

Production and carbon allocation in a clonal *Eucalyptus* plantation with water and nutrient manipulations

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Abstract

We examined resource limitations on growth and carbon allocation in a fast-growing, clonal plantation of *Eucalyptus grandis* × *urophylla* in Brazil by characterizing responses to annual rainfall, and response to irrigation and fertilization for 2 years. Productivity measures included gross primary production (GPP), total belowground carbon allocation (TBCA), bole growth, and net ecosystem production (NEP). Replicate plots within a single plantation were established at the midpoint of the rotation (end of year 3), with treatments of no additional fertilization or irrigation, heavy fertilization (to remove any nutrient limitation), irrigation (to remove any water limitation), and irrigation plus fertilization. Rainfall was unusually high in the first year (1769 mm) of the experiment, and control plots had high rates of GPP (6.64 kg C m⁻² year⁻¹), TBCA (2.14 kg C m⁻² year⁻¹), and bole growth (1.81 kg C m⁻² year⁻¹). Irrigation increased each of these rates by 15–17%. The second year of the experiment had average rainfall (1210 mm), and lower rainfall decreased production in control plots by 46% (GPP), 52% (TBCA), and 40% (bole growth). Fertilization treatments had negligible effects. The response to irrigation was much greater in the drier year, with irrigated plots exceeding the production in control plots by 83% (GPP), 239% (TBCA), and 24% (bole growth). Even though the rate of irrigation ensured no water limitation to tree growth, the high rainfall year showed higher production in irrigated plots for both GPP (38% greater than in drier year) and bole growth (23% greater). Varying humidity and supplies of water led to a range in NEP of 0.8–2.7 kg C m⁻² year⁻¹. This difference between control and irrigated treatments, combined with differences between drier and wetter years, indicated a strong response of these *Eucalyptus* trees to both water supply and atmospheric humidity during the dry season. The efficiency of converting light energy into fixed carbon ranged from a low of 0.027 mol C to a high of 0.060 mol C per mol of absorbed photosynthetically active radiation (APAR), and the efficiency of bolewood production ranged from 0.78 to 1.98 g wood per MJ of APAR. Irrigation increased the efficiency of wood production per unit of water used from 2.55 kg wood m⁻³ in the rainfed plot to 3.51 kg m⁻³ in irrigated plots. Detailed information on the response of C budgets to environmental conditions and resource supplies will be necessary for accurate predictions of plantation yields across years and landscapes.

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1. Introduction

Forest plantations cover approximately 1% of the tropics (40–50 million ha) supporting increasing local and global demands for wood (FAO, 1999; Fox, 2000), with *Eucalyptus* being the dominant hardwood species planted. These forests have also been advocated as carbon sinks (Vitousek, 1991;

Hoen and Solberg, 1994; Cannell, 1999; Sands et al., 1999; Hunter, 2001) to slow the rise of atmospheric CO₂ concentrations. A potential expansion is possible of 345 millions ha as trees are planted in disturbed forest, pastures or abandoned agriculture areas (Cannell, 1999). Complete carbon (C) budgets are needed as the foundation for understanding both wood production and C sequestration, especially in response to environmental conditions. Few complete C budgets are available for tropical forest plantations, and even model-based estimates are limited in value by available information to parameterize models for varying environmental conditions

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(Ryan et al., 1996; Landsberg and Waring, 1997; Nabuurs et al., 2001; Almeida et al., 2004; Stape et al., 2004a; Litton et al., 2007).

The ecology of forest production can be evaluated in terms of resource supplies, rates of use, and growth. This approach was first used by Monteith (1977) for crops and then adapted for forests (Hunt, 1994; Jarvis and Leverenz, 1983; Linder, 1985; Landsberg and Waring, 1997; Binkley et al., 2004), and can be represented as: $GPP = APAR \cdot \alpha^* \cdot f_i$, where α^* is a maximum canopy quantum efficiency (mol C fixed per mol APAR) and f_i represents a series of multiplicative factors which constrain carbon uptake by limiting CO₂ diffusion into the chloroplasts, or by reducing the photosynthetic pathway activity (Jarvis and Leverenz, 1983). Some models of ecosystem productivity have been based on relationships at the stand level between the interception of photosynthetically active radiation (APAR) and gross primary productivity (GPP; Medlyn, 1998; Goetz et al., 1999). This approach can provide insights on the ecology underpinning observed responses to treatments such as irrigation and fertilization.

In Brazil, a study across a geographic gradient found that growth of *Eucalyptus* plantations increased with increasing rainfall, as a result of both higher water use and higher efficiency of water use (Stape et al., 2004b). Aboveground net primary production (ANPP) increased by 2.3 Mg ha⁻¹ year⁻¹ for each 100 mm increase in rainfall, but this descriptive study could not separate the effects of water supply per se from other potentially confounding factors, such as soil fertility and air humidity, across the geographic gradient. In this paper, we address some of the same issues examined across that gradient, but with experimental manipulations of water supplies within a single stand. We estimated the complete C budget for 2 years in a 4–5-year-old, fast-growing plantation of clonal *Eucalyptus* trees in Brazil, characterizing the influences of wet versus normal precipitation, irrigation, fertilization, and irrigation plus fertilization. We also used the production ecology approach to examine how differences in production resulted from differences in resource use and efficiency of resource use.

2. Methods

2.1. Site description

The study site is located on the northeastern coast of Bahia State, Brazil, about 20 km SW of Entre-Rios (11°58'S, 38°07'W) at 250 m elevation with a mean annual temperature of 25.3 °C and an average rainfall of 1040 mm year⁻¹. Precipitation varies substantially between years, with an inter-annual coefficient of variation of 20%. About 2/3 of the rain falls between April and September, with dry summers (CEI, 1991). The slopes are gentle (<3%), with sandy isohyperthermic Typic Haplustox soils that are deep (>3 m), excessively drained, and acidic (pH 4.3 in 0.01 M CaCl₂).

The 26-ha plantation was first planted with *Eucalyptus grandis*, by Copener Florestal Ltda, in July of 1987. This plantation was established by slashing and burning an old pasture, followed by disking, bedding and harrowing to raise

beds 1.5 m wide and 0.5 m high. Seedlings in this original rotation received a fertilization of 39 kg N ha⁻¹, 56 kg P ha⁻¹ and 29 kg K ha⁻¹ in furrows, at planting. At harvesting time in 1995 (8 years old) the forest had a final stocking of 800 trees ha⁻¹, mean height of 17 m and an aboveground wood biomass of 7.5 kg m⁻².

The second-rotation plantation (the focus of the present study) was established in June 1996 with a *E. grandis* × *urophylla* clone (clone COP-0321) after controlling eucalypt sprouts and weeds with a herbicide (glyphosate). Site preparation used a chisel-like subsoiler 0.6 m into the soil (between the prior beds). The 4-month-old cuttings were produced in a shade-house and selected for uniform size (25–35 cm in height) (Stape et al., 2001). A 3.0 m × 3.0 m spacing was used, and fertilizer was applied twice: at planting (14 kg N ha⁻¹ as ammonium sulphate, 30 kg P ha⁻¹ as superphosphate, 12 kg K ha⁻¹ as KCl) along the furrows, and at 6 months old by broadcasting 38 kg N ha⁻¹, 32 kg K ha⁻¹ and 100 kg Ca ha⁻¹ and 50 kg Mg ha⁻¹ as lime. Chemicals were applied yearly to control leaf-cutting ants (sulfluramid) and weeds (glyphosate). The experimental treatments were installed when the plantation was 3 years old, the trees were 15 m tall, with aboveground bole biomass of 37 Mg/ha.

2.2. Experimental design and treatments

A 2 × 2 factorial was used with two-levels of nutrient and water regimes in a completely randomized block design with four replicates. Each plot was 30 m × 30 m (approximately 100 trees), with the central 36 trees used for measurements. An analysis of variance of the initial aboveground biomass showed no pretreatment effects ($P = 0.37$). The experimental treatments ran for 2 full years. The first year, from October 1999 to September 2000, was characterized by a high annual rainfall (1769 mm, the wetter year) with an uniform distribution year round, while the second year (from October 2000 to September 2001) had a more-typical annual rainfall of 1207 mm (the drier year) with a seasonal drought period from November 2000 to May 2001 (Fig. 1).

Fertilization and irrigation regimes were designed to eliminate any limitation on *Eucalyptus* growth. Trenches were dug around the plot boundaries (to 0.8 m) to reduce the potential influence of the fertilization and irrigation treatments on adjacent plots. The fertilization regimes consisted of a control (no additional fertilization) and a high fertilization rate of: 600 kg Ca ha⁻¹ and 300 kg Mg ha⁻¹ (as lime); 4 kg B ha⁻¹, 2 kg Cu ha⁻¹ and 2 kg Zn ha⁻¹ in September of 1999, followed by quarterly fertilizations with 126 kg N ha⁻¹ (as ammonium sulphate), 21 kg P ha⁻¹ (as superphosphate) and 79 kg K ha⁻¹ (as KCl). All fertilizers were broadcast.

The water treatments were rainfed (control), and rainfed plus irrigation. The micro-sprinkler irrigation system used water from a nearby pond to provide a minimum input of 35 mm week⁻¹ based on water balance for the region that showed an average potential evapotranspiration of 28 ± 2 mm week⁻¹ (Stape et al., 1997). A pluviometer was installed in an open area close to the site, and the amount of water to be applied during a week was

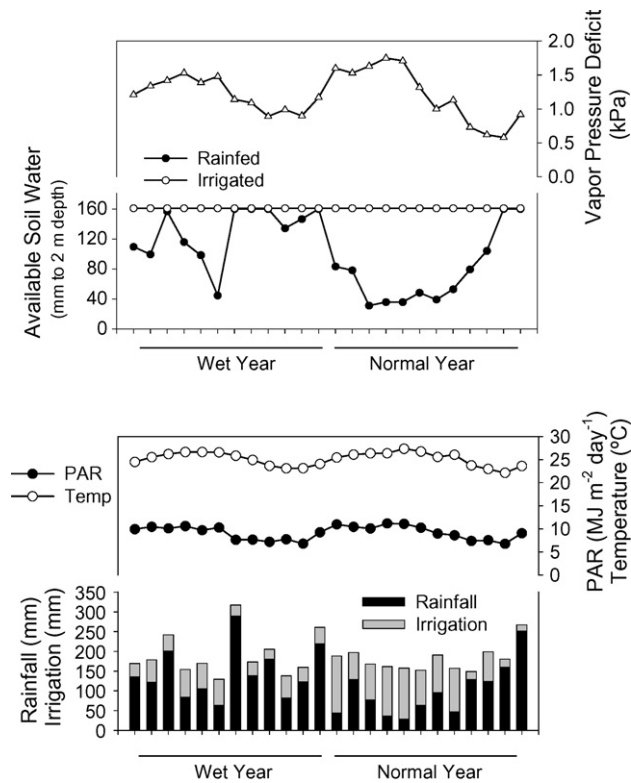


Fig. 1. Environmental conditions for the plantation for 24 months of the study period, characterized by a wet year (October 1999–September 2000) and a normal year (October 2000–September 2001).

Table 1
Methods and periodicity of sampling for C fluxes and pools (DBH = diameter at 1.4 m height, C_R = coarse root, ST = stumps, AW = aboveground woody material (including bark), BR = branch, FO = foliage)

Component	Method	Periodicity	C concentration	Samples (# plot ⁻¹)	Allometric
TBCA					
Soil CO ₂ flux	F_S	IRGA	–	15	
Litterfall	F_A	Litter trays	Foliage = 0.48, woody = 0.44	6 × (0.25 m ²)	
ΔCoarse root	Δ C_R	Allometrics	0.42		C_R , kg = 0.02898 $DBH^{2.4979}$ $r^2 = 0.60$, $P < 0.001$, $n = 24$
ΔO horizon	Δ C_L	Quadrats	Foliage = 0.48, woody = 0.43	6 × (0.25 m ²)	
Δ0–30 cm mineral soil C	Δ C_S	Soil sampling, Bulk density	Variable	9	
ΔStumps	Δ C_T	Allometrics	0.42		ST, kg = 0.0199. $DBH^{2.1372}$ $r^2 = 0.87$, $P < 0.001$, $n = 20$
Fine roots	–	Coring	0.44	12	
ANPP					
Litterfall	F_A	Litter trays	Foliage = 0.48, woody = 0.44	6 × (0.25 m ²)	
ΔWood	Δ C_W	Allometrics	0.45		AW, kg = 0.0276 $DBH^{2.36} H^{0.56}$ $r^2 = 0.96$, $P < 0.001$, $n = 24$ BR, kg = 0.0045 $DBH^{2.86026}$ $r^2 = 0.78$, $P < 0.001$
ΔFoliage	Δ C_F	Allometrics	0.50	Sep/99 and Aug/00	FO, kg = 0.0389 $DBH^{1.8836}$ $r^2 = 0.67$, $P < 0.001$, $n = 10$
		Optical		Every 6 months	FO, kg = 0.0104 $DBH^{2.2287}$ $r^2 = 0.40$, $P < 0.001$, $n = 24$

based on the precipitation of the previous week (no irrigation if >35 mm). The flow rate of the irrigation system was checked every other month.

A meteorological data set for the site was interpolated from two meteorological stations (18 km NE and 20 km NW of the site), yielding monthly values of minimum and maximum temperatures, rainfall, vapor pressure deficit and photosynthetically active radiation (PAR). Soil water balance was obtained as the difference between estimated precipitation (control plots) or precipitation plus irrigation (irrigated plots), and transpiration. Soil water holding capacity, between -0.01 MPa (0.11 g g⁻¹, field capacity) and -1.50 MPa (0.06 g g⁻¹, wilting point), was determined using the pressure plate technique. Canopy transpiration was estimated monthly for each plot using the Penman–Monteith model with an algorithm from the 3-PG model to estimate stomatal conductance (Stape et al., 2004a).

2.3. Tree measurements

The diameter and heights of 36 trees/plot were measured every 6 months for 2 years. Woody biomass was estimated based on an allometric equation developed from 24 trees harvested and measured from this stand (at age 4; see Table 1 for details on sampling methods and periods). Treatments did not affect allometries, and the same equations were used for all treatments.

Foliage biomass was estimated on four occasions: age 3 (September 1999), age 4 (August 2000) and twice for age 5

(February and October 2001). For the first two occasions site-specific allometrics were developed. For the last two occasions, foliage biomass was estimated based on light interception using a Ceptometer-AccuPAR Model 80 (Decagon Devices, Pullman, USA), specific leaf area (SLA, $8.6 \text{ m}^2 \text{ kg}^{-1}$), and a light extinction coefficient of 0.36 (Stape et al., 2004b). Average carbon content for all vegetation and soil samples were determined in a LECO 1000 CN analyzer (Leco Corp., St. Joseph, MI) using 0.1-g of dried and ground samples.

Coarse-root biomass was estimated with an allometric equation developed from 24 trees sampled at age 4. Roots >10 mm diameter were sampled by digging up all coarse roots from the stem base. We expect that the sampling recovered >95% of the coarse root system. The biomass of 2–10 mm roots was estimated based on the proportion (17%) of 2–10 mm roots to roots greater than 10 mm for *E. grandis* in a site with similar productivity in Brazil (Reis et al., 1985).

Fine root biomass (<2 mm) was estimated once at age 4 to confirm that it was a small fraction of total root C. A total of 12 cores (7.6 cm in diameter and 0.6 m long) per plot were collected, soils were sieved and fine roots were hand picked, washed and dried at 65°C until constant weight. Fine roots occur in deeper soil layers, but we expect the upper 0.6 m contained 90% or more of the fine root mass (see Bouillet et al., 2002). Fine root C stock did not differ among treatments and averaged 0.06 kg C m^{-2} at 4.2 years old, representing less than 4% of the coarse root C content.

2.4. Soil C measurements

Total mineral soil C was evaluated at age 3 and 5 with core samples (0.0–0.15, 0.15–0.30, and 0.30–0.45 m) from 45 fixed locations in each plot. Samples were composited by depth for each plot, giving nine composite samples per plot. Bulk density was determined for each plot and sampling period using a standard 92 mL steel-cylinder with four samples taken at the three depths, and dried at 105°C . The C content on the top 0.45 m of the soil profile represented 60% of the total C down to 2 m depth (based on eight samples taken up to 2.0 m, every 0.2 m). We expected the rate of change in soil C would be very small below 0.45 m depth relative to the upper soil, based on results from Bashkin and Binkley (1998). Soil C contents were converted to an area basis by multiplying concentrations by average bulk density and sampling depth and summing the three depths.

The O horizon was sampled at age 3, 4, and 5 using six random 0.25 m^2 quadrats per plot. Samples were composited by plot, dried at 65°C to constant weight, separated into leaf and woody material, and weighed. O horizon mass was converted to an ash-free basis by correcting for ash content (which ranged from 10 to 28% of oven-dry mass).

Stumps from the previous rotation also comprised a substantial portion of soil C. We surveyed the old stumps in each plot ($\cong 590$ stumps ha^{-1}) at age 3, measuring the diameter on the top of the stump (which ranged from 6.9 to 36.4 cm). Based on the diameter distribution, 20 stumps were selected and dug completely out of the soil and weighed. Subsamples

were taken from each stump and dried at 65°C to a constant weight to estimate total stump dry mass. The mass of all stumps in each plot was estimated by regression.

2.5. Estimating C fluxes

Gross primary production was obtained as the sum of aboveground net primary production (ANPP), aboveground plant respiration (R_P) and total belowground C allocation (TBCA) (Ryan, 1991, Giardina and Ryan, 2002). Aboveground plant respiration (R_P) was estimated as a fixed proportion of ANPP based on respiration equations developed on tropical *Eucalyptus* plantations (Giardina et al., 2002). All dry matter estimates were converted to a C basis using the component-specific C content (Table 2) and the measured or interpolated monthly fluxes were summed annually for the 2 years of the study and expressed in $\text{kg C m}^{-2} \text{ year}^{-1}$.

TBCA was estimated by difference by measuring carbon (C) fluxes into and out of the soil–litter system and any change in C storage (Giardina and Ryan, 2002):

$$\text{TBCA} = F_S - F_A + \Delta[C_S + C_R + C_L + C_T] \quad (1)$$

where TBCA is the total belowground carbon allocation, F_S is the soil efflux or “soil” respiration, F_A is the litterfall and Δ represents the change in the C content on mineral soil (C_S),

Table 2

Gross primary production (GPP), aboveground net primary production (ANPP) and total belowground carbon allocation (TBCA) were higher in the wetter year, and in the irrigated treatment

Annual flux component ^a	Rainfed	Irrigated
Wet year production ($\text{kg C m}^{-2} \text{ year}^{-1}$)		
GPP	6.64 (0.18) b	7.80 (0.24) a
ANPP	2.17 (0.07) b	2.56 (0.07) a
Branch	0.17 (0.01) b	0.20 (0.01) a
Foliage	0.19 (0.01) b	0.23 (0.01) a
Bole	1.81 (0.07) b	2.13 (0.05) a
TBCA	2.14 (0.14) b	2.46 (0.14) a
F_S	1.96 (0.11) b	2.31 (0.12) a
F_A	0.25 (0.01) b	0.28 (0.01) a
ΔC	0.43 (0.05) a	0.43 (0.06) a
Normal year production ($\text{kg C m}^{-2} \text{ year}^{-1}$)		
GPP	3.08 (0.07) b	5.64 (0.14) a
ANPP	0.95 (0.04) b	2.05 (0.06) a
Branch	0.09 (0.01) b	0.17 (0.00) a
Foliage	0.14 (0.01) a	0.15 (0.02) a
Bole	0.72 (0.03) b	1.73 (0.05) a
TBCA	1.10 (0.11) b	1.37 (0.04) a
F_S	1.26 (0.07) b	1.41 (0.04) a
F_A	0.22 (0.01) b	0.26 (0.01) a
ΔC	0.07 (0.06) b	0.22 (0.04) a

The drier atmosphere in the year with normal precipitation limited the ability of *Eucalyptus* trees to take advantage of irrigation water. Values are means with standard errors given in parentheses ($n = 8$ plots). Values (within rows) followed by different letters differ at $P = 0.05$. TBCA = total belowground carbon allocation; F_S = C efflux from the soil as CO_2 , F_A = C flux to the soil surface in aboveground litterfall, and ΔC = net change in soil C storage (O horizon +0–45 cm mineral soil).

^a Within columns, all fluxes differ by year ($P = 0.05$).

coarse roots (C_R), litter layer (C_L) and stumps (C_T). The loss of C from erosion, leaching and the change in the pool size of fine root biomass were assumed to be zero.

Soil CO_2 efflux and soil temperature (at 0.10 m depth) were measured monthly at 15 fixed points along each plot diagonal using a PP Systems CIRAS-1 gas analyzer (PP System, Haverhill MA, USA) with a PP Systems soil respiration chamber (area = 7800 mm²) via a closed system. The chamber was inserted into soil and litter layer immediately before readings were taken. Because the PP System equipment sometimes has higher efflux measurements when compared with LI-COR 6400-9 (LI-COR, Lincoln, NE, USA) (Dantec et al., 1999; Janssens et al., 2000), we compared them (Stape, 2002). Soil CO_2 efflux was measured from all 16 plots were measured with both instruments on 2 consecutive days, with five sub-samples per plot in each day, taken 0.2 m apart. For the LI-COR, collars were inserted 2 cm into the soil 12 h prior to measurements. Plot means ranged 1.88–7.84 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the PP systems and 1.76–5.73 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the LI-COR. Average plot effluxes differed significantly between instruments ($P < 0.001$, paired-samples t -test, $n = 32$), but fluxes correlated strongly with a zero-intercept linear regression ($F_S \text{ LI-COR} = 0.796 F_S \text{ PPSystem}$, $r^2 = 0.589$, $P < 0.0001$). We expect the LICOR provides better quantitative flux estimates, so we use this regression to adjust the PP Systems estimates of F_S (direct use of the PP Systems fluxes would increase our soil CO_2 estimates by 26%).

We also evaluated the effect of soil temperature (which showed little daily variation) on the plot-level F_S through a 24 h measurement period. Efflux measurements were taken every 3 h from all four plots of one block, with 10 sub-samples per plot. No correlation between average effluxes and soil temperature was observed ($r^2 = 0.06$, $P = 0.11$), and no temperature correction was used.

Litterfall was collected monthly in six trays (0.25 m² each) per plot. Samples in a plot were combined and separated into leaf material and woody material (branches, twigs and fruits), and dried at 65 °C to constant weight. Because of the rapid decomposition of leaf material at this tropical site, we corrected leaf mass from litter traps using an exponential decay rate ($k = 0.0072 \text{ day}^{-1}$) obtained for leaf material in a 1-year decomposition study using litter bags in the region (Stape, unpublished data).

The rate of change in C content of the O horizon and 0–45 cm mineral soil C was calculated as linear rates between the two soil sampling times (described above), the decomposition rate of old stumps (estimated using an exponential decay model, $k = 0.190 \text{ year}^{-1}$), and the estimated mass of live and old stumps (described above).

Annual aboveground net primary production was calculated as the sum of the aboveground biomass change (bark, branches, stem and live leaves) and the biomass released as litterfall (woody and leaf litterfall):

$$\text{ANPP} = F_A + \Delta C_W + \Delta C_F \quad (2)$$

where F_A is the litterfall, ΔC_W is the change in carbon content on the aboveground woody biomass (stem, bark and branches),

and ΔC_F is the change in carbon content on the foliage in the canopy. Leaf herbivory was assumed to be zero as no defoliation was observed. Change in aboveground woody carbon (ΔC_W) was estimated as the summation of the estimated individual tree aboveground woody biomass increment.

The respiration of aboveground tree tissues (R_P) was not measured directly. We estimated R_P based on equations developed by Giardina et al. (2002) for respiration associated with growth and maintenance of foliage and wood. The average estimate of R_P -to-ANPP ratio for all plots and years was 1.08, which was close to the 1.10 ratio found by Giardina et al. (2002) for a plantation of *Eucalyptus saligna* (a closely related species to *E. grandis* × *urophylla* hybrid) in Hawaii with two fertilization regimes. A literature review by Landsberg and Waring (1997) found that R_P -to-ANPP ratios typically range from 1.0 to 1.5, so we are confident that our estimates of aboveground tree respiration are reasonable.

We estimated the amount of sequestered C by summing the change in stored C in the aboveground biomass and in the litter–soil compartments:

$$\text{NEP} = \Delta C_W + \Delta C_F + \Delta C_R + \Delta C_L + \Delta C_S + \Delta C_T \quad (3)$$

where NEP is net ecosystem production, ΔC_W is increment in C content of aboveground wood, ΔC_F is increment in leaf C, ΔC_R is increment in root C, ΔC_L is increment in litter layer (O horizon) C, ΔC_S is the change in soil organic C, and ΔC_T is the loss of C from decomposing stumps. Yearly estimations of NEP per plot were based on the yearly estimates of each of the components.

2.6. Quantifying light use and efficiency

Absorbed photosynthetic active radiation was estimated per plot using monthly PAR, LAI estimates and Lambert Beer's law ($\text{APAR} = \text{PAR} (1 - e^{-k \cdot \text{LAI}})$, Runyon et al., 1994) with $k = 0.36$. For each year and plot, we estimated the apparent canopy quantum efficiency (α , mol C GPP mol photon⁻¹) and a light-use-efficiency (ϵ , g ANPP MJ⁻¹) following Landsberg and Waring (1997):

$$\alpha = \frac{\text{GPP}}{\text{APAR}} \quad (4)$$

$$\epsilon = \frac{\text{ANPP}}{\text{APAR}} \quad (5)$$

with APAR and α estimates, changes in GPP among treatments could be explicitly associated with the change in light use (APAR) or quantum-efficiency (α).

2.7. Statistical analysis

Analyses of variance used block, fertilization and irrigation as main effects; year was used as a repeated measurement factor for variables estimated more than once. Where necessary, logarithmic transformations were used to meet statistical assumptions for the errors. No interaction between water and nutrient regimes was observed, and as the majority of the

variables were not affected by fertilization, all variable means were pooled across fertilization treatments. Simple linear regressions were also used. All analyses were performed on SAS 8.1 (SAS Institute Inc., Carry, NC, USA 2001) and Tukey's studentized range test (HSD) was employed for multiple comparisons with a significant level of 0.05 (protecting against type I error).

3. Results

3.1. Water and nutrient supplies

The study period was characterized by a uniform thermal regime with average mean, minimum and maximum daily temperatures of 25, 21 and 29 °C. Precipitation was irregular, totaling 1769 mm in the wet year (age 4) and 1207 mm in the normal year (age 5) when the 8-month drought season supplied only 44% of the year's precipitation (Fig. 1). Irrigation added 531 mm of water during the wet year and 962 mm during the normal year, yielding a 115% increase ($\cong 2150$ mm) above historical average. For the rainfed plots, average available soil water was 81% of the maximum capacity for the wet year and 47% for the normal year (assuming no net annual change in water content of the subsoil below 2 m). Rainfed plots transpired an estimated 1261 mm in the wet year (outflow of 243 mm), and 894 mm in the normal year (outflow of 132 mm), while the transpiration rates of irrigated plots were close to 1250 mm for both years (outflow of 764 mm). No water accumulation was observed on the soil surface during irrigation events due to its coarse texture (85% sand) and high drainage (saturated hydraulic conductivity of 22 mm h⁻¹, based on Ritchie et al., 2001). Vapor pressure deficit correlated negatively with rainfall on a monthly basis ($r^2 = 0.32$, $P < 0.01$, $n = 24$).

3.2. Tree growth

Aboveground woody biomass averaged 37 Mg ha⁻¹ at the beginning of the experiment (age 3, Fig. 2). At age 5.5 years, wood biomass reached 107 Mg ha⁻¹ for rainfed and 141 Mg ha⁻¹ for irrigated plots (coefficient of variation of 4.6%). No fertilization effect was observed. Leaf area index (LAI) averaged 3.3 at age 3 and increased to 4.0 at the end of the wet year, with no difference among treatments. During the drought period of the normal year, LAI decreased to 2.3 on rainfed plots and to 3.4 on irrigated plots (Fig. 2). The decrease in LAI was coupled with leaf shedding in the rainfed treatment detected as an increase in litterfall (Fig. 3), which was the only period when litterfall of rainfed plots surpassed the irrigated plots. At 5.4 years during the rainy season, LAI was again similar among treatments (2.8).

3.3. Forest production and C allocation

All forest production measures (TBCA, ANPP and GPP) differed by year and water regime. Fertilization had a minor effect in some of the production components, and only for the wet year and results are not presented separately.

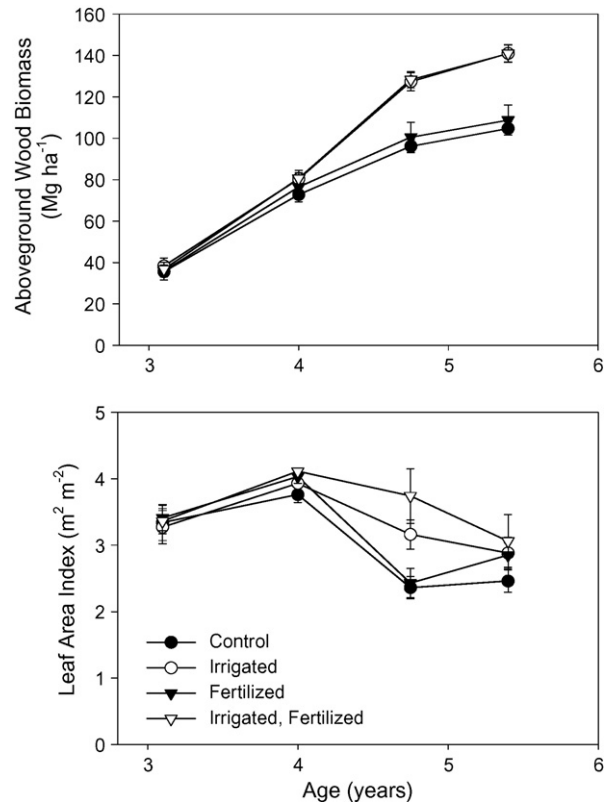


Fig. 2. Aboveground wood (bole) biomass (upper) and leaf area index (lower). Error bars are standard errors of the means ($n = 4$ plots).

Total belowground carbon allocation for the wet year was almost twice the rate of the normal year (2.3 kg C m⁻² year⁻¹ versus 1.2 kg C m⁻² year⁻¹, Table 2) and irrigation increased TBCA in relation to the rainfed plots (1.9 kg C m⁻² year⁻¹ versus 1.6 kg C m⁻² year⁻¹). The coefficient of variation for TBCA across years and treatments was 15%.

Soil CO₂ efflux was the dominant component of the TBCA equation, and litterfall (in the normal year) and change in stored C (in the wet year) alternated as the second in importance (Fig. 4). Soil surface C efflux (F_S) was 60% higher for the wet year (2.1 kg C m⁻² year⁻¹) than the normal

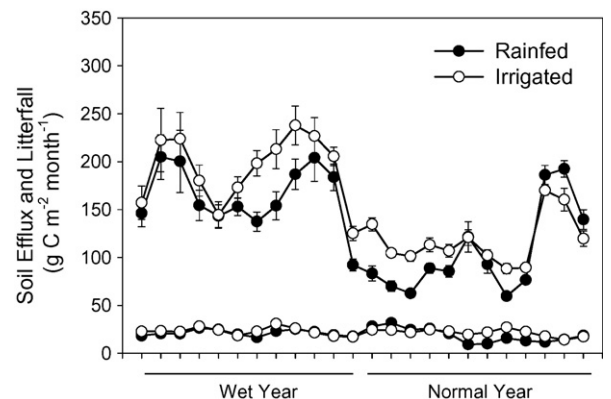


Fig. 3. Monthly soil CO₂ efflux (top lines) and litterfall (bottom lines) by water regime ($n = 8$ plots). Error bars are standard errors of treatment means.

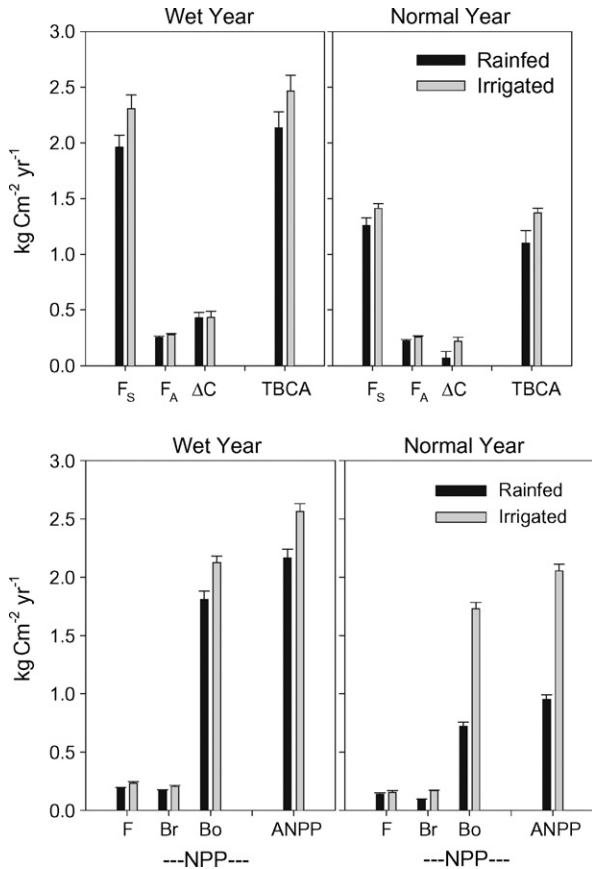


Fig. 4. Components of total belowground carbon allocation (upper) by water regime and year ($n = 8$ plots), and aboveground net primary production (lower). Error bars are standard errors of the means. F_S = soil CO_2 efflux, F_A = litterfall, ΔC = annual change in C stored in coarse roots, litter layer, stumps and mineral soil. F NPP = foliage net primary production, Br.NPP = branch net primary production, Bole NPP = stemwood plus bark net primary production.

year ($1.3 \text{ kg C m}^{-2} \text{ year}^{-1}$), and was also greater for irrigated ($1.9 \text{ kg C m}^{-2} \text{ year}^{-1}$) than rainfed treatments ($1.6 \text{ kg C m}^{-2} \text{ year}^{-1}$), with no interaction between year and water regime. Soil CO_2 efflux dropped during the drought period of the normal year (Fig. 3), and returned to pre-drought values during the rainy season. On a monthly basis, soil CO_2 efflux did not correlate with temperature, even in the irrigated plots that had no water limitation ($r^2 = 0.04$, $P = 0.16$, $n = 24$).

Litterfall (F_A) was marginally higher for the wetter year compared with the drier year, for the rainfed and irrigated treatments, and for the fertilized treatment during the wet year (differences $< 0.04 \text{ kg C m}^{-2} \text{ year}^{-1}$, Table 2). Yearly soil CO_2 efflux averages did not correlate with litterfall at the plot level ($r^2 = 0.01$, $P = 0.29$, $n = 32$). The residence time of foliage in the canopy ranged from 0.8 to 1.1 year⁻¹ (average of 1.0 year). Yearly soil CO_2 efflux correlated with ANPP ($r^2 = 0.47$, $P < 0.001$, $n = 32$) and GPP ($r^2 = 0.71$, $P < 0.001$, $n = 32$).

Total change in stored C (ΔC) in the soil (O horizon plus 0–45 cm mineral soil) was similar for water regimes in the wet year ($0.43 \text{ kg C m}^{-2} \text{ year}^{-1}$) but in the normal year irrigated treatments had a greater ΔC ($0.22 \text{ kg C m}^{-2} \text{ year}^{-1}$ versus $0.06 \text{ kg C m}^{-2} \text{ year}^{-1}$, Table 2). Coarse root accumulation (ΔC_R) was the main component of ΔC (Eq. (1)). Other

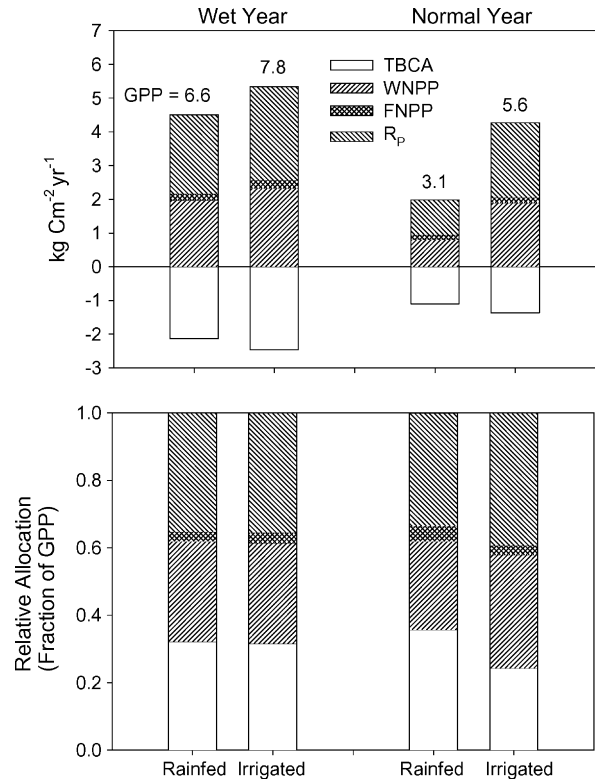


Fig. 5. Absolute (upper) and relative (lower) estimates of gross primary production (GPP) and above and belowground components for the wet year and normal year by water regime and year ($n = 8$). TBCA = total belowground carbon allocation, WNPP = aboveground woody net primary production, FNPP = foliage net primary production and R_p = aboveground autotrophic respiration.

components of ΔC had a small impact on its estimate. Mineral soil C (ΔC_S) showed a significant net decline of $-0.09 \text{ kg C m}^{-2} \text{ year}^{-1}$, which represented 2.3% of initial C stock of 4.2 kg C m^{-2} . Across treatments, C stored in the O horizon did not change, but old stumps lost $0.03 \text{ kg C m}^{-2} \text{ year}^{-1}$.

Irrigation increased ANPP by 18% from 2.2 to $2.6 \text{ kg C m}^{-2} \text{ year}^{-1}$ in the wet year, and by 116% from 0.9 to $2.0 \text{ kg C m}^{-2} \text{ year}^{-1}$ in the normal year (Table 2). Fertilization increased ANPP only in the wet year (from 2.2 to $2.5 \text{ kg C m}^{-2} \text{ year}^{-1}$). Across all years and treatments, bole NPP was the dominant component of ANPP (83%), followed by foliage NPP (9%) and branch NPP (8%) (Table 2, Fig. 4).

Irrigation increased GPP by 18% in the wet year ($6.6 \text{ kg C m}^{-2} \text{ year}^{-1}$ versus $7.8 \text{ kg C m}^{-2} \text{ year}^{-1}$) and by 83% in the normal year ($3.1 \text{ kg C m}^{-2} \text{ year}^{-1}$ versus $5.6 \text{ kg C m}^{-2} \text{ year}^{-1}$, Table 2), and no fertilization effect was detected. All treatments had the same relative belowground allocation during the wet year (32%, Fig. 5), but irrigated plots had a lower relative belowground allocation compared with rainfed plots on the normal year (24% versus 36%). Averaged across years, irrigation decreased the fraction of GPP allocated belowground from 34 to 28%, increasing the fraction allocated to ANPP from 32 to 34%.

Net ecosystem production increased with irrigation both in the wet year ($2.3 \text{ kg C m}^{-2} \text{ year}^{-1}$ versus $2.7 \text{ kg C m}^{-2} \text{ year}^{-1}$) and normal year ($0.8 \text{ kg C m}^{-2} \text{ year}^{-1}$ versus $2.0 \text{ kg C m}^{-2} \text{ year}^{-1}$)

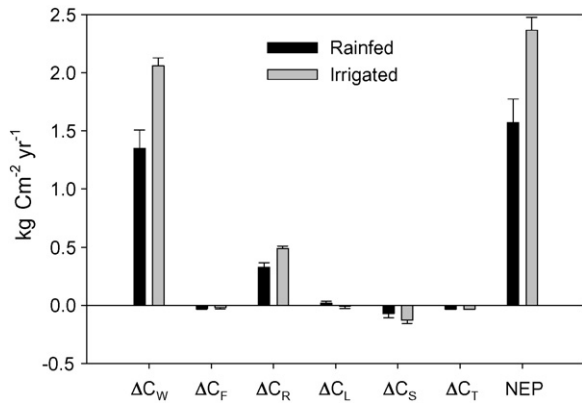


Fig. 6. Components of net ecosystem productivity (NEP) by water regime for both years ($n = 16$ plots). Error bars are standard errors of the means. ΔC_W , ΔC_F , ΔC_R , ΔC_L , ΔC_S , ΔC_T are the change in C stored in aboveground woody biomass, foliage, coarse roots, litter layer, soil and stumps.

with a significant year interaction. NEP increased in the wet year on the fertilized treatments (from 2.4 to 2.7 kg C m⁻² year⁻¹) but no fertilization effect was observed in the normal year. Aboveground (ΔC_W) and coarse root (ΔC_R) components dominated the NEP (Fig. 6).

3.4. Light use efficiency

Absorbed photosynthetically active radiation was similar for rainfed and irrigated treatments in the wet year, but was 14% higher for the irrigated plots in the normal year (Table 3). Canopy quantum efficiency (α) showed an interaction between year and water regime, averaging 0.051 mol C mol⁻¹ APAR (rainfed) and 0.060 mol C mol⁻¹ APAR (irrigated) on the wet year (16% increase by irrigation). In the normal year α dropped to 0.027 mol C mol⁻¹ APAR (rainfed) and 0.044 mol C mol⁻¹ APAR (irrigated) (61% increase by irrigation effect). Light use efficiency (ϵ) also showed a significant year and water regime interaction, averaging 2.0 g C MJ⁻¹ APAR and 2.4 g C MJ⁻¹ APAR on the wet year for rainfed and irrigated

Table 3
APAR, canopy quantum efficiency (α), light use efficiency (ϵ) and bole growth per unit APAR by water regime and year

Year	Rainfed	Irrigated
Absorbed PAR (mol APAR m ⁻² year ⁻¹)		
Wet year	10770 (100)	10940 (100)
Normal year	9420 (180) b	10700 (250) a
α , Canopy quantum efficiency (mol C mol ⁻¹ APAR)		
Wet year	0.051 (0.001) b	0.060 (0.002) a
Normal year	0.027 (0.001) b	0.044 (0.002) a
ϵ , Light use efficiency (g ANPP MJ ⁻¹ APAR)		
Wet year	2.05 (0.06) b	2.39 (0.05) a
Normal year	1.03 (0.05) b	1.97 (0.09) a
Bole growth per unit APAR (g bole MJ ⁻¹ APAR)		
Wet year	1.71 (0.11) b	1.98 (0.09) a
Normal year	0.78 (0.08) b	1.66 (0.16) a

Values are means with standard errors given in parentheses ($n = 8$ plots). Values (within rows) followed by different letters differ at $P = 0.05$.

treatments. For the normal year ϵ decreased by half to 1.0 g C MJ⁻¹ APAR on the rainfed treatments and to only 2.0 g C MJ⁻¹ APAR on the irrigated plots. Bole production efficiency was lowest in the drier year in the control plots (0.78 g bole MJ⁻¹ APAR), and highest in the wetter year in the irrigated plots (1.98 g bole MJ⁻¹ APAR).

The rate of NEP in our study ranged from 0.8 kg C m⁻² year⁻¹ for the normal in the rainfed plots to 2.7 kg C m⁻² year⁻¹ in the wet year in the irrigated plots. The efficiency of using water (kg C of NEP per m³ of water used) increased with improving water supply and increasing atmospheric humidity, climbing from 1.36 kg C m⁻³ without irrigation in the normal year to 2.16 kg C m⁻³ with irrigation in the wet year. Across both years, rainfed treatments produced 2.55 kg of wood per m³ of water used, compared with 3.51 kg of wood per m³ of water with irrigation.

4. Discussion

Water supply limited growth on this typical sandy Oxisol site, but inherent soil fertility and operational rates of fertilization were sufficient to prevent nutrient limitation. Other irrigation and fertilization trials with *Eucalyptus* also reported increased wood growth associated with greater water supply (Pereira and Pallardy, 1989; Stewart et al., 1990; Olbrich et al., 1992; Myers et al., 1996; Honeysett et al., 1996; Hunter, 2001). The wood increment of this clonal *E. grandis* × *urophylla* with irrigation in the wet year (92 m³ ha⁻¹ year⁻¹, based on a wood density of 0.42 kg/m³) is among the highest values ever reported for forests (Birk and Turner, 1992; Cromer et al., 1993; Santana et al., 2000; Binkley et al., 2002). This prominent effect of water matched that observed in the geographic gradient study in this same area (Stape et al., 2004b), indicating that the magnitude of response to increased water supply was similar in response to irrigation as it was to the rainfall gradient. Clearly the supply of water is a key factor in mapping regional potential growth of *Eucalyptus* plantations (Golfari et al., 1977; Coops et al., 1998), and in accounting for substantial variation in growth among years (Olbrich et al., 1992; Sands et al., 1999; Hunter, 2001).

The absence of a fertilization effect on wood production in this site contrasts with experiments where *Eucalyptus* responded strongly to fertilization (Yost et al., 1987; Birk and Turner, 1992; Cromer et al., 1993; Barros and Novais, 1996; Stape and Benedetti, 1997; Fernandez et al., 2000; Laclau et al., 2000; Hunter, 2001; Giardina et al., 2002). At our site, nutrient requirements of the control plots were probably achieved by a combination of the fertilization at time of planting, native nutrient availabilities and efficient nutrient cycling of *Eucalyptus* (Goncalves et al., 1997; Binkley and Ryan, 1998).

Leaf area index values were typical for *Eucalyptus* in Brazil (Mielke et al., 1999; Binkley et al., 2002), Africa (Olbrich, 1998; Laclau et al., 2000), and Australia (Stewart et al., 1990; Cromer et al., 1993; Myers et al., 1996 and Hunter, 2001). The response of LAI to irrigation was similar to other *Eucalyptus* irrigation experiments (Olbrich et al., 1992; Hunter, 2001; Pereira and Pallardy, 1989). The drop in LAI associated with a

near-absence of height increment on rainfed treatments during the normal year (data not shown) indicated low rates of leaf production associated with continued leaf shedding, which is common for *Eucalyptus* (Cromer et al., 1993; Pook, 1985; Honeysett et al., 1996).

The high rates of soil CO₂ efflux (1.2–2.5 kg C m⁻² year⁻¹) were similar to rates obtained on other fast-growing plantations (Binkley and Ryan, 1998; Giardina et al., 2004; Maier and Kress, 2000), and the absence of soil respiration response to temperature agreed with data from another tropical site (Giardina and Ryan, 2002). Approximately 15% (0.25 kg C m⁻² year⁻¹) of the soil CO₂ efflux in our site came from litter layer decomposition, close to the 20% obtained for *E. saligna* in Hawaii by Giardina and Ryan (2002). The remaining 85% of the soil CO₂ efflux (1.5 kg C m⁻² year⁻¹) appeared to be strongly coupled with root respiration, but not with current canopy photosynthesis. Experiments with tree girdling at this site (as well as another site in Brazil) showed plots with girdled trees sustained 75–85% of the rates of control plots for 3 months (Binkley et al., 2006). Given the relatively low soil C content, we expect the soil respiration in girdled plots resulted from continued root respiration, fed from large carbohydrate reserves.

Our highest canopy quantum efficiency estimate (0.060 mol C mol⁻¹ APAR) was obtained on the irrigated and fertilized treatment during the wet year (lower VPD), and is greater or equivalent to theoretical maximum α^* used in previous *Eucalyptus* studies (Beadle and Turnbull, 1992; Landsberg and Waring, 1997; Sands, 2000). This efficiency represents a conversion of 12% of the absorbed PAR into assimilates (\cong 4% of the incoming shortwave radiation). Hunt (1994) reviewed the forest literature and indicated a maximum conversion of 2 g NPP MJ⁻¹ APAR for forests with more than 100 Mg ha⁻¹ of standing biomass and 3.5 for pot experiments. At our site, the average value was 3.0 g NPP MJ⁻¹ APAR indicating that more data from tropical forests are needed.

By decomposing GPP into its multiplicative components (GPP = APAR · α) we could credit the 18% greater GPP in the irrigated treatments in the wet year to a higher canopy quantum efficiency (+18%), while the 83% greater GPP in the normal year was a combination of higher light interception (+14% APAR) combined with a higher canopy quantum efficiency (+61%). Giardina et al. (2002) attributed a 37% increase in GPP of *E. saligna* to a 10% increase in APAR and 25% in α due to better nutrition. The observed light use efficiencies ($\varepsilon = 1.0$ – 2.4 g ANPP MJ⁻¹ APAR) of this *Eucalyptus* clone (Table 3) are similar to C₃ and C₄ crop efficiencies (1.0–4.0 g ANPP MJ⁻¹ APAR) and above the mean of the observed forest values (0.2–2.5 g ANPP MJ⁻¹ APAR) (Cannell, 1989; Hunt, 1994; Haxeltine and Prentice, 1996; Goetz, 1997), and was extremely dependent on C allocation patterns. For instance, the 91% increase in ε for the irrigated plots during the normal year was a combined effect of a 61% increase in α and 18% increase in the aboveground allocation (Table 3). Averaged over the 2 years, the increase in ANPP by the irrigation effect was primarily dependent on canopy quantum efficiency (67%), followed by shift in allocation (18%) and then increasing in LAI (15%). These results show that interpretation of light use

efficiency is limited without belowground data (Jokela and Martin, 2000; Balster and Marshall, 2000), and that belowground carbon allocation responds strongly to water supplies (Litton et al., 2007). Besides that, complete C budgets are needed as the foundation for understanding both wood production and C sequestration, especially in response to environmental conditions (Hoen and Solberg, 1994).

The production ecology of a single *Eucalyptus* clone at a single site may not represent the environmental responses of other *Eucalyptus* genotypes on other sites. The results from this study can be extrapolated to other sites based on functional production models (e.g. Almeida et al., 2004; Stape et al., 2004a). We are also repeating this experiment at seven diverse sites across southeastern Brazil, with a variety of *Eucalyptus* genotypes, as part of the Brazil Eucalyptus Productivity Project (BEPP, www.ipef.br/bepp).

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