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Leaf Dynamics of Two Bamboo Species (*Neohouzeua dulloa* A. Camus and *Dendrocalamus hamiltonii* Nees and Arn.) in Successional Environments in North-East India

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Neohouzeua dulloa A. Camus and *Dendrocalamus hamiltonii* Nees and Arn. are light demanding early successional species, the former being more relatively shade tolerant. Based on leafing characteristics *N. dulloa* belongs to 'periodic growth—evergreen type' whereas *D. hamiltonii* belongs to 'periodic growth—deciduous type'. The deciduousness of *D. hamiltonii* is compensated by faster production of a larger total leaf area in the early part of the growing season, whereas in *N. dulloa* leaf production is more extended. Leaf production reached a maximum in a 15 yr old fallow, in the two species.

Key Words: Bamboos, Leaf area and longevity, Leaf population flux

Introduction

The total leaf area available for photosynthesis on a tree is primarily determined by the patterns of production and fall, and the longevity of leaves (Watson 1956, Newhouse & Madgwick 1986). The leaf with its axillary bud, is the smallest module of organized structure in higher plants, and leaves have many of the properties associated with members of a population, such as abscission rates (Kozlowski 1973, Addicott 1978), longevity (Gill & Tomlinson 1971) and age structure (Kinerson et al. 1974). Little is known on the leaf dynamics of tropical tree species (Boojh & Ramakrishnan 1982, Shukla & Ramakrishnan 1984) and information on tree grasses (bamboos), that colonize disturbed sites, is even less.

An understanding of the leafing characteristics of bamboo is important not only for its own sake but also for their effective management and utilization. The present study, therefore, deals with the leaf population dynamics of two bamboo species, *Dendrocalamus hamiltonii* Nees and Arn. and *Neohouzeua dulloa* A. Camus, of early successional environments at lower elevations of north-east India. The former is less shade tolerant and restricted to fallows upto 25 yrs, whereas the latter being more plastic and more shade tolernt, could occur upto 60 yrs of fallow regrowth, after slash and burn agriculture (Ramakrishnan et al. 1981, Toky & Ramakrishnan 1983).

Study Area and Climate

The study was done at Lailad (200 m altitude), situated in the Khasi Hills of Meghalaya, about 75 km north of Shillong (26°N and 91°5′E). The pre-cambrian rocks are represented by gneiss, schists and granites. The soil is a red sandy loam of laterite origin, with *p*H 5–7. The angle of the slope generally ranged from 20° to 40°.

The climate has three distinct seasons: (i) a brief summer extending from mid-February to May, (ii) a rainy season from May to September, and (iii) a mild and relatively dry winter from October to mid-February. The average maximum temperature during the summer period was 30.7°C and the average minimum was 10.8°C. 73% of the total annual rainfall of 1800 mm occurred during the rainy season. The average maximum temperature during the rainy season was 31.4°C and the average minimum was 24.1°C, whilst that for winter months were 26.5°C and 14.4°C respectively.

Methods of Study

One year old culms of *D. hamiltonii* and current year's and a year old culms of *N. dulloa* were identified in 5, 15, 25 and 60 yr old secondary successional fallows (*D. hamiltonii* was not considered in a 60 yr old fallow) developed after slash and burn agriculture (jhum) in north-east India. Identified culms were protected from herbivory by fencing. All observations are based on five replicates.

All existing leaves of *N. dulloa* and the newly-formed ones of both species were tagged with small and light weight colour-coded aluminium tags. Detailed observations on leaf area, leaf emergence and fall were made individually on those of the first to fifth-order branches, at monthly intervals over a one year period starting from April, 1983. Leaf area was calculated on the basis of 150 leaves harvested separately from other ramets of each fallow, using regression equations developed relating blade length and breadth and leaf area.

Result and Discussion

Leafing Pattern

Both species of bamboo bear leaves on a sympodial leafy shoot continuation of extension growth of the main axis by a lateral meristem after abortion of the terminal meristem shoot produced at the tip of each of the aerial branch orders, except the zero-order branch. These sympodial leafy shoots of *Neohouzeua dulloa* are produced on the sylleptically (the lateral bud produces branch system during the current year of its formation without any dormancy) produced branch system and are subsequently replaced with new sympodial leafy shoots, starting from the second year of the production of the culm. In *Dendrocalamus hamiltonii,* on the other hand, leafy shoots are produced on the proleptically (by the activation and growth of the lateral dormant buds laid during the previous year's growth) produced branch system and are subsequently replaced (after a deciduous naked phase of one to two months) with new sympodial leafy shoots starting from the third year of the production of the culm. In *D. hamiltonii,* the leafy shoot for the first time is produced in April–June itself but in *N. dulloa* it happens in August–September (table 1). This delay in *N. dulloa* is because, the leafy shoots appear only after the production of the sylleptic branch system is completed. Therefore, leaf production on the currently produced ramets of *N. dulloa* occurs only for 245 days. In subsequent years, however, leaf production in this species is continuous throughout the year. The replacement of the leafy shoots of both the species occur in April–June.

There is much clump to clump variation in the time of leafy shoot initiation and the termination time for leaf emergence, which may depart upto about one to two weeks from the mean. More than one factor may be involved in individuals of a given species leafing out at different times at the same site. In clonal populations of herbaceous species, Brown et al. (1985) have been implicated ramet size with phenological behaviour. This is an aspect which needs further study for bamboos.

Table 1 *Important leafing characteristics in current year's and last year's culms of bamboos in successional fallows. (values within parentheses are for last year's culm)*

Parameters	*N. dulloa*	*D. hamiltonii*
(a) Leafy shoot: initiation	August-September	April-June
Exchange/replacement	April-June	April-June
(b) Termination of leaf emergence	Continuous	October-November
(c) Leaf production period (days)	245 (365)	— (180–210)
(d) Leafing behaviour	Evergreen	Deciduous

Leaf Production and Fall

The early successional tree species have been shown to have unrestricted leaf production occurring throughout the growing season (Boojh & Ramakrishnan 1982, Shukla & Ramakrishnan 1984) and this rather than the efficiency of energy conversion is considered to be important for faster growth of these species and for exploiting high light environment (Coombe & Hadfield 1962). However, the two bamboo species follow two distinct strategies for exploiting high light regimes. *N. dulloa* has unrestricted leaf production (figure 1), though the total leaf area attained is lesser than in *D. hamiltonii.* The latter has restricted leaf production period confined to just six months in a year with a faster rate of production so that the area attained is many-fold than that of *N. dulloa.* Leaf production in *D. hamiltonii* peaked in June–July. On the current year's branch system of *N. dulloa,* peaking occurred in September–October, whereas on the last year's branch system peaking was in June-July itself in all the fallows. This is because leaf production in the former situation does not start until extension of the shoot is completed whereas in the latter situation leaf initiation starts earlier on the pre-formed shoot system. However, in a 15-yr-old fallow peaking occurred in September. This may be related to reduced light availability in older fallows since these bamboo species are light demanders that are eliminated during succession because of shading (Toky & Ramakrishnan 1983).

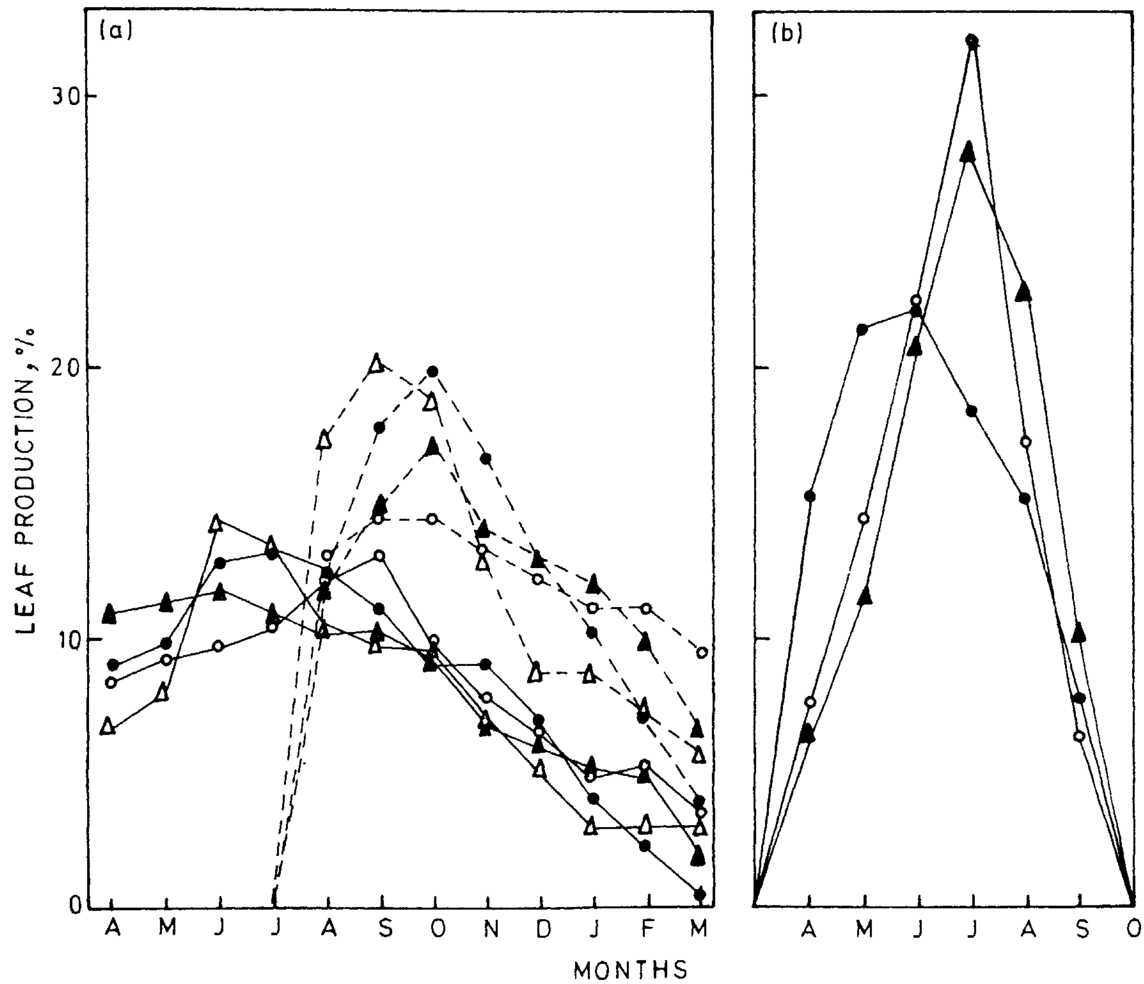


Figure 1 Variation in monthly leaf production (%) in current year's and last year's culms of *N. dulloa* (a) and last year's culms of *D. hamiltonii* (b) in successional fallows. Current year's culm, (---); Last year's culm, (———); Closed circle, 5yr; Open circle, 15yr; Closed triangle, 25yr and Open triangle, 60yr old fallows

Annual leaf area (cumulative total leaf area produced in a year) achieved in *N. dulloa* was generally higher on the last year's culm compared to the current year's culm (table 2). Leaf area was maximum in a 15-yr-old fallow for both species. The monthly pattern of leaf area changes in a given species in the different fallows are similar except the differences in the leaf area produced which was maximal in 15-yr-old fallow (figure 2). This is related to the peaking in the vigour of the culm largely related to increased biomass of the underground rhizomatous storage system with fallow age. Besides, *N. dulloa* growing in a 15-yr-old fallow also had maximum leaf sustained on the branch system over a longer time period (with no clear-cut peaking), unlike in the other fallows. The sharp increase in the leaf area in the second year's branch system of *N. dulloa* in a 15-yr-old fallow is because of an additional fifth-order leaf bearing branch system produced here unlike in the other fallows where branch production is upto the fourth-order only.

Leaf longevity pattern in the two species of different fallows are not different and therefore that for a 5-yr-old fallow alone is shown here (figure 3). The leaves on current year's culm of *N. dulloa* produced during November–December had maximum longevity whereas the last year's culm had maximum longevity for the leaves produced in August. The longevity of the leaves of *D. hamiltonii* declined gradually starting from April to September.

Leaf fall pattern did not differ in the different fallows of the two species and therefore the fall pattern for the last year's culm of the two species in a 15-yr-old fallow alone is given (figure 4). Leaf fall in *N. dulloa* was continuous throughout the year and peaked in November–December. On the other hand, leaf fall in *D. hamiltonii* starting from April is completed by January–February, with a subsequent naked phase. Unlike in the tree species of this area where leaf fall peaked during March-April (Shukla & Ramakrishnan 1984), maximum leaf fall in the two bamboo species occurred during November-January. Lower temperature conditions of the winter months and dryness of the season (Longman & Jenik 1974) may be contributing factors for greater leaf fall during the winter months.

Leaf Population Flux

Leaf production and loss was maximum in a 15-yr-old fallow for *N. dulloa* (table 3). In a 5-and 60-yr-old fallows there was a net negative change in the leaf population of the last year's culm of *N. dulloa*, whereas in all other cases there was a net positive change, at the end of one year period of observation. Rate of change for leaves on the last year's culm of *N. dulloa* reached a maximum in a 25-yr-old fallow. The leaf population on the last year's culm had more

Table 2 *Annual leaf area production* ($\times 10^3$ cm^2) *of bamboos (mean ± SE) in successional fallows*

Bamboo species	Fallow age (years) 5	15	25	60
N. dulloa				
Current year's culm	5.4 ±0.5	17.7 ±1.7	7.1 ±0.6	2.4 ±0.2
Last year's culm	12.6 ±1.0	75.7 ±4.3	16.5 ±1.3	4.9 ±0.5
D. hamiltonii				
Last year's culm	108.5 ±5.4	998.8 ±30.0	862.6 ±25.7	—

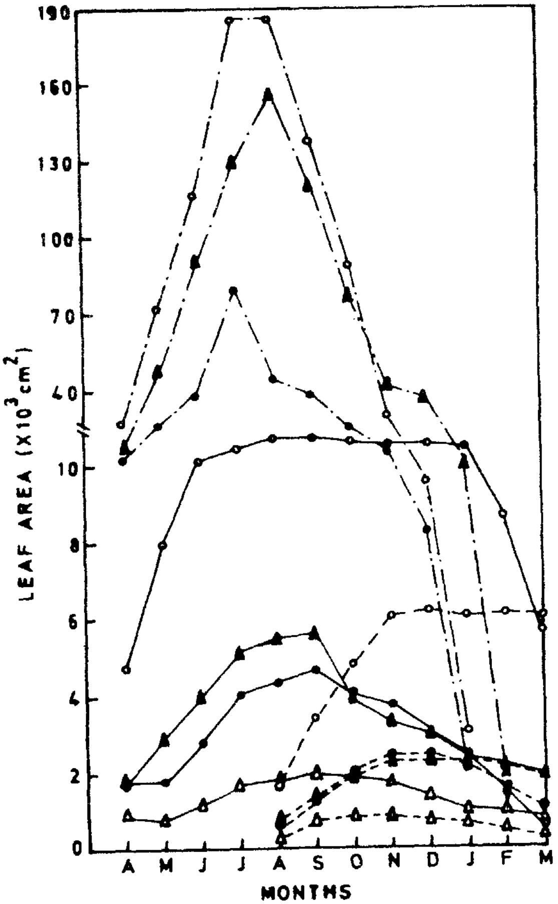
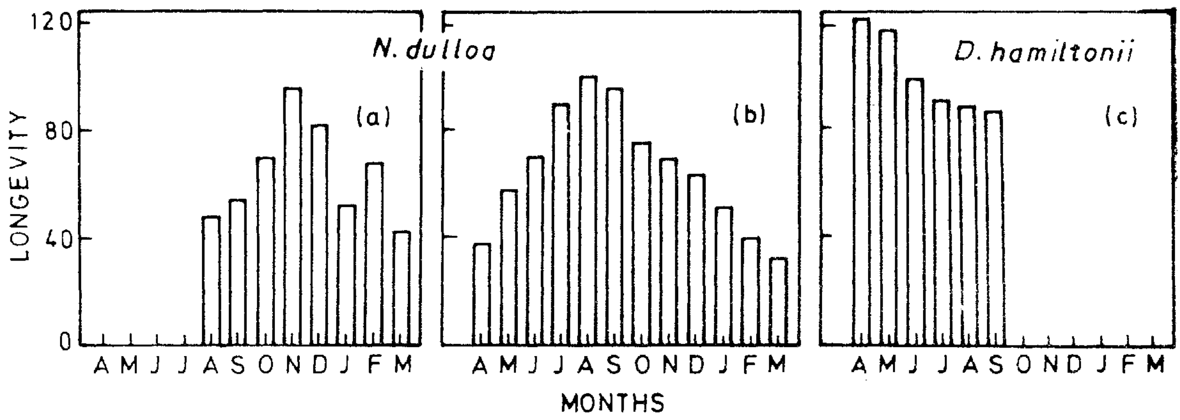


Figure 2 Monthly variation in leaf area in current year's culms (---) and last years culms of *N. dulloa* (———) and that of *D. hamiltonii* (—●—●—) in successional fallows Closed circle, 5yr; Open circle, 15yr; Closed triangle, 25yr and Open triangle, 60yr old fallow



Figre 3 Variation in the longevity of leaves recruited in different months on current year's culm (a) and last year's culms of *N. dulloa* (b) and that of *D. hamiltonii* (c) in a 5-yr-old fallow

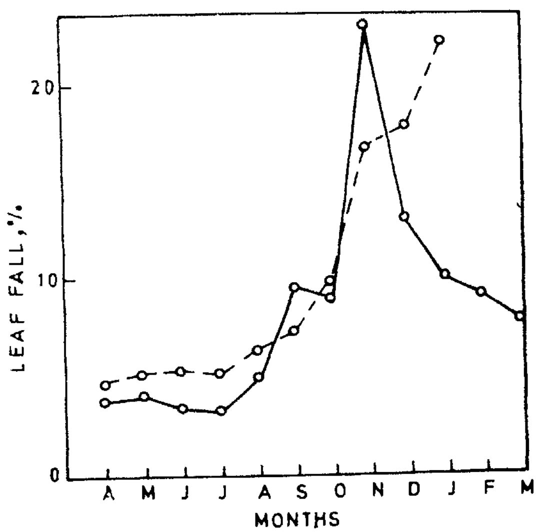


Figure 4 Monthly leaf fall pattern in last year's culm of *N. dulloa* (———) and *D. hamiltonii* (—●—●—) in a 15-yr-old fallow

than 93% mortality, whereas 30-40% leaves on the current year's culm were carried over to the next year. However, complete turnover of the leaf population of *D. hamiltonii* occurred within a year. Leaf production and loss was also maximum in *D. hamiltonii* in a 15-yr-old fallow.

N. Dulloa was more plastic with ability to withstand shade and limited adverse effect on leaf population dynamics of even a 60-yr-old fallow. This is evident from the ability of this species to survive as a sub-canopy species even in a 60-year-old forest fallow unlike *D. hamiltonii.* However, high population flux of leaves in both species occurred with maximum leaf area in a 15-yr-old fallow.

If cumulative leaf area is considered in both the species, 50% leaf area production is completed in the early part of the growing season, by July in *D. hamiltonii* and by September–October in *N. dulloa.* With elongation of all the branch systems of a culm of both the species being completed, just within a month, during April itself (Rao 1986). These C_4 species are able to maximize photosynthesis and production during the more favourable early environments of high temperature regimes. Thus, Saxena and Ramakrishnan (1984) have found distinct seasonal patterns for productivity in C_3/C_4 photosynthetic herbs, with distinct photosynthetic advantages (Ehleringer & Bjorkman 1977). Thus, C_4 species were shown to be more effective in dry matter production during the early part of the growing season

Table 3 *Leaf population flux on current year's culm and last year's culm of* N. dulloa *and that of* D. hamiltonii *in different successional fallows (values within parentheses are for current year's culm)*

		Fallow age (years) for						
		N. dulloa				*D. hamiltonii*		
(a)	No. of leaves/culm at the beginning of study period	90 (0)	169 (0)	65 (0)	33 (0)	415	864	611
(b)	No. of leaves produced/ culm during study period	411 (191)	1853 (456)	531 (228)	170 (90)	2507	10586	8503
(c)	No. of leaves lost/culm during study period	482 (127)	1943 (281)	562 (144)	189 (62)	2507	10586	8503
(d)	No. of leaves/culm at the end of study period	19 (64)	200 (175)	82 (84)	26 (28)	100	871	589
(e)	Total no. of leaves/culm recorded during study period	501 (191)	2022 (456)	596 (228)	203 (90)	2507	10586	8503
(f)	Net change (d-a)	−71 (64)	37 (175)	17 (84)	−7 (28)	−22	7	−22
(g)	Rate of change (d/a)	0.21	1.18	1.26	0.77	0.95	1.01	0.96
(h)	% annual mortality (c/e × 100)	96.2 (66.5)	96.0 (61.6)	94.3 (63.2)	93.1 (68.9)	100	100	100

when solar radiation is more intense, accompanied by warmer temperatures, unlike C_3 herbs that have peak growth during the latter part of the growing season (October-December), when temperature is lower.

Since no sharp line can be drawn between evergreen and deciduous species of the tropics (Holttum 1940, Koriba 1958), Longman and Jenik (1974) recognised four distinct patterns of leafiness on the basis of relative timings of bud-break and leaf abscission. With growth and elongation of the different branch orders being confined to a very brief period of the year, all bamboos are periodic in their growth pattern. While *N. dulloa* belongs to the 'periodic growth-evergreen type', *D. hamiltonii* belongs to the 'periodic growth-deciduous type'. Evergreen habit is advantageous to an early successional species (Shukla & Ramakrishnan 1984) such as *N. dulloa* and the deciduous habit of *D. hamiltonii* is to certain extent compensated by the faster growth and leaf production with a larger leaf area early in the growing season.

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