Journal of Tropical Forest Science 12(4):707–716 (2000)

EARLY SHOOT AND DIAMETER GROWTH IN FOUR *PINUS MERKUSII* POPULATIONS FROM THAILAND

Jarkko Koskela*

Department of Forest Ecology/Tropical Silviculture Unit, P.O. Box 28 (Koetilantie 3), FIN-00014 University of Helsinki, Finland

Received September 1998

KOSKELA, J. 2000. Early shoot and diameter growth in four *Pinus merkusii* populations from Thailand. Early shoot and diameter growth in four *Pinus merkusii* populations from Thailand was monitored between the ages of 8 and 47 weeks under controlled environment. Based on earlier studies concerning shoot development of the grass stage *P. merkusii* seedlings, it was hypothesised that the northern high-altitude populations have slower shoot growth and faster diameter growth than the northeastern low-altitude populations. Variation in timing of shoot and diameter growth among the populations was also investigated. Statistically significant variation in hypocotyl length and total shoot and diameter growth during the experiment was found among the populations. The timing of shoot and diameter growth was similar in all populations. A short hypocotyl length seems to indicate slow shoot growth during the early grass stage. This suggests that hypocotyl length can provide indicative information concerning the duration of the grass stage. The results also confirmed the earlier findings that there is genotypic variation in the rate of progress through the grass stage among the mainland Southeast Asian populations. However, the results did not verify the assumption that the high-altitude populations have slower shoot growth and faster diameter growth than the low-altitude populations. Only one of the two high-altitude populations exhibited rather slow shoot growth during the experiment, whereas the other exhibited significantly faster shoot growth which was similar to the low-altitude populations. Furthermore, only one of the low-altitude populations differed significantly from the high-altitude populations with the slowest total shoot growth. Slow shoot elongation seems be related with intensive diameter growth and *vice versa* during the early grass stage. Genotypic variation in total diameter growth suggests that there is also variation among the populations in their ability to withstand fire.

Keywords: Grass stage - *Pinus merkusii* - shoot elongation - shoot growth

KOSKELA, J. 2000. Pertumbuhan awal pucuk dan garis pusat dalam empat populasi *Pinus merkusii* dari Thailand. Pertumbuhan awal pucuk dan garis pusat dalam empat populasi *Pinus merkusii* dari Thailand dipantau pada umur antara 8 dan 47 minggu di bawah persekitaran yang dikawal. Berdasarkan kajian yang dibuat lebih awal mengenai perkembangan pucuk pada peringkat rumput anak benih *P.merkusii*, satu hipotesis dibuat bahawa populasi di kawasan altitud tinggi di utara mempunyai pertumbuhan akar yang lebih perlahan dan pertumbuhan garis pusat yang lebih cepat berbanding dengan populasi di kawasan altitud rendah di timur laut. Perbezaan masa pertumbuhan pucuk dan garis pusat bagi populasi tersebut juga disiasat. Terdapat perubahan bererti secara statistik dalam panjang hipokotil dan jumlah pertumbuhan pucuk dan garis pusat semasa uji kaji. Masa pertumbuhan pucuk dan garis pusat adalah sama dalam

**Present address: International Plant Genetic Resources Institute (IPGRI), Regional Office for Asia, the Pacific and Oceania, P.O. Box 236, UPM Post Office, Serdang, 43400 Selangor Darul Ehsan, Malaysia. Fax: (603) 8948 7655, E-mail: j.koskela@cgiar.org*

kesemua populasi. Hipokotil yang pendek menunjukkan pertumbuhan pucuk yang perlahan pada peringkat awal rumput. Ini menunjukkan bahawa panjang hipokotil dapat menyediakan maklumat mengenai tempoh peringkat rumput. Keputusan juga mengesahkan penemuan awal bahawa terdapat perubahan genotip dalam kadar perkembangan melalui peringkat rumput di kalangan populasi di Asia Tenggara darat. Bagaimanapun, keputusan tidak mengesahkan anggapan bahawa populasi di altitud tinggi mempunyai pertumbuhan pucuk yang lebih perlahan dan pertumbuhan garis pusat yang lebih cepat berbanding dengan populasi di altitud rendah. Hanya satu daripada dua populasi altitud tinggi mempamerkan pertumbuhan pucuk yang perlahan semasa uji kaji manakala yang lainnya mempamerkan pertumbuhan pucuk lebih cepat dengan bererti, iaitu sama dengan populasi di altitud rendah. Tambahan pula, hanya satu daripada populasi altitud rendah berbeza dengan bererti daripada populasi altitud tinggi dengan jumlah pertumbuhan pucuk yang paling perlahan. Pemanjangan pucuk yang perlahan nampaknya berkaitan dengan pertumbuhan garis pusat secara intensif dan sebaliknya semasa peringkat awal rumput. Perubahan genotip dalam jumlah pertumbuhan garis pusat mengesyorkan bahawa terdapat juga perbezaan di kalangan populasi dari segi keupayaannya untuk melawan kebakaran.

Introduction

In Southeast Asia, as well as elsewhere in the tropical zone, both natural and man-made fires have occurred since prehistoric times (e.g. Goldammer 1991). As a result, fire has been and still is an important ecological element which affects the development of vegetation especially in pine forests (Goldammer & Peñafiel 1990, Stott *et al.* 1990). The occurrence of fires enables pines to colonise disturbed sites as pioneers and to occupy sites which otherwise would not be maintained as pine forests (Turakka *et al.* 1982, Knight *et al.* 1994). Frequent, short-interval fires also maintain open pine–savannas as fire-climax forest communities (cf. Mueller-Dombois & Goldammer 1990).

The scattered natural distribution range of *Pinus merkusii* Jungh. *et* de Vriese extends from Myanmar through Thailand, Laos and Cambodia to Vietnam in the mainland Southeast Asia (e.g. Mirov 1967, Cooling 1968). It can also be found in certain islands of Indonesia and the Philippines (Critchfield & Little 1966). Due to the wide geographical distribution, isolated populations are subjected to different climates from seasonal to constantly humid equatorial with no dry season. The climatic variation and subsequent variation in the frequency of fire have resulted in a clear distinction in the seedling growth habit between the mainland and the insular populations (Cooling 1968). The mainland populations have evolved an adaptive trait to fire, called a grass stage, whereas the insular populations exhibit a normal shoot development (Cooling 1968, Luukkanen *et al.* 1976, Sirikul 1990).

During the grass stage, shoot growth is depressed and long needles are densely attached to a short, branchless stem. A major part of diameter growth results from the expansion of cortex which forms approximately two-thirds of the diameter (Koskela *et al.* 1995). At the end of the grass stage, inhibited internodal elongation turns into normal internodal elongation and the seedlings start rapid shoot growth (see Brown 1964).

Considerable variation in the duration of the grass stage has been reported among *P. merkusii* populations under natural conditions. In Thailand, the grass stage may last up to 7 y in the northern highlands while it lasts only 1–3 y in the northeastern plateau (e.g. Stott *et al.* 1990). Sirikul (1990) studied the morphological shoot development of *P. merkusii* seedlings in detail and observed that the seedlings may pass through up to four ontogenic stages, i.e. the primary growth stage, the early and the late grass stages and the emergence stage. During the early grass stage, shoots are characterised by free or pre-determined growth, and during the late grass stage and the emergence stage, shoots are characterised only by pre-determined growth (Sirikul 1990). Shoots of the high-altitude mainland Southeast Asian populations were formed by free growth whereas in the low-altitude mainland Southeast Asian populations, shoots were formed either by free or pre-determined growth during the early grass stage (Sirikul 1990). Sirikul (1990) also reported that the rate of progress through the grass stage was faster in the low-altitude populations than in the high-altitude populations but no quantitative data on how shoot elongation differed among the populations were presented.

Diameter growth is also of particular interest since the faster the growth the better the seedlings are protected against surface fires. In addition to physical protection, the secondary cortex also works as a carbohydrate store (Cooling 1968). Shoot and diameter growth may also be synchronised since it has been observed that once shoot growth starts to increase at the end of the grass stage, diameter growth decreases (Koskela *et al.* 1995).

Improved management is urgently needed to secure existence of the fragmented *P. merkusii* populations in the mainland Southeast Asia. In Thailand, for example, the remaining natural pine forests cover only about one percent of the total forest area (RFD 1998) and many pine stands are rather old, which has already decreased the regeneration potential. *Pinus merkusii* regenerates well even under a dense cover of grass but seedling mortality due to competition by grass is high and severe fires can also kill the seedlings despite the grass stage (Koskela *et al.* 1995). Thus the seedlings should be exposed to annual weeding treatments for a number of years in order to reduce the mortality and to guarantee successful natural regeneration. Weeding is also found to shorten the grass stage (Cooling 1968). For how many years weeding should be continued depends on the duration of the grass stage in a given site which is difficult to determine if no prior information exists. In addition to altitude, hypocotyl length may also provide information concerning the duration of the grass stage, since Brown (1964) reported that the grass stage seedlings of *P. palustris* had distinctly shorter average hypocotyl length after germination than the non-grass stage *P. taeda* and their semi-grass stage hybrid, *P.* x *sondereggeri*.

The aim of this study was to investigate genotypic variation in hypocotyl length and early shoot and diameter growth among four *P. merkusii* populations originating from Thailand. It was hypothesised that the northern high-altitude populations have slower shoot growth and faster diameter growth than the northeastern low-altitude populations. Patterns of shoot elongation and diameter extension were also studied to find out whether there is variation in timing of shoot and diameter growth among the populations during the early grass stage.

Material and methods

Seeds from four natural populations of *P. merkusii* (Table 1) were germinated in containers filled with a sand-peat mixture (1:1) in a growth chamber. Doi Huey Meing (DHM) and Huey Bong (HB) represented high-altitude populations, and Khong Chiam (KC) and Sangkha (S) low-altitude populations. Germinated seedlings were transplanted into 40-cm-tall pots (5.5 litres) filled with homogenised sand (grain size 0.1–0.6 mm) and thereafter fertilised weekly. The weekly dose was 50 ml of a solution with a 0.1% concentration of a nitrogen poor fertiliser (9–25–20, $N-P_2O_5-K_2O$). The seedlings were irrigated through small holes at the bottom of the pots which were kept in continuous contact with water. This allowed cohesion to guide water movement into the pots. Soil water potential was monitored with standard jet-fill tensiometers at depths of 15 and 30 cm in four pots. Soil water potential was fairly constant throughout the experiment at both depths (600 and 400 Pa respectively).

Table 1. Seed origins of the four populations of *Pinus merkusii* from Thailand used in the study

Geographical location	Latitude	Longitude	Elevation (m)	Annual rainfall (mm)
Doi Huey Meing, Prao [1]	19° 06' N	99° 10' E	800	1500
Huey Bong, Hot [2]	18° 10' N	98° 25' E	800	1300
Khong Chiam, Ubon Ratchatani[1]	15° 28' N	105° 30' E	150	2100
Sangkha, Surin [1]	14° 41' N	103° 46' E	160	1300

Seed sources: [1] Danida Forest Seed Centre, Denmark; [2] Royal Forest Department, Thailand.

Length of the daily photoperiod was set to 13 h with an irradiance level of approximately 200 $\mu mol\ m^{-2}\ s^{-1}$ at a seedling level. Air temperature during the photoperiod was kept at 26 ± 1°C and during the dark period at 18 ±1°C. Relative air humidity was set to 60 ±10% and 70 ±10% respectively.

Six seedlings from each population were randomly selected for the shoot and diameter growth experiment. When the seedlings were transplanted into the pots, the length of a hypocotyl was measured and a thin pin was pushed through the hypocotyl just below the cotyledons as a datum point. Shoot length and diameter measurements were started at the age of 8 weeks and continued thereafter weekly until the age of 47 weeks. The length of the shoot was measured from the datum point to the shoot tip with an accuracy of 1 mm. Diameter was measured below the datum point with the same accuracy.

Homogeneity of variances in the measured data was evaluated by residual analysis before statistical analyses. In the case of total diameter growth during the experiment (final–initial diameter), heterogeneity of variances was detected. Therefore, the diameter data were analysed with non-parametric Kruskal-Wallis one-way test and Mann-Whitney U-test was used for subsequent paired tests. The rest of the data, i.e. hypocotyl length, initial and final shoot lengths, and total shoot growth during the experiment (final–initial shoot length), were analysed with one-way analysis of variance and Tukey's HSD-test was used for pairwise comparisons.

Variation in shoot elongation and diameter extension patterns among the populations were tested using a method developed by Estabrook *et al.* (1982), which is a modified Kolmogorov-Smirnov two-sample test (e.g. Sokal & Rohlf 1995). The method is based on the maximum difference (D) in relative shoot length or diameter of the two populations. Since the final shoot lengths (s_i) and diameters (d_i) of the populations were lower than 25 mm at the end of the experiment, D was multiplied with s_1 and s_2 (or d_1 and d_2) to obtain a test statistic (Sokal & Rohlf 1995). The result was then compared with its critical value obtained from a statistical table for the Kolmogorov-Smirnov two-sample test (Rohlf & Sokal 1995).

Results

Statistically significant differences in mean hypocotyl length were found among the populations (p=0.014). The northern Doi Huey Meing (DHM) had the shortest mean hypocotyl length which differed significantly from those of Khong Chiam (KC) and Sangkha (S), and almost from that of Huey Bong (HB) (p=0.084). No statistically significant differences in mean hypocotyl length were found among KC, S and HB (Table 2).

Table 2. Mean hypocotyl length after germination and mean total shoot and diameter growth during the experiment of the four Thai populations of *P. merkusii.* Standard deviation is presented in parentheses. Means followed by different letter are statistically different (p<0.05).

Population	Hypocotyl length (mm)	Total shoot growth (mm)	Total diameter growth (mm)
Doi Huey Meing	43.3 (6.9) a	13.5 (1.9) a	3.5 (0.8) a
Huey Bong	51.3 (4.4) ab	20.0 (4.9) b	2.0 (0.9) b
Khong Chiam	54.2 (4.7) b	16.0 (2.2) ab	1.5 (0.5) b
Sangkha	52.2 (5.5) b	20.0 (4.1) b	2.0 (-) b

Statistically significant differences in mean shoot length were detected among the populations both at the beginning of the experiment (p = 0.006) and at the end of the experiment (p = 0.003). Analysis of variance also showed statistically significant differences in mean total shoot growth during the experiment among the populations (p = 0.010). HB and S had larger mean total shoot growth than DHM and KC but only DHM differed significantly from HB and S (Table 2).

From the beginning of the experiment until the age of 15 weeks, initiation and extension of primary leaves were still continuing in all populations and the first secondary needle fascicles were formed in the axils of the primary leaves. After this period, the formation of secondary needle fascicles continued, but not in every axil and the formation of primary leaves decreased. DHM did not continue the initiation of primary leaves as long as the other populations did. The rate of shoot elongation was less rapid after the age of 15 weeks than during the first few weeks of the experiment in all populations (Figure 1). No statistically significant differences were found in the pattern of relative shoot elongation among the populations, i.e. the timing of the shoot growth was similar in all populations during the experiment (Table 3).

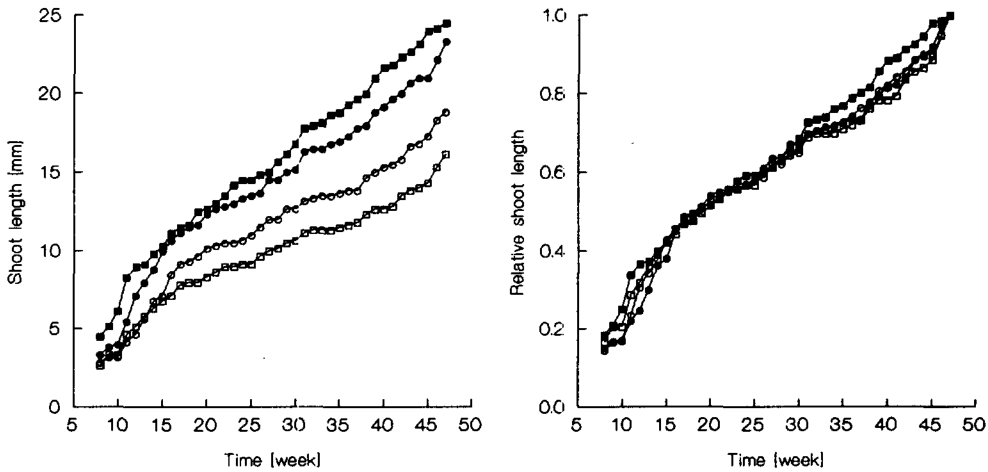

Figure 1. Shoot elongation and development of relative shoot length in four *Pinus merkusii* populations (❑ Doi Huey Meing, ■ Huey Bong, ○ Khong Chiam, ● Sangkha) during the experiment

Table 3. Matrix of test statistics based on maximum difference (*D*) in relative cumulative shoot length between populations and their critical values of the four *P. merkusii* populations

	$D \times$ shoot length$_1 \times$ shoot length$_2$			
Population	Doi Huey Meing	Huey Bong	Khong Chiam	Sangkha
Doi Huey Meing	-	40.0	21.9	20.0
Huey Bong	167	-	54.9	59.5
Khong Chiam	133	187	-	25.9
Sangkha	157	216	177	-

Critical values, $\alpha = 0.05$.

Diameter growth started several weeks later than shoot growth in all populations (Figure 2). DHM started diameter extension at the age of 17 weeks and the other populations a few weeks later. The rate of diameter extension was more rapid in DHM than in the other populations throughout the experiment and thus statistically significant differences in total diameter growth were detected among the populations ($p<0.001$). Mean total diameter growth was significantly larger in DHM than in the other populations (Table 2). No significant differences in total diameter growth were found among HB, KC and S. Although DHM exhibited distinctly more intensive diameter growth than the other populations, no statistically significant differences were found in the pattern of relative diameter extension among the populations (Table 4). Some critical values could only be obtained with $\alpha=1$ (Table 4) since the diameters of all populations except DHM were less than 4 mm at the end of the experiment. The stepwise behaviour in diameter growth (Figure 2) suggests that the used measurement could have been more accurate, 0.5 mm for example.

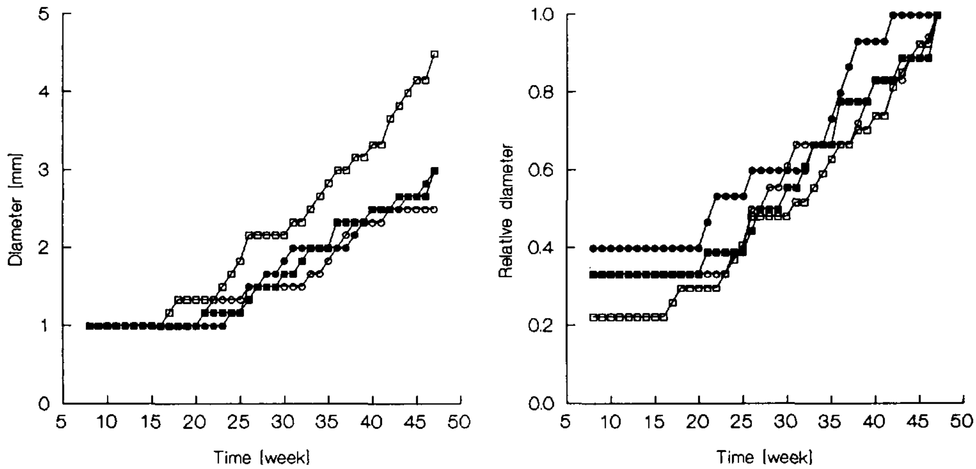

Figure 2. Diameter extension and development of relative diameter in four *P. merkusii* populations (❑ Doi Huey Meing, ■ Huey Bong, ○ Khong Chiam, ● Sangkha) during the experiment

Table 4. Matrix of test statistics based on maximum difference (D) in relative cumulative diameter between populations and their critical values of the four *Pinus merkusii* populations

	$D \times diameter_1 \times diameter_2$			
Population	Doi Huey Meing	Huey Bong	Khong Chiam	Sangkha
Doi Huey Meing	-	1.5	2.7	2.0
Huey Bong	15	-	1.3	1.0
Khong Chiam	15	9*	-	1.6
Sangkha	15	9*	9*	-

Critical values, α = 0.05, * α = 1.

Discussion

Mean hypocotyl length was the shortest in DHM which also had the slowest progress in shoot elongation during the experiment. The differences in mean hypocotyl length were significant between DHM and two out of three populations and almost significant between the third population. Hypocotyl length seems to provide indicative information concerning the duration of the grass stage in a given population of *P. merkusii*. This is in accordance with the earlier observations in *P. palustris* and its hybrid (Brown 1964). As a comparison, *P. merkusii* has longer mean hypocotyl length (43.3–55.5 mm in this study) and shorter grass stage (3–5 years) (Cooling 1968) than *P. palustris* in which mean hypocotyl length is much shorter (6.2 mm) and subsequently the grass stage lasts longer (6–15 years) (Brown 1964). However, hypocotyl length cannot be used for predicting shoot length of individual seedlings at later age (Brown 1964).

Genotypic variation in total shoot growth was detected among the four populations used in this study. The result confirms the earlier findings that there is genotypic variation in the rate of progress through the grass stage among the mainland Southeast Asian populations of *P. merkusii*. A high-altitude population exhibited rather slow shoot growth during the experiment whereas the other high-altitude population exhibited significantly faster shoot growth which was similar to the low-altitude populations. Only one of the low-altitude populations significantly differed from the high-altitude populations with the slowest total shoot growth. The results contradict the classification based on altitude (Sirikul 1990) to distinguish the populations into two groups having either an intermediate or a pronounced grass stage. Furthermore, only one of the northern high-altitude populations exhibited a shoot type which morphologically resembled the shoot type with free growth as described by Sirikul (1990) for all high-altitude populations in his study. Shoots of the other high-altitude population and the two low-altitude populations resembled the shoot types with either pre-determined or free growth (Sirikul 1990).

Different pine species express their adaptation to a wide range of environmental conditions with a number of shoot growth patterns (Lanner 1976). Northeastern Thailand is subjected to warm tropical, semi-humid climate with hydric vegetation period of 5–6 months while the northern parts of the country experience cold tropical, semi-humid or humid climates with hydric vegetation period of 7–9 months (Lauer 1993). In the case of non-grass stage *P. kesiya*, which is also native to Thailand, genotypic variation in timing of shoot growth exists reflecting adaptation to varying environmental conditions (Sirikul & Kanninen 1990). In *P. merkusii*, it seems that the differences in environmental conditions have not resulted in genotypic variation in timing of shoot growth during the early grass stage. The existing genotypic variation in the rate of progress through the grass stage cannot be explained by variation in environmental conditions or altitude alone. Thus other factors, like the frequency of fire in a given site, should be taken into account in further studies.

Slow shoot elongation seems to be related with intensive diameter growth and *vice versa* during the early grass stage. DHM, which had slow shoot growth during the experiment, showed the most distinct diameter extension, whereas the other populations had faster shoot growth but less intensive diameter growth. The revealed genotypic variation in early diameter growth suggests that there is also variation among the populations in their ability to withstand fire. The thicker the bark grows, the better the seedlings can resist frequent surface fires.

The influence of fire on the evolution of *P. merkusii* has also been emphasised in genetic studies. The species has a very low intrapopulational variability in contrast to most pine species but a high level of interpopulational differentation (Szmidt *et al.* 1996). In Thailand, Changtragoon and Finkeldey (1995) found that the genetic differentiation among *P. merkusii* populations does not reflect the geographical distributions of the populations. The low intrapopulational variability may be explained by sparsely distributed small populations and asynchronous flowering (Szmidt *et al.* 1996). Thus it is conceivable that only few parent trees were able to reproduce during the favourable conditions after fires (Changtragoon & Finkeldey 1995) and that the proportion of the survived offsprings was depended on their ability to withstand fire in a given site.

In conclusion, the classification based on altitude may not always provide reliable information concerning the variation in the duration of the grass stage among the mainland Southeast Asian populations of *P. merkusii.* Altitude provides tentative information which can be confirmed by monitoring the early development of the seedlings. Populations having a short hypocotyl after germination can be expected to have a pronounced grass stage with slow shoot growth but intensive diameter growth. The obvious genotypic variation in the ability to withstand fire has silvicultural implications, i.e. seedling survival can be guaranteed with a less intensive but a longer weeding programme in those populations which demonstrate intensive diameter growth during the early grass stage. Sirikul (1990) suggested that breeding programmes with *P. merkusii* may be directed to selecting seedlings which show early pre-determined growth to shorten the grass stage. This selection criterion, however, may decrease the ability of the new *P. merkusii* genotypes to withstand fires.

Acknowledgements

The author is grateful to Olavi Luukkanen for his comments on the manuscript. Seed material for this experiment was kindly provided by the Danida Forest Seed Centre in Denmark and the Royal Forest Department in Thailand. Chunyang Li and Jukka Hilpinen helped in maintaining the experiment at the facilities of the Faculty of Agriculture and Forestry, University of Helsinki. Financial support was provided by the Academy of Finland under the framework of the Graduate School in Forest Ecology and Research Project No. 10119451.

References

BROWN, C. L. 1964. *The Seedling Habit of Longleaf Pine.* Georgia Forest Research Council and School of Forestry, University of Georgia. 68 pp.

CHANGTRAGOON, S. & FINKELDEY, R. 1995. Patterns of genetic variation and characterization of the mating system of *Pinus merkusii* in Thailand. *Forest Genetics* 2(2):87–97.

COOLING, E. N. 1968. *Pinus merkusii. Fast Growing Timber Trees of the Lowland Tropics No. 4.* Commonwealth Forestry Institute, Oxford. 169 pp.

CRITCHFIELD, W. B. & LITTLE, E. L. 1966. *Geographic Distribution of the Pines of the World.* U.S. Department of Agriculture, Washington. 97 pp.

ESTABROOK, G. F., WINSOR, J. A., STEPHENSON, A. G. & HOWE, H. F. 1982. When are two phenological patterns different? *Botanical Gazette* 143(3):374–378.

GOLDAMMER, J. G. 1991. Tropical wild-land fires and global changes: prehistoric evidence, present fire regimes, and future trends. Pp. 83–91 in Levine, J. S. (Ed.) *Global Biomass Burning. Atmospheric, Climatic, and Biospheric Implications.* The MIT Press, Cambridge, Massachusetts.

GOLDAMMER, J. G. & PEÑAFIEL, S. R. 1990. Fire in the pine-grassland biomes of tropical and subtropical Asia. Pp. 45–62 in Goldammer, J. G. (Ed.) *Fire in the Tropical Biota. Ecosystem Processes and Global Challenges.* Ecological Studies 84. Springer-Verlag, Berlin.

KNIGHT, D. H., VOSE, J. M., BALDWIN, V. C., EWEL, K. C. & GRODZINSKA, K. 1994. Contrasting patterns in pine forest ecosystems. Pp. 9–19 in Gholz, H. L., Linder, S. & McMurtie, R. E. (Eds.) *Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: a Comparative Analysis.* Ecological Bulletins 43. Munksdgaard International Booksellers and Publishers, Copenhagen.

KOSKELA, J., KUUSIPALO, J. & SIRIKUL, W. 1995. Natural regeneration dynamics of *Pinus merkusii* in northern Thailand. *Forest Ecology and Management* 77:169–179.

LANNER, R. M. 1976. Patterns of shoot development in *Pinus* and their relationship to growth potential. Pp. 223–243 in Cannell, M. G. R. & Last, F. (Eds.) *Tree Physiology and Yield Improvement.* Academic Press, London.

LAUER, W. 1993. Climatology. Pp. 95–164 in Pancel, L. (Ed.) *Tropical Forestry Handbook, Volume I.* Springer-Verlag, Berlin.

LUUKKANEN, O., BHUMIBHAMON, S. & PELKONEN, P. 1976. Photosynthesis in three provenances of *Pinus merkusii. Silvae Genetica* 25(1):7–10.

MIROV, N. T. 1967. *The Genus Pinus.* Academic Press, New York. 602 pp.

MUELLER-DOMBOIS, D. & GOLDAMMER, J. G. 1990. Fire in tropical ecosystems and global environmental change: an introduction. Pp. 45–62 in Goldammer, J. G. (Ed.) *Fire in the Tropical Biota. Ecosystem Processes and Global Challenges.* Ecological Studies 84. Springer-Verlag, Berlin.

RFD. 1998. *Forestry Statistics of Thailand 1997.* Royal Forest Department, Bangkok, Thailand. 149 pp.

ROHLF, F. J. & SOKAL, R. R. 1995. *Statistical Tables.* Third edition. W. H. Freeman and Company, New York. 208 pp.

SIRIKUL, W. 1990. *Shoot Growth and Flower Development in Tropical Pines: Studies on Genetic and Environmental Variation.* University of Helsinki Tropical Forestry Reports 6. Helsinki University Press, Helsinki. 148 pp.

SIRIKUL, W. & KANNINEN, M. 1990. Shoot growth and its clonal variation in *Pinus kesiya. Silva Fennica* 24(3):303–313.

SOKAL, R. R. & ROHLF, F. J. 1995. *Biometry: the Principles and Practice of Statistics in Biology.* Third edition. W. H. Freeman and Company, New York. 887 pp.

STOTT, P. A., GOLDAMMER, J. G. & WERNER, W. L. 1990. The role of fire in the tropical lowland deciduous forests of Asia. Pp. 32–44 in Goldammer, J. G. (Ed.) *Fire in the Tropical Biota. Ecosystem Processes and Global Challenges.* Ecological Studies 84. Springer-Verlag, Berlin.

SZMIDT, A. E., WANG, X. -R. & CHANGTRAGOON, S. 1996. Contrasting patterns of genetic diversity in two tropical pines: *Pinus kesiya* (Royle ex Gordon) and *P. merkusii* (Jungh. *et* De Vriese). *Theoretical and Applied Genetics* 92:436–441.

TURAKKA, A., LUUKKANEN, O. & BHUMIBHAMON, S. 1982. Notes on *Pinus kesiya* and *P. merkusii* and their natural regeneration in watershed areas of northern Thailand. *Acta Forestalia Fennica* 178. 33 pp.