

# An Investigation of Initial Regeneration in an Evergreen Broadleaved Forest. II. Seedfall, Seedling Production, Survival and Age Distribution of Seedlings\*

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## Introduction

In the literatures seedling production or growth of seedlings have been discussed in relation to regeneration of communities (MOORE, 1928; WOOD, 1938; HARLEY, 1939 and 1949; FERRELL, 1953; OVERTON and MACRAE, 1960; PETERKEN, 1966; HETT and LOUCKS, 1971; MILES, 1972 and 1973), age distribution and the distribution in tree size (HETT and LOUCKS, 1968), biogeographical distribution of tree species (TAGAWA, 1973) and diagnosis of climax forest (TAGAWA, 1977).

Since 4 November 1967, the present author has collected fruits and seeds fallen into traps displayed in the warm temperate evergreen broadleaved forest of IBP research area at Minamata, Kyushu, SW Japan. This investigation originally started for making clear the regeneration of the forest along with the domestic theme of IBP of Japan, 'Biological Production of Warm Temperate Evergreen Forest'. It is still continued even though the Programme was completed in 1972.

The investigation has two stages of study; Preparatory study had been carried out from November 1967 to May 1969, and since then onward Definitive study has been going on.

In the previous paper (TAGAWA, 1973), the number of fallen seeds in one mast year and seedling production coming on the heels of it were described in the following two dominant species, *Castanopsis cuspidata* Schottky (Fagaceae) and *Machilus thunbergii* Sieb. et Zucc. (Lauraceae), and discussion covered the comparison of seedling production and of mortality rate of fresh seedlings as well as the different pattern of biogeographical distribution of both species.

The present paper concerns with the oscillation of seed production in 9 bearing seasons from 1968 to 1976 by *C. cuspidata* and *M. thunbergii*, its effect on the seedling production, pattern of natural thinning of seedlings and the simplified simulation for the age distribution of seedlings.

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### I. Methods

#### 1. Seed trap and its display

Detailed structure of seed trap which catches fallen seeds and fruits was already described in TAGAWA (1973), but is briefly reappeared again. The trap is shaped like a funnel with 3 feet using polyvinyl-chloride circular frame from

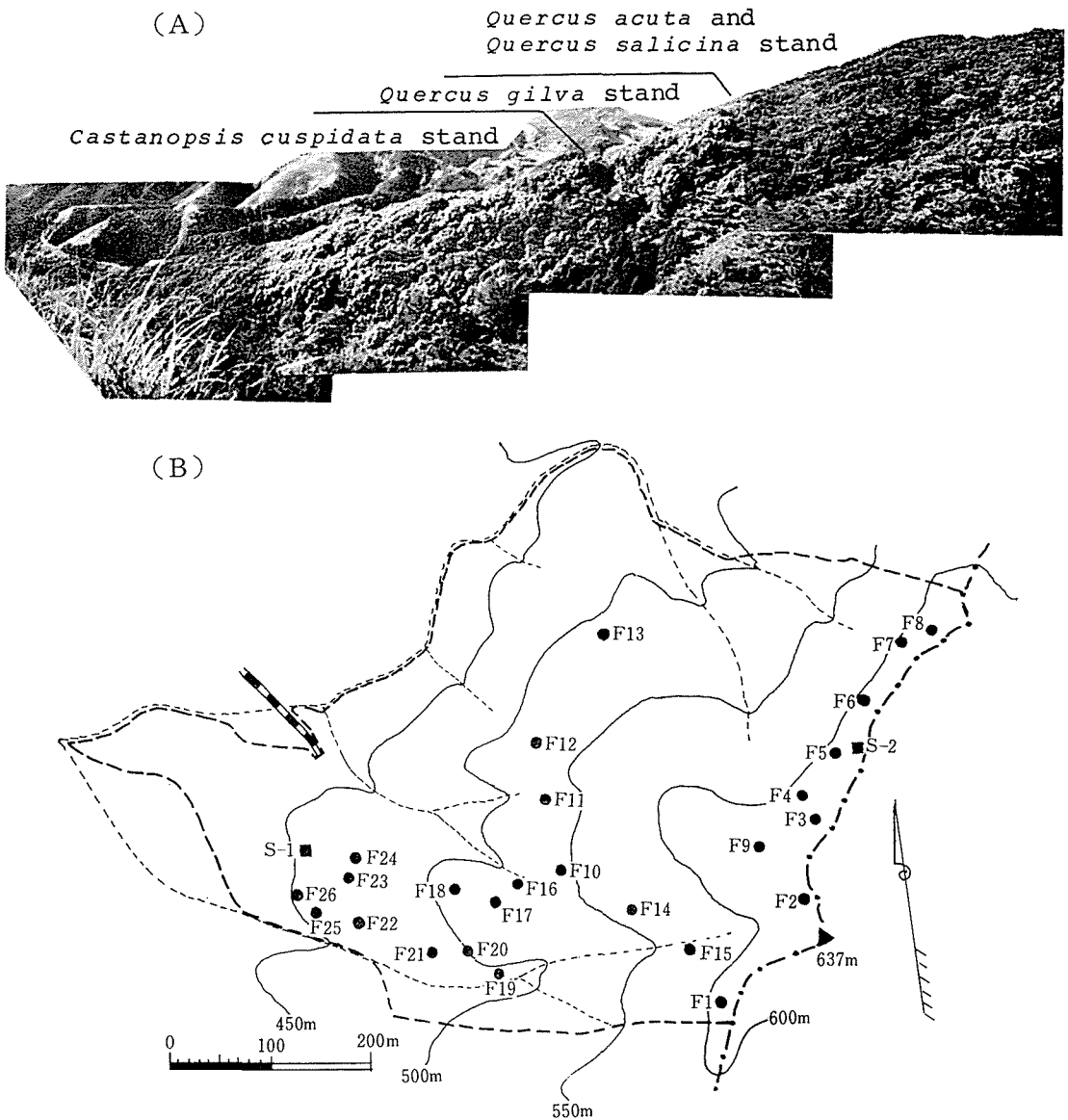


Fig. 1. Minamata Special Research Area of IBP.

(A) General view of the southernmost ridge in the area.

(B) Display of 26 seed traps (F1 to F26) and 2 squares (S-1 and S-2) for the observation of seedlings.

which tetron cloth is hung, and top of the funnel is covered by 13 mm meshed hardware screen to prevent invasion of small rodents and birds. The area of the top of the trap is 1 m<sup>2</sup>.

The number of traps necessary for the estimation of seed fall in reasonable way was calculated to be 26 by I<sub>s</sub>-method (ONO, 1967) which is based on variance of the number of fallen seeds among 14 traps used in the preparatory study. Twenty-six seed traps were assorted into 4 groups, and they were placed in 4 types of vegetational stand (OMURA *et al.*, 1969) i. e. 10 traps were placed in *Quercus acuta* stand, 6 in *Q. salicina* stand, 2 in *Q. gilva* stand and 8 in *Castanopsis cuspidata* stand in the definitive study. Location of these traps in the forest is illustrated in Fig. 1. Most traps were placed near the track in the forest in order to save time in collecting vegetable matter in the trap.

The matter collected was brought back to the laboratory and classified into species and furthermore into sound, immature, damaged, infected and empty seed groups under binocular. Collection of the vegetable matter in the trap was carried out once a month, but several times it was inevitably delayed on account of unavoidable circumstances, namely, weather, accidents and school duties. Seeds and fruits may suffer from loss of their number and viability from desiccation and damages given by such organisms as insects and fungi while they are in the trap. The loss becomes greater as the time they stay in the trap grows. Considering this situation, the obtained number of seeds by the trap method may be underestimate to some extent.

According to the results of seed fall hitherto been observed, seeds fell throughout the year manifesting more or less uneven distribution of fall. May is the least harvesting month in the evergreen broadleaved forest, and early in June cherry (*Prunus jamasakura*) stones begin to fall. It is, therefore, quite natural that the term from June to May of the year ensuing is thought to be one bearing season in the sense of a community as a whole (TAGAWA, 1969), not in the sense of individual population. In the present paper the term bearing season is used in this definition.

## 2. Observation of seedlings

A square of which four sides are 10 m long was placed in each of *Q. acuta* and *C. cuspidata* stands as illustrated in Fig. 1. The square was divided into 4 smaller grids. The individual seedlings found in a grid (5m×5m) was marked with white vinyl tape on which the marking number was written around the young stem, and those in the rest 3 grids and those germinated afterwards were completely uprooted. Observation was carried out in November every year.

In autumn of 1969, *C. cuspidata* in *C. cuspidata* stand produced a lot of acorn followed by the origination of great many seedlings. Acorn of *C. cuspidata* matures in November and December after twenty months from pollination in April of the preceding year, and hypocotyl and radicle come out immediately after fall. But, the leaf does not bud out until next spring. Whilst, *M. thunbergii* had a mast year in 1971 and produced many berries. The berry which holds one seed develops in July, and germinates soon after their fall. It is said that both acorns and seeds are not resistant to desiccation after fall, and they germinate immediately under a favorable condition in the soil without showing any dormancy.

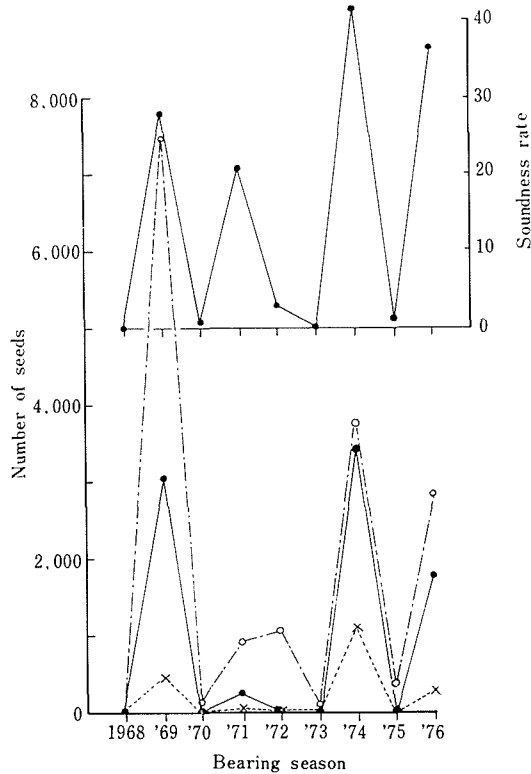
**Table 1.** The number of sound (S), immature (I) and damaged (D) seeds fallen in the area of

Bearing season Species/Stand	1968*			1969			1970			1971		
	S	I	D	S	I	D	S	I	D	S	I	D
<i>Castanopsis cuspidata</i> Schottky												
in <i>Q. acuta</i> stand	—	—	—	—	6	4	—	50	—	2	12	6
in <i>C. cuspidata</i> stand	—	—	—	3800	9338	551	1	149	3	321	1116	100
<i>Machilus thunbergii</i> Sieb. et Zucc.												
in <i>Q. acuta</i> stand	74	400	76	—	—	—	—	—	—	209	1312	112
in <i>C. cuspidata</i> stand	—	—	—	—	—	—	—	—	—	19	33	8

## II. Results and Discussion

### 1. Seed fall

Entire aspect of seed fall of both species *Castanopsis cuspidata* and *Machilus thunbergii* in *Quercus acuta* and *C. cuspidata* stands is shown in Table 1. The number of fallen seeds in 1968 bearing season was based on 5 traps used in the preparatory study. In the definitive study from 1969 bearing season onward



**Fig. 2.** Yearly fluctuation of seed fall by *Castanopsis cuspidata*.

- : Developed and sound seeds
- -○: Immature seeds
- ×.....×: Developed and damaged seeds

10m<sup>2</sup>. \*Data in 1968 season were obtained in the preparatory study.

1972			1973			1974			1975			1976		
S	I	D	S	I	D	S	I	D	S	I	D	S	I	D
—	—	—	2	2	—	—	4	4	—	9	7	2	3	—
43	1323	58	—	133	3	4295	4670	1403	5	478	13	2226	3536	360
—	—	—	—	—	—	—	—	—	482	883	176	—	5	—
—	—	1	—	—	—	—	—	—	86	84	15	—	—	—

10 traps have been used in *Q. acuta* stand as described above. While in *C. cuspidata* stand 3 traps in 1968 bearing season and 8 traps since 1969 were used for the estimation. There is, therefore, a difference in accuracy of estimation of the number of seeds between 1968 and the other bearing seasons.

According to Table 1, the seeds of *C. cuspidata* are very few in *Q. acuta* stand, which may have arisen from the poverty of mother trees. *M. thunbergii* is in the same situation in *C. cuspidata* stand.

Fluctuation of seeds of *C. cuspidata* fallen in *C. cuspidata* stand is illustrated in Fig. 2 together with soundness rate—rate in percentage of the number of sound seeds against the total seeds fallen. In the figure the number of the sound, immature and damaged seeds show the same trend of fluctuation. So the people can foresee the abundant crop of acorns in winter from the fall of a large quantity of the immature seeds in summer. The similar pattern of fluctuation was observed in many other species such as *Q. acuta*, *Cornus macrophylla* and so on. On the other hand, there is another type of relationship between the number of the sound and the immature seeds. *Q. gilva* produced the maximum number of acorns at the minimum sacrifice of the immature seeds in 1974 season (Fig. 3B). In this case the abundant fall of the immature seeds is not a prelude to the corresponding heavy production of the mature acorns.

Soundness rate of *C. cuspidata* is high in high production of acorns. From the statistics of long-term observation the greater parts of the immature seeds fell damaged by insects, and the reciprocal number of soundness rate may be roughly equal to damaged rate of seed. The fact that the damaged rate of seeds is higher in a lean year and it is very low in a mast year rouses our warm interest in the mutual influences between the amount of fruits and seeds and densities of a swarm of the insects feeding upon them. This type of ecological relationship has never been studied in our project team of IBP. In Fig. 3 rather high seed production of *Q. gilva* in 1974 season may be the result of low damage rate.

The yearly fluctuation of the number of the sound seeds shown in Fig. 2 seems to be somewhat irregular. Mast years observed by *C. cuspidata* were 1969, 1974 and 1976 seasons. The other two acorn-producing oaks, *Q. acuta* and *Q. gilva* had their own mast years in different seasons. *Q. acuta* had rather outstanding seed year in 1972, and *Q. gilva* a neutral peak in 1974. Lack of synchronized mast year in a community may give a hint for finding factors

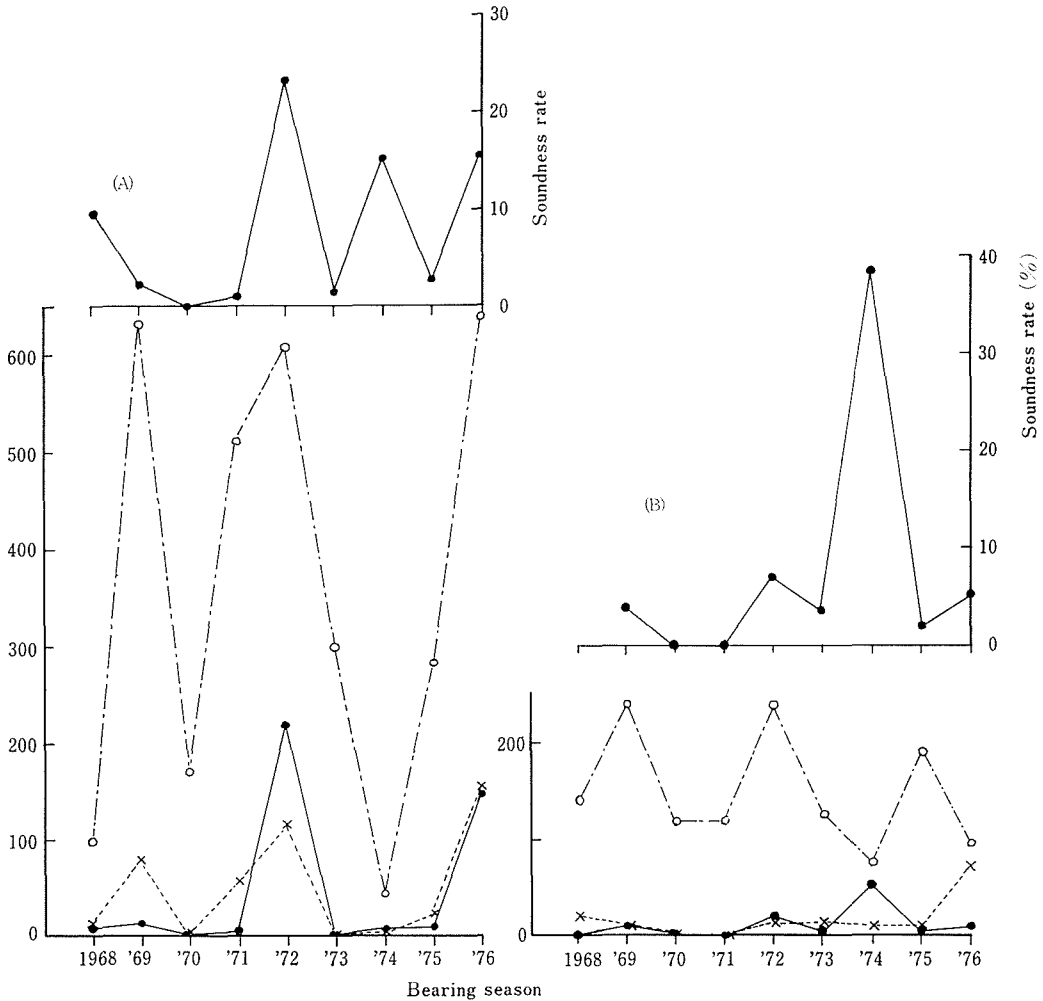


Fig. 3. Yearly fluctuation of seed fall by *Quercus acuta* (A) and *Q. gilva* (B). See also the explanation of Fig. 2.

controlling seed production.

DOWNS and MCQUILKIN (1944) surveyed acorn fall for 7 years from 1936 to 1942 in southern Appalachian oak forest, and found that yearly fluctuation of acorn drop of the following 5 species, *Q. borealis maxima*, *Q. velutina*, *Q. coccinea*, *Q. alba* and *Q. montana*, was not so divergent between the oak group which develops seed in one year and the other group which requires two years, so they could not assume weather condition to be a factor affecting seed crop.

CHRISTISEN (1955) observed seed production of 5 oak species, *Q. velutina*, *Q. marilandica*, *Q. coccinea*, *Q. stellata* and *Q. alba*, for 6 years from 1947 to 1952 in Missouri Ozarks, and described that *Q. stellata* produced acorns constantly every year, three oaks, *Q. velutina*, *Q. marilandica* and *Q. alba*, showed several seed years and the seed year corresponded with each other in some seasons but not in others, and that *Q. coccinea* produced acorns in all-or-nothing pattern, that is, acorn fell heavily in some season and none in other seasons. He did not,

however, introduce any factors to explain the irregularity of acorn production.

In Minamata both *C. cuspidata* and *Q. acuta* bloom simultaneously in April and produce developed seeds in November of the next year, and they had mast years in different season from each other but for 1976 season. It is, therefore, hard to think that only weather controls their seed production.

*M. thunbergii* is a characteristic dominant of an evergreen broadleaved forest in Japan and grows in S China and Taiwan. It showed distinct pattern of bearing season like *Q. coccinea* in Missouri. Mast years of this laurel species in 1968, 1971 and 1975 did not coincide with those of *C. cuspidata* even when the time necessary for the maturation of seeds was taken into consideration.

Growth of vegetative organs such as stem, branch and twig is deeply influenced by the consumption of organic matter for producing a number of fruits as well as the photosynthetic activity. GROSS (1972) reported that *Betula alleghaniensis* and *B. papyrifera* had their crowns deteriorated and the growth of tree boles was reduced as the result of excessive seed production. As far as the species are concerned in Minamata 'die-back' phenomenon has never been observed, but there may be reduced growth of the trees associated with seed production. Consideration in this connection will be given in near future.

## 2. Production of seedlings

The observation of seedling production was carried out in two squares, S-1 in *C. cuspidata* stand and S-2 in *Q. acuta* stand (see Fig. 1) in every November when a part of seeds fallen and stocked in the soil of the forest had finished germination. The number of observed fresh seedlings is shown in Table 2. Seed-

**Table 2.** The number of seedlings observed in the squares of 100m<sup>2</sup>. S-2 square was not yet placed in *Quercus acuta* stand in 1970. \*One-hundred-and-ninety-eight seedlings were found dead in November (1971w in Table 3), but seemed to be alive in summer (1971s).

Species	The number of seedlings (100m <sup>2</sup> )								
	Observation in	1970	1971	1972	1973	1974	1975	1976	1977
In <i>Quercus acuta</i> stand (S-2)			288						
<i>Machilus thunbergii</i>			198*	6.7	5.3	86.7	295	32	2
<i>Trachelospermum asiaticum</i>			—	392	181.3	86.7	56	81.3	221
<i>Quercus acuta</i>			—	1.3	14.7	—	5	—	29
<i>Castanopsis cuspidata</i>			2	1.3	—	—	—	—	—
<i>Neolitsea sericea</i>			2	1.3	—	2.7	3	—	1
<i>Ligustrum japonicum</i>			—	—	—	1.3	—	—	—
<i>Neolitsea aciculata</i>			4	—	—	—	1	—	—
<i>Quercus myrsinaefolia</i>			—	—	—	4	—	—	—
In <i>Castanopsis cuspidata</i> stand (S-1)									
<i>Castanopsis cuspidata</i>		956	302	94	122	50	58.7	432	335
<i>Machilus thunbergii</i>		52	26	4	2	—	292	38	27
<i>Trachelospermum asiaticum</i>		—	—	78	34	56	4	16	46
<i>Prunus spinulosa</i>		4	—	—	2	2	—	—	1
<i>Quercus gilva</i>		8	—	—	—	2	—	—	1
<i>Cinnamomum japonicum</i>		—	—	—	—	—	2.7	—	—

ling group of *C. cuspidata* based on the acorns fallen heavily in winter 1969 in S-1 was checked individually by the observation one year later in November 1970. On the other hand, the summer-germinating species, *M. thunbergii*, yields its seedlings in summer to be examined in November of the year.

Yearly fluctuation in seedling production of *C. cuspidata* and *M. thunbergii* is illustrated in Fig. 4. The large number of seedlings of *C. cuspidata* produced in 1970 corresponded with the heavy acorn fall in 1969, but the other peaks of fall were out of accord with those of seedling production. The great many acorns fallen in 1974 were not followed by the production of a number of seedlings in 1975 but in 1976, two years after the acorn fall. This phenomenon is not satisfactory explained by assuming that if acorn is unsuccessful in germinating immediately after fall in November and December, it will be decayed without lying dormant in the soil. The present author would consider that the acorn of *C. cuspidata* was probably stored in the soil at most for one year if the condition of soil humidity was effective for keeping it alive and for disturbing desiccation of acorn. There is a possibility that the majority of acorns fallen in 1974 was mostly removed by rodents and birds, and that for 1976 many acorns were brought from other forests with good harvest by the avian agency. But it may be denied by the inference that the avian influence on seed fall and seedling production through the carriage of acorns may be equally exercised on the seed traps and on

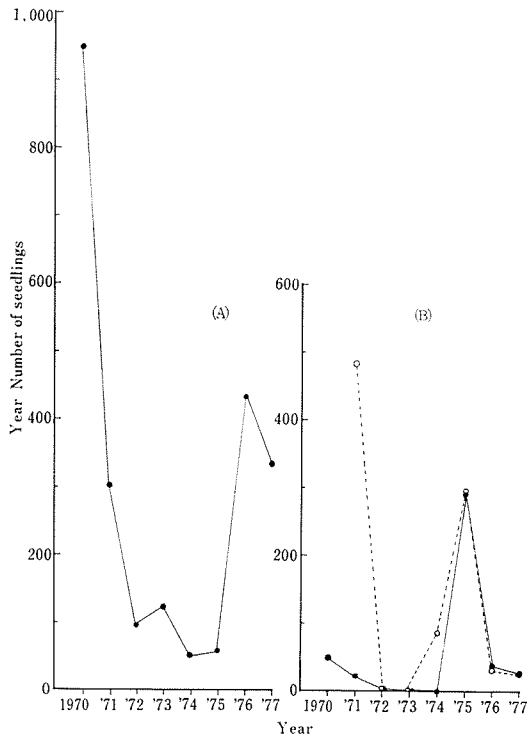


Fig. 4. Yearly fluctuation of seedling production by *Castanopsis cuspidata* (A) and *Machilus thunbergii* (B) in *C. cuspidata* stand (●—●) and in *Quercus acuta* stand (○·····○).



the squares.

Most years in *M. thunbergii* population, on the other hand, shown in Table 1 corresponded sharply with the years showing peaks of seedling production. This may be the result of complete loss of dormancy from the seed due to a thin and soft coat of seed. The fruits of this species are eaten by raccoondog (*Nyctereutes viverrinus*) by preference together with those of *Diospyros lotus*, and the seeds are evacuated in a heap of excrement. We can find frequently such a large mass of faeces overwhelmed by seedlings of *M. thunbergii* in places in the forest. To be lucky, those mass of faeces was not found in the squares for seedling observation.

### 3. Natural thinning of seedlings

Figure 5 shows two contrasting survivorship curves and death rate curves of *C. cuspidata* and *M. thunbergii* seedlings. The survivors of the former decrease linearly with time, and those of latter in negative-exponential way.

Gradually increasing age-specific mortality rate by *C. cuspidata* and linear thinning of seedlings may be due to a certain factor, supposedly light paucity, which blights seedlings year to year. In the population of *M. thunbergii* three mortality factors may contribute to the natural thinning of the seedlings. From summer to winter in 1971, the seedlings were abruptly decreased in their number by the extreme summer desiccation coming after the rainy season in June and July. In the xeric condition on the forest floor radicle can hardly reach the mineral soil due to disturbance from thick accumulation of fresh litter which falls heavily from April to May in the evergreen broadleaved forest. The second factor causing gradual decrease in number may be due to the paucity of light. In addition to these two factors of mortality in seedling growth, there is the third factor causing destructive result to the seedlings brought about by a few herbivore. It was very hard to assign the number of the dead seedlings to any factor responsible for.

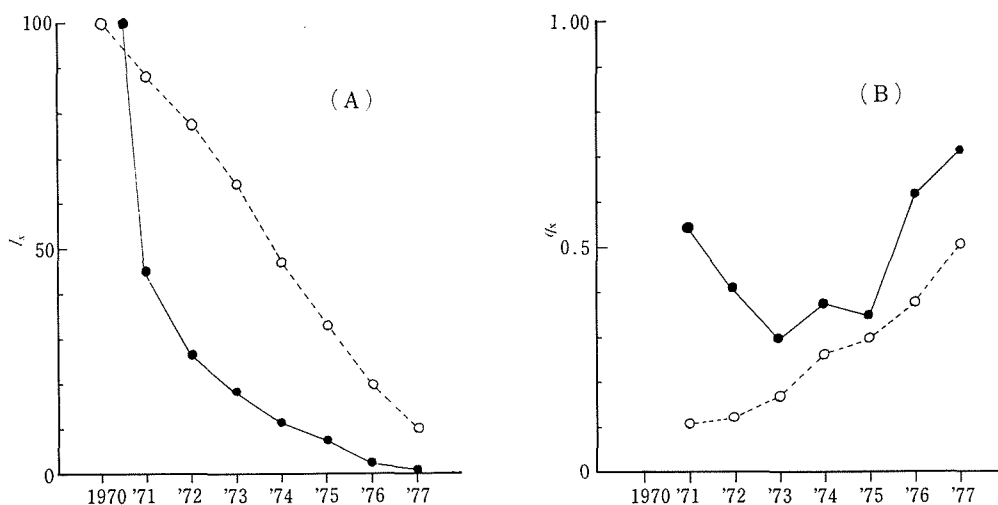


Fig. 5. Survivorship curves (A) and age-specific mortality curves (B) of *Castanopsis cuspidata* (○·····○) and *Machilus thunbergii* (●——●).

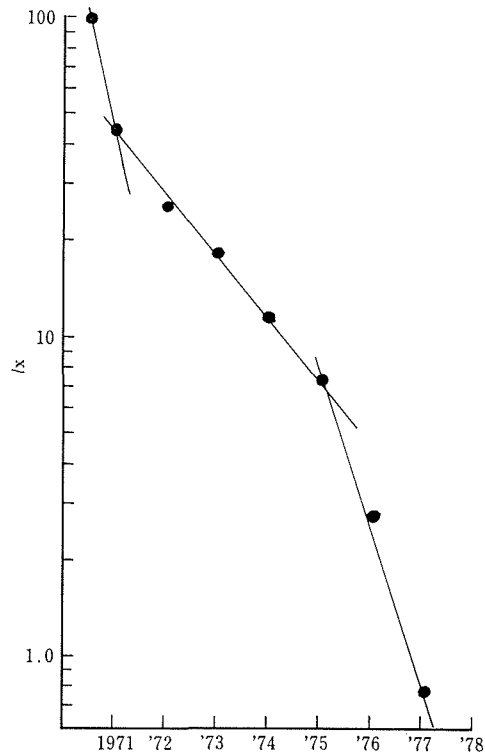


Fig. 6. Survivorship curve of *Machilus thunbergii* in semi-logarithmic scale.

From the different standpoint of view HETT and LOUCKS (1971) applied the negative exponential and power function models to the age distribution of the seedlings of *Acer saccharum*, and found that the power function was adequate to describe the exhaust of seedlings, and that the effects of the environment was not detectable in the survivor of the seedlings. In his case mortality constant,  $b$  in the power function,  $y=y_0x^{-b}$ , was fixed through 10 years from the date of germination. By the application of the negative exponential model,  $y=y_0e^{-bx}$ , to the data of *M. thunbergii*, the survivorship curve shown in Fig. 5 was replaced by three straight lines with different values of  $b$  (Fig. 6). The author supposes that these different values of mortality constant agree with that there were three factors responsible for the death of seedlings. The power function was not fitted to the description of the survivorship curve of *M. thunbergii*.

WOOD (1938) who worked on the seedling production of *Quercus montana* in southern New Jersey, described many types of seedling destruction given by animals and insects, and gave eight unfavorable conditions for the seedling growth. He mentioned 'lack of litter cover, or excessively deep litter for the seed' at the top, and also gave attention to 'lack of moisture in the soil' and 'prolonged presence of the old overwood after germination'. PETERKEN (1966) studied on the mortality of *Ilex aquifolium* seedlings, and stressed such factors causing the death of holly seedlings as lack of soil moisture, deep shade, nibbling, browsing and physical disturbance. He reached the conclusion that the great majority of seedling died in five years, but that only a few remainder was enough to regenerate the same type of forest again.

From the cumulate data obtained in the forest of Minamata by the author, gregariously originated seedlings of every species shortly after the seedfall in a mast year disappear completely or leaving a few stems in one decade or so along the characteristic way of thinning as shown in Fig. 5. The extremely small number of the seedlings left must exist and grow up to saplings in inanition on the dark floor under the multiple layers of foliage. A number of seedlings killed in the process of their growth is a waste of organisms from the forest, but the

**Table 3.** Simply simulated number of seedlings. The italic characters show the number of sound seeds fallen in each year (Table 1). The numerical characters shown at the top in Roman indicate the number of seedlings observed in the field (Table 2), and those shown below them are the estimated number of seedlings from the survivorship curves illustrated in Fig. 5.

Year	<i>Castanopsis cuspidata</i>								Total
	The number of seedlings								
1969	<i>38000</i>								
1970	956	<i>10</i>	..	..	..	..	..	..	956
1971	848	302	<i>3210</i>	..	..	..	..	..	1150
1972	740	268	94	<i>430</i>	..	..	..	..	1102
1973	612	234	83	122	<i>0</i>	..	..	..	1051
1974	448	193	73	108	50	<i>42950</i>	..	..	872
1975	315	142	60	94	44	59	<i>50</i>	..	714
1976	196	100	44	78	39	52	433	<i>22260</i>	941
1977	96	62	31	57	32	46	383	335	1037
1978	..	30	19	40	23	38	334	297	781
1979	..	..	9	25	17	28	276	259	614
1980	..	..	..	12	10	19	203	214	458
1981	..	..	..	..	5	12	143	157	317
1982	..	..	..	..	..	6	89	111	206
1983	..	..	..	..	..	..	43	69	112
1984	..	..	..	..	..	..	..	34	34

Year	<i>Machilus thunbergii</i>								Total
	The number of seedlings								
1971 s	<i>2090 : 486</i>								
1971 w	288	..	..	..	..	..	..	..	288
1972	130	<i>0 : 7</i>	..	..	..	..	..	..	137
1973	90	4	<i>0 : 5</i>	..	..	..	..	..	99
1974	56	3	3	<i>0 : 87</i>	..	..	..	..	149
1975	36	2	2	51	<i>0 : 295</i>	..	..	..	386
1976	14	1	1	34	172	<i>4820 : 32</i>	..	..	254
1977	4	0	1	22	116	19	<i>0 : 2</i>	..	164
1978	..	0	0	14	74	13	1	..	102
1979	..	..	0	5	48	8	1	..	62
1980	..	..	..	2	18	5	1	..	26
1981	..	..	..	..	5	2	0	..	7
1972	..	..	..	..	..	1	0	..	1
1983	..	..	..	..	..	..	0	..	0

periodical production of seedlings is understood as the provision of the forest against fall of trees, lumbering and destruction of the forest.

#### 4. *A simplified simulation for age distribution from seedling production and survivorship curve*

Now, we can estimate the age distribution of seedlings from the data shown in Table 2 and Fig. 5 on the assumption that the survivorship curves of the two species are fixed anytime. For example, 38000 acorns  $100\text{ m}^{-2}$  of *C. cuspidata* fell in 1969 season (Table 1), and produced 956 seedlings in 1970 in *C. cuspidata* stand. The seedlings are assumed to disappear at the rate shown in Fig. 5. One year later, 956 seedlings decrease to 848 ( $=956 \times 88.7\%$ ), two years later to 740 and so on. The result of calculation is shown in Table 3. There is no datum available for the calculation of seedling production before 1969. According to Fig. 5, however, the seedlings of *C. cuspidata* born in 1970 were calculated to come to the complete disappearance from the forest floor by 8th year. If so, a probable age distribution of the seedlings is obtained in the complete form for 1977 only as follows.

Age of seedling	1	2	3	4	5	6	7	8
The number of seedlings	335	383	46	32	57	31	62	96

The age distribution shown above shows wavy fluctuation which meets our expectation, and, of course, it does not agree with the periodicity of seedfall and of seedling production.

The number of seedlings of *M. thunbergii* produced in 1968 is unknown, and the tail of the survivorship curve is seemed to be endless. The calculated number of seedlings in each year shows steep ups and downs in number because of all-or-nothing feature of seed fall and abrupt disappearance of the seedlings.

The reverse process is possible, too. If we know the age distribution of seedlings of some species in the field and its survivorship curve, we can estimate the seedling production by calculating backwards. In this type of forest, however, it is difficult to recognize the annual ring in the stem of evergreen broadleaved species and so the age of its seedling.

### Summary

1. The amount and the yearly trend of seed fall were described on *Castanopsis cuspidata* (Fagaceae) and *Machilus thunbergii* (Lauraceae) which are dominant and co-dominant in the evergreen broadleaved forest at Minamata (JIBP research site).
2. The observation of seed fall for 8 years showed that the fluctuation of immature and developed seeds were parallel with each other, but that in some bearing seasons *M. thunbergii* dropped a number of berries with premonitory fall of a few undeveloped seeds. This may be caused from the low damage rate of seeds. Making use of the data on *Quercus acuta* and *Q. gilva*, discussion was focussed to that the weather was not always responsible for the alternate bearing of these

two species.

3. Yearly trend of seedling production was closely correlated with seed fall by *M. thunbergii* but ambiguous by *C. cuspidata*. The reason of this inconsistency found in the latter may be due to a shallow dormancy of the acorn.

4. The survivorship curves were obtained from the successive observation of seedlings for 8 years. The seedlings of *C. cuspidata* disappeared linearly and those of *M. thunbergii* in the negatively exponential way. Probable factors concerned in the disappearance of seedlings are desiccation of forest floor, light paucity under the multiple layers of foliage and biotic agents.

5. Wavy distribution of age in seedlings was obtained by synthesizing the data concerning seedling production on the forest floor every year and the survivorship curve on the assumption that the curve of survivorship was fixed anytime. There was described the possibility of estimating seedling production from the age distribution of a species.

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