qui décroît de façon monotone. Par contre, les modèles diffèrent dans la distance maximum à partir du tronc à laquelle on peut trouver des racines. Il y a d'étroites corrélations entre la biomasse observée et prédite par tous les modèles dans la partie du peuplement où les arbres sont distribués moins uniformément et où la biomasse des racines est la plus hétérogène. Dans une section du peuplement où la densité est moyenne, le modèle du facteur de dispersion des racines qui est fonction du diamètre à l' hauteur de poitrine produit des coefficients de corrélation plus élevés comparativement à l'approche qui utilise une distance fixe dans les deux autres modèles. Des corrélations significatives entre les prédictions du modèle sur la distribution des racines et les mesures du potentiel hydrique dans le sol supportent la validité des modèles. Les résultats des estimations du modèle impliquent des différences dans la distance maximale de dispersion latérale des racines selon la densité du peuplement.

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Introduction

The importance of the spatial dimension of plants in population ecology has often been stressed (Harper 1977; Tilman 1994). The basic reasons for the importance of this spatial dimension are firstly, the sessile property and, sec-

ondly, the spatial quality plants have; this is particularly pronounced in trees. These plant properties become relevant to population ecology in combination with the spatial property of the resource pool plants rely on; the availability of resources such as radiation, water, and nutrients can be highly heterogeneous within the ecosystem in which a plant lives (Rhoades 1997; Kleb and Wilson 1999). The heterogeneous resource availability is caused by abiotic (van Breemen et al. 1997) as well as by biotic factors (Finzi et al. 1998), e.g., competition (Tilman 1982). The latter has become a focus of attention in improving the understanding of plant-plant interactions (Wagner 1999). Thus, the particular effect of plants on the resource pool (Goldberg 1990) is a key issue with regard to resource heterogeneity and competition between plants; each individual tree affects the resource availability to other individuals within a defined area, e.g., by means of leaves, branches, bole, and roots. This feature has been elegantly stressed by Wu et al. (1985) in their work on the "ecological field theory". The ecological field theory and related ideas have been used successfully in some recent mod-

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elling applications, e.g., small-scale distribution patterns of ground vegetation (Kuuvulainen and Pukkala 1989; Yastrebov 1996) or successional processes after clear-cuttings (Mou and Fahey 1993). However, the shape, size, and intensity of the area of influence of a single plant depends upon many factors, such as the resource measured, the environmental conditions (such as latitude and soil properties), the species, or the age and social class of the individual concerned. Much progress has been made in modelling the radiation regime within tree stands (Anderson 1964; Ross 1981; Oker-Blom 1986; Norman and Campbell 1989) and even single-tree effects on radiation can be appropriately modelled now (Knyazikhin et al. 1996). However, comparatively less success has been achieved with regard to the effects on belowground resources, e.g., water and nutrients (for a recent review, see van Noordwijk et al. 1996). In this context it is important to mention that the application of the concept of Wu et al. (1985) does not require mechanistic models of tree root distribution in a stand, the more so as those models are not available for every tree species. In contrast, applications of the ecological field theory to field data were performed using rough estimations of belowground resource effects of single trees (e.g., Kuuvulainen and Pukkala 1989). This approach is based on the assumption that within a specific zone, trees are determining the availability of belowground resources, e.g., soil water. This hypothesis was recently confirmed by an exhaustive literature review on root competition (Coomes and Grubb 2000). Thus, Coomes and Grubb (2000) pointed out that the impact of overstorey trees on the availability of belowground resources is strongly correlated with the amount and length of fine roots in the soil.

To improve our knowledge about the effects trees impose on belowground resources, it is necessary to perform measurements on roots. However, measuring a single-tree root system is much more laborious than measuring its branch- or leaf-distribution patterns. This holds true especially for pure forest stands; the root system lies obscured in the soil and, hence, cannot be effectively measured. Thus, the single root in the soil cannot easily be related to an individual tree. The difficulties in the assignment of single roots and root samples to particular trees within a forest stand, hence, should be stressed as a main obstacle in improving our knowledge of single-tree root systems. Nielsen and Mackenthun (1991) proposed a statistically based method of analysing soil core samples within a forest stand that does not require identifying the specific tree to each fine root. This method calibrates fine-root biomass functions of single trees by comparing fine-root distributions with tree distributions via a least squares fit analysis. Regarding a particular soil core it is assumed that the amount (number, dry mass, or length) of fine roots results from additive contributions from a fixed number of neighbour trees. Recently, Ribbens et al. (1994) used a very similar approach to predict recruitment dispersal patterns in forests. The prerequisites of computations are identical in both papers and only computation techniques (least squares fit vs. maximum likelihood) are markedly different. Thus, a test of the elegant method of Ribbens et al. (1994) in root data is suggested. However, only little is known about the necessities in the technique of data sampling when using the above-mentioned computing

Table 1. Description of study sites and stand.

Parameter	Stand characteristic
Latitude and longitude	48°25'N, 11°41'E
Elevation (m)	490
Precipitation (mm/year)	790
Soil texture	Sandy loam, loamy sand
Site index (at 100 years)*	
Height (m)	38
Volume (m ³ ·ha ⁻¹ ·year ⁻¹)	13
Age in 1997 (years)	75
Density (stems/ha)	498

*According to the yield table of Assmann and Franz (1963).

methods (Stoyan and Wagner 2001), and some of the model's assumptions (e.g., constant maximum spread distances in all diameter at breast height (DBH) classes of a particular stand) are to be questioned when applied to root data.

Thus, the aims of our study were (i) to test the above mentioned method of Ribbens et al. (1994) for appropriateness in root data, (ii) to look for possibilities for model improvement using an alternative approach, and (iii) to test whether the model estimations can be validated with regard to the ecological field theory of Wu et al. (1985) with data of soil water potential.

Materials and methods

Study sites

The study was carried out in a pure Norway spruce (*Picea abies* (L.) Karst.) stand located in southern Germany (Bavaria) near the town of Freising. The rather homogenous soil originates from loess and is very productive (Table 1). These site conditions are representative for many other pure Norway spruce stands in Germany.

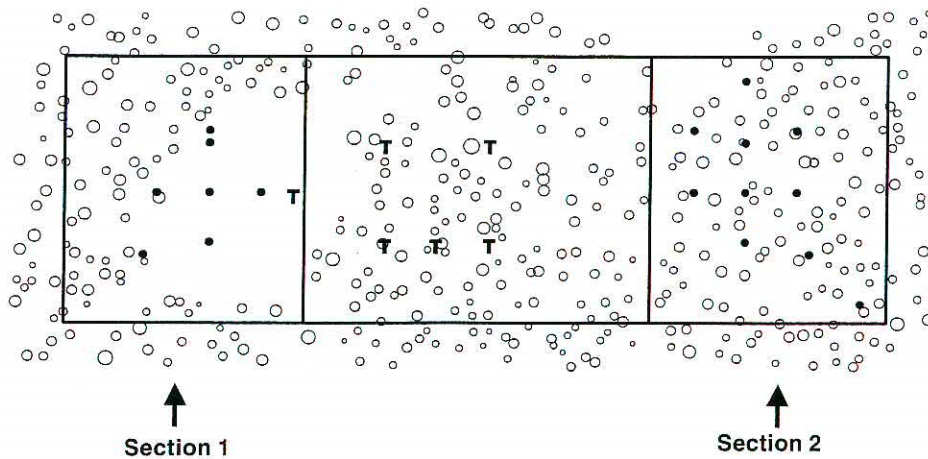
The stand is subdivided into three parts by skidding lines. As can be seen in Fig. 1, which shows the coordinates of all stems, the stand differs in stand density. Whereas the western part of the stand (section 1) includes a gap, the eastern part (section 2) is uniformly stocked. The gap within section 1 was caused by bark beetles in 1990.

Core sampling

Soil cores were taken at 17 points at both parts of the stand. These points were predetermined by another study and correspond to spots where the canopy closure was measured by fish-eye photographs (Ammer 2000). Thus, the soil cores were not selected randomly but scattered throughout both parts of the stand. The coordinates of all spruces as well as those of all positions where soil cores were taken were recorded. Stand map shows both tree and core sampling positions (Fig. 1).

The sampling procedure started with the collection of roots from the forest floor organic horizons using a steel frame (size 20 × 20 cm). Roots in the mineral soil were collected in two steps. First, a 16 cm steel tube corer was driven to a depth of 10 cm. After the removal of the soil, the corer was driven to a depth of 30 cm in a second step. The three samples per core hole (organic horizon, mineral soil up to

Fig. 1. Positions of trees (open circles, the size of the circle is proportional to the DBH of the tree) and soil core samples (solid circles). The positions where the soil water potential was measured with tensiometers are labelled with T.



10 cm, mineral soil up to 30 cm) were placed in separate plastic bags. The samples of mineral soil plus roots were washed over 1-mm sieves to separate root material from mineral soil. According to Böhm (1979) only roots ≤ 2 mm diameter are classified as fine roots. These roots were selected irrespective of their shape. Finally, the dead roots were separated. The distinction between living and dead components was made according to Murach (1984). Following separation, samples of live roots were oven-dried at 65°C for 96 h. Mycorrhizae were not separated from root material.

Measurements of soil water potential

At six measuring points (Fig. 1, T) measurements of soil water potential were conducted with tensiometers (T4-60/10, UMS, Germany) at a depth of 30 cm in 1999. Data were read every 30 min from May 17 at 13:00 (CET) to September 17 at 08:00 (CET) by a data logger (Delta-T DL2e, Delta-T-Devices LTD, U.K.).

Calculations and statistical analysis

To obtain information of horizontal single-tree root distribution patterns, two statistically based methods were used, which will be referred to as the "Ribbens model" (RM) and the "polynomial model" (PM). In both methods a two-step approach is applied.

(1) In the first step (the single-tree step) the frequency distribution of the fine-root density per square metre is deterministically described. In either model the frequency distribution is supposed to be distance dependent regarding the position of the tree. Both models are diameter dependent. Hence, the total amount of fine roots per tree is supposed to increase with increasing DBH of the tree (Hilf 1927; Vater 1927; Drexhage 1994). The formula of Ribbens et al. (1994) was used to compute the total fine-root biomass of a particular tree by $N \times (\text{DBH}/30)^{\beta}$, where N is the total fine-root biomass (g) of a tree with 30 cm diameter at breast height and β is a constant with a value of 4. In contrast to this congruence, only the PM takes the diameter as a means to assess the maximum distance to which roots are spread horizontally (Hilf 1927; Puhe 1994).

(2) In the second step (the step connecting the single-tree information to field information) an additive algorithm is applied in both models. Thus, it is assumed that the total amount of fine roots in a particular core results from additive contributions of the surrounding trees. Interactions among tree roots are not taken into account.

Ribbens model (RM)

All computations were carried out using the program RECRUITS (version 3.0) made available by Dr. Eric Ribbens.

The model can be characterized as follows:

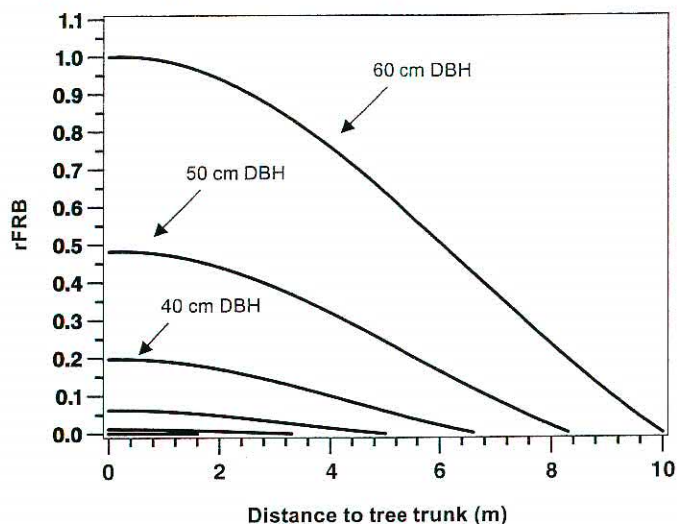
- (1) The maximum distance from the stem where roots of a particular tree can be found is equal in all trees of an even-aged stand.
- (2) Describing the fine-root density depending on the distance to the trunk of the tree a monotonously decreasing function of the form $e^{-Dx^{\theta}}$ is applied, where D shapes the function and the distance reached by roots, θ is a constant with a value of 3, and x is distance to tree trunk in metres.
- (3) The parameter estimation for N and D is calculated via a maximum likelihood algorithm (see Ribbens et al. 1994). Details of the formula can be found in the Appendix.

Polynomial model (PM)

In the PM, relative fine-root biomass (rFRB) for any point in a system of coordinates is calculated on the basis of position and dimension of the canopy trees (Fig. 2). The artificial unit rFRB is transformed to absolute biomass values following calibration. The model is based on the following assumptions:

- (1) Maximum distance where roots of a tree can be found depends on the dimension of the tree. This maximum root spread distance in metres is defined as $\text{SD}_3 = \text{DBH (cm)}/6$.
- (2) The relative fine-root biomass of a tree with $\text{DBH} = 60$ cm at distance SD_0 (stem trunk) is defined as 1. The relative fine-root biomass at distance SD_1 (one-third of the maximum root spread distance) is 0.83 and that of distance SD_2 (mean distance between SD_1 and SD_3 or two-thirds of the maximum root spread distance) is half

Fig. 2. Relative fine-root biomass (rFRB) in relation to distance of stem trunk and dimension of the tree as predicted by the PM model (PM2). All curves are third-degree polynomials.



of 0.83. At distance SD_3 (the maximum root spread distance) the root biomass equals zero by definition.

- (3) Based on the distances SD_0 to SD_3 a polynomial of third degree for each DBH can be calculated using the Gregory–Newton procedure to fit a polynomial of n th degree to $n + 1$ equidistant points of support (Stöcker 1995). The formulae can be found in the Appendix. In a final step, the model sums all relative fine-root biomasses (rFRB), reaching a given point in the system of coordinates.

A comparison of the two basic underlying functions for the fine-root frequency distribution of the PM and the RM is given in Fig. 3.

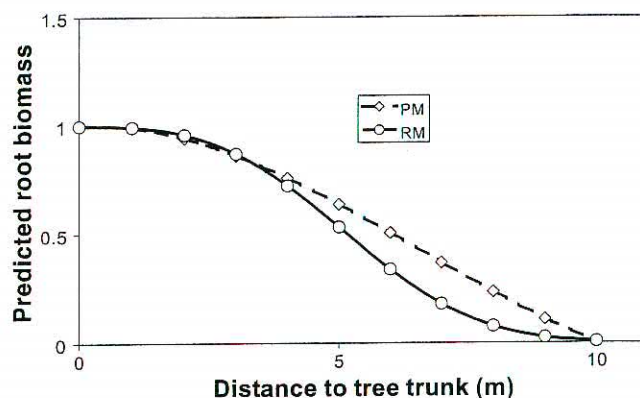
Three different computations were performed to test the correlation between the predicted fine-root biomasses (RM) and relative fine-root biomasses (PM), respectively, and the related measured biomasses. The computations were (i) the RM with fixed β and θ values (4 and 3, respectively) to optimize for the D and N parameter, (ii) the PM with a fixed maximum root spread distance for all DBH classes and an initial root density dependent on the DBH analogous to the RM to mimic the RM by the PM, and (iii) the PM with an initial root density dependent on the DBH analogous to the RM and a DBH-dependent maximum root spread distance (see Appendix) to improve model fits. The three computations will be referred to as RM, PM1, and PM2.

Each of these computations utilized the data of the two sections of the Norway spruce stand mentioned in the description of the study site.

Statistical analysis

Simple correlation analysis (Pearson) was used to evaluate the relationship among the values calculated by the different types of models and the measured fine-root biomasses. All statistical analyses except those performed with RECRUITS were conducted with SAS® (Statistical Analysis System version 6.12; SAS Institute Inc., Cary, N.C.). As a measure of spacing in plant populations the Clark–Evans index of aggregation R (Clark and Evans 1954, extended by Donnelly

Fig. 3. Comparison of the two basic single-tree model functions used in the computations. Given is an example with fixed maximum root spread distance of 10 m for a tree with a DBH of 60 cm. The abscissa is given in units of relative fine-root biomass (rFRB). PM, polynomial model; RM, Ribbens model.



1978) was calculated per section. In a random distribution, $R = 1$. An R value > 1 indicates a tendency towards uniform patterns of distribution (perfect uniformity: $R = 2.1491$); aggregated distributions are characterized by R values < 1 (completely aggregated: $R = 0$).

Results

Fine-root biomasses on stand level and tree distribution patterns

The mean fine-root biomass of the stand up to 30 cm depth was 2404 kg/ha. Fifty-seven percent of the fine-root biomass per square metre was detected in the upper mineral soil (0–10 cm depth) (Table 2). The organic horizons accounted for 15%, the lower mineral soil (10–30 cm) contained 38% of the total fine-root biomass per square metre. However, as compared on a volume basis, the fine-root density in the organic layer exceeded that of the mineral soil between 10 and 30 cm depth (Table 2). The maximum fine-root density was found in the upper mineral soil. All strata show a wide range of fine-root biomasses within the stand because of the differences in stand density (Table 2). Thus, section 1, where some samples were taken in the gap, shows lower fine-root biomasses and with one exception a higher variability of values than section 2 (Table 2).

As Table 3 shows, only the trees of section 1 are randomly distributed. In contrast to this finding, the departure of R from a random distribution pattern towards uniformity was significant at the 99.9% level for the other section. Whereas the two sections differ in the number of stems per hectare, the mean DBH of the trees showed nearly no variation (Table 3).

Model estimations on single-tree level

RM application

The RM was applied separately to the two sections to test for appropriateness in root data. As a criterion for appropriateness of the estimations, product–moment correlations were used. Table 4 shows a higher goodness of fit in section 1. However, the correlations are significant at a mini-

Table 2. Fine-root densities (g/m^3) and fine-root biomasses (g/m^2) in different soil depths for the total stand and fine-root biomasses for the two sections.

	Total stand density (g/m^3)		Total stand biomass (g/m^2)		Section 1 biomass (g/m^2)* ($N = 7$)	Section 2 biomass (g/m^2)* ($N = 10$)
	Mean ($N = 17$)	Range	Mean ($N = 17$)	Range		
Organic horizons	737.65	10.00–2395.00	36.88	0.50–119.75	34.57±47.25	39.98±32.42
Mineral soil, 0–10 cm	1371.25	49.74–2571.35	137.13	4.97–257.13	100.89±89.45	167.96±63.52
Mineral soil, 10–30 cm	332.21	39.79–1032.02	66.44	7.96–206.40	31.76±26.38	83.86±53.82
Total	693.27	67.23–1343.41	240.45	25.37–418.41	167.22±145.10	291.79±77.11

*Values are means \pm SDs.**Table 3.** Stem numbers, measure of spacing (R), and DBH of the sections.

	Section 1	Section 2
Stems/ha	393	545
R^*	0.999 (–0.020)	1.277 (4.585)
DBH [†]	35.9±8.5	35.8±6.9

*Standard variates of the normal curve are given in parentheses.

[†]Values are means \pm SDs.**Table 4.** RM parameter estimates for the sections; both estimations are significant (minimum 95% level).

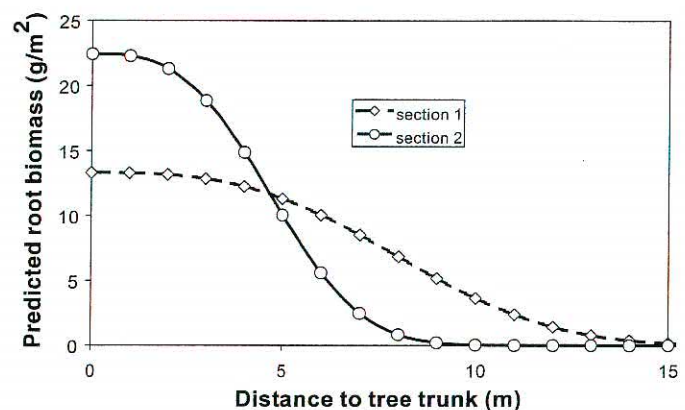
Section	No. of cores	MAXD (m)	r	N (g/tree)	D
1	7	15	0.935	3170	0.001 294
2	10	9	0.590	1831	0.006 414

Note: The MAXD value is the root spread, the distance from a stem over which 99.5% of the tree's fine roots are distributed; the N value (total amount of fine roots per tree in grams) is computed for a tree with DBH of 30 cm; the D value, which determines MAXD, refers to eq. 2 given in the description of the Ribbens model in the Materials and methods.

imum 95% level in both sections. The parameter estimates in Table 4 reveal important differences between section 1 and section 2: the roots in the section with the gap (section 1) spread further than in the other fairly dense part of the stand, and it is obvious that a 30-cm tree in section 2 has only a little bit more than half the fine-root biomass of a 30-cm tree in section 1 (N is 3170 g in section 1 and 1831 g in section 2). The predictions for root-density spatial distributions are given in detail in Fig. 4.

PM application

The functions underlying RM and PM1, describing the decrease of fine-root biomass with increasing distance from tree trunk, are rather similar (Fig. 3). Hence, it is not surprising that the correlations between rFRB calculated by PM1 and measured fine-root biomass is comparable with the estimations of RM (Tables 4 and 5). Note that PM1 as well as RM assume an equal maximum distance of lateral root spread for all trees, regardless of their DBHs. In contrast PM2 is based on the assumption that the roots of a thinner tree do not extend as far as those of a thick tree, as it is de-

Fig. 4. Predicted (Ribbens model, RM) single-tree root-density profiles for the sections 1 and 2 of the Norway spruce stand. Each line shows the predicted distance-dependent root biomass (g/m^2) for a tree with 30 cm DBH.

scribed in the methodical section. This supposition improves the model estimations in the case of section 2 considerably, while the correlation between rFRB and measured fine-root biomass in section 1 is not augmented (Table 5).

Model validation on stand-data level

The validation of the model predictions was done in two ways, both on stand-data level. Firstly, we examined the gap predictions (section 1) more carefully. As shown in Fig. 5 the model adaptations result in predicting a monotonous root density decrease from the edge of the stand towards the centre of the gap. This is quite similar to the decrease in measured root biomasses, although the maximum value in this case is not observed at the edge, but 2 m apart.

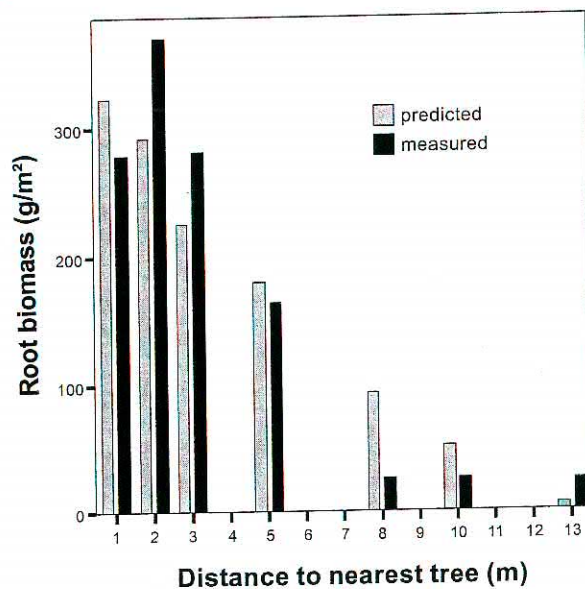
Secondly, a comparison was performed to test the relationship between the relative fine-root biomasses calculated by PM2 in section 2 and the measurements of soil water potential in the intermediate part of the stand, where no model parameterization was performed. Thus, rFRB was calculated for the points where the tensiometers were installed and used as the independent variable (Fig. 6). Regression analysis (through the origin) was done using mean soil water potentials of a day at the end of a rainy period (17 June 1999) as well as of a day in a rather dry week (31 July 1999). It can be seen that the measured soil water potential is decreasing with increasing rFRB. Pearson's correlation coefficient is statistically significant ($t < 0.1$) during dry periods

Table 5. PM parameter estimates for the sections.

Section	No. of cores	PM1			PM2		
		MAXD (m)	<i>r</i>	<i>p</i> > <i>F</i>	MAXD (m)	<i>r</i>	<i>p</i> > <i>F</i>
1	7	15	0.957	0.0007	2.8, 9.5	0.853	0.0146
2	10	9	0.537	0.1091	3.5, 8.3	0.660	0.0380

Note: PM1 is the polynomial model with equal maximum distances (MAXD) of fine roots for trees of all DBHs. PM2 is the polynomial model with variable distances of fine roots depending on the DBH of the tree. Thus, MAXD for PM2 is given for the thinnest and the thickest tree of the related section, respectively.

Fig. 5. Predicted (Ribbens model, RM) and measured root density (g/m^2) in the gap (section 1); data are presented in relation to distance to the nearest tree respectively. Data are not related to single-tree fine-root biomass but to the biomass of the entire stand.



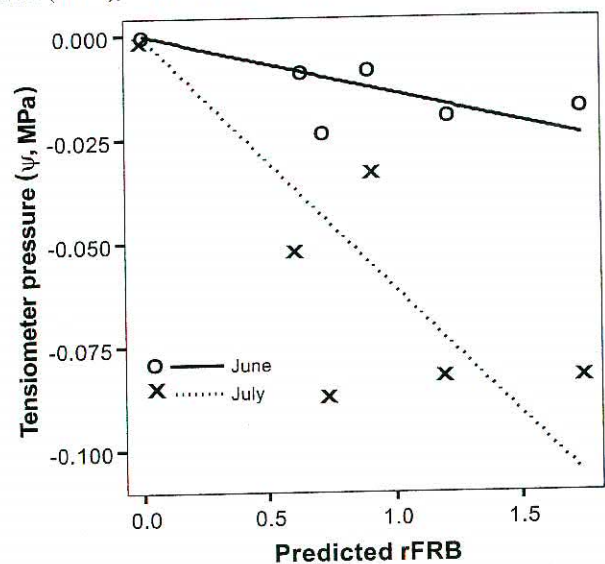
(Fig. 6). It might also be worth pointing out that this worked even within the limits of the model for the regularly spaced section, which has a fairly poor fit (i.e., it would presumably work even better in section 1 with the adapted model).

Discussion

Fine-root biomasses on stand level

The observed fine-root biomass of approximately 2500 kg/ha is in accordance with the results of investigations in somewhat older Norway spruce stands (Murach 1984; Friedrich 1992) and in spruce stands comparable as far as site, age, and yield class are concerned, investigated by Ulrich and Pirouzpanah (1986) and Wittkopf (1995). The vertical distribution of the fine roots is characterized by a concentration in the upper mineral soil. This finding also confirms similar results of previous studies (Kalela 1950; Meyer 1967; Murach et al. 1993; Wittkopf 1995). As the core sampling was restricted to a depth of 30 cm, an underestimation of the real fine-root biomass of the stand is probable. According to the data given by Kalela (1950) and Murach et al. (1993) an underestimation of the amount of

Fig. 6. Mean soil water potential on 2 days in summer 1999 as a function of predicted rFRB. Regression through origin for July 31 (crosses): $\psi = -0.0608(\text{rFRB})$, correlation coefficient $r = -0.744$, $\alpha = 0.09$. Regression through origin for June 17 (circles): $\psi = -0.0139(\text{rFRB})$, correlation coefficient $r = -0.630$, $\alpha = 0.18$.



fine roots of 5–10% should be assumed. By use of eq. 2 from the appendix we computed a mean fine-root biomass (g/m^2) in section 2 by combining the diameter distribution of that section with the estimated parameter values from Table 4 for the RM. The result for the entire stand in section 2 was a mean biomass of 234 g/m^2 estimated by use of the single-tree model (RM). This estimation is in fairly good accordance with the mean value of 292 g/m^2 from the 10 cores considering the standard deviation of 77 g/m^2 of those measurements. The same procedure performed with the data of section 1 gave quite less good concurrence (305 g/m^2 estimated by the single-tree model to a measured mean of 167 g/m^2). However, this can be explained by the location of core samples in section 1 and the very special situation of the edge trees.

- (1) The estimations of the model parameters are only influenced by the edge trees (see Fig. 1). Indeed, these trees are not considered representative to the entire stand of that section but were favoured by the formation of the gap 10 years ago. Thus, the model estimations are based on samples that represent extraordinarily good growing conditions and presumably high fine-root biomasses of very special trees.

- (2) The mean value of the core samples in section 1 can only be taken as a true mean of the gap-edge situation in that section, because no samples were taken within the dense part of the stand. Thus, the simple mean of the core samples represents extraordinary low fine-root biomasses away from tree trunks.

Model assumptions

Presumably because of methodological difficulties, only a few studies about the lateral fine-root distribution patterns of mature trees exist (Böhm 1979; Bédéneau and Auclair 1989). This also holds true for Norway spruce. However, all investigations available to us indicate that (i) the fine-root biomass decreases with increasing distance from the tree trunk (Friedrich 1992; Drexhage 1994), (ii) the maximum extent of lateral tree roots exceed the edges of the crown by far (Hilf 1927; Vater 1927; Wiedemann 1927; Drexhage 1994; Polomski and Kuhn 1998), and (iii) fine-root biomass increases with the DBH of the tree. However, nearly nothing is known about details of these findings, for example, regarding the most appropriate function to describe the decrease in fine-root density with increasing distance, the extent to which roots really spread, or the physiological mechanisms underlying the relation between DBH and fine-root biomass. The latter relation could, for example, be assumed to parallel the so-called "pipe model" (Shinozaki et al. 1964) and could then be derived from well-known allometric functions. Because we know so little about the questions in regard, this model approach is difficult to validate. Thus, the papers cited and the correlation coefficients as well as levels of significance given in the tables are the only measures of appropriateness that we could apply. However, as Fig. 4 shows, the model predictions as well as the measured root biomasses meet the assumption of more or less smoothly decreasing root density with distance to trees. This feature was recently observed in other ecosystems (Brockway and Outcalt 1998) as well. In recently disturbed stands, decreasing root density with distance to the trunk results in belowground gaps (Ostertag 1998). These belowground gaps are appropriately predicted by the models in regard.

Models estimating fine-root biomass in grams per square metre are expected to become valuable tools in modelling the belowground competition emanating from, for example, an overstorey tree on regeneration. As Coomes and Grubb (2000) pointed out, the belowground resource availability decreases with increasing fine-root biomass per square metre. In addition, various experiments primarily by using trenches revealed the strong impact of overstorey tree roots on soil moisture (Gerhardt 1996; Hauskeller-Bullerjahn 1997; Fritz 1999; Irrgang 1999; Ammer 2002) as well as on growth of seedlings in the understorey (van Hees 1997; Madsen 1994; Löf 2000; Ammer 2002). In the present study we observed a significant relationship between soil water potential measured by tensiometers and rFRB calculated by the DBH-dependent model PM2 (Fig. 6). Thus, models like PM2 enable rough identifications of areas with different levels of root competition.

In contrast to RM and PM1 as well as to the model of Nielsen and Mackenthun (1991), PM2 assumes that not only the total amount of fine roots per tree is controlled by DBH,

but also the maximum extent of lateral root spread. This approach is supported by previous works of, for example, Hilf (1927) and Puhe (1994) and by the comparison of the model estimations of PM1 and PM2 (Table 5) or RM, respectively. When the different models were applied to the same data set of the two sections, different levels of degree of fit were achieved (Tables 4 and 5). The models PM1 and RM yielded nearly identical correlation coefficients, which indicates the very similar model algorithms. The PM2 model, which is characterized by a DBH-dependent maximum distance of root spread, differs from this in so far as it yielded a higher correlation coefficient compared with the fixed distance approach (RM and PM1) in section 2 but not in section 1. This indicates that the DBH-dependent root spread may not be as pronounced in heterogeneously spaced and less dense stands as in homogeneously spaced and dense stands. The finding that correlations coefficients of all models are lower in section 2 might be due to the additive algorithm inherent to all three models tested here. Model RM as well as the models PM1 and PM2 predict fine-root biomass at a given point as the sum of the fine roots of all trees assumed to contribute roots to that point. This approach ignores the fact that there might be a maximum fine-root biomass, which cannot be exceeded. More generally, the approach ignores interactions between trees, which would prevent extreme fine-root biomasses. Despite this, interactions are probable. Thus, in samples that are shared by several trees, maximum root biomasses might systematically be constrained by interactions. Constrained biomasses in several cores would cause parameters which result in a systematic underestimation of root biomasses by the models in relation to not constrained samples, because the models are not capable of distinguishing between sample types. Thus, the model functions would be adapted to constrained values, which would affect the estimations for the unconstrained samples also. In other words, if the algorithm of fixing the parameters could distinguish between constrained and unconstrained samples the mean of the model would be raised.

Regarding the high tree number and the low variation in fine-root biomass in section 2, it seems possible that a threshold of maximum fine-root biomass is reached there, causing relatively homogenous root distributions (see below). The models are not capable of taking a maximum fine-root mass into account.

Sample scheme and stands

A fairly heterogeneous degree of fit of either model to the data of the two different sections of the stand is obvious. The best fit was achieved with the data of section 1. Hence, a closer look at the sections using the data of Table 3 is appropriate; this table reveals similar values for the mean DBH of the trees per section but also shows a remarkable difference in the degree of homogeneity and in stem number. The Clark-Evans index R as a measure of regularity of tree spacing differs between sections 1 and 2. Only the distribution pattern of the trees of section 1 can be interpreted as random, whereas the pattern of the other section differs significantly from a random distribution towards regularity. In addition to the differences between the distribution patterns of the trees, the sections can be separated by stand density. The higher stem number occurs in section 2. As a conse-

quence of the gap, a lower stem number can be observed at section 1 (Table 3). Looking at the values of the standard deviations of the root biomass of the sections (Table 2) reveals an interesting feature: the variation is lower in section 2 and higher in section 1. Hence, the models did fit best in that part of the stand, where the trees are distributed less uniformly and where root biomasses are most heterogeneous. From these observations it can be concluded that to fit the models, it is necessary to choose heterogeneous stands and to position the soil cores in those locations within the stands where extremes are expected and where the additive model algorithms appear to be correct.

Root dynamics

In an exhaustive literature review, Stone and Kalisz (1991) found no information as to whether the maximum spread extent of tree roots differs between trees in stands of different density. However, the results of the model estimations imply the existence of such differences. In the case of the trees surrounding the gap in the sparsely stocked section 1, the highest correlation coefficients were reached with a maximum distance of root spread of 15 m, whereas in the denser part of the stand (sections 2) a maximum of 9 m revealed the strongest correlation (Table 4). As the gap was caused approximately 10 years ago, these results reveal that the roots of spruces can effectively tap unoccupied soil compartments. Corroborating observations in gaps of red spruce (*Picea rubens* Sarg.) old-growth stands were also reported by Battles and Fahey (2000).

Concluding remarks

As already mentioned it seems to be of great interest to develop models that estimate fine-root biomass at a given point via variables, which are easy to measure. The approaches presented here should be understood as the first steps in this direction. Further investigations in modelling root architecture are necessary. According to Berntson (1994) they should integrate size-dependent and size-independent aspects of root architecture as well as patterns of root development. It is, therefore, of great interest to elucidate how effectively tree roots can occupy free areas and how the ability of a tree to spread its roots is restricted by other trees in dense stands. Investigations in this field should be borne in mind particularly the orientation of lateral roots, where less is known (Coutts and Nicoll 1991).

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Appendix A

The Ribbens model (RM)

$$n = \int_0^{20} 2\pi x(e^{-Dx^\theta}) dx$$

$$RM(x) = \left[N \left(\frac{DBH}{30} \right)^\beta \right] \frac{1}{n} e^{-Dx^\theta}$$

where $RM(x)$ is the predicted distance-dependent root biomass (g/m^2); DBH is diameter at breast height given in centimetres, x is distance to tree trunk in metres; and D , β , θ , and N are parameters to be estimated.

Estimating the mean fine-root biomass in a section (g/m²) from single-tree data

$$\text{FRB} = \frac{\sum_{i=1}^j \left[N \left(\frac{\text{DBH}_i}{30} \right)^4 \right]}{A}$$

where FRB is mean fine-root biomass (g/m²) in a particular section, N is the estimated root biomass of a single tree in that section with DBH of 30 cm, i is an individual tree, j is the total number of trees in that section, and A is the area of the section in question.

The polynomial model (PM2)

$$x_0 = 0 \quad y_0 = \left(\frac{\text{DBH}}{30} \right)^4$$

$$x_1 = \frac{x_3}{3} \quad y_1 = 0.83y_0$$

$$x_2 = 2x_1 \quad y_2 = \frac{y_1}{2}$$

$$x_3 = \frac{\text{DBH}}{6} \quad y_3 = 0$$

$$h = x_2 - x_1$$

$$b_0 = y_0$$

$$b_1 = \frac{y_1 - y_0}{1!h}$$

$$b_2 = \frac{(y_2 - y_1) - (y_1 - y_0)}{2!h^2}$$

$$b_3 = \frac{[(y_3 - y_2) - (y_2 - y_1)] - [(y_2 - y_1) - (y_1 - y_0)]}{3!h^3}$$

$$\text{PM2}(x) = b_0 + b_1(x - x_0) + b_2(x - x_0)(x - x_1) + b_3(x - x_0)(x - x_1)(x - x_2)$$

where PM2(x) is the predicted distance-dependent relative fine-root biomass (in proportions of the fine-root biomass of a tree with 60 cm DBH), x_i is the distance from tree trunk in metres, y_i and b_i are relative fine-root biomasses without dimension, and DBH is diameter at breast height given in centimetres.