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Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests

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ABSTRACT

The major part of carbon (C) flow into forest soil consists of continually renewed fine roots and aboveground litterfall. We studied the belowground C input from the fine root litter of trees and understorey vegetation in relation to their aboveground litterfall in two Norway spruce (*Picea abies* L.) stands located in northern and southern Finland. The production of fine roots was estimated by using turnover and biomass data from minirhizotrons and soil cores. The foliage litter production of trees was estimated from litter traps, and that of the understorey vegetation from its annual growth and coverage. Finally, we augmented the data with four spruce plots in Sweden in order to study the above- and belowground litter ratios along latitudinal and soil fertility gradients.

The fine root biomass of spruce trees per stand basal area was almost double in the northern site compared to the southern site. Furthermore, spruce fine roots in the north persisted significantly longer (97 ± 2 weeks) than spruce roots in the south (89 ± 2 weeks) or understorey fine roots at both sites. The annual production of tree foliage litter was higher in the southern stand, but the total amount of litter (including trees and understorey, above- and belowground) was similar at both sites, as was the ratio between the above- and belowground litter production.

The role of understorey vegetation was greater in the northern site where it was responsible for 23% and 33% of below- and aboveground litter production, respectively, compared to 11% and 15% in the south. Thus, both below- and aboveground understorey C input is substantial and should be taken into account in ecosystem C cycle models.

The regression between the aboveground:belowground litter production-ratio and the C:N-ratio of the organic layer (combined data from Finland and Sweden), showed that the share of belowground litter production increased when site fertility decreased. This shift in the litter production pattern from above- to belowground in the least fertile sites may have an impact on litter C quality and soil C storage.

1. Introduction

The largest pools of terrestrial organic carbon (C) are found in soils, especially boreal forest soils and wetlands (IPCC, 2007). In the boreal region, *Picea* forests have the highest forest floor C stocks, followed by *Pinus* and broadleaf forests (Gärdenäs, 1998; Ågren et al., 2007; Stendahl et al., 2010; Vesterdal et al., 2013). Soil C stocks are controlled by the input of C by litter production and the output of C by decomposition (heterotrophic respiration), autotrophic respiration and leaching. Forest floor C turnover is most influenced by foliar litter quantity and quality, whereas mineral soil C turnover is affected by root litter and dissolved organic C (Vesterdal et al., 2013). Many studies have quantified C pools and fluxes (Gaudinski et al., 2000; Lehtonen, 2005; Jansson et al., 2008; Kleja et al., 2008; Hansson et al., 2013b), but as there are a large number of influencing factors in each ecosystem the estimates vary considerably.

Abundant data is available for C input through aboveground litter (Starr et al., 2005; Saarsalmi et al., 2007; Ukonmaanaho et al., 2008), whereas belowground litter C input is more laborious to

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quantify. Therefore, it is often predicted using biomass allocation functions (e.g. Marklund, 1987; Repola, 2009) and a constant turnover ratio. Several empirical methods exist for quantifying root biomass and turnover rate and litter production, such as sequential cores, ingrowth cores and nets, rhizotrons and minirhizotrons, all with their pros and cons. Some of the methods give more comparable results than others (Neill, 1992; Samson and Sinclair, 1994; Makkonen and Helmisaari, 1999; Jose et al., 2001; Tierney and Fahey, 2002; Ostonen et al., 2005; Guo et al., 2008b and references therein, Gaul et al., 2009; Brunner et al., 2013). As a result, one of the major uncertainties in C flow studies is estimating the fine root litter production. According to Peltoniemi et al. (2004) fine root turnover affected the average C stock and C accumulation rate most when the turnover rate of other tree compartments were kept constant. Fine root litter production ranged from 0.65 (with low turnover) to three times (with high turnover) the needle litter production.

For estimating fine root turnover, we used the minirhizotron (MR) method, acknowledged by Hendricks et al. (2006) as the most reliable method for root production estimates. In addition to choice of the method, the extremely heterogenic soil environment and continuously renewed roots also challenge root research. Changes in environmental conditions, the length of the study period, vertical distribution of roots in the soil, and root order and diameter have all been shown to affect root survival (Godbold et al., 2003; Baddeley and Watson, 2005; Guo et al., 2008a,b; Valenzuela-Estrada et al., 2008; Kitajima et al., 2010). According to the cost-benefit hypothesis (Eissenstat et al., 2000) fine roots should live longer in harsh environmental conditions, where the construction costs in means of expended C are higher, compared to the sites with more favorable temperature, water and nutrient availability conditions.

During the past few decades the main interest in forest research has been in net primary production, whereas currently the whole C cycle, especially the annual C input into the forest soil and the soil C storage, has also become an important topic (Lehtonen, 2005; Lal, 2005; Meier and Leuschner, 2010; Hansson et al., 2013b). However, litter or net primary production studies often focus either on the aboveground or the belowground part, which results in a poor understanding of the whole tree and stand level interactions. Complete C cycle studies include soil C inputs by trees, understorey and mycorrhizal fungi and C outflows by auto- and heterotrophic respiration as well as by leaching. In Scandinavian conifer forests C cycle studies have been performed e.g. by Lehtonen (2005), Kleja et al. (2008), Ilvesniemi et al. (2009) and Hansson et al. (2013b). However, the conclusions regarding the major litter sources, or even the C balance, have not been consistent.

Norway spruce (*Picea abies* (L.) Karst) is one of the two most common coniferous tree species of the European boreal region. It has a large canopy with 6–10 needle cohorts (Sander and Eckstein 2001). Norway spruce does not shed needles of one needle cohort at a time, but the long-term mean can be considered as being equivalent to such a behavior. Norway spruce aboveground litterfall has been quantified at many different sites in Scandinavia (Bille-Hansen and Hansen, 2001; Saarsalmi et al., 2007; Ukonmaanaho et al., 2008; Nilsen and Strand, 2013), but fine root litter production only at a few sites (Majdi and Andersson, 2005; Hansson et al., 2013a; Leppälammi-Kujansuu et al., 2014). The annual aboveground understorey litter production is generally estimated as being equal to annual growth (Helmisaari, 1995; Schulze et al., 2009) or as biomass multiplied by turnover rate (Lehtonen, 2005; Kleja et al., 2008; Hansson et al., 2013b). The contribution of understorey to the total aboveground litter production in spruce forests varies widely, between 14 and 35% (Kleja et al., 2008; Hansson et al., 2013b). At northern latitudes, especially belowground understorey vegetation is known to play an important role in annual biomass production and carbon and nutrient cycling (Helmisaari et al., 2007; Olsrud and Christensen, 2004; Kleja et al., 2008; Helmisaari, 1995). Nevertheless, it is still neglected in most litter production studies. This may lead to substantial underestimations of C flux into the soil, as fine roots can produce more biomass annually than the other parts of the tree combined (Helmisaari et al., 2002), and half of the fine root biomass in the soil can be understorey fine roots and rhizomes (Helmisaari et al., 2007). According to Peltoniemi et al. (2006), turnover rates of fine roots and understorey vegetation comprise one of the most significant parameters for soil C stock. Overall, in order to obtain a better understanding of the function of the whole ecosystem, it is important to include both above- and belowground parts of both trees and understorey in the analyses.

In this study two, and eventually six, climatically different Norway spruce stands were investigated regarding their C input into the soil via below- and aboveground litter production. The amount of root-origin litter was determined from tree and understorey fine roots and rhizomes and the quantity of aboveground litter from foliage litterfall and from the litter produced by understorey vegetation. As the growing season is shorter and soil organic layer C:N-ratios are higher in the north, we hypothesized that more of the litter production would be directed belowground than aboveground in the northern site compared to the southern site, in order to guarantee sufficient acquisition of nutrients. Based on the cost-benefit hypothesis, we expected that plants growing in the northern site would have a longer root lifespan than plants growing in the south. We also hypothesized that the share of belowground litter production would increase along the latitudinal gradient.

2. Material and methods

2.1. Site descriptions

The northern (N) site, Kivalo, was located in the northern boreal region in Finnish Lapland (66°20′N/26°40′E) and the southern (S) site, Olkiluoto, in the southern boreal region in Eurajoki, southwestern Finland (61°13′N/21°28′E) (Fig. 1). Understorey vegetation at Kivalo represented mesic site type (Hylocomium–Myrtillus type, HMT) and the most abundant species were *Vaccinium myrtillus* and forest mosses (*Pleurozium schreberi*, *Hylocomium splendens and Dicranum* spp.). Olkiluoto represented a more fertile site type (Oxalis–Myrtillus type, OMT) and was characterized by an abundant forest moss layer with many herb and fern species. The cover of dwarf shrubs was only 2–4% (Aro et al., 2012). Soil type in Kivalo was podsolic loamy sand (Smolander and Kitunen, 2011) and in Olkiluoto fine-textured till (Rautio et al., 2004). At Olkiluoto, there were birch trees (17% of overall tree number) growing among the spruces. Root biomass and foliage litterfall of these birch trees were excluded from the data. Stand, climate and soil characteristics of the sites are described in Helmisaari et al. (2009), Aro et al. (2012) and in Tables 1 and 2.

For widening the variation in above- and belowground litter C input and discussing it in relation to site nutrient availability, we included four additional Norway spruce sites from a north–south transect in Sweden (Fig. 1): Flakaliden (64°07′N/19°27′E), and Knottåsen (61°00′N/16°13′E) in the boreal zone, Asa (57°08′N/14°45′E) in the boreo-nemoral zone (Kleja et al., 2008) and Tönnersjöheden (56°40′N/13°03′E) in the cold temperate vegetation zone (Hansson et al., 2011). Climatic conditions (Table 1) as well as nutrient availability change along the latitude gradient: Tönnersjöheden, the southernmost site, is a site with high N deposition (18 kg ha^{-1} yr^{-1}, Bergholm et al., 2003), leading to high N mineralization and availability (Olsson et al., 2012) whereas at