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GROWTH, FOLIAR AND NUTRIENT STATUS OF *TERMINALIA AMAZONIA* PLANTED IN SOUTHWESTERN COSTA RICA

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NICHOLS, J.D., GILLESPIE, A.R. & RICHTER, D.D. 1997. Growth, foliar and nutrient status of *Terminalia amazonia* planted in southwestern Costa Rica. A study was conducted to examine the growth of *Terminalia amazonia,* a promising plantation species native to the humid neotropics, in relation to soil and foliar nutrient levels, its nutrient requirements and suitable management practices, and to suggest further research. Plots of 49 trees were established in 25 three-year-old plantations of *Terminalia amazonia,* at sites ranging from sea-level to 1200 m above sea-level in tropical wet and premontane life zones in southwestern Costa Rica. Measurements of total tree height, diameter at 10 cm above the ground surface, and crown width at its widest point were taken for all trees in each of the 25 plots. Soil was collected at five points and included three depths: 0 to 5 cm for bulk density and physical and chemical property evaluation, 15-30 cm and below 50 cm for chemical and physical property sampling. Sun leaves from seven healthy trees in each plot were also collected. Soil samples were analysed for pH, exchangeable acidity, total C, total N, extractable P, K, Ca, Mg, Na, CEC, base saturation and bulk density. Foliage samples were analysed for concentrations of total N, P, K, C, Ca, Mg and Na. Using the formula d^2h to calculate tree volume, the greatest growth measured in each of three different life zones at three years was: tropical wet forest zone, 29.5 $m^3 ha^{-1}$, tropical moist forest zone, 67.1 $m^3 ha^{-1}$; and tropical premontane forest zone, 49.6 $m^3 ha^{-1}$. Surface-soil phosphorous levels were generally below 4 ppm and foliar P levels were 0.16% or less in vigorously growing trees, indicating that *T. amazonia* is quite efficient in its use of P. The species appeared to be growing better as N levels increased and at lower surface-soil bulk densities.

Key words: *Terminalia amazonia* - native species - reforestation - foliar - nutrition

NICHOLS, J.D., GILLESPIE, A.R. & RICHTER, D.D. 1997. Status pertumbuhan, daun dan nutrien *Terminalia amazonia* yang ditanam di barat daya Costa Rica. Kajian dijalankan mengenai pertumbuhan *Terminalia amazonia,* spesies asli di ladang yang berpotensi di kawasan neotropika lembap, kaitannya dengan tahap tanah dan tahap nutrien daun, keperluan nutrien dan kesesuaian amalan pengurusan serta mencadangkan kaji selidik selanjutnya. Plot bagi 49 pokok ditubuhkan di 25 ladang *Terminalia amazonia* berumur tiga tahun di tapak dari aras laut sehinggalah 1200 m di atas aras laut di zon basah tropika dan pra gunung di barat daya Costa Rica. Jumlah ketinggian pokok, diameter pada 10 cm di atas permukaan tanah, dan lebar silara pada tempat yang paling lebar disukat di semua pokok dalam setiap 25 plot. Tanah diambil di lima tempat termasuk tiga kedalaman: 0 hingga 5 cm bagi ketumpatan pukal dan penilaian ciri-ciri fizikal dan kimia, 15-30 cm dan di bawah 50 cm bagi pensampelan ciri-ciri kimia dan fizikal. Daun dari tujuh pokok yang baik dalam setiap plot juga diambil. Sampel tanah dianalisis bagi pH, keasidan boleh tukar, jumlah C, jumlah N, keboleh ekstrakan P, K, Ca, Mg, Na, CEC, penepuan asas dan ketumpatan pukal. Sampel daun dianalisis untuk kepekatan jumlah N, P, K, C, Ca, Mg dan Na. Dengan menggunakan formula d^2h untuk mengira isi padu pokok, pertumbuhan tertinggi disukat di setiap tiga zon hayat yang berbeza pada umur tiga tahun ialah: zon hutan basah tropika, 29.5 m^3 ha^{-1}; zon hutan lembap tropika, 67.1 m^3 ha^{-1}; dan zon hutan pra gunung tropika, 49.6 m^3 ha^{-1}. Tahap fosforus permukaan tanah biasanya di bawah 4 ppm dan tahap P daun ialah 0.16 % atau kurang dalam pokok yang tumbuh cergas menunjukkan bahawa *T.amazonia* agak efisien dalam penggunaan P. Spesies tersebut didapati tumbuh lebih baik apabila tahap N bertambah dan juga pada ketumpatan pukal permukaan tanah yang rendah.

Introduction

There are 758 million hectares of degraded lands in the tropics which have a potential for some sort of reforestation (Grainger 1988). Reforestation could be accomplished through natural regeneration of forest species or through the establishment of forest plantations. Plantations, while differing in structural complexity and biological richness from natural forests, offer the potential of high production of firewood and timber when species are correctly chosen and the plantations are well managed. Evans (1992) notes that production of industrial wood from plantations is expected to increase fourfold in Latin America by the year 2000, when they will be satisfying 50% of the region's needs.

In 1980, 85% of tropical plantations comprised three genera - *Eucalyptus, Pinus,* and *Tectona* (Evans 1992). There is a need to investigate the production and end-use of native species, for both their economic usefulness and the role they might play in maintaining biodiversity.

Costa Rica is known for its high rates of deforestation in this century (Quesada 1990). Large areas of the country, mostly in mountainous terrain, were deforested during the period 1950 - 1980, and were often converted to pastures for beef production. Resultant degradation through erosion and compaction has been severe on these sites (Tropical Science Center 1982). In response, the Costa Rican government has promoted the conversion of pastures to tree plantations, primarily for timber production, providing incentives for 52 255 ha of land for reforestation between 1987 and 1991 (MIRENEM 1992). In the Zona Sur (the southwestern fifth of the country), the recommended exotic species *Eucalyptus deglupta* and *Pinus caribaea* have performed poorly on many sites. In this region, some of the two hundred commercial tree species native to Costa Rica may be viable alternatives for establishing plantations on thousands of hectares of degraded land. In the Atlantic zone of Costa Rica, preliminary results have indicated that some native species may outperform exotics on degraded pastures (Butterfield 1990), while informal plantings on farms indicate the same in the Zona Sur (Nichols & González 1992).

One of the most promising of the native species is *Terminalia amazonia.* It produces a wood which is in high demand locally for construction and furniture (Allen 1956, Carpio 1992) and it is moderately hard, heavy and durable; density ranges from 0.61 to 0.80 g cm^{-3}. The colour is yellow, frequently streaked with red. Initial results from one planting, where an average height of 21.3 m was attained at 12 y, indicate the species may be suitable for plantations (Nichols 1994). Other species of *Terminalia,* especially *T. ivorensis* and *T. superba* from Africa, are used in plantations (Lamprecht 1989, Evans 1992). *Terminalia amazonia* also has potential for use in regeneration systems other than plantations, where sufficient seed trees are left standing, and abandoned pastures can be converted into nearly pure stands, creating areas which produce large volumes of wood at relatively low cost. This species is also used in agroforestry systems.

The species has been widely planted in southwestern Costa Rica since 1990, particularly in conjunction with the Desarrollo Campesino Forestal project of the Dirección General Forestal (Farm Forestry Development Department of the Costa Rican Forest Service). These plantations provide a useful data set to evaluate *T. amazonia* for reforestation, and can be used to amend the species' nutrient requirements.

The objective of this study was to define the environmental requirements, particularly in terms of climate, soil and nutrient status of *Terminalia amazonia* and how to manage the species under plantation conditions. First approximation techniques for plantation management and establishment may then be recommended over the wide natural range of the species - from southern Mexico to Peru, Brazil, and Trinidad - and on sites with similar characteristics in the rest of the humid tropics.

The plantations examined in this study had been established by farmers in three climatic life zones under a variety of edaphic conditions and using a range of management techniques. By measuring tree growth and collecting foliar and soil nutrient data it was possible to examine correlations between a number of factors and growth and therefore define priorities for future research.

Methods

Field methods

Plantations of *Terminalia amazonia* in the Zona Sur of Costa Rica were located with the assistance of the Costa Rican Forest Service, the Dirección General Forestal (DGF), specifically the Department of Farm Forestry Development, Desarrollo Campesino Forestal (DeCaFor). The plantations were established through a government incentive programme designed to encourage forestry on small- and medium-sized farms.

Sites where *T. amazonia* was reported to have been planted were visited and 25 plantations were selected for sampling. In each plantation, a block of seven by seven trees (49 in total) was laid out, at least three rows from the plantation edge. These blocks were picked to be representative of the plantations in which they occurred. The 21 × 21 m plot (at 3 × 3 m spacing) was marked on four corners with aluminium tags and each tree was marked and numbered with flagging. Survival of planted *T. amazonia* was recorded for each plantation.

Total height (cm), crown width at the widest point of the crown (cm) and stem diameter (cm) at 10 cm above the ground were measured for each tree. Soil samples (0-5 cm) were collected at the centre and in the four quadrants of each plot and combined for bulk density measurement. Soil sampling for bulk density was restricted to the upper 5 cm because *T. amazonia* roots appeared to predominate in the surface horizon. Three samples were also collected from a depth of 15-30 cm, at the centre and in the northwest and southeast or northeast and southwest corners, and one at 50 cm in the centre of the plot for additional chemical and physical analyses. In each plot, fully-expanded leaves having full exposure to the sun were collected from the second whorl below the top of seven co-dominant trees. Foliage sampling took place in June and July 1993, beginning at least six weeks after the start of the rainy season. The leaves from the seven trees were combined and air dried for laboratory analysis.

Elevations of plantation sites were taken from 1:50 000 topographical maps published by the Instituto Geografico Nacional. Information on climatic life zones was taken from Tosi (1969). Annual precipitation and annual temperature data were taken from 13 weather stations in the Zona Sur maintained by the Instituto Meteorologico Nacional (1988).

Farmers and foresters were interviewed to determine plantation history. Management was divided into three categories: "poor", where undersized seedlings were planted, not fertilised, and few or no cuttings of competing vegetation were made; "good", where some efforts at plantation management were made; and "excellent", where trees were carefully tended.

Soil and foliar analyses

For each plot, composited soil samples from each of the three soil depths were analysed for: pH by the H_2O and $CaCl_2$ methods (McLean 1982); exchangeable acidity; $BaCl_2$ acidity (Thomas, 1982); exchangeable Ca, Na, Mg and K using a atomic absorption spectrophotometer (Perkin-Elmer Corporation 1982, Thomas 1982); bulk density (Blake 1965); exchangeable cation exchange capacity as the sum of all base cations plus exchangeable KCl acidity; cation exchange capacity using a saturating salt solution and taking the sum of exchangeable cations in the reacted "leachate" (Rhoades 1982); base saturation by dividing the total sum of bases by the sum of bases plus exchangeable acidity; phosphorus by the Mehlich III method (Mehlich 1984); and total soil C and N using a Elmer 2400 CHNO-S analyser (Perkin-Elmer Corporation 1991).

Foliar analysis was performed on dried, ground leaf samples. Total nitrogen and total carbon were measured on a Perkin-Elmer 2400 Series II CHNO-S analyser. Calcium, Mg, K, Na, Mn, Fe, Zn, Cu and Al were measured by atomic absorption after digestion of leaf tissue (Hach Company 1989).

Analysis

The estimated volume in a plantation was correlated with the independent variables. This quantity is called d^2h in Figures 1 through 7 and was calculated by squaring the measured diameter (d^2) and multiplying by height (h) for each tree (Clutter *et. al.* 1992); these approximate volumes were summed on a plot basis and expressed on a per hectare basis.

Heights and volumes were correlated with 29 site, plant, and management variables. Correlation and multiple regression analyses were used to relate standing volume at three years to individual independent variables and combinations of variables. To examine the potential mechanisms of plantation response to management, tree productivity was plotted against soil and foliar variables. Limiting factors were determined by the pattern and magnitude of plantation response. The boundary representing the potential maximum productivity for the most limiting factor was quantified using non-linear regression analysis. Each stand below this maximum was then examined on a case by case basis to develop an understanding of the relative importance of additional limiting factors.

Results and discussion

Mensurational and site parameters

Survival of *Terminalia amazonia* varied from 65 to 100% (mean=88%), even under conditions where growth was slow (Table 1). Mean height at 3 y varied from 0.89 to 7.16 m, mean diameter at 10 cm above ground level varied from that of seedlings too small to measure to 8.15 cm, and mean crown width from 69.2 to 371.1 cm (Table 1). The tallest individual tree was 10.89 m and the largest diameter measured was 11.0 cm. The volume d^2h measured on the plots varied from negligible where trees were little more than seedling-sized to 67.14 $m^3 ha^{-1}$ at 3 y, with a mean of 15.62 $m^3 ha^{-1}$.

Table 1. Three-year growth, selected foliar and soil nutrient levels in 25 plantations of *Terminalia amazonia*

Plantation	Elevation (m)	Precip. (mm)	Survival (%)	Mean ht. (m)	Mean dia. (cm)	d^2h vol. (m^3 ha^{-1})	Foliar N (%)	Foliar P (%)	BD (g cm^{-3})	pH	Soil N* (%)	Soil P * (ug g^{-1})
A	650	2238	65	3.54	5.34	12.9	1.84	0.21	1.66	5.04	0.40	4.27
B	700	2238	98	2.76	4.49	6.6	1.36	0.15	1.43	4.99	0.53	0.55
C	1200	3811	85	3.63	4.39	5.7	1.21	0.15	1.01	5.07	0.56	0.85
D	600	3088	95	3.04	4.90	7.7	1.33	0.11	1.41	5.22	0.47	0.79
E	50	3707	100	5.41	6.71	29.6	1.40	0.16	1.39	4.71	0.42	1.87
F	1200	3176	78	0.89	negligible	0	1.05	0.09	1.16	5.42	0.55	0.81
G	600	3088	72	2.31	3.23	1.5	1.66	0.15	1.09	4.90	0.65	1.54
H	1000	2336	84	1.84	4.26	3.0	1.49	0.11	1.48	5.12	0.43	0.51
I	600	3804	98	2.48	3.89	4.8	1.42	0.10	1.42	4.84	0.41	0.98
J	500	3176	98	2.85	5.04	9.8	1.69	0.14	1.60	5.38	0.38	0.33
K	900	3804	98	1.96	3.59	4.2	1.63	0.11	1.14	5.51	0.92	0.47
L	800	3176	94	3.10	6.25	11.8	1.76	0.18	1.43	4.82	0.45	2.66
M	1000	3804	98	4.28	7.87	17.4	1.77	0.14	1.13	5.30	0.79	0.58
N	1000	3804	92	4.04	6.65	11.1	1.76	0.12	1.13	5.29	0.88	0.51
O	900	3142	88	3.99	9.69	16.4	1.80	0.16	1.31	5.84	0.53	0.72
P	670	2598	96	6.41	8.04	67.1	2.14	0.10	1.26	4.43	0.56	1.68
Q	600	3088	74	2.32	3.34	2.8	1.33	0.12	1.34	5.23	0.45	1.00
R	600	3088	76	1.45	negligible	0	1.02	0.08	1.53	5.18	0.35	0.47
S	50	3707	88	7.16	8.15	47.8	1.60	0.11	1.16	4.75	0.43	2.15
T	500	2366	86	1.76	3.74	3.0	1.61	0.11	1.61	5.52	0.35	1.67
U	500	2336	85	3.93	6.48	17.9	1.77	0.12	1.63	5.41	0.36	1.12
V	800	3176	69	2.16	5.39	4.9	2.29	0.13	1.51	4.79	0.42	0.69
W	600	2500	100	3.73	5.79	16.6	1.35	0.10	1.73	5.42	0.32	1.20
X	800	3000	96	6.05	8.15	49.7	1.65	0.11	0.91	4.87	0.54	1.43
Y	800	3000	90	3.16	4.23	7.2	1.96	0.10	1.03	4.87	0.63	1.40

* Values from top 10 cm of soil.

Calculated d^2h at 3 y was greater than 30 m^3 ha^{-1}, for a wide range of elevations (Figure 1), on four sites, with the remaining sites having less than 20 $m^3 ha^{-1}$. There are two cases of high growth (>30 m^3 ha^{-1} at 3 y) for stands E and S, at coastal locations less than 50 m above sea-level, and two more for stands P and X, at 650 and 800 m in elevation respectively. The remaining plantations with poor to moderate growth span a range of 500 to 1200 m in elevation. Thus, all sites in this study appear to be within the elevation range where *T. amazonia* potentially grows quite well.

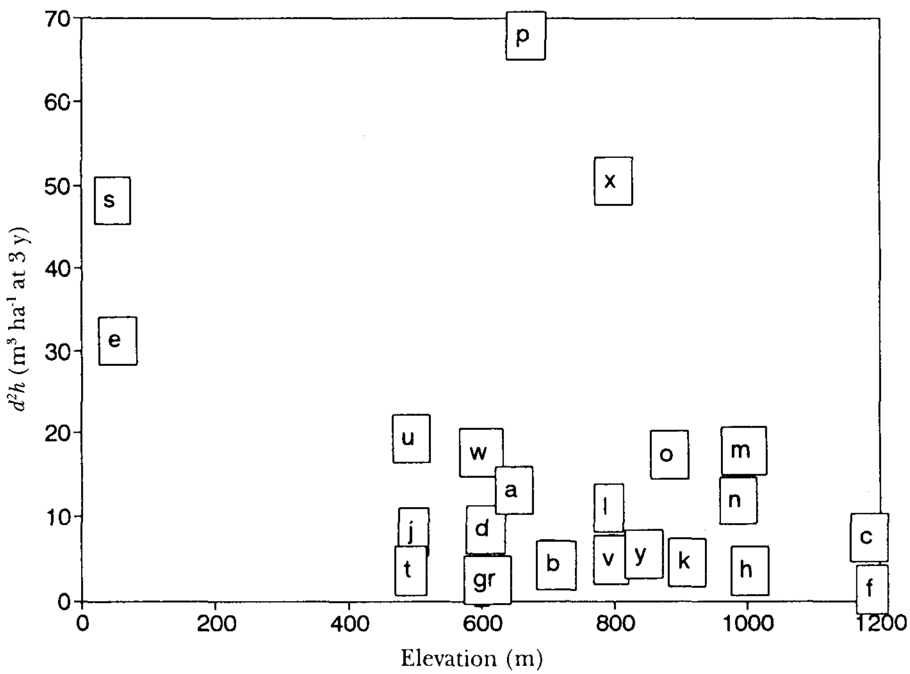

Figure 1. Elevation vs. d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

Considering precipitation, plantations with both high and low productivity were again found across a wide range, in this case from 2200 mm y^{-1} to nearly 4000 mm y^{-1} (Figure 2). The Holdridge life zone system, mapped for Costa Rica by Tosi (1969), is based on precipitation and temperature. According to this system, the highest-producing plantations spanned a number of life zones. Plantation P is in the tropical moist forest region where there is a distinct dry season and the original vegetation had a considerable deciduous component. Plantation X is in the premontane wet forest province, higher and cooler, and plantations S and E are in the hottest and wettest zone, classified as tropical wet forest, also known as "rain forest". Thus, rainfall in the range 2200-4000 mm y^1 was not limiting to growth. One question which future work on this species might address is whether *T. amazonia* might grow adequately in drier environments, in the rain shadows of the Zona Sur where precipitation ranges between 1300 and 2200 mm y^{1} and in the higher areas of the premontane zone above 1200 m elevation. One-way analysis of variance showed only a marginal difference between productivities among the life zones ($p=0.07$) though 2-way ANOVA showed this effect actually to be due to management intensity.

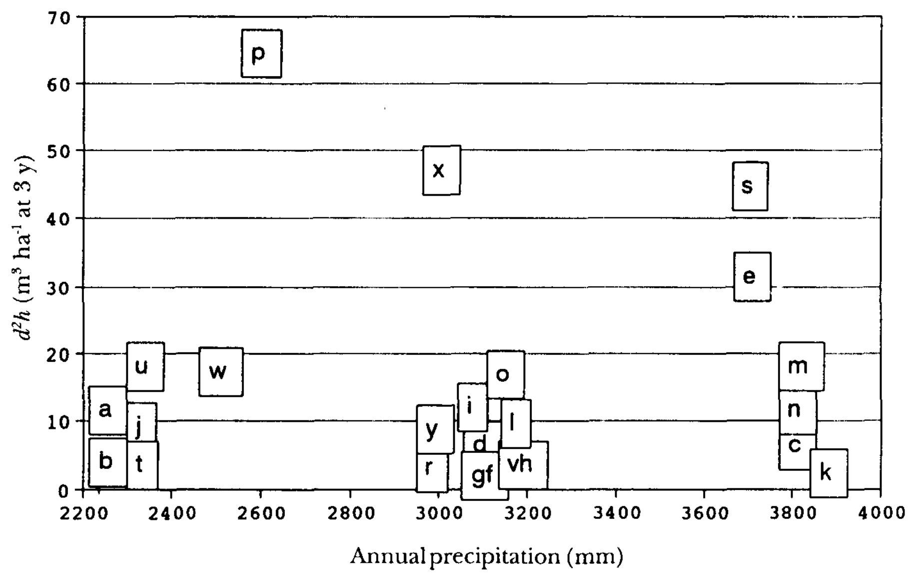

Figure 2. Precipitation vs. d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

Foliar and soil parameters

Values for foliar N varied from 1.02 to 2.29%, foliar P ranged from 0.08 to 0.21%, and foliar K had values of 0.63 to 1.37%. Bulk density ranged from 0.91 to 1.73 g cm^{-3} with a mean of 1.34 g cm^{-3} (Table 1). Means (and ranges) for several chemical properties in surface soils follow: H_2O pH, 5.12 (4.43 - 5.84); base saturation (in % of exchangeable cation capacity), 76.54 (25.34 - 99.17); exchangeable cation exchange capacity (cmol kg^{-1}), 9.18 (3.10 - 22.72); total N (%), 0.51 (0.32 - 0.92); extractable PO_4-P (ug g^{-1}), 1.21 (0.33 - 4.27); and exchangeable K (cmol kg^{-1}), 0.51 (0.05 - 2.00).

In some reported studies, volume increment and soil nutrient levels have been fairly well correlated (Chijioke 1988, Evans 1992) but in this study, soil variables and plantation growth showed little correlation (Table 2). One of the largest correlations found for volume and soil characteristics was for surface soil pH ($r = -0.47$), which ranged from 4.43 to 5.98. The lowest pH (H_2O) for any horizon in any of the plantations, 4.43, was found in the surface soil of plantation P which had the greatest volume production. The pH range for the four most productive plantations was 4.43 to 4.87 indicating that *T. amazonia* performs well on more acid soils. Perhaps a lower pH is associated with the acidifying effect of fertilisers, or some nutrients are made more available under high acidity.

Total nitrogen in the top 5 cm of soil (0.31- 0.92 %) was poorly correlated with foliar N concentrations (r=0.19). Soil N contents for the top four plantations were intermediate in this range (0.43 to 0.56%).

Table 2. Pearson correlation coefficients for 3-y d^2h and foliar and soil nutrient levels

Environmental variables		Soil variables	0 - 5 cm	15 - 30 cm	> 50 cm
Elevation	- 0.33	pH (H_2O)*	- 0.47	- 0.28	- 0.28
Precipitation	0.01	pH (salt)	- 0.37	- 0.31	- 0.05
Annual temperature	0.23	$BaCl_2$	- 0.01		
		Exch. acidity*	0.51	0.29	0.29
Foliar nutrient levels		Total C	- 0.13	- 0.04	- 0.07
		Total nitrogen	- 0.05	- 0.17	
Foliar N	0.28	Mehlich 3P	0.28	- 0.01	- 0.15
Foliar P	- 0.16	Potassium	0.25	0.23	- 0.03
Foliar K	- 0.24	Calcium	0.10	- 0.12	0.15
Foliar C	0.46	Magnesium	0.24	- 0.02	0.18
Foliar Ca	- 0.03	Na	0.10	0.15	0.13
Foliar Mg	0.15	Bulk density	0.26		0.25
Foliar Na	0.15	Exch. CEC	0.32	0.19	- 0.09
N:P ratio	0.38	CEC	0.17	0.04	0.11
N:K ratio	0.41	Base sat.	0.32	- 0.19	- 0.15
P:K ratio	0.04				
Ce:Mg ratio	0.17				

* (p = < .05).

Soil P was also poorly correlated with volume growth. Plantation X, with the second highest volume increment of all plantations, had an extractable P level of 1.43 ppm, plantation P 1.68 ppm, plantation S 2.15 ppm and plantation E 1.87 ppm (mean for the top four 1.72 ppm P, coefficient of variation 23%). Surface soil P had a moderately strong correlation with foliar P (r = 0.56). All of the surface soil P values for the top four plantations were below the 3 ppm P which has been recommended as the level indicating a need for P fertilisation in loblolly pine (Binkley 1986). It thus appears that *T. amazonia* is relatively efficient in its use of P and can grow well on sites with apparently negligible amounts of P in the mineral soil (as extracted by the Mehlich 3 method). The relative amounts of litter, which can provide considerable P in organic form, were not recorded. Neither were the rooting patterns of *T. amazonia*, which may be extracting some P from lower soil horizons. Thus, it is not clear how nutrient cycling limits long-term P availability nor can we exclude a potential P limitation with the amelioration of another limiting factor.

Plantation management

Standard management as recommended by private foresters and those working for the Dirección General Forestal is to use seedlings approximately 30 cm tall grown in plastic bags. Alternatively, "stumps" of 1 cm diameter or greater with stems and roots each 10-20 cm in length are recommended. Vegetation is to be cleared down to mineral soil in a meter wide circle and a seedling planted at the centre. Grass and brush competition is controlled either manually or chemically. Seedlings are fertilised at the time of planting with 50 g of 10(N)-30(P)-10(K), a fertiliser commonly used in coffee production in the region.

In practice, management on private farms has been highly variable and it was difficult, at least in the 25 plantations studied, to find even one which met the standard management recommendation. In spite of extensive interviews with farmers and forestry workers, a complete history of each plantation was impossible to recreate although in some cases fairly good records were kept, particularly of fertilisation. Information on seed and nursery source was not available in most cases. Management intensity explained much of the variation in standing volume at 3 y (r^2=0.81). The mean standing volume for the 9 sites where management was "poor", meaning that substandard seedlings were planted, not fertilised, and weeds were not controlled, was only 3.4 m^3 ha^{-1} at 3 y (range: no measurable diameter to 7.7 m^3 ha^{-1}). This contrasts with a mean volume of 11.4 m^3 ha^{-1} at 3 y (range: 3.0 - 17.4 m^3 ha^{-1}) for 12 "good" sites and a mean of 48.5 m^3 ha^{-1} at 3 y (range: 29.5 - 67.1 m^3 ha^{-1}) for 4 plantations with "excellent" manage-ment (Figure 6).

"Excellent" management involves a system of cultivation more intensive than that usually used in plantation forestry, similar to that used for coffee or fruit tree cultivation. In fact, the farmer in charge of plantation P used techniques applied in coffee farming, especially the provision of 10-30-10 fertiliser at time of planting and the application of a "complete" fertiliser with 18% N at the beginning of the second growing season. These techniques, though expensive, resulted in a closed-canopy plantation ready for thinning at 3 y with a d^2h value of 67.14 m^3 ha^{-1}.

Plantations E and S were both in the coastal region near Uvita de Osa, and so had similar climatic regimes. These plantations were also well tended, but plantation E had been in pasture for many years and had heavy grass competition for tree seedlings, whereas S had been in secondary forest and had little history of recent use. These differences were reflected in plantation E's lower foliar N concentration and higher bulk density (Figures 5 and 6) with a d^2h of 29.9 m^3 ha^{-1} at 3 y for E as opposed to 47.7 m^3 ha^{-1} for S.

The "poor" sites most frequently had major problems with competing vegetation, in many cases having been planted and more or less abandoned. The effects of this competition were reflected in poor height growth and generally low foliar N concentrations. Surface soil N levels in plantations F and P, with the poorest and best volume increments respectively, were virtually the same, but in plantation F pasture grasses were left uncontrolled, whereas in plantation P competing vegetation was controlled and the stand closed in less than 3 y. In stands D, F, G, H, Q, and R, apparently very small (10 cm) seedlings were planted in August, three months after the beginning of the rainy season, and left untreated without further control of competing vegetation. In spite of these conditions, survival was 76% in F, the plantation with least growth, and 78% in R, the second worst. It is possible that these trees may still respond if released from competition.

Mechanisms of management response

As expected, intensive management provided large growth responses and, again, explained the majority of variation in productivity (r^2= 0.81). However, the mechanisms through which management provides this response must be identified to understand the nature of site limitations and to prescribe the appropriate and cost-effective silvicultural treatments needed to overcome these limitations. Thus, correlation analyses and data plots were used to discern patterns of stand volume response to foliar and soil variables. Pearson correlation coefficients for 3-y volume vs. environmental and foliar and soil nutrient factors showed high variability due to non-linear relationships among the variables (Table 2). It was apparent that no strong linear relationship existed between volume and any one of the independent variables considered singly. Even when combining four variables, foliar N, foliar P, surface soil P and total surface soil N [in a manner similar to that employed by Lamb (1976, 1977) or cited by Evans (1992) in work with *Eucalyptus*], only 26% of the variation in volume production was explained.

Traditionally, these highly-weathered tropical soils have been described as P deficient. Volume ha^{-1} at 3 y was examined in relation to foliar P levels (Figure 5). Phosphorus appeared not to be limiting the growth of *T. amazonia* on most of the sites studied, as growth excelled even at low foliar P concentrations. The data showed a dilution pattern where enhanced growth from management decreased foliar P concentrations to very low levels. Only in plantations R and F were deficiency symptoms visible in the trees sampled, where, in fact, there were no individuals from which to collect "healthy" foliage. The three plantations with the greatest volume increment (P, S and X) were near the lower end of the range for foliar P, with concentrations between 0.10 and 0.12%. The range in surface soil P for these three sites was 1.43 to 2.15 ug g^{-1}. Of course, foliage biomass was much greater on these sites, implying large quantities of P in the canopies. Nevertheless, the physiological functioning of these leaves (photosynthesis) was efficient even at these low concentrations, providing the large canopy mass. The levels of foliar P were consistent with those found in *T. ivorensis* and *T. superba* in Africa (Drechsel & Zech 1991) although the level at which *T. amazonia* exhibited deficiency in our study was lower, at 0.08 - 0.09% P rather than 0.11%.

For the other macro-nutrients, the correlation coefficients were 0.28 for foliar N and - 0.24 for foliar K. Foliar K showed a similar dilution effect to that shown by P. The relationship of volume growth to foliar N appeared to be curvilinear (Figure 3) and was the strongest response observed when examining data plots of both soil and foliar chemical and physical variables. This was mirrored in the nutrient ratios incorporating N. A curvilinear relationship would be expected for essential nutrients as growth increases and then levels off with "luxury" consumption or the limitation of some other resource. The plot of 3-y standing volume vs. foliar N showed the strong response of well-managed stands, forming an upper boundary to the data. This boundary is the approximate maximum productivity to be expected at a particular foliar N concentration. Nine plantations follow this upper boundary curve. Fitting a linear model to the 3-y standing d^2h vs. foliar N relationship for those nine plantations yielded an r^2 value of 0.87. This linear model would estimate a critical level of 1.92% foliar N below which productivity is less than 90% of the maximum. Fitting a nonlinear regression model increases the precision of the delineation of the productivity boundary (r^2= 0.95). This model would estimate a critical limit of 1.84% foliar N. The non-linear equation predicting 3-year standing volume was:

$$\text{Standing volume } (d^2h) = 82.2(1-e^{(-2.0(\text{folN}-1.2))})$$

where 82.2 represents the asymptote of productivity, or the highest attainable production estimated from these data. Growth for well-managed plantations on this curve was: at E, 29.5 m^3 ha^{-1} at 3 y compared to 47.7 m^3 ha^{-1} for S, and 49.6 and 67.1 m^3 ha^{-1} for X and P respectively. Since growth at all plantations was less than 90% of that at P, we suggest that 1.83% foliar N based on the curvilinear model for volume growth approximates the critical level for foliar N of *T. amazonia*. Twenty-two of the 25 plantations had foliar N levels lower than 1.83%. Two plantations had foliar N levels above 1.83% but had low to moderate productivity, i.e. they fell below the boundary line.

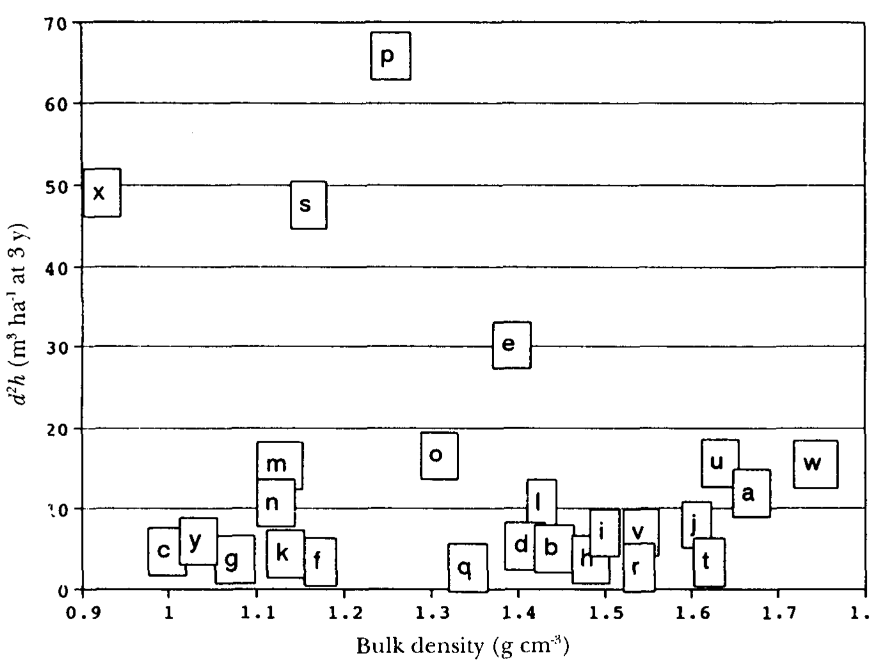

Figure 3. Foliar N vs. d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

Bulk density in the top 5 cm of soil appeared to be limiting growth on some of these sites despite adequate or marginal N nutrition (Figure 4), especially in the case of V, with a bulk density of 1.51 g cm^{-3}. High bulk densities may have restricted root growth, impacting water and nutrient uptake. Several plantations had both low bulk density and moderate to high foliar N but low productivity, specifically plantations M, N, K, G and Y. Plantations M and N were in a coffee plantation on an Andisol or volcanic soil. These stands were planted at a 4 × 4 m spacing whereas most of the other plantations were planted at 3 × 3 m. As a result, standing d^2h volume was less than that of denser stands having the same survival. If plantations M and N (where surface soil total N and foliar N were high) had been planted at 3 × 3 m, they would be fifth and sixth in ranking after the leading four plantations. Also in plantations M and N the lower two or three whorls of branches on each tree had been pruned reducing photosynthetic capacity and thus volume increment. Plantation K was actively being pastured and most trees had suffered from animal damage, again slowing growth though foliar N levels were relatively high. Plantation G had some loss in biomass due to moderate survival (72%), as did plantations V (68%) and A, Q, R and F, impacting increment through a reduction in growing stock despite the relatively high foliar N concentrations. Here in plantation Y, shade, rather than a nutrient or water limitation, was clearly slowing growth.

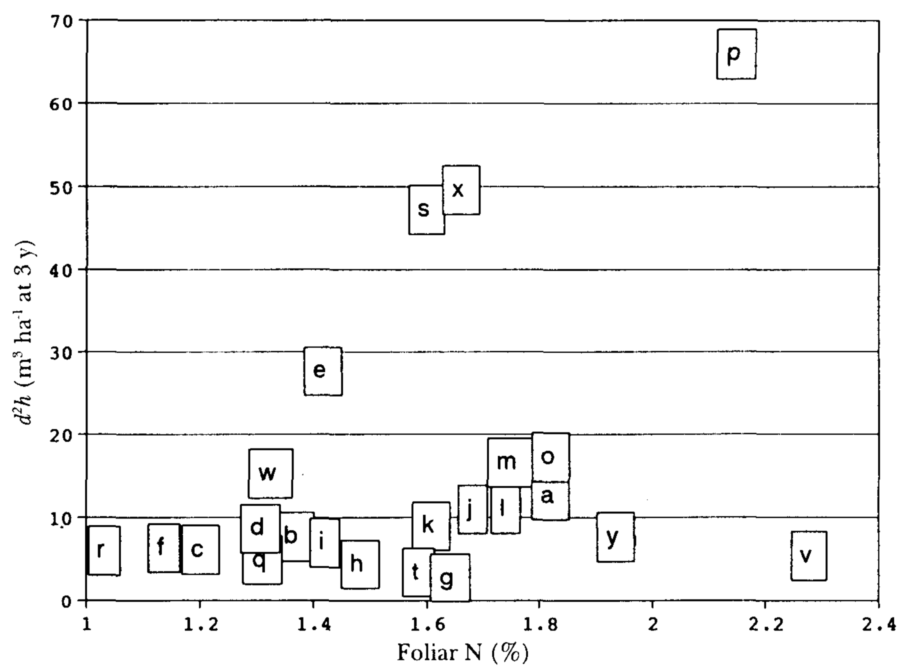

Figure 4. Bulk density vs d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

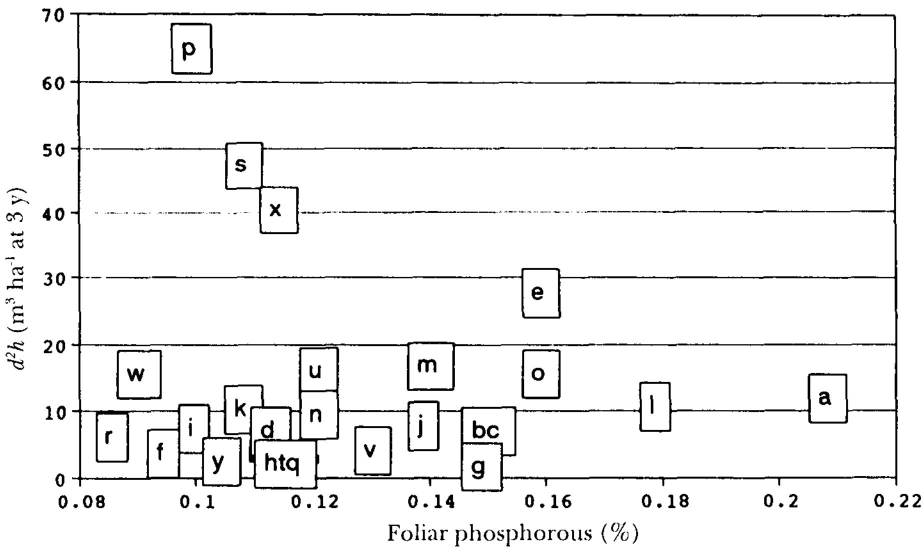

Figure 5. Foliar P vs. d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

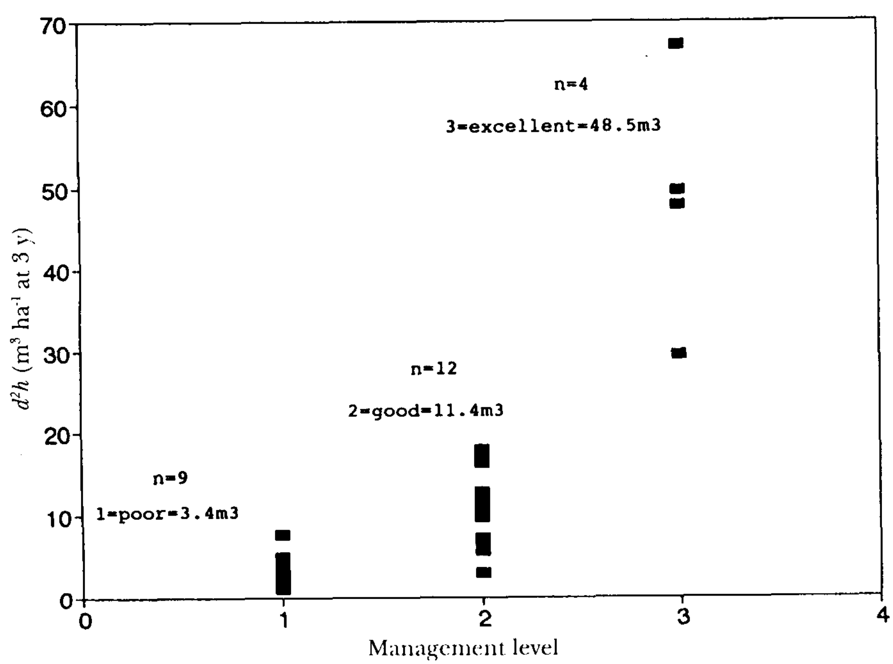

Figure 6. Management level vs. d^2h volume for 25 3-y-old plantations of *Terminalia amazonia*

Site preparation for plantation establishment should focus on the specific limitations of a site. Introduced African pasture grasses are strong competitors on many sites in Costa Rica. Our results suggest that weeds are competing primarily for nutrients, particularly N, since foliar N levels increased with plantation volume. Simple weed control or soil cultivation, with no fertilisation, may be the most effective treatment on many sites. On fertile sites, where trees are competitive with weeds for N, no treatment may be necessary. Ineffective weed control, where fertiliser intended for seedlings actually ends up benefiting weeds, is counterproductive. Where N availability is inherently low, fertilisation may be necessary. The feasibility of these various prescriptions would be based on their relative ability to impact N availability in relation to their cost of implementation.

By examining foliar nutrient status and several soil variables, an attempt was made to understand how management was influencing growth. It was concluded that the species can grow well (>10 m^3 ha^{-1} y^{-1}) under conditions of low soil phosphorus. However, low nitrogen availability and high bulk density in surface horizons limit growth.

Further research should concentrate on developing efficient and cost-effective means for fertilising with nitrogen and alleviating high bulk density. Systematic development of nursery techniques, methods for control of competing vegetation, and a genetic improvement programme could be combined with experiments on nitrogen nutrition and bulk density amelioration to realise the potential of *T. amazonia* in plantations. A logical first step would be experimental planting of the species in the three life zones studied here to test different rates of N fertilisation, weed control and bulk density amelioration.

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