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Effect of site management on leaf area, early biomass development, and stand growth efficiency of a *Eucalyptus grandis* plantation in South Africa

Ben du Toit and Steven B. Dovey

Abstract: The effects of intensive site management operations on leaf area index (LAI), aboveground woody biomass (WB) development, and stand growth efficiency were studied in a South African *Eucalyptus grandis* (Hill ex Maiden) stand from establishment to 3.5 years of age. Site management treatments included slash removal, slash retention, fertilization, slash burning, and slash disturbance through mechanized harvesting operations. Stand LAI development responded strongly and significantly to the site management treatments imposed at establishment. Responses were driven by nutrient supply but were apparently limited by a severe drought after establishment. At 1.3 years, LAI in the slash removal treatment reached 2.1, compared to 4.5 following fertilization or slash burning. Treatments also significantly affected the development of aboveground WB, which ranged from 53.6 (slash removal) to 64.9 (fertilization) and 65.8 Mg·ha^{-1} (slash burning) at 3.5 years. Biomass allocation to roots and stand growth efficiency (i.e., WB increment per unit of LAI) did not differ significantly between treatments. We conclude that the fast-growing treatments produced more WB because of more rapid development of maximum LAI. The possible implications of this response mechanism for management operations that aim to improve growth through improved nutrient supply are discussed, with reference to unthinned, short-rotation crops.

Résumé : Les effets des travaux intensifs de préparation de terrain sur l'indice de surface foliaire (LAI), la production de biomasse ligneuse et l'efficacité de croissance du peuplement ont été étudiés dans un peuplement d'*Eucalyptus grandis* (Hill ex Maiden) d'Afrique du Sud à partir du moment où il a été établi jusqu'à l'âge de 3,5 ans. Les traitements de préparation du terrain incluaient l'enlèvement ou non des déchets de coupe, la fertilisation, le brûlage des déchets de coupe et le brassage des déchets de coupe dû aux travaux mécanisés de récolte. L'indice de surface foliaire du peuplement a réagi fortement et significativement aux traitements de préparation de terrain effectués lors de l'établissement. Les réactions étaient contrôlées par la disponibilité des nutriments mais elles ont vraisemblablement été atténuées par une sécheresse sévère survenue après l'établissement. À l'âge de 1,3 ans, la valeur de LAI a atteint 2,1 dans le traitement où les déchets de coupe avaient été enlevés comparativement à 4,5 après la fertilisation ou le brûlage des déchets de coupe. Les traitements ont aussi significativement affecté la production de la biomasse ligneuse aérienne qui variait de 53,6 (enlèvement des déchets de coupe) à 64,9 (fertilisation) et 65,8 Mg·ha^{-1} (brûlage des déchets de coupe) à l'âge de 3,5 ans. L'allocation de biomasse aux racines et l'efficacité de croissance du peuplement (c.-à-d., l'accroissement de la biomasse ligneuse par unité de LAI) ne différaient pas significativement d'un traitement à l'autre. Les auteurs arrivent à la conclusion que les traitements où la croissance était rapide produisaient plus de biomasse ligneuse parce que la valeur maximum de LAI était atteinte plus rapidement. Les répercussions potentielles de ce mécanisme de réponse sur les travaux d'aménagement qui visent à améliorer la croissance via un meilleur apport en nutriments sont discutées dans le contexte des plantations non éclaircies à courte période de révolution.

[Traduit par la Rédaction]

Introduction

This study forms part of the Karkloof Project, which is situated in the Midlands of the KwaZulu-Natal province, South Africa. The objective is to study the effects of intensive site management operations during the interrotational period on a stand of *Eucalyptus grandis* (Hill ex Maiden), to improve our understanding of two key issues: (1) the short-

term effects of management operations on soil water and nutrient availability to trees and (2) the impact of these operations on the soil's physical, chemical, and biological properties. A more comprehensive description of all the components of the full project is given by du Toit et al. (2000). This paper deals specifically with the response mechanism of a stand of trees to increases in growth resource availability.

Operations that increase the availability of water and nutrients in forest stands have the potential to increase wood production. The mechanism for this response is the stand's ability to capture incoming radiation and the efficiency by which this energy is used to convert CO_2 into woody biomass (WB) (Linder 1985; Linder 1987; Ericsson et al. 1993; Landsberg and Hingston 1996; Binkley et al. 2004). In practical terms, we hypothesized that the response can manifest as (1) an increased leaf area or (2) an increased stand growth efficiency (i.e., aboveground WB production per unit of leaf area) (Waring 1983). This report explores the nature of the relationship between leaf area, aboveground WB, and coarse roots with changing levels of available soil water and nutrients (brought about by site management treatments) and subsequently reflects on the implications of these effects for the management of commercial forests.

Materials and methods

Location, site, and stand description

The trial was situated at 29°S and 30°E in the Province of KwaZulu-Natal, South Africa, at an altitude of 1260 m above sea level. The Humic Ferralsol (FAO classification) on the site has a clayey texture, low base status, and high phosphorus (P) sorption capacity. A well-developed microstructure ensures high levels of porosity and good drainage. Soil depth across the trial site varies from approximately 0.7 to 1.1 m (average 0.92 m). The mean annual precipitation is approximately 950 mm: rain falls mostly in summer; and the period from May to August is typically dry, with sporadic frost in midwinter. The long-term mean monthly minima for the coldest month (June) and the warmest month (January) are 3.7 and 14.8 °C; the corresponding maxima are 19.0 and 25.0 °C. More details on the location, soil, and historic climate records of the experimental site are documented in du Toit et al. (2000). The site supported a 7-year-old stand of *E. grandis*, which had a mean annual increment of 21 $m^3 \cdot ha^{-1} \cdot year^{-1}$ when it was clear felled in December 1998. *Eucalyptus grandis* is an evergreen tree with an open, spreading crown. In the juvenile stage, it has large, dark green, ovate leaves, which become more slender and lanceolate with age. It is capable of rapidly forming a dense canopy in plantations under suitable establishment conditions (Poynton 1979; Boland et al. 1997). The site was replanted in February 1999 with genetically improved seedlings of *E. grandis* that had been raised in containerized planting trays. Seedlings were planted in small notch pits at a density of 1680 stems·ha⁻¹ and treated with a pesticide drench (deltamethrin, a synthetic pyrethroid) suspended in 2 L of water.

Experimental design and treatments

The design and layout of the experimental program were described by du Toit et al. (2000). All treatments were kept weed-free until canopy closure. The trial design was a randomized complete block and had four replications. Five treatments (each as a stand-alone set of site management options) were implemented:

(1) 0S, slash removal: All harvesting residue (including bark, branches, and foliage) and litter layer manually removed from the plot. Partly decomposed material in the forest floor remained on site.

(2) 1S, slash retention (regular slash load): Harvesting residue retained and broadcast on the plot. This is regarded as the control treatment.

(3) SB, slash burning: Harvesting residue burnt in a medium-intensity fire.

(4) SD, slash disturbance: Slash disturbed and mixed with soil through mechanical loading and stacking of timber with a three-wheeled loader.

(5) SF, fertilization: Regular slash load, followed by the application of 16.6 kg nitrogen (N)·ha⁻¹ + 33.3 kg P·ha⁻¹ + 0.7 kg zinc (Zn)·ha⁻¹ in localized positions near seedlings at time of planting.

Data collection

Climatic data were collected with an automatic weather station. The reference evapotranspiration from a short grass surface was calculated with the Penman–Monteith equation (Monteith 1965). Soil water retention characteristics were determined at matric potentials ranging between saturation and the wilting point. We used a tension table apparatus (Smith and Thomasson 1974) for high matric potentials and a pressure plate apparatus (Klute 1986) for matric potentials from –100 to –1500 kPa. Soil water content in the field experiment was measured with time domain reflectometry (TDR) sensors (model CS615; Campbell Scientific Africa, Stellenbosch, South Africa), placed at 15 cm depth. Four sensors were used per treatment (two per plot in replications 1 and 3). The permanent wilting point in this soil was estimated from the water retention curve as 25.2% volumetric soil water content. This level was used to normalize the readings from all TDR sensors in the first dry winter period (the soil water was drawn down to near wilting point and remained at that level for more than 30 days across all treatments). Small differences between treatments were recorded in soil water content during the first growing season (data not shown). However, for the bulk of the remaining observation period, soil water levels were remarkably similar between treatments at a given point in time; hence, mean values across treatments are presented.

The development of woody tissues and other biomass components over time was determined by destructive harvesting of 20 ± 3 trees at 0.3, 0.5, 0.8, 1.0, 1.8, and 3.0 years after planting (YAP). An additional sample of 12 trees was harvested at 3.5 YAP. The fresh wet mass of the foliar components and that of the woody components were determined separately for destructive samples in the field. Subsamples were oven dried to constant mass at 65 °C in preparation for nutrient analysis and were weighed for conversion of fresh sample mass to oven-dry mass. Coarse root samples (diameter > 2 mm) were collected from the 20 sample trees at 3.0 YAP. The area occupied by each sample tree (2.44 m × 2.44 m) was divided into four quadrats. The soil in one such

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Table 1. Mean values for slash dry mass and nutrient content after implementing three slash management options that formed part of treatments (adapted from du Toit 2003).

Treatment	Dry mass ($kg \cdot ha^{-1}$)	N ($kg \cdot ha^{-1}$)	P ($kg \cdot ha^{-1}$)	K ($kg \cdot ha^{-1}$)	Ca ($kg \cdot ha^{-1}$)	Mg ($kg \cdot ha^{-1}$)
1S, slash retention (regular slash)	116 527	1 044	53	193	823	201
0S, slash removal	79 854	710	39	111	233	116
SB, slash burning	31 415	604	27	96	747	151

Note: Treatments SD (slash disturbance) and SF (fertilization) had regular slash loads, similar to treatment 1S.

quadrat was excavated in layers to a depth of 60 cm and sieved to obtain the coarse roots (Q). The taproot (TR) was excavated separately to the same depth. The coarse root mass associated with the tree was estimated as $4Q + TR$ and was reported on an ash-free basis to eliminate potential errors arising from soil contamination. Coarse root mass and WB of destructive sample trees were regressed against diameter at breast height (DBH) and total tree height, and the models explaining the largest portion of the variation were used to estimate individual tree WB. Individual tree estimates were summed per plot and scaled up to a hectare basis.

Subsamples from the four bulk foliar samples per treatment were analysed for nutrient concentration according to the methods described by Kalra and Maynard (1991). The dried material was ground, dry ashed, dissolved in 0.6 $mol \cdot L^{-1}$ HCl, filtered, and diluted to an appropriate level with deionized water. Concentrations of calcium (Ca) and magnesium (Mg) were determined by atomic absorption spectroscopy, and flame emission spectroscopy was used for potassium (K). The concentration of P was determined spectrophotometrically (molybdenum blue method). The concentration of N was determined by the Kjeldahl procedure, with selenium as a catalyst (Nicholson 1984). Nutrient accretion in the foliar and woody tissues was calculated as the product of the nutrient concentration (mean of four sample trees per treatment) and the dry mass of that component per plot. Nutrient accretion in WB is the sum of foliar and woody components at each age, and periodic values were obtained by difference.

The specific leaf area was determined by scanning subsamples of leaves with a LI-COR™ 3200 area meter (Li-COR Inc., Lincoln, Nebraska) before oven drying. The leaf area index (LAI) for the treatments was determined using two different techniques during stand development. From planting up to 1.3 years of age, the leaf area of individual trees (destructive samples) was regressed against tree height (tree height and canopy length were virtually identical during this period, as the canopy had not started to lift from below). The regressed leaf areas of individual trees per plot were summed and divided by the ground area to determine LAI.

After canopy closure (1.8–3.5 YAP), plant area index was estimated with optical methods that used two LI-COR plant canopy analysers in remote mode. All measurements were taken on windless days, under uniform sky conditions, and with the sun at a low angle (LI-COR 1992). The relationship between plant area index and LAI varied with age. Relationships appropriate to the stand age-class (developed from Dovey and du Toit 2005) were used to convert LAI from plant area index readings at different intervals between 1.8 and 3.5 years of age.

For this paper, the stand growth efficiency (GE) is defined as the periodic increase in aboveground WB ($Mg \cdot ha^{-1} \cdot year^{-1}$) per unit leaf area (after Brix 1983; Waring 1983; Albaugh et al. 1998; Jokela and Martin 2000). The LAI, rather than leaf mass, was chosen as the indicator of the photosynthetic capacity of the stand, since it is related to absorbed photosynthetically active radiation (Linder 1985; Landsberg and Hingston 1996) and since specific leaf area is not constant in developing stands (Linder 1985; Sands et al. 1992; Cromer et al. 1993; Osório et al. 1998; Job et al. 2003). Measurement periods were of unequal length, making it necessary to express GE on an annual basis. Since leaf area was increasing, the average value of LAI over the observation period was used. Levels of GE were depicted on graphs at the midpoint of each observation period.

Data for nutrient accretion, LAI, WB, and GE were analysed with a standard one-way analysis of variance (ANOVA) procedure using Genstat® for Windows™ (Lane and Payne 1996). By following the guidelines described by McConway et al. (1999), we made sure that the basic assumptions of ANOVA were not violated.

Results

The mass of slash on the site after harvesting amounted to 116.5 $t \cdot ha^{-1}$ on average, of which approximately 40% (by mass) was from the harvesting residue and 60% from the forest floor. This large build-up of material on the forest floor has been ascribed to a combination of dry and cold conditions during winter (du Toit 2003). The oven-dry mass and nutrient content for slash management treatments are shown in Table 1. Slash burning markedly reduced the quantities of N, P, and K in the remaining ash, but the total amounts of Ca and Mg were affected to a lesser degree. Slash removal strongly reduced levels of all elements, especially Ca.

Foliar nutrient concentrations and nutrient accretion in WB (Table 2) were monitored to reflect differences in plant-available nutrients between treatments. Nutrient accretion in treatment 0S was significantly lower than in the control (1S) for virtually all elements across all monitoring periods, as shown in Table 2. On the other extreme, the uptake of N and P in the fertilized treatment remained significantly superior to that in the control for the entire first year. Nutrient accretion in treatments 1S, SD, and SB remained statistically similar during midwinter (0.25–0.50 YAP). However, by 0.75 YAP, the trees in the SB and SD treatments had already

Table 2. Nutrient accretion in the aboveground biomass of treatments for specific intervals during the first year of growth.

Event No.	Period (years)	Time of year	Nutrient	Treatment[a] (kg·ha⁻¹) 0S	1S	SD	SB	SF	Mean	LSD[b]
1	0.00–0.25	Feb.–Apr.	N	0.56a	1.37c	1.43c	1.07b	1.76d	1.24	0.25
			P	0.03a	0.08c	0.07bc	0.06b	0.10d	0.06	0.02
			K	0.18a	0.49c	0.47c	0.34b	0.46c	0.39	0.08
			Ca	0.11a	0.25c	0.25bc	0.21b	0.29c	0.22	0.04
			Mg	0.11a	0.30c	0.27bc	0.23b	0.29c	0.24	0.05
2	0.25–0.50	May–July	N	0.61a	2.51b	2.15b	2.18b	3.26c	2.14	0.72
			P	0.04a	0.15b	0.15b	0.16b	0.22c	0.14	0.04
			K	0.14a	0.62b	0.46b	0.52b	0.95c	0.54	0.20
			Ca	0.13a	0.67cd	0.45b	0.53bc	0.83d	0.52	0.16
			Mg	0.10a	0.43b	0.38b	0.43b	0.57c	0.38	0.13
3	0.50–0.75	Aug.–Oct.	N	2.09a	4.59bc	6.12bc	6.41bc	7.23c	5.29	2.47
			P	0.11a	0.29b	0.33bc	0.38bc	0.45c	0.31	0.15
			K	0.52a	1.42b	2.41c	2.37c	2.19bc	1.78	0.79
			Ca	0.31a	0.67a	1.44b	1.68b	1.35b	1.09	0.51
			Mg	0.43a	1.05b	1.59bc	1.92c	1.74c	1.35	0.61
4	0.75–1.00	Nov.–Jan.	N	20.50a	39.60b	42.00b	51.50c	52.00c	41.12	8.19
			P	1.04a	2.08b	2.33b	3.20c	3.04c	2.34	0.51
			K	7.89a	15.37b	16.29bc	19.39c	18.79c	15.55	3.30
			Ca	5.47a	12.68b	17.97c	15.82c	22.97d	14.98	3.13
			Mg	6.15a	13.88b	15.36bc	18.68c	18.08c	14.43	3.65

Note: Values within rows followed by the same letter are not significantly different at $p < 0.05$. LSD, least significant difference.
[a]Treatment over the period in question.
[b]Least significant difference at $p = 0.05$.

taken up significantly more K and Ca than those in the control (1S). Finally, by 1.0 YAP, the nutrient accretion in treatment SB was significantly superior to that in the control for all elements in Table 2.

Cumulative monthly data for rainfall and for evapotranspiration were recorded for each growth year (August to July). The rainfall for each of the four years (August to July) totalled 618, 1003, 810, and 1013 mm (the long-term average is 918 mm). Cumulative evapotranspiration over the same periods totalled 1262, 1159, 1130, and 1189 mm. The first year of the project (1998–1999) was abnormally dry in the late summer with relatively high evapotranspiration levels. In addition, the winter period was unusually dry and long; the period with monthly rainfall less than 20 mm spanned 6 months during the winter of 1999 compared to only 3 months during the following two seasons. In strong contrast, the second year (1999–2000) had above-average rainfall with relatively low evapotranspiration rates.

Figure 1 shows the volumetric soil water content over the monitoring period, with lines indicating the soil water contents at –10, –1000, and –1500 kPa of tension. Despite the fact that soil moisture was very similar between treatments, large differences existed between years, specifically with regard to the duration of the water stress period during each dry (winter) season. Another important difference between seasons was the level of soil moisture in the wet season. The low rainfall toward the end of the first summer led to a rapid depletion of soil moisture (Fig. 1).

During the second growing season (1999–2000), soil water was held at less negative tensions, and the soil water content regularly exceeded field capacity after large rainfall events. The large differences in LAI that existed between treatments during the second growing season did not give

Fig. 1. Mean soil water content across treatments at 0.15 m depth from time of planting until 2.7 years of age. The volumetric soil water contents at field capacity (42.2%), at –1000 kPa tension (26.0%), and at the wilting point (25.2%) are shown as horizontal lines on the graph. The three pairs of vertical lines indicate the onset and the end of each of the first three dry winter periods, when soil moisture was held at tensions more negative than –1000 kPa for more than 30 consecutive days.
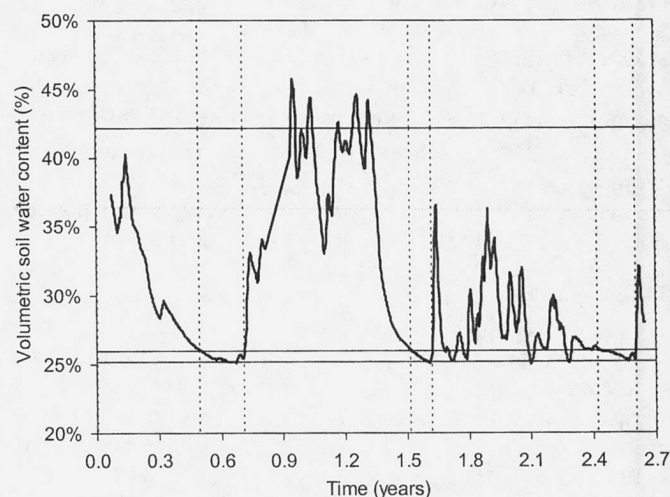
rise to meaningful differences in soil moisture, apparently because soil water was available in such abundant supply during this time.
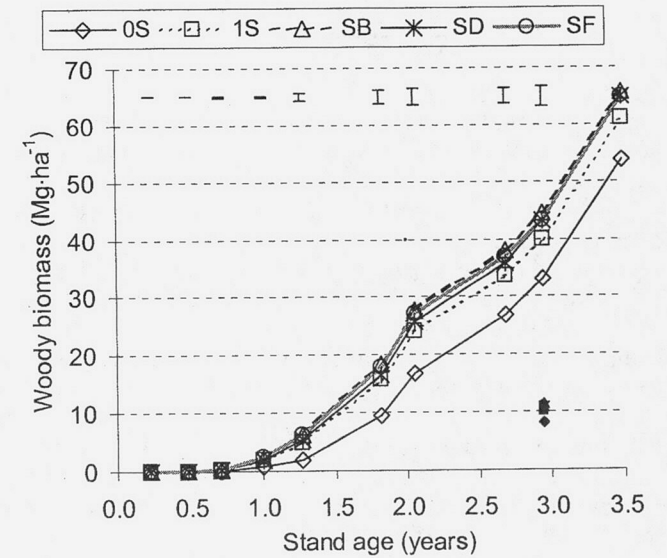
Tree survival immediately after planting was generally very good and was similar between treatments. The average stocking for plots on the trial site was 1582 stems·ha⁻¹. The

Fig. 2. Development of leaf area index up to 3.5 years of age. The least significant difference ($p = 0.05$) is shown as an error bar for each measurement event. The three pairs of grey vertical lines indicate the onset and the end of each of the first three dry winter periods as defined in Fig. 1. Treatments: 0S, slash removal; 1S, slash retention (regular slash load); SB, slash burning; SD, slash disturbance; and SF, fertilization.

Fig. 3. Development of aboveground woody biomass during the first 3.5 years after planting (open symbols linked by lines) and coarse root biomass at 3.0 years (filled symbols without lines). The least significant difference for the aboveground data ($p = 0.05$) is shown as an error bar for each measurement event. Treatments: 0S, slash removal; 1S, slash retention (regular slash load); SB, slash burning; SD, slash disturbance; and SF, fertilization.
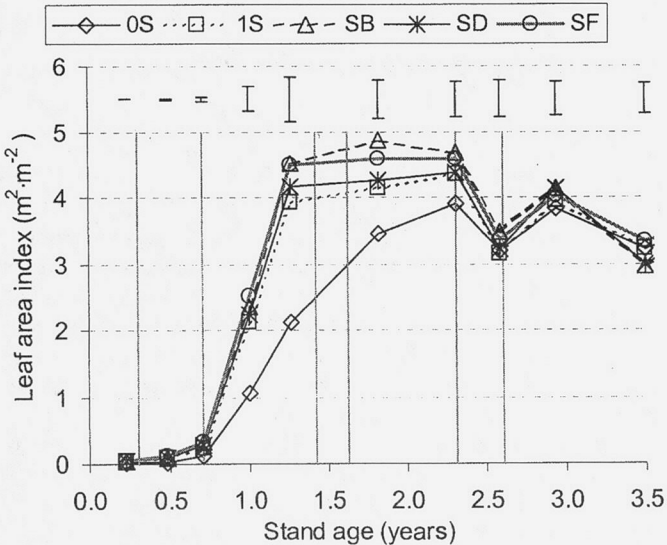
development of LAI in the treatments is shown in Fig. 2. The duration of the dry winter periods, when soil moisture decreased to tensions more negative than –1000 kPa, appeared to have a pronounced influence on the development of LAI in the treatments. The LAI developed slowly during the dry winter period of 1999 (0.5–0.7 YAP in Fig. 2). The onset of spring rains in October 1999, coupled with higher temperatures, triggered rapid growth in leaf area (0.7 YAP). The above-average rainfall in the second growing season kept the soil moist (Fig. 1) and allowed trees in the fast-growing treatments (SB, SF, SD, and 1S) to develop LAI values in excess of 4 by the end of that season (1.4 YAP in Fig. 2). Within the group of fast-growing treatments, SB was significantly superior to 1S (control) from 0.5 to 1.8 YAP, whereas SF was significantly superior to the control from 0.8 to 1.0 YAP. Trees in the SD group had a slightly higher leaf area than those in the control group for long periods of time, but this difference was never significant. On the other extreme, LAI development in treatment 0S was significantly slower than in all other treatments, reaching a value of approximately 2.1 by the end of the second summer season (Fig. 2). The difference in LAI between 0S and the other treatments remained highly significant ($p < 0.001$) from 0.3 to 2.1 YAP, and it was still significant ($p < 0.05$) at 2.3 YAP. The LAI in treatment 0S finally reached a maximum of 3.95 at 2.3 YAP (approximately 400 days after the fast-growing treatments reached or exceeded that level). The last substantial rainfall event of the third growing season lasted 3 days and ended on 2 May 2001, when 12 mm was recorded. The LAI of most treatments was still virtually unaffected by the dry conditions when measured at 2.3 YAP (27 days after the last significant rainfall event). Intense water stress set in at approximately 2.4 YAP (Fig. 2), that is, 63 days after the last rains, when the soil water contents dropped below 26%.

The dry conditions in the third winter (this time of fairly average duration, i.e., 106 days) caused LAI to decline sharply in all treatments. No significant differences were detected between treatments from this point forward. LAI again increased in the fourth growing season (2.6–3.2 YAP), but this peak was lower than that of the third summer (Fig. 2).

The development of the WB (mass of the stem wood plus bark and branches) over time is shown in Fig. 3. The values for treatment 0S were significantly ($p < 0.001$) lower than in all other treatments for all measurement events recorded (Fig. 3). This was expected, given the slow development of LAI in that treatment. A significant "block effect" was observed in the WB data toward the end of the observation period (2.7–3.5 YAP), with replications 1 and 2 having greater WB than replications 3 and 4. A summary of the ANOVA for WB from 1.8 to 3.5 YAP is shown in Table 3. In all treatments, WB was slow to develop initially, since early tree growth favours the development of leaves and roots. However, from the onset of the second growing season WB increased at exponential rates in all treatments (Fig. 3). The slopes of the lines showing WB increment over time for individual treatments all decreased after 2.1 YAP but then increased again slightly from 2.6 YAP (Fig. 3). As expected, these fluctuations coincided with the decline in LAI observed in all treatments during the third winter and with its subsequent increase thereafter (Fig. 2). The rate of increase in WB for the 0S treatment diverged from that for the other treatments from 0.3 YAP (Fig. 3); however, from 2.1 YAP, the WB increment lines for all treatments run in parallel. Here again, the WB development mirrors the fact that LAI, the main driver of growth rate, had converged to similar levels in all treatments and remained similar, despite seasonal fluctuations. Coarse root mass at 3.0 YAP is also shown in

Table 3. Summary of analysis of variance results showing mean squares for woody biomass 1.8–3.5 years after planting (YAP).

Source of variation	df	Woody biomass (Mg·ha^{-1})				
		1.8 YAP	2.1 YAP	2.7 YAP	3.0 YAP	3.5 YAP
Replication	3	3.58ns	11.63ns	21.32*	26.21*	46.89*
Treatment	4	52.36***	77.97***	81.24***	83.38***	101.98***
Residual	12	2.70	4.62	5.54	7.09	11.07
Total	19					

Note: df, degrees of freedom; ns, not significant; *, $p < 0.05$; ***, $p < 0.001$.

Fig. 3. The ratio of coarse root mass to WB at 3.0 YAP was not significantly different between treatments, ranging from 21.7% (OS) to 21.0% (SF and SB).

Fluctuations in the periodic stand GE (periodic WB increment per unit leaf area) are shown in Fig. 4. During the principal period of canopy development (0.0–1.3 YAP), levels of GE were generally lower than in the third growing season. This is an expected result, as trees shift from initially allocating large portions of carbon to developing canopies and roots to gradually allocating increasing portions of carbon to stem wood. The GE for treatment OS was consistently lower than that for treatments SD, SB, and SF (Fig. 4). The difference between the fastest growing treatment (SB) and the slowest (OS) was significant during this entire period. Some tree mortality occurred during the first winter in the control treatment. The net effect was that the leaf area of the plots recovered more rapidly than the WB increment. This explains the very low levels of GE in the control at the end of the first winter. The stand GE curves for treatments changed markedly after canopy closure. Treatment OS recorded significantly greater GE than the fast-growing SB treatment during the last two measurement intervals (Fig. 4).

The fraction of dry matter production allocated to WB varies among trees of different size- and age-classes (Ledig 1983; Cromer and Jarvis 1990). Significant differences in GE between treatments (Fig. 4) may also be attributed (at least in part) to trees being at different physiological phases of development at specific times. The fact that LAI in OS peaked 400 days after the fast-growing treatments (Fig. 2) may have resulted in it reaching maximum GE considerably later than the other treatments (Fig. 4). To rule out the effect of the physiological development phase and the differences in time span of individual measurement events, we calculated the mean values of LAI and GE. (Measurement intervals were of unequal length, and this was taken into account in the calculation of the true annual mean values.) The mean annual values of LAI differed significantly between treatments (Table 4). Although the GE differed significantly between treatments at specific time intervals in our study, the mean values were statistically similar (Table 4).

Discussion

Growth resource availability

Historic climate data (du Toit et al. 2000) show that rainfall at the site is strongly seasonal and that both the intensity and the duration of dry winter periods are highly variable. Severe drought (annual rainfall < 650 mm), as experienced in the present study, has a probability of 0.04 of occurring in

any given year at this site (Kunz and Smith 2001). A block effect, observed in the WB data (Table 3), exists between groups of adjacent replications (1 and 2 vs. 3 and 4) and appears to be linked to differences in the soil parent material and soil depth. The soil in replications 1 and 2 had a higher incidence of doleritic intrusions in the predominantly shale parent material and was slightly deeper than the soil in replications 3 and 4. The block effect may be an indication of gradients in resource availability that exist across the experimental site, despite being located in a single compartment of the plantation. The fact that we observed the same treatment responses in two groups of replications that differed significantly in WB growth suggests that our results may have wider applicability to other sites in the region.

Our treatments created large gradients in total nutrient quantities (Table 1), but this gradient was not the only driver of nutrient uptake into the biomass. It appears that plant-available nutrient fractions differed between treatments and across time, judging by differences in foliar nutrient concentrations and nutrient accretion in aboveground tissues (Table 2). Slash removal significantly decreased the availability of macronutrients relative to the control, whereas fertilization significantly increased it (specifically for N and P). There were no significant ($p < 0.05$) differences between treatments with respect to foliar macronutrient concentration at 0.25 and 0.5 YAP (with mean levels for N, P, and K at 0.5 YAP being 3.03%, 0.15%, and 0.66%, respectively). Spring rains for 1999 started during October 1999, and the nutrient concentrations responded immediately with highly significant ($p < 0.001$) differences for N, P, K, and Ca between treatments in the November sample (0.75 YAP; data not shown). The nutrient uptake values (being the product of biomass and nutrient concentration) responded somewhat slower than the concentrations themselves (Table 2). Differences in nutrient availability between 1S and SB (which had been apparent since treatment implementation) manifested as significant differences in nutrient accretion only toward the end of the first year. It appears that the dry (and cold) winter conditions limited nutrient uptake across all treatments and prevented differences in nutrient availability from manifesting in terms of nutrient accretion. Fertilization would increase nutrient availability through direct supply. Other studies have also shown that burning (Romanyà et al. 1994; Fisher and Binkley 2000) and topsoil disturbance (Smith and du Toit 2005) indirectly increase nutrient availability, at least temporarily. Removal of the forest floor or harvesting residue from a site constitutes a loss of nutrient capital from that system and, in addition, has been shown to negatively affect the rate of nutrient mineralization in the topsoil (Gonçalves et al. 2000).

Fig. 4. Periodic stand growth efficiency, i.e., periodic woody biomass increment per unit leaf area, from planting to 3.5 years of age. The least significant difference ($p = 0.05$) is shown as error bars for each measurement event. Treatments: 0S, slash removal; 1S, slash retention (regular slash load); SB, slash burning; SD, slash disturbance; and SF, fertilization.

Table 4. Mean annual values for leaf area index (LAI) and stand growth efficiency (GE) calculated over 3 years of growth.

Treatment	Mean LAI ($m^2 \cdot m^{-2}$)	Mean GE ($Mg \cdot ha^{-1} \cdot year^{-1} \cdot LAI^{-1}$)
0S	2.35a	4.59a
1S	2.85b	4.70a
SB	3.11c	4.58a
SD	2.96bc	4.66a
SF	3.08bc	4.56a

Note: Values in columns followed by the same letter are not significantly different at $p < 0.05$. 0S, slash removal; 1S, slash retention (regular slash load); SB, slash burning; SD, slash disturbance; and SF, fertilization.
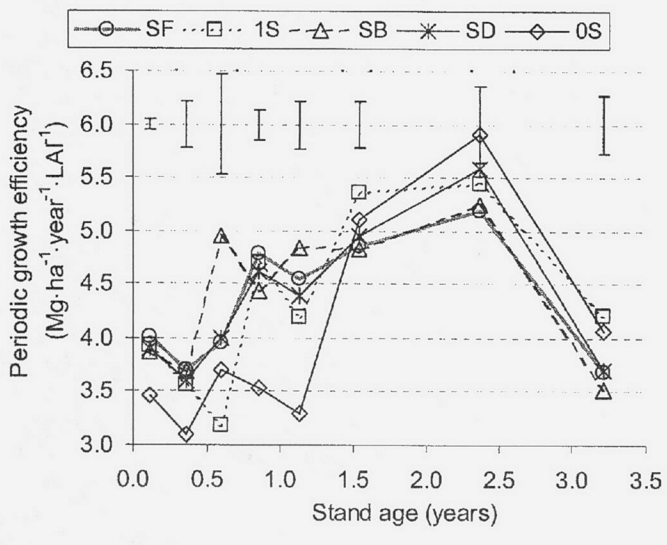
Leaf area and growth

With adequate supplies of growth resources, *E. grandis* stands are capable of rapid canopy expansion and height growth. Coetzee (1994) showed 1-year top height to range from 2.1 to 5.5 m for various site productivity classes of *E. grandis* in South Africa. ("Top height" in this paper is defined as the mean height of those 20% of trees in the population that have the largest DBH.) Height growth of 3–6 m in the first year has been documented by Gonçalves et al. (2000) in Brazil. However, we achieved height growth ranging from only 1.7 m (0S) to 2.8 m (SF) and an LAI ranging from 1.1 to 2.5 across treatments at that age. Stand growth rates may be constrained by reductions in the availability of growth resources (water, nutrition, light) or planting of a species under unfavourable climatic conditions for that species. In the present study, the site is climatically suited to *E. grandis* (Boland et al. 1997). Light per se is not limiting at our latitude (although light capture is reduced when LAI is too small for adequate quantities to be absorbed). Nutrient supply was generally good (unpublished foliar nutrient concentration data) and was increased in treatments SB, SD, and SF. A periodic decrease in the specific leaf area (from approximately 17 to 10 $m^2 \cdot kg^{-1}$) was brought about during the first season (Job et al. 2003), which is typical of water stress (Osório et al. 1998). We conclude that the development of leaf area in all treatments (Fig. 2) was severely curtailed by the dry conditions during the first growing season (Fig. 1).

The response in LAI for treatments SB and SF during the second summer season was mainly driven by increases in nutrient supply (0.75 and 1.00 YAP in Table 2), since rainfall was present in abundance, and prolonged, significant differences in soil moisture levels between these treatments could not be detected during this time (Fig. 1). Cromer et al. (1993) and Hunter (2001) both observed strong responses in the leaf area (or leaf mass) of young stands of *E. grandis*

with increasing levels of fertilization. From 1.8 to 2.3 YAP, the LAI of the fast-growing treatments (SB, SF, SD, and 1S) remained relatively constant around a level of 4.5. Linder (1985) showed that LAI for eucalypts in Australia usually peaks at values of approximately 5–6, since (theoretically) light interception at these values already exceeds 90%. From a tree perspective, the building of leaf area is resource hungry, and any increases in LAI from this high base will result in small gains with respect to light harvesting. This relationship explains why the LAI approached, but never exceeded, 5 in our experiment (where soil water was limiting). Smethurst et al. (2003) presented data for *Eucalyptus nitens* (Deane & Maiden) plantations where LAI exceeded a value of 6, but this occurred only on high-rainfall sites subjected to high levels and multiple applications of fertilizer.

In general, LAI can be expected to reach a maximum in developing stands, and after canopy closure it commonly declines, reaching an equilibrium value for an extended period of time (Beadle 1997). As described by Linder (1985), this decline in LAI coincides with the decrease in specific leaf area (SLA), which is a function of the physiological age of the trees (Sands et al. 1992). The third growing season in the present study experienced fairly average rainfall conditions; however, the soil water content (Fig. 1) remained at low levels. The inability to recharge the soil to field capacity is apparently due to the high levels of LAI in all treatments (Fig. 2), which maximized the actual evapotranspiration during the third growing season. The leaf area for any eucalypt stand on the study site is also expected to vary seasonally because of the pronounced dry season commonly experienced in winter. Seasonal fluctuations of LAI around an equilibrium value are common in eucalypt forests in seasonally dry climates (Beadle 1997). An LAI of 3.2 was determined on the present study site by destructive harvesting in the original mature crop before reestablishment (du Toit et al. 2000). This value (determined August 1998) was taken as a realistic estimate of the lower end of the range of "equilibrium" LAI values for this specific stand. Values of LAI across treatments ranged from 3.2 to 3.5 (third winter) and from 2.9 to 3.3 (fourth winter), which is in close agreement with the mature crop value.

The absolute difference in WB between the extreme treatments (0S and SB) at 3 years amounts to approximately 11 $Mg \cdot ha^{-1}$ (Fig. 3). Fertilization of eucalypts at establishment is highly likely to yield significant growth responses in short

rotations (8–10 years) under most site conditions in and around the study area. Schönau (1983) listed a variety of trials from the same region, where responses in wood production ranged between 18 and 70 Mg·ha^{-1} on a 10-year rotation, with generally slightly lower N and P fertilizer doses than in our trial on similar soils. Du Toit and Freimond (1994) documented a significant growth response to fertilization at planting for a stand of *E. grandis* growing on the same soil type and on the same plantation as our current trial. They reported an increase of 47 m^3·ha^{-1} (approximately 22 Mg·ha^{-1}) of utilizable timber at 7 years of age, while we recorded a nonsignificant improvement with fertilization in the Karkloof experiment. We conclude that the potential magnitude of the response to those treatments that increased nutrient supply to young trees (most notably SB and SF) has not been realised. This was apparently caused by low levels of soil water, which inhibited rapid leaf area development.

The mean level of GE in our study (4.6 Mg·ha^{-1}·year^{-1}·LAI^{-1}) remained relatively constant in treatments that manipulated stand nutrition (Table 4). Smethurst et al. (2003) reported levels of GE ranging from 3 to 5 Mg·ha^{-1}·year^{-1}·LAI^{-1} for 5- to 7-year-old *E. nitens* plantations in Tasmania. Giardina et al. (2003) studied the effects of fertilization at 4 years of age in a stand of *Eucalyptus saligna* Smith in Hawaii. From their data, we calculated stand GE as 2.1 and 3.1 Mg·ha^{-1}·year^{-1}·LAI^{-1} for control and fertilized treatments, respectively. Jokela and Martin (2000), working with *Pinus taeda* L. and *Pinus elliottii* Engelmann in Florida, USA, showed that GE declined strongly as the plantation aged from 7 to 16 years. An age-related decline may explain the fact that we (in a trial with young trees on a dry site) recorded higher levels of GE than the aforementioned eucalypt studies (with wetter sites but mid-rotation age-classes).

Several authors showed that GE can be strongly affected by resource availability (Brix 1983; Albaugh et al. 1998; Bergh et al. 1999; Jokela and Martin 2000; Giardina et al. 2003; Binkley et al. 2004). In contrast to the aforementioned results, Cromer et al. (1993) found a linear relationship between net primary production (or WB increment) and LAI in stands of *E. grandis* up to 3 years of age, which was constant for unfertilized and heavily fertilized treatments. In cases where one resource is strongly limiting, GE may be low despite large increases in the availability of another group of growth resources. For example, Stoneman et al. (1996) found no significant response in GE of an unthinned stand of *Eucalyptus marginata* Donn ex Smith following large N and P fertilizer inputs ("growth efficiency" was defined in that study as the basal area increment per unit leaf area). However, GE was significantly improved by fertilization after thinning in that study. The authors ascribed this response to an alleviation of water stress. The nonsignificant differences in GE between treatments in our study (despite significant differences in stand nutrition) could have been caused by the overriding effect of water stress or by the diminishment over time of the nutrient gradients created by the treatments.

Implications for research and management

Silvicultural treatments that increase the availability of growth resources can affect stand growth in several ways. They may lead to (1) increased leaf area (Brix 1983; Linder

1985; Linder 1987; Linder et al. 1987; Turnbull et al. 1988; Nambiar 1990; Ericsson et al. 1992; Cromer et al. 1993; Jokela and Martin 2000; Stape 2002; Smethurst et al. 2003); (2) increased photosynthetic efficiency (Waring 1983; Linder and Rook 1984; Fife and Nambiar 1997; Stape 2002; Giardina et al. 2003); and (3) changes in allocation of carbon to plant parts (Ledig 1983; Linder and Rook 1984; Keith et al. 1997; Misra et al. 1998; Hunter 2001; Stape 2002; Giardina 2003). Some authors have also reported an increased conversion of light energy into aboveground biomass or WB (Brix 1983; Linder 1987; Linder et al. 1987; Landsberg and Hingston 1996; Stoneman et al. 1996; Albaugh et al. 1998), that is, combining factors (2) and (3). Stand GE, as defined in our study, is likewise most closely aligned with combined factors 2 + 3.

The mechanism of response to changes in resource availability in our experiment is clear: we found large changes in LAI (factor 1), but no significant change in mean GE (factors 2 + 3). The fractions of biomass contained in the coarse roots at 3.0 YAP were similar between treatments. In addition, Nkosana (2002), studying fine root (<2 mm diameter) turnover in this experiment, found large seasonal variations but could not demonstrate significant differences between treatments. We conclude that treatment responses through factor (3), that is, changes in the allocation of assimilates to roots, do not apply in our study. If there were no significant changes in factors (2 + 3) or (3), it follows that there were no changes in factor (2) either. Strong responses to early development of LAI, similar to what we saw in our trial, were reported by Turnbull et al. (1988) and Cromer et al. (1993).

At the fundamental level, forest production can be determined from the product of the intercepted photosynthetically active radiation (PAR) and the radiation utilization coefficient (Landsberg and Hingston 1996). It is difficult to obtain reliable measurements of intercepted PAR in crops before and during canopy closure because of variations in the canopy structure and the light extinction coefficient (Dovey and du Toit 2005). On a practical (forest management) level, the use of LAI and GE, as defined earlier, presents useful surrogates. Forest production can be taken as approximately driven by LAI and GE (Waring 1983).

The fact that increases in LAI (rather than changes in GE) drove increases in the production of woody fibre has some implications for management on similar sites (unthinned, short-rotation crops on fairly fertile sites). It has been argued that the level of LAI peaked and probably will stabilize at a lower level, reflecting the soil water availability of the site. This implies that the period immediately after reestablishment (when the soil profile has been recharged with water and actual evapotranspiration has not yet peaked) is most conducive to boosting the development of LAI (i.e., first and second growth seasons in our study). Treatments that can potentially improve immediate nutrient availability to the tree (e.g., burning, fertilization, tillage, or soil disturbance) are highly likely to have the greatest impact on leaf area development (and hence also on growth in general) during this early period. This hypothesis supports the responses in production, obtained through a combination of several empirical studies testing intensive silvicultural operations in young, short-rotation hardwood crops around South Africa, described by Schönau (1984, 1989). Cromer et al. (1993) and Leuning et

al. (1991) also emphasized that optimum nutrition has a potentially large impact on growth through its effect on early development of SLA and on photosynthetic efficiency, specifically in young stands. It is likely that improved nutrition (e.g., fertilization) of unthinned stands after canopy closure will have a less marked effect on LAI (because of limitations with respect to soil water), as was found in the study of thinned stands by Stoneman et al. (1986). In unthinned, short-rotation crops where soil water availability is generally limiting, we hypothesize that the window of opportunity for increasing the productivity falls in the early stages of development, before soil water limitations constrain leaf area development.

Conclusions

Leaf area development over the first 2 years responded strongly to a nutrient availability gradient brought about by site management treatments imposed at time of establishment. Slash burning or fertilization accelerated LAI development, and slash removal slowed it down. The GE (WB produced per unit leaf area) differed temporally between treatments, but the mean values were statistically similar over the first 3 years of growth. The magnitude of the response (9–11 Mg·ha^{-1} of WB) was smaller than that recorded in other fertilizer trials, and this was attributed to the abnormally severe winter drought at the end of the first growing season. Rapid deployment of the maximum leaf area in treatments (and rapid SLA recovery after the drought), rather than increases in stand GE, resulted in the observed increases in wood production. In unthinned, short-rotation eucalypt stands, treatments that increase nutrient availability to plants are most likely to yield responses in young stands when soil water availability is usually sufficient for developing canopies. Any treatments that increase nutrient availability (e.g., fertilization) are therefore less likely to yield large responses if applied after culmination of leaf area development or during severe droughts. Our study shows that continuous monitoring of LAI is needed to obtain reliable estimates in areas with strong seasonal and interannual rainfall variations.

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