THE LIFE HISTORY OF PALIGA DAMASTESALIS WALKER (LEPIDOPTERA: PYRALOIDEA: CRAMBIDAE), A TEAK SKELETONISER IN MALAYSIA

J. Intachat

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

Received February 1998

INTACHAT, J. 1999. The life history of Paliga damastesalis Walker (Lepidoptera: Pyraloidea: Crambidae), a teak skeletoniser in Malaysia. The life history of Paliga damastesalis Walker was studied under laboratory and field conditions. Paliga damastesalis took between 23 and 32 days in the laboratory and between 22 and 29 days in the field to complete its life cycle from egg to adult. The developmental periods for the egg, larva and pupa varied respectively from 4 to 6, 14 to 15, and 5 to 11 days in the laboratory and from 4 to 6, 13 to 15, and 5 to 8 days under field conditions. The life history had five larval instars and a distinct prepupal period. The longevity of male and female adults, reared on different diets, ranged from 3 to 10 days. Females laid an average of 135 eggs in the laboratory.

Key words: Paliga damastesalis - teak skeletoniser - biology - life history - Tectona grandis - Malaysia

INTACHAT, J. 1999. Sejarah hayat Paliga damastesalis Walker (Lepidoptera: Pyraloidea: Crambidae), ulat perangka jati di Malaysia. Sejarah hayat Paliga damastesalis Walker telah dikaji dalam keadaan makmal dan lapangan. Paliga damastesalis mengambil masa antara 23 hingga 32 hari di makmal dan 22 hingga 29 hari di lapangan untuk melengkapkan kitaran hayatnya daripada telur hingga dewasa. Kala perkembangan untuk telur larva dan pupa berubah masing-masing daripada 4 hingga 6, 14 hingga 15, dan 5 hingga 11 hari di makmal dan daripada 4 hingga 6, 13 hingga 15, dan 5 hingga 8 hari di lapangan. Sejarah hayat mempunyai lima instar larva dan satu kala prepupa yang nyata. Kelanjutan umur dewasa jantan dan betina yang dipelihara dengan gizi yang berlainan, berjulat daripada 3 hingga 10 hari. Betina, secara puratanya, menghasilkan 135 biji telur di makmal.

Introduction

Until recently teak (*Tectona grandis* L.) was believed to perform well in terms of growth only in the drier parts of Malaysia. However, various trials carried out in the wetter regions of the country over the last 20 to 30 years show that teak can perform equally well in these areas (Krishnapillay et al. 1998). Since then teak has become a popular exotic plantation tree species cultivated in Malaysia. Along with most cultivated crops in Malaysia, teak has a number of insect pests. Among them is the teak skeletoniser *Paliga damastesalis* Walker, which is a different species from the teak skeletonisers found in India and Myanmar (Intachat 1998).

Paliga damastesalis is the most common teak defoliator species in Malaysia. Low levels of defoliation are usually observed throughout the year although P. damastesalis

has been reported to cause heavy defoliation on teak trees in the plantations in Malaysia (Tho 1981, Chey 1996). Heavy defoliation as high as 100% can be recorded during serious outbreaks. These outbreaks, however, have been observed to be seasonal, occurring more during wetter periods (Chey 1996).

Little is known about the biology of *P. damastesalis* although it is a common pest of teak planted in Malaysia. Understanding its biology is important in ensuring the success of management strategies formulated for this insect. This paper describes the duration of egg, larval, pupal, and adult life stages of *P. damastesalis* under laboratory and field conditions, and provides additional observations on its biology and life history.

Materials and methods

The moth pupae were first collected randomly from two different planting blocks of the Boonrich Plantation, Sabah, at the end of an outbreak in May 1996. In total, 85 pupae were collected. The insects were then maintained in $36 \times 46 \times 46$ cm and $30.5 \times 25.5 \times 25.5$ cm perspex cages. All data collections on the life history and experiments were conducted under laboratory conditions at a temperature of 26.6 ± 0.6 °C, relative humidity of $72.4 \pm 2.8\%$, and a photoperiod regime of 8L:16D, using the subsequent moth generations from June 1996 to May 1997. For field studies, the insects were reared in $70 \times 35 \times 35$ cm aluminium wire cages in the field at a maximum temperature of 32.9 ± 1.4 °C, a minimum temperature of 22.7 ± 0.5 °C, a relative humidity of $69.2 \pm 15.5\%$, and a photoperiod regime of 12L:12D. All measurements were in arithmetic mean \pm standard deviation, whilst the development periods were reported at 95% confidence.

Data were analysed using MINITAB for Windows Release 10.2 (1994). The normality and homogeneity of the data were checked. Data transformations were carried out when necessary. For detailed observations, methods used for each developmental stage were as follows.

Adults

The longevity of newly emerged adults fed with 10% honey solution for both sexes was observed under laboratory and field conditions. Due to insufficient numbers of adults emerging at the same time, the adult longevity for those reared on water and without any food was conducted under laboratory conditions only. Females and males of the newly emerged adults were separated and released in their respective cages. Mortality rates were recorded daily. Observations of the morphological differences between the males and females were also recorded.

In a separate experiment, the number of eggs produced by each female was conducted only in the laboratory. Based on a preliminary observation that the newly emerged females copulated more readily with older males, newly emerged females were kept singly with two 2-day old males in 7.0 cm diameter × 4.0 cm high transparent plastic containers and fed with 10% honey solution. Teak leaves were provided in each of the containers as a substrate for oviposition sites. The

containers, the cotton wool soaked with 10% honey solution and the teak leaves were changed daily. Eggs oviposited in the containers and on the leaves were recorded daily.

Eggs

Eggs laid on the leaves were measured in millimetre (mm) using a micrometer fixed to a stereo microscope. Portions of the leaves where the eggs were intact were then cut and placed on water agar in 8.5 cm diameter disposable Petri dishes. The portions of the leaf were kept in water agar to allow the leaf tissue to remain fresh until the eggs hatched. Observations were carried out daily until all the eggs hatched. In the field the eggs were left intact on the leaves and the number of eggs which hatched was recorded.

Larvae

Newly emerged larvae, kept in threes, were then transferred to 8.5 cm diameter disposable Petri dishes layered with leaf discs (portions of a teak leaf cut into the shape and size of the Petri dish). Unlike the method above where the portions of leaf were kept moist using water agar, the leaf discs were kept moist by spraying some water on them. Measurements of the head widths and the body lengths in mm were taken on the newly emerged larvae daily using a micrometer fixed to a stereo microscope until all larvae had pupated. The number of moults was determined by the number of the head casts.

Pupae

An attempt to sex the pupae was made based on morphology. Pupae that had slight differences in their structure were kept individually in glass vials. Drawings of the structures were made using a camera lucida that was attached to a stereo microscope. When the adults emerged, their sexes were then determined and correlated with these drawings. The total pupal period (in days) and the anterior-posterior length (in mm) for both the sexes were also recorded.

Results

Adults

The mean lengths of the life spans for both males and females under each condition are given in Table 1. Analysis of variance showed that adult survivorship for males and females differed significantly depending on whether they were reared in the laboratory or in the field $[F(3,156)=14.56;\ p<0.001]$. Tukey's pairwise comparisons with a family error of 5% showed that under laboratory conditions the males lived significantly longer than the females but there was no significant difference between the longevities of the males and the females in the field. The

males also lived significantly longer in the laboratory than in the field whilst there was no significant difference in the adult longevities for the females in both the environments.

	Field		Laboratory	
	+ honey	+ honey	+ water	- honey or water
Males	4.9-6.5	8.6-10.4	3.9-4.7	2.4-3.0
Females	5.1-6.7	5.9-8.1	4.0-5.0	2.8-3.4

Table 1. Adult longevities of *Paliga damastesalis* reared under different conditions (in days with 95% confidence; n = 40)

By providing the adults with different diets, analysis of variance showed significant difference in adult longevities for males and females reared in the laboratory [F(5, 204) = 49.96, p<0.001]. Tukey's pairwise comparisons with a family error of 5% showed that the males reared on honey lived significantly longer than females reared on honey but there was no significant difference for males and females reared on water or without food. Adults reared on water in the laboratory could survive up to eight days. Without food, males lived up to four days, and females up to five days.

Males in general have a larger wing span than the females although their mean lengths were not statistically different [t(60) = 1.68, p > 0.05]. The mean wing spans for the males and the females were 20.0 ± 1.4 mm and 19.4 ± 1.2 mm respectively. The sex ratio for males to females was 1:1 (n = 120) in the laboratory and 1: 2 (n = 87) in the field.

Newly emerged adult females were observed to copulate more readily with the older males (at least two days older) compared to the newly emerged males. Copulation usually occurred in the dark hours or early in the morning. The number of eggs produced varied with the life span of the female adults. There were cases where a female adult was observed to lay up to 240 eggs on a single day but died soon after that, or cases where a female laid as few as two eggs in an 11 days life span. The highest recorded number of eggs produced by a female was 337 eggs over its life span of nine days. The mean number of eggs produced by a female adult in the laboratory was 135 ± 93.4 (n = 35), and the mean life span, with 95% confidence, was 7.3–8.7 days (n = 35).

Eggs

Eggs were usually laid singly, although they were at times found in groups of two, three, or four on the underside of the teak leaves, especially between the veins. On the leaves, they were rather irregular in shape but tending more towards ovoid shape. Eggs laid on the side of the cages, however, were almost spherical. They were creamy in colour with cryptic colouration. The diameter of an egg was 0.66 ± 0.06 mm (n = 32). The eggs, with 95% confidence, took 4.8-5.1 days

(n = 50) to hatch in the laboratory and 5.0 - 5.2 days (n = 50) to hatch in the field. The percentage of eggs hatched in the laboratory was higher, 84.7% (n = 125), whilst in the field it was 76.6% (n = 137).

Larvae

Newly-hatched larvae were whitish in colour and were covered only with fine setae on their bodies. They also appeared to be patternless. As they grew older, their colour changed to green with two dorsal rows of cream-coloured markings. There were five larval instars. The measurements for each instar are given in Table 2. The duration of each instar varied from one to four days (n = 30). In total, the larval period for *P. damastesalis* in the laboratory with 95% confidence was 14.0–14.2 days whereas in the field, the larval period was significantly reduced to 13.6–14.0 days [t(58) = 3.37, p<0.05].

Table 2. The measurements of the head capsule and the body length (in mm \pm S.D) of the larva at different stages of its development and the duration (in days at 95% confidence) of each stage

	Head width ± S.D. (mm)	Length ± \$.D. (mm)	Duration (days)
Newly emerged	$0.25 \pm 0.01 \text{ (n = 30)}$	$1.65 \pm 0.08 \; (n = 30)$	
1st instar	$0.25 \pm 0.01 \text{ (n = 30)}$	$2.07 \pm 0.41 \ (n = 120)$	2.7-3.2 (n = 32)
2nd instar	$0.36 \pm 0.02 \ (n = 51)$	$3.43 \pm 0.43 \text{ (n = 81)}$	2.6-3.1 (n = 32)
3rd instar	$0.54 \pm 0.05 (n = 70)$	$5.35 \pm 0.41 \ (n = 70)$	3.0-3.5 (n = 32)
4th instar	$0.89 \pm 0.08 (n = 60)$	$10.94 \pm 2.51 \ (n = 60)$	2.9-3.4 (n = 32)
5th instar	$1.34 \pm 0.07 \; (n = 84)$	$18.19 \pm 2.02 \ (n = 84)$	2.7-3.2 (n = 32)

Upon hatching, the young larvae would begin feeding on the lamella of the teak leaf from the underside, avoiding the upper epidermis and the veins. They were also observed to take refuge at the side of the veins, especially the bigger veins such as the main lateral vein. As the young larvae matured, their ability to build and produce silk webs increased, allowing them to feed on other parts of the leaf. These included the upper epidermis, but still avoiding the veins, while taking refuge under the webs. The young and mature larvae were observed using the silk web to move from one leaf to another.

Pupae

Prior to pupation, the mature larvae would cease feeding and begin to spin cream-coloured cocoons. At times, some cocoons could be found in leaf folds. Within these cocoons, the larvae would enter the prepupa phase where they would remain immobile, with 95% confidence, for 1.9-2.2 days (n=30). During the prepupa stage, the colour of the larvae was observed to change to paler green and the markings on their bodies became less distinct. The actual pupation stage started soon after that and the external appearance of the larvae changed to that of the pupae.

The new pupae were pale green in colour, similar to larvae at the prepupal stage. Towards the end of the cycle, the colour changed to brown. At this stage, the pupae of the females could be differentiated from males by the presence of the genital opening on the 8th segment (Figure 1). In the female the genital opening is located ventroanteriorly, and in the male it is located ventroposteriorly on the 8th segment. The mean lengths of the male $(11.2\pm1.0\,\mathrm{m})$ and female pupae $(10.8\pm1.0\,\mathrm{mm})$ were not significantly different $[t(67)=1.82,\,p>0.05]$.

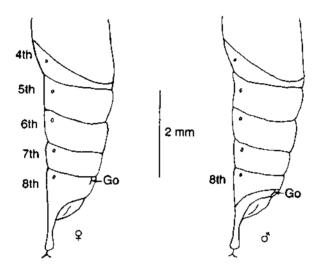


Figure 1. Female and male pupae of *Paliga damastesalis* (lateral ventral view); female pupa with genital opening (Go) on the 8th segment

The incubation periods for the male and female pupae in laboratory and field environments are listed in Table 3. Analysis of variance showed significant differences in pupal incubation period after the effects of environments and different sexes were taken into account [F(3,116)=23.32, p<0.001]. Tukey's pairwise comparisons with a family error rate of 5% showed that the incubation period for the male pupae is significantly longer than for the female pupae in the laboratory whilst there was no significant difference for male and female pupae incubated in the field. The male pupae also took significantly longer time to incubate in the laboratory than in the field whilst there were no significant differences in incubation period for female pupae in both environments.

Table 3. Incubation periods (in days with 95% confidence) for male and female pupae in the laboratory and in the field (n = 30)

Labor	ratory	Fi	eld
Male pupae	Female pupae	Male pupae	Female pupae
8.1-9.1	5.9-7.1	6.4-6.8	6.3-6.8

Discussion

Generally, the habits and the life history of *P. damastesalis* were found to be rather similar to those of *Paliga machoeralis* Walker, another species of teak skeletoniser that occurs in India, Myanmar and China. *Paliga machoeralis* is frequently referred to in the literature as *Eutectona* or *Pyrausta machoeralis* Walker, and has often been misspelt as machaeralis (see Intachat 1998 for details). The variations in the duration of the life cycle that occur in *P. machoeralis* in India at different periods of the year (Patil & Thontadarya 1987a) were not observed in *P. damastesalis*, although the latter was estimated to produce 12 to 13 generations a year.

The adult longevity of *P. machoeralis* has been recorded as up to 20 days, especially in the winter (Patil & Thontadarya 1987a), whereas the highest adult longevity ever recorded for *P. damastesalis* was 14 days. The morphological characteristics, such as the wing span of the adult males and females of *P. damastesalis*, were similar to those of *P. machoeralis* as reported by Misra (1975). Males of both species generally have wider wing spans than the females. Despite having similar body size, the mean number of oviposited eggs was lower for *P. damastesalis* (135 eggs/female) compared to *P. machoeralis*, where a mean of 217 eggs was recorded in China (Wu et al. 1979) and 374 eggs in India (Patil & Thontadarya 1987a). The egg incubation period was longer in *P. damastesalis* compared to *P. machoeralis* at the maximum temperature of 32.5 °C. Having a similar body size to *P. machoeralis*, the lower number of eggs oviposited by *P. damastesalis* suggests that the eggs were larger and therefore took a longer time to hatch.

Both teak skeletoniser species have five larval instars. Depending on the temperature, the mean larval period for *P. damastesalis* may be longer or shorter than that of *P. machoeralis*. At lower temperatures and relative humidity, the larval period for *P. machoeralis* was prolonged (Patil et al. 1984, Patil & Thontadarya 1987b). The larval period of *P. damastesalis* was significantly longer in the laboratory, where the temperature was generally cooler, but relative humidity was higher than in the field. This suggests that temperature and/or relative humidity may also have some effect on the duration of the *P. damastesalis* larval stage although this may not be true in some of the stages or sex (see above results). Between the two environmental parameters, the influence of relative humidity in some species of Lepidoptera is trivial compared to temperature (Haugen & Stephen 1984, Reichenbach & Stairs 1984).

Another environmental parameter that may influence larval development, especially the occurrence of diapause, in many species of Lepidoptera is photoperiod (Gomi 1995, Wipking 1995, Fantinau et al. 1998). Diapause was not evident in P. damastesalis although there were differences in the photoperiod regimes and the temperatures in the laboratory and the field. Environmental conditions in tropical countries such as Malaysia do not go through obvious changes throughout the year. For diapause to occur, environmental conditions are usually extreme with low temperature, short photoperiod regime and in some cases low relative humidity. The larvae of P. machoeralis were also not observed to enter diapause in the winter in China (Wu et al. 1979), but in India, the occurrence of facultative

diapause was evident (Patil & Thontadarya 1987a) with diapause induced by high temperature and high relative humidity (Patil & Thontadarya 1987b). There is a possibility that the *P. machoeralis* studied by Wu et al. (1979) is in fact *P. damastesalis*, as the morphological difference between these two species of *Paliga* is trivial (Intachat 1998).

The two teak skeletoniser species were similar in the duration of the pupal developmental period. The method for sexing *P. damastesalis* at the pupal stage was also similar to that for *P. machoeralis*, where the male and female pupae can be differentiated by the position of the genital opening as reported by Misra (1975). The male and female pupae of both species were similar in size (length) although not necessarily in weight. The female pupae in some species of Lepidoptera can be heavier than the males (see Clancy 1991) but not in other species (Miller *et al.* 1991). In this study, the pupal weight of the *P. damastesalis* was not recorded.

Acknowledgments

The author thanks Saimas Ariffin and Faridah Din of the Forest Research Institute Malaysia for their assistance. The author is also grateful to Harry Staines of Abertay-Dundee University, United Kingdom, for his statistical advice and Chey Vun Khen of the Forest Research Center, Sandakan, Sabah, three anonymous referees and A. J. Hurrell for their comments. The research was supported by IRPA 01-04-01-0054.

References

- CHEY, V. K. 1996. Forest Pest Insects of Sabah. Sabah Forest Record No. 15. 111 pp.
- CLANCY, K. M. 1991. Multiple-generation bioassay for investigating western spruce budworm (Lepidoptera: Tortricidae) nutritional ecology. *Environmental Entomology* 20(5):1363-1374.
- Fantinau, A. A., Tsitsipis, J. A. & Karandinos, M. G. 1998. Diapause termination in Sesamia nonagrioides (Lepioptera: Noctuidae) under laboratory and field conditions. Environmental Entomology 27(1):53-58.
- GOMI, T. 1995. Effect of temperature on diapause response to photoperiod in *Hyphantria cunea* with special reference to local divergence. *Applied Entomology & Zoology* 30 (3):490-492.
- HAUGEN, D. A. & STEPHEN, F. M. 1984. Development rates of Natucket pine tip moth, Rhyacionia frustrana (Comstock) (Lepidoptera: Tortricidae), life stages in relation to temperature. Environmental Entomology 13(1):56-60.
- INTACHAT, J. 1998. A note on the identity of a Malaysian teak skeletoniser, *Paliga damastesalis* Walker (Lepidoptera: Pyralidae). *Journal of Tropical Forest Science* 10(4):561-563.
- Krishnapillay, B., Mohd. Noor, M., Norini, H., Ahmad Zuhaidi, Y., Ab. Rasip, A.G. & Mahmud, A. W. 1998. Viability of planting teak and sentang in Malaysia. Pp. 23-33 in Ahmad Zuhaidi, Y., Ab. Rasip, A. G., Mohd. Noor, M. Mahmud, A. W., Wickneswari, R. & Nik Zanariah, N. M. (Eds.) Proceedings of the Seminar on Commercial Cultivation of Teak, Sentang, Acacia and Hevea for Timber. 9 January 1997, Renaissance Hotel, Kuala Lumpur.
- MILLER, J. C., HANSON, P. E. & KIMBERLING, D. N. 1991. Development of the gypsy moth (Lepidoptera: Lymantriidae) on Garry oak and red alder in western North America. *Environmental Entomology* 20(4):1097-1101.
- MINITAB Release 10.2. 1994. Minitab Incorporated, 3081 Enterprise Drive, State College.
- MISRA, M. P. 1975. Sexing of pupae and adult moths of teak skeletonizer, *Pyrausta machaeralis* Walker (Lepidoptera: Pyralidae). *Indian Forester* 101:301-304.

- Patil, B. V. & Thontadarya, T. S. 1987a. Biology of teak skeletonizer, *Pyrausta machaeralis* Walker (Lepidoptera: Pyralidae). *Mysore Journal of Agricultural Science* 21:32–39.
- Patil, B. V. & Thontadarya, T. S. 1987b. Studies on the induction and termination of hibernation on the teak skeletonizer, *Eutectona machaeralis* Walker (Lepidoptera: Pyralidae). *Entomon* 12 (3):179-182.
- PATIL, B. V., THONTADARYA, T. S. & AWAKKANAVAR, J. S. 1984. Effect of temperature and relative humidity on the development and survival of teak skeletonizer, *Pyrausta machaeralis* Walker. *Indian Journal of Ecology* 11(1): 32-36.
- REICHENBACH, N. G. & STAIRS, G. R. 1984. Response of western spruce budworm (Lepidoptera: Tortricidae) to temperature and humidity: developmental rates and survivorship. *Environmental Entomology* 13(2):611-618.
- WIPKING, W. 1995. Influences of day length and temperature on the period of diapause and its ending process in dormant larvae of burnet moths (Lepidoptera, Zyaenidae). *Oecologia* 102(2):202-210.
- Wu, S. H., Chen, C. C. & Wang, T. H. 1979. A preliminary study on the teak defoliator *Pyrausta machaeralis* Walker. *Acta Entomologica Sinica* 22 (2):156–163.

THE EFFECTS OF DEFOLIATION AND INORGANIC FERTILISERS ON THE GROWTH OF SOME TROPICAL TREE SEEDLINGS

D. A. Agboola & M. Kadiri

Department of Biological Sciences, University of Agriculture, Abeokuta, P.M.B. 2240, Abeokuta, Ogun State, Nigeria

Received May 1996

AGBOOLA, D. A. & KADIRI, M. 1999. The effects of defoliation and inorganic fertilisers on the growth of some tropical tree seedlings. The effects of defoliation and some inorganic fertilisers on the growth of 3-month-old seedlings of six tropical tree species, i.e. Terminalia ivorensis, Terminalia superba, Ceiba pentandra, Gmelina arborea, Tectona grandis and Leucaena leucocephala, were studied. The removal of two to three leaves significantly decreased root length and dry weights of root and shoot of seedlings of the six species. Seedling height was unaffected by defoliation. Removal of part of a previously intact leaf had no adverse effect on the total growth. There was increase in total leaf area and dry weight of seedlings treated with five inorganic fertilisers, that of Mg(NO₃)₂ being the most effective.

Key words: Defoliation - inorganic fertilisers - seedlings - tropical trees - growth - root - shoot

AGBOOLA, D. A. & KADIRI, M. 1999. Kesan peranggasan dan baja tak organik terhadap pertumbuhan beberapa anak benih pokok tropika. Kesan peranggasan dan beberapa baja tak organik terhadap pertumbuhan anak benih berumur 3 bulan bagi enam spesies pokok tropika iaitu Terminalia ivorensis, Terminalia superba, Ceiba pentandra, Gmelina arborea, Tectona grandis dan Leucaena leucocephala dikaji. Pembuangan dua hingga tiga daun mengurangkan dengan bererti panjang akar dan berat kering akar serta pucuk anak benih enam spesies tersebut. Ketinggian anak benih tidak dipengaruhi oleh peranggasan. Pembuangan sebahagian daripada daun yang masih berkeadaan baik tidak memberi kesan yang buruk terhadap jumlah pertumbuhan. Terdapat pertambahan dalam jumlah luas daun dan berat kering anak benih yang dirawat dengan lima baja tak organik, dan rawatan Mg(NO₄)₂ didapati paling berkesan.

Introduction

The tropical forest in its original state is exceptionally rich supporting more than a hundred different species per hectare compared to 10–15 in many temperate forests (Spore-CTA 1991). The natural vegetation has been faced with over-exploitation. Natural regeneration of forests in the tropics is threatened with many problems including poor seed germination, seedling establishment and survival (Onochie 1990).

Various nursery practices have been geared towards successful seedling establishment. However, successful seedling establishment of some species in plantation is still faced with some handicaps, mainly, loss of leaves by the young seedlings. Leaf can be lost through diseases, insect and animal feeding and infestation, and by physical means. For example, the heavy winds that accompany tropical rainstorms are a common source of leaf loss (Remison 1978). Leaf loss interferes with the metabolic processes of the plant in general and hence growth. This can be critical during the early vegetative phase especially when young seedlings have limited surfaces for photosynthesis (Devlin 1969).

The demand for nutrients by trees is very high and response to a lack of it, probably is the most common form of mineral deficiencies in trees. Nitrogen deficiency is readily manifested by chlorosis and wilting (Kozlowski 1971). Magnesium deficiency in trees is shown to form chlorosis, pigmentation which may later be followed by necrotic spotting (Devlin 1969). The easiest and fastest methods of correcting nutrient deficiencies are through the use of fertilisers which are mostly applied directly to the soil or indirectly to the plant foliage in liquid form (FDDP 1989).

This present study aims to verify the extent to which leaf removal and application of five inorganic fertilisers affect early vegetative growth of seedlings of six economically important tropical trees. Terminalia ivorensis, Terminalia superba and Ceiba pentandra, inhabitants of the tropical rain forest, are sources of high quality timber for furniture and construction in Nigeria. Leucaena leucocephala, Tectona grandis and Gmelina arborea are exotic species introduced into Nigeria from other tropical zones of the world, especially Southeast Asia. Of these L. leucocephala has been successfully used in various agroforestry practices (Kang & Wilson 1987, Beets 1989).

Materials and methods

Three-month-old seedlings of the six tree species were raised in nursery bags from seeds previously treated for dormancy release according to the methods of Agboola and Etejere (1991). The seedlings were divided into seven lots and then thinned to one plant per bag three weeks after germination.

Seedlings were subjected to seven defoliation treatments 10 weeks after germination using a modified method of Remison (1978). Most tree seedlings are more susceptible to premature death due to loss of leaves at this age in their natural habitat in Nigeria. The seedlings at this stage had 5-7 leaves. The defoliation treatments were designated D_0 to D_6 as listed below:

- D₀ Control (no leaf removed)
- D, One whole leaf removed
- D₂ One half leaf removed
- D. Two whole leaves removed
- D₄ Two halves removed
- D₅ Three whole leaves removed
- D₆ Three leaf halves removed

In the defoliation treatment, a whole leaf blade was either detached (excluding the petiole) or cut into half with scissors. Leaves were carefully cut into half from the leaf apex to the base of the leaf along the side of the mid-rib. The experiment was carried in a greenhouse with minimum and maximum daily temperatures of 28 °C and 30 °C respectively. Trees were arranged in a randomised block design with five replicates. The root and shoot lengths, total plant height and dry weights of shoot and root were recorded 2 weeks after defoliation treatments were applied when seedlings would have been 12 weeks old. Means of replicate values were calculated while the analysis of variance (ANOVA) was used to interprete the data.

In a separate experiment, five inorganic fertilisers, NH₄NO₃, Mg(NO₃)₂, NaNO₃, Al(NO₃)₃, and NH₄Cl were used. Seedlings were raised in nutrient - free sandy loam in planting bags. Two grams of fertiliser per plant were applied when seedlings were two months old. Control seedlings received no fertiliser. Seedlings were watered with gentle mist spray every second day. A randomised block design of 6 species × 6 treatments × 5 replicates was used. Means of replicate values were also taken and the analysis of variance, ANOVA, used to interprete the data. Mean values were compared by the least significance difference, LSD at 0.05 probability level. Seedling growth was evaluated at the 3-month stage by measuring leaf area and total dry weights. Leaf area was measured using the electronic planemeter while the dry weights were determined after drying to constant weight by the method of Etejere and Osatimehin (1984).

Results

The values obtained for the growth parameters investigated under the effects of defoliation treatments D_3 and D_5 in all the species were significantly different from the control D_0 (p=0.05) (Tables 1-4). It was observed that the removal of 2 and 3 leaves from the seedlings of the tree species significantly affected the total dry weights of root and shoot and root length as compared to the control in Terminalia ivorensis, T. superba, Tectona grandis, C. pentandra and G. arborea and L. leucocephala (Tables 1-3). For example, the total plant height of 3-month-old seedlings of T. ivorensis when no leaf was removed was 27.8 cm compared to 21.3 and 18.9 cm observed when 2 and 3 leaves were removed respectively (Tables 3 & 4). The dry weights of root and shoot in the same seedling in the control were 5 and 9 g respectively in comparison to 2.5 and 5.2 g in seedlings with 2 leaves removed, 2.0 and 4.3 g in T. ivorensis with 3 leaves removed (Tables 1 & 2). This trend was also observed in the other tree species.

The results showed that the shoot length of the seedlings of all the six species were mostly not affected by the defoliation treatment (Table 4). It was observed generally in all the species investigated that removal of part of an intact leaf had no adverse effect on the growth of the seedlings (Tables 1-4).

Tables 5 and 6 show the observed values for the effects of five fertilisers on the total leaf areas and dry weights of the 3-month-old seedlings of the six tree species investigated. There was an increase in the total leaf area and dry weight of seedlings

treated with the five inorganic fertilisers (Tables 5 & 6). However, $Mg(NO_3)_2$ had the most significant effect in increasing the total leaf area (Table 5). None of the fertilisers tested, with the exception of $Mg(NO_3)_2$, had any significant effect on the total dry weight. Magnesium nitrate caused very high increase in total dry weight in all the seedlings, especially those of *C. pentandra* and *L. leucocephala* (Table 6), where 300 and 400% growth increases were observed respectively.

Table 1. Effect of defoliation on the root dry weight of 3-month-old seedlings of six tropical tree species. Data are mean values \pm s.e. of five replicates.

Defoliation treatment	Dry weights of root (x10 ² g)									
	Ts	Tv	Tg	Cb	Ga	Leu				
$\mathbf{D_o}$	7.9 ± 0.5	5.0 ± 1.2	130.0 ± 1.7	15.0 ± 1.3	33.4 ± 0	23.0 ± 0.2				
D ₁	9.7 ± 0.3	4.8 ± 1.2	127.3 ± 0.6	14.7 ± 0.2	33.6 ± 0.1	22.8 ± 1.6				
D ₂	7.2 ± 0.4	4.6 ± 1.0	128.4 ± 0.3	14.2 ± 0.5	33.7 ± 0	22.7 ± 1.2				
D,	5.1 ± 0.1	$2.5 \pm 0.61*$	102.3 ± 0.2	9.3 ± 0.3*	26.3 ± 1.2*	15.2 ± 1*				
D,	7.3 ± 0.3	4.7 ± 0.1	126.8 ± 0.1	14.8 ± 1.5	34.0 ± 0.6	22.6 ± 0.3				
	$4.6 \pm 0.4 *$	2.0 ± 0.1	94.2 ± 1.0	$10.4 \pm 2.4*$	22.3 ± 0.1*	13.3 ± 1.1*				
${f D_5} \\ {f D_6}$	7.1 ± 0.4	4.4 ± 1.2	126.2 ± 0.7	14.6 ± 2.2	32.9 ± 0.1	22.8 ± 3.9				

^{*}Significantly different from control (p = 0.05).

 $D_0 = \text{no leaf removed (control)}$

 D_2 = one half leaf removed D_4 = two leaf halves removed

D = three leaf halves removed

D = two whole leaf removed

D₃ = two whole leaves removed

 \mathbf{D}_{k} = three whole leaves removed

Ts = Terminalia superba Cb = Ceiba pentandra Tv = Terminalia ivorensis Ga = Gmelina arborea Tg = Tectona grandis

Leu = Leucaena leucocephala

Table 2. Effect of defoliation on the shoot dry weight of 3-month-old seedlings of six tropical tree species. Data are mean values \pm s.e. of five replicates.

Defoliation treatment	Dry weights of root $({ m x}10^2{ m g})$									
	Ts [†]	Tv	Tg	Съ	Ga	Leu				
D ₀ †	12.6 ± 0.4	9.0 ± 0.4	60.0	99.0 ± 4.0	89.0 ± 0.3	48.0 ± 1.6				
D ₁	12.4 ± 0.7	8.8 ± 0.6	57.3 ± 0.1	94.0 ± 2.6	86.3 ± 0.2	47.3 ± 0.2				
$\mathbf{D}_{\mathbf{z}}^{'}$	12.5 ± 0.2	8.7 ± 0.3	58.0	96.0 ± 6.3	87.2 ± 0.3	47.6 ± 1.2				
D,	8.4 ± 0.7	5.2 ± 0.1	46.4 ± 1.2	64.6 ± 2.4*	63.4 ± 1.7*	31.3 ± 1.1*				
D,	12.2 ± 1.3	8.6 ± 0.4	57.2 ± 1.3	96.2 ± 4.2	87.2 ± 0.5	47.7 ± 1.3				
D ₅	6.7 ± 0.1 *	4.3*	39.6 ± 0.4	$70.1 \pm 1.6 *$	56.7 ± 1.3*	27.2 ± 1.4*				
D_6	12.2 ± 0.1	8.2 ± 0.2	57.1 ± 0.3	97.3 ± 3.4	87.6 ± 0.3	47.3 ± 2.4				

^{*}Significantly different from control (p = 0.05).

^{&#}x27;As in Table 1.

Defoliation	Root length (cm)									
treatment	Ts [†]	Tv	Tg	Съ	Ga	Leu				
D,†	20.0 ± 0.3	16.4 ± 0.3	18.0 ± 2.0	20.4 ± 1.8	19.4 ± 1.3	18.2 ± 0.5				
Ď,	19.7 ± 0.2	16.2 ± 0.2	17.3 ± 0.1	18.9 ± 0.3	19.0 ± 0.1	16.4 ± 0.4				
D,	19.4 ± 0.3	16.0 ± 0.1	17.0 ± 0.1	18.8 ± 0.3	19.2 ± 0.2	18.0 ± 0.3				
D,	13.0 ± 0.1	$10.0 \pm 1.2 ^{\bullet}$	12.3 ± 0.1	13.3 ± 0.6*	19.3 ± 1.2	13.9 ± 0.8*				
D,	19.8 ± 0.4	16.3 ± 0.4	17.4 ± 0.1	19.4 ± 0.7	18.8 ± 1.3	16.9 ± 1.3				
D ₀ † D ₁ D ₂ D ₃ D ₄ D ₅	12.3 ± 0.5*	$8.0 \pm 1.2 *$	9.6 ± 0.3	$11.1 \pm 0.3*$	19.2 ± 0.7	12.0 ± 0.5*				
$\mathbf{D_6^2}$	18.3 ± 0.4	16.0 ± 0.2	17.0 ± 0.1	18.6 ± 0.4	18.7 ± 1.1	18.0 ± 0.5				

Table 3. Effect of defoliation on root length of 3-month-old seedlings of six tropical tree species. Data are mean values ± s.e. of five replicates.

Table 4. Effect of defoliation on the shoot length of 3-month-old seedlings of six tropical tree species. Data are mean values ± s.e. of five replicates.

Defoliation treatment	Shoot length (cm)										
	Ts*	Tv	Тg	Сь	Ga	Leu					
D ₀ [†]	16.4 ± 0.1	11.4 ± 0.1	10.9 ± 0.4	16.4 ± 0.5	23.0 ± 0.1	20.0 ± 1.6					
D,	16.0 ± 1.3	11.4 ± 0.1	11.3 ± 0.1	17.5 ± 0.2	22.9 ± 0.3	18.9 ± 1.3					
D,	16.2 ± 0.9	11.2 ± 0.2	10.8 ± 0.1	16.8 ± 0.1	22.8 ± 0.1	19.4 ± 0.6					
D.	16.3 ± 0.6	11.3 ± 0.1	8.9 ± 0.2	16.0 ± 0.2	$15.0 \pm 1.2 $	12.6 ± 0.5					
D ₂ D ₃ D ₄	16.2 ± 0.7	11.0 ± 0.1	10.2 ± 0.4	16.3 ± 0.1	22.9 ± 0.1	20.7 ± 1.2					
D.	15.9 ± 0.4	10.9 ± 0.3	7.8 ± 0.1	16.4 ± 0.2	$13.3 \pm 0.9*$	12.5 ± 0.6*					
D, D ₆	15.6 ± 0.1	11.2 ± 0.4	10.4 ± 0.1	16.3 ± 0.4	21.5 ± 1.3	20.1 ± 0.2					

^{*}Significantly different from control (p = 0.05).

Table 5. Effect of inorganic fertilisers on the leaf area of 3-month-old seedlings of six tropical tree species. Data are mean values ± s.e. of five replicates.

Fertiliser	Leaf area of seedling (cm²)									
treatment	Ts*	Tv	Тg	Сь	Ga	Leu				
Control	1435.0 ± 4.6	350.0 ± 2.7	6550.0 ± 7.3	1175.0 ± 9.1	4611.0 ± 18.1	788.0 ± 3.0				
NaNO.	1610.0 ± 11.3	412.0 ± 1.5	6730.0 ± 6.2	1360.0 ± 6.4	4764.0 ± 9.2	920.0 ± 7.4				
Mg(NÖ,),	1620.0 ± 11.2*	476.0 ± 2.5*	6947.0 ± 7.3*	1642.0 ± 3.5*	5102.0 ± 4.1*	1020.0 ± 8.1				
NH,NO,	1536.0 ± 9.7	436.0 ± 1.7	6714.0 ± 3.9	1260.0 ± 2.7	4821.0 ± 10.1	640.0 ± 4.1				
Al(NO,)	1497.0 ± 11.7	410.0 ± 6.4	6614.0 ± 11.2	1210.0 ± 4.2	4721.0 ± 8.7	360.0 ± 3.5				
NH,C1	1560.0 ± 5.4	386.0 ± 5.1	6783.0 ± 8.4	1320.0 ± 6.1	4801.0 ± 7.2	802.0 ± 5.6				

^{*}Significantly different from control (p = 0.05).

^{*}Significantly different from control (p = 0.05).

^{&#}x27;As in Table 1.

^{&#}x27;As in Table 1.

^{&#}x27;As in Table 1.

Fertiliser treatment	Total dry weight of seedling (g)									
	Ts*	Tv	Tg	Сь	Ga	Leu				
Control	1.62 ± 0.01	1.65 ± 0.02	8.84 ± 0.14	12.65 ± 0.09	18.46 ± 0.19	7.47 ± 0.18				
NaNO,	3.01 ± 0.02	1.97 ± 0.03	8.77 ± 0.14	12.94 ± 0.14	18.76 ± 0.87	7.86 ± 0.18				
Mg(NO.).	5.24 ± 0.04**	$4.87 \pm 0.06**$	16.29 ± 0.17**	34.64 ± 0.11**	30.0 ± 0.76**	28.92 ± 0.144				
NH NO.	4.6 ± 0.06	3.70 ± 0.22	8.93 ± 0.03	13.01 ± 0.46	18.6 ± 1.24	8.01 ± 0.26				
AL(NO,),	1.72 ± 0.04	1.75 ± 0.01	8.19 ± 0.39	12.12 ± 0.01	18.77 ± 1.26	7.48 ± 0.27				
NH,Cl	2.46 ± 0.03	1.74 ± 0.01	8.74 ± 0.01	13.53 ± 0.4	18.73 ± 0.06	7.95 ± 0.36				

Table 6. Effect of inorganic fertilisers on the total dry weights of 3-month-old seedlings of six tropical tree species. Data are mean values ± s.e. of five replicates.

Discussion

The removal of 2 or 3 leaves in the 3-month-old seedlings of all three species in this study significantly affected dry weights of root and shoot compared to the control trees. Root length was the most adversely affected by defoliation especially in T. ivorensis, T. superba, C. pentandra and T. grandis (Table 3).

Removal of half a leaf from the seedlings had no effect (Tables 1-4). The result of the present study compared favourably with that of Remison (1978) on the effect of defoliation on growth of maize. He found that in the field, defoliation of all leaves from the plant at 50% silking reduced the dry matter accumulation severely. Removing half of the leaves above or below the ear did not affect cob and grain weight to the same extent as removing all leaves above and below the ear. Leaves are essential for photosynthetic and respiratory activities and their loss by any means can retard or inhibit growth processes.

This study has shown that defoliation of young seedlings of tree species in the early vegetative phase impaired root growth and consequently may affect the uptake and distribution of nutrients (Tables 1-4). In turn, this may result in reduced growth rate of defoliated plants. A number of workers (Davidson & Milthorpe 1965, Evans 1973) have shown that defoliation has deleterious effects on plant growth. Dry matter accumulation was most affected when a greater number of leaves (2-3) were defoliated at especially at 2- to 3-month stage (Tables 1 & 2).

Presumably with 2-3 leaves removed the tender plants depended in part on the green stems for their photosynthetic activities and less leaf material for growth was deposited. Martin and Leonard (1967) reported that stripping corn leaves at an early stage of growth checked grain development and reduced yield. When half the leaves were removed, there was no effect on growth. This showed that the undefoliated halves, other green parts of shoot and the intact leaves provided enough photosynthates needed for growth at this stage.

^{**}Highly significantly different from control (p = 0.05).

^{&#}x27;As in Table 1.

Removal of leaves in this investigation is perhaps a semblance of conditions where leaf-eating insects or diseases and physical removal by wind or heavy rain remove leaf area. Insects, according to Martin and Leonard (1967), may not remove all leaves on plants although some insects such as locusts and army worms can devour large parts leaving only bare stalks or sometimes only stubs in the field. Occurence of greater damage on shoot of young seedlings of *Chlorophora excelsa* (*Milicia excelsa*) by leaf gall-forming aphids has been clearly documented by Fasidi and Olofinboba (1975).

The present results of the effect of inorganic fertiliser on growth compare well with those of Etejere and Osatimehin (1984). Magnesium nitrate, NH₄NO₃ and KNO₃ significantly increased the dry weight of above-ground tissue of seedlings of baobab, *Adansonia digitata*, with KNO₃ being the most effective. Ammonium nitrate and KNO₃ enhanced the plant root length and shoot height. Ekwebelam and Reid (1984) found that application of three levels of ammonium nitrate led to significantly larger biomass in 16-week-old seedlings of *Pinus contata*.

If a plant is supplied with high concentrations of fertiliser, especially that containing nitrogen, there is a tendency for the plant to have increased leaf cell number and cell size with an overall increase in leaf production (Njoku 1957). This explains the observed enhancement of leaf area of the tree seedlings by the five fertilisers (Table 5). Magnesium nitrate apart from enhancing leaf area also caused increased total dry weight. Magnesium is a constituent of chlorophyl and hence plays a prominent role in the production of photosynthates and assimilable materials (Nanson & Mcleroy 1963).

Acknowledgements

The authors are grateful to the technical staff of the seed store and library of the Forestry Research Institute of Nigeria (FRIN) for their technical assistance.

References

Acboola, D. A. & Etejere, E. O. 1991. Studies on seed dormancy of selected economic tropical forest tree species. Nigerian Journal of Botany 4: 115-126.

BEETS, W. C. 1989. The Potential Role of Agroforestry in ACP-Countries. Technical Centre for Agriculture and Rural Cooperation (CTA). ACP-EEC. Lome Convention, Netherlands. 18 pp.

DEVLIN, R. M. 1969. Plant Physiology. 2nd edition. Van Nostrand Renthol Co., New York: 41-43.

Davidson, J. L. & Milthorpe, F. L. 1965. Carbohydrate reserves in the growth of cocksfoot. *Journal of British Grassland Society* 20:15-18.

EKWEBELAM, S. A. & REID, C. P. P. 1984. Nitrogen fertilization and light effects on the growth and photosynthesis of lodge pole pine seedlings. *Annals of Applied Biology* 105:117-127.

ETEJERE, E. O. & OSATIMEHIN, D. A. 1984. Some aspects of growth of Adansonia digitata L. Indian Journal of Plant Physiology 27:190-250.

Evans, P. S. 1973. The effect of repeated defoliation to the different levels on root growth of five pasture species. The New Zealand Journal of Agricultural Research 16:31-34.

FASIDI, I. O. & OLOFINBOBA, M. O. 1975. Studies on *Chlorophora excelsa* (Welw) Benth: effect of light and herbicide on seed germination. *Nigerian Journal of Forestry* 5:9-20.

- FDDP. 1989. Fertilizer Use and Management Practices for Crops in Nigeria. Fertilizer Distribution Department, Federal Ministry of Agriculture, Lagos, Nigeria. Technical Series 2.
- KANG, B. T. & WILSON, G. F. 1987. The development of alley cropping as a promising agroforestry technology. Pp. 227-243 in Stepler, H. A. & Main, P. K. R. (Eds.) Agroforestry: A Decade of Development. ICRAF, Nairobi, Kenya.
- KOZLOWSKI, T. T. 1971. Growth and Development of Trees. Academic Press Ltd., London. Vol. 1:77-81.
 MARTIN, J. A. & LEONARD, W. H. 1967. Principles of Field Crop Production. Macmillan Co., New York: 77-106.
- Nanson, A. & McElroy, W. D. 1963. Mode of action of the essential mineral elements. Pp. 451-456 in Steward, F. C. (Ed.) *Plant Physiology*. Academic Press, New York.
- NJOKU, E. 1957. The effect of mineral nutrition and temperature on the leaf shape of *Ipomea. New Phytologist* 56:154-156.
- Onochie, C. F. A. 1990. The dying forest: declining forest resources of Nigeria. Keynote address. 4th Annual Conference of the Botanical Society of Nigeria. University of Nigeria, Nsukka.
- Spore-CTA. 1991. Halting the disapperance of the rain forest. Africa takes initiative. Bulletin of the Technical Centre for Agriculture and Rural Cooperation, Wagenigen, Netherlands 34:1-3.
- REMISON, S. U. 1978. Effect of defoliation during early vegetative phase and at silking on growth of maize (Zea mays). Annals of Botany 42:1439-1445.

PHYSIOLOGICAL EFFECTS OF TEMPERATURE AND THERMAL STRESS ON THE SEED GERMINATION OF STRYPHNODENDRON POLYPHYLLUM

M. Tambelini & S.C.J.G.A. Perez

Seed Germination Laboratory, Botany Department, Federal University, Rodovia Washington Luis, Km 235, CP 676, CEP 13565-905, São Carlos, SP, Brazil

Received May 1996

TAMBELINI, M. & PEREZ, S. C. J. G. A. 1999. Physiological effects of temperature and thermal stress on the seed germination of Stryphnodendron polyphyllum. The thermal effects brought about by temperature on the seed germination of Stryphnodendron polyphyllum were studied in relation to the germination percentage and relative frequency distribution of germination along the incubation time. Stryphnodendron polyphyllum seeds were found to be eurithermic, having the following cardinal temperatures: the minimum between 5 and 10 °C, the maximum between 40 and 45 °C, the optimum between 25 and 30 °C. The germination rate was temperature dependent. However, the distribution of relative frequency of germination did not fit the adjusted gaussian and did not give good linearity in the Arrhenius graphs of their isothermal germination rates. Hence, in these seeds the thermal communication between the environment and the seed growth effector is made through a temperature signal superimposed upon the random thermal noise at all germination isotherms. The absolute values of enthalpy activation of germination (ΔH_n^*) were less than 12 Kcal mol between 20 and 30 °C, 12 and 30 Kcal mol at 15 °C and higher than 30 Kcal mol' above 35 °C. Therefore, the germination of the seeds was only limited by diffusion process between 2 and 30 °C. Below 15 and above 35 °C phase transitions and protein denaturation occurred. The lowest values of informational entropy occurred between 25 and 30 °C, showing a higher synchronisation of the germination process. Seeds without imbibition were resistant to exposure at 70 °C for 24 h, without showing a significant reduction in the rate and percentage of germination. Thermal stress of imbibed seeds at 50 °C for 24 h gave only 10% germination.

Key words: Germination - temperature - thermal stress - Brazilian "cerrado".

TAMBELINI, M. & PEREZ, S. C. J.G. A. 1999. Kesan fisiologi suhu dan tegasan terma terhadap percambahan biji benih Stryphnodendron polyphyllum. Kesan terma yang dibawa oleh suhu terhadap percambahan biji benih Stryphnodendron polyphyllum dan kaitannya dengan peratus percambahan dan kekerapan relatif taburan percambahan di sepanjang tempoh pengeraman dikaji. Biji benih Stryphnodendron polyphyllum didapati lebih euritemik, mempunyai suhu utama yang berikut: minimum antara 5 dan 10 °C, maksimum antara 40 dan 45 °C, optimum antara 25 dan 30 °C. Kadar percambahan bergantung kepada suhu. Bagaimanapun, taburan kekerapan relatif percambahan tidak sesuai dengan taburan biasa yang diselaraskan. Ia juga tidak memberikan kelinearan dalam graf Arrhenius bagi kadar percambahan isotermanya. Oleh yang demikian, dalam biji benih ini, komunikasi terma antara alam sekitar dan

penindak pertumbuhan biji benih dilakukan melalui isyarat suhu yang ditindih di atas bunyi bising terma secara rawak pada kesemua percambahan isotem. Nilai mutlak pengaktifan entalpi percambahan (ΔH^a_n) ialah kurang daripada 12 Kcal mol⁻¹ antara 20 dan 30°C, 12 dan 30 Kcal mol⁻¹ pada 15 °C dan lebih tinggi daripada 30 Kcal mol⁻¹ di atas 35 °C. Oleh itu, percambahan biji benih hanya dihadkan oleh proses resapan antara 2 dan 30 °C. Di bawah 15 dan di atas 35 °C wujud peralihan fasa dan penyahaslian protein. Nilai terendah entropi bermaklumat terjadi antara 25 dan 30 °C, mewujudkan penyelarasan yang lebih tinggi dalam proses percambahan. Biji benih tanpa pendapan tahan kepada pendedahan pada 70 °C selama 24 jam, tanpa menunjukkan pengurangan bererti dalam kadar dan peratus percambahan. Tegasan terma biji benih yang dipendap pada suhu 50 °C selama 24 jam hanya memberikan 10% percambahan.

Introduction

Stryphnodendron polyphyllum Mart, a member of the Leguminosae, occurs in Brazilian "cerrado" and is locally known as "barbatimão". Its trunk has a high content of tannin that can be used in tanning and the bark has medicinal properties. The tree is also ornamental, and may be used in landscape gardening and in urban forestry; its wood is good for construction. This species is also recommended for mixed plantation in degraded and permanent conservation areas.

According to Labouriau (1983), it is important to determine the extreme cardinal temperatures (T_m and T_M) and the optimum range of germination percentage to understand the biology and ecology of the species.

The main physiological interest in studying the temperature dependence of germination is the search for limiting factors and partial processes of seed germination.

Temperature effects can be determined from changes in the percentage, rate and relative frequency of germination (Labouriau & Agudo 1987). The extreme temperature limits of seed germination are easily determined empirically and provide biogeographical and ecological information (Labouriau 1983).

Since the overall process is strongly affected by temperature, its mechanisms may be subjected to thermobiological analysis, and germinating seeds provide the basis for many thermobiological investigations (Labouriau 1983).

One approach to studying the temperature dependence of the germination rate is to determine the activation enthalpy. This makes possible the identification of the temperature intervals in which the germination is limited by photochemical reactions (very small values), by diffusion processes ($/\Delta H^*/<12$ Kcal mol⁻¹), by phase transitions or thermal transconformation of proteins ($/\Delta H^*/>30$ Kcal mole⁻¹). Another approach is to evaluate the synchronisation of individual seed germination, using the synchronisation index, that expresses the informational entropy or uncertainty associated with relative frequences distribution at germination (Labouriau & Agudo 1987).

According to Heydecker (1973), an environmental factor present at extreme values may be of considerable biological stress. However, thermal stress could promote the germination of seeds with hard coats (Egley 1989).

Thus, due to the lack of information about tropical wood species, the objective of this study was to determine the cardinal germination temperatures and the impact of thermal shock on the germination of Stryphnodendron polyphyllum seeds.

Material and methods

Seeds of Stryphnodendron polyphyllum were collected from "cerrado" vegetation areas. The seeds were then scarified with 98% concentrated sulphuric acid for 60 min (Tambelini 1994), washed in water, disinfected in 2% sodium hypochlorite and finally washed in distilled water. Four replications of 50 seeds were used for each treatment and incubated in Petri dishes (15 cm diameter) using filter paper moistened with 15 ml of fungicide solution (Benomyl). Observations were daily recorded and germinated seeds (with radicle ≥ 2 mm length) were removed as soon as detected. The cardinal germination temperatures were determined under growth chamber conditions with constant temperatures, ranging from 5 to 45 °C, with intervals of 5 °C.

The thermal stress was evaluated at 3 levels: a) intact seeds were exposed at 50, 60, 70 and 80 °C for 48 h; b) scarified and unimbibed seeds exposed at 50 °C for 24 h and 50, 60, 70 and 80 °C for 48h; c) scarified and imbibed seeds were exposed at 50 and 60 °C for 24 h. The seeds were incubated at 30 °C after the thermal shock exposure.

The parameters of germination were estimated using expressions described by Labouriau and Agudo (1987):

- germination rate, v=1/t (in day¹)
- relative frequency distribution, $f_i = n_i / \sum n_i$ (where n_i = number of seeds germinated between observations t_{i-1} and t_i);
- enthalpy, $\Delta H_n^* = [R(T_m + T_M).(\theta T).T]/[T T_m).(T_M T)]$ (where R is the universal gas constant, T is the incubation temperature in the Kelvin scale and θ is the average between T_m and T_M);
- informational entropy of activation, $E = -\sum f_i \cdot \lg_9 f_i$ (where $f_i = n/N$).

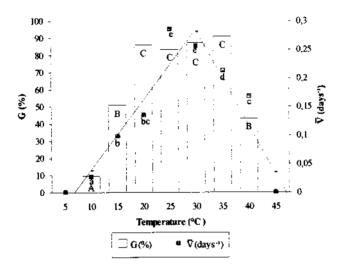
The germination percentages were arcsin transformed and the results were compared using Ftest (Sokal & Rohlf 1980).

Results and discussion

Temperature effects

Germination of Stryphnodendron polyphyllum seeds occurs from a minimum between 5 and 10 °C up to a maximum between 40 and 45 °C with optimal range

from 25 to 30 °C (Figure 1). At 5 °C the seeds showed no germination even after two months at this temperature and at 45 °C the seeds presented a black coat with an extrusion of gelatinous substance. The highest rates of germination were observed at 25 and 30 °C without significant differences among them. Above and below this optimum range, the rate decreased significantly.

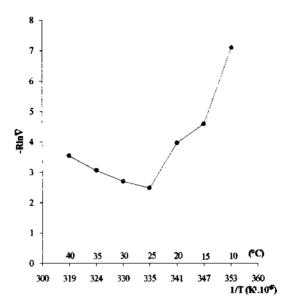


(Continuous line - V theoretical points: V = 0.01358 T - 0.09410 r = 0.9551; V = -0.01628 T + 0.7700, r = -0.9362). Means followed by the same letters do not differ at p<0.05.

Figure 1. Influence of different temperatures on germination percentage (G) and germination rate (V) in Stryphnodendron polyphyllum seeds

Due to the germination temperature range, Stryphnodendron polyphyllum may be classified as a tropical species, having a high temperature tolerance, with a maximal limit of or above 35 °C, and a minimum limit generally above 5 °C (Okusanya 1978 in Perez 1988). Similar cardinal temperatures have been found for other "cerrado" species like Magonia pubescens (ranging from 10 to 40 °C) (Joly et al. 1980) and Dimorphandra mollis (ranging from 12 to 33°C) (Zpeväk 1994).

An approach to identifying the activation energy of this process is in the use of the Arrhenius equation. This type of analysis assumes that a physiological process does not occur unless the system overpasses an energy threshold and that the distribution of energy within the system takes place only through elastic molecular collisions. In this case, the graphs should give only straight lines. There are physiological processes in which this condition is indeed fulfilled, but in many instances, the Arrhenius plots are definitely curved, as the germination rates of Stryphnodendron polyphyllum seeds show (Figure 2). Several other species that present a non-linear Arrhenius plot are Salvia hispanica (Labouriau & Agudo 1987), Prosopis juliflora (Perez & Moraes 1990) and Dimorphandra mollis (Zpevåk 1994).



(\overline{V} : rate of germination; R: universal gas constant (0.08205 atm.K⁻¹ mol⁻¹); T: absolute temperature (K)

Figure 2. Arrhenius plot of germination rate in Stryphnodendron polyphyllum seeds

It is apparent that seed germination rates of this species must be analysed by another approach, like the partition of energy within the seed system (Labouriau 1983). The Eyring theory reported by Perez and Moraes (1990) postulated that a) the system must have several degrees of freedom, among which its energy is partitioned, b) the system must be always in equilibrium with its environment, and c) the process cannot take place unless the system has overpassed a certain potential energy barrier. The same theory says that there are two parcels of energy spent in the activation process: enthalpy and entropy. In seed germination systems with linearly temperature dependent rates, high variations of enthalpy activation take place near the temperature limits, and at the optimum range the enthalpy variations present low values.

The absolute values of enthalpy variation of Stryphnodendron polyphyllum seed germination (ΔH*_n) (Table 1) were lower than 12 Kcal mol¹ between 20 °C (293K) and 30 °C (303K). Values between 12 and 30 Kcal mol¹ take place at 15 °C (288K), and above 35 °C (308K) the values were higher than 30 Kcal mol¹. Thus, the germination of Stryphnodendron polyphyllum seeds would only be limited by the diffusion process between 20 and 30 °C. Below 15 °C and above 35 °C phase transitions and protein denaturation may occur.

Γ (°C)	T(K)	v	T (°C)	I/T (K ⁴ .10 ⁵)	-Rin V	ΔH [*] _n (Kcal/mol ⁻¹)	E (bits)
5	278	No ge	ermination				
10	283	0.028	5-10 °C	353	7.10		2.17 A
15	288	0.099	10-15 °C	347	4.59	21.018	2.37 A
20	293	0.135	15-20 °C	341	3.97	7.363	2.00 A
25	298	0.286	20-25 °C	335	2.48	- 1.185	1.10 B
30	303	0.256	25-30 °C	330	2.70	- 10.327	1.75 A
35	308	0.214	30-35 °C	324	3.06	- 31.385	2.36 A
40	313	0.168	35-340 °C	319	3.54		2.57A
45	318	No ge	ermination				,. .

Table 1. Temperature dependence on net enthalpy variation ΔH^{*}, and entropy (E) variation for germination activation in Stryphnodendron polyphyllum seeds

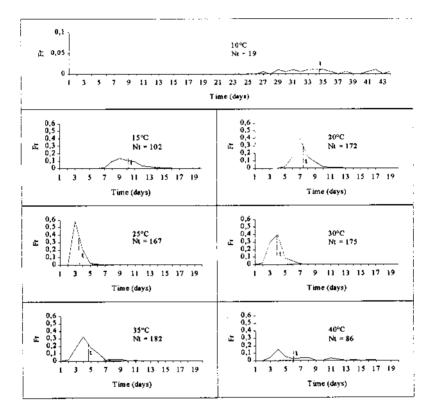
Means followed by the same letters do not differ at p<0.05.

The approach using the theory of absolute reaction rates requires the understanding of the physiological meaning of large values of activation enthalpy. Two phenomena show activation enthalpy of this magnitude: phase transitions and protein denaturation. Either one may be the cause. Phase transitions, i.e. the melting of lipids, has previously been suggested to be involved in several physiological phenomena with very high activation energies. The denaturation of an amylase and an oxidase has been suggested as the cause of the decrease in germinability (with very high Q10 values) and of the lowering of the activity of these enzymes when seeds are submitted to thermal shocks (Labouriau 1978).

Phase transitions, thermodenaturations and damage to cytomembranes have been all presented by Cohen (cited by Labouriau 1978) as possible causes of high values of activation enthalpy in the germination of lettuce seeds. An investigation of the leakage of amino acids from incubated seeds of several species showed that the leakage is enhanced at supra-optimal incubation temperatures, but the results are consistent both with the melting of lipids and with the denaturation of proteins of cytomembrances. One way of discriminating between these two possibilities is in the study of the effects of deuterium oxide on isothermal seed germination, which has a protective action against protein thermodenaturation (Labouriau 1978). This we did not do.

Whenever seed germination rates are temperature dependent, the frequency distributions along the time of isothermal incubation must be different for different temperatures. Thus, for Stryphnodendron polyphyllum the graph (Figure 3) shows the temperature specification of the embryo growth which is necessary and sufficient for its emergence from the seed coat. In the isothermals from 15 to 30 °C, they are unimodal. However, polymodality is clearly shown at 10, 35 and 40 °C indicating a physiological heterogeneity of seeds as to their individual germination. Furthermore, the relative position of the average germination time and the main mode can show whether the heterogeneity is due to a minority of

slower germinating seeds (optimum range) or to a minority of faster germination seeds (extreme cardinal temperatures). In this study, the medium time is displaced to the right of the main mode, within the optimum range and at the temperatures near to maximum (Figure 3). This may be due to a few seeds presenting slower germination (optimum range), or due to many seeds with slower germination (near to maximum).



The Fr values represent the replications sum and 't' represent the mean germination time (Nt = total number of germinated seeds)

Figure 3. Relative frequency distribution (Fr) on seed germination of Stryphnodendron polyphyllum along the time of isothermal incubation for different temperatures

Since relative frequency distribution describes the specification of seed germination by external temperatures, it can be looked upon as expressing a thermal communication between the environment and seed growth effector. The measurement of the information content of this communication is given by the uncertainty value attached to the distribution (Shannon 1948, in Labouriau 1978). Thus, two situations can be envisaged. Either this thermal communication follows the mechanism of random molecular shocks, or else there is a more organised system of heat transmission superimposed upon the random molecular collisions.

The quantitative discrimination between the two alternatives is made possible by a theorem (Shannon 1948, in Labouriau 1983) which states that for a given variance, the gaussian is a distribution of maximum uncertainty. In the case of Stryphnodendron polyphyllum seeds, the graphs (Figure 3) did not fit adjusted normal curves and so, the thermal communication would be made through a temperature signal superimposed upon random thermal noise.

Seeds of Stryphnodendron polyphyllum presented the lowest value of informational entropy at 25 and 30 °C, and the highest values in 15 and 40 °C (Table 1). At 25 and 30 °C, the system has higher information conditions, presenting high rates and germination percentages in these isotherms.

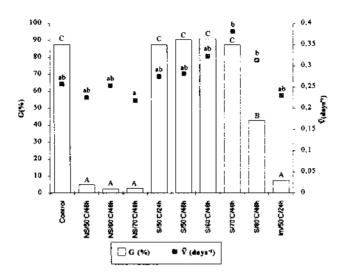
Thermal stress

According to Rolston (1978), Egley (1989) and Bell et al. (1993), thermal stress may promote the germination of hard coat seeds and increase the germination percentage. Perez and Fanti (1996) achieved a higher rate and percentage of germination using thermal stress on Peltophorium dubium seeds. However, this procedure is not effective in breaking the mechanical dormancy of Stryphnodendron polyphyllumseeds without scarification pretreatment, when exposed to a thermal stress at 50, 60, 70 °C (Figure 4). Scarified seeds were resistant to thermal stress up to 70 °C for 48 h, but a significant reduction of the radicle length and coat alterations were observed. Exposure of the scarifieds seeds to 80 °C for 48 h promoted a leakage of gelatinous substances throughout the coat and a reduction in the viability and radicle length. Imbibed seeds were sensitive to thermal stress, presenting germination percentage as low as 10%. Sometimes, the thermal stress could affect the seedling development adversely (Mayer & Poljakoff-Mayber 1989) as has been obtained in Prosopsis juliflora (Perez & Moraes 1990) and Leucaena leucocephala (Cavalcante & Perez 1995).

A probable effect of high temperatures on germination is an increased respiration rate, leading to a high energy production, available for the growth (Okusanya 1980). This would be the reason for the slight increase in the rates observed in scarifieds seeds exposed to 60 and 70 °C.

Conclusion

The germination of Stryphnodendron polyphyllum seeds is a eurithermic process, occurring from a minimum between 5 and 10 °C up to a maximum between 40 and 45 °C, with optimal range from 25 to 30 °C. It is limited by diffusion process between 20 and 30 °C, and probably by phase transitions or proteins denaturation below 15 and above 35° C. Thermal stress of 50–70 °C is not effective in breaking the mechanical dormancy of Stryphnodendron polyphyllum seeds. Stryphnodendron polyphyllum scarified seeds are thermal resistant until 70 °C during 48 h when not imbibed, but imbibed seeds already show thermal stress when exposed to 50 °C for 24 h.



(NS: seeds without scarification; S: seeds after scarification; Im: imbibed seeds). Means followed the same letters did not differ at p<0.05.

Figure 4. Influence of distinct thermal stresses on germination percentage (G) and germination rate (V) in Stryphnodendron polyphyllum seeds. The values of G and V represent the replications means

References

Bell, D. T., Plummer, J. A. & Tayler, S. K. 1993. Seed germination ecology in southwestern Western Australia. *Botanical Review* 59(1):24-73.

CAVALCANTE, A. M. B. & PEREZ, S. C. J. F. A. 1995. Efeitos da temperatura sobre a germinação de sementes de Leucaena leucocephala (Lam.) de Wit. Revista Brasileira de Sementes 17:1-8.

EGLEY, G. H. 1989. Water-impermeable seed coverings as barriers to germination. Pp. 207-223 in Taylorson, R. B. (Ed.) Recent Advances in the Development and Germination of Seeds.

HEYDECKER, W. 1973. Seed Ecology. Butterworth Group, London. 577 pp.

JOLY, C. A., FELIPPE, G. M., DIETRICH, S. M. C. & CAMPOS-TAKAKI, G. M. 198. Physiology of germination and seed gel analysis in two populations of *Magonia pubescens*. Revista Brasileira de Botanica 3:1–9.

LABOURIAU, L.G. 1978. Seed germination as a thermobiological problem. Ration and Environment Biophysics 15:345-366.

LABOURIAU, L.G. 1983. A Germinação das Sementes. Organização dos Estados Americanos (OEA), Washington, United States of America. 174 pp.

LABOURIAU, L. G. & AGUDO, M. 1987. On the physiology of germination in Salvia hispanica L. Temperature effects. Anais da Academia brasileira de Ciencias 59:37-56.

MAYER, A. M. & POLJAKOFF-MAYBER, A. 1989. The Germination of Seeds. 4th edition. Pergamon Press, New York, United States of America. 270 pp.

OKUSANYA, O. T. 1980. Germination and growth of Celosia cristata L. under various light and temperature regimes. American Journal of Botany 6:854-858.

Perez, S. C. J. G. A. 1988. Aspectos Ecofisiológicos da Germinação de Sementes de Prosopis juliflora (Sw) D.C. Sao Carlos, Brazil. 214 pp.

- Perez, S. C. J. G. A. & Fanti, S. C. 1996. Influência da temperatura e do estresse térmico na velocidade e porcentagem de germinação de *Peltophorium dubium* (Spreng) Taubert. VIII Seminario Regional de Ecologia, Programa de Pos-Graduocao em Ecologia e Recursos Naturais/Univesidade Federal de São Carlos, São Carlos, Brazil.
- Perez, S. C. J. G. A. & Moraes, J. A. P. V. 1990. Influências da temperatura, da interação temperaturagiberelina e do estresse térmico na germinação de *Prosopis juliflora* (Sw) D. C. *Revista Brasileira* de Fisiologia Vegetal 2(1):53.
- ROLSTON, M. P. 1978. Water impermeable seed dormancy. Botanical Review 44:365-396.
- SOKAL, R. R. & ROHLF, F. J. 1980. Introduccion a la Bioestatistica. Barcelona, Editorial Reverte. 362 pp. Tambelini, M. 1994. Tratamentos pré germinativos e aspectos ecofisiologicos na germinação de sementes de Stryphnodendron polyphylum Mart. Sao Carlos: UFS Car. Dissertação de mestrado. 112 pp.
- ZPEVAK, F. A. 1994. Efeitos do ácido abscisico, potential hidrico, temperatura e tratamentos para quebra de dormência na germinação de sementes de *Dimorphandra mollis* Benth. São Carlos: UFS Car. Dissertação de mestrado. 104 pp.

EFFECTS OF ABIOTIC AND BIOTIC FACTORS ON THE SEEDLING RECRUITMENT OF HERITIERA FOMES IN THE MANGROVES OF THE SUNDARBANS, BANGLADESH

Neaz Ahmad Siddiqi

Bangladesh Forest Research Institute, Chittagong 4000, Bangladesh

Received February 1997

SIDDIQI, N. A. 1999. Effects of abiotic and biotic factors on the seedling recruitment of Heritiera fomes in the mangroves of the Sundarbans, Bangladesh. Influences of abiotic and biotic factors on the seedling regeneration of Heritiera fomes Buch.-Ham. were investigated. The average number of seedlings appearing in a year was 6680 had although recruitment density varied among different parts of the forests and from year to year. Of the many mangrove species in the area, H. fomes alone constituted 24% of the recruits. Salinity of the area apparently influenced the recruitments which decreased with increasing levels of salinity. Seedling half-life values for H. fomes in less, moderate and strongly saline zones were 13.7, 8.8 and 6.3 months respectively. The relationship between seedling recruitment and stand density was insignificant. Similarly, up to 33 months, canopy closure was not found to affect the seedling recruitment and survival. A lower recruitment and survival of seedlings were noticed in areas with higher level of tidal inundation. As regards the biotic factors, the spotted deer (Axis axis) was not found to affect the natural regeneration of H. fomes, rather it might influence the dominance of this mangrove species through its preferential browsing habit. The wild boar(Sus scrofa) did not appear to have any significant impact on regeneration. Crabs were not found to cause mortality of seedlings, while the role of the rhesus macaque (Macaca mulatta) also appeared to be insignificant. However, the black rat (Rattus rattus) caused substantial damage to the new seedlings of H. fomes, but only in relatively raised and less saline areas.

Key words: Seedling regeneration - Heritiera fomes - abiotic - biotic - mangrove - Bangladesh

SIDDIOI, N. A. 1999. Kesan faktor abiotik dan faktor biotik terhadap penokokan Heritiera fomes di hutan bakau di Sundarbans, Bangladesh. Pengaruh faktor abiotik dan biotik terhadap pemulihan anak benih Heritiera fomes Buch.-Ham. dikaji. Purata bilangan anak benih yang muncul dalam setahun ialah 6680 ha⁻¹ walaupun kepadatan penokokan berubah-ubah di kalangan bahagian-bahagian yang berbeza di hutan tersebut daripada setahun ke setahun. Daripada banyak spesies bakau di kawasan tersebut, H. fomes sahaja membentuk 24% daripada penokokan. Kemasinan kawasan tersebut jelas mempengaruhi penokokan yang berkurang dengan bertambahnya tahap kemasinan. Nilai-nilai anak benih separuh-hayat bagi H. fomes di zon yang kurang, sederhana dan kuat kemasinannya masing-masing ialah 13.7, 8.8 dan 6.3 bulan. Kaitan antara penokokan anak benih dan kepadatan dirian adalah tidak bererti. Begitu juga, sehingga 33 bulan, penutupan sudur tidak mempengaruhi penokokan dan kemandirian anak benih. Penokokan dan kemandirian yang rendah bagi anak benih dapat dilihat di kawasan yang mempunyai penimbunan pasang surut yang lebih tinggi. Mengenai faktor biotik, rusa berbintik (Axis axis) tidak mempengaruhi pemulihan semula jadi H. fomes. Kemungkinan ia lebih mempengaruhi keunggulan

spesies bakau ini melalui keistimewaan tabiat meragutnya. Babi hutan (Sus scrafa) tidak mempengaruhi pemulihan dengan bererti. Ketam tidak menyebabkan kematian anak benih, manakala peranan monyet resus (Macaca mulatta) juga tidak bererti. Bagaimanapun tikus hitam (Rattus rattus) menyebabkan kerosakan yang teruk kepada anak benih baru H. fomes, tetapi hanya di kawasan yang secara relatifnya bertambah dan kurang masin.

Introduction

Heritiera fomes Buch.-Ham. has a limited distribution and is restricted to the mangroves of Myanmar, Bangladesh and the Indian Sundarbans (Troup 1921, Kostermans 1959). In the Bangladesh Sundarbans, the tree is moderate in size and grows to a height of 15 to 20 m. Once trees of girth up to 2 m were found, but owing to heavy exploitation, trees over 1 m in girth are no more common. Heritiera fomes is a highly valuable species and noted for its use in house construction, boat building, electric poles, fuelwood, etc. (Das & Siddiqi 1985). This alone constitutes 63.8% of the merchantable timber (Rahman 1990). It is the dominant species in 52.7% and codominant in 14.8% of the forest area (Chaffey et al. 1985).

The Sundarbans is managed under a selection system on sustained yield basis (Khuttak 1979, Imam 1982). But a depletion by 40% of the merchantable growing stock of *H. fomes* was noticed through two successive forest inventories (Forestal 1960, Chaffey *et al.* 1985). A number of factors may have contributed to this decline. Nevertheless, an adequate regeneration, which depends on a variety of abiotic and biotic factors, would assist in improving the stocking. Chaffey *et al.* (1985) recommended carrying out research into the factors affecting the natural regeneration of the main tree species.

Materials and methods

Study area

The Bangladesh Sundarbans (20°31'-22°30' N, 89°-90° E) covers an area of about 6200 km² and is located in the delta of the Ganges River. Administratively the forest is divided into four ranges and 55 compartments. Tides in the Sundarbans are semi-diurnal with a small diurnal irregularity. The whole forest is in intertidal region, but there is variation in the depth, duration and frequency of tidal inundation. Mean spring tide range in the mouth of the Passur River (east delta) is 2.4 m, whereas this range is 4.3 m in the mouth of the Hoogli River (west delta). The hydrology of the Sundarbans is related to the high seasonal rainfall, as well as the depth and duration of tidal inundation. The entire area is intersected by a complex network of streams and rivers (Figure 1). The forest has been divided into three salinity zones (Hassan et al. 1990) based on the degree of soil salinity—(i) less saline (<2mS cm¹), (ii) moderately saline (2-4mS cm¹) and (iii) strongly saline (>4mS cm¹). Salinity reaches its peak in April—May and drops after June with the appearance of the monsoon. The climate of the Sundarbans is humid. Highest

temperatures occur in April and May and lowest in December and January. Mean annual maximum and minimum temperatures vary between 30 and 21°C. Annual rainfall is in the range 1640–2000 mm. June, July and August are the wettest months and December, January and February the driest. Unlike many other mangroves, the Sundarbans is rich in floristic composition. About 70 species of plants have been recorded from the Bangladesh Sundarbans (Khan 1978, Chaffey & Sandom 1985, Khatun & Alam 1987).

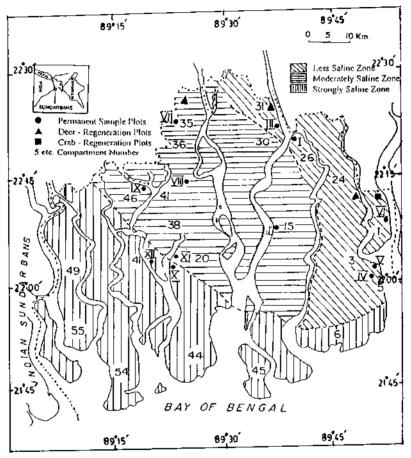


Figure 1. Map of the Sundarbans showing the locations of permanent sample plots and experimental plots

Experiments and observations

Abiotic influences on seedling recruitments (age <3 months) and their survival were studied based on data collected during 1982 to 1991 from twelve permanent sample plots (PSP) established at stratified random design in three salinity zones. Figure 2 shows the lay-out of a PSP. Regeneration data were collected twice a year (pre-monsoon and post-monsoon) from the PSPs (400 m² each). Sixteen points

were demarcated in each plot by four stakes each to the north, the south, the east and the west equidistant from the centre of the plot. Data were collected from only these fixed spots using a circular quadrat (0.75 m²). Soil salinity, soil texture, frequency of tidal inundation, stand density and the canopy closure of the PSPs were also recorded. Soil salinity was determined from 1:2.5: soil: water suspension using electric conductivity meter and soil class texture by the USDA texture classification. Frequency of tidal inundation (days in a year) was assessed by continuous visual observations.

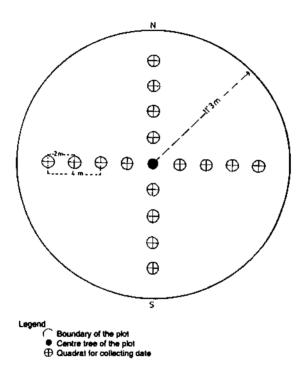


Figure 2. Sketch diagram of a permanent sample plot

Biotic influences were studied during 1990 and 1991 by laying out experimental plots, direct observations and indices (browsing of deer, girdling by crabs, cutting collars by rats, trampling or soil digging by wild boars). To ascertain the role of deer, the experiment was set in Randomised Complete Block Design (RCBD) in three salinity zones with different floristic composition (Figure 1). In each place, five plots each with an area of 25 m^2 ($5 \times 5 \text{m}$) were fenced with barbed wire to prevent access by deer. Five more unfenced plots of the same size, accessible to deer, were established 5 m apart from the fenced plots. Data on the availability and survival of new seedlings (age < 1 year) of H. tomes in the plots were recorded every two months up to 10 months following the appearance of seedlings. Similar data on

old seedlings (age>1 year, height<1.3m) were recorded up to 14 months. Mortality of seedlings due to browsing by deer was identifiable by careful observations of the dead or damaged seedlings. So, a comparison of the seedling survivals between fenced and unfenced plots would provide information on the damage caused by deer.

As regards wild boars, they were more active in the dark. So, the role of this animal was studied by the indices, e.g. earth digging, trampling, uprooting. To access the role of crabs, an experiment was set with H. fomes and six other species in Factorial Design in a less saline zone (Figure 1). Sixteen seedlings of H. fomes (one month old) were planted in cages with additional 16 seedlings outside each cage. The cage $(0.25 \text{ m}^2 \text{ surface area and 1 m tall})$ was covered with nylon mesh $(1 \times 1 \text{ cm})$ in all six sides to prevent entrance of the crabs. There were three replicate pairs. Final data on seedling survival were collected one year after initiation of the experiment. The activities of the monkeys on regeneration were directly observed. Rodents use incisors for cutting which can be distinguished clearly. So, their role was studied from the nature of the damage to the seedlings.

Results and discussion

A. Influences of abiotic factors on regeneration

Seedling recruitment status

The condition of seedlings was recorded in November after the monsoon. These three-month-old seedlings were regarded as seedling recruits. In addition to Heritiera fomes, recruits of 12 other species were found in the PSPs during the study period. Heritiera fomes alone constituted 24% of the total recruits.

A total of 962 new seedlings of H. fomes were recorded during ten years in the PSPs over an area of 144 m^2 ($0.75 \times 16 \times 12 \text{ m}$). The average number of seedlings appearing per year was 6680 ha⁻¹. Recruitment density varied considerably among the PSPs. At PSP No. 6, recruits were 28 165 seedlings ha⁻¹, whereas at PSP No. 7, no recruit was there. Chaffey et al. (1985) recorded an average of 11 630 seedlings ha⁻¹ (height < 1.3 m) of H. fomes for the entire Sundarbans.

Yearly variation in recruitments

A remarkable yearly variation in seedling recruitments of *H. fomes* was noticed. In 1982 and 1986, recruitment was much higher (Table 1, Figure 3). The reason was not clearly understood. Usually, there is a significant reduction in seed production following a very heavy seed year for different species (Hocker 1979). However, Hasan and Howlader (1970) claimed no periodicity in *H. fomes*. Siddiqi et al.(1991) reported probable existence of periodicity in fruit production of this species. Jimenez (1988) reported year to year variation in seedling density for *Rhizophora racemosa* in the mangroves of Costa Rica.

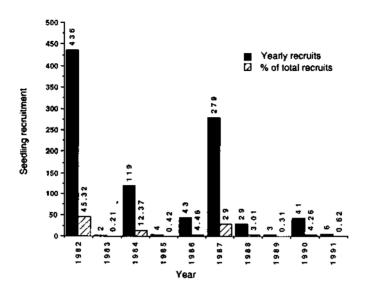


Figure 3. Yearly seedling recruitments (3 months) of Heritiera fomes

Table 1.	Characteristics of the permanent sample plots (PSPs) and seedling
	recruitments of Heritiera formes

PSP No.	Location compt/ zone	Mean soil salinity (mS cm ⁻¹)	texture	Inundation (days per year)	H. fomes trees (No.)	Total trees (No.)	Canopy closure (%)	H. fomes seedling (No.)	Survival up to 33 months (%)
1	26/LS*	2.85	Silty- clay-loan	105–120	102	168	90	164	19.38
2	15/MS	3.80	-do-	105-120	85	121	70	28	3.85
3	30/LS	2.85	-do-	90-105	42	145	60	80	0
4	3/LS	1.80	-do-	105-120	92	148	80	102	16.30
5	5/LS	1.80	-do-	105-120	106	168	70	109	12.48
6	1/1.\$	0.78	-do-	75-90	02	18	30	338	18.95
7	35/MS	3.50	Silty-clay	120-135	14	47	80	0	0
8	36/MS	4.00	-do- ´	120-135	04	165	70	17	ő
9	46/SS	3.85	-do-	135-150	23	29	30	-6	ŏ
10	20/MS	4.05	-do-	135-150	58	68	40	11	ő
11	38/SS	4.00	-do-	135-150	37	81	40	64	ŏ
12	41/SS	4.75	-do-	135-150	46	87	50	43	ő

LS: Less saline, MS: Moderately saline, SS: Strongly saline.

Tree density and recruitment

A non-significant relationship (r = 0.06) was obtained between the number of H. fomes trees in the PSPs and seedling recruitments (Table 1). The fruits of the species are non-viviparous and buoyant in nature. Possibly the seeds, after falling on the floor of the PSPs were washed away by tide water and either failed to

germinate or germinated elsewhere. Jimenez (1991) pointed out that in the mangroves of Costa Rica, propagule establishment seemed to be unrelated to the occurrence of the reproductive trees.

Salinity and recruitment

The number of newly appearing seedlings for ten years in different PSPs was plotted against soil salinity of the respective plots (Figure 4). Seedlings of *H. fomes* significantly decreased with increasing level of salinity (r = -0.815; p<0.01). This species prefers a level of lower salinity (Troup 1921, Saenger 1986). Salinity plays a vital role on the distribution of species in the Sundarbans (Choudhury 1968). *Heritiera fomes* predominates in the less saline areas of the forests.

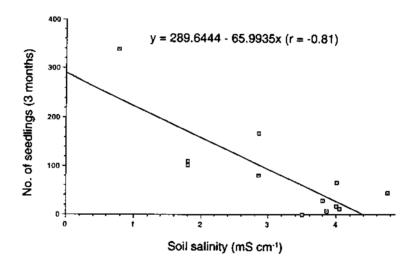


Figure 4. Relationship between salinity and seedling recruitment of Heritiera fomes

Salinity and seedling survival

Seedling survival was recorded for a period of 33 months following appearance. A large proportion of seedlings disappeared during this period. Only 16.53 and 1.92% seedlings of *H. homes* survived up to 33 months in less and moderately saline zones respectively with no survival in the strongly saline zone. Seedling half-life values (i.e. time required for 50% of seedlings to disappear) in less, moderate and strongly saline zones were 13.7, 8.8 and 6.3 months respectively (Figure 5). This shows greater preference of the species for lower salinity level. In the Indian Sundarbans, where salinity is higher, this species is not abundant (Karim 1988) and natural regeneration is unsatisfactory (Mukherjee 1975). With regard to growth, Latif *et al.* (1992) mentioned higher increment in diameter in less saline areas.

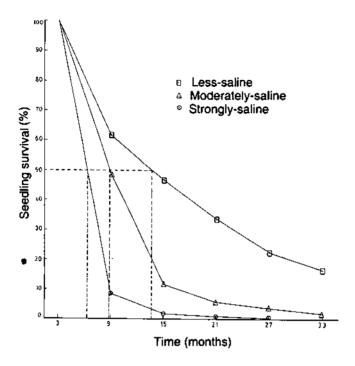


Figure 5. Depletion curves showing seedling half-life for *Heritiera fomes* in different salinity zones

Canopy closure and recruitment

Usually some plants are shade tolerant while others are light demanding. Thus recruitment and disappearance of seedlings are influenced by the canopy closure of the forests (Whitmore 1986, Kimmins 1987). No significant relationship was found between canopy closure and recruitment (r=0.14). The relationship was also insignificant at 33 months with respect to seedling survival (r=0.11). Heritiera fomes is shade tolerant in the early stage (Troup 1921, Dalmacio et al. 1991). It seems that factors other than canopy closure, e.g. tidal range, current, salinity, seed availability, etc., affect seedling recruitment.

Inundation and recruitment

The rate of inundation was higher in the western part of the Sundarbans. Maximum growth of *H. fomes* is noticed in areas where the forest floor remains dry for about 3-4 months a year. Seedling recruitment and survival were higher in PSPs where inundation rate was lower (Figure 6). No seedling of *H. fomes* survived up to 33 months from emergence where the PSPs got inundated for more than 120 days a year. However, PSP 3 (inundation 90-105 days a year) was subjected

to much wave action and that might be a reason for failure of *H. fomes* to survive. Mangrove seedling establishment is regulated by depth and frequency of tidal inundation (McMillan 1971, Chapman 1975, Kjerfve 1990, Siddiqi & Khan 1990, Jimenez 1991).

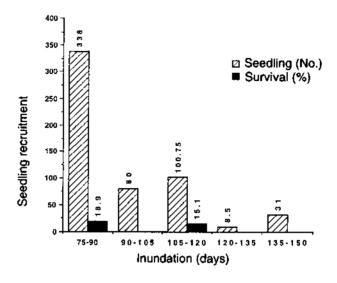


Figure 6. Seedling recruitment and survival up to 33 months for *Heritiera fomes* in relation to degree of inundation

B. Influences of biotic factors on regeneration

Role of deer

Data collected on seedling survival from the fenced and unfenced plots were analysed in RCBD with several observations per cell. Seed shedding continued up to September. So, for new seedlings the analysis was based on the data collected after September (Table 2). For old seedlings, analysis was made for the data collected from July (Table 3). The survival of seedlings showed non-significant difference between fenced and unfenced plots at compartment 24 for new ($F_{1,48}$ = 1.09) and old ($F_{1,64}$ = 0.96) seedlings. The difference was also insignificant for new ($F_{1,48}$ = 0.98) and old ($F_{1,64}$ = 0.38) seedlings at compartment 31. Only a few seedlings of H. fomes appeared at compartment 35 and were inadequate for analysis. Plots in compartments 24 and 31 were located in Excoecaria agallocha-Heritiera fomes and H. fomes-E. agallocha forest types respectively. The plot in compartment 35 was in Heritiera fomes-Xylocarpus mekongensis-Bruguiera sexangula forest type.

Hendrichs (1975) gave a rough estimate of population size of the spotted deer (Axis axis) as 80 000 individuals for the Bangladesh Sundarbans. Deer are considered to play a vital role in regulating regeneration density of the forests through their browsing habits (Champion et al. 1965, Choudhury 1968, Blasco 1977, FAO 1982,

Gomez et al. 1986). They cause substantial damage to the natural regeneration. Deer are reported to cause damage to mangrove seedlings in Myanmar (Troup 1921) and Malaysia (Chai & Lai 1984). In Bangladesh, deer were harmful to the regeneration of Avicennia officinalis, Sonneratia apetala, Xylocarpus mekongensis, Bruguiera sexangula and Aegiceras corniculatum (Siddiqi & Husain 1994), but they were not found to feed on the leaves of H. fomes. It is possible that deer influenced the dominance of H. fomes through their preferential browsing habits.

Table 2. Survival percentages of new seedlings (age <1 year) of Heritiera fomes in fenced (protected from deer) and unfenced plots

Location	Condition	Survival percentage overtime (months)							
		0	2	4	6	8	10		
Compt.24	Fenced	100	85.00	35.0	26.7	23.3	20.0		
	Unfenced	100	80.65	41,9	22.6	19.4	19.4		
Compt. 31	Fenced	100	89.2	71.6	71.2	62.2	57.2		
comput-	Unfenced	100	83.6	64.1	57.8	53.9	46.1		

Table 3. Survival percentages of old seedlings (age >1 year) of *Heritiera fomes* in fenced (protected from deer) and unfenced plots

Location	Condition			Survival	percentage :	overtime (m	onths)		
		0	2	4	6	8	10	12	14
Compt.24	Fenced	100	99.4	98.8	98.4	96.7	96.1	95.6	95.1
	Unfenced	100	99.9	99.5	99.1	98.2	98.0	97.0	96.7
Compt. 31	Fenced	100	100	99.5	96.5	96.9	96.7	96.5	96.1
•	Unfenced	100	99.8	99.8	99.8	96.7	96.2	95.8	95.2
Compt. 35	Fenced	100	81.8	81.8	81.8	81.8	91.8	81.8	72.7
•	Unfenced	100	83.3	83.3	83.3	83.3	83.3	83.3	50.3

Role of crabs

Seedling mortality of all the seven species including H. fomes planted inside cages or in the open was low. In all, 48 (3x16) seedlings of H. fomes were planted within the cages and another 48 (3x16) in the open. A total of 42 seedlings in the cages and 46 in the open survived when data were collected after one year. Average seedling survival was 87.5% inside cages and 95.8% in the open (control). The impact of crabs was insignificant (t = 0.85 with p = 0.05 & d.f. = 4) on regeneration of H. fomes.

The crabs belonging to the family Grapsidae were reported to cause severe damage to mangrove regeneration in many countries of the world (Siddiqi 1995, 1996). Hendrichs (1975) reported occurrence of six species of grapsid crabs in less saline areas of the Sundarbans. He estimated population density of crabs as

50 animals m⁻² at the water edge along the high water line and the density was lower away from the water. Further studies covering all the representative areas of the Sundarbans are necessary to ascertain the role of crabs on regeneration.

Role of monkeys

The rhesus macaque (Macaca mulatta) is an arboreal animal. However, in the afternoons the animals are found to play in groups on the banks of rivers and canals in the Sundarbans. They were not found to eat the leaves or damage the seedlings of H. fomes. In raised experimental plantations of mangroves, damage attributable to monkeys did not occur. Monkeys are reported to cause damage to mangrove seedlings in Malaysia (Salleh & Chan 1987) and Thailand (Aksornkoae 1987). In the Bangladesh Sundarbans, the population size of the rhesus macaque is 40 000 (Hendrichs 1975) while Gittins and Akonda (1982) estimated it to be 126 000 individuals. The diet of the monkeys consists of plant materials (S. apetala leaves, young Nypa fruticans, grasses), crabs and fishes (Sanyal 1983, Salter 1984). From visual observations, the monkeys were not found to affect the regeneration of H. fomes in the Sundarbans.

Role of wild boars

Unlike deer, the wild boar (Sus scrofa) can potentially damage the plants via their roots, even uprooting them. In the Sundarbans, the population size of wild boar is 20 000 individuals (Hendrich 1975). Foraging damage to H. fomes seedlings by wild boars was not noticed in the forests. Trampling of these animals might affect some seedlings. But they do not have any substantial role on seedling mortality.

Choudhury (1968) mentioned that in the Sundarbans wild boars used to uproot the seeds and seedlings but the extent of damage was not high. The animals feed on roots, stems, seeds, crustaceans, molluscs, marine turtle eggs, dead fish and other animals (Sanyal 1983). As the food habit of the animals is diverse, they were not found to deliberately harm the seedlings.

Role of rodents

In compartment 24, six-month-old seedlings of *H. fomes* were found to be attacked by rodents as apparent from the nature of injury to the collars. When estimated in a plot, it appeared that 41% of the newly recruited seedlings were destroyed by the black rat (*Rattus rattus*). Out of 76 seedlings appearing in the plot, 37 seedlings were killed when six months old. Identification of the animals was made following trapping. No seedlings of the previous years were damaged by the rats. Damage to *H. fomes* seedlings was also noticed at compartment 1. Rat attack was not detected in other parts of the forests. Damage was confined to a few places with lower salinity and higher ground elevation. The *R. rattus* in Australia occupied many habitats including mangroves. This species cannot survive on full strength sea water, and consequently must depend on water in its food or perhaps

temporary fresh water during rains (Dunson & Lazell 1982). Higher level of salinity in other parts of the Sundarbans might limit the activities of rats.

Conclusion

Of variously available species, *Heritiera fomes* alone constitutes 24% of the seedling recruits in the Sundarbans. Recruitment density varied considerably among different parts of the forests. Rate of seedling establishment was low.

Level of salinity and tidal inundation influenced the regeneration of *H. fomes*. Higher recruitment and survival of seedlings were noticed with lower level of salinity and inundation. As regards biotic factors, the spotted deer (Axis axis) did not adversely affect regeneration; rather they might help dominance of *H. fomes* through their preferential browsing habit. The role of wild boar (Sus scrofa), rhesus macaque (Macaca mulatta) and crabs on regeneration was insignificant. The black rat (Rattus rattus) caused damage to new seedlings but only in restricted areas.

Heritiera fomes is the dominant species of the mangroves of Bangladesh. It has a great economic importance because of its multiple uses. Decline in stocking of the species has been reported. Therefore, further studies on various factors that affect the survival and establishment of the seedlings of H. fomes need to be undertaken. This could help develop methods to ensure adequate natural regeneration and improve the stocking of the species.

Acknowledgements

I am grateful to M. Shahidullah, Research Officer, M. A. H. Shahjalal, Field Investigator, M. M. Rahman, Deputy Ranger, and other staff members of the Mangrove Silviculture Division, Bangladesh Forest Research Institute (BFRI) for their help in the lay-out of experiments, maintenance of the plots, and collection and compilation of data. I also thank M. Shahadat Hossain, of the Minor Forest Products Division, BFRI, for typing the manuscript.

References

- AKSORNKOAE, S. 1987. Country report: Thailand. Pp. 231–261 in Mangroves of Asia and the Pacific. Status and Management. UNDP/UNESCO (RAS/79/002). Philippines.
- Blasco, F. 1977. Outline of ecology, botany and forestry of the mangals of the Indian subcontinent. Pp. 241-260 in Chapman, V.J. (Ed.) Wet Coastal Ecosystems. Elselvier, Amsterdam.
- CHAFFEY, D. R., MILLER, F. R. & SANDOM, J. M. H. 1985. A Forest Inventory of the Sundarbans, Bangladesh. Main Report. Overseas Development Administration, England. 196 pp.
- CHAFFEY, D. R. & SANDOM, J. H. 1985. Sundarbans Forest Inventory Project, Bangladesh. A Glossary of Vernacular Plant Names and a Field Key to the Trees. Overseas Development Administration, England. 23 pp.
- CHAI, P. P. K. & LAI, K. K. 1984. Management and utilization of mangrove forests in Sarawak. Pp. 785-795 in Proceedings of Asian Symposium on Mangrove Environment Research & Symposium Mangrove Management.
- Champion, H. G., Seth, S. K. & Khattak, G. M. 1965. Manual of Silviculture for Pakistan. Pakistan Forest Institute, Peshawar. 543 pp.

- CHAPMAN, V. J. 1975. Mangrove biogeography. Pp. 3-22 in Walsh, G. E., Snedaker, S. C. & Teas, H. J. (Eds.) Proceedings of the International Symposium on Biology and Management of Mangroves. Vol. 1. University of Florida, Gainesville.
- CHOUDHURY, A. M. 1968. Working Plan of the Sundarbans Forest Division for the Period for 1960-61 to 1979-80. East Pakistan Government Press, Dacca. 82 pp.
- Dalmacio, M. V., Rahman, Z. & Ahmad, I. U. 1991. Coastal Afforestation Management Manual. (Draft paper). Bangladesh Forest Department. 95 pp.
- Das, S. & Siddigi, N. A. 1985. The Mangroves and Mangrove Forests of Bangladesh. Mangrove Silviculture Division Bulletin No. 2. Bangladesh Forest Research Institute. 142 pp.
- DUNSON, W. A. & LAZELL, JR., J. D. 1982. Urinary concentrating capacity of Rattus rattus and other mammals from the lower Florida Keys. Comparative Biochemistry and Physiology 71 A:17-21.
- FAO. 1982. Management and Utilization of Mangroves in Asia and the Pacific. FAO Environment Paper 3. FAO, Rome. 160 pp.
- FORESTAL. 1960. Forest Inventory 1958-59, Sundarbans Forests. Forestal International Incorporated, Oregon, Canada.
- GITTINS, S. P. & AKONDA, A. W. 1982. What survives in Bangladesh? Oryx 16(3): 276-81.
- GOMEZ, E. D., BINOHLAN, C. D. & CHAVEZ, V. B. 1986. National stressors in a mangrove ecosystem. Biotrop. Indonesia:15-22.
- HASAN, S. M. & HOWLADER, N. I. 1970. Coastal afforestation in Noakhali district. Forest Dale News 2(3):41-49.
- HASSAN, M. M., MAZUMDER, A. H., NURUL ISLAM, A. T. M. & EMDAD HOSSAIN, A.T. M. 1990. Soil hydrology and salinity of the Sundarbans in relation to top dying, regeneration and survival of sundri (Heritiera fomes) trees. Pp. 1-11 in Proceedings of the Seminar on Top Dying of Sundri (Heritiera fomes) Trees, 1988, BARC, Dhaka.
- HENDRICHS, H. 1975. The status of the tiger *Panthera tigris* (Linne, 1758) in the Sundarbans mangrove forest (Bay of Bengal). *Saugetierkundliche Mitteilungen* 23:161-199.
- HOCKER, H. W.1979. Introduction to Forest Biology. John Wiley and Sons, USA. 467 pp.
- IMAM, S. A. 1982. The Sundarbans and its future. Pp. 19-24 in Proceedings of the Second Bangladesh National Conference on Forestry. January 21-26, 1982, Dhaka.
- JIMENEZ, J. A. 1988. The dynamics of *Rhizophora racemosa* Meyer forests on the Pacific Coast of Costa Rica, *Brenesia*:1-12.
- JIMENEZ, J. A. 1991. Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries* 14(1):49–56.
- KARIM, A. 1988. Environmental Factors and the Distribution of Mangroves in Sundarbans with Special Reference to *Heritiera fomes* Buch. Ham. Ph.D. thesis, University of Calcutta. 222 pp.
- KHAN, M. S. 1978. Flora of Bangladesh No. 7. Family Rhizophoraceae. Bangladesh National Herbarium, Dhaka. 19 pp.
- KHATTAK, G. M. 1979. History of forest management in Bangladesh. Pakistan Journal of Forestry 29(3):121-128.
- KHATUN, B. M. & ALAM, M. K. 1987. Taxonomic studies in the genera Avicennia Linn. from Bangladesh. Bangladesh Journal of Botany 16(1):39-44.
- KIMMINS, J. P. 1987. Forest Ecology. Macmillan Publishing Company, New York. 531 pp.
- KJERFVE, B. 1990. Manual for Investigation of Hydrological Processes in Mangrove Ecosystems. UNESCO/ UNDP Regional Project RAS/79/002 and RAS/86/120. 79 pp.
- Kostermans, A. J. G. J. 1959. A monograph of the genus *Heritiera* Aiton (Sterenl.). *Reinwardtia* 4(4): 465-583.
- LATIF, M. A., RAHMAN, M. F., DAS, S. & SIDDIQI, N. A. 1992. Diameter increments for six mangrove tree species in the Sundarbans forest of Bangladesh. *Bangladesh Journal of Forest Science* 21:7–12.
- McMillan, C. 1971. Environmental factors affecting seedling establishment of the black mangrove on the Central Texas Coast. *Ecology* 52(5):927-930.
- MUKHERJEE, A. K. 1975. The Sundarbans of India and its biota. *Journal of Bombay Natural History Society* 72(1):1-20.
- RAHMAN, M. A. 1990. A comprehensive report on sundri (Heritiera fomes) trees with particular reference to top dying in the Sundarbans. Pp. 12-63 in Proceedings of the Seminar on Top Dying of Sundri (Heritiera fomes) Trees. 1988, BARC, Dhaka.

- Saenger, P. 1986. Bangladesh Mangrove Afforestation Project. Report prepared for the Government of Bangladesh. Shedden Pacific Pty. Limited, Melbourne, Australia. 63 pp.
- SALTER, R. E. 1984. Integrated Development of the Sundarbans Bangladesh (Status and Utilization of Wildlife).

 Report prepared for the Government of Bangladesh. FAO, Rome. 59 pp.
- Salleh, M. N. & Chan, H. T. 1987. Sustained yield forest management of the Matang mangrove. Pp. 319-324 in *Mangroves of Asia and the Pacific Status and Management*. UNDP/UNESCO (RAS/79/002). Philippines.
- Sanyal, P. 1983. Mangrove tiger land, the Sundarbans of India. Tiger Paper 10(3):1-4.
- Siddle, N. A. 1995. Role of crabs on the natural regeneration of mangroves in the Sundarbans forest of Bangladesh. Australian Journal of Ecology 20:340–343.
- Siddle, N. A. 1996. A review on the impact of animals on regeneration in the mangroves with particular reference to Bangladesh. *Tiger Paper* 23(1):3–10.
- Siddle, N. A. & Husain, K. Z. 1994. The impact of deer on the natural regeneration in the Sundarbans mangrove forest. *Bangladesh Journal of Zoology* 22(2): 223-234.
- SIDDIQI, N. A. & KHAN, M. A. S. 1990. Growth performance of mangrove trees along the coastal belt of Bangladesh. *Mangrove Ecosystems Occasional Papers*, UNDP/UNESCO Regional Mangroves Project. Thomson Press No. 8:5-14.
- SIDDIQI, N. A., SHAHIDULLAH, M. & SHAHJALAL, M. A. H. 1991. Studies on the size, viability and germination of seeds of sundri (*Heritiera fomes* Buch.-Ham.). *Indian Journal of Forestry* 14(2):119–124.
- TROUP, R. S. 1921. The Silviculture of Indian Trees. Clarendon Press, Oxford. Volume 1. 336 pp.
- WHITMORE, T. C. 1986. Tropical Rain Forests of the Far East. English Language Book Society/Oxford University Press. 352 pp.

STAND STRUCTURE AND FLORISTIC COMPOSITION OF A PRIMARY LOWLAND DIPTEROCARP FOREST IN EAST KALIMANTAN

Plinio Sist

CIRAD-Forêt/CIFOR (Center for International Forestry Research), P.O. Box 65, 96 JKPWB, Jakarta 10065

&c

Amiril Saridan

BPKS: Balai Penelitian Kehutanan Samarinda, Ministry of Forestry, Jalan Pandan Wangi Sempaja, Samarinda, Kalimantan Timur, Indonesia

Received March 1997

SIST, P. & SARIDAN, A. 1999. Stand structure and floristic composition of a primary lowland dipterocarp forest in East Kalimantan. This paper presents the structure and species composition of the primary lowland dipterocarp forest in Berau, East Kalimantan, Indonesia. This study was based on three undisturbed forest plots. 4 ha each, totalling 12 ha, where 93% of the trees (dbh \geq 10 cm) were identified at the taxa level. The density, basal area and standing volume were on average and respectively 521 trees ha⁻¹, 31 m² ha⁻¹ and 383 m³ ha⁻¹. The dipterocarps represented about 25% of the tree population, 50% of the basal area and 60% of the standing volume. In primary forest 538 different taxa were recognised representing a mean of 182 tree species per ha. The families Dipterocarpaceae and Euphorbiaceae were the main important taxa in both density and number of species (61 species each). The structure of the forest of Berau is very similar to that of Sabah or other parts of Northern Borneo. However, the main characteristic of this forest is its remarkable richness in dipterocarps, in comparison with the northern parts of Borneo, which exhibits in mean 29 species had and 61 species for the 12 ha surveyed. The forests of Sabah are mainly dominated by light-demanding dipterocarp species such as Parashorea spp. and Dryobalanops spp. This could result from important canopy disturbances caused by climatic events like long period of drought or cyclone. The high species richness of the Berau forest may be linked to a longer stability and a relative constancy of the climate in the region. The hypothesis of a possible impact of drought events on the forest dynamics and consequently on species distribution and richness in Borneo is discussed. However, it is stressed that the lack of data for Kalimantan is undoubtedly an handicap for the analysis of phytogeographical variations within the region. In the study area, the first record for Indonesia of the two dipterocarps species Shorea leptoderma Meijer and Shorea symingtonii Wood demonstrates that our knowledge of the flora of Kalimantan is still to be improved.

Key words: East Kalimantan - Borneo - primary lowland dipterocarp forest -structure - species richness

^{*}Present address: CIRAD-Forêt, Campus International de Baillarguet BP 5035, 34032 Montpellier Cedex 1, France. E-mail: sist@cirad.fr

SIST, P. & SARIDAN, A. 1999. Struktur dirian dan komposisi flora hutan dipterokarpa tanah pamah primer di Berau, Kalimantan Timur, Artikel ini membentangkan mengenai struktur dan komposisi spesies hutan dipterokarpa tanah pamah primer di Berau, Kalimantan Timur, Indonesia. Kajian ini didasarkan kepada tiga petak hutan tidak rosak, setiap satu seluas 4 ha, berjumlah 12 ha iaitu 93% daripada pokok tersebut (dbh > 10 cm) dikenal pasti pada peringkat taksa. Kepadatan, luas pangkal dan isipadu dirian ialah pada kadar purata dan masing-masing ialah 521 pokok sehektar, 31 pokok sehektar, dan 383 m⁵ ha¹. Dipterokarpa mewakili kira-kira 25% daripada populasi pokok, 50% daripada luas kawasan dan 60% daripada isipadu dirian. Di dalam hutan primer, 538 taksa yang berbeza dikenali mewakili sebanyak 182 spesies pokok sehektar. Famili Dipterocarpaceae dan Euphorbiaceae merupakan taksa yang penting dalam kedua-dua kepadatan dan bilangan spesies (61 spesies setiap satu). Struktur hutan di Berau sama dengan struktur hutan di Sabah atau bahagian-bahagian lain di Borneo Utara. Bagaimanapun, ciri utama hutan ini jalah kekayaan dipterokarpanya, berbanding dengan bahagian utara Borneo, yang mempamerkan secara purata 29 spesies sehektar dan 61 spesies bagi 12 hektar yang disurvei. Hutan di Sabah kebanyakannya didominasi oleh spesies dipterokarpa yang memerlukan banyak cahaya seperti Parashorea spp. dan Dryobalanopsspp. Ini mungkin terjadi akibat gangguan sudur yang penting akibat gangguan cuaca seperti tempoh kemarau atau taufan yang lama. Kekayaan spesies di hutan Berau mungkin ada kaitannya dengan kestabilannya dan ketetapan cuaca secara relatif di kawasan tersebut. Hipotesis mengenai kemungkinan kesan kemarau terhadap dinamik hutan dan seterusnya terhadap taburan dan kekayaan spesies di Borneo juga turut dibincangkan. Bagaimanapun, ditekankan bahawa kekurangan data bagi Kalimantan tidak syak lagi merupakan satu hambatan untuk menganalisis kepelbagaian fitogeografi di kawasan tersebut. Di kawasan yang dikaji, catatan pertama bagi Indonesia untuk dua spesies dipterokarpa iaitu Shorea leptoderma dan Shorea symingtonii menunjukkan bahawa pengetahuan kita mengenai flora di Kalimantan masih perlu ditingkatkan.

Introduction

Borneo is widely acknowledged as one of the most important centres of plant diversity in the world as well as the centre of distribution and species diversity for a large number of families and genera (Van Steenis 1950, Whitmore 1984, Soepadmo 1995). Within the Malesian archipelago, the greatest number of dipterocarp species has been recorded in Borneo which includes 267 species with 59% of endemicity (Ashton 1982). In comparison, species number and endemicity are respectively in Malaysia 156 and 19%, in Sumatra 96 and 12%, in the Philippines 45 and 47%. Although New Guinea shows the highest endemicity for dipterocarps (73%), and generally speaking for the other taxa, it is also the poorest island with only 15 species (Ashton 1982). In the western block of the Malesian archipelago, the lowland evergreen tropical rain forest is called lowland dipterocarp forest because of the dominance in the canopy and the emergent stratum of the family of the Dipterocarpaceae. This forest shows the greatest number of species of any rain forest ecosystem in Malesia (Whitmore 1984, Philips et al. 1994). The dipterocarp forests of Borneo are also one of the most productive in the tropics since harvesting rates range from 80 to 100 m³ ha⁻¹ whereas in other parts of the tropics they do not exceed 30 to 50 m³ ha⁻¹ (Schmidt 1991, Bertault & Sist 1997, Sist et al. 1998).

The ecology of dipterocarp forests has been widely studied particularly in Peninsular Malaysia and in the northern parts of Borneo (most important references: Symington 1943, Wyatt-Smith 1966, Poore 1968, Kochummen et al. 1991, Appanah & Weinland 1993 for Peninsular Malaysia; Burgess 1961, Ashton 1964, Bruenig 1973, Proctor et al. 1983, Baillie et al. 1987, Ashton & Hall 1992, Newberry et al. 1992, Davies & Becker 1996 for Sabah, Sarawak and Brunei). Several studies have demonstrated that floristic variation within tropical rain forest is linked to the complex interaction of both physical (climate variation, cyclone, edaphic conditions, topography) and biological factors (forest dynamics, species growth requirements during development) (Ashton 1969, 1989, Raich & Khoon 1980, Bruenig 1970, Gentry 1989, Hartshorn 1989, Philips & Gentry 1994). For the Indonesian part of the Island (Kalimantan), studies on the ecology of mixed dipterocarp forest are relatively new (Kartawinata et al. 1981, Riswan 1987, Suselo & Riswan 1987, Soedjito & Kartawinata 1995). Although a species check list of all the families with at least one timber size species has been published for Indonesia (Whitmore et al. 1990), the tree flora of Indonesia is still at a preliminary stage.

This study was carried out in the framework of STREK (Silvicultural Techniques for the Regeneration of Logged-over Forests in East Kalimantan) project which aimed to maintain sustained productivity of the forests of East Kalimantan by the experimentation of logging improvement techniques (Reduced-Impact Logging or RIL) in primary forest and silvicultural treatments in logged-over forests (Bertault & Sist 1995, 1997, Sist et al. 1998). Because sound forest management cannot possibly be applied without an understanding of the basic ecology of the forest, research on forest structure and species composition was an important component of the project. This paper presents the main results of the project regarding the structure and species composition of three 4-ha plots in a primary undisturbed lowland dipterocarp forest in East Kalimantan.

Materials and methods

Study area

The study area was located in East Kalimantan (Indonesia) in the district of Berau (2°N, 117° 15'E), in a 500 000 ha of forest concession (Figure 1). The concessionaire, PT INHUTANI I, a state-owned company, has been harvesting timber in this area for the past fifteen years. The climate is equatorial with a mean annual rainfall of 1870 mm (SD = 240 mm, records for Tanjung Redeb, 1984-1994) and a mean annual temperature of about 25 °C. August and September are usually the driest months while January is the wettest one (Figure 2). The bedrock is primary alluvial deposits (mudstones, siltstones, sandstone and gravel) dating from Miocene and Pliocene. The topography is gently undulating with elevations above sea-level below 500 m.

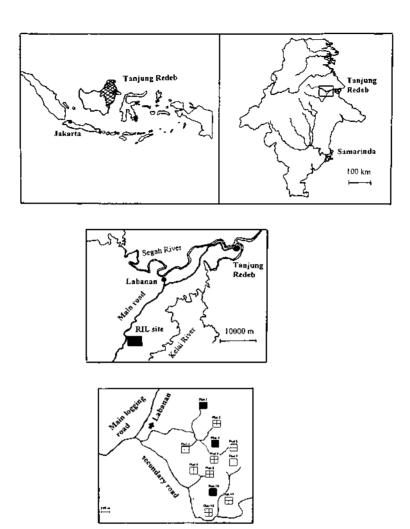


Figure 1. Map of Indonesia, East Kalimantan and location of the experimental plot network in the study area

Methods

A 5% inventory within the 1000-ha zone scheduled for logging provided the data base for sample plot selection. Twelve 4-ha plots $(200 \times 200 \text{ m})$, each divided into four 1-ha subplots, were set up in 1989. From November 1991 to March 1992, logging operations were carried out in nine plots following conventional and RIL techniques (Bertault & Sist 1995, 1997, Sist et al. in press) whereas three plots (1, 4, 10) remained undisturbed as control plots. In each control plot, slopes were measured every 10 m, along 20 tracks, 200 m long with a south-north direction. These data were then processed with Surfer software for the map drawing and used

as base maps for soil survey. In each control plot 25 augerings, displayed every 50 m, up to 110 cm depth, were collected and the following soil characteristics described: geomorphology, slope classification, soil drainage, soil type, parent material and texture. On the basis of information provided by the augerings, representative sites were selected for the detailed description of soil profiles in pits with a 150 cm depth.

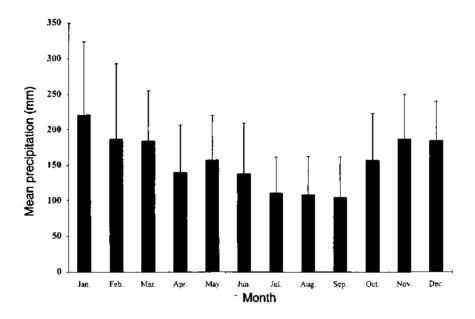


Figure 2. Mean annual rainfall (+SD) in Tanjung Redeb for the period 1984-1994

Before logging commenced, all trees with dbh ≥ 10 cm were measured (girth at 1.30 m or 20 cm above buttresses), numbered and marked. Plant collections were made and herbarium samples identified in Bogor (Herbarium Bogoriense). Because of time constraint in the logging operation schedule, tree identification at the species level could not be achieved before logging. However, this was completed in the three undisturbed plots in 1994.

Jaccard's coefficient was used to compare the floristic similarity of the three control plots. This coefficient was: J = c/(a+b-c) where c is the number of common species between a pair of plots, a and b the total number of species in each plot (Dajoz 1982).

Results

Soil characteristics

The analysis of the 75 augerings in the three undisturbed forest plots gave the following records (SSS classification, 1987): Ultisols (93%), Entisols (7%). Ultisols comprised Paleudults and Hapludults which are deep with an illuvial B horizon of low base saturation (BS<35%). These two types of soil differ mainly from each other in the deeper illuvial horizon of Paleudults. Paleudults and Hapludults were recorded in roughly similar proportions, 41% and 52% respectively. Paleudults and Hapludults are classically divided in Typic (well to moderately drained) or Aquic (bad or impeded drainage). Most of the Paleudults (74%) were well drained (typic) whereas Hapludults showed in general a bad drainage pattern (79%). Entisols were described as Lithic Troporthents mainly characterised by their shallow development (less than 40 cm deep), a good drainage pattern and a loamy to sandy loamy texture.

Plots 1 and 4 were very similar in both soil type, drainage and topography (Table 1). They were mainly located on a plateau with Typic Paleudult and Typic Hapludult suggesting therefore good drainage conditions. In contrast, plot 10 showed a much steeper relief and lay on poor drained Ultisols (Table 1).

Table 1.	Soil characteristics in plots 1, 4 and 10 (results of the 75 augerings
	collected in the three plots, 25 augerings in each)

	Ultisols		ols		Entisols	Drainage	
	TP	AP	TH	AH	LT	1-2	3-
Plot I	14	5	4	2	0	7	18
Plot 4	8	2	4	6	5	16	9
Plot 10	1	1	0	23	0	23	;
Total	23	8	8	31	5	46	29
%	30	11	11	41	7	61	38

TP: Typic Paleudults, AP: Aquic Paleudults, TH, AH: Typic and Aquic Hapfudults, LT: Lithic Troporthents. Drainage: 1-2: Poorly to imperfectly drained, 3-4: Moderately well to well drained.

Forest structure and tree family

In primary forest, tree density, basal area and standing volume were on average and respectively, 521 trees ha⁻¹, 31 m² ha⁻¹ and 383 m³ ha⁻¹ (Table 2). The family of Dipterocarpaceae was the dominant taxon gathering about 25% of the total tree density (126 stems ha⁻¹ in mean), 50% of the total basal area (15 m² ha⁻¹) and 61% of the stand volume (234.5 m³ ha⁻¹, Table 2).

Table 2. Mean density (MD), mean basal area (MBA), and mean stand volume (MSV) of all trees and dipterocarps only according to the dbh classes in the three control plots (12 ha) of primary forest

	10–20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90–100	>100 cm	Total
All trees											
Mean density (No. had)	329.1	93.6	45.3	20.9	12.0	8.6	4.2	3.1	1.5	3.1	521.5
SD	41.8	11.8	7.3	5.1	4.2	3.5	2.6	1.7	1.3	1.9	53.1
Mean basal area (m² ha-i)	5.0	4.4	4.3	3.3	2.8	2.8	1.8	1.7	1.1	4.0	30.6
SD	0.6	0.6	0.7	0.8	1.0	1.2	1.1	0.9	1.0	2.2	3.1
								2	> 90 cm		Total
Mean standing volume	37.8	43.7	49.4	40.8	36.5	42.8	28.2	26.2	77.4		382.9
SD	4.4	6.3	10.1	10.2	16.8	17.7	17.5	11.7	39.7		60.7
Dipterocarps											
Mean density	60.3	21.9	13.4	7.4	7.1	6.2	2.6	2.6	1.4	3.0	125.8
SD	12.4	5.3	6.9	3.9	3.8	2.7	2.6	1.6	1.4	1.9	25.1
Mean basal area	0.9	1.0	1.3	1.2	1.6	2.0	1.1	1.4	1.0	3.2	14.9
SD	0.21	0.2	0.6	0.6	0.9	0.9	1.1	0.9	1.0	2.5	3.3
									> 90 cm		Total
Mean standing volume	10.1	11.8	16.2	18.4	27.4	32.8	23.9	28.0	74.0		234.4
SD	2.3	3.6	8.2	9.9	14.0	14.0	19.6	29.9	44.4		53.8

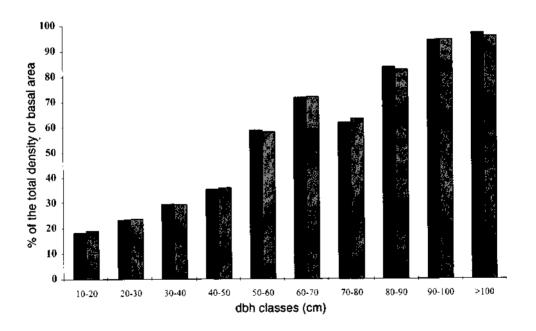


Figure 3. Proportions of dipterocarps in basal area and density in each diameter class (solid bars: % of the total basal area; hatched bars: % of the total tree density, area surveyed: 12 ha, 3 undisturbed forest plots)

Table 3. Cumulated density of each family in the three control plots according to the dbh classes

					DE	H classes	(cm)				
	10–19	20-29	30-39	40-49	50-59	60-69	>70	Total	N sp	% dens.	% BA
Dipterocarpaceae	727	263	160	86	89	72	113	1510	61	24.14	48.75
Euphorbiaceae	551	164	83	38	7	1	1	845	61	13.51	9.02
Sapotaceae	312	58	16	4	4	3	1	398	20	6.36	3.14
Myristicaceae	287	58	7	3	0	0	0	355	19	5.68	2.22
Burseraceae	235	46	11	11	3	1	2	309	21	4.94	2.80
Муткасеве	140	77	32	11	3	2	2	267	22	4.27	3.50
Ebenaceae	165	55	21	5	1	ī	O	248	17	3.96	2.28
Leguminosae	131	33	31	15	12	4	8	234	26	3.74	4.60
Anacardiaceae	142	36	21	11	4	0	2	216	26	3.45	2.56
Lauraceae	104	83	26	18	4	3	ï	189	23	3.02	2.96
Annonaceae	144	19	4	1	0	0	0	168	18	2.69	0.98
Rubiaceae	121	31	9	ī	ō	i	ŏ	163	20	2.61	1.26
Guttiferae	86	27	9	5	2	ò	ō	129	20	2.06	1.25
Jnknown	94	29	12	5	6	3	4	158	5	2.45	2.16
doraceae	68	18	15	5	ì	i	ó	108	12	1.73	1.26
terculiaceae	44	14	14	9	2	3	ĭ	87	7	1.73	1.68
'olygalaceae	59	8	4	3	ō	Õ	i	75	14	1.20	0.68
agaceae	32	17	14	3	ì	ŏ	ō	67	20	1.07	0.92
Aeliaceae	42	ii	6	1	ś	ő	ì	64	16	1.02	0.92
erbenaceae	37	17	š	ô	ő	Õ	2	64	6	1.02	0.92
apindaceae	28	15	4	ž	Õ	ő	ō	49	11	0.78	_
delastomataceae	41	2	i	Ô	0	ő	0	44	8	0.70	0.47 0.20
ecythidaceae	31	13	ò	Ö	ő	0	0	44	4		
laeocarpaceae	31	6	5	ŏ	o	0	0	42	12	0.70 0.67	0.31
Thymelaeaceae	27	5	4	ŏ	ĭ	a	0	37	9		0.32
hrysobalanaceae	24	8	2	3	o	0	0		9	0.59	0.41
iliaceae	21	6	3	0	5	ì	0	37	_	0.59	0.36
lacourtiaceae	23	9	2	0	0	0	_	36 20	4	0.58	0.67
iacouroaceae iombacaceae	18	8	ó	3	0	-	1	29	6	0.46	0.30
Pilleniacaceae	25	2	ì	0	_	0	0	29	5	0.46	0.29
nuemaceae Cacinaeae	25 21	7	0	-	0	0	0	28	2	0.45	0.18
	20	4	0	0	0	0	0	28	4	0.45	0.16
Jimaceae			-	0	0	0	0	24	3	0.38	0.24
elastraceae	16	9	4	1	0	0	0	24	6	0.38	0.12
oganiaceae	18	4	0	0	0	0	0	22	2	0.35	0.57
Dleaceae	14	5	2	0	1	0	0	22	2	0.35	0.12
pocynaceae	8	5	3	3	0	3	0	22	2	0.35	0.21
lyrsinaceae	18	1	0	0	0	0	0	19	1	0.30	0.10
hamnaceae	15	2	0	0	0	0	0	17	3	0.27	0.07
heaceae	8	5	0	0	0	1	0	14	4	0.22	0.22
Chnaceae	6	6	0	0	0	0	0	12	1	0.19	0.11
ymplocaceae	6	2	1	0	0	0	0	9	1	0.14	0.08
lagnoliaceae	6	0	0	0	0	0	0	6	1	0.10	0.02
raucariaceae	2	0	0	0	0	2	1	5	1	0.08	0.61
imaroubaceae	2	1	1	0	0	0	0	4	1	0.06	0.07
lacaceae	0	0	2	0	0	0	0	2	1	0.03	0.05
'etrameristaceae	0	0	1	0	0	0	0	1	1	0.02	0.02
otal	3950	1127	539	247	149	102	141	6255	538	100	100

Nsp: Cumulated total number of species in the family, % dens.: % of the family in the tree population. % BA: % of the family's basal area of the total basal area.

The distribution of the basal area according to diameter classes clearly indicated that dipterocarps mainly dominated the upper dbh classes and were therefore canopy and emergent trees (Table 3, Figure 3). In the three undisturbed forest plots, 70% of the trees with dbh (50 cm belonged to the Dipterocarpaceae family and to the following genera: Anisoptera, Cotylelobium, Dipterocarpus, Dryobalanops, Parashorea and Shorea. The other two genera of dipterocarps, Vatica and Hopea,

rarely exceeded 50 cm in diameter and were found mainly in the understorey and subcanopy layers. The Euphorbiaceae was the second most abundant family comprising 13.5% of the total tree density and 9% of the basal area (Table 3). This taxon comprised mainly understorey and medium-sized trees which did not generally exceed 50 cm in diameter (Table 3). The few species reaching a dbh greater than 50 cm that have been recorded in the control plots were *Chaetocarpus castanocarpus*, *Drypetes kikir* and *Elateriospermum tapos*. The number of taxa recorded in the second richest families, namely Anacardiaceae and Leguminosae, dropped to only 26.

Fourteen families (Dipterocarpaceae, Euphorbiaceae, Sapotaceae, Myristicaceae, Burseraceae, Myrtaceae, Ebenaceae, Leguminosae, Anacardiaceae, Lauraceae, Annonaceae, Rubiaceae, Guttiferae, Moraceae) comprised 82% of the total tree density and 68% (i.e. 366) of the taxa recorded in the three control plots (Table 3).

The distribution of the families according to the dbh classes allowed distinguishing four main groups of trees: 1) canopy and emergent trees, 2) mediumsized trees (subcanopy to canopy trees), 3) small trees of the understorey, 4) pioneer species. The first group is mainly dominated by dipterocarps with, however, some Leguminosae such as Koompassia excelsa, K. malaccensis and Sindora spp. Some Sterculiaceae (Heritiera simplicifolia, Scaphium macropodum) and Tiliaceae like Pentace adnophora can be also found in the canopy layer. The second includes medium-sized trees which did not generally exceed 70 cm in diameter. In primary forest, this group comprised mainly the following families: Anacardiaceae, Burseraceae, Ebenaceae and Sapotaceae. The commonest species in this group were Gluta renghas and Buchanania spp. (Anacardiaceae), Canarium sp. Dacryodes costata and D. rostrata (Burseraceae), Diospyros endertii and D. bornensis (Ebenaceae), Madhuca malaccensis, Madhuca sp. 2 and Palaquium eriocalyx (Sapotaceae). Group 3 comprised small trees (dbh < 50 cm) which mainly belong to the following families: Annonaceae (Polyalthia rumphii, P. sumatrana, Goniothalamus macrophyllus), Euphorbiaceae (Aporusa spp. Baccaurea sumatrana), Guttiferae (Mesua borneensis), Moraceae (Artocarpus anisophyllus, A. lanceifolius), Myristicaceae (Knema laurina, K. furfuracea, Gymnacranthera forbesii, Myristica iners) and Rubiaceae (Nauclea sp.). The fourth group includes fast-growing pioneer species colonising opened areas like big gaps. These trees are mainly Macaranga gigantea, M. hypoleuca, M. pruinosa, M. triloba (Euphorbiaceae), Anthocephalus chinensis (Rubiaceae), Duabanga mollucana (Sonneratiaceae) and Octomeles sumatrana (Datiscaceae).

Species identification rate

The three control plots comprised 6255 trees with dbh ≥10 cm. Among these 6255 trees, 6102 (97.5%) were identified at the family level whereas 153 (2.5%) remained as unknown taxa or unidentified trees. All the trees could not be collected and identification was achieved for 5764 trees (92.3% of the tree population) sorted into 538 different taxa comprising 45 families and 128 genera. Among these taxa, 280 were identified to species level (n= 4320 trees or 69.2% of the total tree

population) while 185 (n=1122 or 17.9 % of the trees) and 68 (n=293 or 4.7%) were identified to the genus and family levels respectively. Five taxa (n=29 or 0.5 %) remained as unknown families.

Species richness

The tree (dbh \geq 10 cm) taxa were 329 in plot 1, 358 in plot 4 and 322 in plot 10 with on average, 182 species per hectare (SD = 16.6, n = 12, minimum = 160 species in plot 10 square 3, maximum = 201 species in plot 1 square 3). A 4-ha sample plot was not representative of the species richness of the primary forest since it comprised on average 63% of the total taxa identified in the overall 12-ha sampled area. The species-area curve confirms this result and shows that, in each plot the asymptote was not reached for a 4-ha inventory (Figure 4).

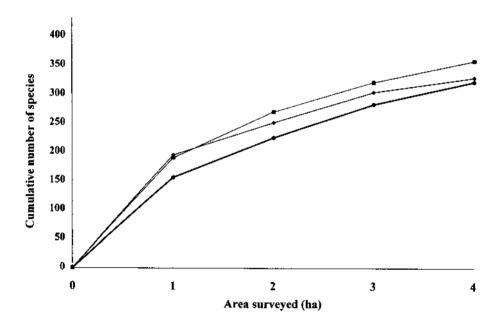


Figure 4. Species-area curve in the three undisturbed forest plots (4 ha each)

The Shannon index H' for the three control plots was 8.0 and the equitability 0.88 (Hmax = 9.07). H' indices and the equitabilities calculated in each plot were very similar (plot 1 H'= 7.54 & E = 0.90, plot 4 H'= 7.57 & E = 0.89, plot 10 H'= 7.36 & E = 0.88). More than 70% of the species (i.e. 394 taxa) were recorded with a density equal or lower than one stem per ha (n \leq 12 for the overall 12-ha area). Roughly 22% of the species (i.e. 117 taxa) were recorded only once whereas half of the total tree population was represented by 72 taxa.

The commonest species recorded in the primary forest was *Elateriospermum tapos* (Euphorbiaceae) with a mean density of 16 stems ha⁻¹ which represented only 3% of the total tree density in the three control plots. The second and third ranked species were *Diospyros endertii* (Ebenaceae, n = 9 trees ha⁻¹ and 1.7% of the total tree density) and *Madhuca* sp. 2 (Sapotaceae, n = 8 trees ha⁻¹ and 1.6% of the total tree density). The first dipterocarp, *Shorea parvifolia*, was ranked fourth (n = 7.8 trees ha⁻¹ or 1.5% of the total density).

The plots shared 153 species in common, comprising 58.3% (n = 3650 trees) of the total tree population but only 28% of the total taxa were recorded in the plots. The most similar plots in terms of species composition were 1 and 4 (Jaccard's coefficient $J_{14} = 0.53$, 239 common species). Plot 10 was different from the other two plots ($J_{101} = 0.40$, $J_{104} = 0.41$ sharing respectively 186 and 199 species with plots 1 and 4).

Dipterocarp richness and composition

In the three control plots, Dipterocarpaceae and Euphorbiaceae, with 61 species each, were the richest families (Table 3). The dominance of dipterocarps in the density and basal area was therefore also recorded in term of species richness. On average, 29 species of dipterocarps had were recorded in primary forest, ranging from 20 to 41 species ha⁻¹. In the three control plots, the most abundant and richest dipterocarp genera were Shorea (31 species and 61 stems ha-1), Dipterocarpus (12 species and 30 stems ha-1), Vatica (8 species and 19 stems ha⁻¹, Figure 5). These three genera comprised 88 and 68% of the dipterocarp tree population and species in the undisturbed forest plots respectively. The commonest dipterocarps species recorded (n ≥ 5 stems hail) were Shorea parvifolia, Dipterocarpus acutangulus, S. pinanga and S. hopeifolia. In plot 10, the dominant dipterocarp species was Parashorea smythiesii (9% of the total dipterocarp density in the plot) a light-demanding and fast-growing species, In contrast, this species in the other two plots was recorded in much lower density (1% and 2% of the dipterocarp density respectively in plots 1 and 4). The lowest dipterocarp species richness was recorded in plot 10 exhibiting 39 species against 49 and 46 in plots 1 and 4 respectively (cf. Annex 1). Comparison of dipterocarp species composition between the three plots with Jaccard's coefficient showed that as for the overall population, plots 1 and 4 were very similar ($I_{14} = 0.69$ and 39 species in common) whereas plot 10 was different from the other two plots (J_{101} = 0.51, $J_{104} = 0.52$, with respectively 31 and 29 species in common with 1 and 4). In contrast with the other two plots and beside its different topography and soil feature, plot 10 exhibited also big gaps where pioneer species were recorded (Macaranga hypoleuca n = 31, M. gigantea n = 3, M. pruinosa n = 4). The data on forest dynamics during the period 1989–1994 showed that gap formation in plot 10 occurred more often than in the other two plots (unpublished data).

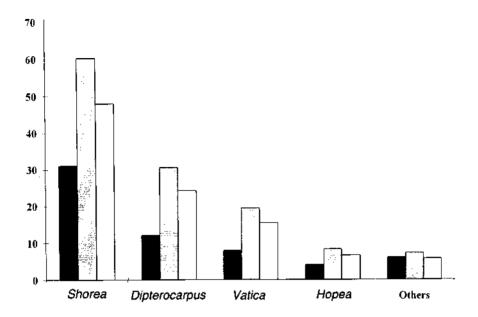


Figure 5. Species richness (number of species, hatched bars), density (stems hat, dotted bar) and proportion of the main dipterocarp genera (% of all dipterocarps density, empty bars) in the three control plots (12 ha). Others include: Anisoptera costata, A. laevis, Cotylelobium melanoxylon, Dryobalanops beccarii, Parashorea malaanonan and P. smythiesii.

The genus Shorea, which is one of the most demanded for timber, includes several commercial groups known by Indonesian foresters as red meranti, white meranti, yellow meranti and balau. In the primary forest, red meranti, the highest quality timber within the genus, were dominant (52% of the Shorea density) followed by yellow meranti (24%) and balau (20%) which showed similar densities. In contrast, white meranti were very few and represented only 4% of the genus density.

Discussion and conclusion

The data presented in Table 4 demonstrate the considerable variations in both stem density and basal area among the lowland mixed dipterocarp forests in Borneo. Tree density and basal area of the Berau forest were very similar to those recorded in Brunei at Belalong by Poulsen et al. (1996, in Davies & Becker 1996) and at Ladan by Davies and Becker (1996), and in East Kalimantan at Wanariset by Kartawinata et al. (1981). Tree density and basal area (521 stems ha-1 and 30 m² ha-1) were much lower than those recorded by Nicholson (1965) in Sandakan, Sabah (608 trees ha-1 and 42 m² ha-1) and in Sarawak (G. Mulu, Proctor et al. 1983, and Lambir 3,4,5, Philips et al. 1994, Table 4). However, proportions of dipterocarps in stem density (25.5%) and basal area (50%) were similar to those recorded by Nicholson (1965) in Sabah where dipterocarps comprised 27% of the tree density, and in Sarawak, ha-1 in Gunung Mulu National Park, where Proctor et al. (1983) recorded 120 dipterocarps ha-1 comprising 49% of the total basal area (Table 4).

Table 4. Species richness, stem density and basal area for trees ≥ 9.5, 9.7 or 10 cm dbh in primary lowland dipterocarp forest in Borneo (updated from Davies and Becker 1996)

Site	Altitude (m)	Soil	Plot size (ha)	Species (ha¹)	No. trees (ha¹)	% dipt. (ha ⁻¹)	Basal area (m²ha¹)	% Dipt. basal area	Reference
arawak									
3. Mulu	200	Red-Yellow Podsol	0.95	214+	778	16.2	57	49.1	Proctor et al. (1983)
ambir 2	114	Clay Udult	9.0	212*	462	•	43		Phillips et al. (1994)
Lambir 3,4,5	114	Sandy Humult	3×0.6	240*	739	,	53		Phillips et al. (1994)
Brupei									
Belalong	250	Shale-derived Acrisol	1.0	231	550	•	41		Poulsen et al. (1996)
adang	70	Haplic Acrisol	96.0	194	200	18	40	56	Davies & Becker (1996)
nelnpu	3	Sandy Haplic Acrisol	96.0	256+	621	ð,	35	324	Davies & Becker (1996)
		and Dystric Acrisol							
Sabah									
Sepilok-RP 17	9 5	Red-yellow Podsolic	1.8	157	999	27	42		Nicholson (1965)
Danum Valley	8	Haplic Acrisol & Dystric Cambisols	2 X 4	130	470	91	27	6	Newberry a al. (1992)
East Kalimantan									
Lempake	40-80	Red-yellow Podsolic		1 67 *	445	9	34	33	Riswan (1987)
Kutai	358	Red-yellow Podsolic		,			43	24	Suselo & Riswan (1987)
Wanariset	ሜ	Red-yellow Podsolic	1.6	174	541	16	æ	55	Kartawinata et al. (1981)
Berau	×100	Hapludult & Paleudult	3×4	182	5211	251	31,	5.05	This paper

+ = observed number of species in plots slightly smaller than 1 ha

^{1 =} mean of 12 unit squares, 1 ha each (3 plots, 4 ha each)

^{\$ =} from dbh ≥ 5 cm

The forest of Berau is dominated by Dipterocarpaceae and Euphorbiaceae which comprised 37% of the total tree density and 57% of the basal area. More than 70% of the species were recorded with a density lower or equal to one stem per ha but this pattern of low species density is commonly reported in tropical rain forests (Proctor et al. 1983, Whitmore, 1984, Gentry 1989, Phillips et al. 1994). In the study area, on average, 182 tree species (dbh ≥10 cm) ha¹ were recorded in the three control plots (12 ha). This species richness is very similar to that commonly found in other parts of Borneo which is generally close to 200 species ha⁻¹. The Dipterocarpaceae and Euphorbiaceae families, each with 61 species or 29 species ha⁻¹, were the richest taxa. Before logging, in the 12 plots totalling 48 ha, 74 species of dipterocarps were recorded. In comparison, Nicholson (1965), in Sabah, reported 198 tree species including 21 dipterocarps in a 1.9-ha plot. In East Kalimantan, Kartawinata et al. (1981) counted 239 species (14 dipterocarps) in a 1.6-ha plot. In Sabah (Danum Valley), Newbery et al. (1992) recorded 247 species in a 2-ha plot. In Sarawak, Proctor et al. (1983) counted 214 tree species in a 1-ha plot. The forest of Berau is therefore much richer in dipterocarps than the neighbour forests of Sabah which are mainly dominated by light-demanding dipterocarps like Parashorea spp. and Dryobalanops spp. The higher species richness of the Brunei and Sarawak dipterocarp forest, in comparison with those of Sabah (Table 4), could result from a higher stability of the northwest of Borneo which experienced less dramatic drought periods than the eastern part of the Island (Goldammer et al. 1996, Walsh 1996). However, the data from the present study demonstrate that in spite of its eastern location, the forest of Berau has a higher species richness than the forest of Sabah, particularly in dipterocarps. Because of its inland situation (about 75 km from the coast), the STREK area may have experienced less dramatic drought periods than coastal stations in East Kalimantan (Balikpapan, Samarinda and Tanjung Redeb for the study area) or Sabah. The high species richness of the Berau forest could be correlated to a longer stability of this forest which faces less dramatic drought events. However, our knowledge on the floristic variation occurring in Borneo is based on data mainly collected in the northern part of the island (Sabah, Sarawak and Brunei). The first record of Shorea leptoderma and S. symingtonii for Indonesia in the study area (Sist 1996) demonstrates that botanical surveys in East Kalimantan are still needed to improve our knowledge of the flora of Borneo. The lack of data for Kalimantan is undoubtedly an handicap for the analysis of phytogeographical variations within the region. The hypothesis of a possible impact of climatic variations and particularly of drought events on the species distribution and richness in Borneo must therefore be confirmed by further inventories and research in Kalimantan associated with meteorological data monitoring.

Previous studies in lowland dipterocarp forest reported that species richness and composition could be correlated with soil nutrients, particularly with phosphorus and magnesium concentrations (Ashton 1976, 1989, Baillie et al. 1987, Pemadosa & Gunatilleke 1981). In contrast, in Malaysia, on a 18-km² surveyed area, Wong and Whitmore (1970) could not find any significant correlation between species distribution and soil features. In Berau, the species richness of dipterocarps was

higher on well-drained soils with gentle slopes than poorly drained zones with steep relief (Sist 1996). In the study area, floristic variations between plots could be correlated with forest dynamics rather than with soil chemical features. In plot 10, the dominance of light demanding species such as *Parashorea smythiesii* and *Dryobalanops beccarii* is likely the result of a higher rate of canopy opening. The higher occurrence of gap formation in plot 10 might be linked to the steep topography of the plots which favoured tree falling. For this reason, logging operations, by creating gaps, are likely to promote the growth and development of such light-demanding dipterocarps and have therefore important consequences on the future forest composition for the next rotation.

The high commercial value of the Berau forest was earlier demonstrated by the assessment of the harvested volume (47 m³ ha¹ in mean) during logging operations in the area (Bertault et al. 1995). This richness is enhanced by the dominance of red merantis which are the chief timber export in Southeast Asia. Ultisols are the dominant soil covering 87% of the study area (Sumaryono 1996). Those soils have a poor nutrient status and the most fertile part is the thin surface layer (Bremen et al. 1990). Under these conditions, selective logging associated with a long-term forest management plan remains the most suitable and economic profitable land-use system.

References

- APPANAH, S. & WEINLAND, G. 1993. A Preliminary Analysis of the 50-ha Pasoh Demography Plot. I. Dipterocarpaceae. FRIM Research Pamphlet 112, Kuala Lumpur. 183 pp.
- Ashton, P. S. 1964. Ecological Studies in the Mixed Dipterocarp Forests of Brunei State. Clarendon Press, Oxford. 75 pp.
- Ashton, P. S. 1969. Speciation among tropical forest trees, some deductions in the light of recent evidence. Biological Journal of the Linnean Society 1:155–196.
- Ashton, P. S. 1976. Mixed dipterocarp forest and its variation with habitat in the Malayan lowlands: a re-evaluation at Pasoh. *Malaysian Forester* 39:56–72.
- ASHTON, P. S. 1982. Dipterocarpaceae. Flora Malesiana Serie 1, 9, Part 2:237-552.
- Ashton, P. S. 1989. Species richness in tropical forests. Pp. 239–251 in Holm-Nielsen, L. B., Nielsen, I. C. & Baslev, H. (Eds.) Tropical Forests Botanical Dynamics, Speciation and Diversity. Academic Press, London.
- Ashton, P. S. & Hall, P. 1992. Comparison of structure among mixed dipterocarp forests of northwestern Borneo. *Journal of Ecology* 80:459-481.
- Baillie, I. C., Ashton, P. S., Court, M. N., Anderson, J. A. R., Fitzpatrick, E. A. & Tinsley, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201-220.
- Bertault, J-G. & Sist, P. 1995. Impact de l'exploitation en forêt naturelle. Bois et Forêts des Tropiques 245:5-20.
- Bertault, J-G. & Sist, P. 1997. An experimental comparison of different harvesting intensities with reduced-impact and conventional logging in East Kalimantan, Indonesia. Forest Ecology and Management 94:209–218.
- Bremen, H. (van), Iriansyah, M. & Andriesse, W. 1990. A Study Soil and Site Characteristics in Twelve Permanent Plots in East Kalimantan. Tropenbos Technical Series 6. 188 pp.
- Bruenig, E. F. 1970. Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. *Tropical Ecolology* 11(1):26–43.
- Bruenic, E. F. 1973. Species richness and stand diversity in relation to site and succession of forests in Sarawak and Brunei. *Amazoniana* IV 3:293–320.

- Burgess, P. F. 1961. The structure and composition of lowland tropical rainforest in North Borneo. *Malayan Forester* 24:66–80.
- Dajoz, R. 1982. Précis d'Ecologie. Bordas, Paris. 503 pp.
- DAVIES, S. J. & BECKER, P. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. Journal of Tropical Forest Science 8 (4):542-569.
- GENTRY, A. H. 1989. Speciation in tropical forests. Pp. 113-134 in Holm-Nielsen, L. B., Nielsen, I. C. & Baslev, H. (Eds.) Tropical Forests Botanical Dynamics, Speciation and Diversity. Academic Press.
- GOLDAMMER, J.G., SIEBERT, B. & SCHINDELE, W. 1996. Fire in dipterocarp forests. Pp. 155-185 in Schulte A. & Schöne, D. (Eds.) Dipterocarp Forest Ecosystems, Towards Sustainable Management. World Scientific Publishing, Singapore.
- HARTSHORN, G. S.1989. Gap phase dynamics and tropical tree species richness. Pp. 65-73 in Holm-Nielsen, L. B., Nielsen, I. C. & Baslev, H. (Eds.) Tropical Forests Botanical Dynamics, Speciation and Diversity. Academic Press.
- KARTAWINATA, K., ROCHADI, A. & PARTOMIHARDJO, J. 1981. Composition and structure of a lowland dipterocarp forest at Wanariset, East Kalimantan (Indonesia). Malaysian Forester 44, 2/3:397-406.
- Kochummen, K. M., LaFrankie, J. V. & Manokaran, N. 1991. Composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Science* 3(1):1-13.
- Newbery, D. McC., Campbell, E. J. F., Lee, Y. F., Ridsdale, C. E. & Still, M. J. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Philosophical Transactions of the Royal Society* B 335:341-356.
- NICHOLSON, D. I. 1965. A study of virgin forest near Sandakan, North Borneo. Pp. 67-87 in Proceedings of the Symposium on Humid Tropics Vegetation. Kuching. UNESCO, Paris.
- Pemadosa, M. A. & Gunatilleke, C. V. S. 1981. Pattern in a rainforest in Sri Lanka. *Journal of Ecology* 69:117-124.
- PHILIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VASQUEZ, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences* 91:2805–2809.
- PHILIPS, O. L. & GENTRY, A. H. 1994. Increasing turnover rate through time in tropical forests. Science 263:954-958.
- Poulsen, A. D., Nielsen, I. C., Tan, S. & Balslev, H. 1996. A quantitative inventory of trees in one hectare of mixed dipterocarp forest in Temburong, Brunei Darussalam. In Edwards, D.S., Booth, W. E., & Choy, S. C. (Eds.) Tropical Rain Forest Research-Current Issues. Kluwer Academic Press. Dordrecht, the Netherlands. (In press, cited by Davies & Becker 1996).
- Poore, M. E. D. 1968. Studies in Malaysian rain forests. I. The forest on triassic sediments in Jengka Forest Reserve. *Journal of Ecology* 56:148-196.
- PROCTOR, J., ANDERSON, J. M., CHAI, P. & WALLACK, H. W. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park. I. Forest environment, structure and floristics. *Journal of Ecology* 71:237-260.
- RAICH, J. W. & KHOON, G. W. 1980. Effect of canopy openings on tree germination in a Malayan dipterocarp forest. *Journal of Tropical Ecology* 6:203-217.
- RISWAN, S. 1987. Structure and floristic composition of mixed dipterocarp forest at Lempake, East Kalimantan. Pp. 435–457 in Kostermanns, A. J. G. H. (Ed.) Proceedings of The Third International Round Table Conference on Dipterocarps. UNESCO, Jakarta, Indonesia.
- SCHMIDT, R. C. 1991. Tropical rainforest management: a status. Pp. 181-203 in Gomez-Pompa, A., Whitmore, T. C. & Hadley, M. (Eds.) Rainforest Regeneration and Management. MAB Series, Parthenon Publishing, UNESCO, Paris, Vol. 6.
- Sist, P. 1996. Structure and diversity of dipterocarps in a lowland dipterocarp forest in East Kalimantan. Pp. 60-86 in Appanah, S. & Khoo, K. C. (Eds.) Proceedings of the Fourth Round Table on Dipterocarps. FRIM, Malaysia.
- Sist, P., Nolan, T., Bertault, J.-G. & Dykstra, D. 1998. Harvesting intensity versus sustainability in Indonesia. Forest Ecology and Management 108:251-260.
- Soedjito, H. & Kartawinata, K. 1995. Long-term ecological research in Indonesia: achieving sustainable forest management. Pp. 129-139 in Primack, R. B. & Lovejoy, T. E. (Eds.) Ecology, Conservation and Management of South East Asian Rainforests. Yale University Press, United States of America.

- SOEPADMO, E. 1995. Plant diversity of the Malesian tropical rainforest and its phytogeographical and economic significance. Pp. 19-40 in Primack, R. B. & Lovejoy, T. E. (Eds.) Ecology, Conservation and Management of South East Asian Rainforests. Yale University Press, United States of America.
- SSS (SOIL SURVEY STAFF). 1987. Keys to Soil Taxonomy. Third SMSS Technical Monograph 6. Agency for International Development/United States Department of Agriculture. Cornell University, Ithaca, New York, United States of America.
- SUMARYONO, S. M. 1996. Distribution spatiale des espèces forestières de Kalimantan Est en relation avec la topographie et la nature des sols. Thèse de Doctorat de l'Université Paris 6.
- Suselo, T. B., Riswan, S. 1987. Compositional and structural pattern of lowland mixed dipterocarp forest in the Kutai National Park, East Kalimantan. Pp. 459-470 in Kostermanns, A. J. G. H. (Ed.) Proceedings of the Third International Round Table Conference on Dipterocarps. UNESCO, Jakarta, Indonesia.
- Symington, C. F. 1943. Foresters' Manual of Dipterocarps. Malayan Forest Records 16. Reprinted 1974. Kuala Lumpur. 242 pp.
- Van Steenis, C. G. G. J. 1950. The delimitation of Malaysia and its main plant geographical divisions. Flora Malesiana Serie I, 1: LXX-LXXV.
- Walsh, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:385–407.
- WHITMORE, T. C. 1984. Tropical Rain Forests of the Far East. 2nd edition. Clarendon Press, Oxford. 352 pp.
- WHITMORE, T. C., TANTRA, I. G. M. & SUTISNA, U. (Eds.) 1990. Tree Flora of Indonesia, Check List for Kalimantan. Parts I, II.1 and II.2. Ministry of Forestry, FORDA, Bogor.
- Wong, Y. K. & Whitmore, T. C. 1970. On the influence of soil properties on species distribution in a Malayan lowland dipterocarp rain forest. *Malayan Forester* 33:42-54.
- WYATT-SMITH, J. 1966. Ecological Studies on Malayan Forest. Research Pamphlet 52. Forest Research Institute, Kepong, Malaysia.

Annex. List of dipterocarp species identified in the 12 plots (4 ha each) in RKL 4 before logging. Codes: 0: species not recorded in control plots; 1,4, 10: species recorded only in plots 1, 4 and 10 respectively; 3: species recorded in all the 3 plots; 14: species recorded in both plots 1 and 4 only; 101: species recorded in both plots 10 and 1 only; 104: species recorded in both plots 10 and 4 only.

Species	Cod
Anisoptera costata Korth.	14
Anisoptera laevis Ridl.	14
Cotylelobium melanoxylon (Hook. f) Slooten	1
Dipterocarpus acutangulus Vesque	14
Dipterocarpus confertus Slooten	3
Dipterocarpus conformis Slooten	0
Dipterocarpus costulatus Slooten	1
Dipterocarpus elongatus Korth.	3
Dipterocarpus glabrigemmatus Ashton	0
Dipterocarpus gracilis Blume	10
Dipterocarpus grandiflorus Blanco	14
Dipterocarpus hasseltii Blanco	0
Dipterocarpus humeratus Slooten	3
Dipterocarpus kunstleri King	10
Dipterocarpus pachyphyllus Meijer	1
Dipterocarpus palembanicus Slooten ssp. borneensis Ashton	14
Dipterocarpus stellatus Vesque ssp. parvus Ashton	1
Dipterocarpus verrucosus Foxw. ex Slooten	3
Dryobalanops beccarii Dyer	101
Hopea bracteata Burck	0
Hopea dryobalanoides Miq.	3
Hopea ferruginea Parijs	4
Hopea nervosa King	0
Hopea pachycarpa (Heim) Symington	9
Hopea sangal Korth.	G
Hopea semicuneata Symington	4
Parashorea malaanonan (Blanco) Merr.	10
Parashorea smythiesii Wyatt-Smith ex Ashton	9
Shorea agamii ssp. agamii Ashton	9
Shorea almon Foxw.	9
Shorea angustifolia Ashton	9
Shorea atrinervosa Symington	9
Shorea beccariana Burck	14
Shorea confusa Ashton	0
Shorea exelliptica Meijer	9
Shorea faguetiana Heim	104
Shorea falciferoides ssp. glaucescens (Meijer) Ashton	(
Shorea fallax Meijer	101
Shorea guiso (Blanco) Blume	(
Shorea hopeifolia (Heim) Symington	5
Shorea inappendiculata Burck	2
Shorea johorensis Foxw.	1
Shorea laevis Ridl.	14
Shorea lamellata Foxw.	104
Shorea leprosula Miq.	9
Shorea leptoderma Meijer	14
Shorea longisperma Roxb.	104
Shorea macrophylla x pinanga	(

Annex (continued)

Shorea macroptera spp. sandakanensis (Symington) Ashton	14
Shorea maxwelliana King	1
Shorea mecistopteryx Ridl.	10
Shorea ochracea Symington	4
Shorea ovalis ssp. ovalis Burck	14
Shorea parvifolia Dyer ssp. parvifolia Ashton	3
Shorea parvifolia Dyer ssp. velutinata Ashton	8
Shorea parvistipulata Heim ssp. albifolia Ashton	3
Shorea parvistipulata Heim ssp. parvistipulata Brandis	3
Shorea patoiensis Ashton	3
Shorea pauciflora King	3
Shorea pinanga Scheff.	3
Shorea scrobiculata Burck	101
Shorea seminis (De Vriese) Slooten	0
Shorea smithiana Symington	3
Shorea superba Symington	101
Shorea symingtonii Wood	0
Shorea virescens Parijs	4
Shorea xanthophylla Symington	0
Vatica albiramis Slooten	10
Vatica micrantha Slooten	3
Vatica nitens King	14
Vatica oblongifolia ssp. multinervosa Hook.f.	3
Vatica odorata (Griff.) Symington ssp. mindanensis (Foxw.) Ashton	14
Vatica rassak (Korth.) Blume	14
Vatica sarawakensis Heim	101
Vatica umbonata (Hook.f.) Burck	3
Vatica vinosa Ashton	3

LEAFING, FLOWERING AND FRUITING OF AZADIRACHTA INDICA (NEEM) IN INDIA

V. S. Kishan Kumar & M. L. Arrawatia

Arid Forest Research Institute, Jodhpur 342 005, India

Received May 1997

KISHAN KUMAR, V. S. & ARRAWATIA, M. L. 1999. Leafing, flowering and fruiting of Azadirachta indica (neem) in India. Some basic phenological observations on neem were carried out at different locations situated in six different agro-ecological zones (ER2, ER4, ER8, ER9, ER10 and ER15) of India. The neem tree is generally in heavy leafing during May-November. Leaf shedding in general starts from November and the trees are back in full leafing by April. There is an appreciable drop in percentage of trees flowering immediately after May. The flowering peak is April for arid locations (ER2) and the semi-arid regions (ER4 and ER8) have a broad peak spread between March and May. Among the sub-humids, ER10 has a single flowering peak in March whereas ER9 and ER15 have broad peaks spreading between April and May. Some restricted flowering during August and November is indicated at some locations both in the semi-arid and sub-humid regions. As far as fruiting is concerned, neem trees in the arid and semi-arid areas start fruiting in May and June whereas in the sub-humid regions it varies between April and July. In ER15 there is an overlapping of flowering and fruiting patterns. Mature fruit availability time in the arid region is in June whereas in the semi-arid region it is in June and July extending up to August-September in ER8. In the sub-humid region June-July is also the best time for seed collection. Secondary flowering found in some regions is followed by fruiting and a few of the fruits mature subsequently. This provides an additional seed collection time in these regions.

Key words: Neem - phenology - leafing - flowering - fruiting - seed collection - India

KISHAN KUMAR, V. S. & ARRAWATIA, M. L. 1999. Pendaunan, pembungaan dan pembuahan Azadirachta indica (neem) di India. Beberapa cerapan fenologi asas bagi neem dijalankan di lokasi yang berbeza di enam zon ekologi-tani yang berbeza (ER2, ER4, ER8, ER9, ER10 dan ER15) di India. Pokok neem pada amnya berdaun lebat pada bulan Mei-November. Peluruhan daun kebiasaannya bermula pada bulan November dan pokok mula mengalami pendaunan penuh pada bulan April. Selepas bulan Mei, terdapat penurunan dalam peratus pembungaan pokok. Kemuncak musim berbunga ialah pada bulan April bagi lokasi gersang (ER2) dan kawasan separagersang (ER4 dan ER8) mempunyai masa kemuncak yang panjang antara April dan Mei. Di kawasan sublembap, ER10 mengalami kemuncak pembungaan hanya pada bulan Mac manakala ER9 dan ER15 mengalami kemuncak pembungaan yang lebih panjang antara bulan April dan Mei. Beberapa pembungaan yang terbatas pada bulan Ogos dan November terdapat di beberapa lokasi di kedua-dua kawasan. Mengenai pembuahan, pokok neem di kawasan gersang dan semi-gersang memulakan pembuahan pada bulan Mei dan Jun manakala di kawasan sublembap ia berubah-ubah antara bulan April dan Julai. Dalam ER15 terdapat pola bertindih bagi pembungaan dan pembuahan, Buah matang di kawasan gersang ialah pada bulan Jun manakala di kawasan separa gersang ia matang pada bulan Jun dan Julai sehinggalah ke bulan Ogos dan September dalam ER8. Di kawasan sublembap juga, masa yang paling sesuai untuk pengutipan biji benih ialah pada bulan Jun-Julai. Pembungaan sekunderyang didapati di beberapa kawasan diikuti oleh pembuahan dan sesetengahnya matang selepas itu. Ini memberikan pertambahan masa bagi pengutipan biji benih di kawasan ini.

Introduction

Azadirachta indica A. Juss. of family Meliaceae, widely known as neem, has a variety of uses ranging from medicinal applications to use as fodder. The ability of this plant to grow in hardy conditions makes it a preferred species for the arid regions. Although its value as a utility tree has already been established, detailed studies on its morphological and phenological aspects are found wanting in India. The processes of flowering and fruiting, which are generally connected with each other, are important from the point of view of silviculture. Often one finds that an abundant flowering is not followed by an equally abundant fruiting. And due to its important role in regeneration, fruiting of any tree species deserves special attention. Though abundant fruiting is a prerequisite, it cannot always ensure vigorous regeneration. The time of flowering (and subsequent fruiting) may vary in a given region. The leaves of neem tree are acknowledged fodder for goat and camel and also are well known for their pesticidal properties. Apart from these, the spermicidal, antifertility and anti-implantation properties of neem leaves have attracted the attention of researchers in the recent past (Shaikh et al. 1993). Hence a clear understanding of the availability of neem leaves and leaf shedding period of the tree is also of much importance. It is in these contexts that a pilot study on the phenological aspects of neem was initiated in April 1993. This paper discusses some of the important observations which came out of the study.

Locations and methods

Studies on the phenology of neem were taken up to understand its leafing, flowering and fruiting behaviour throughout the year at twelve different locations in India which are situated in six different agro-ecological zones as classified by the National Bureau of Soil and Land-use Planning. The twelve different locations and the six agro-ecological zones in which they are situated are tabulated below.

Region	Location	State	Agro-ecologica zone
Hot arid	Jaisalmer Jodhpur	Rajasthan	ER2
Hot semi-arid	Ahmedabad Allahabad Jaipur New Delhi Bangalore Coimbatore	Gujarat Uttar Pradesh (UP) Rajasthan Delhi Karnataka Tamil Nadu (TN)	ER4 ER8
Hot sub-humid	Pinjore	Haryana	ER9
	Jabalpur	Madhya Pradesh (MP)	ER10
	Jorhat Midnapore	Assam West Bengal (WB)	ER15

Note:

ER2: Western plains and Kucchh Peninsula with desert and saline soils ER4: Northern plains and central highlands with alluvium derived soils

ER8: Eastern Ghats (Tamil Nadu uplands) and Deccan Plateau with red loamy soils

ER9: Northern plains with alluvium-derived soils

ER10: Central highlands (Malwa and Bundelkhand) with medium and deep black soils

ER15: Assam and Bengal plains with alluvium derived soils

At each location, ten trees were marked for monthly observations. The study was initiated in April 1993 and data up to December 1994 were analysed to generate information regarding flowering and fruiting times, maximum leafing period, seed availability time, etc. As neem is seldom leafless in India, the data on leafing were collected based on whether or not a tree is in heavy leafing. A tree with more than two-third portion of its crown covered with leaves was considered to be in heavy leafing. As far as flowering and fruiting are concerned, a tree which bears at least a few flowers/fruits was considered to be in flowering/fruiting. The percentages of the total number of trees bearing flowers, bearing young and mature fruits and found in heavy leafing were then calculated for each agro-ecological region.

Results and discussion

Leafing

Most of the trees are in heavy leafing during May-November. The notable exception is in the case of the northern plains represented by ER4 and ER9 where heavy leafing is observed in most of the trees even up to January. Otherwise it can be assumed that leaf shedding in general starts from November and the trees are back in full leafing by April. Only in very dry areas the tree is found leafless for a short period during February-March (Dwivedi 1993). Neem is already reported to be in full foliage when most other trees are leafless (Troup 1981).

Flowering

From the point of view of natural pollination, flowering season is very important. Figures 1(a) and 1(b) show the distribution of flowering intensity (percentage of trees which bear at least a few flowers) for the calendar year. At almost all the locations there is an appreciable drop in the percentage of trees flowering immediately after May. This is preceded by peak flowering in March-April-May. Only in the arid locations (Jodhpur and Jaisalmer in Rajasthan) is there a sharp drop in percentage of trees flowering after April itself. In this agro-ecological region (ER2), less than 35% of the trees are flowering in May whereas, in all other regions 60% or more of the trees are flowering in this month. But the situation changes considerably in June. While 80 to 100% of the trees are flowering in May in most of the locations, only a few of them (less than 35%) bear flowers in June except in ER2 and ER9 where there are no flowering trees in this month.

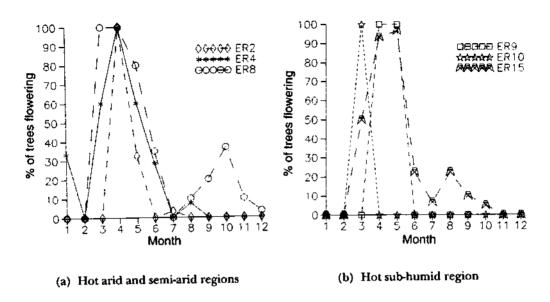


Figure 1. Flowering of neem

Some restricted flowering is indicated during July-October in the sub-humid locations in Assam and Bengal (ER15). In August, nearly 23% of the trees are flowering here. At the semi-arid locations of Eastern Ghats and Deccan Plateau (ER8) also there is some restricted flowering during August-December. The secondary peak in this case is in October with about 4% of the trees being found flowering. In the semi-arid regions of northern India represented by ER4, some restricted flowering is indicated in January and August with about 34% and less than 10% of trees being flowering respectively.

These observations are largely in agreement with other reports. In a study in Tamil Nadu the primary and secondary flowering seasons were reported as April and September respectively (Shanti et al. 1996). Mahadevan (1991) has reported the two flowering periods to be March to mid-May and mid-August to September based on his observations in Tamil Nadu and Andhra Pradesh. In Malaysia, these seasons were reported to be February–April and July–September respectively (Loke et al. 1992).

Fruiting

The beginning of fruiting was studied by observing young fruits. It is observed that generally May-June is the season when fruiting starts in neem. However, there are different peak patterns for fruiting in different regions [Figures 2(a) and 2(b)]. In the arid locations (ER2) more than 80% of the trees have young fruits on them in May and June and there is no observation of young fruits for the other periods of the year. In the semi-arid parts of northern India (ER4), the peak is distinct in May (more than 85%) with June showing only 40% of the trees bearing young

fruits. The flowering pattern for this agro-ecological zone is a wider one ranging from March to May showing more than 60% of the trees to be flowering and peaking in April. But the fruiting peak is sharper with a distinct peak in May indicating that the fruiting pattern is quite different from that of flowering for this zone. The restricted flowering in January is accompanied by some fruiting too. In the semi-arid parts of southern India (ER8), more trees start to fruit in June and the restricted flowering found in October is accompanied by some fruiting in November-December.

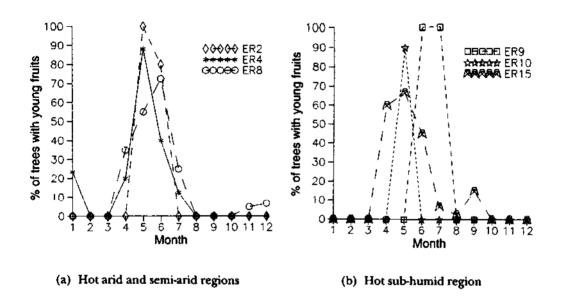
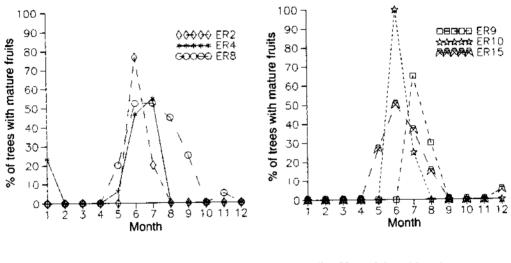


Figure 2. Young fruits of neem

Among the sub-humid parts, the central highlands (ER10) have only a single peak in May which follows its corresponding flowering peak in March. There is no record of young fruits during the rest of the year in this zone whereas in ER9 (northern parts) the only fruiting peak is found in June-July following the flowering peak of April-May. In the Assam and Bengal plains (ER15), there is a broad peak between April and June with 45–65% of the trees showing young fruits which closely follows its corresponding flowering peak of March-May. This is followed by a few trees (less than 20%) showing some young fruits in September following the secondary flowering peak of August. One can see that the flowering and fruiting peaks of ER15 somewhat overlap. Such an overlap of flowering and fruiting in young trees of neem was reported in a provenance trial also (Gupta et al. 1995).

Seed collection

This case was studied by taking stock of the intensity of mature fruits. It is reported that the optimum period for seed collection is when the colour of the drupe turns from full green to yellow-green (Lauridsen & Souvannavong 1993). Yellow-brown, wrinkled or already fallen drupes should be avoided as their viability declines rapidly in storage (Suri & Mehrotra 1994). Figures 3(a) and 3(b) give the times of occurrence of mature fruits in the different agro-ecological zones. In the arid region (ER2), maximum ripened fruits occur in the month of June. In the semi-arid regions, it is in June and July. But a notable exception is in the case of semi-arid regions of southern India (ER8) where about 45 and 25% of the trees still have mature fruits in August and September respectively. In Tamil Nadu fruits from the primary flowering have been reported to be ready for harvest in July-August and those from the secondary flowering in December (Shanti et al. 1996). The respective seasons were reported by Mahadevan (1991) to be June and October from his studies in Andhra Pradesh and Tamil Nadu.



(a) Hot arid and semi-arid regions

(b) Hot sub-humid region

Figure 3. Mature fruits of neem

In the sub-humid regions also the analysis shows diversity in peaks of ripened fruits. In ER9 the peak is in July whereas ER10 and ER15 show the peaks in June. But about 40 and 25% of trees in ER15 and ER10 respectively have mature fruits in July too. In Malaysia, ripened fruits from the two flowerings were reported to be available in June-August and October-December (Loke et al. 1992). A study on the characteristics of seeds of neem collected from the two seasons (primary and secondary) indicated that those collected in the secondary season have higher seed weight, larger size and lower moisture content (Mishra & Tomar 1995).

The various phenological observations, viz. leafing, flowering, occurrence of young and mature fruits, etc., from this study are summarised in Table 1.

	Arid	Semi	i-arid		Sub-humid	
	ER2	ER4	ER8	ER9	ER10	ER15
Heavy leafing	May-Nov.	AprJan.	AprDec.	June-Feb.	AprDec.	June-Oct.
Flowering	April	Mar.–May	Маг.–Мау	АргМау	March	AprMay
Young fruits	May-June	May	May–June	June-July	May	AprJune
Mature fruits	June	June-July	June-Sept.	July	June	June

Table 1. Peak months in which various phenological characteristics take place in neem in India

Conclusion

Flowering and fruiting characteristics of neem generally show up during March and August. The fruiting pattern closely follows the flowering pattern in the various agro-ecological zones studied except in the case of the semi-arid parts of northern India falling in ER4. Moreover, some of the agro-ecological regions show restricted flowering and fruiting. The seed collection period is the month of June for most of the regions except for ER4, ER8 and ER9 where the best seed collection periods are June–July, June–September and July respectively.

Acknowledgements

The authors wish to thank the Director, Arid Forest Research Institute, for his keen interest in this work and all the staff members of the different Indian Council of Forestry Research and Education (ICFRE) institutes and centres who carried out the data collection. The help of Prem Singh Sankla in data entry is appreciated.

References

- DWIVEDI, A. P. 1993. National level neem provenance trials at Jodhpur. Pp. 18-28 in Read, M. D. & French, J. H. (Eds.) Genetic Improvement of Neem: Strategies for the Future. Proceedings of the International Consultation on Neem Improvement. Kasetsart University, Bangkok, Thailand, 18-22 January, 1993. Winrock International.
- GUPTA, P. K., PAL, R. S. & EMMANUEL, C. J. S. K. 1995. Initial flowering and fruiting of national provenance trial. *Indian Forester* 121:1063-1068.
- LAURIDSEN, E. B. & SOUVANNAVONG, S. 1993. Neem provenance selection and seed handling. Pp. 137–149 in Read, M. D. & French, J. H. (Eds.) Genetic Improvement of Neem: Strategies for the Future. Proceedings of the International Consultation on Neem Improvement. Kasetsart University, Bangkok, Thailand, 18–22 January, 1993. Winrock International.
- LOKE, J. H., HENG, C. K., REJAB, A., BASIRUN, N., & MARDI, H. C. A. 1992. Studies on neem (Azadirachta indica A. Juss.) in Malaysia. Pp. 103-107 in Proceedings 3rd International Conference on Plant Protection in the Tropics. Genting Highlands, Malaysia, March 1990.
- MAHADEVAN, N. P. 1991. Phenological observations of some forest tree species as an aid to seed collection. *Journal of Tropical Forestry* 7:248-247.

- MISHRA, D. K. & TOMAR, U. K. 1995. Comparative studies on seeds of Azadirachta indica A. Juss. (neem) collected at different seasons. Neem: News Letter of International Neem Network Vol. II: 18.
- SHAIKH, P. D., MANIVANNAN, B., PATHAN, K. M., KASTURI, M. & NAZEER AHAMED. 1993. Antispermatic activity of Azadirachta indica leaves in albino rats. Current Science 64:688–89.
- Shanti, K., Manimuthu, L. & Singh, B. G. 1996. Genetic significance of late flowering forms in neem (Azadirachta indica A. Juss.) as reflected by germination studies. *Indian Forester* 122:263–264.
- Suri, R. K. & Mehrotra, A. 1994. Neem (Azadirachta indica A. Juss.), A Wonder Tree. Society of Forest and Environment Managers, Dehra Dun. 36 pp.
- TROUP, R. S. 1981. The Silviculture of Indian Trees. Volume III. Edited by Joshi, H. B. Controller of Publications, Government of India, New Delhi:147-154.

SPATIAL PATTERNS OF COMMON TREE SPECIES RELATING TO TOPOGRAPHY, CANOPY GAPS AND UNDERSTOREY VEGETATION IN A HILL DIPTEROCARP FOREST AT SEMANGKOK FOREST RESERVE, PENINSULAR MALAYSIA

K. Niiyama*,

Forestry and Forest Products Research Institute, Matsunosato 1, Kukisaki, Inashiki, Ibaraki, 305 - 8687, Japan

K. Abd. Rahman,

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

S. Iida,

Forestry and Forest Products Research Institute, Hokkaido Research Center, 7, Hitsuzigaoka, Toyohiraku, Sapporo 062, Japan

K. Kimura,

Department of Biology, Faculty of Education, Fukushima University, Matsukawa, Fukushima 960-12, Japan

R. Azizi & S. Appanah

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

Received August 1997

NIIYAMA, K., ABD. RAHMAN, K., IIDA, S., KIMURA, K., AZIZI, R. & APPANAH, S. 1999. Spatial patterns of common tree species relating to topography, canopy gaps and understorey vegetation in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. The spatial patterns of the 30 most common tree species and their associations with topography (ridge, slope and valley), canopy gaps, and understorey vegetation (bertam palm, Eugeissona tristis, and a common bamboo, Gigantochloa scortechinii) were analysed in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. We enumerated all trees≥5 cm dbh and performed a census on the distribution of gaps, palm and bamboo in a 6-ha

^{*}Corresponding author: Fax: 0298-73-1542. E-mail: niiya@ffpri-affrc.go.jp

permanent plot. Most species showed significant aggregated patterns and only two species, Payena lucida and Scaphium macropodum, were randomly distributed through all quadratsizes. Thirteen species showed significant positive association with topography; two species were associated with valley, ten species with ridge, and one species with slope. The 30 most common tree species were separated into three groups by a cluster analysis based on the dissimilarity index: $D = (1-\omega)/2$, where ω is Iwao's ω -index which reflects the degree of inter-species spatial association. Species group A (7 species) contained two randomly distributed valley species (Vitex longisepala and Crypteronia griffithii). Group B (11 species) consisted of ridge species. Shorea curtisii, Lithocarpus wallichianus, Eurycoma longifolia and others were positively associated with typical ridge sites and/or the distribution of the palm. Group C (12 species) consisted of slope species (Pimelodendron griffithianum), gap-associated species, (Macaranga triloba, Millettia atropurpurea and Knema conferta) and others. Gap species were also associated with bamboo. Distinctive habitat guild was recognised only on the ridge species.

Key words: Canopy gaps - common tree species - hill dipterocarp forest - Peninsular Malaysia - spatial distribution - topography - understorey vegetation

NIIYAMA, K., ABD. RAHMAN, K., IIDA, S., KIMURA, K., AZIZI, R. & APPANAH, S. 1999. Corak taburan spesies pokok utama serta hubungannya dengan topografi, ruang-ruang silara dan tumbuhan bawah di hutan bukit dipterokarpa di Hutan Simpan Semangkok, Semenanjung Malaysia. Analisis terhadap corak taburan 30 spesies pokok utama hutan bukit dipterokarpa serta hubungannya dengan topografi (permatang, cerun dan lembah), ruang-ruang silara, dan tumbuhan bawah (bertam, Eugeissona tristis, dan buluh, Gigantochloa scortechinii) dijalankan di Hutan Simpan Semangkok, Semenanjung Malaysia. Kami telah mengukur semua pokok≥5 cm ppd dan membanci taburan ruang-ruang, palma dan buluh di dalam petak kekal seluas 6 hektar. Kebanyakan pokok menunjukkan taburan kelompok bererti melainkan Payena lucida dan Scaphium macropodum, taburannya adalah rawak pada setiap kelas saiz. Tiga belas spesies menunjukkan hubungan positif bererti dengan topografi, dua spesies menunjukkan hubungan dengan lembah, sepuluh spesies dengan permatang dan satu spesies di cerun. Tiga puluh spesies utama ini dibahagikan kepada tiga kumpulan berdasarkan analisis kelompok menggunakan indeks ketidaksamaan: $D=(1-\omega)/2$, di mana ω ialah indeks Iwao ω yang menggambarkan darjah hubungan taburan antara spesies. Spesies kumpulan A (7 spesies) mengandungi dua spesies taburan rawak dan di lembah (Vitex longisepala dan Crypteronia griffithii). Kumpulan B (11 spesies) mengandungi spesies di permatang. Shorea curtisii, Lithocarpus wallichianus, Eurycoma longifolia dan lain-lain spesies mempunyai hubungan positif dengan permatang dan/atau taburan palma, Kumpulan C (12 spesies) mengandungi spesies cerun (Pimelodendron griffithianum), dan spesies yang menunjukkan hubungan dengan ruang, (Macaranga triloba, Millettia atropurpurea dan Knema conferta) dan lainlain. Spesies ruang juga ada hubungan dengan buluh. Habitat berkelompok yang ketara hanya dikenal pasti pada spesies permatang.

Introduction

The spatial patterns of tropical rain forest are an important key to understanding the coexistence and abundance of tree species. Tree community is an assemblage of tree species which have specific spatial patterns: random, regular, and aggregated patterns in temperate forests (Masaki et al. 1992, Yamamoto et al. 1995) and also in tropical forests (Ogawa et al. 1961, Poore 1968, Armesto et al. 1986, Hubbell & Foster 1986b, Manokaran et al. 1992). The spatial distributions of tropical trees were

usually analysed to test Janzen-Connell model (Janzen 1970, Connell 1971). They predicted that the adult trees were less aggregated than seedlings or saplings. However, many species were aggregated both at sapling and adult stages (Okuda et al. 1997, He et al. 1997). Although aggregated patterns are dominant, very diverse spatial patterns of tree species were described in a 50-ha plot in Pasoh Forest Reserve in Peninsular Malaysia (Manokaran et al. 1992), where distribution of tree species appears to depend on topography, wet soil, the position of large mother trees, and on canopy gaps.

Habitat separation as a result of differentiation in habitat niche is a simple and obvious mechanism that explains species coexistence in plant communities (Grubb 1977). However, the cause of aggregated distribution, the differentiation of habitat niche among tree species, and the intra-community structure such as habitat guild have not been sufficiently studied in tropical forests.

Hill dipterocarp forests, which are well developed on the ridges throughout Peninsular Malaysia and Borneo, are characterised by the distinctive topographic categories, namely ridge, slope and valley. It is expected that habitat separation of tree species that depends on topography and other environmental conditions is more clearly detected in the hill dipterocarp forest than in lowland dipterocarp forest where topography is less undulated.

Canopy gap dynamics also contribute to the spatial patterns of tree species. Armesto et al. (1986) reported that large-scale disturbances (such as landslides, fire, volcanic eruption and hurricanes) increase the proportion of random distribution species, whereas canopy gaps due to tree falls act to increase aggregated patterns. In addition to the difference of topography, densities of understorey palm or bamboo colonies differ between lowland and hill dipterocarp forests. Bertam palm (Eugeissona tristis) and a common bamboo species (Gigantochloa scortechinii) seem to affect the spatial distribution of common tree species in a hill dipterocarp forests (Symington 1943, Wyatt-Smith 1959, 1963, Burgess 1969, 1971, 1975, Whitmore 1984, Wong 1995).

We aimed to study the spatial distribution patterns of the 30 most common tree species according to topography, canopy gaps, and understorey vegetation in a hill dipterocarp forest. The following questions were addressed:

- Do common tree species show aggregated or random distribution?
- Are habitat guilds dependent on topography recognised in the hill dipterocarp forest?
- Does understorey vegetation affect the spatial pattern of common tree species?
- Are there gap-dependent species in the common species?

Materials and methods

Study area

In 1992, we set up a 6-ha plot $(200 \times 300 \text{ m})$ in a hill dipterocarp forest at the Semangkok Forest Reserve (SFR), which is located beside the road on the way to

Fraser's Hill about 65 km north of Kuala Lumpur, Selangor, Peninsular Malaysia. The study plot is located within compartment 30 of SFR. It is a virgin jungle reserve of about 28 ha surrounded by secondary forests that were selectively logged in the 1980s. A typical hill dipterocarp forest has developed on the narrow ridge and steep slope (Putz 1978), ranging from 340 to 450 m above sea-level. The plot has east and west facing slopes and a ridge (Figure 1). The nearest meteorological station is at Kuala Kubu Bahru, 15 km southwest of the plot; the average annual rainfall is 2414 mm and the average annual minimum and maximum temperatures are 21.9 °C and 33 °C respectively (Saifuddin Sulaiman et al. 1991).

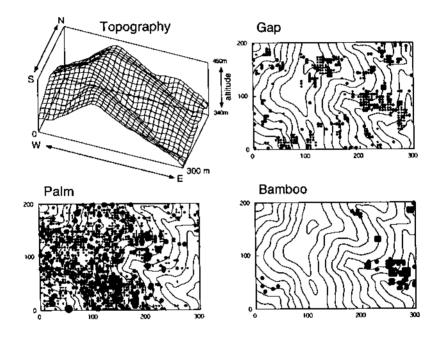


Figure 1. Topography of the 6-ha plot and the distributions of canopy gaps, palm (Eugeissona tristis) and bamboo (Gigantochloa scortechinii) on the 6-ha plot in Semangkok Forest Reserve, Peninsular Malaysia. In the map of gaps, small and large closed circles show 5-m and 10-m height gaps respectively. In the map of palm, the size of closed circles shows the abundance of palm individuals per 5×5 m quadrat. In the map of bamboo, closed circles show the presence of bamboo culm at the 5×5 m quadrat.

Plot establishment

We divided the 6-ha plot into $150\ 20 \times 20$ m quadrats and $2400\ 5 \times 5$ m subquadrats. All young and mature trees ≥ 5 cm diameter at breast height (dbh) were tagged, measured, and identified in 1993, 1995 and 1997. The position of each tree was coded to each 5×5 m that was the smallest unit of spatial distribution. This method follows that used for a temperate 6-ha plot (Masaki et al. 1992).

To examine the distribution of canopy gaps in the 6-ha plot, we checked tree height at the center of 5×5 m subquadrats using a 10-m pole and by visual observation in January-February 1994. This is similar to the gap census in the 50-ha plot at Barro Colombo Island (BCI) (Hubbell & Foster 1986a). We defined '5 m gap', '10 m gap' and 'closed canopy' in tree heights of 0-5 m, 5-10 m and >10 m respectively. The number of palm individuals (Eugeissona tristis) and the presence or absence of bamboo culm (Gigantochloa scortechinii) were checked in each 5×5 m subquadrat simultaneously with gap census.

Analysis

The 30 most common tree species among a total of 455 species \geq 5 cm d.b.h. were analysed using the recensus data set in 1995. Spatial patterns were analysed by Morisita's I δ -index where the significance of aggregation or randomness was tested by F-value (Morisita 1959). Pairwise interspecific spatial association was estimated by Iwao's ω -index (Iwao 1977) with the unit quadrat of 400 m² (20 \times 20 m). Dissimilarity index for cluster analysis was calculated as follows:

$$D = (1 - \omega) / 2 \tag{1}$$

where D is dissimilarity index ranging from 0 (complete overlap) to 1 (complete separation). See Masaki et al. (1992) and Yamamoto et al. (1995) for examples of this index used in forest ecology. The ω -index is as follows:

$$\omega_{(\star)} = (\gamma - \gamma_{(ind)}) / (1 - \gamma_{(ind)}) \text{ for } \gamma \ge \gamma_{(ind)}$$
 (2)

or

$$\omega_{(.)} = (\gamma - \gamma_{(ind)}) / \gamma_{(ind)}$$
 for $\gamma \le \gamma_{(ind)}$ (3)

where

$$\gamma = \sqrt{\left[\frac{m_{YX}^{*}}{m_{X}} \cdot \frac{m_{XY}^{*}}{m_{Y}}\right] / \left[\frac{m_{X}^{*}+1}{m_{X}} \cdot \frac{m_{Y}^{*}+1}{m_{Y}}\right]}$$
(4)

$$\gamma_{\text{(ind)}} = \sqrt{\frac{m_{\chi}}{m_{\chi}^* + 1} \cdot \frac{m_{\gamma}}{m_{\gamma}^* + 1}}$$
 (5)

and m_{χ} , m_{χ}^* , m_{γ} and m_{χ}^* are mean density and mean crowding (Lloyd 1967) of species X and Y respectively. In the equation (4), $m_{\chi\chi}^*$ and $m_{\chi\chi}^*$ are mean crowding on species Y by species X and that on species X by species Y respectively. More details of equations are shown in Iwao (1977). Species groups were recognised by cluster analysis with the group-average method (Greig-Smith 1983) that is one of common clustering procedure. Cluster analysis was carried out by the statistics program SYSTAT (SYSTAT, Inc. 1992).

The associations among the distribution of 30 most common tree species and topographic categories (ridge, slope and valley), canopy gap, and understorey vegetation types (palm and bamboo) were tested by Fisher's exact probability test using the statistics program StatView (Abacus Concepts Inc. 1992). One hundred and fifty 20 × 20 m quadrats were separated into ridge, slope, and valley. The ridge quadrat was defined as a 20 × 20 m quadrat less than 15 m in undulation and higher than 400 m in mean elevation. Valley quadrats were decided by the counter map and the visual observation at each quadrat. The other quadrats except ridge and valley quadrats were defined as slope quadrats. In the Fisher's test (2×2 test) 150 quadrats were always divided into three types; ridge quadrats and the others, slope quadrats and the others, and valley quadrats and the others. The gap quadrat was defined as a 20 × 20 m quadrat containing more than four gap-subquadrats (one subquadrat, 5×5 m = 25 m²). The palm quadrat was defined as a 20×20 m quadrat which included more than 20 palm individuals. This stemless palm usually develop to a multi-leaved individual. The bamboo quadrat was a 20×20 m quadrat which included a living culm of bamboo. In the Fisher's test 150 quadrats were divided into gap quadrats and the others, palm quadrats and the others, and bamboo quadrats and the others in each calculation. The associations among the topographic categories (ridge, slope, valley) and other three factors (gap, palm, and bamboo) were also analysed by the Fisher's test.

The reasons we used a 20×20 m quadrat as the size to analyse spatial distribution were as follows: 1) smaller quadrats such as 5×5 m or 10×10 m contain too few individuals to analyse interspecific spatial association, 2) larger quadrats such as 50×50 m or 100×100 m contain heterogeneous topography, complex canopy layers, and different densities of palm or bamboo patches. These quadrats, therefore, are inadequate to analyse the spatial associations among the distribution of common species, topography, gaps, palm, and bamboo. The size of 20×20 m is an arbitrary size to analyse the spatial distribution of common tree species in a hill dipterocarp forest.

Results

A total of 455 tree species were identified in the plot. The total basal area of stems ≥ 5 cm dbh in the plot was 42.9 m² ha¹ where *Shorea curtisii* dominated with 29.0% of the total basal area (Table 1). The 30 most common tree species contain emergent, main canopy and understorey tree species (Table 1).

Total gap area was 15.6% of which about half were 5-m gaps and another half were 10-m gaps (Figure 1). About 11% of canopy gaps were overlapped by bamboo colonies, because tree recruitments were sometimes inhibited by bamboo culms, and bamboo invaded into new gaps. Although most of the gaps had originated from tree falls, a small landslip had also made a gap at the upper part of slope in the plot.

Bertam palm, Eugeissona tristis, occupied 40% of 5×5 m quadrats in the 6-ha plot except in the shallow valley (Figure 1). In particular, palm density was high on the ridge; the maximum density was 55 individuals/400 m² and the mean density of palm was 380 individuals ha¹. The distribution area of palm largely overlapped with that of Shorea curtisii. The distribution of bamboo was restricted to the lower slope (Figure 1). This bamboo occurred in 3% of the 6-ha plot.

Most species showed significant aggregated patterns and only two species, Payena lucida and Scaphium macropodum, were randomly distributed through all quadrat sizes (Table 2). However, aggregation depended on the quadrat size; Crypteronia griffithii, Myristica iners and Artocarpus lanceifolius were not aggregated under 20×20 m quadrat sizes and Dacryodes rostrata was not aggregated over 50×50 m quadrat sizes. As a result, 24 species showed significant aggregated pattern in the 20×20 m quadrat size.

Table 1. Population parameters and abbreviations of the 30 most common tree species

Species	Den	sity	Basal	area	Max. dbh	Abbreviations
· · · · · · · · · · · · · · · · · · ·	(No. ha ⁻¹)	(%)	(m² ha-1)	(%)	(cm)	
Shorea curtisii	53.3	5.7	12.44	29.0	161.1	SHORCU
Lithocarpus wallichianus	30.2	3.2	1.13	2.6	54.5	LITHWA
Teijsmanniodendron coriaceum	24.2	2.6	0.61	1.4	42.5	TEIJCO
Antidesma cuspidatum	20.3	2.2	0.44	1.0	61.9	ANŤICU
Scaphium macropodum	19.2	2.0	2.24	5.2	101.7	SCA2MA
Diospyros latisepala	18.8	2.0	0.01	0.0	28.7	DIOSLI
Eurycoma longifolia	18.7	2.0	0.11	0.3	27.1	EURYLO
Pimelodendron griffithianum	13.0	1.4	0.38	0.9	41.9	PIMEGR
Aiđia wallichiana	13.0	1.4	0.20	0.5	34.8	AJDIWA
Macaranga triloba	12.7	1.4	0.09	0.2	24.1	MACATR
Canarium patentinervium	12.2	1.3	0.11	0.2	37.8	CANAPA
Artocarpus lanceifolius	10.8	1.2	0.49	1.1	56.0	ARTOLA
Xanthophyllum griffithii	10.5	1.1	0.38	0.9	55.4	XANTGR
Dacryodes rostrata	10.3	1.1	0.21	0.5	45.7	DACRRO
Myristica iners	10.2	1.1	0.48	1.1	61.9	MYRIIN
Vatica odorata	9.7	1.0	0.22	0.5	39.8	VATIOD
Diospyros venosa	9.7	1.0	0.08	0.2	20.0	DIOSVE
Dacryodes rugosa	9.3	1.0	0.21	0.5	35.1	DACRR1
Payena lucida	9.2	1.0	0.55	1.3	*150.2	PAYELU
Archidendron bubalinum	8.7	0.9	0.13	0.3	31.8	ARCHBU
Milletia atropurpurea	8.0	0.9	0.17	0.4	50.8	MILLAT
Vitex longisepala	7.8	0.8	0.07	0.2	25.6	VITELO
Diospyros styraciformis	7.7	0.8	0.07	0.2	22.4	DIOSST
Anisoptera curtisii	7.5	0.8	0.97	2.3	123.8	ANIICU
Eugenia ridleyi	7.2	0.8	0.26	0.6	60.0	EUGERI
Ochanostachys amentacea	7.0	0.7	0.51	1.2	57.8	OCHAAM
Crypteronia griffithii	6.5	0.7	0.22	0.5	55.8	CRY2GR
Knema conferta	6.3	0.7	0.10	0.2	29.5	KNEMCO
Diosyros sumatrana	6.3	0.7	0.07	0.2	23.5	DIOSSU
Dialium platysepalum	6.0	0.6	0.37	0.9	73.3	DIALPL
Other species	543.2	57.9	19.60	45.7		
Total	937.3	100.0	42.9	100.0		

^{*}Large buttress.

Three species groups, A, B and C were recognised by the cluster analysis (Figure 2). The statistical significance between the distribution of the 30 most common tree species and ridge, slope, valley, gap, palm, and bamboo is shown in Table 3 where species order followed the result of the cluster analysis (Figure 2). The 20×20 m quadrats defined as ridge, slope, valley, gap, palm and bamboo quadrats were numbered as 31, 95, 24, 39, 51 and 22 respectively.

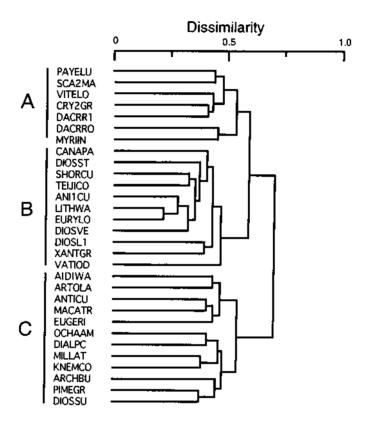


Figure 2. Cluster diagram of spatial association for the 30 most common tree species based on dissimilarity derived from Iwao's ω -index calculated for 20×20 m quadrats

Group A (7 species) was randomly distributed or aggregated around valleys (Figure 3). Vitex longisepala and Crypteronia griffithii showed positive association with valley and negative association with gap or bamboo. These two species are recognised as valley species. Dacryodes rugosa showed positive association with palm and negative association with gap. Myristica iners showed negative association with slope. Payena lucida and Scaphium macropodum and Dacryodes rostrata were randomly distributed throughout all quadrat sizes or on the sizes over 50 m (Table 2). They did not show significant association with any category. Although Scaphium macropodum was widely distributed, large trees were not distributed on the ridge.

Table 2. Analysis of distribution pattern and spatial association based on Morisita's 18-index and Iwao's ⊕-index. Grid sizes are 10 × 10 m to 100 × 100 m. Abbreviations of species name are shown in Table 1. Species order and group follow the result of cluster analysis (Figure 2).

Species	Group			18					to - index	
į		10×10m	10×20	20×20	50 × 50	50 × 100	100×100	Total	Мах.	Min.
PAYELU	4	0.84	0.84	0.84	1.07	1.12	1.00	-3.14	0.17	-0.56
SCA2MA	∀	0.82	0.73	96.0	66.0	1.00	1.03	-1.92	0.14	-0.52
WITELO	∢	12.77**	10.55**	8.19**	5.71**	3.33**	1.75**	90.9	0.19	-1.00
CRY2GR	¥	2.43	1.62	1.42	1.55**	1.77**	1.77**	-2.74	0.20	.1.00
DACRRI	V	3.12**	2.73**	1.95**	1.62**	1.67**	1.31**	4.89	0.20	-1.00
DACRRO	K	2.22*	1.90*	1.82*	1.19	1.07	1.06	4.69	0.15	-0.75
MYRIIN	4	1.31	1.48	1.31	1.23*	1.05	1.06	-2.08	0.12	-0.61
CANAPA	₩.	2.97**	2.40**	2.05**	1.63**	1.47**	1.11•	-3.51	0.30	-0.84
DIOSST	8	6.38**	4.06**	4.64**	2.53**	1.86**	1.50**	-5.35	0.35	-1.00
SHORCU	æ	1.69**	1.64**	1.49**	1.38**	1.30**	1.24**	-2.09	0.42	-0.88
TEIJCO	æ	3,39**	3.10**	2.41**	1.91**	1.74**	1.32**	4.19	0.37	68.0
ANIICU	4	3.03*	3.94**	3.94**	2.50**	1.64**	1.49**	-6.15	0.50	00:1-
LITHWA	4	8.46**	7.27**	3.64**	2.60**	2.31**	1.93**	-5.66	0.59	1.00
EURYLO	æ	3.57**	3.57**	3.09**	2.45**	1.74**	1.53**	4.70	0.59	€.10
DIOSVE	æ	2.54*	3.27**	2.45**	2.15**	1.65**	1.64**	.80 4.80	0.51	1.00
NOSE1	æ	2.09**	2.18**	1.94**	1.75**	1.50**	1.24**	-3.96	0.28	-0.97
KANTGR	æ	2.46**	2.00*	1.31	1.36**	1.23**	1.15*	4.18	0.30	0.75
/ATIOD	m	3.27**	4.72**	4.90**	2.95**	2.14**	2.13**	-7.91	0.33	00:1-
AIDIWA	ပ	1.60	1.50	1.65**	1.54**	1.49**	1.37**	-2.74	0.17	45.0
ARTOLA	O	1.44	1.30	1.01	1.38**	1.16**	1.10	¥.4	0.17	-0.65
ANTICU	ပ	3.01**	2.36**	1.91	1.71**	1.58**	1.16**	-2.68	0.20	-0.58
MACATR	ပ	15.37**	12.74**	7.58**	3.29**	2.07**	1.52**	-9.08	0.20	-0.91
EUGERI	ပ	5.32**	3.32**	1.99*	1.70**	1.44**	1.14	-3.87	0.20	-0.56
OCHAAM	ပ	2.09	2.09	2.26**	1.37*	1.42**	1.25**	-6.47	0.19	0.84
DIALPL	ပ	2.86	1.90	2.38**	1.56**	1.50**	1.32**	-7.75	0.19	-0.95
MILLAT	ပ	1.60	1.60	1.73*	1.68**	1.32**	1.33**	-5.76	0.24	-0.81
KNEMCO	ပ	15.36**	8.53**	7.47**	6.59**	6.69**	4.59**	-15.00	0.24	·1.00
ARCHBU	ပ	3.17**	2.04	1.81	1.25*	1.10	1.17*	-5.63	0.19	-0.83
PIMEGR	ပ	1.60	1.50	1.80**	1.64**	1.47**	1.38**	-5.44	0.26	0.77
DIOSSII	C	***								

**: p < 0.01; *: p < 0.05.

Group B (11 species) was a very homogeneous group. Most species were associated positively with ridge or palm, and negatively with bamboo. Lithocarpus wallichianus and Eurycoma longifolia were strongly aggregated to the main ridge. Large trees of Shorea curtisii were restricted on the ridge, while small trees were distributed from the middle slope to the ridge. Congeneric species, Diospyros styraciformis, D. venosa and D. latisepala, showed largely overlapped distribution. Vatica odorata was distributed on the southern half of the ridge, which might depend on the position of mother trees and the regeneration site.

Table 3. Significance test of spatial association based on Fisher's exact probability test among the distribution of the 30 most common tree species and ridge, slope, valley, gap, palm and bamboo. Species order and group follow the result of cluster analysis (Figure 2).

			Тородтарну		Canopy	Understore	ey vegetation
Species	Group	Ridge (n=31)	Slope (n=95)	Valley (n=24)	Gap (n=39)	Palm (n=51)	Bamboo (n=22)
PAYELU	A						
SCA2MA	A						
VITELO	Α			++	-		
CRY2GR	Α		•	++			-
DACRR1	A				-	++	
DACRRO	A						
MYRIIN	A						
CANAPA	В					+	
DIOSST	В	+				++	-
SHORCU	В	++	-			++	
TEIJCO	В	++			-	++	-
ANI1CU	В	++				++	
LITHWA	В	++		•		++	••
EURYLO	В	++				++	
DIOSVE	В	++					
DIOSLI	В	++		••		++	••
XANTGR	В	+				+	
VATIOD	В	++				++	•
AIDIWA	С						
ARTOLA	C	••				•	
ANTICU	C						
MACATR	C				++		+
EUGERI	C					-	
OCHAAM	C	-					
DIALPL	С						+
MILLAT	С				+		++
KNEMCO	C	-			+	••	++
ARCHBU	С						
PIMEGR	C	•	+				
DIOSSU	С	-				••	

^{+,-:} p < 0.05; ++,--: p < 0.01. +: positive association. -: negative association, n = number of 20×20 m quadrats.

Group C was the most heterogeneous. Pimelodendron griffithianum was the only species that showed positive association with slope. Artocarpus lanceifolius, Ochanostachys amentacea and Diospyros sumatrana were negatively associated with ridge or palm, which showed slope preference. Macaranga triloba, Millettia atropurpurea and Knema conferta were positively associated both with gap and bamboo. Dialium platysepalum was significantly associated with bamboo (Table 3). Eugenia ridleyi showed negative association with palm. The other three species, Aidia wallichiana, Antidesma cuspidatum and Archidendron bubalinum, had no associations with any other categories.

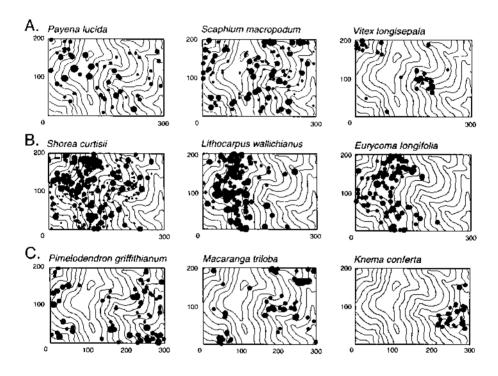


Figure 3. Examples of spatial patterns. Groups A, B and C follow the result of cluster analysis (Figure 2). Closed circles show relative diameter at breast height in each tree species.

As a result, thirteen species showed significant positive association with topographic categories; two species were associated with valley, ten species with ridge, and one species with slope. Six species showed only negative association with topographic categories (Table 3).

Significant association was also detected among the categories. Palm was positively associated with ridge (p<0.01) but negatively with valley (p<0.01). Bamboo was positively associated with gap (p<0.05), and negatively with palm (p<0.01) and ridge (p<0.05). Gap did not have any significant association with the three topographic categories but had positive association with bamboo (p<0.05).

The degree of inter-species overlaps in spatial distribution was well represented by the ω-index (-1:complete separation to 1:complete overlap), and the sum of ω-index with other 29 species ranging from 29 to -29 (Table 2). If a species was completely segregated with other 29 tree species, all inter-species ω-index was -1, and the sum of ω-index became -29. The largest inter-species ω-index of 0.59 was obtained between Lithocarpus wallichianus and Eurycoma longifolia distributed on the ridge. The means of inter-species ω-index in Groups A, B, and C were 0.17, 0.41, 0.27 respectively. This result shows the largest overlap among Group B of ridge species. Knema conferta, which is a typical aggregated distribution species on the lower slope, had the least sum of ω-index of -15.0, because it was completely segregated with many other species. On the other hand, Scaphium macropodum had the lowest inter-species ω-index, 0.14, but showed relatively large sum of ω-index, -1.92.

Discussion

Aggregated spatial patterns were predominant among the 30 most common tree species. However, the degree of aggregation was continuous and the degree of significance depended on the quadrat sizes. This hill dipterocarp forest allows the presence of diverse aggregation patterns and less number of randomly distributed tree species. These spatial patterns are not specific to tropical forests; the forest communities in tropical dry, warm temperate and cool temperate forests also consist of many aggregated species and small numbers of randomly distributed species (Hubbell 1979, Masaki et al. 1992, Tanouchi & Yamamoto 1995, Yamamoto et al. 1995). Patterns of aggregation or randomness, therefore, do not directly explain the higher tree species diversity in the tropical forest and the abundance of each tree species.

The cause of aggregation patterns depends on the spatial scale. At large scales > 2500 m², topography, edaphic factors (Pemadasa & Gunatilleke 1981, LaFrankie 1996), and large historical disturbances contribute to the aggregated patterns. Although there was a distinctive topographic gradient, evidence for large-scale disturbances was not detected in the plot. Variation of species composition among mixed dipterocarp forests has been explained by the soil chemistry such as contents of potassium or magnesium (Baillie et al. 1987, Ashton & Hall 1992). On the other hand, variation of species composition or spatial patterns of tree species within a forest community was not well explained by soil chemistry (Newbery et al. 1996). Topography and soil water condition were emphasised to explain the distribution pattern of tree species in a tropical forest (Newbery et al. 1996, Walsh 1996). Rare drought events restrict the tree species dominating on the ridge where soil is shallower and becomes much drier than the slope or valley sites. However, soil nutrients were dependent on topography in this plot (Tange et al. 1998); total amounts of nitrogen and phosphorus were rich on the ridge. Tree species distributed on the ridge probably depend on both water availability and soil chemistry.

At the micro scale $< 2500~\rm m^2$, tree gaps (Richards & Williamson 1975, Armesto et al. 1986), seed dispersal mode, regeneration around the mother trees and stress factors may cause aggregated patterns. Small- or medium-sized gaps were predominant in the plot. Most of the 30 most common tree species were significantly aggregated at the scale of $10 \times 10~\rm m$ to $20 \times 20~\rm m$ quadrat sizes similar to the size of gaps. Particularly, Macaranga triloba and Knema conferta showed strong aggregation in the quadrat of size less than $20 \times 20~\rm m$. Although new recruits of most tree species probably depend on the canopy gaps, a distinctive association with current gaps was detected for Macaranga triloba, Millettia atropurpurea and Knema conferta. Macaranga triloba is a well-known light-demanding pioneer species, but characteristics of other two species have not been studied.

Aggregation patterns also depend on the seed dispersal ability (Poore 1968). The tree species having lower seed dispersal ability will make a clump around the mother trees. This is in contrast with the spatial pattern of *Scaphium macropodum*, which has an effective organ for wind dispersal and was distributed at random throughout the plot. This random distribution pattern occurs for trees larger than 5 cm dbh in the plot. On the other site, seedlings and saplings of *Scaphium macropodum* showed aggregated patterns around mother trees (Yamada & Suzuki 1997).

Vitex longisepala and Crypteronia griffithii were restricted to the valley and valley head where shade and wet conditions were predominant. This is an example of the aggregated patterns dependent on specific stressed conditions similar to swamp species (Poore 1968, Hubbell & Foster 1986b).

Habitat guild was recognised in ridge species. Species group B was the most distinctive and homogeneous species group. Most species of the group showed significant positive associations with ridge and palm, and negative association with bamboo. The distribution of tree species largely overlapped within the group B but not with other groups. This group, therefore, is recognised as habitat guild dominated on the ridge. Other species groups were mixtures of species whose spatial patterns and associations with the categories were different from each other. In lowland dipterocarp forest, only swamp species were distinctively distributed with other tree species, because topography was homogeneous (Poore 1968). Habitat guilds were also found in a neotropical forest (Hubbell & Foster 1986b) where five habitat guilds, "Slope", "Indifferent", "Plateau", "Streamside/Ravine" and "Swamp" were recognised.

Among the six site categories, ridge and palm were positively associated. The effects of ridge and palm on tree distribution were not completely separated. It has been pointed out that this stemless palm prevents regeneration of canopy trees (Chong 1970, Burgess & Lowe 1971). The large area of foliage interrupts dispersed seeds and shades the seedlings around the palm, and the thick leaf litter of the palm prevents establishment of tree seedlings. However, it was reported that Shorea curtisii, which is the most abundant and largest tree species in the ridge, can survive for several years under these conditions (Whitmore 1984). This species was dominant through most size classes on the ridge. Consequently, water availability and soil chemistry related to ridge topography, regeneration condition related to dense palm cover, and a large stocking of S. curtisii make a fundamental set of environmental conditions on the ridge. Tree species of the ridge guild probably depend on or tolerate these characteristic conditions on the ridge.

Acknowledgements

We are grateful to the Director General of FRIM for the support of and permission to conduct our study. We thank E. Suzuki (Kagoshima University) for his program to analyse spatial pattern, and Y. Maruyama (FFPRI, Hokkaido Research Center), H. Tanouchi (FFPRI, Hokkaido Research Center) and N.Osawa (Kyoto University) for their help in the field work, budget management and arranging the contacts between FRIM and FFPRI. We also wish to thank the field assistants, Muzaid Hj. Salleh, Fizi Mazlan, Mohd. Fauzi Abu Bakar, Ghazali Jaafar, Shahrulzaman Idris, Shahrie Md. Som and Abd Wahab Nali.

This study was supported mainly by the Global Environment Research Program, Grant No. E-1, Japan Environment Agency. This is a part of a joint research project of FRIM (Forest Research Institute Malaysia), UPM (Universiti Putra Malaysia), NIES (National Institute of Environmental Studies, Japan) and FFPRI (Forestry and Forest Products Research Institute, Japan).

References

- Armesto, J. J., Mitchell, J. D. & Villagran, C. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18:1–11.
- Ashton, P. S. & Hall, P. 1992. Comparisons of structure among mixed dipterocarp forests of northwestern Borneo. *Journal of Ecology* 80:459-481.
- BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPATRIC, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201-220.
- Burgess, P. F. 1969. Preliminary observations on the autecology of *Shorea curtisii* Dyer ex King in the Malay Peninsula. *Malayan Forester* 32:438.
- Burgess, P. F. 1971. Effect of logging on hill dipterocarp forest. Malayan Nature Journal 24:231-237. Burgess, P. F. 1975. Silviculture in the Hill Dipterocarp Forests of the Malay Peninsula. Malayan Forestry Department Research Pamphlet No.66. 97 pp.
- Burgess, P. F. & Lowe, J. S. 1971. The control of bertam (Eugeissona tristis Griff.), a stemless palm in hill forests of the Malay Peninsula. Malayan Forester 34:36-45.
- Chong, P. W. 1970. The effect of bertam control on regeneration of Shorea curtisii Dyer. Malayan Forester 33:166-175.
- CORNNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298-310 in Den Boer, P. J. & Gradwell, G. R. (Eds.) Dynamics of Populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers of Populations. Center for Agricultural Publishing and Documentation, Wageningen, Suriname.
- Greic-Smith, P. 1983. Quantitative Plant Ecology. Blackwell Scientific Publications, London. 359 pp.
- GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Review 52:107-145.
- HE, F., LEGEMDRE, P. & LAFRANKIE, J. V. 1997. Distribution patterns of tree species in a Malaysian tropical forest. Journal of Vegetation Science 8:105-114.
- HUBBELL, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203:1299–1309. Hubbell, S. P. & Foster, R. B. 1986a. Canopy gaps and the dynamics of a neotropical forest. Pp. 77–95 in Crawley, M. (Ed.) Plant Ecology. Blackwell, Oxford.
- HUBBELL, S. P. & FOSTER, R. B. 1986b. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. Pp. 205–231 in Soule, M. E. (Ed.) Conservation Biology. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Iwao, S. 1977. Analysis of spatial association between two species based on the interspecific mean crowding. *Research on Population Ecology* 18:243–260.

- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528.
- LAFRANKIE, J. V. 1996. The contribution of large-scale forest dynamics plots to theoretical community ecology. Pp. 63-79 in Turner et al. (Eds.) Biodiversity and the Dynamics of Ecosystems. DIWPA Series Vol. 1. The International Network for DIVERSITAS in Western Pacific and Asia, Kyoto.
- Lioyd, M. 1967. Mean crowding. Journal of Animal Ecology 36:1-30.
- MANOKARAN, N., LAFRANKIE, J. V., KOCHUMMEN, K. M., QUAH, E. S., KLAHN, J. E., ASHTON, P. S. & HUBBELL, S. P. 1992. Stand Table and Distribution of Species in the 50-ha Research Plot at Pasoh Forest Reserve. Research Data No. 1. Forest Research Institute Malaysia, Kepong. 454 pp.
- MASAKI, T., SUZUKI, W., NIYAMA, K., IDA, S., TANAKA, H. & NAKAHIZUKA, T. 1992. Community structure of a species rich temperate forest, Ogawa Forest Reserve, central Japan. *Vegetatio* 98:97–111.
- MORISITA, M. 1959. Measuring of dispersion of individuals and analysis of the distributional patterns.

 Memoirs of the Faculty of Science of Kyushu University Series E 2:215-235.
- Newbery, D. McC., Campbell, E.J. F., Proctor, J. & Still, M.J. 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. *Vegetatio* 122:193–220.
- Ogawa, H., Yoda, K. & Kira, T. 1961. A preliminary survey on the vegetation of Thailand. Nature and Life in Southeast Asia 1:21-157.
- OKUDA, T., KACHI, N., YAP, S. K. & MANOKARAN, N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rain forest—implications for regeneration and maintenance of species diversity. *Plant Ecology* 131:155–171.
- Pemadasa, M. A. & Gunatilleke, C. V. S. 1981. Pattern in a rain forest in Sri Lanka. *Journal of Ecology* 69:117-124.
- POORE, M.E.D. 1968. Studies in Malaysian rain forest. I. The forest on Triassic sediments in Jengka Forest Reserve. *Journal of Ecology* 56:143-196.
- Putz, F.E. 1978. A Survey of Virgin Jungle Reserves in Peninsular Malaysia. Research Pamphlet 73. Forestry Department Peninsular Malaysia, Kepong. 87 pp
- RICHARDS, P. & WILLIAMSON, G. B.1975. Treefalls and patterns of understory species in a wet lowland tropical forest. *Ecology* 56:1226–1229.
- SAIFUDDIN, S., ABDUL RAHMAN, N. & MUHAMMAD FARID, A. R. 1991. Watershed Research in Forest Plantation: I. Establishment and Physical Characteristics of Bukit Tarek Watershed. Research Pamphlet No.110. Forest Research Institute Malaysia, Kepong. 51 pp.
- Symington, C. F. 1943. Foresters Manual of Dipterocarps. Malayan Forest Records No. 16. 244 pp. (Reprinted with plates and a historical introduction, Penerbit Universiti of Malaya, Kuala Lumpur, 1974).
- Tange, T., Yagi, H., Sasaki, S., Niiyama, K. & Abd. Rahman, K. 1998. Relationship between topography and soil properties in a hill dipterocarp forest dominated by Shorea curtisitat Semangkok Forest Reserve, Peninsular Malaysia. Journal of Tropical Forest Science 10(3):398–409.
- Tanouchi, H. & Yamamoto, S. 1995. Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. *Vegetatio* 117:51–60.
- Walsh, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. Journal of Tropical Ecology 12:385-407.
- WHITMORE, T. C. 1984. Tropical Rain Forests of the Far East. 2nd edition. Clarendon, Oxford. 352 pp.
- Wong, K. M. 1995. *The Bamboos of Peninsular Malaysia*. Malayan Forest Records No. 41. Forest Research Institute Malaysia, Kepong. 200 pp.
- Wyatt-Smith, J. 1959. The control of bertam palm—Eugeissona tristis, Griff. Malayan Forester 22:314–326. Wyatt-Smith, J. 1963. Manual of Malayan Silviculture for Inland Forests. (2 volumes). Malayan Forest Records No. 23. Forestry Department Peninsula Malaysia, Kepong.
- Yamada, T. & Suzuki, E. 1997. Changes in spatial distribution during the life history of a tropical tree, Scaphium macropodum (Sterculiaceae) in Borneo. Journal of Plant Research 110:179–186.
- YAMAMOTO, S., NISHIMURA, N. & MATSUI, K. 1995. Natural disturbance and tree species coexistence in an old-growth beech-dwarf bamboo forest, southwestern Japan. *Journal of Vegetation Science* 6:875–886.

USES, MANAGEMENT AND ECONOMIC POTENTIAL OF GARCINIA KOLA AND RICINODENDRON HEUDELOTII IN THE HUMID LOWLANDS OF CAMEROON

Elias T. Ayuk*,

ICRAF/SALWA, BP 320 Bamako, Mali

Bahiru Duguma",

IRAD/ICRAF Collaborative Agroforestry Project, BP 2123, Yaoundé, Cameroon

Steve Franzel,

ICRAF, P. O. Box 30677, Nairobi, Kenya

Joseph Kengue,

IRAD/NCRE Collaborative Project, BP 2067, Yaoundé, Cameroon

Matthias Mollet[†], Theophile Tiki-Manga

IRAD/ICRAF Collaborative Agroforestry Project, BP 2123, Yaoundé, Cameroon

&c

Pauline Zenkeng

IRAD/NCRE Collaborative Project, BP 2067, Yaoundé, Cameroon

Received September 1997

AYUK, E. T., DUGUMA, B., FRANZEL, S., KENGUE, J., MOLLET, M., TIKI-MANGA, T. & ZENKENG, P. 1999. Uses, management and economic potential of Garcinia kola and Ricinodendron heudelotii in the humid lowlands of Cameroon. Garcinia kola and Ricinodendron heudelotii are among the most preferred species in the humid lowlands of Cameroon. Garcinia kola fruits and Ricinodendron heudelotii seeds are highly valued and traded. The species grow in the wild and not much work has been done in domesticating them. As part of a prioritisation exercise a field survey

^{*}Corresponding author: Current mailing address: SADC-ICRAF Agroforestry Project,
c/o DR & SS, P.O. Box CY594 Causeway, Harare, Zimbabwe.
Tel: (263-4) 704531-7; Fax: (263-4) 728340; E-mail: eayuk@samara.co.zw

[&]quot;Current mailing address: USAID, Washington, DC, USA.

[†]Current mailing address: Birmensdorferstr. 299, 8055 Zurich, Switzerland.

was undertaken to quantify, at the farm-level, uses, management and economic potential of the species. Results from this study show that there are several uses of different products of the species including those for medicinal purposes and for home consumption. Desired improvement objectives include reduced time to bearing, reduced tree height, higher yield, increased fruit size and spreading the fruiting period. Improvement research in those lines might increase the value of the species to land users.

Keywords: Humid lowlands of Cameroon - non-timber forest products - Garcinia kola

- Ricinodendron heudelotii improvement farm level economic potential
- farmers' indigenous knowledge

AYUK, E. T., DUGUMA, B., FRANZEL, S., KENGUE, K., MOLLET, M., TIKI-MANGA, T. & ZENKENG, P. 1999. Penggunaan, pengurusan dan potensi ekonomi Garcinia kola dan Ricinodendron heudelotii di tanah pamah lembap di Cameroon. Garcinia heudelotii dan Ricinodendron heudelotii ialah antara spesies yang paling diutamakan di kawasan tanah pamah lembap di Cameroon. Buah-buahan Garcinia kola dan biji benih Ricinodendron heudelotii sangat tinggi nilainya dan didagangkan. Spesies ini tumbuh liar dan tidak banyak usaha dijalankan untuk mendomestikasinya. Sebagai sebahagian daripada keutamaan, satu kajian lapangan dijalankan untuk menjumlahkan, pada peringkat ladang, penggunaan, pengurusan dan potensi ekonomi spesies tersebut. Hasil kajian ini menunjukkan bahawa terdapat beberapa kegunaan produk yang berbeza bagi spesies ini termasuklah untuk tujuan perubatan dan kegunaan di rumah. Pembaikan objektifyang dikehendaki termasuklah mengurangkan masa untuk berbuah, mengurangkan ketinggian pokok, membanyakkan hasil, menambahkan saiz buah dan menyebarkan tempoh musim berbuah. Pembaikan penyelidikan dalam perkara-perkara tersebut mungkin akan dapat meningkatkan nilai spesies tersebut kepada mereka yang mengusahakan tanah di kawasan tersebut.

Introduction

The tropical moist forests which dominate the humid lowlands of Cameroon are known to be among the richest flora on earth. These forests, besides their role in maintaining and enhancing environmental quality, are also a reservoir of enormous quantity of animal and plant communities that are vital for human existence and constitute an integral part of the rural economies. Duguma et al. (1990) found that a great number of species are found in this ecozone. Local communities in the region depend heavily on this resource as a source of food, condiment, medicine and raw materials for various uses.

In the next few years forest products, especially non-timber forest products (NTFPs), will become of even greater economic importance for a number of reasons. First, demographic pressures on land resources have led to the need to explore non-conventional sources for the provision of badly needed food to meet the needs of the rising population. Secondly, owing to population pressure and rural to urban migration, the fallow periods in many areas have declined from over 10 years to less than 5 years (1 to 3 years in most places) rendering the system economically inefficient and environmentally/ecologically unsustainable. Thirdly, forest products provide opportunities for earning cash and consequently achieving the goal of income diversification as a strategy to

minimise risks associated with their conventional farming practices. The cash crop production sector is negatively affected by the low and fluctuating market prices. Many of the products from the tropical rain forest are being currently traded on regional and international markets and can play an essential role in earning badly needed foreign exchange.

The extent to which NTFPs can satisfy the needs of land users depends largely on how the trees can be integrated into the land use system. Multi-strata sequential and simultaneous agroforestry systems can be potential strategies for achieving this goal (Cooper et al. 1996). In fact, in the context of West Africa, these systems already exist (Okafor & Fernandes 1987). The existing multi-strata home garden system is, however, characterised by low species diversity and inferior genetic materials—based more on availability of planting material than on economic value and genetic superiority—that hardly contribute to the well-being of the farmers beyond the subsistence level. This system provides ample opportunities for improvement relying on: (1) a better understanding of farmers' indigenous knowledge of their ecosystem; (2) farmers' intended uses of trees (preferred products and services) and how they are integrated in their land use system; and (3) the introduction of appropriate superior plant material.

Most of the tree species that are of great importance to land users in the humid lowlands of Cameroon grow in the wild since they have not been domesticated. Recently, there has been a great awareness of the need to domesticate indigenous tree species. Domestication is a dynamic process which develops from selecting the species to be domesticated, through background socio-economic studies, to the actual germplasm collections and genetic improvement (Leakey & Jaenicke 1995). Domestication ensures that valuable species are easily accessible to and manageable by land users.

The choice of species that can be improved at any given time is limited by cost considerations. What species to improve should depend on the potential products of the particular species and their value to land users. Previous research has reported information on the type of products and species from which the various products are harvested (FAO 1981, World Resource Institute 1985, Okafor & Fernandes 1987, Falconer 1992). However, despite recent efforts, empirical data on the relative economic importance of NTFPs are not available at the farm level. Detailed quantification of the monetary value of commonly used NTFPs is essential in identifying key products and species that can improve the welfare of local communities. This kind of information can be useful in identifying candidate species for improvement research.

A previous study identified the following 10 species in descending order as the ones most preferred by farmers in the region: Irvingia gabonensis, Baillonella toxisperma, Dacryodes edulis, Elaeis guineensis, Ricinodendron heudelotii, Alstonia boonei, Guibourtia demensei, Entandrophragma cylindricum, Garconia lucida and Chlorophora excelsa (Mollet et al. 1995, Adeola et al. unpublished data). The objective of this paper is to assess, at the farm level, the uses, management and economic value of Garcinia kola and Ricinodendron heudelotii in the humid lowlands of Cameroon.

Description of species

Garcinia kola Heckel (Guttiferae)

The species is found in moist semi-deciduous forest of secondary growth. Its area of distribution extends from Sierra Leone to the Democratic Republic of Congo (former Zaire). In Cameroon, it can be found in some regions in Mamfe and in Bertoua and Moloundou. The large tree reaches 30 to 40 m in height and 100 cm in diameter. The crown is narrowly triangular with sinuous upright branches. The bole is straight, very high, cylindrical or conical, and sometimes enlarged at the base.

Multiplication by seed has been reported with a germination rate of 80%. Young plants must be shaded.

Garcinia nuts are consumed as an aphrodisiac. The nuts figure prominently in national and inter-regional trade and fetch very high prices in the markets. The tree is a good timber and dead branches are used for firewood.

Ricinodendron heudelotii (Baill) Pierre ex Pax (Euphorbiacecae)

Ricinodendron heudelotii is commonly found in the secondary forest extending from Guinea to Angola and in East Africa. It is a dioecious tree and is common and locally abundant in secondary forests in Cameroon. The tree can reach 40 m in height and 120 cm in diameter.

Germination is slow with a rate of less than 40%. However, growth is rapid for young plants in open spaces. Vegetative propagation techniques have been developed for the species (Shiembo 1994, Shiembo et al. 1997).

The main uses of this species include those of the seeds which are a sought-after ingredient for soups and a variety of dishes; the wood is used for making household implements, drums and carvings (Shiembo 1994), and the bark is used as medicine to treat elephantiasis (Abbiw 1990) and leprosy (Bokemo 1984). The oil obtained from the seeds is also used for soap and varnish making (Abbiw 1990). The species is of high cash value to land users in Cameroon. It has been reported that for the period January to July 1995, about 172 tons of the seeds were traded in the humid forest zone of Cameroon for a value of \$US 460 000. These data were based on information collected from farmers, transporters and traders in 31 markets located in 5 provinces (CIFOR 1996).

Methods

Study site

The humid lowlands are defined as areas below 1000 m altitude with an annual precipitation of above 1500 mm, a growing period of 270-365 days and covered by tropical moist forest vegetation. In Cameroon, the humid lowlands are divided

into two zones: the coastal lines with an altitude of 0 to 300 m and the continental plateau with an altitude ranging between 600 and 800 m above sea-level (Tonye et al. 1986). The area delimiting the humid lowlands in Cameroon together with the study sites is shown in Figure 1.

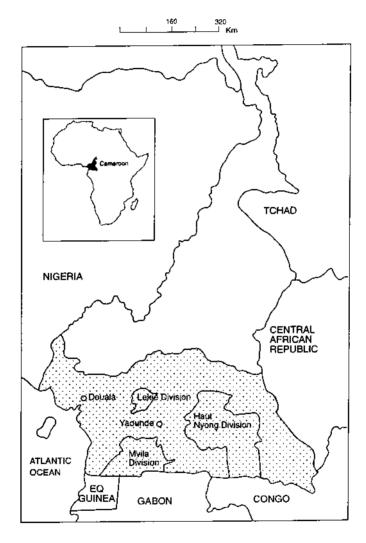


Figure 1. Study sites in the humid lowlands of Cameroon with elevation less than 1000 m above sea-level

Using secondary data on market accessibility, population density, ethnic groups and infrastructure, the priority land use system was divided into three strata corresponding to three divisions (administrative units) located in three different provinces (Table 1). The study was conducted in Mvila (South Province), Lekié (Centre Province) and Haut Nyong (East Province) administrative divisions of Cameroon.

Division	Ethnic group	Market accessibility	Population density
Haut Nyong	Maka, Bama, Pygmies	Low	Low
Lekié	Eton	High, good infrastructure	High
Mvila	Bulu	Medium, export area but poor infrastructure	Medium

Table 1. Variables used to stratify the study area

Mvila is located at latitude 2° 22'-2° 29'N and longitude 10°17'-12°14'E. The division shares boundaries with Equatorial Guinea and the Republic of Gabon. The mean monthly temperature is 24 °C. Market accessibility is moderate in this division and there is modest infrastructure. The population density is medium (10 inhabitants km²) and the dominant ethnic group is the Bulu.

The Lekié division is situated between latitude 3° 50′- 4°30′N and longitude 11° 0′-12° 0′E. Mean monthly of the division is 25 °C. This is a highly populated area (25 inhabitants km²) with good infrastructure and easily accessible to urban markets. The Etons are the major ethnic group in the division.

Haut Nyong division is located at latitude 2°0'-4°30'N and longitude 12°30'-14° 40'E. The mean monthly temperature is 22.5 °C. The division is not easily accessible to urban markets. Population density is low (4 inhabitants km²) and infrastructure is poor. The Makas constitute the major ethnic group.

In all three divisions, the rainfall pattern is bimodal, with two rainy seasons occurring during mid-March to mid-July and mid-August to mid-November. Mean annual rainfall ranges from 1650 mm in Haut Nyong to 1860 mm in Mvila. During the rest of the months, referred to as main (mid-November to mid-March) and minor (mid-July to mid-August) dry seasons, total monthly rainfall hardly exceeds 50 mm.

In Lekié, where the population pressure is high, most of the economically important trees have been removed. Farm activities are very intensive and, therefore, the dominant vegetation type is of degraded secondary forest or fallow lands with patches of grass fallow increasing from south to the north. Tree species such as Musanga cecropioides and Albizia zypia dominate the landscape. Chromoleanae odoratum and Panicum maximum are the common fallow species and are associated with the practice of short fallow cycle.

In Mvila and Haut Nyong, both secondary and primary rain forests are still available. The vegetation is essentially evergreen rain forest with mosaic of raffia swamps near rivers and logging areas. Dominant tree species include Albizia spp, Ficus exasperata, Milicia excelsa, Terminalia superba, Triprochiton scleroxylon and Ceiba pentandra.

The dominant soil types in all three divisions are ultisols and oxisols. However, there is a marked micro variability between the three sites. The soils of Lekié are more fertile and moderately acidic (pH 1:1 $H_2O = 5$ to 6) compared to the very acidic (pH 1:1 $H_2O = < 5$), low cation exchange capacity and high aluminium

saturation (> 40%) associated with the soils of Mvila and Haut Nyong divisions. This probably explains the relatively high population density in Lekié division compared to the low population density in East and South Provinces of Cameroon in general.

The cropping system of all three divisions includes the fallow based food crop production system, the semi-permanent cash crop production system and the multistrata home garden system. The food crops include egusi melon (Cucumeropsis mannü), cassava (Manihot esculenta), maize (Zea mays), groundnuts (Arachis hypogaea), plantain (Musa spp.). The main cash crops are coffee (coffea robusta) and cocoa (Theobroma cacao). In home gardens, farmers plant several crops ranging from vegetable crops such as green pepper to large fruit trees such as mango (Mangifera indica), safou (Dacryodes edulis) and Ricinodendron heudelotii.

Field survey

A field survey was undertaken as part of a prioritisation exercise. The survey was aimed at collecting data on production, consumption and marketing of main tree products so as to determine their economic potential and social value. The sample size is bigger, the sampling is more rigorous and the data are more comprehensive than for the preference surveys reported by Mollet et al. (1995).

A multi-stage procedure was used to choose the villages and farmers from the identified strata. On the basis of grids laid over a divisional area map, grid cells of 2 × 2 inch were formed. The division was then split into four quadrants each containing an equal number (4-5) of contiguous grids. From each quadrant a grid cell was selected randomly from which a village was also randomly selected. Thus, in each division, 4 villages were selected. Upon arrival in the village, 7-8 farmers were randomly chosen. Eighty interviews were held with individuals or groups of individuals. Both male and female members of the household were interviewed. Key informants were also identified from each village and were asked an additional set of questions. The selected villages in the respective divisions were Nkolfeb, Emana, Lobo and Tala (Lekié division), Djouyaya, Ntolock, and Bayong 1 (Haut Nyong division) and Mefoup, Ebolobola, Mang and Yama (Mvila division).

The value of production was estimated as the product of quantity and the price/unit of production. Quantity produced is a sum of quantity sold and quantity consumed plus other uses which include gifts. Production and value data were obtained from 8, 6, and 16 growers/collectors in the Lekié, Haut Nyong and Mvila divisions respectively for *Garcinia kola* and for *Ricinodendron heudelotii* from 26, 18 and 23 growers in the Lekié, Haut Nyong and Mvila divisions, respectively. Farm-gate prices used for this analysis were obtained by deflating the reported market prices by 20% if the distance to markets where the products were sold was greater than 20 km. From the results of this survey the potential farm-level economic value of the species was estimated for each division.

Results and discussion

Tables 2 and 3 summarise information on mode of propagation, niches, management and farmers' improvement objectives for *Garcinia kola* and *Ricinodendron heudelotii* respectively.

Mode of propagation and niches

For Garcinia kola, the most common mode of propagation across all three divisions is by retention/protection of young plants that are found by the farmers in their fields. Some cases of transplanting of wildings were also reported in the Lekié and Mvila divisions. In Lekié, about 38% of the farmers also planted seedlings of the species.

Retainment/protection is also the main mode of propagation of *Ricinodendron heudelotii* in the study area. About 67% of the farmers propagate the species by this method in the Lekié; comparable figures are 89 and 44% in Haut Nyong and Mvila divisions respectively. In fact it is the only propagation method reported in the Haut Nyong division. Few cases of propagation through seedlings are reported in Lekié and Mvila divisions.

These results suggest that, for both species, farmers do not fully master or may be experiencing difficulties with the other propagation methods. The recent developments in the vegetative propagation of *Ricinodendron heudelotii* (Shiembo et al. 1996) need to be brought to the attention of land users in the region.

The niches for Garcinia kola in Lekié and Mvila divisions are home gardens, tree crop fields, fallow land, food crop fields and virgin forests, each of these having on average one tree per grower. In Haut Nyong, tree crop fields and virgin forest are the main niches. Collection from the forest is highest in Haut Nyong—83% of the farmers growing the species—followed by the Lekié (25%) and Mvila divisions (13%). The high proportion collecting from the forest in Haut Nyong indicates the availabilty of virgin forests in the division.

Ricinodendron heudelotii is found in a variety of niches in the study area. In the Lekié and Mvila divisions, it is found mostly in tree and food crop fields, home gardens, fallow land and virgin forests. In Haut Nyong division, the species is found in most of the niches. The proportion of farmers collecting from the forest ranges from 35% in Haut Nyong to only 4% in Lekié. About 13% of the farmers in Mvila collect the species from the forests. The low figure in Lekié is probably related to the disappearance of secondary forest in the region. Generally, Ricinodendron heudelotii seems to be more widely distributed than Garcinia kola with higher averages in each niche.

Table 2. Uses, niches and management of Garcinia kola in the humid lowlands of Cameroon²

	Lekié division (N°=8)	Haut Nyong division (N°=6)	Mvila division (N ^b =16)
Local name	G'niel (Eton)	Ngwell (Mpong Mpong)	Onyae (Bulu)
% Farms with tree (Average # of trees/grower)	29(4)	30(4)	50(7)
Mode of propagation	Retain/Protect-3 Plant seeds-3 Transplant wildings - 2	Retain/Protect-4	Retain/Protect-6 Transplant wildings - 1
Main source of seeds, if planted	Market place-1; Neighbours-1; Nurseries-1.	Not available	Not applicable
Criteria for selection of fruit of tree	Large fruit tree-1; Yearly production-1.	Large fruit tree-2; Good tasting fruit-2; Good production-2; Yearly	Good production-2; Large fruit tree-2; Good tasting fruit-1; Yearly production-1.
Niches	Home garden-2(1); Tree crop fields-2(1); Fallow land-1(1); Food crop fields-1(1); Virgin forest-1(1).	Virgin forest 4(4); Tree crop fields 2(1)	Tree crop fields-9(3); Fallow land-4(4); Virgin forest-3(1); Food crop fields-1(1); Home garden-1(1).
Uses (non-food)	Firewood-3; Medicinal use 2(diarrhoea): bark; Timber-1; Poles-1.	Firewood-4; Medicinal use-3 (diarrhoea): bark; Poles-3; Stakes-3.	Medicinal use-3(diarrhoea): bark; Firewood-3; Timber-1; Poles-1
Management tasks undertaken	Harvesting (climb)-3; Harvesting (gather)-3; Processing-2; Pruning-1.	Processing 4; Harvesting (gather)-3; Pruning-1; Disease/Insect control-1;	Harvesting (gather) 4; Harvesting (climb)-3; Processing-2; Disease and insect control-2; Pruning-1.
Improvement objective	Reduce time to bearing-3; Reduce tree height-2; High yield-1; Fruit size-1.	Fruit size-4; Regularity-2; Spread fruiting-2; Reduce tree height-2; Pest and discase resistance-1.	Fruit size-5; High yield-4; Spread fruiting-3; Reduce tree height-2; Regularity-1.

Notes: a: All numbers denote number of respondents making particular choice; b: Number of growers/collectors; c: The number in parentheses is the average number of trees (to the nearest non-zero integer) in the given niche.

Table 3. Uses, niches and management of Ricinodendron heudelotti in the humid lowlands of Cameroon*

	Lekié division (N°=8)	Haut Nyong division (N°=6)	Mvila division (N ^b =16)
Local name	Esessang (Eton)	Adje Sap, Zool (Mpong Mpong)	Ezang (Bulu)
% Farms with tree (Average # of trees/grower)	93(4)	85(17)	72(6)
Mode of propagation	Retaub/Protect-21 Plant seeds-5 Transplant wildings-4	Retain/Protect-16	Retain/Protect-10 Plant seeds - 1
Main source of seeds, if planted	Neighbours-3; Own farm, any tree-3; Own farm, selected tree-2; Market place-2; Tree experts-2.	Own farm, selected tree-1; Market place-1; Neighbours-1.	Not applicable
Criteria for selection of fruit of tree	Good production-5; Good tasting fruit-3; Yearly production-3; Large fruit tree-2.	Good tasting fruit-5; Good production 4; Parly production 4; Large fruit tree-3; Early maturity-2.	Good production-2; Year production-2; Large fruit tree-2; Early maturity-2; Good tasting fruit-1.
Niches*	Tree crop fields-20(3); Food crop fields-6(1); Home garden-5(1); Fallow land-4(1); Virgin forest-3(1).	Tree crop fields-9(6); Virgin forest-9(5); Food crop fields-8(5); Home garden-6(2); Fallow land-3(1).	Tree crop fields-10(3); Fallow land-7(2); Food crop fields-7(2); Virgin forest-2(1);
Uses (non-food)	Medicinal use-10(yellow fever, dysentery, diarrhoea, hernia, small pox): bark; Firewood-11; Stakes-2; Timber-1; Poles-1; Fodder-1.	Firewood-9; Medicinal use-8(hernia): bark; Poles-1; Stakes-1.	Firewood-9; Timber-6; Medicinal use- 3(diarrhoea): bark; Poles-1; Fodder-1.
Management tasks undertaken	Harvesting (gather)-22; Processing-19; Harvesting (climb)-2; Disease/Insect control-1.	Processing-15; Harvesting (gather)-14; Harvesting (climb)-1.	Harveting (climb)-8; Harvesting (gather)-8; Processing-6; Disease/Insect control-1.
Improvement objective	High yield - 12; Fruit size - 11; Reduce time to bearing - 7; Reduce tree height - 6; Spread fruiting - 5.	Reduce time to bearing-5; High yield-4; Regularity-4; Reduce tree height-3; Spread fruiting-2.	High yield-8; Fruit size-7; Reduce tree height-5; Good tasting fruit-4; Reduce time to bearing-3.

Notes: a: All numbers denote number of respondents making particular choice; b: Number of growers/collectors; c: The number in parentheses is the average number of trees (to the nearest non-zero integer) in the given niche.

Effect on tree and food crops

The proportion of farmers who perceive any effect of Garcinia kola on tree or food crops (Table 4) is low except in the Haut Nyong division where 50% feel that the species has a mixed effect—that is, favourable in some areas and unfavourable in others—on tree crops. These results suggest that the species may be compatible with food crops and therefore suitable for agroforestry systems. In the case of Haut Nyong, this means that appropriate management practices need to be developed to mitigate the negative effect of the species on tree crops.

Table 4. Effect of Garcinia kola tree on different crops in the humid lowlands of Cameroon (% of respondents)

			Division	
		Lekié	Haut Nyong	Mvila
	Increase	13	0	6
Tree crop	Reduce	13	17	0
•	Mixed	0	50	13
	Increase	0	0	0
Food crop	Reduce	13	0	0
•	Mixed	0	17	6

Note: % do not add up to 100 because respondents did not provide answers to all questions.

An examination of the effect of *Ricinodendron heudelotii* on tree and food crops (Table 5) shows that, in Lekié, many more farmers than in the other divisions believe that the tree has a positive effect on tree crops. The reason given for the negative effect is shade which is also given as one of the reasons for the positive effect together with the leaves.

Table 5. Effect of *Ricinodendron heudelotii* tree on different crops in the humid lowlands of Cameroon (% of respondents)

			division	
		Lekié	Haut Nyong	Mvila
	Increase	39	17	9
Тгее сгор	Reduce	19	17	13
	Mixed	8	22	17
	Increase	4	6	17
Food crop	Reduce	19	22	9
•	Mixed	12	11	13

Note: % do not add up to 100 because respondents did not provide answers to all questions.

For Haut Nyong, farmers' perceptions show that the same number of farmers associate the species with both negative and positive effects on tree crops. Concerning food crops the evidence seems to suggest that *Ricinodendron* has a negative effect on these crops due mostly to the shade.

In Mvila farmers' perceptions are somewhat similar to those in Haut Nyong with respect to the effect of *Ricinodendron* on tree crops. This is, however, not the case for the effect on food crops as many more farmers associate a positive effect with the species than those who attribute it a negative effect.

The perception of a mixed effect is balanced across all three divisions with respect to food crops. For the effect on tree crops, however, it is lowest in the Lekié division. Again, the implication of these results is that appropriate management practices need to be developed to enhance the compatibility of these species with tree and food crops.

Uses, management and improvement objectives

The bark of *Garcinia kola* is reported to be used for the treatment of diarrhoea. The wood is used as timber, poles and stakes for yams and its dead branches for firewood in all three divisions. *Garcinia* nuts play a very important social function as they are often offered as gifts to visitors.

Ricinodendron heudelotii is used for treating various ailments including yellow fever, dysentry, diarrhoea, hernia and small pox. The main part used is the bark. Other uses are for firewood(dead branches), timber, poles, stakes and fodder. These uses cut across the three divisions with the exception of timber and fodder which are not mentioned in Haut Nyong.

The above findings highlight farmers' indigenous knowledge of the medicinal value of both species for the treatment of a variety of ailments. This aspect cannot be underestimated especially given the present economic environment whereby pharmaceutical products are becoming out of reach of resource poor farmers.

A variety of management tasks are performed on *Garcinia*. In Lekié, these are pruning, harvesting by climbing, harvesting by gathering and processing. Farmers feel that each of these tasks involves much work. In Haut Nyong, the tasks reported are pruning, disease and insect control, harvesting by gathering and processing. As in Lekié, each of these tasks is rated as involving a lot of work. Pruning, disease and insect control, harvesting by climbing, harvesting by gathering and processing are the main tasks performed on the species; all of which by farmers' rating involve much work.

Key management activities undertaken on *Ricinodendron heudelotii* include disease and insect control, harvesting by climbing, harvesting by gathering and processing. Disease and insect control is mainly for weevils which attack the leaves and for borers and insects that attack the fruits of the species. The key management activities are common in all three divisions except for disease/insect control which is not practised in the Haut Nyong division. In general, farmers rate all these activities as involving a lot of work. Processing is mostly done by women who sometimes form groups of 3-4 to carry out this activity.

The current evidence indicates that pruning is not undertaken on *Ricinodendron heudelotii*. For both species, however, it seems that management practices undertaken are labour intensive. This calls for the need to examine strategies and improvement objectives which may reduce the labour requirement of appropriate management options.

Farmers in Lekié wish to see, for *Garcinia kola*, a reduction of time to bearing, higher yield, increase in fruit size and a reduction of tree height. Increase in fruit size, regular production, spreading of fruiting across the year, reduction of tree height and resistance to pest and disease are the major improvement objectives in Haut Nyong division. In Mvila farmers desire bigger fruits, higher yield, spread of fruiting across the season, reduction in tree height and regular production.

Concerning Ricinodendron heudelotii, the improvement objectives identified by farmers in Lekié are higheryield, reduction of time to bearing, increased fruit size, reduced tree height and spread fruiting throughout the year. In Haut Nyong, the same objectives are expressed with the exception of spreading fruiting which is replaced by regular production. Higher yield, reduction of time to bearing, increasing fruit size, reduced tree height and good tasting fruit are the improvement objectives in Mvila division.

Suggested improvement objectives are consistent with management practices identified above. For instance, in both species, farmers would like the species to be shorter. This may be related to the fact that they perceive harvesting by climbing as a difficult task. In general, the improvement objectives indicate the social and economic importance of both species to land users in the humid lowlands of Cameroon.

Economic value and potential

Mean production estimates and seasonal breakdown of the value of production of *Garcinia kola* and *Ricinodendron heudelotii* are shown in Tables 6 and 7 respectively. Seasonal variation of prices was observed for the species. Early in the season prices are usually high owing to the limited quantity available in the market. The lowest prices are observed at the middle of the season. A seasonal breakdown of the analysis is presented in this paper.

The production season for *Garcinia kola* runs from May to August in Lekié, February to August in Haut Nyong and February to July in Mvila. For *Ricinodendron heudelotii* most production is between February and December in Lekié, January and October in Haut Nyong and March and December in Mvila.

Of the three divisions, the highest level of production of Garcinia kola is in the Haut Nyong division with a mean production of 60 kg/grower or collector, followed by Mvila (34 kg) and Lekié (13 kg). A larger proportion of the production is for household consumption with the exception in Haut Nyong where 75% of the production is sold. On the basis of peak season prices the annual contribution of Garcinia kola ranges from 6500 FCFA (\$US 13.00) in Lekié to 30 000 FCFA (\$US 60.00) in Haut Nyong. The figure in Haut Nyong is based

on data from one grower, though. The value of production of this species is 11 390 FCFA(\$US 23.00)/year in Mvila.

Ricinodendron heudelotii production is highest in the Lekié (48 kg) followed by Haut Nyong (33 kg) and lastly Mvila divisions (17 kg). The proportion of the seeds of this species consumed is greater than that sold except in Haut Nyong where 64% of the production is sold. The potential annual revenue, based on midseason prices, generated by the species is 11 390 FCFA (\$US 23.00) in Lekié, 8580 FCFA (\$US 17.00) in Haut Nyong and 2720 FCFA (\$US 6.00) in Mvila.

The proportions of both species used for household consumption show the roles they play for food security in the region. In the case of *Garcinia*, as mentioned earlier, it is commonly offered as gifts to visitors to demonstrate the host's hospitality. *Ricinodendron's* role is mainly in the preparation of various dishes. In addition both species constitute a source of additional income to land users.

Table 6. Mean annual production estimates (kg/grower) and yearly value of production (FCFA²/grower) of Garcinia kola nuts in the humid lowlands of Cameroon

		Division	
Variable	Lekié	Haut Nyong	Mvila
Production	13	60	34
Sales ^b	5	45	9
	(40%)	(75%)	(27%)
Consumption ^b	8	15	24
	(60%)	(25%)	(72%)
Otherh (e.g. gifts)	0	0	1
	(0%)	(0%)	(2%)
Value of production ^e			
Using beginning	26 000	30 000	34 000
of season prices	(14 000)		(7500)
Using middle	6500	30 000	11 390
of season prices	(3800)		(2515)
Using end of	2600	30 000	42 500
season prices	(1400)		(9500)

Notes:

a. \$US = 500 FCFA.

b. Figures in parentheses are percentages of total production.

c. Number in parenthesis are standard errors. All figures are rounded up to nearest 5 FCFA and value of production is estimated by multiplying total production by deflated farm-gate prices.

d. Deflated farm-gate prices used are 2000 FCFA kg¹, 500 FCFA kg¹ and 200 FCFA kg¹ for beginning, middle and end of season respectively in Lekie; 500 FCFA kg¹, 500 FCFA kg¹ and 500 FCFA kg¹ for beginning, middle and end of season respectively in Haut Nyong and 1000 FCFA kg¹, 335 FCFA kg¹ and 1250 FCFA kg¹ for beginning, middle and end of season respectively in Mvila.

		Division	
Variable	Lekié	Haut Nyong	Mvila
Production	48	33	17
Sales*	20	21	5
	(43%)	(64%)	(27%)
Consumption	22	12	12
•	(45%)	(36%)	(72%)
Otherb (e.g. gifts)	6	0	1
	(12%)	(0%)	(1%)
Value of production.			
Using beginning	20 160	10 560	5440
of season prices	(4650)	(5605)	(1500)
Using middle	11 280	8580	2720
of season prices	(2590)	(5100)	(760)
Using end of	17 520	14 520	2655
season prices	(4025)	(8700)	(740)

Table 7. Mean annual production estimates (kg/grower) and yearly value of production (FCFA²/grower) of *Ricinodendron heudelotii* nuts in the humid lowlands of Cameroon

Notes:

- a. \$U\$ ≈ 500 FCFA.
- b. Figures in parentheses are percentages of total production.
- c. Numbers in parenthesis are standard errors. All figures are rounded up to nearest 5 FCFA and value of production is estimated by multiplying total production by deflated farm-gate prices.
- d. Deflated farm-gate prices used are 420 FCFA kg¹, 235 FCFA kg¹ and 365 FCFA kg¹ for beginning, middle and end of season respectively in Lekié; 320 FCFA kg¹, 260 FCFA kg¹ and 440 FCFA kg¹ for beginning, middle and end of season respectively in Haut Nyong and 320 FCFA kg¹, 160 FCFA kg¹ and 155 FCFA kg¹ for beginning, middle and end of season respectively in Mvila.

Summary and further research needs

Garcinia kola and Ricinodendron heudelotii play a major role in household economies in the study area. The nuts of Garcinia kola fulfil important social functions for producers in the area as they are very frequently presented to visitors. Besides, the bark is used for medicine in the treatment of diarrhoea. It is also used as timber, firewood(dead branches), stakes and poles. Ricinodendron seeds are used in the preparation of sauces which are highly appreciated by the people, thereby fulfilling important function for food security. Both species also secure additional revenue for the farmers in the humid lowlands of Cameroon.

Farmers in the study area have identified important traits which they desire improved. These improvement objectives cut across all three divisions and both species. They include reduction of time to bearing, higher yield, increased fruit size, reduction of tree height, regularity in production, resistance to pests and diseases and spreading of fruiting across the entire year.

Both species seem to be compatible with cropping patterns in the region and hence suitable for agroforestry systems prevalent in the study area. Although Garcinia kola and Ricinodendron heudelotii do not contribute nearly as much as Irvingia gabonensis and Dacryodes edulis (Ayuk et al. unpublished data) to household income in the humid lowlands of Cameroon, they are valuable species. Further research needs to be undertaken in improving our understanding of the market opportunities and constraints of these species. It is also important to identify methods to quantify the non-food uses of these species.

Acknowledgements

We wish to thank Richard Coe, Hannah Jaenicke and Roger Leakey, and an anonymous reviewer for very useful comments on an earlier version of this paper. Remaining errors and omissions are the sole responsibility of the authors.

References

- ABBIW, D.K. 1990. Useful Plants of Ghana: West African Uses of Wild and Cultivated Plants. Intermediate Technology Publications and the Royal Botanic Gardens, Kew. 337 pp.
- BOKEMO, W. 1984. Les plantes antilepreuses de Kasangani, Haut Zaire. Bulletin of the Royal Botanical Society of Belgium 117:305-311.
- CIFOR. 1996. 1995 Annual Report. Jakarta, Indonesia. 62 pp.
- COOPER, P. J. M., LEAKEY, R. R. B., RAO, M. R. & REYNOLDS, L. 1996. Agroforestry and the mitigation of land degradation in the humid and sub-humid tropics of Africa. *Experimental Agriculture* 32:235–290.
- Duguma, B., Tonye, J. & Depommer, D. 1990. Diagnostic Survey on Local Multipurpose Trees/Shrubs, Fallows Systems and Livestock in Southern Cameroon. ICRAF Working Paper No. 60. 34 pp.
- FAO. 1981. Tropical Forest Resource Assessment Project. Forest Resources of Tropical Africa. Part I: Regional Synthesis. FAO, Rome. 108 pp.
- FALCONER, J. 1992. Non-timber Forest Products in Southern Ghana A Summary Report. ODA Forestry Series No. 2.23 pp.
- LEAKEY, R. R. B. & JAENICKE, H. 1995. The domestication of indigenous fruit trees: opportunities and challenges for agroforestry. Pp. 15–26 in Suzuki, K., Subarai, S., Ishii, K. & Norisada, M. (Eds.) *Proceedings 4th BIO-REFOR Workshop.* Tampere, Finland, 6–12 August 1995.
- MOLLET, M., TIKI-MANGA, T., KENCUE, J. & TCHOUNDJEU, Z. 1995. The 'top 10' species in Cameroon: a survey of farmers' views on trees. *Agroforestry Today*, Vol. 7(3-4):14-16.
- OKAFOR, J.C. & FERNANDES, E. C. M. 1987. Compound farms of Southern Nigeria. A predominant agroforestry homegarden system with crops and small livestock. *Agroforestry Systems* 5:153–168.
- SHIEMBO, P. N. 1994. Domestication of Multipurpose Tropical Plants with Particular Reference to *Irvingia gabonensis* Baill, *Ricinodendron heudelotii* (Baill) Pierre ex Pax and *Gnetum africanum* Welw. Ph.D. thesis, University of Edinburgh. 313 pp.
- SHIEMBO, P. N., NEWTON, A. C. & LEAKEY, R. R. B. 1996. Vegetative propagation of Ricinodendron heudelotii, a West African fruit tree. Journal of Tropical Forest Science 9(4):514-525.
- Tonye, J., Ambassa-Kiki, R., Nsangou, M., Depommier, D., Djimde, M., Paitan, F., Raintree, J. & Scherr, S. 1986. In Djimde, M. & Raintree, J. (Eds.) Agroforestry Potential in the Humid Lowlands of Cameroon. AFRENA Report No. 12. 96 pp.
- WORLD RESOURCES INSTITUTE. 1985. Tropical Forest: A Call for Action. Part I. Report of an International Task Force convened by the World Resources Institute. The World Bank and the United Nations Development Programme. Library of Congress Catalogue Card number 85–518664–49. 49 pp.

GROWTH PERFORMANCE OF EUCALYPTUS GLOBULUS AS INFLUENCED BY STAND AND SITE FACTORS IN CHELELEKA CATCHMENT, CENTRAL ETHIOPIA

Amanuel Mehari*1 & B. Å. Näslund²

Swedish University of Agricultural Science, Faculty of Forestry, Department of Silviculture, 901 83 Umea, Sweden

Received October 1997

AMANUEL, M. & NÄSLUND, B. Å. 1999. Growth performance of Eucalyptus globulus as influenced by stand and site factors in Cheleleka Catchment, central Ethiopia. This study was conducted on a 4-y-old fuelwood plantation of Eucalyptus globulus in Cheleleka Catchment, central Ethiopia. Using the General Linear Model (GLM), significant effects of stand density (number of survivors/plot) and altitude on mean tree height and mean diameter were found. As stand density increased, mean tree height and diameter increased. In this study, none of the site factors significantly influenced the number of survivors per plot. The best growth in the catchment was at altitude 2950 m a.s.l. In this topographic position, mean tree height and mean diameter at breast height were greater than those in the valley floor (2850 m a.s.l.) and in the upper parts of the catchment (3050 and 3150 m a.s.l.). Further studies on the influence of site factors on catchment microclimate in relation to tree growth are recommended.

Key words: Altitude - aspect - Eucalyptus globulus - growth performance - slope - soil depth - plot tree density

AMANUEL, M. & NÄSLUND, B. Å. 1999. Prestasi pertumbuhan Eucalyptus globulus seperti yang dipengaruhi oleh faktor dirian dan faktor tapak di Cheleleka Catchment, tengah Ethiopia. Kajian ini dijalankan di ladang kayu api Eucalyptus globulus berumur empat tahun di Cheleleka Catchment, tengah Ethiopia. Menggunakan Model Linear Am (GLM), kesan kepadatan dirian bererti (bilangan pokok yang terselamat/petak) dan altitud bagi ketinggian pokok min dan garis pusat min diperoleh. Apabila kepadatan dirian bertambah, ketinggian pokok min akan bertambah. Dalam kajian ini, tiada satupun faktor tapak mempengaruhi dengan bererti bilangan survivor bagi satu petak. Pertumbuhan yang paling baik dalam kawasan tadahan ialah pada altitud 2950 m a.s.l. Dalam kedudukan topografi ini, ketinggian pokok min dan garis pusat aras dada min adalah lebih tinggi daripada pokok yang terletak di lantai lurah (2850 m a.s.l.). Disyorkan supaya kajian yang lebih mendalam dijalankan mengenai pengaruh faktor tapak terhadap mikrocuaca tadahan yang berkaitan dengan pertumbuhan pokok.

Private address: Blodstensv. 6-110, 752 58 Uppsala, Sweden.

^{*}Author for correspondence

Permanent address: Department of Forest Soils, Swedish University of Agricultural Science, Box 7001, 750 07 Uppsala, Sweden. E-Mail: Amanuel.Mehari@sml.slu.se

²E-mail: Bert Ake Naslund@ssko.slu,se

Introduction

Eucalyptus globulus Labil. subsp. globulus is the dominating tree species in the current reforestation programme on the highlands of Ethiopia, where it is grown for the production of wood for energy and construction. The success of tree cultivation depends a great deal on site factors such as altitude, aspect (compass orientation) and slope (Mitscherlich 1975, Kramer 1988), which directly influence the climatic elements of a growing site (Geiger 1965, Worrell & Malcolm 1990b). The reduction of productivity and tree growth with altitude is an example (Grace 1977, Tranquillini 1979), resulting from the general effects of altitude on meteorological variables such as air pressure, air density, vapour pressure, radiation components, air temperature and wind velocity (Barry 1992).

Temperature decline with altitude reduces the photosynthetic capacity of a plant (Tranquillini 1979), as demonstrated by Slatyer (1977). The reduction in chlorophyll content (Benecke 1972, Covington 1975), and increase in respiration (Piske & Winkler 1958) with altitude are other causes of the decline in plant photosynthetic capacity.

Differences in climatic parameters with change in altitude for the study area are well documented. The mean diurnal temperature of sites 2000 m above sealevel (m a.s.l.) and above falls by an average of 0.8 °C per 100 m rise in altitude (Gamachu 1988). With increase in altitude, wind speed increases (Geiger 1965, Barry 1992) which affects tissue temperatures, water status and the incidence of mechanical damage (Grace 1977).

Aspect and slope influence the microclimate at any site in mountains, valley basins, etc. (Geiger 1965, Barry 1992). Both affect the radiation income and soil heat flux (Rosenberg et al. 1983). Slope affects the receipt of radiation per unit area of absorbing surface, and soil water storage and drainage. Soils on steeper slopes dry more rapidly. The other factor included in this study is soil depth, an important pedogenic property which determines the function of the soil as a reservoir for plants' water supply and directly affects root growth.

Not only site factors, but also stand factors such as tree density, which in this study is defined as number of surviving trees/plot, modify tree growth (Kramer 1988, Wenk et al. 1990, Von Gadow & Bredenkamp 1991).

Because of the influence of site and stand factors on the productivity of forest land, decisions on land acquisition and investment, and the silvicultural operations in forest management, are indirectly affected (Worrell & Malcolm 1990a). An understanding of site and stand factors provides the management with important information on planting limits and for predicting the future yield of a stand (Worrell & Malcolm 1990a). The purpose of this study was therefore to investigate and identify site and stand factors which strongly influence the growth of *E. globulus* in the study area.

Materials and methods

Study area

The study was conducted in a fuelwood plantation, situated in the Cheleleka Catchment, c. 8 km southeast of Chancho (09° 15'N, 38° 45'E) (Figure 1), altitude 2850–3150 m a.s.l. With varied topography, a rugged and undulating surface, the study area belongs to the most heavily eroded regions of the country. The plantation was established on land formerly used for grazing and agriculture.

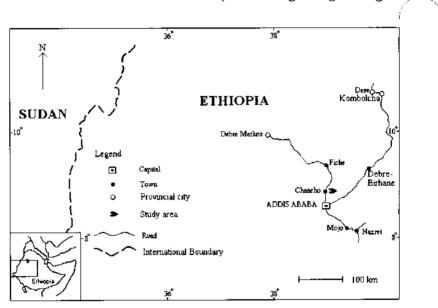


Figure 1. Map of the study area

Soils of the study area are of volcanic origin (Huffnagel 1961, Mohr 1962) and are clayey in texture. Depending on their composition and relief, the soils of the study area differed in colour. On the slopes of the catchment, soils were red to light reddish-brown, whereas in the valley bottom, they were brown to dark in colour.

Under the tree canopy, shrubs and grasses are common. The dominant shrubs along the hillside of the catchment were Erica arborea (2950–3150 m a.s.l.), Rumex nervous (2850–3150 m a.s.l.), Rosa abyssinica (2850–3150 m a.s.l.), Myrsine africana (2850–3150 m a.s.l.), Osyris spp. (2850–3150 m a.s.l.) and Budleja polystachya (2850–3150 m a.s.l.). Few remnant indigenous trees such as Juniperus procera (2850–3050 m a.s.l.), Hagenia abyssinia (2850 m a.s.l.), Olea africana and Acacia abyssinica (2850 m a.s.l.) were also found in the study area. Especially Hagenia abyssinica was common along stream channels in the catchment area. Herbs such as Cypoglossum lanceolatum, Plantageo lanceolata, Satureja paradoxia, Carduus kikuyorum and grasses such as Sporbolus pyramidalis, Stipa capensis, Andropogon abyssinica and Digitaria abyssinica were common in the study area.

Because there are no direct meteorological measurements from the study area, climatic data from Addis Ababa and Fiche (Figure1)were taken as representative for the site. The main rainy season for the study area is between June and September and the period of short rains is between March and April (Figure 2). The drier months are October to February. The mean maximum day temperatures are low during the wet seasons. According to the Ethiopian Mapping Authority (EMA) (1988), frost is frequent in valley bottoms and at higher altitudes in the study area.

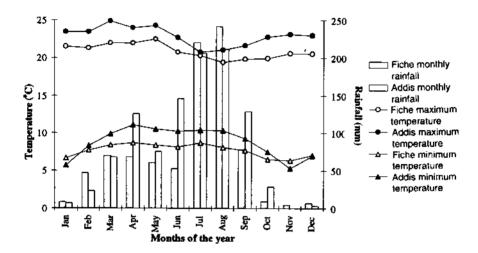


Figure 2. Mean monthly maximum and minimum temperatures and rainfall during the year for Fiche (1984–1989), and Addis Ababa (1984–1989). (Data from the Ethiopian National Meteorology Services Authority)

Field sampling

The sampling was carried out in a 4-y-old fuelwood plantation of *Eucalyptus globulus* in the Cheleleka Catchment. The catchment runs SE-NW, and includes sites of different soil depth, aspect, slope and altitude. This site was selected because it consists of an even-aged plant material raised from seeds collected from Intoto forest, at lower elevation (2550 m a.s.l.) near Addis Ababa. The seedlings were planted at a spacing of 2×2 m, with an initial tree density of 2500 seedlings per ha or 125 seedlings per plot (0.05 ha).

A field sampling was conducted by establishing 100 temporary circular plots (0.05 ha) between January and February 1993 (Table 1). The plots were laid out at 100 m vertical interval along four main contours spanning the upper slopes, 2850 to 3150 m a.s.l. (Figure 3). For the inventory and the establishment of the first plot, the village shown in Figure 3 was used as a reference point on the ground. To minimise the edge effect on our measurements, the first and the last plots on a transect were established inside the forest 2 to 25 m from the forest boundary.

Table 1. Numbers of sample plots, soil depths, slopes, measured number of trees, numbers of trees per plot and survival rates per plot for each alutude grouped by aspect four years after planting, in Cheleleka Catchment. Values for soil depth, slope, number of trees per plot and survival rate per plot are given as means \pm s.e.

Altitude (m a.s.l.)	Aspect	Number of plots (n)	Soil depth (cm)	Slope (%)	Measured No. of trees	Number of trees per plot (0.05 ha)	Survival rate (%) per plot
3150	NE	80	42.7±2.7	63.3 ± 11.7	98	28.7 ± 10.3	22.9 ± 8.3
	S	2	21.5 ± 1.5	30.0 ± 0.0	33	16.5 ± 1.5	13.2 ± 1.2
	MS	91	34.8 ± 3.2	53.5 ± 4.6	322	32.2 ± 5.3	25.8 ± 4.3
	×	er.	39.3 ± 3.0	71.7 ± 11.7	51	17.0 ± 9.2	13.6±7.3
	MN	87	31.5 ± 6.5	42.5 ± 12.5	53	26.5 ± 3.5	21.2 ± 2.8
	z	64	42.5 ± 2.5	72.5 ± 7.5	17	8.5±3.5	6.8 ± 2.8
3050	NE	ĸ	40.0 ± 5.8	63.0 ± 7.0	172	34.4 ± 6.1	27.5 ± 4.9
	s	7	32.9 ± 2.5	67.8 ± 4.9	335	47.9 ± 5.0	38.3 ± 4.0
	MS.	6	24.2 ± 2.3	47.8 ± 5.7	292	32.8 ± 5.7	26.2 ± 4.5
	≯	ιĊ	27.6±2.2	58.0 ± 10.1	201	40.2 ± 5.1	32.2 ± 4.1
	ΜX	8 П	48.0 ± 5.0	65.0 ± 15.0	78	26.0 ± 1.2	20.8 ± 0.9
	Z	1	73.0 ± —	65.0 ± −	27	27.0 ± −	21.6 ±
2950	NE NE	-	73.0±	70.0 ±	4	4.0 ± —	3.2 ± —
	SE	αÛ	15.0 ± 1.2	51.7 ± 1.7	35	11.7 ± 2.0	9.3 ± 1.6
	s	4	20.0 ± 2.0	68.8 ± 2.4	137	34.2 ± 12.0	27.4 ± 9.6
	MS	13	22.4 ± 1.3	58.1 ± 2.8	332	25.5±3.9	20.4 ± 3.1
	≯	5	24.4 ± 2.1	55.0 ± 2.7	186	37.2 ± 10.4	29.8 ± 8.4
	ΜM	œs	27.3 ± 4.3	56.7 ± 9.3	78	26.0 ± 7.0	20.8 ± 5.6
	z	9	26.7 ± 3.5	39.2 ± 6.8	220	36.7 ± 9.3	29.3 ± 7.5
2850	s	2	21.5 ± 1.5	37.5 ± 17.5	33	16.5 ± 15.5	16.5 ± 15.5
	MS	9	23.7 ± 1.7	45.0 ± 3.16	158	26.3±8.9	26.3 ± 8.1
	*	64	25.0 ± 2.0	45.0 ± 10.0	8	30.0 ± 8.0	90.0 ± 8.0
	Z	ąc)	29.3 ± 1.9	41.7 ± 7.3	133	44.3 ± 9.8	44.3±9.8

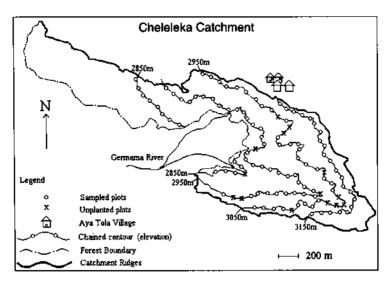


Figure 3. Systematic sampling and layout of the sampled plots at Cheleleka Catchment

All trees in a plot were counted. Tree height (m) and diameter at breast height (cm) of each tree in a plot were measured and recorded. Height and diameter were measured using an aluminium measuring pole and a calliper respectively. The following topographic variables for each plot were also measured and recorded (Table 1):

- Altitude (m a.s.l.) was measured using the Thommen Classic altimeter;
- Slope (S), the angle of inclination of the plot surface, was measured by the Suunto clinometer in percentage;
- Aspect θ (°), which is plot-surface orientation, was measured using the Silva compass by bearing from the north. For the study area, seven aspects were recorded. These were: northeast (NE), southeast (SE), south (S), southwest (SW), west (W), northwest (NW), north (N);
- The soil depth (SD) was measured using a calibrated soil-auger. At each plot, a
 minimum of six soil depths were randomly measured and the average was used
 for the analysis.

Data analysis

Means for the measured variables were computed for each plot. The effects of altitude, aspect, slope, soil depth, plot tree density and their interactions were analysed using the general linear model (GLM) procedure of the SAS software package (SAS Institute Inc. 1990). The discrete variables included in the models were altitude, aspect, slope, soil depth tree density, and their interactions. The models used were:

$$Y_{1} = a + b_{1}x_{1} + b_{2}x_{2} + b_{3}x_{3} + b_{4}x_{4} + b_{5}x_{5} + b_{6}x_{6} + b_{7}x_{7} + b_{8}x_{8}$$
 (1)

$$Y_{2}^{I} = a + b_{1}x_{1} + b_{2}x_{2} + b_{3}x_{3} + b_{4}x_{4} + b_{5}x_{5} + b_{6}x_{6} + b_{7}x_{7}$$

$$Y_{3} = a + b_{1}x_{1} + b_{2}x_{2} + b_{3}x_{3} + b_{4}x_{4} + b_{5}x_{5} + b_{6}x_{6}$$

$$(2)$$

$$Y_{3} = a + b_{1}x_{1} + b_{2}x_{2} + b_{3}x_{3} + b_{4}x_{4} + b_{5}x_{5} + b_{6}x_{6}$$
(3)

where Y_n , Y_2 and Y_3 are dependent variables plot mean tree height, plot mean diameter at breast height and plot survival rate. The values $b_1 \dots b_n$ are coefficients of the independent variables in the models. The independent variables in the models given above are:

$$x_1$$
 = altitude x_2 = aspect x_3 = slope x_4 = $x_2 * x_3$
 x_5 = soil depth x_6 = $x_5 * x_3$ x_7 = tree density x_8 = $x_5 * x_7$

The least square means (adjusted means) were used to assess the significance of effects, after adjusting for other terms in the model. Type III sums of squares were used to test the effects of all the main factors and interactions.

Results and discussion

Influence of site factors (altitude, aspect, slope, soil depth, and their interactions) on tree dimensions and survival

A statistical analysis was performed for the whole data set. The effects of altitude on mean tree height (MTH) [F (3, 79) = 15.34, p < 0.0001] (Table 2a) and mean diameter at breast height (MDBH) [F (3, 79) = 10.96, p < 0.0001] (Table 2b) were strongly significant. Trees at an altitude of 2950 m a.s.l. had a greater least square mean tree height (LSMTH), and least square mean diameter at breast height (LSMDBH) than those at other altitudes (Table 3a).

Four years after planting, the average survival rate in E. globulus plantations in the study area was $24.4 \pm 1.4\%$ which is very low. According to Pohjonen (1989), low annual rainfall (≤ 1000 mm), the desiccating dry-season winds which prevail from October to February, and the shallow soils are causes of low tree density and survival in the region. However, this study shows no statistically significant effects of any of variables tested on the survival rate (Table 2c).

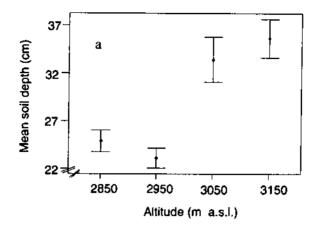
Young trees of Eucalyptus globulus are susceptible to the African mole rat, Tachyoryctes splendens, root damage (Alemayehu & Million 1993, unpublished) and weed competition (Pohjonen 1989), which are probable causes of the poor survival rate in the study area.

In the study area, seedlings are planted inside micro-basins (eyebrow terraces). In a such type of plantation establishment, the pit for the seedling should be dug in the centre of the micro-basin, towards the non-fill area. However, because pit preparation and planting are easy on the fill areas of micro-basins, and because it is difficult for unskilled workers to find the centre of the micro-basin, seedlings are planted almost on the edge of the fill riser (personal observation and inquiry). Seedlings planted on the edge of micro-basins are at risk of being washed away down hill during heavy rainstorms (Vletter 1987), which may also be the cause of poor seedling survival in the study area.

Table 2. Table of multivariate analysis using the general linear models procedure

Source	DF	F Value	Pr > F
Altitude	3	15.34	0.0001
Aspect	6	0.80	0.5724
Slope	1	0.49	0.4862
Aspect * Slope	6	0.62	0.7100
Soil depth	1	0.02	0.8917
Slope * Soil depth	1	0.57	0.4532
Tree density	1	15.28	0.0002
Soil depth * Tree density	1	1.34	0.2510
2b) Dependent variable: mean j	plot diameter at b	oreast height (MDB	H) (cm)
Source	DF	F Value	P r > F
Altitude	3	10.96	0.0001
Aspect	6	0.69	0.6619
Slope	1	0.86	0.3578
Aspect * Slope	6	0.47	0.8283
Soil depth	1	0.00	0.9643
Slope * Soil depth	1	0.50	0.4833
Tree density	1	11.26	0.0012
Soil depth * Tree density	1	2.51	0.1173
2c) Dependent variable: plot su	rvival rate (%)		
Source	DF	F Value	Pr > F
Altitude	3	1.56	0.2043
Aspect	6	0.59	0.7386
Slope	1	0.29	0.5918
Aspect * Slope	6	0.63	0.7066
Soil depth	1	2.74	0.1018
Slope * Soil depth	1	1.65	0.2031

The mean soil depth and slope of the sampled plots at each altitude and their variation within different elevations are summarised in Figure 4. The average slope per altitude class varies from 40 up to 70% (Figure 4). The soil of plot at 2950 m a.s.l. were shallow compared to those at 3150, 3050 and 2850 m a.s.l. (Figure 4a). As Figure 4b shows, plots at 2950, 3050 and 3150 m a.s.l. were steeper than plots at 2850 m a.s.l. As a result, sites on the valley bottom receive transported materials from sites above them, which may contribute to the improvement of the nutrient status of soils on the valley floor. Despite the addition of nutrients from elevated sites and low gradient, trees on the valley floor (2850 m a.s.l.) grew more slowly and were shorter than those at 2950 m a.s.l. (Table 2a). In spite of shallow soils, the growth of trees at 2950 m a.s.l. was better than that of trees grown on sites with similar slope (Figure 4b), but with deeper soils (Figure 4a) on the upper hillside of the valley (3050–3150 m a.s.l.).



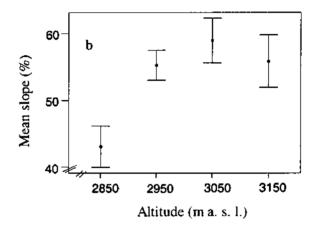


Figure 4. Altitude versus mean soil depth (a) and mean slope (b) in the Cheleleka Catchment (n=100)

The relationship between altitude and least square (adjusted) mean tree height (LSMTH), and least square mean diameter (LSMDBH) is given in Table 3. In general, as altitude increases from valley floor to tree limit, which is about 3200 m a.s.l. for indigenous trees in the region (Uhlig 1988), trees grow slower and become shorter (Tranquillini 1979, Pyrke & Kirkpatrick 1994). However, the LSMTH of trees at 2950 m a.s.l. was 8.4, 21.6, and 22.4% greater than that of trees at 2850 (p=0.0155), 3050 (p=0.0001), and 3150 (p=0.0001) m a.s.l. respectively (Table 3a). The LSMDBH at 2950 m a.s.l. was respectively greater by 6.3, 15.6 and 13.2% than those at 2850 (p=0.0506), 3050 (p=0.0001) and 3150 (p=0.0001) m a.s.l. (Table 3b).

Table 3.	Pairwise contrast of the least square means (adjusted means) of treatments
	using the general linear models procedure

3a) Pairwis	se contrast of lea	st square me	an tree height (I	.SMTH) of each a	ltitude	
Altitude	LSMTH	Pr > lT	HO: LSMEAN(i)=LSMEAN(j)		
(m a.s.l.)	(m)	i/j	1	2	3	4
2850	7.5016	1		0.0155	0.0028	0.0030
2950	8.1313	2	0.0155		0.0001	0.0001
3050	6.6843	3	0.0028	0.0001		0.8524
3150	6.6450	4	0.0001	0.0001	0.8524	

3b) Pairwise contrast of least square mean diameter at breast height (LSMDBH) of each altitude

Altitude	LSMDBH	Pr > 1T	HO: LSMEAN(i)=LSMEAN(j)		
(m a.s.l.)	(m)	i/j	1	2	3	4
2850	7.2025	1		0.0506	0.0057	0.0506
2950	7.6835	2	0.0506		0.0001	0.0001
3050	6.4856	3	0.0057	0.0001		0.3528
3150	6.6728	4	0.0506	1000.0	0.3528	•

The most favourable location for tree growth in the study area was at 2950 m a.s.l. which may be caused by the development of 'thermal belt' around this position. As a result, valley bottoms and higher altitudes (3050–3150 m a.s.l.) become cooler than the middle slope. The development of 'thermal belt' on valleys is well documented by Geiger (1965) and Oke (1987) and its direct effect on tree growth is also discussed elsewhere (Mitscherlich 1971).

The development of a warm zone at about 2950 m a.s.l. at night results in an increase in mean temperature at this position. Due to the increased mean temperature, the growing period of trees increases (Tranquillini 1979), which probably contributed to the better performance of trees at 2950 m a.s.l.

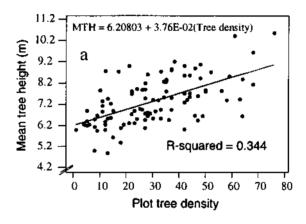
The ground surfaces of the sampled plots with varying slopes were oriented to different aspects, i.e. north (360°), northeast (45°), etc. According to Rosenberg et al. (1983), differences between aspects and slopes are not critical in the receipt of direct-beam solar radiation in the tropics where the sun remains high throughout the year. Tamrat (1994), in his report on the remaining Afromontane forests on the central plateau of Ethiopin, also found no significant variation between community types of different aspects. In this study, aspect was detected to have no significant effect on tree growth in the study area and no significant influence was found on tree parameters for slope, and its interactions with aspect (Tables 2a & 2b).

Effect of plot tree density on tree growth performance

The tree density for the study area varied from 1 to 76 trees (stems) per plot (0.05 ha) and it was found to have a significant effect on plot mean tree height

(MTH) (p=0.0002) (Table 2a), and plot mean diameter at breast height (MDBH) (p=0.0012) (Table 2b).

Plots with low tree density were excessively open and were infested with weeds, mainly grasses and shrubs (personal observation). According to Daniel et al. (1979), tree growth is adversely affected by excessive openings. The trend lines fitted in Figure 5 show the decline of the MTH, and the MDBH as tree density decreases. When tree density is low, much of the solar radiation reaches the ground, which may lead to dominance of grass and shrubs in the site. In such conditions, because of competition in the understorey, trees do not fully utilise the water and nutrients, and their growth rate could consequently be retarded. Similar observations were also made by Spurr and Barnes (1980).



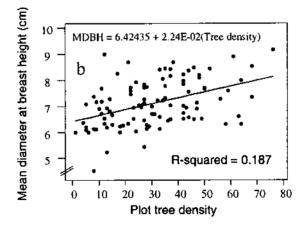


Figure 5. (a) Response of mean tree height (MTH), and (b) mean diameter at breast height (MDBH), to plot tree density after four years in the plantation of *Eucalyptus globulus* at the study area (n=100)

Conclusion and management recommendations

The results of this study show that the growth performance of *Eucalyptus globulus* on the study area was significantly influenced by tree density and altitude.

In the study area, the MTH, and MDBH of Eucalyptus globulus increase as plot tree density increases. In denser plots or plots with a high number of survivors, the canopy closes quickly, which may result in the suppression of the weeds. As a result, trees use sunlight, nutrients and water efficiently; thus trees in plots with high density showed better growth performance than those at lower density.

Altitude and other side factors had no significant effect on the survival rate of the regeneration material from Intoto forest. This indicates the adaptation of *E. globulus* to a range of altitude and site factors in the study area. However, the growth performance of trees from this regeneration material was poor at higher altitudes and in valley bottoms. This may be due to differences in meteorological parameters in various topographic situations, which are probably caused by the change of altitude and by the local wind circulation in the catchment. Therefore, this study suggests that further research is needed into the influence of topography on catchment microclimate in relation to tree growth.

Acknowledgements

The first author thanks Ato Wolde Kidane Nerae and Ato Kidane Menghistu for their permission to get access to Addis-Bah fuelwood project. We thank Rodolphe Schlaepfer, Department of Rural Engineering, Swiss Federal Institute of Technology and Jöran Fries for reading and commenting on the manuscript. We are grateful to Ulf Olssan, Department of Statistics, Swedish University of Agricultural Science (SUAS), for his guidance in statistics. We extend special thanks to Kurth Perttu, Department of Short Rotation Forestry, SUAS, Tom Ericsson and Anders Lindroth, Department of Production Ecology, SUAS, Ingvar Backéus, Department of Ecology Botany, Uppsala University, and two anonymous referees for many useful comments on the manuscript. This work was partly financed by the German Academic Exchange Service (DAAD), the Ethio-German forestry project and Deutsche Gessellschaft für Technische Zusammenarbeit (GTZ) GmbH.

References

ALEMAYEHU, W. & MILLION, T. 1993. Comparison of tree baits and fumigation tablets against African mole rat, *Tachyorcyctes splendens*. (Unpublished).

BARRY, R. G. 1992. Mountain Weather and Climate. 2nd edition. Routledge, London. 402 pp.

Benecke, U. 1972. Wachstum, CO₂-Gaswechsel und Pigment Gehalt einiger Baumarten nach Ausbringung in verschiedene Höhenlagen. *Angewandte Botanik* 46:117-135.

COVINCTON, W. W. 1975. Altitudinal variation of chlorophyll concentration and reflectance of the bark of *Populus tremuloides*. *Ecology* 56:715–720.

Daniel, T. W., Helms, J. A. & Baker, F. S. 1979. Principles of Silviculture. 2nd edition. McGraw-Hill, New York, 500 pp.

EMA. 1988. National Atlas of Ethiopia. Berhanena Selam Printing Press, Addis Ababa. 76 pp.

Gamachu, D. 1988. Some patterns of altitudinal variation of climatic elements in the mountainous region of Ethiopia. *Mountain Research Development* 8:131-138.

Geiger, R. 1965. The Climate near the Ground. Harvard University Press, Cambridge, Massachusetts. 61 pp.

GRACE, J. 1977. Plant Responses to Wind. Academic Press, London. 204 pp.

HUFFNAGEL, H. P. 1961. Agriculture in Ethiopia. FAO, Rome. 484 pp.

Kramer, H. 1988. Wald Wachstums Lehre. Verlag Paul Parey, Hamburg und Berlin. 374 pp.

MITSCHERLICH, G. 1971. Wald Wachstum und Umwelt: Waldhlima und Waserhaushalt. Zweiter Band, J. D. Sauerläner's Verlag, Frankfurt. 351 pp.

MOHR, P. A. 1962. The Geology of Ethiopia. University College of Addis Ababa Press, Asmara. 268 pp. OKE, T. R. 1987. Boundary Layer Climates. 2nd edition. Cambridge University Press, London. 435 pp.

PISKE, A. & WINKLER, E. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Link) in verschiedener Höhlage und der Zirbe (*Pinus cembra*) an der alpinen Waldgrenze. *Planta* 51:518-543.

POHJONEN, V. 1989. Establishment of fuelwood plantation in Ethiopia. Silva Carelica 14:1-338.

Pyrke, A. F. & Kirkpatrick, J. B. 1994. Growth rate and basal area response curves of four *Eucalyptus* species on Mt. Wellington, Tasmania. *Journal of Vegetation Science* 5:13-24.

ROSENBERG, N. J., BLAD, B. L. & VERMA, S. B. 1983. Microclimate: The Biological Environment. Willy-Interscience Publication, New York. 495 pp.

SAS INSTITUTE INC. 1990. SAS/STAT User's Guide. Version 4 edition. Volumes 1 & 2. 1686 pp.

SLATYER, R. O. 1977. Altitudinal variation in photosynthetic characteristics of snow gum, Eucalyptus puaciflora Sieb. ex Spreng. III. Temperature response of material grown in contrasting thermal environment. Australian Journal of Plant Physiology 4:301-312.

Spurr, S. H. & Barnes, B. 1980. Forest Ecology. 3rd edition. John Wiley & Sons, New York. 687 pp.

TAMRAT, B. 1994. Vegetation ecology of remnant Afromontane forests on the central plateau of Shewa. Acta Phytogeographica Suecica 79:1-59.

Tranquillini, W. 1979. Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps. Springer-Verlag, Berlin. 137 pp.

UHLIG, S. K. 1988. Mountain forests and the upper tree limit on the southern plateau of Ethiopia. Mountain Research and Development 8:227-234.

VLETTER, J. D. 1987. Recommendation for construction of micro-basins (eyebrow terraces) in forestry.

Chapter 13 in Ministry of Agriculture (Ed.) Ethiopian Forestry Manual for Professional & Subprofessional Field Staff. Volume 1, Addis Ababa.

Von Gadow, K. & Bredenkamp, B. 1991. Forest Management. Academica, Hatfield. 115 pp.

Wenk, G., Antanaitis, V. & Smelko, S. 1990. Waldertragslehre. Deutscher Landwirtschaft, Berlin. 448 pp. Worell, E. & Malcolm, D. C. 1990a. Productivity of Sitka spruce in northern Britain. 1. The effects of

elevation and climates. Forestry (London) 63:105-118.

WORELL, E. & MALCOLM, D. C. 1990b. Productivity of Sitka spruce in northern Britain. 2. Prediction from site factors. Forestry (London) 63:119-128.

THE ROLE OF TREE SPACING IN MINIMISING FUEL LOAD IN ACACIA MANGIUM PLANTATION—A CASE STUDY IN SOUTH SUMATRA, INDONESIA

Bambang Hero Saharjo

Laboratory of Forest Protection, Division of Forest Management, Faculty of Forestry, Bogor Agricultural University, Indonesia

Received January 1998

SAHARJO, B. H. 1999. The role of tree spacing in minimising fuel load in Acacia mangium plantation—a case study in South Sumatra, Indonesia. A case study examining the role of tree spacing in minimising fuel load in Acacia mangium plantation showed that close rather than wide spacing tends to reduce fuel load. The lowest fuel load, $13.7 \, \mathrm{t}$ ha⁻¹, resulting from the closest spacing $(2 \times 2 \, \mathrm{m})$, was still too high, compared to the fuel load reduction necessary to minimise fire risk. This means that reducing fuel load in the plantation will require not only close spacing, but also proper tree maintenance, i.e. weeding and pruning. This should be conducted regularly at 3-month intervals, and $2 \times 3 \, \mathrm{m}$ spacing is also recommended.

Key words: Acacia mangium - forest fire - fuel load - maintenance - South Sumatra - spacing

SAHARJO, B. H. 1999. Peranan penjarakan pokok bagi meminimumkan beban bahan api dalam ladang Acacia mangium—satu kajian kes di Sumatera Selatan, Indonesia. Satu kajian kes memeriksa peranan penjarakan pokok bagi meminimumkan bahan api di ladang Acacia mangium menunjukkan bahawa jarak yang rapat berbanding dengan jarak yang luas lebih cenderung untuk mengurangkan muatan bahan api. Muatan bahan api yang paling rendah, 13.7 t ha⁻¹, akibat daripada penjarakan terdekat (2 × 2 m), masih lagi terlampau tinggi berbanding dengan pengurangan beban bahan api yang sesuai untuk meminimumkan risiko kebakaran. Ini bermakna, pengurangan beban bahan api di ladang memerlukan bukan sahaja jarak yang dekat, tetapi juga penjagaan pokok yang betul iaitu merumput dan memangkas. Ia perlu dilakukan secara tetap pada setiap selang 3 bulan, dan jarak 2 × 3 m juga disyorkan.

Introduction

Products from industrial forest plantations, which are fulfilling consumer demands, have increased year by year, especially pulp and paper. Because of this, the success of plantation activities is very important. In addition, this success should also reduce cutting in natural forests. Large plantations, however, do not guarantee efficiency in production.

Fire is often the most important danger facing a newly established plantation in the tropics, and the greatest fires occur while a plantation is young, before canopy closure and suppression of ground vegetation (Evans 1992). Fire hazards increase as both living and dead biomass accumulates during the course of a planted forest's development (ITTO 1993). Of the many reasons for this, one is forest fire. In only three months of 1994, 17% of the total *Acacia mangium* planted in the research site in the present study was burnt. One of the reasons so much of the plantation was burnt was the high level of poorly maintained fuels on the adjacent land (Saharjo 1996). The key to saving industrial forest plantation from fire is fuel load reduction. If a plantation has a reduced fuel load, it can be said that the area is in good condition. In addition, ground vegetation should be treated until the tree canopies close. Weeding is recommended three months after planting, and proper tree planting spacing is also advised (Saharjo & Watanabe 1995, Saharjo 1996).

If trees are planted close together, their crowns and roots will soon close and full occupancy of the site is achieved early. High stand density induces small branches, slow diameter growth, a low degree of stem taper, and rapid increase in the length of the bases of the live crowns (Smith 1986). Wider tree spacing leads to some loss in total volume production per hectare, but individual trees grow larger. A stand of trees planted far apart will have a lower photosynthetic surface area per hectare to intercept light in the early years and, consequently, a lower yield at the outset. Wide spacing, however, enables individual trees to develop and maintain large crowns, and their root systems will occupy a large volume of soil before competition starts, both of which enhance growth (Evans 1992). The choice of initial spacing is determined by the end use of the plantation material, and to some extent by the tree form (Srivastava 1993). Onset of between-tree competition depends on species growth rate and initial spacing. Competition occurs when the presence of neighbouring trees begins to slow a tree's own development. Slow development may occur from competition between root systems or once branches touch and shade one another (Evans 1992).

The objective of this study is to clarify the role of tree spacing in minimising fuel load in *Acacia mangium* plantations.

Materials and methods

Site description

This research was carried out in a newly established *Acacia mangium* plantation (1.5, 3, and 6 y old) belonging to PT.Musi Hutan Persada, Barito Pacific Group, at the Subanjeriji forest block, South Sumatra, Indonesia, from August to September 1996 and from August to September 1997.

The mean annual rainfall is about 2800 mm, and monthly rainfall is about 209 mm ranging from 92 mm in July to 278 mm in February. According to the Schmidt and Fergusson (1951) system, the climate of this area belongs to rainfall type A. Mean maximum air temperature in this area is 32.6 °C in August, mean minimum air temperature is 22.6 °C in December and mean annual relative humidity is about 85%.

The soil is red yellow podsolic and the USDA soil classes are: Haplaquox, Dystropepts, Kandiudults, and Hapladux. This area has the following characteristics: slopes < 8 %, 5–125 m altitude, drainage varies from well-drained to imperfectly drained, soil mineral depth is 101–150 cm, cation exchange capacity (CEC) is 4.9–17.9 me 100 g⁻¹, base saturation is 5.6–21.8 %, available phosphorus is 0.4–3.2 ppm, total nitrogen is 0.11–0.20 %, organic carbon is 1.09–3.51 %, free salinity, and soil fertility based on Indonesian criteria are low (Hikmatullah *et al.* 1990).

Understorey vegetation is dominated by Imperata cylindrica, Eupatorium pubescens, Clidemia hirta, Tetracera sp., Artocarpus anisophyllus, Macaranga javanica and Dillinia grandifolia (Saharjo & Watanabe 1996).

Measurements and analysis

Data presented in this paper were derived from field experiments. Tree diameter, height, crown width and fuel load were measured at different ages and tree spacing.

One lot of about 40×40 m was established in the *Acacia mangium* plantations in each of several stand types that ranged from 1.5 to 6 y of age, at different tree spacings. At 1.5 y the five spacings used were 4×3.5 m, 4×3 m, 3×3.5 m, 4×2.5 m and 3.5×2.5 m. At 3 y the four spacings used were 4×4 m, 4×3 m, 3.5×2 m and 3×2 m. At 6 y the four spacings used were 4×4 m, 3×3 m, 3×2 m, and 2×2 m. All trees in the plantation were of the Subanjeriji provenance.

In each plot, tree diameter, height, canopy diameter and fuel load were measured. Diameter at breast height, i.e. 1.3 m above ground (dbh), and height of all trees in the plot were measured. Survival of trees, mean dbh, basal area and crown closure (using crown width data and a digital planimeter, PLANIX 7) were calculated.

Fuel load was measured by collecting and weighing all the living and dead materials in six quadrats of a subplot, each of area 0.25 m^2 ($0.5 \times 0.5 \text{ m}$).

The data calculated were subjected to analysis of variance, and significant difference was tested with the Tukey test (Steel & Torrie 1981). A linear regression was developed to predict the effect of tree spacing and crown closure on tree diameter, height, basal area and fuel load.

Results and discussion

Survival

Survival rate of trees in the plot (Table 1) varied from 80.9% at 3.5×2.5 m spacing (3 y) to 95.0% at a 4×4 m spacing (6 y). In the oldest 6-y-old plantation, survival increased with increasing spacing; at a spacing of 2×2 m, 75 trees died (81.2% survival), the highest number, while the lowest was 5 trees at spacing of 4×4 m (95.0% survival). The causes of the death were probably due to high competition and natural disturbance, i.e. pests and diseases.

Tree growth

Height

Spacing had no significant effect on tree height in the 1.5-y-old and 3-y-old plantations but it was significantly different in the 6-y-old plantation (Table 1). If there is no difference in growth among trees in the stands at young ages, it is reasonable to assume that competition has not yet begun to impact on the growth of the stands (Larocque & Marshall 1993). Differences in height might be due to varied genotypes, enhancing early development. Increase of tree density (and tree cover) at closer spacing tends to increase tree height significantly at 3 and 6 y of age (Table 2).

Table 1. Diameter, height, basal area, crown width, crown closure, and fuel load, at 1.5-, 3- and 6-y-old Acacia mangium plantations at different tree spacings

Spacing (m²)	N ha ⁻¹	No. plor ⁱ	Survival (%)	Height (m)	dbh (cm)	Basal area (m² ha¹)	Crown width (m)	Crown closure (%)
1.5-y								
4 × 3.5	714	102	89.5	$5.3 \pm 0.7a$	$7.7 \pm 2.6a$	3.5	$2.9 \pm 0.9a$	47.5 ± 9.8a
4×3	833	125	93.3	$5.5 \pm 0.6a$	$7.4 \pm 2.3a$	3.7	$2.8 \pm 0.8a$	52.9 ± 9.3ab
3×3.5	952	129	84.9	$5.5 \pm 0.7a$	$8.0 \pm 2.5a$	4.0	$2.7 \pm 1.1a$	56.5 ± 10.6 bc
4×2.5	1000	145	90.6	$5.4 \pm 0.7a$	$7.4 \pm 2.9a$	4.2	$2.6 \pm 0.9a$	62.6 ± 9.3cd
3.5×2.5	1142	183	93.9	5.8 ± 0.9 a	7.4 ± 2.4a	5.1	$2.7 \pm 0.8 a$	65.4 ± 10.4d
3-y								
4 × 4	625	84	84.0	$11.6 \pm 0.9a$	9.6 ± 4.5a	5.2	$3.4 \pm 1.6a$	60.3 ± 16.6a
4×3	833	119	88.8	$11.7 \pm 0.8a$	9.7 ± 3.8a	6.4	$3.2 \pm 1.3a$	68.1 ± 11.2 ab
3.5×2.5	1142	152	83.1	$11.8 \pm 0.7a$	$9.2 \pm 4.8a$	8.0	3.1 ± 1.6a	72.9 ± 15.0 ab
3×2	1666	216	80.9	$12.0 \pm 0.2a$	9.3 ± 4.8a	11.0	$2.9 \pm 1.4 \mathbf{a}$	79.8 ± 18.0b
6-y								
4×4	625	95	95.0	$18.1 \pm 0.3a$	$18.7 \pm 5.9a$	16.9	$3.9 \pm 1.3c$	$66.8 \pm 21.1a$
3×3	1111	151	84.8	18.7 ± 0.5 b	15.9 ± 4.9b	24.0	3.3 ± 2.8b	79.1 ± 17.1b
3×2	1666	221	82.8	$19.5 \pm 0.8c$	$13.5 \pm 4.7c$	25.5	3.2 ± 1.7b	86.3 ± 11.1b
2 × 2	2500	325	81.2	$20.6 \pm 0.5 d$	$11.3 \pm 3.7d$	26.7	$2.3 \pm 1.2a$	87.3 ± 15.5b

^{*} Means are significantly different when standard errors are followed by different letters ($p \le 0.05$).

Diameter

Spacing also had no significant effect on diameter growth in the 1.5-y-old and 3-y-old plantations. A significant effect was seen in the 6-y-old plantation where wide spacing tends to increase diameter more than close spacing (Table 1). This finding was also reported by Kohan (1996). Closer spacing (Table 2) tends to decrease tree diameter significantly at 6 y of age as neighbouring canopies touch each other, as shown by the high percentage of crown closure (Table 3). Diameter

increment of individual trees begins to show the effects of between-tree competition at the onset of canopy closure, the effects appearing last in the most widely spaced plots (Evans 1992).

Table 2. The effect of tree density on tree diameter, height, basal area, crown width, crown closure, and fuel load

Parameter	Plantation age					
	1.5 y old	3 y old	6 y old			
Diameter (cm)	$Y = 8-4.7 \times 10^{4} \text{X}$ ns $r^{2} = 0.09$	$Y = 9.8-3.8 \times 10^4 X \text{ ns}$ $r^2 = 0.51$	$Y = 20.6-3.9 \times 10^{-4}X *$ $r^2 = 0.96$			
Height (m)	$Y = 4.6 + 4.4 \times 10^{-4} X \text{ ns}$ $r^2 = 0.64$	$Y = 11.4+3.8 \times 10^{4}X *$ $r^{2} = 0.98$	$Y = 17.2 + 1.3 \times 10^{3} X^{*}$ $r^{2} = 0.98$			
Basal area	Y = 0.7 + 3.6 X*	Y = 1.0+6.4X *	$Y = 20.58 + 2.25 \times 10^5 X \text{ ns}$			
(m² ha-1)	$r^2 = 0.90$	$r^2 = 0.98$	$r^2 = 0.32$			
Crown width (m)	Y = 2.3-0.04X ns	Y = 2.6 + 0.05X *	Y = 2.1 + 0.12X *			
O. C	$r^2 = 0.62$	$r^2 = 0.98$	$r^2 = 0.85$			
Crown closure	Y = 16.74+0.04X *	Y = 51.50+0.02X *	Y = 64.50 + 0.01X*			
(%)	$r^2 = 0.96$	$r^2 = 0.94$	$r^2 = 0.79$			
Fuel load	$Y = 22.8-4.8 \times 10^{3}X$	$Y = 21.9 - 1.3 \times 10^{-5}X$ *	$Y = 20.96 - 3.06 \times 10^{3} X$ *			
(t ha ⁻ⁱ)	r² = 0.94	$r^2 = 0.98$	$r^2 = 0.92$			

^{*} Significant at $p \le 0.05$; ns, not significantly different.

Table 3. The effect of crown closure percentage on tree diameter, height, basal area and fuel load

Parameter	. <u></u>	Plantation age	<u> ·</u>
	1.5 y old	3 y old	6 y old
Diameter (cm)	$Y = 7.58-0.01X$ ns $r^2 = 0.16$	$Y = 10.89 - 0.02X$ ns $r^2 = 0.49$	$Y = 40.5 - 0.3X$ * $r^2 = 0.90$
Height (m)	Y = 4.45 + 0.02X ns $r^2 = 0.50$	$Y = 10.3 + 0.02X *$ $r^2 = 0.96$	$Y = 11.1+0.1X *$ $r^2 = 0.77$
Basal area (m² ha ⁻¹)	Y = -0.35 + 0.08X * $r^2 = 0.83$	$Y = 16.0+0.4X + r^2 = 0.90$	$Y = -13.2 + 0.04X$ ns $r^2 = 0.98$
Fuel load (t ha ⁻¹)	$Y = 24.4-0.1X *$ $r^2 = 0.92$	$Y = 25.55 - 0.07X *$ $r^2 = 0.96$	$Y = 36.0-0.2X * r^2 = 0.81$

^{*} Significant at $p \le 0.05$; ns, not significantly different.

Crown width and crown closure

The percentage of crown closure increases significantly (Table 1) at closer spacing in each planting age. As a tree gets older and its crown width expands (Table 1), the percentage of canopy cover also increases at closer spacing where tree density is also high (Table 2). Once crown closure takes place, the differences will be as keen as before, even though the more heavily stocked stand will continue to decline (Shepherd 1986). The onset of competition within a stand occurs when the crowns of individual trees begin to interfere with each other for light (Long & Smith 1984, Evans 1992).

Basal area

Basal area increases with closer spacing and age (Table 1). This is especially pronounced in the 3-y-old plantation (at 3×2 m spacing) and the 6-y-old plantation (at all spacings but the widest) (Table 1). The basal area increase is due more to the greater number of standing trees with increase of tree density at closer spacing than to diameter increment since at the same age closer spacing tends to have a negative effect on diameter growth, especially at ages 3 and 6 y (Tables 1 & 2).

Role of tree spacing

Wide spacing tends to give a higher fuel load than close spacing in all the plantations (Table 4). However, in the 3-y-old plantation, spacing did not have a significant effect on fuel load. Fuel load has been reported to increase up to the second year of planting and then decrease in the third and fourth years (Saharjo & Watanabe 1996). This is probably due to the fact that 1-2 y after planting, tree canopy gradually closes as crown width expands (Table 2). Table 3 shows that fuel load at all the years of planting tends to decrease significantly as crown closure increases. At 1.5 years and 3 years, the fuel load was dominated by that from the live component (Table 4), i.e. from the understorey vegetation such as Imperata cylindrica and shrubs, rather than from the trees themselves, i.e. fallen leaves, pod, and branches. As trees get older and space is gradually occupied by the canopy, competition starts especially for light. This competition also indicates unsatisfactory conditions, especially with close spacing. Fuel load tends to decrease significantly at close spacings at all the years of planting (Table 2). In rubber plantations, at low planting density, competition from I. cylindrica restricts tree growth, but at a higher planting density, this grass is controlled (Menz & Grist 1996). Once the canopy of a stand closes, weeds become suppressed by shading (Evans 1992). This is one reason fuel load (especially for live fuel, i.e. I. cylindrica and shrubs) decreases. The suppression of the understorey vegetation leads to the fuel load being contributed mainly by fallen leaves, pods and branches. Lower branches of closely planted trees usually die rapidly and are sometimes shed (Lim 1993).

The lowest fuel load, $13.7 \, \text{t ha}^{-1}$, (Table 4) was found at a spacing of $2 \times 2 \, \text{m}$ (6 y), but this fuel load was too high compared to the fuel load permitted to remain in the plantation, $3 \, \text{t ha}^{-1}$ (Saharjo & Watanabe 1997). This means that, with all the fuel loads measured, wildfires such as those in 1994 and 1997 will destroy the plantations. Wildfires are particularly destructive to timber and soil (McArthur 1962). Thus depending on close spacing alone to minimise fuel load in the forest plantation without proper tree maintenance is inadequate to prevent forest fire. Neglect of weeding is probably the most important single factor contributing to the failure of forest plantation in the tropics (Jackson 1983). This is especially important in a young plantation, as Table 4 shows, where weeds and live fuel load are dominant.

Spacing		Fuel load (t ha')	
(m²)	Total	Dead	Live
1.5-y			
4×3.5	$(19.6 \pm 1.1)a$	(2.9 ± 0.5) b	(16.7 ± 1.1)
4 × 3	$(18.6 \pm 0.8)ab$	$(2.8 \pm 0.1)b$	(15.8 ± 0.9)
3×3.5	$(18.1 \pm 0.8)ab$	(2.6 ± 0.2) ab	(15.5 ± 1.2) :
4×2.5	(17.9 ± 1.3) ab	$(2.5 \pm 0.3)a$	(15.4 ± 0.7) :
3.5×2.5	(17.5 ± 1.1) b	$(2.3 \pm 0.1)a$	(15.2 ± 1.3)
3-y			
4×4	$(21.2 \pm 1.8)a$	$(7.7 \pm 0.6)a$	(13.5 ± 0.9) :
4 × 3	$(20.8 \pm 2.4)a$	$(7.5 \pm 0.1)a$	(13.3 ± 0.7) :
3.5×2.5	$(20.5 \pm 1.8)a$	$(7.3 \pm 0.4)a$	(13.2 ± 1.1)
3×2	$(19.8 \pm 1.0)a$	$(7.1 \pm 0.3)a$	(12.9 ± 0.6)
6-у			
4×4	$(19.0 \pm 1.5)a$	$(15.9 \pm 1.3)b$	(3.1 ± 0.4) b
3×3	$(18.2 \pm 1.3)a$	$(15.5 \pm 1.8) b$	(2.7 ± 0.2) al
3×2	$(14.8 \pm 1.2)b$	$(12.7 \pm 12.7)a$	$(2.1 \pm 0.3)a$
2×2	(13.7 ± 1.7) b	$(12.2 \pm 0.4)a$	$(1.5 \pm 0.4)a$

Table 4. Distribution of total, dead and live fuels at the 1.5-, 3- and 6-y-old plantations at different spacings

High fuel loads found in young A.mangium plantations both at wide and close spacings showed that maintenance activities, i.e. weeding and pruning, were not done well. To obtain optimum tree growth, completely clean weeding and removing all competing and flammable vegetation are the best measures (Jackson 1983, Saharjo 1996). Otherwise a situation is created where the plantation is at a high risk of fire invasion, especially in the dry season. Reducing fuel load with closer spacing is helpful, but only as a complement. Therefore choosing the correct spacing depends on two major factors, ecology and economics. Spacing should have the ability to reduce fuel load due to the role of the closed canopy to prevent fire invasion and spread, and its stand should also be of good quality.

A narrow spacing, for instance 2×2 m, is an option, but if the stand quality is not good, the choice is unacceptable. Wide spacing $(4 \times 4 \text{ m})$ gives a good quality stand with fewer tree deaths, but the high accumulation of fuel load found in the stand is also a negative factor. Wide spacing that delays canopy closure may lengthen the period of fire hazard. As mentioned by Evans (1992), very close spacing is extremely expensive and very wide spacing grossly underuses the site. It is also commonly observed that A.mangium grown at wider spacing produces multishoots, with more and heavier branches that prune poorly and persist for long periods (Srivastava 1993). We suggest that for a pulp and paper plantation, 3×2 m spacing is recommended. Table 4 shows that at 3×2 m spacing, fuel load production was not significantly different from that at the closest spacing of 2×2 m. Live and dead fuels at both spacings also have no significant differences.

^{*} Means are significantly different when standard errors are followed by different letters ($p \le 0.05$).

To keep the plantation free from fire risk, it is also highly recommended that weeding be conducted every three months after planting, with good tree maintenance.

Conclusion

The results of this research show that close spacing tends to minimise fuel load production in the plantation. The lowest fuel load resulting from the closest spacing of 2×2 m at 6 y was 13.7 t ha⁻¹. Unfortunately this fuel load is still too high compared to the safe fuel load level of 3 t ha⁻¹. The decrease of fuel load at closer spacing as trees get older is caused by light competition resulting from increasing crown width and crown closure. When light competition starts, fuel load composition mainly from *Imperata cylindrica* and shrubs is replaced by fuel load mainly from trees, i.e. branches, pod, and dry leaves.

Close spacing also affects tree growth. Trees in close spacing tend to produce low diameter and crown width, but high tree height, basal area and crown closure. In addition, many trees die and tree quality is not as good as that at a wider spacing.

To minimise fuel load in the plantation in order to reduce the high risk of fire it is not sufficient to depend only on close spacing without proper tree maintenance. Proper tree maintenance, especially weeding and pruning and removal of flammable vegetable matter should be done until the tree canopy closes. A 3×2 m spacing is recommended.

References

Evans, J. 1992. Plantation Forestry in the Tropics. 2nd edition. Clarendon Press, Oxford. 403 pp.

ITTO. 1993. ITTO Guidelines for the Establishment and Sustainable Management of Planted Tropical Forests. 38 pp.

HIKMATULLAH, A., HIDAYAT, A., AFFANDI, U., SUPARMA, E., CHENDY, T. F. & BUURMAN, P. 1990. Explanatory Booklet of the Land Unit and Soil Map of the Lahat Sheet (1012), Sumatra. Centre for Soil and Agroclimate Research, Bogor. 135 pp.

JACKSON, J. K. 1983. Why do forest plantation fail? Pp. 277-285 in Wiersum, K. F. (Ed). Strategies and Designs for Afforestation, Reforestation and Tree Planting. Pudoc, Wageningen.

Kohan, S. 1996. Research on intensive cultural treatments in poplar stands in the Latorica River area in Vychodoslovenska Nizina lowland. Lesnictvi 42(12):556–563.

LAROCQUE, G. R. & MARSHALL, P. L. 1993. Evaluating the impact of competition using relative growth rate in red pine (*Pinus resinosa* Ait.) stands. Forest Ecology and Management 58:65-83.

Lim, M. T. 1993. Growth and yield. Pp. 149-161 in Awang, K. & Taylor, D. (Eds). Acacia mangium: Growing and Utilization. Winrock International and FAO, Bangkok.

Long, J. N. & Smith, F. W. 1984. Relation between size and density in developing stands: a description and possible mechanisms. *Forest Ecology and Management* 7:191-206.

McArthur, A. G. 1962. Control Burning in Eucalypt Forest. Leaflet Forest Timber Bureau Australia, No. 80. 31 pp.

MENZ, K. M., & GRIST, P. 1996. Increasing rubber planting density to shade Imperata: a bioeconomic modelling approach. Agroforestry Systems 42(12):291-303.

Saharjo, B. H. & Watanabe, H. 1995. Fire behavior in a newly established *Acacia mangium* plantation in South Sumatra, Indonesia. Paper presented at the 106th annual meeting of the Japanese Forestry Society. Hokkaido, Japan, April 2–5, 1995.

- Saharjo, B. H. 1996. Disappearance of a newly establish Acacia mangium Willd. plantation by fire in South Sumatra. Tropical Forest Management Journal 2(1):65-72.
- Saharjo, B.H. & Watanabe, H. 1996. Fire threatens industrial forest plantation: the case study in South Sumatra, Indonesia. Paper presented at the 13th Conference on Fire and Meteorology: International landscape fires. October 27–31, 1996, Cumberland Conference Center, Lorne, Australia. 23 pp.
- Saharjo, B. H. & Watanabe, H. 1997. Did close spacing reduce fuel load in an *Acacia mangium* plantation? Paper presented at the 7th annual meeting of the Japan Society for Tropical Ecology. Shiga, Japan, June 21–22, 1997.
- Schmidt, F. H. A. & Fergusson, J. H. S. 1951. Rainfall Type Based on Wet and Dry Periods of Ratios from Indonesia with Western New Guinea. Verhandelingen No.42. Directorate of Meteorology and Geophysics, Jakarta. 77 pp.
- SHEPHERD, K. R. 1986. Plantation Silviculture. Martinus Nijhoff Publishers, Dordrecht. 322 pp.
- SMITH, D. M. 1986. Tree Practice of Silviculture. 8th edition. John Wiley and Sons, New York. 527 pp.
- Srivastava, P. B. L. 1993. Silvicultural practices. Pp. 113-147 in Awang, K. & Taylor, D. (Eds.) Acacia mangium: Growing and Utilization. Winrock International and FAO, Bangkok.
- STEEL, R. G. D. A. & TORRIE, J. H. 1981. Principles and Procedure of Statistics: A Biometrical Approach. 2nd edition. McGraw-Hill, Inc., New York, 633 pp.

TREE SPECIES-AREA AND SPECIES-DIAMETER RELATIONSHIPS AT THREE LOWLAND RAIN FOREST SITES IN SUMATRA

Keith Rennolls* & Yves Laumonier**

FIMP, INTAG, Manggala Wanabakti, PO Box 7612, Jakarta 10076, Indonesia

Received January 1998

RENNOLLS, K. & LAUMONIER, Y. 1999. Tree species-area and species-diameter relationships at three lowland rain forest sites in Sumatra. Data from three forest sites in Sumatra (Batang Ule, Pasirmayang and Tebopandak) have been analysed and compared for the effects of sample area cut-off, and tree diameter cut-off. An 'extended inverted exponential model' is shown to be well suited to fitting treespecies-area curves. The model yields species carrying capacities of 680 for Batang Ule, 380 species for Pasirmayang, and 350 for Tebopandak (tree diameter ≥ 10 cm). It would seem that in terms of species carrying capacity, Tebopandak and Pasirmayang are rather similar, and both less diverse than the hilly Batang Ule site. In terms of conservation policy, this would mean that rather more emphasis should be put on conserving hilly sites on a granite substratum. For Pasirmayang, with tree diameter ≥ 3 cm, the asymptotic species number estimate is 567, considerably higher than the estimate of 387 species for trees with diameter ≥ 10 cm. It is clear that the diameter cut-off has a major impact on the estimate of the species carrying capacity. A conservative estimate of the total number of tree species in the Pasirmayang region is 632 species! In sampling exercises, the diameter cut-off should not be chosen lightly, and it may be worth adopting field sampling procedures which involve some subsampling of the primary sample area, where the diameter cut-off is set much lower than in the primary plots.

Key words: Species-area curves - species-diameter curves - non-linear modelling

RENNOLLS, K. & LAUMONIER, Y. 1999. Kaitan antara spesies dan luas pokok dengan spesies dan garis pusat pokok di tiga tapak hutan hujan tanah pamah di Sumatera. Data daripada tiga tapak hutan di Sumatera (Batang Ule, Pasirmayang dan Tebopandak) dianalisis dan dibandingkan untuk mendapatkan kesan sampel bagi potongan kawasan dan potongan garis pusat pokok. Model eksponen songsang diperluas didapati sangat sesuai dengan lengkuk kawasan spesies pokok. Model ini menghasilkan spesies dengan daya muat membawa sebanyak 680 spesies bagi Batang Ule, 380 spesies bagi Pasirmayang, dan 350 spesies bagi Tebopandak (garis pusat pokok≥10cm). Nampaknya dari segi keupayaan spesies, Tebopandak dan Pasirmayang lebih kurang sama, dan kedua-duanya kurang kepelbagaiannya berbanding dengan

France.

^{*}Address for correspondence: University of Greenwich, London SE18 6PF, (k.rennolls@gre.ac.uk).
**Address for correspondence: CIRAD-Forêt, Baillarguet, PO Box 5035, 34032 Montpellier, Cedex,

tapak Batang Ule yang berbukit. Dari segi polisi pemuliharaan, ini bermakna bahawa penekanan perlulah diberikan untuk memulihara tapak berbukit di atas substrata granit. Bagi Pasirmayang, dengan garis pusat ≥ 3 cm, anggaran bilangan spesies asimtot ialah 567, lebih tinggi daripada anggaran 387 spesies bagi pokok bergaris pusat ≥ 10 cm. Jelas bahawa potongan garis pusat mempunyai kesan utama terhadap anggaran daya muat membawa spesies tersebut. Satu anggaran konservatif mengenai jumlah spesies pokok di kawasan Pasirmayang ialah 632 spesies! Dalam pensampelan, potongan garis pusat mestilah dipilih dengan berhati-hati. Penggunaan prosedur pensampelan yang melibatkan beberapa subpensampelan kawasan sampel primer, iaitu potongan garis pusat disediakan jauh lebih rendah daripada plot primer.

Introduction

One of the primary concerns of floristic specialists in studying a particular forest region is the total number of species in the region (Peet 1975, Hubbell 1979, Hubbell & Foster 1983, Magurran 1988, Turner et al. 1997). Rennolls and Laumonier (1998) showed that the number of species in a plot is one of the primary dimensions of species diversity in two distinct forest sites in Sumatra, Batang Ule and Pasirmayang. It is well known that the observed number of species, and indeed any calculated measure of diversity, will depend on the area of the sample plot (Fisher et al. 1943, Pielou 1975). As the area of the sample plot increases, the number of species observed, and any of the measures of diversity will increase. The traditional ecological question is therefore, how many species would be observed on a very large forested region, of which the sampled area is typical (Kent and Coker 1992). A similar question could be asked of measures of diversity (Boyle & Boontawee 1995, Vanclay 1996), but this paper is concerned solely with the estimation of the total number of species. There are two standard approaches: (i) to fit a suitable model to the species frequency distribution (usually negative binomial or lognormal), and to estimate the number of undetected species from the truncated part of these distributions, (ii) to extrapolate the associated collector's curves (i.e. the species-area curves).

In practical field terms it is necessary to use a minimal diameter cut-off, because of the very large number of trees of small diameter. Figure 1 is a plot of log_e [$log_e(number\ of\ observed\ trees)$] against the diameter cut-off, d_{min} , for the Pasirmayang site of this study. It shows how the total number of trees observed varies with the diameter cut-off. The very high rate at which the number of observed trees increases with decreasing minimal diameter is of course the reason that a reasonably high diameter cut-off is adopted in empirical observational studies. Visual extrapolation in Figure 8 to $d_{min}=0$ gives an maximal estimate for the intercept of about 2.3, corresponding to a total stocking on the 3-ha site of about 21 500 trees [= exp(exp(2.3))].

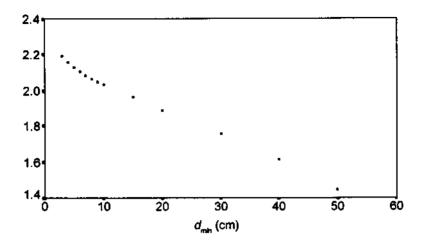


Figure 1. Pasirmayang: plot of log [log (number of observed trees)] v date

It is also clear that use of a minimum diameter cut-off when observing the trees in a sample area will result in an underestimate of the species carrying capacity for all trees. Little attention has been paid to the effect of the choice of the selection criterion for trees on the estimation of the total number of tree species. Usually a minimal size criterion is used, chosen to reflect the part of the forest ecosystem which is of primary concern. Hubbell and Foster (1983) used a minimum diameter of 20 cm, since this reflected their interest in the trees that are part of the upper canopy of the forest. Though the qualitative effect of the use of a diameter cut-off is obvious, it does not seem that quantitative analysis of this diameter cut-off effect has been conducted in observational studies of the tropical rain forests. However, if concern is with the biodiversity of the whole tropical rain forest ecosystem, such arbitrary cut-offs obscure the true range of tree species diversity that occurs. It is therefore of interest to investigate the effect of minimal cut-off diameter on the number of tree species that are observed. Initially the species-area curves for the three sites are analysed by fitting non-linear statistical models for trees with diameter ≥ 10 cm and the extrapolative estimate of the total species carrying capacities determined for each site.

The Pasirmayang site is of area 10 ha, with a 3-ha core plot in which trees have been observed and species and spatial locations recorded, for trees with diameters down to 3 cm. The other sites considered in this paper, Batang Ule and Tebopandak, have species and locations of trees recorded only for trees with diameter ≥10 cm, a diameter cut-off that is typical in many forest inventories or vegetation surveys in tropical forest areas. Other reported studies have used diameter cut-offs of 20, 30 or even 50 cm. Clearly the observed numbers of species in these studies with different diameter cut-offs are not comparable, and neither are the carrying capacities estimated from the use of species—area curves.

The data from the Pasirmayang site (Laumonier 1997) have been used to evaluate the effect of varying the diameter cut-off, and extrapolative methods have been used to estimate the carrying capacity of the site for trees of all diameters. Finally an attempt is made to obtain combined models of the species—area—diameter relationship.

The study site

The data from Tebopandak were collected as part of a Phase-I implementation of the Forest Inventory and Monitoring Project (FIMP) which was designed to obtain both traditional forest inventory data and forest diversity information. The sampling plan uses a standard field assessment plot of 100 m by 10 m directed along the line of maximal topographic slope. In some instances it is not possible because of site conditions to obtain a 100-m field assessment plot, and a 50-m plot is then used. The rationale of the orientation of the plot is that such a choice will maximise the number of environmental conditions encountered, and the number of tree species detected. Though this is a standard floristic sampling strategy, it does pose some problems in constructing unbiased regional forest inventory estimates. A method for doing this has been described in Rennolls (1997a, b).

Data from Batang Ule and Pasirmayang were collected prior to the FIMP Phase-I study. For both these sites the data used in this paper are from a 300 m by 100 m (3 ha) assessment area. In order to allow comparisons between Tebopandak and these sites the 3-ha assessment areas have been divided into 30 100 m by 10 m 'sample-plots' for the purpose of analysis. Other sub-plot choices, such as 10 m by 10 m, have been used in analyses not reported in this paper.

Batang Ule

The sampled area at Batang Ule is rectangular of dimensions 300 m by 100 m, with an area of 3 ha on which 1885 trees of diameter 10 cm or over are observed, being from 502 different species (Trichon 1996). The site is very heterogeneous, including a valley region, steep slopes, and narrow ridges, (see Lieberman et al. 1996, for comparisons). Illustration of the topography, and the way in which diversity measures vary with topography can be found in Rennolls and Laumonier (1999). The plot has been oriented so that the 300-m side of the plot is along the line of maximal topographic gradient. For the purposes of species—area analysis the site has been sub-divided into 30 sub-plots of dimensions 100 m by 10 m, oriented across the line of maximum topographic gradient. The sub-plots are therefore approximately on topographic contours, and are essentially homogeneous, within themselves, but there will be a wide between-plot variation generated by the wide variation in topography over which the plots have been placed. The lower order plots are in the valley, the middle order plots are on a steep slope rising to narrow ridges on which the higher numbered plots lie.

Pasirmayang

The Pasirmayang study site is flat. Since the diversity analysis of the Batang Ule data (Rennolls & Laumonier 1999) showed an increased species diversity associated with ridge plots, it might be expected that the Pasirmayang site would show species diversity measures, including species count, similar to that observed in the flat areas of Batang Ule. The measurements in Pasirmayang are made on all trees down to a diameter of 3 cm. In order to allow a valid comparison between estimates of the species carrying capacities at the three sites considered, the data at Pasirmayang are first analysed using a diameter cut-off of 10 cm, the same as was used at Batang Ule and Tebopandak.

Tebopandak

In the Tebopandak region 45 plots have been assessed, 26 are 100×10 m, 19 are 50×10 m. All were oriented along the line of maximal topographic gradient. A total of 300 species were observed, with a tree diameter cut-off of 10 cm. There were a considerable number of unidentified trees, and these have been lumped into a single species for the purposes of the analysis in this paper. No account has been taken of this in the species-area analysis (see Rennolls 1997a, b and Rennolls & Laumonier 1999, for further analysis and discussion of these issues).

Species-area curves

Ecologists generally obtain their species—area curves by repeatedly halving the study area considered, so that the sequence of areas considered forms a geometric progression. If the area variable in the species—area analysis is to be log-transformed, then this will result in log (area) values which are evenly spaced. Such evenly spaced data are well suited for testing the adequacy of fit of a range of models in terms of log(area), the best of which may then be used for extrapolative purposes. Such an approach focuses consideration predominantly on the numbers of species observed in very small sub-areas. When the main objective of the study of species—area curves is for extrapolation to very high areas this focus on small sub-areas is not statistically efficient. In order to improve the quality of extrapolative predictions more emphasis should be given to the number of species observed on large sub-areas. Hence the conventional area-halving procedure has not been followed here. The area variable has been left untransformed, and the area values in the species—area analysis have been formed by a cumulation of the areas of a number of sub-plots which have an area typically of 0.1 ha.

The way in which a set of sub-plots is selected needs some care. The assumptions of the species-area curve method need to be taken into account. The sample area will usually contain a number of zones which environmentally differ, based for example on elevation, gradient, soil, etc. The extrapolation of the species-area curves allows an estimate of the number of species which would be found in an

(hypothetical) region of area greater than the sample area which has the same environmental sub-zones as the sample area occurring in the same ratio. For it to be valid to extrapolate the fitted species-area curve it is necessary that each sub-area of the sample area should also contain the same environmental sub-zones in the same ratio. However, the nature and areas of all possible relevant sub-zones in the sample area will not in general be known. Hence it is not possible to ensure that the sub-areas strictly satisfy the requirement that they should follow the environmental-zone ratios of the sample area. In such a situation one approach to ensuring that the sub-area is representative of the sample area is to form the sub-area from a random sub-sample of plots in the sample area.

The "wrong" species-area curve

Figure 2 shows the species—area curve for the 3-ha sample area at Batang Ule for the sub-plots of cumulative area i*0.1ha; i=1,2,...,30 when i follows a plot ordering from the valley, up the slope, over the ridge. There is an apparently almost linear increase in the number of species with plot area. However, since the plot index spans the topographic gradient along which new species are expected to be encountered, the near linearity of the species—area curve is not surprising. A cumulative sub-plot constructed from this (natural) ordering of plot numbers is not representative of the whole variability in topography that is present on the whole of the study site. Hence the species—area curve constructed from the cumulative plots from this natural plot ordering is inappropriate for species—area analysis and extrapolation.

Randomised species-area curves

If a sub-area of the 3-ha site is to be made up of a number of the 0.1-ha sub-plots, then in order for the sub-area to be "representative" of the whole of the Batang Ule sample area, the sub-plots may be chosen randomly from the 30 available sub-plots. This can be achieved for all sub-areas of areas from 0.1 ha to 2.9 ha by forming the cumulative sub-areas using a plot numbering formed by a random permutation of the original (natural) plot ordering. There are 30! different permutations of the original plot ordering, each of which will result in a different observed speciesarea curve. One of these will be the original (natural) plot ordering, which we have seen is not suitable for use in species-area curve analysis. However, in a relatively small subset of random permutations each is likely to achieve a high degree of "mixing-up" of the natural plot ordering, and hence ensure that each of the chosen sub-areas is representative (in the random sampling sense) of the whole sample area. A set of ten random permutations has been selected from the set of all permutations. This results in ten randomly sampled sub-areas at each area from 0.1 ha to 2.9-ha, in 0.1-ha steps. Results for Batang Ule are shown in Figure 2. (Software in Visual Basic for Excel has been written for the generation of the permuted data, and may be obtained from the first author.) Clearly the original

species—area plot is anomalous. The permuted-plot-order curves give the fairest indication and hence in the analysis given below, only the permuted-plot-order data are used. A larger sample could have been selected, but it was considered that the ten sample species—area curves gave an adequate representation of the trend and variability for estimation purposes.

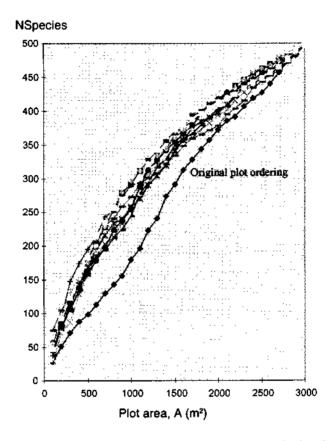


Figure 2. Batang Ule: species-area curves for the original and ten random plot re-orderings, $(d_{min} = 10 \text{ cm})$

Statistical analysis

The ten randomised species—area curves of Figure 2 for Batang Ule pass through two fixed points. First, the origin, for the observed species count is necessarily zero when A=0. A model of the species—area relationship should be constrained to pass through the origin. Second, when A = 3.0 ha the observed species count is 502. It is possible that the species—area relationship could also be constrained to go through the (3.0, 502) fixed point of the randomised species—area curves. However, the upper fixed point is merely a result of the actual area that is sampled.

There are an infinite number of possible sample areas which could have been selected from the larger (hypothetical) region to which we wish to extrapolate. They would yield differing values of the number of species observed in the whole 3-ha area. The variation in the numbers of species observed in specified-area subareas of the 3-ha plot contains information on the variability of the number of species that would be observed if the whole 3-ha plot had been re-sampled from the hypothetical (super-) population of such plots. In fact, the variance of the number of observed species will increase with increasing sampled area, and this is illustrated in Figure 1 by the divergence of the randomised species—area curves as the area of the sub-area increases from A = 0.

In this paper we have adopted a compromise approach which uses ordinary least squares (OLS) to estimate the species—area relationship from the randomised species—area curves. This is equivalent to giving equal weighting to all the data points on the randomised species—area curves. OLS is the maximum likelihood method of estimation if the data have a homogeneous and independent error structure. It is expected that the use of OLS in the fitting of species—area relationships will result in fitted models which are reasonably unbiased. However, the standard errors of the estimated model parameters should not be taken at face value, since the assumptions under which they would be valid, i.e. homogeneity and independence, are not satisfied. They may be useful as a guide to the relative accuracy of estimation on the different sites considered.

Species-area model

Both the inverted exponential model and the "collector's curve" (Pielou 1975, page 39) were found to be unsatisfactory in fitting the species-area curves. An 'extended inverted exponential model' of the form

$$NSpecies = K1*[1-exp(-K2*((Area/1000)**K3))]$$
 (1)

was found to be an adequate representation of the species-area relationships at all three study sites, in terms of residual analyses. The parameter KI represents the asymptotic species carrying capacity.

Species-area results

Batang Ule

Model (1) was fitted to the randomised species—area curves for Batang Ule (tree diameter≥10 cm) shown in Figure 2 using ordinary least squares (OLS) and gave the parameter estimates shown in Table 1.

		Asymptotic	Asymptotic 95 % confidence interval	
Parameter	Estimate	std. error	Lower	Upper
K 1	675.6	22.8	630.6	720.5
K2	0.52	0.024	0.47	0.57
K3	0.83	0.017	0.80	0.87

Table 1. Parameter estimates for Batang Ule for model (1), $(d_{min} = 10 \text{ cm})$

From Table 1 it can be seen that the estimated total number of species in an area as characterised by the Batang Ule plots is 676 [approximate 95% confidence interval (631,720)] which may be compared with the 502 observed species on the site.

Pasirmayang

Tree diameter ≥10 cm

The natural-ordering and randomised species-area curves for Pasirmayang are shown in Figure 3, for trees with diameter greater than or equal to 10 cm. Note that since this site is flat, and there is no environmental gradient, the sequentially ordered sub-plots produce a species-area curve which is not distinguishable from the species-area curves from the randomised plot sequences. Hence in subsequent analysis, all the eleven species-area curves given in Figure 3 are used in the model fitting.

The parameter estimates for model (1) are shown in Table 2. The estimate of the total number of tree species for which the tree diameter is greater than or equal to 10 cm is 376 [approximate 95% confidence interval (367, 386)]. This fitted model has a satisfactory residual plot (Figure 4).

Table 2. Parameter	estimates for Pasirmayang for model (1),	$(d_{\min} = 10 \text{ cm})$

		Asymptotic		otic 95 % ice interval
Parameter	Estimate	std. error	Lower	Upper
K1	376.46	4.63	367.35	385.60
K2	0.93	0.03	0.87	0.99
К3	0.74	0.01	0.72	0.77

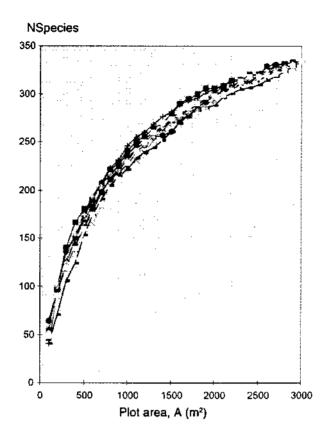


Figure 3. Pasirmayang: species-area curves for the original and ten random plot re-orderings, $(d_{min} = 10 \text{ cm})$

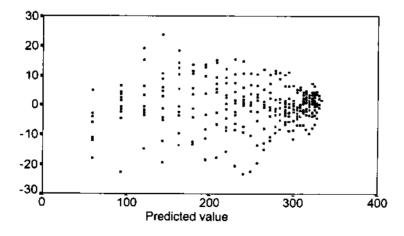


Figure 4. Pasirmayang: residual plot for fitted model, (1), $(d_{min} = 10 \text{ cm})$

Figure 5 shows the species—area curves for the 3-ha plot for trees of diameter greater than, or equal to 3 cm. Fitting model (1) yields the parameter estimates shown in Table 3 with an asymptotic species number estimate of 567 [approximate 95% CI (555, 580)], which may be compared with the estimate of 376 (tree diameter ≥10 cm). Movement from a diameter cut-off of 10 cm to 3 cm results in an estimate of the species carrying capacity which is increased by 51%.

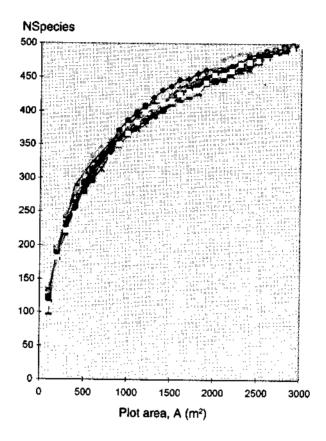


Figure 5. Pasirmayang: species-area curves for the original and ten random plot re-orderings, $(d_{\underline{a}} = 3 \text{ cm})$

Table 3. Parameter estimates for Pasirmayang for model (1); $(d_{max} = 3 \text{ cm})$

		Asymptotic	Asymptotic 95 % confidence interval	
Parameter	Estimate	std. error	Lower	Upper
KI	567.81	6.33	555.35	580.27
K2	1.11	0.04	1.03	1.18
K.3	0.60	0.01	0.59	0.62

Tebopandak

Species-area data for 11 orderings of the area increment process are shown in Figure 6; one, in which the data were collected, and the plots numbered, and 10 random permutations of the plots sequence. Since the cumulative areas differ for each of the illustrated area curves, only the scatter diagram of all the points on all the curves is presented. The fitted parameters of model (1) to the points on the 11 species-area curves are given in Table 4.

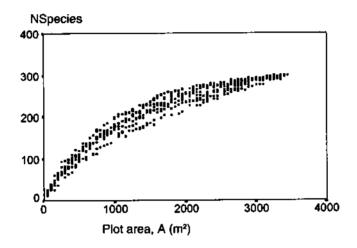


Figure 6. Tebopandak: superimposed species-area curves for 11 plot sequences, $(d_{min} = 10 \text{ cm})$

		Asymptotic		otic 95 % ce interval
Parameter	Estimate	std. error	Lower	Upper
K1	345.33	7.77	330.06	360.60
K2	0.70	0.03	0.65	0.75
К3	0.85	0.02	0.81	0.89

Table 4. Tebopandak: parameter estimates for model (1); $(d_{\perp} = 3 \text{ cm})$

Thus, the estimate of the species carrying capacity (tree diameter ≥ 10cm) is 345 [approximate 95% confidence interval (330, 361)].

Species-diameter curves

The study location at Pasirmayang has been sampled down to a minimal diameter of 3 cm on a 3-ha plot. Figure 7 shows the natural logarithm of the number of observed species (NSpecies) plotted against the diameter cut-off, d_{\min} , and is a

reasonably linear relationship. This would suggest that a reasonable model of NSpecies as a function of d_{min} would be:

$$NSpecies = C1*exp(-C2*d_{...})$$
 (2)

Extrapolation to zero diameter cut-off in Figure 7 leads to an intercept of about 6.3, resulting in a rough estimate of the total number of species, for an area of 3 ha, of about 545 [=exp(6.3)].

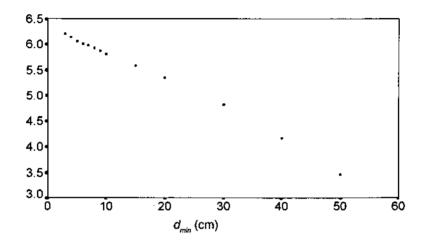


Figure 7. Pasirmayang: plot of log_{i} (NSpecies) as a function of d_{min}

The joint species-area-diameter relationship

How should the empirical species—area relationship, given by model (1), and the empirical species—diameter relationship, given by model (2), be combined into a joint model which adequately summarises the joint variation of the number of species observed with sample area, and diameter cut-off? It is not entirely obvious what the joint form of the model should be. To progress on this, we adopt an entirely empirical approach and examine Figure 8 which shows the relationship between $log_e(NSpecies)$ and d_{min} for the whole plot of 3 ha, and for sub-areas of area 2 ha and 1 ha. It seems that the relationship between $log_e(NSpecies)$ and d_{min} is linear with both intercept and slope depending on area. The three linear trends in Figure 8 may be modelled by:

$$E[log_{e}(NSpecies)] = \beta_{o} + \beta_{1} \delta_{1} + \beta_{2} \delta_{2} + \gamma_{o} d_{min} + \gamma_{1} \delta_{1} * d_{min} + \gamma_{2} \delta_{2} * d_{min}$$
(3)

where δ_1 and δ_2 are dummy variables indicating the sub-areas of area one and two hectares respectively. When model (3) is fitted, using OLS, the parameter estimates given in Table 5 are obtained.

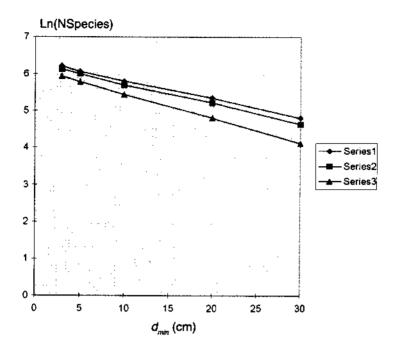


Figure 8. Pasirmayang: relationship between $log_e(NSpecies)$ and d_{min} . Plot areas: 3 ha (Series 1); 2 ha (Series 2); 1 ha (Series 3)

Table 5. Parameter estimates from fitting model (3) to the data in Figure 8

Variable	В	se B	t	p-value
DUMI	-0.23	0.03	-8.42	0.00
DUM2	-0.08	0.03	-2.89	0.01
DMIN	-0.05	8.E-04	-63.40	0.00
DUMID	-0.014	0.002	-8.40	0.00
DUM2D	-0.0013	0.0016	-0.78	0.45
(Constant)	6.36	0.014	445.	0.00

The parameter estimates in Table 5 correspond to the following generic linear relation

$$log_{i}(NSpecies) = intercept(A) + slope(A)*d_{min}$$
 (4)

with A taking values of 3, 2 and 1 ha. Using Table 5 we obtain the following fitted linear relations:

A = 3 ha:
$$log_{\epsilon}(NSpecies) = 6.359 \cdot 0.053d_{min}$$

A = 2 ha : $log_{\epsilon}(NSpecies) = 6.278 \cdot 0.054d_{min}$ (5)
A = 1 ha: $log_{\epsilon}(NSpecies) = 6.124 \cdot 0.067d_{in}$

Supposing that the *intercept* in (4) has a maximal asymptotic value as A approaches infinity, the intercept values given in (5) may be described by the relationship:

$$intercept(A) = 5.831 + 0.6177*[1-exp(-0.6425*A)]$$
 (6)

If we assume that the diameter distribution of every species is such that for $A = \infty$, the observed diameters of trees will exceed any finite diameter cut-off, then as $A \rightarrow \infty$ so will slope(A), in (4), approach zero. The slope values shown in (5) may then be described by the relationship:

$$slope(A) = -0.74*exp(-0.125*A)$$
 (7)

Combining relations (4), (6) and (7) leads to the empirical descriptive joint species-area-diameter model:

NSpecies =
$$632*exp \ [-0.6177*exp(-0.6425A) - 0.74*d_{min}*exp(-0.125A)\]$$
 (8)

It is noted that the form of (8), as a function of A, is different from model (1). A longer sequence of areas in (5) would need to be used in order to fit more complex models than (6) and (7). From (8), as $A \rightarrow \infty$, and $d_{\min} \rightarrow 0$, then NSpecies $\rightarrow 632$, our best estimate of the total species carrying capacity at Pasirmayang.

Conclusion and discussion

The extended inverted exponential model seems to be well suited to fitting speciesarea curves. A summary of the parameter estimates for this model (1), for the three study sites, is shown in Table 6.

		Kl	K2	К3
Batang Ule	$(d_{\min} = 10 \text{ cm})$	676	0.523	0.834
Tebopandak	$(d_{max} = 10 \text{ cm})$	345	0.700	0.847
Pasirmayang	$(d_{min} = 10 \text{ cm})$	376	0.929	0.744
Pasirmayang	$(d_{\min} = 3 \text{ cm})$	567	1.107	0.604

Table 6. Summary of parameter estimates for model (1)

It can be concluded that the hilly Batang Ule site is substantially more diverse, in terms of the total number of species which could be carried, than both the Pasirmayang and Tebopandak sites. In terms of conservation policy this would mean that rather more emphasis should be put on conserving hilly sites on a granite substratum. However, it has not been established that the Batang Ule diversity space encompasses that of Pasirmayang and Tebopandak. A joint analysis of the data sets would be necessary to establish or refute this.

For the Pasirmayang study site, with tree diameter greater than or equal to 3 cm the asymptotic species number estimate of 567 is considerably higher than the estimate of 376 species, from the data for trees with diameter greater than of equal to 10 cm. The empirical modelling of the joint species—area—diameter relationship leads to an estimated maximal carrying capacity on the Pasirmayang-type forest of about 632 species, 68% larger than the species carrying capacity estimated from simple species—area relationships for trees of diameter greater than or equal to 10 cm in diameter. If the same inflation factor is applied to the Batang Ule site then the estimated total carrying capacity of a very large region like Batang Ule would be 1136 species! Hubbell and Foster (1983) showed that patchy distributions of rare species (a factor not considered in this paper) could cause an underestimation of unobserved species resulting in a total species estimate which is 10-20% too low.

The models used in this paper have been descriptive in nature, being chosen to represent adequately the patterns and relationships in the observed data. It would be much more satisfying if the models used were suggested by a theoretical model of forest structure. Unfortunately there is no adequate model of forest structure available at this time to derive the form of the species—area, species—diameter and species—area—diameter relationships.

The model fitting for the effect of d_{\min} has rested largely on the high quality data that has been collected in the Pasirmayang site; all species down to a minimal diameter of 3 cm were identified. However, analysis of data sets collected on larger areas, and to smaller diameter cut-offs than used at Pasirmayang is required. Such data have been collected at a number of sites throughout the world, where the area sampled has been 50 ha, and the diameter cut-off has been 1cm, and subjected to a range of analyses (Ashton 1969, 1976, Appanah & Weinland 1993, Baillie et al. 1987, Manokaran & LaFrankie 1990). Unfortunately these data sets do not seem to be publicly available.

Most of the concern in ecological circles, when considering sampling for the assessment of species diversity, is the effect of using a finite sample area on the estimate of the species carrying capacity. It is clear that the diameter cut-off also has a major impact on the estimate of the species carrying capacity. In sampling exercises, the diameter cut-off should not be chosen lightly, and it may be worth adopting field sampling procedures so as to involve some sub-sampling of the primary sample area, where the diameter cut-off is set much lower than in the primary plots.

References

APPANAH, S. & WEINLAND, G. 1993. A Preliminary Analysis of the 50-hectare Pasoh Demography Plot: I. Dipterocarpaceae. Research Pamphlet No. 112. Forest Research Institute Malaysia. ISSN: 0126–8198. 53 pp.

Ashton, P. S. 1969. Speciation among tropical trees: some deductions in the light of recent evidence. Biological Journal of the Linnean Society 1:155–196.

ASHTON, P. S. 1976. Mixed Dipterocarp Forest and its variation with habitat in Malayan lowlands: a re-evaluation of Pasoh. *Malaysian Forester* 39:56-72.

- Baillie, I. C., Ashton, P. S., Court, M. N., Anderson, J. A. R., Fitzpatrick, E. A. & Tinsley, J. 1987. Site characteristics and the distribution of tree species in Mixed Dipterocarp Forest on Tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201–220.
- BOYLE, T. J. B. & BOONTAWEE, B. (Editors) 1995. Measuring and Monitoring Biodiversity in Tropical and Temperate Forests. CIFOR, Bogor.
- FISHER, R. A., CORBETT, A. S. & WILLIAMS, C. B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12:42-58.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 213:1299–1309.
- Hubbell, S. P. & Foster, R. B. 1983. Density of canopy trees in neotropical forest and implications for conservation. Pp. 25-41 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (Eds.) Tropical Rain Forest: Ecology and Management. Blackwell.
- KENT, M. & COKER, P. 1992. Vegetation Description and Analysis. John Wiley. 363 pp.
- LAUMONIER, Y. 1997. The Vegetation and Physiography of Sumatra. Geobotany 22. Kluger Academic Publishers. 222 pp.
- Lieberman, D., Bieberman, M., Peralta, R., Hartshorn, G. S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84:137–152.
- MAGURRAN, A. E. 1988. Ecological Diversity and Its Measurement. Chapman and Hall. 179 pp.
- MANOKARAN, N. & LAFRANKIE, J. 1990. Stand structure of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3(1):14-24.
- Orlog, L. 1991. Entropy and Information. SPB Academic Publishing. 72 pp.
- PEET, R. K. 1975. Relative diversity indices. Ecology 56:496-498.
- Pielou, E. C. 1975. Ecological Diversity. John Wiley, New York. 165 pp.
- RENNOLLS, K. 1997a. Diversity Issues in the Forest Inventory and Monitoring Project. FIMP-INTAG Technical Series No. 7, 157 pp.
- RENNOLLS, K. 1997b. Inventory and Other Issues in the Forest Inventory and Monitoring Project. FIMP-INTAG Technical Series No. 8, 157 pp.
- Rennolls, K. & Laumonier, Y. 1999. Forest tree species diversity: assessment, analysis and interpretation in the presence of non-identification and non-observance. Pp. 421-432 in Laumonier, Y., King, B., Legg, C. & Rennolls, K. (Eds.) Data Management and Modelling Using Remote Sensing and GIS for Tropical Forest Land Inventory. Rodeo International Publishers, Jakarta.
- TRICHON, V. 1996. Heterogeneite spatiale des structures en foret naturaelle de balle altitude a Sumatra, Indonesia. These doctorat universite Toulouse III. 260 pp.
- Turner, I. M., Wong, Y. K., Chew, P. T. & All, I. 1997. Tree species richness in primary and old secondary tropical forest in Singapore. *Biodiversity and Conservation* 6:537-543.
- VANCLAY, J. K. 1996. Towards more rigorous assessment of biodiversity. Paper presented at IUFRO 4.11, Monte Verde, September 1996.

ALLELOPATHIC EFFECT OF LEUCAENA LEUCOCEPHALA ON ZEA MAYS

H. P. Singh, Daizy R. Batish & R. K. Kohli

Department of Botany, Panjab University, Chandigarh 160 014, India

Received February 1998

SINGH, H. P., BATISH, D. R. & KOHLI, R. K. 1999. Allelopathic effect of Leucaena leucocephala on Zea mays. Allelopathic effect of leaves and litter of Leucaena leucocephala was examined on Zea mays through various greenhouse and laboratory studies. The extracts of dried leaves as well as litter were found to be inhibitory to germination and seedling growth of Z. mays under laboratory conditions. Further, the amendment of leaf powder and litter in the soil as mulch or soil mixture caused detrimental effect on root and shoot growth and biomass which increased with increase in the amount of litter/leaf powder applied. The inhibitory effect was greater when the material was amended as soil mixture. Litter was found to be more inhibitory than leaf powder in both laboratory and greenhouse studies. The amount of phenolics (a well known allelochemical group) was determined from different soil horizons under Leucaena plantations as well as its leaves. Maximum amount was found in leaves followed by the A_{00} - soil horizon containing partially degraded leaf litter of Leucaena.

Key words: Allelopathy - Leucaena leaf mulch - litter - phenolics - growth performance

SINGH, H. P., BATISH, D. R. & KOHLI, R. K. 1999. Kesan alelopati Leucaena leucocephala terhadap Zea mays. Kesan alelopati daun dan sarap Leucaena leucocephala diuji dengan melakukan pelbagai kajian di rumah hijau dan di makmal. Ekstrak daun kering dan juga sarap didapati rencat terhadap percambahan dan pertumbuhan anak benih Z. mays di bawah keadaan makmal. Seterusnya, pindaan serbuk daun dan sarap di dalam tanah sebagai sungkup atau campuran tanah menjejaskan akar dan pertumbuhan pucuk dan biojisim yang bertambah dengan bertambahnya jumlah sarap/serbuk daun yang digunakan. Kesan rencat adalah lebih besar apabila bahan tersebut dipinda sebagai campuran tanah. Sarap didapati lebih rencat berbanding dengan serbuk daun dalam kedua-dua kajian di makmal dan di rumah hijau. Banyaknya fenol (satu kumpulan alelokimia yang sangat dikenali) ditentukan daripada horizon tanah yang berbeza serta daun di bawah ladang Leucaena. Jumlah maksimum di dalam daun diikuti dengan A₀₀- horizon tanah yang mengandungi sarap daun pokok Leucaena separuh usang.

Introduction

Many socio-economic problems have arisen due to over-exploitation of natural resources—caused by rapidly increasing population. Agricultural land and forests are under tremendous pressure to cater to these increasing demands. Diversification of modern agriculture by integrating fast-growing multi-purpose woody perennials has, therefore, been envisaged so as to achieve increased agricultural production as well as that of timber, fuel, wood and forage, etc. in a sustainable way.

Leucaena leucocephala (Lam.) de Wit (hereafter referred to as Leucaena), commonly known as subabul in India, is a fast-growing versatile leguminous tree widely distributed in the tropics (Brewbaker 1987). It is grown extensively under various afforestation programmes and in agricultural fields either in alleys or along field margins as boundary plantations or even scattered. As regards the interaction of this tree with agricultural crops or other vegetation, both positive as well as negative reports are available. Some reports indicate that tree prunings placed as mulch in agricultural field improve the physical characteristics of soil and thus, increase the productivity (Budelman 1989, Tian et al. 1993). On the other hand, reduction in the growth and yield of crops growing either in close proximity to tree lines or alleys cropped with it has been reported (Karim et al. 1991, Rishi & Dhillon 1996). Likewise, Suresh and Vinaya Rai (1988) and Chou and Kuo (1986) reported exclusion of ground vegetation under this tree and ascribed this to allelopathy which refers to the negative effect (but positive too, in some cases) of one plant on the other through the release of chemical substances into the environment (Molisch 1937, Rice 1984, Janovicek et al. 1997). This phenomenon may play a significant role in determining the interactions of Leucaena with agricultural crops as well. We, therefore, hypothesise that the allelopathic chemicals (=allelochemicals) of the tree which are released in the soil through fresh intact leaves and the litter (comprising mainly dead leaves and small twigs which fall in plenty and are in various stages of decomposition) exert a negative effect on the crops and understorey vegetation. The present study was, therefore, undertaken to investigate the

- (i) effect of *Leucaena* leaves and litter extracts and their amendment in the soil on the growth and biomass of *Zea mays* (maize)— an important agroforestry combination, and
- (ii) amount of phenolics in the fresh leaves, the litter enriched top organic layer of the soil and the soil beneath the organic layer.

Material and methods

Collection of material

Fresh leaves and litter were collected from the 6 ± 1 -y-old trees of Leucaena growing near the agricultural fields on the outskirts of Chandigarh (30°42' N, 76° 54' E; 333 m a.s.l.). Because of its perennial and evergreen nature, Leucaena produces litter throughout the year and forms an organic horizon (comprising upper A_{00} - horizon having freshly fallen raw litter, and the lower A_0 -horizon consisting of finely degraded litter mixed with the soil). Soil samples were collected from the A_{00} -, A_0 - and A-horizons (i.e. just below the organic layer comprising a mixture of mineral matrix). The soil was also collected from the upper surface (3-5 cm

depth) of Leucaena free site for the purpose of amendment. The sampling was done in triplicate and the samples of leaves, litter and soil were air dried, milled, sieved and filled in polythene bags for further studies. For the bioassay studies, pure line certified seeds of Zea mays var. EH-114 were used.

Preparation of extracts from Leucaena leaves and litter

Aqueous extracts of leaf and litter were prepared by soaking 10 g dried and powdered material of each in 500 ml of pure water (conductivity < $0.05\,\mu\text{S}$, obtained through Millipore RO - Milli Q Water Purification System) for 24 h and 25 °C so as to get an extract of 2 % concentration. The extracts were filtered through a muslin cloth followed by Whatman # 1 filter paper. Each of these leaf or litter extracts was diluted to 1% and kept at 4 °C until used.

Amendment of soil with Leucaena leaf and litter

Three kilogram of the *Leucaena* free soil was filled in the $10 \times 10 \times 15$ inch earthenware pots. The powdered *Leucaena* leaves and litter were amended in this soil at the rate of 12, 24, 36 and 48 g per pot equivalent to 2.5, 5, 7.5 and 10 t ha¹. Amendment of leaf as well as litter was done in the following two ways in order to simulate the natural conditions, i.e.

- a) as surface mulch (equivalent to Ano-horizon as already described), and
- b) as soil-powder mixture (equivalent to A₀- horizon).

A set of pots amended in a similar way but with peat moss (an inert plant material) in place of leaf or litter powder served as control. Three pots were maintained for each treatment and the entire set-up was placed in a greenhouse in a completely randomised block design.

Determination of phenolic content

The amount of total phenolics was determined from the A_{00} -, A_{0} - and Ahorizons of the soil collected from the *Leucaena* inhabited area and the leaf powder using Folin-Ciocalteu reagent as per the method of Swain and Hillis (1959). In addition, phenolics were extracted from the top A_{00} - layer using the sodium salt of EDTA following the method of Kaminsky and Muller (1977). Two concentrations of these extracted phenolics (0.5 and 1.0 mg ml⁻¹) were prepared in pure water after initially dissolving the requisite amount in a few drops of ethyl alcohol. These were used for the germination and growth studies on *Z. mays* under laboratory conditions.

Germination and growth studies

Under laboratory conditions

The germination studies were carried out in 6" diameter Petri dishes lined with Whatman # 1 filter paper and underlined with a thin absorbent cotton wad. These were moistened with 10 ml of each of the extract or phenolic solutions. Twenty-five seeds of Z. mays imbibed for 10 h in the respective solutions were then equidistantly placed on the Petri dishes. Four replications were maintained for each treatment. Treatment in a similar manner with pure water instead of extracts served as control. All the Petri dishes were maintained at $25 \pm 1^{\circ}$ C and $75 \pm 2\%$ humidity in a seed germinator. After a period of 10 days, percentage germination, seedling length and dry weight of seedlings were measured. The experiment was repeated twice.

Under greenhouse conditions

Five seeds of Z. mays were sown per pot amended with leaf and litter powder as described above. After germination, these were thinned to two seedlings per pot. After eight weeks, the plants were uprooted, their root and shoot length were measured and biomass of root and shoot was determined by the oven-drying method (drying at 80 °C for 24 h). Three replications were made for each treatment and the pots were arranged in a randomised manner.

Statistical analysis

The different treatments were subjected to one-way ANOVA and the comparisons were made using Duncan's multiple range test (Duncan 1955). Correlation coefficients (r values) were also calculated between parameter value and respective concentrations.

Results and discussion

The extracts of Leucaena leaves and litter in concentrations as low as 1 or 2% reduced the germination and seedling growth of Z. mays under laboratory conditions (Table 1). The litter extracts were more inhibitory than the fresh leaves. Further, the amendment of soil collected from Leucaena free site with leaf or litter powder reduced growth (root and shoot length) and biomass of Z. mays compared to peat amended control (Figures 1a-d). Here too, the litter was more inhibitory than the fresh leaves, irrespective of the mode of application. The amendment in the form of soil mixture caused more reduction than as surface mulch. With an increasing rate of amendment, a further decrease in the growth and biomass of Z. mays was noticed as is also evidenced by reciprocal and statistically significant values of r between concentration and effect (Figures 1a-d). The study, therefore, reveals a strong allelopathic effect of leaves as well as litter of Leucaena on Z. mays.

Treatment		Germination (%)	Seedling length (cm)	Biomass (mg)
Control (water)		100°	17.82	92.4
Leaf powder	1 %	86.3 ^b	13.8 ^b	46.3b
•	2 %	68.3°	6.4 ^d	15.2^{a}
Litter powder	1 %	85.0h	10.0°	35.6
-	2 %	61.0°	5.6 ^d	17.20

Table 1. Effect of leaf and litter extracts of *Leucaena* on the germination and initial growth of *Zea mays*

Different letters in a column represent significant difference at 5% level applying Duncan's multiple range test.

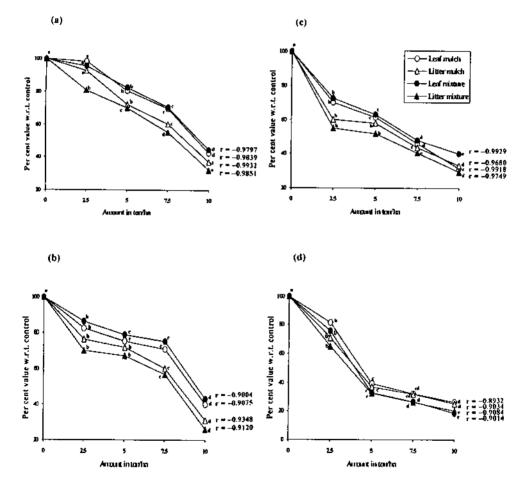


Figure 1. Effect of varying concentrations of leaf and litter of Leucaena leucocephala amended in the soil as mulch or soil mixture on the (a) root length, (b) shoot length, (c) root biomass, and (d) shoot biomass of Zea mays

Similar letters along a curve represent insignificant difference at p = 0.05 level applying Duncan's multiple range test. r along each curve represents correlation coefficient between different concentrations and value of parameter.

In nature, Leucaena leaves fall throughout the year and form a characteristic litter layer dominated by its leaves besides pods and seeds. It hardly supports any understorey vegetation except its own seedlings (Chou & Kuo 1986). The growth of Leucaena is fast although the tree is not very hardy. Even its branches keep falling with the pressure from strong winds and may exert a negative effect on adjoining crops and vegetation. Leucaena when grown as a hedge tree is pruned periodically and the prunings placed in the fields with a motive to incorporate the nutrients in the soil, Facelli and Pickett (1991) have reported that plant litter placed as mulch has an important impact on nutrient availability and their accumulation in the soil. However, a number of reports indicate that several allelochemicals are released upon leachation or decomposition from the litter (Blashke 1979, Rice 1984, Kuiters 1990, Chou & Leu 1992, Gonzalez et al. 1995). A number of reports are available which indicate that litter of several trees/shrubs cause significant toxicity to the understorey and field crops (Younger et al. 1980, Wilt et al. 1988, Molina et al. 1991, Inderjit & Mallik 1996, Singh 1996). Jobidon (1986) reported the reduction in seed germination of grasses by the leaf and litter extracts of coniferous trees. The allelochemicals upon release may cause toxic effect on the vegetation or prevent the emergence and growth of crop plants. In some cases litter mixed in soil significantly reduced growth and biomass accumulation of test plants and even the addition of fertilisers failed to compensate it (Sidhu & Hans 1988, Mallik 1996).

Our studies further show that phenolics are present in considerable amount in Leucaena leaves, the top soil layer containing un- and partially decomposed litter (equivalent to A_m-horizon) and decomposed litter-soil mixture (equivalent to A_n -horizon) and the humus free soil (i.e. A_n -horizon) in the order of leaves $> A_m$ -soil horizon > A-soil horizon > A-horizon (Table 2). Chou and Kuo (1986) have reported the presence of phenolic acids, quercetin and mimosine in the leaf and litter of Leucaena. Chaturvedi and Jha (1992) reported that the reduction in the germination and radicle growth of rice seedlings in response to leaf leachates was due to the presence of mimosine in the leaves. In the present study, however, total phenolic content was studied rather than individual compounds because the allelochemicals act additively or synergistically but not singly (Einhellig 1995). The phenolics collected from the uppermost soil layer (Am-layer) were tested for their phytotoxicity towards Z. mays and seen to inhibit germination and growth under laboratory conditions (Table 3). The presence of phenolics may also affect the nutrient status of Leucaena as phenolics, in general, are known to alter the accumulation, availability and uptake of the nutrients in plants (Appel 1993).

Table 2. Amount of phenolics extracted from the leaves of *Leucaena* and different soil horizons

Material	Amount (mg 100g1)	
Leaves	77.30 ± 2.35	
A _{so} -horizon	45.18 ± 1.45	
A horizon	28.64 ± 0.50	
A-horizon	12.38 ± 0.21	

Table 3.	Effect of different concentrations of phenolics extracted from the A _m -horizon
	under L. leucocephala on the germination and initial growth of Z. mays in the
	laboratory. Values are with respect to control.

Concentration (mg ml ⁻¹)	Germination (%)	Seedling length (cm)	Seedling dry weight (mg)
0 (Control)	100°	100°	100*
0.5	85 ^b	66.47 ^b	45.4b
1.0	47°	25.414	35.3°

Similar letters in a column represent insignificant difference at 5% level applying Duncan's multiple range test. Values in control: seedling length, 15.45 ± 1.32 cm; seedling dry weight, 88.72 ± 3.58 mg.

It is, therefore, concluded that the presence of phenolics in the *Leucaena* litter and leaves is largely responsible for allelopathic effect on *Z. mays.*

Acknowledgements

The first author is thankful to the Centre for Scientific and Industrial Research (CSIR), New Delhi, for financial assistance.

References

- APPEL, H. M. 1993. Phenolics in ecological interactions: the importance of oxidation. *Journal of Chemical Ecology* 19:1521-1552.
- Blashke, H. 1979. Leaching of water soluble organic substances from coniferous needle litter. Soil Biology and Biochemistry 11:581-584.
- Brewbaker, J. L. 1987. Leucaena: a multipurpose genus for tropical agroforestry. Pp. 289-323 in Steppler, H. A. & Nair, P. K. R. (Eds.) Agroforestry: A Decade of Development. International Council for Research in Agroforestry, Nairobi, Kenya.
- BUDELMAN, A. 1989. Nutrient composition of the leaf biomass of three selected woody leguminous species. Agroforestry Systems 8:39-51.
- Chaturvedi, O. P. & Jha, A. N. 1992. Studies on allelopathic potential of an important agroforestry species. Forest Ecology and Management 53:91-98.
- CHOU, C. H. & KUO, Y. L. 1986. Allelopathic research of subtropical vegetation in Taiwan. III. Allelopathic exclusion of understorey by *Leucaena leucocephala* (Lam.) de Wit. *Journal of Chemical Ecology* 12:1431-1448.
- CHOU, C. H. & LEU, L. I. 1986. Allelopathic substances and interactions of *Delonix regia* (Boj.) Raf. Journal of Chemical Ecology 18:2285-2303.
- DUNCAN, D. B. 1955. Multiple range and multiple F-tests. Biometrics 11:1-42.
- EINHELLIC, F. A. 1995. Allelopathy: current status and future goals. Pp. 1-24 in Inderjit, Dakshini, K. M. M. & Einhellig, F. A. (Eds.) Allelopathy: Organisms, Processes and Applications. American Chemical Society, Washington D.C.
- FACELLI, J. M. & PICKETT, S. T. A. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1–32.
- GONZALES, L., SOUTO, X. C. & REIGOSA, M. J. 1995. Allelopathic effects of Acacia melanoxylon R.Br. phyllodes during their decomposition. Forest Ecology and Management 77:53-63.
- INDERJIT & MALLIK, A.U. 1996. The nature of interference potential of Kalmia angustifolia. Canadian Journal of Forest Research 26:1899-1904.

- JANOVICEK, K. J., VYN, T. J., VORONEY, R. P. & ALLEN, O. B. 1997. Early corn seedling growth response to acetic, propionic and butyric acids. Canadian Journal of Plant Science 77:333–337.
- Jobidon, R. 1986. Allelopathic potential of coniferous species to old-field weeds in Eastern Quebec. Forest Science 32:112–118.
- KAMINSKY, R. & MULLER, W. H. 1977. The extraction of soil phytotoxins using a neutral EDTA solution. Soil Science 124:205-209.
- KARIM, A. B., SAVILL, P. S. & RHODES, E. R. 1991. The effect of young Leucaena leucocephala (Lam.) de Wit hedges on the growth and yield of maize, sweet potato and cowpea in an agroforestry system in Sierra Leone. Agroforestry Systems 16:203–211.
- Kutters, A. T. 1990. Role of phenolic substances from decomposing forest litter in plant-soil interactions. *Acta Botanica Neerlandica* 39:329–348.
- Mallik, A. U. 1996. Effect of NPK fertilizations on Kalmia angustifolia: implications for forest disturbance and conifer regeneration. Forest Ecology and Management 81:135-141.
- MOLINA, A., REIGOSA, M. J. & CARBALLEIRA, A. 1991. Release of allelochemical agents from litter throughfall, and top soil in plantations of *Eucalyptus globulus* Labill. in Spain. *Journal of Chemical Ecology* 17:147–160.
- MOLISH, H. 1937. Der Einfluss einer Pflanze auf die andere -Allelopathie. Fischer, Jena. 20 pp.
- RICE, E. L. 1984. Allelopathy. Academic Press, New York, USA. 422 pp.
- RISHI, A. & DHILLON, M. S. 1996. Impact of subabul based alley cropping system on the growth and yield of oat fodder. Pp. 255-258 in Kohli, R. K. & Arya, K. S. (Eds.) Proceedings of the IUFRO-DNAES International Meeting on Agroforestry and Environment. Dayanand National Academy of Environmental Sciences, India.
- Sidello, D. S. & Hans, A. S. 1988. Preliminary studies on the effect of *Eucalyptus* leaf-litter on accumulation of biomass in wheat. *Journal of Tropical Forestry* 4: 328–333.
- Singh, H. P. 1996. Phytotoxic Effects of *Populus* in Natural and Agroecosystems. Ph.D. thesis, Panjab University, Chandigarh, India. 279 pp.
- Suewah, K. K. & Vinaya Rai, R. S. 1988. Allelopathic exclusion of understorey by a few multipurpose trees. *International Tree Crops Journal* 5:143–151.
- Swain, T. & Hillis, W. E. 1959. The phenolic constituents of *Prunus domestica*. I. The quantitative analysis of phenolic constituents. *Journal of Science Food and Agriculture* 10:63–68.
- TIAN, G., KANG, B. T. & BRUSSAAFD, L. 1993. Mulching effect of plant residues with chemically contrasting compositions on maize growth and nutrient accumulation. *Plant and Soil* 153:179-187.
- WILT, F. M., MILLER, G. C. & EVERETT, R. L. 1988. Monoterpene concentrations in litter and soil of single leaf pinyon woodlands of the Western Great Basin. *Great Basin Naturalist* 48:228-231.
- YOUNGER, P. D., KOCH, R. G. & KAPUTSKA, L. A. 1980. Allelochemic interference by quaking aspen leaf litter on selected herbaceous species. *Forest Science* 26: 429-434.

ANALYSIS OF TWO ALTERNATIVE HARVESTING SYSTEMS IN PENINSULAR MALAYSIA: SENSITIVITY ANALYSIS OF COSTS, LOGGING DAMAGE AND BUFFERS

Saharudin Ahmad,

Forest Economics Unit, Forestry Department Headquarters, Jalan Sultan Salahuddin, 50660 Kuala Lumpur, Malaysia

J. Douglas Brodie

Department of Forest Resources, Oregon State University, 237 Peavy, Corvallis, Oregon, 97331-5703, United States of America

&

John Sessions

Department of Forest Engineering, Oregon State University, 223 Peavy, Corvallis, Oregon, 97331-5706, United States of America

Received March 1998

SAHARUDIN, A., BRODIE, J. D. & SESSIONS, J. 1999. Analysis of two alternative harvesting systems in Peninsular Malaysia: sensitivity analysis of costs, logging damage and buffers. An economic study of two alternative timber harvesting systems was carried out in Peninsular Malaysia to evaluate and compare existing and improved harvesting systems in terms of their costs, efficiency and productivity. The results showed that distance and diameter? were significantly related to delay-free cycle time in felling in Jengai and Tembat, the two areas studied with contrasting harvesting systems. In skidding, distance and number of logs were significant in Jengai, while distance and diameter were significant in Tembat. Logging cost excluding cost of conservation, premium and royalty under the new system was RM 50.89 m³ or 4% lower than logging cost under the old system of RM 52.9 m³. Under average conditions, it takes 0.31 h to fell a tree under the new system compared to 0.39 h (simulated) under the old system. This suggests that the improvement made in the Jengai Forest Reserve has increased productivity of felling. In skidding, it takes about 0.55 h to travel one round trip under the new system compared to 0.77 h (simulated) under the old system. This suggests that the improvement in road construction in Jengai has increased productivity of skidding. Under average conditions, the costs of felling and skidding were lower under the new system as compared with the old system (simulated). Simulating the new system, the cost of felling and skidding were slightly higher as compared with the old system. The present value of cost of damage discounted at 4% discount rate was RM 3.62 m³ compared to RM 5.02 m³ under the old system. The Present Net Worth (PNW) of the new system with buffer cost was RM 577.07 m³

compared to PNW of the old system of RM 566.53 m⁻³ without buffer cost. This shows that the reduction in damage to the residual stand has increased the net future harvests as shown by the higher PNW of the new system. The study also shows that it is more economical to install the buffer zone in the new system based on the higher PNW of the new system.

Key words: Productivity - new system - old system - buffer costs - PNW - damage costs - logging costs - opportunity costs

SAHARUDIN, A., BRODIE, J. D. & SESSIONS, J. 1999. Analisis terhadap dua sistem pengusahasilan hutan alternatif di Semenanjung Malaysia: analisis kepekaan bagi kos, kerosakan pembalakan dan penampan. Satu kajian ekonomi terhadap dua jenis sistem pengusahasilan hutan telah dijalankan di Semenanjung Malaysia bertujuan untuk menilai dan membuat perbandingan antara sistem pengusahasilan sedia ada (sistem lama) dan ubahsuai (sistem baru) dari segi kos, kecekapan dan produktiviti. Hasil kajian menunjukkan iaitu jarak antara pokok dan garis pusat² berhubung kait dengan bererti dengan masa pusingan tanpa kelewatan bagi aktiviti penebangan di kedua-dua kawasan kajian, manakala dalam aktiviti penarikan, jarak dan bilangan balak berhubung kait dengan bererti dalam Jengai manakala jarak dan perepang berhubung kait dengan bererti dalam Tembat. Kos pembalakan tanpa kos pemuliharaan, premium dan royalti di bawah sistem baru ialah RM 50.89 m³ atau 4% lebih rendah daripada kos pembalakan di bawah sistem lama iaitu sebanyak RM 52.9 m³. Aktiviti penebangan bagi sebatang pokok di bawah sistem baru mengambil masa selama 0.31 jam berbanding dengan 0.39 jam (simulasi) di bawah sistem lama. Ini menunjukkan bahawa pembaikan yang telah dibuat di Hutan Simpan Jengai telah meningkatkan produktiviti penebangan. Bagi aktiviti penarikan, ia mengambil masa selama 0.55 jam untuk satu pusingan di bawah sistem baru berbanding dengan selama 0.77 jam (simulasi) di bawah sistem lama. Ini menunjukkan bahawa pembaikan yang telah dibuat ke atas pembinaan jalan di Hutan Simpan Jengai telah meningkatkan produktiviti penarikan. Kos penebangan dan penarikan di bawah sistem baru adalah lebih rendah berbanding dengan sistem lama (simulasi). Kos penebangan dan penarikan di bawah sistem baru (simulasi) lebih tinggi sedikit berbanding dengan sistem lama. Nilai kini kadar kerosakan pada kadar diskaun 4% ialah sebanyak RM 3.62 m³ berbanding dengan RM 5.02 m³ di bawah sistem lama. Nilai Bersih Kini (PNW) bagi sistem baru dengan kos penampan ialah sebanyak RM 577.07 m³ berbanding dengan RM 566.53 m3 tanpa kos penampan. Ini menunjukkan bahawa pengurangan dalam kerosakan bagi dirian tinggal telah meningkatkan hasil tebangan pusingan akan datang seperti yang ditunjukkan oleh peningkatan nilai PNW bagi sistem baru. Kajian ini juga menunjukkan bahawa lebih ekonomi untuk mewujudkan zon penampan di bawah sistem baru berdasarkan peningkatan nilai PNW bagi sistem baru.

Introduction

Astudy was carried out under the Project B7: Malaysia-United Kingdom Programme of Cooperation on Forest Management and Conservation to evaluate and compare existing and improved harvesting systems in terms of their costs, efficiency and productivity. Forest harvesting is the most important activity of the forestry sector and how it is being done will directly influence the other related forestry activities. Unfortunately, over the years, insufficient attention has been given to the forest harvesting operations other than the control in areas opened for logging. Most of the loggers are only interested in the short-term benefits with

scant regard to the nation's needs in the long run. The attitudes and actions of the loggers have resulted in damage and pollution of the environment leaving large quantities of potential wood and other forest goods as logging wastes. The main problem currently faced by the Forestry Department is the lack of provisions for adequate rules and regulations for stricter control on the forest harvesting operations and insufficient experience and technology in maximum utilisation and production in forest harvesting operations. The lack of sufficient knowledge and technical know-how was the main obstacle to the planning, evaluation, management and control of forest harvesting activities. This study was carried out to recommend the most efficient forest harvesting system which would minimise damage to the environment with minimum cost. An economic model of harvesting costs in order to assess the opportunity costs of timber left in buffer strips and the costs and benefits of directional felling was developed.

Under the new or improved harvesting system, buffer strips are installed and marked on the ground with width of at least 20 m from either side of the streams¹. There is no marked buffer strips under the old or existing system. Directional felling is incorporated in the new system showing the direction of trees to be felled. There is no directional felling under the old system. Under the new system, there is improved road construction where road location is made on the plan before logging licence is approved, that is road construction according to the standards and specifications of forest roads in Peninsular Malaysia, while under the old system, road location and construction do not follow the standards and specifications of forest roads in Peninsular Malaysia.

The Jengai Forest Reserve which is under the new system is located in Compartment 123, Block B, in the district of Dungun, Terengganu, with an area of 197 ha while the Tembat Forest Reserve which is under the old system is located in Compartment 204, Block 12 A, covering an area of 135 ha. Both study areas were mostly hilly and rocky with elevation between 100 and 600 m and slope ranging from 5 to 22°.

The study areas were managed under the Selective Management System (SMS) with rotation length of 30 y. The cutting limits were 45 cm dbh and above both for the dipterocarp and non-dipterocarp groups for the Jengai Forest Reserve and 50 cm dbh and above both for the dipterocarp and non-dipterocarp groups for the Tembat Forest Reserve, based on the Pre-Felling Inventory (Pre-F Inventory) of the two areas. The Pre-F Inventory was carried out for all trees of diameter classes of 5 cm and above.

In the Jengai Forest Reserve, there was a total of 48 species and the yield was 65 m³ ha⁻¹ and 3.2 m³ per tree. In the Tembat Forest Reserve, there were 51 species with a yield of 92 m³ ha⁻¹ and 3.3 m³ per tree.

The harvesting system used in the Jengai and Tembat Forest Reserves was a combination of chainsaw, crawler tractor and a winch-lorry called San Tai Wong. In the felling site, a chainsaw was used to fell the tree and to cross-cut the log

¹ Buffer strips are forested area on either side of the streams left unlogged for protection of the streams from soil erosion and sedimentation.

immediately at the felling site or at the temporary log-landing. A crawler tractor was used to transport the log from the felling site to the log-landing. The winch lorry was used to transport logs from the temporary log-landing to the permanent log-landing.

Literature review

Other studies on cost studies in harvesting includes comparison of a logging system with only one crawler tractor and a system with a crawler tractor combined with the FMC skidder and a simple model was used. This comparison showed that the system with the combination of crawler tractor and FMC skidder was more economical than using the crawler tractor only when the average skidding distance of the tractor exceeded 0.38 km (Marn et al. 1982).

In another study on logging cost and productivity (Marn et al. 1981), the time study was conducted on the traditional type of skidding operation in which three different ways of skidding were studied, namely down hill skidding, uphill skidding and neutral. Regressions were made for time and distance on main, secondary, no trail and opening trails. Generally good correlations were found. In the case of loading, no good correlation could be found, but on average, good correlations were found in skidding for time related to volume and distance.

Comparison of felling time and cost per m³ between directional felling and traditional felling was studied by Marn (1982). Cost of directional felling was RM 2.29 m³ compared to RM 2.31m³ for the traditional felling. Directional felling was thus achieved without any extra cost. In the log extraction, two different operations both using CAT D6C were compared. A carefully planned operation where felling had been done towards already opened main skidtrails and chokers were used was compared to extraction by traditional method. The results showed that increase in production was 36% compared to traditional felling and reduction of cost was 26% compared to traditional felling.

On the effects of directional felling to the remaining stand, the study showed that the number of trees lost was reduced by 33% and the volume of felled sound timber left was reduced by 48%. The combined effect of the directional felling, the use of chokers and good skidtrail network, planned and opened before the start of the felling, contributed mostly to the increase in production and reduction of damage to the remaining stand.

Methodology

Data were collected using a combination of time-study and survey-questionnaire method. The study sites were randomly selected from those with similar forest types, zones and forest management systems. The forest type selected was the hill dipterocarp forest from the eastern zone of Peninsular Malaysia. Interviews were conducted to obtain information on fixed and operating costs as well as harvesting systems used. Information on forest stand, topography and departmental costs

was collected from the District Forest Office. Production times were taken from the five sub-systems: felling and cross-cutting, skidding or off-road transportation, loading, short distance transportation or short hauling, and road construction.

Comparisons of productivity and costs between the Jengai and Tembat Forest Reserves were made using average conditions in each area. Equations developed for the Jengai Forest Reserve were used to represent the new system while those developed for the Tembat Forest Reserve were used to represent the old system. The same contractor wage rates and equipment costs were used for each area to simulate the new system in Jengai and the old system in Tembat.

For the sensitivity analysis on the damage to the residual stand after logging, comparisons of damage costs between the new and the old systems were made. Comparison of the Present Net Worth (PNW) between the new and the old systems without buffer cost was made to evaluate the impacts of future damage on the PNW returns for each of the systems. Comparison of PNW between the new and the old systems with buffer costs was also made to project the impacts of the future damage and buffer zone on the PNW returns for each system. The percentage damage for breakeven on the new system was determined for each of the analyses to justify the new system.

Statgraphics (Windows Version 2) was used to analyse the Jengai and Tembat Forest Reserves and to find significant independent variables (95% confidence level) that could be used to predict cycle times.

Results and discussion

Felling

The model for the Jengai Forest Reserve (new system) is:

delay-free cycle time(s) = -241.51 + 0.98 distance + 0.20 diameter²

 $R^2 = 68.4\%$, SE = 691.1, MAE = 500.3 t-statistics: distance = 2.3, diameter² = 7.8

The model for the Tembat Forest Reserve (old system):

delay-free cycle time(s) = 47.64 + 5.92 distance + 0.09 diameter²

 $R^2 = 53.4\%$, SE = 502.7, MAE = 313.7 **statistics: distance = 3.9, diameter² = 4.6

The above model shows that distance between trees is relatively more important in the Tembat Forest Reserve as shown by the greater regression coefficient. It shows that for the same distance, the felling operator takes 5.92 s to travel 1m as compared to 0.98 s in the Jengai Forest Reserve. Felling time

increased with increase in distance between trees and diameter². In a similar study carried out by the FAO, 1966-1968, it was found that felling time increased with increase in diameter and number of logs per tree (Anonymous 1974). The improvements made in road construction on the Jengai Forest Reserve had increased productivity. The model also shows that it takes 0.09 s per square centimeter to fell and cross-cut the tree with the same diameter in the Tembat Forest Reserve as compared to 0.20 s per square centimeter in the Jengai Forest Reserve. The longer time taken to fell a tree with the same diameter in the Jengai Forest Reserve as compared to the Tembat Forest Reserve may be due to the longer time taken in directional felling in the Jengai Forest Reserve.

The results showed that under average conditions, under the new system in the Jengai Forest Reserve it takes 0.31 h to fell a tree compared to 0.39 h (simulated) in the Tembat Forest Reserve. This suggests that the improvement made in the Jengai Forest Reserve had increased the productivity of felling.

Skidding

The model for the Jengai Forest Reserve (new system) is:

delay-free cycle time (s) = 569.85 + 1.72 distance + 324.15 log number

 $R^2 = 62.7\%$, SE = 337.3, MAE = 240.5 *statistics: distance = 4.5, log number = 2.3

The model for the Tembat Forest Reserve (old system) is:

delay-free cycle time (s) = 119.3 + 3.67 distance + 4.11 diameter

 $R^2 = 57.6\%$, SE = 270.9, MAE = 203.2*t*-statistics: distance = 8.2, diameter = 3.3

The model shows that skidding distance is more significant in the Tembat Forest Reserve as compared to the Jengai Forest Reserve as shown by the greater regression coefficient. It shows that for the same distance, the crawler tractor takes 3.67 s to travel one round trip meter as compared to 1.72 s in the Jengai Forest Reserve. The improvement in road construction in the Jengai Forest Reserve had increased skidding productivity as compared to the Tembat Forest Reserve. It also shows that the number of logs per trip is significantly related to time in Jengai and diameter of logs per trip in Tembat. In a similar study carried out by the FAO, 1966-1968, it was found that skidding time increased with increase in distance, number of logs and diameter (Anonymous 1974).

In skidding, it takes about 0.55 h to travel one round trip in Jengai as compared to 0.77 h (simulated) in Tembat. This suggests that the improvement

in road construction in Jengai had increased productivity of skidding. It was also found that in Jengai it was more efficient to transport more than one log to increase production as the distance increased.

Short hauling

As only one travelling distance was used in the short hauling system, it is not possible to predict the cycle time using multiple linear regression. The equation for the short hauling system was estimated based on the time taken to travel the hauling distance, excluding the loading and the unloading time as follows:

The model for the Jengai Forest Reserve (new system) is: delay-free cycle time (s) = 1500 + 0.70 distance

The model for the Tembat Forest Reserve (old system) is: delay-free cycle time (s) = 1338 + 0.62 distance

The model shows that hauling distance is more significant in the Jengai Forest Reserve as compared to the Tembat Forest Reserve as shown by the greater regression coefficient of the hauling distance. It shows that for the same distance, the winch lorry takes 0.70 s to travel one round trip meter as compared to 0.62 s in the Tembat Forest Reserve.

For the same average distance of 15 200 m as in the Jengai Forest Reserve, the time taken in short hauling in the Tembat Forest Reserve was 10 762 s which is still lower than the time taken in the Jengai Forest Reserve. However, comparisons of productivity between the two areas was not possible since only one observation for distance was used in the model.

Costs and productivity

Logging costs for the Jengai Forest Reserve using the new system and the Tembat Forest Reserve using the old system are given in Table 1.

Activity	Jengai (RM m³)	Tembat (RM m ⁻³)
Felling and cross-cutting	4.79	6.20
Skidding	10.93	11.03
Loading and unloading	2.49	0.94
Short hauling	8.72	10.60
Supporting costs	23.96	24.14
Total logging cost	50.89	52.91

Table 1. Logging costs for the Jengai and Tembat Forest Reserves

From Table 1, the cost of logging in the new system was RM 50.89 m⁻³ or 4% lower than the cost of logging under the old system, RM 52.91 m⁻³, excluding conservation costs, royalty, and premium.

The study was designed in such a way that comparison of logging costs was made possible using the criteria of similar forest types, zones and forest management systems. However, to make a more even comparison between the new and the old systems we established a standard set of physical, biological, and economical conditions, that is tree size, trees per acre, walk-in distance and contractor costs, and then used these conditions in the models developed from Jengai and Tembat in the simulation process. Two obvious sets of standard conditions are available. We could use either the average values in Jengai or Tembat (machine's cost, operator's cost and volume tree-1) and repeat the analyses first using the average values at Jengai and then the average values at Tembat. In doing this, the model (equation) developed for Jengai would be used to represent the technical relationships of the new system and the model developed from Tembat would be used to represent the technical relationships of the old system.

In terms of costs, under average conditions, the cost of felling under the new system is RM 44.49 tree⁻¹ or 0.34% lower than the old system (simulated) of RM 44.64 tree⁻¹. The cost per tree would be approximately the same using the new system as the old system. Simulating the new system in Tembat, the cost of felling in the new system is RM 50.55 tree⁻¹ (simulated) or 0.28% higher than the old system of RM 50.41 tree⁻¹. The cost per tree is approximately the same under the new system as the old system, but the productivity of the new system (0.22 h tree⁻¹ per tree) is slightly lower under the new system than under the old system (0.19 h tree⁻¹).

In skidding, the cost under the new system is RM 78.12 log¹ or 14 % lower than the old system(simulated) of RM 90.74 log¹. This suggests that under the same conditions of distance, diameter and number of logs as in the Jengai Forest Reserve, the cost per log is lower using the new system.

The cost of skidding under the new system (simulated) is RM 84.48 log¹ or 3.6% higher than the cost under the old system of RM 81.56 log¹. The productivity of the new system (simulated) is 0.30 h per trip compared to 0.22 h per trip under the old system.

Sensitivity analysis on the damage to the residual stand after logging

Volume of trees damaged in the residual stand in the 30-39 cm dbh and >40 cm dbh classes is $0.5 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$. The total volume of trees damaged at 30% damage under the new system in the next rotation is $15 \text{ m}^3 \text{ ha}^{-1}$. Assuming the damage under the new system is about 30%, the damage under the old system is estimated

 $^{^2}$ A 30% damage refers to the damage to the residual trees in the 30-39 cm and >40 cm diameter class under the new system while 40% damage refers to the damage to the residual trees in the 30-39 cm and >40 cm diameter class under the old system.

at about 40% (Johnson & Cabarle 1993). The percentage growth of damaged trees in the next rotation is 18% under the new system and 22.7% under the old system (Forestry Department of Peninsular Malaysia 1991). The total volume of trees damaged at 40% damage under the old system in the next rotation is 20 m³ ha¹. The net future volume of harvests for the next rotation after allowing 30% damage under the new system is 50 m³ ha¹ and 45 m³ ha¹ under the old system at 40% damage. At 30% damage under the new system, the present value of costs of damage discounted at a 4% discount rate is RM 3.62 m³, based on yield of 65 m³ ha¹ and RM 5.02 m³ under the old system at 40% damage based on yield of 65 m³ ha¹, as shown in Table 2. From Table 2, the breakeven percentage damage under the new system was about 41% with a present value of RM 5.02 m³. Hence the percentage damage allowable under the new system should be less than 41% in order to justify the viability of the new system.

When the yield is 92 m³ ha¹ for the old system, the present value of damage cost is RM 3.55 m³ at 40% damage, as shown by Table 3. Breakeven on the new system decreased from 41 to 28%. This shows that yield other than logging cost plays an important role in influencing the viability of the new system.

Table 2. Comparison of present value of damage costs under the new and old systems (RM m³), based on yield of 65 m³ ha⁻¹ for the new and the old systems

Damage (%)	New system	Old system
0	0.00	0.00
10	1.21	1.25
20	2.41	2.51
30	3.62	3.76
40	4.83	5.02
50	6.03	6.27
60	7.24	7.53

Table 3. Comparison of present value of damage costs under the new and old systems (RM m³), based on yield of 65 m³ ha⁻¹ (new system) and 92 m³ ha⁻¹ (old system)

Damage (%)	New system	Old system
0	0.00	0.00
10	1.21	0.89
20	2.41	1.77
30	3.62	2.65
40	4.83	3.55
50	6.03	4.43
60	7.24	5.32

Under the new system, the cost of buffer zones is RM 19.09 m⁻³. The difference between the PNW of the new system with buffer and the PNW of the new system without buffer is the present value of the cost of buffer, which is RM 4.53 m⁻³ or about 7.63% of the present value of logging cost.

Under the old system, the cost of buffer zone is RM 24.50 m⁻³. The difference between the PNW of the old system with buffer and the PNW of the old system without buffer is the present value of the cost of buffer, which is RM 5.92 m⁻³ or about 9.52% of the present value of logging cost.

The PNW of the new system with buffer cost at 30% damage is RM 577.07 m³ compared to the PNW of the old system of RM 566.53 m⁻³ at 40% damage without buffer cost, using the same yield of 65 m3 ha1 and revenue of RM 521 m3 as the new system, as shown by Table 4.

Damage (%)	New system (with buffer cost)	Old system (without buffer cost)
0	609.16	612.40
10	598.46	600.93
20	587.77	589.46
30	577.07	577.08
40	566.38	566.53
50	555.68	555.06
60	544.98	543.59

Table 4. Comparison of PNW between the new and the old systems (RM m³)

This shows that the PNW of the new system is approximately 2% higher than the PNW of the old system. Hence the reduction in damage to the residual stand has increased the net future harvests as shown by the higher PNW of the new system with buffer cost. From Table 4, the percentage damage under the new system for breakeven is about 38%; hence the percentage damage allowable under the new system should be less than 38% in order to justify the viability of the new system.

Without buffer cost, the PNW of the new system is RM 581.60 m⁻³ or approximately 3% higher than PNW of the old system of RM 566.53 m⁻³ based on the yield of 65 m³ ha⁻¹ and revenue of RM 521 m⁻³ as the new system, as shown by Table 5.

Without by	microdit buner cost (NM III)		
Damage (%)	New system (without buffer cost)	Old system (without buffer cost)	
0	615.04	612.40	
10	603.90	600.93	
20	592.75	589.46	
30	581.60	577.00	
40	570.45	566.53	
50	559.30	555.06	

559.30

548 15

60

555.06

543.59

Table 5. Comparison of PNW between the new and the old system without buffer cost (RM m3)

This shows that the reduction in damage to the residual stand has increased the net future harvests as shown by the higher PNW of the new system and the presence of buffers had decreased the PNW of the new system by about 1%, from RM 581.60 m⁻³ to RM 577.07 m⁻³. From Table 5, the PNW of the new system for breakeven is RM 566.53 m⁻³ at about 42% damage; hence the percentage damage allowable under the new system should be less than 42% in order to justify the viability of the new system.

Sensitivity analysis was also done on the new system, with and without buffer costs and on the old system with and without buffer costs. Table 6 shows comparison of PNW between the new and the old systems

Damage (%)	New system (with buffer cost)	Old system (with buffer cost)
0	609.16	534.19
10	598.46	527.65
20	587.77	521.13
30	577.07	514.60
40	566.38	508.08
50	555.68	501.55
60	544.98	495.02

Table 6. Comparison of PNW between the new and the old systems (RM m⁻⁵)

From Table 6, the PNW of the new system with buffer cost was RM 577.07 m³ at 30% damage compared to the PNW of the old system of RM 514.60 m³ with buffer cost. This shows that it is more economical to install the buffer zone in the new system based on the higher PNW compared to the old system with buffer zone.

Conclusion

The new system is more productive at the Jengai Forest Reserve, and less productive at the Tembat Forest Reserve, than the old system.

In felling, it was found that distance and diameter² were the two variables that were significantly related to time in both study areas. The time of felling increases as the distance and diameter² increase in both areas. It takes less time to travel between trees in the Jengai Forest Reserve as compared to the time taken to travel the same distance in the Tembat Forest Reserve. For the same average distance and diameter, it takes a shorter time to fell a tree in Jengai than in Tembat. This suggests that the improvement made in the Jengai Forest Reserve has contributed to the higher productivity in the Jengai Forest Reserve.

Distance and number of logs were significantly related to delay-free cycle time in skidding in the Jengai Forest Reserve while distance and diameter were significant in the Tembat Forest Reserve. The time of skidding increases in Jengai as the distance and number of logs increase while in Tembat the time of skidding

increases as distance and diameter increase. Productivity in the Jengai Forest Reserve is higher than that in the Tembat Forest Reserve based on the same average distance, number of logs and diameter as given by the shorter time taken to skid a log in Jengai than in Tembat. This suggests that the improvements in road construction in the Jengai Forest Reserve increased productivity of skidding. From the study, it was also found that the number of logs was significantly related to delay-free cycle time in the Jengai Forest Reserve. The delay-free cycle time increases with increase in the number of logs skidded. This shows that it is more efficient to transport more than one log as the distance increases in order to increase production.

On average it took a longer time to haul logs in the Jengai Forest Reserve than in the Tembat Forest Reserve. However, due to the lack of a range of operating conditions for the short hauling system, it is not easy to compare productivity between the two study areas. A more detailed study consisting of more than one hauling distance is needed to arrive at a model of the short hauling system.

The new system is cheaper in Jengai than in Tembat because the model for the new system was developed based on the improved conditions with respect to road construction, directional felling and buffer strip.

Under the same conditions of distance and diameter as in the Jengai Forest Reserve, the cost of felling per tree was RM 44.49 or 0.34% lower using the new system than the simulated cost of using the old system (RM 44.64). Under the same conditions of distance and diameter as in the Tembat Forest Reserve, the cost of felling per tree was RM 50.55 or 0.28% higher using the simulated cost of the new system than the old system (RM 50.41).

Under the same conditions of distance, diameter and number of logs as in the Jengai Forest Reserve, the cost of skidding per log in the Jengai Forest Reserve using the new system was RM 78.12 or 14% lower than the simulated cost of using the old system (RM 90.74). Under the same conditions of distance and diameter and number of logs as in the Tembat Forest Reserve, the cost of skidding per log was RM 84.48 or 3.46% higher using the simulated cost of the new system than using the old system (RM 81.56).

On average, the cost of hauling was lower (RM 8.72 m³) in the Jengai Forest Reserve than in the Tembat Forest Reserve (RM 10.60 m³). Because of the lack of predictive model for the hauling system in each area, it was not possible to compare productivity and costs between the two areas.

Yield other than logging costs plays an important role in influencing the viability of the new system. When yield per hectare is increased from 65 to 92 m³ ha⁻¹, breakeven on the new system decreased from 41 to 28%. This shows that viability of the new system is decreased from 41 to 28% damage.

The PNW of the new system with buffer cost is RM 577.07 m³ or approximately 2% higher than PNW of the old system of RM 566.53 m³ without buffer cost. The reduction in damage to the residual stand from 40 to 30% damage had increased the net future harvests as shown by the higher PNW of the new system.

It is more economical to install the buffer zone in the new system based on the higher PNW of RM 577.07 m⁻³ compared to the PNW of RM 514.60 m⁻³ in the old system.

Acknowledgements

This paper is based on work undertaken by the first author in collaboration with his co-authors while on study leave at the College of Forestry, Oregon State University. The project is sponsored by the Malaysia-United Kingdom Programme for the Conservation, Management and Development of Forest Resources under Sub-Programme B which focusses on the valuation of non-timber forest goods and services. The first author thanks the Director General of the Forestry Department, Peninsular Malaysia, and the Public Services Department of Malaysia for granting approval of his study leave from 1995 to 1997.

References

- Anonymous. 1974. Logging and Log Transport in Tropical High Forest: A Manual on Production and Costs. FAO Forestry Series No. 5, FAO Forestry Development Paper No.18.
- FORESTRY DEPARTMENT OF PENINSULAR MALAYSIA. 1991. Current Status of Forestry Sector in Peninsular Malaysia. Forest Planning Unit, Forestry Department Headquarters, Kuala Lumpur.
- JOHNSON, N. & CABARLE, B. 1993. Surviving the Cut: Natural Forest Management in the Humid Tropics.

 World Forest Resources Institute.
- MARN, H. M. 1982. The Planning and Design of the Forest Harvesting and Log Transport Operation in the Mixed Dipterocarp Forest of Sarawak. A technical report to the Government of Malaysia.
- MARN, H. M., VEL, E. & CHUA, D. K. H. 1981. Planning and Cost Studies in Harvesting in the Mixed Dipterocarp Forest of Sarawak. A technical report to the Government of Malaysia.
- MARN, H. M., VEL, E. & CHUA, D. K. H. 1982. Further Cost Studies in Harvesting the Mixed Dipterocarp Forest of Sarawak Including FMC Skidder Operation. A technical report to the Government of Malaysia.

THE PEST STATUS OF THE TERMITE COPTOTERMES CURVIGNATHUS IN ACACIA MANGIUM PLANTATIONS: INCIDENCE, MODE OF ATTACK AND INHERENT PREDISPOSING FACTORS

Laurence G. Kirton,

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

Valerie K. Brown

CABI Bioscience: Environment, Silwood Park, Ascot, Berks SL5 7TA, United Kingdom

&c

M. Azmi

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

Received May 1998

KIRTON, L. G., BROWN, V. K. & AZMI, M. 1999. The pest status of the termite Coptotermes curvignathus in Acacia mangium plantations: incidence, mode of attack and inherent predisposing factors. The incidence and mode of attack by the termite Coptotermes curvignathus in Acacia mangium plantations were determined in 452 living trees sampled using random plots in one eight-year-old and two fouryear-old plantations. The overall incidence of infestations was 2.2%, while the highest infestation rate in a site was 4.5%. A few predisposing factors on the tree trunk of living A. mangium trees were observed to facilitate entry of C. curvignathus into the wood. These were large pruning wounds, abscission scars resulting from natural pruning and damage by an insect bark borer. Infestations restricted to such injuries were much more frequently encountered than severe attack by C. curvignathus, which is characterised by extensive soil cover constructed by the termite on the tree trunk. However, such localised external termite activity is thought to be an indication of heartwood infestations, which have been frequently reported to occur in A. mangium. Predisposition of trees to heartwood infestations of termites, as a result of heart rot infection caused by fungi, is examined. The pest status of C. curvignathus in A. mangium plantations is discussed, and recommendations are given for minimising losses in different end-uses of the wood.

Key words: Termite attack - Coptotermes curvignathus - pest status - Acacia mangium plantations - predisposition

KIRTON, L. G., BROWN, V. K. & AZMI, M. 1999. Status perosak anai-anai, Coptotermes curvignathus di ladang-ladang Acacia mangium: insidens, kaedah serangan dan faktor-faktor predisposisi bawaan. Insidens dan kaedah serangan anai-anai Coptotermes curvignathus di ladang-ladang Acacia mangium telah ditentukan dengan

pensampelan sebanyak 452 pokok hidup menggunakan petak-petak rawak di sebuah ladang dengan pokok berumur lapan tahun dan dua buah ladang dengan pokok berumur empat tahun. Kadar insidens infestasi keseluruhannya ialah 2.2%, manakala kadar infestasi paling tinggi ialah 4.5%. Beberapa faktor predisposisi pada batang pokok-pokok hidup A. mangium didapati memudahkan kemasukan C. curvignathus ke dalam batang kayu. Faktor-faktor tersebut adalah parut-parut besar disebabkan pemangkasan dahan, parut semula jadi dari luruhan dahan dan kerosakan oleh serangga pengorek kulit pokok. Infestasi yang tertumpu pada kecederaan-kecederaan tersebut didapati lebih kerap berlaku dibandingkan dengan penyelaputan menyeluruh dengan tanah pada pangkal pokok yang menjadi petunjuk sesuatu pokok telah diserang dengan teruk oleh C. curvignathus. Bagaimanapun, aktiviti anai-anai yang kelihatan tertumpu pada bahagian luar batang yang cedera ini dianggap sebagai satu tanda infestasi kayu teras, yang mana telah kerap dilaporkan berlaku keatas A. mangium. Predisposisi pokok-pokok kepada infestasi kayu teras oleh anai-anai sebagai akibat daripada infeksi reput teras diteliti. Status perosak C. curvignathus di ladang-ladang A. mangium dibincangkan, dan cadangan-cadangan diberikan untuk mengurangkan kerugian dalam kegunaan hasil kayu yang berbeza.

Introduction

The termite Coptotermes curvignathus Holmgren (Isoptera: Rhinotermitidae) is considered a very damaging pest of cultivated trees in Southeast Asia because of its ability to kill living trees. Its economic importance, host range, behaviour and control have been reviewed by Tho and Kirton (1990). The termite undermines the bark and outer wood of the tree beneath an extensive, constructed cover of soil and faecal matter or, more rarely, gains access to the core of the tree, with little external indication of its presence. A large number of plant species are attacked including agricultural tree crops such as rubber and oil palm and forest plantation trees, particularly conifers. The termite has also been frequently reported attacking Acacia mangium in both East and West Malaysia (Mori 1986, Hamid 1987, Tho & Kirton 1990, Intachat & Kirton 1997).

Acacia mangium Willd. (Leguminosae) was introduced from Australia to Southeast Asia, first as a fire-break and later as a fast-growing forest plantation tree species (Yap 1986). It is now one of the most widely planted forest plantation tree species in Malaysia. In this paper, we report the incidence and mode of attack by C. curvignathus in A. mangium plantations, and discuss factors predisposing the tree species to attack.

Methods

Three A. mangium plantations in Peninsular Malaysia were sampled as part of a larger study to determine the effect of large wood remnants on populations of C. curvignathus. The three sites were in Kemasul, Ulu Sedili and Batu Arang. Trees were about four years old at Kemasul and Ulu Sedili, and about eight years old at Batu Arang. Initial planting density was about 900 stems per ha, with a spacing of 3.7×3.0 m (Anonymous 1989, Weinland & Ahmad Zuhaidi 1991). Sampling was carried out in each site using 25.10×10 m plots located 10-40 m from the

edge of access roads at random distances along a sampling transect of about one kilometre. Detailed sampling methods and characteristics of each site are given in Kirton et al. (1999). Trees occurring within each plot were inspected for the presence of active Coptotermes infestations. A tree was considered to have an active infestation if it had termites present under soil cover or runways on the tree trunk, or in dead branch stubs or exposed wood of the living tree. A heavy knife was used to prise open bark or wood that could harbour infestations in the tree trunk. A small voucher collection of soldier termites was, as far as possible, obtained for each infestation, so that identification could be confirmed in the laboratory. A count was made of the number of infested and uninfested A. mangium trees in each plot.

In addition to the systematic survey conducted in these three plantation sites, other field visits to these or different sites were made, and the observations during these visits are also discussed. Most of the visits were in response to specific requests of State Forest Departments to investigate deaths of A. mangium trees attributed to termite attack.

Results and discussion

Incidence and mode of attack

The overall incidence of infestations of *C. curvignathus* on living trees in the sampling plots was 2.0%, ranging from 4.5% in Ulu Sedili to no infestations in Batu Arang (Table 1). Thinning had been carried out in Batu Arang and, thus, there were fewer trees in the sampling plots in comparison to Ulu Sedili and Kemasul. There was only one dead tree in which mortality may have been due to *C. curvignathus*. This tree, which had the surface of the trunk covered with soil, was in Batu Arang. The only other species of *Coptotermes* that infested living *A. mangium* trees was *C. kalshoveni*, found only once in the hollowed base of a tree trunk in Ulu Sedili. This species has also been found feeding on a dead portion of a living *A. mangium* tree trunk in Kemasul, and feeding in the heartwood of a living tree felled in Batu Arang. Species from other termite genera may also infest the heartwood of *A. mangium*; we have found at least one other termite species in the heartwood of *A. mangium* logs.

Table 1.	Incidence of C. curvignathus infestations in living
	A. mangium trees at three plantation sites

Site	No. of trees sampled	Incidence of infestations (%)
Kemasul	184	1.6
Ulu Sedili	155	4.5
Batu Arang	113	0.0
Total	452	2.0

Acacia mangium appears to be as susceptible as many conifer species to infestations of C. curvienathus, but the infestations do not appear to be as severe, and the resulting mortality is much lower (Kirton et al. 1999). Most of the infestations on living A. mangium trees in the sampling plots were indicated by runways leading to localised infestations, with little soil cover of the tree trunk. Only one of the ten living trees on which C. curvignathus was found had extensive soil plastering the tree trunk. Such soil cover, typical of severe attack by C. curvignathus, is more readily detected by cursory observation than are localised infestations. Thus, severe attack was observed on several occasions outside the sampling plots in all of the three sampling sites. It was also observed in Bukit Tarek and in other areas where A. mangium is grown in the three sampling sites. It is probable that infestations which appeared localised were external indications of more extensive internal infestations of the heartwood, such as is shown in Figure 1. They may also have occurred in trees which had no external signs of termite activity, if the termites gained access through the roots. Thus, the figures reported in the present study may underestimate the incidence of heartwood infestations by C. curvignathus. Internal termite infestations have been widely reported to occur in thinned or harvested A. mangium trees. As many as 17% of 264 five-year-old A. mangium thinnings have been found to have internal termite infestations (Chew 1987 in Weinland & Ahmad Zuhaidi 1992). Mahmud et al. (1993) reported an overall incidence of 4% termite infestation of the heart-wood in a sample of 195 sixto nine-year-old A. mangium trees felled from seven sites in Sabah, East Malaysia. The highest incidence in a site was 23%. These studies enumerated heartwood infestations by termites in general. Hollow cores more specifically attributed to Coptotermes curvignathus were found in 6% of a sample of 115 Acacia mangium logs in Sabah (Chan 1986).



Figure 1. Cross section of a termite infested A. mangium tree trunk in Batu Arang, showing damage to the heartwood

Predisposing factors inherent in plantation A. mangium

A number of predisposing factors on the tree trunk of living A. mangium trees were observed to facilitate entry of C. curvignathus into the wood. Some of the common factors are shown in Figure 2, and Table 2 gives a breakdown of the number of infestations resulting from different predisposing conditions in trees within the sampling plots. Infestations of C. curvignathus localised on some form of injury to the wood or bark accounted for 80% of the ten trees with infestations (Table 2). This was significantly greater than the proportion of trees which had infestations on bark that had no visible injuries (binomial test, p < 0.06, α = 0.10). There was, therefore, a tendency for the termites to infest injured parts of the tree trunk.



Figure 2. Trunk of a living A. mangium tree with an infestation of C. curvignathus in Kemasul, showing some common predisposing factors: A. furrows in the bark, probably caused by a Cerambycid beetle; B. scar left by a dead branch, where the termite appears to have penetrated the heartwood of the trunk; C. pruning wound (the pruned stem can be seen lying on the ground beside the tree)

Table 2.	Number of trees infested by C. curvignathus within the sampling
	plots as a result of different predisposing factors. Data have been
	pooled for the three plantation sites.

Part of tree infested	No. of trees
Pruning wound	4†
Abscission scar exposing wood	3*
Bark damaged by insect borer	1*
Bark damaged by other forms of jury	1
Non-damaged bark	2

One tree had infestations of both a pruning wound and abscission scars;

Pruning wounds were most common in Ulu Sedili, where multiple leaders or side branches of significant size had been pruned. These wounds left the wood of the tree exposed and vulnerable to infestation. In Peninsular Malaysia, A. mangium is prone to heavy early branching, resulting in the formation of multiple leaders from the base of the tree if pruning is not carried out (Yong 1985, Mead & Speechly 1991). Hence, recommendations by the Forest Department of Peninsular Malaysia for the silviculture of this species emphasise pruning, which is carried out four months, one year and four years after planting (Anonymous 1989, Weinland & Ahmad Zuhaidi 1991). In spite of the early pruning at four months to leave a single leader (singling), low branching still occurs and results in large wounds from later pruning exercises (Figure 2). Although wound dressings are used for large pruning wounds, these did not provide long-term protection against termites. One pruning wound was observed to be infested in spite of a visible coat of wound dressing.

Abscission scars resulting from natural pruning also exposed the wood of the tree, though not usually as extensively as pruning wounds. Canopy closure had already occurred in most areas of the four-year-old A. mangium plantations sampled. Rapid canopy closure in A. mangium plantations results in death of the numerous lower branches, which persist on the trunk for years (Weinland & Ahmad Zuhaidi 1991, Lee & Arentz 1997). These branches eventually break off, and the branch stubs decay, leaving a scar that serves as an entry point for termites (Figure 2).

Pruning wounds and abscission scars were the most common causes of infestation (Table 2). However, damage caused to the bark by a borer also appeared occasionally to predispose trees to attack by *C. curvignathus*. The long furrows left in the bark and outer wood (Figure 2) suggest the borer was probably the larva of a Cerambycid beetle which fed beneath the bark. Damage by the borer was most frequently observed in Kemasul. The species may have been *Xystocera globosa* (Cerambycidae), which has been recorded as a pest of *A. mangium*, tunnelling in the inner bark of the trees (Hutacharern 1993). Damage by a borer, thought to be *Xystocera globosa*, has also been reported from three *A. mangium* plantations in the Peninsula, with severe damage resulting in withering and death of some trees in Ulu Sedili (Lee 1997).

^{*} termite infestation associated with borer attack was also observed outside the plots.

The means by which C. curvignathus frequently gains access into the wood is paralleled by heart rot infection in A. mangium, which is associated with a number of Basidiomycete fungi of the Hymenomycete group (Lee et al. 1988, Lee & Maziah 1993). Pruning wounds, branch stubs and dead branches which expose the heartwood or sapwood of the tree are the most common entry points for heart rot fungi in A. mangium (Lee et al. 1988, Mahmud et al. 1993), particularly since A. mangium has a poor wound response, making it susceptible to invasion of the xylem by fungal hyphae (Schmitt et al. 1995). There are also sufficient data to suggest an association between heart rot in A. mangium and termite damage to the heartwood (Mahmud et al. 1993) (Table 3). Although heart rot frequently occurred without termite damage, the latter was largely associated with the former, suggesting that heart rot predisposes the tree to heartwood infestation by termites. Many termite species are attracted to fungus-decayed wood. The relationship between Basidiomycete fungi, the chemical products of decay and termite behaviour have been extensively reviewed (e.g. Amburgey 1979, Gilbertson 1984). Decayed wood is known to contain chemicals that influence shelter tube formation, orientation and trail following in termites. However, decay is not a prerequisite for termite infestation of the heartwood, as one of the trees cored by termites had no fungal decay (Table 3). Termite species were not distinguished by Mahmud et al. (1993), and it is likely that C. curvignathus, with its ability to attack and kill living trees, infests trees both with and without heart rot.

Table 3. Contingency table, based on data of Mahmud *et al.* (1993) for data in Telupid, Sabah, where there was a sufficiently high incidence of heartwood infestations by termites to show its relationship with heart rot. There is a significant association between the two factors (Fisher exact p = 0.025, $\alpha = 0.05$)

	Heart rot present	Heart rot absent	Total	
Termites present	5†	2**	7	
Termites present Termites absent	5	18	23	
Total	10⁺	20	30†	

*Value given by Mahmud et al. (1993); *one tree had another form of decay, but the number of trees with other forms of decay was not stated for trees in which termites were absent.

Lee and Arentz (1997) have put forth a hypothesis to explain the high incidence of heart rot infestations in A. mangium in Peninsular Malaysia. This hypothesis can also explain the ease with which C. curvignathus infests A. mangium trees through abscission scars. They suggest that A. mangium is physiologically adapted to a climate with an annual period of low rainfall which triggers the development of a cleavage zone at the base of dying branches of A. mangium, where abscission eventually takes place. This cleavage zone, which is thought to develop better in the East Malaysian state of Sabah, where there is greater rainfall seasonality than in Peninsular Malaysia, would result in the production of periderm tissue which

protects underlying wood from infection by decay-causing micro-organisms. The absence of strong rainfall seasonality in Peninsular Malaysia prevents this natural abscission process from taking place and, thus, results in the exposure of the wood to infection by decay fungi and infestation by termites.

Pest status and management in A. mangium plantations

Coptotermes curvignathus has been described as the most important pest of A. mangium and other fast-growing tree species planted under the compensatory forest plantation scheme (Yong 1985). This reputation has probably been attained by virtue of it being one of the few pest species that kill mature trees. While significant losses may occur in localised areas of A. mangium plantations (Yong 1985, Intachat & Kirton 1997), overall losses due to tree mortality are relatively low by comparison to conifers, which are inherently more susceptible to severe attack (Kirton et al. 1999). Most infestations of A. mangium in the sampling plots were localised in dead tissue of living trees, or in the heartwood, and did not become more extensive.

In the establishment of conifer plantations and early A. mangium plantations, seedlings were protected by prophylactic treatment of the soil with granular heptachlor applied into the planting hole during transplanting (Tho 1976, Yong 1985). In A. mangium, the treatment was ineffective in providing long-term protection (Chew 1987 in Weinland & Ahmad Zuhaidi 1992), and has been said to last only about two years (Yong 1985). The breaching of this soil barrier by the termites after two years makes it unlikely that the chemical would have affected the incidence or mode of attack in four- and eight-year-old A. mangium sampled in this study. The practice of prophylactic soil treatment was later discontinued, with a shift towards remedial chemical control of infestations (Tho & Kirton 1990). In view of the relatively low susceptibility of A. mangium to severe attack, this has probably been an economically sound decision. There has not, thus far, been any report of severe, widespread losses in more recently established, untreated A. mangium plantations.

Although significant losses due to tree mortality caused by C. curvignathus occur only in localised areas of A. mangium plantations, damage due to heartwood infestations by C. curvignathus, or other termite species, is a more widespread problem. Heartwood infestations reduce the quality of the wood and may render it unusable when the damage is severe, particularly if the wood is to be used for sawn timber. When the wood is to be used for pulp in the manufacture of paper, or for chipboard, as is generally the case at present in Malaysia, heartwood infestations are a less serious defect. In this case, the problem of heartwood infestations can be reduced by avoiding late pruning of low stems that have reached the size of a large leader. Pruning can be carried out more frequently when a clear bole is required for sawn timber, so that stems are pruned while still young. This is thought to facilitate better healing of pruning wounds (Lee et al. 1988). Wound dressings in current use in A. mangium plantations do not provide sufficient protection against heartwood infestations. Site matching of A. mangium

to areas with strongly seasonal rainfall, as proposed for the prevention of heart rot (Lee & Arentz 1997), may also minimise heartwood infestations by termites through the formation of a physiological abscission zone at the base of dying branches. This is because termites and the fungi that cause heart rot have common entry points into the wood and, furthermore, heart rot predisposes the heartwood to termite infestation.

Acknowledgements

We are grateful to the Director General of the Forest Department of Peninsular Malaysia for permission to conduct these studies in the Acacia mangium plantations. We are also thankful for support and assistance rendered by the plantation managers and staff of the Compensatory Forest Plantations of Batu Arang, Kemasul and Ulu Sedili. The first author gratefully acknowledges the advice of S. G. Khoo.

References

- Amburgey, T. L. 1979. Review and checklist of the literature on interactions between wood-inhabiting fungi and subterranean termites: 1960-1978. *Sociobiology* 4:279–296.
- Anonymous. 1989. Panduan Penubuhan Ladang Spesies Cepat Tumbuh. Ibu Pejabat Perhutanan, Kuala Lumpur. [In Bahasa Malaysia; A Guide to the Establishment of Fast-Growing Plantation Species. Forest Department of Malaysia, Kuala Lumpur.] 88 pp.
- CHAN, H. H. 1986. Graded sawn timber recovery study of Acacia mangium. Malaysian Forester 47:116-124.
- CHEW, T. K. 1987. Assessment of termite attack and heart-rot on thinned *Acacia mangium* trees. Unpublished report. Forestry Department, Kuala Lumpur. 2 pp.
- GILBERTSON, R. L. 1984. Relationships between insects and wood-rotting Basidiomycetes. Pp. 130-165 in Wheeler, Q. & Blackwell, M. (Eds.) Fungus-Insect Relationships. Perspectives in Ecology and Evolution. Columbia University Press, New York.
- Hamid, A. A. 1987. Insect Pests of Acacia mangium Willd. in Sarawak. Forest Research Report FE 1. Sarawak Forest Department, Kuching. 10 pp.
- HUTACHARERN, C. 1993. Insect pests. Pp. 163-202 in Khamis, A. & Taylor, D. (Eds.) Acacia mangium. Growing and Utilization. MPTS Monograph Series No. 3. Winrock International and FAO, Bangkok.
- INTACHAT, J. & KIRTON, L. G. 1997. Observations on insects associated with Acacia mangium in Peninsular Malaysia. Journal of Tropical Forest Science 9:561-564.
- Kirton, L. G., Brown, V. K. & Azmi, M. 1999. Do forest-floor wood residues in plantations increase the incidence of termite attack? Testing current theory. *Journal of Tropical Forest Science* 11:218-239.
- LEE, S. S. 1997. Diseases of some tropical plantation acacias in Peninsular Malaysia. Pp. 53-61 in Old, K. M., Lee. S. S. & Sharma, J. K. (Eds.) Diseases of Tropical Acacias. Proceedings of an International Workshop held at Subanjeriji (South Sumatra), 28 April 3 May 1996. Center for International Forestry Research, Jakarta.
- Lee, S. S. & Arentz, F. 1997. A possible link between rainfall and heart rot incidence in Acacia mangium? Journal of Tropical Forest Science 9:441-448.
- LEE, S. S. & MAZIAH, Z. 1993. Fungi associated with heart rot of Acacia mangium Willd. in Peninsular Malaysia. Journal of Tropical Forest Science 5:479-484.
- LEE, S. S., TENG, S. Y., LIM, M. T. & RAZALI, A. K. 1988. Discolouration and heart rot of Acacia mangium Willd. some preliminary results. *Journal of Tropical Forest Science* 1:170–177.
- MAHMUD, S., LEE, S. S. & AHMAD, H. 1993. A survey of heart rot in some plantations of Acacia mangium in Sabah. Journal of Tropical Forest Science 6:37-47.

- MEAD, D. J. & SPEECHLY, H. T. 1991. Growing Acacia mangium for high quality sawlogs in Peninsular Malaysia. Pp. 54-71 in Sheikh Ali, A., Paridah, M. T., LIM, M. S., NOR AINI, A. S., AHMAD SAID, S. & DORAISINGAM, M. (Eds.) Proceedings of a Regional Symposium on Recent Developments in Tree Plantations of Humid/Subhumid Tropics of Asia. Universiti Pertanian Malaysia, Serdang.
- MORI, T. 1986. Hand List of Insect Pests of Forest Plantations in Sabah. FRC Publication No. 28. 54 pp. Schmitt, U., Liese, W., Hong, L. T. & Killmann, W. 1995. The mechanisms of wound response in Acacia mangium. IAWA Journal 16:425-432.
- Tho, Y. P. 1976. Preliminary observations on the use of heptachlor as a protection measure against termites in initial plantings of *Araucaria* spp. Pp. 171-185 in *Proceedings of the Sixth Malaysian Forestry Conference*. 11-17 October 1976, Kuching, Sarawak. Volume II. Information Papers.
- Tho, Y. P. & Kirton, L. G. 1990. The economic significance of Coptotermes termites in Malaysian forestry. Pp. 193-199 in Proceedings of the Third International Conference on Plant Protection in the Tropics. Kuala Lumpur, 1990. Volume IV.
- Weinland, G. & Ahmad Zuhaidi, Y. 1991. Management of Acacia mangium stands: tending issues. Pp. 41-53 in Appanah, S., Ng, F. S. P. & Roslan, I. (Eds.) Malaysian Forestry and Forest Products Research. Proceedings of the Conference. 3-4 October 1990, Forest Research Institute Malaysia, Kuala Lumpur.
- Weinland, G. & Ahmad Zuhaidi, Y. 1992. An Annotated Bibliography on Acacia mangium. 2nd edition. Research Pamphlet No. 102. Forest Research Institute Malaysia, Kuala Lumpur. 170 pp.
- YAP, S. K. 1986. Introduction of Acacia species to Peninsular Malaysia. Pp. 151-153 in Turnbull, J. W. (Ed.) Australian Acacias in Developing Countries. Proceedings of an international workshop held at the Forestry Training Centre, Gympie, Qld., Australia, 4-7 August 1986. ACIAR Proceedings No. 16. Australian Centre for International Agricultural Research, Canberra.
- Yong, C. T. 1985. Compensatory plantations in Peninsular Malaysia. Pp. 35-44 in Liew, T. C., Udarbe, M. P., Tang, H. T., Tang, R. I. E. & Lee, Y. F. (Eds.) Proceedings of the Seminar on Forest Plantation Development in Malaysia. 9-14 July 1984, Kota Kinabalu/Kundasang, Sabah.

PELTOPHORUM DASYRACHIS SEEDLING GROWTH RESPONSE TO DIFFERENT LEVELS OF BORON

Robin Rose,

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, United States of America

Antonio Royo

Unidad de Anatomia, Fisiologia y Genetica Forestal Escuela Tecnica Superior de Ingenieros de Montes Ciudad Universitaria s/n 28040 Madrid, Spain

&

Diane L. Haase

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, United States of America

Received May 1998

ROSE, R., ROYO, A. & HAASE, D. L. 1999. Peltophorum dasyrachis seedling growth response to different levels of boron. Five boron treatments (0, 10, 20, 40, and 60 ppm) were applied to Peltophorum dasyrachis (Kurz) seedlings. Height and diameter were measured after one month. In addition, leaves were partitioned as damaged or undamaged and measured for dry weight and nutrient concentrations and contents. The results demonstrate that boron had both a growth enhancement and a toxic impact on the seedlings. The 10-ppm boron treatment enhanced growth (albeit non-significantly) relative to the control, while the 20-, 40-, and 60-ppm treatments were detrimental to growth. With higher boron treatment levels, the number and dry weight of damaged leaves were significantly higher. Foliar concentrations of potassium, magnesium, and especially boron also increased significantly with higher treatment levels.

Keywords: Toxicity - Thailand - micronutrients - nutrition

ROSE, R., ROYO, A. & HAASE, D. L. 1999. Tindak balas pertumbuhan anak benih Peltophorum dasyrachis terhadap boron yang berbeza tahapnya. Lima rawatan boron (0, 10, 20, 40, dan 60 ppm) dilakukan terhadap anak benih Peltophorum dasyrachis (Kurz). Ketinggian dan garis pusat diukur selepas satu bulan. Di samping itu, daun dibahagikan kepada rosak atau tidak rosak. Berat kering, kepekatan dan kandungan nutrien daun-daun tersebut disukat. Keputusan menunjukkan bahawa boron meningkatkan pertumbuhan dan memberikan kesan toksik terhadap anak benih. Rawatan 10-ppm boron meningkatkan pertumbuhan (walaupun tidak bererti) secara relatif dengan kawalan, manakala rawatan 20, 40, dan 60 ppm menyebabkan pertumbuhan merosot. Tahap rawatan boron yang lebih tinggi menyebabkan bilangan

dan berat kering daun-daun yang rosak lebih tinggi. Kepekatan potasium, magnesium dan terutamanya boron dalam daun juga meningkat dengan bererti dengan tahap rawatan yang lebih tinggi.

Introduction

Boron is an essential micronutrient in plants and one whose role is not fully understood. Boron deficiency is the most widespread micronutrient deficiency in forestry, particularly in the tropics. Boron is thought to be passively taken up by plant roots as undissociated boric acid and translocated to the foliage (Hu & Brown 1997). Until recently, boron has been considered to be phloem-immobile. Although this is true for most species, boron can be readily transported in the phloem of species rich in polyols (Brown & Shlep 1997). Boron plays an important role in cell wall structure, cell membrane integrity, enzyme interactions, sugar transport and other plant functions (Marschner 1995, Match 1997, Power & Woods 1997).

Although boron deficiency and toxicity can be common, this micronutrient has received relatively little attention in the literature for tree species, especially for native tropical tree species. One study (Robinson & Edgington 1942) showed that the leaves of hardwoods such as hickory (Carya spp.), walnut (Juglans spp.), black locust (Robinia pseudocacia) and creosote bush (Larrea mexicana) can have boron levels of ~40 to 77 ppm. A few researchers report beneficial effects of boron for trees. Mitchell et al. (1987) found that 25 ppm borate applied as a mist to the foliage or as a soil drench significantly promoted the colonisation of ectomycorrhizae on shortleaf pine (Pinus echinata). Stone et al. (1982) suggest that southern pines suffering from boron deficiency do poorly after outplanting. Atalay et al. (1988) found significant increases in sugars in both ectomycorrhizal and non-mycorrhizal roots of shortleaf pine in response to boron fertilisation. Other researchers have reported the effects of boron toxicity (Glaubig & Bingham 1985, Vimmerstedt & Glover 1984, Timmer 1991, Nable et al. 1997).

This paper reports on the effect of boron on the important timber species *Peltophorum dasyrachis* (Kurz) (Family: Caesalpiniaceae). This species is native to southeast Asia and grows in many areas throughout Thailand and neighbouring countries, where it is used for everything from wood carvings to furniture. It was chosen for study because Thailand is known to be an area of the world where some soils are deficient in boron (Shorrocks 1997). While not as commercially valuable as teak (*Tectonia grandis*), *P. dasyrachis* is an important species for ecological restoration and conservation and is commonly grown in Thai nurseries.

In a nursery setting, *P. dasyrachis* seedlings are commonly grown in polybags in a medium consisting of local clay soil, rice husks, and chicken manure in various unknown ratios. The formula varies greatly from one area and nursery to another. In some cases, burnt rice husks are added as fertiliser. It can take more than two years for seedlings to reach plantable size (50 cm tall). Sporadic watering, the absence of commercial fertilisers with micronutrients such as boron, and the low fertility of the media greatly contribute to the slow growth.

In 1995 a successful demonstration project carried out by Oregon Woods, Inc. (Eugene, OR) in cooperation with the United States Agency for International Development (USAID) and the Royal Forest Department of Thailand showed that quality *P. dasyrachis* seedlings could be grown in styro-8 (8 cubic inch) containers with modern soluble fertilisers (Peters®) and a peat-vermiculite media mix. With constant fertilisation and irrigation, seedling growth was very rapid. The root systems filled the styro-8 cavities in less than four months.

The objective of this study was to test the null hypothesis that variations in soil boron do not affect growth of *P. dasyrachis* seedlings. Our approach was to vary the level of boron in the media while holding all other growth factors (such as light, temperature, fertilisation, and irrigation) as constant as possible. To the best of our knowledge, this is the first experiment of its kind to look at the influence of boron nutrition on early *P. dasyrachis* seedling growth.

Materials and methods

Seedlings

Peltophorum dasyrachis seed was obtained from Nursery No. 4 of the Royal Forest Department in Korat, Thailand; the seed source is unknown. Seeds were pretreated by pouring boiling water over them and allowing them to soak for 12 h until cool. They were then surface sown in flats containing a peat medium and covered with grit. Seeds were allowed to germinate and grow for several weeks before being transplanted to pots. On 21 June 1996, seedlings (approximately 5 cm tall) were pricked out of a flat bed container and transplanted to individual 15-cm (diameter) x 17-cm (height) pots (approximately 3 l). The medium was Black Gold® (a peat and vermiculite mixture) and a silt loam soil in a 1:1 (v:v) ratio.

The transplanted seedlings were grown on raised benches under ambient light conditions in a Forest Research Laboratory greenhouse, College of Forestry, Oregon State University. The fiberglass roof reduced the amount of full sunlight by as much as 50%. Temperatures in the greenhouse fluctuated from 20 to 35 °C during the day and from 10 to 20 °C at night. These conditions were much cooler than those in northeast Thailand. Another factor that was difficult to control was the cool (7 °C) temperature of the irrigation water. However, the seedlings grew very well under the circumstances.

Treatments

Five boron treatments were used: 0, 10, 20, 40, and 60 ppm of boron. These treatment levels were selected based on their expected ability to bracket responses ranging from deficient to toxic. The source of the boron was Solubor™ (U.S. Borax, Inc., Valencia, CA), which is 20.5% boron. Treatments were applied by pouring 1 l of boron solution (diluted to achieve the desired treatment) into the media of each pot. For each treatment, 20 seedlings were treated on 15 July

1996, and again on 5 August 1996. In addition, each pot was fertilised with other nutrients by adding 400 ml of Peters® 20-20-20 fertiliser diluted to 100 ppm nitrogen I day after the initial boron treatment and approximately twice per week until the end of the experiment. Pots were watered daily or as needed. The level of boron in the Peters® fertiliser (undiluted) was low (0.0068%). Other micronutrient levels were iron 0.05%, magnesium 0.05%, manganese 0.025%, copper 0.0036%, zinc 0.0025%, and molybdenum 0.0008%. The boron contributed by the tap water used in the experiment was considered negligible.

Measurements

Height was measured to the nearest centimeter (cm) from groundline to the highest tip of the plant. Diameter was measured to the nearest millimeter (mm) at groundline. Height and diameter were measured initially on 16 July 1996. Final height and diameter were measured, the number of leaves per plant was counted, and plant parts were harvested on 18 and 19 August 1996. Damage from boron toxicity was assessed visually as chlorosis on the leaflet edges of the pinnately compound leaves (Figure 1). A damaged leaf was defined as having at least 25% chlorosis of the leaflet surface area. Damaged and undamaged leaves were snipped off, counted, pooled together by damage category, and dried in an oven at 65 °C for 48 h. Dry weights of damaged and undamaged leaves were measured separately. There were no damaged leaves in the control treatment.

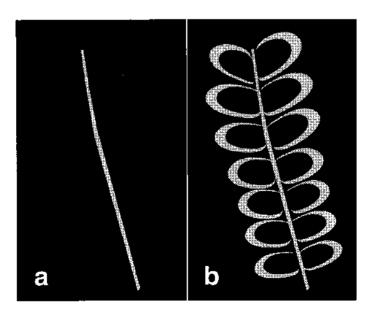


Figure 1. Effect of boron toxicity on leaflets of *Peltophorum dasyrachis:*a) undamaged and b) damaged (chlorosis on leaflet edges)

Nutrient analyses were done at the Soil and Plant Analysis Laboratory at Oregon State University using standard laboratory techniques. The leaves of each plant were separated into two categories: undamaged and damaged. There were four composited samples (consisting of 4 to 5 seedlings each) of damaged and undamaged leaves for each boron treatment. A total of 36 samples were analysed [(5 treatments × 4 undamaged leaf samples) + (4 treatments × 4 damaged leaf samples)].

Nutrient concentration is the percentage of an element in the dried leaf material. Nutrient content is the dry weight of the element in the dried leaf material (nutrient concentration x leaf dry weight). Estimates for nutrient concentrations and contents in the total foliage (i.e. damaged leaves + undamaged leaves) were calculated by adding the data and weighting by leaf dry weight as follows:

$$Total \ foliar \ nutrient \ concentration = \frac{undamaged \ DW}{total \ DW} \quad (undamaged \ concentration) + \\ \frac{damaged \ DW}{total \ DW} \quad (damaged \ concentration)$$

$$Total \ foliar \ nutrient \ content = \frac{undamaged \ DW}{total \ DW} \quad (undamaged \ content) + \\ \frac{damaged \ DW}{total \ DW} \quad (damaged \ content)$$

where DW = leaf dry weight (mg); (un)damaged concentration = nutrient concentration (%) in (un)damaged leaves; and (un)damaged content = nutrient content (mg) in (un)damaged leaves.

To aid in nutrient data interpretation, vector diagrams were plotted according to Haase and Rose (1995). Vector analysis is a technique that allows simultaneous comparison of plant biomass, nutrient concentration, and nutrient content in an integrated graphic format. Nutrient ratios were calculated for each nutrient as a percentage of nitrogen.

Design and experimental analysis

The study was a completely randomised design with 5 treatments and 20 seedlings per treatment. All data were analysed with a one-way ANOVA. Tests for normality, linearity, and constant variance of the residuals were performed, and transformations were made where necessary to assure the validity of these assumptions. Fisher's Protected Least Significant Difference procedure was used

to determine significant differences among treatments at the α < 0.05 level. Statistical Analysis System software (SAS Institute Inc. 1989) was used for analysis of all data.

Results

Boron treatments significantly influenced the growth of *Peltophorum dasyrachis* seedlings. In general, the 10-ppm boron treatment enhanced growth relative to the control (although the difference was not statistically significant), while 20-, 40-, and 60-ppm treatments were significantly detrimental to growth.

Morphology

Seedling morphology was significantly influenced by the boron treatments (Table 1). As expected, initial height and stem diameter were not significantly different among treatments. However, by the end of the experiment, seedlings receiving the 10-ppm boron treatment had the largest total height, stem diameter, height growth, and diameter growth (although not significantly different from the control).

Table 1. Seedling morphology by treatment

	Boron treatment (ppm)				
Measurement	0	10	20	40	60
Seedling height (cm)					
Initial- $16 \text{ July } (p = 0.1679)$	9.55a	10.55a	9.76a	9.08a	10.55a
Final-19 August (p = 0.0199)	15.42abc	16.94c	15.68bc	13.5a	14.73ab
Growth $(p = 0.0002)$	5.87b	6.47b	5.92b	4.43a	4.18a
Stem diameter (mm)					
Initial -16 July (p = 0.2606)	1.97a	2.03a	1.86a	1.76a	2.04a
Final- 19 August ($p = 0.0006$)	3.38cd	3.57d	3.08bc	2.67a	2.82ab
Growth $(p = 0.0001)$	1.41bc	1.55€	1.22b	0.91a	0.78a
Final harvest—19 August					
Damaged leaves per plant (%) $(p = 0.0001)$	0.0a	27.83Ь	50.62c	68.00d	72.01d
No. leaves per plant					
Undamaged 1 (p = 0.0001)	10.14d	7.51c	4.74b	2.81a	2:31a
Damaged 1 (p = 0.0001)	0.00a	2.11b	4.86c	6.07c	6.11c
$Total^{1}(p = 0.0009)$	10.13c	10.65с	9.65bc	9.60ab	8.48a
Dry Weight (g)					
Undamaged leaf (p = 0.0001)	1.24c	1.37c	0.86b	0.41a	0.35a
Damaged leaf $(p = 0.0001)$	-	0.14a	0.28b	0.34b	0.50c
Total leaf $(p = 0.0001)$	1.23bc	1.55c	1.13b	0.77a	0.84a
$Stem^{1}(p = 0.0010)$	0.30c	0.37c	0.27bc	0.19a	0.20ь

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \le 0.05$ level using Fisher's Protected Least Significant Difference procedure;

^{&#}x27;Values were back-transformed from log values used for analysis and are estimates of the median.

Leaf damage reflected the level of the boron treatments (Table 1). The proportion of damaged leaves per plant was higher with higher levels of boron. The influence of the boron treatments was also readily apparent in the dry weights. Seedlings from the 10-ppm boron treatment had the highest undamaged leaf dry weight, total leaf dry weight and stem dry weight, while those treated with 40 and 60 ppm boron tended to be significantly smaller than the other treatments.

Foliar nutrients

The boron treatments significantly affected the concentrations of most nutrients (Table 2). With higher boron treatment levels, the concentrations of potassium, magnesium, and especially boron in the undamaged leaves, damaged leaves, and total foliage increased significantly. None of the other nutrients had significant differences among concentrations in total foliage. However, these nutrients are included in the tables to give the reader an overall understanding of *P. dasyrachis* nutrient levels since this important species has not previously been represented in the literature. Nitrogen and phosphorous concentrations in the damaged leaves were significantly higher in the 40- and 60-ppm treatments than in the 10- and 20-ppm treatments; phosphorous concentrations in undamaged leaves also increased significantly with higher treatment levels. Calcium was the only nutrient that had significantly lower concentrations in the undamaged and damaged leaves with higher treatment levels. Concentrations of manganese, copper, and zinc in undamaged leaves, damaged leaves, or total foliage were not significantly different among the treatments (Table 2).

Foliar nutrient contents (Table 3) showed more significant differences than the foliar nutrient concentration data. This is not surprising given that nutrient content is a function of dry weight, which differed significantly by treatment. With the exception of boron content, higher treatment levels of boron resulted in significantly lower nutrient contents in undamaged leaves and in total foliage, and significantly higher nutrient contents in damaged leaves.

Figure 2 shows vector diagrams for total estimated foliar boron, nitrogen, and potassium. Relative to the control, nutrient content (nitrogen and potassium only) and foliar dry weight were higher for the 10-ppm boron treatment and lower for the 20-, 40-, and 60-ppm treatments.

The nutrient ratios relative to nitrogen provide another look at the effects of the boron treatments on the various elements (Table 4). Ratios of phosphorus, potassium, and magnesium to nitrogen tended to be higher with higher levels of boron. However, the ratios of calcium to nitrogen in damaged and undamaged leaves were significantly lower with higher treatment levels of boron. As expected, the boron/nitrogen ratio showed highly significant changes.

Table 2. Nutrient concentrations (ppm or %) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

	Boron treatment (ppm)					
Measurement	0	10	20	40	60	
Nitrogen (%)						
Undamaged leaves (p = 0.0764)	3.17a	3.33a	3.80a	3.61a	3.58a	
Damaged leaves (p = 0.0011)	_	2.00a	2.35a	2.77b	2.96Ъ	
Total foliar estimate ($p = 0.5301$)	3.17a	3.17a	3.45a	3.18a	3.20a	
Phosphorus (%)						
Undamaged leaves $(p = 0.0001)$	0.31a	0.34Ъ	0.37c	0.40d	0.40a	
Damaged leaves $(p = 0.0001)$	_	0.19a	0.19a	0.28ь	0.28b	
Total foliar estimates (p = 0.1063)	0.31a	0.32a	0.32a	0.34a	0.33a	
Potassium (%)						
Undamaged leaves (p = 0.0001)	1.65a	1.95b	1.93Ъ	2.26c	2.29c	
Damaged leaves $(p = 0.0001)$	-	1.14a	1.48b	1.91c	1.98c	
Total foliar estimate ($p = 0.0001$)	1.65a	1.85b	1.82b	2.10c	2.10c	
Calcium (%)						
Undamaged leaves (p = 0.0001)	1.47bc	1.50c	1.38bc	1.33b	1.06a	
Damaged leaves (p = 0.0311)	-	2.24b	2.26b	2.05ab	1.87a	
Total foliar estimate (p = 0.0781)	1.47a	1.58a	1.59a	1.66a	1.55a	
Magnesium (%)						
Undamaged leaves (p = 0.0001)	0.30a	0.29a	0.33ь	0.39с	0.36c	
Damaged leaves ($p = 0.0093$)	_	0.29a	0.29a	0.35b	0.33b	
Total foliar estimate $(p = 0.0001)$	0.30ab	0.29a	0.32ь	0.37d	0.35c	
Manganese (ppm)						
Undamaged leaves (p = 0.0829)	59.75a	57.00a	52.50a	48.25a	39.75a	
Damaged leaves (p = 0.1970)	_	87.25a	79.75a	81.00a	68.50a	
Total foliar estimate $(p = 0.8928)$	59.75a	60.27a	59.14a	63.69a	56.97a	
Copper (ppm)						
Undamaged leaves (p = 0.1814)	2.50a	2.50a	2.00a	3.25a	2.00a	
Damaged leaves $(p = 0.1522)$	-	3.25a	3.75a	3.25a	3.00a	
Total foliar estimate (p = 0.2449)	2.50a	2.57a	2.43a	3.25a	2.60a	
Вогоп (ррш)						
Undamaged leaves' (p = 0.0001)	51.03a	144.42b	217.13c	271.31d	265.87d	
Damaged leaves $(p = 0.0001)$	-	336.75a	623.25b	878.25c	970.25c	
Total foliar estimates $(p = 0.0001)$	51.03a	165.50b	315.37c	552.14d	686.67e	
Zinc (ppm)						
Undamaged leaves (p = 0.0551)	22.75a	23.00a	23.50a	26.00a	26.00a	
Damaged leaves (p = 0.6348)		20.25a	19.50a	21.00a	20.50a	
Total foliar estimate (p = 0.7161)	22.75a	22.63a	22.52a	23.92a	22.81a	

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \le 0.05$ level using Fisher's Protected Least Significant Difference procedure;

Values were back-transformed from log values used for analysis and are estimates of the median.

Table 3. Nutrient contents (mg) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

	Boron treatment (ppm)					
Measurement	0	10	20	40	60	
 Nitrogen						
Undamaged leaves (p = 0.0001)	43.0bc	50.7c	35.4b	15.4a	13.6a	
Damaged leaves $(p = 0.0001)$	_	3.9a	6.9b	10.6c	16.7d	
Total foliar estimate ($p = 0.0001$)	43.0a	54.6b	42.3a	25.6c	30.6c	
Phosphorus						
Undamaged leaves (p = 0.0001)	4.2c	5.1d	3.8b	1.8a	1.5a	
Damaged leaves $(p = 0.0001)$	_	0.4b	0.6c	0.1a	1.6d	
Total foliar estimate (p = 0.0001)	4.2bc	5.5c	4.0b	2.9a	3.1a	
Potassium						
Undamaged leaves ($p = 0.0001$)	22.4c	29.7d	18.0b	10.2a	8.7a	
Damaged leaves 1 (p = 0.0001)	-	2.2a	4.4b	7.3c	11.2d	
Total foliar estimate ($p = 0.0001$)	22.4b	31.9c	22.3b	17.6a	20.0ab	
Calcium						
Undamaged leaves $(p = 0.0001)$	19.8c	22.8d	12.8b	6.1a	4.0a	
Damaged leaves $(p = 0.0001)$	-	4.3a	6.7b	7.8b	10.5c	
Total foliar estimate (p = 0.0001)	19.8b	27.2€	19.5b	13.9a	14.8a	
Magnesium						
Undamaged leaves $(p = 0.0001)$	4.0c	4.4c	3.1b	1. 7 a	1.4a	
Damaged leaves $(p = 0.0001)$	-	0.6a	0.9b	1.3c	1.9 d	
Total foliar estimates ($p = 0.0007$)	4.0b	5.0c	3.9b	3.1a	3.3ab	
Manganese						
Undamaged leaves (p = 0.0001)	0.0818c	0.0862c	0.0492ъ	0.0219a	0.0150	
Damaged leaves $(p = 0.0001)$	-	0.0169a	0.0237ь	0.0312c	0.0385	
Total foliar estimate (p = 0.0006)	0.0818ъ	0.1032c	0.0730ab	0.0530a	0.0535	
Copper						
Undamaged leaves (p = 0.0001)	0.0033c	0.0039c	0.0019b	0.0015ab	0.0008	
Damaged leaves $(p = 0.0001)$	-	0.0006a	0.0011b	0.0012Ь	0.0017	
Total foliar estimate ¹ (p = 0.0196)	0.0033ab	0.0044b	0.0030a	0.0026a	0.0025	
Boron						
Undamaged leaves! (p = 0.0001)	0.0688a	0.2191c	0.2008c	0.1205Ь	0.1002	
Damaged leaves $(p = 0.0001)$	-	0.0644a	0.1839Ь	0.3372c	0.5453	
Total foliar estimate ¹ (p = 0.0001)	0.0688a	0.28406	0.3851c	0.4597€	0.6471	
Z inc						
Undamaged leaves $(p = 0.0001)$	0.0310c	0.0350c	0.0218b	0.0113a	0.0093	
Damaged leaves $(p = 0.0001)$	-	0.0039a	0.0058b	0.0083c	0.0116	
Total foliar estimate (p = 0.0001)	0.0310b	0.0389c	0.0276b	0.0201a	0.0201	

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \le 0.05$ level using Fisher's Protected Least Significant Difference procedure;

¹Values were back-transformed from log values used for analysis and are estimates of the median.

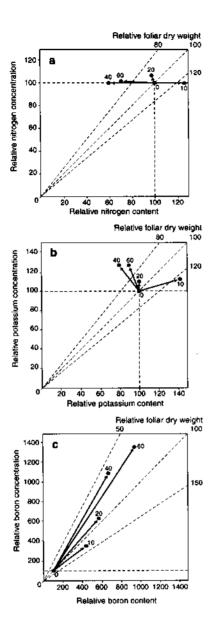


Figure 2. Relative effect of boron treatments on nutrient concentration, nutrient content, and foliar dry weight for a) nitrogen, b) potassium, and c) boron. The control (0-ppm treatment) was normalised to 100.

Table 4. Nutrient concentration ratios relative to nitrogen (nitrogen = 1) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

	Boron treatment (ppm)						
Measurement	0	10	20	40	60		
Phosphorus/Nitrogen	•		<u>.</u>				
Undamaged leaves (p = 0.0154)	0.098a	0.101a	0.097a	0.113Ь	0.1116		
Damaged leaves! $(p = 0.3572)$	_	0.092a	0.083a	0.101a	0.096a		
Total foliar estimate (p = 0.0887)	0.098a	0.101a	0.095a	0.111a	0.103a		
Potassium/Nitrogen							
Undamaged leaves ($p = 0.0016$)	0.520a	0.586ь	0.518a	0.630ъ	0.641Ъ		
Damaged leaves (p = 0.3448)	_	0.574a	0.642a	0.698a	0.670a		
Total foliar estimate (p = 0.0009)	0.520a	0.585a	0.537a	0.667ь	0.656Ь		
Calcium/Nitrogen							
Undamaged leaves (p = 0.0001)	0.463c	0.450c	0.367Ь	0.370ъ	0.297a		
Damaged leaves ¹ (p = 0.0005)	-	1.121Ь	0.967Ь	0.742a	0.641a		
Total foliar estimate (p = 0.2861)	0.463a	0.499a	0.468a	0.521a	0.483a		
Magnesium/Nitrogen							
Undamaged leaves (p = 0.0087)	0.094ab	0.087a	0.088a	0.109€	0.101bc		
Damaged leaves (p = 0.0470)	_	0.146b	0.124ab	0.127ab	0.113a		
Total foliar estimate (p = 0.0024)	0.094a	0.091a	0.094a	0.118Ь	0.108Ъ		
Manganese/Nitrogen							
Undamaged leaves (p = 0.0516)	0.00189a	0.00172a	0.00144a	0.00142a	0.00111:		
Damaged leaves $(p = 0.1970)$	-	0.00433a	0.00340a	0.00292a	0.00230a		
Total foliar estimate (p = 0.0090)	0.00189a	0.00191a	0.00177a	0.00209a	0.001782		
Copper/Nitrogen							
Undamaged leaves (p = 0.0425)	0.000079ab	0.000076ab	0.000054a	0.000100Ь	0.000056		
Damaged leaves (p = 0.0113)	-	0.000162ъ	0.000163b	0.000120a	0.000102		
Total foliar estimate (p = 0.1239)	0.000078a	0.000083a	0.000070a	0.000113a	0.000085		
Boron/Nitrogen							
Undamaged leaves (p = 0.0001)	0.0016a	0.0044b	0.0058c	0.0078d	0.0075d		
Damaged leaves (p = 0.0002)	_	0.017la	0.0268b	0.0321bc	0.0328c		
Total foliar estimate (p = 0.0001)	0.0016a	0.0053b	0.0093c	0.0178d	0.0215e		
Zinc/Nitrogen							
Undamaged leaves (p = 0.5647)	0.00071a	0.00069a	0.00063a	0.00071a	0.00071a		
Damaged leaves (p = 0.0766)	_	0.00100a	0.00083a	0.00071a	0.00071a		
Total foliar estimate (p = 0.7894)	0.00072a	0.00071a	0.00067a	0.00075a	0.00005a		

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \le 0.05$ level using Fisher's Protected Least Significant Difference procedure;

Discussion

The treatments in this study bracketed a level of boron that appears to have stimulated growth as well as levels that are clearly toxic. However, despite the growth response, some toxicity symptoms were still evident in seedlings treated with 10 ppm of boron. It is unfortunate that this study did not include boron treatment levels below 10 ppm, which might have resulted in a significant growth response

Values were back-transformed from log values used for analysis and are estimates of the median.

without toxicity symptoms. No plants died in this experiment even though the concentration of boron in leaves of some plants exceeded 1000 ppm. The leaves may have maintained adequate turgor pressure, which perhaps helped mitigate cell damage and stave off leaf abscission.

The use of *P. dasyrachis* in this study had several advantages. This species has a pinnately compound leaf, which allows for easy tracking of boron toxicity symptoms. The plants grew rapidly, and thus toxicity symptoms could be observed easily across the gradient from older foliage at the base of the plant to the newer foliage at the top. Furthermore, this species appears to be tolerant of abnormally high levels of boron.

Partitioning the leaves according to leaf damage allowed us to examine the concepts of nutrient dilution, toxicity, and mobility in a tropical seedling species as a result of boron application.

"There seems considerable merit...to compare B [boron] concentrations in healthy regions of leaves with those in necrotic/chlorotic regions. If there is a large gradient between these regions, then it is very likely that B toxicity is the causal agent, not other factors such as climate or pathogens. Such an approach could be very informative in species that accumulate B in their leaves." (Nable et al. 1997).

The pattern of boron toxicity shows that boron is an immobile element in the phloem for *P. dasyrachis* (i.e. the undamaged leaves were primarily at the top of the plant, where foliage is newer, while the damaged leaves were primarily toward the base, where foliage is older). The pattern was similar for immobile elements calcium and manganese: the damaged leaves had higher nutrient concentrations than the undamaged leaves. The opposite was true for mobile elements nitrogen, phosphorus, and potassium. Oertli and Kohl (1961) partitioned leaves of several boron-treated herbaceous plant species into three categories (necrotic, chlorotic, and green) and measured the boron concentration in each. They found concentrations of 800–12000 ppm in necrotic tissue, 400–3000 ppm in chlorotic tissue, and 40–1000 ppm in green tissue. The toxicity symptoms observed in this study are similar to those described by Bradford (1966) and Scott (1960), in which the leaflets displayed marginal chlorosis or necrosis.

Although there is literature on boron deficiency and toxicity in numerous plant species, especially agricultural crops, we were unable to find any sources on deficiency or toxicity levels in *P. dasyrachis*. This study provided some insights into how this tropical timber species grows in the presence of various levels of boron. The tendency toward increased growth in seedlings receiving the 10-ppm boron treatment is similar to results from deficiency studies with other species, in which the addition of boron had a positive effect on growth (Stone & Will 1965, Bradford 1966, Stone 1990, Will 1990). In the current study, total foliar boron concentration for the 10-ppm treatment showed a growth enhancement at a level of 165.50 ppm.

By known standards for boron in plants (Marschner 1995), the concentrations found in leaves from the 10- to 60-ppm boron treatments were high. In many species, the range between toxicity and deficiency of boron can be quite narrow

(Eaton 1940, Gupta et al. 1985). In the current study, the highest average boron concentration found in undamaged foliage was 265.87 ppm (60-ppm treatment), while the lowest boron level in damaged leaves averaged 336.75 ppm (10-ppm treatment).

Although the data in Tables 2 and 3 are useful for the quantitative measure of each nutrient, vector diagrams (Haase & Rose 1995) provide a means of visualising shifts in nutrient concentration, nutrient content, and foliage dry weight relative to one another. All three of the vector diagrams in Figure 2 reveal the higher foliar dry weight found in seedlings from the 10-ppm treatment relative to the control. This is especially dramatic in the nitrogen vector diagram, in which there was very little difference in nitrogen concentration but significant differences in dry weight and, hence, nutrient content (Figure 2a). The potassium diagram also shows a similar effect, as well as significantly higher concentrations for the higher boron treatments (40 and 60 ppm) (Figure 2b). The boron diagram shows the huge difference in relative boron concentration as a result of the treatments (Figure 2c).

Conclusion

The on-going reforestation programme in Thailand can greatly benefit from research to determine the optimum levels of boron and other nutrients in the leaves of forest tree seedlings grown in nurseries. Based on our experience, it is obvious how well *P. dasyrachis* and other Thai species respond to full-spectrum soluble fertilisers. In fact, the slow growth of seedlings in polybags could be shortened to as little as four months. Given that boron is not currently used as a supplement in Thailand and that seedlings in this experiment showed some evidence of a positive response to low levels of boron, it is advisable to follow up this experiment with other trials using treatment levels of 10 ppm boron or less.

Acknowledgements

We acknowledge the support of the Royal Forest Department of Thailand and Nursery No. 4 at Korat, Thailand, for supplying the seed for this study. Dr. Apishard of Chiang Mai University, Chiang Mai, Thailand, graciously answered questions from time to time about seed treatment and propagation. This is Paper 3266 of the Forest Research Laboratory, Oregon State University, Corvallis.

References

ATALAY, A. GARRETT, H. E., MAWHINNEY, T. P. & MITCHELL, R. J. 1988. Boron fertilization and carbohydrate relations in mycorrhizal and nonmycorrhizal shortleaf pine. *Tree Physiology* 4:275–280.

Bradford, G. R. 1966. Boron. Pp. 33-61 in Chapman, H. D. (Ed.) Diagnostic Criteria for Plants and Soils. University of California, Division of Agricultural Sciences, Berkeley.

Brown, P. H. & Shlep, B. J. 1997. Boron mobility in plants. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7-11 September 1997. *Plant and Soil* 193:85-101.

- EATON, S. V. 1940. Effects of boron deficiency and excess on plants. Plant Physiology 15:95-107.
- GUPTA, U. C., JAME, Y. W., CAMPBELL, C. A., LEYSHON, A. J., & NICHOLAICHUK, W. 1985. Boron toxicity and deficiency: a review. Canadian Journal of Soil Science 65:381-409.
- GLAUBIG, B. A. & BINGHAM, F. T. 1985. Boron toxicity characteristics of four northern California endemic tree species. *Journal of Environmental Quality* 14(1):72-77.
- HAASE, D. L. & Rose, R. 1995. Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. Forest Science 41:54-66.
- Hu, H. & Brown, P. H. 1997. Absorption of boron by plant roots. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7-11 September 1997. Plant and Soil 193:49-58.
- MARSCHNER, H. 1995. Mineral Nutrition of Higher Plants. 2nd edition. Academic Press, New York. 889 pp.
- MATOH, T. 1997. Boron in plant cell walls. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7–11 September 1997. *Plant and Soil* 193:59–70.
- MITCHELL, R. J., GARRETT, H. E., COX, G. S., ATALAY, A. & DIXON, R. K. 1987. Boron fertilization, ectomycorrhizal colonization, and growth of *Pinus echinata* seedlings. *Canadian Journal of Forest Research* 17:1153–1156.
- Nable, R. O., Banuelos, G. S. & Paull, J. G. 1997. Boron toxicity. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7-11 September 1997. *Plant and Soil* 193:181-198.
- OERTLI, J. J. & KOHL, H. C. 1961. Some considerations about the tolerance of various plant species to excessive supplies of boron. *Soil Science* 92:243–247.
- Power, P. P. & Woods, W. G. 1997. The chemistry of boron and its speciation in plants. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7–11 September 1997. Plant and Soil 193:1–13.
- ROBINSON, W.O. & EDGINGTON, G. 1942. Boron content of hickory and some other trees. *Soil Science* 53:309-312.
- SAS Institute Inc. 1989. SAS/STAT User's Guide. Version 6, Fourth edition. SAS Institute Inc., Cary, NC. 846 pp.
- Scott, E. G. 1960. Effect of supra-optimal boron levels on respiration and carbohydrate metabolism of *Helianthus annuus*. *Plant Physiology* 35:653–661.
- Shorrocks, V. M. 1997. The occurrence and correction of boron deficiency. Boron 97, International Symposium on 'Boron in Soils and Plants', Chiang Mai, Thailand, 7–11 September 1997. *Plant and Soil* 193:121–148.
- STONE, E. L. & WILL, G. M. 1965. Boron deficiency in *Pinus radiata* and *P. pinaster. Forest Science* 11:425-433.
- Stone, E. L., Hollis, C. A. & Barnard, E. L. 1982. Boron deficiency in a southern pine nursery. Southern Journal of Applied Forestry 6(2):108–112.
- Timmer, V. R. 1991. Interpretation of seedling analysis and visual symptoms. Pp. 113-135 in van den Driessche, R. (Ed.) *Mineral Nutrition of Conifer Seedlings*. CRC Press, Boston. Boca Raton, Florida.
- VIMMERSTEDT, J. P. & GLOVER, T. N. 1984. Boron toxicity to sycamore of minsoil mixed with sewage sludge containing glass fibers. Soil Science Society of America Journal 48(2):389–393.
- Will, G. M. 1990. Influence of trace-element deficiencies on plantation forestry in New Zealand. Forest Ecology and Management 37:1-6.

NOTES

EFFECT OF PRESOWING TREATMENTS ON GERMINATION AND SEEDLING GROWTH IN SYZYGIUM CUMINII

K. Vanangamudi, A. Venkatesh, J. Jayaprakash, Mallika Vanangamudi, R. Umarani & R. S. Vinaya Rai

Forest College and Research Institute, Tamil Nadu Agricultural University, Mettupalayam 641 301, India

Syzygium cuminii (L.) Skeels (Myrtaceae) is an evergreen tree, whose moderately hard wood is used in construction, manufacture of agricultural implements and as an excellent firewood. The fruits are edible. The tree is found throughout India, Myanmar, Andamans, Sri Lanka and Malaysia. The tree is not demanding in soil requirements. Fresh seeds are characterised by low germination rates which decrease with time. Seed germination and seedling growth are known to be regulated by exogenous hormones in many tree species (Verma & Tandon 1988, Singh 1990, Kumaran et al. 1994). Similarly, treatments with inorganic ions like KCl (Palani et al. 1995) and KNO₃ (Nagao & Furutani 1986, Maideen et al. 1990) have also been reported to enhance germination in tree species. But similar studies are wanting in Syzygium cuminii. Studies were therefore designed to investigate the effect of some chemicals on seed germination and seedling vigour in S. cuminii and to identify a suitable chemical for maximising both these parameters.

Ripe fruits were collected from a 15-y-old woodlot of *S. cuminii* at the Forest College and Research Institute, Mettupalayam (11° 19'N, 76° 56'E; 300 m a.s.l). The fruits were depulped, stored for two months and then treated with IAA 100 ppm, IBA 100 ppm, GA₃ 100 ppm, NaH₂PO₄ 1%, KCl 1% and water, each for a period of 12 and 24 h. The lower doses were chosen on economic considerations. The experiment was set up in a randomised block design, replicated twice, fifty seeds comprising one replication. The seeds were sown in polybags measuring 15×10 cm, one seed per bag at a depth of 1–2 cm. Thirty days after sowing counts were made on normal seedlings and germination expressed in percentage (ISTA 1993). Five seedlings were selected at random in each replication and measured for shoot length, root length and total dry matter production. Seedlings were oven dried at 85 °C to constant weight. Vigour index for each treatment was calculated (Abdul-Baki & Anderson 1973) as the integral of seedling length and germination per cent. The data were subjected to an ANOVA and treatment differences tested at p \leq .05 following Panse and Sukhatme (1967).

Compared to water soaking all presowing chemical treatments except those with 1% KCl and 1% KNO₃ recorded enhanced germination but the magnitude of increase was maximum in 12-h soaking in 100 ppm IBA followed by 24-h soaking in 1% NaH₂PO₄ (Table 1). For each chemical, doubling the duration of soaking resulted only in marginal increase in germination barring KCl and KNO₃ which recorded improved germination. However, root growth in several cases was inhibited under prolonged soaking.

The enhanced germination due to IBA may be ascribed either to diffusion of the growth regulator (Mathur et al. 1971) or its antagonistic effect on the inhibitor present in dormant seed (Khan 1968). Such augmentative effects of growth regulators have been reported in *Picea smithiana* (Singh 1990) and *Azadirachta indica* (Kumaran et al. 1994).

Root length and seedling dry weight were not influenced by the chemical treatments. But shoot growth and vigour index registered an increase following the treatments. Maximum vigour index was evident under the 12-h treatments of 100 ppm IBA and 1% NaH₂PO₄ (Table 1). Increased shoot growth was discernible in the 12-h treatments of IBA and NaH₂PO₄; it was further enhanced in the 24-h treatments of IAA and GA₈.

Table 1.	Effect of presowing growth stimulants on germination and seedling
	growth in Syzygium cuminii

Treatment		Germination (%)	Root length (cm)	Shoot length (cm)	Total dry matter (mg/seedling)	Vigour index
Dry seed		46	9.17	9.49	922	857
Water soak	12 h	54	9.99	9.83	934	1070
IAA 100 ppm	12 h	60	11.03	10.74	1073	1306
IBA 100 ppm	12 h	67	11.30	12.43	1120	1595
GA 100 ppm	12 h	59	10.43	10.18	1056	1208
NaH,PO, 1%	12 h	65	12.44	12.71	1171	1630
KCI İ%	12 h	45	12.55	10.71	1142	1047
KNO, 1%	12 h	50	9.99	10.20	926	1010
Water soak	24 h	56	10.01	9.77	911	1108
IAA 100 ppm	24 h	61	10.60	13.43	1297	1466
IBA 100 ppm	24 h	65	10.52	12.25	1299	1475
GA, 100 ppm	24 h	64	10.92	12.15	1186	1473
NaH,PO, 1%	24 h	66	9.17	12.98	1381	1464
KCI 1%	24 h	52	9.58	9.01	1139	967
KNO, 1%	24 հ	65	10.93	10.06	1098	1329
CD (p≤0.05)		0.63	ns	2.97	DS	89

CD = critical difference,

The growth promoting action of gibberellin was suggested to be the outcome of an interplay between supplied exogenous GA and endogenous auxin (Wareing & Phillips 1970). The ameliorative action of chemicals like KCl, KNO₃ has been reported in Acacia nilotica (Palani et al. 1995). But in the present study these chemicals proved inferior to IBA and NaH₂PO₄. Though IAA in low concentration has been reported to be beneficial in Cassia obtusifolia (Singh & Murthy 1982), in the present study, the quantum of its contribution was less than that of either IBA or NaH₂PO₄.

From a holistic consideration, soaking for 12 h in 100 ppm IBA is recommended to realise higher viability and vigour in *S. cuminii*. Compared to the control (dry seed), germination under this treatment increased by 21% and vigour index almost doubled.

References

ABDUL-BAKI, A. A. & ANDERSON, J. D. 1973. Vigour determination in soybean seed by multiple criteria. Crop Science 13:630-632.

ISTA. 1993. International rules for seed testing. Seed Science & Technology 20: 29-32.

KHAN, A. A. 1968. Inhibition of gibberellic acid induced germination by abscisic acid removal by cytokinins. *Plant Physiology* 43:1463–1465.

ns = not significant.

- Kumaran, K., Palani, M., Jerlin, R. & Surendran, C. 1994. Effect of growth regulators on seed germination and seedling growth of neem (Azadirachta indica). Journal of Tropical Forest Science 6:529-532.
- MAIDEEN, S. K., JACQUELINE, A. S. & VINAYA RAI, R. S. 1990. Presowing chemical treatment to hasten germination of Casuarina equisetifolia. International Tree Crops Journal 6:173–181.
- MATHUR, D. D., COUVILLON, G. A., VINES, H. M. & HENDRSHOOT, C. H. 1971. Stratification effects on endogenous gibberellic acid in peach seed. *Horticulture Science* 6:538-539.
- Nacao, M. A. & Furutani, S. C. 1986. Improving germination of papaya seed by density separation, potassium nitrate and gibberellic acid. *Horticulture Science* 21:1439–1440.
- PALANI, M., DASTHAGIR, M. G. & KUMARAN, K. 1995. Effect of presowing chemical treatment on germination and seedling growth in Acacia nilotica. International Tree Crops Journal 8:189-192.
- Panse, V. G. & Sukhatme, P. V. 1967. Statistical Methods for Agricultural Workers. Indian Council of Agricultural Research, New Delhi. 361 pp.
- Singh, C. & Murthy, V. S. 1982. Effects of some growth regulators on the seed germination and seedling growth of Cassia obtusifolia. Acta Botanica Indica 15:17-79.
- Singh, V. 1990. Influence of indole acetic acid and indole butyric acid on seed germination of spruce. Indian Forester 116(6):450–453.
- VERMA, A. N. & TANDON, P. 1988. Effect of grown regulators on germination and seedling growth of Pinus kesiya and Schima khosiana. Indian Journal of Forestry 11: 32-36.
- WAREING, P. F. & PHILLIPS, I. D. J. 1970. The Control of Growth and Differentiation in Plants. Pergamon Press, Oxford.

GROWTH OF PLANTATION GROWN KHAYA IVORENSIS IN PENINSULAR MALAYSIA

Ahmad Zuhaidi Yahya, M. Noor Mahat & Ab. Rasip Ab. Ghani

Forest Research Institute Malaysia, Kepong 52109 Kuala Lumpur, Malaysia

Khaya ivorensis, a member of the Meliaceae family, also known as African mahogany, is found naturally in the tropical moist lowlands of West Africa, parts of Côte d'Ivoire, Ghana, Togo, Benin, Nigeria and southern Cameroon. It is large tree, deciduous in drier climates that can attain heights of 40-50 m and diameter at breast height of up to 200 cm (Kinloch & Miller 1949, Lamprecht 1989). The tree is straight with long clear bole to as high as 30 m and bearing well-developed plank buttresses. The timber is moderately durable with a fine, fairly regular grain, easy to work and season, but difficult to impregnate. The timber is categorised as a medium hardwood timber with density averaging 560 kg m³ (Lamprecht 1989). The wood can be used for high quality furniture, panelling, cabinet-making and superior joinery, including other decorative works (Kinloch & Miller 1949).

A 0.3-ha stand of *K. ivorensis* was established in 1957 in the Bukit Lagong Forest Reserve, Selangor, Peninsular Malaysia (3° 14' N, 101° 38' E). The mean daily temperature in this region ranges from 27 to 32 °C. The annual rainfall is between 2000 and 2900 mm. Aspect is easterly. The soil is light reddish loam, shallow with underlying rock and granite. The drainage system is good. In the planting trial, 310 seedlings were line-planted at a spacing of 3×3 m (1111 seedlings ha⁻¹). Line cleaning and cutting of secondary forests and palms were carried out for the first five years at two-month intervals. During this period (1957 until 1962), 4 weeding rounds (first 2 years) and 18 climber cuttings were done. No further treatments and thinning were carried out thereafter and the stand was remeasured for the first time in 1997.

Table 1 presents the average growth results and standing stock of the 40-y-old plot in the Bukit Lagong Forest Reserve in Selangor in comparison with data from a 26-y-old plot in the Gunung Bungsu Forest Reserve in Kedah (as reported by Darus *et al.* 1991). Early assessment shows that 180 or 58 percent of the tree population achieved a diameter at breast height of 9–14 cm (mean diameter 10.6 cm) at the age of 5 years and 4 months after planting (Table 1).

Table 1. Standing stock of planted K. ivorensis, Bukit Lagong and Gunung Bungsu Forest Reserve, Peninsular Malaysia

Age (y)	N (ha ⁻¹)	h _{dom} (m)	d _{dom} (cm)	h (m)	d _g (cm)	h _c (m)	G (m²ha¹¹)	V (m³ha ^{,1})	V _{mai}
5.25*	1033	-	-		10.6	-	-	-	_
26**	-	-	48.3**	26.2	43.6	-	-	192.10	7.39
40***	390	29.7	46.8	23.5	29.5	16.40	26.61	305.48	7.64

Sources: * Anonymous (1957), ** Darus et al. (1991), *** this study.

Note:

N : number of trees han

h_{dom}: mean height of 100 biggest trees ha¹ d_{dom}: mean diameter at breast height of 100

biggest trees had

h_a: mean height of the stand d_e: mean diameter of the stand h, : mean height (clearbole)

G: basal area ha⁻¹ V: volume ha⁻¹

V_{mi}: mean annual volume increment

(m³ha-lyeart)

The stand in Bukit Lagong Forest Reserve was initially planted at a density of 1111 stem ha⁻¹. As a result of mortality caused mainly by tree competition, the density declined to 390 stems ha⁻¹ in 40 y. The dominant trees (100 biggest trees ha⁻¹) had an average diameter of 46.8 cm and average height of 29.7 m. The overall mean diameter was 29.5 cm and the overall mean height 23.5 m. The average clear bole height was 16.40 m. The approximate standing volume (clear bole volume) was 305.48 m³ ha⁻¹, i.e. the current standing stock was produced with a mean annual volume increment of 7.64 m³ ha⁻¹ y¹ at 40 years. The value is lower than for the other Meliaceae species, Azadirachta excelsa, with a mean annual volume increment of 14.4 m³ ha⁻¹ y¹ at 41 y (Ahmad Zuhaidi & Weinland 1995).

Similarly, the 26-y-old K ivorensis planted in Gunung Bungsu Forest Reserve shows comparable growth performance as indicated by the mean annual volume increment. The average diameter at breast height for the dominant class trees was 48.3 cm (Appanah & Weinland 1993) with the overall mean diameter of 43.6 cm and the mean height of 26.2 m. The standing stock was produced with a mean annual volume increment of 7.39 m³ ha⁻¹ y¹ at 26 y (Darus et al. 1991).

The diameter range in the population from Bukit Lagong Forest Reserve is very wide as the large difference between the dominant and overall average diameter indicates (17.3 cm).

Figure 1 shows the diameter distribution of the 40-y-old K. ivorensis stand.

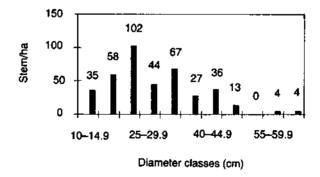


Figure 1. Diameter-class distribution of K. ivorensis, Bukit Lagong Forest Reserve, Peninsular Malaysia at 40 y

The wide diameter range of 12.3–62.4 cm is not necessarily a disadvantage as long as the size of the final crop trees lies within a relatively narrow range. The optimum final crop standing is assumed to be 200–250 trees ha⁻¹. Table 2 gives the main stocking parameter for the 100 and 200 biggest trees ha⁻¹.

Sub- population	h (m)	(cm)	(m)	G (m² ha¹)	V (m ⁵ ha ⁻¹)	dia. range (cm)
100	29.66	46.8	19.30	9.96	134.56	41.2-62.4
200	25.45	38.6	17.20	15.26	185.73	31.2-62.4

Table 2. Stocking parameter for the two sub-populations of biggest trees hard

Note: abbreviations as in Table 1.

While the diameter range for the 100 biggest trees ha⁻¹ is fairly narrow, the range only increases by 10 cm for the 200 biggest trees ha⁻¹. There is also a gradual descent in the average diameter for the group of 100 biggest trees ha⁻¹ (d = 46.8 cm) to that of 200 biggest tree ha⁻¹ (d = 38.6 cm).

The potential of the species for plantations seems to be promising. However, before the species can be planted on a commercial scale, the following aspects have to be addressed. The factors contributing to the distinct differentiation in tree size need to be determined. A tree selection programme might be needed to achieve a more uniform growth performance within the population. Observations in the 40-y-old stand in Bukit Lagong Forest Reserve, Peninsular Malaysia, show that the species is relatively free from serious pests and diseases except for an isolated attacked of shoot borer (*Hypsipyla sp.*) upon the saplings. Some silvicultural measures including line-planting under shade trees and mixed planting have been identified in reducing the risk of shoot borer attacks (Lamprecht 1989). The growth results, however, do provide some guidance with respect to realistic production targets and could be refined by conducting more studies considering different site conditions and stand treatments.

Acknowledgements

We thank Baskaran Krishnapillay for his valuable comments on the draft, and Khalid Tahir, Aziz Mohd Nor and Razani Zakaria for their assistance in data collection.

References

- Ahmad Zuhaidi, Y. & Weinland, G. 1995. A note on Azadirachta excelsa: a promising indigenous plantation species? Journal of Tropical Forest Science 7(4):672-676.
- Anonymous. 1957. Khaya ivorensis. Field Records 30C. Forest Research Institute, Kepong, Peninsular Malaysia. 24 pp.
- APPANAH, S. & WEINLAND, G. 1993. Planting Quality Timber Trees in Peninsular Malaysia A Review. Malaysian Forest Records No. 38, 221 pp.
- DARUS, A., HASHIM, M. N., A. RASIP, A. G. & LOK, E. H. 1991. Khaya ivorensis and Endospermum malaccense as potential species for future reforestation programme. Pp. 60-65 in Appanah, S., Ng, F. S. P. & Roslan, I. (Eds.) Proceedings of the Conference of Malaysian Forestry and Forest Products Research. Forest Research Institute Malaysia, Oct 3-4, 1990.
- Kinloch, W. & Miller, W. A. 1949. Gold Coast Timbers. Forestry Department and Prince Risborough Forest Products Laboratory, England. 34 pp.
- LAMPRECHT, H. 1989. Khaya ivorensis: Tree Species-Possibilities and Methods for their Long-Term Utilization.
 Silviculture in the Tropics. German Agency for Technical Cooperation (GTZ), Eschborn. 296 pp.

EARLY SURVIVAL AND GROWTH IN FIELD TRIALS OF AQUILARIA MALACCENSIS (KARAS) AND AZADIRACHTA EXCELSA (SENTANG)

Lok Eng Hai, Chang Yu Shyun & Aziah Mohd Yusoff

Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

Aguilaria malaccensis Lamk., a member of the Thymelaceae family, is commonly found in the lowland forests of Malaysia, Indonesia, the Philippines, Myanmar and India (Corner 1988). It is locally known as karas and produces aloes wood or 'gaharu' which is fragrant in nature. The production of 'gaharu' is believed to be due to the pathological infection and reaction of the wood caused by injuries. Gaharu is highly sought after and priced both for local use and in the international market particularly in the Arab countries where it is used as incense and in religious ceremonies (Desch 1954, Gianno & Kochummen 1981). The timber, a light hardwood, is suitable for veneer making, packing boxes, indoor light construction and possesses native medicinal values for treating asthma and body healing properties (Burkill 1966, Whitmore 1972, Wong 1978, Lok & Ahmad Zuhaidi 1996, Anonymous 1998). Azadirachta excelsa or sentang, belonging to the Meliaceae family, is fast growing and can reach 50 m in height and 4 m girth. It is a medium hardwood, locally important and used in house-building. An effective botanical insecticide has been identified in the species (Ng 1999). The tree is described by Wyatt-Smith (1952), Ng and Tang (1974), Corner (1988). Further information including the use of its timber has been compiled by Noraini (1997).

Currently, these two species, which occur naturally, have attracted many local planters, enterpreneurs, individuals and researchers into domesticating them on a large scale. Karas trees are normally exploited for gaharu and are often felled while gaharu is being examined and extracted. Thus, planting of the species is strongly recommended to ensure sustainable supply of the wood and its valuable non-wood product. Since information on the early growth perfomance and other silvicultural requirements of the species is scanty, trial plots were established to assess their survival and height growth at Bukit Lagong Forest Reserve, Selangor, Peninsular Malaysia.

The two plots, Field 26(A) (established in April 1996) and Field 52(B) (established in May 1997), are located at 3° 14'N and 101° 38'E. The mean daily temperature ranges from 27 to 30 °C with annual rainfall of between 2000 and 2900 mm. In Field 26(A), only karas were randomly line-planted with 80 selected tissue culture plantlets and 159 seedlings under pine at a close spacing of 1×1 m. The pines are sparsely scattered and the karas seedlings are about 40% shaded. They are located at the lower slope of the lower ridge of Bukit Hari at an altitude of 100–110 m above sea-level. Aspect is southerly. In Field 52(B), 375 karas were randomly interplanted in the open with 406 sentang seedlings at a spacing of 3×3 m. The plot is located on the ridge of Bukit Hari at an altitude of 200–220 m above sea-level. At both sites the soil is a heavy clay loam of granitic origin, reddish-brown with an average pH of 4.5.

Six-month-old seedlings, germinated from freshly collected seeds, were potted and later transferred to and planted in the fields. Initial average height and survival rates of the seedlings and plantlets were measured at one month after planting and then over periods of 24 months for Field 26 (A) and six months for Field 52 (B).

In Field 26 (A), karas tissue culture plantlets performed better than the raised seedlings. The percentage survival of both species decreased gradually over the period; at 24 months

plantlets gave 66.3% survival and seedlings 40.3% (Figure 1a). The initial and final heights of the plantlets were 43.1 and 136.6 cm respectively while those for the seedlings were 27.9 and 114.8 cm respectively (Figure 1b).

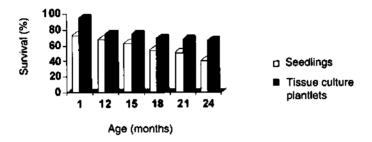


Figure 1a. Survival rates of karas seedlings and tissue culture plantlets

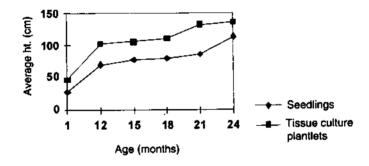


Figure 1b. Average heights of karas seedlings and tissue culture plantlets

In Field 52(B), six-month-old seedlings of both karas and sentang attained a similar higher survival rate of 93% although the value for sentang was initially higher (Figure 2a). They were planted in the open and at wider spacing of 3 x 3m. This further suggests that karas can be planted in the open although it has been regarded as shade loving compared to sentang which is shade intolerant and a faster growing species. The average heights achieved after six months for karas and sentang seedlings were 86.2 and 114.4 cm respectively (Figure 2b).



Figure 2a. Survival rates of karas and sentang seedlings

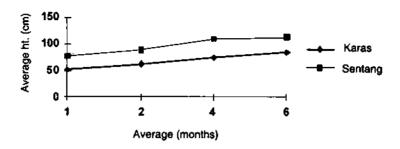


Figure 2b. Average heights of karas and sentang seedlings

These early results suggest that karas can be interplanted with sentang. Shade, especially for the former, can be provided at the early stage of planting to ensure a good survival rate. Planting stocks from karas can also be raised through seeds, wildings or tissue culture plantlets whereas sentang are usually planted using seedlings. In karas, the results shows that higher survival rate and average height growth can be obtained from tissue culture plantlets compared to seedlings. However, to ensure the suitability of the planting stocks on an operational scale, future studies should be conducted for longer durations and in larger trials for which a tree selection programme/provenance trials can be initiated to obtain a more precise conclusion.

Acknowledgements

We thank Baskaran Krishnapillay for his invaluable comments on the manuscript, and Markandan Moorthy, Razali Hamat, Mahat Sudin and Ahmad Sariani for their assistance in plot establishment, maintenance and data collection. We are grateful to the Silviculture Unit and the Division of Medicinal Plants, FRIM for their cooperation and contribution. We also thank the anonymous referees who made useful suggestions and improvements to this paper.

References

Anonymous. 1998. From a rubber tapper to masseur with wood. The STAR, 12 January, 1998.

BURKILL, I. H. 1966. A Dictionary of the Economic Products of the Malay Peninsula. Volume 1. Publisher City:198-206.

CORNER, E. J. H. 1988. Wayside Trees of Malaya. Volume 1. Government Printer, Singapore. 722 pp. Desch, H. E. 1954. Manual of Malayan Timbers. Malayan Forest Records No. 15. FRI, Kepong: 607-608. Gianno, R. & Kochummen, K. M. 1981. Gaharu wood. Malaysian Forester 44(4):567.

LOK, E. H. & AHMAD ZUHAIDI, Y. 1996. The growth performance of plantation grown Aquilaria malaccensis in Peninsular Malaysia. Journal of Tropical Forest Science 8(4):573-575.

No, F. S. P. & Tang, H.T. 1974. Comparative growth rates of Malaysian trees. *Malaysian Forester* 37(1):2-23.

Nc, L. T. 1999. A botanical new source of botanical insecticide - Azadirachta excelsa (sentang). FRIM In Focus. April, 1999:4–5.

NORAINI, A. (Ed.) 1997. Azadirachta Excelsa. A Monograph. Research Pamphlet No. 120. Forest Research Institute Malaysia. 59 pp.

WHITMORE, T. C. (Ed.) 1972. Tree Flora of Malaya. Volume 2. Longman, Kuala Lumpur: 383-386.

Wong, T. M. 1978. Wood Structure of the Lesser Known Timbers of Peninsular Malaysia. Malayan Forest Records No. 28. FRI, Kepong: 26-27.

WYATT-SMITH, J. 1952. Pocket Check List of Timber Trees. Malayan Forest Records No.17. 251 pp.