Fine root biomass and turnover in southern taiga estimated by root inclusion nets.

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Abstract

Fine roots play an important part in forest carbon, nutrient and water cycles. The turnover of fine roots constitutes a major carbon input to soils. Estimation of fine root turnover is difficult, labour intensive and is often compounded by artefacts created by soil disturbance. In this work, an alternative approach of using inclusion nets installed in an undisturbed soil profile was used to measure fine root production and was compared to the in-growth core method. There was no difference between fine root production estimated by the two methods in three southern taiga sites with contrasting soil conditions and tree species composition in the Central Forest State Biosphere Reserve, Russia. Expressed as annual production over standing biomass, Norway spruce fine root turnover was in the region of 0.10 to 0.24 y-1. The inclusion net technique is suitable for field based assessment of fine root production. There are several advantages over the in-growth core method, due to non-disturbance of the soil profile and its potential for very high rate of replication.

Introduction

Fine roots are responsible for the bulk of the water and nutrient acquisition and form the most active part of the root system. About 33% of global net primary production is used in fine root production and functioning (Jackson et al. 1997). As a result, fine root systems contribute substantially to global terrestrial carbon (C) cycle and are a major reservoir of C (Vogt and Persson 1991). Gower et al. (1997) suggested that the proportion of assimilated C allocated to fine roots is greater in coniferous forests than deciduous forest, and fine root production is thought to constitute a greater proportion of total biomass production in boreal forests characterised by low soil fertility and temperatures (Ruess et al. 1996b). However, in an analysis of over 140 sites in Europe, Finér et al. (2007) showed that standing fine root biomass is greater in beech (*Fagus sylvatica* L.) than Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.), but the amount of fine root biomass is strongly linked to above ground biomass. Fine roots have a much shorter lifespan than coarse roots, as a consequence, their biomass varies both seasonally and due to changing environmental conditions. Because of their rapid production, senescence and decomposition, fine roots contribute significantly to forest soil C flux, making accurate measurement of their biomass and rate of production indispensible for closing the boreal forest C budget (Brunner and Godbold 2007).

There are several methods for measuring fine root production in situ, all of which have drawbacks which influence the reliability of the observation, mostly related to the fact that a certain degree of soil environment disturbance is necessary before commencing the measurement. Two of the most commonly used methods which introduce a clear threshold for root growth initiation are in-growth coring and minirhizotrons (Majdi et al. 2005). On the one hand, minirhizotrons - transparent tubes inserted into the soil, are very effective for assessing seasonal changes in fine root growth or comparisons between sites, but they must be installed in the soil long before reliable observations can be made. Minirhizotrons do not allow for a direct measure of root production, even if observation on root growth and mortality can be used together with standing biomass observations to infer root production per unit area. On the other hand, in-growth cores – a root free cylinder or bag of soil inserted into the soil profile separated from it by a mesh or a net, give a ready estimate of fine root biomass per unit soil volume, but suffer from the soil disturbance introduced during their installation (Majdi et al. 2005). When using in-growth cores to measure root production in, for example, arable crops this is not of major importance as the soil profile has been already thoroughly mixed (Steingrobe et al. (2000). However, when measuring root production in an undisturbed natural ecosystem, in-growth coring is fraught with difficulty and very tedious as each in-growth core must be made to resemble the original soil profile. This is especially difficult in soils with multiple and well defined horizons, as each of these have to be re-created inside the core. To limit soil disturbance and the need to re-construct soil horizons, we have tested a modification of the in-growth core method where only two-dimensional net is inserted into the soil. Fahey and Hughes (1994) used a similar method in a study of a Northern hardwood dominated by *Acer saccharum*. In this investigation, Fahey and Hughes (1994) used 2.5 mm mesh screens set at an angle of 45º in the soil, and used the number of root intersection per screen to gain a relative measure of fine root production, but also of fine root disappearance. We have hypothesised (i) that this method can be used to assess fine root growth in situ without the need of laboratory and (ii) this method will provide fine root production estimates comparable with those obtained by standard in-growth cores.

Materials and methods

*Site description and sampling*

The study area is located in the Central Forest State Biosphere Reserve (CFSBR), 250 km north-northwest of Moscow, Russia (Table 1). The area is one of the few remaining pristine unmanaged ecosystems of the Southern Taiga zone in Russia. The mean annual temperature is +3°C, mean annual precipitation is 640 mm. The area is a watershed with a weakly cut relief, the topography ranges from flat to gently undulating. The vegetation is that of a typical southern boreal forest (Vygodskaya et al. 1995), where the main vegetation disturbance takes the form of windthrow, favouring the entrance of broadleaves in an ecosystem otherwise dominated by conifers (Drobyshev 2001). No wild fires have been reported in the CFSBR for at least one hundred years (Ulanova 2000).

Three sites of approximately 2.4 km2 each were selected to represent various degrees of disturbances and consequently, different size of gaps in the spruce canopy. Five replicate plots were selected within each site at least 2 crown lengths apart. Each plot contained 3 canopy dominant Norway spruce (*Picea abies* L. Karst) trees. The vegetation at the sphagnum site is dominated by Norway spruce, while the soil profile is characterised by a well defined sphagnum layer covering nearly 100% of the surface area. The other two sites do not have significant sphagnum cover, but differ in the degree of disturbance. All sites have Norway spruce in the overstorey. One site is dominated by Norway spruce (spruce forest), while at the other site the presence of broadleaves forms a mixed species forest (mixed forest). At both sites in addition to Norway spruce, birch (*Betula pubescens* L.) and aspen (*Populus tremula* L.) are present in the overstorey and mountain ash (*Sorbus aucuparia* L.) is present in the understorey (Bonifacio et al. 2008). The presence of these species is greater in the mixed species stand, where maple (*Acer platanoides* L.), lime (*Tilia cordata* P. Mill.) and elm (*Ulmus glabra* Huds.) are also present. The soils are Albeluvisols and show the presence of an argillic horizon at some depth in the profile. Above the argilic layer, there is a spodic horizon and a bleached albic horizon below a thin organic matter-rich surface mineral layer. Podzolisation is therefore superimposed on a process of clay translocation, as often occurs in this kind of soil (Driessen et al. 2001). At the sphagnum site an organic horizon contained most of the root mass. At all sites a composite organic horizon (Oe/Oa) was found, which we could not separate in its two components because of strong intermixing of material. Below the organic layer, both A and E type horizons were present in 90 % of all samples at mixed species site and the spruce dominated site.

*Root biomass*

In September 2002 and April 2004, two soil cores were taken using an 8 cm diameter auger around the central tree in each replicate plot, causing as little disturbance of the surrounding soil as possible. The maximum distance from the trunk was 2 m, the core position was chosen at random and each core was taken to a depth of 20 cm. Only 8-16% of the fine root biomass was found at depths greater than 20 cm in test cores at all sites (taken to a depth of 1 m). In each core, soil horizons were identified and separated. The roots were removed from the core sections and the resulting root-free soil was used to repack the in-growth cores. The roots were initially air dried in paper bags, then transported to the laboratory where they were washed free of soil, sorted into *Picea abies* roots and other tree species roots, dried at 70ºC and then weighed.

*In-growth cores*

In September 2002, to make the in-growth core, the hole from a root core (8.6 cm in diameter) was lined with a 2mm mesh to a depth of 20 cm, and repacked using the root free soil. Root-free soil was re-compacted inside the mesh according to the horizons and original bulk density. In April 2004, the in-growth core was recovered by cutting the roots on the outside of the core. All roots within the core were removed and washed dried and weighed as described above.

*Inclusion growth root nets*

In September 2002, 6 individual nylon nets (1mm opening, 10cm width and 25 cm length) were inserted vertically into the soil with the help of a steel plate and a hammer in two rows of 3 nets ca. 2m from the central tree of each replicate plot. The plate had a blade along its bottom cutting edge and a steel handle along the top to facilitate its extraction from the soil once the net has been inserted to the appropriate depth. The root nets were then left in the soil for 16 months and extracted in April 2004. To extract the nets, the soil was first cut 5 cm from each side of the net with a 25cm long knife. The 10 cm thick soil block thus created, with the net inside it, was then extracted from the profile and carefully shaken free of soil. Fine roots penetrating the net were quickly counted and the net together with the roots was placed in a plastic bag. The samples were kept cool during transport and then stored at 4ºC for about two week until processed. Once in the laboratory, using a binocular microscope, root fragments were classified into *Picea abies* and other tree roots, shortened to 1cm on either side of the net to create a ‘virtual’ core 2cm thick, 10cm wide and 15 cm deep, then removed from the net, dried at 70 ºC and weighed.

*Root production assessment*

The net and in-growth cores were inserted in September 2002 and recovered in April 2004. Given the present climatic conditions in Central Forest Reserve, the measured fine root production is primarily that of the 2003 growing season (see also Discussion). The rate of fine root turnover was calculated by dividing the estimate of fine root production by the estimate of fine root standing biomass in 2004.

Prior to re-insertion, we re-packed the in-growth cores according to the original stratification of the horizons using root-free material appropriate for each horizon. This allowed for an estimate of fine root production and turnover in different soil horizons (Table 3). We used fine root biomass (coring) and fine root production (in-growth core) found in each soil horizon to calculate Norway spruce fine root turnover.

*Statistical analysis*

Due to the large distance between the five plots within each site, they were considered independent replicates (n=5). All observations (6 nets, 2 ingrowth cores or 2 root cores) from one replicate plot were averaged at this level prior to carrying out statistical analysis (Bonifacio et al. 2008). One- or two-way ANOVA was used to compare the sites or measurement methods. Site and method were considered fixed effects, plot a random effect. Repeated measures ANOVA was used to compare standing root biomass between 2002 and 2004. All tests were carried out using standard procedures in SigmaStat 3.0 (SPSS Inc., Illinois, USA). Data were tested for normality (Kolmogorov-Smirnov test with Lilliefor’s correction) and equality of variance (Levene Median test) prior to ANOVA, a post-hoc (Holm-Sidak test) analysis was used for pair-wise comparisons if significant difference was detected.

Results

Comparison of the estimates of root production using the two methods gives remarkably similar values (Figure 1). A slightly higher fine root production was determined by the net method in comparison to in-growth core, 50.4 g m-2 and 35.0 g m-2 respectively, however the difference between the two methods is not significant (P=0.194). Similarly, there was no difference in the rate of spruce fine root production between the sites (P=0.069). Using the net method values, we also estimated fine root production of other woody species present at each site (Figure 2). These were roots of *Betula pubescens*, *Populus tremula* and *Sorbus aucuparia*, but they were not divided into species. The lowest root production by these species was found on sphagnum site and the spruce forest site. A significant difference was however found only between the sphagnum site and the mixed forest site (P=0.005).

Root net method also gives the opportunity of an in-field estimate of root production. Once the net has been shaken free of soil, it is possible to count the number of fine root incursions and thus carry out an initial assessment of within or between site variability of root production. We have verified the reliability of the field assessment of the inclusions against the data obtained in the laboratory using a stereo microscope (Figure 3). The data shown are the inclusions for all species, a good agreement was found between the field estimate and the laboratory estimate (r2=0.79). We also evaluated the relationship between the number of inclusions and the biomass of the roots crossing the net (Figure 4). The predictive power of the number of inclusions for root mass is not very high, reflecting the variability in fine root thickness in spruce (r2=0.21) and other woody species (r2=0.54).

Standing Norway spruce fine root biomass measured by coring differed significantly between the sites (P <0.001), with average values between the two samplings in September 2002 and April 2004 of 227 (SE ±29) g m-2 at the sphagnum site, 326 (±45) g m-2 in the spruce forest and 409 ( ±38) g m-2 in the mixed forest in the top 20 cm of soil (Figure 5). The amount of live fine roots present in the soil in April 2004 was slightly higher than in September 2002, this difference is however not significant (P=0.106). Total spruce root biomass, however, was not affected by the site (P=0.07); 622 (SE ±122) g m-2, 914 (SE ±113) g m-2 and 902 (SE ±188) g m-2 of live roots were found at the sphagnum, spruce and mixed sites, respectively.

The higher estimate of fine root production determined from the net method compared to the in-growth cores is reflected in the slightly higher estimate of fine root turnover (Table 2). The values of turnover estimated by the different methods do not differ significantly (P=0.185), nor there is a significant difference in the rate of spruce fine root turnover among the sites (P=0.975). Prior to re-insertion, we re-packed the in-growth cores according to the original stratification of the horizons using root-free material appropriate for each horizon. This allowed for an estimate of fine root production and turnover in different soil horizons (Table 3). We used fine root biomass (coring) and fine root production (in-growth core) found in each soil horizon to calculate Norway spruce fine root turnover. None of the differences in fine root turnover among horizons of sites were found significant.

Discussion

*Root net inclusion method*

The application of the in-growth net method was driven by the need to quickly establish and analyse a large number of replicate samples without excessive disturbance of soil profile. The method can also be used at remote sites without the need of specialist equipment, giving it an advantage over the standard in-growth coring or minirhizotron studies. The accuracy of the estimation of fine root turnover using in-growth cores is dependent upon the time that the cores are left in the ground being sufficiently short to minimize root death in the cores (Lukac and Godbold 2001). We have left both cores and nets in the soil for more than a year, and no dead roots were observed in the in-growth cores or nets. This suggests that in boreal forests of the climatic zone we investigated, long incubation periods are required. Persson and Ahlström (1994) similarly suggested that an incubation time of over a year is required in Swedish forest. However, black spruce fine roots in interior Alaska have been shown to decompose relatively rapidly in wet conditions, such as the sphagnum site in this study, and disappear within 97 days (Ruess et al. 2003). Given that ca.100 days is over half the vegetation period in the Central Forest State Biosphere Reserve, it is reasonable to assume that had high rates of mortality occurred in the nets or in-growth cores, some necromass should have been detected. To minimise the possible effect of fine root disappearance, and thus an underestimate of the turnover rate, the time period of in-growth core or net insertion could be shortened according to local conditions. The inclusion net method appears to be especially suitable for this, as inserting and extracting several cohorts of nets during a growing season is not expensive or labour intensive (Fahey and Hughes 1994).

Using the nets, immediately after extraction from the soil, the number of woody fine roots protruding through the net was assessed by the naked eye. This observation agreed well with the laboratory measurement determined with a stereomicroscope (Figure 3). If only a rapid comparison of root production under contrasting treatments or conditions is needed, the in-growth net method can be used in the forest. However, the number of inclusions cannot be used to predict biomass in this type of forest, probably due to differential thickening of fine roots once they have grown through the net. The nets utilised in this work were fashioned from the woven type of nylon netting, where individual fibres are not attached at intersections. This gives growing tree roots sufficient room to expand and does not limit the root diameter to the nominal mesh size.

To make fine root biomass production estimates, all fine roots protruding through the net were shortened to 2 cm in length, and fine root production per soil volume thus calculated. The values obtained for the in-growth nets and the in-growth cores across a range of soil types were very similar (Figure 1). No significant differences were found between the two methods in soils where the top 20 cm was composed only of an organic layer (sphagnum site) or had a well developed mineral soil horizon (mixed forest). It has been shown that fine root biomass of Norway spruce is dependent on organic horizon thickness or other soil characteristics (Helmisaari et al. 2007), the agreement between the two methods is therefore noteworthy. As disturbance is minimal when the nets are inserted, it is unlikely that the insertion alters the soil chemical properties in the immediate vicinity of the net. The agreement between the two methods also suggests that at the boreal sites used in this investigation it is possible to repack the in-growth cores close to the original growth conditions of the soils. Repacking of in-growth cores has been suggested to increase rates of N mineralization and thus increase root growth (Steingrobe et al. 2000), this is clearly not the case in the investigated sites.

Steingrobe et al. (2000) also showed that cutting existing fine roots during the installation of an in-growth core stimulates root growth in potato through the induction of multiple roots. In *Populus* genotypes, Lukac and Godbold (2001) could not find evidence for this. Using the net method, the old cut parts of the root are visible after extraction. Severed roots that have developed multiple new roots can thus be eliminated from the estimate of fine root production. We did not record the exact number of severed roots that regenerated multiple new roots, and although this process occurred, it was rare. The established in-growth core method suffers from the same drawback, but since the severed roots remain outside the core, it is without the possibility to correct for such excessive root growth from roots cut during core installation.

Although we did not perform such analysis, we have observed that since net extraction did not disturb the soil profile, soil horizons can be marked on the net immediately after extraction. This allows for fine root production estimation per soil horizon similar to the in-growth core method.

*Fine root biomass and turnover*

Norway spruce fine root biomass measured in southern Taiga falls well within the range reported for this species in boreal forests. Our values of 288 g m-2 in 2002 and 354 g m-2 in April 2004 correspond to Norway spruce fine root biomass measured in Finland (225-440 g m-2, Helmisaari and Hallbacken (1999)) or Norway (49-398 g m-2, Borja *et al.* (2008)) in stands of varying age and stocking density. The seasonality of fine root production in boreal ecosystems has been well documented, fine roots biomass usually peaks in late spring and decreases thereafter until the following year (Hendrick and Pregitzer 1993). We have found higher fine root biomass in early spring of 2004 than in September 2002, however these two observations do not differ significantly, suggesting that all sites are at equilibrium and that fine root biomass oscillates seasonally but does not change in the longer term.

Our period of observation from September 2002 to April 2004 was chosen to cover the entire growing season of 2003. Very little is known about root growth in boreal ecosystems between late autumn or early spring, largely due to inaccessibility of soils due to freezing and being covered in snow. Root growth initiation and cessation is closely linked to temperature, root growth slows and usually ceases as soil temperature drops below 4ºC (Kuhns et al. 1985; McMichael and Burke 1998). At the Central Forest State Biosphere Reserve, the average length of snow cover is 130 days, and the mean daily air temperatures are below 0 ºC between November and March. Although a certain amount of root growth can occur even at lower temperatures or during the winter, especially in ecosystems adapted to such low temperatures (Billings 1987), we expect the root growth in the Central Forest State Biosphere Reserve to be minimal in winter months. Thus, we suggest that the fine root production we measured in in-growth cores and inclusion nets is a good estimate of root growth during 2003. There was no difference in the rate of fine root turnover estimated by the two methods, fine root turnover calculated as production over maximum biomass reached values around 0.20 y-1. This is a low value in comparison with published turnover values from similar spruce dominated ecosystems. In Norway spruce forests, fine root turnover was between 0.28y-1 and 1.0y-1 in temperate forest in Germany (Godbold et al. 2003), 0.67 y-1 in Belgium (Vanpraag et al. 1988) and 0.76y-1 and 1.3y-1 in northern Sweden (Andersson and Majdi 2005). In two separate studies in boreal systems where the minirhizotron technique was applied, fine root turnover in black spruce forest in Saskatchewan was 0.87y-1 (Kalyn and Van Rees 2006) and in Norway spruce in Sweden 0.5-0.6y-1 (Majdi and Andersson 2005). The difference may reflect the different fine root diameters measured by the minirhizotron and in-growth core methods, and is a recurrent problem in measuring fine root turnover (Majdi et al. 2005; Strand et al. 2008). Estimates of fine root production can ultimately be used to quantify carbon inputs into the soil, however most tree species in boreal ecosystems are ectomycorrhizal. For example, fine roots of all the species used in this work were colonised by ectomycorrhizae to some extent, thus any calculations of C flux based on fine root turnover should contain C from both roots and mycorrhizal fungi. The extramatrical mycelium is also a large C pool in forest (Wallander 2006) and quantification of hyphal production may be possible using a modification of the net method, as suggested by Ruess et al. (1996a). Fine roots of less than 1mm can be found and removed form the nets, and branched ectomycorrhizal roots, and even branched long roots of less than 1 mm remain trapped in the net. It is possible that the production of the smallest diameter roots (below 0.5mm) cannot be accurately measured by the net or the in-growth core methods as these roots are very difficult to separate from the soil. Mini-rhizotron investigations have shown that these finest roots have shorter life-spans, and thus by not including them the net method would underestimate the overall fine root turnover rate. However, in agreement with other studies using in-growth cores, the low turnover rates determined in this study emphasize the slow growth rates in continental boreal forests in Russia. This is may be of critical importance in estimating the C fluxes in boreal ecosystems.

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 References

Andersson P and Majdi H 2005 Estimating root longevity at sites with long periods of low root mortality. Plant Soil 276, 9-14.

Billings W D 1987 Constraints to Plant-Growth, Reproduction, and Establishment in Arctic Environments. Arctic and Alpine Research 19, 357-365.

Bonifacio E, Caimi A, Falsone G, Trofimov S Y, Zanini E and Godbold D L 2008 Soil properties under Norway spruce differ in spruce dominated and mixed broadleaf forests of the Southern Taiga. Plant Soil 308, 149-159.

Borja I, De Wit H A, Steffenrem A and Majdi H 2008 Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in southeast Norway. Tree Physiol 28, 773-784.

Brunner I and Godbold D L 2007 Tree roots in a changing world. Journal of Forest Research 12, 78-82.

Driessen P, Deckers J, Spaargaren O and Nachtergaele F 2001 Lecture notes on the major soils of the world. In World Soil Resources Reports. FAO, Rome.

Drobyshev I V 2001 Effect of natural disturbances on the abundance of Norway spruce (*Picea abies* (L.) Karst.) regeneration in nemoral forests of the southern boreal zone. Forest Ecol Manag 140, 151-161.

Fahey T J and Hughes J W 1994 Fine-Root Dynamics in a Northern Hardwood Forest Ecosystem, Hubbard Brook Experimental Forest, Nh. Journal of Ecology 82, 533-548.

Finer L, Helmisaari H S, Lohmus K, Majdi H, Brunner I, Borja I, Eldhuset T, Godbold D, Grebenc T, Konopka B, Kraigher H, Mottonen M R, Ohashi M, Oleksyn J, Ostonen I, Uri V and Vanguelova E 2007 Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosystems 141, 394-405.

Godbold D L, Fritz H W, Jentschke G, Meesenburg H and Rademacher P 2003 Root turnover and root necromass accumulation of Norway spruce (*Picea abies*) are affected by soil acidity. Tree Physiol 23, 915-921.

Gower S T, Vogel J G, Norman J M, Kucharik C J, Steele S J and Stow T K 1997 Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J Geophys Res-Atmos 102, 29029-29041.

Helmisaari H S, Derome J, Nojd P and Kukkola M 2007 Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol 27, 1493-1504.

Helmisaari H S and Hallbacken L 1999 Fine-root biomass and necromass in limed and fertilized Norway spruce (*Picea abies* (L.) Karst.) stands. Forest Ecol Manag 119, 99-110.

Hendrick R L and Pregitzer K S 1993 Patterns of fine root mortality in 2 sugar maple forests. Nature 361, 59-61.

Jackson R B, Mooney H A and Schulze E D 1997 A global budget for fine root biomass, surface area, and nutrient contents. P Natl Acad Sci USA 94, 7362-7366.

Kalyn A L and Van Rees K C J 2006 Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agr Forest Meteorol 140, 236-243.

Kuhns M R, Garrett H E, Teskey R O and Hinckley T M 1985 Root-growth of black walnut trees related to soil-temperature, soil-water potential, and leaf water potential. Forest Sci 31, 617-629.

Lukac M and Godbold D L 2001 A modification of the ingrowth-core method to determine root production in fast growing tree species. J Plant Nutr Soil Sc 164, 613-614.

Majdi H and Andersson P 2005 Fine root production and turnover in a Norway spruce stand in northern Sweden: Effects of nitrogen and water manipulation. Ecosystems 8, 191-199.

Majdi H, Pregitzer K, Moren A S, Nylund J E and Agren G I 2005 Measuring fine root turnover in forest ecosystems. Plant Soil 276, 1-8.

McMichael B L and Burke J J 1998 Soil temperature and root growth. Hortscience 33, 947-951.

Persson H and Ahlstrom K 1994 The effects of alkalizing compounds on fine-root growth in a norway spruce stand in southwest Sweden. Journal of Environmental Sciences and Health 29, 803-820.

Ruess L, Sandbach P, Cudlin P, Dighton J and Crossley A 1996a Acid deposition in a spruce forest soil: Effects on nematodes, mycorrhizas and fungal biomass. Pedobiologia 40, 51-66.

Ruess R W, Hendrick R L, Burton A J, Pregitzer K S, Sveinbjornsson B, Allen M E and Maurer G E 2003 Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monogr 73, 643-662.

Ruess R W, VanCleve K, Yarie J and Viereck L A 1996b Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can J Forest Res 26, 1326-1336.

Steingrobe B, Schmid H and Claassen N 2000 The use of the ingrowth core method for measuring root production of arable crops - influence of soil conditions inside the ingrowth core on root growth. J Plant Nutr Soil Sc 163, 617-622.

Strand A E, Pritchard S G, McCormack M L, Davis M A and Oren R 2008 Irreconcilable differences: Fine-root life spans and soil carbon persistence. Science 319, 456-458.

Ulanova N G 2000 The effects of windthrow on forests at different spatial scales: a review. Forest Ecol Manag 135, 155-167.

Vanpraag H J, Sougnezremy S, Weissen F and Carletti G 1988 Root Turnover in a Beech and a Spruce Stand of the Belgian Ardennes. Plant Soil 105, 87-103.

Vogt K A and Persson H 1991 Measuring growth and development of roots. In Techniques and Approaches in Forest Tree Ecophysiology. Eds. J P Lassoie and T M Hinckley. pp 477-501. CRC Press, Boca Raton.

Vygodskaya N, Puzachenko Y, Kozharinov A, Zavelskaya N, Tchernyshev M, Tatarinov F, Varlagin A and Milukova I 1995 Long-term effects of climate on *Picea abies* communities in the South European taiga. J Biogeogr 22, 433-443.

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

Table 1. Stand location and selected characteristics for the three experimental sites in Central Forest Biosphere Reserve (values are mean ±S.E.).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | LatitudeLongitude | Canopy cover (%) | Basal area (m2 ha-1) | Canopy height (m) | Max DBH (cm) | Slenderness ratio |
| Sphagnum | 56.27448 N 32.55266 E | 98.3 ±3.5 | 37.0 ±1.0 | 27.8 ±0.4 | 48.0 ±1.0 | 58.0 ±0.7 |
| Spruce forest | 56.29216 N 32.56057 E | 56.0 ±6.2 | 31.0 ±2.1 | 28.9 ±1.4 | 36.5 ±2.9 | 80.2 ±3.8 |
| Mixed forest | 56.27456 N 32.54565 E | 82.5 ±5.9 | 21.8 ±2.8 | 31.3 ±2.1 | 47.1 ±4.3 | 67.6 ±5.3 |

Table 2. Standing fine root biomass [2004, g m-2], fine root production [Sep 2002 to May 2004, g m-2 y-1] and fine root turnover [y-1] of Norway spruce at 3 sites in the Central Forest State Biosphere Reserve. For the purpose of comparison, the depth of the in-growth cores has been altered by calculation to correspond to that of the nets – the nets were 2cm shorter . Values shown are mean ±SE, n=5.

|  |  |  |
| --- | --- | --- |
|  | *Method* | *Site* |
|  |  | Sphagnum | Spruce forest | Mixed forest |
| Fine root biomass | Coring | 267.1 | ±53.29 | 347.5 | ±54.85 | 447.6 | ±64.99 |
| Fine root production | In-growth core | 15.52 | ±3.57 | 47.70 | ±9.97 | 41.70 | ±8.57 |
| Net | 31.57 | ±11.46 | 66.93 | ±28.49 | 52.80 | ±9.74 |
| Fine root turnover | In-growth core | 0.103 | ±0.039 | 0.146 | ±0.038 | 0.125 | ±0.022 |
| Net | 0.236 | ±0.122 | 0.164 | ±0.025 | 0.192 | ±0.081 |

Table 3. Rate of Norway spruce fine root turnover [y-1] determined by in-growth core method at 3 sites in the Central Forest State Biosphere Reserve. Rates of turnover have been calculated using in-growth cores per soil horizons, the core depth (20 cm). There are no significant differences between soil horizons within a site or between sites. Values shown are mean ±SE, n=5.

|  |
| --- |
| Site |
| Sphagnum | Spruce forest | Mixed forest |
| Horizon |  |  | Horizon |  |  | Horizon |  |  |
| Sph | 0.103 | ±0.039 |  |  |  |  |  |  |
| O | 0.209 | ±0.121 | O | 0.130 | ±0.041 | O | 0.109 | ±0.029 |
|  |  |  | A | 0.159 | ±0.043 | A | 0.119 | ±0.041 |
|  |  |  | E | 0.028 | ±0.017 | E | 0.105 | ±0.066 |
| Core | 0.092 | ±0.027 | Core | 0.122 | ±0.029 | Core | 0.125 | ±0.023 |

Figure legends.

Figure 1 Norway spruce (*Picea abies*) fine root production [g m-2 y-1] estimated by net and in-growth core methods at three southern taiga sites at the Central Forest State Biosphere Reserve. Bars are means ±SE, n=5.

Figure 2 Norway spruce (*Picea abies*) and other woody species fine root production [g m-2 y-1] estimated by the net method at three southern taiga sites at the Central Forest State Biosphere Reserve. Bars are means ±SE, n=5.

Figure 3 Relationship between the number of fine root inclusion per net determined by the naked eye in the forest and in a subsequent laboratory investigation using a stereomicroscope.

Figure 4 Relationship between the number of fine root inclusion per net and root dry weight per net for Norway spruce (*Picea abies*) and other woody species.

Figure 5. Norway spruce (*Picea abies*) fine root biomass [g m-2] estimated by coring at three southern taiga sites at the Central Forest State Biosphere Reserve. Bars are means ±SE, n=5.

Figure 1



Figure 2



Figure 3



Figure 4



Figure 5.

