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Biomass, net primary production and impact of bamboo plantation on soil redevelopment in a dry tropical region

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Abstract

Growth and impact of a bamboo (*Dendrocalamus strictus* (Roxb.) Nees) plantation on mine spoil in a dry tropical region were examined. Culm dynamics, biomass, net primary production, soil microbial biomass and N-mineralization were estimated at ages 3, 4, and 5 years. The recruitment of culm population varied between 18% and 36% and shoot mortality from 6–7% per year. Net accumulation of green culms during 3rd and 4th year was 3999 and between 4th and 5th year 10854 ha⁻¹. Total biomass was 46.9 t ha⁻¹ in the 3-year old to 74.7 t ha⁻¹ in the 5-year old plantation with 35% occurring belowground. Total net primary production (NPP) ranged between 20.7 t ha⁻¹ (3-year old) and 32.0 t ha⁻¹ (5-year old), of which aboveground net production was 17.0 to 24.7 t ha⁻¹ (between 3 to 4, and 4 to 5 years, respectively). Accounting for only 14% of the total biomass, foliage contributed 36% to NPP. Nutrient deposition through leaf litter was 45–79 kg N and 6–11 kg P ha⁻¹. Litter bag experiment indicated 235 days for 50% and more than 1000 days for 95% decomposition. Amounts of N and P deposition and release increased with the age of the plantation. Rate of N-mineralization increased from 3.3 (3 years) to 6.9 μg g⁻¹ month⁻¹ (5 years). The proportion of mineralized-N converted into nitrate decreased with age. Soil microbial C increased from 127–319, microbial-N from 19–38 and microbial-P from 9–16 μg g⁻¹ soil between 3 to 5 years. With increasing age of plantation, a greater proportion of soil C, N and P tended to be immobilized in soil microbial biomass. Net primary production and the soil redevelopment process exhibited a positive feed-back relationship. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Dendrocalamus strictus*; Litter decomposition; Microbial biomass; Mine spoil; Net primary production; N-mineralization; Restoration; Soil redevelopment

1. Introduction

Opencast coal mining removes surface earth, piling it over unmined land to form chains of external dumps. Mine spoils are physically, nutritionally and biologi-

cally impoverished habitats, therefore their natural recovery is a slow process (Wali and Pemble, 1982; Wali, 1987; Jha and Singh, 1991, 1992). Restoration of such habitats requires the establishment of a self-sustaining soil/plant system. Artificial restructuring of vegetation is often essential to check the soil erosion, to restore the soil fertility and to accelerate the natural recovery process (Singh and Jha, 1993;

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Dobson et al., 1997). Vegetation contributes to the accumulation of soil organic matter and plant nutrients. Development of a sufficient organic matter pool to serve as an N source and sufficient N-mineralization potential resulting into nutrient release rates that are adequate for plant growth are essential for sustaining vegetation at an acceptable level of production (Bradshaw et al., 1986). Microorganisms contribute to the re-establishment of biogeochemical processes, and play an important role in soil redevelopment and in the maintenance of soil fertility.

The influence of plant species on the soil, redeveloping under plantations on mine spoils could vary from species to species. For example, Alexander, 1989a, b compared the effects of *Acacia albida* and *Eucalyptus camaldulensis* on the tin-mine spoil in Jos Plateau, Nigeria, and found that *A. albida* was able to improve both the nutrient status and physical conditions in the top 20 cm of the soil beneath its canopy, whereas *E. camaldulensis* caused a progressive increase in the soil acidity and reduction of base content. We believe that a desirable species for planting on mine spoils should possess the ability to (i) grow on poor and dry soils, (ii) develop the vegetation cover in a short time and to accumulate biomass rapidly, and (iii) improve the soil organic matter status and microbial biomass, thereby enhancing the supply of plant-available nutrients. In addition, the species should be of multipurpose economic use.

The bamboo *Dendrocalamus strictus*, a perennial woody tropical grass, is a constituent of native dry tropical forests (Tomar, 1963; Singh and Singh, 1991a). It is a quick-growing and hardy species occurring on a wide range of soil conditions with particularly luxuriant growth on porous, coarse-grained dry soils with low moisture retaining capacity and on well-drained, sandy loam soils overlying boulders on hill sides with an optimum pH 5.5–7.6 (Yadav, 1963). On account of extensive shallow root system and accumulation of leaf mulch, bamboo serves as an efficient agent in preventing soil erosion and conserving moisture, and its plantations are effective for the control of soil erosion, stream bank protection, reinforcement of embankments and drainage channels, etc. (Yadav, 1963). Additionally, bamboo is an important commercial source for a variety of purposes, such as manufacture of paper, construction of houses, bridges, furniture, bags and baskets, and is also utilized,

although to a limited extent, as fuel and fodder. The felling cycle varies between 3–5 years.

In this study we assess the impact of *D. strictus* on soil conditions during the early phases of mine spoil restoration. Since mine spoils are characterized by the loss of soil both in the pedological and biological senses, this study provided an opportunity to understand the soil redevelopment processes following a massive ecosystem degradation. We also compare the biomass and net production levels of *D. strictus* attained in plantation on mine spoil with those of native dry tropical forest. Restoring drastically disturbed ecosystems to acceptable levels of production could contribute to counteracting emissions of CO₂ to the atmosphere.

2. Materials and methods

2.1. Study site

The experimental plots were located at the Jayant project in the Singrauli coalfield which extends over 2200 km² (lat. 23°47'–24°12'N, long. 81°48' to 82°52' E, and elevation 280–519 m above msl). The climate is tropical monsoonal and the year is divisible into a mild winter (November–February), a hot summer (April–June) and a warm rainy season (July–September). A meteorological station established on the site showed that the mean monthly minimum temperature within the annual cycle ranges from 6.4–28°C and mean monthly maximum from 20–42°C. The annual rainfall averages 1069 mm, of which about 90% occurs during the period from late June to September. The rainfall is characterized by a high degree of interannual variation, for example during the 1980–1994 period it ranged from 673 to 1450 mm year⁻¹. The bulk density of the soil was 1.67 g cm⁻³, water holding capacity 25.50%, pH 7.03, and soil texture sandy (78.43% sand, 9.13% clay and 12.43% silt). The potential natural vegetation of the area is a dry tropical deciduous forest, in composition similar to that described by Singh and Singh (1991a).

2.2. Stocking density and plant biomass

Plantation of *Dendrocalamus strictus* was raised in July–August 1991 on fresh mine spoil by planting

8-month old nursery-raised seedlings in previously dug pits (40 cm × 40 cm × 40 cm) at a spacing of 2 m × 2 m. Three plots, each 15 m × 15 m in size, were established in 1994. Number of bamboo clumps per plot varied from 45–47. Five clumps in each plot were marked and the number of culms in each clump was counted annually from 1994 (3-year old) to 1996 (5-year old). Bamboo shoots were categorized into current year, old, and standing dead shoots. All culms were measured 10 cm above the ground for circumference and tallied into five size classes between 5 and 15 cm at 2 cm intervals. Fifteen culms of different size classes were harvested. The oven-dry weights of different components, viz. stem, foliage, rhizome, and root were determined. Least squares regression equations were developed to estimate dry weights of each component from culm diameter (Table 1). Biomass for each component for each size class was multiplied by the number of culms in that size class. Summation of values across size classes yielded total biomass, which was calculated separately for each plot for each year.

2.3. Net productivity

Net primary production (NPP) was calculated for the 1994–1995 (4-year old), and 1995–1996 (5-year old) growth cycles separately for each of the three plots, from foliage and current stem biomass and net biomass accumulation in different components using the following expression:

$$\text{NPP}_n = \text{FB}_n + \text{CSB}_n + \Delta\text{OSB} + \Delta\text{DSB} \\ + \Delta\text{RhB} + \Delta\text{RB} + \text{NLL}_n$$

where, NPP_n = net primary production of *n*th year,

FB_n = foliage biomass in *n*th year, CSB_n = stem biomass of current shoots in *n*th year, (OSB = change in old stem biomass between *n* – 1 and *n*th year, (DSB = change in dead shoot biomass between *n* – 1 and *n*th year, (RhB = change in rhizome biomass between *n* – 1 and *n*th year, (RB = change in root biomass between *n* – 1 and *n*th year, and NLL_n = non-leaf litter deposited in *n*th year.

2.4. Leaf litter decomposition

For assessing the dry matter loss through decomposition, freshly fallen leaves were collected during May–June 1994. Nylon net litter bags (10 cm × 10 cm, 1 mm mesh), containing 5 g of air-dried leaf litter were placed on the floor of bamboo plantation in the month of June 1994. Dry weight of the air-dry litter was determined on samples from the same stock. Three litter bags were recovered from each plot at each of the six sampling dates. The recovered litter was air-dried, adhering soil particles were carefully brushed off, and then oven dried at 80°C to constant weight.

The mean relative decomposition rate (MRD) was calculated by using the formula

$$\text{MRD} (\text{mg g}^{-1} \text{day}^{-1}) = \ln(W_1 - W_0) / (t_1 - t_0)$$

where W_0 is the weight of litter at time t_0 , W_1 the weight of litter at time t_1 , and $t_1 - t_0$ is the sampling interval (days). The daily instantaneous decay rate (k) of litter for the study period was calculated using the negative exponential decay model of Olson (1963): $W_t/W_0 = e^{-kt}$, where W_0 is the initial weight and W_t the weight remaining after time t . The time required

Table 1

Constants (a), slopes (b), coefficients of determination (r^2) for regression equations relating biomass to culm diameter. Values in parentheses are 1 SE

Components	a	b	r^2	P
Stem ^a	4.7 (0.2)	1.7 (0.2)	0.93	<0.001
Foliage ^b	4.1 (0.2)	0.5 (0.1)	0.87	<0.001
Rhizome ^c	-155.0 (70.6)	182.1 (19.7)	0.91	<0.001
Root ^a	3.6 (0.3)	1.6 (0.2)	0.83	<0.001

^aLn $Y = a + b \text{ Ln } X$.

^b $Y = \exp(a + bX)$.

^c $Y = a + bX$.

for 50% and 95% weight loss was calculated as $t_{50} = 0.693/k$, and $t_{95} = 3/k$, respectively.

2.5. Soil sampling and analysis

Three soil samples were collected at random from each of the three permanent plots using $15 \times 15 \times 10$ cm monoliths during September in 1994, 1995 and 1996. The samples from within a plot were thoroughly mixed to yield one composite sample per plot. Large pieces of plant materials were removed and the field-moist soil was sieved through a 2 mm mesh screen. Each soil sample was divided into two parts. One part in the field-moist condition was used for the measurement of available nutrients ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$), and for the determination of microbial C, N and P. The other part was used for the determination of dry weight, total organic C, kjeldahl N and total P.

Organic C was determined by dichromate oxidation and titration with ferrous ammonium sulphate (Moore and Chapman, 1986). Kjeldahl N was determined by the microkjeldahl method (Jackson, 1958), and $\text{NH}_4\text{-N}$ was extracted by 2 M KCl and analysed by the phenate method (APHA, 1985). $\text{NO}_3\text{-N}$ was measured by the phenol disulphonic acid method, using CaSO_4 as the extractant (Jackson, 1958). Biocarbonate extractable Pi was determined by the ammonium molybdate-stannous chloride method (Sparling et al., 1985). The soil was digested in a triple acid mixture of HClO_4 , HNO_3 , and H_2SO_4 (1 : 5 : 1) and the digest was analysed for P by a phosphomolybdic acid blue colour method (Jackson, 1958).

2.6. Microbial biomass

The field-moist soil was preincubated by spreading it overnight in a thin layer between two sheets of polyethylene, with the moisture content adjusted to 40% water holding capacity, then transferred to polyethylene bags and incubated for 7 days at 25°C in a large air-tight container that held two vials, one containing 20 ml distilled water to maintain 100% relative humidity and the other containing sodalime to absorb CO_2 . The container was aerated every day by opening the lid for a few minutes. After 1 week, the soil was taken out, mixed and analysed for soil microbial biomass C, N and P by fumigation extraction method

(Brookes et al., 1982, 1985; Vance et al., 1987). In brief, preconditioned soil samples (50 g) were saturated with purified liquid CHCl_3 for 10–20 h (Srivastava and Singh, 1988). The CHCl_3 was subsequently removed by evacuation and then the soil was extracted with 0.5 M K_2SO_4 (1 : 4, soil : extractant) for 30 min for the biomass C and N estimates. For biomass P, another soil sample was extracted with 0.5 M NaHCO_3 for 30 min. Extracts of unfumigated preconditioned soil samples were also obtained.

Microbial C was determined in the mine spoil extracts of fumigated and unfumigated samples by dichromate digestion following Vance et al. (1987). Biomass C (MBC) was then estimated by the equation, $\text{MBC} = 2.64 E_C$, where E_C is the difference between C extracted from the fumigated and non-fumigated soils (Vance et al., 1987). On the same K_2SO_4 soil extracts, biomass N was determined as total N using the kjeldahl digestion procedure. The flush of total N (K_2SO_4 -extractable N in unfumigated soil subtracted from that of fumigated soil) was divided by a KN (fraction of biomass N extracted after CHCl_3 fumigation) value of 0.54 (Brookes et al., 1985). Biomass P was determined as inorganic P in the NaHCO_3 extracts of fumigated and unfumigated soils by the ammonium molybdate-stannous chloride method (Sparling et al., 1985). Biomass P was calculated by dividing the flush of inorganic P (NaHCO_3 -inorganic P in fumigated soil minus that in the unfumigated soil) by a KP value of 0.40 assuming that 40% of P in the soil microbial biomass is released as inorganic P by CHCl_3 (Brookes et al., 1982). All results are expressed on an oven dry soil (105°C , 24 h) basis.

2.7. N-mineralization

N-mineralization was measured by the buried bag technique (Eno, 1960). Two fresh, field-moist, sieved (2 mm) soil samples (150–200 g each) were sealed in large polyethylene bags and buried in soils at 15 cm depth in each plot. Coarse roots and large fragments of organic debris were removed in order to avoid any marked immobilization during incubation. Nitrate-N and ammonium-N were analysed (as mentioned above) at time zero and after 30 days of field incubation. The increase in the concentrations of ammonium and nitrate-N over the course of field incubation is defined as net N mineralization and the increase in

nitrate-N only as nitrification. All results are expressed on an oven-dry soil (105°C, 24 h) basis.

2.8. Statistical analysis

The data were subjected to multifactor Analysis of Variance, and regression analysis using the Statgraphics package (Statistical Graphics Corporation, 1986). Differences in means were tested using multiple range tests.

3. Results

3.1. Culm dynamics, biomass and net primary production

Distribution of live and dead culms in different size classes, for 3rd, 4th and 5th year is summarized in Table 2. The majority of green culms were in the 9–13 cm circumference class, while the dead culms, which averaged 30% of the total culms, dominated the 5–7 cm class. Of the total culms, 14–15% were represented by current year shoots and 54–55% by old shoots. The recruitment to culm population was 5864 ha⁻¹ between the 3rd and 4th year, and 13 679 ha⁻¹ between the 4th and 5th year. Corresponding values for mortality were 1863 culms ha⁻¹

and 2824 culms ha⁻¹; this resulted in net accumulation of 3999 green culms between the 3rd and 4th year and 10 854 green culms ha⁻¹ between the 4th and 5th year.

Total biomass increased from 46.9 t ha⁻¹ in the 3-year old to 74.7 t ha⁻¹ in the 5-year old plantation (Table 3). ANOVA indicated significant differences due to age in the biomass of foliage, old stem, rhizome, root and total biomass. For all the above components only the 5th year biomass was significantly different from that of the previous years (Table 3).

The contribution of different components of the plant to total stand biomass was remarkably consistent across the three ages. A majority of biomass was contributed by live stems (\bar{x} = 42.2%) followed by rhizomes (\bar{x} = 25.3%). Foliage accounted for 14% of the total biomass while roots contributed 9.4%. Thus 65.3% biomass was located above the ground and 34.7% below-ground.

There was a marked temporal variation in the distribution of biomass in the stems of different size classes (Fig. 1). In the stems of current shoots, a majority of biomass resided in the 11–13 cm size class in the 3-year and 4-year old plantation (62.2% and 55.8% respectively), while this size class in the 5th year accounted for only 23.7%. The 11–13 cm size class also harboured a majority of biomass in the old

Table 2
Distribution of green and dead culms in different size classes of *D. strictus* plantation on coal mine spoil

	No. of culms ha ⁻¹ ± 1 SE					Total
	Circumference class (cm)					
	5–7	7–9	9–11	11–13	13–15	
<i>3-year old</i>						
Green	2145 ± 515	3242 ± 2033	10540 ± 773	5502 ± 1958	1046 ± 597	22475 ± 3754
Dead	6500 ± 938	2682 ± 1120	713 ± 645	0	0	9895 ± 764
Total	8645 ± 1210	5923 ± 940	11253 ± 1958	5502 ± 1958	1046 ± 597	32368 ± 3232
<i>4-year old</i>						
Green	2714 ± 390	5027 ± 1714	10117 ± 890	7137 ± 1335	1478 ± 561	26474 ± 2164
Dead	7990 ± 795	2835 ± 1052	933 ± 742	0	0	11758 ± 955
Total	10704 ± 1161	7862 ± 808	11051 ± 1517	7137 ± 1335	1478 ± 661	38232 ± 1651
<i>5-year old</i>						
Green	4998 ± 504	9758 ± 767	10657 ± 1051	8808 ± 699	3108 ± 471	37328 ± 264
Dead	9886 ± 597	3229 ± 990	1467 ± 933	0	0	14582 ± 1323
Total	14884 ± 857	12988 ± 718	12123 ± 1681	8808 ± 699	3108 ± 471	51911 ± 1063

Table 3
Oven-dry stand biomass of bamboo plantation at different ages on mine spoil

Components	Biomass ($\text{t ha}^{-1} \pm 1 \text{ SE}$)		
	3-year old ^a	4-year old ^a	5-year old ^a
Foliage	6.1a \pm 1.2	7.9a \pm 0.6	10.7b \pm 0.3
Current shoot stem	4.5a \pm 0.6	3.7a \pm 0.6	5.4a \pm 0.3
Old shoot stem	15.3a \pm 3.0	19.6a \pm 1.6	26.4b \pm 0.9
Dead shoot stem	4.5a \pm 0.8	5.3a \pm 0.9	6.7a \pm 1.2
Rhizome	11.9a \pm 1.6	14.0a \pm 1.0	18.8b \pm 0.7
Root	3.6a \pm 0.4	4.1a \pm 0.2	5.3b \pm 0.1
Total	46.9a \pm 6.8	55.8a \pm 4.1	74.7b \pm 2.4

^aValues in a row suffixed with different letters are significantly different from each other at $P < 0.05$.

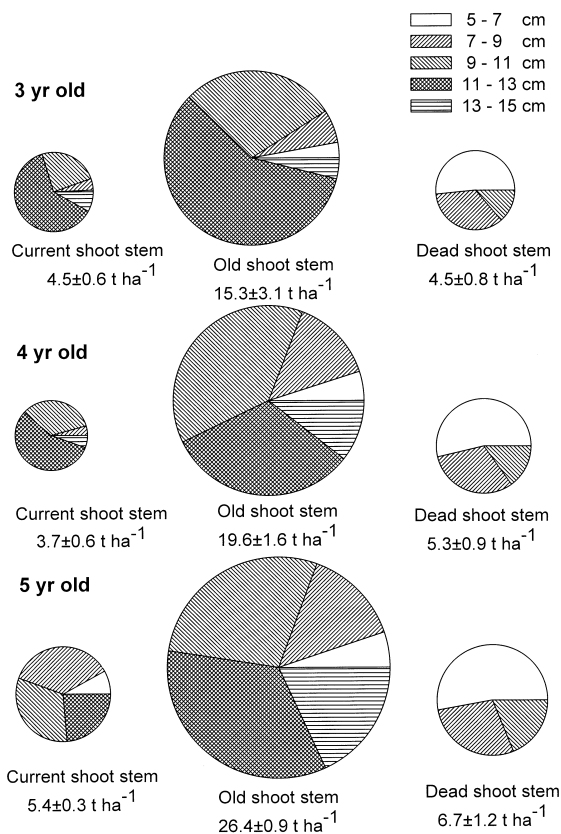


Fig. 1. Distribution of biomass in different size classes of current, old and dead stems of the bamboo plantation at ages 3, 4 and 5 years. Values below the pies are total biomass $\pm 1 \text{ SE}$.

shoots in the 3rd year (58.4%) but contribution of this size class was reduced when the plantation became older (32.3–34.4%). This temporal fluctuation

reflected the different recruitment rates of stems into different size classes. Most of the biomass (>50%) in the dead shoot was accounted by the size class 5–7 cm. Within the stem component, greatest accumulation of biomass occurred in stems of old shoots (Fig. 1).

Net primary production could be calculated only for the 4th and 5th year (Fig. 2). The total net primary production (NPP) of the 5-year old plantation was one and one-half times greater than that for the 4-year old plantation. Net production of each component (foliage, current stem, old stem, dead stem, rhizome and root) was higher for the 5th year compared to the 4th year, but the differences between the 2 years were statistically significant only for foliage, and root. For both the years, stem contributed maximally (42.2%) to NPP followed by foliage (36.1%), rhizome (12.3%) and root (7.9%). The current stems accounted for 40–42%, old stems 48–50%, and dead stems 9–10% of stem production. While the contribution of roots to NPP was remarkably constant (about 7.9%), that of foliage and rhizomes showed mild fluctuation. Thus in comparison to 38.6% and 9.8% contribution, respectively by foliage and rhizomes in the 4-year old plantation, these components accounted for, respectively, 33.7% and 14.7% of NPP in the 5-year old plantation.

3.2. Litter decomposition and nutrient return

The litter bag experiment indicated a significant inverse exponential relationship between per cent weight remaining (Y) and time (X) according to $Y = 100 e^{-0.0032X}$ ($R^2 = 0.9716$, $P < 0.001$) (Fig. 3). Decomposition parameters indicated that for 95%

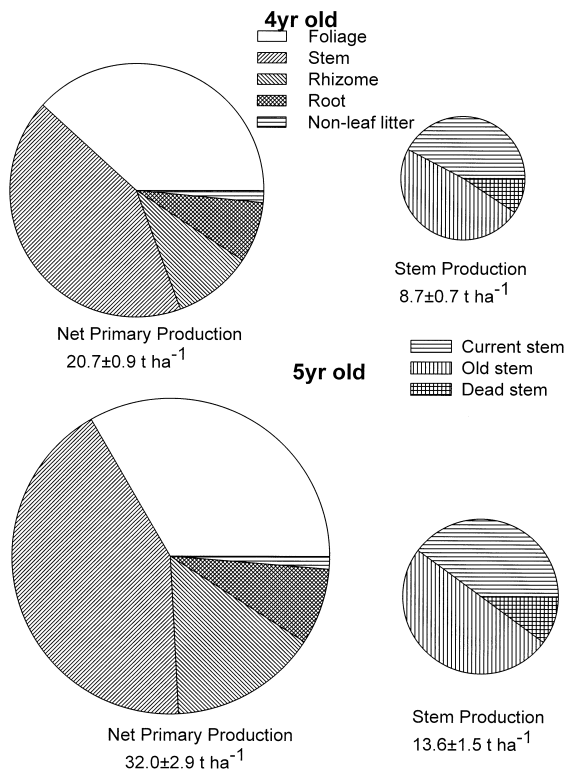


Fig. 2. Share of different plant components in total NPP of bamboo plantation. Values below the pies are total net production \pm 1 SE. The pies on the right represent distribution of stem net production in current, old and dead categories.

Table 4
Decomposition parameters for bamboo leaf litter

	(mean \pm 1 SE)
Decay constant (year^{-1})	-1.08 ± 0.03
Mean relative decomposition rate ($\text{mg g}^{-1} \text{day}^{-1}$)	2.28 ± 0.018
Time for 50% decomposition (days)	235 ± 6
Time for 95% decomposition (days)	1016 ± 27

Table 5
Deposition of N and P through leaf fall and release through decomposition

Age (year)	Leaf fall ($\text{kg ha}^{-1} \text{year}^{-1}$)	N deposition ($\text{kg ha}^{-1} \text{year}^{-1}$)	P deposition ($\text{kg ha}^{-1} \text{year}^{-1}$)	N release ($\text{kg ha}^{-1} \text{year}^{-1}$)	P release ($\text{kg ha}^{-1} \text{year}^{-1}$)
3	6150	45.51	6.33	37.89	5.27
4	7900	58.46	8.14	48.68	6.78
5	10680	79.03	11.00	65.81	9.16

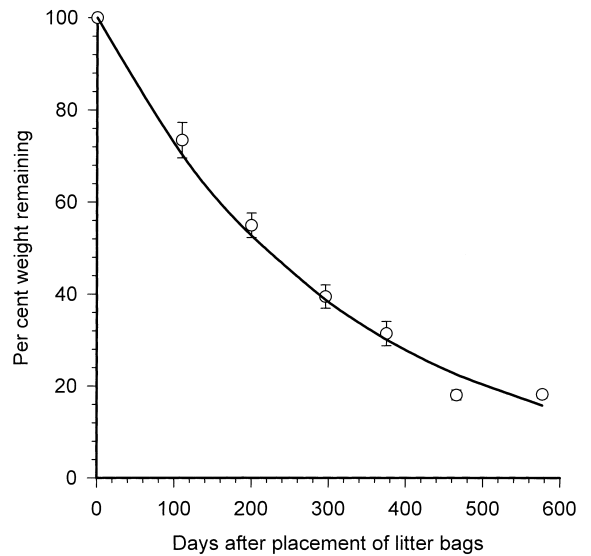


Fig. 3. Relationship between per cent weight of leaf litter remaining and time elapsed since placement of litter bags on plantation floor. Bars are 1 SE and the fitted line represents the regression equation.

mass loss about 2.8 years will be needed, while 50% decomposition occurred within about 8 months (Table 4). The fresh litter of bamboo contained 0.74% N and 0.103% P. Since this bamboo is deciduous, annual leaf fall is equivalent to foliage biomass. On the basis of foliage biomass (Table 3), N and P contents, and mean relative decomposition rate (Table 4), N and P cycling is calculated in Table 5, which shows increasing amounts of deposition and release of N and P with the age of the plantation.

3.3. Soil microbial biomass and nutrient availability

Soil C, N and P contents are given in Table 6. Organic C and kjeldahl N increased with age. ANOVA indicated significant differences in organic carbon and

Table 6
Carbon and nutrient contents of soil and microbial biomass

Parameters	Plantation age (mean \pm 1 SE)		
	3-year ^a	4-year ^a	5-year ^a
Soil organic C (%)	0.34a \pm 0.02	0.50b \pm 0.01	0.67c \pm 0.01
Soil kjeldahl N (%)	0.04a \pm 0.00	0.05b \pm 0.00	0.07c \pm 0.00
Soil total P (%)	0.01a \pm 0.00	0.01a \pm 0.00	0.01a \pm 0.00
SOC : KN	8.48a \pm 0.28	9.22ab \pm 0.56	10.05b \pm 0.13
NH ₄ -N ($\mu\text{g g}^{-1}$)	3.2a \pm 0.2	3.4a \pm 0.2	3.7a \pm 0.1
NO ₃ -N ($\mu\text{g g}^{-1}$)	0.9a \pm 0.1	1.1a \pm 0.1	1.2a \pm 0.2
Mineral N ($\mu\text{g g}^{-1}$)	4.1a \pm 1.7	4.5a \pm 0.3	4.9a \pm 0.1
PO ₄ -P ($\mu\text{g g}^{-1}$)	8.0a \pm 0.6	8.0a \pm 0.6	8.8a \pm 0.4
Microbial biomass C ($\mu\text{g g}^{-1}$)	126.8a \pm 14.2	217.6b \pm 9.8	319.1c \pm 10.6
Microbial biomass N ($\mu\text{g g}^{-1}$)	19.2a \pm 3.0	29.3b \pm 2.4	37.5c \pm 2.9
Microbial biomass P ($\mu\text{g g}^{-1}$)	9.1a \pm 0.2	12.7b \pm 0.1	16.2c \pm 0.2
SOC in biomass C (%)	3.77a \pm 0.55	4.38ab \pm 0.28	4.74b \pm 0.13
TN in biomass N (%)	4.82a \pm 0.86	5.38a \pm 0.19	5.61a \pm 0.47
Total P in biomass P (%)	7.46a \pm 1.14	9.45ab \pm 1.26	12.13b \pm 2.04
MB-C/MB-N	6.72a \pm 0.32	7.47a \pm 0.30	8.56b \pm 0.39
MB-C/MB-P	13.93a \pm 1.27	17.10b \pm 0.82	19.73c \pm 0.42
N concentration of microbial biomass (%)	7.48a \pm 0.36	6.71b \pm 0.28	5.86c \pm 0.26
P concentration in microbial biomass (%)	3.65a \pm 0.35	2.93a \pm 0.14	2.53b \pm 0.05

^aValues in a row suffixed with different letters are significantly different from each other at $P < 0.05$. SOC = soil organic carbon, KN = kjeldahl nitrogen, MB-C = microbial carbon, MB-N = microbial nitrogen, MB-P = microbial phosphorus.

Table 7
Nitrogen mineralization in soils under bamboo plantation

Age (year)	Nitrification ($\mu\text{g g}^{-1} \text{ month}^{-1}$)	N-mineralization ($\mu\text{g g}^{-1} \text{ month}^{-1}$)
3	1.2a \pm 0.2	3.3a \pm 0.4
4	1.7b \pm 0.1	5.2b \pm 0.0
5	1.9c \pm 0.2	6.9c \pm 0.2

Values in a column suffixed with different letters are significantly different from each other at $P < 0.05$.

kjeldahl N due to plantation age. Total P however, did not differ significantly with age of the plantation.

Although mineral P and mineral N contents also increased with age, the increases were not statistically significant. On the other hand, N-mineralization rate increased significantly with the age of the plantation (Table 7). Interestingly, the proportion of mineralized-N converted to nitrate-N decreased with age. NO₃-N was 35.1% of mineralized-N in 3-year old plantation while it was 32.1% and 27.4% at ages 4 and 5 years, respectively.

Microbial C, N and P contents increased significantly with age (Table 6). Proportions of soil organic

C, total soil N and total soil P reflected in microbial biomass increased, while the concentrations of N and P in biomass calculated by assuming that dry biomass contains 50% carbon decreased with the age of the plantations (Table 6). There was a concomitant increase in biomass C : N and C : P ratios (Table 6).

4. Discussion

4.1. Culm recruitment and mortality

In *D. strictus* culms emerge during the rainy season from nodes located on the rhizomes of the previous year culms and grow to full height before branching in about 3–4 months. The production of new culms is linearly related with the number of old culms in a clump, and the majority of new culms is produced by the rhizomes of 1–2 year old culms (Tomar, 1963). Taylor and Zisheng (1987) reported average annual recruitment of culms between 8.2% (*Fargesia spathe-sia*) and 13.7% (*Fargesia scabrida*) in bamboos which form the dominant understorey under montane and subalpine forests of Sichuan, China, and Tripathi and

Singh (1996) found 10.6–12.3% recruitment in a mature *D. strictus* plantation in the Indian dry tropics. The annual recruitment in the present plantation on mine spoil varied from 18 (between the 3rd and 4th year) to 36% (between 4th and 5th year). Among the three species of *Fargesia*, the annual mortality varied between 8.5% and 10.6% (Taylor and Zisheng, 1987), and in a mature *D. strictus* plantation it was 6.6–10.6% (Tripathi and Singh, 1996). These mortality rates are comparable to the rates observed for the present *D. strictus* plantation on mine spoil (6–7%). Thus the mine spoil habitat proved favourable to growth and survival of *D. strictus*.

4.2. Biomass and net primary production

The quantity of biomass per unit area constitutes the primary inventory data needed to understand the flow of nutrients and water through the ecosystem. The bamboo plantation developed on the mine spoil accumulated a substantial amount of biomass. Compared to 30–49 t ha⁻¹ in the present study, several bamboo forests and plantations recorded 0.8 to 24 t ha⁻¹ aboveground biomass (Veblen et al., 1980; Taylor and Zisheng, 1987; Rao and Ramakrishnan, 1989; Tripathi and Singh, 1996). The aboveground biomass recorded for *Sasa kurilensis* in Japan (90 t ha⁻¹, Oshima, 1961), *Chusquea culeou* in San Pablo, Andes (158.8 t ha⁻¹, Veblen et al., 1980) and *Arundinaria alpina* in Kenya (100 t ha⁻¹, Wimbush, 1945). In the native dry tropical deciduous forest, aboveground biomass ranged between 42–78 t ha⁻¹ (Singh and Singh, 1991a). In the native dry tropical forest, 86% of the tree biomass was allocated aboveground and 14% belowground, compared to 65% and 35% in the present *D. strictus* plantation. In the present plantation, foliage accounted for as much as 14% of the total biomass compared to 7% in the native dry tropical forest (Singh and Singh, 1993), which should contribute to a high level of primary productivity.

Comparison with data on biomass from tree plantations on mine spoils also indicated superiority of *D. strictus*. A 3-year old black locust plantation on mine spoils in Kentucky yielded 5.8 to 18.5 t ha⁻¹ aboveground biomass (Creighton et al., 1983). Ten-year old plantations of eastern-cotton wood, virginia pine and black locust accumulated between 36 and 45.4 t ha⁻¹ aboveground biomass (Vail and Wittwer, 1982).

Net primary production in *D. strictus* plantation ranged between 20.7 (3-year old) and 32.0 t ha⁻¹ (5-year old) compared to 11.3–19.2 t ha⁻¹ year⁻¹ of the native dry tropical forest (Singh and Singh, 1991a). Aboveground net primary production in bamboo forests and bamboo plantations ranged between 1.5–11.0 t ha⁻¹ year⁻¹ (Veblen et al., 1980; Taylor and Zisheng, 1987; Tripathi and Singh, 1996) compared to 17.0–24.7 t ha⁻¹ year⁻¹ in the present study. Isagi et al. (1993) have reported 24.6 t ha⁻¹ year⁻¹ aboveground net primary production for *Phyllostachys bambusoides* in Japan. In this study, of the total NPP, foliage accounted for 33.7–38.9%, and of the aboveground net primary production, 43.3–46.5%. In the native dry tropical forest, tree and shrub foliage contributed 30% of NPP (Singh and Singh, 1993) and 38–57% of the aboveground tree net production (Singh and Singh, 1991a). Thus in this plantation foliage accounted for a significant proportion of ecosystem function as is also true for the native dry tropical forest. Production efficiency (i.e., NPP per unit weight of leaf) ranged between 2.6 to 3.0 and compared with 3.3 reported for a variety of deciduous species in south-eastern USA (Hedman and Binkley, 1988).

The high NPP and relatively smaller biomass resulted into short mean residence time (biomass accumulation ratio, biomass : net production) of various plant compartments. The biomass accumulation ratio averaged 1 year for foliage, 5 years for culm, 5 years for rhizome and 2.3 years for roots. Isagi (1994) recorded biomass accumulation ratio of 6 years for culms of *Phyllostachys bambusoides* and this ratio for the dry tropical forest trees averaged 13.7 (Singh and Singh, 1991a). The biomass accumulation ratio of bamboo culms is in consonance with 3–5 years felling cycle. However, since most of the products of bamboo stem are long lasting, the accumulated C would remain sequestered for a long time.

4.3. Litter deposition, decomposition and nutrient release

Fast turnover (1 years) of the foliage compartment and its large share of NPP cause a substantial amount of nutrients to be deposited on the floor by the bamboo plantation each year. The present values of nutrient deposition (45–79 N and 6–11 kg P) compare with the range 51.6–69.6 N and 3.1–4.3 kg P ha⁻¹ year⁻¹

reported for native dry tropical forest (Singh and Singh, 1991b), and 40.8 N and 3.5 kg P ha⁻¹ year⁻¹ for a mature *D. strictus* plantation on unmined Ultisol (Tripathi and Singh, 1995).

The release of deposited litter nutrients depends on the rate of decomposition. Roy and Singh (1994) reported a decay constant between 1.93 and 2.26 for dry deciduous forest litter, and Tripathi and Singh (1992) recorded a decay constant of 1.51 for leaf litter of bamboo planted in natural dry tropical habitat. Thus while *D. strictus* leaf litter takes 235 days for 50% decomposition and more than 1000 days for 95% decomposition on mine spoil, the corresponding values for natural unmined habitat are 168 and 725 days. Leaf litter of natural forest on the other hand, takes only 113–133 days for 50% decomposition, and 488–576 days for 95% decomposition. The relatively slow decomposition of bamboo leaf litter should lead to soil organic matter build up in the long run and is expected to provide benefits of mulching. Because of the accumulation of leaf mulch bamboo serves as an efficient agent in preventing soil erosion and conserving soil moisture (Yadav, 1963).

4.4. Impact of plantation on soil redevelopment

The high inputs of litterfall in the *D. strictus* plantation were reflected in increasing contents of soil organic C and kjeldahl N with the age of the plantation. The soil under 5-year old plantation had 98% greater C, and 67% greater N compared to that under 3-year old plantation. The recorded widening of soil C : N ratio (from 8 to 10) is an indication of vegetation effect. In contrast to soil organic C and kjeldahl N, there was no significant difference with age in mineral N or PO₄-P. On the other hand, the rate of N-mineralization increased significantly with age. The N-mineralization under 5-year old plantation was twice as much as that in the 3-year old plantation. Evidently the increasing demand by the aggrading plant biomass does not permit the mineral N and P to accumulate. Studies on the native forest ecosystems yielded a rainy season range of 2.1–6.8 µg mineral N µg g⁻¹ and 1.2–3.1 µg PO₄-P g⁻¹ dry soil, and N-mineralization rates of 18–48 µg N g⁻¹ month⁻¹ (Roy and Singh, 1994, 1995; Jha et al., 1996). Thus while the mineral N pool in the bamboo plantation was comparable, even in the 5-year old plantation, the

N-mineralization rate was only 14–40% of that in the native forest. This indicates the high nutrient use efficiency of the bamboo. In both the native forest and the bamboo plantation, the dominant form of available N was ammonium, which could indicate a preferential uptake of nitrate by plants (Jha et al., 1996). Nevertheless, in the bamboo plantation, although absolute net rate of nitrification increased with NH₄ availability (N-mineralization), only 35 (3-year old)–27% (5-year old) of mineralized N was converted into NO₃-N by nitrifying bacteria. The greater abundance of ammonium could be at least partly due to less efficient nitrification process, or due to substantial microbial assimilation of NO₃ as argued by Stark and Hart (1997). The increasing abundance of less mobile form of plant-available N is a precursor of progressively tighter nutrient cycle.

Substantial amounts of C, N and P were immobilized in microbial biomass, and the magnitude of immobilization increased with age in conformity with increasing soil organic C and kjeldahl N. The microbial biomass levels recorded in this study are still much lower than in native forest ecosystems but are comparable to those observed in naturally vegetating mine spoils (Srivastava et al., 1989). Studies have indicated positive relationships between microbial C and total soil C, and between microbial N and total soil N (Wardle, 1992; Ruess and Seagle, 1994; Singh and Singh, 1995). Addition of C and N simultaneously, as it happens through litter fall, should increase microbial biomass substantially by satisfying both the C and N limited components. In the present study while microbial C in the 5-year old plantation was 152% greater, microbial N and P were only 96 and 78% greater than in the 3-year old plantation. With the increasing age of plantation, greater proportions of organic C, kjeldahl N and total soil P tended to be immobilized in the microbial biomass indicating the soil redevelopment process. The ratio of microbial C to total soil C is reported to be a reliable soil microbiological index for evaluating the status of a restored ecosystem (Insam and Domsch, 1988). Stark and Hart (1997) have argued that, in ecosystems where soil C and N are accumulating, the microbial biomass will be a net sink for inorganic N, including NO₃.

The biomass C : N and C : P ratios increased with time and the N and P concentrations of microbial biomass decreased. These observations indicate a

possible change in the composition of microbial biomass. As the litter layer builds up, the food web in the soil may progressively become fungus dominated (Hendrix et al., 1986). An increase in the fungal component of microbial biomass during grassland restoration has been reported (Bentham et al., 1992). Fungi and bacteria have considerably different C : nutrient ratios. For example, the C : N ratio of fungal hyphae is higher (10–12) compared to that of bacteria (usually between 3–5) (Jenkinson and Ladd, 1981). Compared with higher turnover and C losses of bacterial population, fungal domination would lead to greater retention of microbial-C (Coleman and Hendrix, 1988; Singh and Singh, 1995). This is consistent with the increasing availability of NH_4 (i.e. N-mineralization), which is a preferred N-source for microbial communities (Recous et al., 1990). Increasing availability of N has been reported to increase immobilization of C in biomass (Elliott et al., 1983).

In this study the proportional increase in microbial biomass was substantially greater than the proportional increase in soil C or N, which is in conformity with Powlson et al. (1987) and Saffigna et al. (1989). Positive relationships have been reported between microbial biomass and soil structure, aggregate size and stability (Drury et al., 1991; Singh and Singh, 1995). Therefore, a rapid development of microbial biomass in the mine spoil is an indication of the efficient restoration potential of *D. strictus* plantation.

5. Conclusions

Dendrocalamus strictus planted on mine spoil attained similar biomass but higher net production levels compared to that of native dry forest within a short time. Accounting for only 14% biomass, foliage contributed 36% ecosystem function resulting into heavy deposition of organic matter on the soil surface. About one-third of plant biomass was located below-ground. As much as 56% of NPP was directed to support the soil redevelopment process, and 44% was sequestered in perennial aerial structure which can be harvested and put to long-term use. These features augmented the soil microbiological processes which resulted in progressively greater proportions of soil C and nutrients being immobilized in microbial biomass,

and a widening of soil C : N and biomass C : N ratios. Increasing availability of organic matter also enhanced N-mineralization and hence the supply of plant-available nutrients. Increasing abundance of less-mobile forms of plant-available N (i.e. $\text{NH}_4\text{-N}$) indicated a progressive tightening of nutrient cycling. During these early years of ecosystem redevelopment, the net primary production and soil processes indicated a positive feedback relationship.

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