EFFECT OF HERBIVORY ON SEEDLING ESTABLISHMENT OF DRYOBALANOPS AROMATICA (DIPTEROCARPACEAE) UNDER PLANTATION FOREST IN PENINSULAR MALAYSIA

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KACHI, N., OKUDA, T. & YAP, S.K. 1995. Effect of herbivory on seedling establishment of *Dryobalanops aromatica* (Dipterocarpaceae) under plantation forest in Peninsular Malaysia. Post-dispersal survival of kapur (*Dryobalanops aromatica*) was monitored in a 60-year-old kapur plantation and a mixed-species plantation at Kepong, Peninsular Malaysia. Kapur seeds showed no dormancy and germination started within 1-3 days after being placed on the forest floor. In both plantations, seeds and cotyledon-stage seedlings were consumed by vertebrates such as rodents and wild pigs. On average, less than 1% of the seeds survived to the four-leaf seedling stage. After reaching the four-leaf stage, predation appeared to be reduced, but seedling mortality probably caused by water stress and/or pathogens increased. Seedlings in the six-leaf stage had low mortality, allowing the establishment of a sapling bank under the canopy. The results indicate that natural regeneration of kapur in plantations may be expected when sufficient seeds produced during mast years compensate for the high mortality during the seed and early seedling stage.

Key words: Dipterocarp - Dryobalanops aromatica - herbivory - kapur - predation - seeds - seedlings - survival

KACHI, N., OKUDA, T. & YAP, S.K. 1995. Kesan herbivori ke atas penubuhan anak benih Dryobalanops aromatica (Dipterokarpa) di bawah hutan ladang di Semenanjung Malaysia. Kemandirian selepas-penyerakan kapur (Dryobalanops aromatica) telah didapati di sebuah ladang kapur berusia 60 tahun dan di sebuah ladang spesies campuran di Kepong, Semenanjung Malaysia. Biji benih kapur menunjukkan tiada kedormanan dan percambahan bermula dalam masa 1-3 hari selepas ditempatkan di lantai hutan. Di dalam kedua-dua ladang, biji benih dan anak benih di peringkat kotiledon dimakan oleh vertibrata seperti roden dan babi hutan. Secara purata, kurang dari 1% daripada biji benih adalah mandiri pada peringkat anak benih empatdaun. Selepas mencapai peringkat empat-daun, pemangsaan didapati berkurangan tetapi kematian anak benih mungkin disebabkan oleh tekanan air dan/atau pertambahan patogen. Anak benih-anak benih pada peringkat enam-daun mempunyai kadar kematian yang rendah, membolehkan penubuhan betau anak pokok di bawah sudur. Keputusan menunjukkan bahawa pemulihan semulajadi kapur di ladang-

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ladang mungkin dijangkakan bila biji benih-biji benih yang mencukupi dihasilkan pada tahun-tahun kematangannya bagi menggantikan pokok-pokok yang mati dengan banyaknya pada peringkat biji benih dan peringkat awal anak benih.

Introduction

In many plant species, plants in the stage from germination to seedling establishment are most vulnerable to mortality in their life histories (Harper 1977). In tropical forests, seeds and seedlings are eaten or trampled by vertebrate animals (Coley 1983, Becker & Wong 1985, Schupp 1988, Clark & Clark 1989, Howe 1990, Osunkjoya *et al.* 1992), infested by insects (Clark & Clark 1985, Khan & Tripathi 1991), attacked by fungi and other microorganisms (Augspurger 1983), buried under forest litter (Molofsky & Augspurger 1992, Vazquez-Yanes & Orozco-Zegovia 1992), washed away by rain, and suppressed by lack of light (Sasaki & Mori 1981, Augspurger 1984), water (Augspurger 1979) and mineral nutrients (Janzen 1974).

In tropical forests, seedlings of several plant species suffer high mortality at the vicinity of their conspecific adult trees due to an abundance of natural enemies (Janzen 1970). Thus, the probability of seedlings to survive in an artificially-established mono-specific dominant forest would be lower than that in areas with mixed-species typical of lowland tropical forests. However, evidence reported from neotropical forests suggested that this situation is not always true (Clark & Clark 1984) and little evidence has been reported from Southeast Asia (Becker & Wong 1985).

Dryobalanops aromatica (local name: kapur) is a canopy tree species (Symington 1943; see also a review by Appanah & Weinland 1993) with its natural distribution in the Malay Peninsula, Sumatra and Borneo (Foxworthy 1932). The altitudinal range is between 70 and 400 m above sea level (Wyatt-Smith 1963). It is common on well-drained fine sandy soils (Symington 1943, Wong et al. 1987). Unlike many other canopy tree species in lowland tropical forests, kapur is very abundant locally. In natural conditions, kapur produces 40 - 60% or more of the total volume of timber in the forests, although it is always accompanied by numerous other tree species (Foxworthy 1932, Vincent 1961). In Peninsular Malaysia, most of the natural kapur forests occur in scattered patches along the east coast, stretching from the southern part of Terengganu south to Johor, where the rainy season extends from November to January (Foxworthy 1932, Wyatt-Smith 1963). A small natural stand of kapur is also found in the Kanching Forest Reserve on the west coast, although its origin is unknown (Wyatt-Smith 1963).

In laboratory conditions, freshly fallen and sound seeds of kapur germinate within a week with over 80% viability at 30 °C (Yap 1981), but the viability is quickly lost within three weeks mainly due to attacks by fungi and microorganisms (Jensen 1971). As in most members of Dipterocarpaceae, the seeds are recalcitrant and regeneration depends largely on the presence of a sapling bank on the forest floor.

The purpose of this study is to investigate post-dispersal survival of kapur in kapur and mixed species plantations to determine if the monoculture kapur plantations can regenerate naturally.

Methods

The site

Within the grounds of the Forest Reserve of Forest Research Institute of Malaysia (FRIM) in Kepong, Peninsular Malaysia (101° 37'E, 3°13'N), a plantation of kapur was established during the late 1920's and early 1930's. The canopy is dominated by kapur with heights of around 40 m. At about 200 m distance from the kapur plantation, there is a mixed species plantation of similar age, where *Shorea bracteolata*, *Dipterocarpus baudii*, *D. semivestitus* (all in the Dipterocarpaceae), *Gymnacranthera forbesii* (Myristicaceae), *Scorodocarpus borneensis* (Olacaceae), and *Paraserianthus falcataria* (Leguminosae) are codominant, and kapur trees are absent. The canopy height is 30 - 35 m and the density of canopy trees is comparable to that of the kapur plantation (17 - 25 per ha for individuals with diameters at breast height more than 10 cm).

Seed-sowing

A series of experiments were conducted to determine the survivorship and causes of mortality following seed fall of kapur. In March 1991, many trees flowered in the kapur plantation and mature fruits fell during June and August in the same year. Fallen fruits were collected from the kapur plantation during August 1991. The fruit is a winged nut with five lobes (7-8 cm long and 1.5-2 cm wide). The size of the nut (hereafter described as seed) is 2.5-3.5 cm long and 1.2-2.0 cm wide and the fresh weight is 5-10 g. Natural density of fruits in the kapur plantation was variable depending on the topography and locality of fruiting trees, ranging from 0 to 10 per m². In all experiments only visually undamaged seeds were used, more than 95% of which germinated in a preliminary germination test.

The seeds were immediately sown in the kapur and mixed-species plantations on 16 August 1991. Two plots $(1 \times 1 \text{ m})$ were established in each plantation and 72 seeds were sown in each plot. Seed survival and causes of mortality were monitored on 2, 6 and 12 days after sowing.

Isolated seeds may have higher probability of survival than seeds occurring in groups, as they are less likely to be discovered by predators (Boucher 1981). To assess whether isolation affects seed mortality, another experiment was carried out. Twelve canopy trees were arbitrarily chosen in the kapur and mixed-species plantations and two seeds were placed in each compass direction at 1 m from the base of each tree. A total of 96 seeds were left among the 12 trees in each plantation on 23 August 1991. To determine the longevity of individual seeds, survival of these seeds was monitored for 76 days from the date of sowing until all but one seedling died or disappeared.

Transplanting of seedlings

Three sets of transplant experiments were conducted to assess seedling survival starting from cotyledon, four-leaf, and six-leaf stages. After removing the wings, kapur seeds were sown in a black polyethylene bags, $10 \, \mathrm{cm}$ in diameter, containing B-layer soil (5-30 cm deep) from the kapur plantation and grown outdoors in a nursery until transplanting. The photon flux densities relative to that at an open site was ca. 3 - 4%. The light measurement was made on a overscattered cloudy day using a photon sensor (LI-COR Model LI-190SA). For the transplanting trials the following numbers of quadrats ($1 \times 1 \, \mathrm{m}$) and seedlings were used:

	No. of quadrats	No. of seedlings/quadrat
Cotyledon stage	6	6
Four-leaf stage	6	10
Six-leaf stage	2	10

The same set-ups were established in both kapur and mixed-species plantations. All plots were randomly distributed in an area of ca. 100×100 m. The respective experiments were started on 4 September, 11 October and 3 December 1991.

Protective cage experiment

To determine the mortality of seeds and seedlings due to predation by small mammals, an experiment using protective cages was conducted in the two plantations. On 29 August 1991, 10 mature kapur seeds were placed on the forest floor and covered with a mesh cage with openings of 18×8.5 mm. Two cages were set in each plantation. Control plots were also set adjacent to the caged plots. The cages were removed on 19 September 1991 (21 days after sowing) and the census was continued until 14 November 1991 for 77 days.

Size distribution of kapur

In the kapur plantation, a $550 \,\mathrm{m}^2$ plot divided into $5 \times 5 \,\mathrm{m}$ grids was established in March 1992. All individual kapur trees including seedlings were marked and the diameters were measured. For plants less than 30 cm high, diameters were measured at the stem base, for plants 30 - $60 \,\mathrm{cm}$ high at $10 \,\mathrm{cm}$ above the ground, for those 60 - $200 \,\mathrm{cm}$ high at $30 \,\mathrm{cm}$ high, and for plants more than $200 \,\mathrm{cm}$ high at $100 \,\mathrm{cm}$.

Results

Survivorship at seed stage

Seeds of kapur showed no dormancy and the majority of sound seeds germinated within three days in the field. Seeds sown in the kapur plantation had 93% mortality

after 12 days. The majority of them were consumed by predators within two days after sowing (Figure 1). In contrast, seeds in the mixed-species plantation had relatively low mortality compared with those in the kapur plantation (p < 0.001, Chisquare test based on data on respective sampling days).

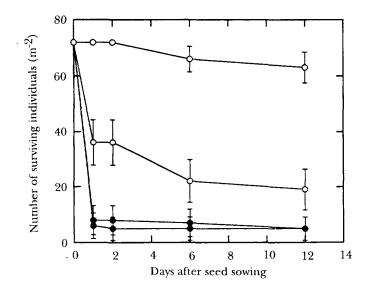


Figure 1. Survivorship of seeds of *Dryobalanops aromatica* (kapur) transplanted in duplicate plots in the Forest Research Institute of Malaysia. (Vertical bars indicate the range of 95% confidence limits; open circle: in the mixed-species plantation; closed circle: in the kapur plantation).

In the other experiment when isolated seeds were placed around individual trees 97% of germinating seeds were lost or dead by the 5th day in the kapur plantation. Seeds similarly placed in the mixed-species plantation suffered 92% mortality after 34 days (Figure 2). The average longevity of seeds was 2.6 days in the kapur plantation and 14.1 days in the mixed-species plantation and the difference between them was highly significant (p < 0.001, Mann-Whitney U-test).

Most of the seeds protected by cages germinated without predation and these seedlings survived until the cages were removed. After removing the cages, the seedlings were eaten by mammals (characterised by leftover seed coats and half-eaten seeds) resulting in a high mortality (Figure 3). On the 21st day when the cages were removed in the experimental plots, 41% of the seedlings in the uncaged control plots situated in the kapur plantation were surviving, while 53% were still present in the mixed-species plantation (Figure 3). By the 77th day all but two seedlings were dead.

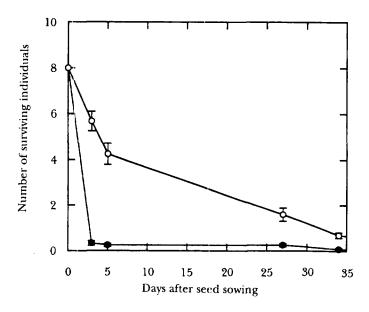


Figure 2. Survivorship of seeds of *Dryobalanops aromatica* (kapur) placed in isolation around a canopy tree in the Forest Research Institute of Malaysia. (Each point is the average over 12 tree plots; vertical bars indicate the range of 95 % confidence limits; open circle: in the mixed-species plantation; closed circle: in the kapur plantation).

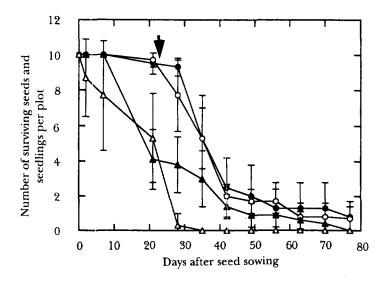


Figure 3. Effects of protective cages on survivorship of seeds and seedlings of *Dryobalanops aromatica* (kapur) transplanted in plantations in the Forest Research Institute of Malaysia. (Vertical bars indicate the range of 95% confidence limits; circles: protected by cages; triangle; control; closed symbols: in the kapur plantation; open symbols: in the mixed-species plantation. The arrow indicates the time when the protective cages were removed).

Survivorship at cotyledon stage

Mortality during the early seedling stage, while the cotyledons were still attached, was also high. The probability of cotyledon-stage seedlings to survive to the four-leaf stage was ca. 2% in both sites. The main cause of mortality was predation by mammals. Some insect damage to leaves was also observed. Three per cent (in the kapur plantation) and 7% (in the mixed species plantation) of seedlings failed to produce any leaves, when their shoot apexes were damaged by insects and/or microbial pathogens.

In the kapur and mixed-species plantations, the survival of cotyledon stage seedlings was approximately linear in a semi-logarithmic plot (Figure 4). There was no significant differences in the regressions of specific mortality rates between kapur and mixed-species plantations (p > 0.05, t-test for comparisons of two regression slopes and intercepts). The mortality rate after pooling all data was 6% per day.

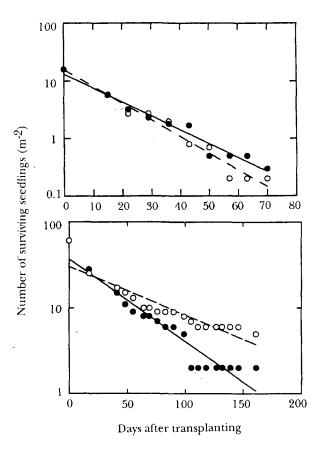


Figure 4. Survivorship of cotyledon stage seedlings (top figure) and four-leaf stage seedlings (bottom figure) of *Dryobalanops aromatica* (kapur) transplanted in plantations in the Forest Research Institute of Malaysia. (Closed circle and solid line: in the kapur plantation: open circle and broken line: in the mixed-species plantation).

Survivorship at four-leaf stage

When seedlings at the four-leaf stage were transplanted in the kapur and mixed-species plantations, they were also eaten by mammals. The mortality rates, however, were reduced to 2.2% per day (in the kapur plantation) and 1.3% per day (in the mixed-species plantation) respectively (Figure 4). These values were about one-fourth of the mortality rate obtained for the cotyledon stage seedlings. The specific mortality rate was higher in the kapur plantation than in the mixed-species plantation (p < 0.05, t-test for comparisons of two regression slopes).

Survivorship after six-leaf stage

Kapur seedlings reaching the six-leaf stage exhibited low mortality when compared with those obtained for the cotyledon and four-leaf stages. By the 7th month after transplanting, only 2 of 20 plants were dead in the kapur plantation and all plants survived in the mixed-species plantation.

Possible causes of mortality

Figure 5 shows relative importance of different mortality factors at the cotyledon and four-leaf stages. Mammalian predation accounted for 92% (in kapur plantation) and 95% (in the mixed-species plantation) of the mortality among cotyledon stage seedlings; 65% (in the kapur plantation) and 93% (in the mixed-species plantation) of the mortality among the four-leaf stage seedlings. In the kapur plantation, 35% of plants at the four-leaf stage were dead due to wilting probably caused by water stress. A part of the mortality may have been attributable to an induced damage of the root system during transplanting.

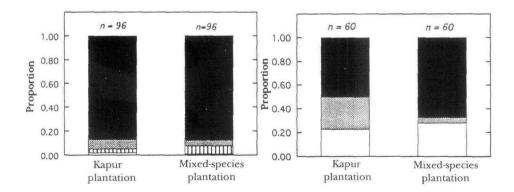


Figure 5. Proportion of survival and mortality factors during cotyledon (left figure) and four-leaf stage of seedlings (right figure) of *Dryobalanops aromatica* (kapur) in plantations in the Forest Research Institute of Malaysia. (Closed area: eaten by mammals; shaded area: wilted and dead; hatched area: the main stem or apical shoot was damaged and dead; open area: surviving plants). (Right hand side is the results from the mixed-species plantation and left hand side is those from the kapur plantation).

Size distribution of kapur

Figure 6 shows frequency distribution of stem diameters of all individuals of kapur in the plantation. The size is classified on a logarithmic scale. All individuals with diameters more than 40 cm are canopy trees belonging to the first generation. The majority of individuals were in size classes 1-3 cm, constituting the sapling bank. There were very few current year seedlings which are included in the smallest size class, reflecting high mortalities in the seed and seedling stages.

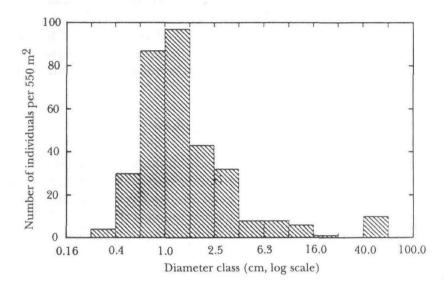


Figure 6. Frequency distribution of stem diameters of *Dryobalanops aromatica* (kapur) individuals including seedlings in a kapur plantation in the Forest Research Institute of Malaysia. (Number of samples is 326).

Discussion

Mortality factors of seeds

Weevils (alcidodes and nanophyes) are known to be the major pests of seed crops of dipterocarps including kapur (Singh 1974). They attack kapur seeds at an early stage of seed development. Other insect species also attack kapur seeds causing 40 - 80% mortality before ripening (Kobayashi 1974). A recent study recorded 90% of the seeds that had been infested by larvae of various insects before dispersal (Y. Tsubaki, K. Takamura & J. Intachat, unpublished).

After dropping onto the ground, kapur seeds are often heavily attacked by predators (Singh 1974). Wild pigs (*Sus scrofa*) could have partly contributed to the mortality of seeds, as their tracks were observed in and around the plots. When kapur seeds were protected by cages, most of them germinated without predation (Figure 2). As the protective cage was effective against only small mammals, it is

most likely that the main predators were rodents, of which murids and sciurids are dominant in the plantations (Nor Azman Hussein, personal communication).

Seed predation by mammals tended to be higher in the kapur plantation than in the mixed-species plantation (Figures 1 & 2). Higher predation pressure in the kapur plantation can be expected, because before and during the experiments seed-fall was continuing in the kapur plantation, which must have attracted predators.

The timing and intensity of predation varied among plots in the mixed-species plantation. Seeds in some plots were discovered and consumed by mammals within a day after being placed on the ground, while in the other plots they remained undisturbed for more than two weeks (Figures 1 and 2). The rate of predation can be variable depending on the density of predators. When the density is low as expected in the mixed-species plantation, some seeds may be quickly discovered by predators while others may not.

Mortality factors of seedlings

Mammalian predation is an important component of mortality during seed and seedling stages of several tropical tree species (Sork 1987, Schupp 1988, Molofsky & Fisher 1993). This had also been observed in kapur, where cotyledons and newly developing shoots were bitten off by animals (Foxworthy 1932). In our experiment, when seedlings at the cotyledon stage were transplanted in the plantations, they were frequently eaten by animals, most likely rodents and wild pigs, although there were no direct observations.

Insect feeding on leaves and apical meristems was occasionally observed during the experiment, but insect herbivory usually does not kill the seedlings. Foxworthy (1932) recorded that young twigs of kapur were often attacked by scolytid beetles belonging to the genus *Cryphalus*, but the attack also did not cause the death of the whole plant.

The low predation of kapur seedlings after reaching the six-leaf stage could be attributed to several factors. It could be that the plants at this stage are no longer attractive to mammalian predators thus reducing predators' activities. Although there has been no evidence so far, the palatability of the plants may have changed during the development of seedlings possibly due to production of secondary substances like phenolics in plant tissues as observed by Freeland and Janzen (1974).

Regeneration of kapur

Kapur forests often show copious natural regeneration. A census of trees 17 cm girth at breast height (GBH) and over in a natural kapur forest at Bukit Bauk Forest Reserve in Terengganu along the east coast of Peninsular Malaysia showed that the kapur trees had a continuous size distribution (Wyatt-Smith 1963). A large number of seedlings and saplings were also found in the same forest. Persistent occurrence of the sapling bank in the kapur forest indicates that the forest is a

self-replacing climax forest rather than a forest in an intermediate stage of plant succession. In our census on the size distribution in the kapur plantation, a considerable number of saplings with diameters 1-3 cm (ca. 50 individuals per 100 m²) were found under the canopy. Therefore, a sapling bank for natural regeneration can be established even in plantation conditions. However, the number of seeds produced in the particular year of our observation may not have been high enough to increase the level of the sapling bank, because very few current-year seedlings were observed in the field (Figure 6).

The results of our transplant experiment showed a high survival rate after reaching the six-leaf stage in contrast to the high mortality in the preceding stages. These findings suggest that in spite of the high predation pressure during seed and early seedling stages, a heavy seed flush in a mast year could let some seeds to germinate and establish after escaping from the predation. A cohort of seedlings could then reach the six-leaf stage to produce a sapling bank under the canopy. Natural regeneration of kapur plantation will be from these seedlings and can be accelerated when appropriate canopy gaps are created. Recent observation on the kapur forest in Kanching by Abd. Rahman et al. (1993) also demonstrated the ability of kapur to regenerate under a dense canopy. As a plantation practice, it is also recommended that nursery-grown seedlings should be transplanted at or after the six-leaf stage.

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References

- ABD. RAHMAN, K., SHAHRULZAMAN, I. & WEINLAND, G. 1993. Growth performances of a naturally regenerated stand of kapur (*Dryobalanops aromatica* Gaertn. f) 37 years after a heavy low thinning treatment. P. 94 in *Abstracts of the International Conference on Tropical Rainforest Research: Current Issues.* Universiti Brunei Darussalam.
- APPANAH, S. & WEINLAND, G. 1993. Planting Quality Timber Trees in Peninsular Malaysia A Review. Malayan Forest Records No. 38. Forest Research Institute of Malaysia, Kuala Lumpur.
- AUGSPURGER, C. K. 1979. Irregular rain cues and the germination and seedling survival of a Panamanian shrub (*Hybanthus prunifolius*). *Oecologia* 44:53-59.
- AUGSPURGER, C. K. 1983. Seed dispersal by the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759-771.
- AUGSPURGER, C.K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72:777-795.
- BECKER, P. & WONG, M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland dipterocarp rainforest. *Biotropica* 17: 230 237.
- BOUCHER, D. H. 1981. Seed predation by mammals and forest dominance by *Quercus eoides*, a tropical lowland oak. *Oecologia* 49: 409-414.

- CLARK, D. B. & CLARK, D. A. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connel model. *American Naturalist* 124: 769 788.
- CLARK, D. B. & CLARK, D. A. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66: 1884-1892.
- CLARK, D. B. & CLARK, D. A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225 230.
- COLEY, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monograph* 53: 209 233.
- FOXWORTHY, F. W. 1932. Dipterocarpaceae of the Malay Peninsula. Malayan Forest Records No. 10. Federated Malay States Government. 289 pp.
- FREELAND, W. J. & JANZEN, D. H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108: 269 289.
- HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London.
- HOWE, H. F. 1990. Survival and growth of juvenile Viroïa surinamensis in Panama: effects of herbivory and canopy closure. Journal of Tropical Ecology 6: 259 280.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528.
- JANZEN, D. H. 1974. Tropical blackwater river, animals, and mast fruiting by the Dipterocarpaceae. Biotopica 6: 69-103.
- JENSEN, L. A. 1971. Observation on the viability of Borneo camphor *Dryobalanops aromatica* Gaertn. *Proceedings of the International Seed Testing Association* 36: 141-146.
- KHAN, M. L. & TRIPATHI, R. S. 1991. Seedling survival and growth of early and late successional tree species as affected by insect herbivory and pathogen attack in sub-tropical humid forest stands of north-east India. *Acta Oecologia* 12: 569 579.
- KOBAYASHI, K. 1974. Ecological study on seed production of kapur and keladan. *Nettai Ringyo* (Tropical Forestry) 34:16-20.
- MOLOFSKY, J. & AUGSPURGER, C. K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68-77.
- MOLOFSKY, J. & FISHER, B. L. 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. *Ecology* 74: 261 265.
- OSUNKJOYA, O. O., ASH, J. F., HOPKINS, M. S. & GRAHAM, A. W. 1992. Factors affecting survival of tree seedlings in North Queensland rainforest. *Oecologia* 91: 569 578.
- SASAKI, S. & MORI, T. 1981. Growth responses of dipterocarp seedlings to light. *Malaysian Forester* 23:319-345.
- SCHUPP, E. W. 1988. Seed and early seedling predation in the forest understory and treefall gaps. *Oikos* 51: 71 78.
- SINGH, D. K. 1974. Seed pests of some dipterocarps. Malaysian Forester 37: 24-36.
- SORK, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68: 1341-1350.
- SYMINGTON, C. F. 1943. Forester's Manual of Dipterocarps. Malayan Forest Records No. 16. (reprinted in 1974 by Penerbit Universiti Malaya, Kuala Lumpur)
- VAZQUEZ-YANES, C. & OROZCO-ZEGOVIA, A. 1992. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiology* 11: 391-400.
- VINCENT, A. J. 1961. A Survey of the Kapur (Dryobalanops aromatica Gaertn f.): Silvicultural Treatment Research Plots in Naturally and Artificially Regenerated Forest, Malaya. Forest Research Institute Research Pamphlet No. 36. Forest Department. Federation of Malaya.
- WONG, K. M., SAW, L. G. & KOCHUMMEN, K. M. 1987. A survey of the forests of the Endau-Rompin area, Peninsular Malaysia: principal forest types and floristic notes. Malaysian Heritage & Scientific Expedition: Endau-Rompin. *Malaysian Nature Journal* 41: 125 144.
- WYATT-SMITH, J. 1963. Manual of Malaysian Silviculture for Inland Forests. Malayan Forest Records No. 23. Forestry Department, Peninsular Malaysia.
- YAP, S. K. 1981. Collection, germination and storage of dipterocarp seeds. *Malaysian Forester* 44: 281 300.