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Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate *Sasa* grassland–deciduous forest series in southwestern Japan

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The effects of dwarf bamboo, *Sasa*, cover on the initial mortality of hardwood seedlings were investigated by transplanting 1-year-old beech (*Fagus crenata*) and current-year oak (*Quercus mongolica* var. *grosseserrata*) seedlings to three different stands; old-growth beech and secondary oak forests with *Sasa* undergrowth, and a *Sasa* grassland in a grassland–forest series near the top of Mt Jippo, southwestern Japan. The most frequent cause of seedling mortality was gnawing of the stems by rodents. In the beech forest, the gnawing was more likely to occur under *Sasa* cover, suggesting that it provides a good habitat for rodents on the beech forest floor. The *Sasa* undergrowth may thus play an important role in regeneration of beech forest. In the oak forest, mortality of both species was low and only a little gnawing occurred during a year. However, no natural oak seedlings were found in the forest even after a mast year. This may be because most of the acorns disappeared before establishment. The early-stage demography of hardwood seedlings such as oak may thus play an important role in regeneration of oak forest. In the *Sasa* grassland where the seed supply is small, almost all of the seedlings died from gnawing regardless of the presence of *Sasa* cover. These factors prevent the recruitment of a sizable seedling bank. Rodents may thus play an important role in maintenance of the *Sasa* grassland.

Key words: forest regeneration; gnawing; rodents; *Sasa*; seedling mortality.

INTRODUCTION

The effect of forest floor vegetation on the performance of tree seedlings is important in the regeneration process of forests (Maguire & Forman 1983; Nakagoshi & Wada 1990). Dwarf bamboo, *Sasa*, is a typical undergrowth vegetation type that could have an effect on forest dynamics; it occurs widely in beech forests in Japan (Shidei 1974). *Sasa* species flower and die simultaneously over a large area once in several decades. Because this natural phenomenon occurs rarely, the relationship between *Sasa* undergrowth and forest dynamics has never been fully understood despite the efforts of many researchers; few studies have investigated the regeneration process of *Sasa* species after their simultaneous death (Makita 1992; Makita *et al.* 1993) or the associated dynamics of beech (*Fagus crenata* Blume) seedlings (Nakashizuka 1988). In a beech forest with dense *Sasa* undergrowth, the absence of beech seedlings was attributed to the effect of shading by *Sasa* (Nakashizuka & Numata 1982). *Sasa* cover was also found to be one of the main causes inhibiting the establishment of hardwood seedlings in a *Sasa* grassland (Ida & Nakagoshi 1994). Hence, the simultaneous death of *Sasa* improves the survival rate of seedlings and a large seedling bank can be produced (Nakashizuka 1988).

Some studies describe factors affecting the mortality of hardwood tree seedlings, such as light deficiency, drought, fungal attack and herbivory (e.g. Nakashizuka 1988; Sahashi *et al.* 1994). These studies, however, did not analyse the mortality factors of the seedlings. Thus the processes leading to death of hardwood seedlings in temperate deciduous forests have not yet been revealed.

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We were concerned with diagnosis of the factors inhibiting the establishment and development of seedling populations of beech and oak (*Quercus mongolica* Fischer var. *grosseserrata* (Blume) Rehd. et Wils.) in different plant communities: old-growth beech and secondary oak forests with *Sasa* undergrowth, and a *Sasa* grassland. In the present study, effects of *Sasa* cover on the initial demography of seedlings were analysed through observations of the mortality process of transplanted seedlings of beech and oak. The patterns and processes of disappearance of these seedlings are discussed.

METHODS

Study area

Vegetation structure and population growth of beech and oak were investigated, focusing on the regeneration of a temperate deciduous forest in a beech forest–oak forest–*Sasa* grassland series located on a northwestern slope toward the ridge of Mt Jippo (34°34′N, 132°09′E, and 1318.9 m a.s.l.) in southwestern Japan. A transect 280 m long and 20 m wide was established from old-growth beech forest on a mountainside to grassland dominated by *Sasa palmata* (Marliac) Nakai on the ridge, through the secondary oak forest. It was divided into 14 quadrats of 20 × 20 m numbered from Q1 (beech forest) to Q14 (*Sasa* grassland). In previous papers (Ida & Nakagoshi 1993, 1994), formation of the zonation and forest regeneration in the *Sasa* grassland were discussed. It was concluded that the beech forest and the *Sasa* grassland had been maintained for at least 330 years. The oak forest, however, developed as a secondary forest, and the disturbance could be due to logging conducted more than 85 years ago.

The present study was performed in three quadrats: Q2 (beech forest), Q8 (oak forest) and Q12 (*Sasa* grassland). Table 1 shows the stand characteristics of these quadrats. From Q2 to Q12, the coverage in the canopy layer and the canopy tree size became gradually lower and smaller, respectively. Among the three quadrats tree density was the highest in Q8, although the total basal area in Q2 was about as much as that in Q8. Mean height of *S. palmata*, which densely developed on the forest floor, decreased from Q2 to Q12.

Table 1 Summary of the stand characteristics of the three quadrats

Quadrat	Q2	Q8	Q12
Coverage in canopy layer (%)	90	70	8
Maximum tree height (m)	18.6	9.8	3.1
Maximum d.b.h. (cm)	85.1	33.0	6.5
Number of stems (400 m^{-2})	32	140	19
Number of individuals (400 m^{-2})	20	77	8
Total basal area (m^2 per 400 m^2)	11.4	11.5	0.2
Mean height of *Sasa palmata* (cm)	200	150	70

Revised from Ida and Nakagoshi (1993, 1994).

Table 2 shows the relative density and relative basal area of each species of living stems larger than 2 cm in diameter at breast height (d.b.h.) in the three quadrats. The main tree species are *Fagus crenata* and *Magnolia obovata* Thunb. in the canopy layer and *Lindera umbellata* Thunb. in the shrub layer of Q2; *Quercus mongolica* var. *grosseserrata*, *Carpinus japonica* Blume, *Acer sieboldianum* Miq. and *Clethra barbinervis* Sieb. et Zucc. in the canopy layer and *C. barbinervis* and *Symplocos coreana* (Léveillé) Ohwi in the shrub layer of Q8. *Sasa* grassland (Q12) is dotted with oak sprouts and shrubs of other species.

There were few current-year to 3–4-year-old beech or oak seedlings in the study transect in 1992 when the present study was carried out. Some beech and oak saplings much older than 3–4 years occurred in the Q2–Q4 and Q7–Q14 areas, respectively (Ida & Nakagoshi 1994).

Transplanted seedlings

In July 1991 current-year beech seedlings whose cotyledons had fallen and primary leaves had appeared were collected at Mt Daisen, southwestern Japan. In October 1991 oak acorns were collected at Mt Hiba, southwestern Japan.

The seedlings and acorns were taken to the university campus in Hiroshima City and were planted singly in vinyl pots (10 cm diameter and 11 cm depth) containing decomposed granite soil and vermiculite. After germination only healthy seedlings were selected and used for this experiment.

Experimental plots

Before May 1992 two 3 × 2 m plots were set up in each of the Q2, Q8 and Q12 quadrats. To

Table 2 Relative density and relative basal area (BA) of each species of living stems (d.b.h. ⩾ 2 cm) in the three quadrats

Species	Q2 Density (%)	Q2 BA (%)	Q8 Density (%)	Q8 BA (%)	Q12 Density (%)	Q12 BA (%)
Acanthopanax sciadophylloides	6.3	4.5	—	—	5.3	1.4
Acer rufinerve	3.1	0.2	—	—	—	—
Acer sieboldianum	—	—	3.6	3.9	—	—
Betula grossa	6.3	0.2	1.4	0.4	—	—
Carpinus japonica	—	—	10.7	4.3	5.3	1.4
Clethra barbinervis	—	—	22.9	3.8	—	—
Corylus sieboldiana	—	—	3.6	0.2	—	—
Fagus crenata	6.3	77.4	0.7	0.1	—	—
Hydrangea paniculata	—	—	2.9	0.4	5.3	1.8
Lindera umbellata	15.6	0.2	—	—	—	—
Lyonia ovalifolia var. *elliptica*	—	—	—	—	31.6	28.6
Magnolia obovata	9.4	11.4	—	—	—	—
Pinus densiflora	—	—	—	—	5.3	1.6
Prunus grayana	3.1	<0.1	—	—	—	—
Pterostyrax corymbosa	3.1	<0.1	—	—	—	—
Quercus mongolica var. *grosseserrata*	—	—	35.7	83.2	26.3	42.2
Rhus trichocarpa	—	—	2.9	0.2	—	—
Sorbus alnifolia	—	—	1.4	2.1	—	—
Sorbus commixta	28.1	5.7	—	—	—	—
Symplocos coreana	9.4	0.1	10.7	0.8	—	—
Tilia japonica	—	—	3.6	0.4	21.1	23.0
Viburnum plicatum var. *tomentosum*	9.4	0.2	—	—	—	—

identify the effects of *Sasa* cover on the transplanted seedlings, all *Sasa* culms were cleared off in one plot of each quadrat (managed plot: M) in order to simulate the conditions after the simultaneous death of *Sasa*. Another plot was left in a natural condition (control plot: C). In the M plot, *Sasa* shoots were cut at the ground so that the surface of the plot was not shaded. The rootstock of *Sasa* was also cut beneath the ground surface as much as possible. Cut culms and leaves were left on the ground as litter. Subsequent *Sasa* shoots were cut off whenever they regenerated.

Seedling transplanting and recording mortalities

Healthy seedlings were removed from pots and transplanted after the soil had been removed from their roots. Initially 25 beech seedlings were transplanted on 8 June 1992 and then 25 more were transplanted on 1 July 1992 (50 individuals in total). Thirty oak seedlings were transplanted on 22 July 1992. The beech and oak seedlings were planted at 20 cm intervals in a 5 × 10 grid and in a 5 × 6 grid, respectively. Seedling survival and seedling damage was recorded every 3–4 weeks until December 1992 and once each in May and June 1993. The differences in the number of surviving seedlings was statistically tested using Fisher's Exact method for every recording period.

The factors affecting mortality of the seedlings were classified into four main types; (i) gnawing, (ii) standing dead, (iii) snapping and (iv) others. Death from gnawing was caused by rodents. The authors were able to judge that the agent was a rodent because the tooth scars left on the dead seedlings were very similar to ones left on hardwood seedlings gnawed by the breeding vole *Microtus montebelli* Milne-Edwards. Most of the gnawed seedlings were gnawed off near the ground surface. We captured four species of rodents in the study area; *Apodemus argenteus* Temminck, *Apodemus speciosus* Temminck, *Eothenomys smithi smithi* Thomas and *M. montebelli*. The standing dead seedlings may have been damaged by drying out or fungal attack (Augspurger 1990; Sahashi *et al.* 1994). Their leaves were wilted and the stems and buds were dry. Sahashi *et al.* (1994, 1995) suggested that the fungus *Colletotrichum dematium* (Pers. ex Fr.) Grove plays an important role in the disappearance of current-year beech seedlings. Death by fungal attack is usually characterized by softening and decaying of stems (Nakashizuka 1988), but such seedlings were not observed in our experiment. The snapped seedlings had their stems broken off near the ground surface. Death by physical causes such as litter fall or winter snowfall resulting in stem breakage was also classified as snapping. Other mortality was due to the disappearance of leaves and buds by insects and obscured factors.

RESULTS

The survivorship curves and the mortality factors of the beech seedlings are shown in Fig. 1 and Table 3. There was a significant difference between Q2C and

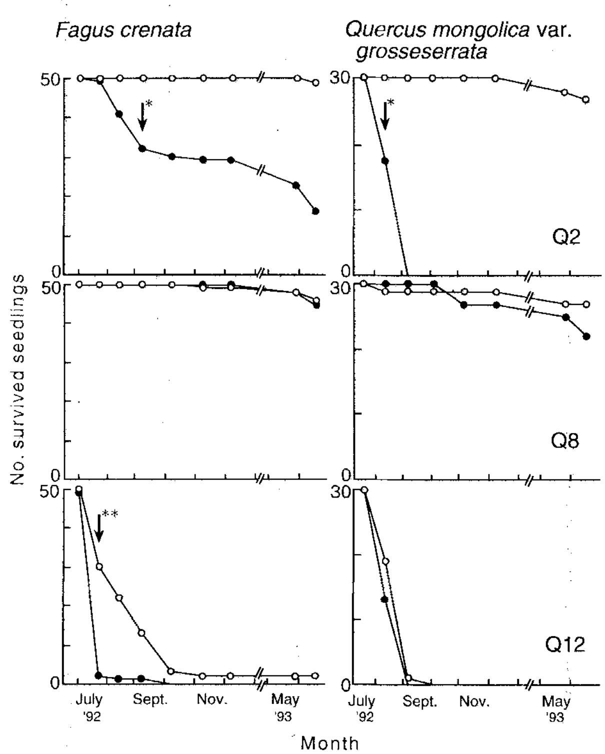

Fig. 1. Survivorship curves of the transplanted seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in the experimental plots: Q2, beech forest; Q8, oak forest; Q12, *Sasa* grassland. (●) Control plots (C); (○) managed plots (M). Arrows show the date when the seedling survivals in the two plots significantly differed (*$P < 0.01$, **$P < 0.001$, Fisher's Exact test).

Q2M in September 1992 ($P < 0.01$). In Q2C 21 individuals died before November 1992 due to gnawing of their stems by rodents. Figure 2 shows the tooth scars left by rodent gnawing on a beech seedling. Thirteen other individuals in Q2C died, eight were standing dead. There was no seedling death in Q2M in 1992. In Q8C and Q8M more than 90% of the seedlings survived and there was no significant difference between the two plots during the observation period. None of the individuals in Q8C and Q8M were damaged by rodents. In Q12C all the seedlings were killed by rodents before October 1992. Compared with Q12C, the survival rate of Q12M decreased more slowly, with 48 individuals killed before November 1992. There was already a significant difference between the two plots by late July 1992 ($P < 0.001$).

Figure 1 and Table 3 show the survivorship curves and mortality factors of the oak seedlings, respectively. In Q2C all of the seedlings died from gnawing by rodents before September 1992, while in Q2M no mortality was observed. The difference between the two plots was significant at $P < 0.01$ in August. The survival rate in Q2M before December 1992 was 100%; however, three individuals were damaged before June 1993 and two of them were standing dead. In Q8C two individuals died from rodent gnawing and one was damaged by snapping before December 1992. After that, four individuals were standing dead and one died by snapping. In Q8M one seedling was killed by rodent gnawing before December 1992 and two were standing dead. There was no significant difference in the seedling mortality between Q8C and Q8M during the observation period. In Q12C and Q12M, almost all individuals were damaged in the first 6 weeks after transplanting. There was no significant difference between treatments. One seedling was standing dead and all the others died from rodent gnawing.

DISCUSSION

Low survival rates of the beech and oak seedlings occurred in plots Q2C, Q12C and Q12M; most deaths could be ascribed to gnawing by rodents. There have been several studies investigating the relationship between small mammals and the regeneration of deciduous broad-leaved forests especially regarding dispersal and disappearance of acorns and

Table 3 Mortality factors and number of dead seedlings of *Fagus crenata* (n = 50) and *Quercus mongolica* var. *grosseserrata* (n = 30) in each plot during the observation period: July 1992–June 1993

Species	Plot	Mortality factor				Total
		Gnawing	Standing dead	Snapping	Other	
Fagus crenata	Q2C	21	8	—	5	34
	Q2M	—	—	—	1	1
	Q8C	—	3	1	1	5
	Q8M	—	2	1	1	4
	Q12C	50	—	—	—	50
	Q12M	46	2	—	—	48
Quercus mongolica	Q2C	30	—	—	—	30
var. *grosseserrata*	Q2M	—	2	—	1	3
	Q8C	2	4	2	—	8
	Q8M	1	2	—	—	3
	Q12C	30	—	—	—	30
	Q12M	29	1	—	—	30

C and M are the abbreviations for control and managed plots in the quadrats Q2, Q8 and Q12, respectively.

Fig. 2. A tooth impression left on a transplanted *Fagus crenata* seedling identified as being made by a rodent.

nuts by acorn-feeding rodents such as field mice (Kanazawa 1975; Kanazawa & Nishikata 1976; Jensen 1985; Kikuzawa 1988; Miyaki & Kikuzawa 1988). In general, caching and disappearance due to feeding on seeds by rodents affects forest dynamics (Shaw 1968; Jensen 1985; Kikuzawa 1988). However, there have been few reports about the effects of rodents on tree seedlings (e.g. Pigott 1985). At least four species of rodents were living in this study area; *A. argenteus, A. speciosus, E. smithi*, and *M. montebelli*. The herbivorous rodents *M. montebelli* and/or *E. smithi* may have been responsible for gnawing damage to the transplanted seedlings, as the tooth scars left on the seedlings were very similar to those of the breeding vole *M. montebelli*.

Sasa cover prevented the regeneration of beech and oak by providing suitable habitat to protect the small rodents which removed the zoochorous seeds from predators (Wada 1993). In the present study, it was found that the damage of seedlings by rodents was more likely to occur under the cover of *Sasa* than without *Sasa* cover in the beech forest. This suggests that *Sasa* cover provides a good habitat for rodents on the floor of the beech forest, and that the survival rate of tree seedlings would increase through decreased gnawing rodents if *Sasa* died. There is a similar prediction for beech seedlings (Nakashizuka 1988). Furthermore, beech seedlings were more vulnerable to fungal attack in shady than in sunny environments (Sahashi *et al.* 1994). Therefore, the *Sasa* undergrowth may play an important role in the regeneration of beech forest.

The survival rates of both beech and oak seedlings in the secondary oak forest were high; only a little gnawing damage to oak seedlings occurred. This suggests that the survival rate would be higher regardless of the presence of *Sasa* cover. However, there were no natural beech and oak seedlings in the oak forest. There were no beech seedlings due to the fact that the density of the reproductive beech population was very low. On the other hand, although a large acorn production was observed all through the oak forest in the autumns of 1990 and 1992, there were no recruited seedlings in the following springs. Most of the acorns on the ground are cached or removed within a few days and eventually eaten by the rodents before the following spring (Sork 1984; Miyaki & Kikuzawa 1988; Borchert *et al.* 1989). In this study area, almost all of the acorns disappear due to feeding by rodents and Japanese black bears (*Selenarctos thibetanus japonicus* Schlegel). This suggests that most of the acorns would disappear before seedling establishment. Therefore, the early stage demography of the hardwood seedlings such as oak will play an important role in the regeneration of oak forest.

Almost all the beech and oak seedlings in *Sasa* grassland died due to gnawing by rodents before the summer of the study year, although the survival rate of beech in Q12C decreased significantly more quickly than in Q12M. This suggests that rodents in *Sasa* grassland do not always appear only under *Sasa* cover. The gnawing damage by rodents, therefore, is one of the most important factors associated with the disappearance of the seedlings in the *Sasa* grassland. The effects of gnawing may depend on the probability of the rodents finding the seedling. If the rodents can find the seedlings, they will eat seedlings even in areas where there is no shading by *Sasa*. However, if the simultaneous death of *Sasa* occurs over a large area, the regeneration patterns of seedlings may be very different from those observed in the present study.

Acorn dispersal from the forest area by rodents, which are associated with acorn disappearance, or other agents is necessary for forest regeneration in *Sasa* grassland (Ida & Nakagoshi 1994). The seed supply, however, will apparently be less in *Sasa* grassland than in the forests even though mast production of the acorns occurs, because the spatial pattern of abundance of large and heavy seeds such as those of *Fagus* species was related to the position of reproductive trees (Houle 1992). In addition, just after emergence seedlings are likely to be killed by fungal atack (Sahashi *et al.* 1994) and seedlings a few years old are likely to be gnawed by rodents, as shown in this study. In the *Sasa* grassland, therefore, both the rates of seed disappearance and seedling death would be inevitably higher than in beech and oak forests. These factors prevent the recruitment of a sizable seedling bank in *Sasa* grassland. Therefore, it was suggested that rodent behavior plays an important role in maintenance of the *Sasa* grassland. Moreover, even seedlings that escaped gnawing by rodents might suffer from shading by *Sasa* cover (Ida & Nakagoshi 1994). These factors would prevent forest regeneration in the *Sasa* grassland.

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