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An approach for modelling the mean fine-root biomass of Norway spruce stands

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Abstract The applicability of a heuristic model for estimating mean fine-root biomass of Norway spruce stands based on the coordinates and the diameters at breast height (diameter at a height of 1.3 m, dbh) of their trees was tested. The model was developed based on the following assumptions which were derived from the literature: (1) the maximum distance the roots of a tree can be found depends on the dimension of the tree and exceeds the edges of the crown; (2) fine-root biomass decreases with increasing distance from the tree trunk; (3) fine-root biomass increases with the dbh; (4) maximum fine-root biomass of a tree is not allocated directly around the tree's trunk but at some distance from the stem. On the basis of these assumptions the model calculates a relative fine-root biomass at a given point within a stand. Four different versions of the model were compared, with each version differing with respect to the assumed decrease in fine roots with decreasing dbh and the approaches used to calculate the contribution of a subject tree to the fine-root biomass at a given point within a stand (additive versus consumptive). Using regression analysis we parameterised each model type with the data of 70 soil cores from a 75-year-old Norway spruce stand in southern Germany (Bavaria). The relative fine-root biomass calculated by the four different model types accounted for 62–72% of the variation of the measured fine-root biomass. The parameterised models were used to predict the fine-root biomass of 60 given points of a second Norway spruce

stand based on its dbhs and stem coordinates. The comparison of measured and predicted mean fine-root biomasses of the second stand revealed no significant differences between the measured mean and the means estimated by three of the four model types. Whereas with two of the model types we achieved means and medians, respectively, nearly identical to the measured average, none of the model types was able to predict values as high as the measured maximum. Constraints of the models and points that need to be considered regarding the minimum number of soil cores needed for a reliable parameterisation of the model are discussed.

Keywords Fine-root distribution · Fine-root biomass prediction · Aboveground stand characteristics · *Picea abies*

Introduction

For both ecological and economic reasons the conversion of pure Norway spruce [*Picea abies* (L.) Karst.] stands into mixed stands has been promoted in central and northern Europe (Kenk 1992; Björse and Bradshaw 1998; von Lüpke et al. 2004). For example, a common way to introduce beech (*Fagus sylvatica* L.) is to plant seedlings or to drill seeds below the canopy of a mature spruce stand (Leder and Wagner 1996; Ammer et al. 2002). As shade affects the morphology of beech seedlings (Collet et al. 2002), the general assumption is that this technique is advantageous to seedling quality (high uprightiness, low branchiness) (Leder and Hillebrand 2001), the avoidance of frost damage and to a reduction in weed competition (Aussenac 2000). However, the overstorey trees have various effects on seedling growth, as they do not only reduce the availability of light, but they also control the availability of belowground resources (Kuuluvainen and Pukkala 1989; Brockway and Outcalt 1998; Wagner 1999; Ammer 2002a). In fact, a recent trenching experiment showed that spruce roots have a significant impact on the growth and biomass partitioning of beech seedlings

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(Ammer 2002a). As the availability of the belowground resources is strongly correlated with the amount of fine roots in the soil (Wu et al. 1985; Coomes and Grubb 2000; Ammer and Wagner 2002), information on the fine-root biomass of the overstorey trees is of great interest in modelling seedling growth (e.g. Kuuluvainen and Pukkala 1989; Wagner 1999). However, it is both difficult and expensive to obtain statistically sound information on the root biomass of a stand in general (Makkonen and Helmisaari 1998; Bolte et al. 2003). This is particularly true for fine roots because of their high degree of heterogeneity within short distances of a few meters (Clemensson-Lindell and Persson 1995; Campbell et al. 1998; Jones et al. 2003). Consequently, models using easy-to-measure data are of great interest (Drexhage and Grupber 1999; Le Goff and Ottorini 2001; Bolte et al. 2003). Three different approaches to modelling fine-root biomass at a given point from aboveground stand characteristics have recently been published (Nielsen and Mackenthun 1991; Ammer and Wagner 2002). However, to date, none of these models has been used for predicting the fine-root biomass of another stand without additional soil cores.

In addition to the importance of developing approaches for predicting fine-root biomass for the generation of reliable regeneration models, fine-root models may also be used for the quantification of the role of fine-root biomass for carbon cycling on stand level. Despite the fact that fine roots are only a small part of the total tree biomass (Vogt 1991) they are important for biomass dynamics and hence carbon cycling (Persson 1983). Fine-root production, which is related to fine-root biomass (Kurz et al. 1996) is a key factor in calculating the carbon budget of the forest sector (Vogt et al. 1996). To determine the potential role of forestry in carbon sequestration, information on the belowground carbon storage in tree roots is needed to verify existing calculations (Böswald 1996; Burschel and Weber 2001; Rohner and Böswald 2001). Hence the first objective of the study reported here was to test the suitability of a model for fine-root biomass predictions on stand level by a heuristic approach modelling the fine-root biomass distribution of Norway spruce trees. At present all existing models for the prediction of fine-root biomass at a given point assume a proportional decrease of fine-root biomass with tree diameter and an additive contribution to the total fine-root biomass by the surrounding trees. However, these assumptions have only been partly verified. The second objective of the study, therefore, was to test whether model modifications result in more accurate fine-root biomass predictions.

Materials and methods

Model description

The model calculates a so-called relative fine-root biomass (rFRB) for any point in a system of coordinates that takes into consideration the distance of the overstorey trees to

that point and their dimensions. The model is based on the following assumptions:

1. The maximum distance from the tree trunk where roots of a subject tree can be found depends on the dimension of the tree and exceeds the edges of the crown by a significant distance (Vater 1927; Wiedemann 1927; Stone and Kalisz 1991; Parsons et al. 1994; Brockway and Outcalt 1998; Polomski and Kuhn 1998; Puhe 1994, 2003; Müller and Wagner 2003).
2. Fine-root biomass decreases with increasing distance from the tree trunk (Friedrich 1992; Drexhage 1994; Bauhus and Bartsch 1996; Brockway and Outcalt 1998; Taskinen et al. 2003).
3. Fine-root biomass increases with the diameter at breast height (diameter at a height of 1.3 m, dbh) of the tree (Drexhage 1994; Le Goff and Ottorini 2001).
4. The maximum fine-root biomass of a tree is not allocated directly around tree's trunk but at some distance from the stem (Hilf 1927; Wittkopf 1995; Taskinen et al. 2003).

These assumptions can be transformed into two models (Fig. 1a,b). Model A defines a proportional decrease of fine root with decreasing dbh (Fig. 1a), whereas model B assumes a stronger decrease (Fig. 1b). The respective algorithms were formulated as follows:

1. Model A: $RD_3 = dbh/6$ assuming a maximum root-spread distance of 10 m for a tree 60 cm in dbh (Ammer 2000).
Model B: $RD_3 = dbh/6 + z$ with $z = -(dbh-60)/10$ if $dbh < 60$ (otherwise as in model A; applying the term z for thicker trees would lead to unreasonable distances of maximum root spread), where RD_3 is the maximum root-spread distance in meters, and dbh is the diameter at breast height in centimeters.
2. Model A and B: $RD_2 = (2/3)RD_3$, $RD_1 = (1/3)RD_3$ and $RD_0 = 0$, where RD_3 is the maximum root-spread distances in meters, RD_2 and RD_1 are two-thirds and one-third, respectively, of this distance and RD_0 marks the trunk.
3. Model A: $rFRB_0 = dbh/100$
Model B: $rFRB_0 = (dbh)/(100 + g)$ with $g = -(dbh - 60)$, where $rFRB_0$ is the relative fine-root biomass at distance RD_0 (trunk), and dbh is the diameter at breast height in centimeters.
4. Model A and B: $rFRB_1 = (5/3)rFRB_0$, $rFRB_2 = (5/6)rFRB_0$ and $rFRB_3 = 0$, where $rFRB_1$, $rFRB_2$ and $rFRB_3$ are the relative fine-root biomasses at distances RD_1 , RD_2 and RD_3 , respectively.

Based on the distances RD_0 to RD_3 in both models we calculated a polynomial of third degree for the dbh of each tree using the Gregory-Newton procedure to fit a polynomial of n th degree to $n+1$ equidistant points of support (Stöcker 1995). This allows the calculation of the rFRB of each tree of a stand at any point x,y . The respective formulae are:

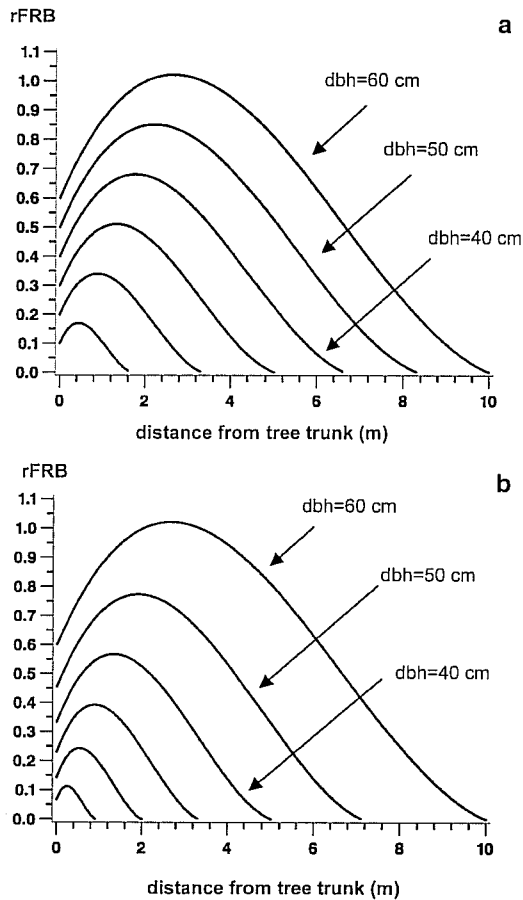


Fig. 1 Relative fine-root biomass (rFRB) of a tree in relation to the distance from the stem trunk and the diameter at breast height (*dbh*) as assumed by the model. **a** Model types A1 and A2, **b** model types B1 and B2

1. If $D \geq RD_3$, then $rFRB=0$, where D is the distance between the tree's trunk and x, y .
2. If $D < RD_3$, then $rFRB$ of a tree at point x, y is calculated as follows:

$$h = RD_2 - RD_1$$

$$b_0 = rFRB_0$$

$$b_1 = \frac{(rFRB_1 - rFRB_0)}{1!h}$$

$$b_2 = \frac{((rFRB_2 - rFRB_1) - (rFRB_1 - rFRB_0))}{2!h^2}$$

$$b_3 = \frac{\left(\frac{((rFRB_3 - rFRB_2) - (rFRB_2 - rFRB_1))}{-((rFRB_2 - rFRB_1) - (rFRB_1 - rFRB_0))} \right)}{3!h^3}$$

$$\begin{aligned} rFRB_{x,y} &= b_0 + b_1(D - RD_0) + b_2(D - RD_0)(D - RD_1) \\ &\quad + b_3(D - RD_0)(D - RD_1)(D - RD_2) \end{aligned}$$

To obtain information about the relative fine-root biomass of all trees contributing roots to point x, y , we tested two different ways of calculation for both models. First an additive total rFRB (TrFRB) at point x, y was calculated as: $TrFRB = \sum_{i=1}^n rFRB_i$, where i is the tree number of the stand (model type A1 and B1). Thus, it is assumed that the total amount of fine roots at a given point results from additive contributions of the trees.

Second, TrFRB was calculated based on the assumption that the consumption of the soil resources by tree fine roots and hence fine-root biomass is negatively influenced by the presence of roots from other trees. This assumption is based on the finding that the root growth of trees is facilitated by the removal of competing trees and compensates for the fine-root biomass loss entailed by the reduction in stem number (Parsons et al. 1994; Jones et al. 2003; Puhe 2003). Thus the second model type (model type A2 and B2) assumes that the contribution of fine-root biomass of a subject tree to a given point decreases with the presence of other trees standing closer to the point of interest. This is realised by the following computations:

1. Defining a rFRB entirely consuming soil resources. According to Wagner (1999), it was assumed that at the point where a tree of 100 cm dbh shows the highest amount of fine roots all soil resources are consumed by this tree. Following the model assumption (see above) a tree of 100 cm dbh exhibits the highest relative fine-root biomass at a distance of 5.55 m from tree trunk. The pertinent rFRB value is 1.6667.
2. Calculating the consuming effect of the tree standing closest to the point of interest (tree no. 1) as $u_1 = 1 - rFRB_1/1.6667$, where u_1 is the relative amount of soil resources left by tree no. 1.
3. Calculating the effect of tree no. 2, standing closer than all other trees except tree no. 1 as: $u_2 = u_1 - u_1 rFRB_2/1.6667$, where u_2 is the relative amount of soil resources left by tree no. 1 and tree no. 2.
4. Calculating the effect of the n th tree with roots reaching the point of interest as: $u_n = u_{n-1} - u_{n-1} rFRB_n/1.6667$, where u_n is the relative amount of soil resources left by all tree fine roots reaching the point of interest.
5. Calculating a consumptive total relative fine-root biomass as: $TrFRB = 1 - u_n$.

Model parameterisation

The model was parameterised with the data of 70 soil cores that were taken in autumn 1998 in a pure 1.45-ha Norway spruce stand located in southern Germany (Bavaria) near Freising. The rather homogenous soil originates from Loess and is very productive (Table 1). The stand differs in stand density as it includes uniformly and densely stocked parts and a larger gap which was created by bark beetles in 1990. Thus, the basal area measured in a grid of 18×18 m ranges between 0 m² ha⁻¹ and 80.1 m² ha⁻¹ (Leder et al. 2003). The points where the soil cores were taken had been predetermined by a study by Ammer (2000) and correspond to light measurement spots. The spots were located in 18 of 36 randomly selected 18×18-m plots. Within the plots the light measurement spots, and hence the points where the four to five soil cores were taken, had been evenly spaced in a regular grid throughout the entire plot. As the 18 plots and corresponding samples were scattered throughout the whole stand, the data include soil cores from the gap (b. a. 0 m² ha⁻¹), medium stocked (up to 50 m² ha⁻¹) and dense parts of the stand (up to 80 m² ha⁻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. Following removal of the soil, the corer was driven to a depth of 30 cm in a second step. As Norway spruce exhibits a particularly shallow root system, the zone of the upper 30 cm is known as the section where normally more than three-quarter of the fine roots of spruce are located (Kalela 1950; Wittkopf 1995; Schmid and Kazda 2002). For that reason the depth of 30 cm was chosen, as in other studies (e. g. Clemensson-Lindell and Persson 1995; Helmisaari and Hallbäck 1999). The three samples per core hole (organic horizon, mineral soil down to 10 cm, mineral soil down to 30 cm) were placed in separate plastic bags. The samples of mineral soil plus roots were washed individually over 1-mm sieves to

separate the root material from mineral soil. Following the guidelines of Böhm (1979), we classified only roots ≤2 mm in diameter as fine roots. These roots were selected irrespective of their shape. Finally, the dead roots were separated out. The distinction between living and dead components was made according to Murach (1984) by assessing the colour and elasticity of the roots and the existence of the root cortex. Following separation, samples of live roots were oven-dried at 65°C for 96 h. Mycorrhizal root tips were not separated from root material. For the parameterisation of the model, the measured fine-root biomasses of the three root samples per core hole were combined to one sample. As in previous studies, only the total fine-root biomass per soil core was analysed (Nielsen et al. 1991; Müller and Wagner 2003).

Coordinates of all trees and soil core sampling points were taken; the dbh of all trees was measured the year before (1997).

Model validation

The parameterised models (A1, A2, B1, B2) were used to predict fine-root biomass at given points of another Norway spruce stand (1.25 ha in size) based on its dbhs and stem coordinates. This second stand is located 28 km from the first stand and stocks on a similar site. Both stands are even-aged pure Norway spruce stands. The soil type and soil texture of the two sites are comparable (Table 1). Both soils are very fertile Typic Hapludalfs of the same geological origin (Ammer 2000). In addition, the stands are of the same age and yield class but differ in stand volume and tree number (Table 1). Model validation was carried out by comparing the fine-root biomass of another 60 soil cores which had been taken in the second stand with the predicted values that had been calculated for these 60 sample points by the parameterised models. The soil samples were taken from 12 of 36 randomly selected 18×18-m plots. Within each plot five evenly spaced soil

Table 1 Characteristics of stands and sites

Parameter	Stand no. 1	Stand no. 2
Latitude and longitude	48°25'N, 11°41'E	48°34'N, 11°59'E
Elevation (m)	490	465
Precipitation (mm year ⁻¹)	790	780
Soil texture	Sandy loam, loamy sand	Sandy loam, loamy sand
Soil type	Typic Hapludalf (U.S. soil taxonomy) derived from Pleistocene loess over Tertiary sediments	Typic Hapludalf (U.S. soil taxonomy) derived from Pleistocene loess over Tertiary sediments
Site index (at 100 years)		
Height	38	38
Volume	13	13
Age in 1997	75	78
Density (stems ha ⁻¹)	553	377
Basal area (m ² ha ⁻¹)	54.78	40.91

cores were taken in a regular grid throughout the entire plot.

Calculations and statistical analyses

The parameterisation of the different model types was done by regression analysis using the measured fine root biomass (mFRB) as the dependent variable and the relative fine-root biomass calculated by models A1, A2, B1 and B2 (TrFRB) as the independent variable. To comply with the regulations underlying linear regression, we computed logarithmic transformations of dependent and independent variables according to Quinn and Keough (2002). This resulted in a linearisation of the regression model and constant variance. Model validation was conducted by testing the means of the predicted and the measured fine-root biomasses of stand no. 2. As both predicted and measured fine-root biomasses showed non-normal distributions, the non-parametrical two-sample test after Wilcoxon was used to test the H_0 that the distribution functions of the two sets of observations do not differ in location (Dufner et al. 1992). Model programming, calculations and statistical analyses were conducted using the SAS (Statistical Analysis System ver. 6.12; SAS Institute, Cary, N.C.).

Results

Model parameterisation

For each of the four model types it was possible to get a highly significant relationship between the measured fine-root biomass and the TrFRB calculated by the models (Table 2). Thus, the calculated TrFRB accounted for 62–72% of the variation of the measured fine-root biomass. However, the coefficients of determination of model types B1 and B2 were substantially lower than those of the two other variants. This indicates a better fit of the A1 and A2 model variants, both of which assume a proportional decrease of fine roots with decreasing dbh while calculating TrFRB. In contrast to the difference between models A and B no differences between model types 1 and 2 within a model could be detected. This means that the two approaches tested, and additive and consumptive

contribution of tree roots to soil cores, could be parameterised equally by the data.

Model validation

The comparison of the measured and predicted mean fine-root biomasses of the second stand revealed that the null hypothesis—assuming that the distribution functions of the two sets of observations do not differ in location and, hence, there are no significant differences of the means—could not be rejected for model types A1, A2 and B1 at the 0.05 significance level (Table 3). However, when the statistical attributes given in Table 3 are examined, it is obvious that there are differences between the model types. Whereas model type A1 showed the closest median, model type A2 achieved a mean nearly identical to the measured average. In addition, model type A2 showed the widest range and the lowest standard error (Table 3). Nevertheless, none of the model types was able to predict values as high as the measured maximum. The only model type with a predicted mean significantly different from the measured average was model type B2 (Table 3) and, consequently, the mean fine-root biomass predicted by this model type was significantly different from the measured data.

Given the applicability in principle of at least the three model variants A1, A2 and B1 for predicting the mean fine-root biomass the question arises of just how many soil cores have to be sampled and analysed for the parameterisation of the model to guarantee precise estimations of the fine-root biomass in additional stands. To answer this question we randomly selected nine of the 70 soil cores taken from stand no. 1. We then added a tenth soil core that represented a situation in which none of the surrounding trees contributed fine roots as assumed by the model. This measure helped to reduce the fluctuation of the intercept and to yield highly significant relationships in every case between the ten soil core values and the TrFRB in the following parameterisation procedure. With the parameterised model (model type A1) we then predicted the FRB-values for the 60 sample points of stand no. 2 and subsequently calculated the mean and the median of these predicted values. This procedure was carried out 100 times using the random generator of SAS (Statistical Analysis System ver. 6.12). It can be seen from Fig. 2 that even with ten samples used for the parameterisation of the model the measured mean fine-root biomass of stand no. 2 could be predicted. Of the means calculated on the basis of the predicted values, 45% lay within the range of the measured mean \pm standard error. The lowest predicted value was 35% smaller than the measured mean; the highest overestimation was 120% of the measured mean (Fig. 2).

Table 2 Results of regression analyses for the parameterisation of the four model types. Regression equation: $\ln(\text{mFRB}) = b_0 + b_1 \ln(\text{TrFRB})$, where mFRB is the measured fine-root biomass and TrFRB is the total relative fine-root biomass per soil core estimated by each model type. *MSE* Mean standard error

Model type	b_0	b_1	r^2	MSE	df	P
A1	5.3635	0.4664	0.721	0.1052	69	<0.0001
A2	5.8521	0.5788	0.721	0.1051	69	<0.0001
B1	5.6857	0.4154	0.615	0.1450	69	<0.0001
B2	6.0755	0.5241	0.620	0.1465	69	<0.0001

Table 3 Measured and predicted values (mg m^{-2}) for the validation stand (stand no. 2) and test statistics: Wilcoxon's two-sample test comparing measured and predicted data. *Prob* denotes the proba-

	Mean	SE	Median	Minimum	Maximum	Probability
Measured	245.37	17.92	223.52	11.70	646.05	
Predicted by A1	230.30	6.35	224.86	33.01	314.26	0.5135
Predicted by A2	246.42	6.11	243.96	25.53	316.66	0.1209
Predicted by B1	234.51	8.57	241.37	43.50	385.77	0.6574
Predicted by B2	181.95	7.73	188.56	24.21	313.27	0.0196

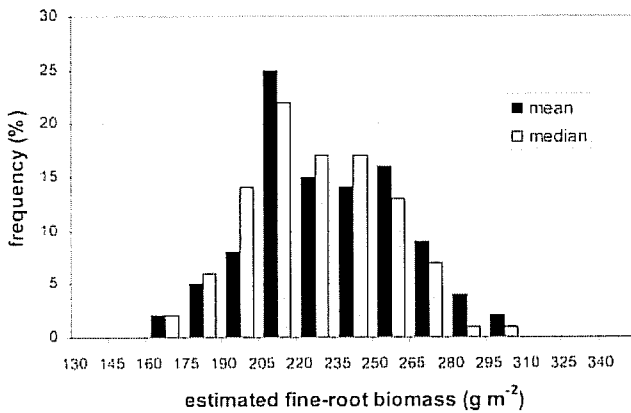


Fig. 2 Frequency distribution of the means and medians of stand no. 2 predicted by model type A1. Each value represents the mean (median) predicted fine-root biomass of 60 given points. The predictions are based on the same model but differing model parameters. The parameters were computed by regression analysis using TrFRB as the independent variable and measured fine-root biomass of nine randomly selected and one fixed soil core of stand no. 1 as the dependant variable. The random selection and the regression analysis, respectively, were repeated 100 times, resulting in 100 parameters and 100 predictions. The means (medians) were grouped to width classes of 15 g m^{-2} .

Discussion

Model types and model assumptions

As our regression analyses show (Table 2), we were able to detect a strong and highly significant relationship between the TrFRB calculated by the model types and the measured fine root biomass. Thus, 62–72% of the variability of the measured fine-root data was explained by the different model types. This result reveals that in addition to other model approaches assuming exponential or logistic fine-root distribution functions (Nielsen et al. 1991; Müller and Wagner 2003), simple heuristic models can also be parameterised adequately by measured data. For given points of the same stand these models can therefore be used to predict the fine-root biomass (Ammer and Wagner 2002). More importantly, following the parameterisation by the data of a specific stand, two of the four model types tested within the framework of the present study yielded reliable results when used for the prediction of the mean fine-root biomass of another stand (see section Model predictions). Hence, there is some evidence that the assumptions on root spread derived from

literature and implemented in the models do properly reflect reality. However, 28–38% of the variability of the data could not be explained by any of the model variations. A potential source of this unexplained variability is that the maximum root spread of a tree of a given dbh is likely to be dependent on stand density (Stone and Kalisz 1991). In fact, Ammer and Wagner (2002) found that maximum root spread for a given tree is higher in less dense stand sections including a gap. The same is suggested by the results of studies where the fine-root extension from edge trees into gaps was investigated (Parsons et al. 1994; Bauhus and Bartsch 1996; Müller and Wagner 2003). In addition, the results presented by Parsons et al. (1994) and Jones et al. (2003) indicate that until a threshold gap size is reached differences in stem number are not reflected in different fine-root biomass densities. These results suggest that the relationship between fine-root biomass and dbh of a tree varies within a determined range.

When models A and B are compared, it is evident that the assumptions of the smaller decrease in fine-root biomass and distance of root spread (model types A1 and A2) seem to be more realistic than the rapid diminution represented by model types B1 and B2, as indicated by the larger r^2 and smaller MSE (Table 2). Unfortunately, no data is available to compare the model assumptions with measured fine-root data of single trees. However, the extent of the decrease of the relative fine-root biomass calculated by the models with decreasing dbh is similar to the relationships between coarse-root biomass and dbh referred to by Drexhage and Grupber (1999) and Bolte et al. (2003). These authors estimated the coarse-root biomass of Norway spruce (y) at dbh using the equation: $\ln(y) = a + b \ln(\text{dbh})$ and found that the slopes (b) of the regression lines were between 2.36 and 2.85. The comparable computation, i.e. calculated relative fine-root biomasses of model A1 and B1 regressed against dbh, resulted in slopes of 2.0 (A1) and 2.55 (B1).

In contrast to models A and B, the respective model types 1 and 2 did not differ in the amount of explained variability of the measured fine-root data. However, for the prediction of the mean fine-root biomass of stand no. 2 model type 2 was suitable only for model A but not for model B (see section Model predictions).

The basic assumption underlying model types A2 and B2 is that a spruce of a defined diameter (here 100 cm, dbh) entirely occupies and consumes a given soil

compartment at distance RD_1 . Regrettably, this was not verified, but the approach is based on the biologically founded supposition that a maximum fine-root threshold of a given soil volume does exist. However, varying the tree diameter, which is assumed to entirely consume the soil resources at distance RD_1 , did not result in more precise estimations. Larger diameters cause slightly increased parameters b_0 and b_1 of the regression equation given in Table 1. This is caused by lower TrFRB values, which always result if the diameter of a tree entirely consuming the soil resources at distance RD_1 is enhanced. Increased parameters, however, reduce the accuracy of the predicted mean fine-root biomass of stand no. 2. Thus, the predicted fine-root biomass decreases with increasing entirely-consuming tree diameter (i.e. an entirely-consuming tree diameter of 150 cm corresponds to a predicted mean fine-root biomass of 237.65 mg m^{-2} ; a diameter of 200 cm results in 232.82 mg m^{-2} ; a diameter of 250 cm, in 229.75 mg m^{-2} ; a diameter of 300 cm, in 227.34 mg m^{-2}). However, the assumption that the presence of the fine roots of a tree reduces the belowground resource availability for other trees was derived from the finding that soil moisture decreases with increasing fine-root biomass (Coomes and Grubb 2000), which was recently confirmed by trenching experiments (Gerhardt 1996; Irrgang 1999; Ammer 2002a). In addition, Vanninen and Mäkela (1999) pointed out that the soil nutrient status is inversely related to the amount and production of fine roots. Although the coefficients of determination given in Table 2 show no differences between model types A1 and A2 and B1 and B2, respectively—i. e. between the additive and the consumptive approach—the consumptive approach yielded the most precise prediction of mean fine-root biomass of stand no. 2 (Table 3).

As presented elsewhere (Ammer and Wagner 2002), the additive model A1 can also be parameterised assuming that the maximum relative fine-root biomass occurs at the trunk. Thus, although reported repeatedly and biologically plausible, the reduction of fine-root biomass in the area overtopped by the tree's crown described by all model types seems to be not as important for a strong relationship between measured and calculated data as the distance-dependent root spread.

Model predictions

All model types except model type B2 predicted means and medians of fine-root biomass that were not statistically different to the measured values ($P < 0.05$). Whereas model type A1 predicted the median most precisely, model type A2 nearly met the measured mean fine-root biomass. However, none of the model types was able to reflect the high variation-inherent spatial fine-root biomass distribution commonly found in tree stands (Clemensson-Lindell and Persson 1995; Vogt et al. 1996; Vanninen and Mäkela 1999; Mäkela and Vanninen 2000; Schmid and Kazda 2002). This is problematic if estimations of the full range of fine-root biomass are required, e.g. for modelling

seedling growth on a single-tree basis, whereas it seems to be acceptable if information on fine-root biomass at the whole-stand level is required. In a pilot test with model A1 at the single-point level under- and overestimations of fine-root biomass occurred frequently (Ammer 2002b). As shown in the present study these under- and overestimations were mutually equalised by calculating a mean. However, despite their surprising accuracy regarding predicted mean fine-root biomass three constraints of all model types have to be mentioned. Firstly, the model predictions cannot be used for estimating fine-root production over time by comparing estimated fine-root biomasses at different times. As Kurz and Kimmins (1987) and Santantonio and Grace (1987) pointed out, the production and mortality of fine roots proceed at the same time. Thus, the simple subtraction of fine-root biomasses of two inventories would ignore the turnover during the growing period.

Secondly, for periodic repeated inventories during a year the model requires repeated parameterisations. This is necessary because fine-root biomass shows a seasonal and annual change (Santantonio and Herrmann 1985; Burke and Raynal 1994; Clemensson-Lindell and Persson 1995; Makkonen and Helmisaari 1998; Leuschner et al. 2001; López et al. 2001; Müller and Wagner 2003), whereas TrFRB computed by the model is relatively static as it is related to aboveground biomass. This means the TrFRB at the end of the year should be higher than at the beginning of the growing period due to tree growth, whereas the fine-root biomass could have decreased due to abiotic factors such as soil temperature, mean annual temperature-precipitation ratio, mineralisation rates and so on (Santantonio and Grace 1987; Nadelhoffer and Raich 1992; Persson 1996; Vogt et al. 1996). Consequently, production estimates are not possible with the model presented here. Thus, if changes during the year or comparisons between years are of interest a new parameterisation of the model is necessary. However, summarising the results from the analysis of the minimum number of soil cores required for an reliable parameterisation of the model we can state that, depending on the desired accuracy, estimations based on only ten soil cores are possible.

The third constraint of the model is that different sites require new parameterisations as site quality, nutrients and, in particular, soil texture affect fine-root biomass (Meyer 1967; McClaugherty et al. 1982; Nadelhoffer et al. 1985; Kurz et al. 1996; Vogt et al. 1996; Makkonen and Helmisaari 1998; Schmid and Kazda 2002; Puhe 2003). Whether the model is transferable to younger stands without parameterisation cannot be answered within the scope of the present study. However, because the model is based on tree dimension (dbh), which is closely correlated to age, its applicability in younger stands and/or other tree species is expected. Nevertheless, once parameterised the model allows reliable predictions on the single-point level within the same stand and sound estimations of mean fine-root biomass of stands comparable in age and located at a comparable site.

Conclusions

Vanninen and Mäkela (1999) stated that methods of estimating fine-root biomass by allometric relationships with aboveground compartments “does not seem to apply to fine roots because they cannot usually be estimated on an individual tree basis”. However, based on the study presented here, we believe that it is possible to use aboveground information not only for estimations of structural roots (Santantonio et al. 1977; Drexhage and Gruber 1999; Drexhage and Colin 2001; Le Goff and Ottorini 2001) but also for estimations of fine-root biomass. Despite the high spatial and temporal variability of fine-root biomass and the numerous abiotic and biotic factors influencing root growth (Makkonen and Helmi-saari 1998; Jones et al. 2003), reliable estimations of fine-root biomass at the stand level have been achieved within the framework of the present study. We therefore accept the hypothesis outlined in the Introduction that a simple model based on aboveground stand characteristics is able to predict the mean fine-root biomass of a Norway spruce stand. In contrast, we cannot confirm that the presented model modifications (e.g. A2, B1, B2) resulted in improved predictions. However, the general approach presented here requires further research into various areas, including the applicability of our approach to other systems. We mentioned in the Introduction that the overstorey trees determine seedling growth not only by reducing light availability but also, and in some situations exclusively, by controlling the availability of belowground resources (see Brockway and Outcalt 1998). Against this background future research should focus on the question of to what extent reliable model predictions of fine-root biomass are linked to belowground resource availability and to seedling establishment and growth.

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