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Effects of species replacement on the relationship between net primary production and soil nitrogen availability along a topographical gradient: Comparison of belowground allocation and nitrogen use efficiency between natural forests and plantations

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ABSTRACT

Changes in dominant plant species can influence the net primary production (NPP) via changes in species traits, including nitrogen use efficiency (NUE) and belowground allocation enhancing N uptake, as well as soil N availability. We investigated changes in above- and belowground NPP, N uptake, and NUE in response to changes in soil N in natural forests and plantations, with and without changes in species compositions among the environmental gradient, respectively. In plantations, NPP increased with increasing availability of soil N in the presence of constant NUE and the proportion of belowground NPP to total NPP. However, in natural forests, aboveground, belowground, and total NPP were high for the available middle range soil N. Belowground NPP and the proportion of belowground NPP to total NPP in natural forests was positively related to aboveground NPP. Both belowground NPP and soil N mineralization rates explained stand N uptake rates. These results indicated that belowground allocation might facilitate aboveground NPP with enhancement of N uptake by root allocation. Stand NUE decreased with soil N availability in natural forests and was stable in plantations, and resulted in lower production in natural forests and higher production in plantations under high soil N availability. The community weighted mean (CWM) of N resorption efficiency was positively related to NUE. The CWM of juvenile root growth, as reported previously for planted juveniles, was positively related to belowground NPP allocation. In addition, the ranges of CWMs were broader in natural forests than in plantations. This suggested that the different changes in NPP in response to changes in soil N between natural forests and plantations was due to the changes in leaf and root species traits via changing in species composition among sites. In conclusion, the present study showed that the changes in species specific traits in root growth and leaf N strongly affected the relationship between soil N availability and stand carbon and N dynamics.

1. Introduction

Net primary production (NPP) is the fundamental ecosystem service of forest ecosystems. Soil nitrogen (N) often limit the aboveground NPP (Pastor et al., 1984; Reich et al., 1997); however, NPP including the belowground component does not always follow soil N availability, which suggests there are site-specific soil or species composition influences (Tateno and Takeda, 2010). In local scale studies, the dominant species-specific characteristics are more important for forest NPP than the actual species diversity with complementary resource use (Jacob et al., 2010). A large-scale study using remote sensing found a positive relationship between changes in local species composition and regional variation of forest productivity (He and Zhang, 2009). These findings imply that changes in local species composition and their functions might be critical for NPP, as well as soil N availability. However, the mechanism behind how the interaction between changes in local species composition and soil N availability influences stand NPP is still not well understood.

For tree species trait effects, two important species-specific strategies influence the relationship between soil N availability and NPP. The

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first is the strategy of increasing NPP allocation to belowground parts to maximise soil N resource capture (Gower et al., 1992; Tateno et al., 2004). Belowground allocation patterns are often different to aboveground NPP patterns, and strongly influence the entire stand NPP and N use patterns in response to the availability of soil N (Tateno and Takeda, 2010). In addition, species-specific root traits as the driving force of plant growth and ecosystem processes have recently been studied (Bardgett et al., 2014; Comas and Eissenstat, 2009). In general, plant belowground allocation increases with decreasing soil N rather than a decrease in aboveground growth (Aerts and Chapin, 2000; Gower et al., 1992; Tateno et al., 2004), although opposite patterns in belowground allocation have been recorded (Hendricks et al., 2006; Nadelhoffer et al., 1985).

The second strategy is increasing N use efficiency (NUE), which is defined as the production per unit N, to maximise NPP with low N cost to plants (Killingbeck, 1996; Vitousek, 1982). In general, NUE has a negative relationship with soil N (Aerts and Chapin, 2000; Birk and Vitousek, 1986). However, often NUE does not decrease with soil N availability when wood organ growth increases under high soil N availability. Berendse and Aerts (1987) divided NUE into two components, N productivity and mean residence time of N (MRT_N). N productivity is defined as production rate per unit N in plants and MRT_N is defined as plant N content divided by plant N uptake. These authors predicted that lower N productivity and higher MRT_N might be more important under low soil N availability than high NUE.

When tree species have different belowground allocations and NUE or its components, species turnover variations affect the relationship between NPP and soil N availability via changes in dominant species traits. In ecosystems limited by N, a negative relationship between belowground allocation or NUE and soil N availability might reduce changes in NPP in response to changes in soil N, because high belowground allocation and NUE might compensate for the low supply of soil N. Leaf and root N concentrations (Aerts and Chapin, 2000; Killingbeck, 1996; Kong et al., 2014) and root growth (Comas and Eissenstat, 2009; Levang-Brilz and Biondini, 2002), relating to NUE and belowground allocation, are considerably different among species. In multi-species dominant natural forests, tree species are distributed in habitats based on preferences and functions. For example, in mesic or high availability of soil N habitats, fast-growing plant species with low NUEs are dominant, whereas in xeric or low availability of soil N habitats, slow-growing plant species with high NUEs are dominant (Aerts and Chapin, 2000; Tateno and Takeda, 2010). In contrast, in mono-species dominant plantations under most soil conditions, the species spatial turnover and community trait changes are lower than in natural forests. This might result in narrower ranges of physiological buffering functions for NPP regarding soil N deficiencies, such as belowground allocation or NUE, in plantations than in natural forests. Thus, the relationship between the availability of soil N and NPP between natural forests and plantations should be different owing to belowground allocation and NUE.

Topography, such as slope position and direction, is one of the main determinants of soil fertility and the formation of soils at local scales (Hishi et al., 2014; Jenny, 1941). Therefore, topography results in a natural contrast in soil N fertility under the same climate, parent material conditions, and regional species pool at a local scale. In natural forest ecosystems, the slope ridge is characterised by low soil N availability and aboveground NPP and dominant high NUE species, whereas the slope bottom is characterised by high soil N availability and aboveground NPP and dominant low NUE species (Tateno et al., 2004). Slope direction also affects soil fertility. South-facing slopes are generally dryer than north-facing slopes owing to differences in amount of sunlight received. Moreover, soil N availability and stand productivity (Newman et al., 2006) is lower in south-facing slopes than in north-facing slopes. These topographical changes in NPP in terms of soil conditions could be related to changes in species composition and in species-specific traits.

We hypothesised that changes in species composition might create differences in the positive linear relationship of NPP to soil N availability between multi-species dominant natural forests and mono-species dominant plantations, because mono-species dominant plantations might have narrower strategies for N capture and NUE in response to changes in soil N gradients than multi-species dominant natural forests. First, this could result in NPP in plantations being more positively related to the availability of soil N than in natural forests, because higher variations in N capture and use strategies in natural forests might weaken the positive relationship between NPP and soil N availability. Second, the ecosystem functions in NUE and belowground allocation might be explained by variations of tree species traits as well as soil N availability. To verify the hypotheses, we investigated the effects of soil N availability on ecosystem functions of forest stands, such as above- and belowground NPP, N uptake, and NUE in topographical sequences, both in natural forests and larch plantations. In addition, the contributions of species functional traits to ecosystem functions were evaluated.

2. Materials and methods

2.1. Study site

The study site was located at the Ashoro Research Forest (ARF) in inland Hokkaido, Japan (near central Ashoro, 43°15′ N, 143°33′ E). Ashoro has an inland climate with cool temperatures, low precipitation, and temporal soil freezing between late December and April. Annual precipitation and mean temperature averaged from 2004 to 2013 were 832 mm and 6.4 °C, respectively (Japan Meteorological Agency, 2018). The soil was covered with snow from late December to mid-April. The maximum snow depth near the study plots was 46 cm from December 2011 to May 2012. Soil freezing occurred from December to early May.

We studied two forest types: deciduous broad-leaved natural forests and larch plantations. To include various topographical traits, five square study plots (0.04 ha) in natural forests and plantations were established in the ARF. The ages of the natural forests were greater than 150 years old, which was estimated from the large growth rings in the trees within each plot. *Larix kaempferi* was planted in the plantation sites, and the stand age of the trees in the middle parts of a north-facing slope (P-NM) was 43 years old and the other plantation sites were 51 years old in 2008. In the natural forests, two plots were established in the upper and middle parts of a south-facing slope (N-SU and N-SM, respectively), two plots in the upper and middle parts of a north-facing slope (N-NU and N-NM, respectively), and at the bottom of a slope (N-L). Similarly, plots in the plantation were established at P-SU, P-SM, P-NU, P-NM, and P-L on the upper and middle parts of the south- and north-facing slopes and at the bottom of a slope, respectively. Exact locations of the study sites are provided in supplementary materials (Interactive map viewer in Elsevier).

2.2. Soil and vegetation census

Soil mineralization was estimated by the *in-situ* buried bag method (Eno, 1960) during one year using surface soil (0–10 cm) during May 2011 and May 2012. The south-facing and upper slope were dry, whereas the north-facing and lower slope experienced wet soil conditions, mainly because of solar radiation and location of the watershed area (Table 1). The soil N mineralization rate was lower in the south-facing and upper slope than in the north-facing and lower slope areas. The changes in soil characteristics at each plot in this site are detailed in Hishi et al. (2014).

At the study site, the gradient of solar radiation mediated by topography also strongly influenced the vegetation present (Table 1), as well as soil N availability. Regarding species compositions on different slope aspects and positions in natural forests, the south-facing upper slopes were dominated by oak species and the north-facing lower slopes were dominated by mesic species. This vegetation pattern was consistent