

The effects of understory grazing by deer on aboveground N input to soil and soil N mineralization in a forest on Mt. Ohdaigahara in Japan

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According to some studies, herbivores reduce plant productivity, N input to the soil, and soil N mineralization, hence decelerating N cycling in forest ecosystems. However, few studies have been conducted on plant productivity and N dynamics in forest ecosystems, where herbivores have grazed on understory plants. In the temperate mixed forests of Ohdaigahara in central Japan, sika deer (*Cervus Nippon centralis*, Temminck, hereafter "deer") graze on understory dwarf bamboo (*Sasa nipponica*, Makino et Shibata, hereafter "sasa"). We studied the effects of deer grazing on the aboveground N input to the soil and soil N mineralization at the deer enclosure in the forest for 4 years. Deer exclusion increased the aboveground biomass of sasa, and thus the N input from sasa litter to the soil. The N input from the aboveground sasa litter inside the enclosure was nearly twice the sum of the N input from the aboveground sasa litter and the N input from the deer excrement outside the enclosure. This suggests that deer grazing decreased the aboveground productivity of sasa. We could not verify that deer grazing decelerated the soil N mineralization rate. Because the difference in the total N input was relatively small when N from woody litter was added to the N input, and the acceleration of the soil N mineralization rate by N input through excrements may partly compensate for depression by the decrease in the total aboveground N input. Long-term monitoring is needed to understand the effect of grazing on N dynamics in forest ecosystems.

Key words : deer, grazing, N input, N mineralization, *Sasa nipponica*

古澤仁美, 日野輝明, 金子真司, 荒木 誠: 大台ヶ原山の森林においてシカによる下層採食が地上部から土壌への窒素供給と土壌窒素無機化に及ぼす影響. 森林立地53:1-8, 2011.

今までのいくつかの研究で, 植食者は森林生態系の植物生産性, 土壌への窒素供給, 土壌無機化を減少させ, したがって窒素循環を減少させると報告されてきた。しかし, 下層植生が採食されている森林生態系での植物生産性と窒素動態を研究した例はほとんどない。大台ヶ原山の針広混交林では, ニホンジカが下層のミヤコザサを採食している。この森林で, 4年間ニホンジカを排除したシカ排除区を用いて, 採食が地上部から土壌への窒素供給と土壌窒素無機化におよぼす影響を検討した。シカ排除によって, ミヤコザサの地上部現存量が増加し, ミヤコザサリターによる窒素供給量が増加した。シカ排除区内のミヤコザサ地上部リターによる窒素供給量は, シカ非排除区のミヤコザサ地上部リターと糞尿による窒素供給の合計量のおよそ2倍であった。このことから, ミヤコザサ地上部の生産性は採食によって減少していると示唆された。土壌中の窒素無機化速度における採食の影響は明らかでなかった。なぜなら, 上層木のリターによる窒素供給を加えた全窒素供給量においてシカ排除区とシカ非排除区間の違いは相対的に小さかったため, そしてシカの排泄物としての窒素供給による無機化の加速が全地上部窒素供給量による抑制をある程度相殺したためと考えられる。採食が森林生態系の窒素動態におよぼす影響を明らかにするには長期的モニタリングが必要である。

キーワード: ニホンジカ, 採食, 窒素供給量, 窒素無機化, ミヤコザサ

1. Introduction

Grazing or browsing by herbivores often influences the N cycling in grassland ecosystems (McNaughton, 1979; Holland *et al.* 1992; Frank and McNaughton 1993; Ritchie *et al.* 1998; Olofsson *et al.* 2004) and forest ecosystems (Pastor *et al.*, 1993; Smit and Kooijman, 2001; Stark *et al.*, 2003). Herbivores have been shown to sometimes enhance (McNaughton, 1979; Frank and McNaughton, 1993) and sometimes retard (Pastor *et al.*, 1993; Ritchie *et al.*, 1998) the rate of N cycling in these ecosystems. Changing the quantity and quality of litter by grazing or browsing is an important factor that drives N cycling in ecosystems affected by herbivores.

In a study of north temperate grassland grazed by elk and bison in the Yellowstone National Park, Wyoming, herbivores increased the aboveground productivity (Frank and McNaughton, 1993), increased the N content and reduced the C/N ratio of plant materials (Tracy and Frank, 1998), thus increasing the N input from plants to the soil. Frank and Groffman (1998) observed that net soil N mineralization was faster in the grazed grassland than in enclosures. They indicated two possible reasons for this. First, the relative increase of the N input compared with the C input of grazed plant materials would increase the net N mineralization because of the reduced microbial demand for N (i.e., microbial immobilization) during decomposition. Another possibility is that N added as herbivore

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excrement, which be thought to have more easily decompose composition (Hobbs, 1996), may increase the rate of N mineralization in the grassland soil. An increased N availability to plants through an increase in the soil N mineralization rate helps grazed plants re-grow. Thus, herbivores enhance a positive feedback process, which increases aboveground plant productivity and the rate of N cycling.

In forest ecosystems, the situation is more complicated than grassland ecosystems because trees dominate the upper layer and there are understory plants on the forest floor. In boreal forests in Isle Royale, Michigan, selective foraging of hardwoods by moose increased the abundance of conifer species that have a slow growth rate, a low N demand, a low N content and a high C/N ratio in litter (Pastor *et al.*, 1993). Moose diminished both the mass and N content of litter input to the soil by increasing the abundance of conifer species, and as a result, the N mineralization and net primary productivity outside the exclosures were lower than inside the exclosures. In the case of boreal forests, where nutrient availability is generally low, changing the quantity and quality of litter may have a considerable effect on N mineralization and N availability.

Browsing dominant tree species in the upper layer may also have important effects on the N dynamics of the forest ecosystem in temperate regions. However, herbivores would affect the N dynamics through grazing on understory plants even if herbivores do not change the quantity and quality of litter from the upper layer. Herbivores in a Scots pine forest in the Netherlands do not directly browse the forest stands but graze dominant understory grasses (Smit and Kooijman, 2001). Grazing leads to an overall decrease in grass productivity and N input, and presumably slows down N cycling because of the decrease in importance of the grass layer. In general, the biomass herbivores consume would be relatively large compared to standing crops, particularly in low-productivity environments such as forest understories with an overabundant population (Brathen and Oksanen, 2001). Thus, Côté *et al.* (2004) hypothesize that herbivore grazing reduces plant productivity and decelerates nutrient cycling in forest ecosystems. However, few studies have been conducted on plant productivity and N dynamics, such as the N input from plants and soil N mineralization in forest ecosystems where herbivores grazed understory plants.

Populations of sika deer (*Cervus nippon centralis* Temminck; hereafter, “deer”) have grown for the past several decades in many areas of Japan (Natural Environmental Research Center, 1997). In forests, this increase in the deer population has changed the species composition (Takatsuki, 1977) and biomass of plants, especially for dwarf bamboo species, which are the dominant species in the forest understory in Japan (Furubayashi and Yamane, 1997; Yokoyama and Shibata, 1998).

Mt. Ohdaigahara in central Japan also has a high population density of deer, estimated to be 20 to 30 individuals per km², and this population has remained stable for the past 20 years (Fukushima *et al.*, 1984; Maeji *et al.*, 1999; Environmental Agency of Japan, 2001). Deer grazing has decreased the culm height and biomass of *Sasa nipponica* Makino et Shibata (hereafter, “sasa”), a species of dwarf bamboo that dominates the forest floor on Mt. Ohdaigahara. Within 4 years of the establishment of deer exclusion areas in the forest, the aboveground biomass of sasa increased to between 123 and 550 g m⁻² there (Furusawa *et al.*, 2003). However, we still do not know whether deer decrease both aboveground N input from sasa to the soil by decreasing the net aboveground productivity and soil N mineralization rate.

In order to study the impact of understory grazing on N dynamics in the sasa-dominated forest at Ohdaigahara, we conducted a 4-year study using an experiment based on deer treatments (exclusion and control). The aim of this paper is to describe the effect of deer grazing on the aboveground N input to the soil and the soil N mineralization rate.

2. Materials and methods

2.1 Study area and experiment design

This study was carried out in a temperate mixed forest with a 5° to 9° slope at Mt. Ohdaigahara on the Kii Peninsula in central Japan (lat. 34°10′44″N, long. 136°5′22″E; altitude 1,540 m). The annual precipitation exceeded 4,000 mm. The mean annual temperature was 6.4°C at the study site in 2001 (Furusawa *et al.*, 2006). The stem density and total basal area of live trees were 693.3 trees ha⁻¹ and 40.6 m² ha⁻¹ respectively at the study site (Ito and Hino, 2004). The dominant tree species are *Fagus crenata* Blume (48.2% of basal area) and *Abies homolepis* Sieb. et Zucc. (23.9%) (Ito and Hino, 2004).

Although sasa covers more than 90% of the forest floor, it remains less than 0.1 m tall as a result of deer grazing. The mean deer population density has been estimated to be 20 to 30 individuals km⁻² from 1982 to 2000 (Fukushima *et al.*, 1984; Maeji *et al.*, 1999; Environmental Agency of Japan, unpublished data). Deer usually use the study area during the snow-free season from April to November (T. Hino, unpublished data).

We used five pairs of plots (each plot was 5 × 10 m), established in May 1997 in the forest. One plot of each pair excluded deer by means of a surrounding 2-m-high fence (hereafter, the “deer-exclusion plot”), and the other did not exclude deer (control, hereafter, the “deer-grazing plot”). These two plots were adjacent to each other, and were also used for other research, including research on seedlings, insects, and soil invertebrates (e.g., Hino *et al.*, 2003; Ito and Hino, 2004; Ito and Hino, 2005; Ueda *et al.*, 2006). Thus, we could not obtain

samples from all five plot pairs for some measurements because we had to avoid any physical disturbance that would have resulted from taking large samples. A more detailed description of the study site is provided by Furusawa *et al.* (2003) and Furusawa *et al.* (2005).

2.2 Field and laboratory methods

2.2.1 Biomass, N concentration and N stock of sasa

We measured the aboveground biomass of sasa in May 1997, and September or October from 1998 to 2001. Aboveground sasa was clipped into a 0.5 m × 0.5 m quadrat in each plot in three of the five pairs chosen randomly at each sampling. We measured the dry weight of the leaves and the culms. The total N concentrations of the leaves and the culms in each plot in 2001 were measured using an automatic NC analyzer (NC800, Sumika Chemical Analysis Service, Ltd., Japan), which was also used for all measurements of the N concentrations described below. The N stock in sasa aboveground in each plot in 2001 was determined by multiplying its biomass by its N concentration.

The N stock in the sasa belowground in 2000 was determined by multiplying the biomass of new roots with the total N concentration of new roots, and the biomass of old roots with the total N concentration of old roots. We used the biomass data of new and old roots measured by Terai *et al.* (2009). To determine these biomass values, the sasa belowground was dug up to a depth of 0.2 m in a 0.5 m × 0.5 m quadrat in each plot in all five plot pairs and was divided into old and new roots, then was dried and weighed (Terai *et al.*, 2009). New roots were distinguished from old roots by their white color, their softness and their epidermis-covered nodes. We then measured the N concentration in the samples they collected.

2.2.2 The aboveground N input from sasa litter

The N input from aboveground sasa litter in 2001 was not measured directly. Instead, we estimated it by multiplying the above-mentioned biomass in 2000 by the total N concentration in dead leaves and culms. The culms and leaves of this species sprout in spring, stop growing by autumn, overwinter, and die by the autumn of the next year. Thus, we assumed that the biomass in October in 2000 represented the litter input for 2001. We used the total N concentration of the dead leaves and culms sampled and measured in 2006 (16.5 mg g⁻¹, 5.4 mg g⁻¹ in the deer-exclusion plots, and 16.9 mg g⁻¹, 8.6 mg g⁻¹ in the deer-grazing plots, respectively) (Furusawa *et al.*, submitted).

2.2.3 The N input from woody litter

We used previously published data for the N input from woody litter, which was measured with a litter-trap technique (Furusawa *et al.*, 2003), to compare it with the N input from aboveground sasa litter. The trapped woody litter was collected

from May 1997 to June 2000 in the forest (n = 10), and their oven-dried weights and N concentration were measured. It was assumed that the N input from the woody litter was not (yet) seriously affected by deer exclusion.

2.2.4 The amount of sasa consumed by deer and the deer's N intake from sasa

We investigated deer's N intake from sasa, which was presumed to equal the N input from deer excrement, from May to December 2001. To determine the amount of sasa consumed by deer, we established 40 quadrats (each 1.5 m × 1.5 m) outside the plots. We established a 1.5-m³ cage made of steel pipes, with the sides and top enclosed by a 40-mm mesh nylon net, in each of the 20 quadrats to exclude deer grazing in May, while the other 20 quadrats were used as control. We clipped the sasa aboveground in each quadrat in December, and oven-dried and weighed the leaves and culms (105°C, 24 hr). The difference in the quantity of leaves and culms between the deer-grazing and the deer-exclusion quadrats was considered to be equal to the annual quantity of sasa consumed by deer in the study area, as the deer were unable to graze on sasa in winter because of the deep snow. The deer's N intake from the sasa leaves and culms was determined by multiplying the quantity consumed by deer and the overall mean N concentration (measured in the deer-grazing plots for 5 years, 1997-2001). We assumed that the quantity consumed by deer did not change during the study because the deer density had remained roughly stable for the past 20 years (Environmental Agency of Japan, unpublished data).

2.2.5 Litter decomposition rate

We investigated the decomposition rate of the litter from the leaves of *F. crenata* (hereafter, "beech leaves"), sasa leaves, and sasa culms using the "mesh bag" technique in 1998. We chose the beech leaves because it was the most abundant species in the study area, and because beech leaves accounted for more than half of the litter collected in the litter traps. The beech leaves were collected from September to October 1997 using the litter traps described above. Because fresh dead material of sasa is difficult to collect in the forest, we obtained dried samples (70°C, 24 h) of living leaves and culms that were clipped in October 1997, and used these samples to measure the litter decomposition rate. The C and N concentrations in these materials were obtained using the NC analyzer. Each litter type was placed in a separate mesh bag (0.15 m × 0.15 m with a 1-mm mesh size), with 4.28 g of beech leaves, 1.61 g of sasa leaves, and 1.54 g of sasa culms (based on their ash-free and oven-dried weight at 105°C). In May 1998, one bag of each litter type was then fixed to the forest floor of each plot in all five plot pairs using metal pins. All bags were collected 1 year later, and their contents were dried and weighed in the laboratory.

2.2.6 Potential net N mineralization

Potential net N mineralization was measured in May, July, and October 2000. Soil samples were taken from each plot of the five plot pairs in May, July and October in 2000. The samples were taken from an 0.1 m × 0.1 m sampling area (0.01 m²) from 0 to 0.05 m in depth. The soil samples were transported in an icebox and refrigerated at 8°C in the laboratory on the same day. Incubation started in the laboratory on the next day and was based on the method of the Committee of Analysis and Measurement for Forest Environment (1999). Two 50 g subsamples were sieved through a 2 mm screen, and then transferred into 100 mL glass jars. The jars were covered with thin aluminum foil to prevent the samples from drying out. The soil samples were then incubated for 6 weeks at 15°C, which is the mean soil temperature during the growing season (May to October) at the study site.

At the start and end of the 6-week incubation period, we extracted mineralized ammonium (NH₄-N) and nitrate (NO₃-N) with the 2 M KCl, and quantified these components using the steam-distillation method described by the Committee of Standard Soil Analysis and Measurement (1986). The increases in NO₃-N and the sum of increase in NH₄-N and NO₃-N during the 6-week incubation were defined as the net nitrification rate and the net soil N mineralization rate respectively.

2.2.7 The N stock of the O layer and surface soil

To evaluate the N stock in the O layer of the soil, all the materials in this layer were collected from 0.5 m × 0.5 m sampling areas (0.25 m²) in each plot of three randomly selected pairs in October 2000. The samples were sorted into fine (< 4 mm) and coarse (> 4 mm) fractions using sieves. Coarse materials were further separated into woody and sasa residues. The dry weight (70°C, 24 h) of each fraction of the residues was measured and corrected on an oven-dry basis (105°C, 24 h). The N stock of each fraction was determined by multiplying the oven-dried mass by the corresponding N concentration. We then calculated the N stock in the O layer as the total N stock for all fractions combined.

We determined the total N concentration and bulk density to evaluate the N stock in the surface soil (0–0.05 m in depth per 1 m²). The total N concentration was measured in the samples used for measuring the soil N mineralization rate. To estimate bulk density, in July 2000 we took three core samples of the surface soil outside the plots using a 0.0004-m³ stainless-steel cylinder (0.1128 m in diameter, 0.04 m in depth). Bulk density was estimated to be 284.4 kg m⁻³ according to the method of the Committee of Analysis and Measurement for Forest Environment (1999). We then calculated the mass of the surface soil (0–0.05 m in depth) as 14.2 kg m⁻². We determined the N stock in the surface soil by multiplying this mass by the total N concentration of the soil in each plot at each sampling sea-

son and then taking the average of the three sampling seasons.

2.2.8 Statistical analysis

All the statistical tests were performed with Statview software (Hulinks Co., Japan). The Mann-Whitney test was used to reveal the effect of deer on the aboveground biomass of sasa in 2001, and the total N concentration of sasa leaves, culms, and roots. The Mann-Whitney test was also used to reveal the effect of the N stocks in sasa, the O layer, and the surface soil when the sampling seasons were pooled, as well as the N input from the aboveground sasa litter.

We analyzed the effect of deer and the litter types on the proportion of the litter mass remaining after 1 year using the materials in the mesh bags and a two-way ANOVA after arcsine transformation. Two-way ANOVA was also used to examine the effect of deer and of the sampling on the potential net soil N mineralization rate (NH₄-N + NO₃-N), the net nitrification rate and the N stock in the soil.

3. Results

3.1 The aboveground biomass and N concentration of sasa

While the aboveground biomass tended to increase slightly in the deer-grazing plots throughout the study period, the aboveground biomass showed a ten-fold increase in the deer-exclusion plots by September 2000 and remained at that level in the following autumn (Table 1). The aboveground biomass was significantly higher in the deer-exclusion plots than in the deer-grazing plots in 2001 ($p < 0.05$). The N concentrations of leaves and culms were 29.6 ± 1.8 mg g⁻¹ and 6.2 ± 0.6 mg g⁻¹ in the deer-exclusion plots and 30.1 ± 1.9 mg g⁻¹ and 8.8 ± 0.4 mg g⁻¹ in the deer-grazing plots (average ± SD). Deer exclusion had a significantly negative effect on the total N concentration in the culms ($p < 0.05$), but not in the leaves.

The N concentrations of new and old roots were 10.1 ± 1.0 mg g⁻¹ and 8.9 ± 1.4 mg g⁻¹ in the deer-exclusion plots and 9.4 ± 1.9 mg g⁻¹ and 7.2 ± 2.2 mg g⁻¹ in the deer-grazing plots (average ± SD). Significant differences were not found between plots in the N concentration of new and old roots.

Table 1. Aboveground biomass of sasa (g m⁻²) (n = 3)

	May 1997	Oct. 1998	Sep. 1999	Sep. 2000	Oct. 2001
Deer-exclusion	33.5 (1.7)	90.3 (32.7)	185.0 (87.1)	319.4 (197.7)	339.0 (190.7)
Deer grazing	23.5 (7.3)	40.9 (5.1)	43.3 (13.1)	61.0 (17.8)	82.3 (6.4)

Values in parentheses represent SD.

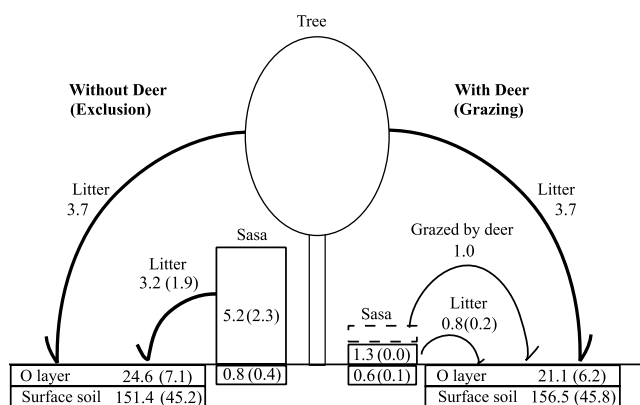


Fig. 1. N stocks in sasa (n = 3) and in the O layer of the soil (n = 3), surface soil (n = 5), and annual N input from plants to the soil (n = 3 for N input from litter, n = 20 for N input from deer)

Soil depth was defined as 0 to 0.05 m for surface soil. The units of N inputs and stocks are g m⁻² yr⁻¹ and g m⁻², respectively. Values in parentheses represent SD. The numerical values presented in the figure were measured in 2001, with the following exceptions: N in tree litter represents the average from 1997 to 1999 (n = 10), and N stocks in the O layer, in soil and in belowground Sasa components (n = 5) were measured in 2000.

3.2 The N stock and aboveground N input to soil

Fig. 1 summarizes our results on the N stock and N input in 2000 or 2001, except the N input from woody litter that was measured from 1997 to 1999. Deer exclusion had a significantly positive effect on the N stock in sasa aboveground (p < 0.05). The effect of deer exclusion was not significant on the N stock in the sasa belowground. Deer exclusion had no significant effect on the total N stock of the O layer. The N stock in the surface soil ranged from 141.0 to 163.6 g m⁻² 0.05m⁻¹ in the deer-exclusion plots, and from 121.8 to 174.0 g m⁻² 0.05m⁻¹ in the deer-grazing plots for three sampling seasons. The effects of deer exclusion and sampling season on the N stock in the surface soil were not statistically significant. When sampling seasons were pooled, deer exclusion had no significant effect.

The quantities of leaves and culms consumed by deer were estimated at 31.3 and 5.4 g m⁻² respectively, based on a comparison of sasa biomass between caged and uncaged quadrats. The mean N concentrations of leaves and culms for 4 years were 30.1 mg g⁻¹ and 9.5 mg g⁻¹ in the deer-grazing plots. The N amounts for leaves and culms consumed by deer were calculated at 0.9 g m⁻² and 0.1 g m⁻² respectively. Accordingly, the deer's N intake from sasa and the N input from excrement to soil was estimated at 1.0 g m⁻².

The N input from aboveground sasa litter in the deer-exclusion plots (3.2 g m⁻² yr⁻¹) was four times higher than in the deer-grazing plots (0.8 g m⁻² yr⁻¹) (p < 0.05), and was nearly double the total N input from aboveground sasa litter and deer excrement (1.8 g m⁻² yr⁻¹) in the deer-grazing plots.

Table 2. The proportion of the litter mass remaining after one year, the soil N mineralization rate, and the nitrification rate in the deer-exclusion plots and the deer-grazing plots (n = 5 at each plot)

	Deer-exclusion	Deer-grazing
The proportion of the litter mass remaining		
Sasa leaves	0.55 (0.03)	0.55 (0.04)
Sasa culms	0.71 (0.03)	0.69 (0.02)
Beech	0.80 (0.04)	0.83 (0.03)
The soil N mineralization rate (mg kg ⁻¹ day ⁻¹)		
May	3.6 (1.9)	2.5 (1.6)
July	4.2 (2.4)	3.3 (1.6)
October	2.3 (0.9)	3.6 (2.3)
The nitrification rate (mg kg ⁻¹ day ⁻¹)		
May	2.3 (1.0)	2.2 (1.5)
July	2.4 (0.6)	2.1 (0.7)
October	2.1 (0.9)	2.3 (0.7)

Values in parentheses represent SD.

Table 3. Two-way ANOVA results for the proportion of the litter mass remaining, the soil N mineralization rate, and the nitrification rate

	F	p
The proportion of the litter mass remaining		
Deer treatment	0.3	0.60
Types of litter	155.7	<0.01
Deer treatment×Types of litter	1.7	0.20
The soil N mineralization rate		
Deer treatment	0.1	0.73
Sampling season	0.5	0.61
Deer treatment×Sampling season	1.2	0.31
The nitrification rate		
Deer treatment	0.1	0.78
Sampling season	0.01	0.99
Deer treatment×Sampling season	0.2	0.82

If the N input from woody litter was not seriously affected by deer exclusion, the N input was 3.7 g m⁻² yr⁻¹ in the both plots. The total aboveground N input, including from sasa, wood, and deer excrements, was 6.9 g m⁻² yr⁻¹ in the deer-exclusion plots, and 5.5 g m⁻² yr⁻¹ in the deer-grazing plots respectively. The N input from excrement to soil was 22% of the N input from sasa and woody litter in the deer-grazing plots.

3.3 Litter decomposition rate

The proportion of the litter mass remaining after 1 year differed significantly between the three types of litter. It was low-

est for sasa leaves and highest for beech leaves in all treatments (Table 2 and 3). The initial C/N ratios were 15.0 in sasa leaves, 31.9 in sasa culms and 40.1 in beech leaves, corresponding to the order of the proportion of the litter mass remaining. Deer exclusion had no significant effect on the proportions of the litter mass remaining (Table 3).

3.4 Potential net N mineralization

The net soil N mineralization rate ranged from 2.3 to 4.2 mg kg⁻¹ day⁻¹ in the deer-exclusion plots, and from 2.5 to 3.6 mg kg⁻¹ day⁻¹ in the deer-grazing plots for three sampling seasons (Table 2). The net nitrification rate ranged from 2.1 to 2.4 mg kg⁻¹ day⁻¹ in the deer-exclusion plots, and from 2.1 to 2.3 mg kg⁻¹ day⁻¹ in the deer-grazing plots for the three sampling seasons (Table 2). The effects of deer exclusion and of sampling season on the net soil N mineralization rate and the net nitrification rate were not statistically significant (Table 3). The ratio of nitrification to mineralization ranged from 0.71 to 0.91 in the deer-exclusion plots, and from 0.74 to 0.82 in the deer-grazing plots for three sampling seasons. The effects of deer exclusion and of sampling season on the ratio were not statistically significant.

4. Discussion

Deer exclusion increased the aboveground biomass of sasa and thus the N input from its litter to soil. The N input from aboveground sasa litter in the deer-exclusion plots was nearly twice the total N input from the aboveground sasa litter and deer excrement in the deer-grazing plots. This result suggests that the aboveground productivity of sasa was decreased by deer grazing, and supports the hypothesis of Côté *et al.* (2004). We took the aboveground biomass of sasa in September or October as the N input from aboveground sasa litter in the deer-grazing plots. This may lead to an overestimation of sasa litter because deer grazing continues until November (T. Hino, unpublished data). The aboveground biomass tended to increase slightly in the deer-grazing plots throughout the study period, probably because of spatial and temporal variation in the measurement of sasa biomass. In fact, according to additional observation of the aboveground biomass from 2002 to 2005, the aboveground biomass ranged from 31.7 to 58.1 g m⁻², and thus did not increase (Furusawa, unpublished data).

The biomass of old roots and the total biomass of roots were not significantly different between plots (Terai *et al.*, 2009), nor were the N concentration of roots and the total N stock of sasa belowground. These results suggest that sasa would initially increase its aboveground biomass and leaf area to acquire more energy from sunlight than belowground when deer are excluded (Terai and Shibata, 2002). Thus we propose that belowground productivity and the amount of root litter would not increase through deer exclusion.

Deer grazing has a few properties that depress rates of N accumulation in the forest ecosystem at Ohdaigahara. In the deer-exclusion plots, sasa keeps N in its large biomass and the input N of litter to the soil is the same as woody litter. Sasa would help to maintain N in the forest ecosystem at Ohdaigahara. Deer grazing decreased this effect of sasa by decreasing sasa productivity. Instead, deer input N through excrement. Forty percent of excreted N by ungulate (cattle and sheep) is urea N that is soluble and would rapidly mineralize (Haynes and Williams, 1993) and tends to leach easily. Therefore, N from excrement by deer may not so accumulate as well.

A decrease in N input from plant to soil decelerates the soil N mineralization rate (Pastor *et al.*, 1993). However, we could not verify that deer grazing decelerated the soil N mineralization rate. There are two possible reasons for this. First, the difference of the total aboveground N input (from sasa, wood, and deer excrement) was relatively small between the experimental plots (6.9 g m⁻² yr⁻¹ in the deer-exclusion plots, and 5.5 g m⁻² yr⁻¹ in the deer-grazing plots) if woody litter input were the same. There might have been a time lag between the change of litter N input from sasa and N mineralization. Deer exclusion had no effect on the total N stock in the O layer and the surface soil, which are substrates for mineralization. The relatively rapid decomposition rate of sasa litter, as shown in the mesh-bag experiment, also may decelerate the accumulation of sasa litter in the O layer. The rapid decomposition rate of sasa, especially its leaves, was probably due to its lower C/N ratio (Kawahara, 1985; Berg and McLaugherty, 2003). The increase in litter input from sasa aboveground through deer exclusion would lead to an increase in N stock in the O layer and surface soil in the future. It will take several decades because the difference in the total aboveground N input between the experimental plots is small (1.4 g m⁻² yr⁻¹) compared to the N stock of the surface soil. The second reason is the soil N mineralization rate would increase by adding soluble N, which would rapidly mineralize in the excrements of herbivores (Hobbs, 1996). This positive effect of herbivore excrement is important when most of the N returns through excrement rather than plant material. For example, Frank *et al.* (1994) showed that the estimated rate of N input from ungulates to the soil was approximately 4.5 times the amount of N in senescent plants in temperate grassland in Yellowstone National Park, and that the soil N mineralization rate for the grassland was higher than that measured in other temperate grassland ecosystems. In our study, the N input from deer to the soil was only 22% of the N input from sasa and woody litter to the soil in the deer-grazing plots. However, the acceleration of the soil N mineralization rate by N input through excrements may partly compensate for depression by the decrease in the total aboveground N input.

Many long-term studies that use herbivore exclosures have demonstrated the significant effect of grazing on soil N mineralization (e.g. 15–30yr, Stark *et al.*, 2003; 33–37yr, Frank and Groffman, 1998; 37–39yr, Pastor *et al.*, 1993). These experimental periods of these experimental sites were longer than our sites. At our study site, the increase of aboveground litter input from sasa because of deer exclusion may increase the N mineralization in soil in the future, as already discussed above. Moreover, we predict that belowground sasa in deer-exclusion plots will increase in biomass and its litter due to the increased photosynthetic products. In fact, the increase in belowground biomass was confirmed in a study in 2004 (S. Shibata, personal communication). The belowground litter input from sasa to soil may also influence the N mineralization in the soil. Long-term monitoring is needed to understand the effect of grazing on N dynamics in forest ecosystems.

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