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Title

Spatial pattern of soil nitrogen availability and its relationship to stand structure in a coniferous-broadleaved mixed forest with a dense dwarf bamboo understory in northern Japan

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Abstract

Natural disturbances create spatial patterns of the ecosystem processes and functions in natural forests. However, how dynamics and the spatial structure of forests relate to soil nitrogen dynamics is not well understood. We examined the spatial relationship between the distributions of canopy and understory species, and soil nitrogen dynamics in a natural coniferous-broadleaved mixed forest with a dense understory of *Sasa* dwarf bamboo in northern Japan. The O horizon was thick where coniferous litter predominated, and it was thin where broadleaved litter predominated. The soil water content was low in areas with a thick O horizon and a high abundance of coniferous trees. The soil nitrate content was low where the soil water content was low, and the soil nitrate content increased linearly with increasing net nitrification potential. These results suggest that the soil nitrate content under the coniferous canopy was lower because of the low nitrification potential of soil microbes in soils with low water contents. The soil nitrate content and nitrification potential were higher in the canopy gap than under the canopy. Our results suggest that forest structure, specifically the thickness of the forest floor, significantly affects the spatial pattern of the soil water content, thereby creating a spatial pattern of soil nitrogen availability at a relatively small scale with flat topography. The higher nitrification potential under the canopy gap could pose a long-term risk of nitrate leaching because of the suppression of the natural regeneration of canopy species by dense *Sasa* dwarf bamboo in this forest ecosystem.

Keywords: canopy gap; disturbance; litterfall; spatial pattern; understory vegetation

Introduction

Natural disturbances are fundamental factors that drive the development and maintenance of the structure and function of forest ecosystems (Attiwill 1994). To maintain biodiversity and ecosystem functions, forest management is shifting toward approaches that are based on understanding natural disturbance regimes (Franklin 1993; Attiwill 1994). Treefall, which creates canopy gaps, is a consequence of the disturbance regime, and it leads to the creation of a complex forest structure in many forest ecosystems (Attiwill 1994). In Hokkaido, northern Japan, occasional strong typhoons and windstorms are major natural disturbance regimes, and they create various sizes of canopy gaps in the forests (Yoshida and Noguchi 2009). The creation of a canopy gap alters the supply of light, water, and litterfall to the ground, which then alter various ecosystem processes, such as litter decomposition, soil microbial activity, soil nutrient and organic matter dynamics, and water and nutrient uptake by vegetation. These changes in ecosystem processes then feedback to the productivity of the ecosystem and the vegetation composition; therefore, understanding the impact of the change in vegetation structure on the ecosystem processes would aid the design of sustainable forest management treatments that aim to balance timber production and ecosystem processes. However, how a complex forest structure, which consists of both overstory and understory vegetation, is related to these ecosystem processes is not well understood.

Plants synthesize organic matter, and then litterfall supplies the organic matter, which is a source of energy, carbon (C) and nutrients (e.g., nitrogen (N), phosphorous, and potassium) to soil biota (Wardle et al. 2004). Nitrogen is a limiting nutrient for the growth of organisms in boreal and temperate forests (Vitousek and Howarth 1991), and its dynamics in soil not only affects plant growth, but also influences various ecosystem functions and services. For example, soil N availability affects carbon sequestration by influencing CO₂ balances between the forest and atmosphere via gross photosynthesis by vegetation, as well as organic matter decomposition (Compton et al. 2011). Additionally, nitrification affects water quality via NO₃⁻ leaching from soil to streams (Vitousek et al. 1997; Compton et al. 2011). Plant species affect soil N dynamics via their litter traits (Binkley and Giardina 1998), nutrient uptake by roots (Hobbie 1992),

mycorrhizal type (Chapman et al. 2006), and throughfall and stemflow chemistry (Knops et al. 2002). Therefore, in forests with a complex forest structure, the plant community composition and configuration will regulate the distribution of soil nutrients, which in turn affects plant community and ecosystem dynamics (John et al. 2007; Boyden et al. 2012).

Litter traits are some of the major factors that control litter decomposition, which is related to soil N dynamics (Chapin et al. 2011). Plant litter with high C/N (Enriquez et al. 1993) or lignin/N ratios (Melillo et al. 1982) generally decomposes slowly, and net N transformation rates in soils under slow-decomposing litter are often lower than those under fast-decomposing litter (Scott and Binkley 1997). Differences in litter decomposition rates often lead to differences in the C/N ratios of soil organic matter (Finzi et al. 1998), which affects N transformation rates (Booth et al. 2005). Additionally, the cations and aluminum (Al) contained in plant litter can modify soil pH, which can in turn influence soil N cycling (Tietema et al. 1992; Reich et al. 2005).

Soil moisture affects soil N dynamics through microbial biomass and its activities (Bengtson et al. 2005; Baldrian et al. 2010). Soil moisture conditions are influenced by the interception of precipitation by the canopy (Barbier 2009), the reduction in evaporative losses from soil by canopy shade (Muscolo 2007), transpiration by vegetation (Oren et al. 1998), and the redistribution of soil moisture via water uptake by roots (Burgess et al. 1998) according to the spatial structure of the vegetation. The creation of water repellency by the production of hydrophobic compounds by living or decomposing plants (Doerr et al. 2000) also affects water infiltration and storage, which influence soil moisture.

Our understanding of the effects of plants on soil N dynamics has largely been advanced by studies that compared the soil N dynamics among monospecific stands or beneath individual trees of different species (Scott and Binkley 1997; Finzi et al. 1998; Reich et al. 2005). However, most natural forests consist of multiple plant species, and their spatial structures are complex because of natural disturbances and succession. In mixed-species forests, the supplies of light, rainfall, and litterfall to the ground are spatially heterogeneous, which creates spatial variations in the available soil N that influence the growth of both existing plants and newly established seedlings. Soil N dynamics are spatially heterogeneous at various spatial scales, and apart from plant

species composition, spatial patterns of topography, bedrock geology, and hydrology, it is known to affect the heterogeneity of soil N dynamics at local scales, such as watersheds. In the forested watersheds in most parts of Japan, where the topography is usually steep, spatial patterns in soil N transformation have been observed along slopes because of the variation in the soil water content that affects the vegetation pattern and the soil C/N ratio (Hirobe et al. 1998; Isobe et al. 2015). Plant distribution caused by natural disturbances and succession creates highly diverse patterns of litterfall and soil moisture even in small spatial scales with flat topographies, consequently resulting in diverse soil N dynamics patterns. However, how the complex forest structure of natural forests is related to the spatial pattern of soil N dynamics in relatively small and flat areas is not well understood.

Understory vegetation plays an important role in forest dynamics. The density and cover of understory species largely increase after the creation of canopy gaps (by natural disturbances, etc.), and in many cases they prevent or inhibit the regeneration of canopy species, thereby leading to their domination of canopy gaps (Royo and Carson 2006). Despite the importance of understory vegetation in forest dynamics, its effects on belowground processes have usually been overlooked in biogeochemical studies. Nilsson and Wardle (2005) found that the dominant understory species in boreal forests affect soil microbial activity and soil N availability through the effect of their litter traits, thereby demonstrating that understory vegetation should be taken into account if we are to understand the forest structure–soil N dynamics relationship in natural forests. Many of the natural forests in Hokkaido, northern Japan, are cool-temperate conifer-broadleaved mixed forests with dense undergrowth of dwarf bamboo (*Sasa* species) (Hiura et al. 1996; Yoshida et al. 2006; Yoshida and Noguchi 2009). After treefall, *Sasa* dwarf bamboos tend to dominate in canopy gaps and inhibit the regeneration of other plant species (Hiura et al. 1996). *Sasa* dwarf bamboo leaf litter has been reported to decompose more slowly than the litter of overstory species (Tripathi et al. 2006; Watanabe et al. 2013). Hence, it can be expected that the influence of *Sasa* dwarf bamboo on soil N dynamics differs from that of canopy species in these forest ecosystems.

In this study, we examined the spatial relationship between the distributions of coniferous and broadleaved species, and understory *Sasa* dwarf bamboo and soil N

dynamics in a natural mixed stand with relatively flat topography in northern Japan that contains canopy gaps that are covered with dense undergrowth. We hypothesized that the spatial pattern of soil N dynamics would be controlled largely by the spatial pattern of canopy trees and understory *Sasa* dwarf bamboo through the interacting effects of soil moisture and litter chemical properties on litter decomposability.

Methods

Study site

This study was conducted in the Uryu Experimental Forest (UREF) of Hokkaido University (44°21'N, 142°16'E), a core site of the Japan Long-Term Ecological Research Network that is located in northern Hokkaido, Japan. According to the meteorological data recorded in the UREF from 2000 to 2009, the mean annual temperature is approximately 4 °C, and the mean annual precipitation is approximately 1,150 mm. The forest floor is usually covered by snow from November to May, with a maximum snow depth of approximately 200 cm. The soil is a Cambisol (IUSS Working Group 2006) that is situated on Pleistocene sedimentary rock. The organic horizon mainly consists of an Oe/Oa horizon with a relatively thin Oi horizon. The annual wet N deposition is approximately 7 kg N ha⁻¹ yr⁻¹ (Ogawa et al. 2006). Coniferous-broadleaved mixed forest is a major forest type of the UREF, with the dominant coniferous species being *Abies sachalinensis* and *Picea glehnii*, and the dominant deciduous broadleaved species being *Quercus crispula*, *Acer mono*, and *Betula ermanii* (Noguchi and Yoshida 2004). Dense *Sasa* dwarf bamboo covers the forest floor in areas where tree densities are low. We established a study site (approximately 800 m² in area) in a primary coniferous-broadleaved mixed stand in the UREF. The study site has no record of human disturbances (i.e., timber production) during the past 100 years. Occasional strong typhoons are a primary disturbance regime in this region, and they play an important role in creating the complex forest structure and various sizes of canopy gaps, which are covered with *Sasa* dwarf bamboo (Yoshida and Noguchi 2009). The site is located on relatively flat topography, and the elevation is approximately 340 m a.s.l. The total basal area of evergreen coniferous species is

greater than that of deciduous broadleaved species in the site (Table 1). The coniferous species consist of *A. sachalinensis* and *P. glehnii*, while the dominant deciduous broadleaved species are *B. ermanii* and *Q. crispula* (Table 1). The forest floor is mainly covered by the dwarf bamboo *Sasa senanensis* (hereafter referred to as *Sasa*). The site contains a canopy gap that has existed for at least 7 years according to 2004 tree census data obtained by the research group of the UREF. The size of the canopy gap is approximately 190 m². We used intensive grid and quadrat samplings to examine the spatial relationships among the plant community composition and configuration (including trees and understory vegetation), and litterfall, the organic horizon, and mineral soil properties.

Intensive grid sampling

A 4 × 4 m grid system was established in a 768-m² area within the site (Fig. 1). The number of sampling grids was 48. We measured a number of properties at each grid in September 2012, which comprises the latter part of the growing season, and in June 2014, which constitutes the beginning of the growing season after the snowmelt. The *Sasa* biomass, the thickness of the Oe/Oa horizon (hereafter referred to as the O horizon), the soil inorganic N content, and the soil water content were measured in each grid. A sampling point was selected approximately 1 m from the northwest corner of each grid for the September sampling, and approximately 1 m from the southeast corner of each grid for the June sampling. The sampling points for the two sampling periods were approximately 2 m from each other. At each sampling point, one soil core was taken using a 4.2-cm diameter auger, and the top 10 cm of the mineral soil was collected after the thickness of O horizon was measured. The soil samples were transported to the laboratory for further analysis. The *Sasa* biomass was calculated by multiplying the total culm number by the average height of standing *Sasa* within a 1-m radius from each sampling point. To assess soil acidity, the exchangeable calcium (Ca) and Al concentrations in the soil, as well as soil pH, were measured for the soils that were collected in September.

Sampling at quadrats

We categorized the forest structure into three types in terms of the dominant vegetation: 1) canopy gaps with dense *Sasa* cover on the forest floor (*Sasa* quadrats), 2) canopy trees with *Sasa* understory (*Sasa*/tree quadrats), and 3) canopy trees without *Sasa* understory (tree quadrats). We established five quadrats (1 × 1 m) in each category (Fig. 1). Their locations were selected so that they were not clumped in a particular part of the site (Fig. 1).

At one point within each quadrat, the thickness of the O horizon was measured, and approximately 200 g of surface mineral soil (0–10-cm depth) was collected to analyze the soil physicochemical properties (inorganic N contents, potential net N mineralization and nitrification rates, concentrations of exchangeable Ca and Al, total C and N concentrations, pH, and the water content). *Sasa* biomass was obtained by harvesting all the aboveground parts of each *Sasa* within each quadrat, and their oven-dried (70 °C, 48 h) weight was measured. All samplings were conducted in early September 2011. Leaf litterfall was collected at a location adjacent to each quadrat using litter traps constructed of a plastic basket (collecting area: 0.18 m²) covered with a 1-mm mesh net. The litter traps were fixed at a 30-cm height. Litterfall was collected monthly in August and September 2012, and biweekly during October 2012. The leaf litters were air dried, separated into four types (coniferous canopy species, broadleaved canopy species, *Sasa*, and others), oven-dried at 70 °C for 48 h, and weighed. The dried litter samples were analyzed for total C and N, Ca, and Al concentrations.

Analysis of litter and soil chemical properties

Total C and N concentrations in the litter were analyzed using a CHNS/O analyzer (PE2400II; PerkinElmer, Waltham, MA, USA) after the dried subsample was ground using a ball mill. Ground litter (0.5 g) was digested with 5 ml of nitric acid (60 %) and 2 ml of hydrogen peroxide (30 %) in an automatic microwave digester (Microwave Digestion System; O.I. Analytical, Tokyo, Japan). The Ca and Al concentrations in the digested solution were analyzed by inductively coupled plasma–atomic emission spectrometry (IRIS Advantage, Nippon Jarrell Ash Co., Kyoto, Japan).

The fresh soil samples were passed through a 4-mm sieve to remove rocks and coarse roots prior to further analysis. Total C and N concentrations in the soil were analyzed using a CHNS/O analyzer after the subsample was air-dried and ground. Ten grams of fresh soil was extracted with 100 ml of 2 M potassium chloride, and the extract was analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) concentrations by a colorimetric method using an auto analyzer (AACS-4, BL-TEC Inc., Osaka, Japan). Another 10-g subsample was extracted with 100 ml of 1 M ammonium acetate (pH 7) to analyze the exchangeable Ca and Al concentrations by inductively coupled plasma-atomic emission spectrometry. The gravimetric soil water content was measured by drying the soil at 105 °C for 24 h. Soil pH was measured using a glass electrode (1:2.5 soil:water ratio).

Potential net N mineralization and net nitrification rates

Potential N mineralization and nitrification rates were measured by laboratory incubation for 7 d. Thirty grams of sieved, fresh soil was placed in a glass jar and covered with aluminum foil with ventilation holes. The temperature was maintained at 25 °C, and the soil moisture was kept at 60 % of the field capacity. The net N mineralization rate is the net difference in the $\text{NH}_4^+ + \text{NO}_3^-$ contents, and the net nitrification rate is the net difference in NO_3^- contents during the incubation period.

Mapping the spatial patterns of soil and vegetation properties

The locations of canopy trees (stem diameter at breast height > 10 cm) were mapped using ArcGIS (Arc Desktop version 10, Esri Japan, Tokyo, Japan). We used the data from a tree census that was conducted at the site in 2007, and we assumed that the tree distributions in the data are similar to those in 2011–2014. The *Sasa* biomass was measured only for the September sampling, and we assumed that its spatial variation did not change significantly between the two samplings.

Data processing and statistical analysis

Properties of the forest floor and soil at each sampling point are influenced by adjacent trees through canopy cover, litterfall, root, and mycorrhiza. The spatial range of the influence of trees varies among studies. Hence, to understand the range of influence of the trees, we calculated the number and total basal area of coniferous and broadleaved trees within 5-, 10-, and 15-m radii buffers around each sampling point and sampling quadrat. We then compared the number of significant correlations between the canopy trees and the other variables, as well as the fitting of the models obtained by a stepwise multiple regression analysis.

We analyzed the spatial relationships between the response and explanatory variables obtained in the intensive grid samplings using a stepwise multiple regression analysis. The variance inflation factor was assessed to ensure that multicollinearity among the explanatory variables did not significantly affect the model results. Spatial autocorrelation in the data could lead to incorrect assessments of hypotheses (i.e., a high tendency to reject the null hypothesis) and biased coefficients in the prediction model (Legendre 1993; Dormann 2007). When model residuals exhibit spatial autocorrelation, the spatial autocorrelation needs to be incorporated into regression models (Legendre 1993). Therefore, we first assessed the spatial structure of the observations using Moran's I statistics (Plant 2012). Some of the variables in our data, such as the soil NO_3^- content and the soil water content, were spatially autocorrelated (Table 2). For these variables, we assessed the spatial structure of the model residuals using Moran's I test for regression residuals for the selected model with the highest degree-of-freedom adjusted R^2 (Plant 2012). In our analysis, the selected models did not have spatially autocorrelated residuals; thus, the results of ordinary least square models were used for further analysis and discussion. Spearman's rank correlation coefficient was used to examine the relationships between the variables measured in the quadrats and in the grids. Comparisons of measured variables across litter types and sampling quadrats were conducted using a single factor analysis of variance with a post-hoc Tukey's honestly significant difference test. Prior to the analyses, all data were transformed ($\log(x+1)$) to achieve a normal distribution. All statistical analyses were performed using R software (version 3.1.1, The R Foundation).

Results

Spatial patterns of plants, soil properties, and soil N availability

Coniferous trees predominated in the closed canopy, while small-to-medium sized broadleaved trees were mainly found near the canopy gap (Fig. 1). *Sasa* biomass tended to be high in the canopy gap that is located in the western part of the study site, and it tended to be low under groups of medium-to-large coniferous trees in the middle and eastern parts of the study site (Fig. 1).

The mean soil NH_4^+ contents were 11.7 and 11.1 mg N kg soil⁻¹ in September and June, respectively (Table 2). The mean soil NO_3^- contents were 1.17 and 1.62 mg N kg⁻¹ soil in September and June, respectively (Table 2). The mean soil water content was significantly higher in June than in September (Table 2). Moran's I values indicated that the soil NO_3^- content and the soil water content exhibited a positive spatial autocorrelation at both sampling dates (Table 2).

The soil NO_3^- contents were higher in the canopy gap and near the southeastern corner of the site where a few broadleaved trees grew, compared with those under the dense coniferous canopies in both sampling dates (Figs. 2a and b). The soil water contents were higher under the canopy gap than under the dense coniferous canopy on both sampling dates (Figs. 2d and e). The thicknesses of the O horizons tended to be high around coniferous trees and low in the canopy gap and around broadleaved trees on both sampling dates (Figs. 2g and h). The spatial patterns of the soil NO_3^- content, the soil water content, and the thickness of O horizon were similar between the two samplings dates (Fig. 2c, f, and i), although the ranges and coefficients of variation for the soil NO_3^- contents and soil water contents were larger in June than in September (Table 2).

Spatial relationships among plants, soil properties, and soil N availability

The number of broadleaved trees within the 10- and 15-m radii buffers exhibited more significant correlations with the measured variables (11 and nine variables, respectively, for $P < 0.01$; 14 and 14 variables, respectively, for $P < 0.05$) than that within the 5-m radius buffer (two variables for $P < 0.01$; seven variables for $P < 0.05$), while the

number of coniferous trees within the 5-m radius buffer exhibited more correlations with the variables (11 variables for $P < 0.01$; 16 variables for $P < 0.05$) than those within the 10- and 15-m radii buffers (10 and eight variables, respectively, for $P < 0.01$; 13 and 13 variables, respectively, for $P < 0.05$) (Table 3). The total basal area of trees showed a similar trend in the correlation analysis, but the number of significantly correlated pairs was less than that in the analysis using the number of trees (data not shown).

The *Sasa* biomass showed positive correlations with the number of broadleaved trees within the 10- and 15-m radii buffers, while it showed stronger negative correlations with the number of coniferous trees within the 5-m radius buffer, compared with those within the other radii (Table 3).

The proportions of broadleaved litter to the total litterfall were significantly and positively correlated with the numbers of broadleaved trees within the 10- and 15-m radii buffers, and the proportion of coniferous litter was significantly and positively correlated with the number of coniferous trees within any of the three buffers (Table 3). The proportion of *Sasa* litter was significantly and negatively correlated with the number of coniferous trees, especially within the 5-m radius buffer (Table 3).

The proportion of *Sasa* litter was significantly and positively correlated with the *Sasa* biomass (Table 4). The thickness of the O horizon was significantly and positively correlated with the proportion of coniferous litter, and it was significantly negatively correlated with the proportions of broadleaved litter and *Sasa* litter (Table 4).

The spatial variation in the soil NO_3^- content was best explained by the spatial variation in the soil water content, the number of broadleaved trees within the 5-m radius buffer, and the thickness of O horizon on both sampling dates (Table 5). The spatial variation in the soil water content was explained by the spatial variation in the thickness of the O horizon, as well as the number of coniferous trees within the 5-m radius buffer, on both sampling dates; these variables had significantly negative effects (Table 5). The spatial variation in the number of coniferous trees within the 5-m radius buffer had a positive impact on the spatial variation of the O horizon thickness on both sampling dates (Table 5).

Plant, litter, and soil properties in different forest structures

In the *Sasa* quadrats, the numbers of broadleaved trees and coniferous trees were significantly higher and lower, respectively, than those in the other two types of quadrats, except for the number of broadleaved trees within the 5-m radius buffer (Table 6). The proportion of broadleaved litter in the total litterfall was significantly higher in the *Sasa* quadrats than in the *Sasa*/tree quadrats (Table 6). The proportion of coniferous litter was lowest in the *Sasa* quadrats (Table 6). In the *Sasa* quadrats, broadleaved litter was the dominant litter type; on average, broadleaved litter accounted for 68 % of the total litter, while *Sasa* litter accounted for 20 % (Table 6). The O horizon thickness was significantly lower in the *Sasa* quadrats than in the other quadrats (Table 6).

The coniferous litter had a significantly higher C/N ratio and Al concentration than the broadleaved and *Sasa* litters, while the coniferous litter contained significantly less N than the broadleaved litter (Table 7). The *Sasa* litter had a significantly lower Ca concentration than the broadleaved and coniferous litters (Table 7).

The soil NO_3^- content and net nitrification rate were significantly higher in the *Sasa* quadrats than in *Sasa*/tree and tree quadrats, while there were no significant differences in the soil NH_4^+ content and soil pH among the quadrats (Table 6). The soil in the *Sasa* quadrats had the highest concentration of exchangeable Ca, while the soil in the tree quadrats had the highest exchangeable Al concentration (Table 6). There was a significantly positive correlation between the soil NO_3^- content measured at the quadrats and the net nitrification potential measured in the laboratory (Table 8). Neither the soil C/N ratio nor the net N mineralization rate in the soil explained the net nitrification rate (Table 8).

Discussion

Relationships between forest structure and dynamics and the spatial pattern of soil properties

Current spatial forest structure is shaped not only by species competition for resources (light, water, nutrients, etc.), but also by past disturbances and the following forest succession. Occasional windstorms and typhoons are major natural disturbance regimes in Hokkaido (Yoshida and Noguchi 2009), and they create spatially

heterogeneous canopy structures. The spatial pattern of light availability, which is regulated by the canopy structure, is a major determinant of the distribution of *Sasa* undergrowth, and it results in high biomass in canopy gaps and low biomass under coniferous trees (Noguchi and Yoshida 2005). The distribution of *Sasa* biomass in our study site was consistent with this common pattern (Fig. 1). The positive correlation between the *Sasa* biomass and the broadleaved tree abundance, and the negative correlation between the *Sasa* biomass and the coniferous tree abundance indicate that the distribution of the two functional types of trees creates a spatial variation of *Sasa* growth even under the tree canopy (Table 3). In general, *Sasa* quickly covers the forest floor under a canopy gap once the gap is formed, and it exclusively dominates the area and inhibits the regeneration of canopy species; hence, canopy gaps with dense *Sasa* coverage tend to be sustained for a long time (Noguchi and Yoshida 2004). Tree regeneration under canopy gaps is usually restricted to occasionally disturbed microsites such as tip-up mounds (Hiura et al. 1996; Yoshida et al. 2006; Vodde et al. 2011). Shade-intolerant broadleaved species (e.g., *B. ermanii*, *B. platyphylla*, and *Kalopanax septemlobus*) are usually the first tree species (pioneer species) to become established on these microsites, and they grow faster than shade-tolerant coniferous species (Hiura et al. 1996; Yoshida et al. 2006; Vodde et al. 2011). In contrast, the seedling and sapling densities of tree species tend to be higher under conifer canopies because of the lower inhibition by *Sasa* cover (Noguchi and Yoshida 2004). In our site, some shade-intolerant broadleaved trees (*Phellodendron amurense*) grew around the canopy gap (Fig. 1), implying that these trees were established after the forest floor of the canopy gap had been covered by *Sasa*. However, the timing of the establishment of *Sasa* and shade-intolerant broadleaved species varies depending on canopy-gap conditions such as gap size, the species composition of adjacent vegetation, and light availability.

The spatial range of influence of broadleaved trees on *Sasa* biomass, litter composition, and soil properties was relatively large (10- to 15-m radii), while the influence of coniferous trees was strongest within the 5-m radius, although the 10- and 15-m radii buffers also showed significant relationships with these variables (Table 3). This could be explained partly by the fact that the lower density of broadleaved trees made the variation of the number of broadleaved trees within the 5-m radius buffer insufficient to capture the variation of the *Sasa* biomass and other variables, compared

with the more abundant coniferous tree in this study site. However, our result showing that the *Sasa* biomass was positively correlated with the abundance of broadleaved trees within the 10- and 15-m radii buffers and negatively correlated with the abundance of coniferous trees within the 5-m radius buffer could reflect the generally brighter forest floor under the deciduous broadleaved canopy, compared with that under the evergreen coniferous canopy. The negative influence of conifer abundance was also found on the proportion of *Sasa* litterfall (Table 3). These radii of tree influence could also reflect the wider range of leaf litterfall by the broadleaved species, compared with that of the coniferous species (Ferrari and Sugita 1996), because the number of broadleaved trees within the 10- and 15-m radii buffers was positively correlated with the proportion of broadleaved litter, and the number of coniferous trees within the 5-m radius buffer was positively correlated with the proportion of coniferous litter (Table 3).

We observed that the litter composition was determined largely by the surrounding plant community composition (Table 3). Locations where coniferous litter was dominant exhibited a relatively thick O horizon, while those where broadleaved and *Sasa* litters were dominant exhibited a relatively thin O horizon (Table 4). The coniferous litter had a lower N content and a higher C/N ratio than the broadleaved and *Sasa* litter (Table 7). These results indicate that the dominance of recalcitrant coniferous litter in the litterfall leads to the accumulation of organic matter on the forest floor, suggesting that the spatial pattern of the O horizon thickness is regulated by the spatial distribution of trees. An increase in O horizon thickness because of the recalcitrant litter quality was also reported in previous studies (Rothe et al. 2002; Guckland et al. 2009).

In the canopy gap, the O horizon was relatively thin (Figs. 2 g and h, Table 6). The thin O horizon appeared to have resulted from the small contribution of recalcitrant coniferous litter to the total litterfall, as well as the dominance of fast-decomposing broadleaved litter in the total litterfall in the canopy gap (Table 6). The observed litter composition is probably caused by the narrow dispersal range of coniferous litter, compared with that of broadleaved litter (Ferrari and Sugita 1996), as well as the concentration of broadleaved trees around the canopy gap (Table 1). In addition to the litter composition, the wet condition of the forest floor in the canopy gap may have enhanced litter decomposition, as moisture is one of the major factors that controls litter decomposition (Prescott 2010). The forest floor under the canopy gap is likely to have

received more precipitation than that under the canopy, as coniferous and broadleaved canopies intercept 23–33 % of total precipitation (Barbier et al. 2009). Additionally, understory vegetation cover prevents an increase in soil temperature by attenuating the input of radiant energy to the ground (Balisky and Burton 1993), which consequently reduces evaporation (Muscolo et al. 2007). Previous studies indicated that the decomposition rate of *Sasa* litter is slower than that of overstory species (Tripathi et al. 2006; Watanabe et al. 2013), suggesting that the dense *Sasa* in the canopy gap area increases the thickness of the O horizon. However, our results indicate the opposite pattern (i.e., a thin O horizon in the gap area), implying that the positive effects of the absence of coniferous litter, the dispersed input of deciduous litter, and the wet conditions outweigh the negative impact of *Sasa* litter on litter decomposition in the canopy gap. We also observed that there were large spatial and temporal variations in the thickness of O horizon within the study site (Fig. 2i), possibly caused by large spatial differences in litterfall amount, litter storage (e.g., the degree of physical fragmentation and compaction), and litter decomposition. Further investigations of the temporal and fine-scale spatial variations of the O horizon thickness are needed.

The soil water content tended to be low near coniferous trees (Table 5). Differences in water uptake by roots are often attributed to be a factor that contributes to soil moisture heterogeneity (Asbjornsen et al. 2011; Naithani et al. 2013). Canopy interception of precipitation is another factor. Coniferous trees tend to intercept more precipitation than broadleaved species owing to their larger leaf area index and bundled needle arrangement (Barbier et al. 2009). In addition, spatial variation in snowpack depth is suggested to cause spatial variation in the soil water content during the growing season because of soil moisture recharge by snowmelt water (Maurer and Bowling 2014), and the snowpack amount is usually lower under coniferous canopies, compared with that in canopy gaps (Harpold et al. 2015).

The thick O horizon had a negative influence on the soil water content (Table 5). The negative effect of the thick forest floor on the soil water content might be attributed to the presence of hydrophobic compounds. Hydrophobic compounds derived from plants can induce soil water repellency, which can impede water infiltration; severe soil water repellency is usually found under slow-decomposing litter layers under evergreen coniferous species (Doerr et al. 2000). Therefore, the spatial variations in soil moisture

observed in September 2012 and June 2014 could be the result of the interacting effects of canopy interception of rainfall and snow (especially for the soil moisture condition in spring), and of soil water repellency under slow-decomposing litter in this snow-dominated forest ecosystem.

Controlling factor of the spatial pattern of soil N dynamics in a forest with a complex structure

The selected regression model for the spatial pattern of the soil NO_3^- content showed that the soil water content has a positive influence on the soil NO_3^- content (Table 5). Additionally, the soil NO_3^- content in the field was strongly related to the net nitrification rate that was measured in the laboratory, and it was used as an index of nitrifier activity (Table 8). These results suggest that differences in nitrifier activity (i.e., nitrification) strongly affect the spatial pattern in the soil NO_3^- content. They also suggest that the nitrification potential differs under various soil moisture conditions. Thus, our results suggest that the spatial pattern of the soil water content, which was created by the plant distribution, influences the spatial pattern of soil microbial activity, which is related to NO_3^- production in the soil. However, there was no significant difference in the soil moisture among the quadrats, although the nitrification rate in the *Sasa* quadrat was significantly higher than that of the other quadrats (Table 6). These might be caused by the large spatial variation of the soil moisture in the study sites. A further study with finer spatial resolution will be necessary to analyze these relationships.

The spatial influence of the soil water content on net nitrification rates, microbial biomass, and enzyme activities was also observed in previous studies (Robertson et al. 1988; Baldrian et al. 2010). A positive influence of soil moisture on nitrifier abundance and gross nitrification was found along a hillslope of another broadleaved forest in Japan (Isobe et al. 2015). Additionally, Bustamante et al. (2012) found that the addition of water to semiarid soil microcosms increased the net nitrification rate by changing the nitrifier composition. These findings suggest that the spatial pattern of the soil water content creates spatial patterns of nitrifier abundance and composition, which might be

responsible for the spatial pattern of the soil NO_3^- content at the study site, but further investigations of the microbial community are necessary to confirm this.

The regression model for the soil NO_3^- content also showed a positive influence of the abundance of broadleaved trees within the 5-m radius buffer on the soil NO_3^- content, suggesting that the soil NO_3^- content is high near groups of broadleaved trees and low where broadleaved trees are scarce (Table 5). This reflects the plant distribution of our site: most of the broadleaved trees are found in and around the canopy gap, while coniferous trees are abundant where broadleaved trees are scarce (Fig. 1). Locations near the broadleaved trees in the canopy gap receive fast-decomposing broadleaved litter, while the contribution of slow-decomposing conifer litter is small in the canopy gap because of the narrow dispersal range of conifer litter (Table 6). This leads to the thinner O horizon and higher soil moisture near the broadleaved trees in the canopy gap as discussed earlier. Therefore, our results suggest that the characteristics of forest dynamics in a cool-temperate mixed forest with a dense understory, in which canopy gaps are created by occasional natural disturbances, subsequently leading to the subsequent dominance of *Sasa* understory and the establishment of broadleaved pioneer species on limited locations, determines the spatial pattern of soil N dynamics, especially the soil NO_3^- content. As we examined only one representative forest stand that contains a single canopy gap, our results can serve as an important case study, as few studies have investigated how soil N dynamics are controlled in complex, disturbed, and mixed forests in detail.

Among the variables measured in our study, the O horizon thickness, the soil NO_3^- content, and the soil water content obtained from the intensive grid sampling were spatially dependent. Statistical analyses of spatially autocorrelated data could lead to incorrect assessments of hypotheses (Legendre 1993; Dormann 2007). Therefore, when the relationships between these variables and controlling factors were modeled, an ordinary linear regression analysis was used after confirming that the model residuals were not spatially structured. In contrast, we used a correlation analysis and a single factor analysis of variance to test for significant relationships and differences among data obtained across the sampling quadrats. We believe that these methods are valid because previous studies dealing with the spatial patterns of soil variables used these statistical analyses (Gross et al. 1995; Hirobe et al. 2003; Bengtson et al. 2006).

However, it is still possible that the assumption of mutually independent data may have been violated. Therefore, the incorporation of spatial autocorrelation into the analysis of data obtained from the quadrats will be required to better understand the spatial relationship between the forest structure and soil N dynamics.

Nevertheless, our results suggest that canopy gap creation and subsequent plant succession create high soil moisture conditions via biological and hydrological processes that are influenced by plants growing in and around the canopy gap in cool-temperate conifer-broadleaved mixed forests with dense undergrowth (Figs. 2d and e), and that the high soil water content may be responsible for the relatively high nitrification potential, which explains the high soil NO_3^- content in the canopy gap (Figs. 2a and b). Our findings suggest that even in a relatively small and flat area within the watershed, the complex forest structure caused by occasional gap creation, and long-term maintenance of the gaps by the dense *Sasa* understory affect the spatial patterns of litterfall and hydrology, which create the spatial variation of soil N dynamics. Furthermore, our results imply that natural disturbances that create patchy canopy gaps will result in the long-term presence of locations with relatively high nitrification rates and soil NO_3^- contents in this forest. Further studies of soil N dynamics in other forest stands with canopy gaps are necessary because nitrification and the soil NO_3^- content affect plant N uptake, NO_3^- leaching to deeper soil, and N_2O emissions in forest ecosystems; additionally, the frequency of strong typhoons, which is a major factor that creates canopy gaps, is predicted to increase because of global warming (Emanuel 2005; Webster et al. 2005).

Conclusions

Figure 3 shows a summary of our findings. We found that the distributions of overstory and understory vegetation, which reflect the current species competition for resources and the legacy of past disturbances, create spatial patterns of nitrification potential and soil NO_3^- content in a conifer-broadleaved mixed forest with a dense *Sasa* undergrowth. Coniferous trees, which were dominant in the closed canopy, and broadleaved trees, which grew mainly around the canopy gap, largely determined the spatial pattern of the O horizon thickness via differences in litter decomposition. The

dominance of recalcitrant coniferous litter resulted in a thick O horizon, while the dominance of fast-decomposing broadleaved and *Sasa* litters led to a thin O horizon. Differences in the canopy interception of precipitation between the conifer-dominated area and the canopy gap could also contribute to the spatial pattern of O horizon thickness through its influence on the moisture conditions of the forest floor. Locations around coniferous trees where the O horizon is thick had dry soils, whereas locations beneath broadleaved trees and in the canopy gap where the O horizon was thin exhibited high soil water contents. High soil water content was related to high nitrification rates and, hence, high soil NO_3^- contents. Our results suggest that the distribution of plant species affects the spatial patterns of litterfall and hydrology, which create the spatial variation of soil N dynamics even in a relatively small and flat area within the watershed. Additionally, our results suggest that the high level of nitrification and the high soil NO_3^- content in the canopy gap may last for decades, given that canopy species have difficulty in naturally regenerating once the canopy gap is dominated by *Sasa*. Further investigations are necessary to understand the influence of soil N dynamics in canopy gaps on the biogeochemical cycle in forests with dense undergrowth.

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Figure legends

Fig. 1 Spatial pattern of canopy trees, *Sasa* biomass, the sampling grid, and the locations of sampling quadrats (*Sasa*, *Sasa*/tree, tree). Locations and diameter at breast height of overstory vegetation are indicated for filled circle (broadleaved trees) and filled square (coniferous trees). *Sasa* biomass was calculated by multiplying the total number of culms by the average height of standing *Sasa* within a 1-m radius from each sampling point. The sampling grids (4 × 4 m) are indicated by gray lines. DBH: diameter at breast height

Fig. 2 Spatial patterns of the measured variables and the distribution of overstory vegetation. (a) soil NO₃⁻ content (mg N kg soil⁻¹), (d) soil water content (%), and (g) thickness of the O horizon (cm) in 2012 September. (b) soil NO₃⁻ content (mg N kg soil⁻¹), (e) soil water content (%), and (h) thickness of the O horizon (cm) in 2014 June. The relationships between the observed values in 2012 September and those in 2014 June for (c) soil NO₃⁻ content (mg N kg soil⁻¹), (f) soil water content (%), and (i) thickness of the O horizon (cm). The dashed line shows that the ratio of the value in September to that in June is 1. Locations and diameters at breast height of overstory vegetation are indicated for filled circle (broadleaved trees) and filled square (coniferous trees). The symbol sizes of overstory vegetation are the same as those in Fig. 1

Fig. 3 Schematic diagram describing how plants affect the spatial pattern of soil NO₃⁻ contents in the coniferous-broadleaved mixed forest stand with dense *Sasa* undergrowth. Detailed explanations of each process and relationship are found in the Discussion and Conclusion sections. The boxes and arrows with solid lines indicate the observed variables and influences, and those with a dashed line indicate unmeasured variables and influences. + and - signs indicate positive and negative influences, respectively

Table 1 Density, DBH, and total basal area of overstory vegetation and the abundance of understory vegetation at the study site

Vegetation	Species	Tree density (tree ha ⁻¹)	Mean DBH (cm)	Basal area (m ² ha ⁻¹)
Coniferous	<i>Abies sachalinensis</i>	691.2	22.46 (9.42)	32.1
	<i>Picea glehnii</i>	46.1	67.33 (37.47)	20.2
	Not identified	80.6	14.79 (13.42)	2.4
	Total	818.0	24.23 (16.38)	54.7
Broadleaved	<i>Betula ermanii</i>	57.6	36.44 (25.79)	8.4
	<i>Quercus crispula</i>	57.6	33.98 (27.65)	8.0
	<i>Betula platyphylla</i>	57.6	22.38 (9.33)	2.6
	<i>Phellodendron amurense</i>	80.6	18.20 (4.69)	2.2
	<i>Aria alnifolia</i>	69.1	14.97 (2.1)	1.2
	<i>Kalopanax septemlobus</i>	34.6	15.47 (2.16)	0.7
	<i>Tilia japonica</i>	11.5	16.40	0.2
	Not identified	69.1	8.44 (2.68)	0.4
	Total	437.8	20.91 (16.14)	23.8
Understory	<i>Sasa senanensis</i> *		0.69 (0.75)	

Note: DBH: diameter at breast height. Data for overstory species are derived from the tree census data of the Uryu Experimental Forest.

*The value for *Sasa senanensis* is mean biomass (kg DW m⁻²). Data were obtained in this study.

Standard deviations are given in parentheses

Table 2 Spatial variation of soil properties measured in the intensive grid sampling

Soil properties	September 2012					June 2014				
	Mean		Range	CV	Moran's I	Mean		Range	CV	Moran's I
O horizon thickness (cm)	3.3	<i>a</i>	1.0–7.0	0.43	0.11	3.6	<i>a</i>	0.5–8.0	0.55	0.27 **
Soil NH ₄ ⁺ (mg N kg soil ⁻¹)	11.70	<i>a</i>	6.56–23.72	0.30	0.07	11.10	<i>a</i>	6.72–22.13	0.26	0.08
Soil NO ₃ ⁻ (mg N kg soil ⁻¹)	1.17	<i>a</i>	0.31–4.03	0.74	0.23 **	1.62	<i>a</i>	0.12–6.40	0.93	0.33 **
Soil water content (%)	31.8	<i>b</i>	26.4–40.0	0.11	0.40 **	34.2	<i>a</i>	27.7–47.6	0.14	0.29 **
Soil pH	4.6		4.2–5.4	0.05	0.03	–				
Soil exchangeable Ca (mg kg soil ⁻¹)	165.2		25.0–553.8	0.79	0.22 **	–				
Soil exchangeable Al (mg kg soil ⁻¹)	26.9		5.8–64.7	0.41	–0.01	–				

Note: Different letters indicate significant differences ($P < 0.05$) between sampling dates. Asterisks indicate significant autocorrelation in the variable. ** $P < 0.01$, * $P < 0.05$

Table 3 Spearman's rank correlation coefficients between the number of trees and the measured variables

Variable	Sampling	Number of broadleaved trees			Number of coniferous trees		
		5-m radius	10-m radius	15-m radius	5-m radius	10-m radius	15-m radius
Number of Brd trees (5 m)		1.00	0.36	0.46 **	-0.20	-0.40 **	-0.37 **
	(10 m)	0.36	1.00	0.77 **	-0.55 **	-0.70 **	-0.65 **
	(15 m)	0.46 **	0.77 **	1.00	-0.62 **	-0.77 **	-0.67 **
Number of Cnf trees (5 m)		-0.20	-0.55 **	-0.62 **	1.00	0.77 **	0.77 **
	(10 m)	-0.40 **	-0.70 **	-0.77 **	0.77 **	1.00	0.90 **
	(15 m)	-0.37 **	-0.65 **	-0.67 **	0.77 **	0.90 **	1.00
<i>Sasa</i> biomass	Grid I	0.16	0.39 **	0.39 **	-0.52 **	-0.37	-0.32
	Quadrat	-0.14	0.51	0.62 *	-0.90 **	-0.62 *	-0.79 **
Litterfall (mass)							
Total litter	Quadrat	0.59 *	-0.02	0.03	0.31	0.31	0.21
Broadleaved litter	Quadrat	0.64 *	0.37	0.46	0.02	-0.04	-0.07
Conifer litter	Quadrat	0.11	-0.81 **	-0.80 **	0.63 *	0.77 **	0.52 *
<i>Sasa</i> litter	Quadrat	-0.33	0.35	0.42	-0.69 **	-0.48	-0.62 *
Litterfall (proportion)							
Broadleaved litter	Quadrat	0.46	0.66 **	0.73 **	-0.38	-0.40	-0.37
Conifer litter	Quadrat	-0.18	-0.88 **	-0.88 **	0.60 *	0.68 **	0.53 *
<i>Sasa</i> litter	Quadrat	-0.35	0.45	0.48	-0.76 **	-0.58 *	-0.65 **
O horizon thickness	Grid I	-0.17	-0.22	-0.11	0.33 *	0.27	0.30
	Grid II	-0.12	-0.38 **	-0.38 **	0.56 **	0.50 **	0.57 **
	Quadrat	0.24	-0.69 **	-0.59 *	0.65 **	0.81 **	0.66 **
Soil water content	Grid I	0.26	0.37 **	0.37 *	-0.56 **	-0.53 **	-0.52 **
	Grid II	0.25	0.40 **	0.39 **	-0.55 **	-0.53 **	-0.60 **
	Quadrat	-0.63 *	0.08	-0.05	-0.23	-0.44	-0.30
Exchangeable Ca	Grid I	0.33 **	0.42 **	0.60 **	-0.41 **	-0.48 **	-0.47 **
	Quadrat	0.18	0.56 *	0.57 *	-0.68 **	-0.54 *	-0.51
Exchangeable Al	Grid I	-0.32 *	-0.22	-0.32 *	0.18	0.21	0.18
	Quadrat	0.05	-0.03	-0.05	0.59 *	-0.14	0.15
Soil NO ₃ ⁻	Grid I	0.42 **	0.43 **	0.47 **	-0.44 **	-0.40 **	-0.43 *
	Grid II	0.34 *	0.40 **	0.41 **	-0.28	-0.24	-0.25
	Quadrat	-0.07	0.60 *	0.46	-0.50	-0.62 *	-0.57 *
Net nitrification	Quadrat	-0.08	0.64 *	0.50	-0.53 *	-0.68 **	-0.59 *
Correlated pairs ($P < 0.05$)		7	14	14	16	13	13
Correlated pairs ($P < 0.01$)		2	11	9	11	9	7

Note: Only the variables that showed significant correlations with the number of trees are shown. Brd, Broadleaved; Cnf, Coniferous; Grid I, Grid sampling in September 2012; Grid II, Grid sampling in June 2014. Correlated pairs ($P < 0.05/0.01$): the number of pairs between the number of trees and other variables that showed significant ($P < 0.05/0.01$) correlations; Asterisks indicate significant correlation in the variable. ** $P < 0.01$, * $P < 0.05$

Table 4 Spearman's rank correlation coefficients among *Sasa* biomass, litterfall, and the thickness of the O horizon

		<i>Sasa</i> biomass	<u>Litterfall (mass)</u>				<u>Litterfall (proportion)</u>			O horizon
			Total	Broadleaf	Conifer	<i>Sasa</i>	Broadleaved	Conifer	<i>Sasa</i>	
	<i>Sasa</i> biomass	1.00								
Litterfall mass	Total litter	-0.39	1.00							
	Broadleaved litter	-0.09	0.81**	1.00						
	Conifer litter	-0.57*	0.27	-0.21	1.00					
	<i>Sasa</i> litter	0.86**	-0.24	-0.09	-0.49	1.00				
Proportion	Broadleaved litter	0.24	0.34	0.81**	-0.62*	0.09	1.00			
	Conifer litter	-0.51	-0.11	-0.53*	0.89**	-0.43	-0.78**	1.00		
	<i>Sasa</i> litter	0.90**	-0.37	-0.15	-0.61*	0.96**	0.12	-0.50	1.00	
	O horizon thickness	-0.53*	0.18	-0.17	0.77**	-0.48	-0.52*	0.72**	-0.55*	1.00

Asterisks indicate significant correlations among variables. ** $P < 0.01$, * $P < 0.05$

Table 5 Summary of the stepwise multiple regression analysis for soil nitrate concentration, soil water content, and O horizon thickness

Response variable	Sampling date	Independent variable	Coefficients	<i>P</i> value	Model <i>R</i> ²	Moran's I error
Soil NO ₃ ⁻	September 2012	Intercept	-2.3E-16	1.000	0.40	NS
		Soil water content	0.36	0.011		
		Number of Brd (5 m)	0.32	0.010		
		O horizon thickness	-0.21	0.120		
	June 2014	Intercept	1.4E-16	1.000	0.39	NS
		O horizon thickness	-0.33	0.019		
		Soil water content	0.30	0.034		
		Number of Brd (5 m)	0.24	0.044		
Soil water content	September 2012	Intercept	1.1E-15	1.000	0.43	NS
		Number of Cnf (5 m)	-0.44	0.001		
		O horizon thickness	-0.39	0.002		
	June 2014	Intercept	1.7E-17	1.000	0.39	NS
		Number of Cnf (5 m)	-0.40	0.004		
		O horizon thickness	-0.33	0.018		
O horizon thickness	September 2012	Intercept	1.6E-16	1.000	0.08	NS
		Number of Cnf (5 m)	0.31	0.031		
	June 2014	Intercept	7.8E-17	1.000	0.26	NS
		Number of Cnf (5 m)	0.52	< 0.001		

Coefficients: standard partial regression coefficients. Model *R*²: degree of freedom adjusted *R*². Number of Brd, number of broadleaved trees; Number of Cnf, number of coniferous trees. All models are significant at *P* < 0.05; Moran's I error: *P* value of the Moran's I test for regression residuals. NS: not significant

Table 6 Properties of vegetation, total litterfall mass, and the proportion of each litter type in the total litterfall in three types of quadrats (*Sasa*, *Sasa*/tree, and tree)

			<i>Sasa</i>			<i>Sasa</i> /tree			tree		
			Mean		Range	Mean		Range	Mean		Range
Vegetation	Number of Brd 5 m	(tree buffer ⁻¹)	0.8	<i>a</i>	0–1	0.6	<i>a</i>	0–2	1.4	<i>a</i>	0–3
	10 m	(tree buffer ⁻¹)	7.6	<i>a</i>	5–10	3.0	<i>b</i>	1–4	4.2	<i>b</i>	3–5
	15 m	(tree buffer ⁻¹)	17.4	<i>a</i>	15–19	8.0	<i>b</i>	5–13	9.2	<i>b</i>	6–10
	Number of Cnf 5 m	(tree buffer ⁻¹)	0.0	<i>c</i>	0–0	3.8	<i>b</i>	2–5	5.2	<i>a</i>	5–6
	10 m	(tree buffer ⁻¹)	8.0	<i>b</i>	7–10	14.2	<i>a</i>	13–16	13.0	<i>a</i>	10–16
	15 m	(tree buffer ⁻¹)	19.8	<i>b</i>	18–21	28.2	<i>a</i>	25–35	28.4	<i>a</i>	25–31
	<i>Sasa</i> biomass	(kg m ⁻²)	1.6	<i>a</i>	1.1–2.4	0.5	<i>b</i>	0.4–0.5	0.0	<i>b</i>	0.0
Litterfall	Total amount	(g m ⁻²)	18.4		9.5–34.9	19.6		17.3–23.4	24.4		19.5–32.6
	Broadleaved	(%)	67.9	<i>a</i>	36.7–81.3	37.2	<i>b</i>	18.7–50.9	56.3	<i>ab</i>	29.2–71.2
	Coniferous	(%)	10.3	<i>b</i>	5.6–15.5	58.0	<i>a</i>	48.4–76.8	43.6	<i>a</i>	28.5–70.8
	<i>Sasa</i>	(%)	19.7	<i>a</i>	7.0–54.6	4.8	<i>ab</i>	0.6–10.1	0.1	<i>b</i>	0.0–0.4
	Others	(%)	2.1		0.0–10.5	0.0		0.0	0.0		0.0
Forest floor	O horizon thickness	(cm)	1.8	<i>b</i>	1.5–2.0	3.5	<i>a</i>	2.5–5.0	3.0	<i>a</i>	2.3–4.0
Soil	Soil water content	(%)	32.3		29.4–34.8	32.4		26.4–39.5	28.7		23.9–32.9
	Soil pH		4.6		4.4–4.9	4.5		4.4–4.7	4.4		4.3–4.5
	NH ₄ ⁺	(mg N kg soil ⁻¹)	6.04		3.02–11.37	7.67		3.21–11.24	5.38		4.16–7.37
	NO ₃ ⁻	(mg N kg soil ⁻¹)	1.97	<i>a</i>	0.48–2.94	0.39	<i>b</i>	0.06–0.70	0.55	<i>b</i>	0.06–1.40
	Net N mineralization	(mg N kg soil ⁻¹ day ⁻¹)	4.58		2.84–5.85	8.03		3.01–14.13	2.75		1.00–4.26
	Net nitrification	(mg N kg soil ⁻¹ day ⁻¹)	2.28	<i>a</i>	0.36–3.69	0.24	<i>b</i>	0.08–0.53	0.41	<i>b</i>	0.03–1.20
	Exchangeable Ca	(mg g soil ⁻¹)	0.24	<i>a</i>	0.08–0.32	0.08	<i>b</i>	0.02–0.12	0.08	<i>b</i>	0.03–0.15
Exchangeable Al	(mg g soil ⁻¹)	0.04	<i>b</i>	0.02–0.05	0.03	<i>b</i>	0.02–0.05	0.07	<i>a</i>	0.05–0.10	

Note: Different letters indicate significant differences ($P < 0.05$) among quadrat types. Number of Brd, number of broadleaved trees; Number of Cnf, number of coniferous trees

Table 7 Chemical properties of leaf litter

		Broadleaved		Coniferous		<i>Sasa</i>				
		Mean	Range	Mean	Range	Mean	Range			
Carbon	(mg g ⁻¹ litter)	527.4	<i>b</i> (n = 15)	499.8–556.2	552.8	<i>a</i> (n = 15)	530.1–587.3	423.3	<i>c</i> (n = 11)	378.4–479.9
Nitrogen	(mg g ⁻¹ litter)	17.4	<i>a</i> (n = 15)	13.7–28.3	8.3	<i>b</i> (n = 15)	7.5–9.1	13.0	<i>b</i> (n = 11)	10.4–17.3
C/N ratio		31.3	<i>b</i> (n = 15)	17.7–39.0	66.8	<i>a</i> (n = 15)	61.7–72.5	33.4	<i>b</i> (n = 11)	22.7–43.8
Calcium	(mg g ⁻¹ litter)	7.68	<i>a</i> (n = 15)	5.87–10.46	8.07	<i>a</i> (n = 15)	6.86–9.72	3.08	<i>b</i> (n = 9)	1.46–3.90
Aluminum	(mg g ⁻¹ litter)	0.064	<i>c</i> (n = 15)	0.043–0.097	0.322	<i>a</i> (n = 15)	0.237–0.420	0.137	<i>b</i> (n = 9)	0.073–0.187

Note: Different letters indicate significant differences ($P < 0.05$) among litter types

Table 8 Spearman's rank correlation coefficients between net N transformation rates and soil properties in the quadrat survey

	Net N mineralization	Net nitrification	Soil C/N	Soil pH	Soil NH ₄ ⁺	Soil NO ₃ ⁻
Net N mineralization	1.00					
Net nitrification	0.13	1.00				
Soil C/N	-0.04	-0.42	1.00			
Soil pH	-0.29	-0.31	-0.41	1.00		
Soil NH ₄ ⁺	-0.25	-0.26	-0.51	0.73 **	1.00	
Soil NO ₃ ⁻	0.08	0.99 **	-0.40	-0.31	-0.29	1.00

Note: Asterisks indicate significant correlation among variables. ** $P < 0.01$, * $P < 0.05$





