

Ecology of *Bambusa arudinacea* (Retz.) Willd. growing in teak plantations of Kerala, India

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Accepted 28 March 1996

Abstract

A study was undertaken to assess the contribution of bamboo to the vegetation structure, biomass productivity and nutrient cycling pattern in 15- and 20-year-old teak plantations in the Kariem-muriem Forest Range, Kerala, India. Based on the distribution pattern of bamboo colonised in these plantations, three types of site were recognised: site type A (bamboo-rich area), site type B (moderately bamboo-rich area) and site type C (bamboo-poor area). Density, basal area, number of culms per hectare, biomass, litter and net primary production of bamboo were greater in site type A than in site types B and C. While the soils of site types A and B were rich in potassium, those of site type C were rich in calcium. In addition to this, a negative correlation between above-ground biomass of bamboo and teak was recorded in site type A. In the case of teak, the rate of accumulation and the enrichment ratio of calcium were more than those of other elements. However, in bamboo, the enrichment ratio and accumulation rate of potassium were higher than in teak. The values for these parameters in bamboo were higher for potassium than for other elements. These results show that even from the nutrient conservation and cycling point of view, bamboo is a suitable species for site type A and teak is suitable for site types B and C. It is recommended that interplanting of bamboo in teak plantation, especially in areas like site types B and C, is not advisable. Instead, patch-planting may be more appropriate both to get better yield and to maintain ecosystem stability. It was also concluded that management of key elements of the ecosystem, such as potassium, is crucial for the stability of the ecosystem after disturbance or the conversion of natural forests into plantations.

Keywords: *Bambusa arudinacea*; Biomass productivity; Nutrient cycling; Teak plantation

1. Introduction

Recolonisation of forest plantations by colonisers like bamboo appears to be a common phenomenon, particularly in the tropics. Teak plantations of site quality II and III are often invaded by *Bambusa arudinacea* or other bamboos (FAO, 1956). Even in plantations of better site quality, invasion of bamboo is not uncommon, especially in water-logged areas and areas bordering swamps (Browne, 1928). In

Kerala State (India) where teak is raised extensively, bamboo is one of the important plant components of several plantations. Although bamboo growing in these teak plantations is an additional source of revenue and bamboo is being extracted on a commercial scale at frequent intervals, so far no attempt has been made to examine its distribution pattern in teak stands and its contribution to vegetation composition, biomass production and nutrient cycling. While studies on biomass are essential for estimating

net primary productivity, studies of nutrient cycling help in assessing the stability of the ecosystem, nutrient mobilization and conservation processes. Furthermore, quantitative knowledge of the structural and functional patterns of density, basal cover, biomass, net productivity and nutrient cycling by the component species in man-made ecosystems is a basic requisite for silvicultural decision-making. In addition to this, information on differing ecological requirements and growth characteristics, and thus the intensity of interspecific competition between the component species, will also help in the design of appropriate planting techniques. The present study was undertaken in order to examine these diverse ecological aspects. The main objectives of the study were to understand the distribution pattern of bamboos in teak plantations and to study the vegetation structure, biomass, productivity and nutrient cycling, with particular reference to the contribution of bamboo to the above-mentioned parameters.

2. Study area and climate

Two teak plantations of 15 and 20 years of age, located in the Kariem-muriem reserve (11°17'–11°23' N, 76°16'–76°18' E) of the Nilambur Forest Division, were selected. Both plantations are at an altitude of 100–150 m above mean sea level with a south or south-easterly aspect and an eastern or southern side slope. The underlying rocks are laterite and the soil is sandy loam. The distance between plantations varied from 0.5 to 4.0 km.

The climate of the region is typically monsoonic with an average rainfall of over 2500 mm. The major proportion (70%) of the annual rainfall occurs from the south-west monsoon, which usually starts in early June and continues until the end of August. The north-east monsoon starts in October and lasts until the end of November. The mean annual maximum temperature is 35°C and the mean annual minimum is 19°C.

The natural forests of the area were tropical moist deciduous, and the predominant tree species were *Terminalia crenulata* Roth, *Terminalia paniculata* Roth, *Lagerstroemia microcarpa* Wt. and *Xylia xylocarpa* (Roxb.) Taub. *Bambusa arundinacea* (Retz.) Willd., *Calycopteris floribunda* Lam. and *Helicteres*

isora L. were the important undergrowth species. In teak plantations, seedlings, saplings and a few mature individuals of miscellaneous tree species such as *Bombax ceiba* L., *Dalbergia latifolia* Roxb., *Gmelina arborea* Roxb., *Mallotus tetracoccus* (Roxb.) Kurz, *Terminalia paniculata* Roth. and *Xylia xylocarpa* (Roxb.) Taub. are seen, as well as shrubs such as *Chromolaena odorata* (L.) King and Robin, *Clerodendrum viscosum* Vent., *Helicteres isora* L. and *Leea indica* (Burm.f.) Merr. and herbs such as *Amomum cannaecarpum* (Wt.) Benth., *Crotolaria filipes* Benth., *Cynodon dactylon* (L.) Pers., *Oldenlandia caerulea* Benth and *Triumfetta rotundifolia* Lamk.

3. Materials and methods

3.1. Site selection

Bamboo clump distribution and clump size were analyzed at different distances from the water course. In each plantation, three quadrats, each 300 m long and 100 m wide, were marked along a transect so as to cover both the swampy areas and upward sloping areas. The distance between two transects was 200–300 m. The slope of the plots varied between 8% and 15%. The maximum elevation recorded on the upward slope was 32 m, and the minimum at the bottom of the swamp was 2 m, from the nearby stream. The distance between the stream and the margin of the plantation varied between 2 m and 5.2 m. Each quadrat was further subdivided into 20 m × 20 m plots, and the total number of bamboo clumps and culms in each plot was recorded. The following three arbitrary but convenient types of bamboo distribution were recognized:

Type A, plots having 3 or more clumps per 400 m², each clump with more than 20 culms;

Type B, plots having 1–3 clumps per 400 m², each clump with 10–19 culms;

Type C, plots having 0–3 clumps per 400 m², if clumps are present each has less than 9 culms.

The highest number (83–100%) of type A plots were within 100 m of the edge of the plantation bordering the nearest stream or swamp, whereas 72–100% of type B plots occurred 120–200 m from the edge of the plantation. Beyond 220 m, 72–100% of the plots studied were type C plots. Three repli-

cate plots, each of 1 ha, were demarcated for each site type.

3.2. Vegetation analysis

Phytosociological studies of herbs, shrubs, tree seedlings and saplings followed standard methods (Kershaw, 1973). Vegetation analysis of herbs was based on twenty-five 1 m × 1 m quadrats, while that of shrubs and tree seedlings was based on five 5 m × 5 m quadrats. Tree saplings were studied using ten 10 m × 10 m quadrats. Bamboo, teak and mature individuals of miscellaneous tree species were studied by laying out eight 25 m × 25 m quadrats. Species diversity among herbs, shrubs, tree seedlings, saplings and mature trees of miscellaneous species was calculated using the formula given by Shannon and Wiener (1963).

$$H = -\sum[(n_i/N) \log(n_i/N)]$$

where H is the Shannon index of general diversity, n_i is the importance value index of each species, and N is the total importance value index of all species.

However, for bamboos and teak only the density, basal area and percentage frequency were calculated. In the case of bamboo, the number of culms per hectare was also estimated.

3.3. Biomass and productivity

The biomass of teak was measured by a non-destructive volume estimation method. Twenty-four trees (12 from each of the 15- and 20-year-old plantations) were randomly selected over the entire girth range and their height and girth at breast height (at 1.37 m above ground level) were measured. The girth at breast height (GBH) was taken as the mean girth of the bottom 2.74 m sector of the bole. Mid-girths above the bottom sector were measured in successive 3–5 m sectors. Sector volumes (V) were $V = r^2l$, where r and l are the mid-radius and length of the sector. The volumes of the sectors were summed to estimate total bole volume. The specific gravity for teak wood (Nazma et al., 1981) was multiplied by the total wood volume to obtain the

bole biomass. Regressions were established between bole biomass values and GBH.

The total number of the first-order branches in individual trees was recorded. From each tree, three branches (small, medium and large) were randomly selected, cut and weighed. Sub-samples were oven-dried at 80°C to a constant weight. Branch biomass per tree was calculated by multiplying the total number of branches by the mean branch dry weight. Regressions between GBH and total branch weight were calculated.

The total number of second-order branches was recorded for each of the three branches selected. Three branches were randomly selected for leaf count. Leaf biomass was estimated as the product of leaf number and individual leaf weight. The total leaf biomass of the tree was estimated as the product of the leaf biomass in second-order branches and number of secondary branches on the tree.

Through girth/biomass regression the mean bole and branch weights were determined for each girth class. The number of trees in each girth class was multiplied by the corresponding mean tree biomass, and the computed biomass of all girth classes was summed to derive the stand biomass.

Biomass estimation in bamboo was based on destructive sampling, and some of the culms in these plantations which had been marked for felling were used for the purpose. On the basis of culm colour and the presence or absence of a leaf sheath, bamboo culms were classified into four age groups (Khan, 1962): 1-, 2-, 3- and > 3-year-old culms. Five culms from each of five girth classes in each age group were selected at random. Thus a total of 25 culms were selected as destructive samples for every age group. GBH and the total length of the culm were recorded. Immediately after felling, the fresh weights of the foliage, branches and culms were determined individually. Sub-samples were taken to the laboratory for oven-drying at 80°C. Simple regression equations were developed between the weights of foliage, branches, culms and above-ground parts and d^2h (d , diameter; h , height) for each age group.

Through the girth/biomass regressions the mean culm, branch and foliage weights were determined in each girth class. The number of culms of a given age class and in each girth class was multiplied by the corresponding mean above-ground biomass value,

and the computed biomass of all girth classes was summed to derive the stand biomass.

The biomass of herbs, shrubs and tree seedlings was determined separately by harvesting above-ground biomass during October–November 1992, when most plant categories were at peak biomass. In each replicate site, twenty-five 1 m × 1 m quadrats were laid out for biomass estimation. The biomass of each plant category was further separated into the main stem, branches and leaves, before oven-drying at 80°C to constant weight. Biomass estimation of saplings and mature trees of miscellaneous species was based on regression equations already derived from earlier studies (Rai, 1981).

Annual biomass increment of herbs, shrubs, seedlings and saplings was estimated based on sequential measurements of biomass. In the case of teak and miscellaneous trees, differences in the above-ground biomass values of 1992 and 1993 represented the annual increment in above-ground biomass. In the case of bamboo, the annual increment in above-ground biomass was the sum of the differences in recorded biomass values for 1992 and 1993 and the biomass produced in the form of new culms in 1993.

3.4. Litter production

Ten 1 m × 1 m litter traps with sides 20 cm high were laid out at each of the three locations on a given site in each plantation. Litter was collected at monthly intervals (except during the rainy season when fortnightly collections were made) from February 1992 to January 1993 and categorized into leaf and non-leaf litter, and then further separated into teak, bamboo and miscellaneous plants litter. The dry weight of litter produced was based on the constant weight attained after oven-drying the samples at 80°C.

3.5. Net productivity

The annual litter production was added to the annual biomass increment to obtain net primary productivity. No data on herbivory were collected.

3.6. Soil and plant chemical analysis

Soil sampling from three replicate plots at each site was done in November 1992 at depths of 0–10 cm, 10–20 cm and 20–30 cm. Ten random samples were collected from each plot and a composite sample was prepared for each depth. The air-dried soil was ground, passed through a 2-mm sieve and stored in plastic containers. The sand, silt and clay contents in 2 mm air-dried soil samples were estimated by preparing soil suspensions with a dispersant (sodium carbonate + sodium hydroxide) and measuring the density of suspension at stipulated times using a standardized hydrometer.

The pH of soil was determined electrochemically in a soil–water suspension (1:2.5 by weight) using a glass electrode. Chemical analyses were done following standard procedures (Jackson, 1968; Allen et al., 1974; Association of Official Analytical Chemists, 1980). Total nitrogen was determined by the micro-Kjeldahl method, by digestion of the soil with sulphuric acid and Kjeldahl distillation of the ammonium sulphate which was formed. Exchangeable calcium was extracted using 1 M ammonium acetate solution (pH 7) and estimated by EDTA titration. Exchangeable potassium was extracted with sodium acetate extractant (Morgan's reagent) and estimated using a flame photometer.

The weight of each element in the soil was calculated using bulk density estimates (the quotient of the dry weight of the soil to the total volume it occupies in the field) from the air-dried mass of a known field volume. The soil was removed as a disturbed sample and the excavated hole was filled with a measured volume of sand (British Standard Institution, 1967).

For the elemental analysis of vegetation, the samples of teak and bamboo were analyzed separately; the herbs, shrubs and miscellaneous tree species were combined into a composite sample. However, in each case, leaves, branches and main stems (boles in the case of teak and culms in the case of bamboo) were analyzed separately. Litter samples were also separated into leaf and non-leaf parts, and leaf litter was further categorized as bamboo, teak and miscellaneous species.

Oven-dried plant and litter samples were ground and passed through a 0.5 mm sieve and analyzed

following standard procedures (Allen et al., 1974). Nitrogen was determined from Kjeldahl digestion. After wet digestion with triple acid, calcium was estimated titrimetrically, while potassium was estimated by the flame-photometry method.

The quantities of the various elements in the biomass were estimated based on the biomass values obtained for the plant categories at each sampling site. In the same way, the amounts of the various nutrients returned through the litter was computed based on the annual litter production by the different plant categories.

3.7. Nutrient cycling

In the present study, only the cycling of elements between the soil and ground vegetation was considered. The fractional annual turnover of each element was calculated by dividing the weight that left the compartment by the weight held in the compartment, expressed as a percentage (Reiners and Reiners, 1970). Thus for the vegetation, the weight of a given element lost through litterfall was divided by the weight of that element held in the vegetation. Similarly, for the soil, the weight of an element taken up by the species/vegetation was divided by the weight of that element held in the soil. To compare the rates at which elements were incorporated into the vegetation, the enrichment ratio was calculated for each element as the quotient of its weight in the above-ground vegetation of a stand divided by its increase in the above-ground living biomass plus litterfall (Woodwell et al., 1975).

3.8. Statistical analysis

Statistical differences between the three sites (the bamboo-rich area, site type A; the moderately bamboo-rich area, site type B; the bamboo-poor area, site type C) for each of the parameters studied were examined through analysis of variance (ANOVA). If the ANOVA value was found to be significant ($P \leq 0.05$ – 0.001), the parameter mean values were compared using Fisher's least significant difference (LSD) test. The correlation coefficients were computed to measure the mutual relationship between teak and bamboo for any given parameter in a given type of site studied.

4. Results

4.1. Floristic composition

The density, basal area and species diversity index of various plant categories in the three site-types of teak plantations of different ages are given in Table 1. While shrubs, seedlings, saplings and mature trees of miscellaneous species showed generally higher values for all three parameters in site type C, herbs were denser and had more basal cover in site type A and more species diversity in site type B. Although the density of teak did not show any significant difference among the three site types ($P > 0.05$), its basal area was significantly higher ($P < 0.05$) in site type C than in site types B and A. In the case of bamboo, the highest values for density and basal area were recorded in site type A, followed by site types B and C. Similarly, the number of bamboo culms recorded was also higher in site type A, followed by B and C, but no significant difference ($P > 0.05$) was observed between site types A and B for percentage frequency values (Table 2).

4.2. Biomass productivity

Simple linear equations developed between d^2h and the biomass of different components of bamboo (culm, branches, foliage and total above-ground plant body) of different ages are given in Table 3. There was a significant correlation between the d^2h values and the dry-weight values of different components ($r = 0.769$ – 0.9653 , df 13, $t = 4.348$ – 13.323). The predicted and initial estimates of each component were also strongly correlated ($r = 0.565$ – 0.969 , df 13). Similarly, d^2h values of teak trees were also strongly correlated with the dry weights of their different components (Table 4). A strong correlation was found between the values of the actual dry weight and the predicted dry weight of each plant component of teak.

Total above-ground biomass estimated in 20- and 15-year-old teak plantations was 157.3 ± 19.6 and 141.7 ± 11.8 t ha⁻¹, respectively, in site type A, 184.3 ± 15.7 and 112.1 ± 11.5 t ha⁻¹, respectively, in site type B and 192.0 ± 10.1 and 164.9 ± 27.8 t ha⁻¹, respectively, in site type C. No significant difference was noted in the values of total above-

Table 1

Density, basal area and species diversity index values of different categories of plants in three site types^a in 20- and 15-year-old teak plantations in Kariem-muriem, Nilambur, Kerala, India

Plant categories and site types	Density (individuals ha ⁻¹)		Basal area (m ² ha ⁻¹)		Species diversity index (<i>H</i>)	
	20 years	15 years	20 years	15 years	20 years	15 years
Herbs						
Site type A	876 400	1 086 000	4.10	7.88	0.0788	0.0635
Site type B	786 000	84 000	2.92	5.99	0.1351	0.0747
Site type C	548 400	742 000	2.43	4.68	0.1144	0.0702
Shrubs						
Site type A	5200	12 400	0.13	0.07	0.5367	0.3820
Site type B	3440	–	0.18	–	0.6271	–
Site type C	18 320	3320	0.95	0.28	0.4024	0.3168
Miscellaneous trees						
Tree seedlings						
Site type A	120	80	0.03	0.04	0.6931	0.6931
Site type B	320	600	0.09	0.20	0.3487	0.1890
Site type C	920	1200	0.21	0.31	0.6692	0.1846
Tree saplings						
Site type A	40	–	0.13	–	0.6931	–
Site type B	120	120	0.30	0.39	0.2688	0.3500
Site type C	160	180	0.53	0.54	0.2253	0.2454
Mature trees						
Site type A	22	28	0.33	0.45	0.1830	0.2400
Site type B	36	26	1.53	0.37	0.1290	0.1620
Site type C	50	52	3.14	1.29	0.1070	0.1010

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

Table 2

Density and basal area of bamboo and teak and percentage frequency and size of bamboo clumps in site types A, B and C^a in teak plantations of different ages in Kariem-muriem, Nilambur, Kerala, India. Data are mean ± SE, *n* = 3; values in parentheses are SE

Plant categories and parameters	Age of plantation (years)					
	20			15		
	A	B	C	A	B	C
Bamboo						
Density (number of clumps ha ⁻¹)	80 (2.9)	37 (1.7)	12 (1.7)	120 (2.9)	80 (2.9)	22 (1.7)
Percentage frequency	100.0 (0)	91.6 (8.3)	45.8 (8.3)	100.0 (0)	100.0 (0)	70.8 (4.2)
Number of culms ha ⁻¹	1876.7 (57.9)	1520.0 (58.7)	300.0 (14.5)	2968.3 (16.4)	1425.0 (48.6)	208.3 (8.3)
Basal area (m ² ha ⁻¹)	12.7 (1.22)	8.34 (0.86)	2.38 (0.45)	21.17 (3.12)	9.02 (1.02)	0.67 (0.08)
Teak						
Density (individuals ha ⁻¹)	216.7 (33.4)	250.0 (0)	300.0 (28.9)	233.3 (60.2)	216.7 (16.7)	333.3 (33.3)
Basal area (m ² ha ⁻¹)	12.17 (2.54)	17.96 (1.19)	23.64 (1.37)	5.97 (1.55)	10.34 (1.34)	17.92 (5.61)

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

Table 3
Predicted equations for compartmental dry weights of culms of *Bambusa arundinacea* of different ages

Component (kg)	Culm age (years)	Simple linear equations ^a	r-value	t-value (df 13)
Culm ^b	1	$9.599 + 111.303d^2H$	0.9071	7.768 *
	2	$9.457 + 77.815d^2H$	0.9329	9.338 *
	3	$10.170 + 97.031d^2H$	0.9255	8.619 *
	> 3	$8.298 + 77.672d^2H$	0.9279	8.974 *
Branch	1	$4.310 + 17.690d^2H$	0.9237	8.657 *
	2	$4.530 + 33.510d^2H$	0.9284	9.008 *
	3	$4.099 + 66.236d^2H$	0.9312	9.212 *
	> 3	$4.068 + 36.608d^2H$	0.9012	7.499 *
Leaf	1	$1.578 + 5.787d^2H$	0.9201	8.4688 *
	2	$33.876d^2H - 0.6154$	0.9315	9.235 *
	3	$2.102 + 5.601d^2H$	0.7698	4.348 *
	> 3	$2.302 + 6.545d^2H$	0.9358	9.568 *
Total	1	$15.487 + 134.779d^2H$	0.9212	8.5340 *
	2	$13.371 + 145.202d^2H$	0.9653	13.3230 *
	3	$16.372 + 148.869d^2H$	0.9290	9.0500 *
	> 3	$14.668 + 120.826d^2H$	0.9242	8.7240 *

^a d , diameter at breast height (m); H , height of culm (m).

^b Culm without branches or leaves.

* $P < 0.001$.

ground biomass in the three sites in each plantation ($P > 0.05$). For each site type in a given plantation, the contribution of teak to the total above-ground biomass was generally higher (58.4 and 25.7% in site type A of 20- and 15-year-old plantations, respectively, 64.6 and 56.5% in site type B, and 84.3 and 92.7% in site type C). However, the contribution of bamboo to the total above-ground biomass was greater in site type A (39.8 and 71.9% in 20- and 15-year-old plantations, respectively), followed by site type B (30.2% and 40.9%) and site type C (5.7

and 3.0%). Comparison of the above-ground biomass of teak and bamboo was made for the three site types in each plantation. While a significantly higher value for teak biomass was recorded in site type C than in site type A ($P < 0.05$), bamboo showed a higher value in site type A than in B or C ($P < 0.001$).

Correlation coefficients were computed to measure the mutual relationship between the above-ground biomass of bamboo and that of teak. In the case of site type A, the biomass of bamboo and teak were negatively correlated ($r = -0.7207$, $n = 9$, P

Table 4
Predicted equations for compartmental dry weights of 15–20-year-old *Tectona grandis*

Component (kg)	Simple linear equations ^a	r-value	t-value (df 23)
Bole	$0.942 + 512.69d^2H$	0.999	611.59 *
Branch	$0.156 + 144.89d^2H$	0.977	21.97 *
Leaf	$74.0d^2H - 2.72$	0.994	43.97 *
Total	$0.26 + 730.55d^2H$	0.999	124.26 *

^a d , diameter at breast height (m); H , height of bole (m).

* $P < 0.001$.

Table 5

Element concentrations (% dry weight) in different plant components of teak, bamboo and other plants in 15–20-year-old teak plantations in Kariem-muriem, Nilambur, Kerala, India. Values in parentheses are SE

Elements	Main branches	Other branches	Leaves	Leaf litter	Non-leaf litter
Bamboo					
Nitrogen	0.50 (0.01)	0.56 (0.02)	0.77 (0.04)	0.86 (0.06)	0.51 (0.02)
Potassium	0.16 (0.01)	0.18 (0.02)	0.32 (0.03)	0.16 (0.04)	0.20 (0.03)
Calcium	0.28 (0.02)	0.32 (0.04)	0.48 (0.04)	0.50 (0.04)	0.30 (0.05)
Teak					
Nitrogen	0.26 (0.04)	0.32 (0.02)	0.86 (0.09)	0.69 (0.08)	0.31 (0.02)
Potassium	0.12 (0.02)	0.20 (0.06)	0.58 (0.06)	0.13 (0.04)	0.18 (0.02)
Calcium	0.36 (0.05)	0.53 (0.09)	0.36 (0.07)	0.36 (0.06)	0.40 (0.09)
Miscellaneous plants					
Nitrogen	0.52 (0.06)	0.52 (0.08)	0.56 (0.04)	1.64 (0.20)	0.48 (0.03)
Potassium	0.12 (0.04)	0.12 (0.02)	0.23 (0.03)	0.10 (0.02)	0.09 (0.02)
Calcium	0.44 (0.01)	0.42 (0.03)	0.36 (0.01)	0.24 (0.01)	0.20 (0.03)

Table 6

Enrichment quotient elements of vegetation in three site types ^a of teak plantations of different ages in Kariem-muriem, Nilambur, Kerala, India. Data are mean \pm SE, $n = 3$

Element, age of plantation and site type	Plant categories			
	Teak	Bamboo	Others	Total
Nitrogen				
20 years				
A	54.1 \pm 4.6	71.9 \pm 2.7	62.9 \pm 0.9	68.0 \pm 2.1
B	41.8 \pm 0.9	74.3 \pm 3.6	56.4 \pm 2.6	62.9 \pm 2.2
C	38.2 \pm 3.4	64.3 \pm 7.8	56.4 \pm 0.6	42.4 \pm 2.7
15 years				
A	60.6 \pm 3.1	54.5 \pm 2.6	60.1 \pm 1.7	56.0 \pm 2.9
B	44.9 \pm 1.6	51.8 \pm 2.6	60.7 \pm 0.8	50.0 \pm 2.0
C	48.1 \pm 2.8	89.8 \pm 3.2	59.1 \pm 0.6	45.2 \pm 0.6
Potassium				
20 years				
A	77.5 \pm 3.4	83.8 \pm 1.8	73.6 \pm 0.9	82.4 \pm 1.5
B	68.1 \pm 0.8	85.3 \pm 2.4	73.7 \pm 2.1	80.0 \pm 1.7
C	64.5 \pm 3.3	77.8 \pm 5.5	69.0 \pm 0.5	67.4 \pm 1.4
15 years				
A	82.0 \pm 1.9	70.8 \pm 2.2	70.8 \pm 0.6	73.2 \pm 2.5
B	70.8 \pm 1.4	68.5 \pm 2.2	75.7 \pm 0.7	69.7 \pm 1.9
C	73.2 \pm 2.3	94.4 \pm 3.3	71.0 \pm 0.6	66.7 \pm 0.5
Calcium				
20 years				
A	78.4 \pm 3.3	69.5 \pm 2.9	76.5 \pm 0.7	72.8 \pm 2.4
B	69.3 \pm 0.7	72.1 \pm 3.8	74.4 \pm 2.1	70.6 \pm 2.2
C	65.7 \pm 3.2	61.9 \pm 8.2	75.1 \pm 0.4	65.5 \pm 1.6
15 years				
A	82.8 \pm 1.8	51.6 \pm 2.8	74.0 \pm 1.3	62.5 \pm 3.9
B	71.9 \pm 1.3	48.9 \pm 2.5	76.5 \pm 0.6	61.3 \pm 2.3
C	74.3 \pm 2.2	81.0 \pm 3.0	76.8 \pm 0.5	64.1 \pm 0.5

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

< 0.05), while in site types B and C, no significant correlation was found (site type B, $r = -0.6009$; site type C, $r = -0.469$; for both types of site, $n = 9$, $P > 0.05$).

The annual litter production recorded in 20- and 15-year-old plantations was 8.0 ± 0.5 and 9.9 ± 0.9 t ha⁻¹ year⁻¹, respectively, in site type A, 10.0 ± 0.4 and 9.5 ± 0.5 t ha⁻¹ year⁻¹, respectively, in site type B, and 7.9 ± 0.7 and 6.0 ± 0.2 t ha⁻¹ year⁻¹, respectively, in site type C. Significantly higher litter production ($P < 0.05$ – 0.01) was recorded for bamboo in site type A (4.2 ± 0.5 and 6.7 ± 0.7 t ha⁻¹ year⁻¹ for 20- and 15-year-old plantations, respectively) than in site types B (3.5 ± 0.7 and 4.6 ± 0.4 t ha⁻¹ year⁻¹, respectively) and C (0.63 ± 0.2 and 0.23 ± 0.01 t ha⁻¹ year⁻¹, respectively). However, for teak significantly higher litter production ($P < 0.05$ – 0.01) was recorded in site type C (6.0 ± 0.9 and 4.5 ± 0.3 t ha⁻¹ year⁻¹ for 20- and 15-year-old plantations, respectively) than in site types B (4.9 ± 0.5 and 3.6 ± 0.2 t ha⁻¹ year⁻¹, respectively) and A (2.2 ± 0.1 and 1.7 ± 0.1 t ha⁻¹ year⁻¹, respectively). No significant differences in litter production for total vegetation was noticed among the three site types ($P > 0.05$).

The annual rate of biomass production of the total vegetation in 20- and 15-year-old teak plantations was 23.0 ± 0.9 and 21.3 ± 1.1 t ha⁻¹ year⁻¹, respectively, in site type A, 23.1 ± 0.5 and 16.53 ± 1.2 t ha⁻¹ year⁻¹, respectively, in site B, and 10.8 ± 0.9 and 13.4 ± 1.2 t ha⁻¹ year⁻¹, respectively, in site type C, with significantly higher values in site type A than in site type B ($P < 0.05$ – 0.001). Similarly, the net primary production of the total vegetation (27.9 ± 0.8 and 30.8 ± 1.7 t ha⁻¹ year⁻¹, respectively, in site type A, 23.6 ± 0.3 and 25.0 ± 1.4 t ha⁻¹ year⁻¹, respectively, in site type B, and 22.0 ± 1.2 and 22.3 ± 0.7 t ha⁻¹ year⁻¹, respectively, in site type C) was also significantly higher in site type A than in site type C. In the case of bamboo in 20- and 15-year-old plantations, the annual rate of biomass production (15.9 ± 0.3 and 13.3 ± 0.3 t ha⁻¹ year⁻¹, respectively, in site type A, 14.5 ± 0.5 and 5.9 ± 0.2 t ha⁻¹ year⁻¹, respectively, in site type B, and 1.7 ± 0.08 and 0.6 ± 0.06 t ha⁻¹ year⁻¹, respectively, in site type C) and the net primary productivity (18.3 ± 0.8 and 19.0 ± 0.9 t ha⁻¹ year⁻¹, respectively, in site type A, 11.8 ± 0.5 and 9.0 ± 0.5 t ha⁻¹

year⁻¹, respectively, in site type B, and 6.3 ± 0.4 and 0.9 ± 0.02 t ha⁻¹ year⁻¹, respectively, in site type C) were also significantly higher in site type A than in other site types ($P < 0.05$ – 0.001). However, teak had higher values for both annual rate of biomass production (6.2 ± 0.8 and 7.1 ± 1.2 t ha⁻¹ year⁻¹ for 20- and 15-year-old plantations, respectively, in site type A, 8.1 ± 0.7 and 9.7 ± 1.4 t ha⁻¹ year⁻¹, respectively, in site type B, and 8.2 ± 0.8 and 11.6 ± 1.2 t ha⁻¹ year⁻¹, respectively, in site type C) and net primary productivity (8.3 ± 1.5 and 10.5 ± 1.7 t ha⁻¹ year⁻¹, respectively, in site type A, 10.3 ± 0.4 and 14.7 ± 1.5 t ha⁻¹ year⁻¹, respectively, in site type B, and 14.1 ± 0.8 and 19.7 ± 0.7 t ha⁻¹ year⁻¹, respectively, in site type C) in site type C than in site type A ($P < 0.05$ – 0.01).

4.3. Nutrient cycling

Nutrient concentrations were generally highest in leaves and lowest in main branches, with other branches, leaf litter and non-leaf litter having intermediate values (Table 5). The exception was calcium, the concentration of which was highest in the branches and bole of teak and other plants. In the case of bamboo, no significant difference in calcium or nitrogen concentration was recorded ($P > 0.05$) between leaves and leaf litter.

The quantities of elements in the various compartments of living above-ground biomass, the rate of release of elements through litter fall, the rates of accumulation and uptake of elements in teak, bamboo and a composite mixture of other plants (herbs, shrubs, seedlings, saplings and mature trees of miscellaneous tree species), as well as of pooled vegetation in each plantation site, were calculated as described in the methodology. Since the values of these parameters were essentially a function of the changes in biomass, litter production, annual rate of biomass production and net primary productivity pattern, respectively, these values have not been given in this paper. However, they were used to calculate the enrichment quotient of elements and the fractional turnover of elements in the vegetation.

Table 6 shows the enrichment quotient of elements of teak, bamboo, miscellaneous species and the total vegetation in different site types. In general, enrichment quotients of potassium and nitrogen were

Table 7

Fractional annual turnover of elements in the vegetation in three site types^a of teak plantations of different ages in Kariem-muriem, Nilambur, Kerala, India. Data are mean \pm SE, $n = 3$

Element, age of plantation and site type	Plant categories			
	Teak	Bamboo	Others	Total
Nitrogen				
20 years				
A	6.3 \pm 1.4	10.2 \pm 1.4	34.6 \pm 6.8	8.8 \pm 1.4
B	10.2 \pm 2.2	9.2 \pm 1.7	4.0 \pm 0.2	9.2 \pm 0.9
C	9.2 \pm 1.4	9.6 \pm 2.7	5.1 \pm 0.5	8.7 \pm 0.8
15 years				
A	14.1 \pm 4.1	9.7 \pm 1.1	17.0 \pm 3.6	10.2 \pm 1.2
B	14.2 \pm 2.6	17.1 \pm 2.7	22.4 \pm 1.7	15.2 \pm 0.7
C	7.8 \pm 2.1	6.9 \pm 2.1	14.9 \pm 2.9	9.2 \pm 2.4
Potassium				
20 years				
A	2.1 \pm 1.5	5.0 \pm 1.7	10.0 \pm 1.0	3.9 \pm 0.7
B	3.4 \pm 0.7	4.5 \pm 0.8	1.9 \pm 0.1	3.7 \pm 0.3
C	2.8 \pm 0.3	4.7 \pm 1.3	2.1 \pm 0.2	2.9 \pm 0.2
15 years				
A	4.7 \pm 1.4	4.8 \pm 0.5	10.3 \pm 2.2	4.8 \pm 0.6
B	4.7 \pm 0.9	7.3 \pm 1.5	11.0 \pm 0.9	6.1 \pm 0.2
C	2.6 \pm 0.7	3.7 \pm 0.4	6.1 \pm 1.2	2.9 \pm 0.6
Calcium				
20 years				
A	2.0 \pm 0.5	11.5 \pm 1.6	8.7 \pm 0.8	5.1 \pm 1.0
B	3.2 \pm 0.7	10.4 \pm 1.9	1.8 \pm 0.1	4.6 \pm 0.5
C	2.7 \pm 0.3	10.8 \pm 3.0	1.5 \pm 0.1	2.9 \pm 0.2
15 years				
A	2.1 \pm 0.2	24.7 \pm 3.5	8.8 \pm 1.9	9.5 \pm 1.6
B	1.9 \pm 0.4	16.7 \pm 1.7	10.5 \pm 0.8	4.5 \pm 0.7
C	4.1 \pm 1.1	8.2 \pm 0.8	4.5 \pm 0.9	2.5 \pm 0.3

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

Table 8

Soil physical and chemical properties in site types A, B and C^a of teak plantation of different ages in Kariem-muriem, Nilambur, Kerala, India. Data are mean \pm SE, $n = 3$. Values in parentheses are SE

Soil properties	Age of plantation (years)					
	20			15		
	A	B	C	A	B	C
Sand (%)	85.0 (1.3)	64.0 (3.2)	49.0 (2.2)	84.0 (2.4)	60.0 (4.2)	48.0 (1.8)
Silt (%)	8.7 (0.9)	15.0 (1.2)	29.3 (1.5)	9.6 (1.6)	19.8 (2.4)	34.6 (3.2)
Clay (%)	6.3 (1.0)	21.0 (4.4)	21.7 (1.5)	6.4 (0.8)	20.2 (1.7)	17.4 (3.2)
pH	5.03 (0.05)	5.36 (0.08)	5.74 (0.06)	5.05 (0.05)	5.36 (0.02)	5.81 (0.04)
Total nitrogen (%)	0.230 (0.006)	0.287 (0.014)	0.376 (0.008)	0.234 (0.018)	0.329 (0.030)	0.440 (0.043)
Extractable potassium (%)	0.029 (0.002)	0.036 (0.003)	0.027 (0.002)	0.031 (0.001)	0.038 (0.003)	0.026 (0.003)
Extractable calcium (%)	0.086 (0.003)	0.112 (0.006)	0.125 (0.003)	0.084 (0.004)	0.097 (0.002)	0.118 (0.005)
Mass (kg ha ⁻¹)						
Total nitrogen	7387 (138)	9737 (430)	14336 (408)	7650 (78)	11249 (210)	16896 (192)
Extractable potassium	935 (42)	1245 (94)	1065 (75)	1014 (24)	1300 (42)	998 (17)
Extractable calcium	2811 (99)	3842 (192)	4808 (132)	2747 (64)	3317 (27)	4531 (48)

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

significantly higher in bamboo than in teak. However, teak had higher enrichment ratios for calcium. Comparison of the three site types in each plantation showed that enrichment ratios of elements for teak were significantly higher in site type A, followed by site types B and C, whereas no clear trend was evident for this parameter in the cases of bamboo and the total vegetation. While the general trend of enrichment quotients of elements for teak was $Ca \geq K > N$, the trends for bamboo and the total vegetation were $K > Ca \geq N$ and $K \geq Ca > N$, respectively.

The percentage annual turnover of nitrogen and potassium for bamboo and teak generally showed no significant differences ($P > 0.05$), but the fractional

annual turnover of calcium was significantly higher in bamboo than in teak (Table 7). The general trend of the fractional turnover of elements in teak was $N > K \geq Ca$ and those for bamboo and total vegetation were $Ca > N > K$ and $N > Ca \geq K$, respectively. Comparison between sites for the fractional annual turnover rates of elements for teak, bamboo and the total vegetation revealed that there was no significant difference between sites for these values, and no regular trend in these values in any given plant category.

Soils of site type A were more sandy than those of site types B and C, while the clay and silt contents were higher in site type C, followed by site type A (Table 8). Significantly higher values for pH, and the

Table 9
Fractional annual turnover of elements in the soil in three site types^a of teak plantations of different ages in Kariem-muriem, Nilambur, Kerala, India. Data are mean \pm SE, $n = 3$

Element, age of plantation and site type	Plant category			
	Teak	Bamboo	Others	Total
Nitrogen				
20 years				
A	0.46 \pm 0.03	1.75 \pm 0.04	0.14 \pm 0	2.47 \pm 0.05
B	0.60 \pm 0.05	1.17 \pm 0.02	0.06 \pm 0	1.95 \pm 0.03
C	0.46 \pm 0.06	0.11 \pm 0.01	0.09 \pm 0	0.69 \pm 0.03
15 years				
A	0.41 \pm 0.07	1.63 \pm 0.08	0.16 \pm 0.02	2.31 \pm 0.1
B	0.40 \pm 0.01	0.72 \pm 0.04	0.12 \pm 0	1.30 \pm 0.04
C	0.36 \pm 0.02	0.12 \pm 0.01	0.80 \pm 0	0.55 \pm 0.01
Potassium				
20 years				
A	1.1 \pm 0.1	4.5 \pm 0.3	0.1 \pm 0	5.7 \pm 1.4
B	1.2 \pm 0.2	3.0 \pm 0.1	0.1 \pm 0	4.3 \pm 0.4
C	1.6 \pm 1.2	0.5 \pm 0.1	0.2 \pm 0	2.2 \pm 0.3
15 years				
A	1.0 \pm 0.1	3.6 \pm 0.3	0.2 \pm 1.0	4.8 \pm 0.4
B	1.0 \pm 0.3	1.8 \pm 0.2	0.2 \pm 0.5	2.9 \pm 0.3
C	1.7 \pm 0.4	0.7 \pm 0.2	0.2 \pm 0.7	2.6 \pm 0.5
Calcium				
20 years				
A	1.3 \pm 0.2	2.5 \pm 0.2	0.1 \pm 0	4.0 \pm 0.2
B	1.5 \pm 0.1	1.6 \pm 0.2	0.1 \pm 0	3.1 \pm 0.3
C	1.3 \pm 0.2	0.2 \pm 0.1	0.1 \pm 0	1.5 \pm 0.2
15 years				
A	1.4 \pm 0.2	2.5 \pm 0.3	0.2 \pm 0	4.0 \pm 0.4
B	1.3 \pm 0.1	1.4 \pm 0.1	0.2 \pm 0	2.9 \pm 0.2
C	1.4 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0	1.6 \pm 0.2

^a Site type A, bamboo-rich area; site type B, moderately bamboo-rich area; site type C, bamboo-poor area.

concentrations and quantities of nitrogen and calcium in the soil were recorded in site type C than in the other two site types. However, both the concentration and mass of potassium in the soil were higher in site types B and A than in site type C.

The fractional annual turnover of elements in the soil showed a clear difference among plant categories (Table 9). While the percentage annual turnover of each element was higher in site type A than in site type C for bamboo and the total vegetation, in general, no clear trend was observed for teak. Comparison of the fractional annual turnover of elements in the soil showed that while the values for each element for bamboo were higher in site type A, teak had higher values in site type C. The trend of fractional annual turnover rate of elements in the soil with respect to teak was $Ca \geq K > N$, and the trends for bamboo and total vegetation were $K > Ca > N$ and $K \geq Ca > N$, respectively.

5. Discussion

The three site types, i.e. the bamboo-rich area (site type A), the moderately bamboo-rich area (site type B) and the bamboo-poor area (site type C) were chosen on the basis of the distribution pattern of bamboo in teak plantations in the Kariem-muriem Reserve of the Nilambur Forest Division, Kerala. These three site types were also different from each other with respect to their vegetation structure, soil quality, above-ground biomass production and nutrient cycling patterns. The negative correlation between the biomass of bamboo and teak observed in site type A may indicate that the bamboo suppresses the growth of teak by competing with it for soil nutrients and space. The poor performance of shrubs, tree seedlings and saplings in terms of biomass production on site type A may also be attributed to the dominance of bamboo at that site. For any given teak plantation, although type A sites have less teak biomass production than type C sites, there is no significant difference between them in biomass production by the vegetation as a whole. This is because the low biomass production by teak on site type A is compensated by the high biomass production by bamboo. Thus, the colonized bamboo on type A sites makes these as productive as type C sites.

The role of a particular species in nutrient cycling in a given ecosystem is evident when the enrichment quotients, and the fractional turnover rates of elements in the vegetation and the soil are studied to compare these parameters among the different species in the system. For example, in the present study, it was observed that the enrichment quotient values of potassium and nitrogen were higher for bamboo than for teak. Similarly, in bamboo, while the percentage annual turnover rate of potassium is lower than those of other elements studied, the fractional turnover rate of potassium in the soil with respect to bamboo was greater than for other elements. These two observations are important in terms of understanding the role of bamboo in the accumulation and release patterns of elements such as nitrogen and potassium. Although bamboo stores more nitrogen in its biomass, it has a much higher turnover rate of nitrogen than of potassium. This is because of a much higher concentration of nitrogen than of potassium in the leaves and leaf litter. However, as potassium is a labile element it is more readily lost than divalent cations through run-off and percolation of water in disturbed ecosystems (Allen, 1964; Lloyd, 1971). Therefore, the rapid accumulation of this element in the biomass is significant in view of the losses in disturbed areas of tropical forest ecosystems. During the ecosystem recovery phases, one or more species play an important role in conserving nutrients, especially easily leachable elements such as potassium (Bartholomew et al., 1953; Greenland and Kowal, 1960; Swamy and Ramakrishnan, 1987; Chandrashekara and Ramakrishnan, 1994). The role of bamboo species in conserving nutrients, especially potassium, during secondary succession following slash-and-burn agriculture in north-east India has also been reported (Toky and Ramakrishnan, 1982; Rao and Ramakrishnan, 1989). At this juncture, an attempt may be made to ascertain the possible role played by *Bambusa arundinacea* in the conservation of potassium in the teak plantations studied. The soil of site type A is characterized by having more potassium than the soil of site types B and C. It should also be noted here that the soils of site type A are prone to temporary water logging, and the loss of nutrients in run-off can also be expected. The better performance of bamboo under conditions which appear unsuitable for teak, and the capacity of bamboo to accumulate potassium

in larger amount than other nutrients suggest that bamboo not only makes the site productive, but also helps in conserving easily leachable element, e.g. potassium. The lower accumulation of calcium in bamboo biomass and the higher fractional annual turnover rate of calcium, especially on site type A, may indicate faster cycling of calcium in this species and its adaptability to calcium-poor soils.

From the nutrient conservation and cycling point of view, teak is not a suitable species for site type A. This is because teak has got the capacity to store calcium in its biomass, as observed in this study, which leads to a calcium deficiency in the soil of type A sites which is already calcium-poor. The inability of teak, as compared with bamboo, to conserve potassium may lead to loss of potassium from the site owing to the absence of any vegetation that can accumulate it at faster rate. However, on type C sites, which are richer in calcium than type A sites, the fact that teak has a higher enrichment ratio, a low release pattern and a faster assimilation rate for calcium makes it a suitable crop. Thus from the nutrient cycling point of view, it can be concluded that bamboo is a suitable species for type A sites and teak is an ideal species for type B and C sites. It may be worth mentioning here that Kallarackal et al. (1992) reported a relationship between the water blister problem and the proximity of teak trees to a water course.

6. Management implications

These observations of the different performances of bamboo and teak in the areas studied, the ecological requirements of these two species and their role in biomass production and nutrient cycling have many implications for the management of teak plantations, especially those of site qualities II and III. Since even in a given landscape bamboo and teak perform differently, managing these two species demands different approaches based on a greater appreciation of their ecology. As recorded in this study, teak does not perform well in terms of biomass production and nutrient stability in areas of the plantation like site type A (bamboo-rich). Thus attempts to cultivate teak in such areas are not advisable.

However, the presence of bamboo is preferable in type A sites than in site types B and C (moderately bamboo-rich and bamboo-poor, respectively). Thus, interplanting of bamboo in teak plantations, especially in areas like site types B and C, may not give the expected yield. Instead, patch-planting may be more appropriate for sites of type A from the point of view of better yield. In many tropical forest ecosystems conserving potassium seems to be crucial, as it is a labile element. This function is achieved remarkably well in widely scattered forest ecosystem types through some keystone species such as early secondary *Musunga cecropioides* in Africa, *Dendrocalamus hamiltonii* in north-east India, a set of shrubs and trees at the seedling–sapling stage in canopy gaps in rainforests in Kerala, and *Bambusa arundinacea* in teak plantations in Kerala. Management of such key elements of the ecosystem after perturbation or conversion of natural ecosystems into plantation systems is crucial for the stability of the ecosystem. Thus attempts to retain or introduce bamboo in teak plantations in areas like site type A (bamboo-rich) can also help in the conservation of nutrients as well as making such land as productive as site types B and C (moderately bamboo-rich and bamboo-poor, respectively).

Acknowledgements

I am grateful to Dr. K.S.S. Nair, Director, and to Dr. S. Chand Basha, former Director, for their keen interest and encouragement. Drs. R. Gnanaharan and S. Sankar are gratefully acknowledged for their support and the laboratory facilities made available for soil and plant chemical analyses. Thanks are due to K.C. Chacko, Dr. R.C. Pandalai and Dr. K.V. Bhat for their help, valuable comments and suggestions. I wish to thank Dr. B. Mohan Kumar, Kerala Agricultural University, for his helpful comments on an earlier version of the manuscript. This investigation is part of a project on silviculture, management and utilisation of bamboo resources of Southern India funded by the International Development Research Centre (IDRC), Canada, to the Kerala Forest Research Institute.

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