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Nutrient concentration age dynamics of teak (*Tectona grandis* L.f.) plantations in Central America

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Abstract

Aim of study: Appropriate knowledge regarding teak (*Tectona grandis* L.f.) nutrition is required for a better management of the plantations to attain high productivity and sustainability. This study aims to answer the following questions: How can it be determined if a teak tree suffers a nutrient deficiency before it shows symptoms? Are nutrient concentration decreases in older trees associated with age-related declines in forest productivity?

Area of study: Costa Rica and Panama.

Material and methods: Nutrient concentration in different tree tissues (bole, bark, branches and foliage) were measured at different ages using false-time-series in 28 teak plantations.

Research highlights: Foliar N concentration decreases from 2.28 in year 1 to 1.76% in year 19. Foliar Mg concentration increases from 0.23 in year 1 to 0.34% in year 19. The foliar concentrations of the other nutrients are assumed to be constant with tree age: 1.33% Ca, 0.88% K, 0.16% P, 0.12% S, 130 mg kg^{-1} Fe, 43 mg kg^{-1} Mn, 11 mg kg^{-1} Cu, 32 mg kg^{-1} Zn and 20 mg kg^{-1} B. The nutrient concentration values showed can be taken as a reference to evaluate the nutritional status of similar teak plantations in the region. The concentrations of K, Mg and N could be associated with declines in teak plantation productivity as the plantation becomes older. Whether age-related changes in nutrient concentrations are a cause or a consequence of age-related declines in productivity is an issue for future research with the aim of achieving higher growth rates throughout the rotation period.

Key words: age-related decline in productivity; forest nutrition; nutrient bole concentration; nutrient foliar concentration; resorption.

Introduction

Teak (*Tectona grandis* L.f.) has been planted extensively in Central America, acquiring socio-economical relevance due to its productivity (Pandey and Brown, 2000; FAO, 2002). Reference foliar nutrient concentrations have been summarized for teak (Drechsel and Zech, 1991; Boardman *et al.*, 1997), and a preliminary Diagnosis and Recommendation Integrated System (DRIS) has been developed for West African planted teak forests (Drechsel and Zech, 1994). However, appropriate knowledge regarding teak nutrition is still required for a better management of the plantations to attain high productivity and sustainability.

The concentrations of nutrients in tissues depend mainly on species, environmental factors (climate and soil availability) and plantation management. Whether comparing different species or within a single species, genetic requirements, root distribution and age (developmental stage) are usually the most important factors affecting nutrient absorption. At early growth stages, tree nutrition is considered crucial to sustain high growth rates and rapid expansion of the crown and roots. After the crown is fully developed, if seedling nutrition has been adequate, tree requirements during the remainder of the rotation are assumed to be satisfied by environmental inputs, nutrient recycling and nutrient translo-

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cation (Miller, 1981, 1984, 1995). Nutrients in foliage are considered to represent 20-40% of the total amount of nutrients in a stand, and lower nutrient concentrations found in the tree bole (*e.g.* Miller, 1995). Kumar *et al.* (2009) found teak reproductive parts to contain the highest nutrient concentrations, while twigs and foliage also showed high values; the Ca and B concentrations in bark are higher than in other tissues.

Foliar concentration is considered a useful parameter to evaluate the nutritional status of a stand and as a reference to evaluate plantation fertilizer recommendations because (a) its variation is highly dependent on site and soil parameters; (b) it reflects the current nutrient supply; (c) it allows diagnosis of nutritional deficiencies when they are not severe enough to cause visually observable symptoms and, thus, allows action to be taken before the effects on productivity are significant; and (d) deficiency symptoms are confused easily with other effects when visual guidelines are used (Mead, 1984; Drechsel and Zech, 1991; Barker and Pilbeam, 2006; Lehto *et al.*, 2010).

The nutrient concentrations presented in this paper for dominant and co-dominant teak trees, which were developed for a variety of soils and environmental conditions in Central America (Costa Rica and Panama), should be taken as reference values for evaluating the nutritional status of similar teak plantations in the region.

Material and methods

Study sites

Three teak (*Tectona grandis* L.f.) plantations were studied in Central America: two in Costa Rica (Guanacaste and northern region) and one in Panama (Panama Canal watershed) (Fig. 1). The three areas are classified as tropical wet forest according to Holdridge's life zones, with similar mean annual rainfall (2,500-3,100 mm), although in Guanacaste the dry season is longer than at the other two sites. The soils of the study areas are also similar, although the northern region of Costa Rica is less fertile than the other sites and it has higher soil acidity (Table 1).

The studied stands were chosen to be representative of properly managed teak plantations in Central America. In general, management of these plantations consists on continuous silvicultural activities: weed control, pruning, thinning regimen (approximately from 800-1,000 trees ha^{-1} at establishment to 150-200 trees ha^{-1} at final felling) and fertilization during the establishment. The use of clones is common in recent years, so they were not sampled in the study. An expected commercial volume of 100-150 m^3 is expected for this kind of plantations in approximately 20 years rotation.

Field sampling and design

False time series (chronosequences) method was used to analyze nutrient concentration dynamics of teak trees from 1 to 19 years of age. Despite of the critiques of this method (Johnson and Miyanishi, 2008), it was considered to be valid as all the studied stands are considered to be similar in environmental conditions (soil and climate) and management practices.

A total of 28 stands were analyzed, seven in Panama, 12 in the northern region of Costa Rica and nine in Guanacaste (Costa Rica). In order to analyze a maximum yield research experiment (Bertsch, 1998; Alva-

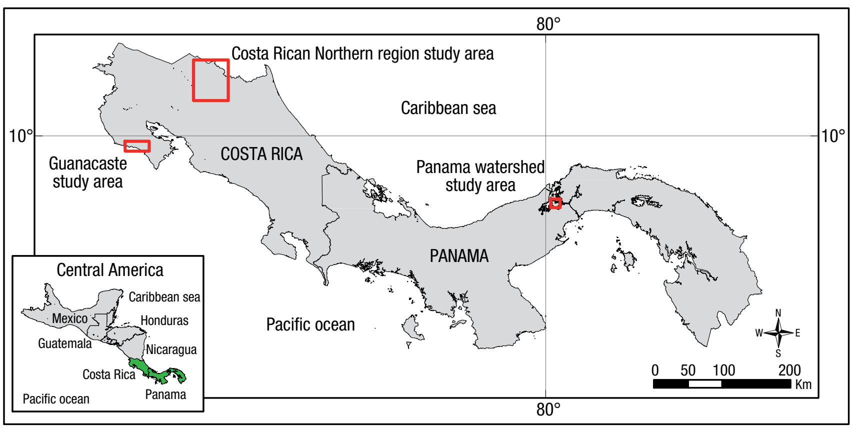

Figure 1. Locations of the study teak (*Tectona grandis* L.f.) plantations: Guanacaste (Costa Rica); northern region (Costa Rica) and Panama Canal Watershed (Panama).

Table 1. Summary of soil properties at the different study areas; means and coefficients of variation (in parentheses) are provided. Soil information was only available for 23 of the 28 sampled stands

	Northern region, Costa Rica (n = 11)	Guanacaste, Costa Rica (n = 9)	Canal Zone Panama (n = 3)	Total (n = 23)
pH	5.11 (6)	5.90 (6)	6.70 (12)	5.63 (12)
Acidity [cmol(+)$^{-1}$]	0.70* (5)	0.31 (30)	0.15 (33)	0.48 (81)
Ca [cmol(+) L^{-1}]	4.45 (44)	21.36 (28)	20.97 (38)	13.22 (74)
Mg [cmol(+) L^{-1}]	1.46 (47)	6.89 (54)	5.25 (64)	4.08 (89)
K [cmol(+) L^{-1}]	0.13* (109)	0.33 (87)	0.36 (82)	0.24 (101)
ECEC [cmol(+) L^{-1}]	6.74 (31)	28.90 (32)	26.72 (40)	18.02 (71)
AS (%)	11.96* (84)	1.22 (58)	0.65 (55)	6.28* (139)
P (mg L^{-1})	3* (114)	3* (146)	2* (0)	3* (124)
Zn (mg L^{-1})	2* (84)	3 (58)	3 (107)	2* (77)
Cu (mg L^{-1})	8 (19)	11 (85)	4 (83)	9 (71)
Fe (mg L^{-1})	165 (23)	37 (81)	65 (154)	102 (75)
Mn (mg L^{-1})	43 (171)	38 (82)	19 (101)	38 (142)
Organic matter (%)	4.6 (27)	3.8 (28)	4.6 (16)	4.3 (27)
Sand (%)	24.9 (23)	23.4 (56)	29.0 (31)	24.8 (38)
Silt (%)	18.4 (13)	36.9 (42)	36.8 (43)	28.0 (51)
Clay (%)	56.7 (11)	39.7 (22)	34.3 (50)	47.1 (27)

ECEC: effective cations exchange capacity. AS: acidity saturation. * Values outside the adequate reference soil levels (Bertsch, 1998).

rado, 2012), dominant and co-dominant trees were selected: (a) without visible symptoms of diseases or nutritional deficiencies and (b) that were representative of the best-performing trees of the plantations, assuming optimal nutrition and a full expression of genetic potential. By analyzing nutrient concentration in the most productive soils without soils deficiencies (and in dominant or co-dominant trees in a site), the maximum species requirements are assessed; hence, if the considered minimum inputs for these high-fertility sites are applied in sites of lower fertility where tree nutrient uptake would be lower, the productivity of the plantation is still achieved (Bertsch, 1998; Alvarado, 2012).

In stands younger than ten years of age, two trees were sampled per stand, whereas only one tree was sampled in older stands. Trees were felled and tree components (bole, bole's bark, foliage and primary and secondary branches) were analyzed for nutrient concentration. Tissue samples (1 kg per tissue per tree) were collected and analyzed at the "Centro de Investigaciones Agronómicas" of the University of Costa Rica (hereafter CIA-UCR) to determine nutrient concentrations (N, P, Ca, Mg, K, S, Fe, Mn, Cu, Zn and B, hereafter referred to as nutrients) after samples were dried and water content was assessed. Dry combustion was used to measure the N concentration, and wet digestion and atomic spectrometry were used to extract and determine other nutrients (Bertsch, 1998). Primary and secondary branches were weighted averaged and are reported as "branches". Foliage samples were collected as representative homogeneous mixture of all the foliage of the sampled trees. All the field work was performed during July-September, at the trees optimal nutritional status during the period of maximum growth activity, to avoid effects of seasonality. In order to estimate soil nutrient availability, topsoil samples were collected (0-20 cm). Soil information was only available for 23 of the 28 sampled stands (Table 1). Soil samples were analyzed at CIA-UCR to determine: pH (in water), Ca, Mg, K, P, Fe, Cu, Zn, Mn, exchangeable acidity and Al, following the KCl-modified Olsen method, as described by Díaz-Romeu and Hunter (1978). Organic matter was determined by the wet combustion method of Walkey and Black, as described by Briceño and Pacheco (1984). Soil texture was determined using the modified Bouyoucos method, as described by Forsythe (1975).

Statistical analysis

Generalized linear mixed models (GLMMs) were used to study the relationships between the concentration of nutrients (N, P, Ca, Mg, K, S, Fe, Mn, Cu, Zn and B) in each tissue (bole, bark, bole and bark, branches, foliage and total) and tree age. The use of GLMMs was required, as most of the study variables did not approach the normal distribution hypothesized in traditional models. Appendix 1 summarizes the complete list of the 44 response variables analyzed and the distribution approached by the data used to construct the GLMMs. The exponentially distributed variables were modeled using a Gamma distribution approach with $\alpha = 1$.

To evaluate the best fitted model for each study variable, a total of 83 different models were constructed, selecting the one with lowest deviance. Appendix 2 summarizes a complete list of the models constructed for each study variable. Three groups of models were constructed: (1) a null model considering only an intercept $[y_i = b_0]$; (2) a model considering an intercept in addition to age as an explanatory variable $[(y_i)^\lambda = b_1 \cdot age + b_0]$; and (3) a model without an intercept $[(y_i)^\lambda = b_1 \cdot age]$. For groups (2) and (3), 41 different power link functions $[g(\mu) = \mu^\lambda]$ were tested for each one, with λ varying between $\lambda = 2$ to $\lambda = -2$ and a $\lambda_{gap} = 0.1$. When no model including age as a parameter was statistically significant, or when the data did not follow any of the studied distribution functions (Appendix 1), the resulting model included only an intercept representing the mean of the variable, and no age effect was taken into account.

The sampled stands in each study area were spatially correlated. The spatial correlation was taken into account by including a random effect for the study area, modeling the working correlation matrix with a first-order autoregressive structure. The goodness-of-fit of the models was estimated by measuring the percentage difference between the deviance of the model and the deviance of a model with no covariates (hereafter referred to as efficiency, EF), which is a pseudo-R^2 measure reported for GLMMs. All statistical analyses were performed using SAS 9.0 (SAS Institute Inc., 2002). All statistical tests throughout the text are considered significant with $\alpha = 0.05$.

Results

N concentrations decreased with age in all tissues (Fig. 2, Table 2); the N concentration was higher in the foliage (1.7-2.3%) than in the other tissues. Ca concentrations did not show any relationship with age in any tissue (Fig. 3, Table 2) but were highest in the bark (1.9%), followed by the foliage (1.3%) and finally the

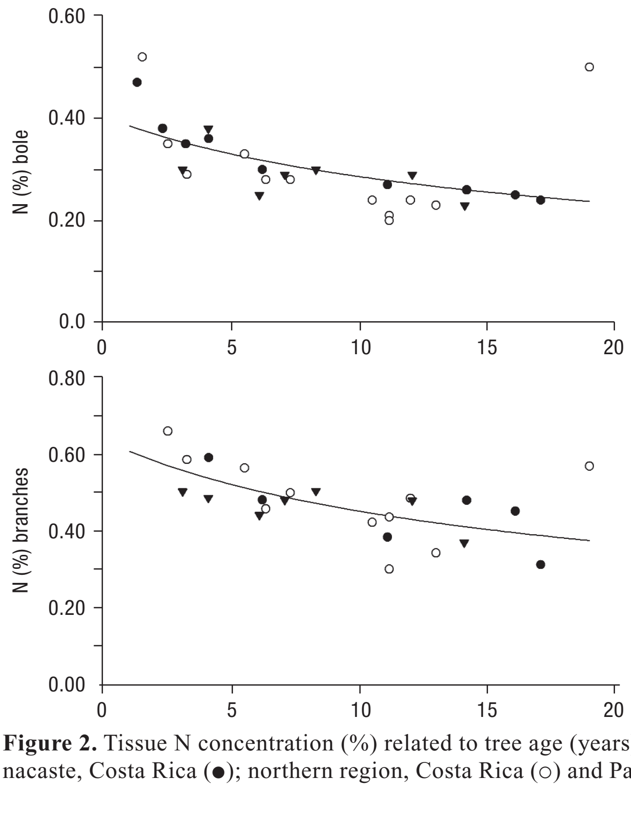

Figure 2. Tissue N concentration (%) related to tree age (years). Points represent trees sampled at three different locations: Guanacaste, Costa Rica (●); northern region, Costa Rica (○) and Panama (▼). Lines represent fitted models (Table 2).

Table 2. Regressions between tissues' nutrient concentration and tree age (years) in 1 to 19 years old teak (*Tectona grandis* L.f.) plantations in Costa Rica and Panama. Below specified models are in the form $[y = (b_0 + b_1 \cdot age)^{1/\lambda}]$, where the response variables (y) are the nutrients concentration at tree tissues. When no model including age as a parameter was statistically significant, the model only included an intercept (b_0) representing the mean of the variable

Tissues	Macronutrient (%)	b_0	b_0 (std. error)	b_1	b_1 (std. error)	λ	EF (%)	Micronutrient (mg kg^{-1})	b_0	b_0 (std. error)	b_1	b_1 (std. error)	λ	EF (%)
Foliage	N	0.1845	0.0170	0.0073	0.0004	–2	34	Fe	129.6087	22.9492				
	Ca	1.3363	0.1062					Mn	42.5507	1.7941				
	K	0.8759	0.0736					Cu	11.0761	0.4361				
	Mg	0.0501	0.0151	0.0033	0.0003	2	90	Zn	31.9978	3.7041				
	P	0.1589	0.0198					B	19.6158	0.6613				
	S	0.1181	0.0047											
Bark	N	1.4506	0.1306	0.1258	0.0246	–2	36	Fe	97,791.3100	1,9837.4200	–5,106.0	1,043.8660	2	29
	Ca	1.9098	0.2409					Mn	0.0004	0.0002	0.0002	0.0001	–2	43
	K	1.2218	0.0234	–0.0205	0.0042	0.4	30	Cu	3.4615	0.3050				
	Mg	0.2349	0.0072					Zn	29.8471	4.5945				
	P	0.0772	0.0112					B	30.6635	1.1832				
	S	32.0732	1.6898	2.2538	0.3823	–1.4	23							
Bole	N	6.1237	0.9564	0.6100	0.1253	–2	26	Fe	72.4639	23.0074				
	Ca	0.1093	0.0057					Mn	1.2500	0.3113				
	K	0.6179	0.0197	–0.0229	0.0029	0.5	72	Cu	2.0907	0.2691				
	Mg	18.9991	3.2787	7.2370	1.5985	–1.7	30	Zn	10.3356	4.4177				
	P	0.0645	0.0162					B	2.7143	0.2763				
	S	0.0446	0.0098											
Branches	N	2.4636	0.4475	0.2449	0.0420	–2	36	Fe	162.7561	8.7137				
	Ca	0.9122	0.0544					Mn	13.9337	1.2417				
	K	0.4282	0.0458					Cu	–0.0060	0.0026	0.0085	0.0010	–2	48
	Mg	14.5100	3.9542	5.9444	0.3472	–2	39	Zn	3.3847	0.1286	–0.0648	0.0088	0	28
	P	0.0751	0.0221					B	11.1654	0.1765				
	S	0.0673	0.0064											

EF (%): model efficiency, pseudo R^2 estimate for Generalized Linear Mixed Models.

bole (0.1%). K concentrations decreased with age in the bole, bark and branches but were constant in the foliage (Fig. 4, Table 2). K-bark (0.6-1.6%) was higher than in the other tissues during the early growth years, but after 14 years, K-foliage was highest (0.88%). Mg-bole and Mg-branches decreased with age, whereas Mg-foliage increased and Mg-bark was constant (Fig. 5, Table 2). The Mg-foliage (0.23-0.34%) was highest, although Mg-bark was also high (0.23%) compared with Mg-bole and Mg-branches. P concentrations did not show any relationship with age in any tissue (Table 2). P-foliage (0.16%) was higher than in the other tissues (< 0.08%). S-bark decreased with age but remained constant in the other tissues (Table 2). In most tissues, the macronutrient concentrations generally followed the trend N > Ca = K >> Mg > P > S.

Fe-bark decreased with age but remained constant in the other tissues (Table 2); in young trees, Fe-bark (28-304 mg kg^{-1}) was higher than in other tissues, although after 14 years, Fe-branches (163 mg kg^{-1}) was highest. Mn-bark decreased with age but remained constant in the other tissues (Table 2). Cu-branches decreased with age but remained constant in the other tissues (Table 2). Zn-branches decreased with age but remained constant in the other tissues (Table 2). Zn-foliage (32 mg kg^{-1}) was higher than the Zn concentration in the other tissues, although the Zn-bark (30 mg kg^{-1}) was also high as was Zn-branches in younger trees (9-28 mg kg^{-1}). B concentrations did not show any relationship with age in any tissue (Table 2); B-bark (31 mg kg^{-1}) was highest, although B-foliage (20 mg kg^{-1}) was also high compared to B-branches (11 mg kg^{-1}) and B-bole (3 mg kg^{-1}). In general, the micronutrient concentrations in the tissues followed the trend Fe >> Mn > Zn = B > Cu.

Ca was found to be the most concentrated nutrient in the tree bark; its concentration in the bark remained constant with age, which was also found for Mg, P, S,

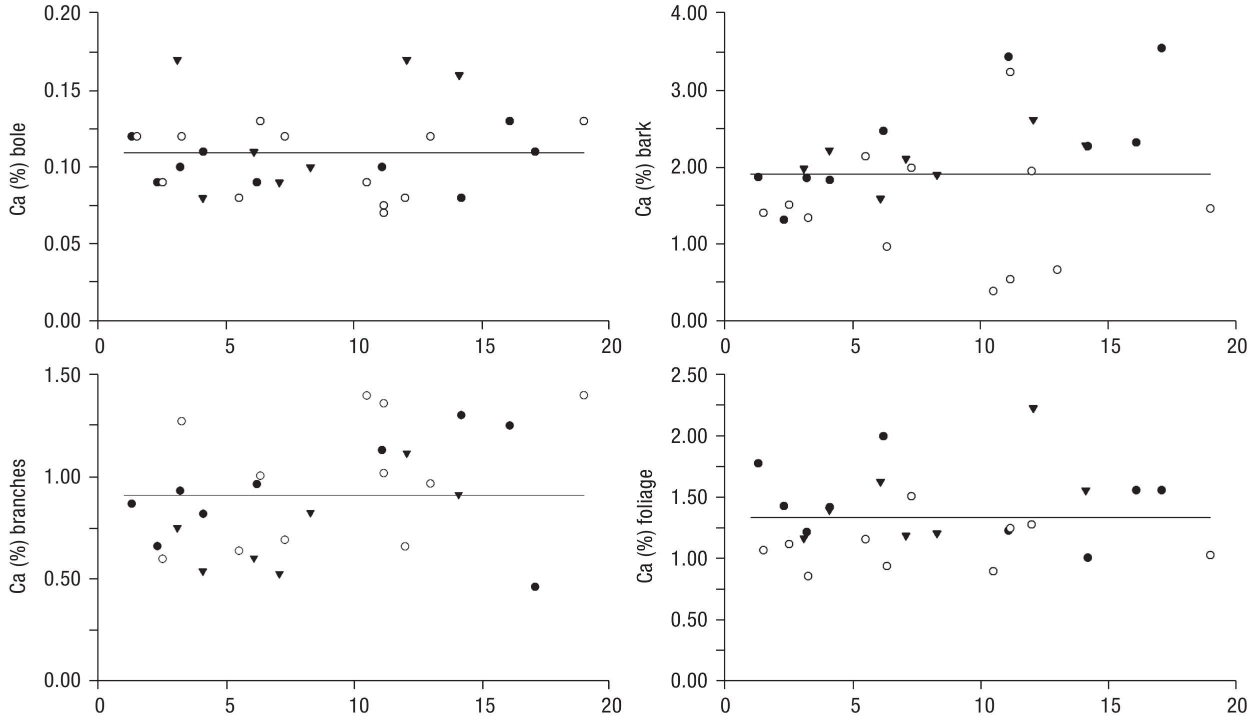

Figure 3. Tissue Ca concentration (%) related to tree age (years). Points represent trees sampled at three different locations: Guanacaste, Costa Rica (●); northern region, Costa Rica (○) and Panama (▼). Lines represent fitted models (Table 2).

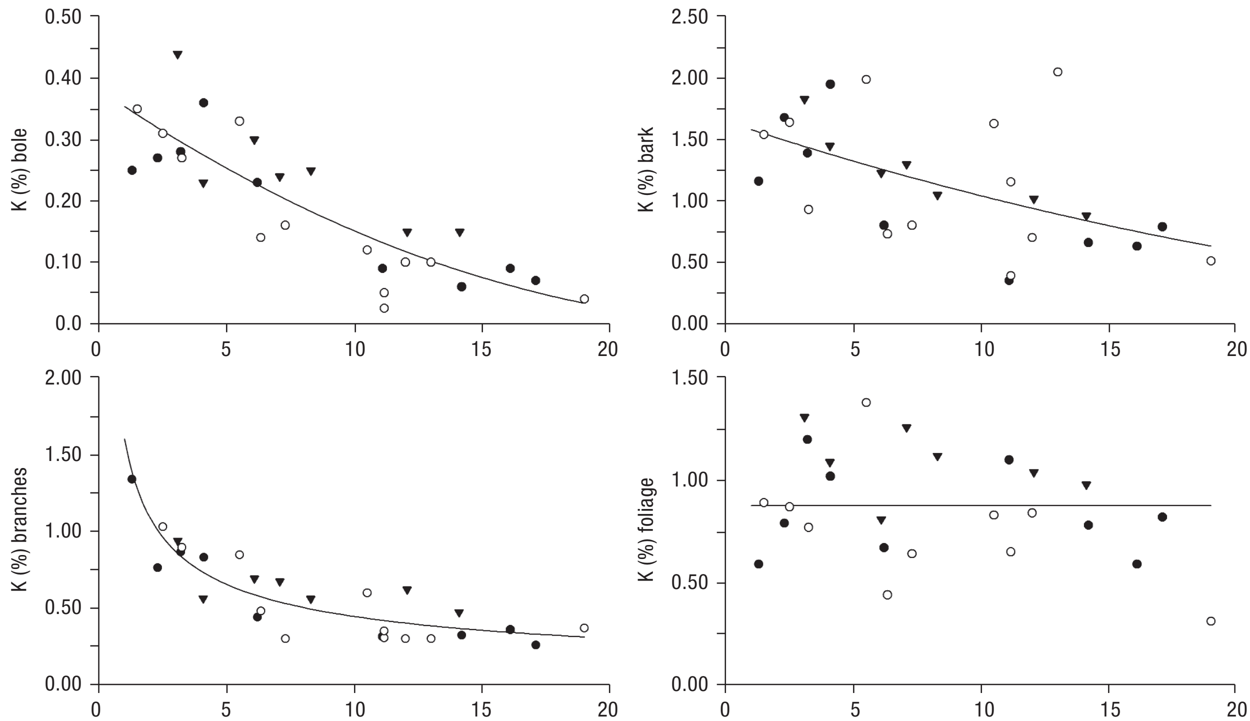

Figure 4. Tissue K concentration (%) related to tree age (years). Points represent trees sampled at three different locations: Guanacaste, Costa Rica (●); northern region, Costa Rica (○) and Panama (▼). Lines represent fitted models (Table 2).

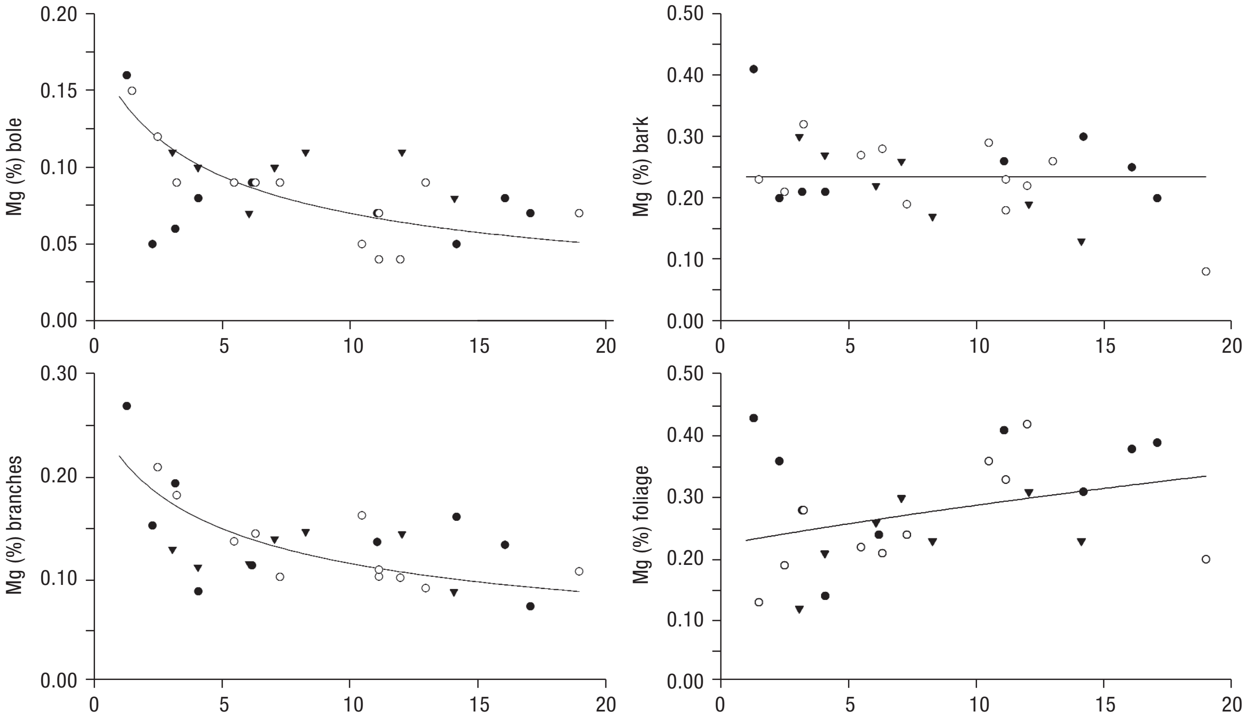

Figure 5. Tissue Mg concentration (%) related to tree age (years). Points represent trees sampled at three different locations: Guanacaste, Costa Rica (●); northern region, Costa Rica (○) and Panama (▼). Lines represent fitted models (Table 2).

Cu, Zn and B. In contrast, the N, K, Fe and Mn concentrations in the bark declined with tree age. N was the most concentrated nutrient in the tree bole and had decreasing concentrations with age. K-bole was also high in young trees but decreased sharply with age, with very low values at the end of the rotation. Mg-bole declined slowly with age due to the low values found in young trees. The relatively low concentrations of Ca, P, S, Fe, Mn, Cu, Zn and B in the bole showed no relationship with tree age. K was the most concentrated nutrient in young tree branches but decreased sharply with tree age. Ca-branches was highest in trees older than approximately 3 years. The concentrations of other elements in the tree branches, including N, Mg, Cu and Zn, also declined with age, whereas those of Ca, P, S, Fe, Mn and B did not show any relationship with tree age. N was the most concentrated nutrient in the foliage and decreased with age, while the other elements did not show any relationship with age, with the exception of Mg, which increased with tree age.

Discussion

In West African planted teak forests, Drechsel and Zech (1994) observed decreases in foliar N and P concentrations with tree age; Montero (1999) also reported foliar N, P and K concentrations decrease in Costa Rica. Similarly, Siddiqui *et al.* (2009) found foliar N, P, K and Zn concentration decrease with age, whereas Ca and Mn increase. Siddiqui *et al.* (2007) also reported a significant reduction in nutrient concentrations in teak roots with trees age. These previously reported patterns do not correspond to the dynamics found in the present study, in which the only foliar nutrient concentration found to decline with tree age was N (Fig. 2, Table 2), whereas there was a tendency for the Mg concentration to increase with tree age (Fig. 5, Table 2).

N concentrations decreased with age in all tissues (Fig. 2), especially in the foliage (2.3 to 1.7%), as has been previously reported for teak (Montero, 1999) and is considered to be a general trend in plant nutrition (Barker and Pilbeam, 2006; Yuan *et al.*, 2007). High N concentrations in young trees could be due to the large requirements of plants at this fast-growing stage, as N is usually related to plant growth (Fölster and Khanna, 1997; Barker and Pilbeam, 2006). However, as greater soil N availability leads to higher plant N concentrations, the high N concentration at the beginning of the rotation could also be explained by the large amount of N available from the soil at this stage, which could be supplied either by large amounts of organic residues combined with high mineralization rates and/or by fertilization. Thus, a plant would absorb large amounts of N, store it as a reservoir and use it later during the rotation by translocation from one tissue to another (Miller, 1984; Yuan *et al.*, 2007; Yuan and Chan, 2010). Hence, the application of N fertilizer at this stage could be futile or could cause even greater losses due to leaching, resulting in contamination and economic losses (Fölster and Khanna, 1997).

The decreases in N concentration observed in several tissues with tree age (Fig. 2) could be explained by (a) decreasing plant requirements as plants age and decline in productivity and require less N to support these lower growth rates; (b) a growth dilution effect, as plant biomass increases with age and usually tends to allocate more structural and storage materials containing little N (Yuan *et al.*, 2007); or (c) a decline in the soil N supply, which would result in lower N uptake and greater nutrient translocation using the nutrients stored during younger years. However, declines in N concentration with age are also considered one of the causes of *age-related declines in forest productivity* because (i) N is usually considered to be the limiting nutrient in forest ecosystems, particularly in young tropical soils (Hedin *et al.*, 2009); (ii) the N mineralization rate in older forest soils is lower than in younger stands, causing a diminishing soil N supply in older stands; and (iii) plant N supply and forest nutrition are generally related to the photosynthesis rate, so a decrease in plant N supply would cause lower net primary production (Gower *et al.*, 1996; Ryan *et al.*, 1997; Binkley *et al.*, 2002). Understanding whether N concentration declines are a cause or a consequence of planted forest productivity declines is an important issue that should be addressed in further research. One way to resolve this issue could be to establish a fertilization experiment in mature planted teak forests (combined with a thinning program), monitoring the N concentration before and after fertilization and evaluating whether an increase in the N concentration would eventually result in an increase in growth rates.

High Ca concentrations in teak bark have also been reported by other authors (Nwoboshi, 1984; Totey, 1992; Negi *et al.*, 1995). The Ca concentration in teak bark tended to increase with tree age in the trees sampled in Guanacaste (Costa Rica) and Panama, but we could not fit a sound statistical model reflecting this tendency, as some trees in the northern region of Costa Rica presented low Ca bark concentrations (Fig. 3). These low concentrations probably reflect Ca deficiencies or certain disorders, as the soils in this region exhibited lower values of available soil Ca and high acidity (Table 1). However, the foliar Ca concentration of the trees in this region was adequate and comparable to that of trees from other regions (Fig. 3). If Ca deficiency occurs it would mainly affect new leaves (Barker and Pilbeam, 2006), so trees with lower bark Ca concentrations could have suffered a Ca deficiency in the past but then recovered, thus exhibiting adequate nutritional status at sampling time. This phenomenon could be explained by lime application at intermediate tree ages.

Zech and Drechsel (1991) consider values of 0.96-1.21 for the Ca:K ratio in foliage as adequate for healthy teak trees; the average ratio value found in our study was 1.53, reflecting a nutrient imbalance involving a Ca excess and/or a K deficiency. It could also reflect a difference between African planted teak forests and the investigated Central American teak stands in terms of environmental, management or even genetic differences. The foliar K concentration ($0.88 \pm 0.07\%$) fell at the lower end of the range (0.80-2.32%) considered as adequate (Drechsel and Zech, 1991; Boardman *et al.*, 1997), higher than the values reported by Negi *et al.* (1990) in India (0.83%) and Benin (0.29%). K is a mobile nutrient that plays key roles in photosynthesis and CO_2 assimilation (Barker and Pilbeam, 2006) and exerts a regulatory effect on stomatal movement and transpiration rates; thus, foliar K requirements would be expected to increase with tree age because modifying transpiration rates to control increased hydraulic resistance and sustaining a higher photosynthesis rate are two of the key physiological mechanisms underlying the plant response to the aforementioned age-related decline in plant productivity (Gower *et al.*, 1996; Ryan *et al.*, 1997; Binkley *et al.*, 2002). However, the foliar K concentration showed no relationship with tree age, in spite of the foliar K decreases associated with age in the sampled trees reported by Montero (1999). The decreasing K concentrations in the bole, bark and branches observed with increasing tree age (Fig. 4) are probably related to the constant foliar K concentration, as the increasing foliar K requirements are probably supplied by the K in those tissues by nutrient translocation.

An increase in the foliar Mg concentration with tree age, as found in this study, has also been reported by Montero (1999) in teak plantations in Costa Rica. This increase could be related to the decline in the Mg concentrations in the bole and branches because Mg is probably translocating from these tissues to leaves. Foliar Mg may increase with age to meet the physiological demands of older trees; these physiological needs include the following: a) to sustain high photosynthesis efficiency; b) to partially inhibit excess photophosphorylation; and c) to regulate leaf stomatal conductance (Gower *et al.*, 1996; Gholz and Lima, 1997; Ryan *et al.*, 1997; Binkley *et al.*, 2002; Barker and Pilbeam, 2006). However, some of the foliar Mg concentrations found in young trees (Fig. 5) are considered low relative to the adequate reference range values (0.20-0.37%) proposed for teak in the literature (Drechsel and Zech, 1991; Boardman *et al.*, 1997); in fact, during the dry season in the northern region of Costa Rica, symptoms of foliar Mg deficiency are common. Hence, the translocation of Mg from the bole and branches and the increase in the foliar Mg concentration can be considered as mechanisms to achieve an adequate Mg level to ensure plant productivity.

The P concentration was higher in the foliage than in the other tissues analyzed, as previously reported by Nwoboshi (1984), showing no tendency associated with tree age. The average foliar P concentration lies at the lower limit of the reference range (0.14-0.25%) for adequate values reported in the literature for teak (Drechsel and Zech, 1991; Boardman *et al.*, 1997), although many of the foliage samples showed values lower than this reference. S was found to be concentrated mainly in the teak foliage, showing values in the lower end of the reference range (0.11-0.23%) considered as adequate for teak (Drechsel and Zech, 1991; Boardman *et al.*, 1997).

The tissue Fe and Mn concentrations showed high variability, probably due to sample contamination with soil during fieldwork; however, prior to statistical analysis, the values determined as too high were considered as outliers and removed from the dataset. This contamination was most noticeable in the bole, the branches and especially the bark, where the Fe and Mn concentration declines with tree age were probably caused by a decrease in the proportion of contaminated vs. properly collected samples as the biomass increased. The foliar Fe (58-390 mg kg^{-1}) and Cu (10-25 mg kg^{-1}) concentrations were within the ranges considered adequate for teak, while the foliar Mn (50-112 mg kg^{-1}) values were below it (Drechsel and Zech, 1991; Boardman *et al.*, 1997).

The foliar Zn concentration lies within the range (20-50 mg kg^{-1}) considered as adequate by other authors (Drechsel and Zech, 1991; Boardman *et al.*, 1997), although Zn is usually deficient in plants growing in highly weathered soils (Barker and Pilbeam, 2006), such as the ones in our study areas. The overall average among the locations showed low available soil Zn; this low average was influenced by the low values found in the northern region of Costa Rica, as the soil Zn values in Guanacaste and Panama are considered adequate (Table 1). Montero (1999) reported an increase in the foliar Zn concentration with age, in contrast with the lack of a relationship found in this study, where the variability of the data was high. The foliage B concentration lies within the range (15-45 mg kg^{-1}) considered adequate by other authors (Drechsel and Zech, 1991; Boardman *et al.*, 1997), which is higher than the requirements reported for other species (Lehto *et al.*, 2010). Of all tested tissues, the highest B concentration was in the bark, as has been reported for other tree species (Lehto *et al.*, 2010).

Generally, relatively high values of microelements are required to maintain an appropriate nutritional status in teak and to ensure forest productivity and sustainability, although little attention has been paid to this issue in other studies of teak nutrition (Nwoboshi, 1984; Totey, 1992; Negi *et al.*, 1995; Kumar *et al.*, 2009). Tropical soils are usually characterized as highly weathered soils that are rich in Fe or Mn but generally deficient in Zn, B, Cu, and Mo (Barker and Pilbeam, 2006). B is commonly deficient in soils throughout the world and is difficult to evaluate in routine soil fertility analyses (Lehto *et al.*, 2010). Hence, special care should be taken to evaluate the B and Zn status in planted forests throughout the tropics.

Tissue nutrient concentrations, especially those for foliage, are considered to be a management tool for evaluating the nutritional status of planted trees (Mead, 1984; Drechsel and Zech, 1991; Barker and Pilbeam, 2006; Lehto *et al.*, 2010). Foliar concentrations have been reported to be remarkably useful for this purpose because they are sensitive indicators of nutritional deficiencies due to their direct relation with productivity, as foliage is where photosynthesis takes place (Mead, 1984). Table 2 summarizes the models and values that we put forth for consideration as adequate concentration reference levels to be used in nutrient management of planted teak forests in Central America. By selecting dominant and co-dominant trees within well-managed and highly productive plantations, we sampled trees with an appropriate nutritional status and higher nutrient requirements than average, so if the plantations are managed to ensure the aforementioned levels, and if fertilizers are added accordingly, the trees would have good nutritional status. Hence, the nutrient concentration values found in this study can be taken as a reference to evaluate the nutritional status of similar teak plantations in the region, *i.e.,* as teak nutrition guidelines for Central America.

Decreases in N concentration with tree age are considered to be either a cause or a consequence of the decline in productivity associated with increasing tree age; the K and Mg concentrations could also be related to this phenomenon, which is a key issue in applied ecology. Future research about these relationships should be performed with the aim of achieving higher growth rates throughout the rotation period, which would allow shorter cycles to be used.

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