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Short-term changes affecting regeneration of *Fagus crenata* after the simultaneous death of *Sasa kurilensis*

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Abstract

Question: The aim of the present study is to determine whether seed/seedling predation will increase and *Fagus* survival will decline with the recovery of the *Sasa* cover.

Methods: We examined *Fagus crenata* regeneration for seven years in an old-growth *Fagus-Sasa* forest near Lake Towada, northern Japan, by examining the effects of simultaneous death of *Sasa*, tree canopy gap formation, mast seeding of *Fagus* and seed and seedling predation by rodents on the survival of *Fagus* seeds and current year seedlings. We established four types of sites differing in forest canopy (closed or gap) and *Sasa* status (dead or alive) following the simultaneous flowering and death of *Sasa kurilensis* (dwarf bamboo) in 1995.

Results: Fallen *Fagus* seed was abundant in 1997 and 2000 (mast years). In sites with alive *Sasa*, survival from the first growing season was low due to high seed and seedling predation. In sites with dead *Sasa*, seed survival under the canopy was high for both mast years, but in gaps it varied between years. Seedling survival was highest in canopy gaps with dead *Sasa* (gap-dead) in 1998, because of higher light levels and lower predation by rodents. However, seedling survival in these plots was low in 2001, apparently because rapid *Sasa* recovery favoured rodent predation. In both mast years, *Sasa* die-back had significant positive effects on seed and seedling survival under closed canopies because the seedlings there were more successful in escaping predation.

Conclusion: The change in successful sites for the early stage of regeneration of *Fagus* appears to reflect the combined effects of canopy gap, seed/seedling predation and revegetation of *Sasa*.

Keywords: Dwarf bamboo; Beech; Canopy gap; Mast seeding; Seed predation; Seedling predation; Understorey.

Nomenclature: Satake et al. (1989).

Abbreviations: PPFD = Photosynthetic photon flux density; RPPFD = Relative photosynthetic photon flux density.

Introduction

Among the various causes of mortality, plant-animal interactions may be a key factor regulating tree regeneration, and sometimes may become a limiting factor in the population dynamics of trees (Myster & McCarthy 1989; Shupp 1990; Caccia & Ballaré 1998; Bonfil & Soberón 1999; Maron & Simms 2001). Variations in the habitat of seed and seedling predators influence the survival patterns of plant propagules (Schupp 1988a, b; Schupp et al. 1989; Myster & Pickett 1993; Ostfeld & Canham 1993; Ostfeld et al. 1997; Russell & Schupp 1998). In addition, as ground cover changes during succession (Myster & Pickett 1993; Ostfeld & Canham 1993; Ostfeld et al. 1997), following canopy gap creation (Schupp 1988a, b; Schupp et al. 1989) or following human disturbance (Hayashida & Igarashi 1995), interactions may change both spatially and temporally, because a dense vegetation cover provides foraging habitat for rodents (Hayashida & Igarashi 1995; Hulme 1998; Manson & Stiles 1998; Flowerdew & Ellwood 2001).

The growth cycle of *Sasa* (bamboo) also causes fluctuations in regeneration in many forests, including Chinese *Abies-Betula* mixed forest (Taylor & Qin 1992; Taylor et al. 1995, 1996), Chilean *Nothofagus* forest (Veblen 1985, 1988), tropical forest in Thailand (Marod et al. 1999) and Japanese *Fagus crenata* (beech) forests. In Japan, *Sasa kurilensis*, a dominant bamboo in the undergrowth (Miyawaki 1977), grows vegetatively for 60-100 yr or more before flowering synchronously and dying over a large area (Makita 1998). Therefore, simultaneous death of *Sasa* and canopy gap formation are main determinants of community structure in *Fagus* forests in Japan (Nakashizuka 1987; Peters et al. 1992; Yamamoto et al. 1995; Abe et al. 2001). Damping off (Nakashizuka 1988; Sahashi et al. 1994) and seed and seedling predation by rodents (Miguchi 1994; Homma et al. 1999; Ida & Nakagoshi 1996) are the main causes

of mortality of *F. crenata* propagules in cool temperate forests. *Sasa* cover strongly prevents the regeneration of beech not only by shading seedlings (Maeda & Miyakawa 1971; Nakashizuka 1988), but also by facilitating seed/seedling predation (Wada 1993; Ida & Nakagoshi 1996). Canopy gaps provide favourable conditions for *Fagus* seedling establishment after the death of *Sasa* through both increased light and reduced predator activity (Abe et al. 2001). However, the favourable conditions provided by disturbances do not last long, because of canopy development.

The aim of the present study is to determine whether seed/seedling predation will increase and *Fagus* survival will decline with the recovery of the *Sasa* cover.

Methods

Study site

We selected an old-growth *Fagus* forest to the south of Lake Towada, Akita prefecture, northern Japan (40°24' N, 140°53' E; 670 m a.s.l.). Characteristics of the stand structure are reported in Abe et al. (2001).

The forest floor of this area had been dominated by *Sasa kurilensis* (dwarf bamboo). In 1995, *Sasa* simultaneously flowered and then died over an area of 1000 ha in this region (Makita et al. 1995), with some patchy populations that did not flower remaining intact. The area of the remaining *Sasa* occupied ca. 33% of a 1-ha study plot (Abe et al. 2001).

In the 1-ha plot (50 m × 200 m), four types of sites were recognized according to the combination of canopy (closed or gap) and *Sasa* (dead or alive): closed-alive, closed-dead, gap-alive and gap-dead. Sites were selected randomly, with three replicates for each type.

Rodent density

Within the 1-ha study plot, we established a 8 by 5 trapping grid with a spacing of 12.5 m between traps. Habitats at the trapping grid comprised of the four site types.

Two Sherman live traps were set at each grid point (total 80 traps). A three night trapping run was conducted 2-5 times in one season from June 1997 to October 2001. Captured rodents were identified by toe-clipping. Species, sex, reproductive condition and body-weight of all captured individuals were recorded before release at the point of capture.

Seed fall

We used seed traps with a 0.5-m² collection area from 1996 (year after *Sasa* flowering) to 2000. Three seed traps were placed at each sample site. The seed traps were the same as those used in previous studies (Abe et al. 2001, 2002). *Fagus* seeds that fell into the traps were collected once a month from June to October each year. The collected seeds were sorted, and viable *Fagus* seeds were counted. A viable seed was defined as having no damage to pericarp or embryo.

Seedling dynamics

Six 1 m × 1 m seedling quadrats (three pairs of neighbouring quadrats) were established at each sample site. Seedlings were observed once a month in 1996 and 1997 from late July to October. From 1998, seedlings were observed bi-weekly or three times a month from early May to early July when the density changed rapidly, and once a month afterward. Surviving seedlings were observed after their first growing seasons every autumn until 2002. Newly emerged *Fagus* seedlings were marked, and their survival followed, as reported by Abe et al. (2001). Factors causing seedling mortality were categorized into damping off, rodent-damage, insect-damage and unknown.

Seed predation experiment

Seed predation during winter was evaluated by a seed predation experiment. Seeds were collected from a local seed source near the sample plot. Each seed was marked with a permanent marker. Cages (800 cm² and 5 cm depth), each containing 50 *Fagus* seeds, were placed at the site in November 2000. To prevent predation by birds, each cage was covered with a 3-cm wire mesh. This protection was sufficient to allow rodents to enter, but not seed eating birds (M. Abe pers. obs.). Seeds and pericarp remaining were counted in May 2001. Seeds that disappeared from the cage or with gnaw marks on the coat were classified as predated.

Sasa recovery

To measure the degree of recovery, *Sasa* seedling density was monitored annually from 1996 in each 1 m × 1 m quadrat at dead-sites at the end of every growing season. Heights of the *Sasa* seedlings were measured every October since 1997.

Light conditions

To measure light conditions at each site, we took a hemispherical photograph with a fish-eye lens (1998: SIGMA, 8 mm, F4S; 2001: Nikon, 8 mm, F2.6) at 15 cm above the ground surface in the middle of each pair of quadrats in late June 1998 and early September 2001. The photographs were digitized, and the photosynthetic photon flux density (PPFD) was estimated with HEMIPHOTO software (ter Steege 1993). The relative PPFD (RPPFD) compared to that at an open site was calculated for each site, and was used as an index of light condition for each site.

Statistical analyses

We used a three-way ANOVA to determine the effect of year, *Sasa* cover, canopy cover and their interaction on RPPFD. The mean RPPFD value for each site was analysed as a dependent variable and three factors (1998 or 2001, gap or closed, with or without *Sasa*) were analysed as independent variables.

We used the log-linear model to analyse the effect of year (1998 or 2001), *Sasa*, canopy condition and their interaction on the survival rates and mortality of seeds and seedlings. Our dependent variables were categorical rather than continuous; therefore, we used a multifactored contingency table. Damped-off seedling and seedling predation were also compared by log-linear model. Factors included were year, *Sasa* condition, canopy condition and seedling performance (damping-off and seedling predation). We excluded cohorts 1996, 1997 and 2002 from seed and seedling survival because cell count (number of seedling observations) of some combination(s) of the factors for these three cohorts were less than five. In contrast, more than one seedling emerged at all combinations of the factors in 1998 and 2000. Therefore, the expected value for each cell is greater than zero, and thus structural zeros are not included for these two cohorts.

For the seed predation experiment, a log-linear model was also used. Factors included were seed survival, *Sasa* condition and canopy condition for each mortality.

To compare seed density between 1997 and 2000, the Wilcoxon signed-rank test was used. Seed density was analysed as a dependent variable, and the two years were analysed as independent variables.
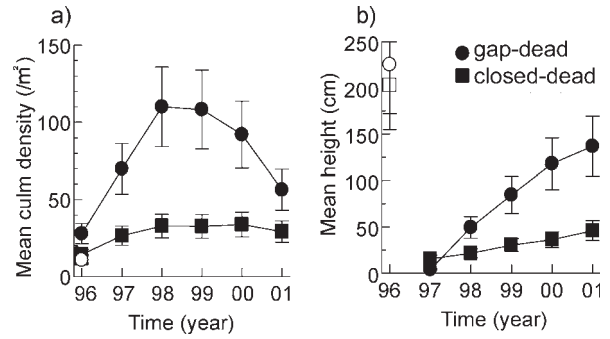
Fig. 1. Changes in **(a)** mean density and **(b)** mean height of *Sasa* seedlings in each canopy condition. ■ = closed-dead; ● = gap-dead. Empty marks indicate flowering population in 1996 (Makita et al. unpubl. data). □ = closed-dead; ○ = gap-dead. Error bars show one s.e.

After a mass flowering of *Sasa*, some of the surviving bamboo usually flowers sporadically (Makita et al. 1995; Widmer 1999). In this study, some areas of *Sasa* within alive patches died and culm density declined after 1998. Therefore, in 2001, the quadrats in alive-sites where *Sasa* density decreased to half of that for 1996 were excluded from the analysis.

STATISTICA software (Anon. 1998) was used for all statistical tests.

Results

Sasa recovery

Sasa recovery was faster at gap-dead sites than closed-dead sites (Fig. 1). Culm density in gap-dead plots dropped abruptly in 2001 (Fig. 1a), probably due to activity by mice or voles (some culms in gap-dead areas were found gnawed at the bottom; M. Abe & A. Honda pers. obs.). This may have been related to the population increase of rodents after *Fagus* masting (Fig. 2). The growth rate of the *Sasa* seedlings was also higher in canopy gaps (Fig. 1b), probably associated with high light levels (Table 1). *Sasa* cover, canopy cover, *Sasa* × canopy and year × canopy interaction all had significant effects on RPPFD, but there was no significant year × *Sasa* × canopy effect (Table 2). The height of *Sasa* reached ca. 66% of that of the flowered population at the gap-dead sites in 2001 (Fig. 1).

Table 1. Mean relative photosynthetic photon flux density (%) at each site (mean ± SD).

Year	Closed-dead	Closed-alive	Gap-dead	Gap-alive
1998	2.27 ± 1.11	2.76 ± 1.88	12.02 ± 7.33	4.57 ± 4.70
2001	4.20 ± 1.74	4.86 ± 1.46	5.97 ± 2.87	3.87 ± 3.32
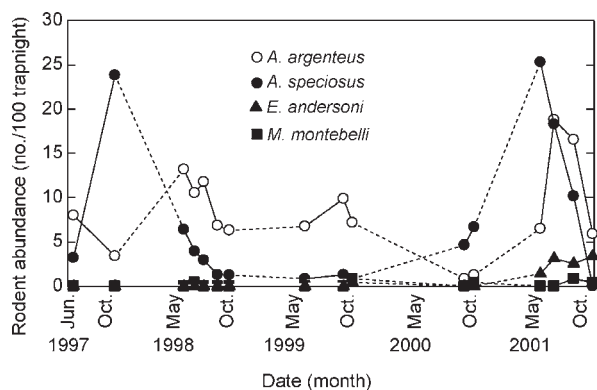
Fig. 2. Annual fluctuations in population size of rodents. ○ = *Apodemus argenteus*; ● = *Apodemus speciosus*; ▲ = *Eothenomys andersoni*; ■ = *Microtus montebelli*.
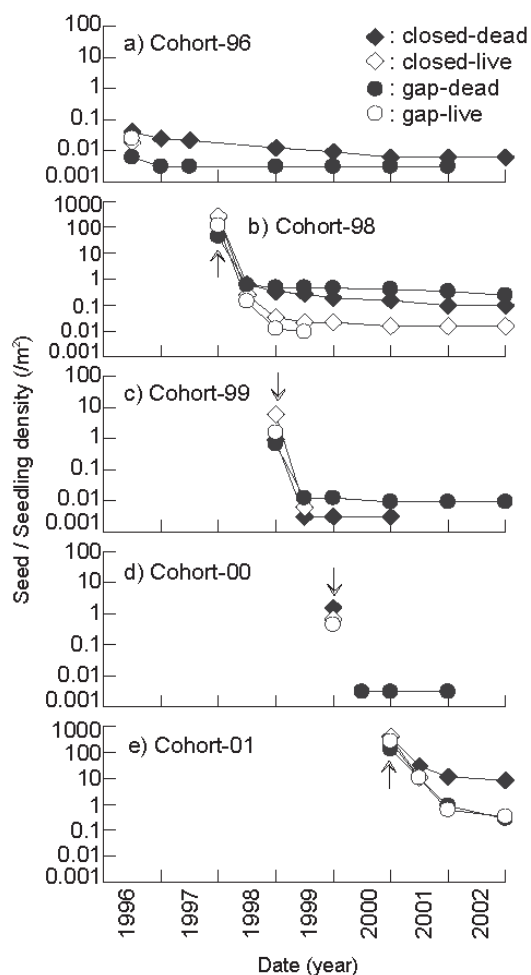
Fig. 3. Changes in *F. crenata* seed and seedling density at each site (mean ± SD). ■ = closed-dead; □ = closed-alive; ● = gap-dead; ○ = gap-alive. (**a**) cohort-96; (**b**) cohort-98; (**c**) cohort-99; (**d**) cohort-00; (**e**) cohort-01, respectively. The arrow indicates seed fall in each year. No seedlings emerged in 1997 and 2002.

Table 2. Result of ANOVA examining the influence of year, canopy condition, and *Sasa* condition on RPPFD.

Factor	df	MS	F	p
Year	1	2.17	0.43	0.5205
Canopy	1	51.74	10.34	0.0058
Sasa	1	23.61	4.72	0.0463
Year × Canopy	1	42.76	8.54	0.0105
Year × *Sasa*	1	11.66	2.33	0.1477
Canopy × *Sasa*	1	42.17	8.43	0.0109
Year × Canopy × *Sasa*	1	8.67	1.73	0.2079
Error	15	75.08		

Rodent population

Four species of rodents were captured (*Apodemus argenteus*, *A. speciosus*, *Eothenomys andersoni* and *Microtus montebelli*), their population densities are shown in Fig. 2. The densities of *E. andersoni* and *M. montebelli* were consistently quite low, whereas those of *A. argenteus* and *A. speciosus* increased after the *Fagus* seed mastings in 1997 and 2000. The density of *A. argenteus* increased in the following spring in both years. The density of *A. speciosus* was also highest in May 2001 (following year of masting); however, that in 1997 was highest in October in the mast year.

Seed dynamics

Density of emerged seedlings reflected the masting character of *F. crenata*. *Fagus* seed fall was very low in 1998 and 1999. Only seven and one seedlings emerged in 72 quadrats in these years, respectively (Fig. 3c, d). No seedling emergence was observed in 1997. Levels of seedling emergence in 1998 (cohort-98) and 2001 (cohort-01) were substantially high (Fig. 3). Large number of seedlings of these cohorts survived until 2002, especially in dead sites (Fig. 3b, e). In 1996, some seedlings emerged and survived for six years after germination in closed-dead sites (Fig. 3a).

In the two mast years (1997 and 2000), *Fagus* seed fall was higher under the closed canopy (dead and alive sites in 1997: 252.0 ± 128.8 and 268.4 ± 168.2; in 2000: 404.4 ± 154.8 and 337.1 ± 118.3) than in the gaps (in 1997: 43.8 ± 17.2; 116.4 ± 68.6; in 2000: 136.4 ± 23.7 and 270.4 ± 133.8), and higher in 2000 than in 1997 (Wilcoxon signed-ranks test; $Z = 6.15$; $p < 0.0001$). Seed fall was lower in 1997 than in common mast years, whereas in 2000 it was comparable to that in mast years reported by Miguchi (1995).

The pattern of seed survival differed between 1998 and 2001. Seedling emergence fractions in both years were higher at dead-sites, being especially high in gap-dead sites in 1998 (Fig. 3). Year, canopy and *Sasa* interaction effects were significant at $p < 0.05$ (Table 3).

Seedling dynamics

In 1998 and 2001, the current year seedling survival ratio was highest where *Sasa* is absent. In one set of plots (gap-dead), seedling survival was significantly lower in 2001 than in 1998 (Fig. 3), because of *Sasa* recovery (Fig. 1). This was a significant difference ($p < 0.01$ for year × canopy × *Sasa* interaction, Table 3. Many other factors were also significant but are not relevant to our main question. As a consequence, in 1998, the densities of emerged and surviving seedlings were higher both at closed-dead (emerged and survived: 11.5 ± 5.7 and 5.9 ± 4.0) and at gap-dead (10.8 ± 7.6 and 8.7 ± 7.1) sites than at alive-sites (closed-alive: 4.4 ± 3.6 and 0.6 ± 1.2, gap-alive: 2.3 ± 2.2 and 0.2 ± 0.4). In contrast, those in 2001 were highest at closed-dead sites (emerged and survived: 30.2 ± 26.1 and 11.7 ± 12.9).

The main causes of seedling mortality in the two years were predation by rodents and damping-off. In both years, most seedling predation occurred soon after germination, and deaths due to damping-off occurred frequently in June and July (Fig. 4).

In 1998, seedling predation was intense at all sites except for dead sites (Fig. 4). In 2001, seedling predation was higher overall, but dramatically so at gap-dead sites. That at closed-dead sites was the lowest among the four sites (Fig. 4). All main effects and interaction terms were significant (log-linear model; $p < 0.001$).

In 1998, the fraction of emerged seedlings killed by damping-off was lowest at gap-dead sites (Fig. 4),

Table 3. Results of log-linear model examining the influence of year, canopy condition and *Sasa* condition on the survival of *Fagus* seeds and seedlings. **a.** Emergence ratio (the proportion of emerged seedlings to seed fall in the preceding year); **b.** Seedling survival (proportion of living seedlings in autumn to total emerged seedlings).

Factor	df	χ^2	p
a. Emergence ratio			
Year	1	13.39	<0.001
Canopy	1	45.58	<0.001
Sasa	1	430.67	<0.001
Year × Canopy	1	82.58	<0.001
Year × *Sasa*	1	22.44	<0.001
Canopy × *Sasa*	1	7.45	0.006
Year × Canopy × *Sasa*	1	59.03	<0.001
b. Seedling survival			
Year	1	162.97	< 0.001
Canopy	1	0.40	0.525
Sasa	1	282.08	< 0.001
Year × Canopy	1	111.06	< 0.001
Year × *Sasa*	1	0.01	0.920
Canopy × *Sasa*	1	0.88	0.347
Year × Canopy × *Sasa*	1	46.96	< 0.001

reflecting high light levels (Table 1) as reported by Sahashi et al. (1994) and Nakashizuka (1988). In 2001 it was highest at closed-dead sites possibly because predation was so intense at the other three sites. Year, canopy and *Sasa* interaction significantly affected the level of damped-off seedlings (log-linear model; df = 1, $\chi^2 = 4.58$, $p = 0.032$).
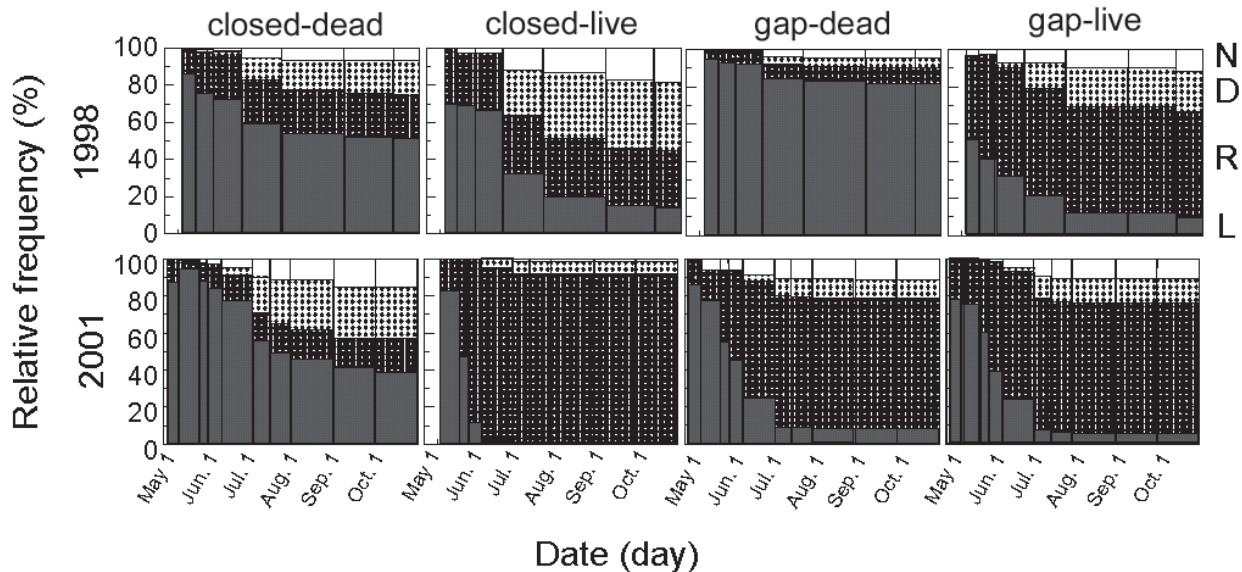
Fig. 4. Seedling survival and mortality factors. L = alive seedlings; R = rodent-damaged; D = damping-off; N = not found.

Seed predation experiment

Most of the seeds disappeared from each site. Fractional rates of seed survival were higher in closed-dead sites (17.1 %) compared from other sites (0 - 2.4%). Effects of *Sasa* (log-linear model; df = 1, $\chi^2 = 118.30$, $p < 0.001$) and canopy (df = 1, $\chi^2 = 56.63$, $p < 0.001$) were significant. Seeds damaged by rodents in the cages accounted for only 10-20% of the total seeds offered. The proportion of decayed seeds was negligible.

Discussion

The formation of the *Fagus* seedling bank is facilitated by masting (Fig. 3). The importance of masting year for *Fagus* seedling bank formation is consistent with other studies on *Fagus* regeneration (e.g. Nakashizuka 1988; Alvarez-Aquino & Williams-Linera 2002).

The effect of *Sasa* on the demography of *Fagus* seeds and seedlings varied greatly between the two mast years. In 1998, the death of *Sasa* reduced seed/seedling predation (Fig. 4; Abe et al. 2001). In addition, a combination of the death of *Sasa* and canopy gaps provided a higher light level (Table 1), which resulted in reduced damping-off (Fig. 4; Abe et al. 2001). However, in canopy gaps, *Sasa* recovery was vigorous (Fig. 1), and the amount of light for *Fagus* seedlings was lower in 2001 (Table 1). With the recovery of the vegetation, seed/seedling predation brought about heavy mortality among *Fagus* seedlings at many sites. Several studies have reported that rodent abundance (Wada 1993) and seed and seedling predation (Ida & Nakagoshi 1996; Bonser & Reader 1998; Caccia & Ballaré 1998; Schreiner et al. 2000) are intense under dense vegetation cover, because the dense cover facilitates foraging activity of rodents (Hayashida & Igarashi 1995; Hulme 1998; Manson & Stiles 1998; Flowerdew & Ellwood 2001). Therefore, changes in habitat quality for rodents caused by *Sasa* die-back and subsequent recovery would have substantial influence on the changes in the spatial pattern of seed and seedling survival.

In contrast to the previous findings for cohort 1998 (Abe et al. 2001), canopy gaps had a minor effect on the seed and current year seedling survival of *Fagus* in 2001. This suggests that even though overall survival from seed fall to seedling establishment was best in gaps just after the *Sasa* death, this was a transient phenomenon. In canopy gaps, vigorous revegetation would facilitate intense competition between *Fagus* seedlings and recovering *Sasa*. Moreover, some fast growing tree species (e.g. *Betula maximowictiana*; Abe et al. 2002) also dominated over *Fagus* seedlings in canopy gaps. These results indicate that successful sites for the early

stage of regeneration of *F. crenata* changed during our observation.

It may be significant that *F. crenata* can avoid seed/seedling predation and survive well at closed-dead sites. Because the recovery of *Sasa* under a forest canopy is slow, *Fagus* seedlings recruited to closed-dead sites in 2001 may be competitive and able to persist for several years under the closed canopy. This is consistent with several earlier studies that documented that *F. crenata* adopts the seedling bank strategy (Nakashizuka 1987; Yamamoto 1989). Because seedling/sapling bank dynamics is influenced by understorey light levels (Duchesneau & Morin 1999; Szwagrzyk et al. 2001), simultaneous death of *Sasa* may have the effect of keeping seedling density under the canopy at a relatively high level, and thus contribute to advanced regeneration. In addition, this effect was multiplied, because total area of closed-dead sites was much greater than the area of gap-dead (Abe et al. unpubl.). Therefore, this multiplied effect of *Sasa* die-back, masting of *Fagus* and extent of canopy area may be important in determining long-term *Fagus* dynamics.

In summary, the positive effect of *Sasa* death in canopy gaps on *Fagus* seedlings (Abe et al. 2001) is short-alive and is restricted to a period of a few years after the death of *Sasa*. Nevertheless, the density of *Fagus* seedlings recruited in 1998 was still greater in gap-dead than closed-dead sites, and these seedlings may survive for several years (Fig. 3b). This observation indicated that the transient effect of canopy gaps could still contribute to *Fagus* regeneration. That is, cohort-98 seedlings might survive under pioneers or other species which regenerate at gap-dead sites, and possibly replace them in the long-term. Further study examining the contribution of multiple cohorts established at different stages of *Sasa* recovery to the seedling bank would benefit our overall understanding of the role of gaps and *Sasa* death in the regeneration dynamics of *Fagus crenata*.

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