# Fluctuation of nut production and seedling appearance of a Japanese beech (*Fagus crenata* Blume)

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The nut productivity, density of fallen nuts, seedling appearance and seedling survival of a Japanese beech (*Fagus crenata* Blume) were investigated at three localities, Mt Gozaisho, Mt Hodaka and Mt Bandai, Japan, from 1976 to 1992. Two patterns of cycles, a short cycle and a long one, were confirmed in the beech nut productivity. Synchronization in the long cycle was recognized both on Mt Hodaka and Mt Bandai. On Mt Gozaisho, the beech nut productivity was quite low, and the seedlings disappeared within 1 year. The phenomenon on Mt Gozaisho seemed to be caused by the low matter production mainly due to erosion and poor soils. A large number of seedlings appeared in the next spring of heavy mast years on Mt Hodaka and Mt Bandai. The large beech nut productivity contributed to the large seedling supply, and this enhanced the survival probability of beech seedlings. This demonstrates the possibility that beech seedlings survived longer even under dense dwarf bamboos, particularly if the seedling supply was large.

Key words: Fagus crenata; mast year; nut production; seedling survival.

## INTRODUCTION

One Japanese beech, *Fagus crenata* Blume, forms a climax forest as a representative tree species in the cool-temperate zone of Japan, although the forests are nowadays under human impact of interference. The clarification of seed- and seedling-stages of the constituent species is one of the bases for understanding the regeneration mechanism of beech forests.

Among some characteristics of seed- and seedlingstages, the productivity of beech nuts has received some attention for its large fluctuations, since the phenomenon was reported at the end of the last century (Schwappach 1895). Many data have been reported up to date on the fluctuation of beech nut productivity at various localities (Matthews 1955; Kikuchi 1968; Maeda & Miyakawa 1971; Hashizume & Yamamoto 1974; Sasaki 1985; Hilton & Packham 1986; Maeda 1988; Suzuki 1989). However, as far as we know, there are few studies about the relationship between nut productivity and seedling appearance or survival in beech forests. Maeda (1988) and Nakashizuka (1988) reported the seedling appearance in the following year of a heavy mast year. In addition, Nakashizuka (1988) reported the disappearance process of beech seedlings which occurred in the next year of heavy mast. The principal focus of these two studies was on the survival of beech seedlings with relation to the occurrence of dwarf bamboos in the fields. However, the effects of nut productivity fluctuation on seedling appearance or survival was not taken into consideration.

In this article we report and discuss the results of observations about the following characteristics of seed- and seedling-stages of the Japanese beech at three localities, from 1976 to 1992: (i) the synchronization and the periodicity of the productivity of beech nuts with reference to the ratio of sound beech nuts; (ii) the seedling appearance or seedling survival in relation to the fluctuation of beech nut productivity. In the case of Mt Gozaisho, we discuss the unique conditions of almost no successive beech saplings.

#### **METHODS**

#### Estimation of beech nut productivity

The fluctuation of beech nut productivity of a Japanese beech, *Fagus crenata*, was investigated at

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three localities, at about 1100 m in altitude on Mt Gozaisho (136°26′E, 35°01′N) in the Suzuka Mountains, at about 1400 m in altitude on Mt Hodaka (137°40′E, 37°17′N) in the Hida Range and at about 1300 m in altitude on Mt Bandai (140°04′E, 37°36′N) at the southern part of the Tohoku District, from 1976 to 1992.

The ground sampling method (Hilton & Packham 1986) was basically employed for the estimation of nut productivity. More than 100 nuts were picked up in heavy mast years, and as many nuts in lean years, in each area of the localities from 1976 to 1983. From 1984 to 1992, to determine the fluctuation of the nut production of each individual mother tree, nuts were collected within the area under the crown of each individual beech tree of more than 40 cm in diameter at breast height (d.b.h.). The number of investigated beech trees was three on Mt Gozaisho, 10 on Mt Hodaka and six on Mt Bandai. One to three quadrats of 1 m<sup>2</sup> were used for each mother tree. There was only one case in each locality where the mother tree of fallen nuts could not be identified because of the closing of beech crowns. The number of nuts in each quadrat was counted. The nuts were examined for whether they were sound or empty. Damaged nuts (by insects etc.) were classified as empty ones, because it was proved by the germination and growth tests that almost all of the damaged nuts did not germinate or did not grow to healthy seedlings (Hiroki & Matsubara 1982). The indices of sound nuts were obtained by calculating the average value of the per cent ratio of sound nuts in each tree. The density of fallen nuts was also obtained in each tree.

To compare the nut weight among the three localities, more than 25 nuts per mother tree were collected at the three localities. The sample number of mother tree was 2, 4 and 5 on Mt Gozaisho, on Mt Hodaka and on Mt Bandai, respectively. Nuts were dried at about 80 °C for 48 h, and then weighed.

#### Observation of beech seedling appearance

To determine the relationship between fallen sound nuts and the appearance of current seedlings in the next year of heavy mast years, two stands, A and B, were selected in a beech forest on Mt Bandai. Each stand included only one crown of beech trees that were used for the estimation of the ratio of sound nuts and the density of fallen nuts. In each stand, one quadrat of  $5 \times 5$  m was laid, and the number of current seedlings that appeared in each quadrat was counted on June in 1985 and 1991, which were both the next years of heavy mast on Mt Bandai. Dwarf bamboos densely occupied the under layer of both stands.

The appearance of current seedlings and their survival were investigated in three stands (C, D, E) under the crowns of beech trees, which grew at the foot of a col of Mt Gozaisho, from the spring of 1983 to the summer of 1985. One quadrat of  $5 \times 5$  m was laid each in the former two stands and one quadrat of  $10 \times 10$  m in the last stand. The investigation was made only in 1985 in the case of stand E. The dwarf bamboos densely occupied the under layer of these stands, except for denuded portions where granite rocks were exposed due to erosion. Beech saplings less than 4 cm in d.b.h. were not found in the beech forests on Mt Gozaisho.

The age distribution of beech seedlings was analyzed on Mt Bandai in June 1983 and on Mt Hodaka in June 1992. The analysis was carried out in the same two stands (A, B) as used for the investigation of the appearance of beech seedlings on Mt Bandai. One quadrat of  $25 \times 25$  m was laid in the stand on Mt Hodaka. The forest floors of the two stands on Mt Bandai were covered with dense dwarf bamboos on a flat ridge. The stand on Mt Hodaka almost lacked dwarf bamboos, located at a steep slope with large gaps in the canopy. In this stand, instead of dwarf bamboos, many shrub trees grew with many beech saplings. The shrubs included *Viburunum furcatum, Lindera umbellata* var. membranacea and Acer japonicum.

The age of beech seedlings less than 50 cm in height on Mt Bandai and less than 1 m in height on Mt Hodaka was counted by means of reading their annual bud scars with naked eyes or a small magnifier (rupe). Individuals with annual bud scars that were difficult to distinguish were dug up, and brought to the laboratory. Their ages were determined by observing annual bud scars with a stereoscopic microscope. When leader shoots were dead and disappeared, the age was judged by tracing the bud scars from branch until the top current shoots. The height and leaf number of beech seedlings in the same population in stand A on Mt Bandai were measured or counted. The height and leaf number of beech seedlings were measured or counted also in the stand on Mt Hodaka.

## RESULTS

Heavy mast years of *Fagus crenata*, which were regarded when the values of the indices of sound nuts were higher than 50%, were 1976, 1982, 1984 and 1990 on Mt Hodaka, and 1976, 1984 and 1990 on Mt Bandai (Table 1). The heavy mast year on Mt Bandai in 1976 was judged from the result of the seedling analysis in 1983, as described later. The values of the indices were generally low on Mt Gozaisho.

Almost all individuals of 10 beech trees on Mt Hodaka and six on Mt Bandai showed the synchronized fluctuation of nut production from 1984 to 1992 in the former and from 1984 to 1990 in the latter (Tables 2, 3). The high ratio of sound nuts did not always correspond with the large density of fallen nuts in individual level. However, it can be concluded that high productivity of the beech nuts generally showed high value of the ratio in heavy mast years. The densities of fallen nuts per 1 m<sup>2</sup> were high in heavy mast years, ranging from 179.3 (1990) to 247 (1984) on Mt Hodaka, and from 228.9 (1990) to 237.3 (1984) on Mt Bandai. The maximum density of fallen nuts per 1  $m^2$  was 612.5 in sample tree no. 9 on Mt Hodaka in 1990 (Table 2). This individual also showed a large density of fallen nuts in 1984. Cycles of 2 years of the nut productivity were recognized in almost all of

 Table 1. The indices of sound nuts of Fagus crenata

 obtained at three localities.

Year	Mt Gozaisho	Mt Hodaka	Mt Bandai
1976	2.5	69.0	*
1977	0	-	_
1978	2.5	14.0	_
1979	0	_	_
1980	0.4	_	_
1981	0	_	_
1982	13.1	62.7	21.0
1983	0	_	_
1984	24.0	52.2	69.2
1985	0	_	0
1986	0	4.7	1.1
1987	0	0.7	0
1988	0	20.1	10.2
1989	0	0	_
1990	5.0	55.9	71.6
1991	_	0	_
1992	_	0	_

\*This year was judged to be a heavy mast year from the observation in 1983 as shown in the results.

the individuals, although low or no nut production continued 3 years from 1985 to 1987 on Mt Bandai. Nut falling was observed only in two individuals on Mt Hodaka in 1987. In this year many individuals bore quite a small number of cupules on their crowns both on Mt Hodaka in this study and on Mt Hakkoda in the Tohoku District.

The mean dry weight of beech nuts was 0.088 g on Mt Gozaisho, 0.138 g on Mt Hodaka and 0.126 g on Mt Bandai. The value on Mt Gozaisho was quite smaller than the other two. The value of beech nuts in 1976 on Mt Hodaka was 0.14 g (Hiroki & Matsubara 1982).

The estimated number of sound nuts per 25 m<sup>2</sup> in the two stands (A, B) on Mt Bandai was 4176 and 3436 in 1984, and 1593 and 1959 in 1990 (Table 4). Both years were heavy mast years. The number of current seedlings appearing in the same stands varied from 34 to 343 in the following spring of the heavy mast years (Table 4). The survival rates from the stage of sound nuts to seedlings ranged from 2.1 to 17.5%, and the mean was 7.8%.

All of the current beech seedlings disappeared within 1 year on Mt Gozaisho in stands C and D in 1983 and in stand E in 1985 (Table 5). The seedlings in stand D had disappeared until the beginning of July in 1983 and those in stand E until the end of July in 1985. Six of eight surviving seedlings in the stand C showed poor vitality or had their leaves partly chewed by insects already on 27 May 1983. Two seedlings survived until October in this stand, and disappeared the next spring.

Yearly beech seedling appearance varied largely in both stands (A, B) on Mt Bandai for 12 years (Fig. 1). It was justified from Fig. 1 that 1976 was a heavy mast year on Mt Bandai. The individuals, of which leader shoots died, are not included in these distributions. The oldest individual was 12 years old and appeared in stand B. The age class distributions of stand A and B showed similar patterns to each other. The number of current seedlings (age class 0) were 12 in stand A, and six in stand B. These small numbers of current seedlings reflected the poor productivity of beech nuts on Mt Bandai in 1982. The index of sound nuts was 21% in that year (Table 1). Contrary to the current seedlings, a large number of seedlings of age class 6 occurred in both stands (97 in stand A, and 130 in stand B). It can be concluded from this result that 1976 was a heavy mast year. Heavy mast years before 1976 could not

	1	984	1	986	1	987	1	988	1	989	1	990	1	991	1	992
Sample tree number	Ratio (%)	Density (m <sup>-2</sup> )														
No. 1	45.7		10.0	1	0	0	60.0	9.1	0	0	62.2	37	0	0	0	0
No. 2	49.0	80	0	0	0	0	11.6	25.7	0	0	22.4	116	0	0	0	0
No. 3	38.4	-	2.0	5	0	0	21.7	3.0	0	0	54.0	63	0	0	0	3
No. 4	· -	_	4.0	10.7	0	0	10.0	4.0	0	0	64.6	82	0	0	0	0
No. 5	58.1	-	10.0	2	7.0	15	15.4	22.0	0	0	61.5	14	0	0	0	1
No. 6	-	-	13.4	3	0	. 3	3.0	34.5	0	0	62.3	122	0	0	0	0
No. 7	42.5	86	0	1	0	0	19.7	1.0	0	0	54.5	121	0	0	0	0
No. 8	-	-	6.0	17	0	0	12.5	31.5	0	0	57.5	127	0	0	0	3
No. 9	65.4	514	0	7.0	0	0	38.0	29.5	0	0	61.8	612.5	0	0	0	2.0
No. 10	66.1	308	2.0	11.0	0	0	8.6	72,0	0	0	58.3	498.5	0	0	0	0
Mean	52.2	247	4.7	5.8	0.7	1.8	20.1	23.2	0	0	55.9	179.3	0	0	0	0.9

**Table 2.** The ratio of sound nuts of *Fagus crenata* and the density of fallen nuts under 10 beech trees on Mt Hodaka from 1984 to 1992.

Table 3. The ratio of sound nuts of Fagus crenata and the density of fallen nuts under six beech trees on Mt Bandai from1984 to 1990.

	1984		1985		1986		1987		1988		1990	
Sample tree number	Ratio (%)	Density (m <sup>-2</sup> )	Ratio (%)	Density (m <sup>-2</sup>	Ratio (%)	Density (m <sup>-2</sup> )						
No. 1	34.6	500	0	0	0	0	0	0	10.4	_	62.0	296.0
No. 2	85.4	247	0	0	0	0	0	0	-	-	80.7	384.5
No. 3	62,1	145	0	0	0	0	0	0	11.8	-	74.3	269
No. 4	75.5	147	0	0	6.3	7.5	0	0	22.2	7.3	77.0	212
No. 5	74.7	184.0	0	0	0	2.5	0	0	6.7	8.3	63.7	123
No. 6	83.1	201	- 0	0	0	0	0	0	0	0	71.6	89
Mean	69.2	237.3	0	0	1.1	1.7	0	0	10.2	5.2	71.6	228.9

Table 4. Estimated density of fallen sound nuts of *Fagus* crenata in heavy mast years, 1984 and 1990, and the density of emerged current seedlings in the next spring of those heavy mast years at two stands on Mt Bandai.

	Density of (25	sound nuts m <sup>-2</sup> )	Density of cu (25	urrent seedlings m <sup>-2</sup> )
Sample plot	1984	1990	1985	1991
Stand A	4176	1593	255 (6.1)	34 (2.1)
Stand B	3436	1959	192 (5.6)	343 (17.5)

Figures in the parentheses denote the percentage of the density of current seedlings to the estimated density of fallen sound nuts.

be discerned from Fig. 1. The number of those seedlings, where leader shoots died, were 4, 8, 11 and 13 in age class 3, 4, 5 and 6, respectively, in stand A, and 4, 8, 26, 2 and 6 in age class 4, 5, 6, 7 and 8, respectively in the stand B.

Figure 2 shows the height class distribution and the leaf number class distribution in the same population in stand A on Mt Bandai. The largest Table 5.Appearance of current seedlings of Fagus cre-nataand its survival in three stands of beech forests on MtGozaisho from the spring of 1983 to the summer of 1985.

		Number of seedling	of seedlings				
Date	Stand C (25 $m^{-2}$ )	Stand D (25 m <sup>-2</sup> )	Stand E (100 $m^{-2}$ )				
27 May 1983	10	5	_				
2 July 1983	8	0	_				
7 Oct. 1983	2	<b>_</b> .	-				
12 June 1984	0	-	-				
24 May 1985	0	0	42				
24 July 1985	0	0	0				

cohort of age 6 involves more individuals that grew better. The largest individual in height and leaf number occurred in the largest cohort of age 6.

One beech sapling of 75 cm in height under dwarf bamboos was found outside the two stands in the same beech forest on Mt Bandai. The base of its stem was sectioned and stained with saccinated carbonic acid, and its annual rings were counted with a mineralogical microscope. The age of this sapling



**Fig. 1.** Age class distributions of *Fagus crenata* seedlings in  $5 \times 5$  m quadrats of stand A ( $\blacksquare$ , n = 114) and B( $\Box$ , n = 162) in a forest on Mt Bandai investigated in the spring of 1983.

was estimated to be 29 years. This sapling had 38 leaf number, and was 8.5 mm in diameter at the base.

Beech seedlings appeared every 2 years, and the number of seedlings of each age showed large variation in a  $25 \times 25$  m quadrat on Mt Hodaka in 1992 (Fig. 3). Fourteen individuals were omitted from this age class distribution on account of an inability of age determination. The oldest seedling was 19 years old in the quadrat. Two large cohorts (age 1 and 9) and a middle one (age 7) were recognized in this age class distribution. The two large cohorts corresponded to the populations of the fallen nuts in 1990 and 1982, and the middle one to that of the nuts in 1984. This seedling appearance coincides well with the indices of sound nuts in Table 1. Heavy mast years before 1982 could not be discerned from Fig. 3.

Figure 4 shows the height class distribution and the leaf-number class distribution of the same population in Fig. 3. The two larger cohorts in older age (7 and 9) included some individuals with many more leaves. The seedlings of the latter cohorts, however, did not show better growth in height



**Fig. 2.** (a) Height class distributions and (b) leaf-number class distributions in the same populations in stand A of Fig. 1. (n = 12, 1, 97, 3 and 1 in age 0, 2, 6, 8 and 10, respectively).



Fig. 3. Age class distribution of *Fagus crenata* seedlings in a  $25 \times 25$  m quadrat in a beech forest on Mt Hodaka investigated in the spring of 1992. Fourteen individuals were omitted from this age class distribution on account of inability of age determination (n = 198).



**Fig. 4.** (a) Height class distributions and (b) leaf-number class distributions in the same population in Fig. 3 (n = 85, 2, 9, 39, 123, 13, 3, 7, 1 and 1 in age 1, 3, 5, 7, 9, 11, 13, 15, 17 and 19, respectively).

compared with other cohorts. The only exception was one individual in age 9, which was about 1 m in height, having more than 50 leaves. The seedlings in this stand were larger both in height and leaf number than those in the stand on Mt Bandai.

# DISCUSSION

Two patterns of cycles in nut productivity of the Japanese beech were recognized from the result of this study at two localities, Mr Hodaka and Mt Bandai, in 17 years from 1976 to 1992. One is a short cycle, in which the nut production basically occurs once every 2 years, as suggested by Yoshioka (1939). The other is a long cycle, in which heavy mast years occur once every 6 or 8 years. This coincides with the result of Maeda and Miyakawa (1971), although Maeda (1988) revised the average term of the long cycle to be once in every 5.3 years and pointed out that the term of the long cycle was changeable.

The result of this study showed a tendency of synchronization in the occurrence of heavy mast years both on Mt Hodaka and Mt Bandai. The information about heavy mast years in Japan since 1976 (Table 6) shows that the synchronization occurred within each region. Hashizume (1987) and Maeda (1988) have already pointed out that the

**Table 6.** Localities in which heavy mast years of Faguscrenataoccurred in recent years.

Year	Locality	
1976	Mt Hodaka	*
	Mt Bandai	*
	Sanin District	(Hashizume 1987)
	Mt Moriyoshi	(Maeda 1988 Nakashizuka 1988)
1981	Mt Iide	(Miguchi & Maruyama 1984)
	Mt Naeba	(Maeda 1988)
1982	Mt Hodaka	*
	Sanin District	(Hashizume 1987)
1984	Mt Hodaka	*
	Mt Bandai	*
	Niigata Prefecture	(Kamitani 1986)
	Sanin District	(Hashizume 1987)
	Mt Naeba	(Maeda 1988)
	Ashiu District	(Saito et al. 1991)
1986	Kanto-Koshinetsu District (the Japan Sea side)	(Suzuki 1989)
1990	Mt Hodaka	*
	Mt Bandai	*

\*Present study.

synchronization did not occur in all localities. Suzuki (1989) reported that seed bearing was found widely in the Pacific Ocean side, while not in the Japan Sea side in 1986. This poor seed bearing on the Japan Sea side corresponded with that on Mt Hodaka and Mt Bandai in the same year. The regional synchronization might be correlated with regional climate as suggested by Matthews (1955). He suggested that the beech nut productivity was affected with weather conditions such as temperature and late spring frosts.

The mean survival rate from sound beech nuts to seedlings was 7.8% in the present study. We reported previously that healthy sound beech nuts germinated almost 100% under snow cover (Hiroki & Matsubara 1982). It can therefore be considered that the reason for the low survival rate of 7.8%could be due to predation by animals such as rodents etc. Miguchi and Maruyama (1984) reported that about 70% of sound beech nuts were attacked by rodents in an artificial experiment. This value may be an underestimation, considering that it was described that the rodent attacks became reduced as nut falling increased in the fields. Ohkubo et al. (1989) reported that the ratio of appeared seedlings to sound nuts was about 1% in the next year of comparatively heavy mast year in Fagus crenata. These data show that nut predation by animals has a large effect on seedling appearance. But even if the survival rate is only a slight percentage, the amount of survived nuts is quite large in heavy mast years. In the case of this study, the number of remained sound nuts amounted to more than 80 000 per hectare. This implies that the predation satiation (Janzen 1971) is fully tenable. This does not mean, however, that surplus nuts are wasted as considered by Smythe (1970) and Janzen (1971). We consider that the hypothesis of predation avoidance by Miguchi and Maruyama (1984) was confirmed. We also considers that the large supply of beech nuts in heavy mast years, together with the existence of large seedling banks under dense dwarf bamboos discussed in the following paragraph, contributes to the conspicuous phenomenon that the beech predominates in the Japan Sea side in the temperate region in Japan.

A large amount of surplus nuts must further result in larger seedling survival under dwarf bamboos. As the forest floor in climax beech forests is quite dark even for beech seedlings, which are considered to be

extremely shade tolerant (Nomoto 1956), it is difficult for the seedlings to survive longer years. However, the existence of 12 year old seedlings under dense dwarf bamboos in a beech forest on Mt Bandai suggests that there is a possibility of much greater survival of beech seedlings in closed beech forests than regarded up to this time (Yoshioka 1939; Yanagiya et al. 1971; Nakashizuka 1988). The survivorship of beech seedlings might depend not only on the existence of dwarf bamboos (Maeda 1988; Nakashizuka 1988) but on the amount of nut supply according to the fluctuation of the productivity of the beech. The large nut supply results not only in the increase of the initial number of seedlings but, as a result of this increase, in the enhancement of the chance of seedling survival. Larger cohorts must have the possibility of remaining larger individuals compared with smaller ones (Figs 2, 4), and larger individuals probably survive more years because the longer survivorship depends on better growth. Although a larger number of leaves does not always reflect better growth, it can be a good indication of growth when the ages of individuals are well known as in the present study, or when individuals are within the same cohorts.

Although the dwarf bamboo cover prevented the establishment of a beech seedling bank (Nakashizuka 1988), it was suggested that simultaneous death of the dwarf bamboos might contribute to beech regeneration (Nakashizuka & Numata 1982). On the other hand, Hara (1983) showed the existence of long suppressed beech saplings on Mt Kurikoma, which penetrated the dwarf bamboo layer, and pointed out the importance of the existence of such individuals in closed climax beech forests. The fact that an individual 29 year old beech sapling was found in the dwarf bamboo layer in the present study suggests that it needs to survey a wider range of area to find out such rare individuals. The relationship between the density of dwarf bamboos and light conditions under the dwarf bamboos, and that of the growth of seedlings under the dwarf bamboos, also need to be established.

The three localities in this study pose a different problem of the survival of beech seedlings. Mt Gozaisho, in particular, showed a peculiar feature about the regeneration of the beech. Though the beech nut production showed a cyclical fluctuation, the nut productivity was quite low on Mt Gozaisho (Table 1). This may be caused by the low matter production due to the poor soil and erosion of weathered granite rocks on this mountain. The small dry weight of the nut on Mt Gozaisho also suggests the low productivity of beech forests on the mountain. These results explain the lack of successor beech saplings in beech forests on Mt Gozaisho, which are supposed to be a relic of the past predominance (Hiroki & Matsubara 1984).

The following conclusions are made about the nut production and appearance of seedlings of *Fagus crenata*: (i) even if the year is a heavy mast year in other regions, a locality similar to Mt Gozaisho, at which some erosion occurs, does not produce so many nuts, and survivorship becomes minimal; and (ii) in beech predominated forests such as Mt Hodaka and Mt Bandai, the regeneration occurs normally, but the important seedling population for regeneration should come from nuts of heavy mast years.

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