Shoot growth and its clonal variation in *Pinus kesiya*

Winai Sirikul & Markku Kanninen

TIIVISTELMÄ: PINUS KESIYAN VERSONKASVU JA SEN GENEETTINEN YKSILÖVAIHTELU

Sirikul, W. & Kanninen, M. 1990. Shoot growth and its clonal variation in *Pinus kesiya*. Tiivistelmä: *Pinus kesiya*n versonkasvu ja sen geneettinen yksilövaihtelu. Silva Fennica 24(3):303–313.

Shoot elongation of *Pinus kesiya* Royle ex Gordon was studied using 2-year-old grafts in a clonal seed orchard of the Pine Improvement Centre, located at the Huey Bong Experimental Station near Chiangmai, Thailand (19° 17' N , 99° 15' E , 900 m a.s.l.).

The seed orchard had a completely randomized block design with 30 blocks and 80 single-tree plots (clones) in each block. Eleven clones in four blocks were selected out of the total of 80 grafts (clones). From each graft, three lateral branches at the height of 1.6 m from the ground level were selected. Thus, total of 109 branches were measured.

Shoot length of branches was measured between July 3, 1983 and March 11, 1984 at approximately bi-weekly intervals. Methods of classical growth analysis were used in describing the shoot growth. Clonal differences in the pattern of shoot elongation were statistically tested using the analysis of variance and a modified Kolmogorov-Smirnoff Two-Sample Test.

The annual shoot growth pattern of *P. kesiya* exhibited two consecutive sigmoid growth curves, i.e it consisted of two flushes of shoot elongation, both formed by free growth. Thus the pattern of shoot growth of *P. kesiya* resembled the *caribaea* pattern. However, the annual shoot was composed of summer and winter shoots. These could be distinguished from each other by the reproductive organs, which always occur on winter shoot. The summer shoot contributed 61 % of the total annual shoot length.

There were significant differences in the pattern of shoot elongation between the studied clones, which may reflect differences in the adaptation to different environmental conditions.

---

*Pinus kesiya*n (Royle ex Gordon) versonkasvua tutkittiin Huey Bongin koeaseman männynjalostuskeskuksessa Chiangmaissa Thaimaassa (19° 17' N , 99 ° 15' E , 900 m m.p.y.). Koeaineistona käytettiin kaksivuotiaita kloonisiemenviljelmän vartteita.

Siemenviljelmä on perustettu täydellisesti satunnaistaen ja siinä on 30 lohkoa, jossa kussakin 80 yhden puun (kloonin) muodostamaa koealaa. Kokeeseen valittiin yksitoista kloonia, jotka sijaitsivat yhteensä neljässä lohkossa. Jokaisesta vartteesta valittiin kolme näyteoksaa noin 1,6 m:n korkeudelta maanpinnasta. Aineiston muodosti yhteensä 109 näyteoksaa.

Oksien pituuskasvua mitattiin noin kahden viikon välein 3.7.1983–11.3.1984 välisenä aikana. Kasvun analyysissä käytettiin perinteisiä kasvututkimuksen menetelmiä. Kloonien pituuskasvun ajoittumisen välistä eroa tutkittiin tilastollisesti varianssianalyysillä ja muunnettua Kolmogorov-Smirnoff kahden populaation vertailutestiä käyttäen.

*Pinus kesiya*n vuotuisessa pituuskasvussa havaittiin kaksi peräkkäistä kasvujaksoa. Näin *Pinus kesiya*n kasvurytmi noudattaa *caribaea*-tyyppiä. Vuosikasvain koostui kesä- ja talviversoista. Ne olivat erotettavissa toisistaan kukkasilmuista, joita oli vain talviversoissa. Kesäverson osuus vuosikasvaimen kokonaispituudesta oli 61%.

Tutkittujen kloonien välillä oli tilastollisesti merkitseviä eroja pituuskasvun rytmissä kasvujakson aikana. Nämä erot heijastavat ilmeisesti alkuperien erilaisia sopeutumismekanismeja ympäristöön.

1. Introduction

The shoot growth patterns and factors controlling growth in pines have received special attention in ecophysiological growth studies, mainly because of apparent regularity of growth in this genus. It is known, for instance, that the pine shoot usually contains stem units along its axis which determine the potential length of the final shoot and the number of the stem units is controlled by environmental conditions (Lanner 1976). However, most of these studies are dealing with pines growing in cold and temperate regions.

Lanner (1976) listed ten different patterns of shoot growth in genus *Pinus*. Later Lanner (1978) and Slee and Shepherd (1978) described the formation of buds and elongation of shoots in subtropical species *Pinus elliottii* Engelm. In addition, a model has been constructed which describes the shoot growth in the tropical species *P. merkusii* Jungh & de Vries during its grass-tree stage (Sirikul 1980). Srivastava and Elias (1982) found three different shoot growth patterns in *P. caribaea* var. *hondurensis* grown in Malaysia.

Pinus kesiya Royle ex Gordon is a species indigenous to Thailand. It is principally found on ridges of higher mountains in northern and northwestern Thailand. Its altitudinal range is from 300 to 1,800 m a.s.l (Turnbull et al. 1980). As a plantation species *P. kesiya* grows very well on sites within the altitudinal range of 700–1,800 m, characterized by a summer rainfall of 1,000–2,000 mm and a distinct dry season (Pousujja et al. 1986). Thus, the species has been recommended for industrial pulpwood plantations in Thailand. The Thai-Danish

Pine Project was established in 1969 through the co-operation between the governments of Thailand and Denmark to genetically improve pine species for large scale plantations in the country. Provenance trials, gene conservation plantations and seed research have since been carried out to study *P. kesiya* together with other tropical pine species.

Although sufficient information on many aspects concerning *P. kesiya* has been obtained, the genetic variation in the shoot growth pattern and environmental factors controlling the growth of this species are unfortunately not well understood. However, this information is needed to predict the performance of the species. For instance, Slee (1982) has emphasized the need to study the shoot growth phenology and to establish a model for shoot growth of tropical trees. He pointed out how the knowledge on the shoot elongation patterns has facilitated the silvicultural practices and breeding programmes of *P. caribaea* planted in Australia. In addition, studies on the phenology of flowering and seed development in relation to the pattern of shoot elongation and factors controlling them are obviously also of great potential importance.

The aim of the present study is to study and describe the pattern of terminal shoot elongation in *Pinus* kesiya grown in Thailand. Furthermore, clonal variation in the shoot growth is studied in order to obtain information which is needed for selecting well-adapted genotypes of this species for plantation forestry.

2. Material and methods

The experiment was carried out on 2-year-old grafts in a clonal seed orchard of the Pine Improvement Centre, located at the Huey Bong Experimental Station near Chiangmai, Thailand (19° 17' N , 99° 15' E , 900 m a.s.l.). The seed orchard had a completely randomized block design with 30 blocks and 80 single-tree plots (clones) in each block. The spacing was 9x9 m. All scions, which originated from registered plus trees, had been top-cleft grafted on potted stocks at the nursery of the Pine Improvement Centre, where the grafts were kept in a glass house for one year prior to planting out in the seed orchard. Unfortunately, due to the clonal variation in graft compatibility, not all the clones were included in every block when the experiment was conducted. Eleven clones (those with the largest number of grafts) were selected out of the 80 clones planted in the field. These clones were registered in the plus tree file of Pine Improvement Centre as 161, 182, 209, 218, 221, 222, 223, 225, 230, 236 and 237. Four blocks (replications) were randomly selected from total of 30.

Three lateral branches at the height of approximately 1.6 m from the ground level were selected from each graft. Due to wide spacing, all selected branches were free from competition. A thin pin was placed under the terminal bud of every branch as a datum point. Shoot length was measured during the period from 3 July 1983 to 11 March 1984 at

approximately bi-weekly (13 to 16 days) intervals. The length of each shoot was measured from the datum point to the shoot tip with an accuracy of one millimeter.

Shoot growth patterns were determined by deriving the relative shoot length, RSL, and the relative shoot growth rate, RGR (1/week), for each shoot. The latter was calculated according to the formula described by Causton and Venus (1981), Evans (1972), Hunt (1982) and Richards (1969):

$$RGR = (1/W) \times (dW/dT)$$
$$= (\ln W2 - \ln W1)/(T2 - T1),$$

where W is the shoot length (cm) and T is time (weeks).

Clonal differences in the pattern of shoot elongation were tested using a method developed by Estabrook et al. (1982), which is similar to the Kolmogorov-Smirnov Two-Sample Test (Sokal and Rohlf 1981). The method involves the observation of the maximum difference (D) in the relative shoot length (RSL) of the two clones. Then it is determined for what critical value (T) it is true that P(D>T) = .05. This is calculated using the formula:

$$P(D > 1.36 \times [(m+n)/(m \times n)]^{1/2}) = .05,$$

where m and n, respectively, are the shoot lengths of the two clones being compared.

3. Results

31. Shoot growth characteristics

Shoot elongation had already begun when the first measurements were made. The shoot length attained at the onset of the measuring period represented 21 per cent of the total annual shoot length.

The annual shoot growth pattern of *P. kesiya* exhibited two consecutive sigmoid growth curves (Fig. 1). They consisted of

two flushes of shoot elongation. In this paper, the flushes are named according to the local meteorological season during elongation, i.e. summer shoot (June to September) and winter shoot (November to February).

The timing of terminal bud formation and shoot elongation is shown in Fig. 2. Summer bud formation begins around the end of February and continues until the end of May

or the beginning of June. Summer shoot elongation follows immediately without bud dormancy and continues to the middle of September. While the summer shoot elongation is still taking place, the winter bud starts to form during the middle of August continuing towards the beginning of November. Immediately following the completion of winter bud formation, the winter shoot elongation commences and continues until the end of February or the beginning of March.

Summer and winter shoots can be distinguished from each other by the reproductive organs which always occur on winter shoots. The summer shoot is composed of a basal sterile scale zone at the proximal portion and a fertile scale zone with secondary needles in the axils. Above these two zones, there is a lateral bud and fertile scale zone which covers the next subsequent terminal bud at the most distal portion. The winter shoot can comprise six different appendage zones. The most proximal zone (1) bears basal sterile scales, and above it the male flower zone (2) is followed by the fertile scale zone (3) with a secondary needle bud in the axil. Distal to the fertile scale zone is the female flower zone (4), with the lateral long shoot zone (5) distal to it. The fertile scale zone (6) is the most distal one comprising a few fertile scales covering the next subsequent terminal bud. A winter shoot without reproductive structures resembles the summer shoot.

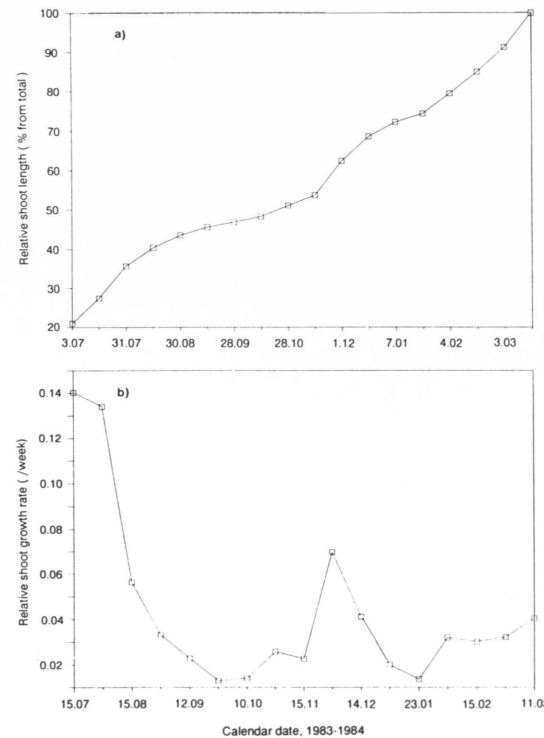The mean relative shoot growth rate increased rapidly during the early stage of the

Fig. 1. The development of a) mean relative shoot length (% of final length), b) the annual pattern of mean relative shoot growth rate (1/week).

shoot development. Terminal bud increased in size and length rapidly with more scales being added to along the axis. Relative shoot growth rate was at its maximum by the beginning of the summer shoot elongation (Fig. 1 b). It decreased during the shoot
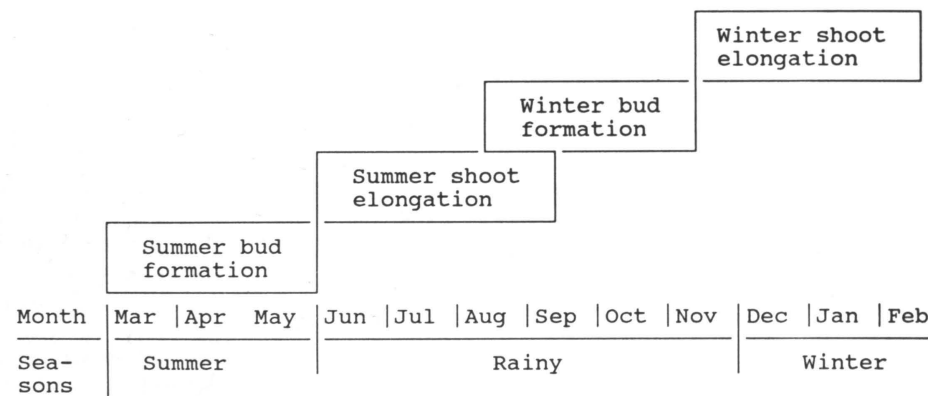

Fig. 2. The timing of terminal bud formation and shoot elongation of *Pinus kesiya*.

elongation and reached its minimum when the shoot attained its maximum length. During this stage, the only shoot activity was the expansion of microscopic organs which were already laid down on the bud and therefore relatively small shoot length was attained.

As an average, the summer shoot contributed 61 percent of the total annual

Fig. 3. Clonal variation of a) annual shoot length (cm) and b) the summer shoot percentage (%). The top and bottom of the rectangle represent the upper and lower quartiles, respectively, and the median is portrayed by a horizontal line within the rectangle.

shoot length, whilst the winter shoot contributed only 39 percent (Fig. 3 and Table 5). The difference between the relative length of summer and winter shoot was highly significant.

32. Clonal variation in shoot growth

The clonal variation in the shoot growth pattern was determined by studying the variation of timing of the shoot elongation with a modified Kolmogorov-Smirnov Two-Sample Test (Estabrook et al. 1982). The shoot growth pattern in Clone 237 was significantly different ($P < 0.05$) from that of Clones 209, 221, 222, 223 and 236, but not from the remaining ones (Fig. 4, Table 2). After applying the techniques suggested by Estabrook et al. (1982) for comparative studies, we observed that the Clone 237 had commenced its shoot elongation about two weeks earlier than those five clones mentioned above (Table 1). Moreover, its shoot was about 10 cm longer than that of those five clones.

The relative shoot growth rate for the overall period of observation (R-mean) as well as separate values for individual measurements (bi-weekly) were calculated for each individual clone (Fig. 5). Subsequently, an analysis of variance and a Duncan test (Table 3) revealed a significant difference in the relative shoot growth rate among the clones for the overall period of observation (R-mean). Clones that exhibited a late start of shoot elongation, 209, 221, 223 and 236, demonstrated higher overall relative growth rate than an early starter, Clone 237.

There is a large amount of clonal variation in the relative growth rate at individual measurement points within the growing period. However, significant differences in the relative growth rate between the clones were detected twice, during August 15 to 30 and January 7 to 23 (Table 3). Both of these significant differences were observed during the late part of shoot elongation, i.e the first being during the late period of summer shoot elongation, whereas the later being during the late period of winter shoot elongation.

An analysis of variance was carried out to determine the clonal variation in summer and winter shoot lengths in relation to the annual
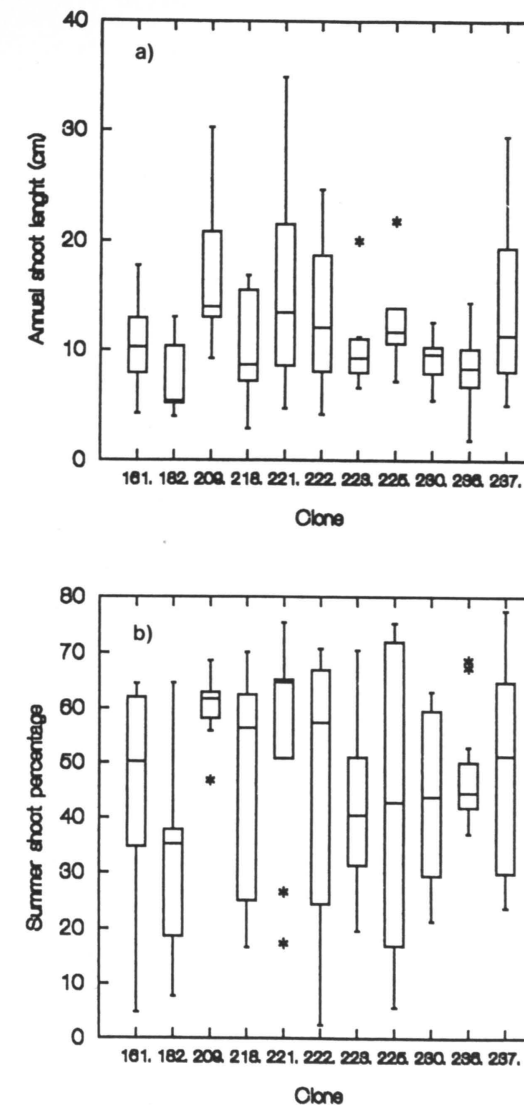
Winai Sirikul & Markku Kanninen

shoot length. No significant differences between the clones were detected either in relative summer or winter shoot lengths. The average clonal shoot length of summer and winter shoots in relation to the annual shoot length is shown in Table 5. However, there are significant differences between the clones in the length of annual shoot (Tables 4 and 5).

Table 1. Mean shoot growth and development of P. kesiya (eleven clones), during the period of 3 July 1983 to 23 January 1984.

Clone	161	182	209	218	221	222	223	225	230	236	237	AVG
Date			Terminal shoot length (cm)									
3.07	4.4	5.6	4.5	4.4	4.3	5.1	1.9	9.8	4.2	2.3	14.5	5.5
15.07	5.9	6.5	7.2	5.8	6.9	7.3	2.5	11.7	5.7	3.1	15.1	7.1
31.07	7.5	7.3	11.2	7.6	10.5	10.6	3.8	14.2	7.0	4.0	15.7	9.0
15.08	8.6	7.6	13.1	8.6	12.9	11.9	4.5	15.1	7.2	4.7	16.2	10.0
30.08	9.1	7.8	13.8	9.6	14.0	12.2	5.1	15.5	7.7	5.5	16.6	10.6
12.09	10.1	8.0	14.3	9.6	14.3	12.4	5.6	15.7	7.9	6.2	16.9	11.0
28.09	10.4	8.2	14.6	9.9	14.6	12.6	5.8	15.9	8.2	6.4	17.3	11.3
10.10	10.5	8.5	15.0	10.2	14.9	12.9	6.2	16.1	8.6	6.6	17.7	11.6
28.10	11.1	9.0	15.6	10.7	15.5	13.2	6.8	17.0	9.2	7.1	18.2	12.1
15.11	11.6	9.5	16.4	11.1	16.2	13.8	7.2	17.8	9.6	7.5	18.7	12.7
1.12	13.3	10.7	19.1	12.5	20.8	15.6	8.7	19.6	11.5	8.8	19.3	14.5
14.12	14.5	12.1	20.1	13.8	21.8	17.5	9.6	20.9	12.3	9.8	19.8	15.7
7.01	15.0	12.6	20.7	14.3	22.6	18.0	10.3	21.8	12.9	10.4	20.3	16.3
23.01	15.3	12.9	21.0	14.6	22.9	18.3	11.4	22.3	13.3	10.7	20.7	16.7

Table 2. Matrix of maximum difference in relative cumulative shoot length between clones and their critical values of eleven clones of *P. kesiya*.

					Maximum difference between clones						
Clone	161	182	209	218	221	222	223	225	230	236	237
161	X	0.15	0.10	0.13	0.20	0.07	0.30	0.10	0.17	0.30	0.36
182	0.44	X	0.14	0.08	0.18	0.09	0.22	0.12	0.09	0.19	0.29
209	0.40	0.42	X	0.07	0.11	0.05	0.23	0.18	0.11	0.23	0.44
218	0.43	0.45	0.41	X	0.09	0.06	0.18	0.12	0.07	0.18	0.38
221	0.38	0.40	0.36	0.39	X	0.12	0.13	0.22	0.09	0.14	0.48
222	0.41	0.43	0.39	0.42	0.37	X	0.24	0.13	0.11	0.24	0.39
223	0.44	0.46	0.42	0.45	0.41	0.44	X	0.28	0.15	0.06	0.50
225	0.39	0.41	0.37	0.40	0.35	0.38	0.42	X	0.15	0.28	0.26
230	0.43	0.45	0.41	0.44	0.40	0.42	0.46	0.41	X	0.15	0.39
236	0.44	0.46	0.42	0.45	0.40	0.43	0.47	0.41	0.45	X	0.48
237	0.40	0.43	0.38	0.42	0.37	0.39	0.43	0.38	0.42	0.43	X

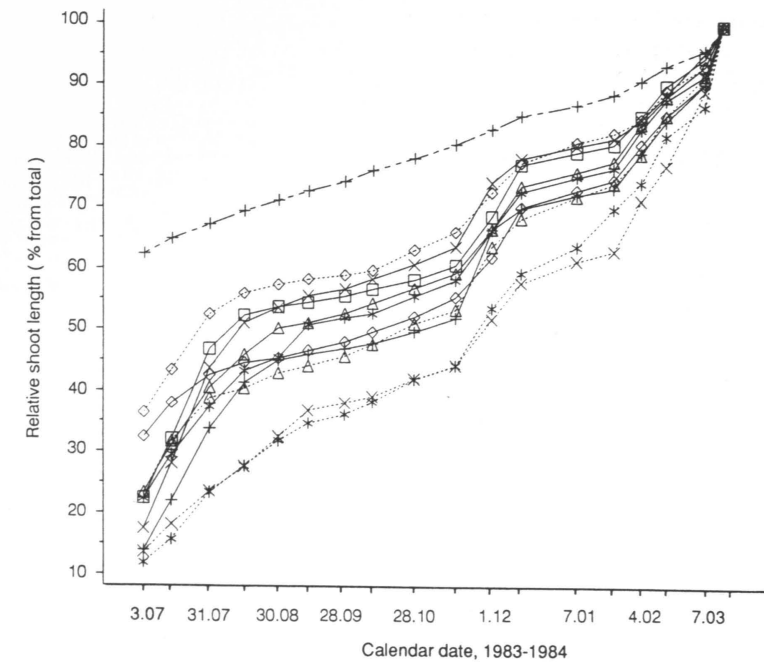$P(D > 1.36 \times [(m+n)/(m \times n)]^{1/2}) = 0.05$

Fig. 4. Clonal variation of the rate of shoot elongation (% of total). The clones are: (*—*) 161; (◇—◇) 182; (△—△) 209; (X—X) 218; (+—+) 221; (□—□) 222; (*-- *) 223; (◇ -- ◇) 225; (△ -- △) 230; (X -- X) 236; (+ -- +) 237.
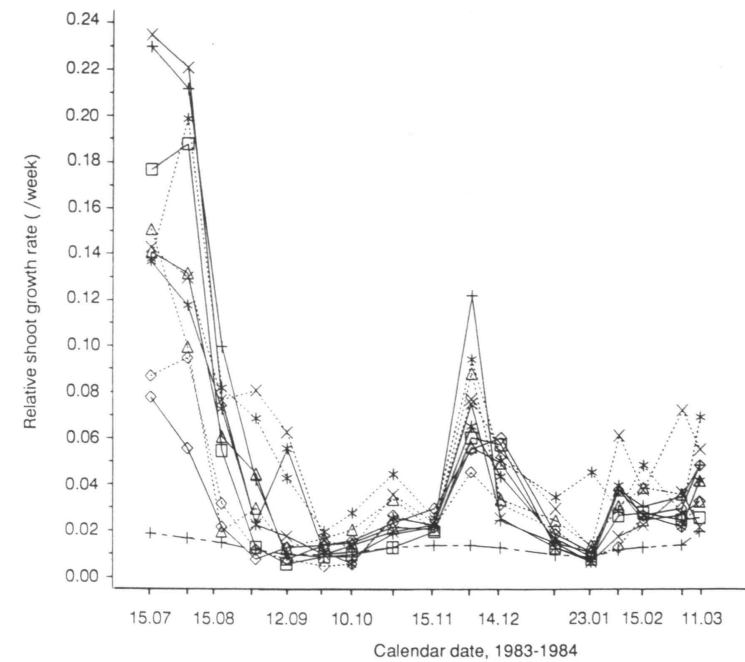

Fig. 5. Clonal variation of the relative shoot growth rate (1/week). The clones are: (*—*) 161; (◇—◇) 182; (△—△) 209; (X—X) 218; (+—+) 221; (□—□) 222; (*-- *) 223; (◇ -- ◇) 225; (△ -- △) 230; (X -- X) 236; (+ -- +) 237.

Table 3. Clonal variation in relative shoot growth rate (1/week). RMEAN is the relative shoot growth rate for overall annual shoot growth period (3 July 1983–23 January 1984). R6-8 is the relative shoot growth rate during the period August 15 to 30 1983. R24–26 is relative shoot growth rate during the period January 7 to 23 1984. Clones that are connected by the same vertical line are not significantly different.

RMEAN	Clone	R6-8	Clone	R24-26	Clone
0.066159	223	0.10669	223	0.049867	223
0.061594	236	0.09351	236	0.019387	236
0.061153	221	0.07096	237	0.014881	182
0.055273	209	0.05879	218	0.014469	237
0.050092	237	0.05458	221	0.013595	230
0.049663	161	0.04680	209	0.012751	218
0.049655	218	0.03334	230	0.012737	221
0.046549	222	0.01990	161	0.012500	161
0.045039	230	0.016570	222	0.011367	222
0.042409	182	0.012200	225	0.009694	225
0.034210	225	0.008220	182	0.009094	209

| P > 0.0009 | | P > 0.0185 | | P > 0.0019 | |

Table 4. Analysis of variance on terminal shoot length of *P. kesiya*. (Eleven clones).

Source	DF	MS	F	PR>F
Clone	10	182.974	3.33	0.001
Block	3	81.454	1.48	0.224
Rep.	2	22.889	0.42	0.66
Error	93	54.925		

Table 5. Annual total shoot length and the relative length of summer and winter shoots of *P. kesiya* (clonal mean). Clones linked with the same vertical line are not significantly different.

Clone	Annual shoot length (cm)	Relative shoot length (%)	
		Summer shoot	Winter shoot
221	22.94	59.76	40.24
225	22.31	70.23	29.77
209	21.03	68.72	31.28
237	18.60	65.30	34.70
222	18.38	60.12	39.88
161	15.38	60.37	39.63
218	14.64	64.88	35.12
230	13.37	60.99	39.01
182	12.90	58.01	41.99
223	11.40	50.82	49.18
236	10.74	59.72	40.28

| P > 0.001 | | P > 0.1529 | P > 0.2641 |

4. Discussion

The annual shoot of *P. kesiya* is composed of summer and winter shoots. The summer shoot bears only vegetative organs, whereas the winter shoot bears both vegetative and reproductive organ structures along the shoot axis (Pousujja and Kingmuangkau 1983, Sirikul and Luukkanen 1986).

In temperate and semi-temperate pine species, the spring shoot is derived from a terminal bud which has initiated in the autumn, overwintered, and elongates in the next spring. The summer shoot, in turn, is derived from a terminal bud, which initiates and elongates within the same growing season. In *P. kesiya* growing in Thailand, the summer shoot develops from a terminal bud initiated early in the summer (March) and elongates until the rainy season at the end of summer (September). For consistency with the definitions used for other pine species, we maintain the term summer shoot. Winter shoot, in turn, is initiated during the end of the rainy season (August) and it elongates during the winter (November to February) without a stage of dormancy. Thus, we call it the winter shoot.

Lanner (1976) pointed out that the cycle of shoot growth of different pine species is an adaptive response shown by the species to its environment. In our study, *P. kesiya* had two consecutive flushes of shoot formed by free growth during one year. Thus, the pattern of shoot growth of *P. kesiya* in Thailand resembles the *caribaea* pattern as classified by Lanner (1976), i.e. the shoot is formed by free growth and the elongation follows immediately after the bud formation without a rest.

However, *P. kesiya* forms two different kinds of shoots, winter and summer shoots. These could be distinguished from each other by the reproductive organs, which always occur on winter shoot. In *P. kesiya* summer shoot contributed longest portion (61%) of the total annual shoot length. These two features may be a demonstration of the effect of environmental conditions on shoot growth and development, i.e. low precipitation in combination with low temperatures during
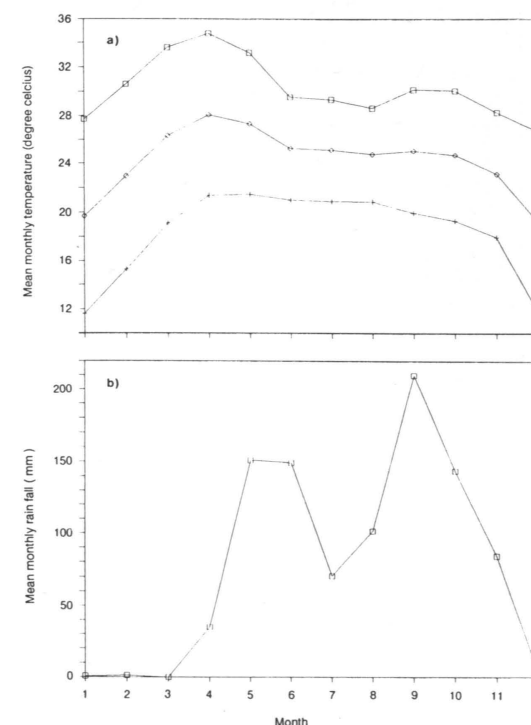

Fig. 6. Climatic conditions at Huey Bong Experimental Station (average of 1982-84). a) Mean (◇—◇), maximum (□—□) and minimum (+—+) monthly temperatures, and b) mean monthly precipitation.

the winter months cause both organological differentiation within the winter shoot and its low rate of elongation (Fig. 6). The two-week interval of the shoot length measurements used in this study is long and did not permit any detailed analysis of the shoot structure at different phases of growth (cf. Ford 1980).

There were significant differences in the pattern of shoot growth between the studied clones. Clone 237 commenced its shoot growth about two weeks earlier than Clones 209, 221, 222, 223, and 236, suggesting that these clones were at different stages of shoot development.

The relative shoot growth rate decreased in a simple manner with increasing shoot

length. Clonal differences in the overall relative shoot growth rate were significant (P < 0.05). Clone 223, which started to elongate about two weeks later than the Clone 237 had a significantly higher overall relative growth rate than the Clone 237 (Table 3). In addition, Clones 209, 221 and 236 also had higher overall relative growth rates than the Clone 237. This may reflect differences in the adaptation of these clones to different environmental conditions. High relative growth rate may facilitate rapid completion of the shoot elongation as a result of conservative growth strategy in adverse conditions. Clones which begin shoot elongation earlier but have low relative growth rate may be more flexible in adapting to a wider range of environments (Cannell et al. 1976).

Clonal differences in the relative growth rate of separate individual measurements during August 15 to 30 and January 7 to 23 (Fig. 4). These periods occur during the late stage of summer and winter shoot elongation, respectively. During the late part of summer shoot elongation, the relative shoot growth rates of slow starters, i.e. Clones 223 and 236 were higher, although not significantly, than that of an early starter – Clone 237 (Table 3). During winter shoot elongation the result was consistent with that of summer shoot, but the relative shoot growth rate of a late starter,

Clone 223 was significantly different from that of the early starters, e.g. the Clone 237. Moreover, Clones 209, 221, 223, and 236 were still elongating actively, whilst the Clone 237 had already completed its shoot elongation and was developing a new terminal bud.

Shoot growth of pines is composed of many stages of shoot development that are controlled by four regions of cell division and cell elongation (Cannell et al. 1976; Slee 1982). This study demonstrates the complexity of the shoot growth of *P. kesiya*. The result, although preliminary, can provide basic information for more detailed physiological and morphological studies. A microscopic study on the terminal shoot in its different stages of development would make possible to determine the condition of the bud in the field. The flowering habit could be better understood and subsequently, artificial floral induction could be carried out with more accuracy.

In addition, a closer analysis is required on the contribution of summer and winter shoots to total annual shoot length. The formation of summer and winter shoots obviously require different sets of environmental conditions. This may reflect an adaptation strategy that has evolved in response to particular environmental conditions characterizing the range of distribution of the studied species.

References

Cannell, M.G.R., Thompson, S. & Lines, R. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. In: Cannell, M.G.R. & Last, F.T. (eds.). Tree physiology and yield improvement. Academic Press, London. p. 173–206.

Causton, D.R. & Venus, J.C. 1981. The biometry of plant growth. Edward Arnold, London. 307 p.

Estabrook, G.F., Winsor, J.A., Stephenson, A.G. & Howe, H.F. 1982. When are two phenological patterns different? Bot.Gaz. 143(3):374–378.

Evans, G.C. 1972. The quantitative analysis of plant growth. studies in ecology. Vol.I. Blackwell Scientific Publications, Oxford - London - Edinburgh - Boston - Melbourne. 734 p.

Ford, E.D. 1980. Impact of environment on the shoot elongation of conifers: short term effects. In: Little, C.H.A. (ed.) Control of shoot growth in

trees. Maritimes Forest Research Centre, Fredricton, New Brunswick. p. 107–126.

Hunt, R. 1982. Plant growth curves. The functional approach to plant growth analysis. Edward Arnold, London. 248 p.

Lanner, R.M. 1976. Patterns of shoot development in Pinus and their relationship to growth potential. In: Cannell, M.G.R. & Last, F.T. (eds.).Tree physiology and yield improvement. Academic Press, London. p. 223–243.

— 1978. Development of the terminal bud and shoot of Slash pine saplings. Forest Science 24(2):167–179.

Pousujja, R., Granhof, J. & Willan, R.L. 1986. Pinus kesiya Royle ex. Gordon. DANIDA Forest Seed Centre. Seed Leaflet.5. 26 p.

— & Kingmuangkau, S. 1983. Flowering and seed formation of P. kesiya in northern Thailand. In:

Thai-Danish Pine Project 1969–1979. Vol.II. Research Papers, Royal Forest Department, Bangkok and DANIDA, Copenhagen. p 5A1–5A5.

Richards, F.J. 1969. The quantitative of growth. In: Steward, F.C. (ed.). Plant physiology – a treatise. Vol. VA. Analysis of growth: behavior of plants and their organs. Academic Press, New York – London. p. 3–76.

Sirikul, W. 1980. The grass tree stage of Pinus merkusii Jungh & de Vriese. M.Sc. Thesis. The Australian National University. 151 p.

— & Luukkanen, O. 1987. Promotion of flowering using exogenous plant hormones in tropical pines. For.Ecol.Manage. 19:155–161.

Slee, M.U. 1982. The importance of modelling the growth patterns of tropical species. In: Tropical forests – source of energy through optimisation & diversification. Faculty of Forestry, University Pertanian Malaysia. p. 311–316.

— & Shepherd, K.R. 1987. Summer shoot production and the change to the resting bud in

young seedling of Pinus elliottii. Aust. For. 41:37–48.

Srivastava, P.B.L. & Elias, A.B.H. 1982. Phenology of shoot development of Pinus caribaea var. hondurensis under Malaysian conditions. In: Tropical forests – source of energy through optimisation & diversification. Faculty of Forestry, University Pertanian Malaysia. p. 335–348.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. The principles and practice of statistics in biological research. Second edition. W.H.Freemand and Company, New York. 859 p.

Turnbull, J.W., Armitage, F.B.& Burley, J. 1980. Distribution and ecology of the Pinus kesiya complex. In: Armitage, F.B. & Burley, J. (eds.). Pinus kesiya Royle ex. Gordon. Tropical Forestry Papers 9. Unit of Tropical Silviculture, Commonwealth Forestry Institute, University of Oxford. p. 13–45.

Total of 18 references