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Dwarf bamboo as an ecological filter for forest regeneration

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Abstract Quantitative relationships between the above-ground biomass of dwarf bamboo, *Sasa nipponica*, and the survivorship and emergence of seedlings of *Abies homolepis*, *Fraxinus lanuginosa* f. *serrata*, and *Fagus crenata* were estimated. We show that dwarf bamboo acts as an ecological filter since the responses of tree species differ according to the biomass of dwarf bamboo. Deer exclusion without management of dwarf bamboo would make it impossible for any tree species to regenerate due to rapid increases in the biomass of dwarf bamboo.

Keywords *Abies homolepis* · *Fagus crenata* · *Fraxinus lanuginosa* f. *serrata* · *Sasa nipponica* · Tree seedlings

Introduction

George and Bazzaz (1999a) pointed out that the fern understory modifies the forest floor microenvironment and that it differentially influences tree-seedling species emergence and establishment. They described the function of it as “a selective filter that influences future forest composition through reducing density, altering species composition, and determining spatial distribution of the seedling bank.” This selectivity was due to a differential response of tree-seedling species to the fern understory, which affects not only emergence and establishment, but also seedling growth and survival (George and Bazzaz 1999b). They suggested that the fern understory acts as an “ecological filter.” In addition to fern, Lei et al. (2002) reported on another understory plant, the evergreen understory shrub *Rhododendron*

maximum L., the effects of which differ depending on the degree of shade tolerance of tree seedlings.

Besides the studies described above, it is well-known that some understory plants can inhibit the emergence, establishment, and survival of tree seedlings in forests (Cross 1981; Maguire and Forman 1983; Smith and Vankat 1991). In East Asia, many studies have shown that dwarf bamboos typically act in this way (Nakashizuka and Numata 1982; Nakashizuka 1987, 1988; Taylor and Qin 1988; Hiura et al. 1995; Taylor et al. 2004). However, most previous studies have investigated the responses of tree seedlings to the presence or absence of understory plants, rather than developing quantitative relationships between seedling performance and the abundance of the understory plants.

Sasa nipponica Makino et Shibata, a species of dwarf bamboo that can dominate forest understories, is also known to be an important forage for sika deer (*Cervus nippon* Temminck) in Japan (Takatsuki 1983, 1986, 1990; Yokoyama and Shibata 1998a). In previous papers, we reported the results from a nine-year field experiment that combined exclusion of browsing by sika deer and the removal of *S. nipponica* in a mixed forest in an area with large deer populations (Itô and Hino 2004, 2005). These studies revealed that (1) dwarf bamboo quickly recovered its biomass after the exclusion of deer, (2) increasing the biomass of dwarf bamboo decreased the survivorship of tree seedlings, and (3) the magnitude of the negative impact on the seedlings differed among tree species. These findings suggest that *S. nipponica* works as an ecological filter. However, we have not previously documented the effects of the bamboo biomass on seedling survival, even though the bamboo biomass varied among plots or among years.

Exclosures are widely used to protect vegetation from deer grazing pressure. However, deer can act as a “keystone herbivore” (Waller and Alverson 1997; Rooney 2001), and exclusion of deer may cause other effects on the ecosystem, such as the dominance of dwarf bamboo, which suppresses seedlings of tree species, as described above. Therefore, not only exclusion of deer

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but also control of dwarf bamboo will be required for smooth tree regeneration. From this perspective, it is important to know the quantitative relationships between the abundance of dwarf bamboo and the emergence/survival of tree seedlings.

In this paper, we report on the results from a study that estimated the effect of aboveground biomass of *S. nipponica* on the survival rate of seedlings and on the number of emerging seedlings of three major species in the forest: *Abies homolepis* Sieb. et Zucc., *Fraxinus lanuginosa* Koidz. f. *serrata* (Nakai) Murata, and *Fagus crenata* Blume. Based on these relationships, we discuss quantitatively how dwarf bamboo works as an ecological filter, and the implications of this for forest restoration in areas with excessively large deer populations.

Methods

Study site

The study site was located in a temperate mixed forest on Mt. Ōdaigahara, in Nara Prefecture of west-central Japan (lat. 34°11'N, long. 136°06'E, 1,540 m a.s.l.). The forest on the site consisted mainly of evergreen coniferous trees such as *Abies homolepis* and deciduous broadleaved trees such as *Fagus crenata* (Itô and Hino 2003). The forest floor was extensively covered with *S. nipponica*, but its aboveground biomass was kept at relatively low levels by deer browsing (Yokoyama and Shibata 1998b). The population density of the deer around the study site was estimated at 22.3–34.1 individuals/km² (Maeji et al. 1999).

Species to be studied

Statistical analysis was conducted for the three major regenerating tree species (*A. homolepis*, *F. lanuginosa* f. *serrata*, and *F. crenata*). These species had a sufficient number of emerging seedlings (Itô and Hino 2005). *A. homolepis* and *F. crenata* were the two dominant tree species in the study site (Itô and Hino 2003). It is said that *Abies* is more shade-tolerant than *Fagus* at the sapling stage, though *F. crenata* seedlings can establish on thick litter, while *A. homolepis* seedlings do not seem to be able to do this (Nakashizuka 1991). *F. lanuginosa* is a shade-tolerant species (Koike 1986), and Wada (1993) showed that the sapling density of this species was not significantly correlated with the coverage of dwarf bamboo.

Data collection

We established five experimental plots in 1996; each plot was a square of 20 × 20 m. We divided each plot into eight subplots corresponding to eight different

experimental treatments based on combinations of the presence or absence of deer, mice, and dwarf bamboo: deer exclusion or control-mice exclusion or control-dwarf bamboo clipping or control (Table 1). Two 1 × 1 m quadrats were established within each subplot to monitor the emergence and disappearance of tree seedlings. Details of the study plots are described in Itô and Hino (2004, 2005). In 1999, we established an additional plot (10 × 10 m) to make the sample size larger. It contained eight 1 × 1 m quadrats corresponding to each of the eight treatments. The total number of quadrats was initially 80, and this increased to 88 in 1999 due to the eight additional quadrats. In the present paper, however, we have only used the data from the deer-exclusion quadrats to isolate the effects of dwarf bamboo, and we have not distinguished between the exclusion or presence of mice because our previous studies showed insignificant effects of mice on seedling survival (Itô and Hino 2004, 2005). As a result, we used data from 40 quadrats (1997–1999) or 44 quadrats (2000–2004).

We began monitoring the seedlings in the initial 80 quadrats in 1997, and in the eight supplemental quadrats in 2000. We marked all tree seedlings that emerged in the 1 × 1 m quadrats from 1997 to 2003 and checked their status (alive or dead) every 0.5–2 months from 1997 to 2004, except during the winter when the plots were under snow cover.

The abundance of *S. nipponica* was estimated from the aboveground parts of this plant every fall from 1997 to 2003 in each subplot where the dwarf bamboo had not been removed. Six sample plots covering a circle of

Table 1 The composition of each experimental set-up, and the combination of treatments in each plot

Plots	Start year	Number of treatments	Number of 1 × 1 m quadrats in each treatment
A	1997	8	2
B	1997	8	2
C	1997	8	2
D	1997	8	2
E	1997	8	2
F	2000	8	1

Treatments in each plot			
	Deer	Mice	Dwarf bamboo
1	Exclusion	Exclusion	Removal
2	Exclusion	Exclusion	Control
3	Exclusion	Control	Removal
4	Exclusion	Control	Control
5	Control	Exclusion	Removal
6	Control	Exclusion	Control
7	Control	Control	Removal
8	Control	Control	Control

The number of 1 × 1 m quadrats was 80 (5 plots × 8 treatments × 2 replications) from 1997 to 1999, and 88 (5 plots × 8 treatments × 2 replications + 1 plot × 8 treatments × 1 replication) after 2000

radius 10 cm were randomly selected within each subplot. In each sampling plot, the *S. nipponica* plants were clipped at ground level, and the dry weights of these samples were measured. The biomass value for each plot is represented by the mean of the six samples.

Statistical analysis

We developed a statistical model to explain the relationship between seedling survival and the biomass of the dwarf bamboo using a generalized linear mixed model (GLMM) approach:

$$\log\left(\frac{p_{ijk}}{1-p_{ijk}}\right) = \beta + \beta_w w_{ijk} + \beta_a a_{ijk} + \omega_i + \omega_j + \varepsilon_{ijk} \quad (1)$$

where i is the plot number, j is the cohort number, k is the individual number, p_{ijk} is the probability of survival, w_{ijk} is the aboveground biomass of the dwarf bamboo (kg d.w./m²) where the seedling is located, and a_{ijk} is the age of the seedling (years). β_w and β_a are fixed effect coefficients for w and a , respectively, and β is the intercept. ω_i and ω_j correspond to the random effects of the i th plot and j th cohort, respectively. ε_{ijk} is the individual error factor for a given individual, cohort, and plot. Equation 1 can be transformed into

$$p = \frac{1}{1 + \exp[-f(w, a)]} \quad (2)$$

where $f(w, a)$ is the linear predictor.

In this analysis, we defined survival and death based on whether a seedling that emerged in or survived until a given year was found alive or dead, respectively, in the next spring. We used the value of the aboveground biomass of the dwarf bamboo in the plot corresponding to the treatment and the plot in the year when survival was assessed. This analysis was conducted for each tree species using the lmer function provided by the Matrix package for the R software package (version 2.2.1; R Development Core Team 2005) with Laplace's approximation method. The number of seedlings of *Fagus crenata* was only high enough to use this analysis in 1999, so we used only this cohort and did not allocate a random cohort factor to the analysis of this species.

We then analyzed the relationships between the aboveground biomass of dwarf bamboo and the number of emerging seedlings for cohorts that emerged in 2002 for *A. homolepis* and *F. lanuginosa* f. *serrata*. There were not enough *Fagus crenata* seedlings to emerge after 1999 to permit this analysis. A GLMM procedure with a logarithmic link function and a Poisson error distribution was used for this analysis. For both species, the number of seedlings that emerged in 2002 was used as the dependent variable, and the aboveground biomass of the dwarf bamboo was used as the independent variable. The differences between plots were allocated to the random factor, which only affected the intercept.

Results and discussion

In the 40 quadrats in the deer-exclusion plots established in 1997, the aboveground biomass of *S. nipponica* increased from an average of 0.09 kg/m² (range 0.07–0.12) in 1997 to 0.65 kg/m² (range 0.40–0.87) in 2003. This large change and the interplot variation in dwarf bamboo biomass caused differential survival of the tree seedlings and enabled us to analyze these relationships for each tree species and age class. Table 2 shows the sample sizes for each cohort and each species.

For all three-tree species, increasing the biomass of the dwarf bamboo decreased the seedling survival (Fig. 1), and the fixed-effect coefficients differed significantly from zero (Table 3). The more dense the dwarf bamboo, the more severely it shaded the forest floor (Itô and Hino 2004). Differences in shade tolerance among the tree species might thus explain their different responses to bamboo biomass. The fixed-effect coefficients for age also differed significantly from zero for *A. homolepis* and *F. lanuginosa*. The positive values for this coefficient mean that survival improved with increasing seedling age, and the ratio of these two coefficients was about 1/10. This meant that one year of seedling growth could compensate for 0.1 kg/m² of aboveground biomass of *Sasa*.

Of the three species, the survival of the *F. crenata* seedlings was affected most strongly by dwarf bamboo. The survival curve for this species decreased more steeply than those for the other two species in Fig. 1 (i.e.,

Table 2 Sample sizes of each cohort and each species

Age	Cohort						
	1997	1998	1999	2000	2001	2002	2003
<i>Abies homolepis</i>							
0	546	47	3	1	0	124	0
1	345	30	3	1	0	69	
2	189	18	2	0	0		
3	124	15	2	0			
4	91	15	1				
5	80	13					
6	56						
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>							
0	8	217	4	11	3	158	2
1	6	160	2	10	2	106	
2	5	138	1	10	2		
3	5	115	1	10			
4	4	107	1				
5	4	105					
6	4						
<i>Fagus crenata</i> ^a							
0			78				
1			42				
2			36				
3			35				
4			34				

^aOnly the cohort which emerged in 1999 was used because none of the other cohorts had sufficient numbers of seedlings

Fig. 1a–c Estimated relationships between the aboveground biomass of dwarf bamboo (*Sasa nipponica*) and seedling survival in each age class. **a** *Abies homolepis*, **b** *Fraxinus lanuginosa* f. *serrata*, and **c** *Fagus crenata*. Curves for age classes are not shown for *F. crenata* because age was not a statistically significant parameter (see Table 3)

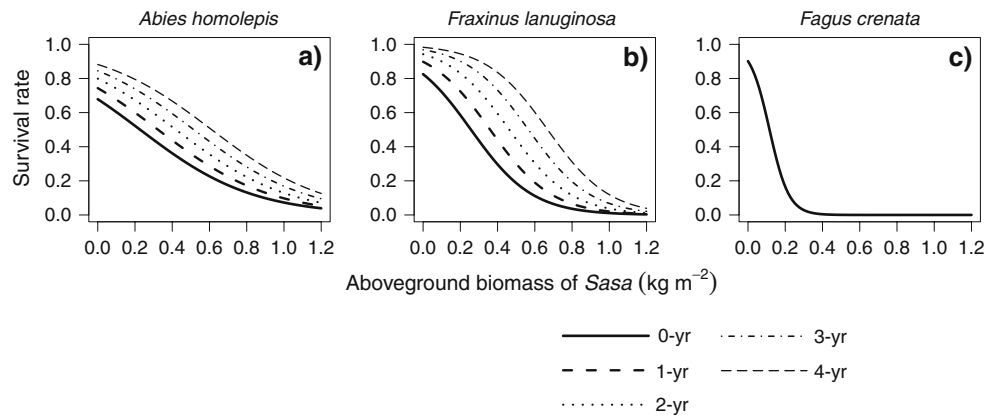


Table 3 Intercepts and coefficients of fixed effects estimated using the generalized linear mixed model approach to the seedling survival of *Abies homolepis*, *Fraxinus lanuginosa* f. *serrata*, and *Fagus crenata*

	Intercept	Coefficient		AIC
		Dwarf bamboo	Age	
<i>Abies homolepis</i>	0.751 (\pm 0.154)	−3.30*** (\pm 0.350)	0.317*** (\pm 0.039)	2124.5
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>	1.56 (\pm 0.193)	−6.07*** (\pm 0.527)	0.624*** (\pm 0.085)	765.9
<i>Fagus crenata</i>	2.19 (\pm 0.447)	−19.5*** (\pm 3.84)	0.434 ^{ns} (\pm 0.250)	105.2

Numbers in parentheses are standard errors for the estimated values. AIC values provided are approximations. Significance levels: *ns*, not significant; *** $P < 0.001$

survival decreased most rapidly with increasing dwarf bamboo biomass). Specifically, an estimated 89.9% of seedlings of *F. crenata* would survive for one year if all dwarf bamboo was removed ($1/[1 + \exp(-2.19 + 19.5 \times 0)] = 0.899$). However, only 0.05% were estimated to survive at a biomass of 0.5 kg/m², which was the minimum biomass attained by the dwarf bamboo in the deer-exclusion plots. At a typical dwarf bamboo biomass of 0.1 kg d.w./m², and in the presence of deer foraging at our study site, 56.0% were estimated to survive. This survival rate is comparable to that of 0–1 year seedlings of *F. crenata* in the bright location after the simultaneous death of dwarf bamboo (59.4%; Nakashizuka 1988). However, if the dwarf bamboo was to grow to 0.2 kg d.w./m² (double the current natural state), the survival rate would decrease to 15.3%.

Dwarf bamboo had the least effect on seedling survival of the coniferous species *A. homolepis*, which had the most gently sloping curve in Fig. 1. The survival rate for seedlings younger than one year with complete removal of dwarf bamboo was 67.9%. While this was lower than that of *F. crenata* (Fig. 1), they survived better for a higher density of dwarf bamboo. An estimated 28.9% of *A. homolepis* seedlings younger than one year would survive to the following year, even at 0.5 kg d.w./m² of dwarf bamboo biomass, versus a value of ~0% for *F. crenata*. The estimated 52.3% survivorship at a dwarf bamboo biomass of 0.2 kg d.w./m² is also much higher than that for *F. crenata* (15.3%). This survival rate indicates that the capacity for regeneration

in this species is as strong as the value reported for *F. crenata* by Nakashizuka (1988) under the condition of simultaneous death of dwarf bamboo, but this would not require complete elimination of dwarf bamboo.

Fraxinus lanuginosa f. *serrata* had survivorship curves with slopes that were intermediate between those of the other two species (Fig. 1). For this species, an estimated 82.6% of the seedlings younger than one year would survive in plots where dwarf bamboo was removed, and 18.6% would survive at 0.5 kg d.w./m² of dwarf bamboo biomass. The estimated survival rate for seedlings younger than one year at a dwarf bamboo biomass of 0.2 kg d.w./m² is 58.5%, which is equivalent to that of *A. homolepis*.

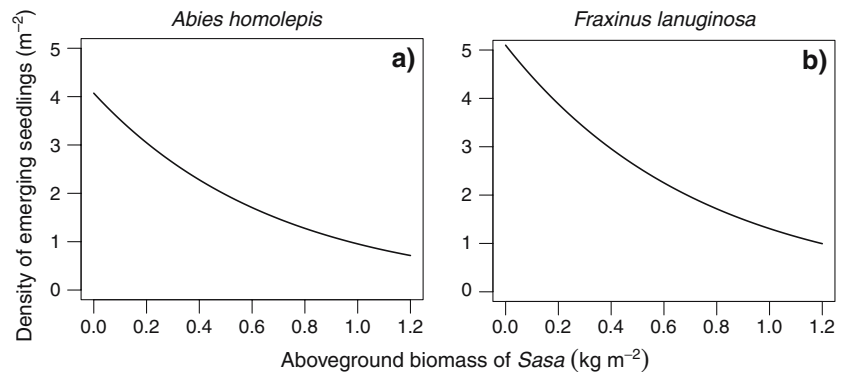
Increasing aboveground biomass of the dwarf bamboo also significantly decreased the number of emerging seedlings in *A. homolepis* and *F. lanuginosa* ($P < 0.001$; Table 4). When the aboveground biomass of dwarf bamboo reached 0.5 kg d.w./m², the number of emerging seedlings of *A. homolepis* was about half the natural level observed at the current dwarf bamboo biomass of 0.1 kg d.w./m² (Fig. 2; $\exp(-1.43 \times 0.5)/\exp(-1.43 \times 0.1) = 0.564$). *F. lanuginosa* revealed a similar relationship. Dense dwarf bamboo generates a large amount of litter, and increased litter is known to inhibit seed germination in many plant species (Xiong and Nilsson 1999). *S. nipponica* retains its aboveground parts for about 18–20 months (Agata and Kamata 1979), so an aboveground biomass of 0.5 kg d.w./m² for this plant contributes about 0.3–0.33 kg/m²/year of litter to the

Table 4 Intercepts and coefficients of fixed effects estimated using the generalized linear mixed model approach to the seedling emergence of *A. homolepis* and *F. lanuginosa* f. *serrata*

	Intercept	Coefficient Dwarf bamboo	AIC
<i>Abies homolepis</i>	1.34 (± 0.242)	-1.43 ^{***} (± 0.389)	62.1
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>	1.44 (± 0.276)	-1.42 ^{***} (± 0.282)	143.9

Numbers in parentheses are standard errors for the estimated values. AIC values provided are approximations. Significance levels: *ns*, not significant; ^{***} $P < 0.001$

Fig. 2a, b Estimated relationships between the aboveground biomass of dwarf bamboo (*Sasa nipponica*) and the number of emerging seedlings of **a** *Abies homolepis* and **b** *Fraxinus lanuginosa* f. *serrata*



forest floor. This value was larger than the amount of litter fall from trees in this site (0.2268 kg/m²/year; Furusawa et al. 2003). This additional supply of leaf litter may influence seedling emergence of the various tree species differently, though the responses of *A. homolepis* and *F. lanuginosa* were not so different.

In conclusion, dwarf bamboo appears to function as an ecological filter because different tree species responded differently to its biomass in terms of seedling emergence and survival. In addition, our quantitative analysis revealed some implications for forest restoration in areas with large deer populations. In many areas of Japan, including the Ôdaigahara region, large-scale deer exclosures have been established to prevent deer grazing from impeding forest restoration. However, this may lead to rapid growth of understory plants, often reaching densities that can adversely affect tree regeneration. In areas where *S. nipponica* dominates the forest floor, exclosure allows it to rapidly reach an aboveground biomass greater than 0.5 kg d.w./m². Our results indicate that this level of biomass would prevent *F. crenata* from regenerating and would greatly reduce seedling emergence and survival of *A. homolepis* and *F. lanuginosa*. If we assume that about 50% survival of seedlings is required for successful regeneration, dwarf bamboo biomass must be kept below 0.2 kg d.w./m² for *A. homolepis* and *F. lanuginosa* and below 0.1 kg d.w./m² for *F. crenata*. Accordingly, forest managers must somehow reduce the biomass or the area of *S. nipponica* where deer exclosures have been established. In forests where dwarf bamboo dominates the forest floor, excluding it from some parts of the forest floor will facilitate seedling establishment and forest regeneration. In addition, preserving suitable seedbeds such as fallen

logs for *Abies* species (Narukawa and Yamamoto 2002) and tip-up mounds for *F. crenata* (Peters et al. 1992) will also enhance seedling establishment.

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