

## Architectural plasticity 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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**Abstract.** Two bamboo species, *Neohouzeua dulloa* A Camus and *Dendrocalamus hamiltonii* Nees and Arn. show plasticity in architecture, biomass and nutrient allocation patterns over a successional gradient of up to 60 yr for the former and 25 yr for the latter. However, optimal biomass accumulation rate was attained in a 15 yr old fallow for both species. Maximum elongation and thickness of the zero-order branch (main axis) is attained in a 15 yr old fallow for *Neohouzeua dulloa* and in a 25 yr old fallow for *Dendrocalamus hamiltonii*. The lower order branches produced on the zero-order branch of *Neohouzeua dulloa* are generally sylleptic whereas those of *Dendrocalamus hamiltonii* are proleptic. Maximum elongation and thickness for the zero-order branch, and least bud dormancy on them occurred in a 15 yr old fallow for *Neohouzeua dulloa* and in a 25 yr old fallow for *Dendrocalamus hamiltonii*. *Dendrocalamus hamiltonii* in a 5 yr old fallow had a well developed first-order branch system with diffusely placed lower order branch clusters appearing as if borne on the first-order branch, unlike in older fallows where first-order branch production was continuous and lower order branch clusters appeared as if borne on the zero-order branch itself. In older fallows both species tend to allocate more biomass and nutrients to the below-ground rhizomatous component, as an adaptation for survival and vegetative regeneration after slash and burn disturbance. The growth and architecture of both species are generally geared to capitalize upon the high light regime of the early successional environment, but with a limited ability by *Neohouzeua dulloa* to tolerate shade.

**Keywords.** Bamboos; architecture; growth pattern; allocation pattern; secondary succession.

### 1. Introduction

During secondary succession after slash and burn agriculture in north-east India, edaphic (Ramakrishnan and Toky 1981; Toky and Ramakrishnan 1983b) and micro-environmental changes such as reduction in light availability occur with the development of a closed community (Singh and Ramakrishnan 1982; Toky and Ramakrishnan 1983a). Species of the early successional environment show varying degrees of plasticity to such fast changing situations. Canopy architecture that is adapted to changing light environment during succession (Boojh and Ramakrishnan 1982a, b; Shukla and Ramakrishnan 1984, 1986) could be highly plastic. Much of the work on canopy architecture in relation to succession pertains to temperate broad-leaved tree species (Brunig 1976; Kramer and Kozlowski 1979; Borchert and Slade 1981; Nelson *et al* 1981). It is only in recent times that tropical woody species have started receiving some attention (Ramakrishnan and Shukla 1982; Shukla and Ramakrishnan 1984, 1986). However, all these studies refer to different species over a successional gradient. No information is available on architectural plasticity of the

same species in such a gradient. Further, information on bamboos are largely qualitative (Hallé *et al* 1978).

The present paper deals with the architectural plasticity and biomass and nutrient allocation patterns of two early successional bamboo species, *Neohouzeua dulloa* A Camus and *Dendrocalamus hamiltonii* Nees and Arn. The former is more plastic occurring in successional fallows of upto 60 yr whereas the latter is restricted to the first 25 yr of secondary succession after slash and burn agriculture (Ramakrishnan *et al* 1981; Toky and Ramakrishnan 1983a) at lower elevations in Meghalaya in north-east India.

## 2. Study area

The study was carried out 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 precambrian rocks are represented by gneiss, schists and granites. The soil is a red sandy loam of laterite origin, with pH 5–7. The angle of the slope generally ranged from 20–40°.

The climate has 3 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. Seventy three per cent 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 and 14.4°C, respectively.

## 3. Methods of study

Fallows of 1, 5, 15, 25 and 60 yr old were identified based on our own observations and the records available with the village headman and the Forest Department. Care was taken to ensure similar topography, soil type, exposure and slope.

### 3.1 Architectural studies

Culms are produced in both species during the monsoon season. These culms of *D. hamiltonii* would produce branches and leaves only during the next monsoon season. Hence the culms produced in June 1982 and 1983 were separately tagged. *N. dulloa* produce branches and leaves during the same growing season when the culms are initiated. In this case, the culms produced in April 1983 alone were tagged. For both species, 10 replicate culms from different clumps selected randomly were considered. Observations from a raised platform were made at weekly intervals during the period of culm elongation. When the growth slowed down, these observations were made at monthly intervals. These observations on the two species made in 5–25 yr old fallows pertained to: (i) elongation of the branches of different orders, (ii) branch production, (iii) internodal length and (iv) bud dynamics on the main axis (zero-order branch). Observations on *N. dulloa* were also made in a 60 yr old fallow.

### 3.2 Allocation studies

*N. dulloa* is a gregariously flowering bamboo species, that flowered last in 1968 in the study area, before total death. Therefore the entire population under observation in 1983 had a stock age of 15 yr. *D. hamiltonii* has both sporadic and gregarious flowering habits. The last gregarious flowering in the study area was in 1956. The stock age of this species in 1983 was, therefore, not more than 30 yr. This inference is also based on the very short viability for the seeds which necessitates that they should germinate soon after dispersal.

The age of a clump was measured as regeneration age which was equivalent to fallow age upto 15 yr in *N. dulloa*. Regeneration age for *D. hamiltonii* may be the same or even less than the fallow age depending upon whether the clump arose after gregarious flowering or a subsequent sporadic flowering. The population of *N. dulloa* present in 25 and 60 yr old fallows, however, would have the same stock/regeneration age of 15 yr. With uniform stock age, the clumps of *N. dulloa* in a given fallow were all of the same size. This permitted random selection of clumps. On the other hand, *D. hamiltonii* with possible differences in stock age because of gregarious and sporadic flowering had clumps of different sizes. Therefore clumps of similar size were selected in a given fallow.

Ten replicate clumps of the two species selected from each site were harvested in August 1984. The above-ground parts were separated into main axis (zero-order branch), branches (all orders except zero-order branch) and leaves. Below-ground parts (rhizome and roots) were carefully excavated, washed thoroughly and weighed. Samples were dried at 80°C and dry weights computed.

All the samples were ground and passed through a 0.5 mm sieve and analysed for elemental composition after acid digestion using methods suggested by Allen *et al* (1974). Thus, nitrogen was estimated by Kjeldahl method, phosphorus colorimetrically by ammonium molybdate blue method, potassium by flame-photometry and calcium and magnesium by EDTA-titration method.

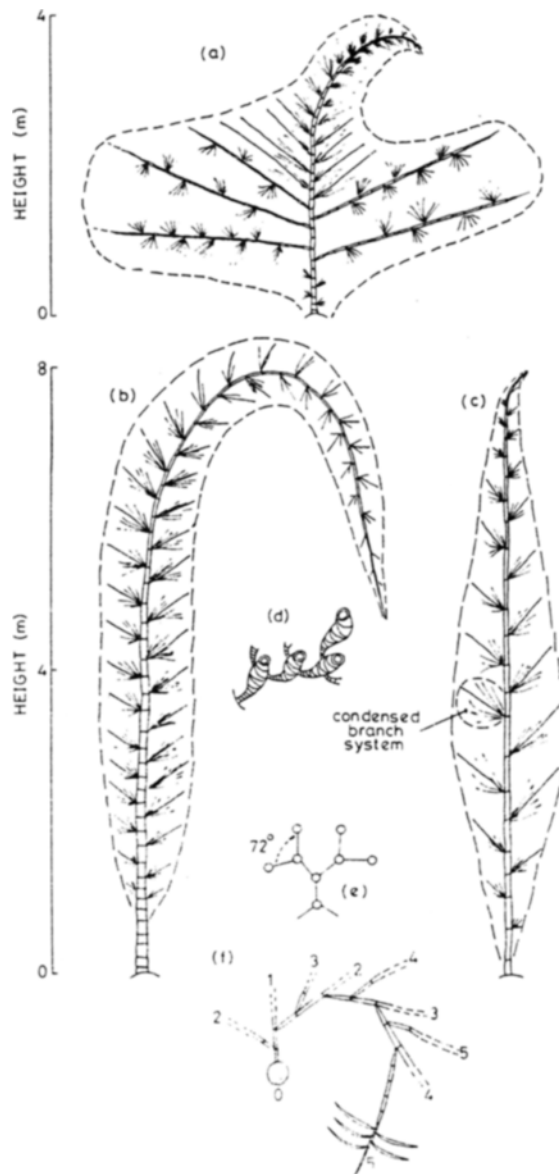
The results were subjected to one way analysis of variance. The mean  $\pm$  S.E. is a pooled estimate over the mean monthly observations with ten replications.

## 4. Results

### 4.1 Architectural studies

*N. dulloa* and *D. hamiltonii* have extensive sympodially branched under-ground rhizomes. Each branch 9–14 cm long in *N. dulloa* and 12–24 cm in *D. hamiltonii* has a narrow neck which broadens out into a thick base (figure 1d). Rhizomatous branches are produced from two of the lateral buds whereas the apical bud would give rise to the above-ground shoot system. With thinner rhizome and aerial branch systems in *N. dulloa* the clumps are more loosely organized in this species than in *D. hamiltonii*.

The crown shape of *D. hamiltonii* is highly variable. In a 5 yr old fallow because of predominantly herbaceous vegetation and the consequent better light availability, the crown is broader, tapering towards the tip (figure 1a). In older fallows, where other larger species compete for aerial space, the crown of *D. hamiltonii* becomes cylindrical in shape with a whip like tip (figure 1b). In *N. dulloa*, the crown form is more uniform in all the fallows, being broader in the middle and tapering on either side (figure 1c).



**Figure 1.** Canopy architecture of *D. hamiltonii* in a 5 yr old fallow (a), in a 15 yr old fallow (b) and that of *N. dulloa* in a 15 yr old fallow (c), Rhizome architecture of the two species (d) along with a diagrammatic representation (e). Diagrammatic representation of the organization of branch orders in a branch complement in the two bamboo species. Zero to fifth-order branches are shown along with the leafy shoots (e).

Branch production in both species is determinate. The orthotrophic zero-order branches of the two species complete their elongation within 90–120 days after initiation (figure 2) through syllepsis (in the same year) in *N. dulloa* but through prolepsis in *D. hamiltonii* (in the following year only). Reiteration (Hallé *et al* 1978) of the zero-order branch may occur in *D. hamiltonii* only. In *N. dulloa*, damage to the

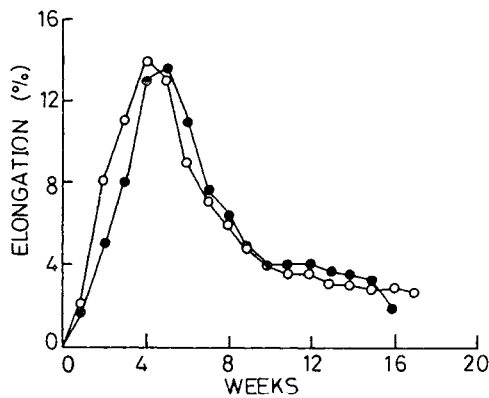


Figure 2. Elongation rate of the zero-order branch of *N. dulloa* (●) and *D. hamiltonii* (○) in a 15 yr old fallow.

apical bud would arrest further growth. All the branches on the zero-order are produced and elongation completed simultaneously. *N. dulloa* would normally produce branches upto the fourth-order except in a 15 yr old fallow where the fifth order branches may be produced, but in the subsequent year only. *D. hamiltonii* would normally produce branches upto the fifth-order. Branches in the two species are produced continuously on all nodes except in *D. hamiltonii* growing in a 5 yr old fallow, where branching was diffuse (figure 1a). The first-order branches and the subsequent orders all look as if arising in a cluster from the same point from a given node on the zero-order axis. However, each branch order is a condensed axis, one arising on the other. Thus, the axillary buds of the two basal nodes of the first-order branch would produce two second-order branches, similarly the second-order branch would produce the third-order branches and so on, so that a maximum of 31 units may be produced in a condensed form (figure 1f). However, branch production may stop at the first-order stage (one unit only), at the second-order stage (3 units only), at the third-order stage (7 units only), or at the fourth-order stage (15 units only).

The two species conform to the Mc Clure's model as described by Hallé *et al* (1978). The essential feature of this model is that all the aerial parts are vegetatively determinant in their growth. They consider the determinant axis and the branch systems to be a determinant organ, something like an elaborate compound leaf.

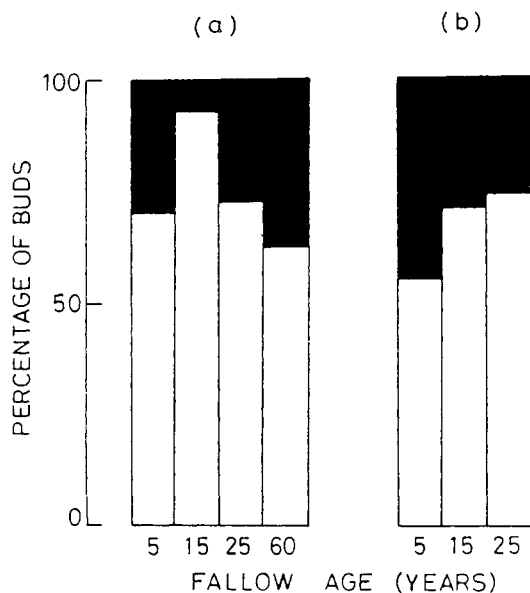
Leaves on both species are borne on all branches towards their tip, except the zero-order branch. These branches are shed off every year and new leafy shoots arise in their place simultaneously in *N. dulloa*, but after a brief dormancy of upto 60 days in *D. hamiltonii*. While *N. dulloa* was evergreen leaf exchanging type, *D. hamiltonii* was deciduous. Growth parameters reached its maximum in a 15 yr old fallow for *N. dulloa* ( $P < 0.05$ ) and in a 25 yr old fallow ( $P < 0.05$ ) for *D. hamiltonii* (table 1). Sylleptic bud dormancy in *N. dulloa* was minimal (6%) in a 15 yr old fallow whereas the proleptic (previous year's) buds of *D. hamiltonii* had declining bud dormancy with fallow age upto 25 yrs (figure 3).

The elongation of the first-order branch presented in table 2 shows that the variation in *D. hamiltonii* in a 5 yr old fallow was very high. This high variation in *D. hamiltonii* is evident from the larger differences in the elongation of the first-order

**Table 1.** Important characteristics (mean  $\pm$  SE) of *N. dulloa* and *D. hamiltonii* in 5–60 yr old fallows.

Parameters	Fallow age (years)			
	5	15	25	60
Rhizomatous branch elongation (cm/yr)	9.7 $\pm$ 0.63 (12.7 $\pm$ 1.14)	13.5 $\pm$ 1.23 (21.5 $\pm$ 1.77)	11.2 $\pm$ 0.82 (23.6 $\pm$ 1.93)	9.5 $\pm$ 0.92
Clump area (cm <sup>2</sup> )	0.41 $\pm$ 0.03 (1.16 $\pm$ 0.11)	1.21 $\pm$ 0.11 (2.27 $\pm$ 0.17)	0.61 $\pm$ 0.05 (2.53 $\pm$ 0.21)	0.30 $\pm$ 0.03
Number of culms/clump	19 $\pm$ 1.30 (32 $\pm$ 2.85)	51 $\pm$ 3.20 (63 $\pm$ 4.11)	42 $\pm$ 2.90 (63 $\pm$ 2.53)	29 $\pm$ 1.90
Number of culms/ha	2000 (2200)	4600 (6000)	3300 (7300)	3000
Culm length (m)	1.35 $\pm$ 0.12 (3.80 $\pm$ 0.35)	8.30 $\pm$ 0.82 (13.70 $\pm$ 1.23)	2.90 $\pm$ 0.21 (16.90 $\pm$ 1.68)	2.05 $\pm$ 0.16
Culm diameter at 10 cm from base (cm)	2.5 $\pm$ 0.20 (5.9 $\pm$ 0.58)	5.2 $\pm$ 0.38 (14.2 $\pm$ 1.14)	2.9 $\pm$ 0.21 (16.8 $\pm$ 1.36)	2.5 $\pm$ 0.16
Annual elongation in current year's culm (cm)	145 $\pm$ 12.9 (400 $\pm$ 28.6)	835 $\pm$ 50.8 (1420 $\pm$ 73.8)	300 $\pm$ 25.8 (1750 $\pm$ 101.3)	215 $\pm$ 17.9
Total height to crown width ratio	1.69 (0.91)	6.91 (10.60)	3.22 (13.00)	2.56

Values in parentheses are for *D. hamiltonii*.



**Figure 3.** Variation in the dormancy of buds (%) on the current year's culm (zero-order branch) of *N. dulloa* (a) and last year's culm of *D. hamiltonii* (b), with fallow age. (■), Dormant buds; (□), active buds.

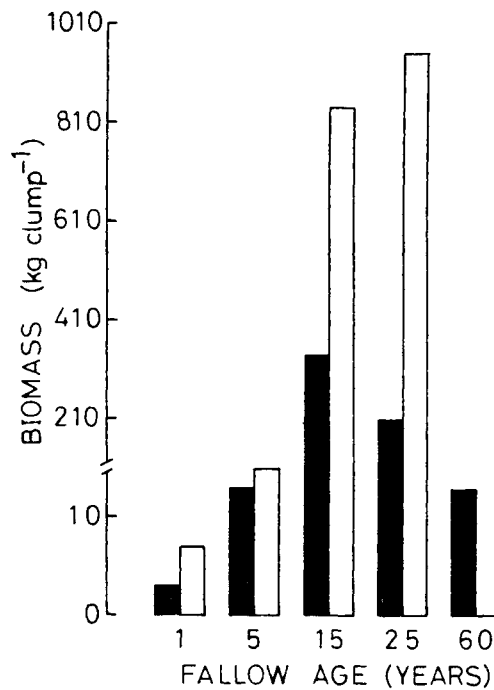
branches at different canopy positions (table 3). *N. dulloa* had, however, maximum elongation in a 15 yr old fallow and *D. hamiltonii* in a 25 yr old one. The elongation pattern for the lower order branches was similar (hence not presented here) except that elongation decreased in higher order branches.

**Table 2.** Variation in first-order branch elongation (cm) (mean  $\pm$  SE) of two bamboos in 5–60 yr old fallows.

Species	Fallow age (years)			
	5	15	25	60
<i>N. dulloa</i>	40.1 $\pm$ 3.57	65.3 $\pm$ 4.00	35.2 $\pm$ 3.07	30.9 $\pm$ 3.00
<i>D. hamiltonii</i>	71.3 $\pm$ 20.50	65.7 $\pm$ 9.60	60.3 $\pm$ 9.70	

**Table 3.** Variation in elongation (cm) (mean  $\pm$  SE) in first-order branches of *D. hamiltonii* at different canopy positions on zero-order branch in 5–25 yr old fallow.

Fallow age (years)	Canopy position (node number from base)			
	0–10	10–20	20–30	< 30
5	14.3 $\pm$ 0.92	254.1 $\pm$ 10.7	25.3 $\pm$ 2.6	
15	13.9 $\pm$ 0.98	75.3 $\pm$ 4.2	51.6 $\pm$ 4.7	18.7 $\pm$ 1.6
25	12.6 $\pm$ 0.81	73.9 $\pm$ 5.6	59.2 $\pm$ 2.9	23.6 $\pm$ 1.8

**Figure 4.** Standing biomass (kg clump<sup>-1</sup>) of bamboos in successional fallows. (■), *N. dulloa*; (□), *D. hamiltonii*.

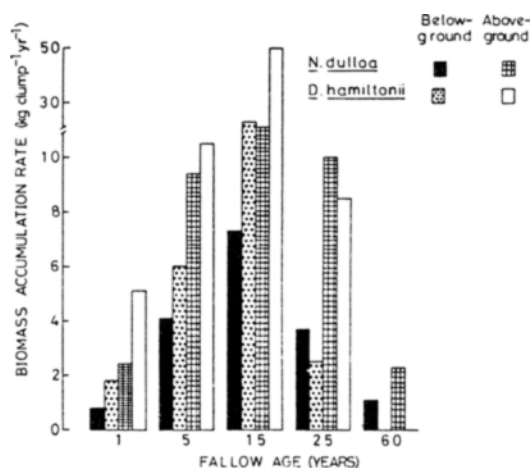
#### 4.2 Allocation studies

The total standing biomass per clump was maximum ( $P < 0.05$ ) in a 15 yr old fallow for *N. dulloa* and in a 25 yr old fallow for *D. hamiltonii* (figure 4). However, the rate of

accumulation for the below-ground and above-ground organs peaked in a 15 yr old fallow, for both species (figure 5). It may be noted here that the rate of accumulation in *N. dulloa* in 25 and 60 yr old fallows, was calculated on the assumption that the age of the clump was 15 yr, based upon the previous gregarious flowering.

The above-ground/below-ground ratio of *N. dulloa* declined significantly ( $P < 0.05$ ) in a 5 yr old fallow (table 4) compared to a 1 and 15 yr old ones. This ratio was significantly lower ( $P < 0.05$ ) in a 60 yr old fallow as compared with 15 and 25 yr. The ratio for *D. hamiltonii* declined sharply ( $P < 0.05$ ) in 15 and 25 yr old fallows, compared to younger ones.

The allocation of biomass to the below-ground organs in *N. dulloa* was higher in 5 and 60 yr old fallows (figure 6a). In *D. hamiltonii*, 1 yr old fallow had maximum biomass allocation ( $P < 0.05$ ) to the zero-order branch whereas the lower branch orders had more allocation ( $P < 0.01$ ) in a 5 yr old fallow. Nitrogen allocation to the leaf component in *N. dulloa* increased ( $P < 0.01$ ) with fallow age but decreased in the case of the zero-order branch (figure 6b). Allocation of nitrogen to the zero-order branch of *D. hamiltonii* was minimal and to the leaf component was maximal in a 5 yr old fallow. In general nitrogen allocation to the leaf component was higher ( $P < 0.01$ ) than biomass allocation. Phosphorus allocation to the below-ground parts of both species increased ( $P < 0.05$ ) and to the zero-order branches decreased in older fallows (figure 6c). The leaves of *N. dulloa* had more phosphorus ( $P < 0.01$ ) allocation

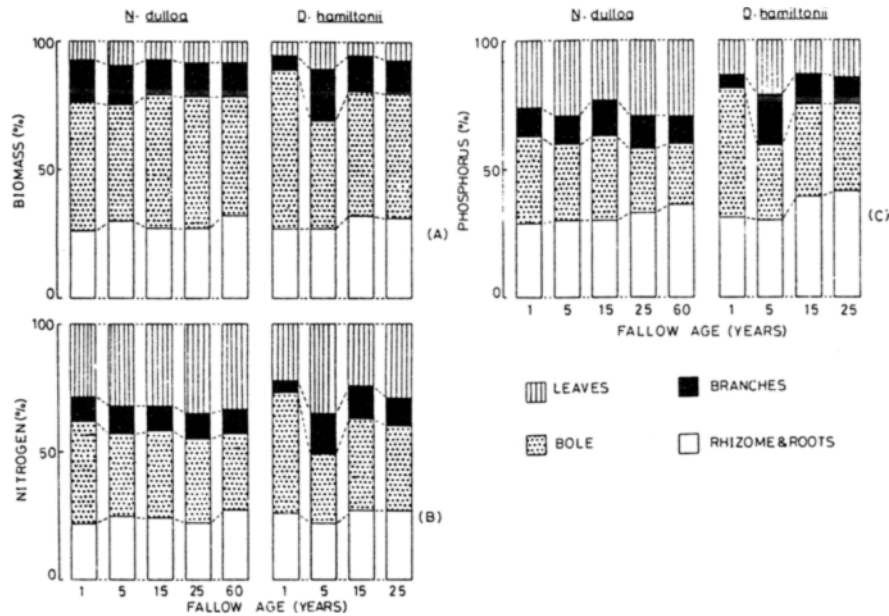


**Figure 5.** Biomass accumulation rates ( $\text{kg clump}^{-1} \text{yr}^{-1}$ ) in above-ground and below-ground components of two bamboos in successional fallows.

**Table 4.** Above-ground/below-ground ratio of bamboos in 5–60 yr old fallows.

Fallow age (years)	<i>N. dulloa</i>	<i>D. hamiltonii</i>
1	2.89	2.76
5	2.34	2.69
15	2.77	2.13
25	2.75	2.24
60	2.15	—





**Figure 6.** Allocation pattern (%) of biomass (a), nitrogen (b) and phosphorus (c) to different organs in two bamboos in successional fallows.

than those of *D. hamiltonii*. The allocation of potassium, calcium and magnesium showed a pattern similar to biomass allocation and therefore not presented here.

## 5. Discussion

### 5.1 Architectural studies

Hallé *et al* (1978) established Mc Clure's model to accommodate the basic architecture of bamboos. There are differentiated axes of two kinds: first sigmoid trunk axes which are essentially mixed, originate by basal branching and bear, second, plagiotropic leafy branches; both kinds show determinate growth due to a high degree of preformation. Takemouchi (1931) and Mc Clure (1966), however, differentiated the below-ground and above-ground parts as solid (internodes filled) and hollow (internodes empty) axes respectively. Based on this difference and also based on the fact that the zero-order branch of Hallé *et al* (1978) is in fact a number of branch systems that are sympodially produced, ordering was done, for the present study, with respect to above-ground branches alone, the above-ground main axis being designated as the zero-order branch.

The canopy architecture of *D. hamiltonii* showed plasticity depending upon the fallow age. In a 5 yr old fallow the culm assumes a conical form which is related to more space and light availability. With reduction in space and light in older fallows the culm assumes a cylindrical form. *D. hamiltonii* has limited plasticity with a range of upto 25 yr of the fallow since it is an emergent and shade intolerant species, but optimum growth occurred in 15 and 25 yr old fallows. Partly because of reduced

light availability in fallows older than 25 yr and partly because the intermast phase for *D. hamiltonii* is 30–40 yr depending upon the geographical zone (Varmah and Bahadur 1980; Janzen 1976) this species is eliminated during succession after 25 yr (Toky and Ramakrishnan 1983a). Over a successional gradient, *N. dulloa* showed great plasticity extending upto 60 yr old fallow, as an emergent upto 15 yr of fallow regrowth and as an undergrowth in 25 and 60 yr old forests. *N. dulloa* with a reported intermast phase of 15–17 yr (Janzen 1976) is, however, able to regenerate through seeds and survive upto 60 yr of fallow age because of its shade tolerance, though with reduced vigour.

Unlike trees where extension and radial growth are continuous activities throughout the life cycle of the species, growth and elongation in bamboos occur just when the culm is produced. Extension growth is through mere elongation of the zero-order branch, whilst radial growth is through cell enlargement and thickening of preformed tissue. Since successive generations of zero-order branches within a given clum tend to be thicker than the earlier ones (Hallé *et al* 1978) it should be expected that the culms produced in older fallows would be generally thicker, as the stock/regeneration age would increase, though upto a point being constrained by species plasticity. Thus in the larger *D. hamiltonii* maximum diameter for the zero-order branch occurred in a 25 yr old fallow, whereas in the smaller *N. dulloa* it occurred in a 15 yr old fallow.

The extension of the zero-order axis through internodal elongation starts from base upwards with peak elongation occurring during the fifth week as also reported for *Phyllostachus* species (Ueda 1960; Mc Clure 1966). With lesser resource storage in the below-ground organs of *N. dulloa*, sylleptic branch production with leafy shoots on them is helpful for immediate photosynthesis and thus for quicker growth. On the other hand, with more resource availability in the below-ground parts of *D. hamiltonii*, the resources are diverted initially for the growth of the larger zero-order axis with postponement of branch production to the second year. Being light demanders, the two species had a high degree of branch drop-off as light availability decreased at lower canopy positions, a feature which helps in rapid upward shift of the canopy of early successional species (Boojh and Ramakrishnan 1982a; Shukla and Ramakrishnan 1986).

## 5.2 Allocation studies

The biomass of *D. hamiltonii* increased with fallow age upto 25 yr and that of *N. dulloa* declined sharply in fallows older than 15 yr. However, the biomass accumulation rate in both the species peaked in a 15 yr old fallow suggesting that growth conditions are, perhaps, more favourable in this fallow than in others, apart from increased regeneration age of the clump.

During the first 15 yr, considerable fluctuation occurred in the above-ground/below-ground ratio of *N. dulloa*. During the first year of shoot growth, rapid transfer of resources from below-ground to above-ground compartment occurred. Subsequently the photosynthates from the above-ground parts are retranslocated to the below-ground organs resulting in a lower ratio. Subsequently, the shoot growth picked up because of another upward translocation of resources from the below-ground parts resulting in a higher ratio in a 15 yr old fallow. The lowest ratio attained in *N. dulloa* in a 60 yr old fallow may be an adaptation for survival through

vegetative growth during the subsequent slash and burn operation. Such a survival strategy was observed in many rhizomatous species such as *Imperata cylindrica* developed in successional fallows after slash and burn agriculture (Saxena and Ramakrishnan 1983) and in *D. hamiltonii* during the present study.

Proportional allocation of phosphorus compared to other nutrients to the below-ground parts was much higher for the two species. A more effective distribution of this element compared to many others for vegetative reproduction was also reported in *Ixia polystachya* (Hocking 1984) and in *Solidago* species (Abrahamson and Caswell 1982). Higher allocation of nitrogen to the leaf component of both the species may be related to photosynthetic efficiency, since leaf nitrogen content is shown to be positively related to photosynthetic rate (Murata 1969; Terry and Ulrich 1973; Nätr 1975; Field 1983). Such a differential allocation of biomass and nutrients suggest that it is often difficult to establish a connection between fitness and resource allocation based on any one currency, and emphasizes the importance of nutrient allocation in such studies (Van Andel and Verma 1977; Chapin 1980; Williams and Bell 1981; Saxena and Ramakrishnan 1983).

A useful strategy for any species establishing after slash and burn of a forested ecosystem should be to capitalize upon the resources of an enriched substratum, which is transient, and make adequate growth as quickly as possible. The species establishing in such environments could have strategies for establishment from seed or for establishment from vegetative sprouts (Saxena and Ramakrishnan 1983). The bamboo species that are predominantly clonal, with high allocation of resources to the below-ground organs of reproduction (Keeley and Keeley 1977; Gadgil and Prasad 1984), represent an extreme stage among vegetative strategists with seed reproduction occurring once during the life cycle, with very low regeneration (Rao and Ramakrishnan 1987) due to predation and rapid loss in viability and weaker seedlings derived from small seeds.

Thus the growth and architectural patterns of bamboo species are geared to capitalize upon high light regime of an early successional environment to make quick growth before light become limiting, and quickly utilize the nutrient resources of a transient soil environment.

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### References

- Abrahamson W G and Caswell H 1982 On the comparative allocation of biomass, energy and nutrients in plants; *Ecology* **63** 982-991
- Allen S E, Grimshaw H M, Parkinson J A and Quarmby C 1974 *Chemical analysis of ecological materials* (Oxford: Blackwell)
- Boojh R and Ramakrishnan P S 1982a Growth strategy of trees related to successional status. I. Architecture and extension growth; *For. Ecol. Manage.* **4** 359-374

- Boojh R and Ramakrishnan P S 1982b Growth strategy of trees related to successional status. II. Leaf dynamics; *For. Ecol. Manage.* **4** 375–386
- Borchert R and Slade N A 1981 Bifurcation ratios and the adaptive geometry of trees; *Bot. Gaz.* **142** 394–401
- Brunig E F 1976 Tree forms in relation to environmental conditions: an ecological view point. in *Tree physiology and yield improvement* (eds) M G R Cannell and F T Last (New York: Academic Press) pp 139–156
- Chapin F S III 1980 The mineral nutrition of wild plants; *Annu. Rev. Ecol. Syst.* **11** 233–260
- Field C 1983 Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program; *Oecologia* **56** 341–347
- Gadgil M and Prasad S N 1984 Ecological determinants of life history evolution of two bamboo species of India; *Biotropica* **16** 161–172
- Hallé F, Oldeman R A A and Tomlinson P B 1978 *Tropical trees and forests: an architectural analysis* (New York: Springer Verlag)
- Hocking P J 1984 Accumulation, partitioning and redistribution of dry matter and mineral nutrients in *Ixia flexuosa* L., with special reference to its coramaceous habit; *Ann. Bot.* **53** 489–501
- Janzen D H 1976 Why bamboos wait so long to flower; *Annu. Rev. Ecol. Syst.* **7** 347–391
- Keeley J E and Keeley S E 1977 Energy allocation patterns of a sprouting and non-sprouting species of *Arctostaphylos* in the California Chaparral; *Am. Mid. Nat.* **98** 1–10
- Kramer P J and Kozlowski T T 1979 *Physiology of woody plants* (New York: Academic Press)
- Mc Clure F A 1966 *The bamboos: A fresh perspective* (Massachusetts: Harvard University Press)
- Murata Y 1969 Physiological responses to nitrogen in plants; in *Physiological aspects of crop yield* (eds) J D Eastin, C Y Sullivan and C H M Van Bavel (Madison: Wisconsin Agronomy Society of America) pp 235–259
- Nátr L 1975 Influence of mineral nutrition on photosynthesis and the use of assimilates; in *Photosynthesis and productivity in different environments* (ed.) J B Cooper (Cambridge: Cambridge University Press) pp 537–556
- Nelson N D, Burk J and Icebrands J G 1981 Crown architecture of short-rotation, intensively cultured populus. I. Effects of close spacing on first order branch characteristics; *Can. J. For. Res.* **11** 73–81
- Ramakrishnan P S and Shukla R P 1982 On the relation among growth strategies, allocation pattern, productivity and successional status of trees of a sub-tropical forest community; in *Improvement of forest biomass* (ed.) P K Khosla (Solun: Indian Society of Tree Scientists) pp 403–412
- Ramakrishnan P S and Toky O P 1981 Soil nutrient status of hill agro-ecosystems and recovery pattern after slash and burn agriculture (jhum) in north-eastern India; *Plant Soil* **60** 41–64
- Ramakrishnan P S, Toky O P, Mishra B K and Saxena K G 1981 Slash and burn agriculture in north-eastern India; in *Fire regimes and ecosystem properties* (eds) H A Mooney, J M Bonneksen, N L Christensen, J E Lotan and W A Reiners USDA, Forest Service, General Technical Report, WO26 pp 570–584
- Rao K S and Ramakrishnan P S 1987 Comparative analysis of the population dynamics of two bamboo species, *Dendrocalamus hamiltonii* Nees and Arn. and *Neohouzeua dulloa* A. Camus in successional environment; *For. Ecol. Manage.* **21** 177–189
- Saxena K G and Ramakrishnan P S 1983 Growth and allocation strategies of some perennial weeds of slash and burn agriculture (jhum) in north-eastern India; *Can. J. Bot.* **61** 1300–1306
- Shukla R P and Ramakrishnan P S 1984 Leaf dynamics of tropical trees related to successional status; *New Phytol.* **97** 697–706
- Shukla R P and Ramakrishnan P S 1986 Architecture and growth strategies of tropical trees in relation to successional status; *J. Ecol.* **74** 33–46
- Singh J and Ramakrishnan P S 1982 Structure and function of a sub-tropical humid forest of Meghalaya. I. Vegetation biomass and its nutrients; *Proc. Indian Acad. Sci. (Plant Sci.)* **91** 241–253
- Takemouchi Y 1931 Systematisch-Vergleichende Morphologie und Anatomie der Vegetationsorgane der Japanischen Bambus-Arten; *Tahoki Imp. Univ. (Formosa) Facul. Sci. Memo* **3** 60
- Terry N and Ulrich A 1973 Effects of phosphorus deficiency on the photosynthesis and respiration of leaves of sugarbeet; *Plant Physiol.* **51** 43–47
- Toky O P and Ramakrishnan P S 1983a Secondary succession following slash and burn agriculture in north-eastern India. I. Biomass, Litterfall and Productivity; *J. Ecol.* **71** 735–745
- Toky O P and Ramakrishnan P S 1983b Secondary succession following slash and burn agriculture in north-eastern India. II. Nutrient cycling; *J. Ecol.* **71** 747–757

- Ueda K 1960 Studies on the physiology of Bamboo, with special reference to practical application; *Bull. Kyoto Univ. For.* No 30
- Van Andel J and Vera F 1977 Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition; *J. Ecol.* **65** 747-758
- Varmah J C and Bahadur K N 1980 Country report and status of research on bamboos in India; *Indian For. Rec. (Botany)*, **6** 28
- Williams R B and Bell K M 1981 Nitrogen allocation in Mojave desert annuals; *Oecologia* **48** 145-150