DISSERTATION

PRODUCTION ECOLOGY OF CLONAL *EUCALYPTUS* PLANTATIONS IN NORTHEASTERN BRAZIL

Submitted by

Jose Luiz Stape

Department of Forest Sciences

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2002

UMI Number: 3064023

UMI Microform 3064023

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COLORADO STATE UNIVERSITY

June 17, 2002

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOSE LUIZ STAPE ENTITLED PRODUCTION ECOLOGY OF CLONAL *EUCALYPTUS* PLANTATIONS IN NORTHEASTERN BRAZIL BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Committee on Graduate Work

Co-adviser

Adviser

Department Head

ABSTRACT OF DISSERTATION

PRODUCTION ECOLOGY OF CLONAL EUCALYPTUS PLANTATIONS IN NORTHEASTERN BRAZIL

Although millions of hectares of *Eucalyptus* are intensively managed for wood production in Brazil, little is known about the physiological processes that control growth and how these processes are regulated by internal and external factors. These uncertainties limit the testing of process-based models, which are necessary to evaluate both production and ecological feedbacks of plantations across spatial and temporal scales.

I used one gradient study and two manipulative studies with clonal *E. grandis* x *urophylla* in northeastern Brazil to achieve three objectives: (1) identify the main environmental factors controlling growth and the associated resource use (Chapter I); (2) quantify water and nutrient supply effects on carbon (C) gain and C allocation patterns (Chapter II); and (3) evaluate the ability of a process-based model to simulate *Eucalyptus* response to changes in fertility and climate (Chapter III).

For the first objective, fourteen stands with aboveground net primary production (ANPP) spanning from 9 to 39 Mg ha^{-1} yr^{-1} were characterized in their supply and use of water, light and nitrogen. Water was the most limiting resource, and ANPP increased by 2.3 Mg ha^{-1} yr^{-1} for each 100 mm yr^{-1} increase in rainfall. Indirectly, water supply also increased light and nitrogen use by increasing LAI and N-uptake-efficiency. The most productive sites were the most efficient in using water (3.21 kg of ANPP per m^3 of transpired water), light (1.14 kg per GJ of APAR) and nitrogen (381 kg per kg of N taken up). Lower VPD, soil water stress and root-to-aboveground ratio were associated with these high-efficiency stands.

For the second objective, an irrigation-fertilization 2 x 2 factorial design was used in a 3-year-old plantation. Carbon budgets were obtained for two years, including ANPP, total belowground C allocation (TBCA), and estimates of aboveground autotrophic respiration. These estimates were summed to obtain the gross primary production (GPP). Irrigation increased GPP by 38% (from 4.8 to 6.7 kg C m^{-2} yr^{-1}), primarily by increasing canopy quantum efficiency from 0.034 to 0.052 mol C mol^{-1} PAR and secondarily by increasing LAI. Despite the increase in TBCA (from 1.6 to 1.9 kg C m^{-2} yr^{-1}), irrigation decreased the fraction of GPP allocated belowground from 34% to 28%, increasing ANPP by 48% (from 1.5 to 2.3 kg C m^{-2} yr^{-1}). Wood and coarse root increments were the dominant components of the net ecosystem production, with no change in soil C.

The final objective was met by calibrating the 3-PG model with two tropical *Eucalyptus* trials that had complete production data. Validation was performed using independent data from forty plots (with and without fertilization) monitored for 2 years. The model captured the influence of water and nutrients on C gain and allocation pattern during calibration. The model also responded well to soil fertility and climate conditions during validation, and was particularly sensitive to LAI estimates. Actual wood production ranged from 2 to 51 Mg ha^{-1} yr^{-1}, compared with model estimates of 10 to 42 Mg ha^{-1} yr^{-1} ($r^2 = 0.78$).

Overall, our study indicates that for fertilized *Eucalyptus* tropical plantations water is the most influential resource controlling C gain, allocation, resource use and the efficiency in using these resources; and process-based models can play an important role in improving the management of these almost-agricultural forests.

Jose Luiz Stape
Department of Forest Sciences
Colorado State University
Fort Collins, Colorado 80523
Summer 2002

ACKNOWLEDGMENTS

I do appreciate having Dan Binkley and Mike Ryan as my advisers. Their endless questionings about forest growth behaviors were the ideal guidances to change my perceptions regarding plantations and their functional insertion on a broader ecological perspective. I also thank Frederick Smith to introduce me to the silviculture of temperate species, and to Willian Parton and Tom Hobbs for showing me how to use modeling as a research and management tool.

To my friends from the University of Sao Paulo, Jose L. M. Gonçalves, Fernado Seixas, Luis C. E. Rodrigues, Jose O. Brito and Fatima Juliani, my appreciation for their help in dealing with my responsibilities in Brazil during my doctorate.

My gratitude to Reinoldo Poernbacher, Jose Augusto Resende, Antonio N. Gomes, Jacyr M. Alves and the SETEC crew from Copener Florestal company by supporting all field work necessary for this thesis. I also thank Edson A. Balloni and Admir L. Mora from Pisa Florestal, Jose M. Mendes from VCP Florestal and Nelson B. Leite from the Brazilian society of silviculture for their indirect support to achieve this goal. To the BEPP group companies (Aracruz, Bahia Sul, Copener, International Paper, VCP and Veracel) for keeping me motivated to finish this step in order to return to Brazil and initiate new projects.

To CNPq – Conselho Nacional de Desenvolvimento Cientifico e Tecnologico do Ministerio da Ciencia e Tecnologia of Brazil government – for the scholarship provided to develop this research (201144-97.2).

To my friends from Colorado State University, Christian Giardina, Yowhan Son, Sigrid Resh, Jason Kaye, Margot Kaye, Suzie Bird, Amanda Myers, Holly Barnard and Carol Adair for their frienship and support during this journey.

Finally, thanks to all that directly or indirectly help me to conclude this thesis.

DEDICATION

To my loved wife **Luceni**,

To my loved sons **Thiago** and **Glauco**, and

To my loved parents **Joubert** and **Lourdes**,

I dedicate this work.

In Memory of

My grandmothers

Helena Dall Pozzo Bertin

(1906 – 1981)

and

Emma Elvira Olivieri Stape

(1901 – 2001)

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CHAPTER I

EUCALYPTUS PRODUCTION AND THE SUPPLY, USE AND THE EFFICIENCY OF USE OF WATER, LIGHT AND NITROGEN ACROSS A GEOGRAPHIC GRADIENT

Introduction

Tropical plantations are fascinating systems. They have all the components of a typical forest, but with a high uniformity and with production rates 5 to 15 times higher than the more-studied temperate forests (Roy et al. 2001). Forest plantations are an increasing component of tropical landscapes with approximately 3 million hectares of annual increase in the current extent of 40 to 50 million ha of planted area (Brown et al. 1997, FAO 1999). This expansion is being driven by rising wood demands for local communities, and raw-material for wood-based industries (Gonçalves et al. 1997, Fox 2000). The increase of plantation productivity has been the goal of governmental and private programs to accelerate economic returns and reduce the acreage needed for forestation (Eldridge et al. 1994, Campinhos 1999). *Eucalyptus* is the dominant hardwood planted species (10 to 15 million ha, Neilson 2000), and the productivity of managed forests has increased from 12 m^3 ha^{-1} yr^{-1} in the 1960s to 20-60 m^3 ha^{-1} yr^{-1} due to improved genetics and silviculture (Mora 1986, Schumann 1992, Eldridge et al. 1994, 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 2001). Evaluation of these supplies is important for zoning plantation potential (Golfari et al. 1977, Laffan 1994, Coops et al. 1998) and for establishing silvicultural methods for site preparation, fertilization and competition control to mitigate water and nutrient stresses (Attiwill and Adams 1996, Gonçalves et al. 2000). Nevertheless, rapid forest growth rates are generally coupled with the high use of site resources, which raises questions regarding both plantation ecological impacts and the sustainability of wood production in water- or nutrient-limited sites (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 (Wang et al. 1991, Gholz and Lima 1997). However, our understanding of the basic physiological mechanisms that govern forest C gain, allocation and the associated resource use lag behind of our empirical knowledge of promoting forest growth (McNabb and Wadouski 1999, Gonçalves et al. 1997). For instance, although most of the effects of water and nutrient supply on forest production are mediated by leaf area responses affecting light use and light use efficiency (Landsberg and Gower 1997), studies associating these processes are scarce (McMurtrie et al. 1990, Runyon et al. 1994, Sampson and Allen 1998).

The production-resource equation (Monteith 1977, Charles-Edwards and Fisher 1980, Vitousek 1982, Cannell et al. 1988, Bridgham et al. 1995, Hiremath and Ewel 2000) provides a framework to characterize the production ecology of plantations, identifying the relationship between production and water, nutrient and light resources:

$$\text{Production} = \text{Supply} \cdot \text{RCE} \cdot \text{RUE}$$

where Production is generally measured as aboveground net primary production (ANPP), Supply is the amount of resource available during the period, RCE is the resource-capture-efficiency (resource used-to-resource available ratio), and RUE is the resource-use-efficiency representing the amount of production per unit of resource used. Solving the equation for each resource allows the association of changes in production with changes in the supply, use or the efficiency of use of the different resources, and their potential interactions. The production-resource equation has crucial importance for the management of forest plantations, including establishing forestry practices that enhance resource supplies when they are identified as limiting (Binkley et al. 1997), evaluating rates of resource use and their ecological significance for the biogeochemical and hydrosphere cycles (Burger and Kelting 1998, Bruijnzeel 1997), screening genotypes for high resource-use-efficiencies (Cannell et al. 1988, Boyle et al. 1997, Green et al. 2001), and obtaining values for resource-use parameters of process-based models (Haxeltine and Prentice 1996, Landsberg and Gower 1997).

Although resource-use indices are available at the leaf or plant level (Kaufmann and Ryan 1986, Lindroth and Cienciala 1996, Larcher 1995), their evaluations at the stand level are not commonly obtained (Gower et al. 1994), and comparisons among different studies are constrained by the use of distinct genotypes, ages, forest structures, environmental factors and efficiency concepts (Birk and Vitousek 1986, Easthan et al. 1990, Wang et al. 1991, Olsson et al 1998, Bargali and Singh 1991, Santana et al. 2000, Binkley et al. 2002).

To characterize the range and controls over biomass production and accumulation, and resource use patterns for *Eucalyptus* plantations, a project was established in 1996 among the University of Sao Paulo (Brazil), six forest companies, Colorado State University (USA) and the USDA Forest Service: "Brazil *Eucalyptus* Potential Productivity - BEPP". As a first project, we selected 14 stands of typical clonal *E. grandis* x *urophylla* forests in the final year of their short-rotation regimes (6 to 8 years) along a geographic and climatic gradient in northeastern Brazil and with aboveground net primary production (ANPP) spanning from 9.7 to 39.1 Mg ha^{-1} yr^{-1}. 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 mean annual biomass increment (MAI), aboveground net primary production (ANPP) and the trends in biomass accumulation; and
ii. Quantifying how much of the patterns in ANPP across sites related to the supply, use and the efficiency of use of water, light and nitrogen resources.

Materials and Methods

Site and stands descriptions

The study sites were located in northeastern Brazil, within a 55-km radius of Entre-Rios (11°58'S, 38°07'W; Figure 1.1). Fourteen *Eucalyptus* plantations (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°C, 30.0°C and 20.9°C characterized this tropical area. Rainfall decreases from 1,600 mm yr^{-1} in coastal areas to less than 800 mm yr^{-1} just 120-km inland (Figure 1.1). Two-thirds of the rain falls in autumn and winter, with a dry period in the summer (CEI 1991). The inter-annual coefficient of variation of the rainfall is high (21%), with low growth or tree mortality during the summers of dry years. 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) represent 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 (more than 1.8 m), with high bulk density (more than 1.4 Mg m^{-3}), and low to moderate organic C (2 to 6 kg C m^{-2}, from 0 to 0.6 m) and N (100 to 500 g N m^{-2}).

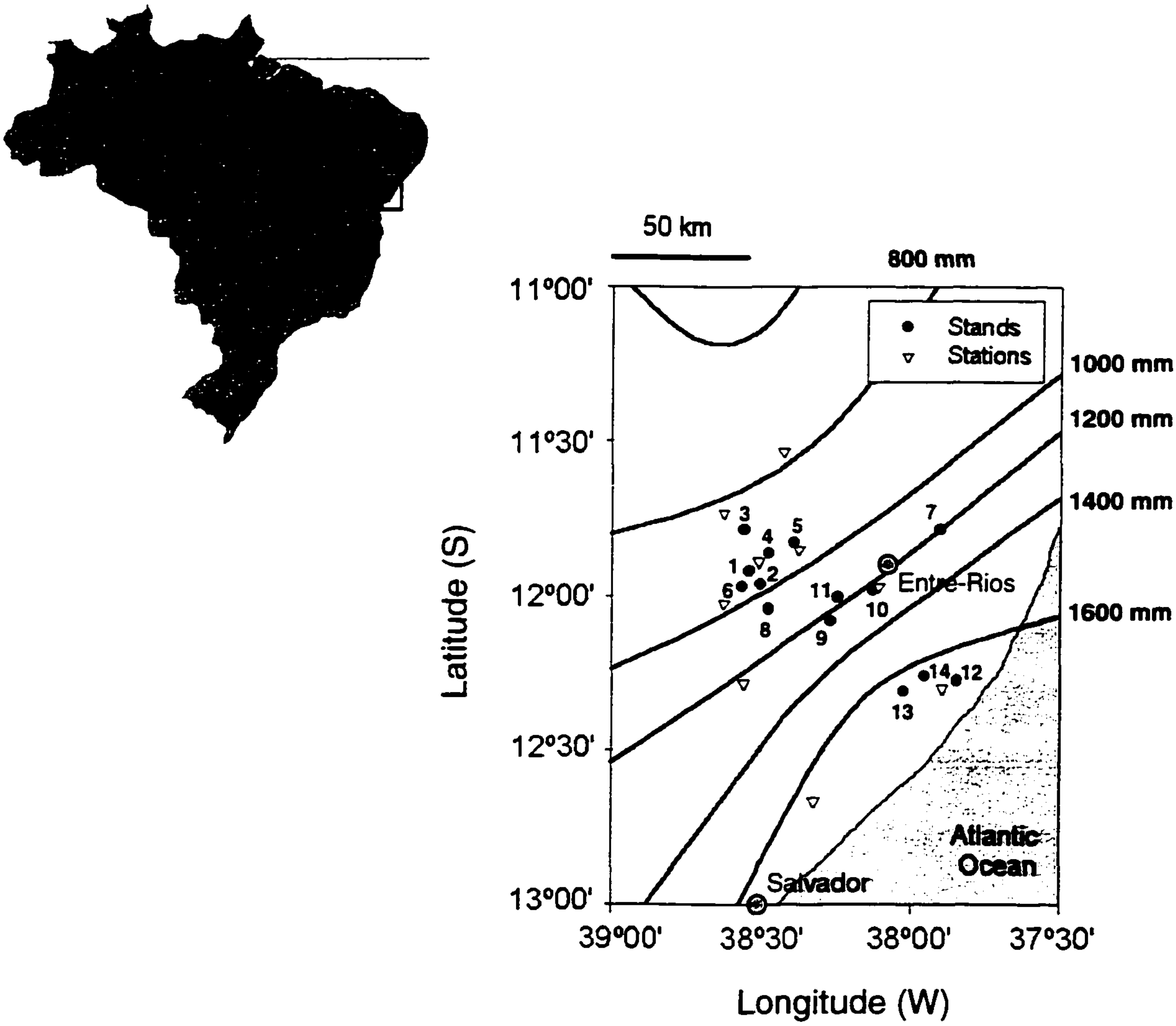


Figure 1.1. Location of the 14 stands of *E. grandis* x *urophylla* in northeastern Brazil and the 9 associated meteorological stations with historical isohyets. Site numbers represent increasing productivity (see Figure 1.2.a).

Table 1.1. 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 x urophylla*.

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

Table 1.2. Biometric characteristics of the stands. Productivity class averages followed by different letters differ at P=0.05.

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

Sampling design and productivity classes

The 14 stands of *E. grandis* x *urophylla* were reaching the end of their first rotation (between 6 and 8 years-old) and were chosen from 320 inventory plots to represent the breadth of regional soil, climate and productivity. Based on the 1996 inventory results, the plots were classified into three groups of mean annual biomass increment (MAI) and two groups of soil texture (lower and greater than 15% clay at 0.5 m depth). Three sites were randomly selected for each of the 6 categories. Due to operational reasons only 14 sites were completely sampled (Table 1.1, Figure 1.1). According to the measured MAI in 1997 and the estimated aboveground net primary production (ANPP), the stands were classified into three productivity categories to facilitate general interpretations: (i) Low (MAI or ANPP < 15 Mg ha^{-1} yr^{-1}, n = 5), (ii) Medium (15 < MAI or ANPP < 20 Mg ha^{-1} yr^{-1}, n = 4), and (iii) High (MAI or ANPP > 20 Mg ha^{-1} yr^{-1}, n = 5) (Table 1.2, Figure 1.2.a). Sites were sorted by ANPP within each productivity class and numbered in ascending order (Figure 1.2.a). All stands were located in flat or 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 1993 at 3.5 m x 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 to control weeds (glyphosate). Eleven of the 14 stands consisted of mixed clonal plantations (30 clonal cuttings randomly mixed in the nursery) and 3 (sites 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 m^2 was measured yearly from 2 years of age until harvest at 6-8 years during 1997 or 1998. The diameters at breast height (DBH, at 1.30 m) were measured for all trees, as well as the first 20 heights and the heights of the 4 dominant trees.

Biomass sampling and allometric equations

Nine trees were selected in each site to represent three size classes (mean DBH, plus one standard deviation, minus one standard deviation) with 3 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 meters. 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 compartment were taken for moisture determination (dried at 65°C) to calculate total dry weight. At the tree level, a root-to-aboveground woody biomass ratio ($R{:}A_T$) was determined. For each site and compartment, allometric equations were established in the form:

$$W_{ij} = a_{ij}.\ DBH^{b_{ij}}$$

where W_{ij} is the dry weight of compartment *i* at site *j*, and *a* and *b* are the allometric and slope parameters to be estimated, respectively. Allometric equations were also derived for each productivity class and for all trees. For foliage, thirty recent fully expanded leaves from the middle of the canopy were selected for specific leaf area (SLA) estimates by photocopying-weighing technique. SLA was calculated by the ratio of measured area (1 side) and dry mass. Forest floor was sampled using six random 0.25 m^2 quadrats, composited, dried at 65 °C, weighted and corrected to soil inclusion (10%).

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

Mean annual biomass increment (stem, bark and branches) was estimated for each site at the biomass harvesting by the summation of the estimated individual tree compartment biomass with site-specific allometrics (Table A.1.4), and dividing by the plot area and age (Table 1.2). Average mean DBH, stand density and basal area were also calculated for each site, together with leaf area index (LAI) based on estimated foliage biomass and specific leaf-area of the stand (Table A.1.5). Site index was directly determined by the average of the 4 dominant trees in each plot at age 5. At the stand level, two biomass distribution indices were calculated: the root-to-aboveground wood biomass ratio ($R{:}A_S$) and the fraction of total biomass (foliage, branch, stem, bark and coarse root) of each forest compartment. A monthly meteorological interpolated file was created for each site for 1990 trough 1998 based on stations located within a 30-km radius of the site (Figure 1.1, Appendix I.B). Averages of the following meteorological variables were estimated for the complete rotation of each site: mean temperature, rainfall, vapor pressure deficit (VPD) and potential evapotranspiration (Table A.1.1).

Aboveground net primary production (ANPP)

Aboveground net primary production (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 in a parallel study. In this study of a 5 year-old clonal *E. grandis* x *urophylla* in the region, canopy turnover was 0.99 year^{-1} with branches representing 31% of the foliage litterfall across a range of water and nutrient treatments (details in Chapter II).

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 8 locations inside each plot using a graduated auger, and subsamples were composited by depth. Samples were dried at 65 °C to a constant weight. Soil texture, pH (in 0.01M $CaCl_2$), labile P, K, Ca and Mg, and total soil C and N were determined using the procedures described in Appendix I.A. Bulk density was determined using a 92 mL steel cylinder with 2 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 site (for a 2 m profile) was estimated based on soil texture at 0.5 m (Table 1.1) and using an equation developed in the region (Appendix I.A).

Resource supply, capture- and use-efficiency

Pastor and Bridghan (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 nitrogen resources (Table 1.3). Transpiration was determined using an algorithm based on Penman-Monteith model calibrated with data from an experimental area of *E. grandis* x *urophylla* in the region where soil moisture in 2 m profile was evaluated weekly during 1.7 years (Appendix I.C, Figure A.1.1). Light extinction coefficient was estimated to be -0.36 for these *Eucalyptus* forests from direct measurements of APAR and LAI for similar plantations (data not shown), and LAI was interpolated from estimates at the beginning and end of the ANPP year, using the specific-foliage allometrics and SLA (Tables A.1.4 and A.1.5). Nitrogen supply was indexed by the total soil N (in kg ha^{-1}, from 0 to 0.60 m) because in a parallel study with 120 plots in the region, total soil N correlated significantly with aerobic and anaerobic N mineralization ($r^2 = 0.37$ and 0.54, $P < 0.001$, Figure A.1.2, Chapter III). The N content of biomass samples was analyzed by acid-base titration after Kjeldahl digestion (Raij et al. 1987). 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 *E. grandis* plantation with 7 years-old, Gonçalves et al. 2000). Throughfall N was estimated as 6% of the N in the litterfall (Attiwill 1980).

Table 1.3. Methods used to estimate resource supply and resource use for the year of the ANPP estimate and derived resource-capture-efficiency and resource-use-efficiency.

Resource	Supply	Method	Used	Method
Water	Rainfall	Interpolation from meteorological stations (Appendix I.B)	Transpiration	Penman-Monteith model with 3-PG algorithm and soil holding capacity (Appendix I.C)
Light	PAR	Interpolation from meteorological stations (Appendix I.B)	APAR	Beer's Law, $k = -0.36$ $APAR = PAR(1-e^{-k.LAI})$
Nitrogen	Soil N	Total soil N (Appendix I.A)	N uptake	N concentration in stem times stem growth plus estimated N on litterfall and througfall

Derived indices:

Resource-capture-efficiency = Resource-use / Supply

Resource-use-efficiency = ANPP / Resource-use

Statistical Analyses

One-way analyses of variance with productivity class as a fixed factor were performed for the biometric variables (Table 1.2), edaphic variables (Table A.1.2), climatic variables associated with MAI (Tables 1.2 and A.1.1), $R:A_S$ ratio and the fractions of total biomass (Table A.1.5), water resource indices (Table A.1.7), light resource indices (Table A.1.8), and N resources indices (Tables A.1.9). The general linear models procedure (GLM) of SAS (SAS Institute Inc., Cary, NC, USA 2001) was used due to the imbalanced design. Tukey's studentized range test (HSD) was employed for multiple comparisons with a significance level of 0.05.

We used logarithmic transformation of the compartment biomass and DBH to estimate the allometric parameters (*a*, *b*) for all sites, productivity classes and all trees together (Tables A.1.3 and 1.5). Analysis of covariance was used to test if the compartment-specific allometric equations differed among productivity classes and interacted with tree size. We used the GLM procedure with the logarithmically transformed biomass of the compartment as the dependent variable, the productivity class (PRO) as the categorical variable, the logarithmically transformed DBH as the covariate and the interaction between productivity class and DBH (lnWi = lnDBH PRO PRO*lnDBH, J.Fownes *personal communication*). If no interaction occurred, we tested if the intercepts differed among productivity classes by dropping the interaction factor, using multiple comparisons with a significance level of 0.05.

$R:A_T$ was analyzed as a mixed model with productivity class and tree size as the fixed factor, while site, site (productivity) and site (productivity x size) were the random factors. Productivity class, tree size and their interaction effects were tested against the appropriate mean squares. We used the mixed procedure of SAS, and multiple comparisons ($p = 0.05$). A non linear regression procedure (Gauss-Newton, SAS) was used to fit the relationship between the fraction of each compartment biomass with MAI and site index, and simple linear regressions were developed between $R:A_S$ and MAI and site index.

To investigate the influence of environmental factors, and stand and canopy attributes on MAI and ANPP, we used multiple regressions with a stepwise procedure in SAS. The minimal inclusion significance of a variable was set at $p = 0.10$. Due to the large number of independent variables (> 40) we utilized the following steps to avoid over parameterisation: (i) independent variables were classified into climatic, edaphic, stand and canopy attribute groups (Table A.1.10); (ii) MAI and ANPP were regressed against the independent variables of each group, separately; and (iii) groups were aggregated by taking the best 3 variables of each group during the isolated analysis and including their interactions. Residual analysis checked for normality and homocedasticity; the final selected independent variables were also based on model parsimony, regarding the facility to obtain the independent variables.

Simple linear regressions between ANPP and resource supply, use and use-efficiency were produced for water, light and nitrogen resources using SAS.

Results

Site attributes

The 14 sites captured a broad variability 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 (eight sites < 90 mm) (Table 1.1). Soil extractable P, K, Ca and Mg varied by 4-, 14-, 17- and 4-fold, respectively (Table A.1.2), and average rainfall ranged from 897 to 1411 mm yr^{-1} (half < 1000 mm yr^{-1}). Mean annual temperatures (25.5 °C), potential evapotranspiration (1470 mm yr^{-1}) and soil bulk density (1.45 to 1.60 Mg m^{-3}) presented low variability across sites (Tables 1.1 and A.1.1) (coefficients of variation < 4%).

ANPP correlated strongly with MAI ($r^2 = 0.76$, $P < 0.001$) and had the same magnitude: MAI varied from 9.4 to 32.6 Mg ha^{-1} yr^{-1}, while ANPP varied from 9.5 to 39.1 Mg ha^{-1} yr^{-1} (Table 1.2, Figure 1.2.a).

Soil properties, climate and biometrics by productivity classes

No soil property differed among low, medium and high productivity classes (Tables 1.1, A.1.2) 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}, Table A.1.5) occurred among classes. Biometric variables did not differ between low and medium productivity classes, except for site index (18.9 *versus* 21.5 m). On the other hand, all biometric variables were larger for the high productivity class comparatively with the other two classes. The high productivity class had greater DBH (23%), basal area (65%), LAI (48%, 4.3 *versus* 2.9), site index (32%, 24.9 *versus* 18.9 m), MAI (100%, 24 *versus* 12 Mg ha^{-1} yr^{-1}) and ANPP (152%, 28 *versus* 11 Mg ha^{-1} yr^{-1}) than the lower class (Table 1.2). Average rainfall systematically increased from low to high productivity classes (57%, 897 *versus* 1411 mm yr^{-1}, Table 1.2) as well as the rainfall associated with the ANPP year (44%, 886 *versus* 1276 mm yr^{-1}, Table 1.7). Average vapor pressure deficit (VPD) and VPD for the ANPP year decreased 7% (1.45 to 1.35 kPa) and 12% (1.46 to 1.28 kPa) from low to high productivity classes (Tables A.1.1 and A.1.7). At harvesting time, across all classes, forest biomass represented 64% of the C stock in the forest plus soil (0.6 m) system (Figure 1.2.b).

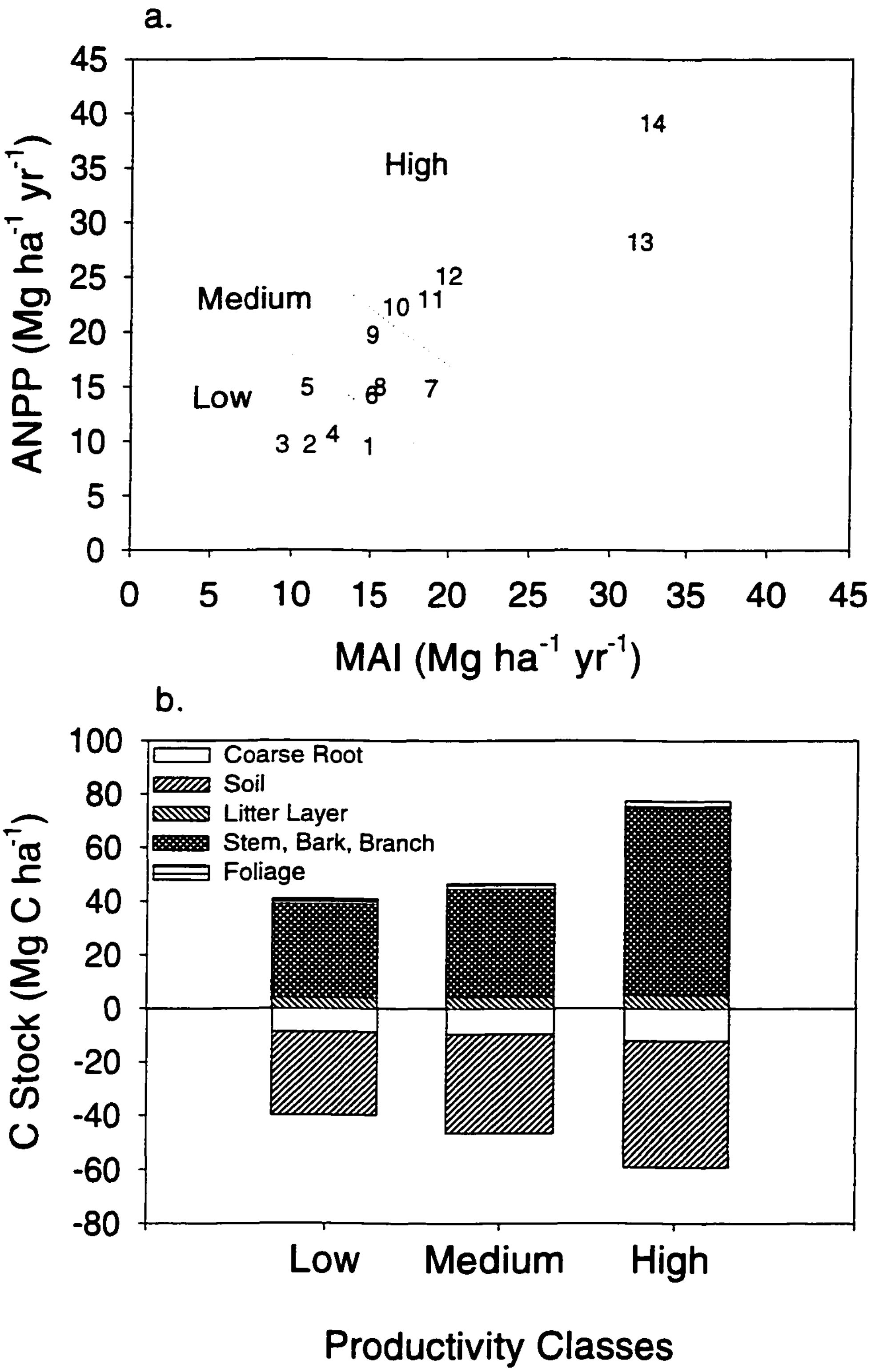


Figure 1.2. Aboveground net primary production (ANPP) at the end of the rotation (6 to 8 years), and mean annual increment (MAI) for the 14 stands and their grouping into low, medium and high productivity classes (a). Forest and soil (0 to 0.6 m) carbon (C) stocks by productivity classes at the end of their 6-year rotations (b).

Allometrics and biomass distribution

Tree $R{:}A_T$ ratio differed by productivity class ($P = 0.02$) but not by tree size ($P = 0.51$), and no interaction between productivity class and tree size occurred ($P = 0.82$). The $R{:}A_T$ ratio for the high productivity class was smaller (0.19) than those of the medium and low classes (0.26) (Table A.1.3, Figure 1.3.b). The allometric equations showed no significant interactions between tree size and productivity class, meaning that the slope coefficients were similar among productivity classes (Table 1.4). In contrast, all intercept coefficients differed between high and low productivity classes for all compartments (Table 1.4). These differences in allometrics resulted in distinct biomass distribution estimates among productivity classes for the same tree size. For instance, a higher stem and a lower coarse root biomass for a given DBH are estimated moving from low to high productivity classes (Figure 1.3.a).

Stand $R{:}A_S$ ratio was lower for the high productivity class (0.18) than medium (0.24) and lower (0.26) classes (Table A.1.5). $R{:}A_S$ related negatively to MAI ($r^2 = 0.36$, $P = 0.01$, Figure 1.4.a) and site index ($r^2 = 0.55$, $P < 0.01$, Figure A.1.4). When compartments were expressed as a fraction of total biomass, only foliage was constant across productivity classes (3%). The high productivity class had smaller branch (4%), bark (7%) and coarse root fractions (15%), and greater stem fraction (69%) compared to the medium (6, 8, 19 and 64%) and lower classes (8, 9, 20% and 54%) (Table A.1.5). These compartment fractions were adequately modeled across all sites by non-linear regressions with MAI or site index as the independent variable (Figure 1.4.b and Table A.1.6).

Table 1.4. Coefficients of the allometric equations by productivity classes and all trees using the general relationship: $W_i=a_i\ DBH^{b_i}$. All regressions were significant at $P=0.01$. There were no differences between slopes coefficients (*b*) within compartments, and allometric coefficients (*a*) followed by different superscript differ at $P=0.05$.

Compartment		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

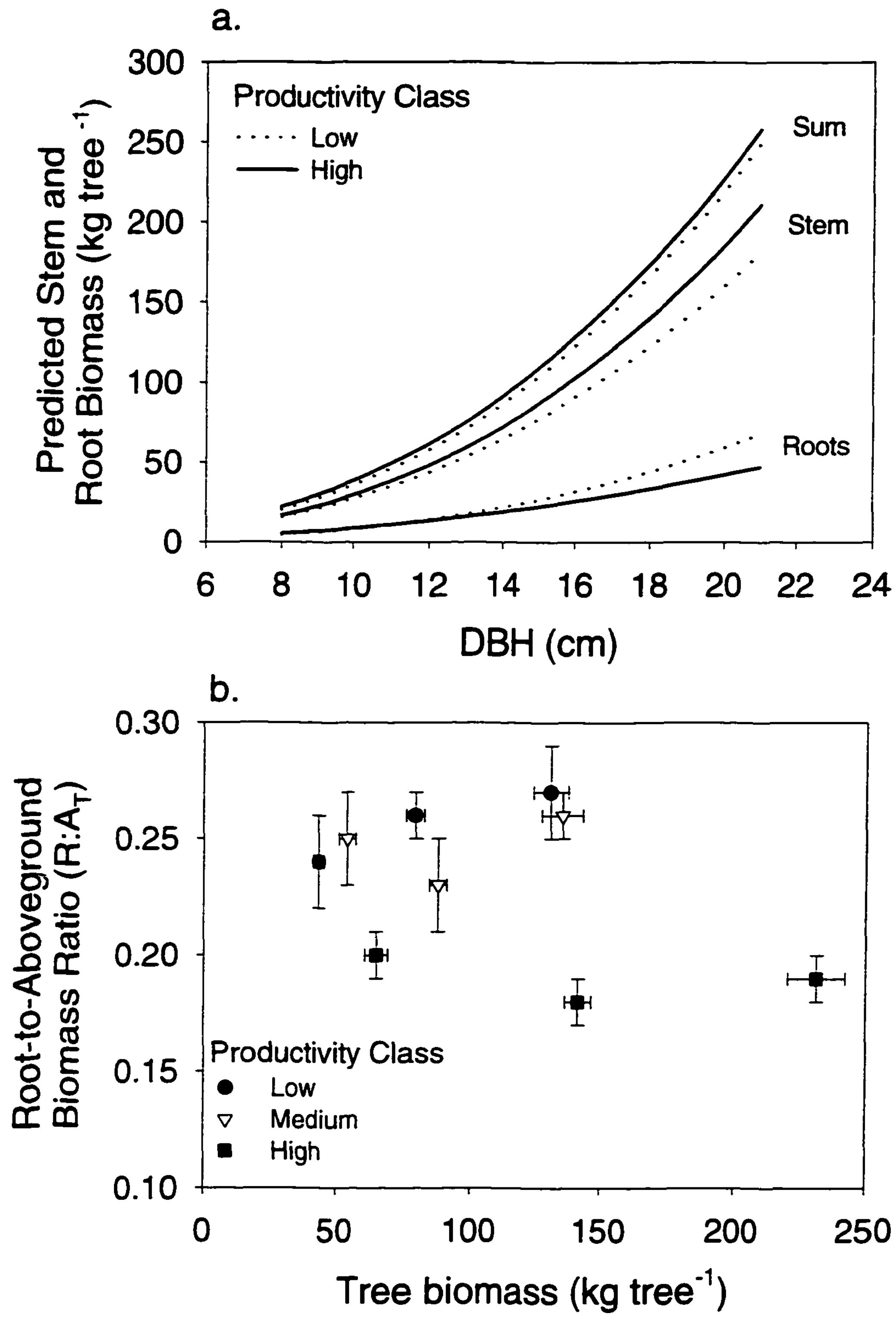


Figure 1.3. Predicted tree stem, coarse root biomass, and their sum, using the specific allometrics obtained for low and high productivy classes. Equations are presented in Table 1.4 (a). Root to aboveground ratio at the tree level by productivity class and the three tree size categories expressed by tree biomass (b).

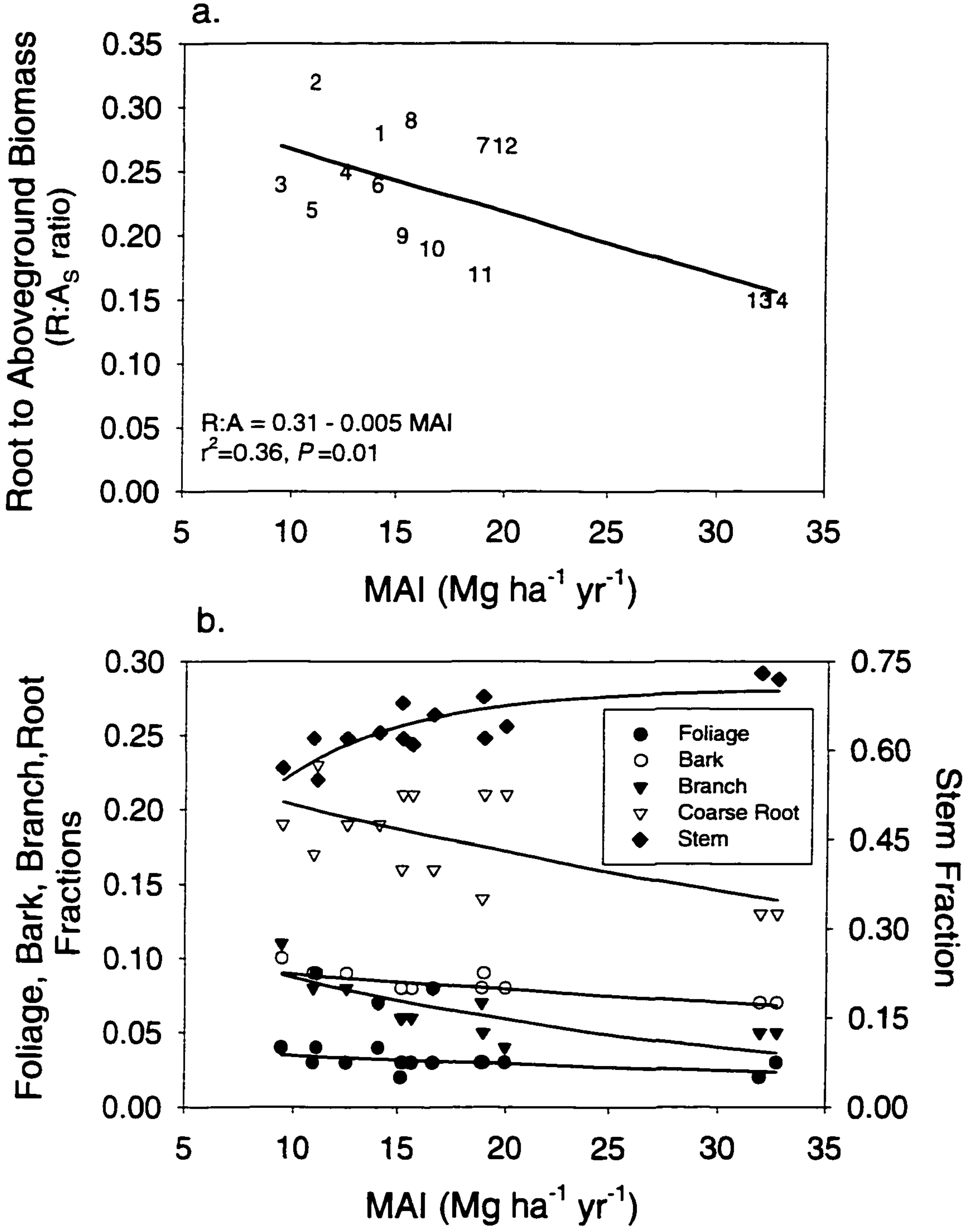


Figure 1.4. Relationship between coarse root to aboveground woody biomass ratio and mean annual increment at the stand level (a). Relationships between the fractions of foliage, bark, branch, stem and coarse root biomass and mean annual increment at the stand level (b). Equations are presented in Table A.1.6.

MAI, and environmental and stand factors

Stepwise regression identified the combination of soil C and N as the best edaphic correlates of MAI ($r^2 = 0.55$, Table 1.5). Rainfall alone explained 80% of the variation in MAI (Figure 1.5). Among stand attributes, site index and LAI together explained 92% of the MAI variation (Table 1.5). For all groups of variables, site index, LAI and outflow accounted for 95% of MAI variability. For the parsimony model we retained rainfall and site index as the independent variables ($r^2 = 0.92$, Table 1.5) due to the high correlation between outflow and rainfall ($r = 0.98$) and the transient dynamics of LAI.

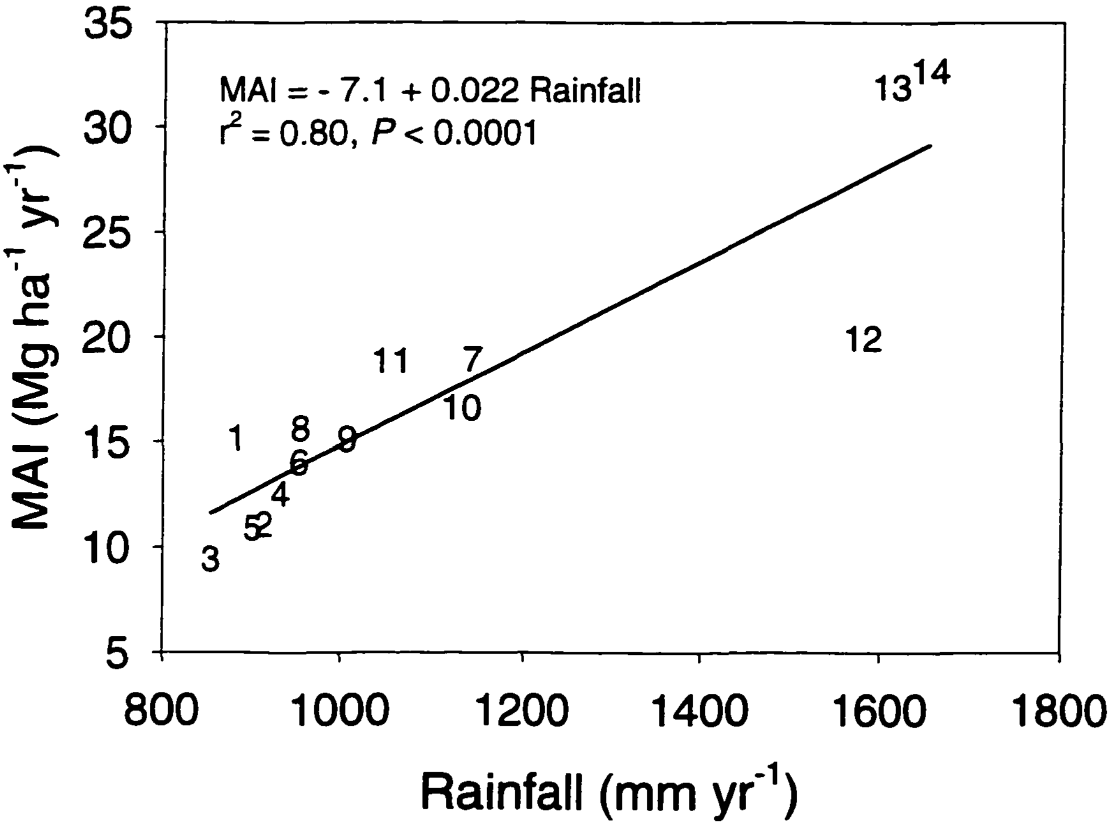


Figure 1.5. Relationship between mean annual increment (MAI) and average rainfall during the complete rotation for the 14 stands.

Table 1.5. Select variables using stepwise regression procedures having MAI (Mg ha^{-1} yr^{-1}), as the dependent variable and the independent variables organized by edaphic, climate and stand type categories.

Category	Variables	Regression*	R^2
Edaphic	Soil C, Soil N	8.9 + 0.00063 C – 0.0057 N	0.55 ($P = 0.013$)
Climate	Rainfall	- 7.1 + 0.022 Rainfall	0.81 ($P < 0.0001$)
Edaphic + Climate	Rainfall	- 7.1 + 0.022 Rainfall	0.81 ($P < 0.0001$)
Stand	SI, LAI	- 24.7 + 1.46 SI + 3.0 LAI	0.92 ($P < 0.0001$)
All	SI,LAI,Outflow	-18.7 + 1.24 SI + 2.0 LAI + 0.010 Out	0.95 ($P < 0.0001$)
Parsimony	SI, Rainfall	-21.2 + 1.17 SI + 0.012 Rainfall	0.92 ($P < 0.0001$)

* Units: C (kg ha^{-1}), N (kg ha^{-1}), Rainfall (mm yr^{-1}), SI (m), LAI (m^2 m^{-2},) Outflow (mm yr^{-1}).

Correlation between Outflow and Rainfall (r = 0.98)

ANPP, and environmental and stand factors

Total soil C and N together were the best edaphic predictors of ANPP (r^2= 0.49, Table 1.6). Rainfall alone explained 39% of ANPP variation, and the textural ratio (clay 0.40-0.60 / clay 0.0-0.2 m) increased model predictability (r^2= 0.51, Table 1.6). Among canopy attributes, LAI alone was able to explain 66% of the ANPP variation, and ANPP was not correlated with any soil or leaf nutrient concentration. For the stand attributes, SI explained 65% of ANPP variability. For all attributes considered, SI and rainfall could account for 74% of its variation (Table 1.6).

Table 1.6. Select variables using stepwise regression procedures having ANPP (Mg ha^{-1} yr^{-1}) as the dependent variable and the independent variables organized by edaphic, climate, canopy and stand type categories.

Category	Variables	Regression*	R^2
Edaphic	Soil C, Soil N	11.0 + 0.00083 C – 0.0088 N	0.49 ($P = 0.009$)
Climate	Rainfall	- 8.4 + 0.025 Rainfall	0.39 ($P = 0.010$)
Edaphic + Climate	Rainfall, BA Clay	- 28.3 + 0.029 Rainfall + 11.1 BAClay	0.51 ($P = 0.007$)
Canopy	LAI	- 7.9 + 7.6 LAI	0.66 ($P = 0.0002$)
Stand	SI	- 27.9 + 2.12 SI	0.65 ($P < 0.0001$)
All, Parsimony	SI, Rainfall	- 31.8 + 1.67 SI + 0.013 Rainfall	0.74 ($P < 0.0001$)

*Units: C (kg ha^{-1}), N (kg ha^{-1}), Rainfall (mm yr^{-1}), BA Clay (none), LAI (m^2 m^{-2}), MAI (Mg ha^{-1} yr^{-1})

Water resource

Among all sites, water supply varied by 2-fold (731 to 1568 mm yr^{-1}), water-capture-efficiency by 1.7-fold (0.48 to 0.86), water-use by 1.7-fold (592 to 999 mm yr^{-1}), and water-use-efficiency by 3.4-fold (1.34 to 4.58 kg m^{-3}) (Figure 1.6). ANPP was not correlated with water-capture-efficiency ($r^2 = 0.14$, $P = 0.19$), but was with water supply ($r^2 = 0.44$, $P = 0.01$), transpiration ($r^2 = 0.39$, $P = 0.02$) and water-use-efficiency ($r^2 = 0.94$, $P < 0.001$) (Figure 1.7). Water-capture-efficiency tended to decrease with water supply ($r = -0.76$, $P = 0.001$). Water-use-efficiency showed a trend to increase with water use ($r = 0.42$, $P = 0.18$) (Figure 1.7) and increased with water supply ($r = 0.60$, $P = 0.02$) (Figure 1.10).

Water supply increased 19% from low to medium productivity classes and 21% from medium to high classes, while water use increased 4% and 21%, respectively. Water-capture-efficiency was similar among classes (0.72, Table 1.7) and water-use-efficiency increased 40% and 43% from low to medium and medium to high classes. The 46% increase in ANPP from low to medium class (11 to 16 Mg ha^{-1} yr^{-1}) was 32% associated with the increase in water supply and 68% with the increase in water-use-efficiency, while the 72% ANPP gain from medium to high classes (16 to 28 Mg ha^{-1} yr^{-1}) was 33% associated with better supply and 67% with larger use-efficiency (Figure 1.11).

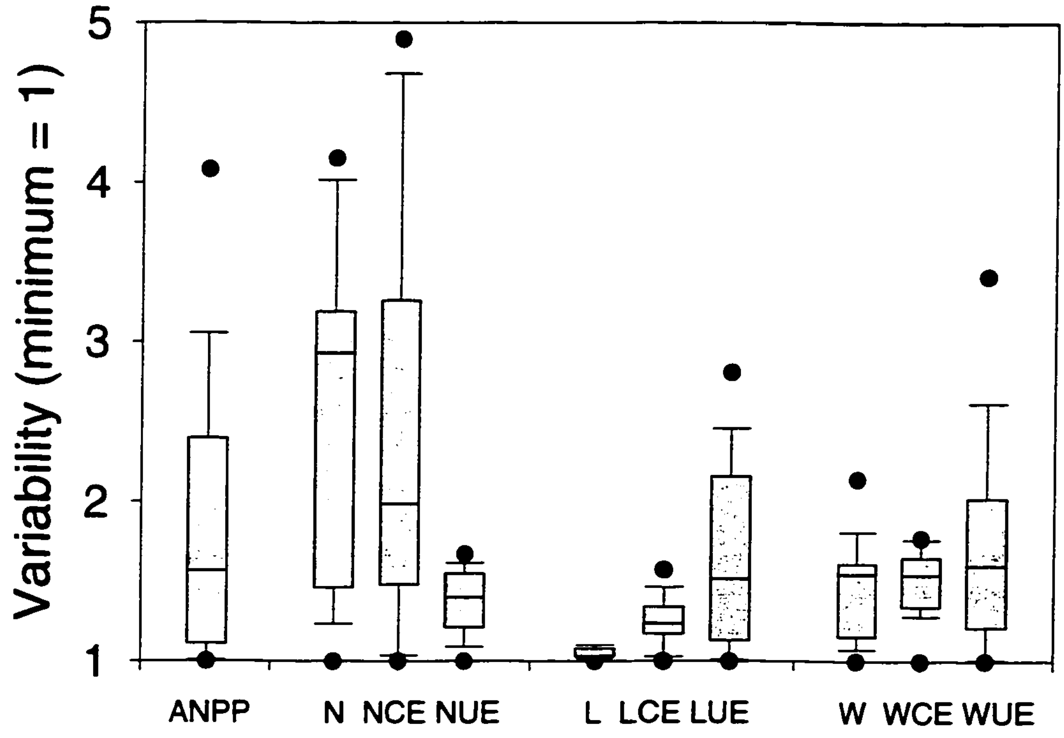


Figure 1.6. Variability of ANPP, nitrogen "supply" (N), nitrogen capture efficiency (NCE), nitrogen use efficiency (NUE), total PAR (L), light capture efficiency (LCE), light use efficiency (LUE), rainfall (W), water capture efficiency (WCE) and water use efficiency (WUE) among the 14 stands. The minimum values were: ANPP = 9.5 Mg ha^{-1} yr^{-1}, N = 1106 kg ha^{-1}, NCE = 0.009, NUE = 248 kg kg^{-1}, L = 30.3 TJ ha^{-1} yr^{-1}, LCE = 0.56, LUE = 0.47 g MJ^{-1}, W = 731 mm yr^{-1}, WCE = 0.48, WUE = 1.34 kg m^{-3}.

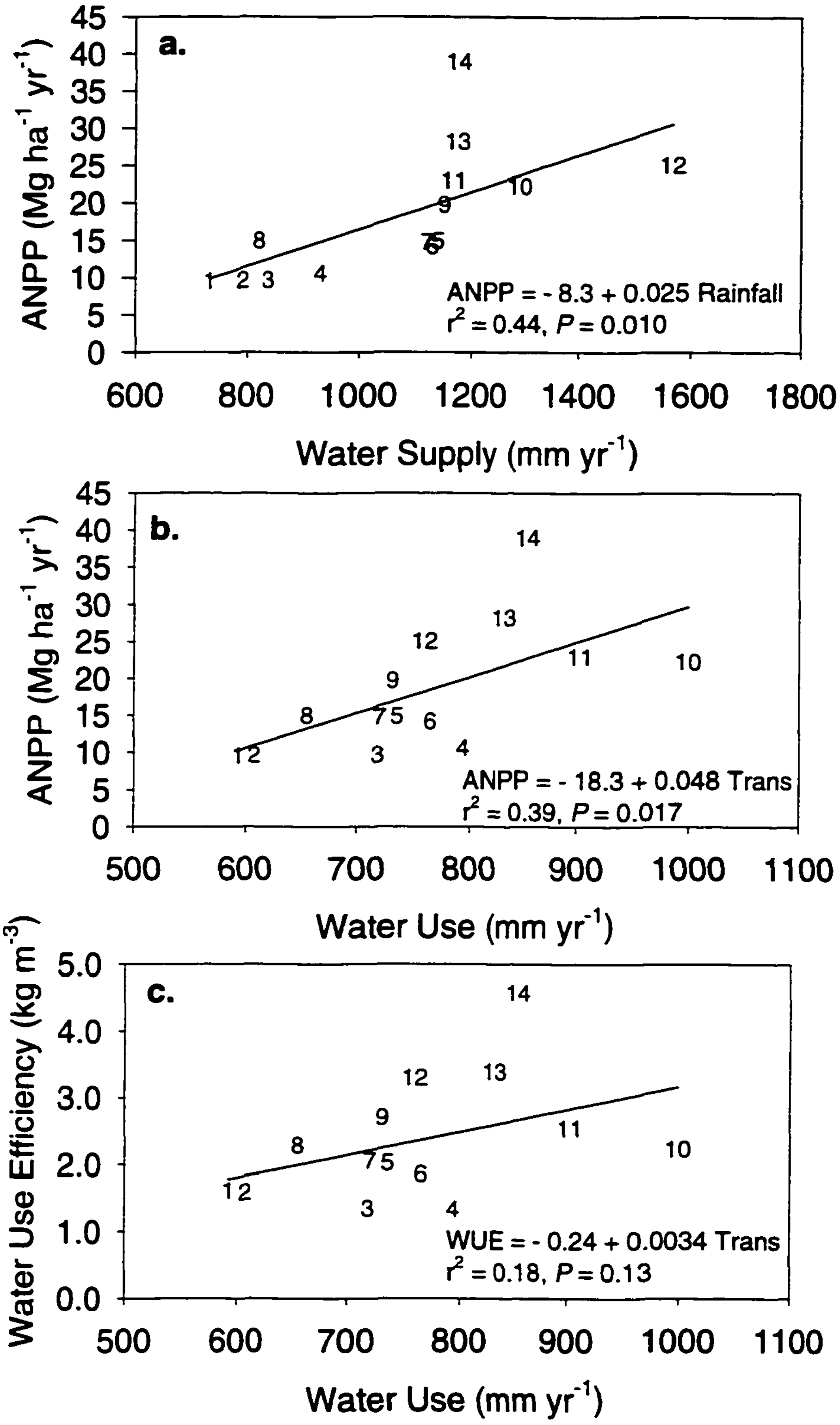


Figure 1.7. Relationships between ANPP and water supply (a), and water use (b), and between water-use-efficiency and water use (c) for the 14 stands.

Light resource

Light supply was similar across sites (31.4 TJ ha^{-1} yr^{-1}), but light-capture-efficiency varied by 1.5-fold (0.56 to 0.87), light-use by 1.5-fold (17.3 to 26.6 TJ ha^{-1} yr^{-1}), and light-use-efficiency by 3-fold (0.47 to 1.47 g MJ^{-1}) (Figure 1.6). ANPP did not correlate with PAR ($r^2 = 0.20$, $P = 0.11$), but related well with APAR ($r^2 = 0.49$, $P < 0.001$), light-capture-efficiency ($r^2 = 0.58$, $P < 0.001$) and light-use-efficiency ($r^2 = 0.92$, $P < 0.001$) (Figure 1.8). Light-capture-efficiency increased with water supply ($r = 0.54$, $P = 0.04$). Light-use-efficiency increased with light use ($r = 0.27$, $P = 0.05$) (Figure 1.7) and water supply ($r = 0.67$, $P = 0.008$) (Figure 1.10).

Productivity classes had equivalent light supplies, but the high class had 18% greater light use and 20% larger light-capture-efficiency than the other two classes. Light-use-efficiency increased by 46% and 44% from low to medium and medium to high classes (Table 1.7). The increase in ANPP from low to medium productivity classes depended 100% on the greater light-use-efficiency, while the increase in ANPP from medium to high classes, was 31% related with larger capture- and 69% with larger light-use-efficiency (Figure 1.11).

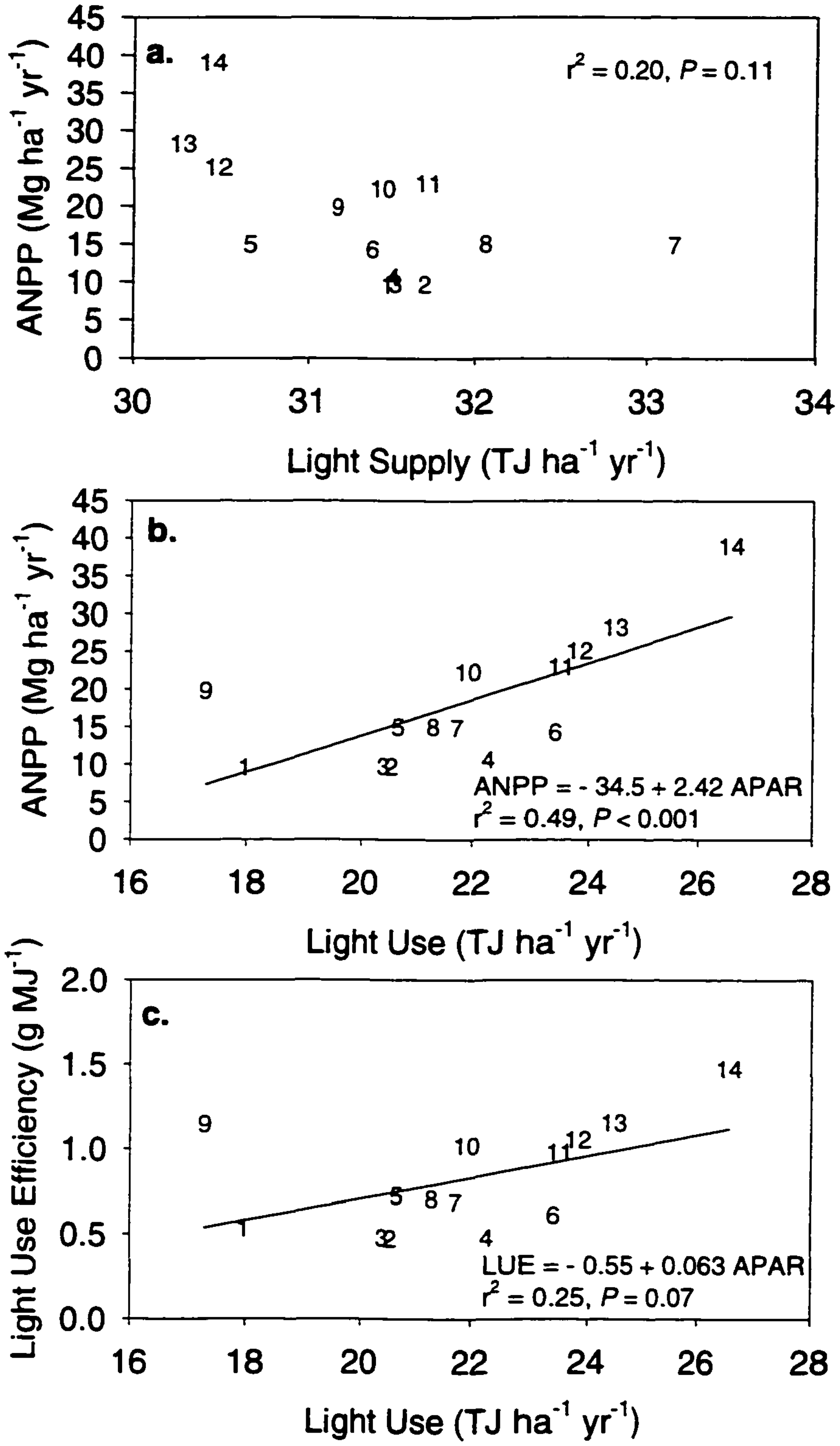


Figure 1.8. Relationships between ANPP and light supply (a), and light use (b), and between light-use-efficiency and light use (c) for the 14 stands.

Nitrogen resource

N supply varied by 4-fold (1106 to 4589 kg N ha^{-1}), N-capture-efficiency by 5-fold (0.009 to 0.045), nitrogen use by 3.5-fold (27.7 to 98.1 kg ha^{-1} yr^{-1}), and N-use-efficiency by 1.6-fold (248 to 415 kg kg^{-1}) (Figure 1.6). Across all sites, ANPP did not correlate with supply ($r^2 = 0.01$, $P = 0.71$) but did correlate with N uptake ($r^2 = 0.95$, $P < 0.001$), marginally with N-capture-efficiency ($r^2 = 0.25$, $P = 0.07$), and with N-use-efficiency ($r^2 = 0.53$, $P < 0.01$) (Figure 1.9). N-capture-efficiency inceased with water supply ($r = 0.57$, $P = 0.03$). N-use-efficiency increased with N use ($r = 0.56$, $P = 0.03$) (Figure 1.7) and water supply ($r = 0.58$, $P = 0.02$) (Figure 1.10).

N supply did not differ among productivity classes (Table 1.7), but N use increased 21% and 58% from low to medium and medium to high classes. N-capture-efficiency increased 53% and 26% and N-use-efficiency 19% and 10% for the same sequence. For nitrogen resource, the increase in ANPP from low to medium and medium to high productivity classes were associated primarily (66%) with an increase in nutrient-capture-efficiency and secondarily (24%) with a greater N-use-efficiency (Figure 1.11).

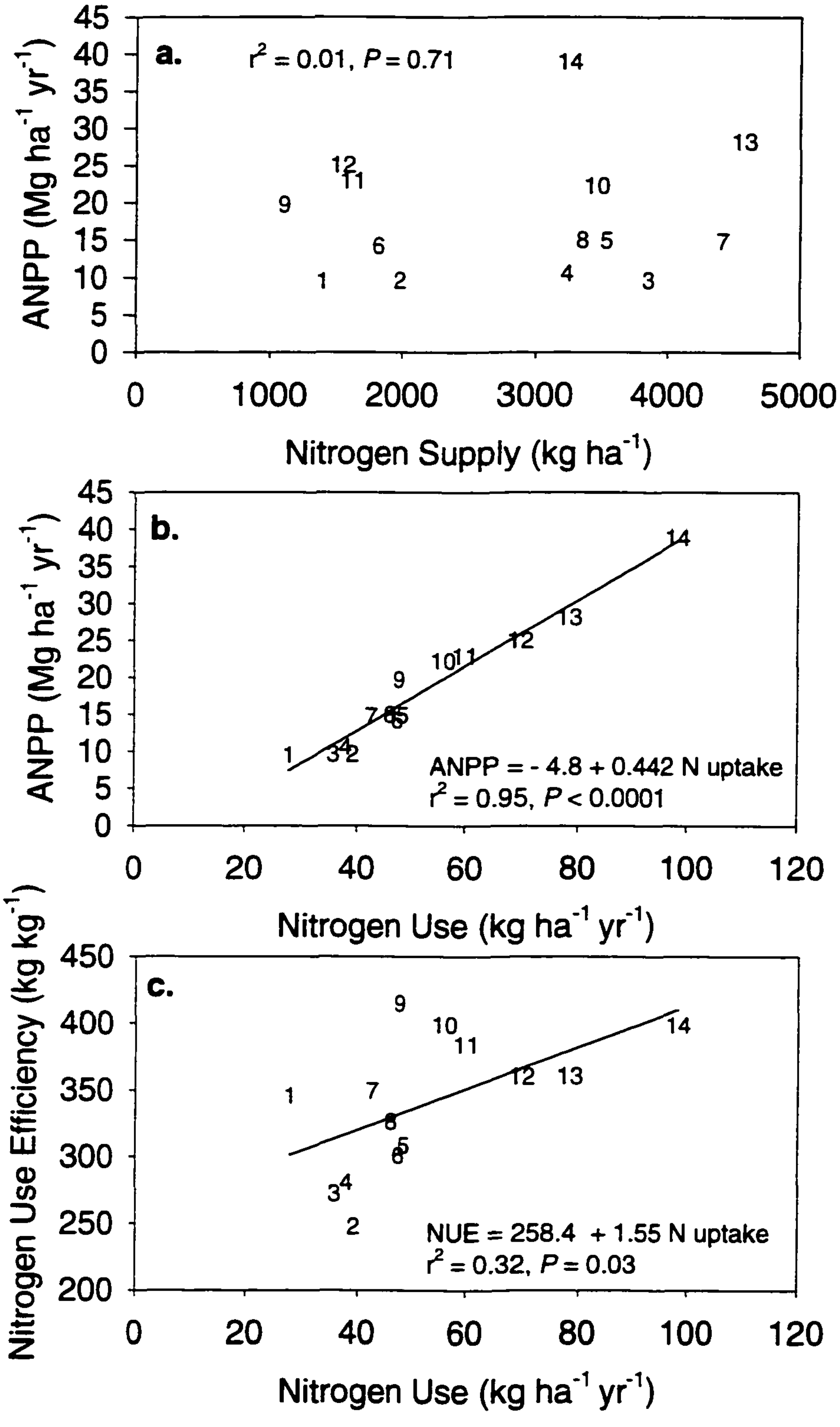


Figure 1.9. Relationships between ANPP and nitrogen supply (a), and nitrogen use (b), and between nitrogen-use-efficiency and nitrogen use (c) for the 14 stands.

Table 1.7. Resource supply, use, capture-efficiency and use-efficiency for water, light and nitrogen by productivity classes. Values followed by different letters differ at $P = 0.05$.

Resource	Supply	Use	Capture-Efficiency	Use-Efficiency
Water Class	**Rainfall ($mm\ yr^{-1}$)**	**Transpiration ($mm\ yr^{-1}$)**	**WCE**	**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 Class	**PAR ($TJ\ ha^{-1}\ yr^{-1}$)**	**APAR ($TJ\ ha^{-1}\ yr^{-1}$)**	**LCE**	**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 Class	**Soil N ($kg\ ha^{-1}$)**	**N Uptake ($kg\ ha^{-1}\ yr^{-1}$)**	**NCE**	**NUE ($kg\ kg^{-1}$)**
Low	2797	37.8 b	0.015 b	291 b
Medium	2674	45.9 b	0.023 ab	348 a
High	2887	72.4 a	0.029 a	381 a

ANPP ($Mg\ ha^{-1}\ yr^{-1}$) = Rainfall ($mm\ yr^{-1}$) . WCE . WUE ($kg\ m^{-3}$) / 100

ANPP ($Mg\ ha^{-1}\ yr^{-1}$) = PAR ($TJ\ ha^{-1}\ yr^{-1}$) . LCE . LUE ($g\ MJ^{-1}$)

ANPP ($Mg\ ha^{-1}\ yr^{-1}$) = N Soil ($kg\ ha^{-1}\ yr^{-1}$) . NCE . NUE ($kg\ kg^{-1}$) / 1000

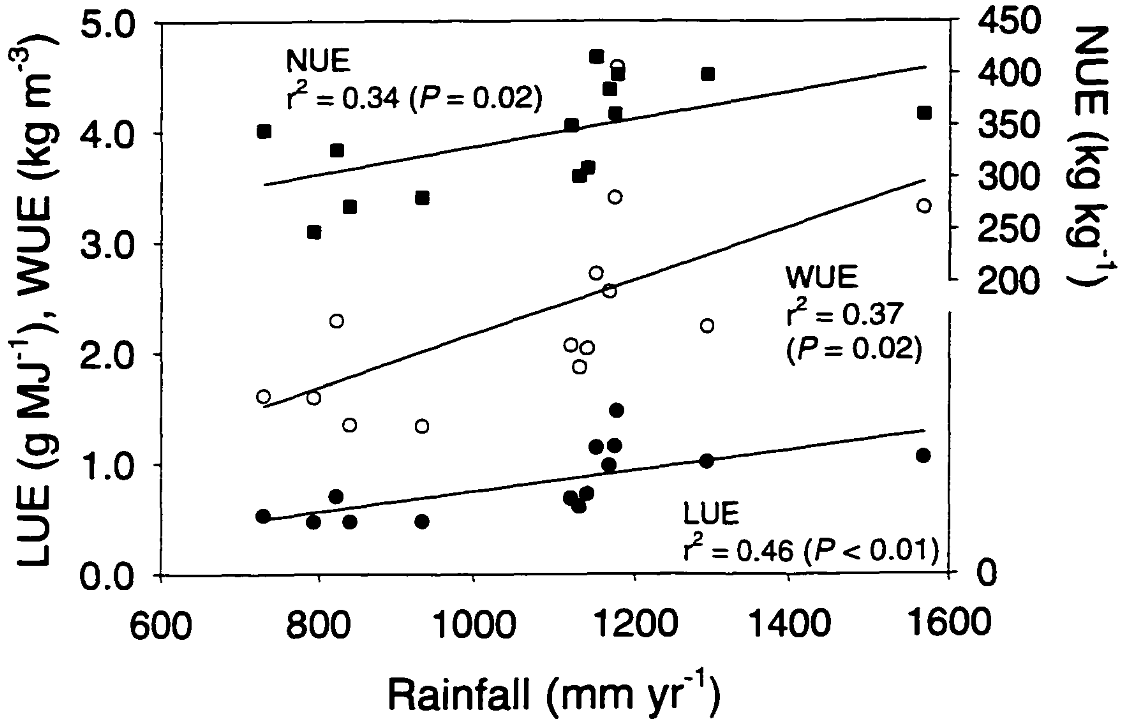


Figure 1.10. Relationships between ligh use efficiency (LUE), water use efficiency (WUE) and nitrogen use efficiency (NUE) with rainfall.

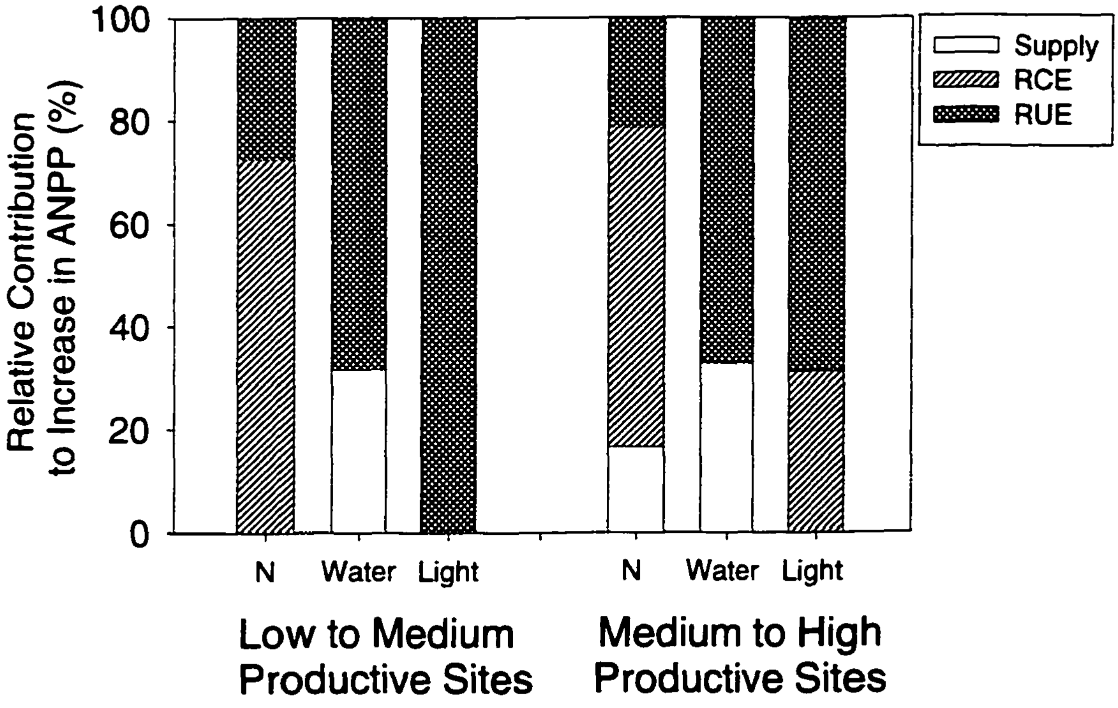


Figure 1.11. Relative contribution of resource supply, capture-efficiency (RCE) and use-efficiency (RUE) on the change of ANPP from low (10.9 Mg ha^{-1} yr^{-1}) to medium (16.0 Mg ha^{-1} yr^{-1}) productivity sites and from medium to high (27.5 Mg ha^{-1} yr^{-1}) productivity sites. Resources are nitrogen (N), water and light.

Discussion

MAI, ANPP and related environmental and stand factors

If managed in a 6 year-rotation, aboveground biomass at harvesting would have spanned from 50 to 200 Mg ha^{-1} among sites. Considering that silvicultural practices (site preparation, spacing, fertilization and forest protection) and survival rates were similar, this 4-fold variation in production can be credited to differences among sites' environmental factors, affecting *E. grandis* x *urophylla* behavior. The high correlation between MAI and ANPP ($r^2 = 0.76$, Figure 1.2.a) suggests that the main external controls throughout the rotation were still the prevalent ones during the year of ANPP estimates.

Rainfall was the environmental variable most strongly associated with both MAI and ANPP (Figures 1.3 and 1.7.a), indicating that water supply is the primary resource controlling productivity in this tropical region. For each 100 mm yr^{-1} increment in rainfall, MAI or ANPP increased by approximately 2.3 Mg ha^{-1} yr^{-1} (Figures 1.5 and 1.7.a). The crucial role played by rainfall in ecosystems productivity has long been recognized (Lieth 1975, Golfari et al. 1977) and has been shown to be determinant of the success of plantations in the tropics (Morais et al. 1990, Snowdon and Waring 1991, Beadle 1997, Gonçalves et al. 1997). For instance, Santana et al. (2000) reported a linear increase in *Eucalyptus* productivity (from 8 to 32 Mg ha^{-1} yr^{-1}) for an increase in water availability measured as the difference between rainfall and potential evapotranspiration (from –200 to 600 mm yr^{-1}).

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). The rainfall-productivity pattern of our study can be also identified geographically on Figure 1.1. Lower site numbers (meaning lower productivity) tend to be located inland as rainfall systematically decreases from east to west, and a "gap" in the MAI – rainfall graph (Figure 1.5), between 1200 and 1500 mm yr^{-1} coincides with the absence of *Eucalyptus* plantations between these isohyets (Figure 1.1). The closer MAI of low and medium productivity classes compared with medium to high classes can be partially explained by their smaller differences in rainfall ($\cong$ 100 mm yr^{-1}), while the differences reached 400 mm yr^{-1} between medium and high productivity classes (Table 1.2).

The fact that total soil C was the only soil attribute that related significantly and positively with both ANPP and MAI may relate to historical land use and water supply (Figure 1.2.b). 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. Besides that, the soil C variable was not significant if rainfall was in the model (Tables 1.5 and 1.6).

Interestingly, despite the high variability in soil fertility status (Table A.1.2), no soil fertility variable related with productivity. This absence of a fertility effect may result from the slash-burning site preparation, initial P fertilization, and adequate weed control allowing a rapid canopy development (in the region, LAI reaches 2.0 to 4.5 at 1.5 year-old). Once the canopies were established, *Eucalyptus* might be highly efficient in cycling nutrients throughout biochemical and biogeochemical cycles decreasing its dependency on soil fertility (Miller 1995, Binkley and Ryan 1998, Misra et al. 1998, Gonçalves et al. 2000).

The inclusion of site index (SI) in addition to rainfall improved the MAI (r^2 = 0.81 to 0.92) and ANPP models (r^2 = 0.39 to 0.69), probably by representing some soil attribute effect (McLeod and Running 1988). For example, among sites 12, 13 and 14 (rainfall > 1500 mm yr^{-1}), site 12 was the least productive, being very sandy (3% clay), having low fertility (lowest P, Ca and Mg values), and presenting a low site index (21 m) compared with the other two (24 and 29 m). This decrease in SI and productivity despite the high rainfall rates was probably associated with low fertility, or with lower water holding capacity (60 mm) and higher water stress during the dry season with only 33% of the yearly rainfall. The inclusion of water supply variables in empirical SI models can provide substantial improvements in their predictions (Tables 1.4 and 1.6), while natural soil fertility variation seems to be less critical for fertilized plantations (Soares and Leite 2000, Sampson and Allen 1999).

For ANPP estimates, inclusion of the textural ratio (clay 0.40-0.60 m / clay 0.0-0.2 m) together with rainfall improved the model (r^2 raised from 0.39 to 0.51), probably reflecting a better water supply on soil with B argilic horizons. Increase in subsoil clay content was related with larger water supply and growth for *Eucalyptus* plantations in Venezuela (Henri 2001), and Australia (Laffan 1994), and *Pinus* in southeastern United States (Sampson and Allen 1999).

Among canopy attributes, LAI correlated strongly with ANPP (Figure A.1.3). On average, for a 1 unit increase in LAI, ANPP was increased by 7.6 Mg ha^{-1} yr^{-1} due to greater absorbed light (LAI and APAR, r = 0.95). This 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 nutrient content in the leaf despite the 2- to 4-fold variation among stands, indicating that LAI may be a better predictor of growth than nutrient foliar concentrations, especially given inexpensive techniques for rapid LAI assessments (Pierce and Running 1988, Cutini et al. 1998, Balster and Marshall 2000).

Allometrics and accumulated biomass

The derived allometrics based on DBH ($W=a.D^b$) captured the different patterns of biomass accumulation by productivity classes with constant “b” slopes and distinct allometric coefficients “a” (Table 1.4). This is in line with Enquist and Niklas's (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 belowground biomass accumulation was larger than for the other two classes (29 *versus* 22 Mg ha^{-1} at age 6). 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} yr^{-1}, $R:A_S = 0.15$) compared with a drier and lower productive site (MAI = 6 Mg ha^{-1} yr^{-1}, $R:A_S = 0.35$), while both sites had the same magnitude of coarse root biomass (11.5 Mg ha^{-1} at age 5). Santana et al. (2000) also reported for *Eucalyptus* an increase in aboveground partitioning (from 78 to 89%) with increasing productivity, and Giardina et al. (2002) obtained a low R:A_T ratio (0.16) for *E. saligna* trees in a high productive site (MAI = 20 Mg ha^{-1} yr^{-1}). Site 12 presented a high R:A_S ratio compared to all other high productivity sites (Table A.1.5), which may relate with its coarse texture and potential water stress (Fabiao et al. 1995). Keyes and Grier (1981) and Brown and Lugo (1982) obtained higher R:A_S ratios in sites with lower productivity and Reed and Tome (1998) detected a change in *Eucalyptus* allometrics by the effect of irrigation. Nevertheless, this trend was not always observed (Cairns et al 1997), and some species seems to be less sensitive to environmental factors and being under strong ontogenetic control (King et al. 1999, Retzlaff et al. 2001). Our study also captured a strong negative correlation between R:A_S ratio and site index ($r^2 = 0.55$, $P < 0.01$, Figure A.1.4), implying that SI can be used for belowground biomass estimates (negative related). The observed partitioning of total biomass into the different forest compartments as a function of site productivity (MAI) was similar to the patterns presented by Battaglia and Sands (1997) for *Eucalyptus* (based on site index) and used in modeling (in our study, SI and MAI were correlated, r = 0.91). Similarly, the obtained fraction biomass equations based on MAI and SI can be used for better estimates of C pools (Cairns et al. 1997) on tropical *Eucalyptus* plantations (Table A.1.6).

Supply, use and efficiency of use of resources

Across our studied geographic gradient of initially fertilized stands, water appeared to be the only resource limiting ANPP (Figures 1.7.a, 1.8.a and 1.9.a). The similar and moderate to adequate level of N concentration on leaves for all productivity classes (average of 16 g kg^{-1}) was consistent with the absence of correlation between N supply and production. In the same region, Louzada and Pacheco (1992) found no *Eucalyptus* fertilization response to N. Light supply was similar among plots with a slight decrease on cloudier (wetter) and more productive areas (Figure 1.8.a).

The increase in water use from the low to the high productivity classes was almost a stable fraction of the larger water supply (72%, Table 1.7, Figure 1.11), but with a trend to decrease with the increase in rainfall. In contrast, the larger use of light and N were associated with the increase in their capture-efficiency (Table 1.7, Figure 1.11) and not supply, and these increments were probably facilitated by the increase in water supply. The higher light-capture-efficiency of the high productivity class (wetter sites), capturing 78% of the incoming PAR compared with 65% for the other two classes (Table 1.7), was related with a larger LAI (4.3 *versus* 2.9). The trend in 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 (Waring 1983, Hatton et al. 1998). In agreement with this hypothesis, LAI estimates were positively related with rainfall ($r = 0.86$, $P < 0.001$) with an increase of 0.3 LAI unit per 100 mm yr^{-1} in rainfall.

The systematic increment in N-capture-efficiency from low to high productivity classes (Table 1.7) may be due to higher N mineralization rates associated with the wetter sites (Gonçalves and Carlyle 1994, Fabiao et al. 1995, Serrano 1997), or higher N mass transport influxes driven by higher transpiration rates of the more productive stands (Cole et al. 1990, Larcher 1995). Although we did not assess fine root production, the increase in fine root was unlikely to contribute to this increase in capture-efficiency because larger water supplies tend to decrease C allocation to roots (see Chapter II) and decrease fine root density (Olbrich et al. 1992, Fabiao et al. 1995).

The observed increase in ANPP from low to high productivity classes could not be explained solely by the increase in resource use, indicating a concomitant increase in the resource-use-efficiencies (Table 1.7, Figure 1.11). For a given amount of resource used, the efficiency of its use can be enlarged 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 aboveground (Cannell 1989a, Landsberg and Gower 1997), for efficiency measured in an ANPP basis. Both processes seem to be operating in our study, once again mediated by the water supply (Figure 1.10). The increase in resource-use-efficiency associated with the increase in resource-use for water, light and nitrogen, clearly indicates that the more productive sites, that use more resources, also presented a higher efficiency in using them (Figures 1.7.c, 1.8.c and 1.9.c).

Along the transect, rainfall and VPD were strongly inversely correlated (Figure A.1.6), with lower VPD values associated with the more productive and wetter sites (Figure A.1.5), and an inverse water-use-efficiency to VPD relation was observed (Figure 1.12). Lindroth and Cienciala (1996) obtained this inverse relation at the stand level. This relationship is also used in some process-based models to estimate water-use-efficiency or photosynthesis based on the actual evapotranspiration (Aber and Federer 1992, Battaglia and Sands 1997).

The increase in *Eucalyptus* stomatal conductance by the effect of both decreasing soil water deficit and VPD is well documented (Pereira 1987, White et al. 1996, Mielke et al. 1999, Barnard 2000), and the larger CO_2 uptake rates for the more productive sites due to such conditions led to increases in the light- and nitrogen use-efficiencies (Myers et al. 1996, Sands et al. 1999) (Figure 1.10). Indeed, this control of soil moisture and VPD over 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).

The relative shift in C allocation from below- to aboveground as water supply increased was also likely to have contributed to the higher resource-use-efficiencies on the more productive sites. Although the $R:A_S$ ratio can be considered just a partial evidence of this partitioning process (Figures 1.3, 1.4 and A.1.4), the decrease in C allocation belowground by the effect of water supply for a *Eucalyptus* clone is fully characterized in Chapter II. Linder and Axelsson (1982), Snowdon and Benson (1992) and Albaugh et al. (1998) had also reported a larger wood production per unit of LAI under higher water supply, crediting these gains to higher quantum efficiency or allocation shift.

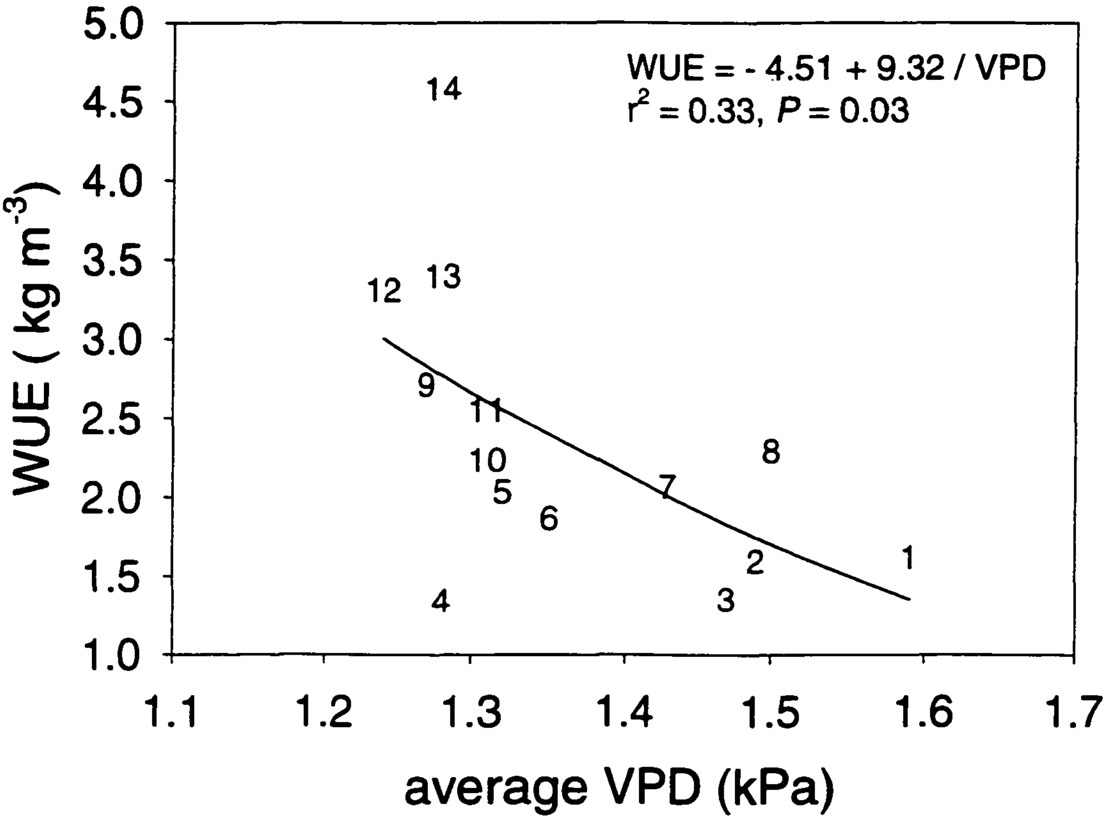


Figure 1.12. Relationship between water use efficiency (WUE) and average vapor pressure deficit (VPD) for the 14 sites of *E. grandis* x *urophylla* in northeastern Brazil.

Water response efficiency (WRE)

The production-resource theory (Monteith 1977, Vitousek 1982, Berendse and Aerts 1987) has been recently expanded with the introduction of the resource-response-efficiency theorem (Pastor and Bridgham 1999), which states that the production per unit of resource available is a unimodal curve, starting at zero for a minimum resource availability, reaching a maximum and then decreasing asymptotically towards zero. The theorem was proposed and tested for natural nutrient gradients (N, P), and was advocated to be applicable to light and water resources.

We used the asymptotic Michaelis-Menten equation (Monod function, Bridgham et al. 1995) to regress production against water supply (rainfall). To increase our scope of water availability range, we included the average of experimental plots for the same *E. grandis* x *urophylla* genotype from the Amazon region with a rainfall of 2500 mm yr^{-1} (Santana et al. 2000), and used MAI as the production variable, and the average rainfall of the rotation as the average water supply. From the three parameters of the function (maximum production, minimum rainfall and the half-saturation constant α in respect to rainfall), we fixed maximum production as 50 Mg ha^{-1} yr^{-1} (low effect on the other parameters estimates), and use non-linear SAS procedure to estimate the other two (Figure 1.13.a).

Monod equation seems to adequately fit the data, and a minimum of 643 mm yr^{-1} of rainfall was associated with this genotype production. The unimodal water response efficiency curve was then derived from the production curve (Figure 1.13.b), and the rainfall for the optimum efficiency (1.74 kg m^{-3} of rainfall) was 1360 mm yr^{-1}. Identifying these ecological limits and efficiencies of water use for plantations has both practical (for zoning) and ecological (for estimating water use, correlation between WRE and WUE, r = 0.92) significance. Moreover, if the assumption made by Pastor and Bridgam (1999) of a tradeoff between minimum resource requirement and maximum production is true, then this curve can be used to simulate the production response and planting recommendations of low and high productive species or clones (as exemplified on Figure A.1.7).

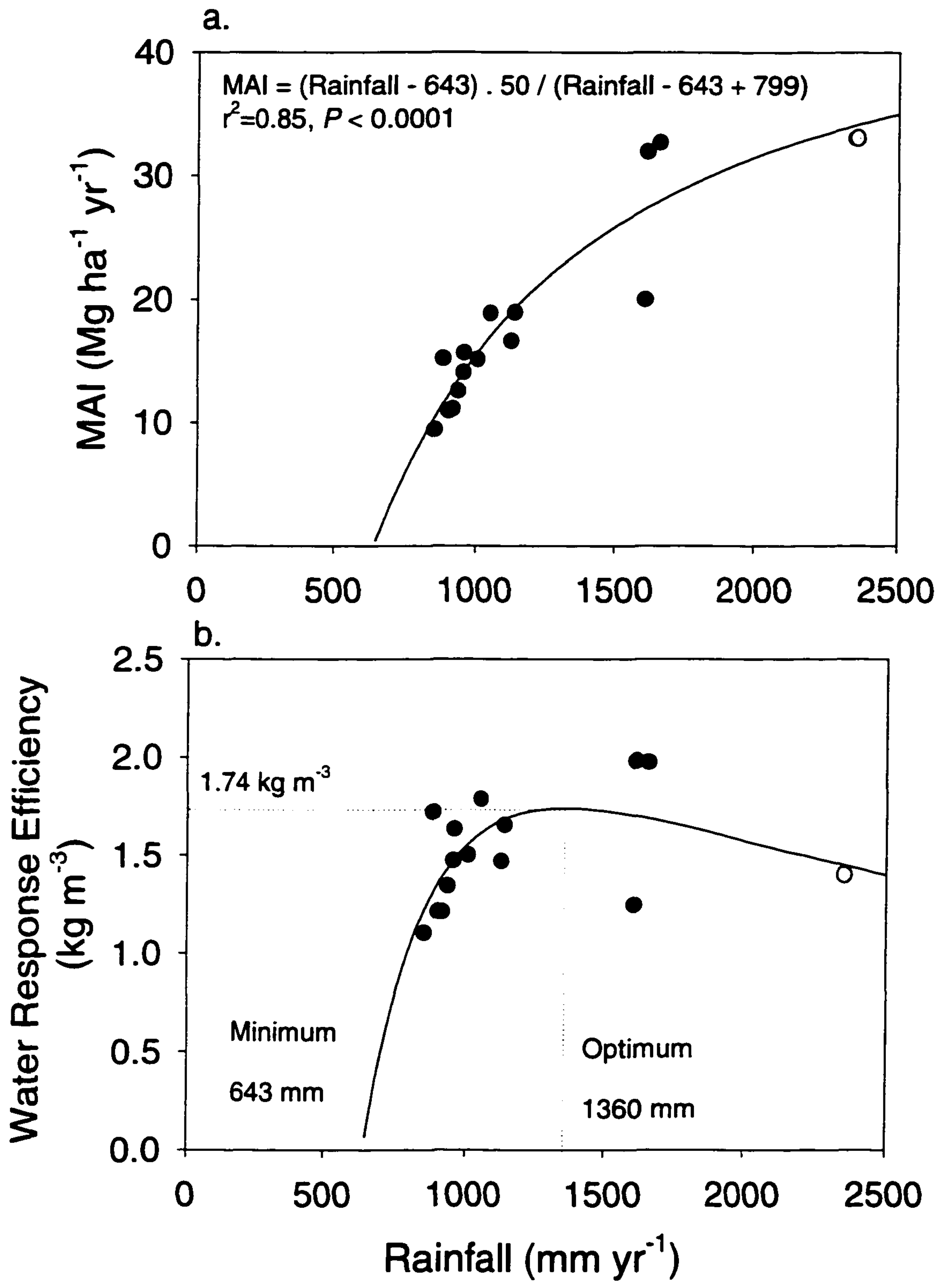


Figure 1.13. Aboveground mean annual increment (MAI) of clonal *E. grandis* x *urophylla* for the 14 studied sites (black circles) and an additional site from the Amazon region (gray circle). Line is the MONOD regression (a). Water response efficiency (MAI per rainfall) by rainfall derived from graph a (b).

Conclusions

Rainfall, leaf area index (LAI) and site index were the environmental and stand factors strongly related with the large range in productivity of the *Eucalyptus* stands observed along the transect in northeastern Brazil (MAI and ANPP from 9 to 39 Mg ha^{-1} yr^{-1}). On average, for each additional 100 mm yr^{-1} in rainfall, LAI increased 0.3 units and productivity 2.3 Mg ha^{-1} yr^{-1}, resulting in an increment of 7.6 Mg ha^{-1} yr^{-1} per added unit of LAI. Site index improved the regional predictive power of rainfall probably by capturing site-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 in their structures. These *Eucalyptus* genotypes also showed high plasticity regarding perennial biomass partitioning with root-to-aboveground ratio varying by 2-fold (from 0.15 to 0.32), with the lowest values associated with the most productive sites. This ratio presented a strong negative relationship with site index, which can be used to improve the belowground C pool estimates in these tropical plantations.

The most productive sites used more water (869 mm yr^{-1}), light (24 TJ ha^{-1} yr^{-1}) and nitrogen (72 kg N ha^{-1} yr^{-1}), but were also the most efficient forests in using these resources: 3.21 kg of ANPP per m^{-3} of transpired water, 1.14 kg of ANPP per GJ^{-1} of absorbed PAR, and 381 kg of ANPP per kg of nitrogen taken up. Increase in rainfall indirectly enlarged light and nitrogen use by increasing their capture efficiency. The inverse relation of rainfall and VPD in our transect led to higher water-use-efficiencies on the most productive sites. These sites also presented larger light- and nitrogen-use-efficiency, possibly due to a joint effect of higher C assimilation rates and aboveground C allocation, driven by the larger stomatal conductance associated with the lower VPD and soil water deficit in these wetter locales.

Combining these relationships, 1 million Mg of wood production in this tropical region in a 6-year rotation would require less land and resources for high productivity sites (24 Mg ha^{-1} yr^{-1}) than low productivity sites (12 Mg ha^{-1} yr^{-1}). Specifically, this would mean 50% less planting area (6,945 *versus* 13,889 ha), 49% less water consumption (311 million m^3 *versus* 629 million m^3 for the entire rotation), exporting 14% less N in the wood at harvesting (2.5 Gg of N *versus* 2.1 Gg of N), and leaving 50% more detritus C belowground in coarse roots per hectare (27 *versus* 18 Mg ha^{-1}).

Although resource supplies have been the main focus of forest growth studies, our results indicate that capture-efficiency and use-efficiency were the key components defining production, and that these efficiencies were under strong water supply influence. This gradient study pointed to some patterns that affect C gain, allocation and use of resources for *Eucalyptus* plantations. A full characterization of the underlying mechanisms that control these processes requires controlled manipulative studies, which was conducted in Chapter II.

CHAPTER II

PRIMARY PRODUCTION AND CARBON ALLOCATION OF A CLONAL *EUCALYPTUS* PLANTATION WITH WATER AND NUTRIENT MANIPULATIONS

Introduction

Forest plantations currently cover approximately 1% of the tropics (40 – 50 million hectares), supporting the increasing local and global wood demands (FAO 1999, Fox 2000), with *Eucalyptus* being the dominant hardwood species planted. These forests have also been advocated as carbon sinks (Vitousek 1991, Fearnside 1995, Cannell 1999, Sands et al. 1999, Hunter 2001) to slow the rise of atmospheric CO_2 concentrations with a potential expansion area of 345 million hectares over disturbed forest, pastures or abandoned agriculture areas (Cannel 1999). Complete C budgets are needed as the foundation for understanding both wood production and C sequestration, especially in response to environmental conditions. However, despite the vast accumulated knowledge regarding silviculture practices, our understanding of the mechanisms that control carbon (C) gain, allocation and resource use, and how these processes are affected by environmental factors remains poorly characterized (Gower et al. 1994). If better understood, these patterns could be used in process-based models of forest production to improve insights into scenarios of forest management and global change (Parton et al. 1994, Ryan et al. 1996b, Landsberg and Waring 1997, Nabuurs et al. 2001).

Determining gross primary production (GPP) of plantations requires accounting for above- and belowground production and respiration, which are challenging tasks (Clark et al. 2001). The belowground processes are the most difficult to evaluate (Cannel 1989b), but the mass balance technique (Raich and Naldehoffer 1989) provides a protocol to determine the total belowground carbon allocation (TBCA) with high accuracy and known variance (Giardina and Ryan 2002). TBCA represents all C sent belowground which supports respiration, coarse, fine root and exudates production, and mycorrizhae growth. TBCA can be added up with aboveground net primary production (ANPP) and aboveground autotrophic respiration (R_P) to estimate GPP (Ryan 1991). ANPP is easily assessed, and the aboveground autotrophic respiration can be reasonably estimated using respiration rate equations developed for commonly planted species (Ryan et al. 1996a, Giardina et al. 2002). Although GPP is known to be sensitive to edaphic and climatic conditions, evaluation of the environmental controls on GPP are scarce for tropical areas (Giardina and Ryan 2002).

The productivity efficiency models (PEM) have been a useful tool to model GPP as a function of environmental factors based on an existing linear relationship at the stand level between APAR and GPP (Medlyn 1998, Goetz et al. 1999). This relation was first identified by Monteith (1977) for crops and was further used for forest studies (Jarvis and Leverenz 1983, Linder 1985, Hunt 1994, Landsberg and Waring 1997). It can be written as: GPP = APAR.α^*.*fi*, where α^* is a theorethical maximum canopy quantum efficiency (mol C fixed per mol APAR) and *fi* represents a series of *i* multiplicative factors which constrain carbon uptake by limiting CO_2 diffusion into the chloroplasts or by reducing the photosynthetic pathway activity (Jarvis and Leverenz 1983). With estimates of GPP, APAR and α^*, *fi* can be assessed.

The fraction of GPP allocated below- and aboveground varies among and within ecosystems due to internal evolved controls (genetics, phenology and hormones) and to external factors like temperature, light, nutrients, water availability and competition (Dewar et al. 1994, Cannel and Dewar 1994, Ingestad and Agren 1995). This relative C allocation has both production and ecological importance because it drives wood growth and the detritus C dynamics (Kurz 1988, Parton et al. 1994, Burger and Kelting 1998). One C-allocation hypothesis predicts an increase in C partitioning to the active organ (shoots or roots) that has the lowest availability of resources (Cannel and Dewar 1994). In line with this theory recent studies have demonstrated that *Eucalyptus* can rapidly shift its C allocation patterns from below to aboveground due to the increment of nutrient supplies (Keith et al. 1997 and Giardina et al. 2002).

Although tropical soils are frequently nutrient-limited (Gonçalves et al. 2000, Fisher and Binkley 2001), fertilization often eliminates these restrictions. The supply of water has been long identified as the main limiting resource for forest productivity in the tropics (Lieth 1975, Golfari et al. 1977, Larcher 1995).

Despite this importance, only a limited number of studies have addressed the above- and belowground production associated with the manipulation of water (Linder and Axelsson 1982, McMurtrie et al. 1990, Snowdon and Benson 1992, Fabiao et al. 1995, Albaugh et al. 1998), and we are aware of no study that evaluates the effect of both water and nutrient supplies in a complete C budget for a tropical plantation.

Therefore, we used a 2 x 2 factorial design to experimentally manipulate water and nutrient supplies in a plantation of clonal *Eucalyptus* in northeastern of Brazil during two dissimilar climatic years (one wet, one normal), measuring ANPP and TBCA and estimating GPP, to achieve four main objectives:

i. To obtain complete C budgets under limited and unlimited water and nutrient supplies;
ii. To associate changes in GPP with changes in light use and canopy quantum efficiency, and identify environmental controls on GPP;
iii. To estimate the effect of water and nutrient supplies on relative and absolute above- and belowground C allocation; and
iv. To evaluate the response sensitivity of the net ecosystem production (NEP, C sequestration) to the increase of water and nutrient supplies.

Materials and Methods

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 yr^{-1}. Precipitation has a high inter-annual coefficient of variation (20%), and 68% of the rain falls between April and September, with dry summer months (CEI 1991). The slopes are gentle (< 3%), with deep (> 3 m), excessively drained, acidic (pH 4.3 in 0.01 M $CaCl_2$) soil classified as sandy isohyperthermic Typic Haplustox.

The 26-ha plantation was first planted with *Eucalyptus grandis*, by Copener Florestal Ltda, in July of 1987. This plantation was established by slash-and-burning an old pasture, disking, bedding and harrowing to raise beds 1.5 m wide and 0.5 m tall. Seedlings 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 an *E. grandis* x *urophylla* clone (clone COP-0321) after controlling *Eucalyptus* sprouts and weeds with 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 to 35 cm in height) (Stape et al.

2001). A 3.0 m x 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 (ghyphosate). The experimental treatments were installed when the plantation was 3 years-old, and the trees were 15 m tall, with aboveground wood biomass of 3.7 kg m^{-2} (Table A.2.7)

Experimental design

A 2 x 2 factorial was used with two-levels of nutrient and water regimes in a completely randomized block design with 4 replicates. Each plot was 30 m x 30 m (approximately 100 trees), with the central 36 trees being used for measurements. An analysis of variance of the initial aboveground biomass showed no pretreatment effects ($P = 0.37$, Table A.2.12). The experimental treatments ran for two complete years. The first year, from October 1999 to September 2000, was characterized by a high annual rainfall (1769 mm, the "wet year") with a uniform distribution year round, while the second year (from October 2000 to September 2001) had an annual rainfall of 1207 mm (the "normal year") with a typical seasonal drought period from November 2000 to May 2001 (Table A.2.1 and Figure 2.1).

Fertilization and irrigation regimes were designed to eliminate any limitation on *Eucalyptus* growth. To reduce the potential influence of the fertilization and irrigation treatments on adjacent plots, 0.25 m wide and 0.80 m deep trenches were opened between 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} (as FTE micronutrient fertilizer) 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 was used to guarantee 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 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. Rainfall and irrigation water analysis were regularly performed (Table A.2.6).

Soil fertility, nitrogen and phosphorus supply

Soil fertility was evaluated at the beginning and end of the study period. In September 1999, and September 2001, soils from all 16 plots were sampled at three depths (0.0-0.15, 0.15-0.30, and 0.30-0.45 m) at 45 locations using a graduated auger. These subsamples were composited by depth to give three samples per plot. Samples were dried at 65 °C to a constant weight. Soil pH and labile P, K, Ca and Mg were determined following procedures described in Appendix I.A. Soil nutrient concentrations were converted to an area basis by multiplying by bulk density (see procedures on soil C sampling) and sampling depth (Table A.2.4).

The availabilities of N and P were indexed with on-site ion exchange resin bag technique (Binkley and Matson 1983) during 3 different periods (September 1999, April 2000 and November 2001). At each time, ten sets of separately bagged anion and cation resins were placed 5 cm below the forest floor along the plot diagonal and left in place for three months. Collection and extraction procedures are described on Appendix III.A.

Meteorological data and water balance

A meteorological data set for the site was interpolated from 2 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). Calculus of the meteorological variables is detailed on Appendix I.B.

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 algorithim from 3-PG model to estimate stomatal conductance (Appendix I.C).

Overview of the C budget

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). TBCA and ANPP were estimated for each of the 16 plots through adequate sampling to capture the spatial and temporal variability associated with different soil and plant C stocks and fluxes of their sub-components (Table 2.1). Aboveground plant respiration (R_P) was estimated as a fixed proportion of ANPP based on respiration equations developed on tropical *Eucalyptus* plantations (Giardina and Ryan 2002). All dry matter estimates were converted to a C basis using the specific-component C content (Table 2.1) and the measured or interpolated monthly fluxes were summed annually for the 2 years of the study and expressed in kg C m^{-2} yr^{-1}.

Total belowground carbon allocation

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

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

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), 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 (Giardina and Ryan 2002).

Table 2.1. Methods and periodicity of C fluxes and stocks measurements for TBCA and ANPP flux determinations.

Component		Method	Periodicity	C Content *	Samples (# plot^{-1})	Allometric†
TBCA						
Soil CO_2 flux	F_S	IRGA	Monthly	-	15	
Litterfall	F_A	Litter Trays	Monthly	Foliage = 0.48 Woody = 0.44	6 x (0.25m²)	
ΔCoarse Root	ΔC_R	Allometrics	Every 6 months	0.42		CR, kg = $0.02898\ DBH^{2.4979}$ $r^2=0.60$, $P<0.001$, n=24
ΔLitter Layer	ΔC_L	Quadrats	Yearly	Foliage = 0.48 Woody = 0.43	6 x (0.25m²)	
ΔSoil C	ΔC_S	Soil Sampling	Every 2 years	Variable	9	
ΔStumps	ΔC_T	Allometrics	Once	0.42		ST, kg = $0.0199.\ D^{2.1372}$ $r^2=0.87$, $P < 0.001$, n=20
Fine Root	-	Coring	Once	0.44	12	
ANPP						
Litterfall	F_A	Litter Trays	Monthly	Foliage = 0.48 Woody = 0.44	6 x (0.25m²)	
ΔWood	ΔC_W	Allometrics	Every 6 months	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	ΔC_F	Allometrics	Every 6 months	0.50	Sep/99	FO, kg = $0.0389\ DBH^{1.8836}$ $r^2=0.67$, $P < 0.001$, n=10
					Aug/00	FO, kg = $0.0104\ DBH^{2.2287}$ $r^2=0.40$, $P < 0.001$, n=24
		Optical			96	

* Average carbon content determined in a LECO 1000 CN analyzer (Leco Corp., St. Joseph, MI) using 0.1-g of dried and ground samples.

† CR = coarse root, ST = stem, AW = aboveground wood biomass, FO = foliage, D = stump diameter

The forest floor was stratified, and procedures related with soil or litter layer measurements within plots sampled proportionately three forest floor strata, each approximately 1 m wide: tree row, intermediate, and old bed. 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 mm^2) via a closed system. The chamber was inserted into soil and litter layers 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 (see procedures on Appendix II.A). The LICOR may provide better quantitative flux estimates and we used the obtained regression ($F_{S\ \text{LI-COR}}$ = 0.796 $F_{S\ \text{PPSystem}}$, $r^2 = 0.589$, $P < 0.0001$, Figure A.2.1) to adjust the PP System's estimates of F_S throughout this study. We also evaluated the effect of soil temperature on the plot-level F_S through a 24 hour measurement period. Efflux measurements were taken every 3 hours from all 4 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 6 trays (0.25 m^2 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 until 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 ($k = 0.0072$ day^{-1}) obtained for leaf material in a 1-year decomposition study using litter bags in the region (Stape and Gomes 2000).

Total mineral soil C was evaluated in the beginning and end of the study period (2 years apart) using the intensive soil sampling procedure with 45 fixed locations within each plot (see fertility evaluation). Samples were composited by forest floor strata and depth for each plot (9 per plot). Samples were dried at 65ºC and analyzed for total C using a LECO 1000 CN analyzer (Leco Corp., St. Joseph, MI). Bulk density was determined for each plot and sampling period using a standard 92 mL steel-cylinder with 4 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 8 samples taken up to 2.0 m, every 0.2 m). We assumed that any rate of change in soil C would be negligible below 0.45 m depth in two years-period 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.

Coarse-root biomass was estimated with a site-specific allometric equation developed from 24 sampled trees on August 2000 (Table 2.1). Roots > 10 mm were sampled by digging following all coarse roots from the stem base. We estimate 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 in September of 2000, 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 root C stock did not differ among treatments and averaged 0.06 kg C m^{-2} at 4.2 years-old (Tables A.2.8 and A.2.12) representing less than 4% of the coarse root C content.

The litter layer was sampled in September 1999, 2000 and 2001 using six random 0.25 m^2 quadrats. Samples were composited by plot, dried at 65° C to constant weight, separated into leaf and woody material, and weighed. To correct for soil inclusion ash content (10-28%) was determined and the mass adjusted to an ash-free basis.

As the site was previously planted with *Eucalyptus* we surveyed the old stumps in each plot (≅ 586 stumps ha^{-1}) in September 1999, measuring the diameter on the top of the stump (6.9-36.4 cm). Based on the diameter distribution, 20 stumps were selected and completely dug out of the soil and weighed, and a subsample for each stump was taken and dried at 65 °C to a constant weight to estimate total stump dry mass. A significant regression was obtained relating stump dry mass and top diameter (Table 2.1). To estimate the monthly decomposition of this carbon compartment, we used the coarse root allometric equation obtained on the site to back-estimate the original dry matter content of the 20 stumps when the forest was harvested (which occurred 4 years before the stump sampling). An exponential decay model was fitted ($k = 0.190\ yr^{-1}$) and used to estimate monthly change in the stump carbon mass (ΔC_T).

Aboveground net primary production

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

$$ANPP = F_A + \Delta C_W + \Delta C_F \qquad \text{Eq. (2)}$$

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. Woody biomass was estimated every 6 months, based on DBH (cm) and total height (H, in meters) measurements and a site-specific allometric equation (Table 2.1). Change in aboveground woody carbon (ΔC_W) was estimated as the summation of the estimated individual tree aboveground woody biomass increment. Foliage biomass was estimated on four occasions: September 1999, August 2000, February 2001 and October 2001. For the first two occasions site-specific allometrics were developed (Table 2.1). The September 1999 sampling was prior to the initiation of treatments, and no significant treatment effect was detected on the August 2000 allometrics. For the last two occasions (February and October 2001), foliage biomass was estimated using indirect optical procedure using a Ceptometer-AccuPAR Model 80 (Decagon Devices, Pullman, USA) associated with specific leaf area (SLA, $m^2\ kg^{-1}$) determination (Pierce and Running 1988) (methodology in Appendix II.B). The estimated LAI of each plot, at each time, was divided by the specific leaf area of the particular treatment to estimate the foliage biomass. Change in foliage carbon (ΔC_F) was estimated as the difference between consecutive measurements. Leaf herbivory was assumed to be zero because no defoliation was ever observed. The availability of separate measurements of foliage and branch litterfall, and branch allometric equations (Table 2.1) also allowed expressing ANPP as the summantion of foliage (FNPP), branch (BrNPP) and bole (BoNPP) net primary productions.

Aboveground autotrophic respiration and gross primary production

No direct measurement of aboveground respiration (R_P) was taken, so we estimated R_P using three indirect approaches. If all approaches provided similar results, then the robustness of one of the estimates of R_P may be adequate to calculate GPP. The first approach used values from the literature; Lansberg and Waring (1997) reported average ratios between NPP and GPP from 0.40 to 0.50 for trees, resulting in R_P-to-ANPP ratios from 1.0 to 1.5. The second estimate of R_P was based on the work of Giardina and Ryan (2002) with *E. saligna* (a closely related species to *E. grandis* x *urophylla* hybrid) in Hawaii with two fertilization regimes. Their estimate of R_P-to-ANPP ratio was stable across treatments, despite the large difference in ANPP, and averaged 1.10. Our third R_P estimate was based on Giardina and Ryan (2002) work, but this time we used their respiration equations to estimate foliage and wood respiration (both construction and maintenance respiration) for our 16 plots (Appendix II.C). The average estimate of R_P-to-ANPP ratio for all plots and years was 1.08, close to Giardina and Ryan's (2002) findings and well within the Landsberg and Waring reported region. This ratio was used across all plots and years to estimate R_P ($R_P = 1.08$ ANPP).

GPP was finally obtained by adding ANPP, R_P and TBCA.

Absorbed PAR and apparent canopy quantum efficiency

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

$$\alpha = \frac{GPP}{APAR} \qquad \varepsilon = \frac{ANPP}{APAR} \qquad \text{Eq. (3)}$$

With APAR and α estimates, changes in GPP among treatments could be explicity associated with the change in light use (APAR) or quantum-efficiency (α). For comparison purpose, Table A.2.11 provides a series of other light use efficiency definitions commonly found in the ecology and forestry literature.

Environmental constraints on canopy quantum efficiency

Jarvis and Leverentz (1983) proposed the use of multiplicative environmental constraint factors to obtain an apparent canopy quantum efficiency

(α) from a theoretical maximum value (α^*). We used this multiplicative method and our experimental design as a tool to obtain yearly estimates of these rating factors for nutrient (f_N), soil moisture (f_W) and vapor pressure deficit (f_D) effects (Runyon et al. 1994):

Eq. (4)

$$\alpha = \alpha^* \cdot f_N \cdot f_W . f_D$$

We assumed f_N and f_W to be 1 in fertilized and irrigated plots, respectively, and derived appropriate ratios among the apparent canopy quantum efficiencies to estimate f_N and f_W for the control plots (Cannell 1989a). For example, for the wet year (year 1), we can write the canopy quantum efficiency for the control (C) , irrigated (I), fertilized (F) and fertilized and irrigated (FI) treatments as:

$$\alpha_C = \alpha^* \cdot f_{N1} \cdot f_{W1} . f_{D1} \qquad \alpha_F = \alpha^* \cdot f_{W1} . f_{D1} \qquad \alpha_I = \alpha^* \cdot f_{N1} \cdot f_{D1} \qquad \alpha_{FI} = \alpha^* \cdot f_{D1}$$

Eq. (5)

The ratio between α_C and α_I produces f_{W1}, and the same is true for the ratio between α_F and α_{FI}. We used the average of these two estimates to obtain the final value for f_W for each block and year. The same procedure was followed for f_N. To obtain an estimate of f_D we used the irrigated treatments for both years, and assumed that f_D for the wet year was 1. We considered that because it was a rainy year (> 1700 mm), the VPD effect was smaller than during the normal year, which was consistent with VPD trends (Figure 2.1.b and Table A.2.1). We did not consider the effects of temperature and age because their changes were minimal during the study period

Leaf $\delta^{13}C$

The ratio of C stable isotopes ($^{13}C/^{12}C$, $\delta^{13}C$) in leaves is determined by stomatal control of the ratio of photosynthesis and transpiration, and the degree of discrimination against $\delta^{13}C$ with a changing ratio of intercellular to ambient CO_2 (Larcher 1995). This signature was used to indirectly evaluate the stomatal conductance among treatments during the drought period of the normal year (Figure 2.1.b), and *Eucalyptus* foliage was sampled on April 2001. For each plot, 5 recent fully expanded leaves from the middle of the canopy of 12 trees were sampled, composited, dried at 65 °C to a constant weight, grounded and analyzed for $\delta^{13}C$ (Hydra 20-20, PDZ-Europa, Cheshire, England).

Net ecosystem production (NEP)

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

$$NEP = \Delta C_W + \Delta C_F + \Delta C_R + \Delta C_L + \Delta C_S + \Delta C_T \qquad \text{Eq. (6)}$$

Yearly estimations of NEP per plot were based on the yearly estimates of each of the components.

Statistical analysis

Analyses of variance were performed considering block, fertilization and irrigation as the main effects, with year as a repeated measurement factor for variables estimated for both the wet and normal years: F_S, F_A, ΔC_L, ΔC_R, total ΔC, TBCA, Foliage NPP, Branch NPP, Wood NPP, ANPP, GPP, NEP, ANPP/GPP, TBCA/GPP, Absorbed PAR, α, ε, LAI, Leaf N, Leaf P, resin N and resin P. For variables evaluated just once, or analyzed independently at the beginning or end of the study period, an ANOVA having block, fertilization and irrigation as the mains effects were used: SLA, $\delta^{13}C$, ΔC_S, ΔC_T, soil C, litter layer biomass, fine root biomass, biometric stand attributes and change in soil fertility. Where necessary, logarithmic transformations were used to meet statistical assumptions for the errors. Because no interaction between water and nutrient regimes was observed, and as the majority of the variables were not affected by the nutrition regime, all variables' means were pooled across fertilization treatments (Appendix II.D contains tables with original means for all 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 stundentized range test (HSD) was employed for multiple comparisons with a significant level of 0.05 (protecting against type I error).

Results

Water and nutrient supplies

The study period was characterized by a uniform thermal regime with average mean, minimum and maximum daily temperatures of 25 °C, 21 °C and 29 °C (Table A.2.1 and Figure 2.1.a). Precipitation was irregular, totaling 1769 mm in the wet year and 1207 mm in the normal year, including a typical 6-month drought season with only 44% of the year's precipitation (Figure 2.1.a). Irrigation added 531 mm of water during the wet year and 962 mm during the normal year (Figure 2.1.a), yielding a 115% increase (≅ 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 (Table A.2.1). No shortage of water was estimated for the irrigated plots (Figure 2.1.b). Rainfed plots transpired an estimate of 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 was negatively related with rainfall on a monthly basis (R^2=0.32, $P < 0.01$, n=24, notice a mirror effect on Figure 2.1.b, Table A.2.1) showing that air humidity was strongly coupled with rainfall.

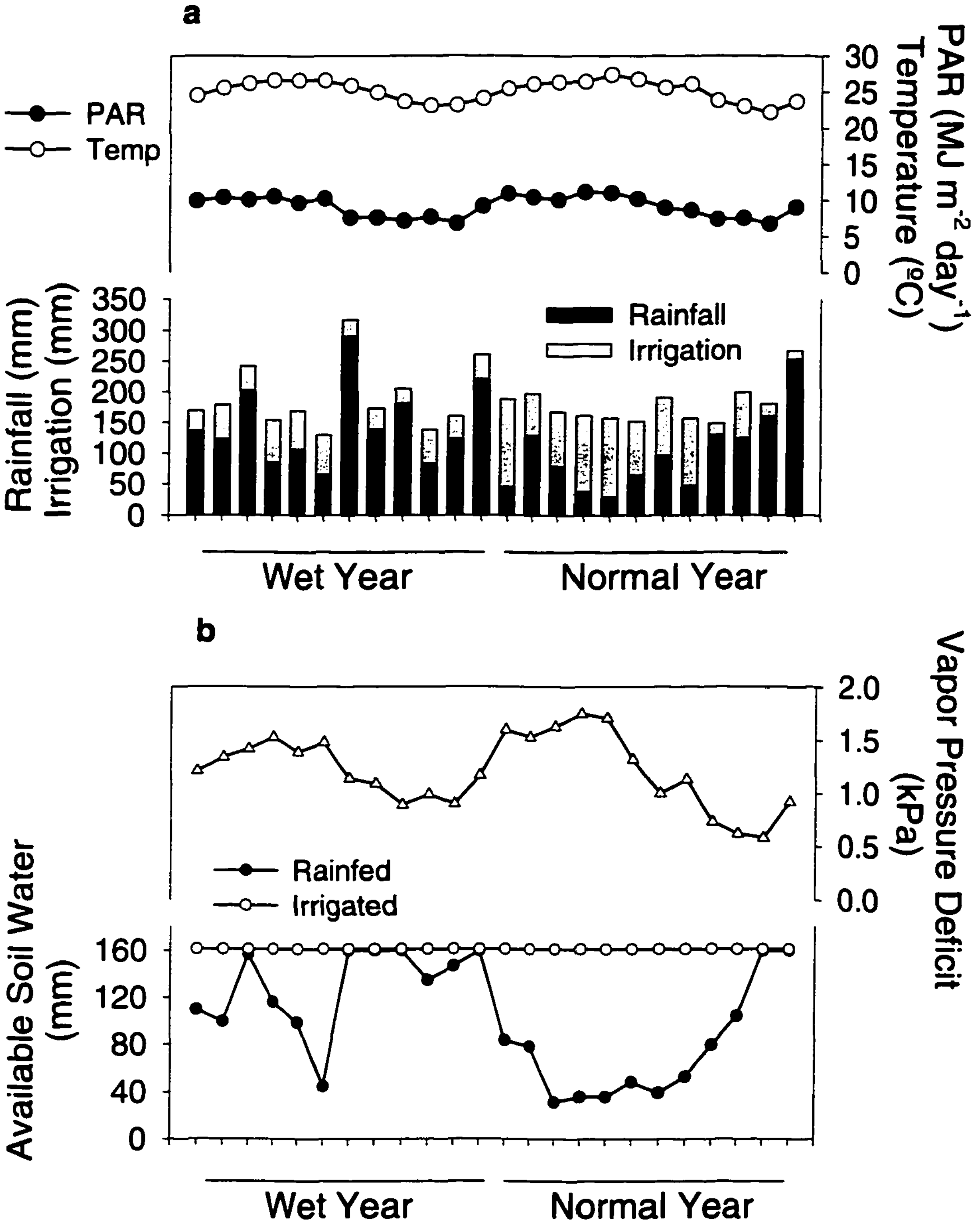


Figure 2.1. Monthly rainfall, irrigation, photosynthetic active radiation (PAR) and average temperature (Temp) during the 24 months of the study period, characterized by a wet year (October 1999 to September 2000) and a normal year (October 2000 to May 2001) (a). Monthly estimated available soil water (2 m profile) for both rainfed and irrigated plots and vapor pressure deficit for the study period (b).

The site had medium soil fertility for *Eucalyptus* production (Novais et al. 1986), and treatments did not differ for total soil C and N, or any other nutrients for the initial sampling (Tables A.2.4 and A.2.14). The amount of nutrients added annually by rainfall (for instance, 4.2 kg N ha^{-1} yr^{-1}) and irrigation (7.1 kg N ha^{-1} yr^{-1}) was modest, representing less than 2% of the fertilization rates used (506 kg ha^{-1} N yr^{-1}) (Table A.2.6). Resin ion values for N and P were higher for the fertilized plots in all three incubations (Table A.2.13) and averaged 0.7 mg N bag^{-1} and 4.3 μg P bag^{-1} for the non-fertilized treatments, and 45.3 mg N bag^{-1} and 253.2 μg P bag^{-1} for the fertilized ones (Table A.2.5 and Figure A.2.2.b). A significant trend in decreasing the availability of P was observed in the non-fertilized treatments with time: 9.9, 2.4 and 0.5 μg P bag^{-1} (Table A.2.13). Water regime had no effect on N and P availability for the non-fertilized treatments or on N availability for fertilized treatments, but averaged across all periods, irrigation increased P capture by anion resin in the fertilized treatments (336 *versus* 170 μg P bag^{-1}, $P < 0.001$). Leaf N and P contents at age 3 presented adequate nutritional values: 19.4 g N kg^{-1} and 1.2 g P kg^{-1} (Table A.2.2). There were small fluctuations around these values for the 4 and 5 year-old leaf sampling, with the fertilized treatments showing on average 10% higher N content and 50% higher P content (Tables A.2.2 and A.2.15). Soil fertility was not affected by water regime (Table A.2.14), but fertilization increased P availability (net change of 2.4 *versus* 0.3 g m^{-2}) and K availability (8.1 *versus* -2.6 g m^{-2}) while maintaining Ca and Mg availabilities, which showed a net decrease on control plots (-20.6 g Ca m^{-2} and -6.0 g Mg m^{-2}) (Table A.2.4 and Figure A.2.2).

Forest growth responses

All biometric variables did not differ initially at age 3 (Tables A.2.7 and A.2.12), with an average aboveground wood biomass of 37 Mg ha^{-1}, but they all differ between water treatments at 5.5 years old, when wood biomass reached 107 Mg ha^{-1} for rainfed and 141 Mg ha^{-1} for irrigated plots (coefficient of variation of 4.6%), and site index (dominant height at 5 years-old) was increased from 24.5 m to 28.0 m (Table A.2.7). No fertilization effect was observed.

Leaf area index (LAI) averaged 3.3 m^2 m^{-2} at age 3 and increased to 4.0 m^2 m^{-2} at the end of the wet year (Figure 2.2.a and Table A.2.2), with no difference among treatments (Table A.2.15). During the drought period of the normal year, LAI decreased to 2.3 on rainfed plots and to 3.4 on irrigated plots (Figure 2.2.a). The decrease in LAI was coupled with leaf shedding in the rainfed treatment detected as an increase in litterfall (Figure 2.3), 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 m^2 m^{-2}, Figure 2.2.a) and at this age fertilization had increased specific leaf area marginally from 8.3 to 8.8 m^2 kg^{-1} (Table A.2.2).

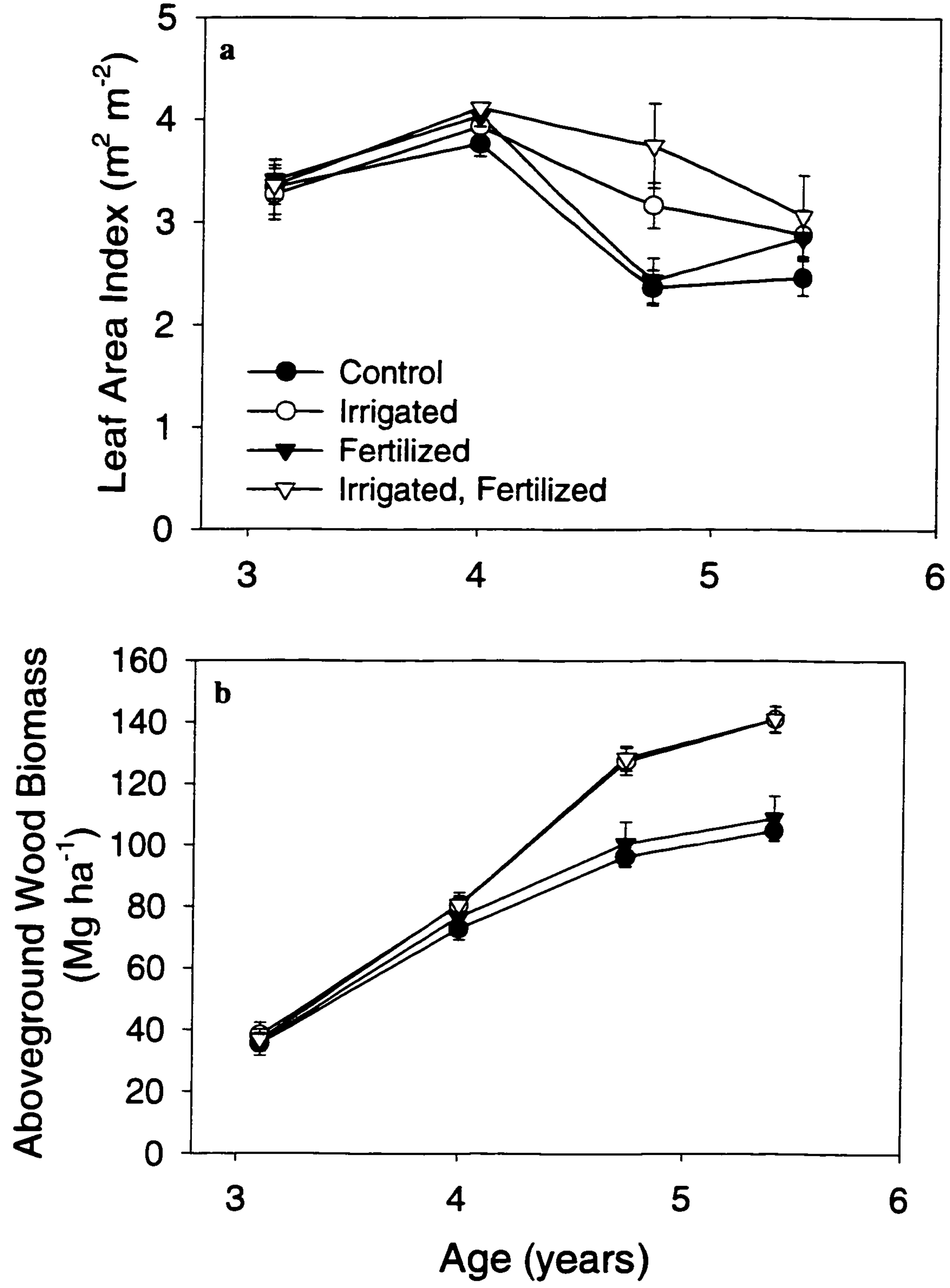


Figure 2.2. Leaf area index (a) and aboveground wood biomass (b). Error bars are standard errors of the means (n=4).

Forest production and C allocation

The repeated measurement analysis showed that all forest production estimates (TBCA, ANPP and GPP) differed by year and water regime (Table A.2.16). Fertilization regime had a minor effect in some of the production components, and only for the wet year (Table A.2.16).

Total belowground carbon allocation

TBCA for the wet year was almost twice the rate of the normal year (2.3 *versus* 1.2 kg C m^{-2} yr^{-1}, Tables 2.2 and A.2.16) and irrigation increased TBCA in relation to the rainfed plots (1.9 *versus* 1.6 kg C m^{-2} yr^{-1}), with no year interaction. The coefficient of variation for TBCA across years and treatments was 15%.

Soil CO_2 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 (Figure 2.4). Soil surface C efflux (F_S) was twice as high for the wet year (2.3 kg C m^{-2} yr^{-1}) as for the normal year (1.2 kg C m^{-2} yr^{-1}, Table 2.2), and was also greater for irrigated treatment (1.9 kg C m^{-2} yr^{-1}) than for the rainfed one (1.6 kg C m^{-2} yr^{-1}), with no interaction between year and water regime (Table A.2.16). Soil CO_2 efflux dropped during the drought period of the normal year (Figure 2.3), and returned to pre-drought values during the rainy season (compare Figures 2.1 and 2.3). 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).

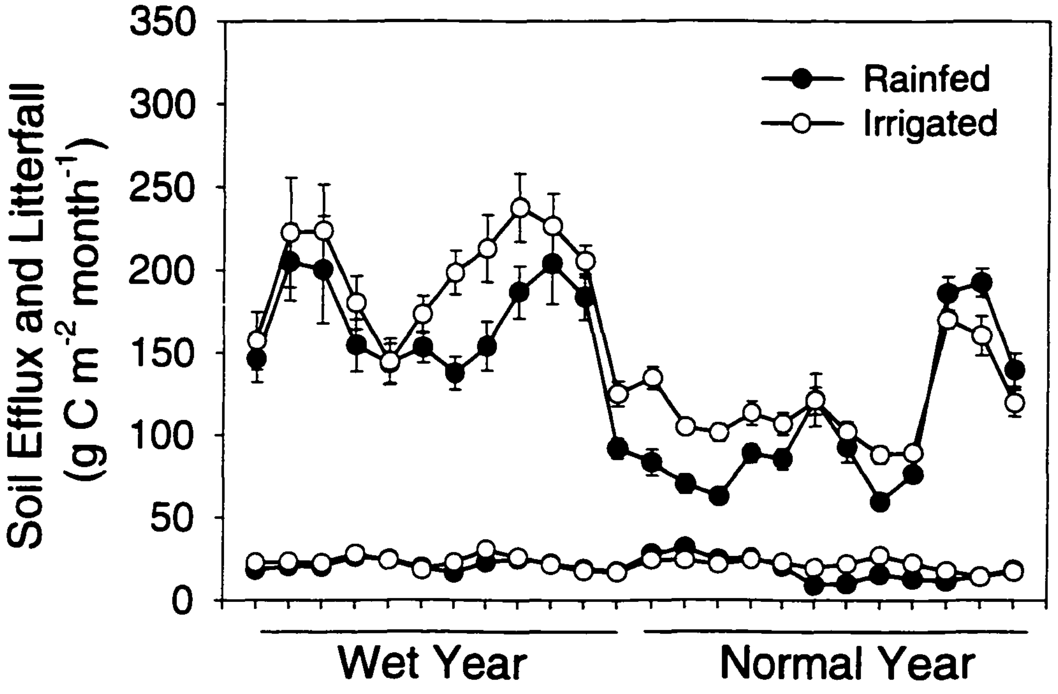


Figure 2.3. Monthly soil CO2 efflux (top lines) and litterfall (bottom lines) by water regime (n=8). Error bars are standard errors of treatment means.

Litterfall (F_A) was marginally higher for the wet year compared with the dry year, for the irrigated treatment compared with the rainfed one, and for the fertilized treatment during the wet year (differences < 0.04 kg C m^{-2} yr^{-1}, Table 2.2). Yearly soil CO_2 efflux averages were not correlated 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 years (average of 1.0 year). Yearly soil CO_2 efflux correlated with ANPP (R^2=0.47, *P* <0.001, n=32, Figure 2.6.a) and GPP (R^2=0.71, *P* <0.001, n=32, Figure 2.6.b).

Table 2.2. Gross primary production (GPP), aboveground net primary production (ANPP) and total belowground carbon allocation (TBCA) of *E. grandis x urophylla* by water regime and year. ANPP is decomposed among its components (foliage, branch and bole NPP). TBCA is presented with the fluxes used on its estimation (F_S = soil CO_2 efflux, F_A = Litterfall and ΔC = change in C stored in the litter layer-soil system). Values are means with standard errors given in parentheses (n=8). Values (within rows) followed by different letters differ at $P = 0.05$.

Annual Flux Component*	Rainfed	Irrigated
	Wet Year Production (kg C m^{-2} y^{-1})	
GPP	6.642 (175) b	7.796 (244) a
ANPP	2.167 (74) b	2.563 (68) a
Branch	0.168 (7) b	0.204 (9) a
Foliage	0.188 (9) b	0.233 (13) a
Bole	1.809 (72) b	2.126 (53) a
TBCA	2.135 (143) b	2.464 (143) a
F_S	1.959 (110) b	2.307 (122) a
F_A	0.254 (12) b	0.275 (12) a
ΔC	0.429 (47)	0.432 (56)
	Normal Year Production (kg C m^{-2} y^{-1})	
GPP	3.081 (69) b	5.642 (135) a
ANPP	0.952 (39) b	2.053 (59) a
Branch	0.090 (5) b	0.169 (3) a
Foliage	0.139 (12)	0.153 (16)
Bole	0.721 (34) b	1.730 (53) a
TBCA	1.100 (112) b	1.370 (42) a
F_S	1.258 (68) b	1.411 (43) a
F_A	0.223 (11) b	0.257 (10) a
ΔC	0.065 (61) b	0.217 (37) a

* Within columns, all fluxes differ by year ($P = 0.05$)

Total change in stored C (ΔC) in the soil-litter layer system was similar for water regimes in the wet year (0.43 kg C m^{-2} yr^{-1}) but in the normal year irrigated treatments had a greater ΔC (0.22 *versus* 0.06 kg C m^{-2} yr^{-1}, Table 2.2). Coarse root accumulation (ΔC_R) was the main component of ΔC (equation 1) (Table A.2.10). Other components of ΔC had a small impact on its estimate. Mineral soil C (ΔC_S) showed a significant net decline of -0.09 kg C m^{-2} yr^{-1} (Table A.2.14), which represented 2.3% of initial C stock (4.2 kg C m^{-2}). Across treatments, C stored in the litter layer did not change (Table A.2.16), and change in C stored in old stumps averaged -0.03 kg C m^{-2} yr^{-1} (Table A.2.10).

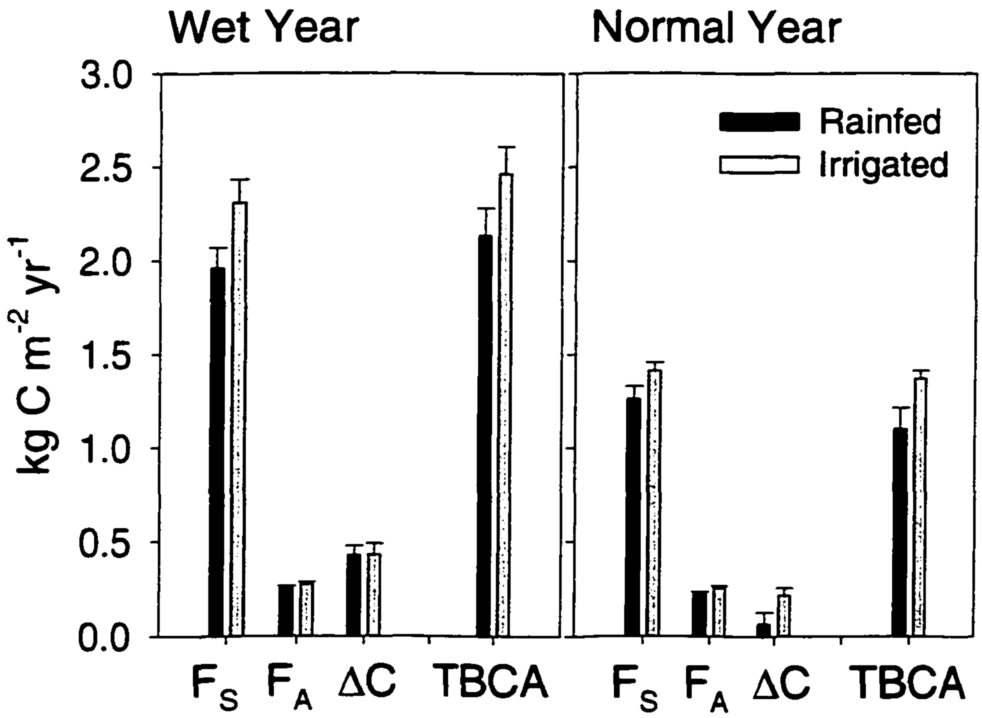


Figure 2.4. Components of total belowground carbon allocation (TBCA) by water regime and year (n=8). Error bars are standard errors of the means. F_S = soil CO_2 efflux, F_A = litterfall, ΔC = annual change in C stored in coarse roots, litter layer, stumps and mineral soil.

Aboveground net primary production

Irrigation increased ANPP by 18% from 2.2 to 2.6 kg C m^{-2} yr^{-1} in the wet year, and by 116% from 0.9 to 2.0 kg C m^{-2} yr^{-1} in the normal year (Table 2.2). ANPP was increased by fertilization only in the wet year (from 2.2 to 2.5 kg C m^{-2} yr^{-1}, Tables A.2.6 and A.2.10). Coefficient of variation for ANPP was 7% on both years. Across all years and treatments, Bole NPP was the dominant component of ANPP (83%), followed by foliage NPP (9%) and branch NPP (8%) (Table 2.2 and Figure 2.5).

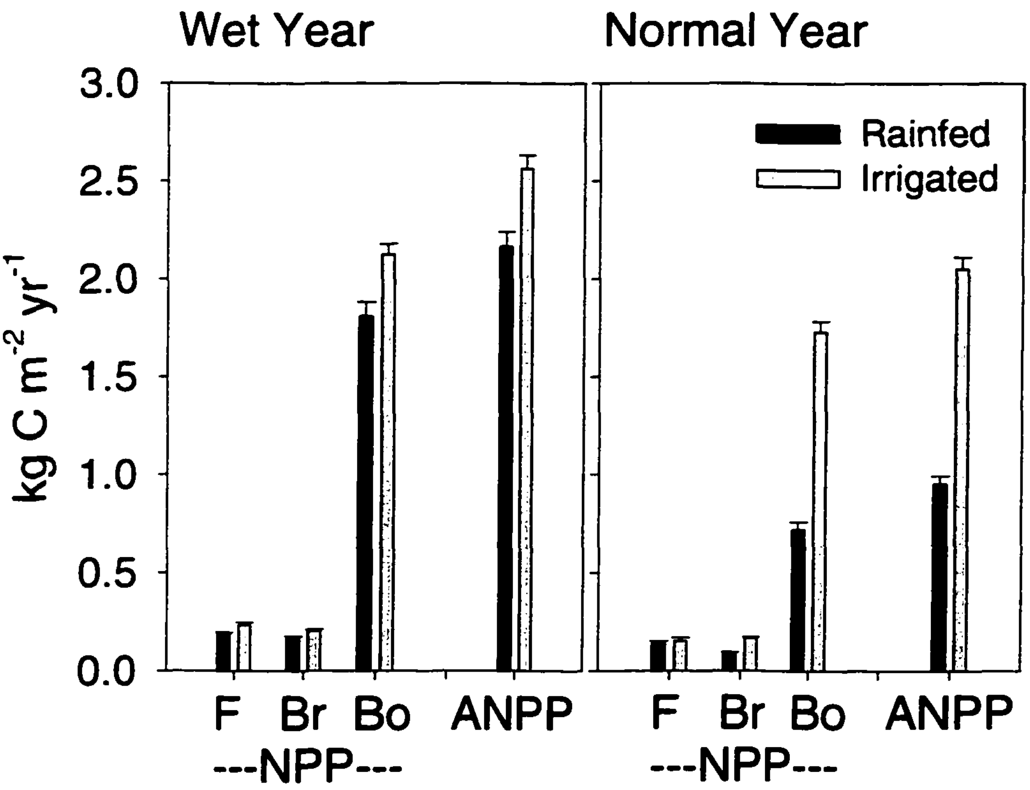


Figure 2.5. Components of aboveground net primary production (ANPP) by water regime treatment and year (n=8). Error bars are standard errors of the means. Fol. NPP = foliage net primary production, Br.NPP = branch net primary production, Bole NPP = stem plus bark net primary production.

GPP and relative allocations

Irrigation increased GPP by 18% in the wet year (6.6 *versus* 7.8 kg C m^{-2} yr^{-1}) and by 83% in the normal year (3.1 *versus* 5.6 kg C m^{-2} yr^{-1}) (Tables 2.2 and A.2.16). No nutrient regime effect was detected. In the wet year, fertilization tended to decrease the relative amount of GPP allocated belowground (33% to 30%, $P = 0.08$, Table A.2.10). All treatments had the same relative belowground allocation during the wet year (32%, Figures 2.7 and A.2.3), but irrigated plots had a lower relative belowground allocation compared with rainfed plots on the normal year (24% *versus* 36%, Figure 2.7, Tables 2.2 and A.2.17). 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% (Figure 2.7 and Table A.2.17).

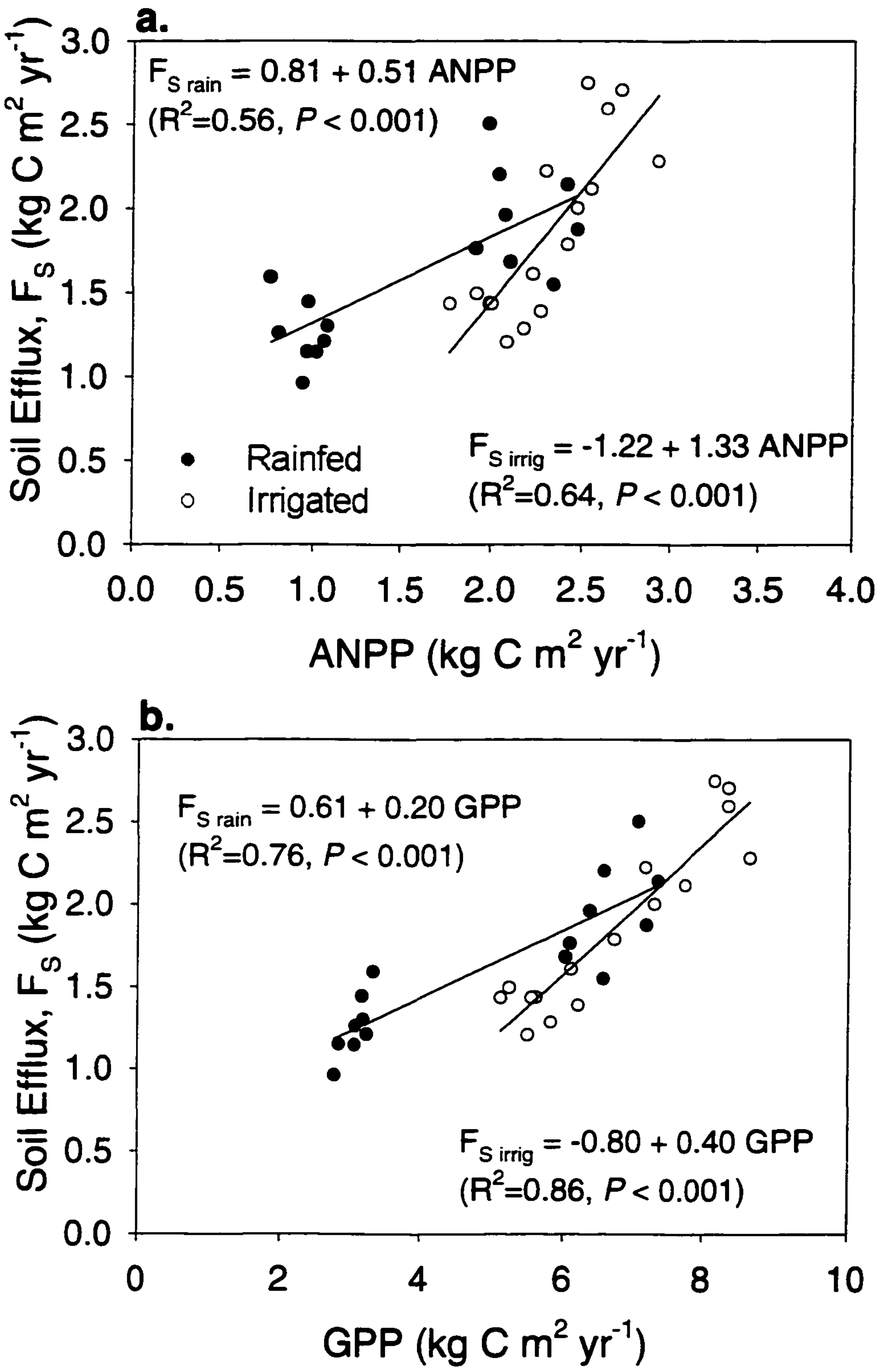


Figure 2.6. Relationship between soil CO_2 effluxes and aboveground net primary production (ANPP) (a) and gross primary production (GPP) (b) for all plots and years (n=32) (b).

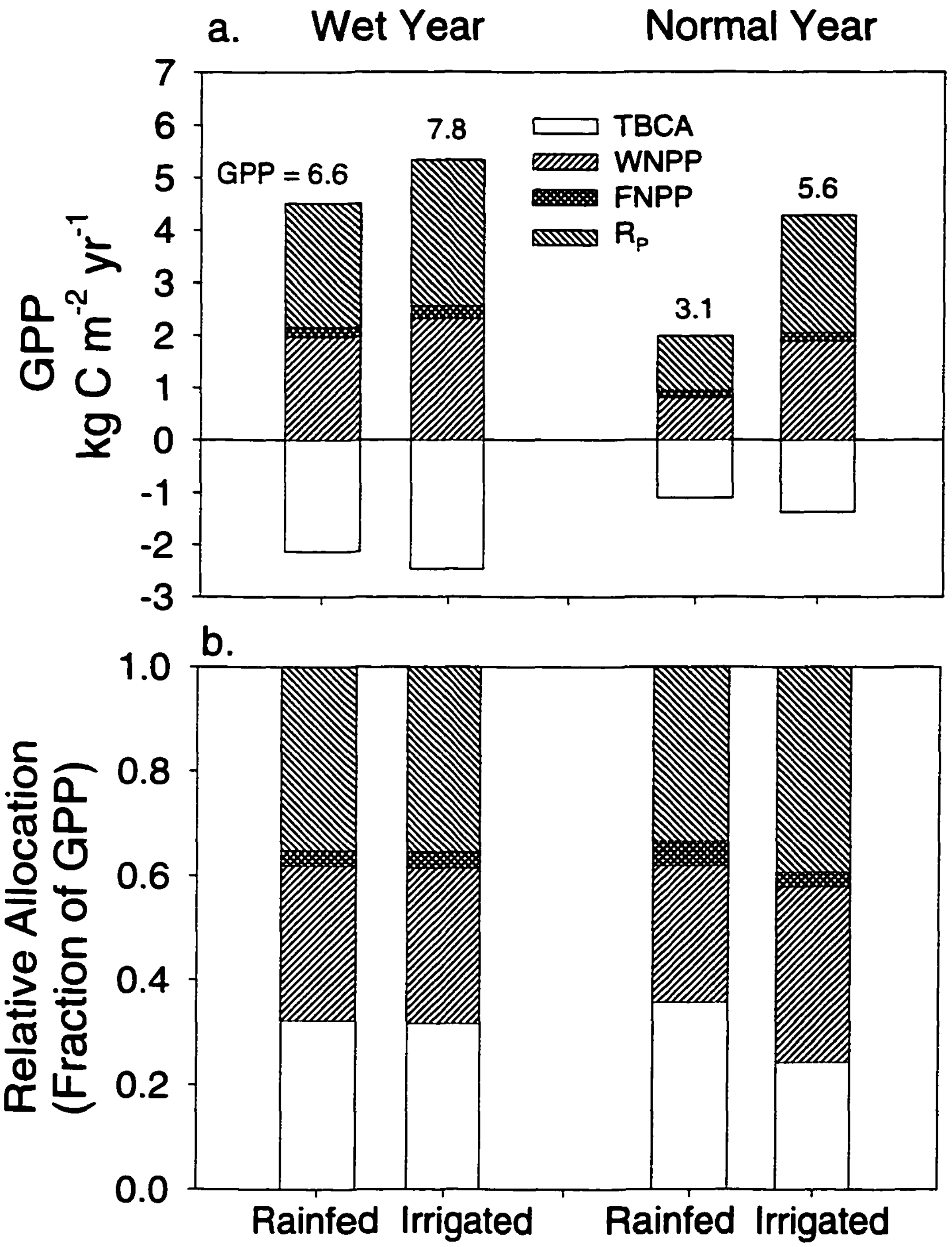


Figure 2.7. Absolute (a) and relative (b) estimates of gross primary production (GPP) and above and belowground components for the wet year and normal year by water regime and year (n=8). TBCA = total belowground carbon allocation, WNPP = aboveground wood net primary production, FNPP = foliage net primary production and R_P = aboveground autotrophic respiration.

APAR, canopy quantum efficiency and light use efficiency

APAR was similar for rainfed and irrigated treatments in the wet year, but was 14% higher for the irrigated plots in the normal year (Table 2.3). Canopy quantum efficiency (α) was not affected by nutrition regime but showed a year and water interaction (Table A.2.17), 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). On 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) (Figure 2.8). Light use efficiency (ε) also showed a significant year and water regime interaction (Table A.2.17) and averaged 2.0 g MJ^{-1} APAR and 2.4 g MJ^{-1} APAR on the wet year for rainfed and irrigated treatments. For the normal year ε decreased by half to 1.0 g MJ^{-1} APAR on the rainfed treatments and to 2.0 g MJ^{-1} APAR on the irrigated plots (Table 2.3 and Figure A.2.4).

Table 2.3. APAR, canopy quantum efficiency (α) and light use efficiency (ε) by water regime and year. Values are means with standard errors given in parentheses (n=8). Values (within rows) followed by different letters differ at $P = 0.05$.

Year	Rainfed	Irrigated
	Absorbed PAR (mol APAR m^{-2} yr^{-1})	
Wet Year	10772 (101)	10938 (98)
Normal Year	9417 (182) b	10702 (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
Dry Year	1.03 (0.05) b	1.97 (0.09) a

Environmental constraints to canopy quantum efficiency and leaf $\delta^{13}C$

The estimates of soil fertility (f_N) constraints for the wet and normal years were close to one (Table 2.4). Soil moisture (f_W) constraints for the wet year was higher (less restrictive) than for the normal year (0.87 *versus* 0.62, respectively). Assuming a vapor pressure deficit constraint of 1.0 for the wet year (no constraint), the vapor pressure deficit (f_D) constraint was lower (more restrictive) for the normal year (0.75) (Table 2.4). Leaves from rainfed plots showed lighter $\delta^{13}C$ (-28.5 ‰) compared with the irrigated plots (–29.1 ‰, Tables A.2.2 and A.2.15).

Table 2.4. Environmental constraints of canopy quantum efficiency by treatment and year. Constraints are expressed as a rating factor (between zero and 1) for soil moisture (f_W), vapor pressure deficit (f_D) and nutrient (f_N) effects. Values are means with standard errors given in parentheses (n=4).

Treatment	Wet Year	Normal Year
	Environmental Constraints	
Control	f_{D1} f_{W1} f_{N1}	f_{D2} f_{W2} f_{N2}
Irrigated	f_{D1} f_{N1}	f_{D2} f_{N2}
Fertilized	f_{D1} f_{W1}	f_{D2} f_{W2}
Irrigated,Fertilized	f_{D1}	f_{D2}
Constraint	**Year Estimates**	
	1	2
f_W	0.87 (0.03)	0.62 (0.03)
f_N	0.98 (0.04)	1.07 (0.04)
f_D	1.00	0.75 (0.05)

Net ecosystem productivity

NEP increased with irrigation both in the wet year (2.3 *versus* 2.7 kg C m^{-2} yr^{-1}) and the normal year (0.8 *versus* 2.0 kg C m^{-2} yr^{-1}) with a significant year interaction (Tables A.2.3 and A.2.16). The coefficient of variation for NEP was 10%. NEP increased in the wet year on the fertilized treatments (from 2.4 to 2.7 kg C m^{-2} yr^{-1}), but no fertilization effect was observed in the normal year. Aboveground (ΔC_W) and coarse root (ΔC_R) components, dominated the NEP (Table A.2.3 and Figure 2.9).

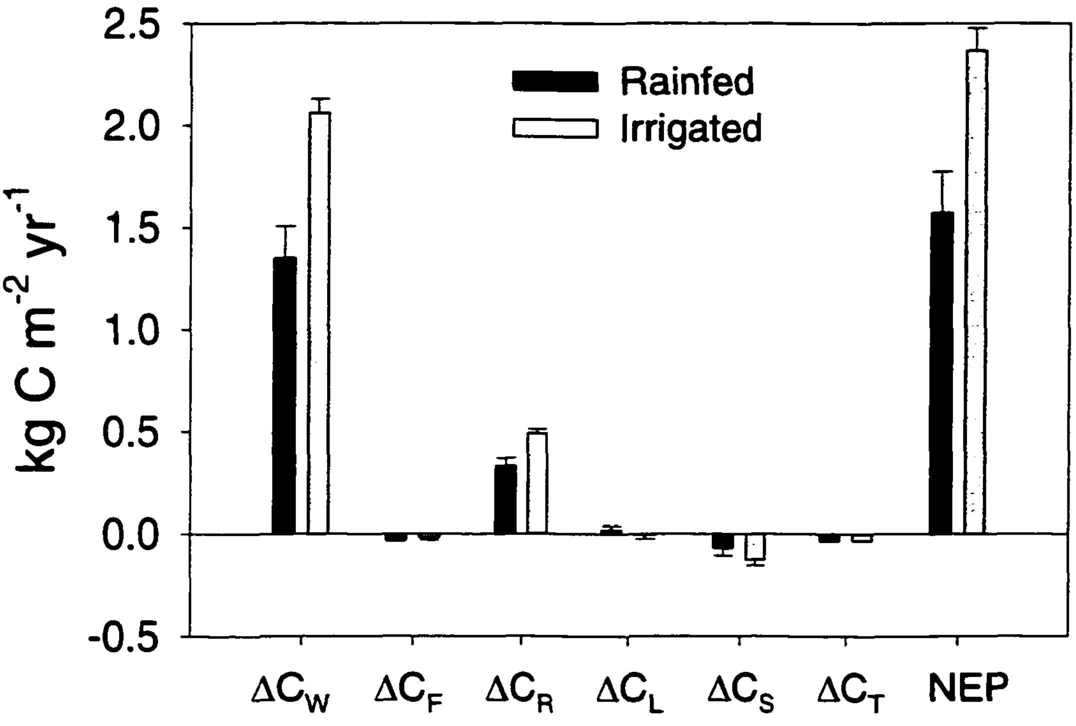


Figure 2.8. Components of net ecosystem productivity (NEP) by water regime for both years (n=16). Error bars are standard errors of the means. ΔC_W, ΔC_F, ΔC_R, ΔC_L, ΔC_S, ΔC_T are the change in C stored in aboveground wood biomass, foliage, coarse roots, litter layer, soil and stumps.

Discussion

Forest growth responses

Water supply limited growth on this typical sandy Oxisol site with little or no current limitation of soil fertility (Figure 2.2.b). Other irrigation and fertilization trials with *Eucalyptus* (Pereira and Pallardy 1989, Stewart et al. 1990, Olbrich et al. 1992, Myers et al. 1996, Honeysett et al. 1996, Hunter 2001) also reported increased wood growth associated with greater water supply. The wood increment (Figure 2.2.b) of this clonal *E. grandis* x *urophylla* in the wet year (92 m^3 ha^{-1} yr^{-1}) 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 on production not only reinforces the importance of water supply on forestation zoning (Golfari et al. 1977, Coops et al. 1998) but also highlights the potential use of irrigation as a management option (Olbrich et al. 1992, Sands et al. 1999, Hunter 2001). The observed rapid rise of the site index by irrigation effect was also observed by Snowdon and Benson (1992), and Albaugh et al. (1998) in pines, and corroborated the positive relationship between site index and rainfall ($r = 0.77$) identified along the studied transect of Chapter I.

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, Cromer et al. 1993, Laclau et al. 2000, Giardina et al. 2002, Birk and Turner 1992, Barros and Novais 1996, Cromer et al. 1993, Stape and Benedetti 1997, Fernandez et al. 2000, Hunter 2001). 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* (Gonçalves et al. 1997, Binkley and Ryan 1998). However, the substantial decrease in resin ion P and soil exchangeable K, Ca and Mg (Tables A.2.4 and A.2.5) on the control plots during the experiment indicates that future nutritional limitations may be likely, due to the high rate of nutrient accumulation in biomass (at 5.4 years-old, for the non-fertilized treatments: 290 kg ha^{-1} N, 24 kg ha^{-1} P, 226 kg ha^{-1} K, 417 kg ha^{-1} Ca and 103 kg ha^{-1} Mg) and low natural inputs (Crane and Raison 1980, Novais and Smyth 1999) (Table A.2.6).

LAI values (from 2.3 to 4.0 m^2 m^{-2}, Figure 2.2.a) are within the range obtained for *Eucalyptus* in Brazil (Mielke et al. 1999, Binkley et al. 2002), Africa (Olbrich et al. 1992, Laclau et al. 2000), Australia (Stewart et al. 1990, Cromer et al. 1993, Myers et al. 1996) and India (Hunter 2001). The absence of fertilization effect on LAI was consistent with adequate initial nutrient contents on leaves (Table A.2.2). The higher LAI obtained during the wet year for all treatments and for the irrigated plots during the drought season of the normal year clearly demonstrated the dependence of LAI on water supply (Figure 2.2.a). Increase of LAI due to better water supplies was obtained for *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 (Table A.2.7) indicated a low leaf growth associated with a shedding behavior, which is a well documented phenomena for *Eucalyptus* (Cromer et al. 1993, Pook 1995, Honeysett et al. 1996). This shedding contributed to the reduction in transpiration rates (Table A.2.1) and kept all trees alive (Honeysett et al. 1996). For the irrigated plots, the increase in tree height during the normal year (3 meters, Table A.2.7) indicated the occurrence of new leaf growth concomitantly with the decrease in LAI, probably representing the establishment of a new equilibrium between reduced assimilation rates (higher VPD and lower stomatal conductances, Table A.2.1) and canopy maintenance costs (Jarvis et al. 1989, Giardina et al. 2002).

C budget

The large measured soil CO_2 effluxes (ranging from 1.2 to 2.5 kg C m^{-2} yr^{-1}, Figure 2.3, Table A.2.10) were similar to rates obtained on other fast-growing plantations (Binkley and Ryan 1998, Giardina and Ryan 2002, and Maier and Kress 2000), and the absence of soil respiration response to temperature agreed with data from a tropical site (Giardina and Ryan 2002). Approximately 15% (0.25 kg C m^{-2} yr^{-1}) of the soil CO_2 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 CO_2 efflux (1.5 kg C m^{-2} yr^{-1}) appeared to be strongly coupled with canopy photosynthesis, with a weak dependence on the “old” mineral soil C pool, as identified in other studies (Arneth et al. 1998, Maier and Kress 2000, Hogberg et al. 2001 and Janssens et al. 2001). This tight coupling was indicated by high CO_2 efflux from a soil with very low C storage, a decline in soil CO_2 efflux on irrigated plots during drought periods with high vapor pressure deficits (Figure 2.3), and the positive relationship between soil CO_2 efflux and both ANPP and GPP (Figures 2.6.a and 2.6.b).

Using the change in soil $\delta^{13}C$ signature (from a sugarcane field converted to *Eucalyptus*), Giardina and Ryan (personnal communication) estimated a 13% contribution of "old C" for the soil CO_2 efflux and 65% coming from root activity. If we use the same ratio between old-C lost per total C content observed in their study, we estimate that on average 5% of our soil CO_2 effluxes came from old-C mineralization, and 80% from recent root activity. If this rough estimate is correct, then soil CO_2 effluxes can be used as method to monitor canopy activity in fast-growing plantations.

Like the study with *E. saligna* in Hawaii (Giardina and Ryan 2002), soil CO_2 efflux at our site was the dominant component of TBCA; C storage changes in soil was very small. However, in our study changes in coarse root C storage (ΔC_R) represented on average 22% of the TBCA, 2-fold higher than Hawaii (11% of TBCA), while litterfall (F_A) averaged 14% of TBCA, lower than the 25% of TBCA in Hawaii. These results indicate that species- and site-specific estimates of litterfall and coarse root allometrics are needed for precise estimates of TBCA. Across all treatments and years, if we assumed no change in C storage ($\Delta C = 0$), we would underestimate TBCA by 16%, while an overestimative of 7% would occur if change in coarse root C were considered.

Our TBCA estimates (ranging from 1.0 to 2.5 kg C m^{-2} yr^{-1}) were higher than values for temperate forests which range from 0.2 to 1.0 kg C m^{-2} yr^{-1} (Raich and Nadelhoffer 1989, Gower et al. 1996, Keith et al. 1997, Smith and Resh 1999), but were similar to *Eucalyptus* stands (Ryan and Binkley 1998, Giardina and Ryan 2002), indicating that these fast-growing forests have a higher potential to interact and alter soil biological, chemical and physical properties. For these fast-growing plantations, litterfall was not a good predictor of TBCA ($r^2 = 0.01$) using the global equation developed by Raich and Nadelhoffer (1989). However, due to the strong relationship between soil respiration and ANPP or GPP (Figure 2.6.a), aboveground wood increment was shown to be a good predictor of TBCA under both rainfed ($r^2 = 0.58$, $P < 0.001$, n=16) and irrigated conditions ($r^2 = 0.72$, $P<0.001$, n=16).

The increase in ANPP by fertilization during the wet year (from 2.2 to 2.5 kg C m^{-2} yr^{-1}) with a stable TBCA (2.3 kg C m^{-2} yr^{-1}, Table A. 2.9) was analogous to the findings of Giardina et al. (2002), fertilizing *E. saligna* in Hawaii, indicating a decrease in relative C allocation belowground under higher soil fertility. The effect of water regime in our study was very prominent. Across both years, irrigation increased GPP (from 4.8 to 6.7 kg C m^{-2} yr^{-1}), ANPP (from 1.6 to 2.3 kg C m^{-2} yr^{-1}) and TBCA (from 1.6 to 1.9 kg C m^{-2} yr^{-1}, Table A.2.2 and Figure 2.7), although the fraction of GPP allocated belowground decreased from 34% to 28% and the fraction allocated to ANPP increased from 32% to 35% (Figures 2.7.a and 2.7.b, Tables 2.2 and A.2.). Most of the ANPP increment (94%) was allocated to woody components and 6% to foliage NPP, explaining the increase in site index probably due to interspecific competition (Makela 1986) and similar to other irrigation results (Linder and Axelsson 1982, Snowdon and Benson 1992, Hunter 2001).

Raich (1998) and Smith and Resh (1999) also found a positive relationship between TBCA and ANPP for natural forests. However, Giardina et al. (2002) measured a stable TBCA associated with different ANPP for control and fertilized *E. saligna*, and Keith et al. (1997) obtained an increase in ANPP to the expense of TBCA for *E. pauciflora* fertilized with P. In our case, the 18% increase in TBCA by irrigation effect (Figures 2.4 and 2.7 and Table A.2.9) was mostly due to structural coarse root growth (Table A.2.10). If we estimate fine root production by assuming that 50% of TBCA is net production, and subtract from that the coarse root increment (Binkley and Ryan 1998, Law et al. 1999), we identify that fine root production was similar between rainfed and irrigated treatments (0.47 kg C m^{-2} yr^{-1}, Table A.2.16). These fine root estimates represented 27% of the TBCA, similar to the fractions (close to 1/3 of TBCA) reported for direct measurements of fine root production and TBCA (Nadelhoffer and Raich 1992, Haynes and Gower 1995, Gower et al. 1996). On average, these estimates of fine root production represented 10% and 7% of the GPP for the rainfed and irrigated treatments, respectively. This indicates a higher efficiency of the fine roots in capturing resources and sustaining growth in the irrigated treatment (Hof et al. 1990), demanding proportionally less belowground C allocation. Olbrich et al. (1992) reported a decrease in fine root density by the effect of irrigation on *Eucalyptus* and credited the superior aboveground growth to a lower belowground allocation to fine roots. Albaugh et al. (1998) observed a stable fine root production and a decreasing fraction of NPP allocated belowground (35% and 31%) when comparing control and irrigated plots of *P. taeda*, and when associated with fertilization, the effects were even greater (23% of NPP allocated belowground). Linder and Axelsson (1982) also found that irrigation and fertilization did not affect fine root production of *P. sylvestris* but reduced its fraction as a percentage of GPP (from 34% to 11%). The quick response of this clone to water supply, both in C gain and allocation shift, indicates that *Eucalyptus* has a strong plasticity (Keith et al. 1997, Gonçalves et al. 1999, Giardina et al. 2002) to respond to environmental factors, but probably within a range dictated by genetic control (Roux et al. 1996, Olbrich et al. 1992). Comparatively, *Pinus* seems to have a much smaller plasticity in responding to amelioration of the soil conditions (Ryan et al. 1996b, Retzlaff et al. 2001).

Despite the distinct behavior of TBCA on some studies (increasing, staying the same or decreasing) with improved soil conditions, all showed that the fraction of the GPP allocated belowground or the relative fine root production decreased (Keyes and Grier 1981, Linder and Axelsson 1982, Kurz 1989, Haynes and Gower 1995, Ryan et al. 1996b, Misra et al. 1998, Albaugh et al. 1998). This indicates that the absolute amount allocated above- and belowground depends firstly on the total pool fixed (GPP) and secondly on the strengths of the above- and belowground sinks, regulated by the adequacy of nutrient- or water-shoot:root balance (Cannel and Dewar 1994, Runyon et al. 1994, Landsberg and Waring 1997). Overall, our results indicate that as water status improves, the fraction of GPP allocated belowground decreases, which is in line with the dominant theory of C allocation driven by nutrition (Vogt et al. 1986, Gower et al. 1994, Cannell and Dewar 1994) and, as proposed by Albaugh et al. (1998), this theory should be expanded to water supply.

Absorbed PAR and efficiencies

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, Table A.2.1), and is greater or equivalent to theoretical maximum α^* used in previous *Eucalyptus* studies (Beadle and Turnbull 1992, Landsberg and Waring 1997, Sands and Landsberg 2002). This efficiency represents a conversion of 12% of the absorbed PAR into assimilates (≅ 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 ($GPP = APAR.\alpha$) 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) jointly 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 a 25% increase in α due to better nutrition. The observed light use efficiencies ($\varepsilon = 1.0$ to 2.4 g ANPP MJ^{-1} APAR) of this *Eucalyptus* clone (Table 2.3, Figure A.2.4) are similar to C_3 and C_4 crop efficiencies (1.0 to 4.0 g ANPP MJ^{-1} APAR), are above the mean of the observed forest values (0.2 to 2.5 g ANPP MJ^{-1} APAR) (Cannell 1989b, Hunt 1994, Haxeltine and Prentice 1996, Goetz 1997), and were extremely dependent on C allocation patterns. For instance, the 91% increase in ε for the irrigated plots during the normal year was a joint effect of a 61% increase in α and 18% increase in the aboveground allocation (Table A.2.3). These results evidence that interpretation of light use efficiency is constricted when no belowground data is available (Colbert et al. 1990, Jokela and Martin 2000, Balster and Marshall 2000).

Averaged over the two years, the 48% increase in ANPP by the irrigation effect was primarily dependent on canopy quantum efficiency (+ 32%), followed by a shift in allocation from below- to aboveground (+ 8%), and then increasing in LAI (+ 7%).

Environmental constraints

The absence of nutritional constraint ($f_N \cong 1$) for both years was consistent with the adequate initial leaf nutrient contents (Table A.2.2), while in a nutrient-limited site Giardina et al. (2002) report a 25% increase in canopy quantum efficiency (α) on *E. saligna* with fertilization (a 22% increasing in N content).

The soil moisture constraint factor estimates in our site ($f_{W1} = 0.85$ and $f_{W2} = 0.62$) indicated that shortages of soil moisture impacted α in both years, and were more intense during the normal year. This decrease in α was caused by the reduction of the stomatal conductance, which was indicated by the decrease of the leaf $\delta^{13}C$ values from –28.5‰ on rainfed to –29.1‰ on irrigated plots for the normal year (Olbrich et al. 1992, Roux et al. 1996). VPD constraints ($f_{D2} = 0.75$, assuming $f_{D1} = 1.0$) indicated that α was reduced by dryer microclimatic conditions of the normal year (Figure 2.1.b, Table A.2.1).

We did not credit the 28% decrease in GPP between years in the irrigated plots to the agė-related decline syndrome (Ryan et al. 1997) because the measurements were just 1 year apart, and GPP decrease in *E. saligna* in Hawaii between age 3 and 5 years was just 3% yr^{-1}. These results are in line with studies showing that the canopy of *Eucalyptus* is strongly coupled with the atmosphere, responding to VPD on a daily basis, and also being influenced by soil moisture status on a seasonal basis (Jarvis et al. 1989, Olbrich et al. 1992, Mielke et al. 1999). Myers et al. (1996) and Barnard (2000) also showed that *Eucalyptus* stomatal conductance can be limited by VPD even with adequate soil water supply, indicating that the VPD control of the stomatal conductance is probably due to a combination of epidermal transpiration and high rates of transpiration during some hours of the day (Pataki et al. 1998).

C sequestration (NEP)

In our study, the dependence of NEP on water supply was large (1.4 and 2.5 kg C m^{-2} yr^{-1} for the normal and wet years). Similarly, Arneth et al. (1998) also observed high NEP for *P. radiata* (average of 0.6 kg C m^{-2} yr^{-1}) on wetter years, which presented a conservative NEP-to-volumetric increment ratio (0.24 Mg C m^{-3}) suggested as an index of C sequestration. At our site, this index also showed to be stable across treatments and years (0.28 ± 0.02 Mg C m^{-3}) and, when applied to the first year growth of our stand (12 m^3 ha^{-1}), indicated that this *Eucalyptus* forest had been a net C sink since planting (NEP of 0.31 kg C m^{-2} in the first year). Maier and Kress (2000) showed that after 12 years the control plots of a *P. taeda* plantation in North Carolina were still a net source of C (-0.1 kg C m^{-2} yr^{-1}), while the managed plots (fertilized and irrigated) were net sinks (0.7 kg C m^{-2} yr^{-1}). After wood production, coarse root increment was the second most important contributor to NEP (21%) in our study (Figure 2.9), being allometrically related with aboveground wood increment ($\Delta C_R = 0.24\ \Delta C_W$) as in many other studies (Kurz 1989, Fabiao et al. 1995, Misra et al. 1998, Reed and Tome 1998, King et al. 1999, Giardina and Ryan 2002). This coarse root production influences the build up of C storage in stumps for sites converted from agriculture, pasture or disturbed savanna. Using our *in situ* estimates of coarse root decay ($k = 0.19$ yr^{-1}), we calculated the long-term C storage in stump compartment to be between 1.0 (rainfed, Figure A.2.5) and 1.2 kg C m^{-2} (irrigated), which is substantial in a site with just 4.2 kg soil C m^{-2}. For these short-rotation forests, changes in C storage in canopy and litter layer were small components of NEP, reaching a steady state after the 2nd or 3rd year.

Across both treatments, the net change in soil C ($\Delta C_S = -0.09$ kg C m^{-2} yr^{-1}) was less than 2.3% of the C content in the soil profile. Bashkin and Binkley (1998) and Binkley and Resh (1999) found no net change is soil C in fast growing *Eucalyptus* plantations; Richter et al. (1999) showed a very low C accretion in a sandy soil under pine plantation after 40 years (0.004 kg C m^{-2} yr^{-1}). Cannell (1999) recommended soils with low C content and able to support high forest productivities as the best for C sequestration, and Katterer et al. (1995, for *Eucalyptus*) and Maier and Kress (2000, for *P. taeda*) reported C accretions on the upper profile of sandy low C soil under irrigation and fertilization management. If the potential of C sequestration in soil increases with higher TBCA fluxes, our results suggest that increasing water availability (and productivity) has the potential to increase C sequestration in soil under fast-growing plantations.

However, the effect of water and nitrogen on C mineralization and stabilization should be evaluated together with the long-term effect of coarse root on soil C dynamics (Parton et al. 1994, Schlesinger 1997, Kaye et al. 2001, Resh et al. 2002).

Time-averaged C storage represents the long-term C content of the forest-soil system for a perpetual forest management (Cannell and Dewar 1995). Using the observed forest growth and coarse root decay rates, and considering no change in soil C, the time-average C storage in this study would be dominated by soil (55%), bole (17%), stumps (13%) and coarse roots (7%) (Figure A.2.5). This storage of 7.6 kg C m^{-2} is an impressive value compared with 15 to 20 kg C m^{-2} estimated for long-rotation temperate forests (Vitousek 1991, Cannell 1999), and can be even higher by delaying harvest (Hoen and Solberg 1994, Cannell 1999). However, the maintenance of this system at this new steady state is dependent on keeping the same production rates, which will demand an adequate nutrient management and soil conservation, mainly during harvesting events (Binkley et al. 1997, Burger and Kelting 1998, Seixas et al. 1995).

Conclusions

For tropical plantations, long-term analyses of wood production and their effects on the global C budget are constrained by the paucity of information of the physiological rules and controls of C gain and allocation. Using the mass balance technique and the production efficiency models (PEM) conceptualiztion, we were able to translate a 2-year C budget of a typical *Eucalyptus* plantation in relation to both wood production and ecological perspectives.

In our study, water supply dramatically affected the C budget, increasing GPP by 38% (4.8 to 6.7 kg C m^{-2} yr^{-1}) and shifting the amount of photosynthate allocated belowground from 34% to 28% of GPP. The increase in GPP could be explained by the combination of a 33% higher canopy quantum efficiency (0.034 to 0.052 mol C mol^{-1} APAR) and 7% higher APAR due to a larger LAI. Despite the allocation shift, TBCA was increased by water supply (1.6 to 1.9 kg C m^{-2} yr^{-1}), indicating an increase in detritus C flows with productivity, pointing to sustainable production systems under intensive management coupled with nutrient additions. Net ecosystem production was composed primarily of wood (0.28 Mg C m^{-3}), but the coarse root plus stump compartment was an important and manageable long-term C pool.

Our results also suggest that the combination of irrigation and fertilization trials, with TBCA methodology and PEM analysis can be used as a tool to estimate at the stand level the relative importance of genetics and environmental factors on forest productivity, guiding both management and breeding strategies.

Overall our results corroborated the gradient study evidences (Chapter I) that distinct physiological processes are affected by water supply, and stress that complete C budgets are crucial for the calibration and testing of ecosystem or forest production models that incorporate the dynamics of C allocation (Chapter III).

CHAPTER III

CALIBRATION AND VALIDATION OF THE 3-PG PROCESS-BASED MODEL TO SIMULATE *EUCALYPTUS* GROWTH

Introduction

Eucalyptus is the dominant and most productive planted forest in Brazil (9 to 39 Mg ha^{-1} yr^{-1}, Chapter I), with more than 3.5 million hectares intensively managed mainly for charcoal, pulpwood and sawtimber products (Simoes et al. 1981, FAO 1999, Neilson 2000). Growth and yield models based on stand attributes are the current tools for predicting wood increments and wood supplies (Campos et al. 1988, McTague et al. 1989). Site index is still the central concept embodying the average environmental quality that sites may have on tree growth (Scolforo and Machado 1990, Burkhart 1997, Reed 1997). Classic growth and yield models limitations for forest production estimates include: (i) they cannot be used to estimate productivity on non-forested landscapes; (ii) in the short term, these models are insensitive to inter-annual climatic variations, which can dramatically affect final production of short-rotation forests due to 1 or more years of bad growing conditions, and (iii) changes in management practices between rotations can alter empirical relationships (Gonçalves et al. 2000, Eldridge et al. 1994, Seixas et al. 1995).

Empirical models do not allow the insertion of the forest production in a broader ecosystem framework regarding the associated use of natural resources (Running and Gower 1991, Landsberg and Gower 1997, Kimmins 1997) and the forest-soil feedback throughout the detritus C and nutrient cycling (Parton et al. 1994, Burger and Kelting 1998), which have increasing economical and social relevance (Brown et al. 1997). For instance, despite the high efficiency of *Eucalyptus* in using water (Lima 1993) and nutrients (Bargali and Singh 1991) to produce biomass, its high productivity leads to high resource use, which may affect the sustainability of forest production (Wang et al. 1991, Hunter 2001) and water from forest catchments (Calder 1992, Bruijnzeel 1997).

Process-based models describe forest productivity based on plant physiological processes that control growth (i.e., photosynthesis, allocation, respiration, transpiration, nutrition and litterfall), and many have been developed (see summary in Landsberg and Gower 1997). Despite the appeal of mechanistic simulations of growth and resource use under different environmental conditions, process-based models are rarely used as management tools (Kimmins 1997, Landsberg and Waring 1997). The limited application of these models likely results from the greater complexity of process-based models, the large number of required parameters (and the difficulties of obtaining estimates), the need of extensive input from environmental files, and models' incomplete documentation. However, recent reviews of process-based models suggest that simple models based on absorbed photosyntheically active radiation (PAR) (Battaglia and Sands 1998, Makela et al. 2000) may overcome these difficulties. APAR models calculate photosynthesis by first estimating the amount of PAR absorbed by the canopy and its ability to fix C. The ability of radiation to produce photosynthesis is modulated with a light-use-efficiency parameter (Monteith 1977), which changes with environmental factors that affect stomatal conductance or the activity of the photosynthesis pathway (Jarvis and Leverenz 1983, Sands 1996, Goetz 1997). This "top-down" approach to the physiology of forest growth reduces the number of required parameters and eliminates many of the non-linearities of these processes at finer scales (Medlyn 1998). Furthermore, water and C sub-models can be coupled throughout canopy processes (McMurtrie et al. 1990, Landsberg and Gower 1997), and the high complexity of nutrient soil dynamics can be lumped into fertility-rating scaling factors (Landsberg and Waring 1997, Battaglia and Sands 1997).

Eucalyptus growth is proportional to intercepted light (Linder 1985, Cromer et al. 1993), and APAR-models have been used in forest plantations (Landsberg and Hingston 1996, Battaglia and Sands 1997, Landsberg et al. 2000, Coops et al. 1998). Further success with these models requires a better understanding of C allocation in response to water and nutrients, because *Eucalyptus* allocation patterns are sensitive to ontogenetic and environmental factors, and these can dramatically affect wood production (Keith et al. 1997, Giardina and Ryan 2002, Chapter II).

The incorporation of process-based models as a management tool by the large and expanding Brazilian forest sector may allow: (i) assessments of the risks of climatic variation on forest productivity and profitability, (ii) estimations of potential productivity for regional forestation planning, (iii) identification of environmental factors limiting growth and estimated resource uses, (iv) a framework for management and breeding programs, and (v) evaluation of the long-term forest productivity when coupled with soil-models. As a step in this direction, we evaluated the 3-PG model (Landsberg and Waring 1997) for *Eucalyptus* plantations in Brazil. The model was selected due to its concise structure, dynamic carbon allocation regulation, sensitivity to environmental factors and site management practices, successful parameterisation and validation for other forest systems (Law et al. 1999, Coops et al. 1998, Landsberg et al. 2000), and adequate documentation (Sands and Landsberg 2002).

Our test of the utility of the 3-PG model had 3 components. First, we calibrated the model with data from one fertilization trial with *E. saligna* in Hawaii. Next, the model was re-calibrated for an irrigation and fertilization trial with *E. grandis* x *urophylla* in Brazil. Third, we evaluated the model's performance against independent growth data from forty pairs of control and fertilized inventory plots monitored for two years in northeastern Brazil, with a further comparison with the predictions of an empirical model. Additionally, we investigated the fertilization response as an index to scale the fertility-rating parameter needed to run the 3-PG model.

Materials and Methods

Overview of the calibration and validation steps

Calibration and validation of the 3-PG model involved three steps (Figure A.3.1): (i) calibration for 6-years of production of an *E. saligna* fertilization trial in Hawaii; (ii) re-calibration for 2-years of production of an *E. grandis x urophylla* irrigation trial in Brazil; and (iii) validation against independent production data of forty paired control-fertilized *E. grandis x urophylla* inventory plots in Brazil, monitored during two distinct climatic (rainfall) years, with a further comparison with a null-empirical yield model fitted for the control plots and used to estimate the 2 years growth. During calibration (steps i and ii), the model was tuned for the treatments with no water or nutrient limitations and verified for the treatments with limited nutrient (Hawaii) or water (Brazil) supplies. Validation of the 3-PG model initially utilized the fertilized inventory plots, because a site-specific fertility rating parameter was required (ranging from zero to 1, and set as 1 in these plots). Based on the validation results for wood increment and LAI outputs, a new parameterisation and second run for 3-PG were undertaken. Finally, 3-PG was run for the control plots, scaling a fertility-rating factor for each site based on the fertilization response of the stands.

3-PG Model

The 3-PG is a monthly-step process-based forest model (Landsberg and Waring 1997, Sands and Landsberg 2002) of the APAR family (after Monteith 1977), for which weather, site and species-specific parameter requirements are supposed to be relatively easy to obtain. 3-PG has a biophysical submodel which estimates monthly evaporation and canopy transpiration using the Penman-Monteith model. Canopy conductance in the Penman-Monteith model is controlled by the most restrictive factor controlling stomatal aperture: vapor pressure deficit (VPD) or soil water limitation. The vapor pressure deficit modifier (f_D) is negatively and exponentially related to average monthly VPD through the coefficient of stomatal response to VPD (k_g). Soil water balance is the difference between precipitation and evapotranspiration. Water is drained if water holding capacity in the rooting zone is exceeded. The soil water modifier (f_θ) is inversely related with soil moisture and depends on soil texture.

The forest production submodel estimates gross primary production (GPP) based on the monthly intercepted PAR times a theoretical maximum canopy quantum efficiency (α^*) reduced by physiological (age, VPD or soil water) or environmental modifiers (temperature, soil fertility and frost). Soil fertility is expressed as a simple rating factor. Intercepted PAR is calculated based on the Beer Lambert's law, and LAI is estimated from the foliage biomass and specific leaf area. Net primary production (NPP) is estimated as GPP times a NPP:GPP ratio (0.45 ± 0.05) to account for respiration. NPP is primarily allocated to the root compartment, inversely proportional to the harshness of the environment (defined as the minimum value between f_D and f_θ) and soil fertility, within maximum and minimum allocation limits defined for the species. The fraction of NPP allocated aboveground is partitioned between stem and foliage growth in a proportion that conserves the allometric relation of the trees, but varies with tree size. The establishment of this proportion can be based on species- and site-specific allometrics for foliage and stem biomass and is represented in 3-PG by two partitioning parameters. Litterfall rate increases with age up to a maximum defined value. For this study, we coded the 3-PG model in Visual-Basic (based on Landsberg and Waring 1997, and Sands and Landsberg 2002). No mortality rate was employed, and the age effect on photosynthesis associated with the hydraulic limitation hypothesis was not implemented because measurements taken in Hawaii showed that stomatal conductance did not differ between 1 (7 meters) and 5 year-old (27 meters) *E. saligna* trees (Barnard 2000).

Hawaii and Brazil trials

The Hawaii fertilization trial and Brazil irrigation and fertilization trial were used for 3-PG calibration due to the fact that they: (i) represented typical high-productive tropical *Eucalyptus* plantations, (ii) had complete C budgets with above- and belowground C allocation estimates during 6 years (Hawaii) or 2 years (Brazil), (iii) had high water and nutrient regime treatments used for calibration, and (iv) presented a control treatment with low fertility (Hawaii) or low water supply (Brazil) for a preliminary test of the model. Although process models should ideally be calibrated for both C and water balances (Waring and McDowell 2002), only the C budget was evaluated in this study because the 3-PG biophysical water submodel had already been shown to adequately estimate the water balance of a clonal *Eucalyptus* trial in Brazil (Appendix I.C).

The Hawaii fertilization experiment was an *E. saligna* (originated from seeds) plantation located 13 km NNE of Hilo (19° 50' N, 155° 07' W) and planted in April 1994. Annual precipitation averages more than 4000 mm/yr, mean annual temperature averages 21.0°C, and the soil is a well-drained, deep (>2 m) Typic Hydrandept. The experimental design consisted of a factorial with two spacings and three fertilization regimes in 3 completely randomized blocks. For this modeling study, just the 3 x 3 m spacing with control and high fertilization regimes were used (control and fertilized treatments). A weather station provided daily averages for photosynthetically active radiation (PAR), air temperature, relative humidity and daily total precipitation, summarized on monthly files. Detailed information regarding the experiment is found elsewhere (Binkley and Resh 1999, Barnard 2000 and Giardina and Ryan 2002).

The Brazil irrigation and fertilization trial (details on Chapter II) was located on the northeastern coast of Brazil, about 20 km SW of Entre-Rios (11° 58' S, 38° 07' W) with a mean annual temperature of 25.5°C and an average rainfall of 1040 mm/yr. The slopes were gentle (< 3%), with deep (> 3 m), excessively drained sandy isohyperthermic Typic Haplustox soil. The plantation was established in June 1996 with an *E. grandis* x *urophylla* clone at 3.0 m x 3.0 m spacing, and treatments were installed when the plantation was 3 years-old. A 2 x 2 factorial with 4 replicates, was used with two-levels of nutrient and water regimes. High fertilization and irrigation regimes (> 2100 mm/yr) were designed to eliminate any nutrient or water limitation on eucalyptus growth. No fertilization effect was observed in the experiment, so we analyzed results as averages across irrigation regimes (rainfed and irrigated treatments), and fertility rating was considered to be 1 (not limiting). A monthly meteorological file with maximum and minimum temperatures, vapor pressure deficit (VPD) and photosynthetically active radiation was derived based on weather data from 2 close meteorological stations (Appendix I.B).

Aboveground woody biomass (AWB) and leaf area index (LAI) were estimated every 3 months (in Hawaii) or 6 months (in Brazil), along with yearly estimates of aboveground net primary production (ANPP), total belowground carbon allocation (TBCA) and gross primary production (GPP) for each plot and year. TBCA was determined by the mass-balance technique (Giardina and Ryan 2002) and represents all C allocated to the roots, while GPP was obtained as the sum of ANPP, TBCA and aboveground autotrophic respiration (Ryan 1991). The Hawaii experiment was used for calibration due to its larger data set. The re-calibration for Brazil conditions allowed the evaluation of the species-specific parameters in the model.

Calibration procedures

The number of parameters to be tuned was minimized by keeping constant all possible site- or species-specific parameters that were locally determined or derived from literature data (Table 3.1). The chosen outputs to evaluate the model during the calibration phase were the yearly estimates of GPP, ANPP, TBCA, average LAI and the AWB at the end of each year. These variables capture three crucial processes: (i) the total amount of C fixed (GPP), (ii) the C allocation pattern (TBCA and ANPP), and (iii) the aboveground partitioning between wood and foliage (AWB and LAI). We estimated TBCA from the model as 2 times the belowground NPP, assuming that respiration equals production (Binkley and Ryan 1998, Law et al. 1999). The tuning process was conducted to simultaneously match predicted and observed values of GPP, ANPP, AWB and LAI (TBCA was not incorporated because it was a linear combination of GPP and ANPP), using a weighted sum of squares (Young et al. 1979), which is a way of normalizing the sum of squares of each variable to its absolute magnitude:

$$WSS = \sum_{i=1}^{v} \frac{n_i \sum_{j=1}^{ni} (P_j - O_j)^2}{(\sum_{j=1}^{ni} O_j)^2}$$

where WSS is the weighted sum of squares, v is the number of variables ($v = 4$), n_i is the number of predicted-observed pairs for the variable i ($n = 6$ and 2 for Hawaii and Brazil), and P_j and O_j are the predicted and observed values. The tuning process used an automated optimization procedure in Visual Basic to minimize WSS with constraints to limit the search within feasible values of the tunable parameters. The optimization routine was initialized several times with different combinations of initial values for the parameters, and the final parameterisation was based on the visual inspection of plotted observed and simulated outputs. As criteria for the goodness of fit of the model, we expected the simulated line to pass within 1 or 2 standard deviations about the observed data points.

Hawaii calibration

The parameters tuned for Hawaii were: fertility rating, coefficient of stomatal response to VPD, and foliage-stem partitioning parameters (Table 3.1). Two tunings were implemented. First, the fertilized treatment data were used, and the fertility-rating parameter was fixed as 1.0. After this calibration, a new tuning was done for the control treatment only for the fertility-rating parameter. The model was initialized using the average 7 month-old biomass (January 1995) and run for 6 years with the same meteorological file for the control and fertilized treatments.

Brazil calibration

The species-specific parameters from the Hawaii *E. saligna* were evaluated for simulating the *E. grandis* x *urophylla* clone production for the irrigated treatment. Next, local SLA, litterfall and allometrics for the clone (see Chapter II) were applied, and tuning was carried out for maximum canopy quantum efficiency and the stomatal response to VPD. With no further tuning, the weather file was changed (without irrigation supply) and the model run to simulate the rainfed treatment. In all cases, the model was initialized at 3.5 years of age (September 1999) and run for 2 years.

Table 3.1. Main parameter values of 3-PG model after calibration for Hawaii (H) and Brazil (B) experimental trials.

Parameter	Hawaii	Brazil	Unit	Source*
NPP/GPP ratio	0.50	0.50	-	Landsberg & Waring 1997
Canopy Quantum Efficiency	0.060	0.080	mol C/mol PAR	Specific (H). Tuning (B)
Specific Leaf Area	10.0	8.5 / 11.0	m^2/kg	Specific (H, B)
PAR Extinction Coefficient	0.5	0.4	-	Specific (H, B)
Age Canopy Cover	1.5	1.5	year	Specific (H, B)
Proportion of Intercepted Rainfall Evaporated	0.15	0.15	-	Lima (1996)
Canopy Albedo	0.2	0.2	-	Landsberg & Waring 1997
Maximum Stomatal Conductance	0.008	0.008	m/s	Mielke et al. 1999
Maximum Canopy Conductance	0.02	0.02	m/s	Landsberg & Waring 1997
Coefficient of Stomatal Response to VPD	0.468	0.324	1/kPa	Tuning (H, B)
Canopy Boundary Layer Conductance	0.2	0.2	m/s	Landsberg & Waring 1997
Maximum Litterfall Rate	0.110	0.070	1/month	Specific (H, B)
Age at which litterfall rate has median value	4	4	month	Specific (H, B)
Foliage/Stem Partitioning DAP=2	1.001	0.096	-	Tuning (H). Specific (B)
Foliage/Stem Partitioning DAP=20	0.212	0.034	-	Tuning (H). Specific (B)
Constant Coefficient at Stem Mass / DAP equation	0.066	0.065	-	Specific (H, B)
Power Coefficient at Stem Mass / DAP equation	2.50	2.68	-	Specific (H, B)
Maximum Fraction of NPP to Roots	0.8	0.8	-	Landsberg & Waring 1997
Minimum Fraction of NPP to Roots	0.25	0.20	-	Landsberg & Waring 1997
Fertility Parameter (FR)	1.00 / 0.85	1.00 - 0.60	-	Tuning (H, B)
Maximum Available Soil Water	300	80/160	mm	Specific (H, B)
Texture Coefficient for Soil Water Modifier	0.7	0.3/0.5	mm	Landsberg & Waring 1997
Power Coefficient for Soil Water Modifier	9	4/7	mm	Landsberg & Waring 1997
Maximum Growing Temperature	40	40	ºC	Sands & Landsberg 2002
Optimum Growing Temperature	22	25	ºC	Specific (H, B)
Minimum Growing Temperature	8	8	ºC	Sands & Landsberg 2002

* Study specific data for Hawaii from Giardina and Ryan (2002) and Giardina et al. (2002), study specific data for Brazil (Chapter II).

Validation: site descriptions and measurements

3-PG performance was evaluated by its ability to predict two years of independent aboveground woody biomass increment measured in forty inventory plots located in five areas of commercial plantations (Table 3.2) in northeastern Brazil (within a 60-km radius of Entre-Rios, 11°58'S, 38°07'W) selected in July of 1999. The final parameterisation obtained for the Brazil experiment was used. Concomitantly, a traditional empirical yield model, based on age, site index and basal area was developed and used as a null-model to estimate the 2 years production of the control plots. This tropical area has a uniform mean annual temperature of 25.5°C and a pronounced inter-annual variability in rainfall (described in Chapter I).

The 6 year-old, first-rotation stands were chosen to capture regional differences in soil and productivity (mean annual increment at age 6 ranged from 7 to 20 Mg ha^{-1} yr^{-1}). All sites were located in flat or modest slopes (< 3%) and site preparation included slash-and-burning of the initial vegetation (pasture, secondary forest or savanna), disking and harrowing. Forests were planted in July of 1993 at 3.5 m x 2.6 m or 3.0 m x 3.0 m spacings and fertilized with 22 kg N ha^{-1}, 36 kg P ha^{-1} and 19 kg K ha^{-1}. The 4 month-old clonal cuttings were produced in a shade-house and selected for uniform size (25 to 35 cm in height) (Stape et al. 2001). Chemicals were applied yearly to control leaf-cutting ants (sulfluramid) and during the first 2 years to control weeds (glyphosate). All stands consisted of monoclonal *E. grandis* x *urophylla* plantations (Clones COP-0204, 0321, 0477, 0670, 1341 or 2361). In each stand, a circular inventory plot of 471 m^2 had been measured yearly since 2 years of age. The diameters at breast height (DBH, at 1.30 m) were measured for all trees, as well as the first 20 heights and the heights of the 4 dominant trees. A high fertilization regime was designed to eliminate any nutrient deficiency and evaluate the fertilization effect on growth. A paired-plot was installed in July of 1999 in each of the stands within 30 meters of the original inventory plot (control plots), with the same form and dimension to be fertilized (fertilized plots). Fertilizers were applied at high rates 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} (as FTE micronutrient fertilizer) 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, applied during 2 years. Trenches (0.25 m wide and 0.80 m deep) between plots minimized any fertilizer effect on the control plots. From July 1999 to August 2001, all paired-plots were measured every 6 months (all DBHs were measured, and heights were estimated with plot-specific hypsometric equations). Aboveground woody biomass (stem plus bark and branches) was estimated between 2 and 4 years-old using a general allometric equation and for measurement at 5 years-old or older local equations were used (Table A.3.4). The annual aboveground woody biomass productions represent the summed growth of individual trees between July 1999 and June 2000, and between July 2000 and June 2001. The site index, defined as the average height of the largest 100 trees per hectare at 5 years-old, was directly determined by the average of the 4 biggest trees in each plot at 5 years-old. Leaf area index was estimated for each plot on July of 1999 and June of 2000 with the regional allometrics (Table A.3.4) and considering an average SLA of 8.5 $m^2 kg^{-1}$ (see Chapter I). On March of 2001 LAI was estimated using optical procedures with a Ceptometer-AccuPAR Model 80 (Decagon Devices, Pullman, USA) (see procedure in Appendix II.B), and the same LAI value was used for June 2001. LAI was interpolated monthly between estimates. For each site, an interpolated meteorological file with monthly PAR, VPD, rainfall and temperatures was created based on daily weather data from local meteorological stations (see Appendix I.B, Table 3.3). A light-use-efficiency was estimated for each year and plot as the ratio between wood increment and APAR. Water holding capacity for each site (a 2 m profile was considered for water budget) was estimated by a general equation developed for the region based on soil texture (Appendix I.A).

Table 3.2. Characterization of the genetics, location, soil taxonomy, soil clay content and total carbon (0 to 0.3 m) of the 40 studied stands of *E. grandis x urophylla*, grouped by area.

Area Nº	Plots (#)	Clones (#)*	Latitude (S)	Longitude (W)	Altitude (m)	Main Soil Order	Clay (%)	Carbon (kg m^{-2})
1	5	2	12º 02'	38º 28'	301	Quartzpsament	13 (7)	3.1 (0.7)
2	20	4	11º 47'	37º 55'	166	Ultisol	29 (10)	3.7 (0.8)
3	3	3	11º 50'	38º 28'	250	Oxisol	22 (3)	3.4 (0.3)
4	7	2	11º 53'	38º 30'	296	Oxisol	16 (3)	2.3 (0.4)
5	5	1	11º 55'	38º 31'	256	Quartzpsament	8 (3)	1.4 (0.3)

* COP-0204, 0321, 0477, 0670 and 1341.

Table 3.3. Rainfall, estimated transpiration and average soil available water (SAW, 0 to 2.0 m) during the two study periods for the 40 stands of *E. grandis* x *urophylla*, grouped by area. Values followed by different letters between years differ at $P = 0.05$.

Area	Rainfall	(mm)	Transp.*	(mm)	SAW*	(mm)
Nº	Wet Year	Normal	Wet Year	Normal	Wet Year	Normal
1	1691	1112	1211	886	65	49
2	2114	1518	1284	1091	116	76
3	1524	1028	1185	883	73	54
4	1520	1001	1180	833	70	52
5	1569	1051	1117	850	58	43
Mean	1845 a	1287 b	1230 a	971 b	92 a	64 b
(SD)	(274)	(234)	(60)	(122)	(25)	(13)

Average VPD wet year = 1.08 kPa, VPD normal year = 1.20 kPa

Rainfall, Transpiration: Area 2 > Area 1 > Areas (3, 4, 5) ($P < 0.001$)

SAW: Area 2 > Areas (1, 3, 4, 5) ($P < 0.001$)

* Transpiration and SAW based on measured and interpolated LAI

Empirical yield-model

The Sullivan and Clutter model (from now on called SC model, Clutter et al. 1983) has been successfully and routinely applied in Brazil for *Eucalyptus* (McTague personnal communication, Campos et al. 1988). This model is derived from two production equations, one for basal area and one for aboveground woody biomass based on age and site index, which are mathematically manipulated to obtain the biomass yield equation:

$$\ln(AWB_2) = \alpha_0 + \alpha_1 S + \alpha_2 / A_2 + \alpha_3 \ln(BA_1) A_1 / A_2 + \alpha_4 (1 - A_1 / A_2) + \alpha_5 S (1 - A_1 / A_2)$$

where BA is basal area ($m^2\ ha^{-1}$), S is the site index (m), A is the stand age (months), AWB is aboveground woody biomass ($Mg\ ha^{-1}$), and α_i are coefficients to be estimated, and the subscripts 1 and 2 on AWB and BA stand for their values at ages A_1 and A_2. The available data from 2 to 6 years-old for the 40 control inventory plots were used to estimate the SC model coefficients using ordinary least square procedures in SAS (Table 3.4).

Table 3.4. Estimated coefficients of the Sullivan-Clutter model based on 40 stands measured yearly between 2 and 6 years-old (control plots). The empirical model predicts the wood biomass (AWB_2, $Mg\ ha^{-1}\ yr^{-1}$) at a future age (A_2, month) based on the initial basal area (BA_1, $m^2\ ha^{-1}$), age (A_1, month) and site index (S, m).

$\ln(AWB_2) = 2.319 + 0.015\ S - 44.508 / A_2 + 0.878\ \ln(BA_1)A_1/A_2 - 0.220\ (1-A_1/A_2) + 0.175\ S\ (1-A_1/A_2)$

$N = 200$

$P < 0.0001$

$R^2adj = 0.942$

Validation: first 3-PG model, and SC model runs

The models were compared by their performance in estimating two growing periods (1999/2000 and 2000/2001), which presented very distinct rainfall totals (wet year with 1845 mm/yr, and normal year with 1287 mm/yr, Table 3.3), for the fertilized (3-PG model, fertility ratings equal 1) and control plots (SC model). The 3-PG model was provided with the initial stand and soil conditions at 6 years-old, together with the respective monthly meteorological files for the two growing years. The monthly growth estimates were summed to obtain the year estimates. For the SC model, basal area at age 6 and site index of the control plots were provided to estimate wood biomass at ages 7 and 8.

Second 3-PG model run

Based on the validation results of wood increments, LAI, and water balance for the first 3-PG run, a slight re-parameterisation was implemented by manually changing the SLA parameter (Figure A.3.1). A second 3-PG run was executed; statistics calculated, and results compared with the first run.

3-PG model run for control plots

Site-specific fertility-rating factors were needed to obtain 3-PG simulated values for the control plots using the second parameterisation. For that purpose, we investigated the use of the fertilization responses as an indirect index for the fertility rating parameter. Fertilization response (FER, in Mg ha^{-1} yr^{-1}) was defined as:

$$FER = (\frac{WNPP_F}{IWB_F} - \frac{WNPP_C}{IWB_C}).(\frac{IWB_F + IWB_C}{2})$$

where WNPP is the wood increment, IWB is the initial wood biomass (at age 6), and the subscripts C and F are for control and fertilized plots. Indeed, this adjusted fertilization response did not differ from the non-adjusted due to the paired-plot design (Figure A.3.2.a). Fertilization responses were evaluated just for the wet year (rainfall > 1500 mm, Table 3.3), because the differences in growth due to fertilization among sites are clearest when water is not a limiting factor (Figure A.3.2.b). Fertilization response did not relate with initial biomass (Figure A.3.3), and no covariate adjustment was needed.

To test if the fertility-rating parameter representation in 3-PG was in line with fertilization responses, we selected the 3 sites with the highest fertilization responses (29.0, 22.9 and 19.0 Mg ha^{-1} yr^{-1}) and 3 sites with no responses (-3.3, -2.3 and -0.8 Mg ha^{-1} yr^{-1}) (Figure A.3.3). For each one, the fertility-rating parameter was tuned to match the wood increment during the wet year. For the high fertilization response sites, the tuned fertility-rating parameters were 0.61, 0.72 and 0.78, while for the non-responsive sites, the fertility-rating parameters were 0.88, 1.01 and 1.10. Due to the coherent directional trend of the fertility-rating values, we estimated all the fertility-rating factors (FR) by scaling between 0.6 (maximum fertilization response, arbitrarily chosen based on highest responsive plot) and 1.0 (no fertilization response), during the wet year (FR = 0.4 (29 – FER)/29 + 0.6), where 29 Mg ha^{-1} yr^{-1} was the highest observed fertilization response. With the site-specific fertility-ratings, 3-PG was run for control plots and compared with the SC model estimates.

Fertilization response and soil fertility and canopy indices

A complete soil and stand characterization were prepared for each site, and a total of 38 soil, 8 bioassay (Table A.3.7) and 16 stand indices (Table A.3.8) were obtained for the control plots. The sampling and laboratory procedures for soil, bioassay and canopy indices are described on Appendix III.A.

Statistical analysis

For each set of simulated and observed aboveground woody biomass production, the following statistics were obtained to help evaluate model performances: model efficiency (EF), root mean square error (RMSE), the *a* and *b* coefficients of the linear relation between predicted (P_i) and observed (O_i) data, and the coefficient of determination (r^2) (Loague and Green 1991):

$$EF = \frac{\sum_{i=1}^{n}(O_i - \bar{O})^2 - \sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2}$$

$$RMSE = \sqrt{\sum_{i=1}^{n}(Pi - Oi)^2 / n}$$

$$P_i = a + b\,O_i \ , \ r^2$$

The best model should have EF and r^2 close to the unity, RMSE close to zero, and *a* and *b* not significantly different from zero and 1, respectively. As we were interested in yearly production estimates, all analyses were done considering a total of 80 observed-simulated pairs (n= 2 years times 40 plots).

Analyses of variances were performed considering fertilization and site (block) as the main effects, with year as a repeated measurement factor for variables estimated for both the wet and normal years: wood increment, LAI, canopy N, canopy P, APAR and LUE. The initial wood biomass of the stands and its interaction with fertilization were tested as potential covariates for the wood increment analysis, but both were shown to be non significant ($P = 0.51$ and $P = 0.33$, respectively) due to the blocking. For variables evaluated just once, or analyzed independently at the beginning or end of the study period, an ANOVA having fertilization and block as the mains effects were used: total soil C, total soil N, and biometric stand attributes. Year and block were the main effects for meteorological data analysis.

To investigate the relation between fertilization response and soil or stand indices, multiple regressions with a stepwise procedure in SAS were used, with fertilization response as the dependent variable and the indices as independent variables. The minimal inclusion significance of a variable was set at $p = 0.10$. Due to the large number of soil independent variables we utilized the following steps to avoid over parameterisation: (i) independent variables were classified into soil-physical, soil-lab incubations, soil-fertility and soil-bioassay groups; (ii) fertilization responses were regressed against the independent variables of each group, separately; and (iii) groups were aggregated by taking, at most, the best 3 variables of each group during the isolated analysis. Residual analysis checked for normality and homocedasticity. For the stand indices no grouping was necessary.

All analyses were performed on SAS 8.1 (SAS Institute Inc., Carry, NC, USA 2001) with multiple comparisons with a significant level of 0.05 to protect against type I error.

Results

Calibration

For the Hawaii trial, a maximum canopy quantum efficiency of 0.060 mol C mol^{-1} APAR was considered because values as high as 0.053 were locally estimated (Giardina et al. 2002). Tuning the coefficient of stomatal response to VPD (k_g, which affects canopy quantum efficiency and allocation to roots) and to the foliage-stem partitioning parameters (which influence wood biomass and LAI estimates) resulted in an adequate time series simulation of the C budget fluxes (GPP, ANPP and TBCA) and the wood biomass and LAI state variables (Table 3.1, Figure 3.1 and Table A.3.1). The model performance for the control treatment was also satisfactorily achieved by decreasing the fertility rating (FR) to 0.85 (Figure 3.2 and Table A.3.2), which reduced canopy quantum efficiency and increased allocation to roots.

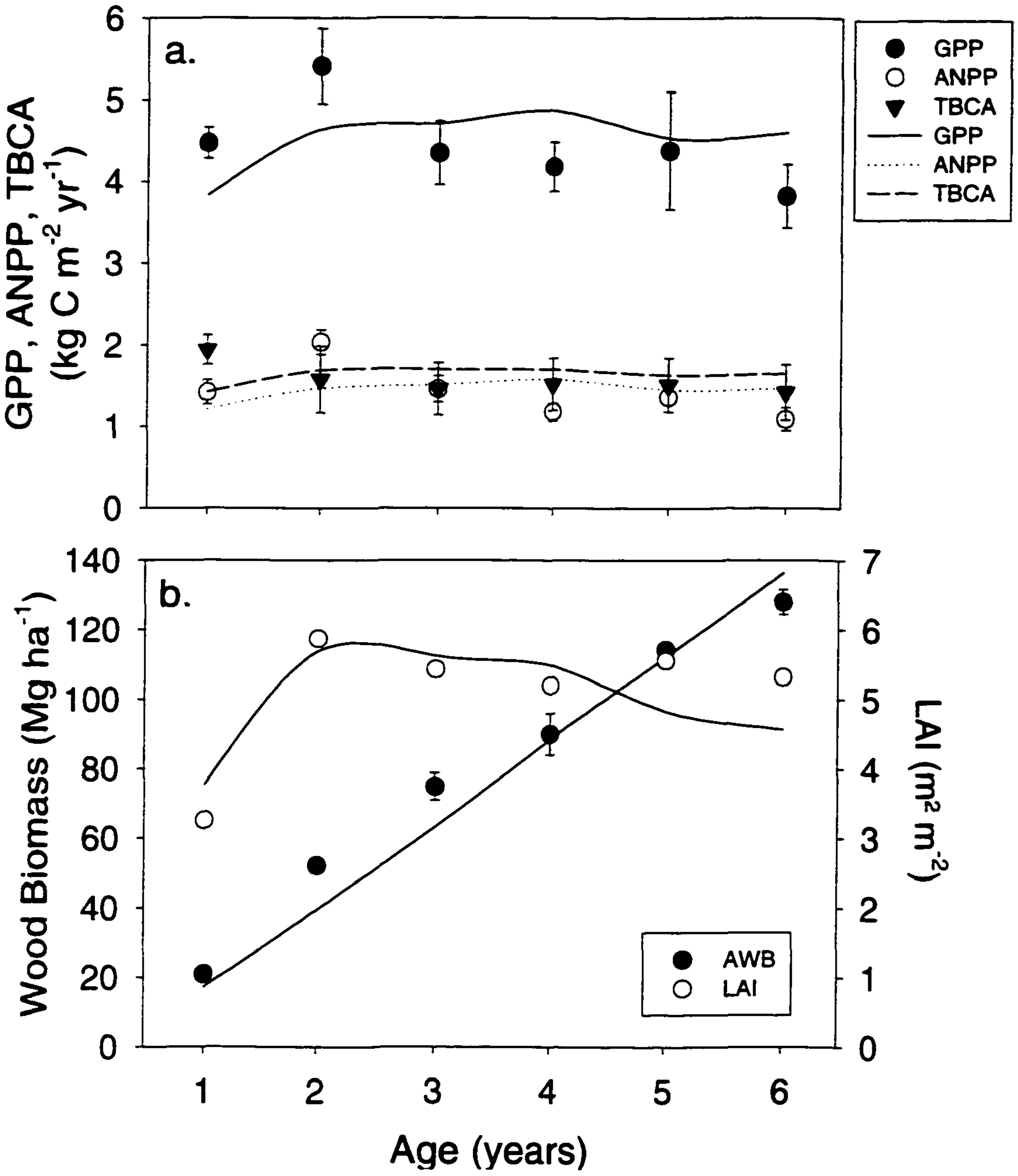


Figure 3.1. Observed (dots with standard deviation bars) and 3-PG simulated (lines) values of GPP, ANPP and TBCA (a), biomass accumulation and LAI (b) for *E. saligna* in Hawaii for the fertilized treatment (fertility rating equals 1.0) after calibration (tuning).

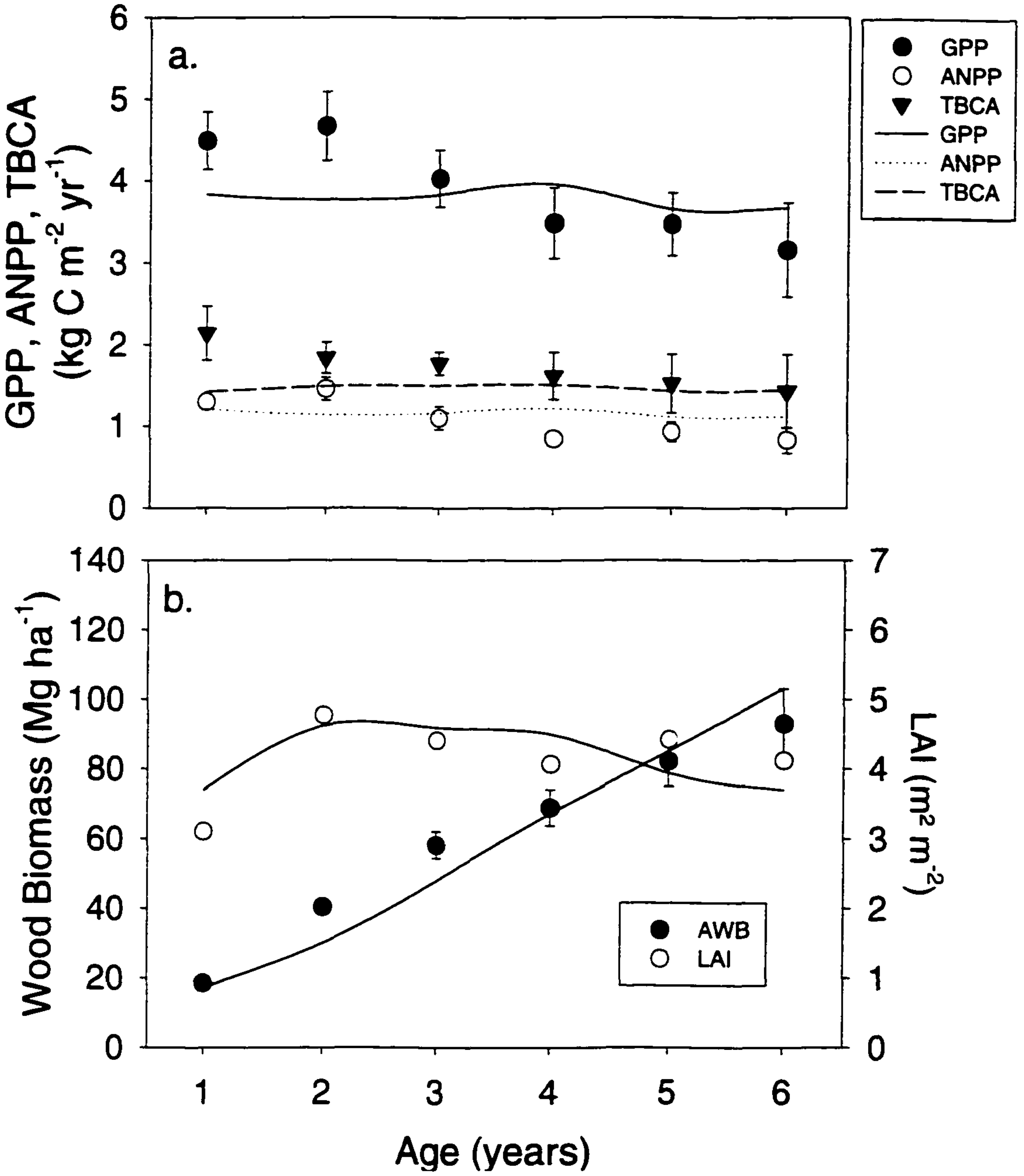
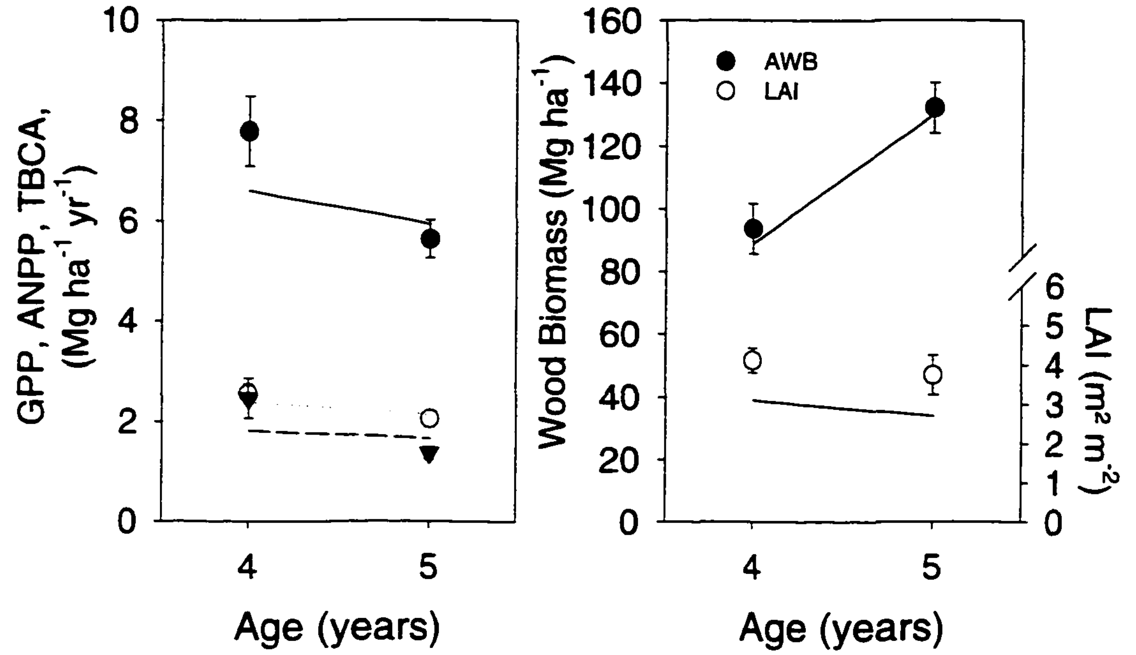


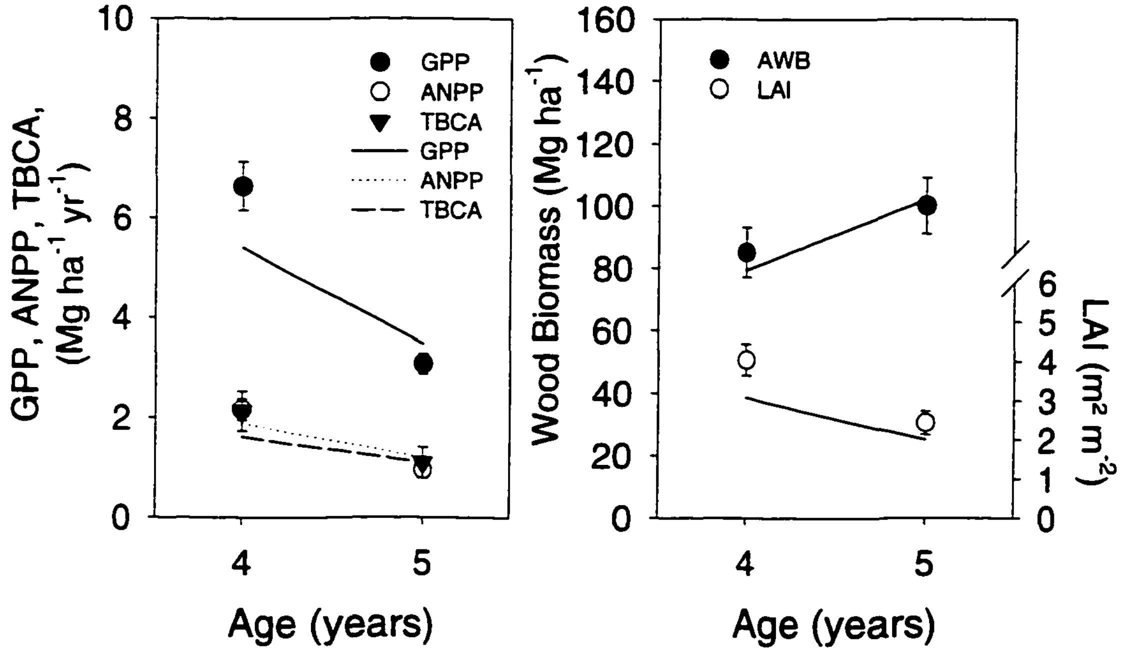
Figure 3.2. Observed (dots with standard deviation bars) and 3-PG simulated (lines) values of GPP, ANPP and TBCA (a), biomass accumulation and LAI (b) for *E. saligna* in Hawaii for the control treatment after calibration by tuning the fertility rating only (FR = 0.85).

Applying the Hawaii calibration of the model to the irrigated clonal *E. grandis* x *urophylla* treatment in Brazil trial led to directionally wrong trends for the C fluxes and LAI, increasing from the first to the second year, instead of decreasing (data not shown). The magnitude and trend of the LAI values were readily adjusted by replacing the foliage-stem partitioning parameters from Hawaii with ones derived from 24 sampled trees in the Brazil trial (see Chapter II, Table 3.1). After this modification, GPP remained low, so a tuning process was carried out for k_g (VPD response) and maximum canopy quantum efficiency, after altering the species-specific parameters based on local data (Table 3.1). The search for quantum efficiency was limited between 0.060 (estimated in the trial, Chapter II) and 0.080 mol C mol^{-1} APAR, and after tuning, the highest value was kept (Table 3.1). Model performance was then considered sufficient, despite the somewhat underestimation of the LAI (Figure 3.3.a and Table A.3.3).

Applying this set of parameters to run 3-PG for the rainfed treatment provided a good simulation of the C fluxes and state variables, except for a slight LAI underestimation (Figure 3.3.b and Table A.3.3). Overall, we considered the calibration for Brazil species and conditions to be satisfactory to begin the validation phase.



a. Irrigated



b. Rainfed

Figure 3.3. Observed (dots with standard deviation bars) and 3-PG simulated (lines) values of GPP, ANPP, TBCA, biomass accumulation and LAI for *E. grandis x urophylla* in Brazil for irrigated treatment (fertility rating equals 1) after calibration (tuning) (a). The same observed and simulated results for the rainfed treatment using the previous parameterisation (b).

Validation

Wood biomass of the 40 stands varied by 3-fold at 6 years of age (42 to 118 Mg ha^{-1}), due to different locations (climate), soil groups and probably clonal genotypes (Tables 3.2 and 3.3). The two production years had distinct rainfall regimes (1845 *versus* 1287 mm, for the wet and normal years, Figure 3.4.a), leading also to higher transpiration rates and available soil water in the root zones for the wet year (Table 3.3). The paired control and fertilized plots did not differ initially for any soil or biometric attributes (Figures A.3.2.a, Figure 3.4.b and Tables 3.5, A.3.5, A.3.9, A.3.10). Wood increments were affected by both fertilization and year, and presented a fertilization-year interaction (Table A.3.11). Increments for both control and fertilized plots were higher for the wet year (29.3 and 37.9 Mg ha^{-1} yr^{-1}, respectively) than for the normal year (15.1 and 17.3 Mg ha^{-1} yr^{-1}) (Figure 3.4.b). Fertilization response was also higher for the wet year (8.6 *versus* 2.2 Mg ha^{-1} yr^{-1}) (Table 3.5), and did not correlate with initial biomass (r^2=0.01, Figure A.3.3).

The SC model effectively described the growth trend of the stands between 2 and 6 years old (r^2=0.94, Figure 3.4.b and Table 3.4), but it was unable to correctly predict the wood production for either wet or normal years (Figure 3.5), underestimating the wood production for the wet year by almost one third (20.2 *versus* 29.3 Mg ha^{-1} yr^{-1}) and overestimating it for the normal year by two thirds (25.0 *versus* 15.1 Mg ha^{-1} yr^{-1}) (Table A.3.6).

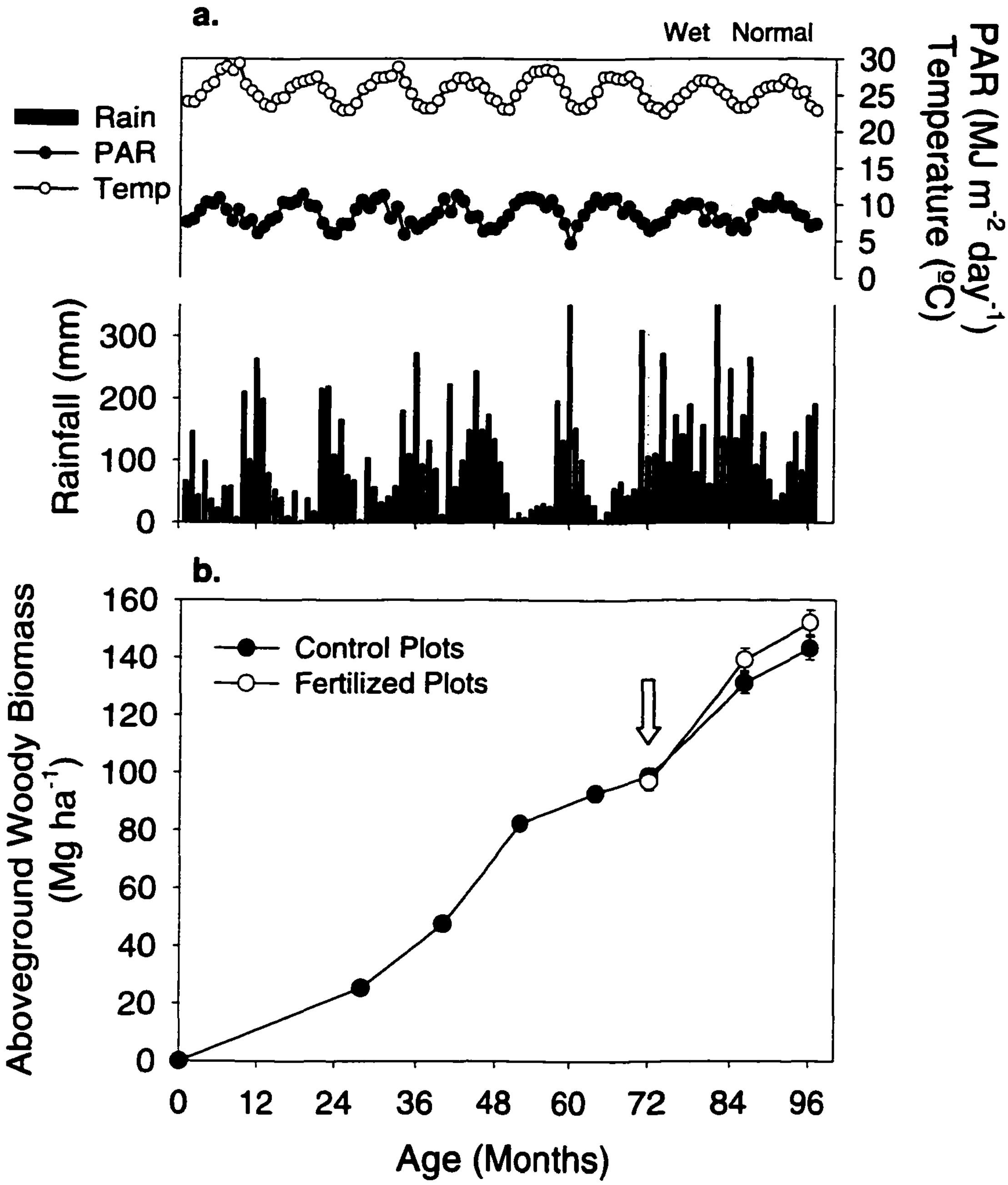


Figure 3.4. Average monthly meteorological variables (rainfall, PAR and temperature) for the complete rotation of the 40 studied sites indicating the last two wet and normal years (a). Average biomass accumulation (and standard error bars) for the control and fertilized plots (b). The arrow indicates the quarterly fertilization initialization.

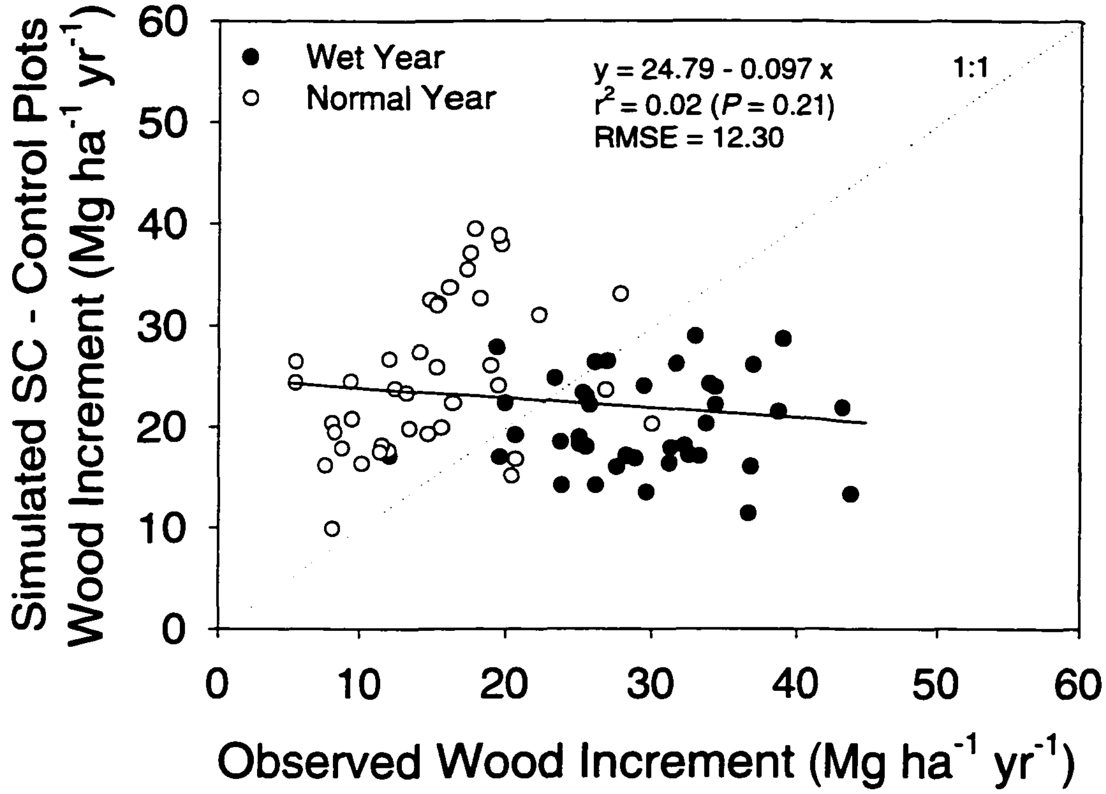


Figure 3.5. Observed and simulated wood increments for the wet and normal years for the SC empirical model on control plots

For the fertilized plots, the 3-PG first run presented a strong correlation between observed and simulated values (r^2 =0.81, Figure 3.6.a), although the slope of the linear regression line (0.48) differed significantly from 1, mainly due to a overestimation of the wood production for the normal year (25.2 versus 17.3 Mg ha^{-1} yr^{-1}). The wet year had satisfactory estimates (36.2 versus 37.9 Mg ha^{-1} yr^{-1}, Table A.3.6, Figure 3.6.a). All statistics for yearly production were consistently better for the 3-PG model simulating the fertilized plots, than for the SC null-empirical model estimating the control plots (Table 3.6).

Table 3.5. Average canopy attributes, absorbed light, wood increment and light-use-efficiency by treatment (control and fertilized) and year (wet and normal), and the respective fertilization response. Values followed by different small letters (between treatments) or capital letters (between years) differ at *P* = 0.05. All significant fertilization responses are presented.

Variable	Year	Control	Fertilized	Response
LAI	Wet Year	3.2 A	3.3	-
($m^2\ m^{-2}$)	Normal Year	2.8 B b	3.2 a	0.4
N content	Wet Year	18.5 A b	20.0 B a	1.5
($g\ kg^{-1}$)	Normal Year	17.6 B b	23.0 A a	5.4
N canopy	Wet Year	7.1 A b	8.0 a	0.9
($g\ m^{-2}$)	Normal Year	5.2 B b	8.6 a	3.4
P content	Wet Year	1.12	1.17 B	-
($g\ kg^{-1}$)	Normal Year	1.10 b	1.72 A a	0.62
P canopy	Wet Year	0.43 A	0.48 B	-
($g\ m^{-2}$)	Normal Year	0.32 B b	0.62 A a	0.30
APAR	Wet Year	20.7 A	21.1	-
($TJ\ ha^{-1}\ yr^{-1}$)	Normal Year	19.7 B b	21.4 a	1.70
Wood	Wet Year	29.3 A b	37.9 A a	8.6
Increment	Normal Year	15.1 B b	17.3 B a	2.2
($Mg\ ha^{-1}\ yr^{-1}$)				
LUE	Wet Year	1.41 A b	1.79 A a	0.38
($g\ MJ^{-1}$)	Normal Year	0.77 B	0.80 B	-

A re-parameterisation of 3-PG was implemented (Figure A.3.1) because the overestimated wood production during the normal year was also associated with both a very low simulated LAI compared with observed values (1.7 *versus* 2.5 m^2 m^{-2}, Table A.3.6 and Figure 3.8.a) and with no soil water deficit (data not shown), despite the low soil available water (Table 3.3). Among the tunable parameters that could affect LAI, model sensitivity was high for the specific leaf area (SLA), which was changed from 8.5 to 11.5 m^2 kg^{-1} (Chapter I), resulting in a better simulation ($r^2 = 0.83$, higher slope, Table 3.6, Figure 3.6.b). This second 3-PG run for the fertilized plots adequately predicted wood increments (≅ 36 Mg ha^{-1} yr^{-1}) and LAI (3.3 m^2 m^{-2}) for the wet year, and improved estimates for the normal year, increasing LAI (from 1.7 to 2.3 m^2 m^{-2}) and soil water deficits (data not shown), and decreasing production (from 25.2 to 21.0 Mg ha^{-1} yr^{-1}, Table A.3.6). No further parameter tunings were done.

This final parameterisation of the model was used to simulate control plot production after scaling a fertility-rating factor for each site (Figure 3.7). The observed and simulated results were strongly correlated ($r^2 = 0.71$), with a high slope coefficient (0.63) and small RMSE (Table 3.6). Across the 40 sites, the observed and simulated wood increments and LAI for wet year were equivalent (29.3 *versus* 30.3 Mg ha^{-1} yr^{-1}, 3.1 *versus* 3.1 m^2 m^{-2}), but small differences persisted for the normal year (15.1 *versus* 18.3 Mg ha^{-1} yr^{-1}, 2.8 *versus* 2.0 m^2 m^{-2}) (Table A.3.6, Figure 3.8.b). The superior predictive ability of the 3-PG model for the yearly productions of the control plot relative to the SC model was clear (Table 3.6, Figures 3.5, 3.7 and 3.8.b).

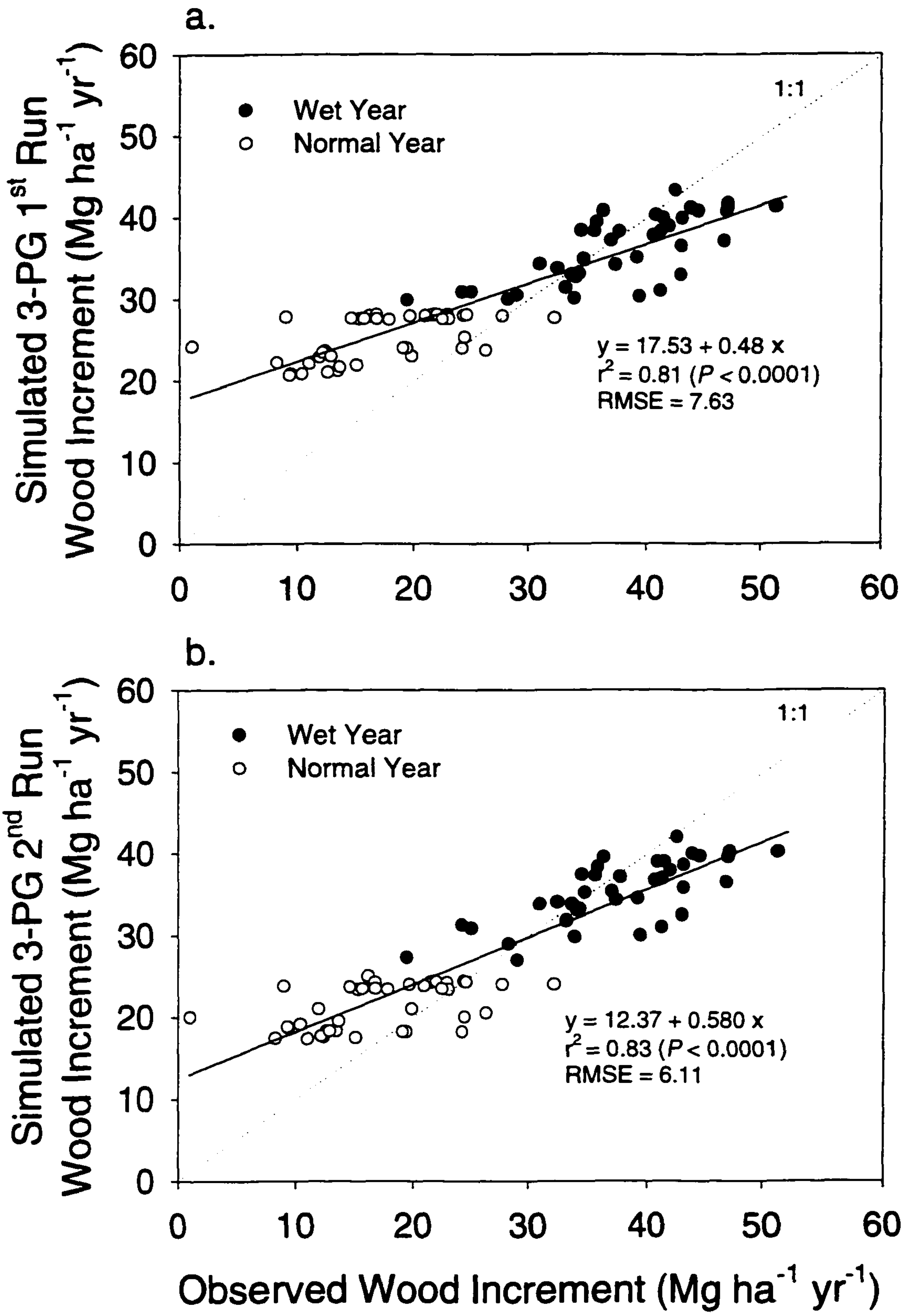


Figure 3.6. Observed and simulated wood increments for the wet and normal years for 3-PG model on fertilized plots before (a) and after re-parameterisation (b).

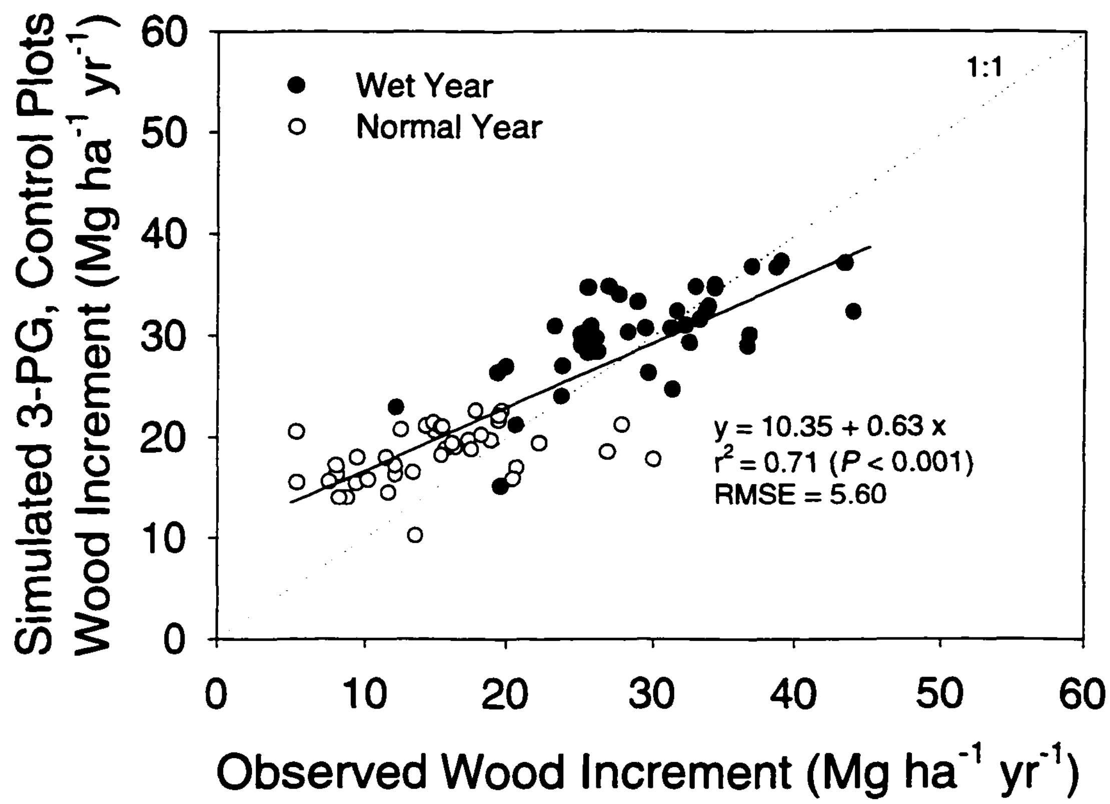
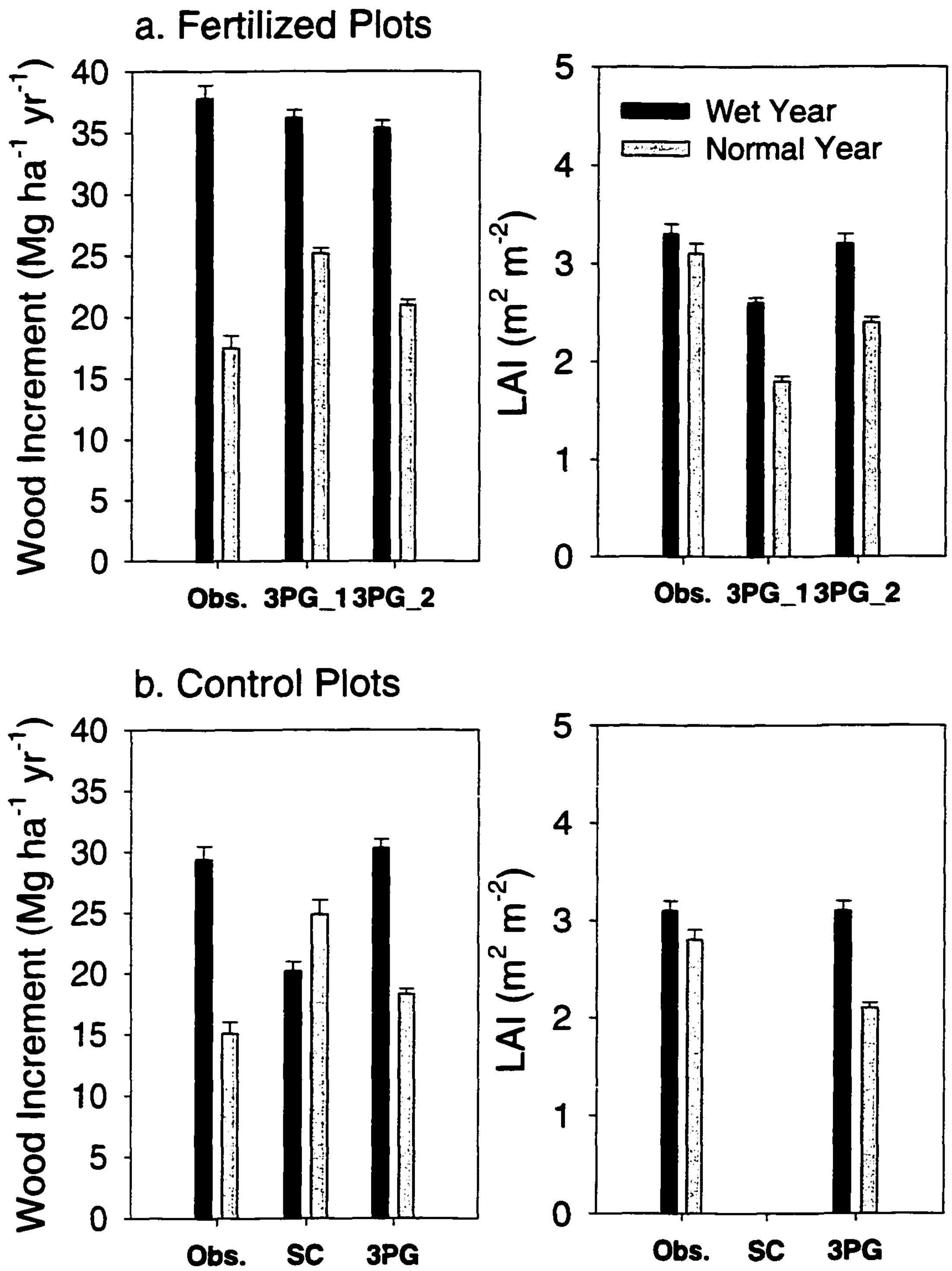


Figure 3.7. Observed and simulated wood increments for the wet and normal years for 3-PG model on control plots.

Table 3.6. Summary of the statistics between observed and simulated wood increment values for both years (N = 80).

Model	SC	3PG 1st Run	3PG 2nd Run	3PG
Plots	Control	Fertilized	Fertilized	Control
Intercept *a*	24.79 (1.87)	17.53 (0.79)	12.37 (0.91)	10.35 (1.08)
Slope *b*	- 0.10 (0.08)	0.48 (0.03)	0.58 (0.03)	0.63 (0.04)
R^2	0.02	0.81**	0.83**	0.71**
RMSE	12.30	7.63	6.11	5.60
Model Efficiency	-0.68	0.61	0.75	0.65

** $P < 0.001$



a. Fertilized Plots

b. Control Plots

Figure 3.8. Average (with standard error bars) wood increment and LAI for the observed (Obs.) and 3-PG first (3PG_1) and second (3PG_2) runs of the 40 fertilized plots (a), and for the observed (Obs.), SC and 3-PG run of the 40 control plots (b) during wet and normal years.

Fertility indices

Very few fertility indices correlated with the fertilization response in the wet year (Table A.3.7). No physical or bioassay indices presented a correlation with fertilization response, while 8 fertility indices showed a negative correlation (mineral N extracted with boiling salt solution, extractable P, extractable K, extractable Mg and cation exchange capacity, from 0 to 15 or 0 to 30 cm depth, Table A.3.7). Interestingly, the majority of the fertility indices correlated negatively (although not all were significant) with the fertilization response (Table 3.7), indicating stronger responses on less fertile soils. Using the stepwise procedure, extractable potassium at 0-0.15 m, phosphorus at 0-0.30 m and cation exchange capacity at 0-0.15 m explained 56% of the variation of the fertilization response. We developed a soil fertilization response index (SFRI) with the linear combination of these soil attributes (Figure 3.9.a). Among the stand properties, only canopy N and canopy P (Tables 3.5 and A.3.8) presented a slight negative correlation with fertilization response. Stepwise procedure retained just N in the model (Table 3.13); fertilization response tended to decrease as the content of N in the canopy increased, which we termed canopy fertilization response index (CFRI, Figure 3.9.b).

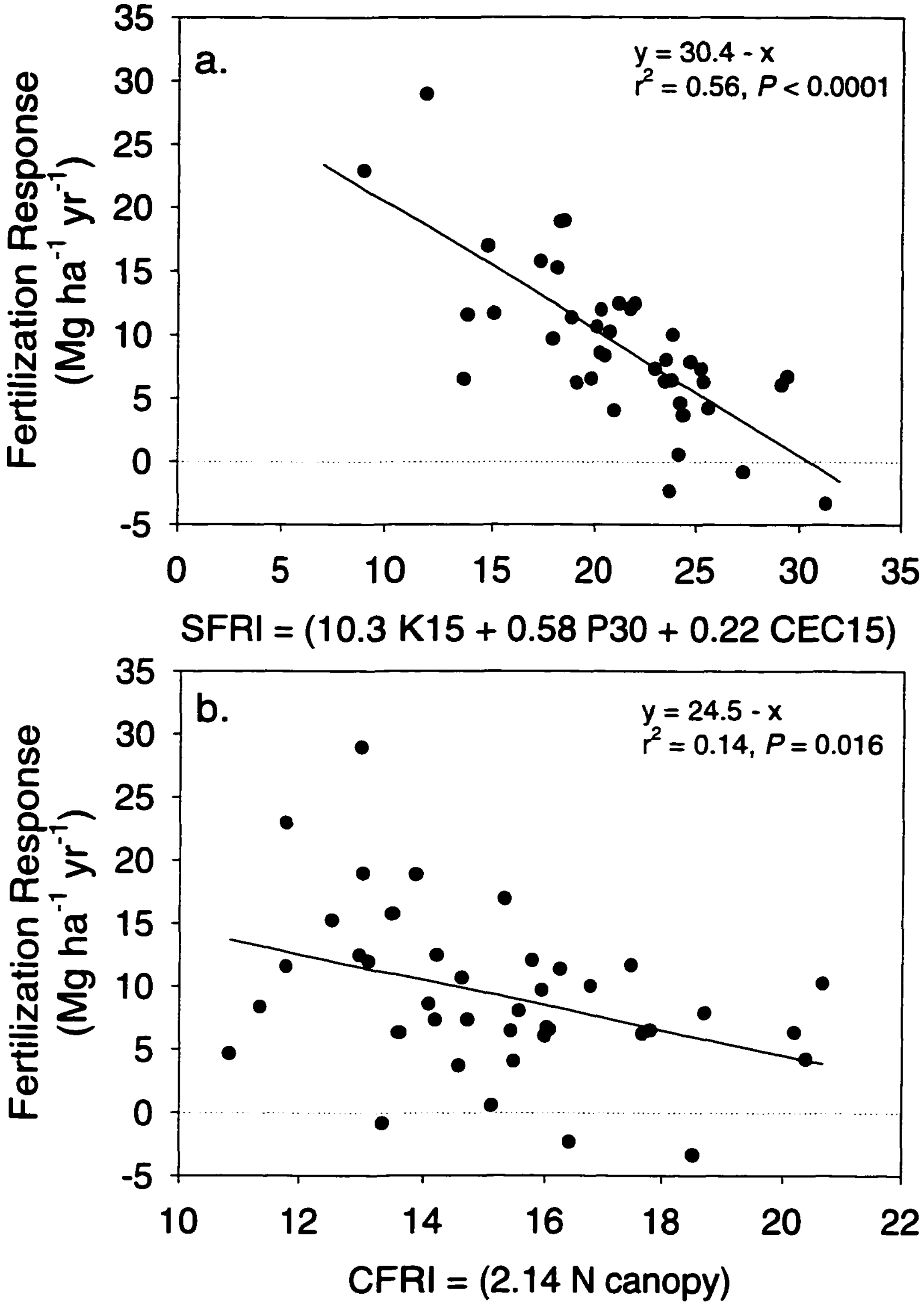


Figure 3.9. Relationship between fertilization response of the 40 stands during the wet year, and soil fertilization response index (SFRI) (a) and canopy fertilization response index (CFRI). K15 = K in mmol$_c$ kg^{-1} at 0-015 m, P30 = P in mg kg^{-1} at 0-0.30 m, CEC = CEC in mmol$_c$ kg^{-1} at 0-015 m, N canopy = N in the canopy in g m^{-2}

Discussion

From the 38 parameters needed to run 3-PG, we tuned a maximum of 3 for each calibration step. The majority of the parameters were locally assessed or obtained from other studies. Maximum canopy quantum efficiency, foliage-stem partitioning parameters and stomatal response to VPD (or the maximum stomatal conductance) were the key parameters tuned in this study, and are recognized as the most influential ones through sensitivity analyzes performed in other studies (Landsberg and Waring 1997, Law et al. 1999, Waring and McDowell 2002, Landsberg et al. 2000).

The complete C budgets from the fertilization and irrigation experiments were critical for the calibration of the 3-PG model and the partial evaluation of its descriptive structure of C fixation, and above- and belowground C allocation. For both the Hawaii and Brazil trials, the calibration using the treatments with the highest supplies of nutrients and water set the fertility and soil moisture modifiers fixed as 1, and let the vapor pressure deficit be the primary modifier control on both C fixation (by affecting canopy quantum efficiency) and allocation (by affecting root partitioning). Under these circumstances, model calibration was achieved satisfactorily. Averaged across years 2 to 6, 3-PG simulated an average GPP of 4.6 kg C m^{-2} yr^{-1} with 36% allocated belowground for *E. saligna* in Hawaii, which is practically identical to the observed GPP of 4.4 kg C m^{-2} yr^{-1} with 34% allocated belowground (Table A.3.1, Figure 3.1). For Brazil, simulated GPP was 6.3 kg C m^{-2} yr^{-1} (28% allocated belowground), well within the 95% confidence interval for estimated GPP of 6.7 kg C m^{-2} yr^{-1} (and 28% allocated belowground) (Table A.3.3, Figure 3.3.a).

After these calibrations, 3-PG runs for the control treatments in each trial were a test for the way the model described effects of nutrition (Hawaii) or soil water (Brazil) on C fixation and belowground allocation. Across all years, decreasing fertility rating from1.0 (fertilized) to 0.85 (control), 3-PG estimated a GPP of 3.7 kg C m^{-2} yr^{-1} with 40% being allocated belowground, almost identical to the observed average GPP value of 3.7 kg C m^{-2} yr^{-1} and 43% allocated belowground (Table A.3.2 and Figure 3.2). The Brazil simulation of the rainfed treatment estimated average GPP as 4.4 kg C m^{-2} yr^{-1} (31% allocated belowground), well within the 95% confidence interval for estimated GPP of 4.8 kg C m^{-2} yr^{-1} (32% allocated belowground) (Table A.3.3 and Figure 3.3.b). These results seem to support the model's description of both water and nutrient effects on C gain and allocation.

GPP estimates for *E. saligna* in Hawaii stayed practically constant over years (Figure 3.1 and 3.2), which resulted from the almost uniform meteorological conditions (and LAI). The 3-PG model has an "age effect modifier" (associated with the hydraulic limitation hypothesis), but this was not activated. The causes of the age-related decline of forest production, prominent in fast-growing plantations, are still under investigation (Ryan et al. 1997, Binkley et al. 2002, Smith and Long 2001).

The production ecology of *E. saligna* in Hawaii clearly differed from that of *E. grandis* x *urophylla* in Brazil, so it is not surprising that the Hawaii calibration was not sufficient for Brazil. *E. saligna* in Hawaii allocated more C to foliage NPP than the Brazilian *E. grandis x urophylla* clone (9 and 4% of GPP, respectively, Giardina et al. 2002 and Chapter II) and the allometrics (tuned for Hawaii and established for Brazil) efficiently captured these trends. Local climate also influences LAI (Waring 1983, Hatton et al. 1998), and the wetter Hawaiian site supported more LAI. The two genotypes also presented distinct parameter values for stomatal response to VPD, canopy quantum efficiency, and litterfall rates, with the Brazil clone being less sensitive to VPD, having higher canopy quantum efficiency and lower litterfall rates. Although the tuned parameters have an unknown degree of uncertainty, they evidence the potential use of process-based models as a framework for breeding programs by identifying the important parameters that control production, and assessing their natural variability among the population (Blake and Suiter 1988, Jarvis et al. 1989).

The empirical structure of the SC model makes it naturally insensitive to inter-annual climatic variations (Clutter et al. 1983, Kimmins 1997). Nevertheless, this adequately fitted SC model was useful to highlight the under- and over-estimation errors associated with the use of empirical model estimates as a surrogate for a specific year production in areas with high climatic variations (Figure 3.5). In contrast, the behavior of 3-PG even for the first run (Figure 3.6.a) showed its generality and flexibility to accommodate distinct sites and weather conditions, especially considering its minimal calibration for just one *Eucalyptus* clone in one experimental trial. The diversity of clones (Table 3.2) among the sites, and differences in environmental conditions (Table 3.3) probably contributed to reduce the performance of the model. The inadequacy of the simulated LAI in the first 3-PG run can be credited to an inadequate calibration phase that had already shown an underestimation of the LAI (Figure 3.3.a). LAI is the most important state variable in APAR-like models because it integrates C and water fluxes (Law et al. 1999). In our study, the second 3-PG run with an increased SLA (from 8.5 to 11.5 $m^2\ kg^{-1}$) resulted in larger simulated LAI and lower wood production (Figure 3.6.b), because higher transpiration rates induced water deficits that counteracted the potential increase in C fixation with the larger LAI. SLA was the only parameter manually changed for the second 3-PG run; other parameters that directly affect LAI (litterfall, foliage:stem partitioning parameters) or water balance (rainfall interception, available soil water) should be better investigated in a second calibration with the irrigation trial. Moreover, shedding of leaves by *Eucalyptus* in response to drought is common in the region (Chapter II) and should be added explicitly to the model given the relevance of LAI (Landsberg and Waring 1997, Sands and Landsberg 2002).

The description of root C allocation in 3-PG as a function of both soil fertility and environmental harshness (water deficit) predicts higher fertility influences for wetter conditions (Stape et al. 1997, Fisher and Binkley 2001). Indeed, 3-PG simulated fertilization responses of 5.1 and 2.7 $Mg\ ha^{-1}\ yr^{-1}$ for the wet and normal year, respectively (Table A.3.6), in line with the observed values of 8.6 and 2.2 $Mg\ ha^{-1}\ yr^{-1}$. Furthermore, the model correctly estimated a higher light-use-efficiency for the fertilized plots during the wet year, but not during the normal year (Table 3.5 and A.3.6). These results show that an adequate description of the C allocation process is crucial for the correct yearly estimates of wood production for *Eucalyptus* in areas with large interannual climatic variability and intense silvicultural practices.

Predictions of wood increment and LAI were reasonable for control plots with the 3-PG model (Figure 3.8.b, Table A.3.6), indicating that the fertility-rating scheme (based on fertilization responses) was adequate. The absence of correlation between fertilization responses and mean annual increment or site index ($r^2 < 0.04$, Table 3.12) made clear that soil fertility needs to be considered as an independent concept. In this region, MAI and site index correlate well with water supply (see Chapter I), and the adequate evaluation of soil fertility restrictions among stands depends on the occurrence of years with regional large rainfall rates or the use of the fertilized paired-plot design (Hart and Binkley 1985). Fertilization responses as a function of soil properties are species-, region- and management-specific (Hart et al. 1986, Gale et al. 1991), and in particular for our study (same basic genotype, management and geology) a soil fertilization response index could be derived (Figure 3.9.a) to predict the fertility-rating parameter. The use of fertilized paired-plots associated with the plantation inventory network over a regional area can be proposed to be used as a process-based modeling tool to estimate the fertility rating factor. Alternativelly, N in the canopy showed up as a more general index, which is in line with the observed increase in LAI (Figure A.3.4) and leaf nutrient content (Table 3.5) on fertilized plots.

In Brazil, LAI is not assessed during inventory surveys on a regular basis (Campos et al. 1988), but this could be implemented easily using light meters (Cuttini et al. 1998), and would provide essential information for process-based APAR model evaluations for tropical plantations.

Conclusions

The empirical yield model was adequate to describe growth for average environmental conditions, but inadequate for a climate that varied between years. Moreover, the empirical model was not sensitive to management factors that would drive production beyond or below historic average situations.

The adaptation of the 3-PG process-based model for tropical *Eucalyptus* plantations was relatively easily achieved through model calibration and testing using complete C budget data from trials with water and nutrient manipulations. For these trials, after 3-PG calibration for the treatments with no-limiting resources, the model representation of the effects of soil water deficit and soil fertility over C gain and allocation was supported by the experimental results of the control treatments.

The use of the paired control-fertilized inventory plots design allowed both the 3-PG validation for the fertilized condition and the identification of a protocol to scale fertility index among sites based on the fertilization responses. Although soil attributes were identified as adequate predictors of these fertilization responses (K, P and CEC), quantifying nitrogen in the canopy sounded like a more generalist approach.

Estimates of LAI were critical for model behavior due to LAI's strong influence over transpiration, and consequently soil water deficit. After the slight re-parameterisation, improving LAI predictions, performance of this moderately tuned model was quite satisfactory to simulate the large observed range of *Eucalyptus* production.

The simulated growth values between 10 and 42 Mg ha^{-1} yr^{-1} (average of 26 Mg ha^{-1} yr^{-1}) for all plots and years was highly correlated (r^{-2} = 0.78, n = 160, P < 0.0001) with the observed values between 2 and 51 Mg ha^{-1} yr^{-1} (average of 25 Mg ha^{-1} yr^{-1}). These results indicate that species- and site-specific parameters that affect LAI are particularly important to be adequately estimated or tuned, and for our study further tuning would likely improve the model's case-specific usefulness.

Overall, the APAR model approach required a reasonable level of localized tuning, and was able to predict yearly growth better than the SC empirical approach. The superiority of the APAR model was especially evident in capturing the effects of interannual variations in precipitation and fertilization effects in northeastern Brazil. We concluded that the 3-PG model presented high suitability to be incorporated as a management tool for *Eucalyptus* plantations, which will require LAI assessment by inventory surveys.

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APPENDIX I.A

Soil texture, fertility, total C and N, and water holding capacity

Soil texture was determined by the hydrometer (Bouyucous) procedure. Soil pH was determined in 0.01M $CaCl_2$ with dry weight/volume ratio of 1:2.5. The suspensions were swirled for 5 minutes, and after 30 minutes the pH electrode was placed in the sediment for reading. Extractable P, K, Ca and Mg were determined using 2.5-g of dry soil, 25 mL of water and a 2.5mL of cationic and anionic resins (Amberlite IR-120, Amberlite IRA-420) shaken during 16 hours. After this period, resins were separated from soil and 50 mL of 0.8N NH_4Cl and 0.2 N HCl solution was added and swirled for 1.5 hour. 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) (Raij et al. 1999). 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.

Water holding capacity for each site was determined based on regression model developed with water retention data established during the soil survey of the company (Kreijc 1998) using the pressure plate technique (Richards, 1965) for moisture content at -0.03 (field capacity) and -1.5 MPa (permanent wilting point). Particle size distribution, bulk density and total C were used as independent variables as suggested by Gupta and Larson (1979) and Ritchie et al. (2000) models and a stepwise procedure was implement to select the significant variables (SAS 2001). The final model retained just sand and clay fractions as predictors of water holding capacity:

$$WHC = 0.1503 - 0.137.Sand - 0.057.Clay \quad (r^2 = 0.21,\ n=654,\ P<0.001)$$

where *WHC* is the water holding capacity (g g^{-1}) and *Sand* and *Clay* are the particle fractions (g g^{-1}).

APPENDIX I.B

Monthly meteorological variable estimates

Daily weather data from 9 meteorological stations were available from 1990 to 2001, 7 belonging to Copener Florestal and 2 from the official Brazilian Meteorological Institute (INMET; Figure 1.1). 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 (p_{sat}) were estimated based on maximum (TX) and minimum (TI) temperatures:

$$p_{SAT} = (0.61078.e^{(17.269*TX/(237.3+TX))} + 0.61078.e^{(17.269*TI/(237.3+TI))})/2$$

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, and average insolation ratio indexes (actual divided by potential sunshine hours) were derived by month and for 3 rainfall classes (zero, between 1 and 10 mm day^{-1}, and greater than 10 mm day^{-1}). All daily data sets were verified and missing temperature and humidity were estimated from the closest meteorological station. Missing sunshine hours were estimated based on month and rainfall using the insolation ratio index of the closest meteorological station. Total short-wave incoming solar radiation was estimated based on Angstron-Prescott equation which relates radiation and insolation ratio :

$$\phi_s = \phi_E (a + b\frac{ns}{nh})$$

Where ϕ_S is the shortwave incoming radiation, ϕ_E is the extraterrestrial shortwave radiation, *ns* is the actual number of sunshine hours, *nh* is daylength in hours, and *a* and *b* are parameters to be estimated for each location. Extraterrestrial shortwave radiation and daylenght were estaimated based on a latitude algorithm, and we used *a* and *b* values proposed for Brazilian conditions by Ribeiro (1980) (*a* = -0.4192 + 0.6971 cos (Latitude); and *b* = 0.52). The photosynthetically active radiation (PAR, wavelengths between 370 and 700 nm) was estimated daily for each station as a fraction of the incoming short-wave radiation. This fraction varied from 44% on sunny days (ns/nh greater than 0.8), 56% on cloudy days (ns/nh lower than 0.2) and 50% on intermediate ones (Pereira et al. 1997). Daily net radiation, used for transpiration estimates (Appendix I.C), was calculated as the sum of net short- and longwave radiations. Net short-wave radiation was the incident shortwave radiation times (1-albedo), and an albedo of 0.20 was used. Net long-wave radiation was estimated after Brunt (1952) (Pereira et al. 1997) using average daily temperature, insolation ratio and relative vapor pressure. For each site, a daily meteorological interpolated data set was created based on meteorological stations located within 30-km radius of the site. Interpolation was done by weighting their meteorological values inversely proportional to their distances to the site. The monthly files were then derived including an estimate of potential evapotranspiration (Thornthwaite and Matter 1951) and transpiration based on Penman-Monteith model (Appendix I.C). Average available water holding capacity and outflow (drained out of the 2m profile) was calculated for each site.

APPENDIX I.C

Transpiration estimates

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

$$\lambda E_c = \frac{sR_n + \rho c_p D g_a}{s + \gamma(1 + g_a / g_c)}$$

where λ (J kg^{-1}) is the latent heat of vaporization of water, E_c (mm month^{-1}) is the canopy transpiration, *s* (kPa °C^{-1}) is the slope of the saturation vapor pressure curve for water, R_n (J m^{-2} month^{-1}) is the net radiation (Appendix B), ρ (kg m^{-3}) is the density of air, c_p (J kg °C^{-1}) is the specific heat of air at constant pressure, D (kPa) is the vapour pressure deficit, γ (kPa °C^{-1}) is the psychrometric parameter, g_a (m s^{-1}) is the aerodynamic conductance and g_c (m s^{-1}) is the canopy conductance. We used a fixed g_a of 0.20 m s^{-1} based on values obtained by Mielke et al. (1999). Canopy conductance (g_c) was estimated monthly using the algorithm proposed by Landsberg and Waring (1997) on the 3-PG model where g_c is controlled by the most restrictive factor for transpiration: vapor pressure deficit or soil water limitation. Soil water balance was obtained as the difference between transpiration estimated by Penman-Monteith model and precipitation (interception of 15%).

Before its implementation, the algorithm was calibrated for an experimental area of *E. grandis* x *urophylla* in the region where soil moisture was gravimetrically evaluated weekly in a 2 m profile and LAI (averaged 2.8 m^2/m^2) was monitored during 1.7 years. The maximum canopy conductance for each month was derived from maximum stomatal conductance (0.008 $m\ s^{-1}$ for *E. grandis* x *urophylla* in the region, Mielke et al. 1999) times the LAI, up to a maximum canopy conductance of 0.02 $m\ s^{-1}$ (Mielke et al. 1999). This maximum value was then corrected by vapor pressure (f_D) or soil water (f_θ) multiplicative modifiers. The vapor pressure modifier was estimated based on the vapor pressure deficit (D) and on a coefficient of stomatal response to vapor pressure deficit (k_g). The soil water modifier was estimated based on the soil moisture ratio (r_θ) and soil-related parameters (c_θ,n_θ) which expressed the soil particle size distribution effects on the water availability dynamics. We started evaluating the algorithm using the values for k_g, c_θ, and n_θ suggested by Landsberg and Waring (1997) for our site characteristics (*Eucalyptus*, clay soil). We tunned the soil parameters (c_θ,n_θ), and on a second step, changed the coefficient of stomatal response to vapor pressure deficit (k_g). The improvement on the algorithm behavior was significant (r^2 = 0.96, Figure A.1.1), and no more tuning was done.

APPENDIX I.D

Supplemental Tables and Figures from Chapter I

Table A.1.1. Meteorological averages for the rotation period of the stands. Averages by productivity classes are presented and values followed by different letters differ at P = 0.05. VPD and PET stand for vapor pressure deficit and potential evapotranspiration.

Site	Temperature	Annual Rainfall (mm)			VPD	PET
Nº	(ºC)	Average	Minimum	Maximun	(kPa)	(mm yr^{-1})
1	25.5	882	731	1129	1.46	1484
2	25.3	916	616	1172	1.42	1448
3	25.4	853	538	984	1.58	1461
4	25.2	935	576	1001	1.47	1416
5	25.2	902	584	965	1.31	1424
6	25.2	955	606	1021	1.43	1422
7	25.8	1143	1083	1302	1.45	1525
8	25.4	958	822	1173	1.35	1473
9	25.6	1008	646	1160	1.38	1483
10	25.8	1131	679	1292	1.49	1529
11	25.6	1054	647	1168	1.38	1484
12	25.7	1605	1161	2136	1.30	1497
13	25.7	1611	1095	2001	1.29	1496
14	25.7	1654	1134	2081	1.28	1493
Low	25.3	897 c	609 c	1050 c	1.45 a	1446
Medium	25.5	1016 b	789 b	1164 b	1.40 a	1475
High	25.7	1411 a	943 a	1735 a	1.35 b	1499

Min. Temp = 21.0 ± 0.4 ºC, Max. Temp = 29.8 ± 0.3 ºC, Wind Speed = 5.4 ± 0.5 m/s and 32% of the rainfall occurred during the dry season (October to March).

Table A.1.2. Soil analysis results for pH and labile P, K, Ca and Mg (0 to 0.6 m). Averages by productivity classes did not differ at *P* = 0.05.

Site	pH	P	K	Ca	Mg
	Ca Cl_2	kg ha^{-1}			
1	3.8	32	23	680	72
2	4.0	26	202	480	121
3	4.1	20	46	520	194
4	4.1	20	241	160	97
5	4.1	24	54	680	315
6	3.9	18	70	420	182
7	4.1	16	23	680	72
8	3.7	36	23	520	72
9	3.8	10	140	400	73
10	4.6	22	210	1680	315
11	4.0	18	62	240	145
12	4.5	12	312	124	72
13	5.0	30	132	2080	291
14	4.4	10	85	680	218
Low	4.0	24	114	504	160
Medium	3.9	20	64	505	100
High	4.6	18	161	960	208

Table A.1.3. Average root-to-aboveground biomass ratio ($R{:}A_T$) per site and tree size (n=3). Averages by productivity classes followed by different letters differ at $P = 0.05$.

Tree size Site	Suppressed	Codominant	Dominant	Average
1	0.30	0.25	0.30	0.28
2	0.30	0.27	0.36	0.31
3	0.25	0.25	0.25	0.25
4	0.20	0.27	0.24	0.24
5	0.17	0.27	0.20	0.21
6	0.28	0.23	0.24	0.25
7	0.29	0.26	0.28	0.27
8	0.22	0.27	0.30	0.26
9	0.22	0.17	0.23	0.21
10	0.19	0.18	0.20	0.19
11	0.22	0.18	0.15	0.18
12	0.26	0.26	0.26	0.26
13	0.18	0.16	0.15	0.16
14	0.17	0.12	0.17	0.16
Low	0.24	0.26	0.27	0.26 a
Medium	0.25	0.23	0.26	0.25 a
High	0.20	0.18	0.19	0.19 b

Table A.1.4. Allometric equations coefficients by site using the general relationship: $W_i=a_i\ DBH^{b_i}$. For all sites n=9 and all regressions were significant at $P=0.01$. For stem, branch and coarse root compartments the slope parameters (b) did not differ among sites at $P=0.05$.

Site	Stem		Branch		Bark		Foliage		Coarse Root	
Nº	a_{st}	b_{st}	a_{br}	b_{br}	a_{bk}	b_{bk}	a_{fo}	b_{fo}	a_{cr}	b_{cr}
1	0.1494	2.3309	0.0008	3.4967	0.0612	1.8978	0.0002	3.6782	0.0532	2.3170
2	0.1963	2.2071	0.0032	3.0607	0.0084	2.7090	0.0003	3.5725	0.0169	2.8054
3	0.0340	2.8336	0.0105	2.6427	0.0440	2.0300	0.0009	3.2316	0.0223	2.5657
4	0.1349	2.3577	0.0478	1.9612	0.0174	2.3884	0.0165	1.9760	0.0151	2.7449
5	0.0412	2.7697	0.0568	1.8949	0.0057	2.7840	0.0030	2.6076	0.0062	2.9982
6	0.0653	2.6346	0.0449	1.9424	0.0250	2.1866	0.0052	2.5380	0.0560	2.2325
7	0.0841	2.5422	0.0030	2.8696	0.1221	1.6917	0.0001	3.8016	0.0385	2.4264
8	0.2559	2.1130	0.0017	3.1621	0.0278	2.1913	0.0001	4.0366	0.0016	3.6646
9	0.0476	2.7927	0.0169	2.2579	0.0146	2.4378	0.0014	2.7750	0.0135	2.7313
10	0.1061	2.4439	0.5473	1.0934	0.0280	2.1740	0.0117	2.0920	0.0384	2.2961
11	0.0396	2.8582	0.4251	1.1464	0.0186	2.3439	0.0026	2.7248	0.1472	1.8009
12	0.1113	2.4416	0.0136	2.2387	0.0218	2.2755	0.0021	2.7592	0.0331	2.4665
13	0.0596	2.7104	0.0359	1.9531	0.0504	1.9607	0.0021	2.6245	0.0364	2.2834
14	0.0598	2.6957	0.0005	3.3975	0.0584	1.9274	0.00001	4.7966	0.0161	2.5528

Table A.1.5. Specific leaf areas, fractions of the total biomass and root-to-aboveground biomass ratio ($R:A_S$) for the 14 stands. Averages by productivity classes followed by different letters differ at $P = 0.05$.

Site Nº	SLA ($m^2 kg^{-1}$)	Total Biomass ($Mg ha^{-1}$)	Foliage	Branch	Bark	Stem	C.Roots	$R:A_S$
			Decimal fraction					Ratio
1	8.8	102.7	0.03	0.06	0.08	0.62	0.21	0.28
2	7.5	110.8	0.04	0.09	0.09	0.55	0.23	0.32
3	9.5	86.8	0.04	0.11	0.10	0.57	0.19	0.24
4	11.0	121.3	0.03	0.08	0.09	0.62	0.19	0.25
5	10.4	98.7	0.03	0.08	0.09	0.62	0.17	0.22
6	8.9	112.0	0.04	0.07	0.07	0.63	0.19	0.24
7	8.4	127.9	0.03	0.05	0.09	0.62	0.21	0.27
8	8.9	109.4	0.03	0.06	0.08	0.61	0.21	0.29
9	7.7	123.8	0.02	0.06	0.08	0.68	0.16	0.20
10	9.9	139.7	0.03	0.08	0.08	0.66	0.16	0.19
11	8.7	149.2	0.03	0.07	0.08	0.69	0.14	0.17
12	7.0	192.9	0.03	0.04	0.08	0.64	0.21	0.27
13	9.7	237.1	0.02	0.05	0.07	0.73	0.13	0.15
14	8.3	242.4	0.03	0.05	0.07	0.72	0.13	0.15
Low	9.4	104.1 b	0.03	0.08 a	0.09 a	0.59 b	0.20 a	0.26 a
Medium	8.5	118.3 b	0.03	0.06 b	0.08 ab	0.64 b	0.19 a	0.24 a
High	8.7	192.3 a	0.03	0.06 b	0.07 b	0.69 a	0.15 b	0.18 b

Table A.1.6. Regressed equations between fraction of the total biomass and MAI and site index (SI, base age 5 year) for each compartment, at the end of the rotation, between 6 and 8 years-old (n=14)

	Biomass Fraction	R^2	P
Foliage	0.0388 exp(- 0.0147 MAI)	0.20	< 0.0001
Branch	0.1262 exp(- 0.0378 MAI)	0.64	< 0.0001
Bark	0.0972 exp(- 0.0097 MAI)	0.47	< 0.0001
Stem	0.7030 [1 – exp (- 0.1604 MAI)]	0.65	< 0.0001
Coarse Roots	0.2448 exp(- 0.0179 MAI)	0.41	< 0.0001
Foliage	0.0797 exp(- 0.0449 SI)	0.42	< 0.0001
Branch	0.2959 exp(- 0.0688 SI)	0.57	< 0.0001
Bark	0.1281 exp(- 0.0204 SI)	0.47	< 0.0001
Stem	0.9188 [1 – exp (- 0.0553 SI)]	0.85	< 0.0001
Coarse Roots	0.4608 exp(- 0.0434 SI)	0.55	< 0.0001

MAI range: 9 to 33 Mg ha^{-1} yr^{-1}

SI range: 17 to 29 m

Table A.1.7. Total rainfall, transpiration, water capture efficiency (WCE), water use efficiency (WUE), water response efficiency (WRE) and average vapor pressure deficit (VPD) for all sites for the ANPP year estimate. Averages by productivity classes followed by different letters differ at P = 0.05.

Site Nº	Rainfall (mm yr^{-1})	Transpiration (mm yr^{-1})	WCE (dec)	WUE (kg/m^3)	WRE (kg/m^3)	VPD (kPa)
1	731	592	0.81	1.62	1.31	1.59
2	793	608	0.77	1.60	1.22	1.49
3	839	718	0.86	1.35	1.16	1.47
4	934	794	0.85	1.34	1.14	1.28
5	1131	735	0.65	2.03	1.32	1.32
6	1130	765	0.68	1.87	1.26	1.35
7	1117	720	0.64	2.07	1.33	1.43
8	822	656	0.80	2.29	1.83	1.50
9	1151	731	0.64	2.71	1.72	1.27
10	1292	999	0.77	2.23	1.73	1.31
11	1168	903	0.77	2.55	1.97	1.31
12	1568	759	0.48	3.31	1.60	1.24
13	1174	832	0.71	3.40	2.41	1.28
14	1177	854	0.73	4.58	3.32	1.28
Low	886 c	689 b	0.78	1.59 b	1.23 b	1.46 a
Medium	1055 b	718 b	0.70	2.24 b	1.54 b	1.37 ab
High	1276 a	869 a	0.70	3.21 a	2.21 a	1.28 b

WCE = Water Capture Efficiency (Transpiration/Rainfall)
WUE = Water Use Efficiency (ANPP/Transpiration)
WRE = Water Response Efficiency (ANPP/Rainfall)

ANPP (Mg ha^{-1} yr^{-1}) = Rainfall (mm yr^{-1}) . WCE . WUE (kg m^{-3}) / 100

Table A.1.8. Total PAR (PAR), absorbed PAR (APAR), light capture efficiency (LCE), light use efficiency (LUE), light response efficiency (LRE) and leaf area efficiency (LAE) for all sites for the ANPP year estimate. Averages by productivity classes followed by different letters differ at $P = 0.05$.

Site Nº	PAR (TJ ha^{-1} yr^{-1})	APAR (TJ ha^{-1} yr^{-1})	LCE	LUE (g MJ^{-1})	LRE (g MJ^{-1})	LAE (g m^{-2} yr^{-1})
1	31.5	18.0	0.57	0.53	0.30	408
2	31.7	20.6	0.65	0.47	0.31	335
3	31.5	20.4	0.65	0.48	0.31	335
4	31.5	22.3	0.71	0.48	0.34	313
5	30.7	20.7	0.67	0.72	0.49	481
6	31.4	23.4	0.75	0.61	0.46	376
7	33.2	21.7	0.65	0.68	0.45	504
8	32.1	21.3	0.66	0.71	0.47	495
9	31.2	17.3	0.56	1.14	0.64	885
10	31.4	21.9	0.70	1.02	0.71	672
11	31 7	23.5	0.74	0.98	0.73	614
12	30.5	23.8	0.78	1.05	0.82	594
13	30.3	24.5	0.81	1.16	0.93	617
14	30.5	26.6	0.87	1.47	1.28	678
Low	31.6	20.4 b	0.65 b	0.54 b	0.35 b	374 b
Medium	31.9	20.9 b	0.65 b	0.79 b	0.50 b	565 a
High	30.8	24.1 a	0.78 a	1.14 a	0.90 a	635 a

LCE = Light Capture Efficiency (APAR/PAR)
LUE = Light Use Efficiency (ANPP/APAR)
LRE = Light Response Efficiency (ANPP/PAR)
LAE = Leaf Area Efficiency (ANPP/LAI)
ANPP (Mg ha^{-1} yr^{-1}) = PAR (TJ ha^{-1} yr^{-1}) . LCE . LUE (g MJ^{-1})
LUE = -0.05 + 0.0017 LAE ($r^2 = 0.76$, $P < 0.001$)

Table A.1.9. Total N, N uptake, nitrogen capture efficiency (NCE), nitrogen use efficiency (NUE), nitrogen response efficiency (NRE) and average residence time (ART) for all sites for the ANPP year estimate. Averages by productivity classes followed by different letters differ at P = 0.05.

Site Nº	Soil N (kg ha^{-1})	N Uptake (kg ha^{-1} yr^{-1})	NCE	NUE (kg kg^{-1})	NRE (kg kg^{-1})	ART (yr)
1	1390	27.7	0.020	346	6.9	5.5
2	1984	39.1	0.020	248	4.9	6.6
3	3850	35.7	0.009	273	2.5	4.7
4	3234	37.9	0.012	281	3.3	6.4
5	3528	48.4	0.014	309	4.2	4.5
6	1813	47.4	0.026	301	7.9	4.3
7	4427	42.5	0.010	350	3.4	5.1
8	3350	46.0	0.014	327	4.5	4.5
9	1106	47.7	0.043	415	17.9	4.5
10	3451	55.9	0.016	399	6.5	4.2
11	1612	59.9	0.037	384	14.3	4.3
12	1536	69.7	0.045	361	16.4	5.5
13	4589	78.3	0.017	361	6.2	5.7
14	3248	98.1	0.030	399	12.0	4.4
Low	2797	37.8 b	0.015 b	291 b	4.4 b	5.6 a
Medium	2674	45.9 b	0.023 ab	348 a	8.4 ab	4.6 b
High	2887	72.4 a	0.029 a	381 a	11.1 a	4.8 b

NCE = Nitrogen Capture Efficiency (Uptake/N Soil)
NUE = Nitrogen Use Efficiency (ANPP/N Uptake)
NRE = Nitrogen Response Efficiency (ANPP/N Soil)

ANPP (Mg ha^{-1} yr^{-1}) = N Soil (kg ha^{-1} yr^{-1}) . NCE . NUE (kg kg^{-1}) / 1000

Table A.1.10. Select variables using 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 evapo-transpiration, 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

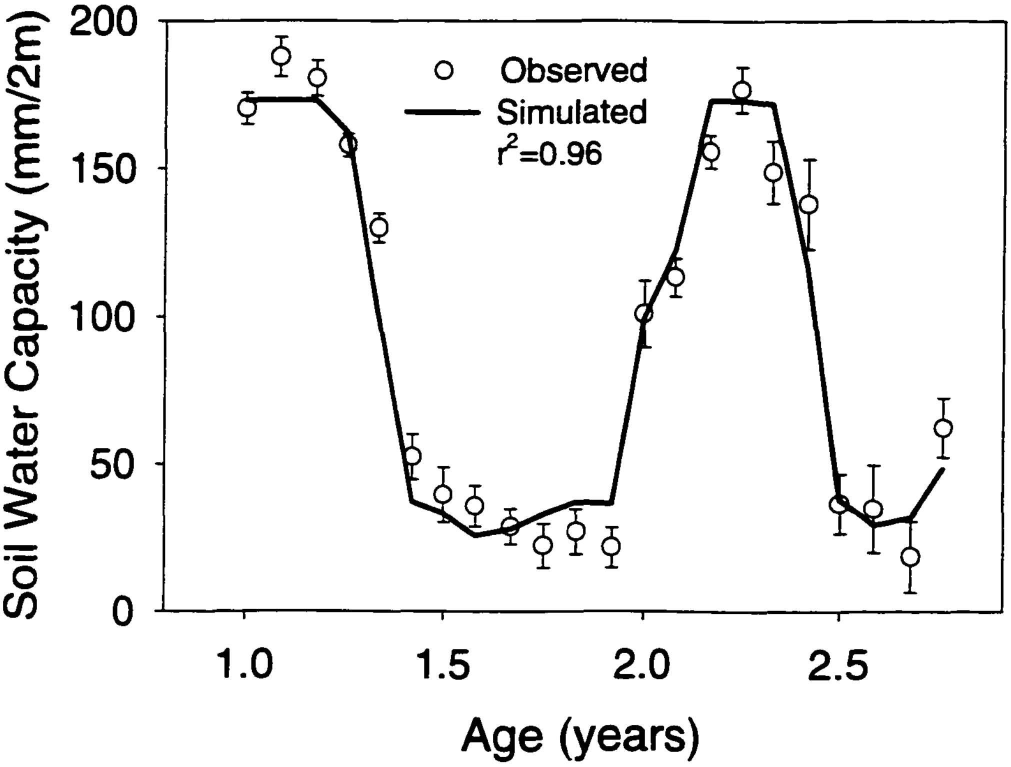

Figure A.1.1. Monthly average soil water capacity for a 2 m profile in northeastern Brazil planted with *E. grandis* x *urophylla* clone. Simulated values were obtained using 3-PG model water balance algorithm (Penman-Monteith). Error bars represent standard errors of the means (n=9 to 18).

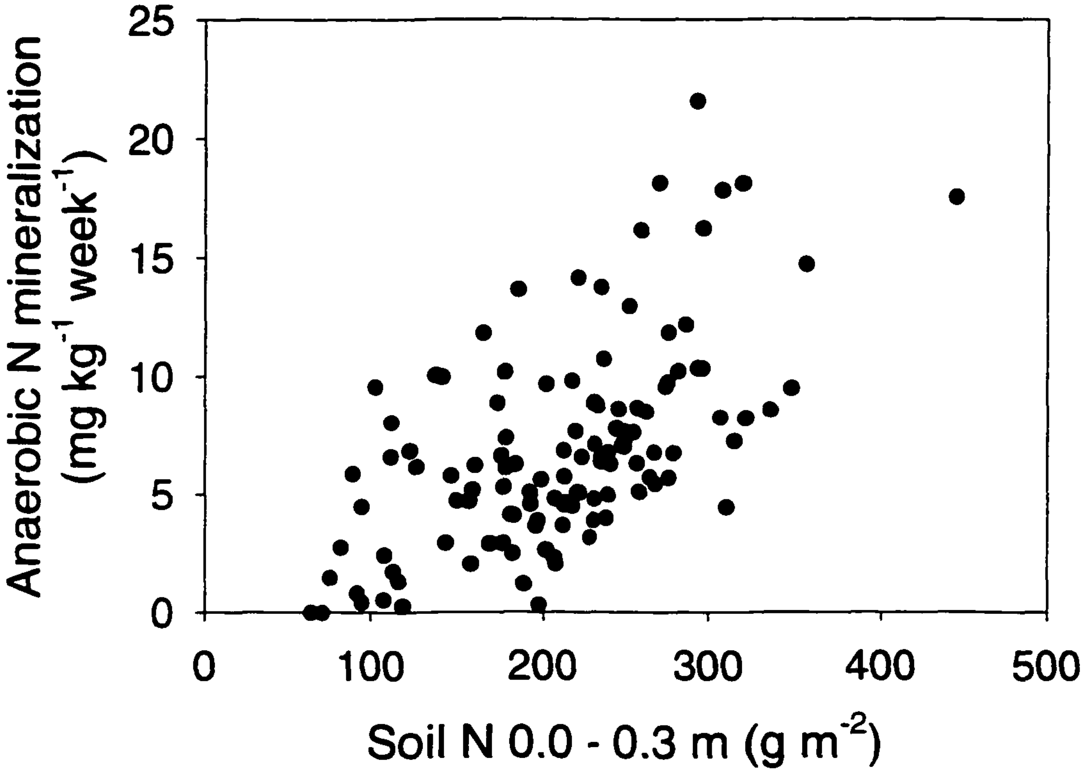

Figure A.1.2. Total soil N and anaerobic nitrate and ammonium in solution after 1 week at 40ºC for 120 stands of *E. grandis* x *urophylla* in northeastern Brazil (r^2 = 0.35, $P < 0.001$).

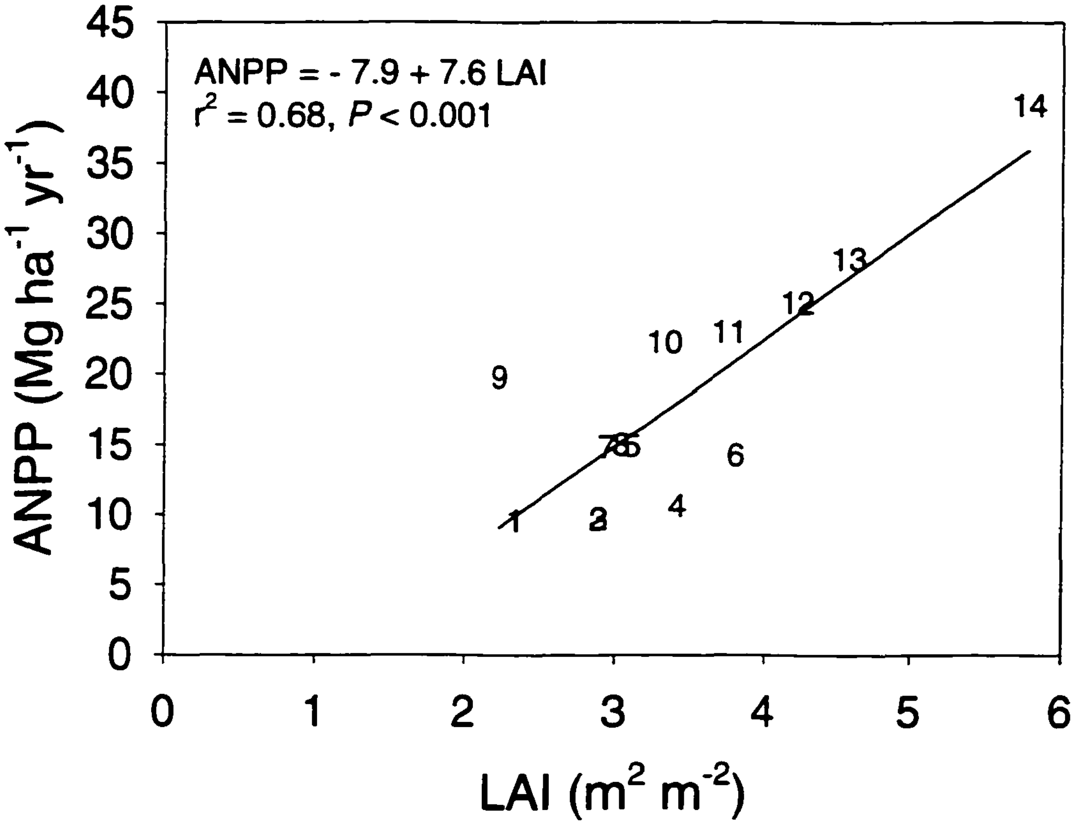

Figure A.1.3. Relationship between ANPP and LAI for the 14 sites of *E. grandis* x *urophylla* in northeastern Brazil.

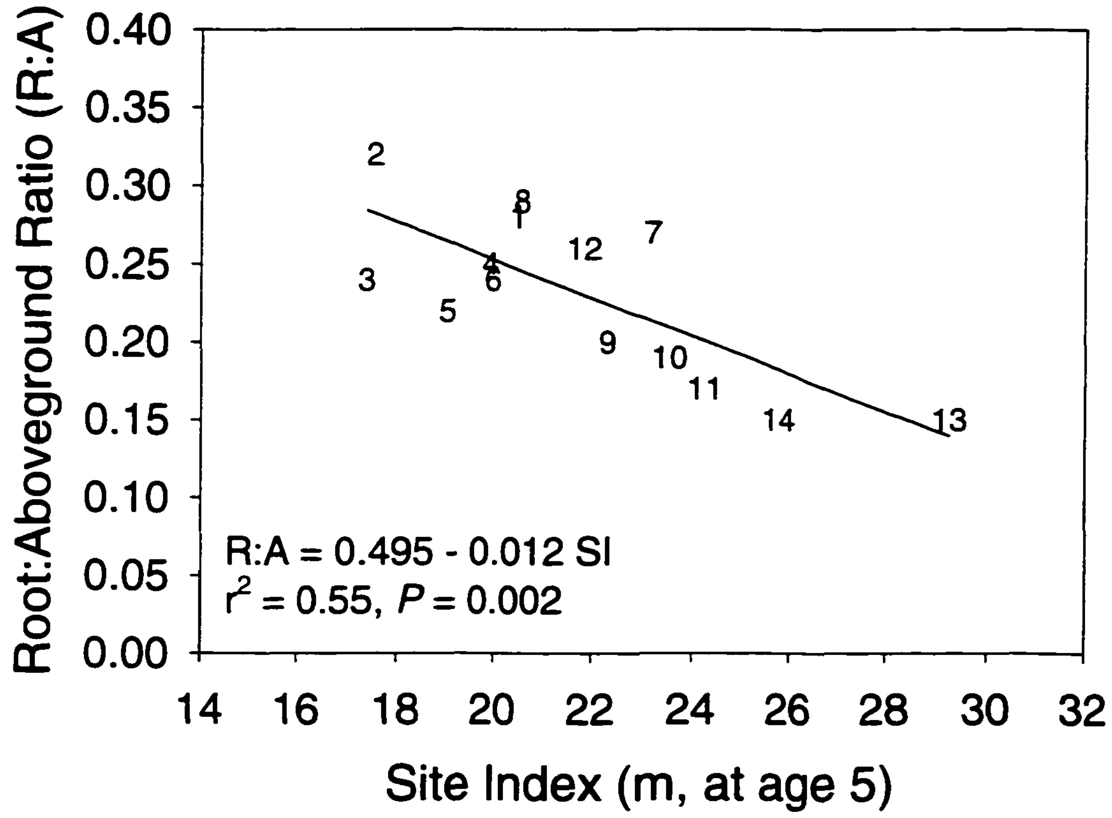

Figure A.1.4. Relationship between R:As ratio at the stand level and site index for the 14 sites of *E. grandis* x *urophylla* in northeastern Brazil.

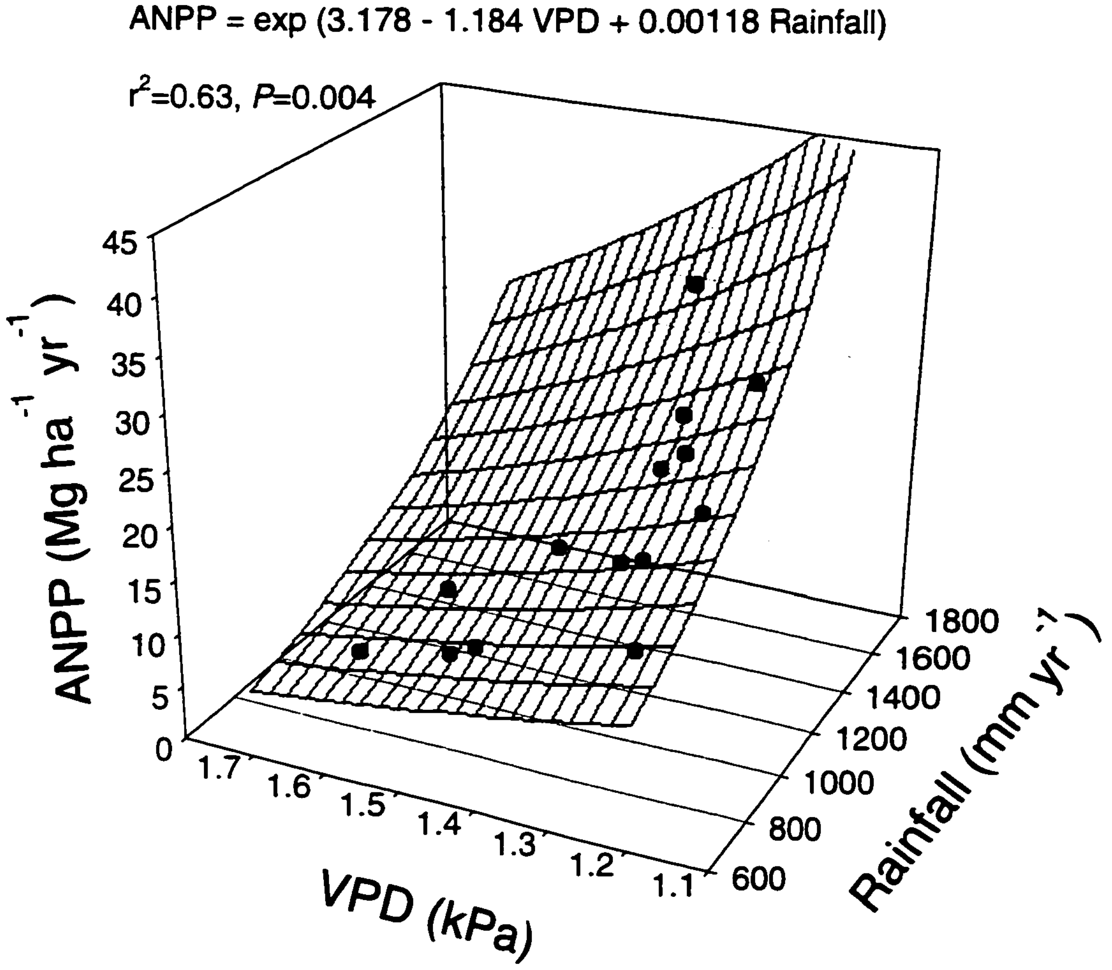

Figure A.1.5. Relationship between ANPP, vapor pressure deficit and rainfall for the 14 sites of *E. grandis* x *urophylla* in northeastern Brazil.

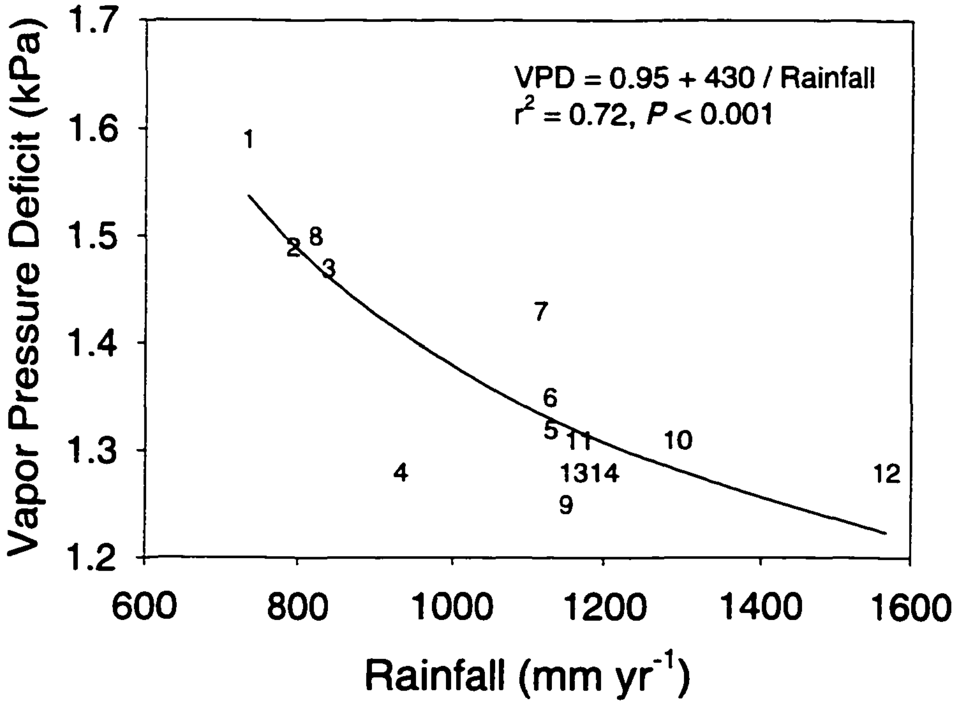

Figure A.1.6. Relationship between vapor pressure deficit and rainfall for the 14 sites during the year of ANPP estimates.

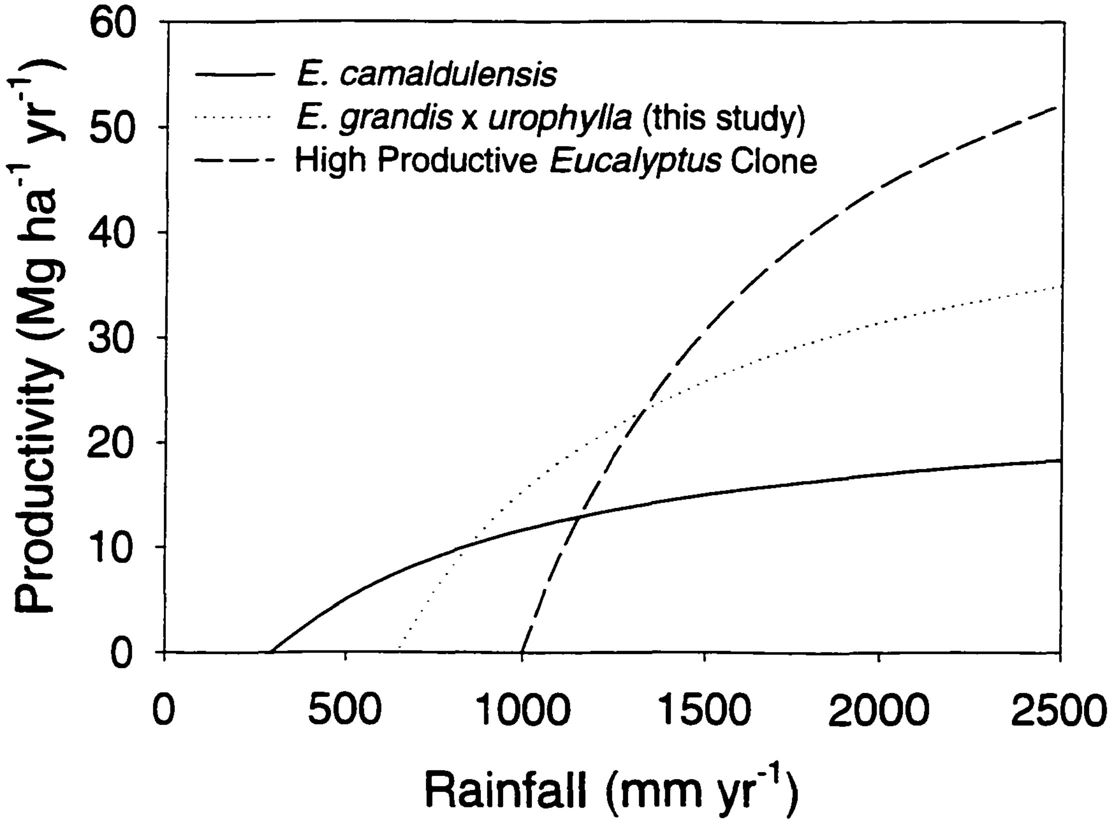

Figure A.1.7. Hypothesized responses of E. camaldulensis, clonal *E. grandis* x *urophylla* of this study, and a hypothetical high productivity clone to water availability (rainfall). For 600 mm yr^{-1}, 1100 mm yr^{-1} and 1500 mm yr^{-1} of water supply, *E. camaldulensis*, *E. grandis x urophylla* and the high productive clone would be the most productive species, respectively. Their water-response-efficiencies could be derived for ecological interpretations.

APPENDIX II.A

PPSystem versus Li-COR 6400 comparison

On January 2001, soil CO_2 effluxes from all 16 plots were measured with both equipments (PPSystem and LiCOR 6400) in two consecutive days, with 5 sub-samples per plot in each day. On the first day the row forest floor position was used and the bed position was used for the second day. The higher effluxes of the row position compared with the bed one, permitted a greater amplitude of the compared effluxes between instruments. The readings were taken for both instruments at the same time from locations 0.20 m apart. For the LI-COR, collars were inserted 2 cm into the soil 12 hours prior to measurements. Plot means ranged 1.88 – 7.84 μmol m^{-2} s^{-1} for the PP systems and 1.76 – 5.73 μmol m^{-2} 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 and a zero-intercept linear regression produced $F_{S\ \text{LI-COR}} = 0.796\ F_{S\ \text{PPSystem}}$ ($r^2 = 0.589$, $P < 0.0001$, the intercept was not significant, Figure A.2.1). We expect the LICOR provides better quantitative flux estimates, so we use this regression to adjust the PP Sytems estimates of F_S (direct use of the PP Sytems fluxes would increase our soil CO_2 estimates by 26%).

APPENDIX II.B

Leaf area index and specific leaf area estimates

Leaf area index (LAI, m^2 foliage m^{-2} ground) was estimated for each plot using a Ceptometer-AccuPAR Model 80 (Decagon Devices, Pullman, USA). The Ceptometer readings were taken between 10 AM and 2 PM on sunny days. For all plots, 24 sampling points were systematically located within the measurement area, with 4 readings per point (the four cardinal directions) totaling 96 readings of transmitted PAR per plot (μmol m^{-2} s^{-1}). The total incoming PAR (μmol m^{-2} s^{-1}) was measured 16 times on an open area before and after each plot's readings. The average values of total incoming PAR and transmitted PAR were used for LAI determination:

$$LAI = -\frac{\ln(\frac{PAR_{PLOT}}{PAR_{SUN}})}{k}$$

where PAR_{PLOT} is the average transmitted PAR measure under the canopy, PAR_{SUN} is the averaged total-incoming PAR and *k* is the light-extinction coefficient determined to be –0.36 for ten *E. grandis* x *urophylla* stands in the region (Stape et al. unpublished data). This value is similar to –0.40 used by Soares et al. (1997) for the same species in a related tropical area. The specific leaf area (SLA) per treatment were determined on October 2001 by sampling twice (two replicates per plot) 5 recent fully expanded leaves from the middle of the canopy of 6 trees (totalizing 30 leaves per replicate). The leaves were immediately placed in plastic bags and coolers and shipped to the lab for area determination using photocopying-weighing technique (a ruler was used to assure no distortion during the copying process). Leaf dry masses were then determined. Specific leaf area was calculated by the ratio of measured area (one-sided) and dry mass (m^2 kg^{-1}).

APPENDIX II.C

Components of Aboveground Respiration (R_P, in g C m^{-2} month^{-1})

(Modified from Giardina et al. 2002)

Wood Construction Respiration (WCR)

$$WCR = (0.9821 - 0.1415\ (AWC/1000))\ WNPP$$

Wood Maintenance Respiration (WMR)

$$WMR = (0.3215 - 0.034 \cdot (5500/1000)) \cdot (AWC/1000) \cdot 30$$

Foliage Construction Respiration (FCR)

$$FCR = 0.25 \cdot FNPP$$

Foliage Maintenance Respiration (FMR)

$$FMR = [NCAN \cdot (1/14) \cdot 0.006278 \cdot 0.012 \cdot 86400 \cdot 30 \cdot 0.5]$$

Where:

WNPP = wood NPP (g C m^{-2} month^{-1})

FNPP = foliage NPP (g C m^{-2} month^{-1})

AWC = aboveground wood carbon (g C m^{-2}), and $3000 < AWC < 6000$;

NCAN = canopy nitrogen (g N m^{-2})

APPENDIX II.D

Supplemental Tables and Figures from Chapter II

Table A.2.1. Yearly averages of the meteorological variables and soil moisture by water regime and age.

Variables		Unit	Wet Year Sep/99-Oct/00	Normal Year Sep/00-Oct/01
Air Temperatures	Minimum	°C	21.1	20.8
	Mean	°C	25.1	25.2
	Maximum	°C	28.7	29.3
Soil Temperature	Rainfed	°C	23.6	24.2
	Irrigated	°C	23.4	23.6
Rainfall	Total	mm	1769	1207
Irrigation	Total	mm	531	962
Transpiration	Rainfed	mm	1261	894
Transpiration	Total	mm	1261	1225
VPD	Mean	kPa	-1.0	-1.2
Available Soil Water	Non-irrigated	mm $2m^{-1}$	129	76
	Irrigated	mm $2m^{-1}$	160	160

Table A.2.2. Leaf characteristics by water regime and age. Values are means with standard errors given in parentheses (n=8). Values (within rows) followed by different letters differ at $P = 0.05$.

Variable	Age (years)	Rainfed	Irrigated
	3.1	3.3 (0.2)	3.3 (0.2)
LAI	4.0	3.9 (0.1)	4.0 (0.1)
($m^2 m^{-2}$)	5.0	2.3 (0.1) b	3.4 (0.2) a
	5.4	2.6 (0.1)	2.9 (0.2)
SLA	3.3	8.9 (0.4) †	-
($m^2 kg^{-1}$)	5.4	8.6 (0.1)	8.5 (0.1)
Leaf N	3.1	19.4 (0.8) †	-
(g kg^{-1})	4.0	22.9 (0.3)	22.0 (0.6)
	5.0	19.3 (0.5)	19.6 (0.5)
Leaf P	3.1	1.2 (0.1) †	-
(g kg^{-1})	4.0	1.6 (0.1)	1.6 (0.1)
	5.0	1.3 (0.1) b	1.5 (0.1) a
$\delta^{13}C$ (‰)	5.0	-28.5 (0.1) a	-29.1 (0.1) b

† Common samples taken before-treatment application

Table A.2.3. Net ecosystem production (NEP) by water regime and year. Values are means with standard errors given in parentheses (n=8). Values (within rows) followed by different letters differ at $P = 0.05$.

	Rainfed	Irrigated
	Wet Year (kg C m^{-2} y^{-1})	
NEP	2.342 (76) b	2.721 (99) a
Δ Aboveground Wood	1.933 (72) b	2.278 (57) a
Δ Foliage	-0.020 (6) b	0.011 (6) a
Δ Coarse Root	0.481 (15) b	0.564 (15) a
Δ Litter Layer	0.054 (23)	0.031 (25)
Δ Soil Carbon	-0.070 (54)	-0.126 (41)
Δ Stumps	-0.035 (3)	-0.037 (1)
	Normal Year (kg C m^{-2} y^{-1})	
NEP	0.794 (39) b	2.013 (77) a
Δ Aboveground Wood	0.766 (33) b	1.843 (51) a
Δ Foliage	-0.037 (8)	-0.047 (15)
Δ Coarse Root	0.178 (10) b	0.417 (10) a
Δ Litter Layer	-0.013 (23)	-0.043 (25)
Δ Soil Carbon	-0.070 (54)	-0.126 (41)
Δ Stumps	-0.029 (2)	-0.030 (1)

Table A.2.4. Total C and N, and extractable pools of P, K, Ca and Mg from soil samples collected between 0 and 45 cm at the beginning and ending of the study period. Values are means with standard errors given in parentheses (n=4). Values (within columns and treatments) followed by different letters differ at *P* = 0.05.

Treatment	Sample year	C	N	P	K	Ca	Mg
		total (g m^{-2})		extractable (g m^{-2})			
Control	1999	3989 (148)	267 (19)	1.4 (0.1)	10.6 (1.5)	40.1 (9.4)	13.4 (1.5) a
	2001	3743 (148)	242 (22)	2.0 (0.1)	8.1 (0.9)	23.2 (4.8)	8.4 (0.6) b
Irrigated	1999	4360 (271)	276 (31)	1.6 (0.1)	11.3 (1.8)	58.1 (10.6)	16.1 (1.9) a
	2001	3971 (206)	273 (10)	1.7 (0.1)	8.4 (1.7)	33.7 (5.8)	9.3 (1.0) b
Fertilized	1999	4233 (233)	278 (23)	1.4 (0.1) b	10.3 (0.9) b	65.6 (18.5)	16.4 (2.6)
	2001	4166 (95)	291 (14)	4.1 (0.3) a	21.4 (2.4) a	64.8 (5.8)	20.9 (2.9)
Irrigated and	1999	4220 (198)	250 (7)	1.5 (0.1) b	8.3 (0.7)	35.6 (4.7)	15.2 (1.9)
Fertilized	2001	4040 (114)	263 (15)	3.5 (0.3) a	13.6 (1.9)	36.3 (6.2)	11.3 (2.7)

* pH $CaCl_2$ = 4.00 (0.09), Bulk Density = 1.61 (0.01), Sand 83%, Silt 2%, Clay 15%, C:N ratio 15:1

Table A.2.5. Nitrogen (ammonium plus nitrate) and phosphorus accumulated on resin bags incubated in situ during three months at three occasions. Values are means with standard errors given in parentheses (n=4). Values (within rows) followed by different letters differ at *P* = 0.05.

Element	Starting Date	Control	Irrigated	Fertilized	Irrigated and Fertilized
N	Sep/1999	0.5 (0.3) b	0.9 (0.5) b	19.7 (2.9) a	32.9 (9.4) a
(mg bag^{-1})	Apr/2000	0.3 (0.2) b	0.3 (0.1) b	66.5 (2.7) a	39.6 (5.6) a
	Nov/2000	1.1 (0.3) b	0.9 (0.3) b	59.7 (6.7) a	53.3 (6.0) a
P	Sep/1999	13.6 (6.3) b	6.2 (1.1) b	187.8 (70.9) a	525.9 (418) a
(µg bag^{-1})	Apr/2000	2.7 (1.5) b	2.1 (0.3) b	187.0 (64.8) a	371.2 (68.3) a
	Nov/2000	0.5 (0.2) b	0.5 (0.2) b	135.5 (53.0) a	111.9 (56.1) a

Table A.2.6. Nutrients (N, P, K, Ca and Mg) inputted by rainfall, irrigation water and fertilization during the two studied years.

Event	Year	N	P	K	Ca	Mg
				kg ha^{-1}		
Rainfall*	Wet	5.0	0.2	3.8	7.7	4.7
	Normal	3.4	0.2	2.6	5.3	3.2
Irrigation†	Wet	5.1	0.2	10.8	10.8	9.7
	Normal	9.1	0.3	19.5	19.5	17.6
Fertilization‡	Wet	506	85	316	600	300
	Normal	506	85	316	0	0

* Based on 39 rainfall analysis and total rainfall

† Based on 4 irrigation water analysis and total irrigation

‡ Based on fertilizer concentrations and amount used

Table A.2.7. Diameter at breast height (DBH), height, dominant height, basal area, stocking, volume and aboveground wood biomass by treatment at 3.1, 4.6 and 5.4 years-old. Values are means with standard errors given in parentheses (n=4). Values (within rows) followed by different letters differ at $P = 0.05$.

Variable	Control	Irrigated	Fertilized	Irrigated and Fertilized
		July of 1999 – 3.1 years-old		
DBH (cm)	10.5 (0.3)	10.6 (0.4)	10.4 (0.4)	10.5 (0.2)
Height (m)	14.8 (0.3)	15.2 (0.5)	14.7 (0.6)	14.9 (0.4)
Dom. Height (m)	15.3 (0.4)	16.0 (0.5)	15.4 (0.6)	15.6 (0.4)
Basal Area (m^2 ha^{-1})	9.3 (0.5)	9.7 (0.7)	9.3 (0.8)	9.5 (0.4)
Stocking (trees ha^{-1})	1070 (21)	1084 (28)	1075 (15)	1083 (14)
Volume (m^3 ha^{-1})	65 (4)	71 (7)	65 (8)	67 (4)
Wood Biomass (Mg ha^{-1})	35.5 (2.6)	38.3 (4.0)	35.9 (4.3)	36.7 (2.2)
		December of 2000 – 4.6 years-old		
DBH (cm)	14.3 (0.3)	14.7 (0.2)	14.5 (0.2)	14.9 (0.2)
Height (m)	22.4 (0.4)	23.2 (0.2)	22.4 (0.7)	23.2 (0.5)
Dom. Height (m)	23.4 (0.4)	24.5 (0.4)	23.7 (0.8)	24.7 (0.5)
Basal Area (m^2 ha^{-1})	17.3 (0.4) b	18.8 (0.5) ab	18.1 (0.8) ab	19.2 (0.4) a
Volume (m^3 ha^{-1})	173 (5) b	194 (7) ab	182 (13) ab	200 (7) a
Wood Biomass (Mg ha^{-1})	91 (3) b	103 (4) ab	97 (6) ab	105 (3) a
		October of 2001 – 5.4 years-old		
DBH (cm)	14.9 (0.3) b	16.3 (0.1) a	15.2 (0.2) b	16.4 (0.2) a
Height (m)	23.7 (0.5) b	26.4 (0.4) a	23.6 (0.8) b	26.0 (0.6) a
Dom. Height (m)	24.7 (0.7) b	28.0 (0.5) a	24.8 (1.0) b	27.8 (0.5) a
Basal Area (m^2 ha^{-1})	19.0 (0.4) b	23.1 (0.4) a	19.4 (0.9) b	23.2 (0.5) a
Stocking (trees ha^{-1})	1070 (21)	1084 (28)	1045 (19)	1075 (21) a
Volume (m^3 ha^{-1})	199 (6) b	266 (9) a	208 (15) b	267 (10) a
Wood Biomass (Mg ha^{-1})	105 (3) b	141 (4) a	109 (7) b	141 (4) a

Table A.2.8. Initial (3.1 years-old) and final (5.4 years-old) C pool sizes for foliage, branches, boles, and fine root pool size (g C m^{-2}). Foliage NPP, branch NPP, bole NPP and aboveground NPP by year and treatment (g C m^{-2} y^{-1}). Values are means with standard errors given in parentheses (n=4).

Compartment	Control	Irrigated	Fertilized	Irrig. and Fert.
	Pool Size July of 1999 – 38 months old			
Foliage	180 (15)	176 (13)	184 (10)	181 (10)
Branch	237 (18)	246 (23)	240 (22)	242 (11)
Bole	1325 (96)	1437 (150)	1336 (165)	1373 (85)
	1st Year Production – October 1999 to September 2000			
Foliage	168 (8)	203 (10)	208 (7)	263 (8)
Branch	152 (3)	195 (6)	185 (7)	213 (16)
Bole	1728 (25)	2067 (61)	1890 (139)	2184 (86)
ANPP	2049 (26)	2465 (72)	2284 (125)	2662 (100)
	Pool Size – 4.2 years old			
Fine Root	74 (19)	67 (23)	64 (24)	48 (6)
	2nd Year Production – October 1999 to September 2000			
Foliage	129 (16)	152 (23)	149 (18)	154 (26)
Branch	93 (9)	170 (5)	87 (4)	168 (3)
Bole	707 (45)	1778 (69)	736 (57)	1682 (83)
ANPP	930 (55)	2102 (85)	973 (62)	2005 (86)
	Pool Size October of 2001 – 65 months old			
Foliage	148 (10)	170 (14)	157 (10)	176 (23)
Branch	472 (19)	581 (12)	505 (19)	600 (9)
Bole	4135 (132)	5621 (173)	4281 (302)	5599 (188)

Table A.2.9. Gross primay production (GPP), net ecosystem production (NEP) and the fractions of GPP allocated to ANPP and TBCA. Values are means with standard errors given in parentheses (n=4).

Compartment	Unit	Control	Irrigated	Fertilized	Irrigated and Fertilized
		1st Year Production – October 1999 to September 2000			
GPP	g C m^{-2} y^{-1}	6499 (215)	7589 (394)	6785 (289.3)	8004 (307)
ANPP	% of GPP	31 (1)	32 (1)	33 (0.9)	33 (1)
TBCA	% of GPP	34 (3)	32 (2)	30 (1.8)	30 (1)
NEP	g C m^{-2} y^{-1}	2198 (73)	2589 (131)	2486 (86.7)	2852 (130)
		2nd Year Production – October 1999 to September 2000			
GPP	g C m^{-2} y^{-1}	3096 (104)	5773 (228)	3065 (105)	5511 (146)
ANPP	% of GPP	30 (2)	36 (1)	31 (1)	36 (1)
TBCA	% of GPP	37 (5)	24 (1)	33 (3)	24 (1)
NEP	g C m^{-2} y^{-1}	758 (62)	2020 (144)	830 (46)	2006 (86)

Table A.2.10. Initial (3.1 years-old) and final (5.4 years-old) C pool sizes for soil, litter, coarse roots and stumps per treatment. Annual fluxes of soil respiration, litterfall, and annual changes in C stored in soil, litter layer, coarse root and stumps, and estimated total belowground carbon allocation (TBCA) by treatment and year. Values are means with standard errors given in parentheses (n=4). Values (within rows) followed by different letters differ at *P* = 0.05.

Variable	Control	Irrigated	Fertilized	Irrigated and Fertilized
Initial		3.1 years-old - (g C m^{-2})		
Soil (0 to 45 cm)	3989 (148)	4360 (271)	4234 (233)	4220 (198)
Litter Foliage	127 (22)	120 (11)	113 (13)	115 (19)
Litter Branch	90 (33)	136 (49)	149 (41)	123 (41)
Coarse Roots	546 (36)	580 (53)	550 (57)	562 (28)
Stumps	220 (10)	216 (6)	206 (36)	228 (10)
		Wet Year - (g C m^{-2} y^{-1})		
Soil CO_2 efflux	2087 (174) ab	2337 (214) a	1832 (123) b	2276 (154) ab
Total Litterfall	229 (12) c	246 (8) bc	278 (11) ab	304 (11) a
Δ Soil C	-110 (76)	-173 (62)	-30 (82)	-80 (52)
Δ Forest Floor	68 (23)	31 (41)	38 (41)	30 (35)
Δ Coarse Roots	455 (2) b	546 (16) a	506 (23) ab	581 (23) a
Δ Stumps	-36 (2)	-35 (1)	-34 (6)	-37 (2)
TBCA	2236 (269)	2461 (285)	2034 (127)	2467 (120)
		Normal Year - (g C m^{-2} y^{-1})		
Soil CO_2 efflux	1333 (111) ab	1482 (47) a	1184 (76) b	1340 (57) ab
Total Litterfall	215 (15) b	253 (14) ab	231 (19) ab	263 (16) a
Δ Soil C	-110 (76)	-173 (62)	-30 (82)	-80 (52)
Δ Forest Floor	7 (26)	-52 (32)	-33 (39)	-34 (42)
Δ Coarse Roots	176 (2) b	425 (15) a	179 (14) b	408 (9) a
Δ Stumps	-30 (2)	-29 (1)	-28 (5)	-31 (1)
TBCA	1161 (202)	1400 (53)	1040 (124)	1341 (69)
Final		5.4 years-old - (g C m^{-2})		
Soil (0 to 45 cm)	3743 (148)	3971 (206)	4166 (96)	4040 (114)
Litter Foliage	159 (20) a	89 (7) b	104 (12) ab	92 (11) b
Litter Branch	150 (13)	156 (14)	173 (22)	152 (5)
Coarse Root	1338 (36) b	1711 (36) a	1389 (74) b	1723 (37) a
Stumps	143 (7)	141 (4)	134 (24)	149 (6)

Table A.2.11. Canopy quantum efficiency (α) and light use efficiency (ε) of E. grandis x urophylla by treatment and year expressed in energy conversion terms (*). A series of leaf area efficiencies (CAI = current annual increment, NPP = total net primary production, ANPP = aboveground NPP, GPP = gross primary production) were estimated by treatment and year. Values are means with standard errors given in parentheses (n=4). Values (within rows) followed by different letters differ at $P = 0.05$.

Efficiency	Control	Irrigated	Fertilized	Irrigated and Fertilized
	1st Year Production – October 1999 to September 2000			
α (J J^{-1} APAR)	0.104 (0.002) b	0.121 (0.006) a	0.106 (0.004) b	0.125 (0.002) a
ε (J ANPP J^{-1} APAR)	0.035 (0.001) b	0.042 (0.001) a	0.039 (0.002) b	0.044 (0.001) a
CAI/LAI (m^3 ha^{-1} y^{-1})	22.0 (0.6) b	25.0 (0.9) a	22.4 (1.7) b	24.8 (0.7) a
NPP/LAI (g C m^{-2} y^{-1})	853 (41) b	961 (62) a	843 (39) b	957 (21) a
ANPP/LAI (g C m^{-2} y^{-1})	551 (18) b	639 (21) a	582 (29) b	654 (13) a
GPP/LAI (g C m^{-2} y^{-1})	1750 (83) b	1972 (125) a	1732 (81) b	1967 (42) a
	2nd Year Production – October 2000 to September 2001			
α (J J^{-1} APAR)	0.056 (0.002) b	0.096 (0.004) a	0.054 (0.002) b	0.088 (0.004) a
ε (J ANPP J^{-1} APAR)	0.018 (0.001) b	0.037 (0.002) a	0.019 (0.001) b	0.034 (0.002) a
CAI/LAI (m^3 ha^{-1} y^{-1})	12.3 (1.3) b	24.8 (2) a	11.9 (1.2) b	20.8 (2.1) a
NPP/LAI (g C m^{-2} y^{-1})	567 (18) b	865 (66) a	538 (19) b	740 (67) ab
ANPP/LAI (g C m^{-2} y^{-1})	352 (32) b	649 (51) a	352 (30) b	555 (53) a
GPP/LAI (g C m^{-2} y^{-1})	1163 (38) b	1781 (137) a	1105 (41) b	1524 (139) ab

* 1 gDM = 18 kJ, 1 gC = 40kJ and 1 mol PAR = 0.23 MJ

Table A.2.12. *P* values obtained from analysis of variances performed at the beginning and ending of the study period for stand biometric attributes and carbon pools used for TBCA estimate.

Variable	Initial – 3.1 years-old			Final – 5.4 years-old		
	Fertilization	Irrigation	Fert x Irrig	Fertilization	Irrigation	Fert x Irrig
Attributes						
DBH	0.570	0.243	0.959	0.328	< 0.001	0.770
Height	0.200	0.141	0.526	0.421	< 0.001	0.731
Dom. Height	0.721	0.085	0.241	0.850	< 0.001	0.628
Basal Area	0.727	0.203	0.656	0.573	< 0.001	0.773
Foliage Biom	0.663	0.742	0.957	0.582	0.176	0.922
Wood Biom.	0.611	0.164	0.453	0.552	< 0.001	0.537
C Pools						
Soil C	0.817	0.434	0.401	0.165	0.761	0.304
Coarse Root	0.684	0.207	0.544	0.411	< 0.001	0.614
Litter Layer	0.718	0.833	0.386	0.447	0.048	0.504
Stumps	0.983	0.665	0.534	-	-	-
Fine Root*	0.269	0.389	0.758	-	-	-

* at 4.2 years-old

Table A.2.13. *P* values obtained from analysis of variances with repeated measurements performed for N and P content of the incubated resin bags. A log transformation of the original data was used to meet statistical assumptions.

Variable	F	I	F x I	T	F x T	I x T	F	I	F	I	F	I
							1st Time		2nd Time		3rd Time	
N Resin	< 0.001	0.963	0.853	< 0.001	< 0.001	0.191	< 0.001	0.406	< 0.001	0.494	< 0.001	0.536
P Resin	< 0.001	0.844	0.634	0.004	0.003	0.551	< 0.001	0.985	< 0.001	0.161	< 0.001	0.281

Table A.2.14. *P* values obtained from analysis of variances with repeated measurements for total C, total N and extractable P, K, Ca and Mg for initial and final soil samples (0 to 0.45 m).

Variable	F	I	F x I	Y	F x Y	I x Y	F	I	F x I	F	I	F x I
							Initial Sampling			Final Sampling		
C	0.419	0.531	0.322	0.020	0.241	0.431	0.816	0.434	0.401	0.164	0.761	0.304
N	0.662	0.761	0.097	0.946	0.156	0.533	0.620	0.522	0.234	0.278	0.929	0.107
P	< 0.001	0.315	0.563	< 0.001	< 0.001	0.078	0.837	0.164	0.523	< 0.001	0.146	0.676
K	< 0.001	0.016	0.006	0.025	< 0.001	0.165	0.197	0.581	0.197	< 0.001	0.024	0.017
Ca	0.138	0.328	0.015	0.029	0.029	0.716	0.888	0.576	0.045	0.003	0.136	0.006
Mg	0.025	0.284	0.046	0.099	0.069	0.125	0.643	0.718	0.389	0.009	0.081	0.041

Table A.2.15. *P* values obtained from analysis of variances with repeated measurements for leaf area index (LAI), nitrogen (leaf N) and phosphorus (leaf P) leaf concentrations. Simple analyses of variances was used for specific leaf area (SLA) and leaf C13 isotope ratio (δ^{13}C).

Variable	F	I	F x I	Y	F x Y	I x Y	F	I	F x I	F	I	F x I
							5.0 years-old			5.4 years-old		
LAI	0.090	0.016	0.814	< 0.001	0.793	0.001	0.214	0.002	0.322	0.257	0.217	0.678
Leaf N	< 0.001	0.301	0.177	< 0.001	0.543	0.039	< 0.001	0.021	0.056	0.013	0.536	0.756
Leaf P	< 0.001	0.037	0.203	0.001	0.019	0.254	< 0.001	0.441	0.028	< 0.001	0.021	0.373
SLA	0.002	0.323	0.256	-	-	-	-	-	-	-	-	-
δ^{13}C	0.746	0.002	0.418	-	-	-	-	-	-	-	-	-

Table A.2.16. *P* values obtained from analysis of variances with repeated measurements for all estimated fluxes (excepted change in soil C and stump which used simple ANOVA).

Variable	F	I	F x I	Y	F x Y	I x Y	F	I	F x I	F	I	F x I
							Wet Year			Normal Year		
F_S	0.047	0.004	0.465	< 0.001	0.909	0.103	0.153	0.007	0.363	0.052	0.044	0.956
F_A	< 0.001	0.002	0.907	0.002	0.006	0.282	< 0.001	0.038	0.621	0.181	0.003	0.755
ΔC_S	0.241	0.431	0.923	-	-	-	-	-	-	-	-	-
ΔC_L	0.431	0.139	0.203	0.063	0.944	0.920	0.675	0.547	0.691	0.783	0.461	0.464
ΔC_R	0.173	< 0.001	0.475	< 0.001	0.025	< 0.001	0.043	0.001	0.667	0.594	< 0.001	0.408
ΔC_T	0.983	0.665	0.534	-	-	-	-	-	-	-	-	-
Total ΔC	0.191	0.263	0.791	< 0.001	0.494	0.041	0.163	0.972	0.883	0.341	0.054	0.735
TBCA	0.396	0.019	0.539	< 0.001	0.947	0.651	0.491	0.039	0.466	0.425	0.033	0.782
FNPP	0.009	0.011	0.958	< 0.001	0.093	0.179	< 0.001	< 0.001	0.278	0.552	0.444	0.607
BrNPP	0.134	< 0.001	0.696	< 0.001	0.012	0.001	0.025	0.005	0.487	0.540	< 0.001	0.798
BoNPP	0.339	< 0.001	0.437	< 0.001	0.101	< 0.001	0.144	0.005	0.802	0.499	< 0.001	0.228
ANPP	0.105	< 0.001	0.415	< 0.001	0.031	< 0.001	0.035	0.001	0.831	0.593	< 0.001	0.185
ΔC_F	0.976	0.221	0.904	0.004	0.707	0.071	0.529	< 0.001	0.344	0.817	0.583	0.673
ΔC_W	0.286	< 0.001	0.431	< 0.001	0.066	< 0.001	0.103	0.003	0.746	0.491	< 0.001	0.264
NPP	0.579	< 0.001	0.896	< 0.001	0.108	< 0.001	0.213	0.001	0.797	0.414	< 0.001	0.529
GPP	0.557	< 0.001	0.881	< 0.001	0.104	< 0.001	0.201	0.001	0.806	0.415	< 0.001	0.516
NEP	0.081	< 0.001	0.728	< 0.001	0.061	< 0.001	0.023	0.004	0.906	0.759	< 0.001	0.646

F_S = soil CO_2 efflux, F_A = litterfall, ΔC_S, ΔC_L, ΔC_R, ΔC_T = change in C sored in soil, litter layer, coarse roots, stumps respectively, Total ΔC = total change in C stored, TBCA = total belowground carbon allocation, FNPP = foliage NPP, BrNPP = branch NPP, BoNPP = stem plus bark NPP, ANPP = aboveground NPP, NPP = total net primary production, GPP = gross primary production, NEP = net ecosystem production

Table A.2.17. P values obtained from analysis of variances with repeated measurements for ANPP:GPP ratio, TBCA:GPP ratio, absorbed PAR (APAR), canopy quantum efficiency (α), light use efficiency (ε), foliage residence time (RT), fine root production (FRP).

Variable	F	I	F x I	Y	F x Y	I x Y	F	I	F x I	F	I	F x I
							Wet Year			Normal Year		
ANPP:GPP	0.238	0.006	0.386	0.100	0.569	< 0.001	0.083	0.665	0.346	0.547	0.001	0.508
TBCA:GPP	0.238	0.006	0.385	0.100	0.569	< 0.001	0.083	0.665	0.346	0.548	0.001	0.507
APAR	0.106	0.003	0.627	< 0.001	0.447	< 0.001	0.078	0.226	0.987	0.158	0.001	0.508
α	0.623	< 0.001	0.617	< 0.001	0.130	0.004	0.491	0.001	0.851	0.171	< 0.001	0.355
ε	0.502	< 0.001	0.152	< 0.001	0.048	< 0.001	0.061	< 0.001	0.745	0.201	< 0.001	0.125
Foliage RT	0.075	0.105	0.462	< 0.001	0.035	0.004	0.006	0.462	0.658	0.810	0.010	0.173
FRP	0.230	0.825	0.419	< 0.001	0.404	0.014	0.198	0.251	0.388	0.473	0.072	0.630

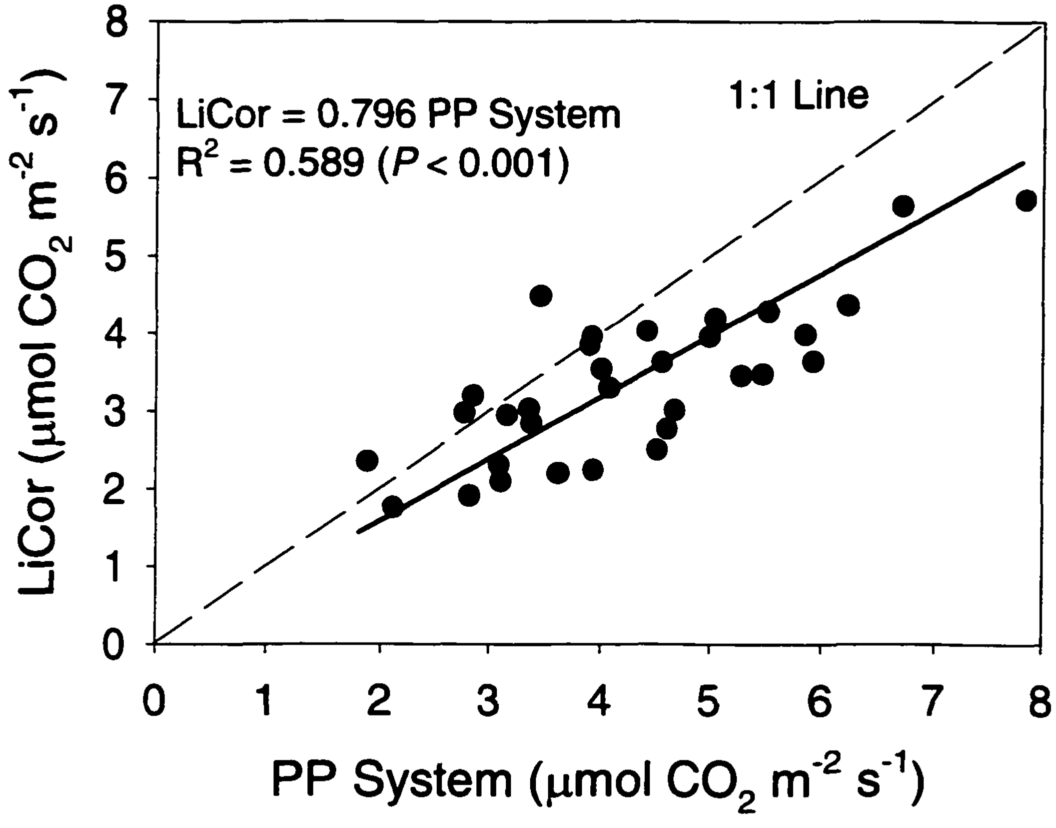

Figure A.2.1. Relationship between LiCor and PP System soil CO_2 effluxes at plot level. Linear regression had no significant intercept.

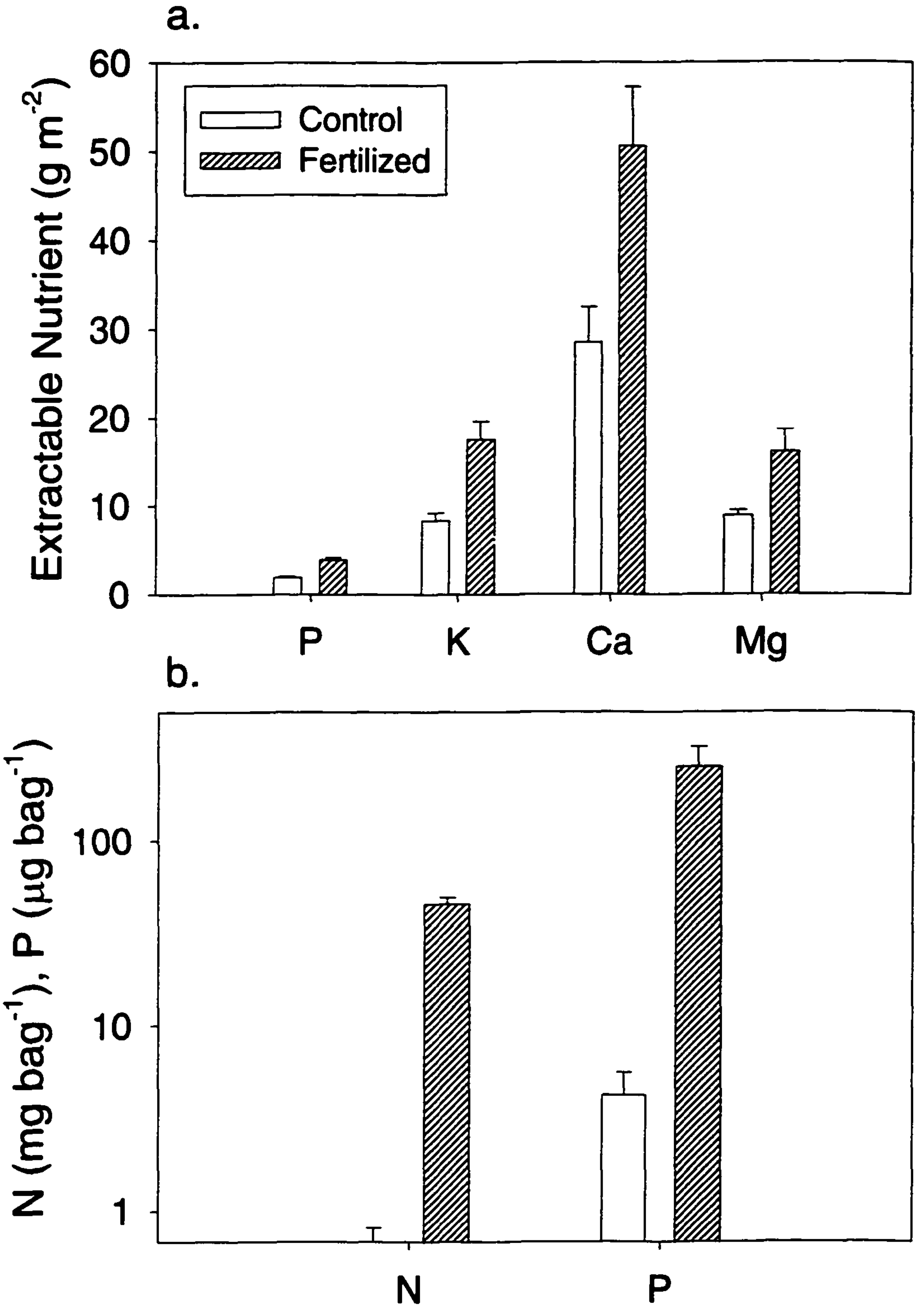

Figure A.2.2. Extractable nutrients from 0 to 0.3 m at the end at 5.5 year-old (n=6) (a). Resin bags N and P concentrations for 3 incubations (n=24) (b). Error bars are standard errors of the means. Note the logarithmic scale.

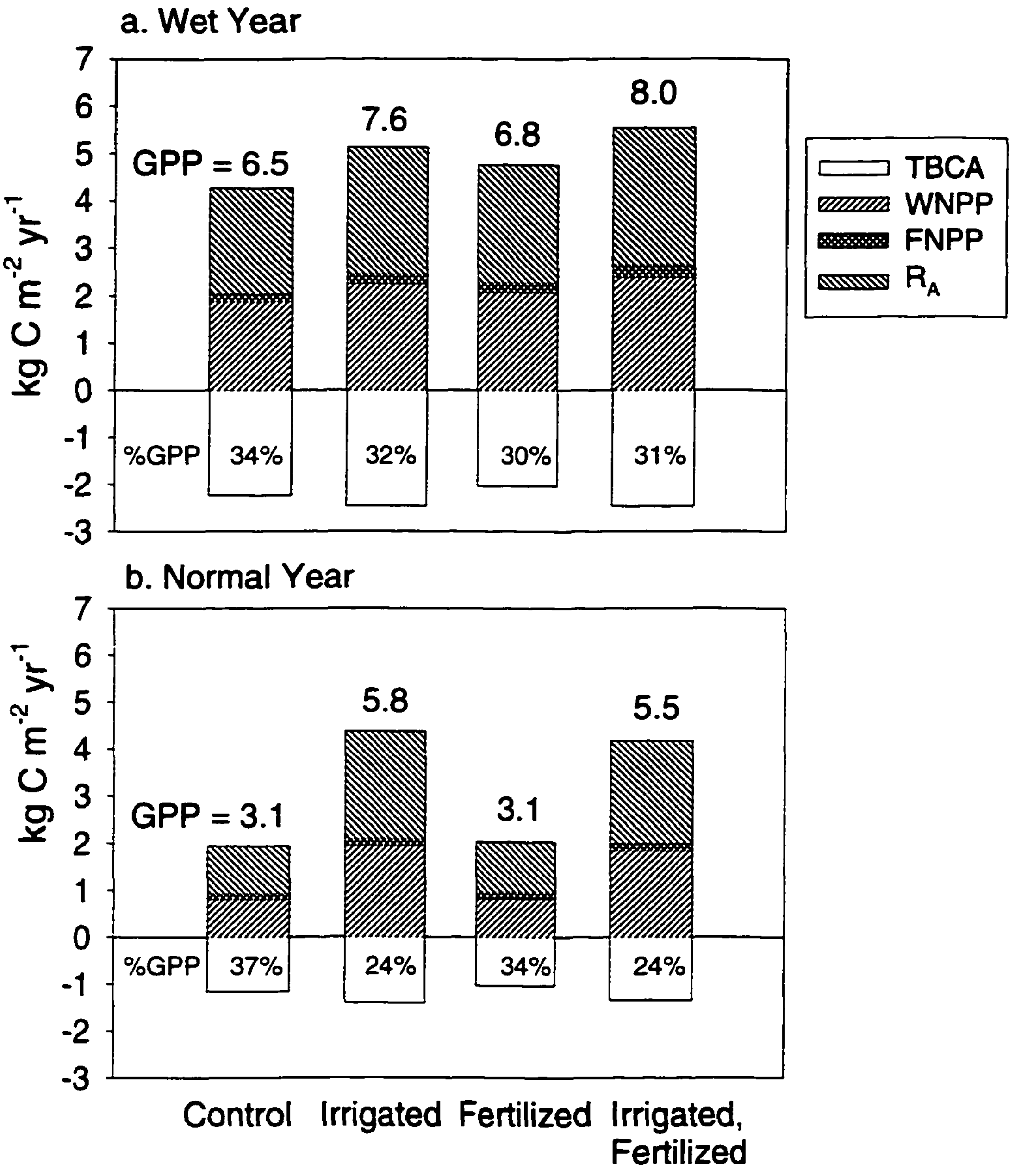

Figure A.2.3. Estimated gross primary production (GPP) and above and belowground components for the wet year (a) and normal year (b): means by treatment and year (n=4). TBCA = total belowground carbon allocation, WNPP = aboveground wood net primary production, FNPP = foliage net primary production and R_P = aboveground autotrophic respiration. Percentages represent the fraction of GPP allocated belowground.

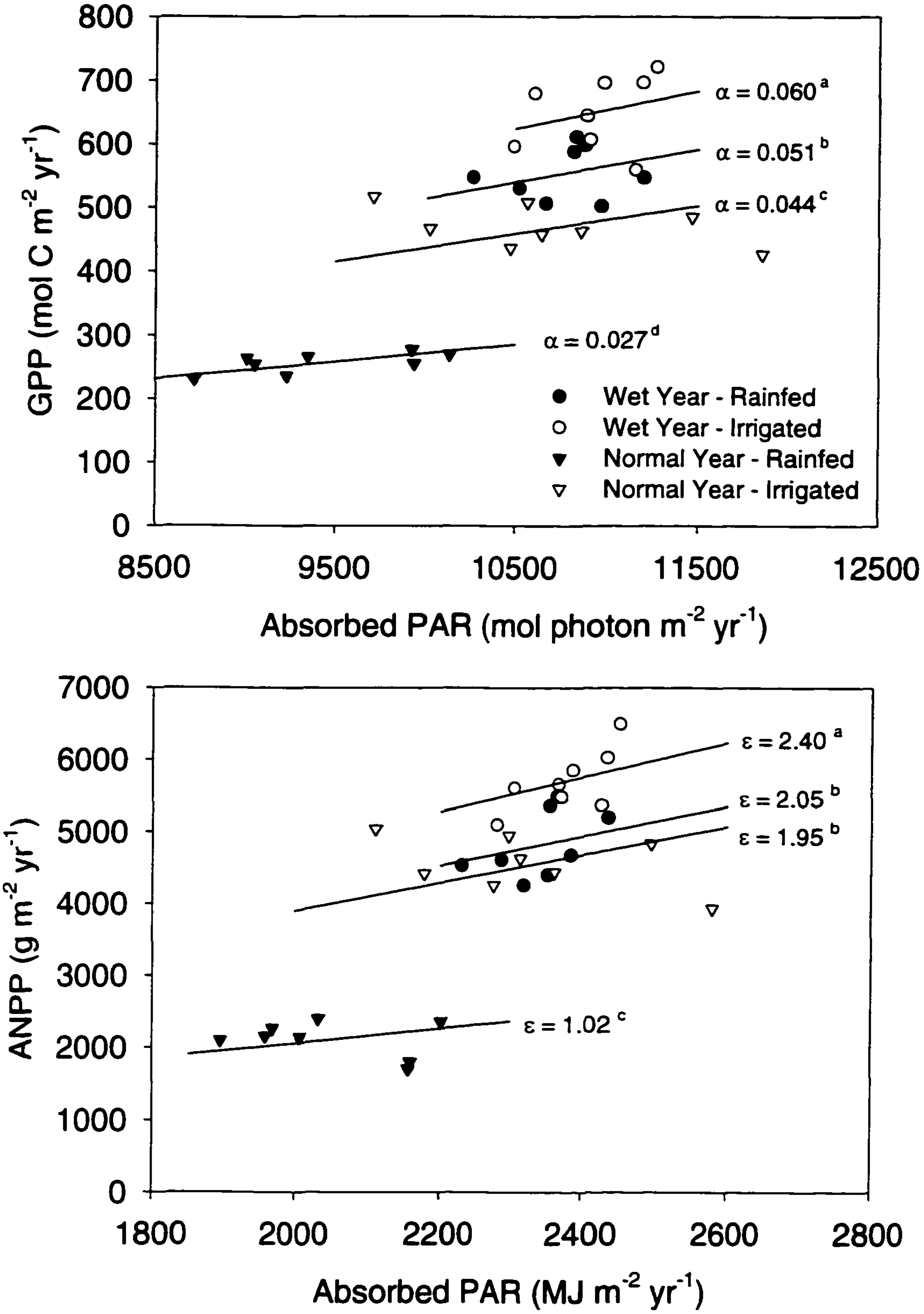

Figure A.2.4. GPP (a) and ANPP (b) *versus* APAR per plot by water regime and year. Linear regressions were forced to the origin and slopes represent light use efficiency (ε). Values followed by different letters differ at $P = 0.05$.

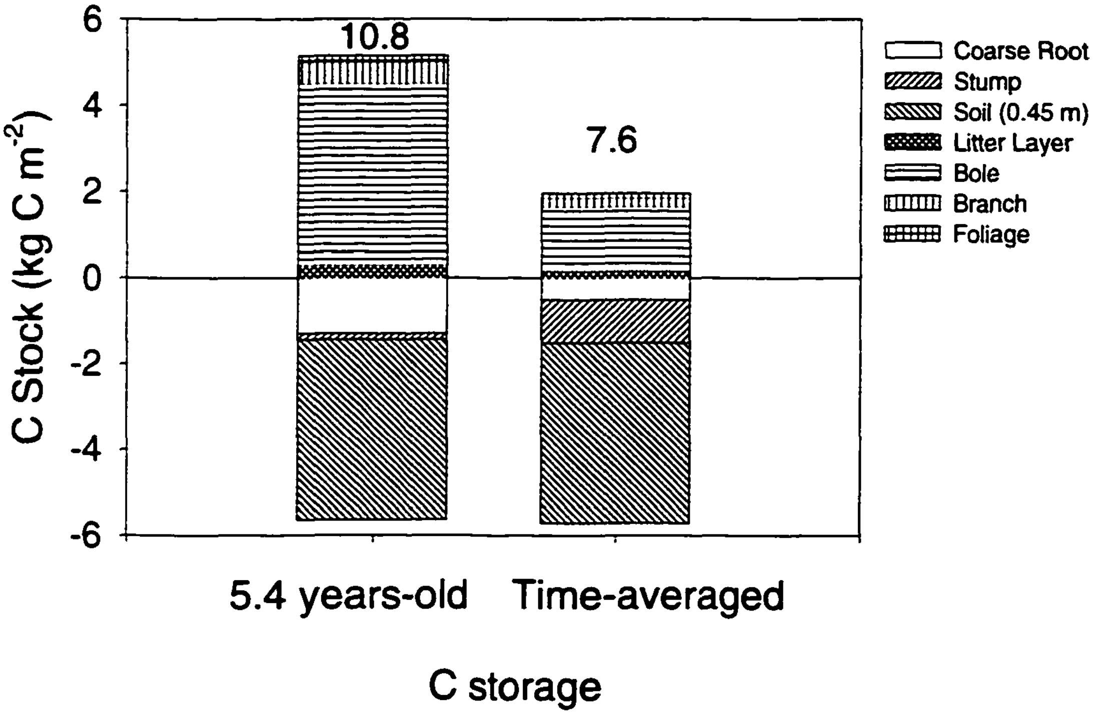

Figure A.2.5. C stocks at the end of the study for the rainfed treatments at 5.4 years-old, and the time-averaged C storage for a 6 year short-rotation, with 1 fallow year.

APPENDIX III.A

Fertility indices and bioassay procedures

On July of 1999, soils from all plots were sampled at two depths (0-0.15 and 0.15-0.30 m) using a graduated auger, and a composite sample (from 8 sub-samples) was obtained for each depth (in the fertilized plots, the samples were taken before any fertilization). Bulk density was determined using a standard 92 mL steel-cylinder with a sample taken at each depth. Samples were placed in plastic bags and dried (before drying, subsamples were taken for fresh aerobic incubation) at 65º C to a constant weight and then sent for analysis.

Soil texture, fertility, total C and N, and water holding capacity

Appendix I.A presents all analytical procedures used for soil texture, fertility, total soil C, total soil N and water holding capacity determination.

N and P soil availabilities

The availabilities of N and P were indexed with on site ion exchange resin bags technique (Binkley and Matson, 1983) during 2 different periods (June 2000 and December 2000). These evaluations were done just on the non-fertilized plots. At each time, six sets of separately bagged anion exchange resins (14 mL Sybron IONAC ASB-IPOH, 4.2 $mmol_c$ per bag) and cation exchange resins (14 mL Sybron IONAC c-251 H^+, 4.9 $mmol_c$ per bag) were placed 5 cm below the forest floor along the plot diagonal (5 between rows and 5 between plants) and left in place for three months. After collection, the resins were air dried and the anion and cation resins from each bag were combined and extracted with 100 mL of 2 M KCl. Concentration of NH_4^+-N and NO_3^--N were determined colorimetrically (Alpkem continuous flow autoanalyzer), and PO_4^{3-}-P (Lachat continuous flow autoanalyzer). The average total N (ammonium plus nitrate) and P content of the six bags in each plot was used as the plot value.

Nitrogen laboratory availability indices

Four laboratory indices were used to estimate N availability in soil (for all non-fertilized plots): anaerobic incubation, boiling-salt extraction, aerobic incubation of fresh soil, and aerobic incubation of dried soil. Soils were collected as described above and the availabilities were determined for both depths. For anaerobic incubation 10-g of dry soil subsamples were incubated in 50 mL of deionized water at 40ºC for 7 days and extracted with 50 mL of 4 M KCl after shaking for 1 hour, suspensions equilibrated for 12 hours and were then filtrated. Concentration of ammonium and nitrate were determined colorimetrically (Alpkem continuous flow autoanalyzer). The average mineral N (ammonium plus nitrate) at 0-0.15 m and 0-0.3 m depths were expressed in mg of N per kg of dry soil. Boiling-salt extraction used 5-g of dry soil subsamples placed in 120 mL specimen cups with 50 mL of 1 M KCl. The covered cups were then boiled in a microwave for 10 minutes, followed by a 15 minutes shaking and allowed to equilibrate for 12 hours. Filtered extracts were analyzed and expressed as previously noted. For dry-soil aerobic incubation two replicates of 10-g of dry soil subsamples per plot were placed in 120 mL specimen cups, humidified with 2.5-g of water and incubated for 5 days at 25ºC. Plastic films covered the containers maintaining moisture content close to field capacity. The first replicates were then extracted with 100 mL of 1 M KCl solution, shaken for 1 hour, let equilibrated for 12 hours and then filtered. The second replicates were incubated for 15 more days (with the plastic cover) and then extracted in the same way. All initial and final filtered extracts were analyzed as previous described. The net total mineralization rates (or immobilization) were obtained by the difference between final and initial values of total mineral N. The net mineralization rates values (N kg^{-1} 15 $days^{-1}$) were estimated for 0-0.15 m and 0-0.30 m depths. For fresh-soil aerobic incubation two replicates of 10-g of field-moist subsamples (collected in the previous day) were placed in 120 mL specimen cups and extracted at day zero (first replicate) and day 15th (second replicate) after incubation at room temperature (average of 25ºC) at field capacity (plastic covers). Extractions followed the procedures described. After filtration the solutions were frozen and sent to N analysis (distillation followed by acid-basic titration). The net rates were estimated and expressed as notice before.

Nutrient contents in the canopy

On February of 2000 and February of 2001, nutrient concentration in the canopy were determined by sampling 5 recent fully expanded leaves from the middle of the canopy of 6 trees, of all plots. Samples were dried out at 65ºC until constant weight. Total N was determined (LECO analyzer, Colorado State University) and P, K, Ca and Mg were mineralized using nitro-perchloric digestion (0.5-g of sample with 5.3 mL of HNO_3 and 0.7 mL of $HClO_4$ for 1 h up to 210ºC) followed by dilution and colorimetric determination for P, flame emission for K and atomic absorption spectrophotometry for Ca and Mg.

Bioassay

A bioassay with *E. grandis* x *urophylla* cuttings was performed to evaluate the supply capacity of each of the 40 sites from soil collected in both plots (previously to fertilization) in July of 1999 at 0-0.15 m depth using the previously described procedures. Soil were then sieved (2-mm mesh) and air-dried and storage. On August 1999 cuttings (clone COP-0321) started been prepared using a special procedure to minimize the nutrient content of the cuttings: uniformed 10-15 cm tall and 3-6 mm tick cuttings with 2 pair of leaves were rooted in a shaded-house in a nutrient free medium (50% of coconut fiber plus 50% of vermiculite) using 50 mL plastic rigid tubes. After 60 days, the rooted cuttings were defoliated and the inferior half of the medium was cut off. Cuttings were allowed to sprout and growth for 30 more days before been selected for uniform size. In December 1999, a 10-L pot was filled with 5 kg of the stored air-dry soils from each plot (total of 80 pots). Pots were placed in an open-area of the Copener's nursery over a suspended structure avoiding root growth out of the pot. Two cuttings were planted per plot to guarantee survival, and after 3 weeks one was removed. Water was provided every other day and the plants were grown for 6 months. Shoot and root biomass (soil was washed out) were harvested and ovendried (at 65ºC). After weighting shoot and root separately, compartments were grounded and mixed thoughtfully for nutrient analysis. N content was determined in a LECO 1000 CN analyzer (Leco Corp., St. Joseph, MI). P, K, Ca and Mg were mineralized by

Kjeldahl digestion, followed by dilution and colorimetric determination for P, flame emission for K and atomic absorption spectrophotometry for Ca and Mg. Dry matter was corrected to an ash-free basis due to potential mineral soil inclusion (ash content varied between 4 and 11%). The averaged dry matter (g per cutting) and nutrient content (mg per cutting) of the two plots in each site was used as the site value.

APPENDIX III.B

Supplemental Tables and Figures from Chapter III

Table A.3.1. Observed (± standard deviation) and 3-PG simulated yearly values of GPP, ANPP, TBCA, wood biomass and LAI for fertilized treatment of *E. saligna* in Hawaii (fertility rating = 1) after tuning.

		GPP	ANPP	TBCA	AWB	LAI
			kg C m^{-2} yr^{-1}		Mg ha^{-1}	m^2 m^{-2}
Year 1	Observed	4.47 ± 0.19	1.42 ± 0.15	1.94 ± 0.18	21.0 ± 1.5	3.3 ± 0.5
	3-PG	3.83	1.21	1.42	17.3	3.8
Year 2	Observed	5.41 ± 0.46	2.04 ± 0.15	1.58 ± 0.41	52.2 ± 1.8	5.9 ± 0.2
	3-PG	4.64	1.47	1.69	39.5	5.7
Year 3	Observed	4.35 ± 0.39	1.46 ± 0.16	1.46 ± 0.32	74.8 ± 4.0	5.4 ± 0.5
	3-PG	4.71	1.51	1.70	63.1	5.6
Year 4	Observed	4.18 ± 0.30	1.18 ± 0.11	1.52 ± 0.32	90.0 ± 6.0	5.2 ± 0.4
	3-PG	4.87	1.58	1.70	88.5	5.5
Year 5	Observed	4.38 ± 0.72	1.36 ± 0.06	1.51 ± 0.33	114.2 ± 1.0	5.6 ± 0.6
	3-PG	4.53	1.45	1.63	112.1	4.8
Year 6	Observed	3.83 ± 0.39	1.09 ± 0.14	1.42 ± 0.34	128.0 ± 3.6	5.3 ± 0.1
	3-PG	4.60	1.47	1.65	136.3	4.6

Table A.3.2. Observed (± standard deviation) and 3-PG simulated yearly values of GPP, ANPP, TBCA, wood biomass and LAI for control treatment of *E. saligna* in Hawaii (fertility rating = 0.85).

		GPP	ANPP	TBCA	AWB	LAI
			kg C m^{-2} yr^{-1}		Mg ha^{-1}	m^2 m^{-2}
Year 1	Observed	4.49 ± 0.35	1.30 ± 0.02	2.14 ± 0.33	18.6 ± 0.4	3.1 ± 0.1
	3-PG	3.07	0.92	1.24	13.2	3.1
Year 2	Observed	4.67 ± 0.42	1.46 ± 0.14	1.84 ± 0.19	40.4 ± 1.0	4.8 ± 0.6
	3-PG	3.77	1.14	1.49	30.0	4.6
Year 3	Observed	4.03 ± 0.35	1.10 ± 0.14	1.77 ± 0.14	58.2 ± 3.8	4.4 ± 0.4
	3-PG	3.83	1.60	1.50	47.9	4.6
Year 4	Observed	3.49 ± 0.43	0.85 ± 0.09	1.62 ± 0.29	69.0 ± 5.2	4.1 ± 0.3
	3-PG	3.96	1.22	1.51	67.2	4.5
Year 5	Observed	3.47 ± 0.38	0.93 ± 0.12	1.52 ± 0.36	82.2 ± 7.3	4.4 ± 0.3
	3-PG	3.65	1.11	1.43	85.0	3.9
Year 6	Observed	3.17 ± 0.57	0.83 ± 0.16	1.43 ± 0.45	93.0 ± 9.9	4.1 ± 0.2
	3-PG	3.67	1.12	1.44	103.1	3.7

Table A.3.3. Observed (± standard deviation) and 3-PG simulated yearly values of GPP, ANPP, TBCA, wood biomass and LAI for irrigated (and fertilized) treatment of *E. grandis x urophylla* in Brazil after tuning. Results for rainfed treatment were obtained by dropping irrigation water supply.

		GPP	ANPP	TBCA	AWB	LAI
		kg C m^{-2} yr^{-1}			Mg ha^{-1}	m^2 m^{-2}
				Irrigated		
Year 1	Observed	7.79 ± 0.69	2.56 ± 0.19	2.46 ± 0.40	93.7 ± 8.0	4.1 ± 0.3
Wet	3-PG	6.61	2.39	1.82	88.9	3.0
Year 2	Observed	5.64 ± 0.38	2.05 ± 0.16	1.37 ± 0.12	132.1 ± 8.0	3.7 ± 0.5
Normal	3-PG	5.93	2.14	1.65	130.1	2.5
				Rainfed		
Year 1	Observed	6.64 ± 0.49	2.16 ± 0.21	2.13 ± 0.40	85.1 ± 8.0	4.0 ± 0.4
Wet	3-PG	5.40	1.89	1.62	79.3	3.0
Year 2	Observed	3.08 ± 0.20	0.95 ± 0.11	1.10 ± 0.31	100.1 ± 9.0	2.4 ± 0.3
Normal	3-PG	3.40	1.19	1.09	102.2	2.0

Table A.3.4. Allometric equations used to estimate aboveground wood biomass and foliage biomass of the 40 *E. grandis* x *urophylla* plots based on DBH (D, cm) and total height (H, m).

Areas and Ages	Aboveground Wood (kg)	Foliage (kg)
All Areas 2 to 4 years-old	$0.0276\ D^{2.36}\ H^{0.56}$ $r^2 = 0.97$, $P < 0.001$, n=24	-
Area 1, 3, 4 and 5 5 years-old or older	$0.0305\ D^{2.11}\ H^{0.79}$ $r^2 = 0.96$, $P < 0.001$, n=63	$0.0162\ D^{3.85}\ H^{-1.37}$ $r^2 = 0.87$, $P < 0.001$, n=63
Area 2 5 years-old or older	$0.0441\ D^{2.09}\ H^{0.67}$ $r^2 = 0.97$, $P < 0.001$, n=63	$0.0154\ D^{3.63}\ H^{-1.37}$ $r^2 = 0.86$, $P < 0.001$, n=63

Table A.3.5. Diameter at breast height (DBH), height, dominant height (D.height), site index, basal area, stocking, wood biomass (W.Biomass) and volume by treatment at 6 and 8 years-old. Values are means with standard deviations given in parentheses (n=40). Values (within rows) followed by different letters differ at $P = 0.05$.

Variable	Unit	Control Plots		Fertilized Plots	
		6 years-old			
DBH	cm	13.2	(1.0)	13.1	(1.0)
Height	m	22.0	(2.1)	21.5	(2.3)
D.Height	m	23.3	(2.3)	23.2	(2.3)
Site Index	m	21.8	(2.0)	21.8	(2.1)
Basal Area	m^2	16.9	(2.3)	16.9	(2.4)
Stocking	trees ha^{-1}	1193	(103)	1215	(101)
W. Biomass	Mg ha^{-1}	98.7	(17.0)	96.9	(18.6)
Volume	m^3 ha^{-1}	181.3	(37.8)	176.7	(41.2)
		8 years-old			
DBH	cm	15.1	(1.2)	15.3	(1.1)
Height	m	24.5	(2.6)	24.7	(3.0)
D.Height	m	26.1 b	(2.8)	26.9 a	(3.2)
Basal Area	m^2	22.2 b	(2.9)	23.4 a	(3.0)
Stocking	trees ha^{-1}	1189	(102)	1213	(105)
W. Biomass	Mg ha^{-1}	143.1 b	(25.1)	152.1 a	(27.2)
Volume	m^3 ha^{-1}	262.8 b	(57.3)	279.0 a	(65.5)

Table A.3.6. Observed and simulated (± standard deviation) wood increment (WNPP) and LAI by year (wet and normal) and treatment (control and fertilized) for the the 40 *E. grandis* x *urophylla* stands using SC and 3-PG models.

		WNPP (Mg ha^{-1} yr^{-1})		LAI (m^2 m^{-2})	
Plots	Data \ Year	Wet	Normal	Wet	Normal
Control	Observed	29.3 ± 1.1	15.1 ± 0.9	3.1 ± 0.1	2.8 ± 0.1
	SC	20.2 ± 0.7	25.0 ± 1.2	-	-
	3PG	30.3 ± 0.7	18.3 ± 0.4	3.1 ± 0.1	2.0 ± 0.1
Fertilized	Observed	37.9 ± 1.1	17.3 ± 1.0	3.3 ± 0.1	3.2 ± 0.1
	3PG 1st Run	36.2 ± 0.6	25.2 ± 0.4	2.5 ± 0.1	1.7 ± 0.1
	3PG 2nd Run	35.4 ± 0.6	21.0 ± 0.4	3.3 ± 0.1	2.3 ± 0.1

Table A.3.7. Summary of the 46 soil fertility indices evaluated at the control plots (N=40) to be associated with the fertilization response during the wet year (R = coefficient of correlation between indices and fertilization response).

Variable	Unit	Minimum	Maximum	Average	SD	R
SC15	g m^{-2}	606	3398	1730	638	- 0.20
SC30	g m^{-2}	1061	5078	3090	1088	-0.18
SN15	g m^{-2}	27	186	106	35	-0.18
SN30	g m^{-2}	64	336	203	62	-0.24
N bag 1	mg bag^{-1}	0.0	1.2	0.1	0.2	-0.06
N bag 2	mg bag^{-1}	0.0	4.4	0.6	0.9	0.05
Nboil15	mg g^{-1}	1.4	25.8	10.4	5.5	-0.34*
Nboil30	mg g^{-1}	2.0	18.9	8.7	4.4	-0.31*
Ndry15	mg g^{-1}	-30.1	4.1	-2.8	5.4	-0.01
Ndry30	mg g^{-1}	-20.0	5.3	-1.6	4.2	-0.07
Nwet15	mg g^{-1}	-5.2	105.4	11.1	18.0	-0.00
Nwet30	mg g^{-1}	0.9	55.7	13.4	9.8	0.01
Nana15	mg g^{-1}	0.0	13.3	5.5	3.1	-0.19
Nana30	mg g^{-1}	0.0	12.9	5.2	2.9	-0.15
pH15	-	3.4	4.3	3.9	0.2	0.04
pH30	-	3.5	4.3	3.9	0.2	-0.23
P bag 1	µg bag^{-1}	2.4	236.5	41.2	63.8	-0.22
P bag 2	µg bag^{-1}	0.3	187.0	31.3	50.1	-0.14
P 15	µg g^{-1}	2.3	36.0	11.5	8.2	-0.43**
P 30	µg g^{-1}	2.4	27.4	10.9	7.7	-0.37*
K 15	$mmol_c$ kg^{-1}	0.1	1.0	0.4	0.2	-0.37*
K 30	$mmol_c$ kg^{-1}	0.1	0.9	0.4	0.2	-0.24
Ca 15	$mmol_c$ kg^{-1}	1.2	15.4	5.5	4.0	-0.10
Ca 30	$mmol_c$ kg^{-1}	1.2	14.8	4.8	3.4	-0.06
Mg 15	$mmol_c$ kg^{-1}	0.8	6.9	3.9	1.7	-0.33*
Mg 30	$mmol_c$ kg^{-1}	0.9	7.5	3.3	1.6	-0.30

* $P < 0.05$, ** $P < 0.01$

Table A.3.7. Continued

Variable	Unit	Minimum	Maximum	Average	SD	R
SB 15	mmol$_c$ kg^{-1}	3.0	22.0	9.9	5.0	-0.21
SB 30	mmol$_c$ kg^{-1}	2.6	20.0	8.5	4.6	-0.16
H AL15	mmol$_c$ kg^{-1}	16.0	64.0	37.1	12.4	-0.31
H AL30	mmol$_c$ kg^{-1}	14.5	60.5	34.9	12.3	-0.29
CEC 15	mmol$_c$ kg^{-1}	20.6	69.0	47.0	13.1	-0.38*
CEC 30	mmol$_c$ kg^{-1}	18.6	65.2	43.4	12.8	-0.34*
Sand 15	%	55.7	96.0	78.9	10.7	-0.05
Sand 30	%	56.3	95.5	76.3	11.5	0.01
Clay 15	%	4.0	40.3	19.7	10.6	0.05
Clay 30	%	3.5	41.6	20.8	10.9	0.01
Bulk D 15	g cm^{-3}	1.4	1.8	1.6	0.1	0.24
Bulk D 30	g cm^{-3}	1.5	1.9	1.7	0.1	0.17
Bio SDM	g plant^{-1}	3.7	10.7	5.4	1.2	-0.03
Bio RDM	g plant^{-1}	1.9	5.9	3.3	0.8	-0.05
Bio TDM	g plant^{-1}	5.8	16.6	8.8	2.0	-0.04
Bio N	mg plant^{-1}	36.2	95.9	52.9	11.4	-0.08
Bio P	mg plant^{-1}	1.9	37.1	10.6	7.9	-0.12
Bio K	mg plant^{-1}	10.6	61.5	26.9	11.7	-0.20
Bio Ca	mg plant^{-1}	19.9	91.4	44.5	12.1	0.01
Bio Mg	mg plant^{-1}	21.1	75.0	33.5	9.3	-0.07

* 15 = 0.0 to 0.15 m, 30 = 0.0 to 0.3 m, SC = total soil C, SN = total soil N, N bag = mineral N index with resin bag, Nboil = mineral N extracted with boiling salt solution, Ndry = Net mineralization using dried soil, Nwet = Net mineralization using fresh soil, Nana = mineral N after anaerobic incubation, P bag = mineral P index with resin bag, P = extractable P, K = extractable K, Ca = extractable Ca, Mg = extractable Mg, SB = sum of bases, H Al = hydrogen plus aluminum, CEC = cation exchange capacity, Bulk D = bulk density, Bio = bioassay, SDM = shoot dry matter, RDM = root dry matter, TDM = total dry matter

Table A.3.8. Summary of the 16 canopy and stand indices evaluated at the control plots (N=40) to be associated with the fertilization response during the wet year (R = coefficient of correlation between indices and fertilization response).

Variable	Unit	Minimum	Maximum	Average	SD	R
MAI	Mg ha^{-1} yr^{-1}	8.22	21.14	16.33	2.84	0.17
Site indexl	m	16.85	25.15	21.87	1.90	0.21
LAI	m^2 m^{-2}	2.10	4.20	3.19	0.45	-0.25
N leaf	g kg^{-1}	14.59	23.70	18.50	1.48	-0.24
P leaf	g kg^{-1}	0.80	1.85	1.12	0.30	-0.27
K leaf	g kg^{-1}	4.70	7.55	6.18	0.75	0.13
Ca leaf	g kg^{-1}	4.65	8.15	6.56	0.78	0.16
Mg leaf	g kg^{-1}	2.95	4.40	3.74	0.37	0.14
N canopy	g m^{-2}	5.05	9.65	7.11	1.13	-0.38*
P canopy	g m^{-2}	0.25	0.79	0.44	0.16	-0.32*
K canopy	g m^{-2}	1.28	3.33	2.38	0.43	-0.14
Mg canopy	g m^{-2}	0.86	1.88	1.44	0.26	-0.14

* $P < 0.05$

Table A.3.9. *P* values obtained from analysis of variances performed for total soil C and N evaluated at beginning of the study period, and meteorological variables on both years.

	Treatment Effect		Year Effect		
	Soil C	Soil N	Rainfall	Transpiration	SAW
P	0.52	0.13	< 0.0001	< 0.0001	< 0.0001

Table A.3.10. *P* values obtained from analysis of variances performed at the beginning (age 6) and end (age 8) of the study period for stand biometric attributes.

Variable	Initial – age 6		Final – age 8	
	Fertilization	Block	Fertilization	Block
DBH	0.07	< 0.0001	0.05	< 0.0001
Height	0.07	< 0.0001	0.52	< 0.0001
D. Height	0.56	< 0.0001	0.001	< 0.0001
Basal Area	0.89	< 0.0001	< 0.0001	< 0.0001
Stocking	0.12	< 0.0001	0.11	< 0.0001
W. Biomass	0.17	< 0.0001	< 0.0001	< 0.0001
Volume	0.08	< 0.0001	0.001	< 0.0001

Table A.3.11. *P* values obtained from analysis of variances performed for canopy attributes, absorbed PAR, wood increment and light-use-efficiency evaluated during both years.

Effects	Fert.	Year	F x Y	Fertilization Effect		Year Effect	
Variable				Wet Year	Normal	Control	Fertilized
LAI	< 0.0001	< 0.0001	< 0.0001	0.02	< 0.0001	< 0.0001	0.13
N content	< 0.0001	< 0.0001	< 0.0001	0.26	< 0.0001	0.01	< 0.0001
N canopy	< 0.0001	0.001	< 0.0001	0.01	< 0.0001	< 0.0001	0.04
P content	< 0.0001	< 0.0001	< 0.0001	0.26	< 0.0001	0.72	< 0.0001
P canopy	< 0.0001	0.37	< 0.0001	0.06	< 0.0001	< 0.0001	< 0.0001
APAR	< 0.0001	0.08	0.001	0.06	< 0.0001	< 0.01	0.20
WNPP	< 0.0001	< 0.0001	0.01	< 0.0001	0.01	< 0.0001	< 0.0001
LUE	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.24	< 0.0001	< 0.0001

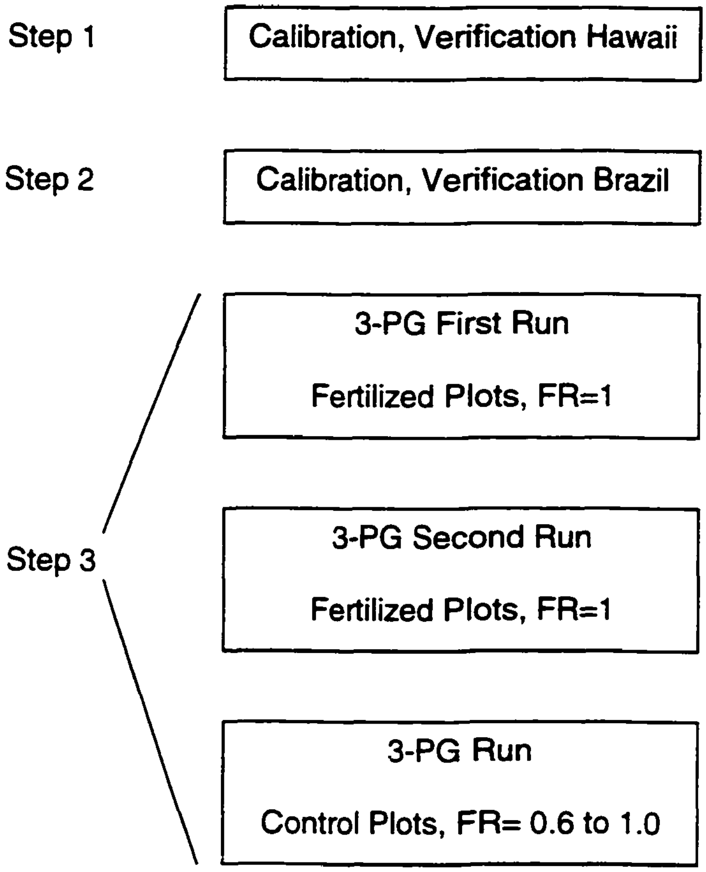

Figure A.3.1. Diagram of the calibration-validation steps used for 3-PG model.

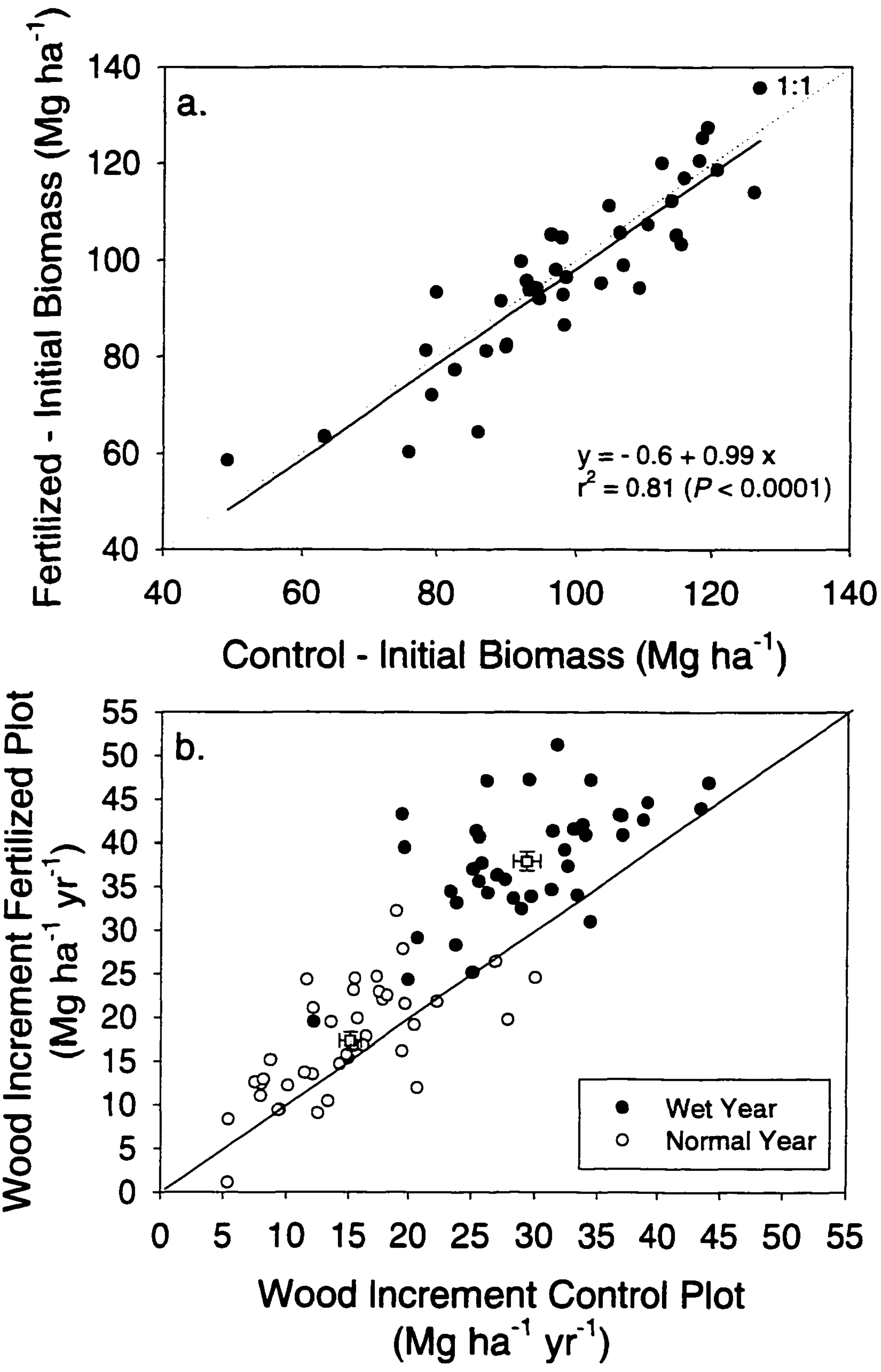

Figure A.3.2. Initial wood biomass of the 40-paired plots (control and fertilized) (a). Wood increments during wet and normal years (b). Gray squares represent the average growth for the years with standard error bars.

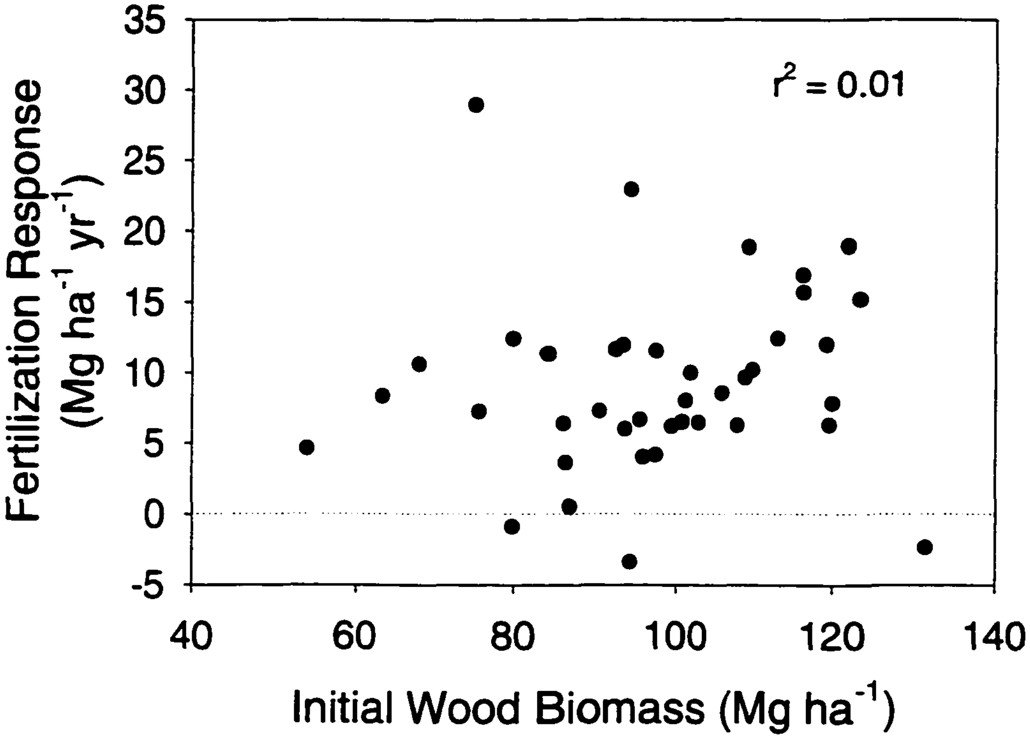

Figure A.3.3. Fertilization responses of the 40 stands during the wet year and the initial wood biomass of the paired plots.

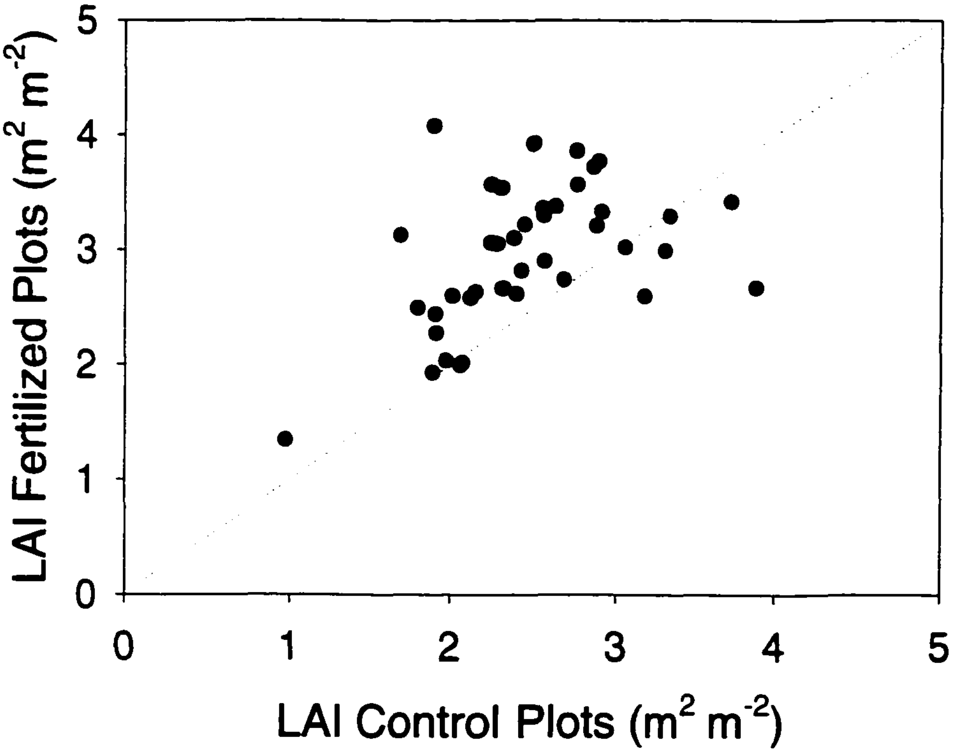

Figure A.3.4. Leaf area index of the control and fertilized plots on March 2001.