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Biomass and nutrient distribution in a highland bamboo forest in southwest Ethiopia: implications for management

K. Embaye[a,b,1], M. Weih[a,*], S. Ledin[c], L. Christersson[a]

[a]Department of Short Rotation Forestry, Swedish University of Agricultural Sciences, P.O. Box 7016, SE-750 07 Uppsala, Sweden
[b]Wondo Genet College of Forestry, P.O. Box 128, Shashemene, Ethiopia
[c]Department of Soil Sciences, Swedish University of Agricultural Sciences, P.O. Box 7014, SE-750 07 Uppsala, Sweden

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Abstract

The Masha natural bamboo forest was stocked with 8840 trees ha^{-1}, uniformly distributed with a mean height of 16.8 m, diameter of 7.6 cm and leaf area index (LAI) of 9.7. Age-structure was 13% of <1 year, 24% of 1–3 years and 63% of >3 years. Culm contributed 82%, branch 13% and leaf 5% to the 110 t ha^{-1} total above ground biomass, while trees mature for harvest (>3 year) made up 73%. The culm component of the mature trees was 60% of the above ground biomass, whereas the biomass of current shoots (<1 year) constituted only 7%. Annual shoot production was 8 t ha^{-1} and contained 44 kg ha^{-1} of N, 6 kg ha^{-1} of P, 122 kg ha^{-1} of K and 1 kg ha^{-1} of Ca. Significant variations in nutrient concentration of plant tissues were found among age-classes and between seasons. More than 8 t ha^{-1} $year^{-1}$ plant litter containing 115 kg N, 8 kg P, 56 kg K and 22 kg Ca returned to the soil surface mainly during the humid season. Resorption efficiency of the foliage was 43% for K, 37% for P and 19% for N. Soil nutrient concentrations declined sharply with soil depth and a large fraction of the total soil nutrient pool was located in the organic layer; the soil was poor in P and K. Management approaches to improve the production efficiency of the forest and the quality of the harvested biomass are discussed.

Keywords: Age structure; Bamboo; Biomass; Ethiopia; Growth; LAI; Nutrients; *Yushania alpina*

1. Introduction

Management of the natural bamboo forests in the tropics in general and in tropical Africa in particular (Kigomo, 1988) should aim to alleviate the prevalent shortages of forest products and to safeguard their potential for sustainable production. In some developing countries like Ethiopia, deforestation and its

* Corresponding author. Tel.: +46 18 67 25 43; fax: +46 18 67 34 40.
E-mail address: martin.weih@lto.slu.se (M. Weih).
[1] Present address: Institute of Biodiversity Conservation and Research, P.O. Box 30726, Addis Ababa, Ethiopia.

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consequences have severely constrained socio-economic growth and development (Embaye, 2000). Proper use of forests for economic growth is a viable option in developing countries for conservation of forests—the ''use it or lose it'' principle (Seydack, 2000). Management must promote optimal production without substantially impairing the potential of the forest resource for perpetual growth and environmental services. The capacity of the environment to perpetuate nutrient supply and substrate quality, combined with the regenerative potential and resource use and recycling efficiency of the plants, determine the sustainability of a forest system (Verwijst, 1996). Stand density, leaf area index (LAI), tree age composition, biomass structure, nutrient distribution and recycling through litter-fall and their temporal variation with tree age and season are all important considerations. These are the foci of this paper.

Biomass, nutrient accumulation and dynamics in bamboo plantations have been studied in a chronosequence (Shanmughavel et al., 2001), but natural bamboo forests (Lakshmana, 2002) and natural bamboo forests of Africa (Kigomo, 1988) have not been well studied. Africa holds about 40 bamboo species, of which two are indigenous to Ethiopia: the lowland bamboo, *Oxytenanthera abyssinica* (A. Richard) Munro and the highland-bamboo, *Yushania alpina* (K. Schumann) Lin.

The objectives of this research are to describe the condition of the Masha natural highland-bamboo forest, southwest Ethiopia, with a focus on spatial distributions and temporal variations of biomass and nutrients and to highlight the implications for its sustainable management at practically achievable production level. Thus, we ultimately will address some management questions related to silvicultural actions such as selective biomass harvests of certain age-classes, fertiliser applications and the optimal timing of harvests and fertilisations.

2. Material and methods

2.1. The species

The species *Yushania alpina* (K. Schumann) Lin., synonym *Arundinaria alpina* (African Alpine Bamboo), is an evergreen, erect, perennial and monopodial (single-stemmed) bamboo with hollow culm. It produces shoots from rhizome buds every humid season until it flowers and dies in about 40 years (local farmers estimate), only to start life again from germinating seeds (Liese, 1985). The growth of new shoots to the size and stature of mature trees in 2–3 months is entirely dependent on nourishment supply from trees interconnected by the rhizome system (Li et al., 2000; Liese, 1985). New shoots produce branches and small leaves upon growth completion towards the end of the humid season. The leaves increase in size and mass until they wither, abscise and fall within a year during the subsequent humid season (Ueda, 1960). Leaves on trees older than 1 year have a 2 year life-span and thus trees of even and odd years carry leaves of different ages: fresh (1 year) and old (2 year) leaves (Li et al., 1998). This pattern is synchronised with the off-year and on-year cycle (Pai-hui, 1985) and goes along with new and old leafing and cyclic changes of nutrient content in the plant body. Nutrient contribution of parent trees to new shoots decreases with age due to declining physiological function after age 3–4 years (Kleinhenz and Midmore, 2001; Ueda, 1960). Culm moisture content also decreases while dry biomass increases with tree age due to cell wall thickening and accumulation of materials like silicon (Liese and Weiner, 1996).

2.2. Study site

The Masha forest is about 19,000 ha in size (Anonymous, 1997) and located in southwest Ethiopia (7°30′N; 35°30′E). The altitude ranges from 2400 m to 3000 m a.s.l. and the relief is gentle to steep sloping terrain and has a uniform soil profile with stable structure and good porosity (Anonymous, 1988). The mean annual rainfall is more than 2300 mm mostly falling during the humid season between April and November (monthly means 100–350 mm and higher than potential evapotranspiration), with dry spells between December and March (dry season, monthly means 40–100 mm and lower than potential evapotranspiration) (Anonymous, 1988). The temperature is moderate throughout the year, with monthly mean range of 16 °C to 20 °C. The soil is deep (>1.5 m) and clayey (46% clay, 27% silt and 8% sand) with about 10 cm thick organic layer and low pH_{H_2O} (4.3–5.2).

2.3. Sampling

Five 10 m × 10 m plots were established at 200 m spacing in the middle of the forest. DBH of all bamboo trees was measured at 1.3 m height and grouped into three age-classes: <1 year, 1–3 years and >3 year. Age was identified in the field based on the indicators used by Wimbush (1945) and Banik (1993). Thus, less than 1-year-old trees were identified by their dark-green and smooth culm, fully or partly covered by fresh looking sheath. The nodes are hairy and the whole culm is free from any spot or sign of infestation by moss or lichen. The youngest ones are with relatively smaller leaf size and no or few branches. The trees of 2–3 years age were distinguished by their faded green or pale green culm, which is slightly rough to the feel, with no sheath or dirty and ragged sheath if present on the lowest (bottom) node. Branches and leaves are fully developed and little moss may be found at the nodes. Trees older than 3 years were identified by their yellowish culm with dry appearance and rough surface. Moss and lichen are prevalent on the nodes and internodes.

Two trees were felled from each age-class and plot (i.e., 30 culms in total) during the humid season in July 2000, i.e., after the completion of new shoot growth, for dry matter, nutrient content and LAI determinations. Sampling was repeated during the dry season in February 2001, following the same procedure, to examine changes in nutrient concentrations. Leaves (two from each of the lower and upper halves of the crown) were sampled from each felled sample tree to estimate LAI of the forest from mean specific leaf area (SLA) and leaf dry weight (LDW). Each sample tree was separated into culm, branch and leaf parts and fresh weights recorded in the field. Two separate sub-samples were taken from each above ground part and weighed: one for dry matter determination and the other for nutrient analyses. The leaf and branch fractions were bulked as foliage sub-sample for nutrient analyses.

Rhizomes and roots were extracted and separated for biomass determination from randomly located soil block samples of 10 cm^3 dimension. Soil samples for nutrient analyses were collected from three soil profiles of about 1.5 m depth, located at selected points in order to include the bottom, middle and top of the landscape. The spacing between consecutive profiles was about 1000 m. Sampling within a profile was done at 20 cm intervals down to 1 m depth. Litter-fall samples (mainly consisting of leaves) were collected during dry and humid seasons by placing 30 plastic sheets (10 during dry season and 20 during humid season) of 50 cm × 50 cm size at 200 m spacing in the forest floor for 3 and 1 month, respectively. The dry and humid season values were extrapolated to the 4 months dry season and 8 months humid season periods of the area to obtain an estimate of total annual dry season and humid season litter-fall. The assumption of similar litter-fall rate across particularly the humid season was made after a pilot study, in which litter-fall was sampled regularly throughout the humid season.

2.4. Bamboo biomass determination

The plant sub-samples were dried to constant weight at 85 °C and mean values of the dry to fresh weight ratios of sub-samples computed. These ratios were used to determine the dry biomass of the plant components in each age-class category. The mean biomass components were multiplied by the mean tree frequency per plot to obtain mean plant biomass of each age-class per plot, another converted to per hectare. Litter-fall was determined in a similar way.

2.5. Plant nutrient analyses

Sub-samples of all plant components from each age-class were dried, ground and analysed for nutrients. Total N contents were analysed by elemental analysis with dry combustion using a Carlo Erba NA elemental analyser NA 1500 (Kirsten and Hesselius, 1983). Total P, K and Ca contents of plant parts were analysed, after acid (HNO_3/$HClO_4$) digestion, by Inductive Coupled Plasma Atomic Emission Spectroscopy (ICP–AES) using JY 70 Plus Spectroanalyser (Winge et al., 1984). Mean nutrient contents of plant components were calculated on per hectare basis for each age-class.

2.6. Assessment of leaf traits

Outlines of 236 sample leaves collected from the different age-class tree samples were traced on paper sheet and areas were measured using a surface area meter (LI-3100; Li-Cor Inc., Lincoln, NE). The leaves were dried at 85 °C and weighed. Mean specific leaf area (SLA) was calculated. The mean leaf area of whole sample trees for each age-class was computed by multiplying the mean leaf biomass by SLA. The LA of sample trees was further converted to leaf area index (LAI) on per plot and ha basis.

2.7. Soil nutrient content and dry mass determination

Soil samples were analysed by the Soil Laboratory of the Department of Soil Sciences, SLU, Uppsala, Sweden, following Swedish standard procedures (SIS, 2001). Nitrogen was determined from finely ground dry samples after dry combustion using an elemental analyser (Leco, CHN-932, Leco corp. MI, USA). P, K and Ca were determined using an atomic absorption spectrometer (AAnalyst 300, Perkin-Elmer, CT, USA), after extraction with .1 M ammonium lactate and .4 M acetic acid from finely ground dry samples, after dry combustion. Soil pH was determined in pure water solution. Dry weight of the 1 m deep mineral soil ha^{-1} was computed based on a bulk density estimated for the soil type and degree of compactness (Brady, 1984) and total nutrient content ha^{-1} was calculated. The true nutrient concentration of the soil is likely to be greater than the estimated value, because the soil included plant materials (rhizomes and roots) while the soil nutrient concentration was determined from soil sample analyses only.

2.8. Data analyses

The Minitab Statistical Software (Release 13.31, Minitab Corp., State College, P.A.) was used to describe and analyse the data. Biomass analyses were based on only one harvest while nutrient analyses were based on two harvests (humid and dry season). Thus, biomass variations among age-classes and nutrient concentration variations among age-classes and between seasons were analysed using analysis of variance (ANOVA). General linear model (GLM) was always used to calculate the ANOVA.

3. Results

3.1. Stocking, culm size and age structure

The forest was composed of living and dead bamboo trees in about 5:1 ratio. The density of the living bamboo population was 8840 ± 1444

Table 1
Biomass (t ha^{-1}), nutrient concentration (%) and nutrient content (kg ha^{-1}) of the above and below ground plant fractions (down to: 10 cm) and the current annual litter fall (h = humid, d = dry season) recorded in a natural bamboo forest grown at Masha, southwest Ethiopia

	Bamboo fraction	Drymass (t ha^{-1})	Nutrients							
			N		P		K		Ca	
			%	kg ha^{-1}	%	kg ha^{-1}	%	kg ha^{-1}	%	kg ha^{-1}
Age-class	Foliage[a]	.2	1.64	4	.19	.4	1.76	4	.16	.4
<1 year	Culm	7.9	.51	40	.08	6	1.50	118	.02	1
Age-class	Foliage[a]	4.2	1.71	71	.14	6	1.03	43	.35	15
1–3 years	Culm	17.6	.36	63	.06	11	1.18	208	.03	5
Age-class	Foliage[a]	14.9	1.78	266	.14	21	.87	130	.36	53
>3 years	Culm	65.0	.30	196	.05	32	.48	314	.02	15
Total above ground[b]		109.8	.58	640	.07	76	.75	819	.08	90
Rhizome[b]		13.6	.74	101	.16	22	1.43	195	.04	5
Root[b]		12.0	.82	99	.06	7	.56	67	.06	7
Total below ground[b]		25.6	.78	199	.11	29	1.02	262	.05	13
Litter (h)		7.5	1.40	105	.10	8	.61	46	.29	22
Litter (d)		.8	1.32	10	.09	1	1.31	10	.26	2
Total litter		11.2	1.39	156	.10	11	.66	74	.29	32

[a] Leaves and branches.
[b] Below ground down to 10 cm mineral soil depth.

Table 2
Mean (±S.D.) leaf area, leaf dry weight and specific leaf area (SLA) of individual leaves, together with the mean leaf biomass ha^{-1} and leaf area index at stand level for various age-classes of the natural bamboo forest at Masha, southwest Ethiopia

Age-class (years)	Leaf area (cm^2)	Leaf biomass (g)	SLA ($m^2 kg^{-1}$)	Leaf biomass ($t ha^{-1}$)	LAI
<1	5.6 (3.2)	.05 (.03)	12.5 (4.8)	.02	.02
1–3	56.0 (12.0)	.56 (.07)	15.8 (3.3)	1.2	1.9
>3	55.2 (10.2)	.33 (.11)	17.7 (4.4)	4.4	7.8
Total				5.6	9.7

trees ha^{-1} (95% C.I., $n = 4$) with mean height and DBH of 16.8 m and 7.6 cm, respectively. Old trees (>3 years) were most frequent (63% of the population or 5570 trees ha^{-1}) while current (<1 year) and 1–3 years old trees constituted 13% (or 1149 trees ha^{-1}) and 24% (or 2222 trees ha^{-1}), respectively. No differences in culm height and DBH among tree age-classes were found.

3.2. Biomass and leaf area

The mean above ground tree biomass of the forest was 110 t ha^{-1}, to which culm, branch and leaf parts contributed about 82%, 13% and 5%, respectively (Tables 1 and 2). Biomass of age-class <1 year was much lower (7% of total above ground biomass) than age-class 1–3 years (20%) and age-class >3 year (73%). Culms mature for harvest (>3 year) constituted 59% of the total above ground biomass. The apparent dry matter density of the forest was .67 kg m^{-3} and was calculated as the ratio of the above ground biomass/m^2 and the mean tree height of the forest. The total below ground bamboo biomass in the top 10 cm mineral soil layer was estimated at 25.6 t ha^{-1}, of which 13.6 t ha^{-1} was rhizome and 12.0 t ha^{-1} root biomass (Table 1).

The total annual litter-fall was estimated at 8.3 ± 2.4 t ha^{-1} (95% C.I., $n = 9$), which is about 7% of the total above ground bamboo biomass and similar to the biomass of current shoots (<1 year; 8.1 ± 1.9 t ha^{-1}) (Table 1). Litter-fall during humid season was higher than dry season by an order of magnitude.

Leaf area (LA) of tree age-classes of 1–3 and >3 years was similar, whereas the LA of tree age-class <1 year was only one-tenth of the LA of the other two age-classes (Table 2). The pattern was similar for SLA. The leaf area index of the forest was 9.7 and the contribution of age-class <1 year shoots was negligible, whilst the contributions of age-classes 1–3 years and >3 years were 19.3% and 80.5%, respectively.

3.3. Mineral nutrients

Nutrient concentrations varied greatly between the different plant parts and among seasons (Fig. 1). The concentration of N and P was highest in the foliage (i.e., the pooled fraction of leaves and branches) and during the dry season, but lowest in culms and during the humid season. However, since old culms formed a large fraction of the total above ground biomass (59%, Table 1), a large amount of the total nutrient pool (N: 30%; P: 42%) was located in the old culms.

Mean nutrient concentrations differed among age-classes in all plant parts (ANOVA, $d.f._{factor} = 2$, $d.f._{error} = 53$, $P < .015$). For example, age-classes <1 year, 1–3 years and >3 year contributed about 8%, 21% and 71% to the total N and P pools in the above ground biomass (Table 1). Mean nutrient concentration ratios across all above ground plant parts and age-classes were 8 N:1 P:11 K:1 Ca (Table 1). The mean N, P and K concentrations in culms were highest in age-class <1 year and lowest in age-class >3 year and the N:P ratio increased with age. The amounts of nutrients located in the rhizome and root biomass of the upper 10 cm of soil were between 12% and 28% of the corresponding nutrient pools in the total plant biomass down to 10 cm soil depth (Table 1).

The N (P) concentration in the litter was between 15 (27)% and 22 (46)% lower than in the foliage, indicating both a higher resorption efficiency for P compared to N and a higher mean residence time (MRT) of P than N in the bamboo plants (Fig. 2). Resorption efficiency for K was also high (between 24% and 63%). At an annual basis, the amount of nutrients returning to the soil through litter was higher

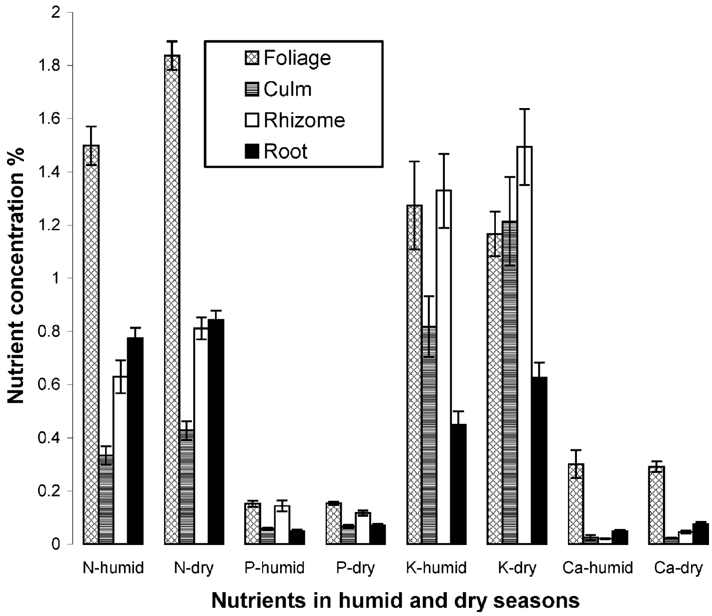

Fig. 1. Seasonal variations (humid and dry season) in mean (±S.E.) concentration of nutrients (N, P, K, Ca) across all age-classes in different bamboo plant parts sampled in the Masha natural bamboo forest, southwest Ethiopia.

than the nutrient amount recovered in the current-year shoots (i.e., age-class <1 year biomass), except for K (Table 1; Fig. 2).

Soil nutrient concentrations declined sharply with soil depth (Table 3). Between 50% and 70% of the total nutrient content estimated in one meter soil depth were located in the organic matter (humus) layer above the mineral soil and between 80% and 97% were located down to 40 cm soil depth. The nutrient concentration ratios in the soil were 261 N:1 P:6 K:21 Ca (Table 3), indicating a soil poor in P and K.

4. Discussion

4.1. Biomass productivity and age structure

Both the above ground standing biomass (110 t ha^{-1}) and annual shoot productivity (8 t) at the Masha forest were lower than the corresponding values reported for bamboo grown in different parts of the world (Veblen et al., 1980; Difan, 1985; Isagi et al., 1997; Kleinhenz and Midmore, 2001). In contrast, the relative allocation of above ground biomass to

Table 3
Soil nutrient concentrations and total amounts per unit ground area (kg ha^{-1}) under the natural bamboo forest at Masha, southwest Ethiopia

		pH (H_2O)	Nutrients							
			N		P		K		Ca	
			%	kg ha^{-1}	%	kg ha^{-1}	%	kg ha^{-1}	%	kg ha^{-1}
Organic layer (6 cm)		5.0	2.43	6560	.032	86	.09	240	.50	1340
Mineral soil (cm)	0–20	4.7	.97	23260	.005	120	.02	550	.15	3600
	20–40	4.7	.55	13240	.001	24	.02	480	.04	1010
	40–60	4.4	.40	9580	.001	24	.01	260	.02	380
	60–80	4.7	.29	6940	.001	24	.00	96	.01	170
	80–100	4.8	.17	4040	.001	24	.00	96	.00	24
Total				63620		302		1720		6520

Nutrient amounts are based on bulk densities of .45 g cm^3 (organic layer) and 1.2 g cm^3 (mineral horizons) (Brady, 1984); the corresponding dry masses of the soil horizons are 270 t ha^{-1} (6 cm organic layer) and 2400 t ha^{-1} (20 cm mineral horizons). The values are means of three soil profiles.

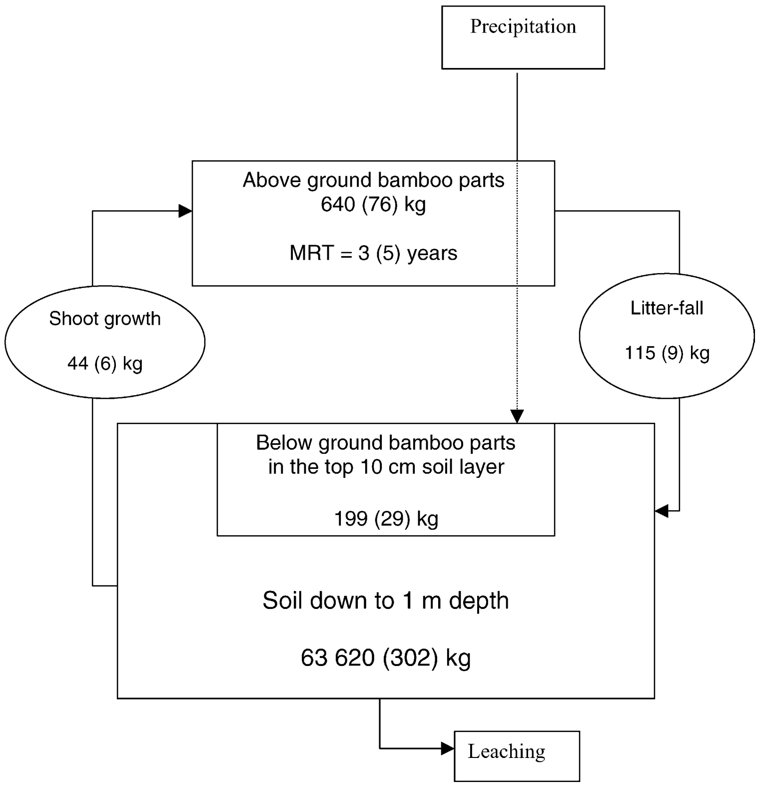

Fig. 2. Gross estimation of the nitrogen and phosphorus (in parentheses) budget of the Masha natural bamboo forest, southwest Ethiopia, at annual basis. The mean resident time (MRT) of N (P) in the above ground biomass is calculated according to Berendse and Aerts (1987). Figures in quadratic boxes indicate (weighted) mean values of the humid and dry season data and arrows indicate nutrient flows. Nutrient addition through precipitation and loss through leaching were not determined.

different plant parts was similar to published values (Ueda, 1960; Kleinhenz and Midmore, 2001). The relatively low biomass productivity at the Masha forest was associated with low dry matter density compared to other reports (Rao and Ramakrishnan, 1989; Shanmughavel et al., 2001). Thus, the hollow nature of the *Yushania alpina* culm and, consequently, low specific gravity compared to bamboo species with solid culms might be an important reason for the low biomass values reported here. In addition, the disproportionately low biomass of current (<1 year) shoots (8% of above ground total) as compared to old (>3 year) trees (72%) could indicate an off-year phase in the cycle of monopodial bamboos (Pai-hui, 1985) and/or an unstable age-structure. The latter is evident from the overwhelmingly old tree (>3 year) composition of the forest. Increased specific gravity with culm age (Liese and Weiner, 1996) may have contributed to the disproportionately high old tree biomass.

A stand age-structure heavily skewed towards older trees, as found in the Masha forest, might indicate low productivity and lack of management. For example, Yuming et al. (2001) recommends an age-class structure of 3:3:3:1 for 1–4-year-old bamboo-trees for optimum culm production.

4.2. Mineral nutrients

Most of the nutrients were concentrated within the upper 40 cm of the soil, where almost all bamboo roots are found (Rui et al., 1999; Yadav, 1963). This could indicate high probability of nutrient uptake by bamboo plants (Singh and Singh, 1999). Nevertheless, a large fraction of the total soil nutrient pools, particularly in the organic horizon, is probably organic bound and becomes available to plants only slowly, after microbial decomposition. The process of soil nutrient mineralisation is inhibited, however, at high soil moisture contents by the lack of aeration (Runge, 1983) and the high amounts of rainfall in the Masha forest might periodically create unfavourable conditions for microbial mineralisation. The artificial drainage of the site could be considered as a management option to improve nutrient availability to plants, if further studies confirm that high soil moisture indeed is an important factor limiting nutrient mineralisation at this site. The localised nutrient accumulation in the organic and upper mineral soil layers over a nutrient-poor substratum suggests the following arguments regarding the stability of the system: (1) the forest system is strongly dependent on nutrient cycling through litter and soil organic matter decomposition and mineralisation; (2) the system is inherently fragile and may quickly lose productive capacity, if the bamboo forest is cleared and the nutrient rich top-soil is removed by erosion. This is a likely scenario considering the periodically high rainfall in the region. The large litter mass returned to the soil surface and in particular the high amount of nutrients contained in it, further supports the former (1) argument. These arguments call for a clear warning to not change the forest into other land-use systems and to prevent organic matter removal from the forest floor by erosion that could be caused by excessive harvesting and/or fire outbreak.

A particularly poor P and K status of the soil was reflected by much higher soil nutrient ratios of N:P and N:K as compared with the corresponding nutrient ratios in the plant biomass (Table 1). We speculate that the higher resorption efficiency for P (37%) and K (43%) compared to N (19%) could indicate that P (and K) was limiting bamboo growth more than N at this site. A similar pattern emerged also when mean residence time (MRT; *sensu* Berendse and Aerts, 1987) was calculated based on nutrient pools (Fig. 2). A longer MRT for P (5 years) than N (3 years) possibly indicates relatively greater growth limitation by P compared to N, because the MRT of growth-limiting nutrients is typically long in infertile sites (Aerts and de Caluwe, 1994; Eckstein et al., 1999). Although the mean relative N:P proportion of 8:1 in the plant tissue appears not to support strong P limitation of plant growth, it is interesting that the N:P ratio of the foliage increased from about 9:1 in the <1 year plants to about 13:1 in >3 year old plants (Table 1). This lends evidence to greater re-allocation of P within the plant compared to N, which indicates an ability of efficient P use in this bamboo species. Higher efficiency of P use compared to N use goes along with relatively higher retention of P than N in the living biomass. Any fertilisation treatment to increase bamboo growth at this site should therefore consider the application of P (and K) in the first place. This conclusion is likely to apply to many bamboo stands grown in the tropics, as tropical soils in many cases are P deficient (Wild, 1996).

The total amount of nutrients located in old culms was large, despite their relatively low nutrient concentrations. Thus, the nutrients that would be removed with the harvest of old culms (>3 year) could impoverish soils with poor nutrient availability after a few cutting cycles. In such sites especially P and K fertilisation should be considered to replenish the nutrients removed from the site through harvest in order to ensure high productivity on a sustainable basis (Lou et al., 1997 cited by Kleinhenz and Midmore, 2001). The accumulated litter and the bamboo plant parts remaining on the site after culm harvest could serve as slow-release fertilisers, if decomposition is not constrained by P limitation (Cleveland et al., 2002) and the nutrients are not washed out by heavy rains or immobilised by microbial biomass.

The generally higher plant nutrient concentrations during dry season than humid season and in young plants than in older ones (Fig. 1; Table 1) are consistent with published results for other bamboo species (Youdi et al., 1985) and with the seasonal activity pattern of monopodial bamboos (Pai-hui, 1985). Humid season is a growing season when nutrient dilution through growth is at its peak and, consequently, nutrient concentrations are low. Dry season is a season of low biomass accumulation and a time for nutrient accumulation and, thus, nutrient concentrations are high. The declining nutrient concentration with age is probably related to the increasing proportion of low-nutrient tissues such as the woody parts of the culms. Fertilisers are consequently applied most effectively early in the humid season and/or towards the end of the dry season, whereas the harvest of culms older than 3 years should be performed during the beginning of the dry season.

4.3. Forest condition and management implications

The high percentage of dead trees (20% of the stem population) and similar or higher annual litter-fall biomass compared to shoot production suggest that the Masha forest has not been managed over a long period of time.

The stand density of >8000 trees ha^{-1} is above the values recommended for optimal culm productivity in China (Hwang, 1975; Cheng, 1983; Shi et al., 1993). Relative productivity i.e., the ratio of fresh (<1 year) to older (>1 year) shoots and culm quality decrease beyond a threshold value with an increase in stand density (Liao and Huang, 1984). Although comparisons of different forest stands are difficult due to genetic constitution, growth condition and management objective variations, the Masha forest appears to be over-stocked above the level favourable for optimum culm production for furniture and construction purposes. Thus, the low percentage of young (<1 year) and prevalence of old (>3 year) trees in the forest, high LAI (9.7) and a litter-fall biomass similar or higher than the new shoot production are all signs of forest degradation (Yuming et al., 2001; Ueda, 1960). For example, biomass production of *Phyllostachys heteroclada* in China was highest at LAI values of 4–6 and declined above LAI of 7 (Tienren et al., 1985). The high percentage of old trees could also lower productivity through adverse effects on the emergence and growth of new shoots (Yuming et al., 2001). Higher energy investment by old trees against deteriorating agents at the cost of biomass production is also a factor for forest degradation (Coley, 1987). Thus, trees >3 years should be removed and the felling operation should result in an age-structure and stand density favourable for optimum biomass production (e.g., Yuming et al., 2001). However, stand density and age-structure and thus harvesting-age threshold should ultimately be decided based on the intended end-use of the product, because culm diameter and property are influenced by stand density and tree age (Kleinhenz and Midmore, 2001; Liese, 2002). For example, only the culm component of bamboo plants is currently of economic value in Ethiopia for construction and furniture uses. As culms of older than 3 year trees constituted about 60% of the total above ground biomass of the 19,000 ha Masha forest, the total amount to be harvested is large. Planning would be necessary for handling and marketing of the products before the actual harvesting operation is performed.

We conclude that silvicultural treatments and harvesting operations are prerequisites for a productive bamboo forest of the type represented by the Masha forest studied here. One of the most important management actions is the sequential removal of old trees by felling each year 25–50% of the trees older than 3 years (Yuming et al., 2001). The appropriate fertiliser type for the site should be rich in P and K and applied before or at the beginning of the humid season. Harvesting operations should be carried out early in the dry season.

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