Belowground interspecific competition in mixed boreal forests: the effect of stand developmental stage and soil fertility on the ectomycorrhiza and fine root characteristics

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ABSTRACT

The role of the belowground interspecific competition in the formation of the stand structure is poorly understood. In boreal forest soils, fine roots and ectomycorrhizas acquire together the soil resources, and therefore have to be studied simultaneously in the same stands.We studied fine roots and ectomycorrhizas in five mixed *Betula pendula* Roth, *Picea abies* (L.) H. Karst., and *Pinus sylvestris* L. stands in Southern Finland. The stands formed continua of developmental stage (15-, 30-, and 50-year-old stands) in the stands of medium fertility, and of site fertility in the young stands (30-year-old fertile, medium fertile, and infertile stands). The biomass of the external hyphae of ectomycorrhizas was the highest, and the diversity of the fungal community the lowest, in the most fertile stand. The vertical distributions of fine roots of the three tree species were mostly overlapping, indicating high inter-specific belowground competition in the stands. We did not find any clear trends in the fine root biomass across the developmental stages of stands. The fine root biomass of the conifers increased towards lower site fertility, whereas in *B. pendula* it was almost constant. In contrast to the conifers, the specific root length (SRL) of *B. pendula* clearly increased from the most fertile to the least fertile stand. This may indicate differences in the primary nutrient acquisition strategy between conifers and *B. pendula*.

KEYWORDS: ectomycorrhizal diversity, fungal biomass, fine root biomass, root morphology

INTRODUCTION

Soil resources, especially the deficit of nitrogen, constrain tree growth in boreal forests (Näsholm and Persson 2001). Therefore, fine roots (diameter < 2 mm) and the mycelia of ectomycorrhizas-forming fungi (ECM) together play an important role in intra- and inter-specific competition. In Finland, the main tree species in mixed stands are *Betula pendula*, *Picea abies*, and *Pinus sylvestris*. The belowground interactions between these species have not been intensively studied and questions like does fine root stratification occur, or does the relative aboveground abundance of different species reflect the belowground situation, have not been answered. Moreover, although the importance of ECM in nutrient uptake has long been understood (Harley and Smith 1983), only a few studies have quantified the characteristics of extraradical ECM mycelium in the field (e.g. Wallander et al. 2001), or the site variation of boreal forests in terms of soil microbial characteristics (Pennanen et al. 1999; Nilsson et al. 2005; Toljander et al. 2006). Our general objective was to assess the belowground interactions in mixed boreal stands of *Betula pendula*, *Picea abies*, and *Pinus sylvestris* forming gradients of developmental stage (15-, 30-, and 50-year-old medium fertile stands) and soil fertility (30-year-old fertile, medium fertile, and infertile stands).

MATERIALS AND METHODS

The stands were located in the vicinity of the Hyytiälä Forestry Field Station of the University of Helsinki in Southern Finland (61°50'N and 24°18'E, 160 m a.s.l.). Five study stands were selected in mixed boreal stands comprising *Betula pendula*, *Picea abies*, and *Pinus sylvestris*. The fine root samples were taken with root corer and the production of external ECM mycelium were estimated with fungal in-growth bag method (Wallander et al. 2001). Statistical analyses for calculated variables were performed using SAS Statistical Software v. 9.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS AND DISCUSSION

Betula pendula had a higher mean fine root biomass than the conifers. The developmental stage of the stand did not have effect on the fine root biomass (Fig. 1 a), which may indicate that the belowground growing space was already closed at the age of 15 years, indicating rapid recovery of fine root biomass after clear-cutting. The fertility gradient had no effect on the fine root biomass of *B. pendula*, while both conifers had the highest fine root biomass on the least fertile site (Fig. 1 b).

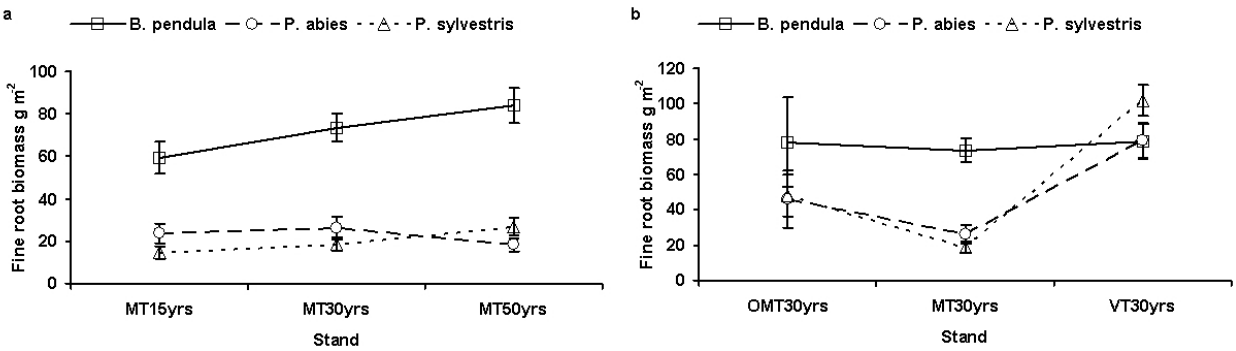

Figure 1. Fine root biomass (g m^{-2}) in the soil layer compromising the humus + uppermost 30-cm mineral soil layer. a) Developmental stage gradient, and b) fertility gradient. Error bars are the standard error of the mean.

Betula pendula had a larger specific root length (SRL, m g^{-1}) than the conifers, which could indicate either a superior competitive ability, i.e. a greater flexibility and potential for effective occupation of nutrient patches in spatially heterogenic soils, or the result of resource depletion by the other species (Bauhus et al. 2000). Ostonen et al. (2007) found the same qualitative difference in fine root morphology between the three species, and our result is also in good agreement with the general hypothesis that evergreen conifers have thicker fine roots and lower SRL than coexisting deciduous trees (Reich et al. 1998). The SRL of both *B. pendula* and *P. sylvestris* was the smallest in the mature stage stand while the SRL of *P. abies* did not deviate between the developmental stages (Fig. 2a). The SRL of *B. pendula* fine roots increased clearly on moving from the most fertile to the least fertile stand, whereas the SRL of the conifers did not change significantly along the stand fertility gradient (Fig. 2b). Ostonen et al. (2007) stated that, on sites of low fertility, the mineral nutrition of the trees is primarily based on an extensive strategy of fine root adaptation, i.e. a higher fine root biomass. Our results for the conifers support this hypothesis, while *B. pendula* appears to have an intensive strategy, i.e. morphological adaptation, to nutrient limitation.

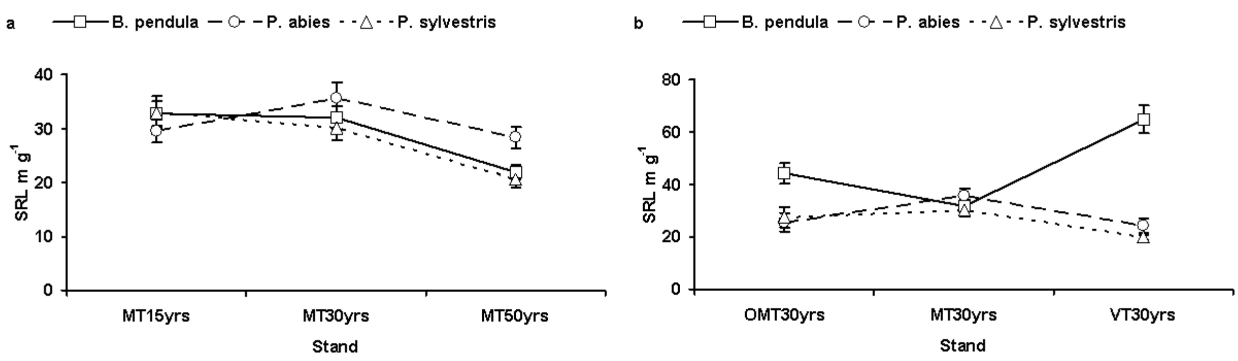

Figure 2. Specific root length (SRL, m g^{-1}) of fine roots (d < 2 mm). a) Developmental stage gradient, and b) fertility gradient. Error bars are the standard error of the mean.

The shapes of the vertical fine root biomass distributions were relatively similar for all species, and in most cases the fine root systems were overlapping (Fig. 3). This lack of vertical rooting space stratification indicates the possibility of high belowground competition in mixed stands of the studied species. In the case of *P. abies* fine root biomass, we observed a clear shift from the humus layer to the mineral soil compared with the vertical distributions obtained in pure stands (Helmisaari et al. 2007). One possible explanation could be that *B. pendula* behaves as a "soil improver" by, for instance, adding amount of the decaying organic material and opening up passages for conifer roots down to depths of 20-30 cm in the mineral soil. Another explanation could be that, under high interspecific competition for the soil resources in the topsoil, the trees have to intensify their rooting also in the deeper less fertile substrate.

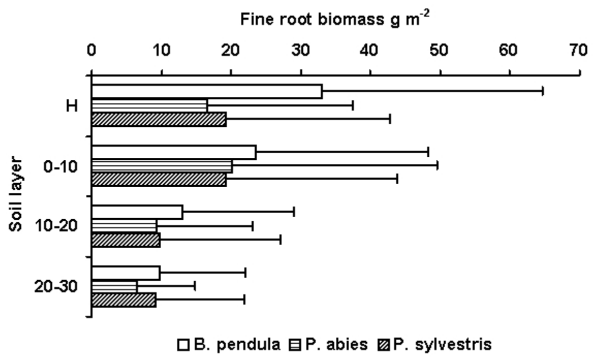

Figure 3. Mean fine root biomass of each species in the different soil layers. H = humus, and 0-10, 10-20 and 20-30 cm are mineral soil layers. Data were pooled over stands because differences between them were not significant. Error bars are the standard deviation

In contrast to the relatively stable fine root characteristics across the developmental stages, the mycelial biomass of ECMs was the highest in the sapling stand (Fig. 4a). The number of ECM taxa was the highest in the pole stage stand, but no developmental stage-related changes were found in the fungal community structure. However, the number of fungal taxa tended to be lower in the samples with a high biomass, which could indicate that the microenvironment in the bag stimulates a few species, which subsequently become dominant in the bags (Hedh et al. 2008). We observed a significantly lower biomass production of ECM mycelia in the least fertile stand, while the number of ECM taxa was the highest on this site (Fig. 4b). Nilsson et al. (2005) reported that ECM mycelial production was the lowest in soils with the highest nutrient availability. However, in their study ECM mycelial production was the highest in the soils with a pH of 4.1-5.3, which correspond the soil pH of our most fertile stand. The clear difference between our and their results was, however, that Nilsson et al. (2005) found the highest ECM mycelial production at the site with the highest fine root biomass, whereas in our study ECM mycelial production was not related to the fine root biomass.

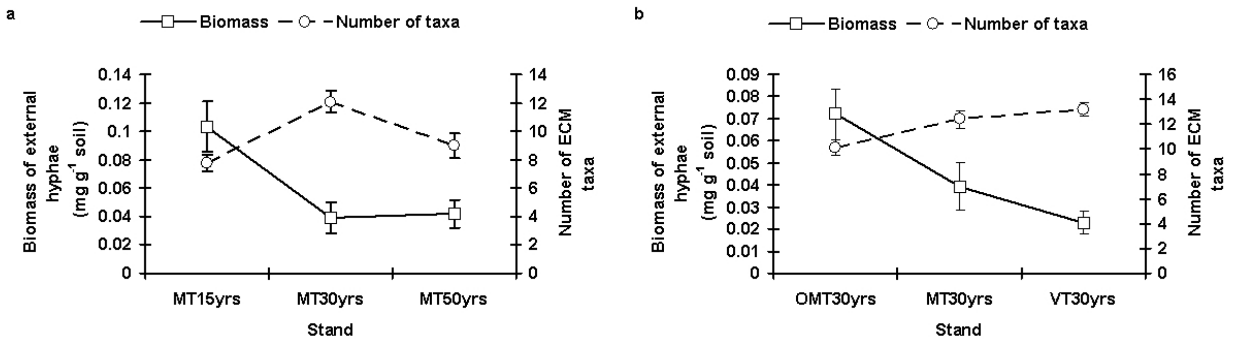

Figure 4. Mean biomass of ECM extraradical hyphae and diversity of ectomycorrhizal community in terms of the number of taxa in a) developmental stage gradient, and b) fertility gradient. Error bars are the standard error of the mean.

Our results show that in the mixed stands of *B. pendula*, *P. abies*, and *P. sylvestris*, species' belowground responses to different soil conditions may differ considerably. *Betula pendula* responded to lower site fertility by adjusting the SRL of fine roots, whereas the conifers increased their fine root biomass. This may indicate differences in the primary nutrient acquisition strategy between conifers and *B. pendula*. The observation that biomass production of the ECM external mycelia was not straightly related to the stand total fine root biomass raises questions, and highlights need for methodological development in order to be able to study fine root and fungal interactions at the individual tree level in the field.

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