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Adaptive growth strategy of Khasi pine (*Pinus kesiya* Royle ex Gordon)

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Abstract. Three year old open grown pine saplings were selected. Three whorls of shoots were begun in one year. The species thus exhibits a recurrent flushing pattern. Two orders of shoots were recognised on the main leader during the study period of one year. Shoots produced at lower canopy levels attained less extension growth and fewer and shorter needles compared to shoots at higher canopy levels. The growth characteristics of shoots indicated shade intolerant nature of the species. The fascicles of 3 flushes appearing at different times of the year had different patterns of fall and life expectancy. The adaptive strategy of the growth pattern with recurrent flushing and short longevity of the needles are discussed and related to faster growth rate of *Pinus kesiya* in an early successional environment.

Keywords. Tree growth strategy; tree architecture; succession; leaf dynamics.

1. Introduction

The pattern of shoot growth, and the seasonality in birth and death of leaves or needles are two important adaptive strategies which ultimately determine the overall architectural pattern of a tree canopy. The importance of canopy architectural design was emphasized by Madgwick (1970) for better understanding of the functioning of forest ecosystem. Kinnerson *et al* (1974) studied the canopy morphology of a 6 year old *Pinus taeda* L. in terms of foliage dynamics and observed that change in quantities of both old and new foliage has direct impact on the production potential of individual trees and of the entire forest. Pravdin (1969) emphasized that a more sensitive organ like the needle reacts rapidly to environmental conditions and affects the growth and development of other organs. Cannel *et al* (1976) emphasized that some factors regulating the onset of needle growth and cessation are adaptive in nature and needle lengths are often a heritable trait. Recently, Bazaz and Harper (1977) treated a plant as a population of leaves having a life cycle—birth, juvenile phase, reproduction (i.e. contributing resources to the birth of other leaves and ultimately to flowering and seed set) in *Linum usitatissimum*. Boojh and Ramakrishnan (1982) and Shukla and Ramakrishnan (1984) have analysed leaf population dynamics in tree species for a better estimate of canopy functioning.

Pinus kesiya, an early successional species, occurs at an altitude of 800–1900 m in subtropical and subtemperate zones in Meghalaya in north-eastern India. The present study deals with the growth pattern of this tree species as related to its successional status.

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2. Study area

The study site is located in Meghalaya at Mawlai, 15 km north of Shillong (25·47°N latitude and 91·56°E longitude) and 1250 m above sea level. The soil is a loam, reddish brown in colour and lateritic in origin. The pH ranges from 5·9–6·2. The climatic data for Shillong are presented in figure 1. Rainfall is heavy from May-September which constitutes the monsoon period. This period is characterized by comparatively maximum and minimum temperatures. The rest of the year (October–April) receives only 525 mm out of a total rainfall of 2149 mm. The winter season extends from November–February. March and early April represent a comparatively dry summer.

3. Materials and methods

Three year old open-grown pine saplings were selected in an even-aged pine plantation at Mawlai in Shillong at an altitude of 1250 m. The tree canopy was divided into 4 equal parts designated at A, B, C and D in that order from the apex down to the base of the canopy. Observations were made on shoots which appeared in 3 successive flushes in 1977 and in one flush in 1978. The 4 flushes were designated F_1 77, F_2 77, F_3 77 and F_1 78. The following characters were studied: shoot length, number of fascicles/shoot and mature fascicle lengths. Mature shoot length was measured to nearest 1 mm accuracy. The number of fascicles on each shoot was counted through a non-destructive method of estimating fascicle number by developing a regression model between fascicle number and shoot length. Ten mature fascicles were selected randomly from each shoot and their lengths measured to nearest 1 mm.

For the estimation of fascicle area (A) and fascicle dry weight (W), two non-destructive models were used (Das *et al* 1982). Both these models are based on fascicle length (L) as an independent parameter. The equations are written as follows: $A = a + bL$ ($a = -3{\cdot}941, b = 1{\cdot}306$) ($r = 0{\cdot}98, n = 69$) $W = aL^b$ ($a = 0{\cdot}419, b = 1{\cdot}703$) ($r = 0{\cdot}99$, $n = 69$).

The fall of fascicles from shoots was recorded at monthly (30 days) intervals. Fascicles produced during a particular flush were considered as one cohort. Life tables were

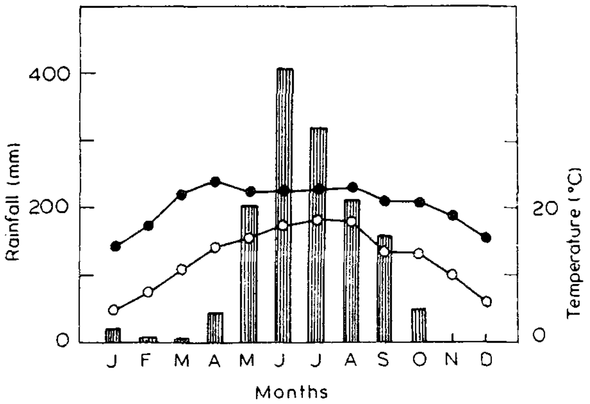

Figure 1. Climate of Shillong (1977) (●), Maximum temperature; (○) minimum temperature; ▥, rainfall.

determined for fascicles of each cohort and from them life expectancy (e_x^0) values were calculated.

To study the effect of light on the growth of shoots, two sets of 15 shoots each were selected. Set I shoots were selected from exposed conditions and designated as 'sun shoots' and set II shoots were from partial shade and was referred to as 'shade shoots'. Shoot length was measured at weekly intervals through the one year period. Three fascicles were randomly selected on each shoot and their length measured also at weekly intervals. Thus lengths of 45 fascicles were measured from each set of shoots. Fascicle of similar lengths ranging from 5–15 cm were selected from sun and shade conditions and oven dried at 80°C for 24 hr for determining the dry weight.

4. Results

The pattern of growth exhibited by the 3 year old pine sapling is shown in figure 2. The annual growth in terms of elongation of the leader or of branch apices, commonly

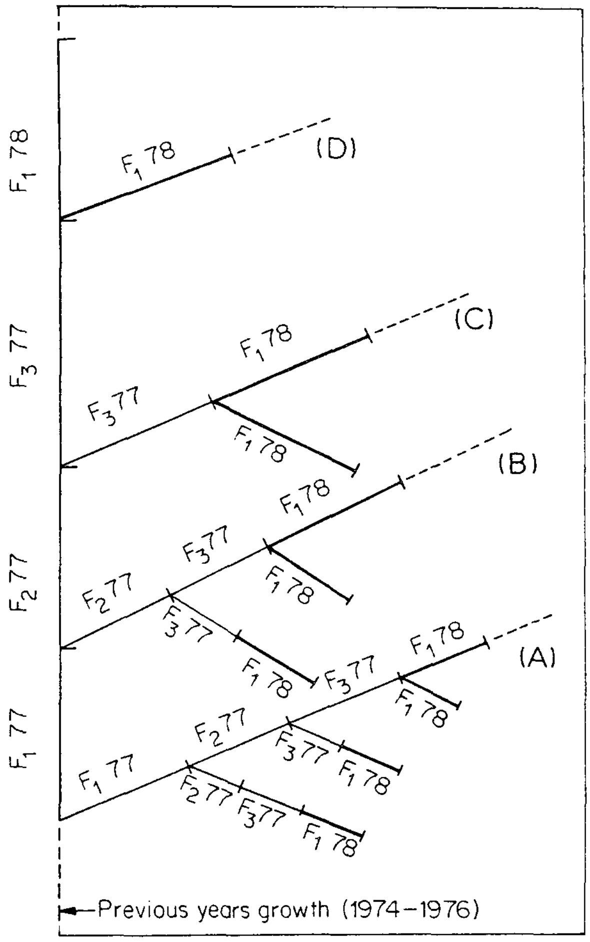

Figure 2. Pattern of shoot growth in a 3-year old *P. kesiya* F_1, F_2, F_3 77 represent 3 flushes of the year 1977 F_1 78 represent first flush of the year 1978.

consists of 3 growth flushes with new apical buds being formed between two flushes. Three whorls of shoots were thus begun in one year: one each in February, June and October. The species thus exhibits recurrent flushing behaviour. Two orders of shoots are recognized from the main leader of the tree: I order shoots are those which arise from the lateral buds on the main axis and its subsequent extensions, II order shoots arise directly from the I order shoots.

4.1 *Extension growth*

Extension growth of main leader during F_1, F_2 and F_3 of 1977 was 27·2, 29·0 and 41·0 cm, respectively. Thus the 3 flushes together contributed a total of 97·2 cm of shoot extension. First order shoots were longer compared to the II order shoots. Shoot extension for the I order shoots of F_1 78 at 4 canopy positions (A, B, C and D) was different, that at position D being longest. Considering shoots produced during the 3 flushes F_1, F_2 and F_3 in a year at canopy position A, the shoot extension attained by F_1 was greater compared to F_2 and F_3 (table 2). The extension in the II order shoots increased from positions A–C (table 3).

4.2 *Fascicle characters*

Fascicle length, fascicle area and fascicle weight on main leader varied considerably and decreased from F_1–F_3. Fascicle number, however, did not show any particular pattern (table 1). Fascicle length, fascicle number/shoot, fascicle area and fascicle weight for I order shoots also varied for the different flushes. Thus fascicle length, area and weight decreased from F_1–F_3 in a given year at canopy position A. Fascicle number of F_1 77 was much higher than that for F_2 or F_3. In a given flush such as F_1 78, the fascicle length, number/shoot, area and weight increased from canopy position A–D (table 2). A similar pattern was also observed on II order shoots (table 3).

Different flushes on the main leader had more fascicle density compared to I order and II order shoots. The fascicle density in a given flush such as F_1 78 was higher at canopy positions A and B than at higher canopy levels (i.e. C and D) (tables 1, 2 and 3).

The fascicle number (y) was linearly related to shoot length (x) (figure 3).

4.3 *Sun and shade strategy*

The rates of elongation of the shoot and fascicles that were exposed to light were faster than those from partial shade (figure 4). The ultimate values obtained at the end of the

Table 1. Shoot and fascicle characteristics of main leader of *P. kesiya*.

Characters	$F_1$77	$F_2$77	$F_3$77	$F_1$78
Shoot extension (cm)	27·2	29·0	41·0	39·0
Fascicle length (cm)	22·54	17·98	12·09	17·22
Fascicle number/shoot	259	178	251	260
Fascicle/cm shoot	9·52	6·14	6·12	6·66
Fascicle surface area/shoot (cm^2)	25·08	19·23	11·70	18·41
Fascicle weight/shoot (mg)	76·02	56·99	29·21	53·71

Table 2. Shoot and fascicle characteristics (mean with standard error values) of I order shoots of *P. kesiya* at 4 canopy positions (A–D).

Characters and flushing numbers		A	B	C	D
Shoot extension (cm)	$F_1$78	14·00 ± 5·36	25·42 ± 1·51	27·75 ± 4·59	39·50 ± 3·97
	$F_3$77	18·20 ± 5·96	18·42 ± 6·13	27·33 ± 4·19	—
	$F_2$77	13·15 ± 7·97	20·95 ± 2·37	—	—
	$F_1$77	24·56 ± 6·46	—	—	—
Fascicle length (cm)	$F_1$78	12·33 ± 0·15	14·73 ± 0·04	15·65 ± 0·01	17·61 ± 0·05
	$F_3$77	9·65 ± 0·04	13·32 ± 0·08	14·72 ± 0·06	—
	$F_2$77	14·90 ± 0·12	17·27 ± 0·07	—	—
	$F_1$77	18·55 ± 0·04	—	—	—
Fascicle number/ shoot	$F_1$78	97·33 ± 47·50	170·50 ± 12·66	116·00 ± 16·77	163·00 ± 15·87
	$F_3$77	83·40 ± 43·99	84·50 ± 38·66	93·00 ± 30·80	—
	$F_2$77	69·00 ± 41·37	78·25 ± 11·78	—	—
	$F_1$77	108·60 ± 57·46	—	—	—
Fascicle/cm shoot	$F_1$78	6·75 ± 1·59	6·70 ± 0·03	4·06 ± 0·08	4·17 ± 0·72
	$F_3$77	5·03 ± 0·81	4·63 ± 1·36	3·33 ± 0·06	—
	$F_2$77	5·38 ± 0·87	3·73 ± 0·32	—	—
	$F_1$77	4·15 ± 1·40	—	—	—
Fascicle area (cm^2)	$F_1$78	12·00 ± 0·29	15·06 ± 0·28	16·68 ± 0·24	18·86 ± 0·31
	$F_3$77	8·77 ± 0·18	13·30 ± 0·24	15·12 ± 0·36	—
	$F_2$77	15·35 ± 0·32	18·37 ± 0·41	—	—
	$F_1$77	22·07 ± 0·25	—	—	—
Fascicle weight (mg)	$F_1$78	30·52 ± 0·95	41·15 ± 0·98	46·75 ± 0·88	55·79 ± 1·30
	$F_3$77	20·52 ± 0·52	36·32 ± 0·23	41·27 ± 1·04	—
	$F_2$77	42·68 ± 1·17	54·07 ± 1·19	—	—
	$F_1$77	61·20 ± 1·09	—	—	—

observations period were also significantly different from each other. The shoot extension growth in a flush of March was completed after 8 weeks whereas needle extension growth was continued upto 13 weeks. The fascicles from exposed situation were longer and heavier than those grown in partial shade. This difference was exaggerated in the case of longer needles (figure 5)

4.4 *Fascicle survivorship and fall pattern*

Fascicles of the 3 flushes appearing at different times in a year had different patterns of fall and life expectancy. The fascicles of F_1 which appeared in February fell off during the subsequent October–March period, the fascicles of F_2 appearing in June were lost in the following January–April period and those of F_3 appearing in October were lost during subsequent March–October. Thus the needle fall of F_1 started after a period of 8 months, that of F_2 after 7 months and that of F_3 after 5 months. Although the fascicles of F_3 started falling earlier than those of the other flushes, the fall of F_3 fascicles continued for a longer period (210 days) compared to fascicles of F_1 (150 days) and F_2

Table 3. Shoot and fascicle characteristics (mean with standard error values) of II order shoots of *P. kesiya* at 3 canopy positions (A-C).

Characters and flushing number		A	B	C
Shoot extension (cm)	$F_1$78	10·07 ± 4·52	14·37 ± 4·74	26·12 ± 9·39
	$F_3$77	11·61 ± 4·29	12·02 ± 2·02	—
	$F_2$77	10·17 ± 3·64	—	—
Fascicle length (cm)	$F_1$78	11·33 ± 0·01	14·63 ± 0·02	16·11 ± 0·02
	$F_3$77	12·49 ± 0·04	6·34 ± 0·02	—
	$F_2$77	11·61 ± 0·02	—	—
Fascicle number/shoot	$F_1$78	50·26 ± 28·19	55·36 ± 19·82	115·40 ± 19·19
	$F_3$77	50·50 ± 20·06	47·20 ± 14·96	—
	$F_2$77	48·43 ± 23·40	—	—
Fascicles/cm	$F_1$78	4·08 ± 1·50	3·82 ± 0·74	4·15 ± 0·56
	$F_3$77	4·30 ± 0·58	3·87 ± 0·91	—
	$F_2$77	4·71 ± 0·76	—	—
Fascicle area (cm^2)	$F_1$78	10·74 ± 0·24	14·99 ± 0·17	16·91 ± 0·25
	$F_3$77	10·07 ± 0·28	4·23 ± 0·24	—
	$F_2$77	12·35 ± 0·23	—	—
Fascicle weight (mg)	$F_1$78	26·75 ± 0·45	41·44 ± 0·65	48·01 ± 0·98
	$F_3$77	25·51 ± 0·65	10·36 ± 0·36	—
	$F_2$77	33·98 ± 0·74	—	—

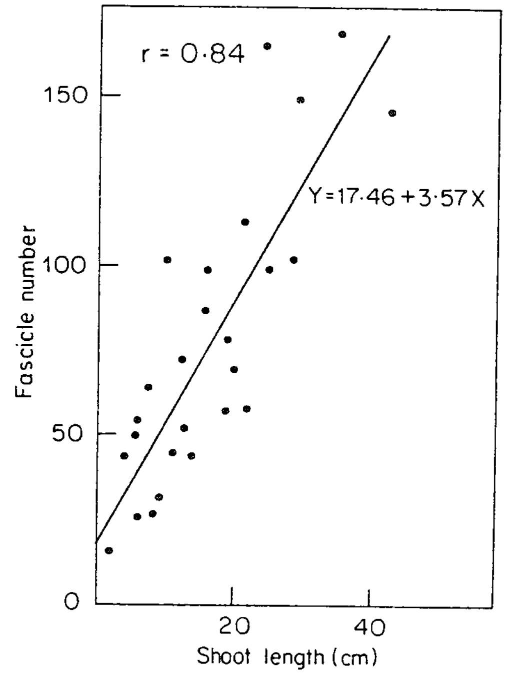

Figure 3. Regression analysis between fascicle number and shoot length of *P. kesiya*.

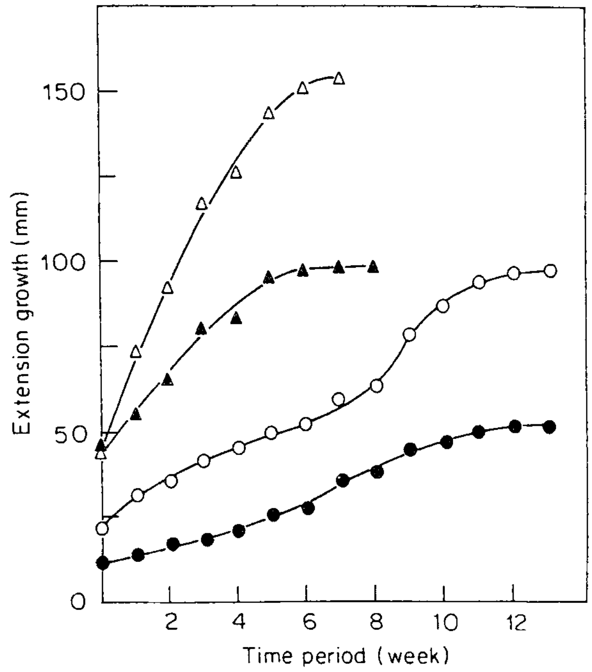

Figure 4. Cumulative extension growth of shoot and needle of *P. kesiya*. (△), Sun shoot; (▲), shade shoot; (○), Sun needle; (●), shade needle.

(90 days) flushes. The life expectancy (e_x^0) values calculated for different flushes (each flush representing one cohort) were 314, 245 and 275 days for flushes F_1, F_2 and F_3 respectively (table 4).

Figure 6 shows the seasonal pattern of fascicle fall of 3 flushes. Maximum fall of needles occurred during February–April (41 % of the total fascicle fall). The fall during the month of March was derived from all the 3 flushes of a given year. From October–December the fall was due only to F_1 fascicles whereas from May–October, the fall was due only to F_3. At other times two flushes contributed towards fascicle fall.

5. Discussion

P. kesiya is an early successional tree species showing recurrent flushing with 3 flushes occurring in a year. This basic growth pattern may be modified to some extent depending upon age and branch position on the tree. Thus, the second and third flushes were absent in some of the lower branches, which may be related to shading. Also two orders of shoots reported in the present study is not an universal phenomenon as shoots of higher orders are seen with increasing age of the plant.

Remarkable differences were seen in the growth characteristics of shoots at 4 canopy positions (A–D). The shoots produced at lower canopy level being comparatively less exposed, had less extension growth and were with fewer and shorter needles as compared to shoots at more exposed higher canopy positions. Similar observations were also made by Harms (1971) and according to him, the leaf growth differences may be brought about by differences in exposure to sun light, variations in nutrient supplies

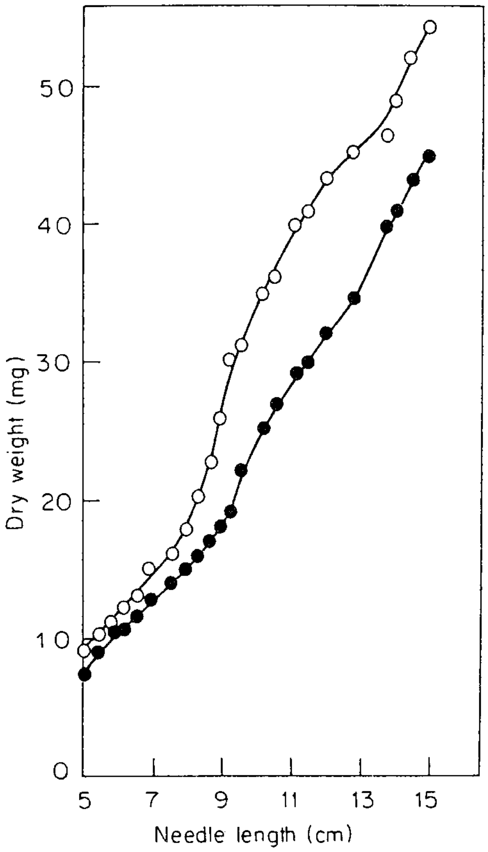

Figure 5. Needle length of *P. kesiya* related to weight in sun and shade. (○), Sun needle; (●), shade needle.

and other factors. In an early successional tulip poplar (*Liriodendron tulipifera* L.), Ramakrishnan P S, Bormann F H and Siccama T (unpublished results) also noted reduced size of twigs and leaves towards the base of the canopy and according to them, this is a strategy for efficient display of leaf tissue towards the light and a mechanism that leads to self pruning of lower branches.

Kondratev (1961) determined the size and weight of pine needles as related to crown formation and found that needle length decreased gradually with increase in age of the whorl from top of the tree downward, an observation also made during the present study. Apart from age and nutrition, light availability may also play an important role.

Remarkable decrease in fascicle length, area and weight were observed from first to third flush. These decreases could be due to low temperature available at the time of growth of the third flush during October. It may also be due to limitation of current photosynthate. While non-recurrently growing pine species use the previous years photosynthate (Kozlowski 1971), the recurrently flushing species like *P. kesiya* may use current photosynthate for their growth as shown by McGregor and Kramer (1963) for *P. taeda*. Thus the important factors that can curtail needle elongation are poor sources of carbohydrates (Gordon and Larson 1968).

Table 4. Number of fascicles surviving (l_x) at different time intervals and life expectancy (e_x^0) of fascicles of 3 flushes (cohorts) of *P. kesiya*.

	l_x	l_x	l_x
	F_1	F_2	F_3
Days	802	1202	2155
0	802	1202	2155
30	802	1202	2155
60	802	1202	2155
90	802	1202	2155
120	802	1202	2155
150	802	1202	2000 (92·80)
180	802	1202	1820 (84·45)
210	802	1100 (91·51)	1668 (77·40)
240	788 (98·25)	620 (51·58)	1600 (74·24)
270	609 (75·93)	202 (16·80)	1200 (55·68)
300	422 (52·61)	101 (8·40)	980 (45·47)
330	301 (37.53)	0	490 (22·73)
360	181 (22·56)	0	310 (14·38)
390	78 (9·72)	0	0
420	0	0	0
Life expectancy (e_x^0) (days)	314	245	275

Figures in parentheses represent per cent values.

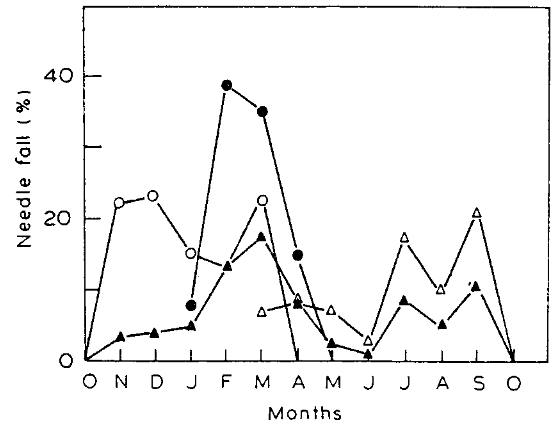

Figure 6. Pattern of fall of needles of the 3 flushes during the year. (▲), Total (including 3 flushes); (○), F_1, (●), F_2; (△), F_3.

The differences in the growth characteristics of shoots and needles under sun and shade conditions indicated clearly the shade intolerant nature of this species. The decrease in needle dry weight in shaded shoots as reported here has also been noted in *Picea sitchensis* (Lewan Dowska and Jarvis 1977). It may be assumed that the length of the live crown is maintained due to shading of the bottom branches so that more nutrients are allocated for rapid height growth. Also, the pattern of growth with 3 flushes in a year may be a strategy to obtain rapid height growth, enabling this species to fulfil its ecological role as a pioneer species. Moreover, the production of needles in 3 flushes in a year results in prolonged photosynthetic activity which in turn contribute towards high rate of assimilation per unit of foliage (4·02 kg/kg leaf/year). This, alongwith typical canopy architecture favouring efficient utilization of light energy results in high net primary productivity (20 mt $ha^{-1} yr^{-1}$) of this tree species (Das 1981).

Data on needle longevity as such are very limited. *P. kesiya* needles showed a much shorter life expectancy compared to the other available published and unpublished data on needle longevity (table 5). The shorter longevity of the needles may be viewed as a strategy to adjust to the existing climate. Gettlieb (1968) mentioned that a plant is at the mercy of a selective environment which favours the modifications best suited for survival in that environment. The comparatively drier period prevailing during February, March and April with very little moisture in the soil may be the cause for shedding of needles at this time to avoid transpiration loss. It seems probable that the longevity of needles originating during the first flush in February is greater due to tolerance to drought at this time of its initial growth phase and the more favourable moisture conditions during the subsequent monsoon? The third flush of leaves though drought tolerant do not obtain a favourable growth period. However, needles arising during the wet period of June as the second flush probably are not drought tolerant resulting in their shorter life expectancy during the subsequent dry winter. In other words, needles arising during drier periods of the year may be more drought tolerant than those arising during the wet season. This, alongwith favourable growing season may, therefore account for the life expectancy decrease from I–III flush. This explanation, however, needs to be tested. According to Wareing and Phillips (1978), in some species competition between old and new leaves may also be a factor for the senescence of the older leaves. Such a competition among successive flushes of needles may also account for the rapid death of needles in *P. kesiya*.

The comparatively short life expectancy of needles of *P. kesiya* along with recurrent flushing pattern may be an additional adaptive strategy for the colonization of this

Table 5. Information on the longevity of needles of different pine species.

Species	Observation	Reference
P. radiata D. Don	Needles retained up to 5 years	Madgwick *et al* (1977)
P. sylvestris L.	Needles retained for 3 years	Ovington (1957)
P. nigra var. maritima (Ait.) Melville	One flush of needles per year; no mortality in the first 2 years; needles may be retained upto 6 years	Maillette (1982)
**P. taeda* L.	Needles retained for 2 years; 2 flushes per year; sometimes 3 flushes during wet years	C W Ralston
P. kesiya Royle ex Gordon	Needles retained for less than a year; 3 flushes per year	Present study

*Personal communication.

species as a pioneer in nutrient poor substrate as this ensures rapid turnover of nutrients through litter. Relatively shorter life span and faster turnover rate of leaf population in early successional broad-leaved species are now well established (Boojh and Ramakrishnan 1982; Shukla and Ramakrishnan 1984). However, slower release of nutrients through slow decomposition of pine litter may avoid heavy losses from the soil through leaching or surface runoff. More rapid and heavier needle fall during the drier season may also be an adaptation towards water economy of the plant at this time of the year. All these characteristics alongwith the fast growth rate and productivity of *P. kesiya* under open conditions are strategies for its success as an early successional tree in a poor soil.

Acknowledgements

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