

Regeneration of Beech (*Fagus crenata*) after the Simultaneous Death of Undergrowing Dwarf Bamboo (*Sasa kurilensis*)

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Abstract

Seedling recruitment and survivorship of beech (*Fagus crenata*) were studied with special reference to the simultaneous death of undergrowing bamboo (*Sasa kurilensis*). The survival rate of beech seedlings on the floor where *Sasa* had withered was much higher than that on the floor where *Sasa* survived. Damping off caused the largest mortality among beech seedlings. However, the allocation pattern of matter to different parts of the seedlings indicated that their survival was greatly affected by production economy. The dense cover of dwarf bamboo prevented the establishment of beech seedling banks on the forest floor. The interval between the times when simultaneous death of *Sasa* occur and the length of its recovery period are thus important factors controlling the dynamics of beech forests in Japan.

Key words: *Fagus crenata*; Regeneration; *Sasa kurilensis*; Seedling bank; Simultaneous death.

Introduction

One of the most unique features of beech forests in Japan is that dwarf bamboos, *Sasa* spp., dominate the forest floor (Shidei, 1974). There are several reports which suggest that *Sasa* produces an inhibiting effect on the regeneration of beech (Maeda and Miyakawa, 1971; Hashizume and Noguchi, 1977). *Sasa* spp. are monocarpic plants: they flower and wither simultaneously over a large area once in several decades (Numata, 1970). Sasaki (1973) speculated that the regeneration of beech forests would proceed when the undergrowing dwarf bamboos had withered. Thus, dominance and simultaneous death of *Sasa* may have a great influence on the regeneration of beech (*Fagus crenata*) in Japan, although there are few data showing tree regeneration after the withering of *Sasa*. This study reports the recovery of *Sasa kurilensis* after its simultaneous death, and the survivorship of beech seedlings during an 8-year recovery period. Also the role of dwarf bamboo on the regeneration dynamics of beech forests is discussed.

The survivorship curves of seedlings are thought to be stable when the environment is stable under canopies of climax forest (Hett, 1971). However, because the environment in a mature forest is generally heterogeneous both in space and time, survivorship of seedlings varies greatly; different types of seedling survivorship curves in gaps and under canopies

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(Skeen, 1976) or on different substrata (Christy and Mack, 1984) have been documented. Such demographic variations are of considerable significance for an understanding of forest dynamics. In the present study, the survivorships on the forest floor under a cover of dwarf bamboo and on the floor where dwarf bamboo withered were compared. Growth of seedlings was also analysed, as it was considered to possibly reflect the physiological conditions influencing their survival. From these analyses, the variations existing in seedling demography were revealed, with special reference to the life history of the dominant undergrowth, *Sasa*.

Study area

The study plots were set up on a gentle slope (about 15° inclination, 1360 m altitude) on Mt. Iizuna (36°44'N, 138°08'E), in central Japan. The surface is covered by thick volcanic soil. Annual precipitation is about 1500 mm, and snow cover is up to 2 m deep from November to March.

The forest studied was a secondary one which had been logged in the 1890s or 1900s for charcoal production. Beech (*Fagus crenata*) was dominant in all the plots, occupying more than 80% of the total basal area. Canopy trees (20–50 cm in DBH) were at the reproductive (seed-bearing) stage when the study began.

Sasa kurilensis, which had been dominant on the forest floor, flowered over an area of several tens of hectares from June to August, 1974 (Uchimura, 1974), and withered in autumn, although some patchy populations which did not wither remained. Many dead culms of *Sasa* were still standing at the beginning of the study in May, 1977, when a large number of beech seedlings appeared.

Methods

Two permanent plots (both 10 m × 10 m) were set up under a closed forest canopy in May, 1977. One was on the forest floor where viable *Sasa* was still present (Plot A), and the other on the forest floor where *Sasa* had withered (Plot B). As Plot B was located near the edge of the forest, the recovery of dwarf bamboo and the growth conditions available for beech seedlings were probably different from those in other locations in the forest. Therefore, another plot (Plot C, of the same size) was set up on an area of forest floor where *Sasa* withered under a well closed canopy in 1981. The three plots were within about 100–200 m of each other, and there were no visible differences in soil and topography among them.

The values of the basal area of the overstory (trees higher than 2 m) of Plots A and B were 30.9 and 39.4 m² ha⁻¹, respectively, in 1977. That of Plot C was 32.1 m² ha⁻¹ in 1981. The mean vegetation cover of the forest floor was 75% in Plot A, and 21% in Plot B in 1977. The value for Plot C was 13% in 1981.

Each plot was divided into 100 small quadrats of 1 m². Germinated beech seedlings in the plots were all tagged. They were enumerated 5 times in 1977, because many seedlings germinated that year. After 1977, the enumerations were conducted twice a year when considerable recruitment occurred, and once a year when it did not. Factors causing seedling death (damping off, herbivory, physical injury, not found) were recorded from 1979. The height and annual increase in height of seedlings were measured every autumn. The length from the top of the seedling to the newest bud scar on the main stem was regarded as the annual increase in height. The seedlings in Plot C, whose age was determined by counting bud scars, were studied in the same way as those in Plots A and B from 1981.

The maximum height of the undergrowth as a whole and that of *Sasa* were measured in every 1 m² quadrat. The means of these values among the 100 quadrats in each plot were used in the analysis of vegetation change.

Ten or twenty seedlings were sampled from the neighboring area of each plot every year. They were divided into leaves, current-year shoots, stems and roots, dried at 80°C for 6 days and weighed. Mean annual net production and its allocation to each part were estimated from these data. Mean annual net production (P_N) was calculated as follows:

$$P_N = w_L + w_C + \Delta w_S + \Delta w_R.$$

where, w_L , w_C , Δw_S , and Δw_R are the mean weights of leaves and current shoots, and mean increments of stem and root weight, respectively. That is,

$$\Delta w_S = w_S - {}_1w_S,$$

$$\Delta w_R = w_R - {}_1w_R.$$

where, w_S and w_R are the mean weights of stem and root in year n , and ${}_1w_S$ and ${}_1w_R$ are those in year $n-1$. The grazed or fallen parts were neglected. The ratios of w_L , w_C , Δw_S and Δw_R to P_N give the allocation ratios to leaves, current shoots, stems, and roots, respectively.

Illuminance at 0.1 m (above the height of recently germinated beech seedlings) and 2.0 m high (above the height of living *Sasa*) were measured in each 1 m² quadrat in the summers of 1977 and 1984 for Plots A and B, and in the summers of 1981 and 1984 for Plot C. The illuminance in the open site was also measured at the same time. All the measurements were carried out under overcast cloudy conditions using photoelectric illuminometers (Toshiba SP-1 in 1977, and Minolta Digital T-1 in 1981 and 1984). Both the instruments have a spectral sensitivity similar to that of the human eye (400–700 nm). Although their spectral sensitivity is different from that of chlorophyll, it roughly reflects the stand structure and its shade conditions. Inter-instrument variation was adequately calibrated. The value found from dividing the illuminance in the forest by that in the open site was adopted as the relative illuminance (RI).

Results

The diffused light conditions reflected the stand structure in each plot. The RI values at a height of 2 m in Plot A were rather large (Fig. 1) because a canopy gap in the neighborhood of the plot increased the RI value at this height. The difference in RI distribution between height of 0.1 m and 2.0 m in this plot was conspicuous (significant by t test at the 0.1% level). This was apparently caused by the cover of *Sasa*. Although the mean RI values at a height of 2 m in Plots B and C were comparable (non-significant at the 0.1% level), the frequency distribution of the former had a wide range. The light conditions in Plot B were heterogeneous, since the plot was located near the forest edge. The light intensity in Plot C was homogeneous, as the stand was well closed.

The change in diffused light conditions in Plots B and C was caused by the recovery of vegetation between the two measurement times. The RI distributions at a height of 0.1 m in Plot B in 1977 and that in Plot C in 1981 did not show any marked difference from those at 2.0 m. In 1984, however, the RI distributions at 0.1 m height shifted to smaller values in both plots (significant at the 0.1% level).

The recovery of vegetation was faster in Plot B than in Plot C (Fig. 2). *Sasa kurilensis* seemed to have dominated considerably in Plots B and C before the withering (as it did in

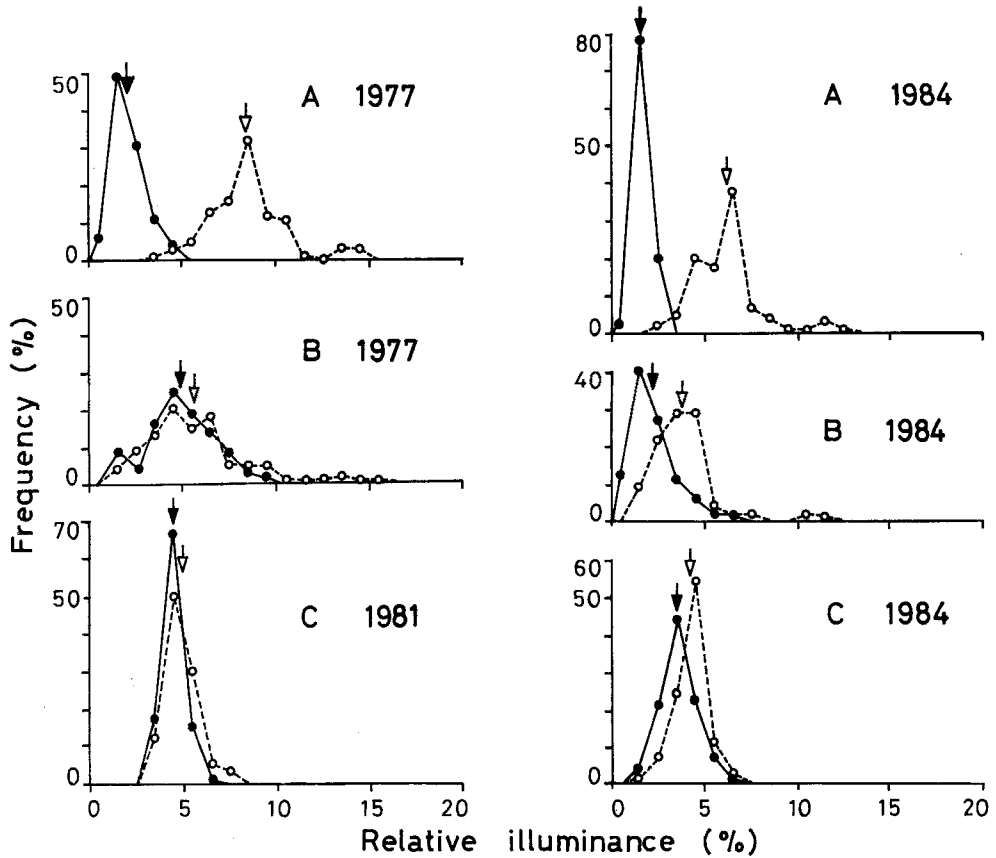


Fig. 1. Frequency distribution of relative illuminance of studied plots in 1977 (left, 1981 for Plot C) and 1984 (right). Clear and solid circles show the distributions at heights of 2.0 and 0.1 m, respectively. Arrows show the means.

Plot A), judging from the height and the density of dead culms. After withering, the forest floor was covered again, mainly by seedlings of *Sasa* and tree species. In Plot B, a community with a high diversity was established. However, the importance of *Sasa kurilensis* had been increasing up to 1984. This interesting floristic change in the course of recovery will be reported in another paper.

The observed numbers of beech seedlings in the study plots are shown in Table 1. The table shows that beech did not produce seeds every year. Germination of great numbers of seeds occurred in 1977 and 1983. This result agrees with the observation by Maeda and Miyakawa (1971) that great mast years occur once every 6–8 years. A smaller number of beech seedlings were recruited in 1979. Seedlings appeared in other years but these recruitments were extremely small.

The survivorship of seedlings varied in the different plots and cohorts. The survivorship curves of Cohorts A77 (the cohorts germinated in Plot A in 1977, the names of other cohorts being abbreviated in the same way), B77, B79, A83, B83 and C83, which consisted of large numbers of seedlings, were analysed.

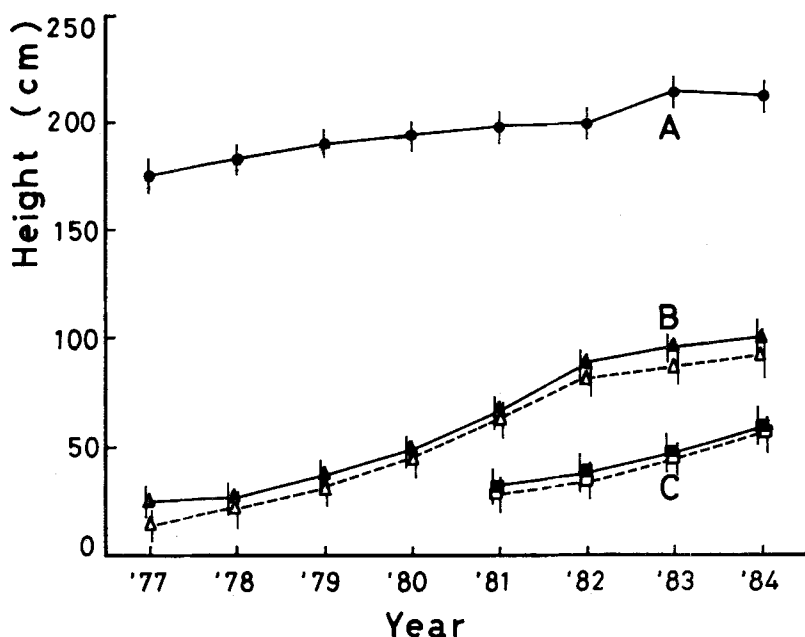


Fig. 2. Mean height of forest floor vegetation in studied plots. Solid and clear symbols indicate the change in vegetation as a whole and the change in *Sasa* populations, respectively. Vertical lines show the 95% confidence limits. The height of *Sasa* in Plot A was almost equal to the height of the vegetation as a whole.

In general, mortalities of current-year seedlings were high, becoming lower thereafter (Fig. 3). The mortality rate of seedlings older than 1 year was almost constant for each cohort. However, the mortality for A77 became low one year after the germination, but rose again gradually. Cohort C77, which is not shown in Figure 3, had almost the same mortality as that of Cohort B77; about 10% annually. In the same plots, mortalities of cohorts germinated in 1983 were all higher than those germinated in 1977 (Table 1). In Plots B and C, the recovery of *Sasa* made the forest floor dark (Fig. 1), being correlated with the higher mortality in the cohorts germinated in 1983.

The causes of mortalities in Cohorts A77 and B77 during 1979–1984, C77 during 1981–1984, and A83, B83 and C83 during 1983–1984 were analysed. The numbers of seedlings in the other cohorts were too small for analysis.

Mortality was classified into four causative factors: (1) damping off, (2) herbivory, (3) physical injuries, and (4) not found. Death from damping off is characterized by wilting of leaves and softening and decaying of stems. Fungi such as *Cylindrocarpon* sp. and others are found on seedlings dying this way (Maeda and Miyakawa, 1971). Herbivory was caused by insects and mammals. Insects eat only the leaves and current-year shoots, although mammals graze on these plus aged stems and roots and sometimes even the whole plant. Seedlings killed by stem breakage due to litter fall or other causes were classified as “physical injury.” Seedlings that could not be found were categorized as “not found.” This category consisted of seedlings which might have been buried by litter during their lifetime, or which had died due to other factors but could not be found due to their decay of their being obscured under litter, and seedlings which, although alive, were simply not found by the researchers. The

Table 1. Survivorship of each cohort. Figures are shown as numbers of seedlings in each 100 m² area.

Year	Date	Cohort								Total
		1977	1978	1979	1980	1981	1982	1983	1984	
Plot A										
1977	27 May	1266								1266
	6 July	844								844
	3 Aug.	684								684
	5 Sep.	609								609
	3 Oct.	555								555
1978	3 June	373	0							373
	12 Sep.	352	0							352
1979	22 May	295	0	18						313
	9 Oct.	232	0	0						232
1980	24 Sep.	157	0	0	1					158
1981	29 July	105	0	0	1	0				106
1982	21 Sep.	55	0	0	1	0	0			56
1983	7 June	—	—	—	—	—	—	47		—
	27 Sep.	35	0	0	1	0	0	7		43
1984	10 Sep.	19	0	0	0	0	0	0	0	19
Plot B										
1977	27 May	783								783
	6 July	656								656
	1 Aug.	594								594
	5 Sep.	546								546
	3 Oct.	513								513
1978	3 June	465	0							465
	11 Sep.	450	0							450
1979	22 May	439	0	24						463
	9 Oct.	425	0	14						439
1980	25 Sep.	388	0	11	0					399
1981	27 July	364	0	10	0	0				374
1982	22 Sep.	344	0	7	0	0	0			350
1983	7 June	—	—	—	—	—	—	588		—
	24 Sep.	307	0	7	0	0	0	272		586
1984	12 Sep.	291	0	6	0	0	0	156	0	453
Plot C										
1981	1 Aug.	224	0	10	0	2				236
1982	23 Sep.	208	0	9	0	2	4			223
1983	7 June	—	—	—	—	—	—	1501		—
	26 Sep.	197	0	9	0	2	4	741		953
1984	11 Sep.	174	0	7	0	2	4	523	0	710

latter case seemed to occur infrequently since seedlings, once classified as “not found,” were seldom found again.

The most important factor was damping off (Fig. 4), occurring more frequently in younger seedlings than in older ones. Since seedlings classified as “not found” must have included many which had been killed by damping off, the proportion of seedlings affected in this way could actually have been higher than recorded.

The current-year seedlings of Cohort 83 suffered greatly from herbivory, especially that by caterpillars. However, death from herbivory in older seedlings was mainly caused by mammals.

“Not found” accounted for a large proportion of the mortality in Plot A, especially in older seedlings. As will be mentioned later, the seedlings were very small, correlating with the dark conditions there. Because the *Sasa* population produced a large amount of leaf

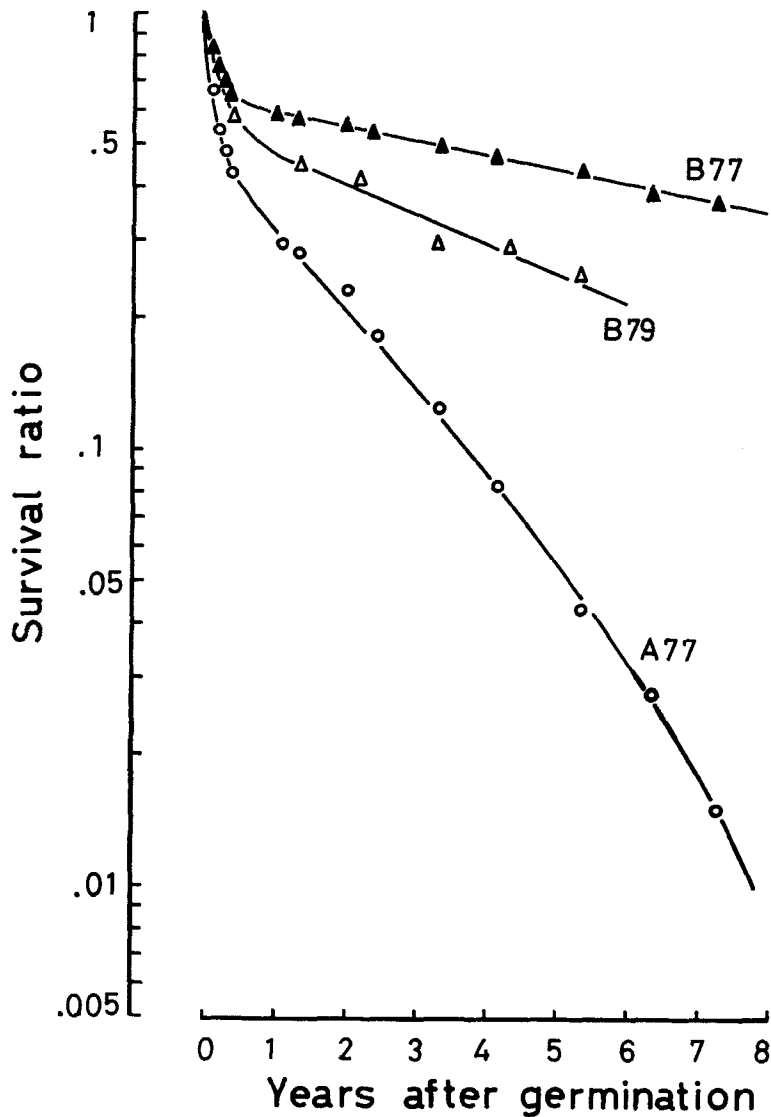


Fig. 3. Survivorship curves of Cohorts A77, B77 and B79.

litter every year in addition to the litter from the canopy, the seedlings might have been easily buried.

Seedlings in Plots A and C grew slowly in height, while those in Plot B showed a rather fast growth (Fig. 5). As Plot B was located near the edge of the forest, the light at the floor level was apparently sufficient for the rapid growth of beech seedlings.

In most cases, the seedlings which died showed a bias towards smaller height classes and towards classes of smaller annual height increase (Fig. 6). Seedlings smaller than about 10 cm and those that had an annual height increase of less than about 2 cm had especially high

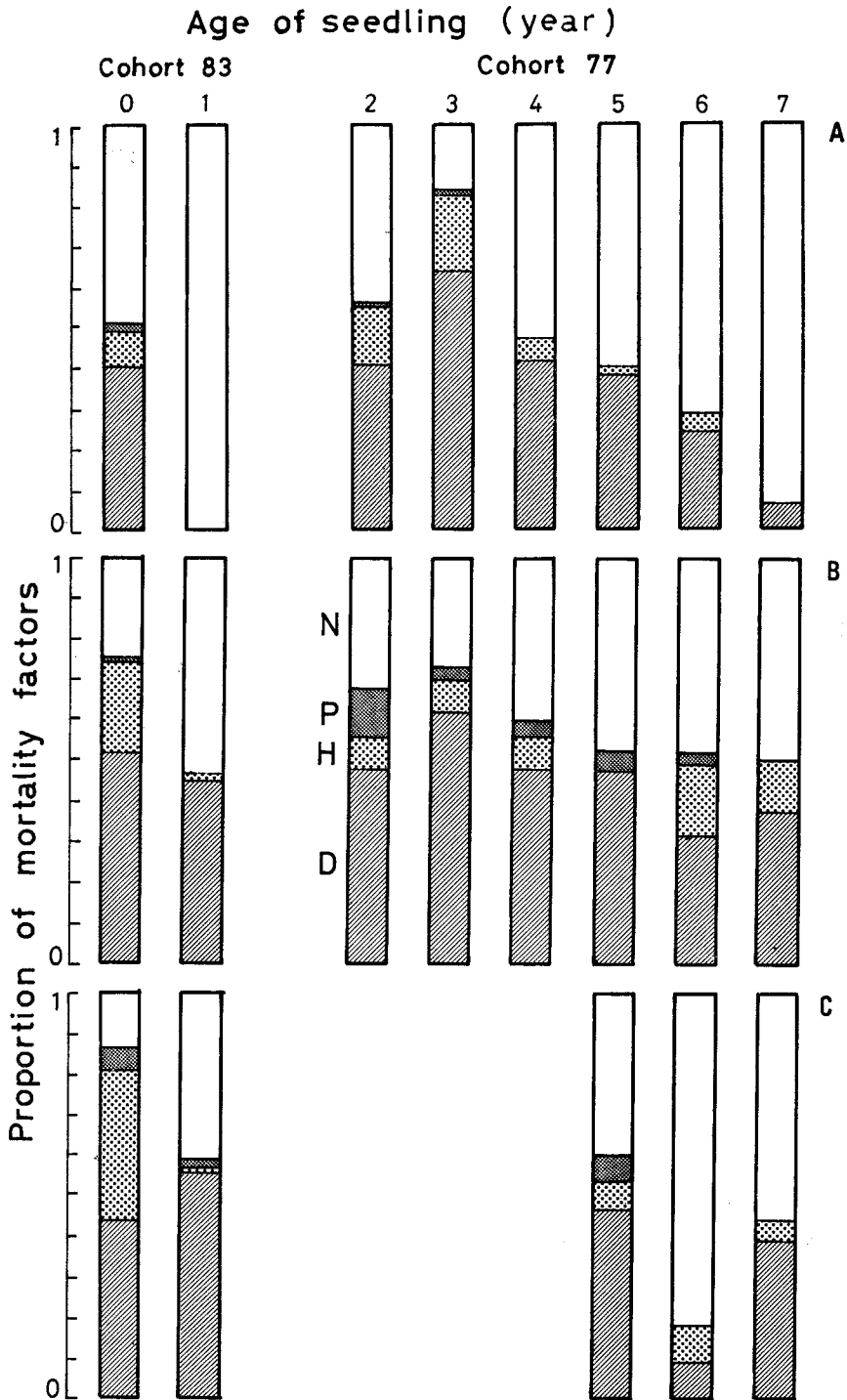


Fig. 4. Mortality factors of seedlings analysed for the cohort germinated in 1977 (2-7 years old) and those in 1983 (0 and 1 year old) in each plot. Mortalities are classified into D (damping off), H (herbivory), P (physical injury) and N (not found).

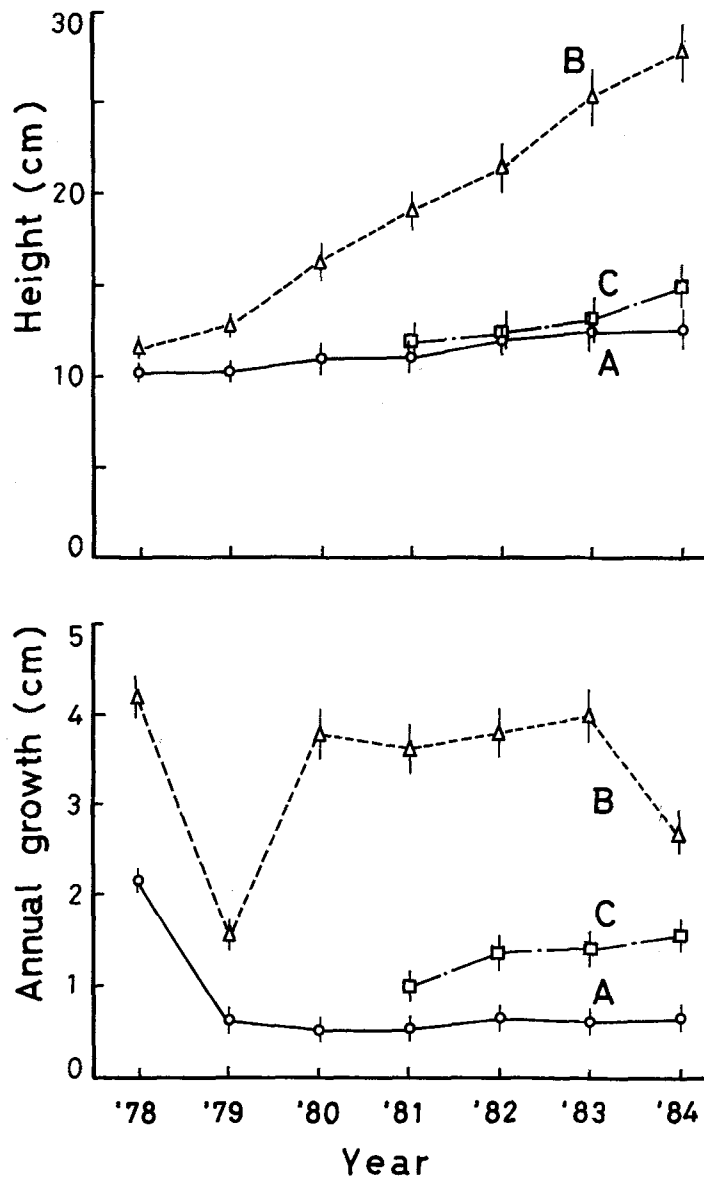


Fig. 5. Mean height and annual height increment of seedlings analysed for the cohort germinated in 1977 in each plot. Vertical lines show the 95% confidence limits.

mortalities. Smaller seedlings might be shaded by other plants and would be easily buried by litter.

The relationship between seedling size, growth and mortality also suggests that the growth rate of seedlings was positively correlated with survivorship. Seedlings in Plot A showed a marked change in the allometric relationship between total weight and leaf weight (Fig. 7). The amount of leaf per unit weight of non-photosynthetic parts decreased with age, especially for small seedlings. A similar phenomenon could also be seen for the seedlings in Plot C, but it was rather obscure for seedlings in Plot B.

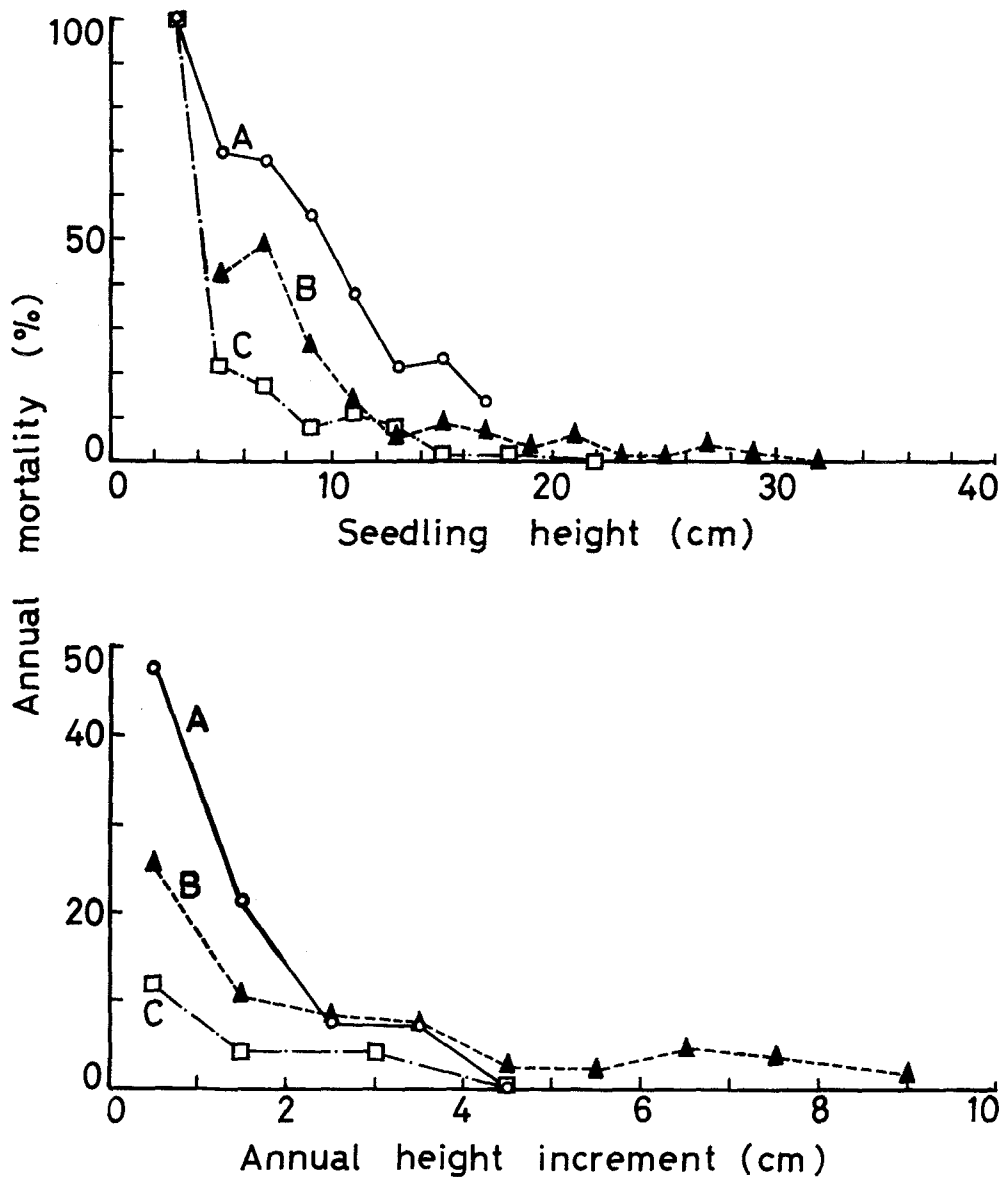


Fig. 6. Relationship between seedling height, annual height increment and seedling mortality for cohort germinated in 1977 in each plot. Annual mortality was calculated for each class using the data during 1978–1984 for Plots A and B, and 1981–1984 for Plot C.

The annual net production of seedlings in Plot A decreased with age, while that in Plot B increased; that in Plot C increased slightly (Fig. 8). The ratio of annual net production allocated to leaves of the seedlings in Plot A increased with age, while the ratio allocated to stems and roots decreased (Fig. 9). Nakashizuka (1983) reported that the number of annual rings of beech seedlings under a closed canopy was usually less than that of bud scars, indicating that the stem did not always grow radially. The six-year-old seedlings in Plot A

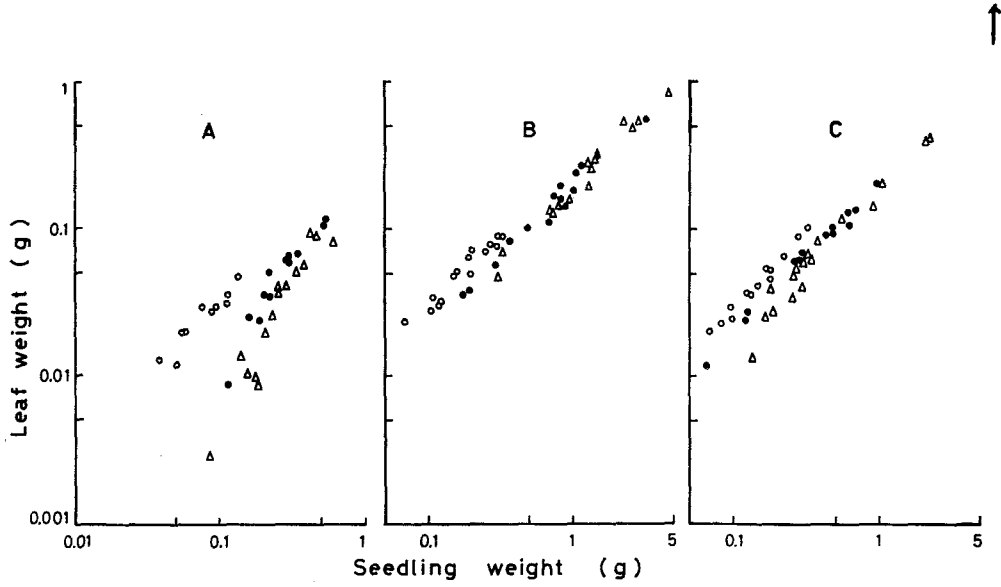


Fig. 7. Allometric relationships between the leaf and total weight of seedlings in each plot. Clear and solid circles and triangles show seedlings of 0, 3 and 5 years old, respectively.

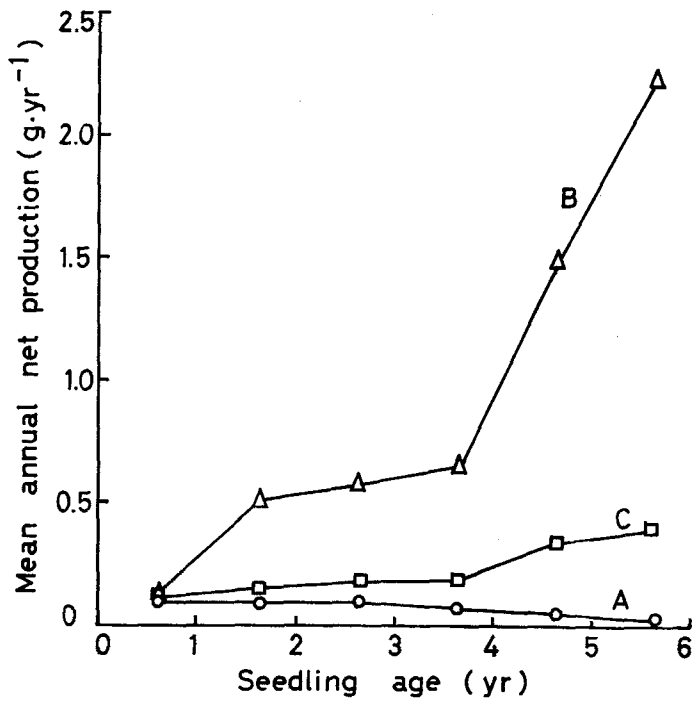


Fig. 8. The change in the mean annual net production with seedling age.

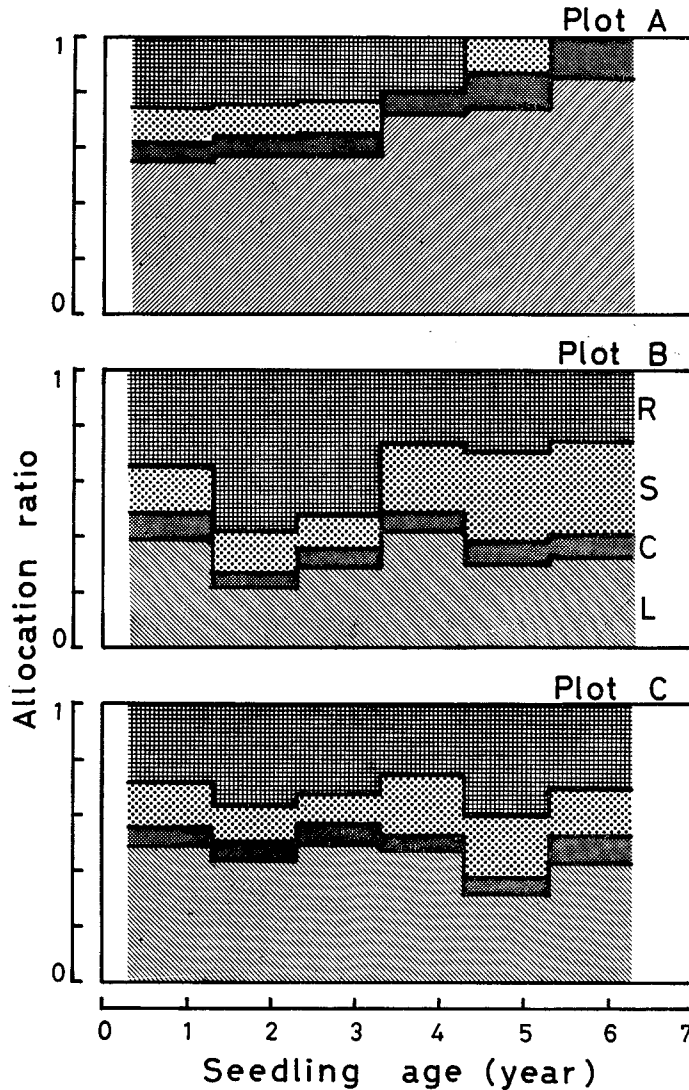


Fig. 9. Ratio of net production allocated to roots (R), stems (S), current shoots (C), and leaves (L) of seedlings in each plot.

allocated almost all their net production to leaves and current-year shoots. Deciduous trees accumulate non-photosynthetic parts, while they renew their leaves every year. As their total net production decreased (Fig. 8), the amount of leaf per unit body weight decreased (Fig. 7), despite such a high allocation ratio for leaves. Thus, seedlings with poor production would suffer severely following only a minor amount of damage, and mortality of such seedlings would be high.

In contrast, the seedlings in Plot B showed an increased net production (Fig. 8) and allocated a large proportion of it to roots and stems (Fig. 9). As net production increased, the proportion allocated to stems also increased, while that allocated to roots decreased. The seedlings in Plot C, which had a slightly increasing net production, showed a rather constant allocation pattern throughout the observation period.

Discussion

High mortalities of seedlings just after germination have been reported for many species: *Shorea* spp. and *Koompassia* (Wyatt-Smith, 1958), *Dipterocarpus* spp. (Chim and On, 1973), *Machilus thunbergii* (Tagawa, 1979), *Acer pennsylvanicum* (Hibbs, 1979), *Tsuga heterophylla* (Christy and Mack, 1984) and *Chamaecyparis obtusa* (Yamamoto and Tsutsumi, 1985a). In many cases, the mortality became low thereafter, and sometimes a constant mortality was observed for several years. Beech seedlings on the forest floor where *Sasa* withered showed such a survivorship. Seedling mortalities of *Machilus thunbergii* and *Castanopsis cuspidata* under a closed canopy were shown to become higher again several years after germination (Tagawa, 1979). Beech seedlings on the floor where *Sasa* survived also showed this type of survivorship curve.

The low matter production and allocation of produced matter by seedlings reflected the poor conditions that were correlated with the high mortality. The proportion of leaf weight to the total body weight of seedlings under the cover of dwarf bamboo declined with age, although the ratio of net production allocated to leaves increased. A seedling with high production would not be killed as easily by fungal attack or grazing animals. The high mortality of older seedlings under poor conditions must be largely affected by such a production economy.

Survivorship curves and mortality factors vary according to the environment surrounding the seedlings. Stand structure (Skeen, 1976), substrate (Christy and Mack, 1984), grazing pressure (Silander, 1983) and disturbance of the soil surface (Yamamoto and Tsutsumi, 1985b) have a great effect on survivorship. In tropical forests, the distance from the mother tree has recently been considered an important factor (Auguspurger, 1983; Howe, Schupp and Westley, 1985). Also, the amount of floor vegetation can affect survivorship (Maguire and Forman, 1983; also this study). Such a variation in seedling survivorship has a great influence on forest dynamics.

A seedling bank (Grime, 1975) is established when recruitment surpasses mortality. Beech seedling banks were established well under a closed canopy without dwarf bamboo. Seedling mortality in Plot C (under a closed canopy without dwarf bamboo) was nearly equal to that in Plot B (near the edge of the forest without dwarf bamboo), although the annual height increment in Plot C was comparable to that of the seedlings in Plot A (under a closed canopy with dwarf bamboo). Thus, dwarf bamboo cover prevents the establishment of beech seedling banks on the forest floor. However, the seedlings in Plots A and C grew little, suggesting that a canopy gap formation is necessary for seedlings in order to grow rapidly even on the forest floor without dwarf bamboo. If a gap were created in a forest with dwarf bamboo, few seedlings would come up there as has been shown in the forest at Kayano-Daira (Nakashizuka and Numata, 1982). Therefore, beech needs both the establishment of a seedling bank and subsequent canopy gap formation in order to regenerate successfully.

Areas of withering of *Sasa* species reach several square kilometers (Muroi, 1968; Okamura and Tanaka, 1979) or more (Yamamoto, 1966). Therefore, their dominance and simultaneous death affect the dynamics of beech forest over a large area. Veblen et al. (1980) have reported on another kind of dwarf bamboo, *Chusquea* sp., in Chile and its role in forest regeneration.

The effects of *Sasa* on beech regeneration may be summarized as follows: (1) its dominance prevents the establishment of beech seedling banks, (2) a longer period is required for the repair of a canopy gap if *Sasa* predominates in beech forests, (3) its death over a large area makes beech regeneration synchronous (Nakashizuka, 1984). As *Sasa* inhibits the repair of

gaps, the proportion of the gap area in a forest would increase as long as *Sasa* was predominant in the forest. Beech forest with *Sasa* sometimes has a very high proportion of gap area (Nakashizuka and Numata, 1982). Thus the interval that the deaths of *Sasa* occur is one of the factors in determining the proportion of the gap area in a forest. Nakashizuka (1987) estimated that gaps of 30–82 m² ha⁻¹ yr⁻¹ are made in beech forests in Japan. If *Sasa* requires 20 years to recover again after withering, the new gaps made during this period would occupy 6–16% of the forested area. When *Sasa* withers over a large area in such a forest, regeneration would begin both in gaps that have not been repaired, and in gaps that are made during the recovery period of *Sasa*. The cover of *Sasa*, therefore, amplifies the fluctuation of community parameters (biomass or tree density) that is also mediated by disturbances.

It is thus clear that more should be learnt about the life history of *Sasa*. Especially, the interval between witherings and the length of the recovery period are important factors relating to the stability of beech forests. Although it is said that *Sasa* species flower and wither once in several decades (Numata, 1970), there are no actual reports or records proving this. Veblen (1982) reported that the dwarf bamboo in Chile, *Chusquea*, withers once in 15–25 years. The withering interval of *Sasa* is longer. The longer the withering interval, the greater the forest fluctuation, i.e., the less stable the forest becomes.

The length of the recovery period has also not been determined either. The above-ground biomass of *Sasa ishizuchiana* in an open site almost recovered to its former value within ten years after withering (Sakurai, 1984). However, in dark conditions as in a forest, it would take a longer time for the populations to recover (Fig. 2). The shorter the recovery period, the more difficult it becomes for beech to establish a seedling bank.

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