J. Plant Res. 107 : 153-159, 1994

Journal of Plant Research

Comparative Studies on Acorn and Seedling Dynamics of Four *Quercus* Species in an Evergreen Broad-Leaved Forest

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The dynamics and regeneration probabilities of *Quercus acuta, Q. gilva, Q. salicina,* and *Q. sessilifolia* were studied in a 0.48 ha plot in an old-growth evergreen broad-leaved forest, Kagoshima prefecture, southwestern Japan. The canopy was well closed and had only one small gap. Seventeen tree species occurred in the canopy. The four *Quercus* species ranked second to fifth in basal area. Excluding the trees originated from sprouts, *Q. acuta and Q. gilva* lacked trees at the subcanopy layer, and *Q. salicina* and *Q. sessilifolia* had some trees at the same layer. For each *Quercus* species, the amount of fallen acorns fluctuated from year to year. The number of current year seedlings was positively correlated with the number of fallen acorns in the previous year. A disproportion between the spatial distribution of fallen acorns and that of established seedlings has been shown. The establishment of seedlings was frequently observed where no acorns had fallen in the previous year. Saplings of four species survived for several years and formed sapling banks under the closed canopy. During the three years of the study, the mortality of *Q. salicina* and *Q. sessilifolia* saplings was lower than that of *Q. acuta* and *Q. gilva*. However, the differences in the average annual height growth of saplings between four species were not significant, and the most of them did not grow much. These results suggest that the saplings of the four *Quercus*, especially *Q. gilva* and *Q. acuta*, have no chance to recruit to the canopy or subcanopy layer within a closed stand, and that some changes in the environment caused by gap formation are required for their recruitment.

Key words : Acorn fall — Evergreen broad-leaved forest — Population dynamics — *Quercus* — Regeneration — Seedling and sapling bank

Many evergreen *Quercus* species are distributed widely in East Asia. *Quercus acuta, Q. salicina* and *Q. gilva* are the major tree species of evergreen broad-leaved forests in the inland of southwestern Japan (Numata *et al.* 1972). *Q. sessilifolia* is a dominant tree species of old-growth forests in Kyushu region (Miyawaki 1981). Together with many other species, the four *Quercus* species exist as canopy trees in old-growth forests in the lowlands of southern Kyushu. Although the coexisting *Quercus* species show the different characteristics from other canopy species on the population structure, it is still uncertain whether the dynamics vary among the *Quercus* species or not. There have been some studies on the dynamics and structure of evergreen *Quercus* populations (Omura *et al.* 1978 ; Naka, 1982). Also, germination and seedling growth of *Quercus* species have been studied (Takenaka 1986 ; Yamashita and Hayashi 1987 ; Matsubara and Hiroki 1989 ; Tanouchi 1990 ; Tripathi and Khan 1990 ; Ono and Suganuma 1991). However, only few attempts have been made to compare the population dynamics of coexisting *Quercus* species.

A full range of each growth stages (from germination through adult) should be studied to clarify life-history and regeneration patterns characteristic of the species in a forest ecosystem. Acorns of *Quercus* do not survive as buried seeds longer than one year (Takeshita personal observation). The acorns germinate almost immediately (Naka and Yoda 1984), and they form seedling and sapling banks (Naka 1982). Experimentally Tanouchi (1990) proved that saplings of some *Quercus* have a high survival rate, but low height growth rate beneath a closed canopy. In old-growth forests, they are not dominant gap successors (Yamamoto 1992), although their growth should be accelerated by gap formation. Therefore, these *Quercus* species have few small sized individuals under a closed canopy (Tanouchi and Yamamoto unpublished). Thus, the dynamics of early stages, from acorn fall to establishment of seedling and sapling bank, need further observations.

We studied the dynamics of four canopy *Quercus* species in a closed forest. We focussed on four aspects : (1) size and spatial distribution of trees, (2) amount of acorn fall and spatial relation between acorn

Abbreviation : ha, hectare ($=10{,}000\ m^2$)

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fall and seedling establishment, (3) survival and growth of the seedlings and saplings, (4) maintenance of seedling and sapling banks in the undergrowth, and then we compare the population dynamics of the four *Quercus* species and characterize the seed and seedling dynamics of each species.

Methods

Study site

The study area is an old-growth evergreen broad-leaved forest in Kagoshima prefecture, Kyushu region, southwestern Japan. The location of site is 32°8′N and 130°32′E and altitude ranges from 485 to 495 m above sea level. The annual mean temperature and precipitation, from 1981 to 1991 in the nearest meteorological station, were 14.9°C and 2,371 mm, respectively. The bed rock is pyroxene andesite. The most abundant soil type is moderately moist brown forest soil by the Forest Soil Division (1976) classification.

According to phytosociological classification, the site is located in the lower area of Distylio-Quercetum salicinae association (Miyawaki 1981). *Quercus salicina, Distylium racemosum, Persea thunbergii* and *Q. acuta*, which are dominant canopy species in the association, were coexisting with *Q. gilva* and *Q. sessilifolia* in the study area.

Methods of study

A study plot (60 m×80 m) was set on an east-facing gentle slope with a stream in 1988. There was only one small gap (ca. 85 m^2) in the plot. The plot was divided into 48 sub-plots (10 m×10 m each) to facilitate the mapping of tree locations and other surveys. The diameter at breast height (dbh), tree height and location of trees taller than 1.3 m were recorded. At the center of each sub-plot, we set up 48 quadrats (2 m×2 m each) for observing seedlings (current year old) and saplings (more than one year old and less than 1.3 m in height). Adjacent to each quadrat, we set up a seed trap (0.5 m^2 each). Of 48 quadrats, seven quadrats were not used for the observation because they covered exposed bed-rocks in the stream bed.

Litter and fallen seeds were collected from the traps monthly from April 1989 to March 1992, and the number of acorns was counted. The acorns were sorted into mature and immature. The determination of either mature or immature depended on their external morphology and the ability to germinate. In this study, acorns whose embryo was damaged by animals or fungi were sorted as immature.

In the quadrats, we followed recruitment and survival of seedlings and saplings, and measured their height and number of leaves. The observation started in April 1989, before shoot elongation, and the saplings were classified as 'one year' or older. From 1989 to 1991, the measurement was repeated in December, after the growing season.

The spatial distribution of tree stems was analyzed by m^*-m and ρ indices (Iwao 1972). Correlations of distributions between each pair *Quercus* species were analyzed by using the ω index (Iwao 1977). The unit quadrat size used was 50 m^2, which was the minimum clump size for all *Quercus* species except *Q. salicina*.

Results

Size and spatial distribution of trees

In the 0.48 ha plot, there was a total of 63 tree species, 3,184 trees taller than 1.3 m and total basal area of 22.19 m^2 (46.23 m^2 ha^{-1}). *Distylium racemosum* was the most abundant species and covered approximately a quarter of the total basal area of canopy species. *Quercus salicina, Q. gilva, Q. sessilifolia* and *Q. acuta* were second to fifth in basal area. The proportions of the total basal area and density of the *Quercus* species were very similar to another old-growth evergreen broad-leaved forest (Tanouchi and Yamamoto unpublished). *Q. sessilifolia* was exceptionally abundant in this plot because it normally favors humid soil (Suzuki 1960). In the dbh distribution, all *Quercus* had high densities in larger size classes corresponding to canopy trees of 27-73% in density and showed bell-shaped or discontinuous distributions excluding sprouts (Fig. 1).

In height, all *Quercus* reached 25 m, and the maximum was a *Q. gilva* individual of 27 m. The distribution patterns were characterized by few or no suppressed trees in the sub-tree layer. *Q. acuta* and *Q. gilva* had no understory trees of 3-12 m in height, while *Q. salicina* and *Q. sessilifolia* had some trees (Fig. 1).

Three *Quercus* species had sprouts, and *Q. gilva* lacked sprouts. The tallest sprout was a *Q. salicina* of 3.4 m. All sprouts were attached to a living mother stem and most of them died when they reached 2-3 m in height.

The four *Quercus* showed contagious distributions, and the mean clump sizes were 50 m^2 for *Q. gilva, Q. acuta* and *Q. sessilifolia*, and 200 m^2 for *Q. salicina*. Each clump, however, was a loose concentration. The interspecific associations were either independent or negative. The values of the index between *Q. gilva* and *Q. acuta*, and *Q. salicina* and *Q. gilva*, were greater than zero (0.028 and 0.090, respectively), but the fact that they were close to zero indicated their independence. The most intense negative interspecific association occurred between *Q. sessilifolia* and *Q. salicina*. ($\omega = -0.424$). All associations between *Q. sessilifolia* and the other *Quercus* species were negative. This is due to the fact that *Q. sessilifolia* was mostly distributed along the stream.

Fallen acorns

Irrespective of species or year, almost all mature acorns were fell from October to December (Fig. 2), with the peak in November. This was consistent with the results reported by Hiroki and Matsubara (1982). Immature acorns mostly fell from July to October, about three months earlier than mature acorns, but in 1991 this period came later and they fell at the same time as mature acorns. Typhoon

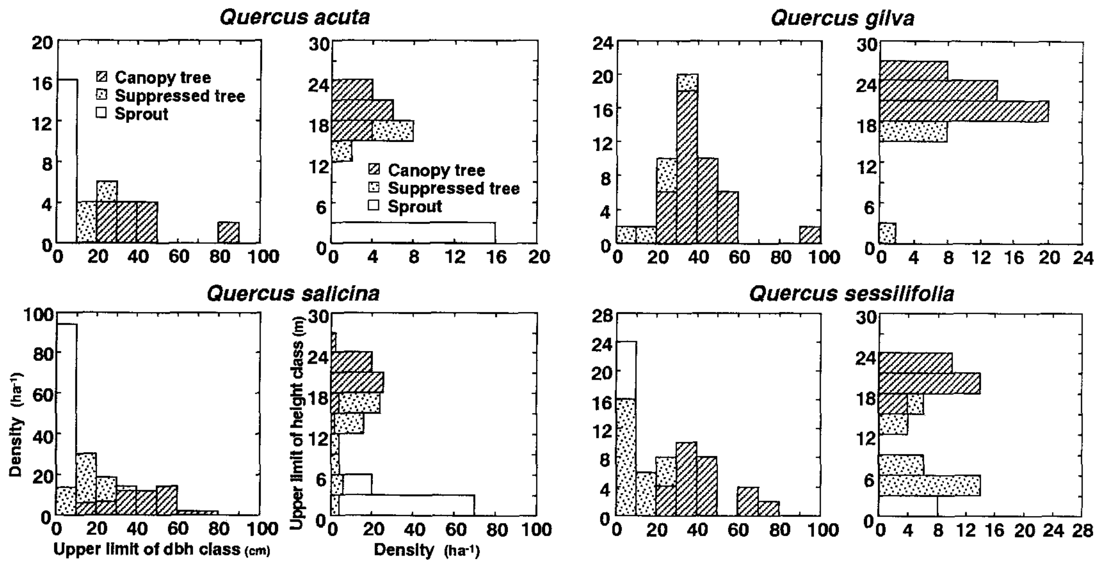

Fig. 1. Dbh and height distribution for four *Quercus* species in the study plot. Included are trees taller than 1.3 m.

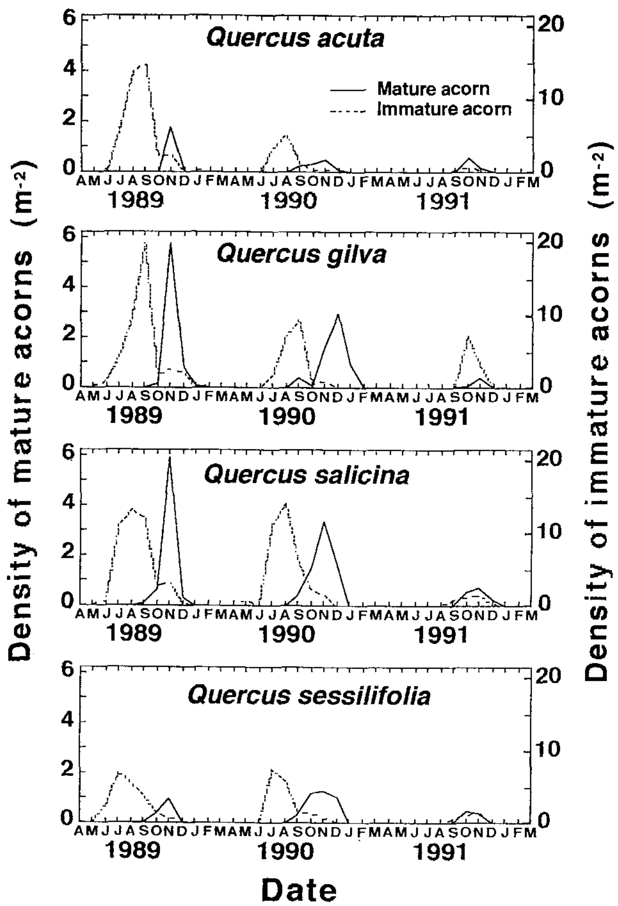

Fig. 2. Monthly amount of fallen acorns of four *Quercus* species for three years in the study plot.

and strong winds in western Kyushu in July, 1989 and 1990 made immature acorn fall, and they were mostly still attached to the branches. In 1991, the crop was smallest, and the minimum density was 0.63 m^{-2} for *Q. gilva* and the maximum 1.54 m^{-2} for *Q. salicina* (Fig. 3). The falling season of immature acorns should depend on timing and frequency of storms with strong winds.

The annual crops of each species were not synchronized except in 1991. The synchronization in a stand has been noted (Kaminaka personal communication), but the mechanism was unknown. If synchronous fruiting occurs, the annual amounts of flowering can not be synchronized because *Q. gilva* fruit takes one year for

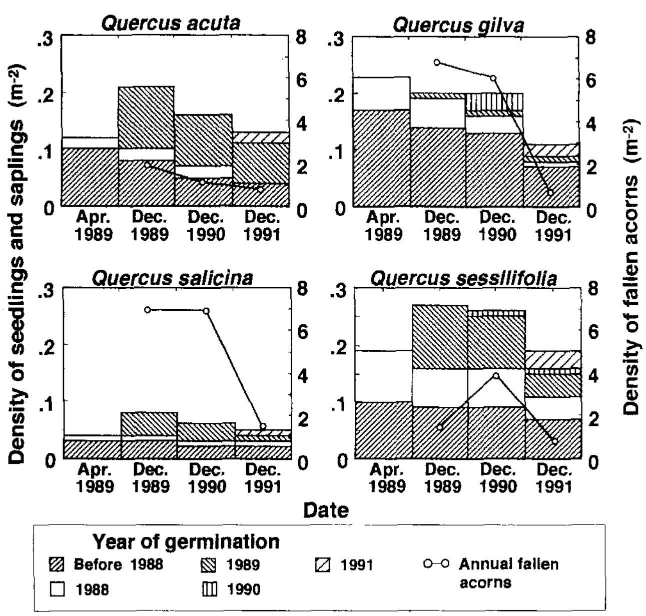

Fig. 3. Number of seedlings and saplings and amount of fallen mature acorns from 1989 to 1991 in the study plot. The densities of seedlings and saplings are the values of four surveys, and the fallen acorns are totals per year.

Table 1. Number of fallen acorns and percentage of seedling establishment for four *Quercus* species

Species	Year	NA[1] (m^{-2})	SR[2] (%)	R1[3] (%)	R2[4] (%)
Quercus acuta	1990	1.88	0		
	1991	1.33	1.63	4.9	0
Quercus gilva	1990	6.83	0.45	6.6	11.1
	1991	6.08	0.30	6.3	6.3
Quercus salicina	1990	6.96	0		
	1991	6.96	0.01	3.8	0
Quercus sessilifolia	1990	1.50	0.81	2.5	12.5
	1991	3.92	0.78	2.3	14.3
All four *Quercus*	1990	17.3	0.15	23.1	2.9
	1991	18.1	0.37	0	19.0

1), number of fallen mature acorns in the previous year; 2), ratio of the number of established seedlings at the late autumn to that of acorns fell in the previous year; 3), percentage of sub-plots where seedlings established in the quadrats without mature acorns fell into the adjacent trap in the previous year; 4), percentage of sub-plots where seedlings established with mature acorns fell.

ripening, whereas other *Quercus* species take two years (Kobayashi and Midorikawa 1959).

Establishment of seedlings

The survival ratio (SR), which is the number of seedlings that survived at the end of the first growing season divided by the total number of fallen mature acorns in the previous year, ranged 0-1.63% for the four *Quercus* (Table 1). The spatial distribution of established seedlings was different from that of fallen acorns in the previous year. The SRs varied but most values were less than 1%. The differences of SRs within and among species were not significant ($P > 0.05$, test of difference among proportions) except that between years in four all *Quercus*.

The percentage of sub-plots where seedlings existed showed no significant difference between in the place with fallen acorns (R2) and with no fallen acorns (R1) ($P >$ 0.05, test of difference among proportions). However, considerable number of seedlings of all *Quercus* were established even where no acorns fell, it means that the seedlings can establish away from the mother trees and are distributed widely.

Survival and growth of seedlings and saplings

All *Quercus* species maintained seeding and sapling banks under the closed canopy (Fig. 3). The densities of these species averaged over four years were 0.16 (*Q. acuta*), 0.18 (*Q. gilva*), 0.06 (*Q. salicina*) and 0.23 (*Q. sessilifolia*) seedlings or saplings per m^2.

The survival ratios of saplings that germinated before 1988 and in or after 1988 (1988-1990) are shown in Fig. 4. At the beginning of the observation, April 1989, the number of saplings was 41, 48, 16 and 51 for *Q. acuta, Q. gilva, Q. salicina* and *Q. sessilifolia*, respectively. The survival ratios for three years after germination in 1988 were higher in *Q. salicina* and *Q. sessilifolia* than *Q. acuta* and *Q. gilva* ($P < 0.05$, test of difference among proportions for three years survival). This difference in the survival ratios between the two groups was also recognized clearly in saplings germinated before 1988 ($P < 0.05$, test of difference among proportions). During the three years of research, the mortality of all *Quercus* saplings that germinated before 1988 was lower than the mortality of younger saplings (≦three years old).

Sapling size structure among the four species did not show as much difference as the survival ratio. The average sapling height of all species in 1991 was taller than in 1989, due to the low mortality rate among large sized saplings (Fig. 5). When larger saplings died, the average height became smaller compared to the previous years (e.g. *Q. salicina* in 1989). The difference in average annual height growth for three years among the four species, e.g. 4.5 cm in *Q. acuta*, 3.3 cm in *Q. sessilifolia*, was not significant ($P > 0.05$, F test). The annual growth of individual trees varied in all species, and several saplings grew more than 10 cm.

The *Quercus* species differed little in the number of leaves per plant. Beneath the closed canopy, they usu-

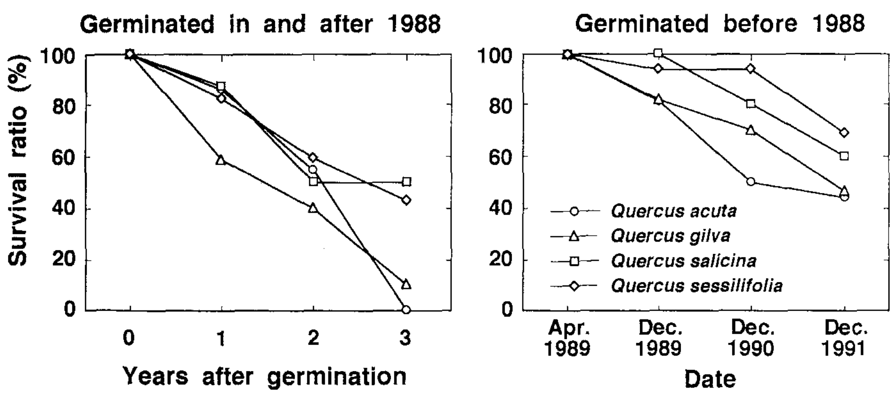

Fig. 4. Survival ratio of saplings beneath a closed canopy. Right and left parts show on the saplings that germinated before and after the beginning of 1988 (the year before the start of the research), respectively.

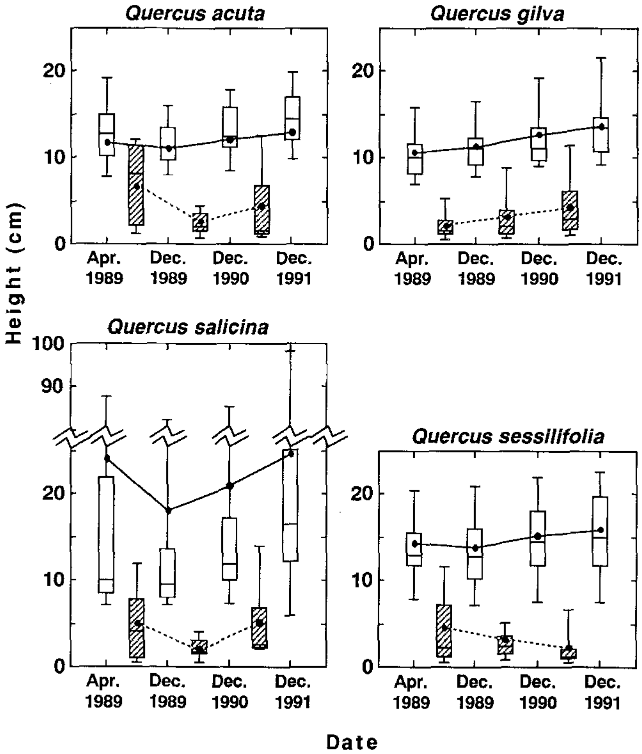

Fig. 5. Height and annual growth of seedlings and saplings of four *Quercus* species beneath the closed canopy in the study plot. The open and shaded boxes show the height and the annual increment of growth, respectively. The center bar in the box denotes the median of height distribution ; upper and lower bars represent the 75th and 25th percentile, respectively ; vertical lines connect the 90th and 10th percentile values ; the circle shows the average. Annual growth means values between dates.

ally elongate a shoot with two leaves once a year, but some saplings did not put forth new shoots. The mean leaf number per seedlings or saplings for the four *Quercus* species was 3.5, and this did not fluctuate sharply for three years. The alternating number of leaves on each individual gradually decreased. The difference between species was not significant ($P>0.05$, F test).

Discussion

Numbers of study have reported on differences in survival under and away from parent trees (e.g. Augspurger 1983, Clark and Clark 1984, Howe *et al.* 1985) and they showed recruitment sites quite far from the parents. Howe (1986) also gave evidence for disproportionate seed and seedling mortality near parent trees. In this study, spatial-disproportionate distribution between fallen acorns and established seedlings was recognized. The spatial distribution of fallen acorns was clumped around the mother tree because the acorns were dispersed from the crown to the ground by gravity. The inconsistent distribution of acorns and established seedlings suggests that considerable amount of acorns were disappeared by predators such as rodents (Kanazawa and Nishikata 1976 ; Price and Jenkins 1986) and birds (Shaw 1968a). Price and Jenkins (1986) noted that rodents cache harvested seeds. Kanazawa and Nishikata (1976) also pointed out the role of rodents in removing and caching *Quercus* acorns. Seedlings that established in sites where no mature acorn fell in the previous year must have originated from acorns that were removed from the foot of the parents, but later they escaped detection and germinated. Removed acorns contribute much to the establishment of the seedlings (R1 in Table 1). This fact signifies that possible sites for establishment extend away from a clump of a large amount of fallen acorns. Further, it should be noted that in some *Quercus* auto-allelopathy causes inhibition of germination of conspecific acorns under the mother tree (Bran *et al.* 1990).

The probability of seedling establishment is greatly influenced by predation and fungal pathogens (Shaw 1968b, Borchert *et al.* 1989, Briggs and Smith 1989). If predators and fungi are not host-specific, a rich or poor acorn fall of a species should influence the survival of other species. Briggs and Smith (1989) reported that the mice consumed *Quercus* acorns selectively, but the selection may be influenced by exposure to acorns. Predators may become specialists in certain species or may not choose depending on the abundance or kind of food available. In our study, although the survival ratios of acorns to be established as seedlings showed various values among the four species (Table 1), the differences were not significant. Consequently a species-specific phenomenon was not recognized during three years observation. Compared with the amounts of fluctuation in the number of fallen acorns, there was little variation in the number of established seedlings each year. Despite the low ratios of establishment, seedling and sapling banks have been maintained (Fig. 3) because of the low mortality of aged saplings.

The four *Quercus* species were divided into two groups by their mortality. One includes *Q. acuta* and *Q. gilva*, and the other includes *Q. salicina* and *Q. sessilifolia*. Because of the lower mortality, we assume that *Q. salicina* and *Q. sessilifolia* are more shade tolerant than *Q. acuta* and *Q. gilva*. Still there was no significant difference in the density of the *Quercus* seedlings and saplings compared to *Distylium racemosum* and *Persea thunbergii* (Sato *et al.* unpublished) and the annual fluctuations of the *Quercus* species were also small. In 1991, saplings over five years old occupied more than 25% in the sapling bank. The survival ratios of saplings that germinated before 1988 were higher than the younger saplings, but they could hardly increase in mean height (Fig. 5). These elder saplings are likely to be individuals that differ in their history or origin (e.g. sprouts after mother stem died).

Generally the population of seedlings and saplings is maintained by seedling recruitment and their survival. When the difference between them occurs, the population level will increase or decrease. Certainly the population of seedlings and saplings for each *Quercus* somewhat fluctuated every year. This was mainly caused by the change in number of seedlings recruited (Fig. 3). *Q. salicina* and *Q. sessilifolia* showed lower mortality, not that this group had larger sapling bank than the other group. During the observation, the difference in the probability of seedling establishment among the *Quercus* species was not significant, although the values varied from year to year. However the population level was determined by the balance between recruitment (seedling establishment) and mortality. When the recruitment is lower than the mortality, *Quercus* species can not maintain the seedling and sapling bank under the closed canopy. If the probability of seedling establishment for two groups are the same, the number of fallen-acorns determines the amount of recruitment. In this case, *Q. acuta* and *Q. gilva* should have a shorter cycle of acorn-fall fluctuation with high acorn production, or they should perform effective dispersion of acorns to realize higher probability of seedling establishment.

Large proportion of canopy trees was a characteristic of the four *Quercus* species. Base on the height distribution, four *Quercus* species were also divided into the same two groups. The number of middle-size trees of *Q. salicina* and *Q. sessilifolia*, such as suppressed trees, was larger than *Q. acuta* and *Q. gilva*. This fact signifies that *Q. acuta* and *Q. gilva* have lower probability of recruitment in the canopy or sub-canopy layer. The difference may mainly depend on the different shade-tolerance of saplings. We think, however, that suppressed trees would not recruit to canopy trees even if the average size opening (ca. 67 m^2 in this type forest, Tanouchi and Yamamoto unpublished) is made, because the suppressed trees of *Distylium racemosum* and *Persea thunbergii* are the common gap successors (Yamamoto 1992). Besides Tanouchi (1990) experimentally showed that saplings of some *Quercus* spp. have a high survival rate, but cannot grow much in height beneath the closed canopy. Tanouchi and Yamamoto (unpublished) also suggested that the saplings can grow up to small trees in the usual gap formation regime of this type of forest and require long-lived or large gaps for regeneration.

In periods where the canopy is well closed, recruitment in the canopy of the four *Quercus* species will not be very successful. However, the seedling and sapling bank was constantly maintained and is patiently waiting for the environmental change caused by the large disturbance, e.g. rare and sever typhoon. The probability of recruitment may depend on the disturbance intensity. Even if the disturbance is not so large, *Q. salicina* and *Q. sessilifolia* which have higher shade-tolerance can recruit. After the larger disturbance, *Q. gilva* and *Q. acuta* should grow faster than *Q. salicina* and *Q. sessilifolia* because the growth speed of species with high shade-tolerance is generally slow. Only *Q. sessilifolia* showed negative interspecific association with the other *Quercus* species, and the distribution depended on geographical features. In the site where *Q. gilva* and *Q. acuta* are coexisting, whether the species can regenerate or not should be decided by a chance factor, e.g. the density of sapling banks or fallen acorns, when the disturbance occurs.

We thank Moriyoshi Ishizuka, Yohsuke Kominami and Shin-ichi Yamamoto for their valuable comments on earlier drafts. Thanks are also due to Rob Peters and Tohru Nakashizuka for reading the manuscript and making a number of critical comments. This study was supported in part by a Grant-in-Aid for the Bio Cosmos Project (BCP-94-III-A-1) from the Ministry of Agriculture, Forestry and Fisheries, Japan.

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(*Received June 28, 1993 : Accepted March 25, 1994*)