



Eucalyptus production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil

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Abstract

Millions of hectares of *Eucalyptus* are intensively managed for wood production in the tropics, but little is known about the physiological processes that control growth and their regulation. We examined the main environmental factors controlling growth and resource use across a geographic gradient with clonal *E. grandis* × *urophylla* in north-eastern Brazil. Rates of production and resource use were estimated for 14 stands that spanned a four-fold range in production. The supply of water appeared to be the most limiting resource in these fertilized plantations. Above-ground net primary production (ANPP) increased by 2.3 Mg ha⁻¹ per year for each 100 mm per year increase in rainfall. Higher water supply was also associated with increased use of light and nitrogen (N). The efficiency of resource use (ANPP per unit of resource used) increased with increasing productivity along the gradient. The most efficient stands produced 3.21 kg ANPP m⁻³ of transpired water, 1.14 kg ANPP GJ⁻¹ absorbed photosynthetically active radiation (PAR), and 381 kg ANPP kg⁻¹ N taken up. The stands with high resource use and high efficiency also had lower mean vapor pressure deficits, less soil water stress, and smaller coarse root to above-ground biomass ratios. Our study indicates that the productivity of fertilized tropical plantations of *Eucalyptus* is most likely constrained by water supply, and that water supply substantially affects the efficiency of resource use as well as biomass allocation to roots, stems, and leaves. At a regional scale, our results indicate that high productivity stands could produce wood in a 6-year rotation on half the land area required for low productivity stands, using only half as much water.

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1. Introduction

Forest plantations are an increasing component of tropical landscapes with approximately 3 Mha of annual increase in the current extent of 40–50 Mha of planted area (Brown et al., 1997; FAO, 1999). *Eucalyptus* is the dominant hardwood planted (10–15 Mha; Neilson,

2000), and the mean annual increment of managed forests has increased from 12 m³ ha⁻¹ per year in the 1960s to 20–60 m³ ha⁻¹ per year as a result of improved genetics and silviculture (Mora, 1986; Eldridge et al., 1994; Campinhos, 1999; Santana et al., 2000; Stape et al., 2001).

Water and nutrient supplies are the main abiotic factors affecting plantation growth in the tropics (Gonçalves et al., 1997; Fisher and Binkley, 2000) and evaluation of these supplies is important for zoning plantation potential (Golfari et al., 1977;

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Laffan, 1994; Coops et al., 1998) and for establishing silvicultural methods for site preparation, fertilization and control of competition (Attiwill and Adams, 1996; Gonçalves et al., 2000). Rapid forest growth rates are generally coupled with the high use of site resources, which raises questions regarding both the ecological impacts of plantations and the sustainability of wood production (Wang et al., 1991; Lima, 1993). To fully address these questions, both the amount of resources used and the efficiency of resource use need to be considered.

The production-resource equation (Monteith, 1977; Charles-Edwards and Fisher, 1980; Cannell, 1989; Pastor and Bridgman, 1999) provides a framework to characterize the production ecology of plantations, identifying the relationship between production and water, nutrient or light resources:

$$\text{production} = \text{supply} \times \text{resource-capture efficiency} \\ \times \text{resource-use efficiency} \quad (1)$$

where production is generally measured as above-ground net primary production (ANPP), supply is the amount of resource available during the period, resource-capture efficiency (RCE) is the proportion of the available resource actually used by the plants, and resource-use efficiency (RUE) is the production per unit of resource used. Solving the equation for each resource allows the changes in production to be understood in relation to changes in the supply, use and efficiency of use of the various resources. For more discussion of this approach for *Eucalyptus* plantations, see Binkley et al. (2004). This equation also forms the heart of some resource-production models, including 3-PG (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Stape et al., 2004).

We selected 14 stands of typical clonal *E. grandis* × *urophylla* forests in the final year of their short-rotation regimes (6–8 years) to characterize biomass production and resource-use patterns for *Eucalyptus* plantations. ANPP along this geographic and climatic gradient in north-eastern Brazil spanned from 9.7 to 39.1 Mg ha⁻¹ per year. A complete characterization of the edaphic, climatic and stand attributes was performed to assess the production ecology of these forests by (i) identifying the environmental and stand factors related with ANPP; and (ii) quantifying patterns in ANPP across stands in relation to the supply, use and efficiency of use of water, light and N.

2. Materials and methods

2.1. Site and stand descriptions

The study sites were located in north-eastern Brazil, within a 55 km radius of Entre-Rios (11°58'S, 38°07'W; Fig. 1). Fourteen *Eucalyptus* stands (owned by Copener Florestal Ltda) were chosen as representative of more than 80,000 ha of forests in the region. Uniform mean, maximum and minimum annual temperatures of 25.5, 30.0 and 20.9 °C characterized this tropical area. Rainfall decreases from 1600 mm per year in coastal areas to less than 800 mm per year just 120 km inland. Two-thirds of the rain falls in autumn and winter, with a dry period in the summer (CEI, 1991) and the inter-annual coefficient of variation of the rainfall is high (21%). Regional soils developed from reworked sediments from tertiary deposits (“Barreiras” formation), which consist of a sandy matrix intercalated with shales and conglomerates (Embrapa, 2000). The relief shifts from a dissected landscape close to the ocean to a gently rolling terrain inland. More erosion-resistant flat areas, called “Tabuleiros”, are formed between drainage valleys and are preferentially used for plantations. Ultisols, Oxisols and Entisols (Quartzipsamments) are the dominant soils in this region (Kreijc, 1998). In general, soils are acidic (pH 3.5–5.6 in water), highly weathered (cation exchange capacity 20–60 mmol_c kg⁻¹), deep (>1.8 m), with high bulk density (>1.4 Mg m⁻³), and low to moderate organic C (2–6 kg C m⁻², from 0 to 0.6 m) and N (100–500 g N m⁻²).

2.2. Sampling design and productivity classes

Existing stands of *Eucalyptus* were used, were near the end of their first rotation (between 6- and 8-year-old) and represented the breadth of regional soil, climate and productivity. Based on the 1996 inventory results of Copener Florestal plantations, the stands were classified into three groups of mean annual biomass increment (MAI) and two groups of soil texture (smaller and greater than 15% clay at 0.5 m depth). Three late-rotation sites were randomly selected for each of the six categories. Due to operational reasons only 14 stands (out of the desired 18) were completely sampled (Table 1). The stands were classified into three productivity categories according to MAI measured in

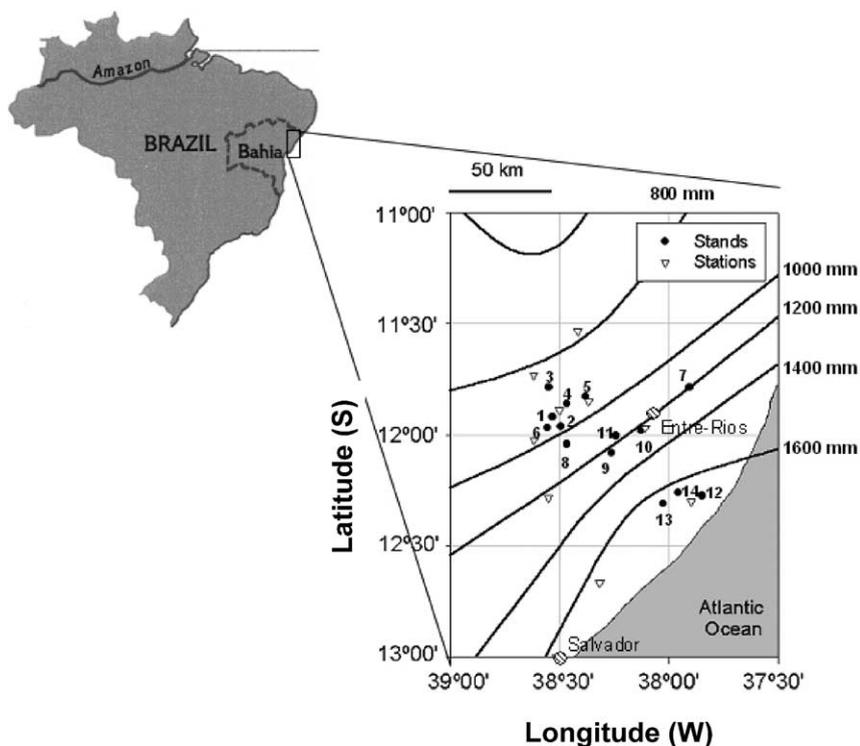


Fig. 1. Location of the 14 stands of *E. grandis* × *urophylla* in north-eastern Brazil and the nine associated meteorological stations with historical isohyets. Stand numbers represent increasing productivity.

Table 1

Location, soil taxonomy, soil texture (0 to 0.2 m), total carbon (0 to 0.6 m) and available water capacity (AWC, 0 to 2.0 m) for the 14 stands of *E. grandis* × *urophylla*

Stand no.	Latitude (S)	Longitude (W)	Altitude (m)	Soil order	Texture (%)		Clay (%) at 0.5 m	Density (Mg m ⁻¹)	Carbon (kg m ⁻²)	AWC (mm/2 m)
					Sand	Clay				
1	11°55'	38°32'	230	Quartzipsamment	94	6	4	1.58	1.8	61
2	11°57'	38°29'	270	Quartzipsamment	95	3	5	1.60	2.3	64
3	11°47'	38°33'	210	Oxisol	89	10	15	1.54	4.4	88
4	11°51'	38°28'	250	Oxisol	80	12	16	1.47	3.2	113
5	11°49'	38°22'	220	Ultisol	85	12	16	1.47	3.7	101
6	11°58'	38°33'	300	Quartzipsamment	92	6	6	1.59	2.2	66
7	11°47'	37°54'	150	Ultisol	63	35	41	1.57	6.4	145
8	12°02'	38°28'	310	Ultisol	88	10	20	1.58	3.9	93
9	12°05'	38°15'	180	Quartzipsamment	98	2	2	1.58	2.5	60
10	11°58'	38°07'	180	Ultisol	82	15	23	1.45	5.4	108
11	12°00'	38°14'	200	Ultisol	92	6	10	1.58	2.7	78
12	12°16'	38°51'	50	Quartzipsamment	96	4	3	1.60	3.5	60
13	12°18'	38°01'	80	Ultisol	89	8	12	1.54	6.6	87
14	12°15'	38°57'	100	Ultisol	84	11	18	1.40	5.2	108

Table 2
Biometric characteristics of the stands

Stand no.	Average rainfall (mm/yr)	Age (year)	DBH (cm)	Site index (m, 5 yr)	Leaf area index (m ² m ⁻²)	Basal area (m ² ha ⁻¹)	Wood biomass (Mg ha ⁻¹)	Mean annual increment			Productivity class
								ANPP	Stem production	(Mg ha ⁻¹ per year)	
1	882	5.1	12.8	20.5	2.4	14.2	78.3	14.9	9.5	6.1	Low
2	916	7.2	12.2	17.6	2.9	14.3	81.0	11.1	9.7	4.7	Low
3	853	6.1	12.1	17.4	2.9	13.7	66.9	9.4	9.7	5.8	Low
4	935	7.1	12.8	19.9	3.4	16.9	94.6	12.5	10.6	6.6	Low
5	902	7.3	12.8	19.0	3.1	15.1	78.7	10.9	14.9	8.8	Low
6	955	6.0	13.2	20.0	3.8	15.8	90.6	15.1	14.2	10.3	Medium
7	1143	5.1	13.7	23.2	3.0	18.5	97.7	18.9	14.8	11.1	Medium
8	958	5.0	12.8	20.6	3.0	15.3	82.2	15.6	15.0	10.6	Medium
9	1008	6.3	13.1	22.3	2.2	16.7	101.3	15.1	19.8	16.0	Medium
10	1131	6.1	15.0	23.5	3.3	19.6	114.1	16.6	22.3	18.0	High
11	1054	6.2	13.8	24.2	3.7	19.0	124.0	18.8	23.0	17.4	High
12	1605	7.9	14.9	21.8	4.2	25.2	147.5	19.9	25.1	16.9	High
13	1611	6.3	16.2	29.2	4.6	28.6	201.9	31.9	28.2	22.1	High
14	1654	6.3	17.1	25.8	5.8	30.1	204.0	32.6	39.1	30.1	High
Low	897 c	6.5	12.5 b	18.9 c	2.9 b	14.8 b	80.0 b	12.0 b	10.9 b	6.4 b	n = 5
Medium	1016 b	5.7	13.2 b	21.5 b	3.0 b	16.6 b	92.0 b	15.9 b	16.0 b	12.0 b	n = 4
High	1411 a	6.5	15.4 a	24.9 a	4.3 a	24.5 a	158.3 a	24.0 a	27.5 a	20.9 a	n = 5

Productivity class averages followed by different letters differ at $P = 0.05$.

1996 and ANPP measured in 1997 or 1998: (i) Low (MAI or ANPP <15 Mg ha⁻¹ per year, $n = 5$), (ii) Medium (15 <MAI or ANPP <20 Mg ha⁻¹ per year, $n = 4$), and (iii) high (MAI or ANPP >20 Mg ha⁻¹ per year, $n = 5$) (Table 2, Fig. 2a). All stands were located on moderate slopes (<3%) and site preparation included slash-and-burning of the initial vegetation (pasture or disturbed secondary forest or savanna), disking and harrowing. Forests were planted between 1989 and 1991 at 3.5 m × 2.6 m spacing and fertilized with 14 kg N ha⁻¹, 43 kg P ha⁻¹ and 14 kg K ha⁻¹. The 4-month-old clonal cuttings were produced in a shade-house and selected for uniform size (30 cm in height) (Stape et al., 2001). Chemicals were applied yearly to control leaf-cutting ants, and during the first 2 years after planting to control weeds. Eleven of the 14 stands consisted of mixed clonal plantations (30 clonal cuttings randomly mixed in the nursery) and three (stands 1, 7 and 8) were monoclonal (Clone COP-0321). Soil taxonomic groups were established during the soil survey (Kreijc, 1998). In each stand, a circular inventory plot of 471 m² was measured yearly from 2 years of age until harvest at age 6–8 years during 1997 or 1998. Trees were numbered systematically along rows, and the diameters at breast height (DBH, at 1.3 m) were measured

for all trees. Heights were measured for the first 20 trees of the plot as well as the four dominant trees.

2.3. Biomass sampling and allometric equations

Nine trees were selected from each stand to represent three size classes (mean DBH, plus one standard deviation, minus one standard deviation) with three trees per size class. The selected trees (with no external damage or defoliation) were harvested, and the coarse root system (>10 mm) was completely excavated by following all coarse roots from the stem base (we estimate that more than 95% of the coarse root system was recovered). The average depth of the pits was 2.5 m. Total fresh stem, coarse root, bark, branch and foliage biomass were determined for each tree, and representative subsamples (ranging from 300 to 2000 g) of each component were taken for moisture determination (dried at 65 °C) to calculate total dry mass. For each stand and biomass component, allometric equations were established in the form:

$$W_{ij} = a_{ij} \times \text{DBH}^{b_{ij}} \quad (2)$$

where W_{ij} is the dry mass of compartment i at stand j , and a and b are the intercept and slope parameters to

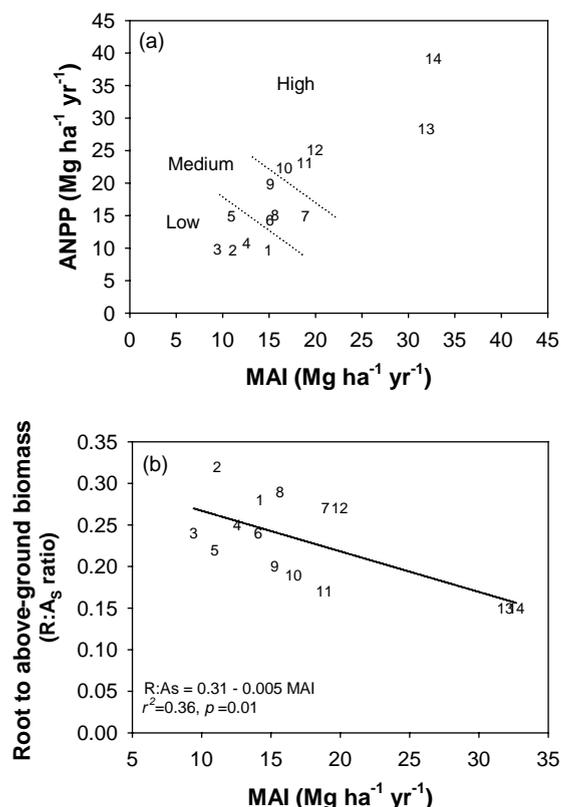


Fig. 2. Above-ground net primary production (ANPP) at the end of the rotation (6–8 years), and mean annual increment (MAI) for the 14 stands and their grouping into low, medium and high productivity classes (a). Relationship between coarse root to above-ground woody biomass ratio ($R:A_S$) and mean annual increment at the stand level (b).

be estimated, respectively. Allometric equations were also derived for each productivity class and for all trees. For foliage, 30 recent fully expanded leaves from the middle of the canopy were selected for specific leaf area (SLA) estimates, calculated as the ratio of single-sided area and dry mass.

2.4. Mean annual biomass increment (MAI), biomass distribution and climate

Mean annual biomass increment (stem, bark and branches) was estimated for each stand by summing the individual-tree biomass (based on stand-specific allometrics, Table 3), and dividing by the plot area and age (Table 2). Average DBH, stand density and basal area were also calculated for each stand, together with

leaf area index (LAI) based on estimated foliage biomass and SLA of the stand (Table 2). Site index (SI) was directly determined as the average of the four dominant trees in each plot at age 5 years. The coarse root (R) to above-ground wood (A_S) biomass ratio ($R:A_S$) was calculated at the stand level.

2.5. Climate

A monthly meteorological interpolated file was created for each stand for 1990 through 1998 based on nine stations located within a 30 km radius of the site (Fig. 1). The meteorological variables measured daily in all stations were minimum and maximum temperatures, day-time relative humidity and rainfall. Daily average temperature and saturated vapor pressure were estimated based on maximum and minimum temperatures (Sands and Landsberg, 2002). Vapor pressure deficit was estimated based on the average of relative humidities measured at 9 a.m. and 1 p.m. and the calculated saturated vapor pressure. In four of the stations, total sunshine hours were measured with Campbell–Stokes heliographs. Total short-wave incoming solar radiation was estimated based on the Angstrom–Prescott equation using site-specific parameters for Brazilian conditions (Pereira et al., 1997). The photosynthetically active radiation (PAR) was estimated daily for each station as a fraction of the incoming short-wave radiation (varying from 44% on sunny days to 56% on cloudy days). Daily net radiation (for transpiration estimates) was calculated as the sum of net short- and long-wave radiation, using average daily temperature, insolation ratio, relative vapor pressure and albedo (Pereira et al., 1997).

2.6. Above-ground net primary production (ANPP)

ANPP was estimated as the sum of the woody biomass production plus branch and foliage litterfall for the year when the biomass sampling was performed. Woody biomass production was the net increment in woody biomass during the year. Litterfall was not directly measured, and was estimated based on the average foliage biomass, the canopy turnover rate, and branch-to-foliage ratio in litterfall available from a parallel study in 5-year-old clonal *E. grandis* × *urophylla* in the region: canopy turnover was 0.99 per year with branches representing 31% of the foliage

Table 3

Coefficients of the allometric equations by productivity classes and all trees using the general relationship: $W = a \text{DBH}^b$ (W in kg and DBH in cm)

Compartment	Coefficient	Productivity class			
		Low ($n = 45$)	Medium ($n = 36$)	High ($n = 45$)	All ($n = 126$)
Stem	a	0.0815 A	0.0681 B	0.0694 B	0.0601
	b	2.5320	2.6342	2.6341	2.6746
Branch	a	0.0111 A	0.0186 B	0.0646 B	0.0429
	b	2.5411	2.2219	1.7616	1.9373
Bark	a	0.0152 A	0.0200 A	0.0301 B	0.0258
	b	2.4463	2.3254	2.1562	2.2245
Foliage	a	0.0014 A	0.0022 A	0.0025 B	0.0034
	b	2.9570	2.7473	3.6563	2.5722
Coarse root	a	0.0134 A	0.0221 A	0.0533 B	0.0516
	b	2.8033	2.6017	2.1814	2.2395

All regressions were significant at $P = 0.01$. Slope coefficients (b) did not differ within compartments, and allometric (intercept) coefficients (a) followed by different capital letters differ at $P = 0.05$.

litterfall across a range of water and nutrient treatments (Stape, 2002).

2.7. Soil sampling and analysis

During the biomass harvesting, soils were sampled at three depths (0.0–0.2, 0.2–0.4 and 0.4–0.6 m) at eight locations inside each plot using a graduated auger. Composite samples were formed by depth and dried at 65 °C to a constant weight. Extractable P, K, Ca and Mg were determined using 2.5 g of dry soil, 25 ml of water and a 2.5 ml of cationic and anionic resins (Amberlite IR-120, Amberlite IRA-420) shaken for 16 h. After this period, resins were separated from soil and 50 ml of 0.8N NH_4Cl and 0.2N HCl solution were added and swirled for 1.5 h. The supernatant was colorimetrically analyzed for P (Hitachi U-2001), for K by flame emission spectrophotometry (Micronal), and for Ca and Mg by absorption spectrometry (Perkin-Elmer Analyst 100). Total C and N concentrations were measured using a LECO 1000 CN analyzer (Leco Corp., St. Joseph, MI) using 0.2 g of ground subsamples. Soil texture was measured by hydrometry, and pH (in 0.01 M CaCl_2) was measured in a 2:1 solution:soil suspension (Rajj et al., 1987). Bulk density was determined using a 92 ml steel cylinder with two samples taken at 0.2–0.3 m depth, and dried at 105 °C. Soil C and nutrient concentrations were converted to an area basis (kg ha^{-1})

by multiplying by bulk density and sampling depth and summing the three depths. Soil water holding capacity for each stand (for a 2 m profile) was estimated based on soil texture at 0.5 m (Table 1) and using an equation developed in the region (Stape, 2002).

2.8. Resource supply, capture- and use-efficiency

Pastor and Bridgham (1999) reviewed the nutrient-use theory by addressing the relationships among production and nutrient supply, uptake-efficiency and use-efficiency. We used this approach to express *Eucalyptus* production (ANPP) as the multiplication of supply, capture- and use-efficiency for water, light and N resources (Eq. (1)).

For the studied year, water and light supplies were considered rainfall and PAR, while transpiration and absorbed PAR (APAR) were the used resources. Water-use efficiency and light-use efficiency express the ANPP per unit of transpired water and absorbed light, respectively. For nitrogen, N supply was not assessed. Estimates of N uptake were used for N use, and N-use efficiency was the ratio between ANPP and N uptake.

Canopy transpiration was estimated using the Penman–Monteith model (Monteith, 1965) on a monthly time-step based on the monthly meteorological stand-specific files and appropriate canopy conductance

value (3-PG model; Landsberg and Waring, 1997). Before its implementation, the algorithm was calibrated for an experimental area of *E. grandis* × *urophylla* in the region where soil moisture was gravimetrically evaluated weekly in a 2 m profile and LAI (averaged $2.8 \text{ m}^2 \text{ m}^{-2}$) was monitored during 1.7 years (Stape, 2002). Potential evapotranspiration (PET) ranged only from 1415 to 1530 mm per year, so the differences in canopy transpiration related largely to rainfall and not to a gradient in PET.

Light extinction coefficient was estimated to be -0.36 from direct measurements of APAR and LAI for similar plantations (data not shown). LAI was estimated at the beginning and end of the year, using the stand-specific-foilage allometrics and SLA (ranged from 7.0 to $11.0 \text{ m}^2 \text{ m}^{-2}$), with a monthly linear interpolation between them.

Nitrogen use was calculated as the average concentration of N in woody tissue times the annual woody mass increment, plus the N content of litterfall. The N concentration of tissues was measured by titration of Kjeldahl digests. The N in the litterfall was estimated as the litterfall production times the N concentration after retranslocation, prior to senescence (61% for foliage and 23% for branches, based on a 7-year-old *E. grandis* plantation (Gonçalves et al., 2000). Throughfall N was estimated as 6% of the N in the litterfall (Attiwill, 1980). We also measured the total N content of soils (0–0.6 m), but did not directly assess the annual rate of supply of soil N.

2.9. Statistical analyses

We used logarithmic transformation of the component biomass and DBH to estimate the allometric parameters (a , b in Eq. (2)) by stand and productivity classes (Table 3). Analysis of covariance was used to test if the component specific allometric equations differed among productivity classes, using multiple comparisons with a significance level of 0.05.

One-way analyses of variance (GLM procedure, SAS Institute Inc., Cary, NC, USA, 2001) with productivity class as a fixed factor were performed for the biometric variables (Table 2), $R:A_S$ ratio, and water resource, light resource, and N resource indices. Tukey's studentized range test (HSD) was employed for multiple comparisons with a significance level of 0.05.

Table 4

Variables used on stepwise regression procedures having ANPP as the dependent variable and the independent variables organized by edaphic, climate, canopy and stand type categories

Category	Variables
Edaphic	Soil C, soil N, extractable nutrients (P, K, Ca, Mg), sum of bases, sand, silt, clay, texture B:A horizons, clay 0.5:clay 0.2 ratio, bulk density, pH, water holding capacity
Climate	Rainfall, transpiration, potential evapotranspiration, outflow, average soil available water, vapor pressure deficit, total PAR
Canopy	LAI, APAR, specific leaf area, foliage biomass, leaf nutrient concentration (N, P, K, Ca, Mg and sum), nutrient in the canopy (N, P, K, Ca, Mg), litter nutrient concentration (N, P, K, Ca, Mg and sum), nutrient in the litter (N, P, K, Ca, Mg)
Stand	Site index, stocking, age

We used multiple regressions with a stepwise procedure in SAS to investigate the influence of environmental factors, and stand and canopy attributes on ANPP. The minimal inclusion significance of a variable was set at $P = 0.10$. Due to the large number of independent variables (>40) we avoided over-parameterization by: (i) grouping independent variables into climatic, edaphic, stand and canopy attribute groups (Table 4); (ii) separately regressing ANPP against the independent variables of each group; and (iii) aggregating groups by taking the best three variables of each group during the isolated analysis and including their interactions. Residual analysis checked for normality and homocedasticity.

Simple linear regressions were examined between ANPP and resource supply, use and use-efficiency using SAS. Simple linear regressions were also developed between $R:A_S$ and MAI and site index.

3. Results

3.1. Site and stand attributes

The 14 sites spanned a broad range of the edaphic and climatic attributes and forest productivity. Clay content varied from 3 to 41% at 0.5 m depth (half <15% clay), total soil C from 1.8 to 6.6 kg C m^{-2} (half < 3.5 kg C m^{-2}), total soil N from 0.1 to 0.5 kg N m^{-2} and water holding capacity from 60 to 145 mm

Table 5

Resource supply, use, capture-efficiency and use-efficiency for water, light and N by productivity classes

Resource	Supply	Use	Capture-efficiency	Use-efficiency
Water	Rainfall (mm per year)	Transpiration (mm per year)	WCE (proportion)	WUE (kg m ⁻³)
Low	886 c	689 b	0.78	1.59 b
Medium	1055 b	718 b	0.70	2.24 b
High	1276 a	869 a	0.70	3.21 a
Light	PAR (TJ ha ⁻¹ yr ⁻¹)	APAR (TJ ha ⁻¹ yr ⁻¹)	LCE (proportion)	LUE (g MJ ⁻¹)
Low	31.6	20.4 b	0.65 b	0.54 b
Medium	31.9	20.9 b	0.65 b	0.79 b
High	30.8	24.1 a	0.78 a	1.14 a
Nitrogen		N uptake (kg ha ⁻¹ yr ⁻¹)		NUE (kg kg ⁻¹)
Low		37.8 b		291 b
Medium		45.9 b		348 a
High		72.4 a		381 a

Productivity class averages followed by different letters differ at $P = 0.05$.

(eight sites <90 mm) (Table 1). Soil extractable P varied by four-fold (average 20 kg ha⁻¹) across the gradient, with similarly high variation in K (14-fold, average 116 kg ha⁻¹), Ca (17-fold, average 667 kg ha⁻¹) and Mg (four-fold, average 160 kg ha⁻¹). Average rainfall ranged from 897 to 1411 mm per year (half <1000 mm per year). Mean annual temperatures (25.5 °C), PET (1470 mm per year) were very similar among sites (coefficients of variation <4%), and soil bulk density ranged from 1.45 to 1.60 Mg m⁻³ (Table 1).

ANPP late in the rotation correlated strongly with MAI for the entire rotation ($r^2 = 0.76$, $P < 0.001$) and had the same magnitude: MAI varied from 9.4 to 32.6 Mg ha⁻¹ per year, while ANPP varied from 9.5 to 39.1 Mg ha⁻¹ per year (Table 1, Fig. 2a). Wood production declined as a proportion of ANPP as ANPP declined ($r^2 = 0.46$, $P < 0.01$).

No soil property differed, on average, between low, medium and high productivity classes (data not shown) indicating an adequate representation of the different soil types within classes. No differences in age (average 6.2 years), stocking (average 1172 tress ha⁻¹) and SLA (average 8.8 m² kg⁻¹) occurred among classes. Biometric variables did not differ between low and medium productivity classes, except for site index (18.9 m versus 21.5 m). On the other hand, all biometric variables were larger for the high productivity class than the other two classes.

The average rainfall across sites increased linearly by 57% from low (897 mm per year) to high (1411 mm per year) productivity classes (Table 2) and by 44% (886 mm per year versus 1276 mm per year, Table 5) in the year that ANPP was determined. Average vapor pressure deficit in that year decreased 12% (1.46 kPa to 1.28 kPa) from low to high productivity classes (data not shown).

At a stand level, the ratio of coarse root to above-ground mass ($R:A_S$) was lower for the high productivity class (0.18) than medium (0.24) and low (0.26) classes. $R:A_S$ was negatively related to MAI ($r^2 = 0.36$, $P = 0.01$, Fig. 2b) and site index ($r^2 = 0.55$, $P < 0.01$).

3.2. ANPP, and environmental and stand factors

Total soil C and N together were the best edaphic predictors of ANPP ($r^2 = 0.49$, Table 6). Rainfall alone explained 39% of variation in ANPP, and the inclusion of textural ratio (BA clay = clay in the 0.40–0.60 depth divided by clay 0.0–0.2 m depth) increased model predictability ($r^2 = 0.51$, Table 6). Among canopy attributes, LAI alone explained 66% of variation in ANPP, which was not correlated with any soil or leaf nutrient concentration. For the stand attributes, SI explained 65% of variability in ANPP. For all attributes, SI and rainfall together explained 74% of variation in ANPP (Table 6).

Table 6

Select variables using stepwise regression procedures having ANPP ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) as the dependent variable and the independent variables organized by edaphic, climate, canopy and stand type categories

Category	Variables	Regression ^a	R ²
Edaphic	Soil C, soil N	$11.0 + 0.00083C - 0.0088N$	0.49 ($P = 0.009$)
Climate	Rainfall	$-8.4 + 0.025\text{rainfall}$	0.39 ($P = 0.010$)
Edaphic + climate	Rainfall, BA clay	$-28.3 + 0.029\text{rainfall} + 11.1\text{BA clay}$	0.51 ($P = 0.007$)
Canopy	LAI	$-7.9 + 7.6\text{LAI}$	0.66 ($P = 0.0002$)
Stand	SI	$-27.9 + 2.12\text{SI}$	0.65 ($P < 0.0001$)
All	SI, rainfall	$-31.8 + 1.67\text{SI} + 0.013\text{rainfall}$	0.74 ($P < 0.0001$)

^a Units: C (kg ha^{-1}), N (kg ha^{-1}), rainfall (mm yr^{-1}), BA clay (none), LAI ($\text{m}^2 \text{ m}^{-2}$), SI (m, 5 years).

Among all sites, water supply varied by 2.0-fold (731–1568 mm per year), water-capture efficiency by 1.7-fold (0.48–0.86 of water supply), water-use by 1.7-fold (592–999 mm per year), and water-use efficiency by 3.4-fold ($1.34\text{--}4.58 \text{ kg m}^{-3}$) (Table 5). ANPP correlated with water supply ($r^2 = 0.44$, $P = 0.01$, Fig. 3a) and transpiration ($r^2 = 0.39$, $P = 0.02$, Fig. 3b), but not with water-capture efficiency ($r^2 = 0.14$, $P = 0.19$). Water-capture efficiency decreased as water supply increased ($r^2 = -0.76$, $P = 0.001$). Water-use efficiency increased with increasing water supply ($r^2 = 0.60$, $P = 0.02$, Fig. 6), and the relationship with water use showed a similar trend ($r^2 = 0.42$, $P = 0.13$, Fig. 3c).

The ANPP of the medium-productivity class was 46% greater than the low-productivity class ($11\text{--}16 \text{ Mg ha}^{-1}$ per year), and about 32% of the difference was associated with the increase in water supply, and 68% with the increase in water-use-efficiency. The ANPP of the high-productivity class was 72% higher than the medium-productivity class ($16\text{--}28 \text{ Mg ha}^{-1}$ per year), and again about one-third of the difference was associated with the increased supply of water, and two-thirds from the greater efficiency of water use.

Light supply (PAR) was similar across sites (31.4 TJ ha^{-1} per year), but light-capture efficiency varied by 1.5-fold (0.56–0.87 of light supply), light-use by 1.5-fold ($17.3\text{--}26.6 \text{ TJ ha}^{-1}$ per year), and light-use efficiency by 3.0-fold ($0.47\text{--}1.47 \text{ g MJ}^{-1}$). ANPP did not correlate with light supply ($r^2 = 0.20$, $P = 0.11$, Fig. 4a), but related well with captured light (APAR, $r^2 = 0.49$, $P < 0.001$, Fig. 4b) and light-capture efficiency ($r^2 = 0.58$, $P < 0.001$). Light-capture efficiency increased with water supply ($r^2 = 0.54$, $P = 0.04$) and light-use efficiency

increased with light use ($r^2 = 0.25$, $P = 0.07$, Fig. 4c) and water supply ($r^2 = 0.67$, $P = 0.008$) (Fig. 6).

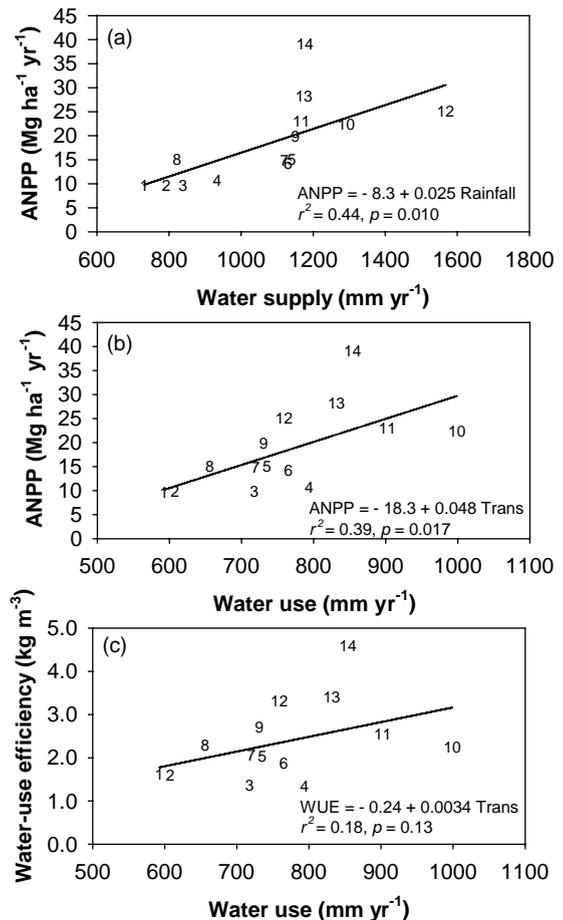


Fig. 3. Relationships between ANPP and water supply (a), and water use (b), and between water-use efficiency and water use (c) for the 14 stands.

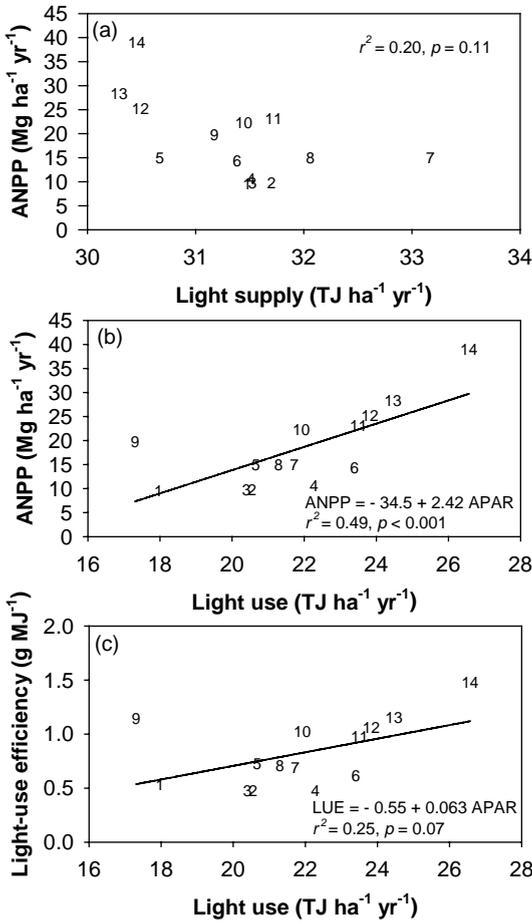


Fig. 4. Relationships between ANPP and light supply (a), and light use (b), and between light-use efficiency and light use (c) for the 14 stands.

The increase in ANPP from low to medium productivity classes derived completely from greater light-use efficiency. About 31% of the increase in ANPP from medium to high classes was related to increased light capture, and 69% with greater efficiency of light use.

The total N content of the soil varied by 4.0-fold (1106–4589 kg N ha⁻¹), N use by 3.5-fold (27.7–98.1 kg ha⁻¹ per year), and N-use efficiency by 1.6-fold (248–415 kg kg⁻¹). Across all stands, ANPP did not correlate with total soil N ($r^2 = 0.01$, $P = 0.71$, Fig. 5a) but did correlate with N uptake ($r^2 = 0.95$, $P < 0.001$, Fig. 5b). N-use efficiency increased with increasing N use ($r^2 = 0.56$, $P = 0.03$, Fig. 5c) and water supply ($r^2 = 0.58$, $P = 0.02$) (Fig. 6).

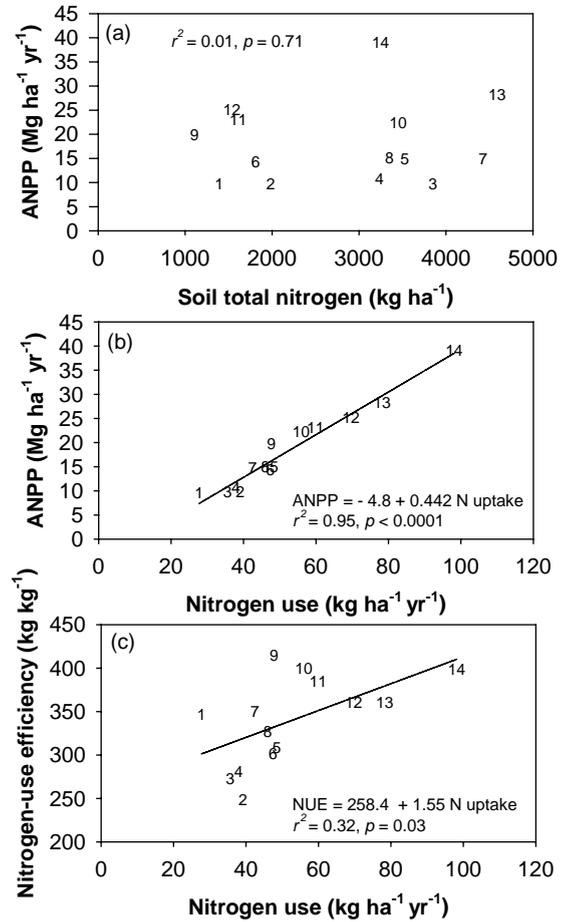


Fig. 5. Relationships between ANPP and total soil N (a) and N use (b), and between N-use efficiency and N use (c) for the 14 stands.

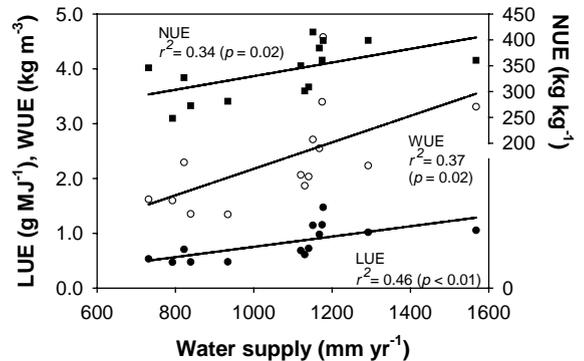


Fig. 6. Relationships between light-use efficiency (LUE), water-use efficiency (WUE) and N-use efficiency (NUE) with water supply (rainfall).

The increase in ANPP from low to medium and medium to high productivity classes was associated primarily (66%) with an increase in N uptake and secondarily (24%) with a greater N-use efficiency.

4. Discussion

4.1. ANPP and related environmental and stand factors

At a rotation age of 6 years, above-ground biomass at harvest would span from 50 to 200 Mg ha⁻¹ among these plantations. The high correlation between MAI and ANPP ($r^2 = 0.76$, Fig. 2a) suggests that the main external controls throughout the rotation still prevailed during the final year of the rotation when ANPP was estimated.

Rainfall (mm per year) was the environmental variable most strongly associated with both MAI (Mg ha⁻¹ per year = $-7.1 + 0.022\text{rainfall}$, $r^2 = 0.81$, $P < 0.001$) and ANPP (ANPP = $-8.3 + 0.025\text{rainfall}$, $r^2 = 0.44$, $P = 0.01$), indicating that water supply is probably the primary resource controlling productivity in this tropical region. For each 100 mm per year increment in rainfall, MAI and ANPP increased by approximately 2.3 Mg ha⁻¹ per year (Fig. 3a). The crucial role played by rainfall in ecosystem productivity has long been recognized (Lieth, 1975; Golfari et al., 1977; Morais et al., 1990; Snowdon and Waring, 1991; Beadle, 1997; Gonçalves et al., 1997). For example, Santana et al. (2000) reported a linear increase in *Eucalyptus* productivity (from 8 to 32 Mg ha⁻¹ per year) for an increase in water availability measured as the difference between rainfall and PET (from -200 to 600 mm per year). Similarly, irrigation trials in dry areas promoted significant *Eucalyptus* productivity increments (Pereira and Pallardy, 1989; Stewart et al., 1990; Olbrich et al., 1992; Myers et al., 1996; Honeysett et al., 1996; Hunter, 2001; Stape, 2002).

The fact that total soil C was the only soil attribute that related significantly and positively with ANPP may relate to historical land use and water supply (Table 6). Tropical forests originally covered the sites of the high productivity class (wetter ones), while the inland sites were associated with dry savannas (Kreijc, 1998), having lower natural productivity and lower C inputs.

No soil fertility variable related with productivity, despite the large range in soil characteristics (data not shown). This absence of a soil fertility effect may result from high nutrient supplies as a result of slash-burning site preparation, initial application of P fertilizer, and adequate weed control.

Among canopy attributes, LAI correlated strongly with ANPP (ANPP = $-7.9 + 7.6 \text{ LAI}$, $r^2 = 0.68$, $P < 0.001$). On average, for a one unit increase in LAI, ANPP was increased by 7.6 Mg ha⁻¹ per year due to greater absorbed light (LAI and APAR, $r^2 = 0.95$). This type of relationship was also identified for *Eucalyptus* by Linder (1985), Jarvis et al. (1989) and Landsberg and Hingston (1996). There was no correlation between ANPP and any foliar nutrient concentration despite the two- to four-fold variation among stands (data not shown), indicating that LAI may be a better predictor of growth than foliar nutrient concentrations.

4.2. Allometrics and accumulated biomass

The derived allometrics based on DBH ($W = a \times \text{DBH}^b$) captured distinct patterns of biomass accumulation by productivity classes with similar “*b*” slopes but different allometric (intercept) coefficients “*a*” (Table 3). This is in line with Enquist and Niklas (2002) findings of general ratios between plant biomass compartments, while the estimates of their absolute biomass values depend on the specificity of the intercept coefficient. Despite the lower $R:A_S$ ratio for the high productivity class ($R:A_S = 0.18$, for medium and lower classes $R:A_S = 0.25$), its absolute coarse root biomass accumulation was larger than for the other two classes (29 Mg ha⁻¹ versus 22 Mg ha⁻¹ at age 6 years). This trend is similar to that observed by Reis et al. (1985) for *E. grandis* in a wetter and more productive site in Brazil (MAI = 20 Mg ha⁻¹ per year, $R:A_S = 0.15$) compared with a drier and lower productivity site (MAI = 6 Mg ha⁻¹ per year, $R:A_S = 0.35$). Santana et al. (2000) also reported an increase in above-ground partitioning for *Eucalyptus* (from 78 to 89%) with increasing productivity, and Giardina et al. (2003) obtained a low $R:A_S$ ratio (0.16) for *E. saligna* trees at a high productivity site (MAI = 20 Mg ha⁻¹ per year). Brown and Lugo (1982) obtained higher $R:A_S$ ratios at sites with lower productivity, and Reed and Tomé (1998) detected a

change in *Eucalyptus* allometrics caused by irrigation. Our study also captured a strong negative correlation between $R:A_S$ ratio and site index ($R:A_S = 0.495 - 0.012 \text{ SI}$, $r^2 = 0.55$, $P < 0.01$), implying that SI can be used for estimates of below-ground biomass (negatively related), similar to the patterns presented by Battaglia and Sands (1997) for *Eucalyptus*.

4.3. Supply, use and efficiency of use of resources

The increase in water use from the low to the high productivity classes was almost a constant fraction of the water supply (72%, Table 5), but tended to decrease with increasing rainfall. In contrast, the larger use of light was associated with the increase in light-capture efficiency rather than light supply, and this increase probably resulted from the higher LAI facilitated by the greater water supply. The highest productivity class (wetter sites) with LAI 4.3 captured 78% of the incoming PAR, compared with 65% for the other two classes with LAI of 2.9. A trend of increasing the LAI of *Eucalyptus* with water supply was observed on a local scale in irrigation trials (Jarvis et al., 1989; Olbrich et al., 1992; Hunter, 2001), while on a regional scale, LAI is postulated to be driven by the regional climate (Hatton et al., 1998). In agreement with this hypothesis, LAI estimates were positively related with rainfall ($r^2 = 0.86$, $P < 0.001$) with an increase of 0.3 LAI units per 100 mm per year in rainfall.

The observed increase in ANPP from low to high productivity classes could not be explained solely by the increase in resource use, demonstrating the importance of the changes in resource-use efficiencies (Table 5, Fig. 6). For a given amount of resource used, the efficiency of its use can be enhanced by the increase in C assimilation by photosynthesis during the same period (Larcher, 1995; Sands, 1996), or by the shift in C allocation from below- to above-ground (Cannell, 1989; Landsberg and Gower, 1997). Both processes seem to be operating in our study, once again mediated by the water supply. Our results clearly indicated a higher efficiency of resource use for stands with higher rates of resource use (Figs. 3–5).

Along the transect, rainfall and vapor pressure deficit were strongly correlated (vapor pressure deficit = $0.95 + 430\text{rainfall}^{-1}$, $r^2 = 0.72$, $P < 0.001$), with lower vapor pressure deficits associated with the more

productive and wetter sites. An inverse relation was found between water-use efficiency and vapor pressure deficit ($\text{WUE} = -4.51 + 9.2 \text{VPD}^{-1}$, $r^2 = 0.33$, $P = 0.03$). This relationship is also used in some process-based models to estimate water-use efficiency or photosynthesis based on the actual evapotranspiration (Battaglia and Sands, 1997).

An increase in *Eucalyptus* stomatal conductance is well documented in response to decreasing soil water deficit and vapor pressure deficit (Pereira, 1987; White et al., 1996; Mielke et al., 1999; Barnard, 2000). Higher CO_2 uptake rates for the more productive sites have also been related to increased efficiency of use of light and N (Myers et al., 1996; Sands et al., 1999). Indeed, this control of soil moisture and vapor pressure deficit on the canopy quantum efficiency is the basic conceptualization of the APAR family models (Jarvis and Leverenz, 1983; Haxeltine and Prentice, 1996; Landsberg and Waring, 1997).

A relative shift in C allocation from below-ground to above-ground as water supply increased likely contributed to the higher resource-use efficiencies on the more productive stands. Although the $R:A_S$ ratio can be considered just a partial evidence of this partitioning process (Fig. 2b), the decrease in C allocation below-ground by the effect of water supply for a *Eucalyptus* clone is well documented (Stape, 2002). Linder and Axelsson (1982), Snowdon and Benson (1992) and Albaugh et al. (1998) also reported a larger wood production per unit of LAI under higher water supply, crediting these gains to higher quantum efficiency or allocation shift.

5. Conclusions

Across our geographic gradient, each additional 100 mm per year in rainfall increased LAI by 0.3 units and productivity by 2.3 Mg ha^{-1} per year. Inclusion of site index improved the regional predictive power of rainfall probably by capturing stand-specific edaphic characteristics. No soil fertility attribute related with production, probably from the adequate site preparation, fertilization and high *Eucalyptus* efficiency in cycling nutrients. Regional empirical yield models based on site index can be improved by incorporating rainfall or LAI variables.

The *Eucalyptus* genotypes in these plantations showed high plasticity in biomass partitioning, with coarse root to above-ground ratio varying by two-fold (from 0.15 to 0.32); low ratios developed in the most productive stands. This ratio presented a strong negative relationship with site index, which can be used to improve the below-ground C pool estimates in these tropical plantations.

The most productive stands used more water (869 mm per year), light (24 TJ ha⁻¹ per year) and N (72 kg N ha⁻¹ per year), but were also the most efficient forests in using these resources: 3.21 kg of ANPP m⁻³ of transpired water, 1.14 kg of ANPP GJ⁻¹ of absorbed PAR, and 381 kg of ANPP kg N⁻¹ taken up. Increasing rainfall indirectly increased light and N use by increasing their capture efficiency. The inverse relation of rainfall and vapor pressure deficit in our transect led to higher water-use efficiencies on the most productive stands. These wetter sites also presented larger light- and N-use efficiency, possibly due to a joint effect of higher C assimilation rates and above-ground C allocation.

Combining these relationships, 10⁶ Mg of wood production in this tropical region in a 6-year rotation would require less land and resources for high (24 Mg ha⁻¹ per year) than low productivity stands (12 Mg ha⁻¹ per year). Specifically, this would mean 50% less planting area (6,945 ha versus 13,889 ha), 49% less water consumption (311 × 10⁶ m³ versus 629 × 10⁶ m³ for the entire rotation), exporting 14% less N in the wood at harvesting (2.5 Gg N versus 2.1 Gg N), and leaving 50% more detritus C below-ground in coarse roots per hectare (27 Mg ha⁻¹ versus 18 Mg ha⁻¹).

Although resource supplies have been the main focus of forest growth studies, our results indicate that capture- and use-efficiency were the key components defining production, and that these efficiencies were under strong water-supply influence. Finally, this gradient study pointed to some patterns that affect C gain, allocation and use of resources for *Eucalyptus* plantations that can be useful for improving both silvicultural and environmental approaches to management.

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