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Initial Regenerative Processes of *Distylium racemosum* and *Persea thunbergii* in an Evergreen Broad-Leaved Forest

Tamotsu Sato[1], Hiroyuki Tanouchi[2]* and Keiko Takeshita[1]

[1] *Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto, 860 Japan*
[2] *Forestry and Forest Products Research Institute, Tsukuba Science City, Ibaraki, 305 Japan*

We studied the initial regenerative processes of *Distylium racemosum* and *Persea thunbergii*, major canopy species, in an old-growth evergreen broad-leaved forest, Kagoshima, southwestern Japan. Although the two species coexisted, the patterns of seed production, seedling emergence, and sapling survival were different between them. During the observation (1989-1991), *P. thunbergii* produced large numbers of seeds in alternate years, while *D. racemosum* had no mast year. The density of established seedlings was high and increased with mass seed production for *P. thunbergii*, but was fairly low for *D. racemosum*. The mortality of seedlings and saplings of *P. thunbergii* was higher than that of *D. racemosum*. In a closed stand, the sapling bank was maintained by dense seedling supply for *P. thunbergii*, and by extremely low mortality of individuals germinated before the beginning of observation for *D. racemosum*. Since saplings of *D. racemosum* showed continuous height growth beneath the closed canopy, the possibility of recruitment into the upper layer seems to be high. The strategy of *P. thunbergii* might be to wait for suitable conditions favoring sapling growth on various site by means of frequent and large seed productivity and wide dispersal of seeds. Thus both species might be able to coexist through environmental heterogeneity.

Key words: *Distylium racemosum* — Evergreen broad-leaved forest — Initial regenerative processes — *Persea thunbergii* — Sapling mortality — Seed production

Differences in regenerative strategies may allow for coexistence of species within a forest community (Forcier 1975, Grubb 1977, Fagerström and Ågren 1979, Denslow 1980). The number of coexisting species may be increased through environmental heterogeneity (Pickett 1980). Gap formation is assumed to play an important role in coexistence and species-richness in forest communities (Hartshorn 1980). Whitmore (1989) suggested that tree species fall into two classes on the basis of gap-phase regeneration behaviour; i.e. climax species, that germinate and establish sapling banks beneath the closed canopy, and pioneers, that germinate only in gaps. Differences in requirements for seedling emergence and sapling growth also exist among climax species (Whitmore 1974), and pioneers (Brokaw 1987). These differences may affect regenerative strategy among tree species (e.g. Denslow 1980). Dynamics of seedlings and saplings can be defined by initial regenerative processes consisting of seed fall, seedling emergence and sapling survival. To clarify the regenerative strategy, many studies have compared the initial regenerative processes of coexisting species within the same community (e.g. Brokaw 1987, Yamamoto 1988, Streng *et al*. 1989, Houle and Payette 1991).

In Japan, evergreen broad-leaved forests are distributed widely and dominated by genera of *Quercus* and *Castanopsis* with associated evergreen tree species (Kira 1991). *Distylium racemosum* Sieb. et Zucc. (Hamamelidaceae) and *Persea thunbergii* (Sieb. et Zucc.) Kosterm. (Lauraceae) are also major species and dominate rather than *Quercus* spp. and *Castanopsis* spp. in the lowland old-growth forests in southern Kyushu (Kitazawa *et al*. 1959, 1960, Sako 1966, Miyawaki 1981). Yamamoto (1992) suggested that *D. racemosum* and *P. thunbergii* are considered climax species and typical gap successors which recruit from the sapling bank. How do both species establish and maintain the sapling banks before disturbance? Only a few ecological characteristics of both species have been documented on shade tolerance (Amano 1938) and population structure (Kitazawa *et al*. 1959) for *D. racemosum*, and mortality of current year seedlings for *P. thunbergii* (Tagawa 1973, 1978). However, regenerative processes of both species are poorly understood. In this paper, we describe patterns of seed-fall, seedling emergence and sapling survival of *D. racemosum* and *P. thunbergii* to fill this deficiency. Then we discuss the characteristics in regenerative processes

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Abbreviation: ha, hectare (=10,000m^2)

* Present address: Japan International Research Center for Agricultural Sciences, Tsukuba Science City, Ibaraki, 305 Japan.

of the two species.

Methods

Study site

The area is in a small valley on a broad ridge of Mt. Onidake (735 m a.s.l.; 32°8′N, 130°7′E), Okuchi City, northwest part of Kagoshima Prefecture, Japan. In 1988, we set up a 0.48 ha plot (60 m×80 m), divided into 48 sub-plots (10 m×10 m each). The diameter at breast height (dbh) and height of trees taller than 1.3 m were recorded. The location of the site is 32°8′N and 130°32′E and the altitude ranges from 485 to 495 m above sea level. According to the climatic data collected at Isa Agriculture and Forestry High school (175 m a.s.l.), the nearest meteorological station, annual mean temperature is 14.9°C, and annual precipitation amounts to 2,371 mm. The bed rock is pyroxene andesite. The most abundant soil type is moderately moist brown forest soil (Forest Soil Division 1976). The area is fairly flat but gently inclined to the westward side. A stream flows from east to west in the center of the area.

A total of 3,184 trees (>1.3 m in height) and 63 tree species were found and the total basal area was 22.19 m^2 in the 0.48 ha plot. The site was characterized by forests in which evergreen species such as *D. racemosum, P. thunbergii* and *Quercus* spp. (*Q. salicina* Blume, *Q. gilva* Blume, *Q. sessilifolia* Blume, *Q. acuta* Thunb.) predominate, with a minor component of deciduous species, e.g. *Idesia polycarpa* Maxim. and *Cornus brachypoda* C.A. Mey. The understory vegetation consists of *Aucuba japonica* Thunb., *Pellionia minima* Makino, *Ophiorrhiza japonica* Blume and others. According to phytosociological classification, this area belongs to the Distylio-Quercetum salicinae association (Miyawaki 1981). The plot was a well closed stand with only one small gap (ca. 85 m^2). The percentage of gap area (percentage of total gap area to total surveyed area) was 2%.

Seedling and sapling survey

To observe mortality of seedlings (current one year old) and saplings (more than one year old, and less than 1.3 m in height), 48 quadrats (2 m×2 m each) were set up at the center of each sub-plot. However, seven quadrats were not observed because they were located on exposed bedrocks in the stream bed. All seedlings of main canopy species were tagged and the individual number, height (*h*) and number of leaves were recorded. Diameter at ground level (d_0) of saplings taller than 30 cm in height were also recorded.

In the first survey made in April 1989, before shoot elongation, saplings were classified into two categories; those germinated in and those germinated before the previous year. From 1989 to 1991, the survey was repeated each December.

Seed traps

Forty-eight circular traps (0.5 m^2 each) for collecting fallen seeds were set up adjacent to each quadrat. Litter and seeds accumulated in traps were collected every month for three years from April 1989. The contents were sorted into seeds or fruit, leaves, branches, flowers and other debris. Maturity of seed was judged by their appearance and the hardness of their seed coats. Seeds in which the embryo was damaged by animals or fungi were treated as immature. Particles that were not developed in appearance were not scored.

Results

Population structure

The number of trees in the 0.48 ha plot was 634 for *Distylium racemosum*, which was the most abundant canopy species and 59 for *Persea thunbergii. D. racemosum* was the most dominant species in basal area (10.23 m^2 ha^{-1}). *P. thunbergii* was ranked sixth (2.34 m^2 ha^{-1}). Densities in each dbh class decreased exponentially as the dbh increased (Fig. 1). The distribution of dbh was inverse J-shaped for *D. racemosum*, and discontinuous for *P. thunbergii*. The height distribution of both species showed a bimodal distribution with most trees in the lower classes (Fig. 2). *D. racemosum* had continuous distribution. On the other hand, *P. thunbergii*

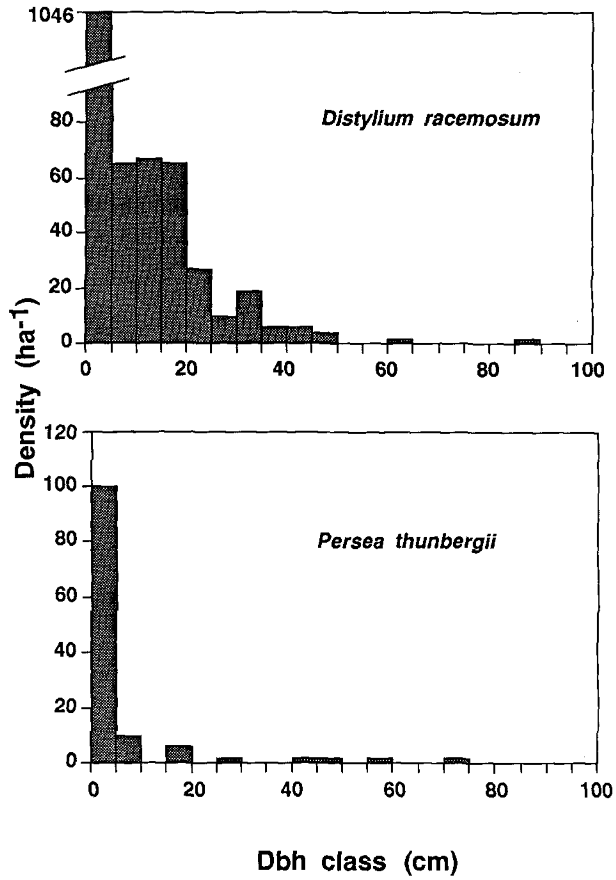

Fig. 1. Dbh distribution of *Distylium racemosum* and *Persea thunbergii* in the study plot.

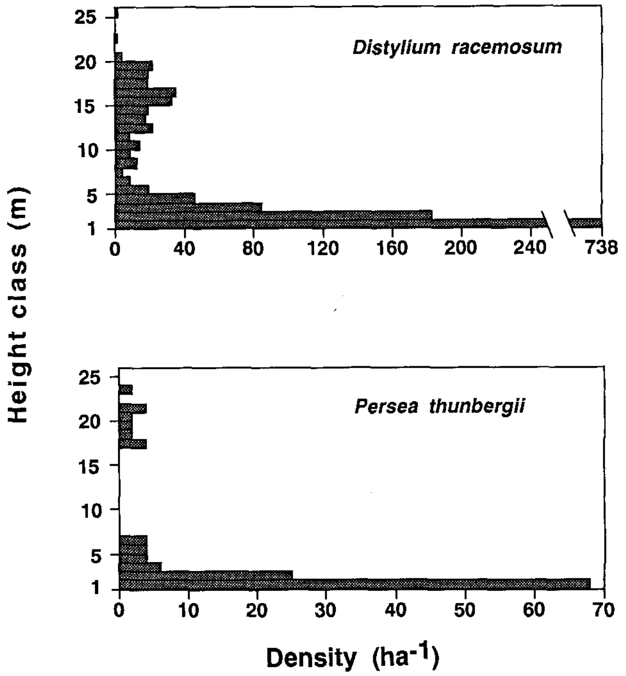

Fig. 2. Height distribution of *Distylium racemosum* and *Persea thunbergii* in the study plot. Included are all trees over 1.3 m in height.

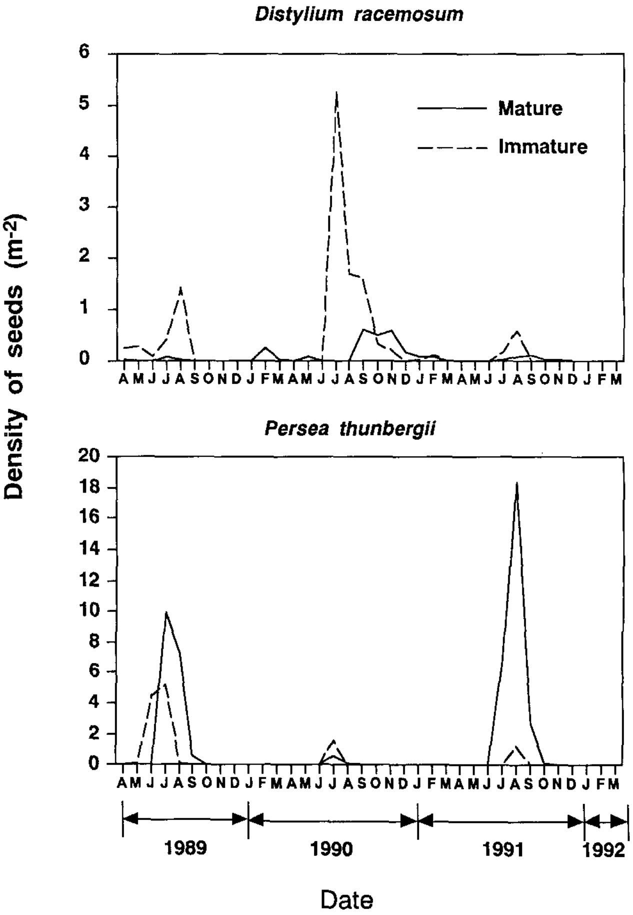

Fig. 3. Monthly quantities of fallen seeds of *Distylium racemosum* and *Persea thumbergii* over three years in the study plot.

size distribution showed bimodal shape; one peak taller than 16 m and another below 7 m. The canopy tree rates (percentage of canopy trees to living trees) were 2.4% for *D. racemosum*, and 8.5% for *P. thunbergii*.

Seed fall

Persea thunbergii flowered in May, and *Distylium racemosum* flowered in April-May. It takes about one year for seeds to be fully ripened in both species. Drupes of *P. thunbergii* contain one seed which is usually dispersed by birds. Capsules of *D. racemosum* enclose two seeds which are dispersed only by dehiscence. Mean length and width (mm±S.D.) of seeds were 10.51±0.84 and 9.40±1.05 for *P. thunbergii*, and 6.10±0.43 and 3.61±0.32 for *D. racemosum*. The seed fall of *D. racemosum* and *P. thunbergii* fluctuated annually (Fig. 3). The average number of annually fallen mature seeds was 17.8, 0.75 and 27.9 per m^2 from 1989 to 1991 for *P. thunbergii*, and 0.46, 2.13 and 0.67 per m^2 for *D. racemosum*. Annual fluctuation was larger in *P. thunbergii* than in *D. racemosum*. The seed fall of *P. thunbergii* attained its peak in July-August (Fig. 3), as is reported by Tagawa (1973, 1978). The peak of immature seed fall was nearly the same as that of mature seed fall. The proportion of immature to mature seeds was lower in *P. thunbergii* than in *D. racemosum*. The relatively large seed production of *P. thunbergii* occurred twice during the observation period (1989 and 1991). There was no clear peak of mature seed fall in *D. racemosum* (Fig. 3), while immature seeds enclosed within capsules fell mostly from July-August. The average of annually fallen seeds was fairly low. The annual fluctuation was also small during the observation.

Seedling emergence

The number of seedlings and saplings fluctuated annually in both species (Fig. 4). The number of established seedlings from 1989 to 1991 were 0.67, 0.08 and 0.59 per m^2 in *Persea thunbergii*, and 0.06, 0.01 and 0 per m^2 in *Distylium racemosum*. Annual fluctuation patterns differed between the two species. In *P. thunbergii*, the number of seedlings increased in the years of mass seed production in 1989 and 1991 (Fig. 4). Seedlings emerged every year, and most died quickly. Thus, total number of seedlings and saplings showed a large variation between years. In *D. racemosum*, the average number of emerged seedlings was 0.02 per m^2 (no emergence in 1991). Density of emerged seedlings was very low despite high density of canopy trees. Low seedling emergence was expected from low mature seed production (1.08 seeds per m^2 for three year's average). Total number of seedlings and saplings did not show extreme variarance between years (Fig. 4).

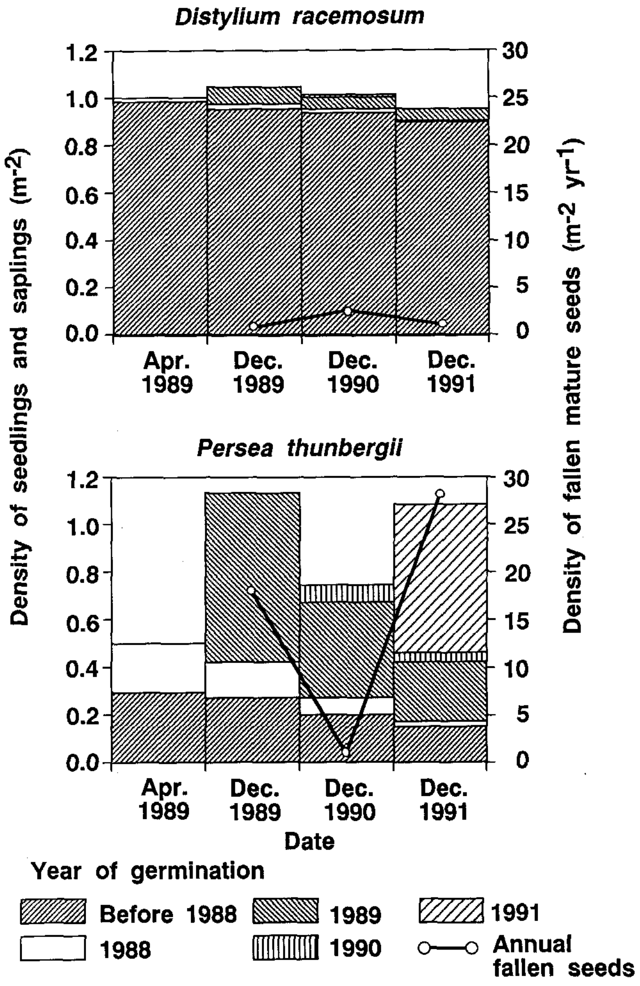

Fig. 4. Number of seedlings and saplings and quantities of annual fallen seeds in the study plot. In the horizontal labels, month and year show survey dates for seedings and saplings, while seeds were collected throughout the entire year shown on the label.

Sapling survival

Saplings of *Persea thunbergii* suffered high mortality (Fig. 5). The number of saplings decreased linearly with time. In the population germinated in and after 1988, fifty-nine percent of seedlings survived for one year after germination and only 8.6% of saplings survived for three years (Fig. 5). The differences in survival rates of emerged seedling population between seed year (1989) and lean year (1990) was not significant ($P > 0.05$, Chi square test).

In *Distylium racemosum*, the survival rate of saplings was extremely high (Fig. 5). The survival rate of saplings that germinated in and after 1988 was high for the first two years after germination. After this period, the survival rate decreased to 33.3% for three year old saplings.

The average sapling height of *D. racemosum* that germinated in and after 1988 was much smaller than that of *P. thunbergii* (Table 1). Saplings of both species slightly increased in height and gave significant differences in each observation period compared with the beginning of the observation. Saplings of both species germinated before 1988 also increased in size slightly over the three years of the study. However, *P. thunbergii* showed no significant differences in height growth during the observation. On the other hand, *D. racemosum* showed significant growth at the end of the observation ($P < 0.01$, Mann-Whitney U test).

Volume (d_0^2h) of saplings that survived beneath the closed canopy increased during the observation. The average volume of saplings increased 16.6% after the first year for *P. thunbergii*, and 2.4% for *D. racemosum*. The difference in increment rate between *D. racemosum* and *P. thunbergii* was significant ($P < 0.01$, Mann-Whitney U test). The volume of *D. racemosum* increased slowly, and the number of saplings also increased slightly. Although *P. thunbergii* showed a larger increment rate than *D. racemosum*, most saplings died after three years beneath the closed canopy.

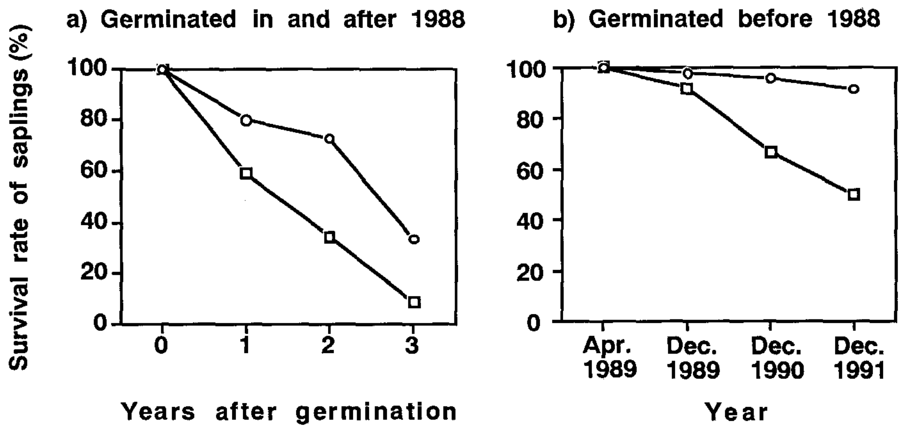

Fig. 5. Survival rate of saplings of *Distylium racemosum* (○) and *Persea thunbergii* (□). Survival rate of sapling population a) germinated in and after 1988, and b) germinated before 1988. The first survey was made in April 1989. From 1989 to 1991, the survey was repeated each December.

Table 1. Height growth of saplings during three years observation of *Distylium racemosum* and *Persea thunbergii* under a closed canopy

Saplings germinated in and after 1988

Years after germination	*Distylium racemosum*	*Persea thunbergii*
0 yr.	4.0 (3.6)	7.2 (7.5)
1 yr.	5.5 (5.4**)	8.8 (9.2***)
2 yr.	5.6 (5.7**)	9.2 (9.3***)
3 yr.	8.0 (8.0†)	11.4 (11.4†)

Saplings germinated before 1988

Date	*Distylium racemosum*	*Persea thunbergii*
Apr. 1989	37.3 (38.0)	19.0 (22.0)
Dec. 1989	39.8 (40.0^{NS})	20.7 (23.7^{NS})
Dec. 1990	42.7 (42.8*)	23.2 (25.2^{NS})
Dec. 1991	44.7 (44.7**)	25.4 (25.4^{NS})

All values are expressed in cm. Values in parentheses show the average height of individuals which had survived until the end of observation, December 1991.

Superscripts indicate the significant difference between the value of the beginning of observation, 0 year or April 1989, and the value of each observation period.

Significance was examined by Mann-Whitney U test.

Symbols : ^{NS} ; not significant, * ; $P<0.05$, ** ; $P<0.01$, *** ; $P<0.001$, † ; data too few for test.

Discussion

Differences in initial regenerative processes between *Distylium racemosum* and *Persea thunbergii* are summarized in Fig. 6. During the observation, *D. racemosum* produced less seeds than *P. thunbergii*, but it maintained relatively high sapling density. There are several factors which maintain sapling density in *D. racemosum*. Extremely low mortality of seedlings and saplings is one of the factors. Another factor could be large seed production in the past; *D. racemosum* might have intervals between mast years longer than five years, because the sapling bank was mostly composed of saplings germinated before 1988. In *P. thunbergii*, mortality of seedlings and saplings was much higher than in *D. racemosum*; most saplings died within three years after seedfall. However, high seed production in 1989 and 1991 supplied dense seedlings which contributed to maintaining the sapling bank. As a result, the sapling bank was mostly composed of saplings germinated after 1989, and its density greatly fluctuated between years. However, the sapling bank of *Persea thunbergii* maintained a certain density beneath the closed canopy (Fig. 4). The results suggest that *D. racemosum* and *P. thunbergii* have diametric tendencies in maintaining sapling bank; i.e. infrequent seedling emergence in *D. racemosum* vs. frequent seedling emergence in *P. thunbergii*.

Yamamoto (1992) suggested that *D. racemosum* and *P. thunbergii* could regenerate from sapling banks in gaps. In the same stand, *Quercus* spp. (major canopy species) also established sapling banks under the closed canopy (Tanouchi *et al.* 1994). These species are recognized as climax species in the sense of Brokaw (1985) and Whitmore (1989) because they can germinate and establish sapling banks under the closed canopy. However, differences in gap regeneration behaviour may exist among climax species in general (Whitmore 1974), and particularly between *D. racemosum* or *P. thunbergii* and other major species in the evergreen broad-leaved forest of Japan, such as *Quercus* spp. (Yamamoto 1992). While *Quercus* spp. have no or a small portion of small trees lower than 6 m in height (Tanouchi *et al.* 1994), *D. racemosum* and *P. thunbergii* have abundant small trees (over 80% of total trees). The saplings of *Quercus* spp. can not grow much in height beneath the closed canopy (Tanouchi *et al.* 1994). This behaviour seems to support the observed difficulty of recruitment into small trees. Some studies have suggested that large disturbance may be required for successful recruitment of *Quercus* spp. (e.g. Yamamoto 1992, Tanouchi *et al.* 1994).

On the other hand, sapling of *D. racemosum* tends to grow steadily in spite of extremely low growth rates (Amano 1938). Although most saplings suffered from high mortality, *P. thunbergii* also showed growth in height beneath the closed canopy. Because of dense seedling supply and high sapling bank density, some saplings may be able to recruit into small trees. However, lack of middle size trees (7-16 m in height) in *P. thunbergii* may suggest that limits of growth in height exist beneath the closed canopy. In any case, population structure of both species suggests that saplings can recruit at least into the small size class beneath the closed canopy. Both species are also considered to be able to maintain a certain density of small trees without disturbance. This behaviour, which differs from that of *Quercus* spp., must enlarge the chance to be a gap successor. The characteristic is in agreement with the observation of gap regeneration behavior in this forest type (Yamamoto 1992).

Dynamics of seedlings and saplings before gap creation may differ between *D. racemosum* or *P. thunbergii* and *Quercus* spp. as well. Fluctuations in fallen seed density reported for *Quercus* spp. (Tanouchi *et al.* 1994) are smaller than in *P. thunbergii*. The mortality of seedlings and saplings of *Quercus* spp. shows intermediate value between *P. thunbergii* and *D. racemosum*. Basically, *Quercus* spp. seem to maintain sapling banks due to low mortality of saplings in the same manner as *D. racemosum*. However, *Quercus* spp. could maintain relatively small density of sapling banks beneath the closed

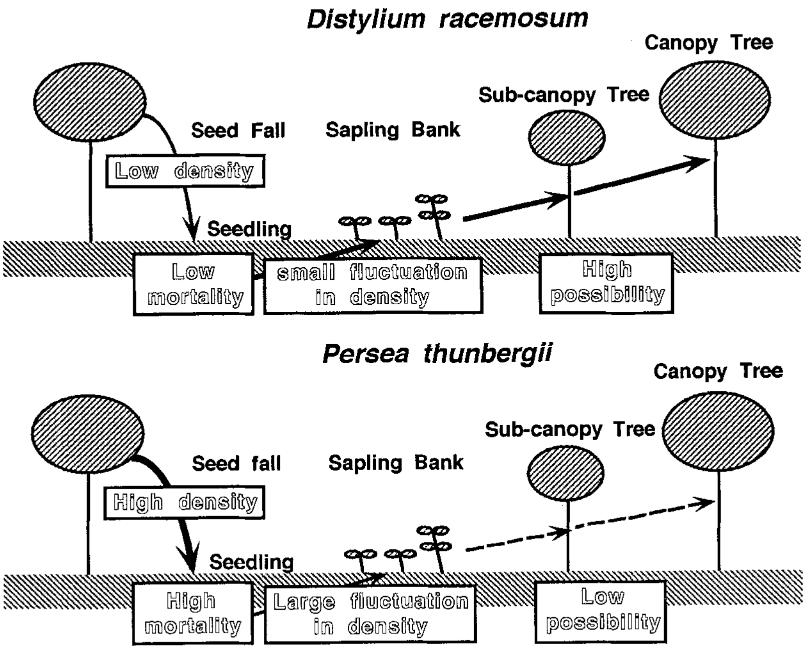

Fig. 6. Schematic diagram of initial regenerative processes of *Distylium racemosum* and *Persea thumbergii* in closed stands. Bold text indicates each regenerative process. Outline text indicates behaviour of each stage. The possibility of recruitment to the layer is presumed from the result of initial regenerative processes.

canopy (Tanouchi *et al.* 1994) because of the balance between low seedling supply and intermediate mortality. Therefore, initial regenerative processes of these species, *D. racemosum, P. thunbergii* and *Quercus* spp., are distinguished from one another on the basis of seedling supply and their mortality.

Canham (1989) suggested that quantitative differences exist among climax species in their responses to gaps, and climax species might respond to even slight increases in understory light level. According to population structure and initial regenerative processes, the possibility of recruitment into the upper layer beneath the closed canopy may be high for *Distylium racemosum*, and low for *Persea thunbergii*. Shade tolerance of *P. thunbergii* seems to be lower than in *D. racemosum*. This is supported by the two observations; lack of middle size trees, and high mortality of seedlings and saplings. *P. thunbergii* produces large numbers of seeds which are dispersed widely by animals, especially by birds. Therefore, *P. thunbergii* may be able to maintain relatively high sapling density and may wait for suitable conditions favoring sapling growth from sapling banks on various sites, either in gaps or in closed canopies. *P. thunbergii* may be able to successfully recruit in a small opening but not beneath a closed canopy.

Comparisons of initial regenerative processes and population structure between both species indicated that environmental heterogeneity is probably necessary for their coexistence within the same community. In future, further studies of developmental processes to maturity are required to clarify the whole community dynamics.

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