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論　文（Original article）

Effects of dwarf bamboo (*Sasa nipponica*) and deer (*Cervus nippon centralis*) on the chemical properties of soil and microbial biomass in a forest at Ohdaigahara, central Japan

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Abstract

In forests at Ohdaigahara, central Japan, the understory is dominated by dwarf bamboo (*Sasa nipponica* Makino et Shibata; hereafter, Sasa), which is the main food of the sika deer (*Cervus nippon centralis* Temminck) that overpopulate the region. We examined the effects of Sasa and deer on the chemical properties of soil and on soil microbial biomass by experimental exclusion of deer or removal of Sasa over 3 years. Clipping and removing Sasa increased the concentrations of NO_3^-, Ca^{2+}, and Mg^{2+} in the soil. This might be caused to decrease of nutrient uptake by Sasa. Inside the deer exclosures, the concentrations of NH_4^+ were higher than those of outside the exclosures, whereas the concentrations of Ca^{2+} and Mg^{2+} were lower. This result suggests that much Sasa litter input and lack of excretion by deer owing exclusion of deer might affect nutrient conditions in the soil. On the other hand, neither Sasa nor deer affected total carbon content, total nitrogen content or microbial biomass C in the soil. These soil properties may be stable for the short duration of the change of Sasa aboveground biomass or deer exclusion.

Key words : *Cervus nippon centralis*, removal experiments, *Sasa nipponica*, soil microbial biomassC, total carbon content, total nitrogen content, water-soluble ions

Introduction

There is some evidence to suggest that the sika deer (*Cervus nippon centralis* Temminck hereafter, deer) population has grown rapidly during the last several decades in Japan (Natural Environmental Research Center 1997). Mt. Ohdaigahara, central Japan, is also known for its high population density of deer, estimated to be 17.5 –30.9 deer/km^2 (Maeji et al. 1999). Deer have grazed a dwarf bamboo (*Sasa nipponica* Makino et Shibata) as their main food at Mt. Ohdaigahara (Yokoyama et al. 1996). Although *Sasa nipponica* is distributed widely as a dominant species in the forest understory owing to its tolerance of deer grazing (Takatsuki 1983), the culm height and biomass of *Sasa nipponica* have recently decreased greatly in Mt. Ohdaigahara (Yokoyama and Shibata 1998a; Hino unpublished).

What effects do *Sasa nipponica* or deer have on the nutrient elements of the forest soil? It has been suggested that the aboveground biomass of *Sasa nipponica* reaches naturally 6400–8800 kg/ha in open areas (Oshima 1961; Kawahara et al. 1977). Considering *Sasa nipponica*'s large biomass and rapid alternation of generations, large quantities of nutrient elements cycle rapidly throuth the *Sasa nipponica* –soil system (Takamatsu et al. 1997). A decrease in biomass of *Sasa nipponica* may increase nutrient concentrations in soil through reduced nutrient-uptake. On the contrary, an increase in biomass of *Sasa nipponica* may also increase the concentrations by supplying more dead tissues to the forest soil for mineralization. Grazing by deer will weaken these effects of *Sasa nipponica*. Large herbivorous mammals such as deer have another effect on soil nutrients. They browse on fresh leaves containing high-quality nutrients, and then excrete urine and feces, increasing available N (McKendrick et al. 1980; Pastor et al. 1993) and nutrient concentrations (Jusoff 1988) in the soil. Accordingly, the effects of *Sasa nipponica* and deer on soil nutrients are expected to be complicated and to vary among nutrients.

The objective of this study was to examine the effects of *Sasa nipponica* and deer on nutrient elements in a forest soil experimentally. We carried out a 2 × 2 factorial experiment with treatments of *Sasa nipponica* (removal

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and control) and deer (exclusion and control) in a mixed forest at Mt. Ohdaigahara over three years. We measured the concentrations of water-soluble ion, total carbon and nitrogen contents, and microbial biomass as indicators of nutrient changes in the soil. The concentrations of water-soluble ions are believed to change in response to changes in forest management (Haibara 1990) and we expected this change to effectively reveal the influence of deer grazing. Total carbon and nitrogen contents reflect the cycling of N and C in the forest ecosystem as a function of turnover of the litter from plants (Arimitsu 1997). Soil microbial biomass C (hereafter, biomass C) also has been considered to be a useful indicator of soil nutrient conditions because soil microorganisms depend on available organic C as their energy source (Dommergues et al. 1978) and because the biomass C acts as a reserve of available nutrients for plants (Sato and Seto 1995; Bauhus et al. 1998).

Materials and Methods

Study area

This study was carried out in a forest at Ohdaigahara on the Kii Peninsula, central Japan (lat 34° 10′ 44″ N, long 136° 5′ 22″ E; altitude 1540 m; Fig. 1). The mean annual temperature is 5.7 °C (Doei et al. 1989) and the annual precipitation ranged from 3235 to 4020 mm from 1997 to 1999 (Nara Meteorological Observatory 1997, 1998, 1999). This area is covered with snow approximately 1 m deep in winter. *Fagus crenata* Blume, *Abies homolepis* Sieb. et Zucc., and *Quercus crispula* Blume are the dominant tree species, and *Sasa nipponica*(hereafter, Sasa) is overwhelmingly the dominant undergrowth species. The soil parent materials are sedimentary rocks with alternation of sandstone and mudstone strata. Soils are classified as a brown forest soil (Forest Soil Division, 1976), and are supposed to fall into the Haplumbrepts (Soil Survey Staff, 1994). The O horizon ranges from 1.5 to 3.5 cm thick. The density of deer there was estimated to be 17.5–30.9 deer km^{-2} (Maeji et al. 1999).

We used parts of 5 experimental setups that had been established for multiple research projects conducted by other researchers in a part of the forest with a 5° to 9° slope. Each experimental setup consisted of 4 plots for each of the 2 × 2 factorial treatments of Sasa (removal and control) and deer (exclusion and control). Deer had been excluded with 2-m-high fences in November 1996, the year preceding the start of our research. The fences were constructed with steel pipes (5 cm in diameter) and a combination of wire and polyethylene netting. In the Sasa-removal plots, the aboveground parts of Sasa were clipped with shears and discarded outside the plots in May or June from 1997 to 1999. In this paper, we call the 4 types of plot D0S0, D0S1, D1S0, and D1S1, where D = deer, S = Sasa, 0 = exclusion or removal, and 1 = control. The size of each plot was 5 m × 10 m, and the whole size of an individual setup was 10 m × 20 m (Fig. 2).

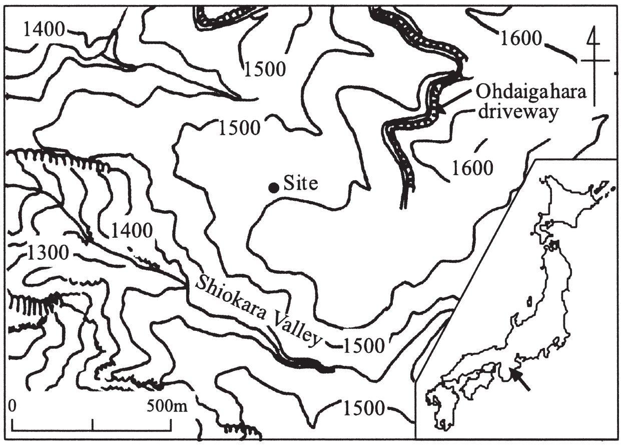

Fig. 1. Location of the experimental site.

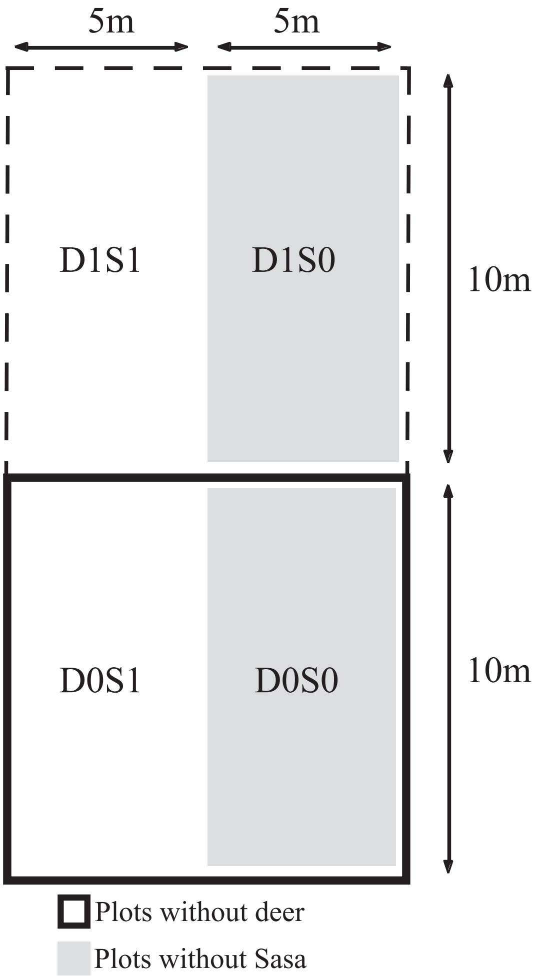

Fig. 2. Design of experimental plots.

Aboveground biomass of Sasa

The aboveground biomass of Sasa was measured in May 1997, May and October 1998, and June and September 1999. Three samples of Sasa were clipped with shears at ground level in 50 cm × 50 cm quadrats in each plot in three of five experimental setups chosen randomly at each sampling time (but only in the D0S0 and D1S0 plots in June 1999). Sampling in May or June was done before removal of Sasa. After measuring dry weights (24h , 70 °C) of Sasa samples, we measured oven-dry weights (24h , 105 °C) of a portion of the samples.

Soil sampling, preparation, and preservation protocol

We only used one of the five experimental setups to take soil samples because we were afraid that soil sampling might disturb the other research being conducted in the setups. We collected 6 samples of mineral soil (0 –5 cm in depth) from each plot of the setup each spring (May or June) and autumn (September or October) from 1997 to 1999. The samples were transported at low temperature and refrigerated at 8 °C in our laboratory on the same day. The soil samples were sieved through a 2-mm screen the next day. Water-soluble ions were extracted as soon as the soil samples had been sieved. Soil microbial biomass C (hereafter, biomass C) was evaluated 7 to 10 days after the soil samples were sieved (next section). Soil samples were refrigerated at 8 °C before analysis. The soil samples used for analysis of total C and N contents were air-dried, then ground in an agate mortar.

Soil analysis

We measured the levels of water-soluble ions in each spring and autumn to correspond with the period of Sasa activity. Sasa starts its first flush of new leaves and culms in the spring, then attains its maximum aboveground biomass in summer (Takatsuki 1992; Yokoyama and Shibata 1998b). Thus we expected that the effect of nutrient absorption by Sasa on the level of water-soluble ions would depend on season. Water-soluble ions were extracted from moist soil (soil: water = 1:5) (Committee of Standard Soil Analysis and Measurement 1986). The extracts were stored at –20 °C until analysis. Concentrations of ions (Ca^{2+}, Mg^{2+}, K^+, NH_4^+, Na^+, NO_3^-, SO_4^{2-}, and Cl^-) were measured by means of ion chromatography (IC7000S, Yokokawa).

We measured the biomass C, total carbon content and nitrogen content in soil for the initial (May 1997) and every autumn. Biomass C was measured by using the chloroform-fumigation–extraction method (Vance et al. 1987; Wu et al. 1990). Extracts were stored at –20 °C until analysis. Organic C in the extracts was measured by wet oxidization in a total organic carbon analyzer (TOC-5000, Shimadzu). Biomass C was calculated as $B_C = 2.22E_C$, where E_C = (C extracted from fumigated soil) – (C extracted from unfumigated soil) (Wu et al. 1990). Total C and total N contents of ground soil samples were measured in a NC automatic analyzer (NC800, Sumika Chemical Analysis Service, Ltd.).

Statistical analysis

All statistical tests were performed with the Statview software (Hulinks.co.). One-way ANOVA was used to examine differences in Sasa biomass between experimental plots at each sampling date. Two-way ANOVA was used to reveal the effects of Sasa and deer on water-soluble ion concentrations in each season. We treated the observed values for three years as replicates because the concentrations of water-soluble ions showed no temporal pattern in our study. Two-way ANOVA was used to reveal the effects of Sasa and deer (presence and absence) on total C and N contents and biomass C at each sampling date. NH_4^+ concentrations were tested only for the 1997 and 1998 data.

Results

Aboveground biomass of Sasa

Sasa biomass differed significantly between experimental plots for all sampling times except May 1998(F = 2.984, p = 0.096). The differences were especially remarkable in Oct. 1998 and Sep. 1999 (F = 4.415, p = 0.041 in May 1997; F = 10.604, p = 0.004 in Oct. 1998; F = 9.747, p = 0.005 in Sep. 1999). The Sasa biomass in the D0S1 plots increased 2.7-fold by autumn 1998 and 5.5-fold by autumn 1999 (Fig. 3). The Sasa biomass in the D1S1 plots did not differ significantly from the biomass in the D0S0 and D1S0 plots.

Water-soluble ion concentrations

In average concentration, NO_3^- was highest (0.060 –0.102 cmol /kg) among anions, and NH_4^+ was highest (0.056–0.158 cmol /kg) and Mg^{2+} was lowest (<0.0082 cmol /kg) among cations (Figs. 4, 5). In spring, neither deer exclusion nor Sasa removal was found to affect any ion (Table 1). In autumn, the effect of Sasa removal was significant for NO_3^-, Ca^{2+}, and Mg^{2+}, all of which had higher concentrations in the S0 plots (Figs. 5; Table 1). Deer exclusion had a significant effect on the concentrations of NH_4^+, Ca^{2+}, and Mg^{2+} (Fig. 5, Table 1). Opposite effects were found for different ions: the concentrations of NH_4^+ were higher in the D0 plots, but the concentrations of Ca^{2+} and Mg^{2+} were higher in the D1 plots. Significant interactive effects between Sasa removal and deer exclusion were not found.

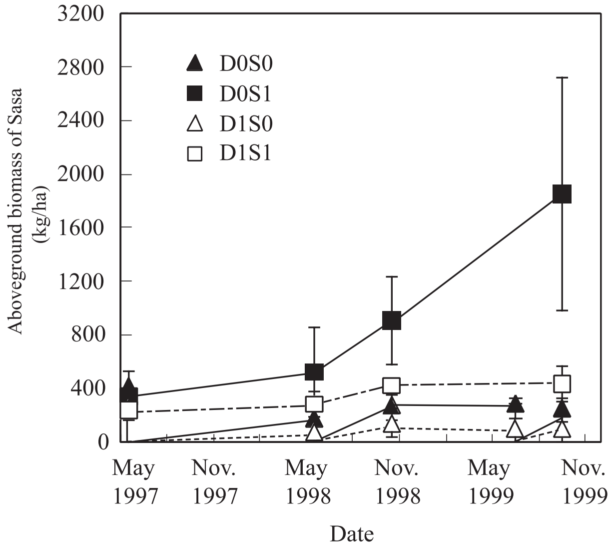

Fig. 3. Temporal changes in mean aboveground biomass of *Sasa nipponica* in each experimental plot (n = 3). D = deer, S = Sasa, 0 = removal or exclusion, 1 = control. Values were measured in May 1997 before the experiment started, and values in May of 1998 and 1999 were measured before the Sasa removal. Vertical bars indicate SD.

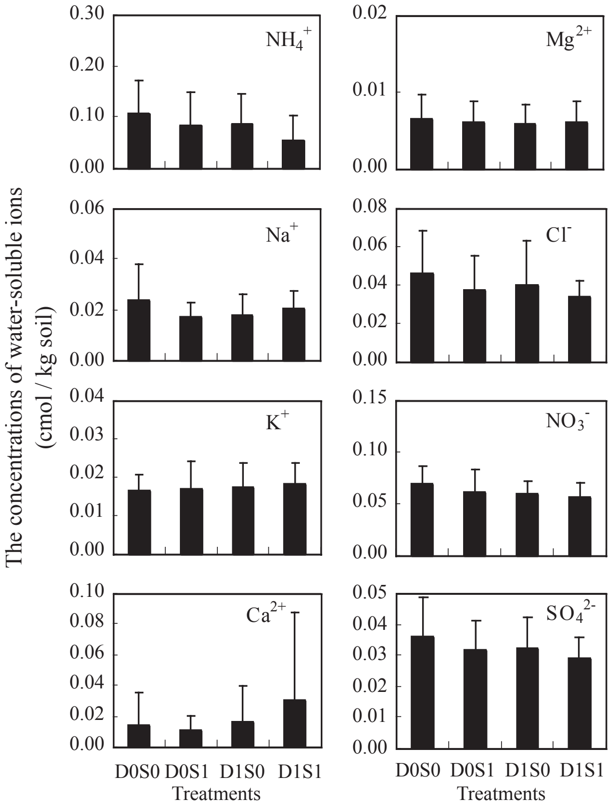

Fig. 4. The concentrations of water-soluble ions in each experimental plot in the spring (n = 18). D = deer, S = Sasa, 0 = removal or exclusion, 1 = control. Vertical bars indicate SD.

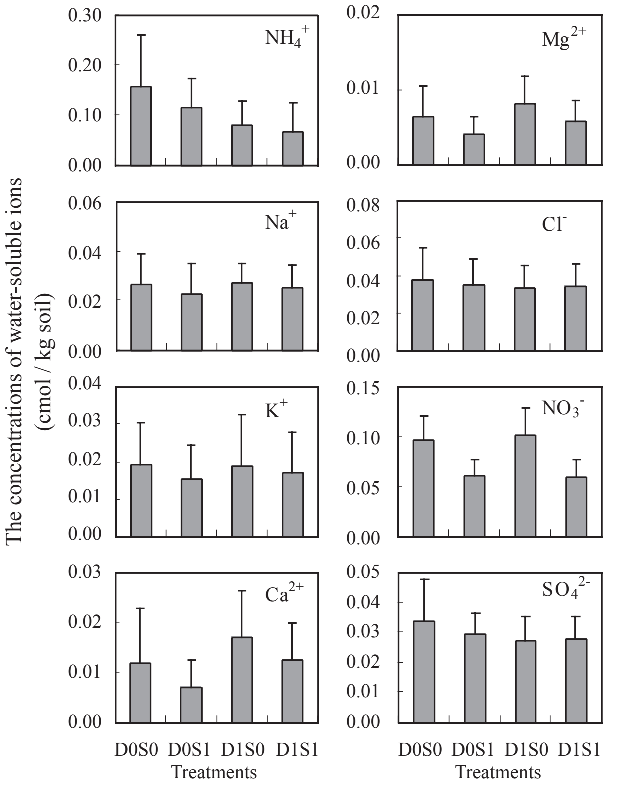

Fig. 5. The concentrations of water-soluble ions in each experimental plot in the autumn (n = 12 for NH_4^+, n = 18 for the others). D = deer, S = Sasa, 0 = removal or exclusion, 1 = control. Vertical bars indicate SD.

Table 1. Two-way ANOVA results for the effects of experimental removal of Sasa (d.f. = 1) or exclusion of deer (d. f. = 1) on concentrations of water-soluble ions in the spring and autumn (n=18 except for NH_4^+ in autumn, for which n=12).

Ion	Sasa		Deer		Sasa × Deer	
	F	*p*	*F*	*p*	*F*	*p*
Spring						
Cl^-	2.514	0.118	1.219	0.274	0.157	0.693
NO_3^-	1.922	0.170	3.476	0.067	0.317	0.575
SO_4^{2-}	2.106	0.151	1.887	0.174	0.065	0.800
NH_4^+	3.632	0.061	3.066	0.084	0.135	0.715
Na^+	0.782	0.380	0.335	0.565	3.366	0.071
K^+	0.309	0.580	0.637	0.428	0.029	0.865
Ca^{2+}	0.556	0.458	2.069	0.155	1.327	0.254
Mg^{2+}	0.005	0.946	0.372	0.544	0.173	0.679
Autumn						
Cl^-	0.048	0.827	0.616	0.435	0.224	0.638
NO_3^-	55.468	<0.0001	0.179	0.673	0.532	0.468
SO_4^{2-}	0.823	0.367	3.041	0.086	1.342	0.251
NH_4^+	1.734	0.195	9.773	0.003	0.509	0.480
Na^+	1.121	0.293	0.339	0.562	0.228	0.635
K^+	1.059	0.307	0.034	0.855	0.118	0.732
Ca^{2+}	5.935	0.018	7.349	0.009	0.008	0.931
Mg^{2+}	9.821	0.003	5.071	0.028	0.003	0.959

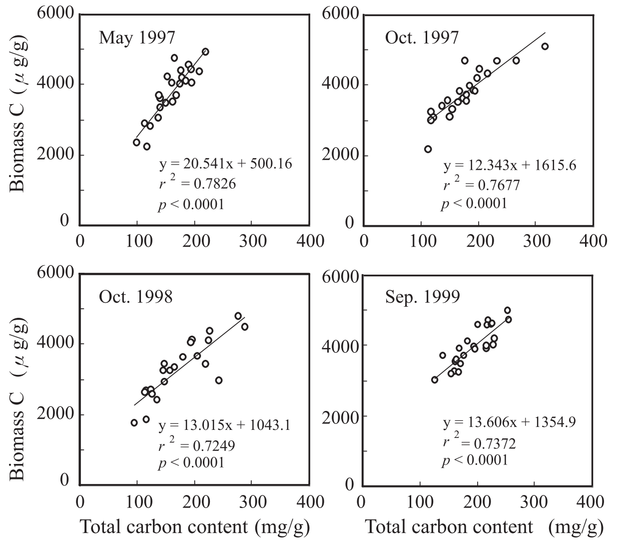

Fig. 6. The relationship between total carbon content and microbial biomass C in the soil at each sampling date.

Total C, total N, and biomass C in soil

The total carbon and total nitrogen contents in the soil are shown in Table 2. The initial values of both total C and total N in the S0 plots were larger than those in the S1 plots (total C: F = 12.503, p = 0.002, d.f. = 5; total N: F = 11.762, p = 0.003, d.f. = 5). Neither Sasa removal nor deer exclusion had a significant effect on total C or total N, except the initial values for Sasa removal. Total C contents in soil ranged from 136.9 to 224.9 mg /g and total N contents ranged from 10.3 to 15.1 mg /g across all plots. There was no significant trend in the temporal variations in either C or N content over the 3-year period.

Biomass C ranged from 2750 to 4310 μ g /g soil in all plots (Table 2). Neither removal of Sasa nor exclusion of deer had a significant effect on biomass C, except the initial values for Sasa removal in May 1997 (F = 8.425, p = 0.009). Biomass C was highly correlated with total soil C at all measurement times (Fig. 6). The ratios of biomass C to total C ranged from 1.24% to 2.89% in all plots. Neither deer exclusion nor Sasa removal affected these ratios.

Discussion

Water-soluble ion concentrations

Sasa removal increased the concentrations of NO_3^-, Ca^{2+} and Mg^{2+}. This result indicates that the decrease in absorption by Sasa due to Sasa removal may increase these nutrients in soil water. Although rainwater is expected to leach Ca and Mg (and K) into the soil from living Sasa plants (Takamatsu et al. 1997), we can neglect these leached ions because of the prompt re-absorption by the roots of Sasa itself.

The responses to deer grazing differed among soluble nutrients in soil. Deer exclusion increased NH_4^+ concentrations but decreased Ca^{2+} and Mg^{2+} concentrations. As Sasa biomass increases, more dead tissues are supplied to forest soil for nitrogen

Table 2. Mean (SD in parentheses, n=6) of total carbon content (mg/g) , total nitrogen content (mg/g) and microbial biomass C (μ g/g) in soil in each experimental plot. D = deer, S = Sasa, 0 = removal or exclusion, 1= control.

Date	Experimental plot			
	D0S0	D0S1	D1S0	D1S1
Total carbon content (mg/g)				
May 1997	179.6 (24.5)	143.7 (33.3)	176.8 (26.6)	136.9 (18.6)
Oct. 1997	224.9 (57.1)	171.8 (36.5)	160.7 (22.8)	150.3 (36.7)
Oct. 1998	221.7 (99.5)	175.3 (50.8)	185.9 (37.5)	163.1 (76.1)
Sep. 1999	190.0 (30.0)	192.7 (40.0)	170.8 (33.2)	220.5 (22.7)
Total nitrogen content (mg/g)				
May 1997	12.8 (1.4)	10.3 (2.1)	12.3 (1.6)	10.3 (1.3)
Oct. 1997	15.1 (3.0)	11.8 (2.3)	11.3 (1.4)	10.7 (2.0)
Oct. 1998	14.5 (5.3)	11.6 (2.7)	12.6 (2.0)	10.9 (4.2)
Sep. 1999	12.8 (1.6)	12.7 (2.4)	11.9 (1.7)	14.3 (1.4)
Microbial biomass C (μ g/g)				
May 1997	4300 (490)	3320 (820)	4050 (630)	3460 (590)
Oct. 1997	4300 (620)	3550 (790)	3700 (440)	3650 (670)
Oct. 1998	4260 (1350)	3110 (450)	3710 (660)	2750 (1120)
Sep. 1999	4180 (520)	3820 (690)	3640 (350)	4310 (430)

mineralization. Owing to this mechanism, deer exclusion may have increased NH_4^+ concentrations in soil. In contrast, the reason why no effect of deer grazing was found on NO_3^- may be that the effects of both N absorption and N supply by Sasa litter offset each other in the deer exclusion plots. The difference in the effect of N from Sasa between NH_4^+ and NO_3^- is indicated by another experiment showing that Sasa removal had a negative effect on ammonification but no effect on nitrification of soil (Furusawa et al. submitted).

Another mechanism is needed to explain the decrease in Ca^{2+} and Mg^{2+} in the deer exclosures. We have 2 possible explanations. One is increased absorption by Sasa, the biomass of which was increased by deer exclusion. The second possibility is the lack of excretion of feces and urine by deer. Although nutrients in excreta are not evenly returned to the pasture but are applied in small areas at very high concentrations (Haynes and Williams 1993), deer feces may spread wider than cow dung (Williams and Haynes 1995). The feces are the main excretory pathway for Ca and Mg (Williams and Haynes 1995), and the Ca and Mg contents of feces are usually in the range of 1.2%–2.5% and 0.3%–0.8%, respectively (Hutton et al. 1965; Hutton et al. 1967; Weeda 1977; Hogg 1981). The release of Ca and Mg is much slower than that of K owing to the lower proportion of water-soluble Ca and Mg present in dung (Weeda 1977). This slow decomposition may lead to continuous supply of Ca and Mg to soil.

No effects of either Sasa removal or deer exclusion were found on Cl^-, SO_4^{2-}, Na^+, or K^+. Because plants do not require much Cl^-, SO_4^{2-}, and Na^+ compared with N and Ca (Kumazawa 1995), the effect of uptake by Sasa was perhaps small for these ions. However, K^+ is an essential nutrient for plants. Because monovalent cations are adsorbed less than bivalent cations onto soil particles, K^+ may leach out owing to the high precipitation at Ohdaigahara.

We also have to explain why effects of Sasa removal and deer exclusion were found in autumn but not in spring in the Ohdaigahara forest. In early May, Sasa starts the first flush of new leaves and culms, and casts off the old ones (Takatsuki 1992; Yokoyama and Shibata 1998b). Nutrient absorption by Sasa and decomposition of dead tissues must continue to influence soil nutrients from spring to autumn. As a result, the effects of Sasa removal and deer grazing will be detected most strongly in autumn. Sasa would lower its activity under deep snow during the winter. From late winter to early spring, however, nutrients in soil will leach out with snowmelt water. Consequently, the accumulated effects of Sasa removal and deer grazing on soil nutrients may disappear in spring. The effect of snowmelt water on soil nutrients has been indicated in Hazlett et al. (1992) and Johnson (1995).

Total C, total N, and biomass C in soil

We expected that the contents of biomass C would be higher in the S1 plots than in the S0 plots because dead tissues of Sasa were supplied to the forest soil. However, unlike with the water-soluble ions, we found no effects of either Sasa or deer on biomass C over the 3 years. Because biomass C is strongly correlated with total C in soil, it may also take a long time for a significant change to be detected in biomass C, as well as in a total soil C. Kieft (1994) reported that biomass C did not change in a pasture that had been ungrazed for 16 years. Biomass C is also affected by soil microclimate conditions. For example, biomass C is low in soils with low moisture (Chang et al. 1995; Taylor et al. 1999) such as occur in forest floors densely covered with undergrowth. The soil in the D0S1 plots was drier than that in the other plots in this study area (Furusawa et al. 2001). Both decreasing moisture and increasing C supply may offset the effect of Sasa's biomass increase on biomass C. This may be one of the reasons why we could not find any effect on biomass C over the 3 years.

Likewise, we found no effect of either Sasa removal or deer grazing on total C and total N contents. A possible reason for the results is that the aboveground biomass of Sasa at Ohdaigahara may be too small to supply sufficient organic materials to show up the effects of either Sasa or deer. Aboveground biomass in Sasa grasslands has been measured at 7700–8800 kg /ha (Oshima 1961) and 6400–8600 kg /ha (Kawahara et al. 1977). Kawahara and Tadaki (1978) suggested that the aboveground biomass of Sasa is halved in forests with 20% relative light intensity at the forest floor; thus, Sasa biomass in forests is expected to be 3200–4400 kg /ha. In our experiment, the biomass of Sasa reached 1850 kg /ha in the D0S1 plots over 3 years. Nevertheless, some research has suggested that long-term exclusion of herbivorous mammals has no significant effect on these contents (7 years, Ritchie et al. 1998; >35 years, Tracy and Frank 1998; 50 years, Berg et al. 1997).

Total soil C contents, N contents, and biomass C may be stable for the short duration (3 years) of the change of Sasa aboveground biomass or deer exclusion. However, because we can expect that Sasa will grow further, longer-term experiments may detect the effects of deer exclusion on them. We need to monitor long-term effects of Sasa and deer by continuing this experimental survey.

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大台ヶ原の森林における土壌の化学性と微生物バイオマスにおよぼすミヤコザサ（*Sasa nipponica*）とニホンジカ (*Cervus nippon centralis*) の影響

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要 旨

大台ヶ原山ではニホンジカ (*Cervus nippon centralis* Temminck、以下シカという) の個体数密度が高く、林床に優占するミヤコザサ（*Sasa nipponica* Makino et Shibata、以下ササと呼ぶ）はシカの主食になっている。我々は，大台ケ原においてシカを排除したプロット，およびササ刈りを行ったプロットを設定して，ミヤコザサとニホンジカが土壌の化学性および微生物バイオマスにおよぼす影響について３年間調査を行った。ササ地上部現存量はシカを排除した区では３年後には初期値の5.5倍に増加した。ササ刈り区では非ササ刈り区に比べて水溶性の NO_3^-，Ca^{2+}，Mg^{2+} が増加することが認められた。これはササによる養分吸収が減少したためと考えられた。シカ排除区では非シカ排除区より NH_4^+ 濃度が高かった一方、Ca^{2+}，Mg^{2+} 濃度は非シカ排除区より低かった。これはササが採食されないためにササリターの供給が多くなったことによって引き起こされたと推察された。３年の試験期間では土壌の炭素，窒素含有率、微生物バイオマス C にはササ、シカ処理の影響は認められなかった。土壌の炭素，窒素含有率および微生物バイオマス C は、ササの地上部現存量の増減やシカの有無に関わらず短期的には安定であると考えられた。

キーワード：水溶性イオン、全炭素含有率、全窒素含有率、ニホンジカ（*Cervus nippon centralis*）、排除試験、微生物バイオマス C、ミヤコザサ（*Sasa nipponica*）

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