

Review

Physiological characteristics of tropical rain forest tree species: A basis for the development of silvicultural technology

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(Contributed by Satohiko SASAKI, M.J.A.)

Abstract: The physiological characteristics of the dominant tree species in the tropical rain forest mainly belonging to dipterocarps as well as the environmental conditions especially for the light in the forest were studied to establish the silvicultural system for the forest regeneration in the tropical South Asia. The flowering patterns of the dipterocarp trees are usually irregular and unpredictable, which make difficult to collect sufficient seeds for raising the seedlings. The field survey revealed the diverged features of the so-called gregarious or simultaneous flowering of various species of this group. Appropriate conditions and methods for the storage of the seeds were established according to the detailed analyses of the morphological and physiological characteristics of the seeds such as the low temperature tolerance and the moisture contents. The intensity and spectra of the light in the forest primarily determine the growth and the morphological development of the seedlings under the canopy. Based on the measurements of the diffused light at the sites in the tropical forest in the varying sunlight, the parameters such as “the steady state of the diffuse light” and “the turning point” were defined, which were useful to evaluate the light conditions in the forest. To improve the survival of the transplanted seedlings, a planting method of “the bare-root seedlings”, the seedlings easy to be handled by removal of all leaves, soil and pots, was developed. Its marked efficiency was proved with various dipterocarps and other tropical trees by the field trial in the practical scale. Tolerance of the various species to the extreme environmental conditions such as fires, acid soils and drought were examined by the experiments and the field survey, which revealed marked adaptability of *Shorea roxburghii* as a potential species for regeneration of the tropical forests.

Keywords: *Dipterocarpaceae*, *Leguminosae*, *Myrtaceae*, seed storage, the light in the forest, bare-root seedlings

In 1980, the Food and Agriculture Organization (FAO) warned of a serious decrease of the areas of the tropical forests for the first time. Since then, the decrease of the tropical forest area has remained at a high level of 10 million hectares every year. The process of the decrease in the tropical forest area is complex. The exploitation of the forests is not the only cause for the decrease, but also other human activities such as the illegal cutting, the forest fire, the shifting cultivation and the conversion to

farmland cause to decrease the tropical forests. These human invasions to the forests frequently result in the creation of the arable land with the infertile soil. Particularly, vast areas in Southeast Asia are originally covered with the infertile soils such as the acid sulfate soil, the waterlogged swamp with pyrite underneath, the dry sand dune, and the saline soil. Peoples in these areas convert the forests to obtain the farmland with better productivity, but the invaded forests are quickly deteriorated as the organic matter is exhausted from the soils. Then the primary forests turn into the unproductive secondary forests,^{1)–4)} which become good targets for next conversions to other land-uses. As the consequence of these processes, the tropical forest areas are rapidly decreasing. We must develop a

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new concept to protect the zone of the tropical forest by emphasizing the environmental functions more than the timber production.^{1),2),5)-7)} It is important to save even the secondary forests maintaining organic matter^{8),9)} as well as to keep the whole zone of the forest. More considerations must be paid for the human factors to improve the general situation of the tropical forests. However, the most urgent matter is to develop the silvicultural methods to rehabilitate the wastelands and to stop the forest declines. Scientific knowledge about the physiological characteristics of the tropical tree species is essential to establish such technologies adaptable to the severe environmental conditions in these areas.¹⁰⁾⁻¹⁹⁾

The Ministry of Education, Culture, Sports, Science and Technology, Japan funded several research projects for the restoration of the tropical forests. "The development of the sustainable technology for the biological productions adaptable to the environment of Asian countries" was one of the largest projects. The researchers of the several universities and the national research institutes in Asian countries as well as those of the Japanese universities joined to carry out the project. In addition, The Ministry of Agriculture, Forestry, and Fisheries, Japan initiated a research association for Japanese private enterprises to restore the tropical forests.²⁰⁾⁻²³⁾ The association conducted cooperative research projects with various institutes in the ASEAN countries. Including the outcome of these projects, the silvicultural researches on the characteristics of the tropical tree species are described in the present review.

I. The flowering and fruiting of the important tropical rain forest species

The prediction of the flowering of major tree species is important to secure the seeds as the planting stocks to regenerate forests, but it is unpredictable with the tropical rain forest tree species. Therefore, we carried out the field survey to explore their flowering and fruiting behaviors in Malaysia.

1. Flowering of *Dipterocarpaceae*

Dipterocarpaceae is a family of the tropical tree species, which are widely distributed in the tropical regions of Asia, Africa, and South America. Among its subfamilies, *Monotoideae* is found in Africa and South America, *Pakaraimoideae* only in South

America, while *Dipterocarpoideae* composed of 15 genera dominate the primary forests of Southeast Asia.²⁴⁾⁻²⁷⁾ The species of *Dipterocarpoideae* grow in wide areas from the Seychelles, India, China, Thailand, Malaysia, Indonesia to the Louisiade Arch of Papua New Guinea. They are typical mesic species adapted to the climate of high temperature and abundant rainfalls throughout the year and more than 500 species have been developed to adapt to the diverse habitats and climatic conditions within these areas.²⁵⁾ Although some species showed the regular flowering in a year, most of them develop the flowers at long irregular intervals.^{28),29)} It is also described that these species in an area develop flowers synchronously when it occurs, which is called "gregarious flowering".^{29),30)} El Niño, the scarce of the rainfall, the high temperature as well as the forest fires are speculated to be the causes for the induction of the flowering of the dipterocarps. However, there is no concrete evidence about the condition to induce the flowering of the dipterocarps.

(1) **The gregarious flowering.** The gregarious flowerings in the Peninsula Malaysia were recorded in 1963, 1968, 1975, 1976, 1980, and 1981.^{24),29),31)-33)} Particularly, the flowering from the end of 1975 to the early 1976 was reportedly intensive as 90% of the dipterocarp species flowered in this period.²⁹⁾ However, our observations described below suggest that the synchronous flowering is limited as to both the areas and the species.³²⁾

The continental divide of the Malay Peninsula runs through the ridges of Fraser's Hill range, and it divides the East Coast and the West Coast.³⁴⁾ The East Coast has the heavy rainy season from October to March, whereas the rainy season in the West Coast is vaguely recognized. The eastern slope of Fraser's Hill along the Kuala Lipis road from Gap at the altitude of 800 m on the ridge to the junction at the altitude of 250 m near Bentung was surveyed for the flowering and fruiting^{31),32)} in the early January 1976 (Table 1). Most of the dipterocarp trees in the Ulu Teranum Forest Reserve (Fig. 1) were observed to flower. The flowering was intensive in the area from the milestone-9 at the altitude of 300 m to the milestone-15 at the altitude of 600 m, where was a part of the dipterocarp forest. At that time, most trees of *Shorea assamica*, *S. parvifolia*, and *S. dasyphylla* already developed young fruits, whereas the trees of *S. leprosula* were

Table 1. Flowering and fruiting of *Shorea* species on the eastern side of Frazer's Hill range (Ulu Teranum Forest Reserve) in the gregarious flowering year 1976. All the trees in the area along with the Kuala Lipis road from Gap to the junction near Benton were surveyed on June 6, 1976.

Species	Distribution of trees													Developmental stages		
	Mile stone to Raub													Flower + Fruit		
	21-20	20-19	19-18	18-17	17-16	16-15	15-14	14-13	13-12	12-11	11-10	10-9	Total	Flower	Fruit	Fruit
<i>Shorea leprosula</i>							2	18	53	23	4	100	48	25	27	
<i>Shorea parvifolia</i>								1	7	21	14	44	4		40	
<i>Shorea ovalis</i>									1	1		2	2			
<i>Shorea platyclados</i>	1							2		5		8				
<i>Shorea assamica</i>						5	3	2	4	2		16			16	
<i>Shorea curtisii</i>										1	3		Stages not confirmed			
<i>Shorea dasyphella</i>											3				3	

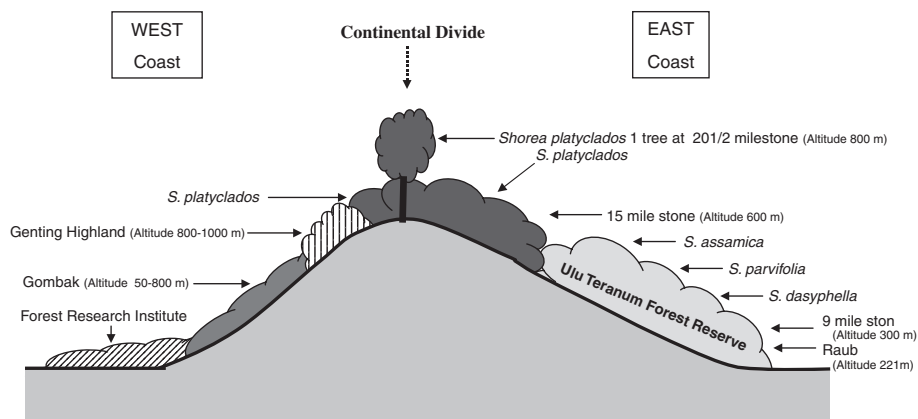


Fig. 1. Gregarious flowering at Frazer's Hill range.

at a stage of the formation of the flower bud. In contrast, the trees of *S. ovalis* showed neither flowering nor fruiting, but flowered much earlier than did those of the gregarious flowering species. At the higher altitudes between the milestone-15 and Gap covered by the pure forest of *S. platyclado*, no flowering was observed except one tree near Gap at the ridge (Fig. 1). According to our records, *S. platyclados* trees located beyond milestone-15 delayed to develop flowers until the end of May 1976 when the trees on the western side flowered.

On the other hand, the dipterocarp trees on the western side of Fraser's Hill range from Gap at the altitude of 800 m down to Kuala Kubu Bharu at the altitude of 117 m developed the flowers at the end of May 1976. In the Ulu Gombak Forest Reserve at a range of the altitude from 50 m to 800 m, the dipterocarps developed the flowers also

at the end of May, and their seeds matured in October 1976. In the Forest Research Institute, Kepong, Kuala Lumpur at the altitude between 75 m and 150 m, the most dipterocarp trees developed their flowers in March, and their seeds matured in August. In Genting Highland at the altitude from 800 m to over 1500 m, which is located above the Ulu Gombak Forest Reserve, the trees of *S. platyclados* flowered in June and their seeds matured in the late November. Although the forest of *S. platyclados* in Genting Highland existed at the same altitude as that of Frazer's Hill, the maturation of their seeds significantly delayed by nearly 6 months from the trees in the Ulu Teranum Forest Reserve on the eastern side.

It was also observed that a few species showed the unusual flowerings during the gregarious flowering year.^{31),32)} The flowering of *S. leprosula* on the

eastern side of Frazer's Hill was intensive, and even small size trees of a 10 cm diameter developed the flowers. Soon after the mature seeds were disseminated, again new flowers were developed on the same tree, but young fruits were aborted before they were matured. In January 1977, these trees of *S. leprosula* developed the flowers for the third time, but those young seeds were prematurely aborted two months later. Yap²⁹⁾ noted similar second flowering with *H. odorata*. A tree of *S. platyclados* located at the ridge of the continental divide flowered twice. The tree flowered together with the dipterocarp trees at the lower elevation on the eastern side of Frazer's Hill range and later flowered together with those trees on the western side (Fig. 1). However, the young seeds that developed for the second time were aborted before they were matured. Similarly, in the Forest Research Institute, the trees of *S. platyclados* flowered twice. It is evident that the seeds developed in the second fruiting are aborted prematurely. The repetition of the flowering followed by the abortion of the seeds might be one of the keys to determine the flowering pattern of the dipterocarp trees.

These observations indicate that the timing of flowering of the dipterocarps in the Peninsular Malaysia is markedly diverged by the species as well as by the location of the forest.

(2) Yearly flowering. The dipterocarp species in the north beyond the boarder of Malaysia were observed to develop the flowers regularly once a year.³²⁾ The trees of *S. roxburghii* in Kuala Lumpur yearly developed the flowers in January and disseminated the matured seeds at the end of April every year. Similarly, the trees of *S. roxburghii* in Perlis, northern Malaysia, and in Narathiwat, Thailand, flowered at the same time with those in Kuala Lumpur. In the north Malaysia, the trees of *Hopea odorata*, *Dipterocarpus alatus*, *D. kerrii*, and *D. chartaceus* flowered yearly at the same time of the year. Yearly flowering was also reported with *H. helferi*, *H. oblongifolia*, and *H. pierrei*.³⁵⁾ These species found in Thailand, Myanmar, and India develop the flowers in a regulated manner.

On the other hand, particular trees in the same species showed the trait to develop the flowers frequently in a year. Such the trait was observed with the trees of *H. wightiana*, *D. oblongifolia*, *S. maxima*, *Neobalanocarpus heimii*²⁸⁾ as well as those of *Dryobalanops aromatica*,³²⁾ which will

allow the selection of the genetically better trees for flowering.

2. Flowering of other tropical species

(1) Flowering of *Leguminosae*. The legumes or *Leguminosae* is one of the major tree families in the tropical rain forests including the various important timber species. Most *Acacia* species in this family have the trait to develop their flowers continually or annually. The seeds of *Acacia mangium* as well as those of *A. auriculaeformis* are produced annually or continually. *Paraserianthes falcatalia* and *Leucaena leucocephala* have the tendency similar to *Acacia*. *Cedrelinga* and *Parkia* develop the flowers and the seeds annually. The trees of *Pterocarpus indicus* shed the leaves early in the year and develop the new leaves as well as the flowers simultaneously. *Intsia palembanica*, one of the dominant legume species in the tropical primary forest, flowers yearly and develops large leathery pods. *Koompassia malaccensis*, another dominant species, develop the flowers in somewhat sporadic manner, but they develop the flowers more often than the dipterocarps do. The trees of *Dialium*, *Intsia*, *Koompassia*, and *Sindora* are the emergent trees of the tropical rain forests, and they have a tendency to develop their flowers together with the dipterocarps in the gregarious flowering year.³⁶⁾

(2) Flowering of *Myrtaceae* trees. The family *Myrtaceae* consists of the genera of the tropical timber trees such as *Eucalyptus*, *Melaleuca*, and *Eugenia*. Among the species of *Myrtaceae*, *Melaleuca cajuputi* as well as *Eucalyptus deglupta* are native in the tropical rain forests in Asian countries, and they are important fast growing species. These species flower almost successively and the seeds can be collected throughout the year.³⁶⁾

II. Morphological and physiological characteristics of the seeds of the tropical trees

Characteristics of the seeds for germination and storage are greatly affected by their morphological structure. The seed of Angiosperms consists of embryo, endosperm, and seed coat. The embryo is composed of the diploid cells of the zygote, and the endosperm is polyploid cells developed from the nuclear fusion, whereas the seed coat is derived from the integuments of the mother tree.¹⁰⁾ In

some Angiosperms seeds, the embryo is small and imbedded in the large endosperm tissue containing most of the reserve substances. Such the seed called "the albuminous seed"³⁷⁾ germinates slowly, as the embryo needs to mature before the germination.¹¹⁾ In contrast, in some of Dicotyledons such as dipterocarps, most leguminous trees, and *Myrtaceae* trees produce "the exalbuminous seed",³⁷⁾ whose embryo consists of large cotyledons containing the abundant reserve substances. In the maturation stages of the seeds, the seeds transfer the reserve substances from their endosperms to the cotyledons of the embryos. This type of seed germinates fast by using the reserve substances in the two large cotyledons.¹¹⁾ We examined these characteristics and established the appropriate conditions for their germination and storage, which are useful for transplantation in the tropical rain forests.

1. Characteristics of the dipterocarp seeds.

(1) **Seed wings.** The dipterocarp seed generally possesses the seed wings developed from the calyx, which originally consists of the five lobes.²⁵⁾ Number of the developed seed wings developed on the mature seeds is five in *Dryobalanops* and *Parashorea*, and three in *Shorea*, whereas dipterocarp genera such as *Dipterocarpus*, *Hopea*, *Upuna*, *Anisoptera*, *Cotylorobium* and *Vatica* develop two wings on the seeds. However, in each genus, there are a few species without the seed wings. *Neobalanocarpus hemii* also has no wings on the seed.

The genus of *Shorea* is divided into the four subgenera groups of *Anthoshorea*, *Rubroshorea*, *Eushorea*, and *Richetia*.²⁵⁾ The seeds of each subgenus show characteristic morphology of the wings. As the maturation of the seed proceeds, the seed wings are desiccated starting from the tips to the bases of the wings. Desiccated portions of the wings become rigid^{31),38),39)} to form solid wing blades. The completely matured seed of *Rubroshorea* shows the rigid brown wings with the clear dark stain at the base of the wings. Below the dark stain, a small portion of the wing tissue is still alive and flexible, showing green color. The green wing base is flexible and facilitates to open wing angles to catch the air. When the fully mature seed is disseminated from the mother tree, the wing blades opened with wide angles rotates to lift the seed to the air. In contrast, the dark stain at the base of the wing did not develop in the seed desiccated artificially or

disseminated prematurely. As the seed reduces the moisture content in maturation processes, the mature seed is much lighter in weight than the immature one. Therefore, the mature seeds are carried away by the wind for a long distance. Although it was believed that dipterocarp seeds were disseminated mostly around the mother tree,³⁰⁾ we often observed that the mature seeds of *S. ovalis* flew for 300 m away from the mother tree. In contrast, the immature seeds as well as those damaged by insects dropped down prematurely underneath the mother tree.^{31),38),39)} On the other hand, the large size seeds of the species including *S. macrophylla* and *D. alatus* are disseminated only around the mother trees due to their heavy weights.

(2) **Cotyledons.** The species of *Dipterocarpaceae* produces the exalbuminous seed. The endosperm is generally absent in the mature seed, and the reserve substances are stored in the cotyledons. During the germination of the seeds, some species expand their cotyledons above the ground, whereas the other species fold their cotyledons under the seed coats in the soil. The former is called "the epigeal seed", whereas the latter is called "the hypogeal seed". The hypogeal cotyledons are protected by the thick seed coat and thus have the tolerance to the drought.^{39),40)}

S. roxburghii and *S. robusta* are the only two species in *Shorea* to produce the hypogeal seeds. We often observed that the seeds of *S. roxburghii* germinated under the drought conditions in the open. The hypogeal seeds such as those of *Dipterocarpus* as well as those of *Vatica* show a similar tolerance to the drought conditions. In the germination of the hypogeal seed, the radicle emerges from the seed coat, and the petioles of the cotyledons are extensively elongated. At the joint of the petioles, an epicotyl is developed. At the apex of the epicotyl, the first paired leaves developed, which are the first organs with the photosynthetic activity. The cotyledons supply the energy necessary for these development processes until the first photosynthetic leaves are formed. Thus the reserve substances in the cotyledons as well as photosynthesis in the first paired leaves possess the important function for the development of the hypogeal seedlings.

In contrast, *Rubroshorea*, *Richetia*, *Eushorea*, *Hopea*, *Dryobalanops*, *Upuna* as well as *Anisoptera* produce the epigeal seeds and expand the green or

reddish cotyledons above the ground. *Parashorea* is known to develop the cataphylls of the needle-shape arranged spirally on the epicotyl in an early stage of the seedling development. Among the epigeal species, the species such as *S. hypochra* and *S. resina-nigra* belonging to the subgenus *Anthoshorea* are unique as to expanding the white cotyledons. In the dark forest, all the seedlings with the white cotyledons faded a few months later due to exhausting the reserve substances. Probably, these *Anthoshorea* species are in an intermediate stage of the development of the epigeal cotyledons from the hypogeal ones. Photosynthesis is important for the early development of the seedling of the epigeal species.

The reserve substances stored in the cotyledons are chemically diverged. The *Dipterocarpus* seeds have starch grains as the reserve substances. Among the subgenera of *Shorea*, *Anthoshorea* seeds have starch grains as the major seed reserve substance, but other groups such as *Rubroshorea*, *Eushorea*, and *Richetia* have oil bodies. *Parashorea* also has abundant oil bodies in cotyledons. *Hopea odorata* mainly has oil bodies, but other *Hopea* species may have starch grains or oil bodies, depending on the species.

(3) Characteristics of seed maturation.

The dipterocarp seeds generally mature within 3 to 5 months after the flowering.^{32),38)} The maturation processes continue until the seed is disseminated from the mother tree.^{11),40)} We often observed that the jelly-like endosperm still filled the cavity of the embryo sac even after the seed reached the fully matured size. In the immature stages, the cotyledons are inconspicuously small. This indicates that the transfer of the reserve substances from the endosperm to the cotyledons continues until the late stage of the seed maturation.¹¹⁾ The maturation of the seeds is associated with fast germination as well as an increase in the germination percentage and a decrease in the moisture content. At the time of dispersal, the seed reduces its moisture content to 70% or less by the dry weight basis. These features can be utilized to select the well matured seeds to germinate faster.^{39),41)}

The process from the maturation to the germination of the seed is continuous in the dipterocarp seeds. In a moist condition, we observed that the *Dryobalanops aromatica* seeds started the germination on the tree by protruding the radicle from the

seeds. It indicates that the germination process is started even before the seeds are shed off from the mother tree.³⁸⁾ Sometimes, the seeds of the temperate zone species such as *Lithocarpus*, *Castanea*, *Quercus* and *Podocarpus*⁴²⁾ also germinate on the trees.

(4) Conditions for seed storage.

1) Moisture content: The dipterocarps are classified as the high moisture seeds, which need the high moisture content of above 20% of the dry weight for their survival.³⁸⁾⁻⁴²⁾ Such seeds are found both in the temperate and tropical species.⁴²⁾ Although the moisture content of the seed is reduced during the maturation process of the dipterocarp seed, the viable seeds still have a high moisture content of over 50% of the dry weight.³⁸⁾ The seeds of *S. ovalis* and *S. roxburghii* lose the viability when the moisture content declined to a level below 20% of the dry weight. Maintaining the moisture content for more than 20% in a sealed container or in a closed plastic bag results in prolonging the viability of the seeds for several months.³⁸⁾

Most of *Rubroshorea* seeds have the thin seed coats, which easily lose water by transpiration. This is one of the reasons that *Rubroshorea* seeds lose their viability quickly in the field. In contrast, the seeds of *Anthoshorea*, *Dipterocarpus*, *Vatica*, and *Parashorea* are covered by thick resinous seed coats. These seeds are viable in the open condition, and often germinate under the strong sunlight. The maturing process on the mother tree reduces the moisture content of the seed without losing the viability. When *S. ovalis* seeds were artificially

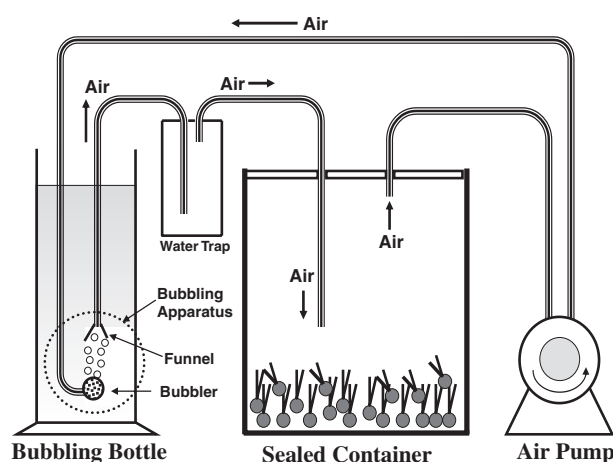


Fig. 2. Air-circulating system for seed storage.

Table 2. Survival of *Anthoshorea* and *Hopea* seeds at 4 °C

Species	Original seeds		Stored seeds at 4 °C		
	% germ.	% moist.	period	% germ.	% moist.
<i>Shorea roxburghii</i>	95	68.1	6 months	69	68.6
<i>Shorea assamica</i>	86	38.1	3 1/4	50	
<i>Shorea hypochra</i>	73		2	10	
<i>Shorea bracteolata</i>	50	48.2	2	4	
<i>Hopea latifolia</i>			2 3/4	10	32.6
<i>Hopea odorata</i>	81	113.0	1 1/2	5	114.0
<i>Hopea wightiana</i>	100		2	5	100.5
<i>Hopea subalata</i>	100	77.4	1 3/4	40	46.8
<i>Hopea ferrea</i>	90	54.7	2	2	49.2
<i>Hopea nervosa</i>	100	95.0	3/4	15	76.0
<i>Hopea beccariana</i>	95	58.7	no storage test, but showing no symptoms.		

dried by leaving in an air-conditioned room, the viability of the seeds was high immediately for a few days after the drying treatment, but distinct decrease was observed after the storage for 30 days.^{38),39)}

In the seeds with the high moisture content, high respiration activity reduces reserve substances in the seed and causes the accumulation of the heat in the storing container. Water is excreted by the respiration as well as by the transpiration of the seeds. The excreted water is re-absorbed by the seed resulting in the premature germination and the fermentation as well as fungus infection of the seeds especially at high temperatures. Therefore, the simple storage of the seeds in a closed plastic bag filled with the moist air often induces the fermentation as well as the premature germination. A device shown in Fig. 2 is effective to keep the seeds viable without causing such the detrimental effects. In the system the air with humidity of 95% is circulated at 25°C, which enables the moisture content of the seeds in the container above 20%. The humidity of the circulating air can be controlled by adding appropriate concentrations of sulfuric acid in the water in the bubbling bottle.

2) *Temperature*: The seeds of *S. roxburghii* are relatively tolerant to the low temperature, as they are alive at a low temperature of 4°C for more than 6 months. The seeds of the other *Anthoshorea* including those of *S. assamica*, *S. bracteolata*, *S. hypochra*, *S. resinosa*, and *S. sericeiflora* survived at 4°C, although the duration of the survival varied depending on the species (Table 2). The

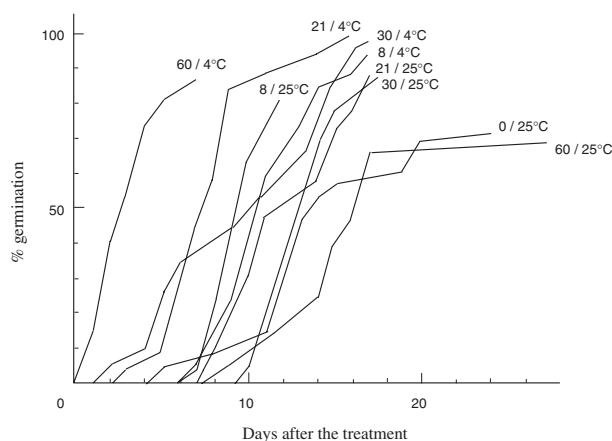


Fig. 3. Effect of prechilling on *Shorea roxburghii* seed germination. Numbers by the each line indicate the duration of the cold treatment (days) and the temperatures (°C).

seeds of some *Hopea* species such as *H. subalata* also showed the tolerance to a low temperature of 4°C (Table 2). According to Tompsett,³³⁾ *Dipterocarpus alatus* seeds have the tolerance to a temperature at -13°C, whereas those of *D. tuberculatus* and *D. intricatus* survive even at -20°C. On the other hand, we observed that the cold treatment of *S. roxburghii* seeds at 4°C accelerated the speed of germination. Furthermore, such the effect of the cold stratification was pronounced when the cold storage period was prolonged (Fig. 3).^{38),39),42)} The phenomenon is related to the after-ripening of the seeds during the cold storage.^{38),42)}

The seeds of *Rubroshorea* are highly susceptible to the low temperatures. The seeds of *S.*

Table 3. Maximum storage period for various *Rubroshorea* seed

Species	Original		25°C			21°C			17°C			4°C*		
	% germ.	% moist.	Days	% germ.	% moist.	Days	% germ.	% moist.	Days	% germ.	% moist.	Days	% germ.	% moist.
<i>S. platyclados</i>	86	59.0				40	20	46.3	40	10	36.2		0	
<i>S. curtisii</i>	90	64.1	35	5	21.6	30	78	72.7	14	15	73.1		0	
<i>S. accuminata</i>	95	75.3				30	70	61.6	14	24	92.9		0	
<i>S. paucifolia</i>	100	103.6	45	67	61.8	45	55	76.5	30	25	91.8		0	
<i>S. argentifolia</i>	100	84.0	51	30	50.2	45	60	64.1	45	10	68.9		0	
<i>S. parvifolia</i>	100	66.7	21	14	60.1	45	53	51.5	45	14	46.0		0	
<i>S. dasyphylla</i>	97	86.9	8	48	55.3	14	24	68.0	8	48	68.0	2	63	118.7
<i>S. leprosula</i>	100	49.5				30	47		27	17	31.4	4 hours	0	
<i>S. ovalis</i>	100	55.2	25	37	40.9	42	80	58.6					0	

*All *Rubroshorea* seeds tested were killed at 4°C for 4 hours, but *Shorea dasyphylla* seeds survived at least for 2 days.

leprosula kept at 4°C developed chilling injury to turn color of the cotyledons brown within 4 hours (Table 3). The seeds of the other *Rubroshorea* groups also developed the chilling injury symptoms within a few days at 4°C. Generally the seeds of *Rubroshorea* lose the viability by the storage at a temperature below 15°C,³⁸⁻⁴⁰⁾ and the reduction of the germination percentage occurred even at 17°C. The chilling injury reveals several symptoms. The embryonic tissues lose the elasticity and become brittle and crumbly. Color of the cotyledons changes from green or white to water-soaked appearance, and finally to necrotic brown. Microscopic observations show that all cells are ruptured with the stained cell wall remained. The development of symptoms in the radicles delays but follows a pattern similar to that of the cotyledons. The seeds of *S. ovalis* placed in a freezer at -20°C did not develop the color change probably due to susceptibility of the browning enzymes or polyphenol oxidases, but the seeds lost viability.

(5) Conditions for the seed storage of various dipterocarps. 1) *Subfamilies of Shorea.* *Anthoshorea:* The fermentation and suffocation of the seeds frequently occurred in the immature seeds with a high moisture content. Therefore, the timing of the seed collection is important to obtain the healthy matured seeds. The seeds of *S. roxburghii* were viable for 6 months at 4°C³⁸⁾ (Table 2), and in a closed polyethylene bag at 21°C, the seeds maintained 90% of survival for more than 7 months with the moisture content of 45.9%. The best storage temperature would be 21°C.

Rubroshorea: The seeds of *S. ovalis* neither tolerate the desiccation below 20% of the moisture

content by the dry weight nor a temperature below 15°C.³⁸⁾ The seeds of *Rubroshorea* are extremely susceptible to low temperatures, as the seeds of *S. leprosula* lose the viability within 4 hours at 4°C (Table 3). The best results were obtained in storage at 21°C in a closed polyethylene plastic bag, which gave the 60% survival of the seeds stored for 100 days. Although the fungus infection was serious in the humid conditions, 10% of the seeds still survived at 21°C even after 168 days. Dusting of fungicide, Benlate, may be helpful for protecting the seeds from infection. *Rubroshorea* groups showed the best results in storage at 21°C with the maximum storage period not exceeding 3 months.³⁸⁾

Eushorea: According to Symington,²⁵⁾ *S. robusta* distributed in India tolerates low temperatures, and Tompsett³³⁾ indicated that *S. robusta* shows some tolerance to 15°C. Similarly, *S. obtusa* growing in dry conditions may have tolerance to low temperature. It is difficult to discuss low temperature tolerance of *Eushorea* collectively.

Richetia: The seeds of *S. resina-nigra*, *S. multiflora*, *S. faguetiana*, and *S. hopeifolia* survived at 4°C for about a month. However, slow development of chilling injury symptoms finally deteriorated the seeds. Therefore, *Richetia* group does not have enough tolerance to low temperatures. The storage of *Richetia* seeds needs a high temperature above 15°C and the temperature suitable for the storage will be in a range around 20°C.

2) *The other dipterocarp genera.* *Hopea:* The seeds of *H. ferrea*, *H. latifolia*, *H. odorata*, *H. nervosa*, *H. beccariana*, *H. subalata*, and *H. wightiana* survived at 4°C for various periods (Table 2).

However, the duration of the survival at 4°C did not exceed 3 months. Probably the tolerance to low temperatures may not be the same as those of *Anthoshorea* group. *H. nervosa* seeds stored at 21°C survived more than 10 months, indicating that a long-term storage is possible for some species of the *Hopea* group.

Dipterocarpus: The seeds of *Dipterocarpus oblongifolius* were viable at 4°C at least for more than 2 months. In addition, the seeds of the unidentified *Dipterocarpus* species tolerated the cold storage at 4°C. Probably *Dipterocarpus* seeds tolerate the low temperatures as low as those of *Anthoshorea* group do. The longest storage was 2829 days at -13°C for *D. alatus* seeds, although the germination percentage decreased during the storage. Similarly, *D. intricatus* seeds survived for 2373 days at -20°C and *D. tuberculatus* seeds were viable for 1369 days at -20°C.³³⁾ These recent data suggest that *Dipterocarpus* seeds are able to tolerate the freezing temperatures.

Parashorea: The seeds of the *Parashorea* species survived at a temperature below 10°C only for one or two weeks. *P. lucida* seeds developed the symptom of the chilling injury at 4°C. However, the *Parashorea* group may need re-examination for the survival at 4°C, because the group includes the species with a wide variety of physiological characteristics.

2. Characteristics of Leguminosae and Myrtaceae seeds

(1) *Leguminosae* seeds. 1) *Structure*: The fruits of *Acacia*, *Cedrelinga*, *Intsia*, *Leucaena*, *Paraserianthes*, and *Parkia* form the long pods similar to those of the beans. Particularly, the pods of *I. palembanica* are large and leathery, but they release the seeds by the dehiscent action of the leathery pod. Among the pods, the pod of *Cedrelinga* is unique. The long pod of *Cedrelinga* contains several seeds in a line. The width of the pod where the seed is located is wide, whereas the widths in between the seeds are narrow. The narrow parts of the pod have the abscission layers. When the pod is released from the tree, it is separated into pieces at the abscission layer to contain one seed in each piece, and then the individually separated seed germinates on the forest floor.

Koompassia and *Pterocarpus* form the papery thin pods, in which usually one seed is enclosed. Particularly, the papery pod of *Koompassia mala-*

ccensis is twisted at the long end, and the twist enables the pod to turn horizontally like the ribbon flying in the air. When the pod separates from the tree, the pod turns horizontally, and it is carried away by the wind. In contrast, *Dialium*, and *Sindora* produce the hard seeds covered by fleshy fruits. Forest animals eat the fleshy fruits and leave the seeds on the ground. The seeds of *Acacia*, *Intsia*, *Leucaena*, *Paraserianthes*, and *Parkia* are disseminated by the dehiscence of their pods. Generally, these seeds are found widely in the forest soil.

Most of the legume seeds are exalbuminous. However, the mature seeds of *Dialium* and *Leucaena* still have the thin endosperm layers surrounding their embryos. This indicates that these species are in an intermediate stage from the albuminous to the exalbuminous seeds. The cotyledons contain the reserve substances of the seeds. The thick cotyledons occupy the most space of the seed, and the other embryonic organs such as the radicle, the hypocotyl, and the epicotyl are connected to the petioles of the cotyledons.

The legume seeds develop two types of the seed coat depending on the species. One is soft seed coat permeable of water, and the other is hard seed coat impermeable of water. In both types, the legume seeds reduce their moisture contents to the level below 10% of the dry weight during the seed maturation.⁴³⁾ Generally, the dry seeds become physiologically dormant, and they have neither respiration nor protein synthesis.^{44)–48)}

2) *Germination*: The legume seeds have the epigeal cotyledons. Although the seeds of *Cedrelinga* and *Koompassia* have soft seed coat and germinate easily on the forest floor, the seeds of *Acacia*, *Dialium*, *Intsia*, *Leucaena*, *Paraserianthes*, *Parkia*, *Pterocarpus* as well as *Sindora* have the hard seed coat, which makes difficult to germinate. They need wound or cracking of the coat to facilitate infiltration of water into the seed for germination. Such the damage of the coat is occasionally achieved by forest fires and attacks by insects or rodents, while abundant numbers of the seeds remain in the soil without encountering the opportunity to germinate. We often observed that after forest fires, the *A. mangium* seedlings were regenerated from the imbedded seeds.

The artificial scarification of the coat is effective to promote germination of the legume seeds

with the hard seed coat.^{42),43)} To make scars on the seed coat by filing is tedious and it is not suitable for small seeds such as *Acacia*, *Leucaena*, and *Paraserianthes*. Hot water treatment is easy, but needs repeated treatments to obtain high germination rates. Effective germination can be obtained by the immersion of the seeds in concentrated sulfuric acid for approximately up to 1 hr. The seed of *Intsia palembanica* is large with 5 cm in length and 3 cm in width. An effective method to scarify the big size seed such as *Intsia* and *Sindora* artificially is to scrape off the small swelling point (strophiole).⁴⁸⁾ The swelling point appears to be the point of the fusion of integuments at micropyle located on the opposite side of the hilum. It is very fragile and easy to make a small hole by rubbing the swelling point on the concrete floor. When the scarified seeds are immersed in water, water infiltrates through the hole into the seeds and the seed coat is swollen and ruptured within 30 minutes.

3) *Storage*: The lesume seeds can reduce the moisture content less than 10% without losing the viability.^{42),43),49)} The moisture content less than 10% means that the seed is physiologically dormant. The seeds resume physiological functions by imbibing water.⁵⁰⁾⁻⁵⁴⁾ The seeds of the legume species such as *A. mangium*, *A. auriculaeformis*, *L. leucocephala*, *P. javanica*, *I. palembanica*, *Paraserianthes falcatalia* as well as *S. coriacea* can be stored at room temperature for more than three years. They are also tolerant to storage at 4°C if the seeds are dry. The seeds of *Koompassia malaccensis* needed the treatment with fungicides, as the infection of fungi became serious after the storage of 100 days. The seeds survived more than 6 months, when they were dusted with 0.1% benlate or dried to reduce the moisture content less than 10%.

(2) *Myrtaceae seeds*. 1) *Structure and germination*: The seeds of *Myrtaceae* are contained in capsules. The capsule of *Eucalyptus deglupta* is conical and contains numerous seeds (12,000 seeds/g).⁵⁵⁾ The seed is exalbuminous without the endosperm, and the moisture content is less than 10% of the dry weight. The capsule of *Melaleuca cajuputi* shows the shape of a small globular cup and also stores numerous numbers of the seeds. The capsule disseminates the seeds with a dehiscent action remaining the vacant capsules on the twigs. The seed germinates fast, as it has a thin seed coat

permeable to water. The *M. cajuputi* seeds germinate on sand dune as well as even under water in swamps. *M. cajuputi* is a good candidate for the rehabilitation of waterlogged areas.

2) *Storage*: As the moisture content of *Myrtaceae* seeds is lower than 10%, they can be stored for a long time at room temperature. It was reported that the dry seeds of *Eucalyptus* of the subtropical regions were stored viable for more than 10 years at a low temperature between 0°C and 4°C.⁴⁹⁾ The seeds of *Eucalyptus deglupta* were able to be stored in a cool airtight container for longer than a year, and those of *M. cajuputi* at the room temperature for several years.

III. Light conditions affecting the seedling growth in the forest

1. Light conditions in the forest

The quantity and quality of the light in the forest primarily determine the growth and the morphological development of the seedlings on the forest floor.^{31),39),56)-60)} The light in the open sky or "the global solar radiation" consists of the sunlight and the diffuse light of the sky, the latter of which becomes constant beyond the 30 degrees of the solar altitude.⁶¹⁾ This constant illuminance of the diffuse light in the sky influences the characteristics of the diffuse light in the forest. In addition, various factors such as absorption and scattering by the green leaves affect not only the illuminance but also the spectral composition of the light under the canopy. Detailed analyses of the characteristics of the light in the tropical rain forests described below were carried out at the sites in the Forest Research Institute, Kuala Lumpur in Malaysia.

(1) *Characteristics of the light illuminance in the forest*. In the tropical regions, the altitudes of the sun are high during the mid-day and the sunlight irradiates from high positions for the most of the day. Not only the sunlight but also the diffuse light of the sky penetrate the canopy layer through transmitting leaves and scattering by foliage and stems of the vegetation to produce the diffuse light in the forest. The illuminance in the shaded area of the forest floor corresponds to the basic level of the diffuse light at the site of the forest. On the other hand, the direct sunlight penetrates the canopy layer passing through apertures between leaves to reach the forest floor. The small apertures function as the pinhole camera and produce bright images of

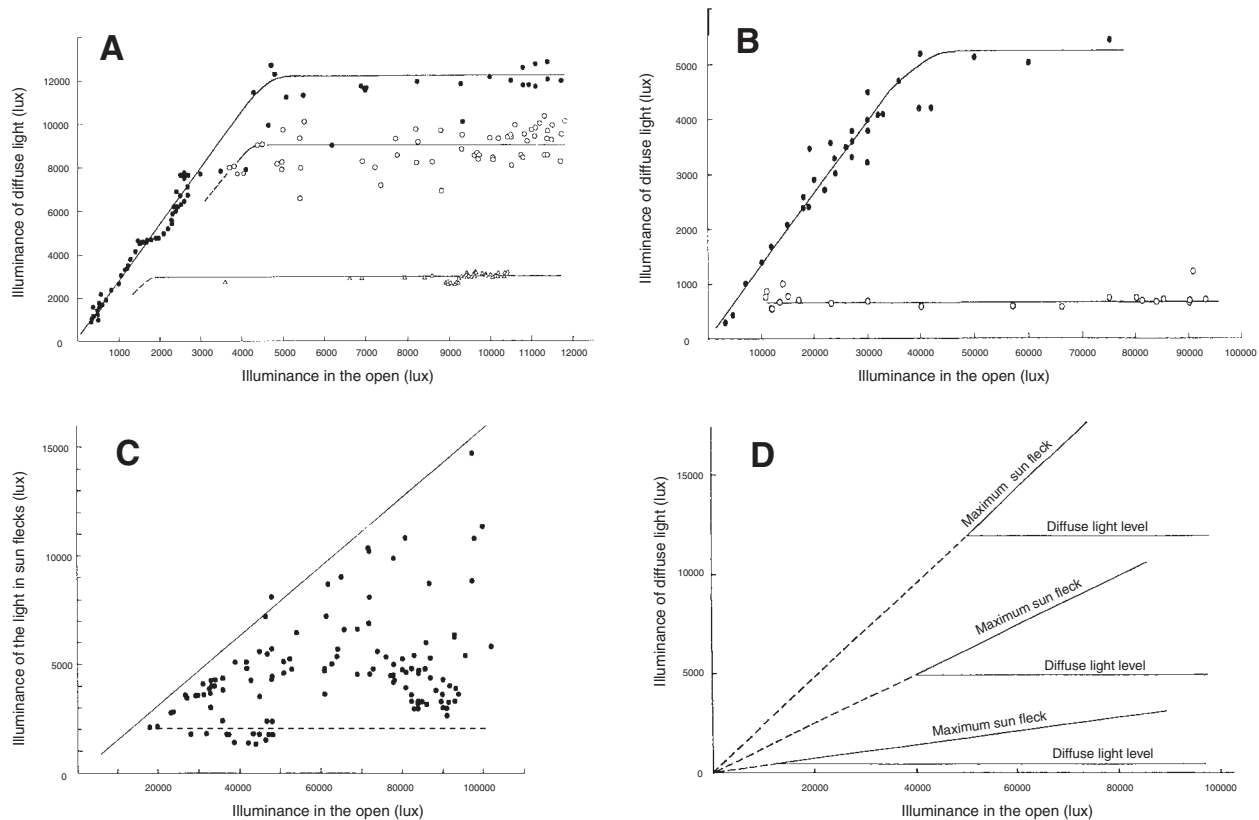


Fig. 4. Relation of the illuminance of the diffuse light in the forest with the illuminance of the light in the open. (A) Diffuse light under the Nipa roofing. The top curve (●): stabilized at 12,000 lux, the second curve (○): stabilized at 9,000 lux, and the bottom curve (△): stabilized at 2,500 lux. (B) Diffuse light measured at the shaded area at the bright (●) and the dark (○) sites under the canopy of the forest. (C) Distribution of the illuminance at a site in the forest. (D) Theoretical relationships of the illuminance at the sun flecks and the diffused light in the forest with the illuminance of the light in the open.

the sun, which are called “sun flecks”. The illuminance in the sun flecks corresponds to the sum of the diffused light and the direct sunlight at the spot.

The characteristics of the diffuse light in the forest were studied at first by measuring the light with two photometers (Toshiba SPI-7 illuminance meters) and a grating spectroradiometer (Iio Electric Co. Spectroradiometer) under a nipa roofing (palm leaf roof) settled in the nursery as a model, where only the shaded area but no sun flecks were present. All the measurements were performed when the illuminance of the light in the open changed in a wide range by shading with a coming thunderstorm. The illuminance at a given site under the roofing was plotted against the illuminance of the light in the open measured at the same time. All the plots were represented by a curve composed of a horizontal line and a slanting one with a specific turning point (Fig. 4A). The results

indicated that, (i) the illuminance of the diffuse light under the roofing linearly increases until the illuminance in the open increases to reach the turning point, and (ii) the illuminance of the diffuse light becomes constant in the region higher than the turning point, even though the illuminance in the open is considerably fluctuated by the clouds.

These observations were confirmed by measuring the illuminance at the sites in the forests, one was composed of *D. aromatica* trees and another was the mixed forest of *S. macroptera* and *S. leprosula*, both of which were 43 year-old. When the illuminance of the diffuse light measured at the spots in the shaded area were plotted against the illuminance of the light in the open, essentially the identical profiles to those under the nipa roofing were obtained with the canopies of the both forests (Fig. 4B). At the relatively bright site in the forest, the illuminance of the diffuse light increased

Table 4. Illuminances of the diffuse light in the forest in relation to the light in the open

Steady state of the diffuse light level lux	The light in the open at the turning point (T) lux	Relative light intensity (%)
500	12,000	4.1
650	13,000	5.0
1,750	20,000	8.8
4,200	32,000	13.0
5,500	39,000	14.0
9,000	45,000	20.0
12,000	50,000	24.0

linearly until the light in the open increased more than 40,000 lux and then became stable at the illuminance of 5,000 lux. At the dark site, the diffuse light reached the stable illuminance of 1,000 lux in the range of the illuminance in the open higher than 10,000 lux.

When all the illuminance measured at a site including the sun flecks, partial sun flecks, and the diffuse light was plotted against the illuminance in the open, all the plots were distributed in an area between the slanting and horizontal lines (Fig. 4C). The slanting line represents the change of the maximum illuminance in the sun flecks or “the linear state of the diffuse light”, while the horizontal line represents “the steady state of the diffuse light” in the shaded area. The generalized profile is presented in Fig. 4D. When the illuminance in the open to give the turning point (here called “T” value) is estimated at the various sites, T becomes higher at the site where the steady state level of the diffused light is higher (Table 4). Thus T or the turning point is a good index to know the light conditions at the site in the forest.

The primary production of various types of the vegetation is in a good correlation with the diffused light in the forest. In order to estimate the diffuse light, the ratio of the penetrating light in the forest to the light in the open or “the relative light intensity” is frequently used. As pointed above, however, the ratio is constant only in the range lower than the turning point T. That is the reason why the condition to measure the relative light intensity should be limited to the cloudy condition as Monsi and Saeki stated.⁶²⁾ The sun flecks in the forest become visible when the light in the open exceeds the T value. Therefore, the relative light intensity can be estimated from the measurements

in the bright sun flecks. In contrast, when a site is as dark as the sun flecks are not visible, the diffuse light is in the linear state, which corresponds to the relative light intensity.

Our studies showed that the linear state, the steady state, and the turning point of the diffuse light are the specific parameters representing the characteristic light condition in the forest.^{31),39),58)} Especially, the steady state of the diffuse light can be assumed as “the baseline light of the site”, which allows easy assessing of the light condition of the forest.

(2) Light quality of the forest. The canopy layer influences the quality as well as quantity of the light in the forest.^{39),42),55)–57)} The light transmitted through the leaf shows the spectra with relatively high ratio of the green (500–600 nm) and far red (>700 nm) light due to the absorption of the red light (Fig. 5A). The shade leaf transmits the green light more efficiently than the sun leaf does, because the shade leaf is thinner than the sun leaf (Fig. 5A). Similar tendency is observed with the thick leaf of *Agathis dammara* and the thin leaf of *S. parvifolia*.

The diffuse light measured in the shaded area in the forest shows a wide spectral distribution especially in the region below 500 nm, because a portion of the diffuse light of the sky is contained (Fig. 5B). On the other hand, the light in the sun flecks contains direct sunlight but not the diffuse light of the sky. As the consequence, the ratio between red light and far red light in the sun flecks is reversed from that of the diffused light (Fig. 5C). The bright sun fleck of full strength contained the relatively abundant red light in the forest that is the most effective spectral region for the photosynthesis. The light in the open showed a peak at

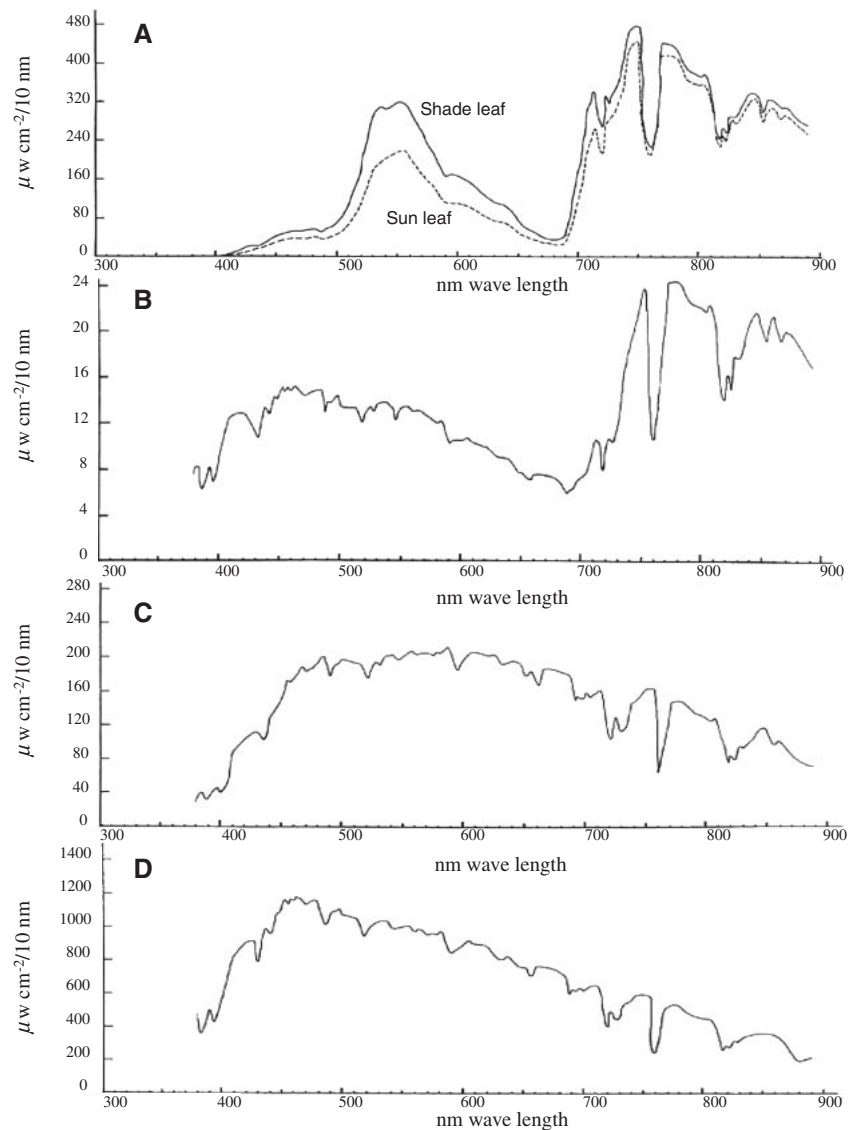


Fig. 5. Spectra of (A) the transmitted light through the leaves of *S. roxburghii*, (B) the diffused light in the mixed forest of *S. macroptera* and *S. leprosula*, (C) the light at the bright sun flecks, and (D) the light in the open.

450 nm, and gradually tapered off toward the far red light (Fig. 5D). Evans⁶³⁾ emphasized that the sun flecks play an important role for the growth of seedlings under the canopy. The growth of seedlings in the forest is affected by not only the relative light intensity but also the spectral characteristics of the light in the forest as described below.

2. Growth of the dipterocarp species seedlings under various light conditions

(1) **Functions of hypogeal cotyledons and first pair leaves.** The photosynthesis of the leaves, the germination of the seeds, as well as the

development of the leaves are affected by the quantity and quality of the light.^{40),57),64),65)} The seedlings of the hypogeal species such as *Shorea roxburghii* utilize the reserve substances of the seeds until the first paired leaves expand to carry out the photosynthesis. Therefore, the function of the cotyledons and the first photosynthetic leaves on the seedling development needs to be studied.

The importance of the hypogeal cotyledons and the first paired leaves in the seedlings of *S. roxburghii* was examined by removing these organs at the stage of the expansion of the first paired leaves.³⁹⁾

The removal of the cotyledons at the development stage of the first paired leaves did not affect the survival of the seedlings, as the most cotyledonal reserve substances were already consumed for the expansion of the first paired leaves. In contrast, the removal of the first paired leaves decreased the survival of the seedlings, because the early seedling development depends on photosynthesis of the first paired leaves. The reduction of the growth was also observed with the survived seedlings after the removal of the first leaves. The survival rate of the seedlings after removing both the cotyledons and the first leaves was reduced by about 50%, which was much less than that of removing the first leaves alone. This indicates that the cotyledons are still functioning for the development of the seedlings even at the stage of the expansion of first paired leaves. It is evident that the photosynthesis in the first paired leaves is particularly important for the development of *S. roxburghii* seedlings.

The removal of both the cotyledons and the first paired leaves caused the decreased growth even one year after the treatments. Particularly under the shade, the seedlings without the first paired leaves showed the retardation of the growth in height. The experiment demonstrates that the enough amount of the sunlight is needed for the initial growth of the *S. roxburghii* seedlings. When the seedlings possessing the first paired leaves intact were placed in the shade, they showed the accelerated internode growth. These seedlings in the shade were slender and tall with the poor root systems, compared with those grown in the open. The shoot/root ratios of the weight for the open grown seedlings were below 2.0, whereas the ratios of the seedlings in the shade were nearly 3.0. The seedlings in the open had a better balance for the shoot/root ratios.

(2) Effect of light on the seedlings growth.

Dipterocarps such as *Shorea roxburghii* and *S. ovalis* had been regarded as the plants growing in the humid condition under the shade. The traditional nurseries used the heavy shades by constructing the roof over the nursery beds or by leaving standing trees in the nursery. These shading practices in the nurseries produced the seedlings having the characteristics of "the shade plants" with the thin leaves and the weak stems. When these seedlings were transplanted in the field, their survival rates were very low. Our results described below clearly

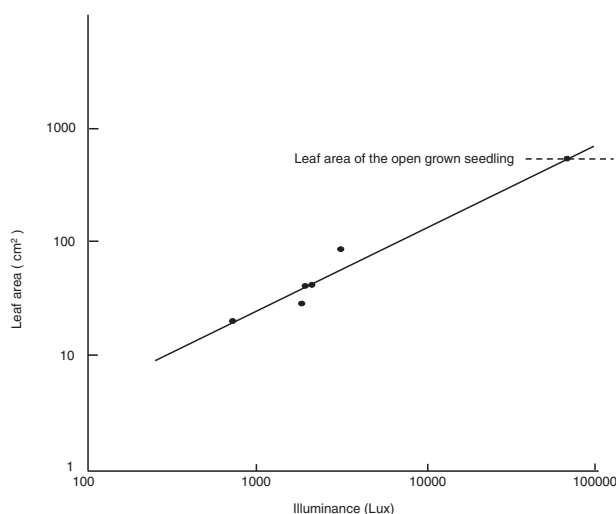


Fig. 6. Leaf area development of one year old *S. roxburghii* seedlings.

demonstrated that these species are distinctly light-dependent.

Among the dipterocarps species, there are some variations in the response of the seedlings to the light conditions. When the seedlings were transferred from the shade to the full sunlight, the *S. leprosula* seedlings showed the adaptation to the strong light by increasing photosynthesis.⁶⁶⁾ However, the seedlings of the *S. ovalis* as well as those of the *Dryobalanops lanceolata* failed to improve the photosynthesis after they were brought to the full sunlight.⁶⁶⁾ Furthermore, various plantations showed that the growth of *S. leprosula* was outstanding in the bright sites, compared with the other *Rubroshorea* species. These results indicate that *S. leprosula* seedlings are adaptable to the bright light conditions.^{65),67),68)}

1) *Effect of the illuminance of the light on the seedling growth:* The seedlings of *S. roxburghii* were placed on various sites in the two forest trails as well as in the nursery. The narrow strip of the canopy opening was present above the forest trails. The sun flecks were continually present on the forest trail of the east-west direction, which was parallel to the sun's orbit. In contrast, on the north-south direction, the sun flecks reached sporadically only during the midday when the sun was in the high altitude. At the sites in the forest, the increase in the height, the numbers of internodes and the internode lengths of the seedlings were poor in

A**B**

Fig. 7. The growth of *S. ovalis* seedlings at the various sites in the forest with different light conditions. (A) The seedlings were placed on the sides of the north-south direction with the steady states of diffused light of 750, 1,080, 1,600 and 3,200 lux, respectively, and (B) and at the sites in the east-west direction with the diffused light of 3,800, 2,600, 2,300 and 2,600 lux, respectively.

comparison with those in the nursery under the bright light.^{31),39),58),59)}

The growth in the total height and the numbers of the internodes were closely correlated with the illuminance of the steady state of the diffused light at the sites. At the dark sites, the seedlings formed only seven internodes for one year. Even at the brightest site in the forest, the seedlings developed only 15 internodes, whereas the seedlings in the open produced 23 internodes for one year. When the leaf area was plotted against the illuminance of the steady state on both logarithmic scales, the linear proportional plot up to the full sunlight was obtained (Fig. 6). These data show that *S. roxburghii* is a light-demanding species.

The effect of light on the growth of *S. ovalis* seedlings was examined in the experimental sites with various light conditions in the forest. Four sites with different illuminance of the steady state of the diffuse light were set on the north-south direction, while another four with the similar illuminance were set in the east-west direction and

the growth was observed during 18 months.^{32),39)} The illuminance of the steady state of the diffuse light was stable at any site and at any time during the day. The illuminance dependent growth of the seedlings was clearly observed as shown in Fig. 7A and 7B. The total leaf area of the seedlings had a good correlation with the steady state of the diffuse light at the sites, but the leaf area reached its maximum at a lower illuminance than that of the *S. roxburghii* seedlings.

The development of the roots of the *S. ovalis* seedlings was also affected by the light condition, and, at a steady state of the diffuse light close to 1,000 lux, almost no roots developed. The shoot/root weight ratios exceeded 5.0 at the steady state of the diffuse light of 1,600 lux. At the sites where the seedlings received the stronger light, shoot/root ratios showed a balanced ratio between 1.0 and 2.0. The seedlings grown at the dark sites showed the extensive elongation of the internodes up to the stage of the first paired leaves. However, the further growth was arrested in the dark sites, resulting in

the typical stunted form for the seedling. The seedlings grown in the brighter sites showed the continuous elongation of the internode.

2) *Effect of the quality of light on the seedling growth:* Chambers covered with various types of colored plastic films to transmit the light with specific spectra were used for studying the effects of the light spectra on the internode growth. The seedlings of *S. roxburghii* under the far red light showed the extensive elongation of the stems, resulting in 3.0 of the shoot/root ratio by the weight. In contrast, the seedlings under the open sunlight as well as under the transparent white film showed 1.0 and 1.2 of the well-balanced shoot/root ratios, respectively. The seedlings in the open as well as those under the transparent white film developed more internodes than those in the other chambers. The excessive elongation of the internode is attributable to a high ratio of the far-red light.³⁹⁾

Similar experiments were carried out with the *S. ovalis* seedlings. The seedlings at the stage of first paired leave expansion were placed in the chambers, and after seven months, the seedlings were harvested to measure the internode elongations and the dry weights. Although the hypocotyls and the first internode of the seedlings had begun to be lignifying at the start of the experiment, the seedlings under the blue film showed the consistent elongation of the internode. The blue film used transmits more than 80% of the blue and far red light but not the red light, which is similar to the diffuse light in the forest. On the other hand, the pale blue film transmitting less than 10% of the far red light at most did not promote the elongation of the internode. It is known that the ratio between the red and the far red light controls the morphological development of the plant through the phytochrome system.^{42),54),56),60)} Our experiments in the field as well as in the color chambers clearly demonstrated that the spectral composition of the forest light affected the seedling growth and morphological development.

In another experiment, the films transmitting UV below 400 nm and the other not transmitting UV were used. The two films showed the significant differences in the growth of the seedlings, particularly in the weights. After seven months, the seedlings in the UV-transmitting chamber had the shoot of dry weight of 1.67 g, whereas the seedlings without UV had 2.68 g of the dry weight.³¹⁾ How-

ever, the height growth and the internode elongation were not affected greatly by UV.

The diffuse light under the canopies is high in the light spectra from 400 to 600 nm as well as high in the far red light spectra above 700 nm. These light spectral regions are known to be low in the efficiency of photosynthesis.⁶⁰⁾ Therefore, the diffuse light in the forest alone does not contribute much to the weight increment. The sun flecks abundantly containing the red light are needed in the forest to enhance the weight increments of the seedlings.^{42),63),69)} In addition, the stout seedlings must be raised under the bright light conditions.

These experiments in the field as well as in the color chambers demonstrated that the spectral composition of the forest light affected the seedling growth.

3. Growth of *Leguminosae* seedlings under light conditions in the forest

(1) *Direct sowing of Intsia palembanica seeds in the field.* Since the large *Intsia* seeds have the abundant reserve substances in the large cotyledons, the seedlings reach 26 cm in height within 15 days after sowing the seeds. Therefore, the direct sowing of the seeds was tested in the forest by using the scarified *Intsia* seeds.⁴⁸⁾

The seedlings in the open developed the 6 or 7 internodes for 143 days after the seeds were sown, whereas the seedlings grown in the forest at the illuminance from 300 to 600 lux by the steady state of the diffuse light developed only the 3 or 4 internodes. In addition, the *Intsia* seedlings in the forest as well as in the color chamber showed the extensive elongations of the hypocotyl and the internode to the first paired leaves.^{48),58),59)} The direct sowing of *I. palembanica* is feasible, but the site must have the good condition of the light for the growth of the seedlings from the stage of the seed germination.

(2) *Natural regeneration trial for Cedrelinga catenaeformis.* The bright condition of the light with probably 5,000–9,000 lux of the steady state of the diffuse light is required for the success of the natural regeneration. The wildlings of the *Cedrelinga catenaeformis* (the local name is Tornijo) were tested for the promotion of the regeneration in the forest. As the *C. catenaeformis* seed has a soft seed coat, the seed germinates easily in the forest. At the experimental site, the small seedlings of the *C. catenaeformis* with an average height of 8 cm

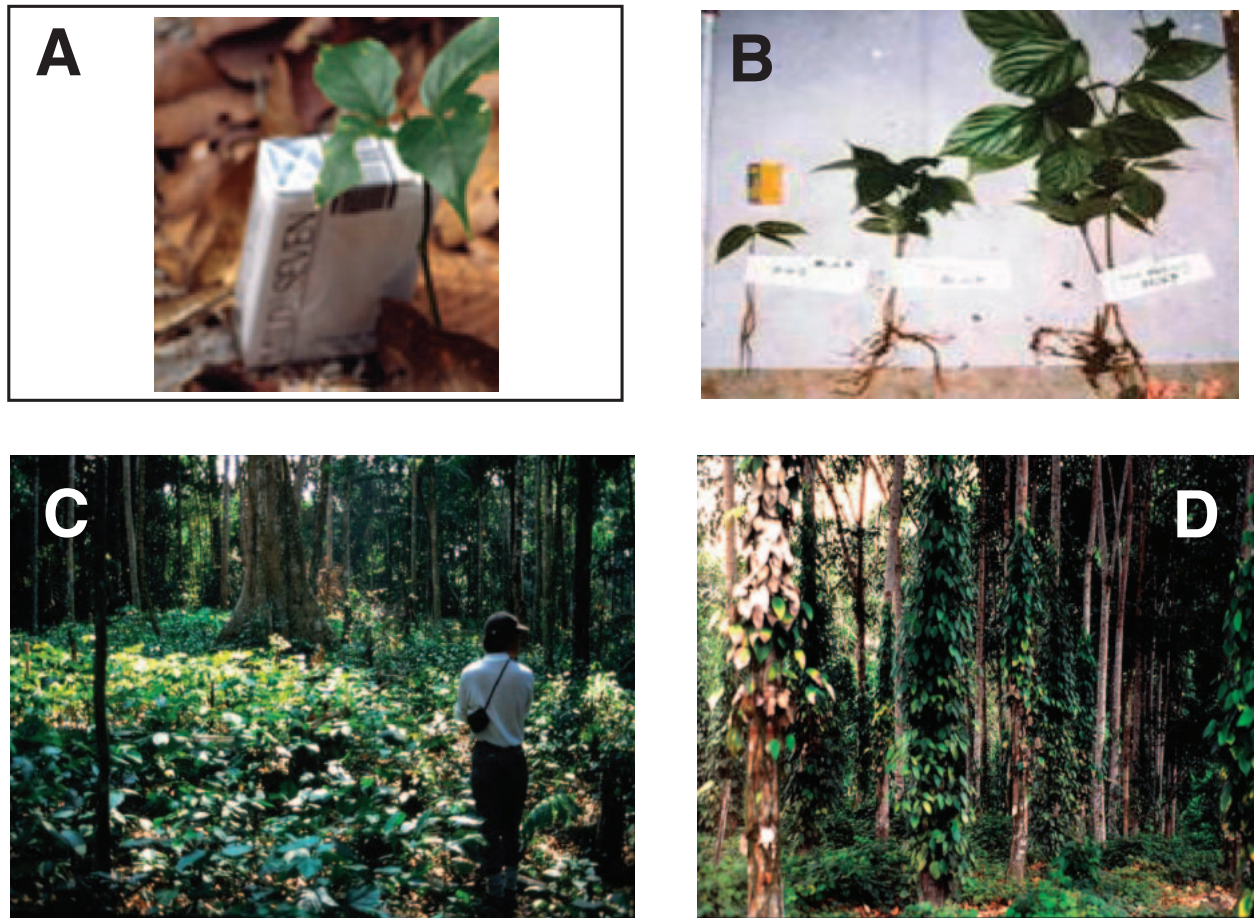


Fig. 8. Photographs showing the promotion of natural regeneration for *Cedrelinga catenaeformis* by thinning the canopy. (A) Natural seedlings grown in the forest, (B) the seedling collected after 6 months of the thinning, and (C) the view of the site one year after the thinning, and (D) the site 13 years after the thinning.

were abundantly present in the forest. However, their growth was arrested in the forest just after a few leaves were developed, because the light in the forest was insufficient. Therefore, the removal of small trees and palms to bring the light into the forest is effective for the promotion of the natural regeneration.⁷⁰⁾ By these operations, the steady state of the diffused light of the forest floor was improved to a maximum of 9,000 lux. The small seedlings of *C. catenaeformis* growing on the forest floor quickly responded to the improved light condition by thinning the canopy and showed the markedly stimulated growth within three months. The responses of the *Cedrelinga* wildings to the canopy opening as well as the establishment of the *Cedrelinga* forest were shown in a series of the photographs (Fig. 8A, B, C and D).

IV. Methods for transplantation

1. Bare-root seedlings

Generally, the potted seedlings have been used for planting trees in the tropical countries, but the survival of the potted seedlings was not satisfactory in the past. The loss of water by the transpiration during the daytime was a serious problem for the transplanting of the seedlings in the field.^{69),71)} The leaves are needed for the growth, but they are detrimental at the time of the transplanting, as the leaves cause loss of water through their high transpiration. In addition, the heavy weight of the pot soil makes the handling in the field difficult and causes the damages to the seedling during the planting. To improve the survival of the transplanted seedlings, a planting method of “the bare-

root seedlings”, the seedlings easy to handle by removal of all leaves, soil and pots, was developed.⁷²⁾

(1) Development of the bare-root seedlings. We performed the following experiments with the *S. roxburghii* seedlings grown in the open in the nursery bed for 1 year and 3 months were pulled out of the soil. The seedlings were treated in three different ways as follows: (i) all leaves, the leader shoot and the taproot were trimmed (named “the bare-root seedlings”), (ii) the leader shoot and the taproot were trimmed, but a few leaves left intact, and (iii) no treatment on the shoot but the taproot was trimmed. These seedlings were transplanted to the nursery bed and kept without watering.^{31),72)}

One week after transplanting, new buds developed from the leaf scars for the bare-root seedlings without leaves. In addition, the fine lateral roots quickly regenerated from these seedlings without the leaves. In contrast, the seedlings with a few leaves intact delayed the new bud development until the old leaves were shed off. Furthermore, the seedlings with all leaves intact showed the symptom of the desiccation and the dieback from the top, but, after all the leaves were shed, the new flush of buds started from the lower portion of the stem. The new flush of the bud on the intact seedling delayed at least one month, compared with the seedlings without the leaves. These observations were verified by the experiment of the bare-root seedlings of *S. ovalis* and *D. lanceolata*.⁷³⁾ The seedling without the leaves and the young portion of the shoot reduced the rate of the transpiration to a level of less than 0.25 g/hour, compared with the rate of the transpiration of 2.0 g/hour for the intact seedling of *S. ovalis* and 1.25 g/hour for *D. lanceolata*. Because there was no transpiration from the leaves for the bare-root seedlings, their moisture contents were maintained at an unexpectedly high level with over 300% of the dry weight.⁷³⁾ In addition, the water potential (or the xylem pressure potential) of the *S. ovalis* seedling with some leaves intact was -4 MP, whereas the water potential of the seedling with all the leaves intact was -15 MP. Although no measurement was taken for the bare-root seedlings, their water potentials of the stem were probably very small. *D. lanceolata* maintained the moisture effectively, and did not develop the water stress as in the case of *S. ovalis*.⁷³⁾

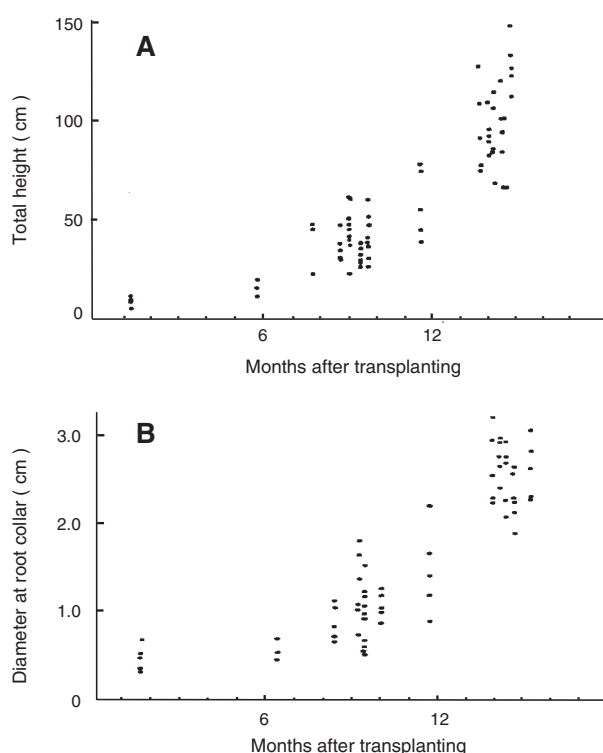


Fig. 9. Growth of the bare-root seedlings after transplantation. (A) Growth in height and (B) growth in diameter at the root collar.

Generally, the uppermost newly formed bud took over the leader shoot role, and none of the seedlings formed multiple leader shoots. The results indicated that the seedlings with their roots and shoots trimmed as well as with all the leaves removed were best suited for transplanting. The shoot trimming enhances the new shoot development.⁷²⁾ Even for the seedling only with the first leaf scars (shortest stem), the new bud takes over as the dominant leader shoot. The bare-root seedlings of *S. ovalis*, *H. odorata*, *D. Lanceolata*, and *D. aromatica* showed the development of new robust leader shoots. A few leaf scars on the stem are sufficient for the bare-root seedlings to develop into the normal seedling with a single main stem. The bare-root planting showed a high survival percentage, but the establishment of the leader shoots as well as the acceleration of the leader shoot growth needed a certain time lag. It takes at least one year for the seedlings to initiate the height growth, as the growth of the height and the diameter restarted to increase 10 months after transplanting (Fig. 9A, and 9B). However, the *S. roxburghii* bare-root

seedlings showed the height growth of 150 cm 1.5 years after transplanting.

The bare-root transplanting is practical in the transplanting work in the forest, because of the easiness of the handling, no desiccation problem, as well as the better survival. The bare-root seedlings are called “stumps” occasionally,²⁴⁾ and the planting of the stump is called “stump planting”.

(2) Field trial of the bare-root seedlings.

The *S. roxburghii* seedlings were suitable to the bare-root planting, as they have the strong regenerative ability of the buds and the roots. A few hundreds of the bare-root seedlings of *S. roxburghii* were planted in 2 ha of the open field in the Sungai Buloh Experiment Forest. All the planted bare-root seedlings survived, and showed the remarkable growth with the height reaching 2 m within 2 years. The bare-root seedlings showed the best performance in the open ground.⁶⁷⁾ We often observed that the planting of the bare-root seedlings failed in dark forest conditions, indicating that the bright light condition is required to succeed the planting of the bare-root seedlings. The bare-root planting method can be applied for the other species such as *Dryobalanops*,⁷⁴⁾ *Anthoshorea*, *Hopea*, and *Dipterocarpus*.

(3) *The storage of bare-root seedlings.* The bare-root seedlings were tested for the storage (Table 5).⁷²⁾ The seedlings were graded by the size of diameter at the root collar. Large seedlings had more than 1.0 cm of the root collar diameter, and small seedlings had a diameter below 0.5 cm. The bare-root seedlings were stored in a closed plastic bag to maintain the moisture content at the level of live seedlings, whereas the control seedlings were kept in an open bag. In addition, the optimum temperature range for the storage was surveyed at the temperatures of 4, 17 and 25°C. To avoid premature bud expansion due to an excess of water during the storage, the seedlings were stored without washing the roots.

The maintenance of the moisture content in the tissue is crucial for the seedling survival. The large size seedlings showed better survival than the small ones, possibly due to available water and reserve substances in the tissue (Table 5). The storage in low temperatures appeared to be detrimental to seedlings. A gradual decline in survival was evident for the small seedlings, even for the seedlings in the closed bags. Although the large seedlings were still

Table 5. Survival % of *Shorea roxburghii* seedlings after storing in various temperature ranges

	Temperature stored	Seedling size*	Storage period (weeks)				
			1	2	3	4	10
Open bag	4 °C	Small	80				
		Large	60				
	17 °C	Small	0				
		Large	0				
	25 °C	Small	0				
		Large	40				
Closed bag	4 °C	Small	100	100	40	20	0
		Large	100	100	100	80	0
	17 °C	Small	100	100	40	80	40
		Large	100	100	100	100	100
	25 °C	Small	100	100	100	100	100
		Large	100	100	100	100	100
	4 °C	Small	100	100	40	20	0
		Large	100	100	100	80	0
	17 °C	Small	100	100	40	80	40
		Large	100	100	100	100	100

*Small seedlings of size in diameter at the collars were below 0.5 cm, while large ones are above 1.0 cm.

surviving after 3 weeks at 4°C, their bud development was markedly delayed. Up to 2 weeks of the storage at 4°C, a detrimental effect of the low temperature did not develop on the large seedlings. However, the storage at 4°C for more than 3 weeks caused the retardation of growth even for the large seedlings. The storage at 17°C also retarded the seedlings after storing for more than 3 weeks. In contrast, the storage at 25°C in an air-conditioned room appeared to be promising for long-term storage, as these stored seedlings at 25°C survived at least for 10 weeks. These stored seedlings resumed the growth after they were transplanted in the nursery. However, the storage of the bare-root seedlings at 4°C showed a gradual deterioration of the growth in the nursery.

Another storage trial of the bare-root seedlings of *S. roxburghii* was conducted in Narathiwat, Thailand. The bare-root seedlings were made from the wildlings (naturally grown seedlings) of *S. roxburghii*. In this experiment, young *S. roxburghii* seedlings with a diameter of 1 cm were pulled out from the open field, and all of their leaves were removed. The stems were cut at 5 cm from the root collar, and these bare-root seedlings were kept in a plastic bag under the desk in a room without the

air-conditioning. These bare-root seedlings were planted in a nursery 3 months after beginning of the storage. All the seedlings developed new shoots and grew well. Similarly, *H. odorata* seedlings survived more than 7 months. On the other hand, *S. ovalis* reduced the survival to 60% after the storage of 2 months.

2. Vegetative propagation

(1) **Cutting and tissue culture.** Propagation of dipterocarps from the cuttings of the seedlings was first succeeded by Momose.^{75),76)} The cuttings of *Anthoshorea*, *Vatica* and *Anisoptera* were prepared by excising a seedling stem into sections, each of which possessed one intact node and one internode with one leaf attached. Initially, the *Rubroshorea* species were difficult to propagate by the cuttings because of the poor callus formation. However, at present, the *Rubroshorea* species such as *S. leprosula*, *S. albida*, *S. selanica*, *S. pinanga*, *S. platy-chrados* and *S. stenoptera*⁷⁷⁾⁻⁸³⁾ can be propagated from the cuttings. Regeneration efficiency of the cuttings of *Rubroshorea* was improved by controlling the temperature under 30°C as well as by maintaining the humidity more than 95% in the cutting chamber with the light intensity of 5,000 lux.^{81),82)} These results suggested that the control of the humidity and temperature for the chamber is important to promote the root development. In addition, the cuttings need photosynthesis to maintain the physiological functions^{78),79)} by keeping a leaf on the stem of the cutting.

The tissue culture has been tried for the several species of *Dipterocarpaceae*. The micro-propagation was successful for the *S. roxburghii*.^{80),81)} In the legume species, *Acacia mangium* has been multiplied by the tissue culture. Since *A. mangium* has the tolerance to acid sulfate soil, the species is a target for breeding the sulfate tolerance clones.⁸⁴⁾⁻⁹¹⁾

(2) **Other propagation methods.** In the forest, we often observed the vertical sprouting of the fallen tree trunks laid down horizontally.⁷²⁾ Therefore, the multiplication of seedlings was attempted by inducing the upright growth of new shoots from the axillary buds of the seedlings horizontally laid and buried in the soil. *S. roxburghii* seedlings were used for the experiment. All the leaves were removed and the shoot tips were trimmed off to release axillary bud development. These seedlings were horizontally placed on the

nursery bed and lightly covered with soil. The *S. roxburghii* seedlings initiated the new shoot growth vertically, with each bud developing into an individual seedling. The roots began to form within a few months after the experiment was initiated. The method can be improved by exposing the seedlings to the light to stimulate the bud development, and then by burying in the soil to stimulate the root formation. In this experiment, *S. roxburghii* showed a strong ability to regenerate the buds on the stem. Probably, the regenerating ability of *S. roxburghii* is related to the tolerance of the species to forest fires.

3. Symbiosis of roots of dipterocarp seedlings with mycorrhiza

The dipterocarp seedlings keep the symbiotic interaction with ectomycorrhiza. In fact, the wildlings and the seedlings grown in the forest soil generally have the mycorrhizal roots. The seedlings after they were infected by the mycorrhizal fungi showed the better growth.^{92),93)} Therefore, the seedlings already forming the mycorrhizal roots were used to infect new seedlings by simply placing the infected seedling pots near the new seedlings in the nursery bed. This method is effective to infect the mycorrhizal fungi.⁹³⁾

4. Transplantation under the extreme conditions of environment

(1) **Tolerance to forest fires.** Our experimental sites in the Forest Research Institute, Malaysia as well as in the Sebulu Forest Experiment Station, East Kalimantan, Indonesia often experienced the forest fires.⁷⁴⁾ In Malaysia, the first forest fire occurred when the bare-root seedlings of *S. roxburghii* reached average 2m in height. The fire burned the stem of the young trees grown from the bare-root seedlings, and the stem of several trees were burned down completely. However, the new seedlings were re-established from the auxiliary buds developed from the root collar of the burned-down stems. In Indonesia, a month after the forest fire, new shoots were developed from the root collars and the plantation was reestablished (Fig. 10A, and 10B). *S. roxburghii* seedlings recover from the forest fire by developing new shoots from the auxiliary buds, which have the strong regenerative capacity. According to Symington,²⁵⁾ the *S. roxburghii* is associated with the Schima-Bamboo forests, which have the influences of the fires and the human activities in the swampy areas.

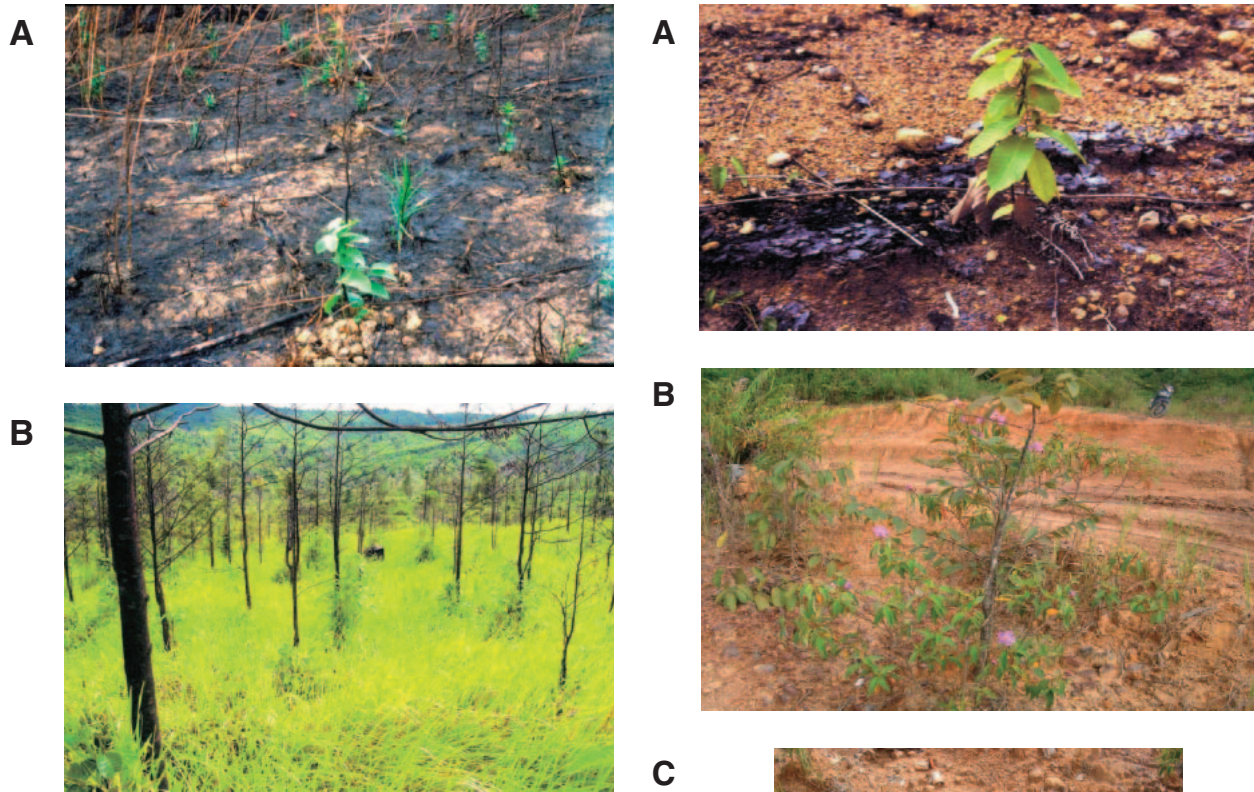


Fig. 10. Recovery of *S. roxburghii* from forest fire. (A) New shoot grown from the root collar after the fire, and (B) the young trees grown after 6 years from the shoots shown above.

Acacia mangium, *Gmelia arborea* and *Penor-ema canescens* were tolerant to the forest fire. *A. mangium* re-establishes the plantation by germinating the seeds buried in the soil, as the heat of the forest fire injures the hard seed coat to stimulate the germination. The *G. arborea* trees survive the fire by shedding the scorched bark as well as by regenerating the new bark. *P. canescens* trees develop the new shoots from the root collar, forming multi-stems. At least, the species tolerant to the fire possess the strong regenerative power of their tissues.

(2) Tolerance to extreme conditions of soil.

1) *Acid sulfate soil*: Acid sulfate soil is originated from pyrite (FeS_2). Pyrite is formed by the volcanic activities or by the submergence of the land under the sea to cause reduction of sulfate to sulfide. Acid sulfate soil and the potential acid sulfate soil spread widely in Southeast Asian countries including Indonesia, Malaysia, Thailand, and Viet Nam, as those landmasses emerged by elevation from the



Fig. 11. Tolerance of *S. roxburghii* to acid sulfate soil. (A) The seedling planted on acid sulfate soil, pH 3.0. A coal layer can be seen. (B) Growth of young trees from the seedlings after 7 years. Vegetation is recovering under the planted trees. (C) Acid sulfate soil without vegetation. Round stones contain iron and manganese.

sea. When pyrite is oxidized, it turns to acid sulfate soil, which lowers pH to 3.0 or below. The strong acidity causes the injury to the tissues of many plant species especially to develop the symptoms of the heavy metal toxicity. In a late stage of the acidification, the symptoms change from the heavy metal toxicity to the nutrient deficiency.^{94),95)} In Malaysia as well as in Thailand, *S. roxburghii*, *A. mangium*, *Melaleuca cajuputi*,^{96),97)} and *Melastoma* species grow on the acid sulfate soil.

The adaptability of *S. roxburghii* seedlings to the acid was tested on the strongly acidic soil with pH 3.0 or below in Sebulu, East Kalimantan, Indonesia. The planting site was chosen on the coal strip layer.⁷⁴⁾ The site was bare, and no vegetation was present before *S. roxburghii* seedlings were planted (Fig. 11A). The seedlings showed the significant growth and ground vegetation was developed under the seedlings seven years after the seedlings were planted (Fig. 11B). In addition, many globular stones were found on the bare soil. They contained heavy metals such as manganese and iron (Fig. 11C). *A. mangium*,⁸⁵⁾ and *Paraserianthes falcataria*⁹⁸⁾ showed the tolerance to aluminum toxicity on the acid sulfate soil.

The acid sulfate soil is often found in swamps, and it tends to be flooded during rainy seasons. In flooding places, *M. cajuputi*^{96),97)} shows the adaptation to anaerobic conditions maintaining the high-energy phosphate level. It is an ideal species for rehabilitating the wasteland of the acid sulfate soil.

2) *Drought conditions:* *S. roxburghii* trees are naturally found on the sandy dune in Kota Baharu and Naratiwat in the Malay Peninsula. Often *S. roxburghii* seeds germinate on the bare sites and eventually form the woodlots. These wood lots extend the territory by the natural regeneration.

In the plantations on the sandy dunes, the seedlings of *S. roxburghii*, *D. alatus*, and *H. odorata* showed the good survival rates.⁹⁵⁾ When *A. mangium* seedlings were planted together with these species, *A. mangium* trees grew quickly on the bare sand, and served as the nurse trees for the three species.⁹⁹⁾ The soil temperature was maintained at a range between 29 and 30°C by the presence of the nurse trees, whereas in the open site the soil temperature fluctuated at a high range between 39 and 40°C.⁹⁹⁾ Similarly, *D. kerrii*, and *S. obtusa* grow on the dry conditions. Interestingly, *M. cajuputi* showed the tolerance to drought as well as the tolerance to flooding.⁹⁶⁾

Among the *Rubroshorea* species, *S. leprosula* showed the tolerance to the drought by forming bud-like structure with the new leaves. In addition, *Dipterocarpus alatus* was tolerant to the sand dune.⁹⁹⁾

3) *Other specific soil conditions:* Various dipterocarp species showed the adaptation to the extreme soil conditions. *S. albida* trees grow in the

swamps of Borneo Island.^{78),79)} In Thailand, *D. chartaceus* trees grow in semi-swamp forests.²⁵⁾ *Melaleuca cajuputi* is the most tolerant species to the flooding and the swamp, as the seedlings are able to grow under water.

In contrast, in upland areas, the trees of *S. curtisii* form the conspicuous aggregates on the specific ridges of the mountains.¹⁰⁰⁾ Soil analysis indicated that the available phosphorus and cation exchange capacity were high in the growing site of *S. curtisii*. In addition, *S. curtisii* did not grow on the soil with iron mottles.¹⁰⁰⁾ This suggests that the species does not grow on the gley soil. Sometimes, we observed that *S. curtisii* grew on the serpentine soil. Probably, divalent cations are effective to prevent the gleization. Other species such as *S. siamensis* grows on the lime stone.

4) *Adaptation to low temperature:* The seedlings were less tolerant to the low temperature, as shown in Table 5. The susceptibility of *S. roxburghii* seedlings to low temperatures less than 15°C were also observed in the storage tests of bare-root seedlings. The temperatures of the growth chambers were set at constant temperatures of 20°C, 19°C, 18°C, 17°C, 16°C, 15°C, 14°C and 13°C. Within a week, the seedlings grown at 14°C and 13°C developed the chlorosis on the leaves. The young leaves became white by losing chlorophylls, and eventually these leaves showed the necrotic symptoms. The susceptibility to the cold temperature is observed in various tropical plants. For example, the tropical species, such as *Cedrela* and *Leucoena*¹⁰¹⁾ developed chilling injuries below 15°C. The development of the chilling injury to the tropical tree species at 15°C is probably related to the vertical and horizontal limits of the distributions of the tropical tree species. The upper limit of dipterocarp distribution is found at an altitude of around 1,200 m, and the minimum temperature at this elevation is close to 15°C. Probably, the minimum temperature for the survival of the dipterocarp species is related to the upper limit of the dipterocarp distribution.

S. roxburghii should be given more attention for the regeneration programs and the rehabilitation of various degraded land in the tropical countries. Other *Anthoshorea* group also may have good traits to adapt to the extreme environmental conditions. One species of *Anthoshorea* in Java Island, *S. javanica* appeared to be very similar to

the *S. roxburghii*, morphologically. Judging from the distribution of the two species, we need detailed studies for the both species. For other species such as *Melaleuca cajuputi*, *Acacia mangium*, *Gmelia arborea* and *Dipterocarpus alatus* need attention for the species to rehabilitate the degraded tropical forests.

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Profile

Satohiko Sasaki was born in 1935 in Otaru, Hokkaido, Japan. In the undergraduate course at the University of Tokyo, he studied the forestry. He studied in the University of Tokyo until he received the master degree of Agriculture. Then, he moved to the Graduate School of the University of Wisconsin in 1961. He chose the joint major in the plant physiology and the tree physiology for his major in the Ph. D. course. He received a degree of the Doctor of the Philosophy (Ph. D.) in January 1967, with the thesis entitled “The effects of the herbicides on the physiological functions of the red pine, *Pinus resinosa* Ait. He continued to work on the growth of the pine seedlings in the University of Wisconsin as a post-doctoral fellow. In September 1968, he moved to the University of Missouri to study processes of the protein synthesis at the germination stage of the pine seeds. In May 1971, he started to work in the Forestry Experiment Station, the Ministry of Agriculture, Forestry, and Fisheries in Japan, and he continued his research on the physiology of the tree species. At the end of 1974, he was sent to the Forest Research Institute, Malaysia for three years as a visiting research officer to carry out the joint researches on the physiology of the tropical forest species. As he was fascinated by the tropical forest species, the tropical forest species have been one of his main research themes. The research outcomes on the physiology of the tropical tree species were applied to establish the plantations in Thailand, Indonesia as well as in Peru. These plantations are already matured, with the height of the trees more than 20 m. He received the Agriculture Prize of Japan in 1996, and in 2004, he was given the Achievement Award of the Forestry Society of Japan for the work of the tropical tree physiology. In 2006, the Duke Edinburgh Prize was given to him, and he was selected as a member of the Japan Academy.

