Manuscript Draft

Manuscript Number:

Title: Effects of site management on growth, biomass partitioning and light use efficiency in a young stand of Eucalyptus grandis in South Africa

Article Type: FLA Full Length Article

Section/Category:

Keywords: dry matter distribution; radiation; net primary production; canopy quantum efficiency; litterfall; fine root turnover

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Manuscript Region of Origin: SOUTH AFRICA

Abstract:

# Effects of site management on growth, biomass partitioning and light use efficiency in a young stand of *Eucalyptus grandis* in South Africa

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## ABSTRACT

The effects of intensive site management treatments at establishment on the production ecology of a stand of *Eucalyptus grandis* were evaluated in South Africa. Treatments mimicked common operational practices in the region, and included slash removal, slash conservation, slash burning, topsoil disturbance through mechanised harvesting and fertilisation. We calculated the carbon distribution in the standing biomass from allometric relationships. Fine root turnover and litterfall measurements were determined using sequential coring techniques and litter traps, respectively, and this data was used to construct a full model of biomass allocation among stand components. Differences in nutrient availability to young trees, brought about by the most extreme site management treatments, produced several small but significant changes in the elements of the production ecology over the three year monitoring period: Absorbed photosynthetically active radiation (APAR) increased from 210 to 247 Mmol photons ha$^{-1}$, apparent canopy quantum efficiency (α) from 0.026 to 0.029 mol C (mol photon)$^{-1}$, and the fraction of carbon allocated to stem wood from 32.7% to 35.6% of net primary production. The magnitudes of these individual responses collectively described the increase in net primary productivity and the Type 1 timber volume response obtained. The biggest changes occurred in APAR, in contrast to published studies from higher rainfall environments where α dominated.

Keywords: dry matter distribution, litterfall, fine root turnover, radiation, net primary production, canopy quantum efficiency.

## INTRODUCTION

*Eucalyptus grandis* is the most important plantation hardwood in South Africa, occupying an area of 311 000 ha, 58% of the total of 541 000 ha planted to the genus *Eucalyptus* as a whole (FSA, 2003). Empirical research conducted during the last 30 years has shown large increases in productivity resulting from early, intensive silvicultural management operations that aim to optimise the supply of growth resources to the newly established crop (Schönau *et al.*, 1981; Schönau, 1983; Schönau, 1984; Schönau, 1989; Herbert and Schönau, 1989 & 1990; Little and van Staden, 2003). This silvicultural regime *i.e.* appropriate slash management and site preparation techniques (Norris, 1995; Smith *et al.*, 2000; Rolando *et al.*, 2002), water planting where necessary (Viero *et al.*, 2002), fertilisation at time of establishment (Herbert and Schönau, 1989 & 1990; Herbert, 1996; du Toit and Carlson, 2000; du Toit and Oscroft, 2003), followed by intensive weed control up to canopy closure (Little *et al.*, 1997; Little, 1999; Little and van Staden, 2003) has since become standard practice in southern African eucalypt plantations. Very few, if any, silvicultural tending operations are carried out from canopy closure until clear felling, since fertilisation and vegetation management practices after canopy closure have not yet been proven to be generally cost effective under water-limiting conditions commonly experienced in the study area (Little and Rolando, 2002). Despite the advances with early, intensive silviculture, a lack of a process-based understanding of tree growth in response to growth resource availability is currently constraining research efforts to increase productivity in a sustainable way. Increasingly, site-specific and operation-specific silvicultural regimes are needed to optimally manage the supply of growth resources (du Toit *et al.*, 2000). An understanding of the response mechanism of the stand to changes in resource availability, brought about by silvicultural practices, will facilitate the extrapolation of results (Binkley *et al.*, 2004; du Toit and Dovey, 2005).

The growth rates of trees are governed by the quantity of absorbed photosynthetically active radiation (APAR) and the efficiency with which this radiation is utilised to convert atmospheric $CO_2$ to carbohydrates (Linder, 1985; Landsberg and Gower, 1997; Stape, 2002; Giardina *et al.*, 2003; Binkley *et al.*, 2004). The quantity of carbon assimilated (after respiration losses have been subtracted), is termed the net primary production (NPP) (Landsberg and Gower, 1997). Changes in the availability of growth resources can modify the quantity of absorbed PAR (through changes in leaf area), the canopy quantum efficiency (α) and the allocation of carbon to different plant parts (Linder and Rook, 1984; Landsberg and Waring; 1997; Landsberg and Gower, 1997; Albaugh *et al.*, 1998 Bergh *et al.* 1999; Jokela and Martin 2000; Stape, 2002; Giardina *et al.*, 2003; Binkley *et al.* 2004; du Toit and Dovey, 2005). We consider the terms allocation and partitioning (in the context of describing the dynamic apportionment of NPP or assimilated carbon) as synonymous in this document, and we use the term distribution to describe the quantity of biomass contained in various parts of a standing crop of trees at a given point in time.

Several papers have been published on carbon distribution among biomass components of eucalypt stands worldwide (Bradstock, 1980; Tandon et al, 1988; Herbert, 1996; Misra, 1998; Hunter, 2001; Laclau *et al.*, 2000; Xu *et al.*, 2002), among many others. However, fewer studies have linked this with allocation to transient components, e.g. fine root production and litterfall, and even fewer have included estimates of above- and below ground plant respiration to calculate a stand-level carbon budget (Stape, 2002; Giardiana *et al.*, 2003). There is also limited information on the effects of changes in resource availability in eucalypt stands on respiration losses (Giardina *et al.*, 2003). The partitioning of carbon, fixed during photosynthesis, is imperfectly understood (Landsberg and Gower, 1997; Gholtz and Lima, 1997) and therefore, further research should focus on measuring whole-forest fluxes of carbon and water. An improved physiological understanding of carbon partitioning at the stand level could facilitate extrapolation of trial results and decision-making in forest management (Gholz and Lima, 1997; Binkley *et al.*, 2004; du Toit and Dovey, 2005), especially through the use of process-based models (Waring, 2000; Mäkelä *et al.*, 2000; Coops and Waring, 2001; Dye, 2001; Esprey, 2001; Landsberg *et al.*, 2001; Sands and Landsberg, 2002; Almeida *et al.*, 2003; Almeida *et al.*, 2004; Binkley *et al.*, 2004).

Experimentation with growth resource manipulation (varying the supply of water, nutrients, light and $CO_2$ concentration) has been done on trees of varying age classes (and on eucalypts in particular). A number of papers have been published to demonstrate that seedlings (Cromer and Jarvis, 1990; Kirschbaum *et al.*; 1992) and tree stands (Keith *et al.*, 1997; Albaugh *et al.*, 1998; Misra, 1998; Berg *et al.*, 1999; Hunter, 2001; Stape, 2002; Giardina *et al.*, 2003) can vary their carbon allocation patterns as a result of changes in the availability of growth resources. Most of these experiments included treatments that resulted in very large and prolonged changes in resource availability, e.g. greenhouse trials with widely differing growth conditions, fertiliser field trials testing large, repeated additions of nutrients, or water and nutrient optimisation experiments. While these experiments have demonstrated that changes in partitioning may occur, it is not certain whether similar changes will take place under less intensive site management treatments commonly used in industrial forestry. Data will be presented to illustrate the production ecology of *E. grandis* subjected to common silvicultural treatments, and to quantify the allocation of the NPP in the young stand. We will demonstrate how changes in growth resource availability affect APAR, α, and the partitioning of NPP to above-ground woody parts ($\eta_w$).

## MATERIALS AND METHODS

### Site, stand and experimental design

The Karkloof trial site is located at 29° 24' south and 30° 12' east at an altitude of 1260 m above sea level. The mean annual precipitation of 950 mm falls mainly in summer and the mean annual temperature is 15.2 ºC. The soil is on average approximately 90 cm deep; it is clayey and rich in organic matter. More details on climatic conditions and the soil physical characteristics (du Toit *et al.*; 2000) as well as basic soil chemical properties (du Toit, 2003), have been published. The site originally supported grassland vegetation, which was converted to an *E. grandis* plantation in 1964. The stand on the site was seven years old at the time of harvest in December 1998. It had been the last of three coppice rotations and had a mean annual increment of 21 $m^3 ha^{-1} yr^{-1}$. After clear felling the standing crop, site management treatments were implemented and a new crop of genetically improved *E. grandis* seedlings were planted. All treatments were subjected to complete chemical weed control up to the time of canopy closure. We studied growth responses across five treatments which were replicated in four separate locations on the trial site, yielding a total of 20 plots, each being 0.17 ha in size. The treatments (except for the 0S treatment) mimicked commonly used silvicultural practices:

***0S*** ***Slash removed:*** All harvesting residue (including bark, branches and foliage) and litter layer manually removed from the plot.

***1S*** ***Regular slash load:*** Harvesting residue retained and broadcast on the plot. This is regarded as the control treatment.

***SB*** ***Slash burnt:*** Harvesting residue burnt in a medium intensity fire.

***SD*** ***Topsoil disturbed:*** Slash disturbed and mixed with soil through mechanical loading and stacking of timber with a three-wheeled loader.

***SF*** ***Fertilised:*** Regular slash, followed by a localised application of an N, P and Zn mixture near each seedling after planting.

**Determination of stand volume and standing biomass**

Tree growth measurements (tree survival, tree diameter and tree height) were conducted at three monthly intervals during the first two growing seasons and six monthly thereafter. Volume was calculated by the equation developed for E. grandis short-rotation crops by Coetzee, 1992 (cited in Bredenkamp, 2000). The development of woody tissues and other biomass components over time were 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). Fresh wet mass of the foliar and woody components were determined separately for destructive samples in field. Sub-samples were oven dried to constant mass and weighed to correct for moisture content. Coarse root samples (roots with diameter > 2 mm) were collected for the 20 sample trees at three YAP. The area occupied by each sample tree (2.44 * 2.44 m) was divided in four quadrats. The soil in one such quadrat was excavated to a depth of 60 cm and sieved to obtain the coarse roots (A). This depth was chosen since a study of root distribution patterns in the previous crop (du Toit et al., 2004) showed that the bulk of the root biomass was located in the upper soil horizons. The taproot was excavated separately to the same depth (B). The coarse root mass associated with the tree was estimated as 4*A + B, and was reported on an ash-free basis to eliminate potential errors arising from soil contamination. Allometric relationships were developed to estimate the biomass of tree components in the coarse root and above-ground biomass (AGB) samples (leaves, branches, stem bark and stem wood) from diameter at breast height (dbh) and total tree height. Individual tree component biomass were estimated from these relationships, summed per experimental plot and reported on a land area basis.

## Estimation of transient biomass components

*Litterfall.*

Foliar and woody litterfall were collected in litter traps on a monthly basis as soon as the first signs of leaf fall could be observed at 14 months of age (unpublished field log file). Eight litter traps were used per treatment, each trap measuring 1.2 * 1.2 m in size (to facilitate the capture of large woody material). Foliar and woody components in monthly samples were separated, oven dried at 65 ºC until constant mass was obtained, and weighed.

*Fine roots.*

Nkosana (2002) collected monthly samples of fine roots (< 2 mm diameter) with a coring device in the top 30 cm of soil during the period 1.6 to 2.6 years after planting (YAP). Fine root turnover has been estimated for this site, using the methodology presented by Santantonio and Grace (1987). The individual treatments (n=4 for monthly observations) were not significantly different, but showed some spikes in the data due to individual outliers (Nkosana, 2002). For these reasons, average values across treatments were used to calculate fine root turnover. These estimates for root production in early summer, late summer and winter seasons of the measurement period (1.6 to 2.6 YAP) were extrapolated to the crop for the period from 0.8 to 3.0 YAP. Fine root turnover immediately following planting (small trees prior to canopy closure) could not be estimated with confidence, but was assumed to make up a small portion of the cumulative fine root turnover during the first three years of stand growth.

*Other removals.*

The consumption of foliage by heterotrophs was assumed to be negligible since *E. grandis* is an exotic tree with relatively few pests and browsers in this country and hence suffers little biological damage in the study region (Midlands of KwaZulu-Natal). The very small seeds could potentially fall through the litter traps mesh, but this was not a factor in our study since the trees are not sexually mature and have not produced any capsules or seed during the study period.

**Light absorption, photosynthesis and NPP**

Daily solar radiation data were collected with an automatic weather station on site. The solar radiation data was converted to photosynthetically active radiation using the approximate conversion under average sunlight conditions given by Landsberg and Gower (1997) as 1W $m^{-2} \approx 2.2$ μmol of photons $m^{-2}$ $sec^{-1}$. The development of leaf area index for treatments in this trial was published previously (du Toit and Dovey, 2005). The exponential relationship between light absorption and leaf area index (Beer-Lambert law) was used to estimate the quantity of PAR absorbed by the stand in each treatment (after Linder, 1985; Sands and Landsberg, 2002). We used a non-constant value for the extinction coefficient (k) since Dovey and du Toit (2005) found k to vary with the stage of physiological development in young stands of *E. grandis*. The values used for k at ages < 2.0, 2.6 and 3.0 YAP were 0.55, 0.48 and 0.42. Values of k for the days in between these ages were linearly interpolated between point data.

The canopy quantum efficiency (α) can be estimated from the following equation (Landsberg and Waring, 1997):

$\alpha = GPP / APAR$, where

GPP is measured in mol of C per unit area and APAR in mol of photons per unit area.

If we assume a constant, unitless fraction to scale NPP to GPP, namely 1/0.47 (Waring *et al.*, 1988), and assume that 1 mol C is equivalent to 24 g dry matter (Sands and Landsberg, 2002); we can calculate α from the data that we have obtained, as follows:

$\alpha = NPP / (24 * 0.47 * APAR)$, where

NPP = Net primary production (Mg $ha^{-1}$)

APAR = Absorbed photosynthetically active radiation (Mmol $ha^{-1}$)

$\alpha$ = Canopy quantum efficiency (mol C (mol photon)$^{-1}$).

### Statistical analysis

The data on stand volume, litterfall, fine and coarse roots, above-ground biomass components, NPP, APAR $\alpha$ and $\eta_w$ were all calculated on a plot basis. The differences between treatments (across the four replications) were analysed with the standard ANOVA procedure in Genstat® for Windows™ (Lane and Payne 1996). The statistical analyses followed the guidelines described by McConway *et al.* (1999), to ensure that the basic assumptions of ANOVA were not violated.

## RESULTS

### Treatment response in terms of volume growth

Figure 1 shows the volume growth of the treatments over time. There are no statistically significant differences between the fast growing treatments (1S, SD, SF and SB). However, treatment 0S had significantly lower volume than all the other treatments at all measurement events from 1.0 to 3.0 years of age. An average volume in the fast-growing treatments of 70 $m^3$ $ha^{-1}$ at three years of age can be considered a moderate growth rate by South African hardwood standards (Coetzee, 1999). Considering that the trial is located on a site with moderate productivity potential (du Toit *et al.*, 2000), and that it had experienced a short, but severe drought at establishment (du Toit and Dovey, 2005), the recorded growth rate was very good. The difference in utilisable timber volume between treatment 0S and the fast growing treatments varied between 18 and 29 $m^3$ $ha^{-1}$ (approximately 7 to 12 Mg $ha^{-1}$) at three years of age, which is smaller than responses obtained in similar treatments on comparable sites (Schönau, 1983; du Toit and Dovey, 2005). The two best treatments (SB and SF) had supplied near optimum levels of nutrients during the early growth phase, judging by foliar nutrient concentrations and nutrient uptake rates (du Toit and Dovey, 2005): For example, N and P concentrations in treatment SF were 3.28% and 0.19%, respectively at 0.7 YAP, while the corresponding concentrations in treatment 0S were 2.69% and 0.13%. However, the trial suffered intensive water stress during a dry period (0.3 to 0.7 YAP), which resulted in soil water being held at tensions more negative than -1000 kPa for 78 consecutive days (du Toit and Dovey, 2005). This led du Toit and Dovey (2005) to conclude that water stress was the major factor limiting the magnitude of the response in this experiment.

Insert Figure 1 here

**Allocations to transient biomass components**

Cumulative values for foliar and woody litter fall are shown in Table 1. When expressed on an annual basis, the average litterfall of foliar and woody components across all treatments amounts to 5.5 and 0.8 Mg ha$^{-1}$, respectively. The differences in foliar and total litterfall between treatment 0S and the remaining treatments were only weakly significant ($p<0.10$). However, the difference was consistent throughout the monitoring period. Cumulative litterfall in treatment 0S over the reported period amounted to 82% of the mean of the other treatments (Table 1).

There were no significant differences between treatments for the live root mass and the root necromass, respectively (Nkosana, 2002). The mean root production, averaged from 16 core samples across treatments, was bi-modal, with peaks in early summer (November) and again in late summer (April). Fine root production during the dry, cold winter was minimal. The mean fine root production observed during the early summer, late summer and winter periods (calculated from Nkosana, 2002; du Toit - unpublished root decay data) is shown in Table 2 (**bold print**). It is likely that root growth would have followed the same seasonal pattern in the unmeasured seasons for the period following canopy closure (bottom section of Table 2). However, fine root production would probably have been less than the seasonal estimates in the very young crop before canopy closure as the trees were very small at this age (mean tree height in the trial was 0.71 and 1.59 m, respectively, at 0.4 and 0.8 YAP). We can therefore arrive at an estimate for fine root turnover in the 0-30 cm soil layer for the period 0.8 to 3.0 YAP, of 7.0 Mg ha$^{-1}$. We used this value as a conservative estimate of fine root turnover for the entire period as it was not realistic to estimate fine root turnover for the period from planting up to 0.8

YAP from the original data collected by Nkosana (2002) that had been determined under bigger trees in a closed canopy stand. The actual fine root turnover for the entire period from planting to three years of age would thus be slightly greater than our conservative estimate (Table 2).

**Allocations to biomass components with slow turnover rates**

The dry mass estimates of various components of the stand (foliage, branches, bark, stem wood and coarse roots) at three years of age are shown for each treatment in Figure 2. The dry mass across treatments follows exactly the same pattern as the utilisable volume growth presented earlier. The 0S treatment recorded the lowest stand biomass while the SD, SF and SB treatments had very similar levels of stand component masses and total biomass. The biomass of all individual components in treatment 0S was significantly smaller than the remaining treatments. There were no significant differences between treatments SD, SF and SB for any of the components shown in Figure 2. The relative contribution of each of the biomass components in the stand was contrasted to published accounts of *E. grandis* stands at a comparable developmental stage (AGB ranging from 45 to 67 Mg ha$^{-1}$) in Table 3. We expressed biomass distribution as a fraction of AGB (and not total biomass) since not all comparable studies included root estimates.

Insert Figure 2 here

The biomass contained in foliage, woody components and roots at 3.0 years of age (Figure 2) was added to the biomass allocated to components with rapid turnover, *i.e.* litterfall (Table 1) and fine root turnover (Table 2), to form a complete synthesis of NPP partitioning in the Karkloof trial system. The allocation to components (a) foliar plus leaf fall; (b) coarse roots plus fine root turnover, and (c) above-ground woody biomass plus woody litterfall are discussed in this paragraph as absolute values and are expressed as percentages of the total NPP in Table 4. Foliar NPP of the 0S treatment (10.0 Mg ha$^{-1}$) was significantly lower than that of the faster growing treatments, which varied between 11.9 and 12.9 Mg ha$^{-1}$ (Figure 2 and Table 1). However, the percentage of the NPP allocated to foliar tissues was statistically similar across all treatments (Table 4). Cumulative woody litterfall contributed only 2.4%, on average, of the total NPP of woody tissues in this young crop. We observed significant differences in total (above-ground) woody NPP between treatments, with 35.5 Mg ha$^{-1}$ in treatment 0S, 45.0 Mg ha$^{-1}$ in 1S and the remaining treatments ranging from 48.8 to 50.3 Mg ha$^{-1}$ (Figure 2 and Table 1). The total root NPP followed the same pattern, with treatment 0S (15.3 Mg ha$^{-1}$), being significantly smaller than the remaining treatments (17.2 to 18.3 Mg ha$^{-1}$) (Figure 2 and Table 2). It was interesting to note, however, in treatment 0S that the fraction of NPP allocated to roots was significantly greater, and the percentage allocated to above-ground woody biomass was significantly smaller than the remaining treatments (Table 4).

### Leaf area development and absorbed PAR

Radiation at the study site varies between monthly averages of 15.9 and 27.8 MJ m$^{-2}$ day$^{-1}$ (du Toit *et al.*, 1999). Cumulative daily radiation at the study site over the three-year period totalled 17.6 GJ m$^{-2}$. Leaf area development in the trial was slow at first, due to the unusually dry conditions from 0.3 to 0.7 YAP referred to earlier. However, leaf area index developed extremely rapidly during the second summer season, reaching values > 4 in the fast growing treatments (Table 1; du Toit and Dovey, 2005). After canopy closure, the LAI levels in all treatments converged to similar levels which followed a pattern dictated chiefly by soil water supply (*i.e.* it increased slightly during the wet summers and decreased during the dry winters) (du Toit and Dovey, 2004; du Toit, and Dovey, 2005). Large differences in LAI between treatments, especially in the developmental phase, resulted in significant differences in radiation interception. The annual and cumulative levels of APAR are shown in Table 5, alongside estimates of NPP and canopy quantum efficiency (α).

## DISCUSSION

### Volume growth

The poor growth in the 0S treatment was attributed to a decrease in the nutrient supply rate relative to other treatments (du Toit and Dovey, 2005). The decrease in volume development of treatment 0S relative to the fast-growing treatments only occurred during the establishment phase, due to a slower rate of development in leaf area index (du Toit and Dovey, 2005). The leaf area index of all treatments converged to similar values by 3 YAP. The mean growth efficiency (GE; stem wood production per unit of leaf area) over the first three years of growth was not significantly different between treatments, despite large differences in nutrient availability (du Toit and Dovey, 2005). This finding suggests that current annual volume increment between treatments will also remain similar from year three onward, since the differences in nutrient and water supply between treatments are likely to become even smaller. The difference in response between 0S and the fast growing treatments can thus be described as a Type 1 response (after Snowdon and Waring, 1984; Snowdon, 2002), since it does not cause a sustained improvement in volume growth, but merely enhances the stage of stand development.

## Litterfall

The bulk of the cumulative litterfall in all treatments are made up by foliar elements. A large portion of the branch mass remains on the tree as dead branches after the leaves had fallen (visual observations), which explains why the litter is dominated by foliar elements in young, developing stands. The average foliar litterfall estimated for the measurement period expressed *per annum,* ranged from 4.79 (0S) to 5.92 (SB) (calculated from Table 1). Dye *et al.* (2004) recorded annual foliar litterfall rates of between 2.4 and 3.0 Mg ha$^{-1}$ for two groups of *E. grandis* plantations in coastal Zululand, South Africa. Turner (1986) documented annual foliar litterfall rates ranging from 4.23 to 5.46 for the same species in New South Wales, Australia, while Bernard-Reversat *et al.* (2001) measured values of 4.31 and 6.84 for eucalypt hybrids grown from seedling crops in Congo. Keith *et al.* (1997) recorded an annual foliar litterfall rate of 2.9 Mg ha$^{-1}$ under *E. pauciflora* in temperate Australia. The period of litterfall reported in this document co-incides with the period of very active tree height growth resulting in the “lifting” of the canopy. LAI in the fast growing treatments already exceeded 4.0 at the onset of the litterfall measurement period but lagged behind in treatment 0S. From 2.5 years of age, LAI’s amongst all treatments started to converge at a common, but lower level of approximately 3.3 (du Toit and Dovey, 2005). The greatest litterfall rates have been recorded in the fast-growing treatments, which experienced the greatest decrease in LAI from 1.6 to 3.0 years (Table 1; du Toit and Dovey, 2005). This may explain why we recorded fairly high annual foliar litterfall rates for the fast-growing treatments (*i.e.* our rates are comparable to the higher end of the spectrum of the cited literature). The foliar litterfall up to 3.0 years of age made up a large fraction of the total foliar allocation (approximately 64% to 66%, depending on treatment), emphasising the importance of the litter as a carbon sink and as a nutrient cycling pathway.

## Fine root production

Fine root production peaked in early summer and late summer/autumn, which roughly co-incided with the peak litterfall periods. The observed annual production of fine roots during one year (in the period after canopy closure) was 2.8 Mg ha$^{-1}$ (Table 2). Working on *E. globulus* in Portugal, Fabiao *et al.* (1985) estimated fine root production to be at least 6.0 Mg ha$^{-1}$, using root ingrowth bags. Using the data of Keith *et al.* (1997), we estimated fine root dry mass production in their control and fertilised *E. pauciflora* stands to be approximately 4.5 and 3.4 Mg ha$^{-1}$, respectively (allowing for 47% respiration loss for the below-ground tissues, as estimated independently by the authors, subtracting coarse root biomass, and assuming a biomass C content of 50%). Lee and Jose (2003) recorded fine root production values of 2.21 and 1.44 Mg ha$^{-1}$, respectively, for stands of cottonwood and pine in Southeastern USA. Santantonio and Santantonio (1987) estimated the fine root turnover in *P. radiata* in New Zealand to be 1.9 and 2.2 Mg ha$^{-1}$ in thinned and unthinned plots, respectively. Our fine root production estimate of 2.8 Mg ha$^{-1}$ yr$^{-1}$ falls in between the cited studies, being slightly greater than the estimates for pines and cottonwood, but slightly lower that the estimate for *E. pauciflora*. Our fine root production estimates are much lower than the value of > 6 Mg ha$^{-1}$ obtained by Fabiao *et al.* (1985) for *E. globulus* in Portugal, using root ingrowth bags. The lower estimate from the corer method is expected, as root ingrowth bags could artificially boost fine root production following increases in nutrient availability from the disturbed soil in the sleeve. Such potential increases using the root ingrowth technique are admitted by Fabiao *et al.* (1985) and have also been demonstrated by Nkosana (2002). However, it is likely that we have underestimated fine root turnover in the first growing season. Although the trees were very small at that age, the abnormally dry conditions may have increased fine root death in winter, followed by an increase in allocation to fine roots to rebuild the fine root biomass after the onset of the first spring rains.

No significant treatment differences could be detected for live and dead fine root mass (Nkosana, 2002), which allowed us to pool data across treatments when estimating fine root production. While there may have been subtle differences in fine root production, it was not possible to detect these with the methods used. It is important to note that the absolute values for fine root production are coupled to different values for the total NPP across treatments. When the fine root production is expressed as a *fraction* of the NPP per treatment (Table 5), it is clear that treatment differences exist. According to this calculation, fine root production constituted 11.5% of the NPP in treatment 0S, but only 8.6% of the NPP in treatment SB. A decrease in the fraction of carbon allocated to fine roots with increases in resource availability has been documented in several forest stands (Keith *et al.*, 1997; Albaugh *et al.*, 1998; Stape, 2002; Giardina *et al.*, 2003).

## Biomass distribution in the standing crop

The foliage makes up a comparatively large portion of the biomass in the young trees in our study (8.9 to 9.0% of the above-ground biomass) (Table 3). This fraction usually decreases with increasing plantation age, since the woody biomass will increase while leaf mass may remain roughly constant in closed canopy stands or decrease slightly (Laclau *et al.*, 2000; Judd, 1996). The contribution of the leaf mass to the above-ground biomass in a 7-year old stand of *E. grandis* (the previous crop on the same study site) was 3.8% (du Toit *et al.*, 2000). The treatments in our study held 37 to 39% of the AGB in the bark plus branch fractions. The branch plus bark mass is commonly expressed as a fraction of the above-ground *woody* biomass for modelling purposes (Landsberg and Waring, 1997). When expressed in this way, the bark plus branch fraction made up between 41 and 43% of the woody biomass in our study. In an age-series study on the same plantation, Job *et al.* (2003) showed that the bark plus branch fraction decreased from approximately 58% in a one year-old stand to 19% in an eleven year-old stand of *E. grandis*. The stem wood mass makes up a comparatively small percentage of the AGB at this young age (between 52.1 and 53.8%). Note that non-utilised stem tops (< 7 cm diameter over bark) were excluded from the stem mass but added to the branch mass for the purposes of our study. The stem mass of *E. grandis* plantations in other studies at comparable stages of development constituted between 58 and 68% of the total biomass (Table 3). We detected significant differences in coarse root mass between treatments. Average annual coarse root production varied from 2.8 (0S treatment) to 3.8 Mg ha$^{-1}$ (SB treatment) (Figure 2). Expressed as a fraction of the AGB, the coarse roots mass in our study ranged between 21.0% and 21.7%, which is slightly greater than that found by Tandon *et al.* (1988). The Karkloof study site has a markedly drier climate than the site at the latter study, which may explain the greater fraction allocated to roots. The fraction reported by Campion *et al.* (2005) was much lower as only a limited soil volume was excavated. Keith *et al.* (1997) found that coarse root mass of a mature *E. pauciflora* stand constituted approximately 22% of the above-ground biomass.

The portion of biomass contained in each structural component remained remarkably similar across treatments in our study. Ranges for structural components were very narrowly distributed around the mean: foliage (0.1%) branches and bark (1.6%); stem wood (1.6%) and coarse roots (0.7%). The biomass contained in each component was strongly related to tree size (represented by dbh), irrespective of treatment. The narrow ranges explain why the treatment effect in the allometric relationships developed for scaling-up purposes was non-significant in all cases. Our results agree with those documented by Birk and Turner (1992). They studied the response of 9.25 year-old *E. grandis* plantations to fertilisation (single or repeated applications), weeding and insecticide treatments. Their treatments resulted in significant differences in the biomass of individual tree components, however, the ratio between above-ground biomass components remained similar. Hunter (2001) tested the effects of irrigation and fertilisation on tree growth and biomass partitioning. The main effect of fertilisation resulted in significant increases in stembark and branches, but the percentage of biomass allocated to woody tissues or foliage remained virtually constant. However, there are also a number of studies that demonstrated shifts in biomass ratio’s following specific treatments. In Hunter’s (2001) study, irrigation resulted in a substantial increase in stemwood and stembark. In addition, there was a shift in the partitioning of AGB reserves; allocation to foliage increased from an average of 13.4 % in two heavily irrigated treatments, up to 17.2% in the control treatment. Misra *et al.* (1998) showed how, in a young (0.8 to 2.8 year-old) *E. nitens* crop, there was a significant reduction in the portion of dry mass allocated to coarse roots following heavy, repeated fertilisation with N and P.

## NPP partitioning

The amount of biomass partitioned to roots make up 22.5 to 25.7% of the total NPP (Table 4). Other studies contrasted the total above- and below-ground carbon allocation (Keith *et al.*, 1997; Stape, 2002; Giardina *et al.*, 2003). In these studies below-ground allocation constituted between 23 and 40% of total GPP, depending on site and growth resource availability. The below-ground estimates for the cited studies included allocation of C to mycorrhizae, which could not be measured in our study. This may be one of the reasons why our estimates fall in the lower end of the range for below-ground C allocation.

We also evaluated shifts in the partitioning of NPP in the system as a whole, brought about by changes in resource availability. The data in Table 4 show that no significant differences could be detected in the portion of NPP allocated to foliar tissues, although the absolute foliage mass produced in the fast growing treatments was greater than in the 0S treatment (Table 1 and Figure 2). However, there was a significant shift in allocation from woody to root biomass in treatment 0S relative to the fast-growing treatments. The changes in NPP as well as the allocation of NPP to foliar, woody or root tissues were calculated from comparable studies on eucalypts, using respiration rates estimated by the authors. We thus contrasted our NPP data (*E. grandis*) with that of a stand of *E. pauciflora* (Keith *et al.*, 1997); *E. saligna* (Giardina *et al.*, 2003) and *E. grandis* x *urophylla* (Stape, 2002). The only study in this group that showed little change in NPP following treatment was the mature *E. pauciflora* stand. Its response to fertilisation consisted of an increase in above-ground NPP at the expense of root NPP. The three young stands responded to changes in growth resource availabilities with significant changes in total NPP. The stand on a very infertile site (*E. saligna*) responded with very large increases in the *absolute* values of NPP allocated to foliage and woody biomass. It appears that virtually the entire increase in NPP following fertilisation was channelled to above-ground tissues. The net effect was a decrease in the *fraction* of NPP partitioned to roots and an increase in the *fraction* allocated to woody tissues. The fraction allocated to foliage remained fairly constant. In the *E. urophylla* x *grandis* stand, irrigation overcame a resource constraint that appears to be intermediate in its severity, relative to the *E. saligna* and *E. grandis* sites (judging by the non-irrigated MAP and the size of the NPP response). The increase in soil water resulted in a large increase in woody NPP, and moderate increases in foliar and root NPP (absolute values). This pattern represented a substantial shift from the fraction of NPP allocated to both foliage and roots in favour of woody tissues. Finally, in our study with *E. grandis* on a fertile soil (by forestry standards), the 0S treatment had a moderate impact on nutrient availability while the effect of other treatments were either small or had a short duration. The only treatment that had a significant impact on NPP was 0S, where it was reduced relative to other treatments. Decreases in NPP allocated to roots, wood and foliage varied between 20 and 40% in absolute terms. The larger decrease in woody NPP over that of roots represents a modest but significant shift in fractional allocation from woody to root NPP, with the foliar allocation fraction remaining constant (Table 4).

**APAR and estimates of canopy quantum efficiency**

The calculation of GPP and α depends on the accuracy of the assumption that NPP is a constant fraction of GPP across all treatments. While it has been shown that the portion of GPP that is respired may change across large gradients of tree age or size (Mäkelä and Valentine; 2001), it is unlikely that it will change considerably among treatments during the short duration of our study. Other studies have found the ratio of NPP:GPP to be relatively constant (Ryan *et al.*, 1996; Waring *et al.*, 1998; Giardina *et al.*, 2003), despite large gradients in resource availability.

Due to the slow initial leaf area development, levels of APAR were low during the first year. Leaf area development in the 0S treatment was significantly slower than the others (du Toit and Dovey, 2005), which explains the significantly lower values for APAR in this treatment. Treatment differences were most striking during year 1 (Table 5). The estimates for α over the three-year period ranged between 0.026 and 0.029 for the treatments in our experiment (Table 5). The 0S treatment had a significantly lower canopy quantum efficiency that the other treatments. Estimates of canopy quantum efficiency obtained in ecosystem-level studies on eucalypts range from 0.027 to 0.060 (Küppers *et al.*, 1986, Wong and Dunin, 1987; Stape, 2002; Giardina, 2003). The higher values in the range were obtained in studies where large quantities of irrigation water and/or fertiliser were applied to treatments. A value of 0.03 mol C (mol photon)$^{-1}$ was suggested for use as a general value for forest systems in the 3-PG model (Landsberg and Waring, 1997), based on the results obtained in pine plantations, as well as deciduous and evergreen forests. Our estimates for α are very close to the values suggested by Landsberg and Waring (1997) and are similar to unfertilised treatments in *E. saligna* (Giardina *et al.*,

2003) and non-irrigated *Eucalyptus grandis* x *urophylla* hybrids under average rainfall conditions in the study of Stape (2002). The parameter α has been shown to be very sensitive in process-based models such as 3-PG (Esprey *et al.*, 2004), underscoring the importance of reliable values for this parameter.

Changes in the availability of light, water and nutrients are within the scope of the plantation manager. Extreme changes in any one of these three growth resources may cause large and significant changes in biomass partitioning to stand components, e.g. light – Little *et al.* (2002); water – Hunter (2001), Stape (2002); nutrition – Misra (1998), Hunter (2001) Giardina *et al.* (2003). However, most of the treatments described above effected extreme changes in resource availability over prolonged periods of time. Commonly used operational treatments (mimicked in our trial) resulted in significant (but smaller) changes to α. The smaller magnitude in our trial appears to be due to shorter duration of the treatment effects and/or the less extreme changes in resource availability.

## Relative contribution of increases in APAR, α and $\eta_w$ to wood production

The production ecology equation states that forest production is a function of the supply of growth resources, the portion of the resources captured by stands and the efficiency of resource use to fix atmospheric $CO_2$ into biomass (Binkley *et al.*, 2004). We have measured two sets of variables that describe the relative contribution of each factor in the production ecology equation. The percentage change (relative to the control treatment) for NPP and mean values for LAI, growth efficiency (GE), APAR, α and $\eta_w$ are shown in Table 6. Our values for α and $\eta_w$ show an increase with increasing nutrient supply. We can thus concur with Stape (2002); Giardina *et al.* (2003) and Binkley *et al.* (2004) that increased use of growth resources at the stand level, leads to increases in the efficiency of resource use. However, our treatments, being less intensive than the studies cited above, yielded more modest responses. The only treatment in our experiment that brought about significant differences from the control (1S) in terms of APAR, α and $\eta_w$, and consequently to stem mass, was 0S. All the treatments commonly used in industrial forestry had no significant effect on mean values for LAI, APAR, α and $\eta_w$ under the prevailing conditions at the site. The differences between the slowest growing and fastest growing treatments are also tabulated in absolute and relative terms in Table 6.

The relative change in factors that govern wood production was similar amongst treatments, and their relative magnitude was proportional to the change in NPP for that factor. The treatment differences in NPP can be explained by the two parameter sets in Table 6 (set A represents a pragmatic approach to describe wood production (after Brix, 1983; Waring, 1983), and set B describes a physiologically-based approach (after Landsberg and Gower, 1997; Landsberg and Waring 1997; Binkley *et al.*, 2004). Using set A, du Toit and Dovey (2005) showed that the differences in woody mass production at three years of age was brought about by changes in mean LAI and that mean GE remained relatively constant (Table 1 and Table 6). However, data presented for set B in this paper show small but significant differences in α (Table 5). It is clear that sets A and B measure approximately equivalent parameters: LAI (set A) is a surrogate for APAR (set B) while the product of α and $\eta_w$ (set B) is approximately equivalent to GE (set A). However, there are important differences in the two sets: Any increase in LAI is not always met with an equivalent increase in APAR, due to the increased shading of leaves with increasing LAI as described by the Lambert-Beer law (Linder, 1985). This explains why the difference between SB and 0S yielded a 31% increase in LAI but only an 18% increase in APAR. Another important difference is the efficiency parameters in the two sets: the GE measures woody mass production *per unit of LAI*, while α expresses C assimilation *per unit of APAR*. This explains why no significant differences could be detected in GE, while we have reported small but significant changes in α in this paper. While set B describes the physiological response more accurately, the data in set A is also useful for our understanding of the system. For example, it emphasises the fact that the difference between 0S and SB stemmed from a disproportionately large (31%) increase in LAI, which only achieved an 18% gain in APAR (*i.e.* the stand had to expand its LAI by that margin to achieve a moderate increase in APAR).

Despite the small differences between the two approaches to describe wood production, they are in agreement on the response mechanism of the stand, namely that the increase in light capture was the major contributor to increased woody production, rather than changes in efficiency or allocation. The difference in NPP between the most extreme treatments (0S and SB) was 14.3 Mg ha$^{-1}$, which represents a difference of 24%. The overall effect was brought about by decreases in APAR, α and $\eta_w$ of approximately 18%, 13% and 5%. Giardina *et al.* (2003) measured a 13% increase in APAR and a 33% increase in α following fertilisation in a stand of *E. saligna* under high rainfall conditions. Stape

(2002) documented improvements in APAR (7%), α (33%), as well as a shift of 8% in allocation from below- to above ground woody biomass, following irrigation treatments of *Eucalyptus grandis x urophylla* hybrids in Brazil. Both studies increased the supply of the most limiting resource (nutrients or water) while the other resources were present at relatively high levels of supply. The response was dominated in both cases by the contribution of α to the increase in NPP, while the contribution of APAR was small. Improvements in NPP in the Karkloof study stemmed largely from improvements in APAR, particularly during the latter half of year one and the whole of year two, when moisture supply was plentiful and the canopy was in a developing phase (du Toit and Dovey, 2005). We also found increases in α, but these were modest compared to the cited studies. Our experiment is located in a comparatively low rainfall area with prolonged dry periods in winter, leading to periodic water stress (du Toit and Dovey, 2005). It is highly likely that soil moisture limited α through increased vapour pressure deficit during dry periods. The increases in $\eta_w$ with increasing resource availability could be associated (at least in part) by increases in wood density which is commonly observed with increase in resource availability of short-rotation eucalypt stands (Wilkins, 1990; Cromer *et al.*, 1998; Little, 1999; du Toit *et al.*, 2001; du Toit and Drew, 2003).

## Implications for management and planning

The quantity of radiation and the concentration of $CO_2$ at a given site cannot be changed by management, however, the quantity of APAR, as well as soil water and nutrient supply can strongly be manipulated through silvicultural operations. The treatments used in this trial closely resemble silvicultural treatments at time of establishment and our trial site is highly representative of forestry sites in the region. The responses obtained are therefore highly applicable to short-rotation eucalypt plantations in the region, and has the following implications for planning and management:

Our study corroborates the general finding (Binkley *et al.*, 2004) that increases in growth resource availability and use (chiefly light and nutrients in our case) will lead to increased efficiencies of resource use at the stand scale. However, the rainfall at our site and in our region is only moderately high, with high pan evaporation rates (du Toit *et al.*, 1999), which means that one growth resource (water) is seldom in plentiful supply. This also implies that, as the stand develops its leaf area, soil water will increasingly constrain stand resource use efficiency since the stand will then be able to transpire at maximum rates. Our study differed from comparable results obtained in eucalypts, namely that resource capture (*i.e.* increases in APAR), and not resource use efficiency, was the most important component of the response in wood production. The window of opportunity to increase chiefly resource capture (light) but also the efficiency of use, is thus in the early developmental phase. This finding agrees with an analysis of the growth efficiency (du Toit and Dovey, 2005), and it underscores the importance of early silvicultural management (appropriate slash management, weed control and early fertilisation) in short rotations crops on sites with moderate to low rainfall. (Broadscale irrigation of plantations is definitely not an option in our region due to higher priority needs of a water-scarce country and due to economic considerations). Growth modellers involved in management planning will need to take the moderate (but temporary) increases in APAR and α into account as it has been shown that wood production estimates in process models are sensitive to these variables. However, it appears that the partitioning coefficients are relatively insensitive to the degree of change in growth resource availability brought about by commonly used treatments.

## ACKOWLEDGEMENTS

The author conducted the research described above while employed at the Institute for Commercial Forestry Research, Pietermaritzburg. The author is extremely grateful to the sponsors and the team of people that contributed to the measurement of individual components of the results presented: Steven Dovey (climatic data and leaf area index), Anthony Job, Greg Fuller and the late Thulani Ngcobo (standing biomass, destructive sampling & litterfall), Mbeko Nkosana (fine root turnover), Zola Sithole (coarse root mass). Mary Scholes, Janine Campion, Luke Esprey and Sally Upfold made valuable inputs to improve the first draft of this document.

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## **Tables**

Table 1. Cumulative litterfall from 1.67 to 3.04 years after planting as well as mean and peak levels of leaf area index. Numbers within rows followed by the same letter superscript are not significantly different at $p<0.10$.

| Litterfall component | Treatment | | | | |
|---|---|---|---|---|---|
| | **0S** | **1S** | **SD** | **SF** | **SB** |
| Foliar components (Mg ha$^{-1}$) | 6.56 $^{a}$ | 7.59 $^{b}$ | 7.90 $^{b}$ | 7.66 $^{b}$ | 8.11 $^{b}$ |
| Woody components (Mg ha$^{-1}$) | 0.80 $^{a}$ | 1.10 $^{a}$ | 1.31 $^{a}$ | 1.17 $^{a}$ | 1.11 $^{a}$ |
| Total litterfall (Mg ha$^{-1}$) | 7.36 $^{a}$ | 8.69 $^{b}$ | 9.21 $^{b}$ | 8.83 $^{b}$ | 9.22 $^{b}$ |
| Mean LAI (m$^{2}$ m$^{-2}$) | 2.35$^{a}$ | 2.85$^{b}$ | 2.96$^{bc}$ | 3.08$^{bc}$ | 3.11$^{c}$ |
| Peak LAI (m$^{2}$ m$^{-2}$) | 3.84 | 4.36 | 4.38 | 4.58 | 4.86 |

Table 2. Observed (Bold entries, calculated from Nkosana, 2002) and estimated seasonal and cumulative fine root production from 0.0 to 3.0 years.

| Period | Stand age (years) | Canopy closure | Observed, estimated or uncertain | Fine root production (Mg $ha^{-1}$) |
|---|---|---|---|---|
| Late summer 1999 | 0.2 | No | Uncertain, likely to be a small number | << 1.0 (?) |
| Winter 1999 | 0.5 | No | Uncertain, likely to be a small number | < 0.1 (?) |
| Early summer 1999 | 0.8 | Partial | Estimated (80% of early summer value) | 1.4 |
| Late summer 2000 | 1.2 | Yes | Estimated (late summer value) | 1.0 |
| Winter 2000 | 1.5 | Yes | Estimated (winter value) | 0.1 |
| **Early summer 2000** | **1.8** | **Yes** | **Observed** | **1.7** |
| **Late summer 2001** | **2.2** | **Yes** | **Observed** | **1.0** |
| **Winter 2001** | **2.5** | **Yes** | **Observed** | **0.1** |
| Early summer 2001 | 2.8 | Yes | Estimated (early summer value) | 1.7 |
| Feb1999–Feb 2002 | 0 to 3 | | Observations and estimates | Approx. 7.0 |

Table 3. Biomass distribution of stand components as percentages of the above-ground biomass.

| Data source | Karkloof Experiment | | | | | *E. grandis* literature | | | |
|---|---|---|---|---|---|---|---|---|---|
| Site and treatment | 0S | 1S | SD | SF | SB | Campion *et al.* (2005)[a] | Hunter (2001)[b] | Bradstock (1981) | Tandon *et al.* (1988) |
| Stand density (stems ha$^{-1}$) | 1601 | 1505 | 1610 | 1549 | 1645 | 1250 | 2500 | 1080 | 1700 |
| Age (Years) | 3 | 3 | 3 | 3 | 3 | 4 | 3 | 5 | 3 |
| Above ground biomass AGB (Mg ha$^{-1}$) | 38.2 | 48.2 | 52.1 | 52.8 | 54.0 | 67.0 | 45.5 | 52.2 | 56.3 |
| Foliage/AGB (%) | 9.0 | 9.0 | 8.9 | 8.9 | 8.9 | 7.0 | 14.7 | 8.6 | 4.7 |
| (Branch+bark)/AGB (%) | 38.9 | 37.6 | 37.4 | 37.3 | 37.3 | 34.3 | 27.5 | 33.1 | 27.2 |
| Stem/AGB (%) | 52.1 | 53.4 | 53.7 | 53.8 | 53.7 | 58.7 | 57.8 | 58.3 | 68.2 |
| Coarse roots/AGB (%) | 21.7 | 21.1 | 21.1 | 21.0 | 21.0 | 7.7[c] | n.d. | n.d. | 15.0 |

[a] Values for the unfertilised control treatment.

[b] Average values given across all treatments which included irrigation and fertilisation gradients.

[c] The coarse root mass was recovered by excavating a limited soil volume and values is therefore an underestimate of total coarse root mass.

Table 4. Total biomass allocation to foliar, woody and below-ground components during the three year monitoring period. Numbers within rows followed by the same letter superscript are not significantly different at $p<0.05$.

| Biomass component | Description | Portion of NPP (%) | | | | |
|---|---|---|---|---|---|---|
| | | 0S | 1S | SD | SF | SB |
| Foliage | Standing foliage mass + foliar litter | 16.4 $^{a}$ | 16.1 $^{a}$ | 15.8 $^{a}$ | 15.5 $^{a}$ | 15.9 $^{a}$ |
| Woody parts | Stem, branches, bark + woody litter | 58.5 $^{a}$ | 60.8 $^{b}$ | 61.5 $^{b}$ | 61.8 $^{b}$ | 61.7 $^{b}$ |
| Roots | Coarse roots + fine root production | 25.1 $^{a}$ | 23.2 $^{b}$ | 22.7 $^{b}$ | 22.7 $^{b}$ | 22.5 $^{b}$ |
| Stem wood | Commercially utilized stem wood | 32.7 $^{a}$ | 34.8 $^{b}$ | 35.3 $^{b}$ | 35.6 $^{b}$ | 35.6 $^{b}$ |

Table 5. Estimates of photosynthetically active radiation absorbed by treatments and canopy quantum efficiencies for the period 0 to 3 years of age. Numbers within rows followed by the same letter superscript are not significantly different at $p<0.05$.

| Treatment | Period | 0S | 1S | SD | SF | SB |
|---|---|---|---|---|---|---|
| APAR (Mmol photons ha$^{-1}$) | Year 1 | 12.1 $^{a}$ | 21.1 $^{b}$ | 22.5 $^{bc}$ | 25.0 $^{c}$ | 23.6 $^{bc}$ |
| | Year 2 | 91.1 $^{a}$ | 107.3 $^{b}$ | 109.0 $^{b}$ | 111.3 $^{b}$ | 111.4 $^{b}$ |
| | Year 3 | 106.5 $^{a}$ | 109.1 $^{ab}$ | 109.0 $^{ab}$ | 110.8 $^{b}$ | 111.4 $^{b}$ |
| APAR (Mmol photons ha$^{-1}$) | Cumulative years 0 to 3 | 209.7 $^{a}$ | 237.4 $^{b}$ | 240.4 $^{bc}$ | 247.1 $^{c}$ | 246.4 $^{bc}$ |
| NPP [a] (Mg ha$^{-1}$) | | 60.8 $^{a}$ | 74.1 $^{b}$ | 79.3 $^{bc}$ | 79.7 $^{bc}$ | 81.6 $^{c}$ |
| α [mol C (mol photon)$^{-1}$] | | 0.026 $^{a}$ | 0.028 $^{b}$ | 0.029 $^{b}$ | 0.029 $^{b}$ | 0.029 $^{b}$ |

[a] Indicates the cumulative total of standing biomass plus litterfall plus fine root turnover

α = Canopy quantum efficiency

Table 6. Two parameter sets describing changes in the production ecology of the stand as brought about by treatments.

| Para-meter set | Variable | Change relative to the control treatment (1S) | | | | Largest treatment difference (SB-0S) | |
|---|---|---|---|---|---|---|---|
| | | 0S | SD | SF | SB | Absolute | Relative |
| | NPP | -18% | 7% | 8% | 10% | 14.3 Mg ha$^{-1}$ | 24% |
| A | LAI* | -18% | 9% | 4% | 8% | 0.73 units | 31% |
| | GE$^{*}$ | -2% | -3% | -1% | -3% | -0.03 Mg ha$^{-1}$ yr$^{-1}$ LAI$^{-1}$ | -1% |
| B | APAR | -12% | 2% | 4% | 4% | 37.4 Mmol photons ha$^{-1}$ | 18% |
| | $\alpha$ | -7% | 6% | 3% | 6% | 0.004 mol C (mol photon)$^{-1}$ | 13% |
| | $\eta_w$ | -4% | 1% | 2% | 1% | 0.025 | 5% |

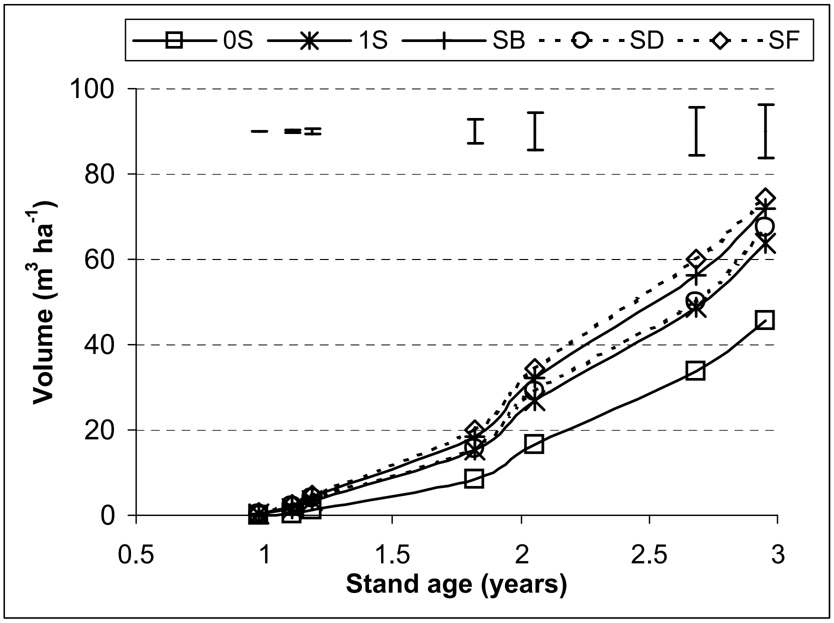
* Calculated from du Toit and Dovey, 2005

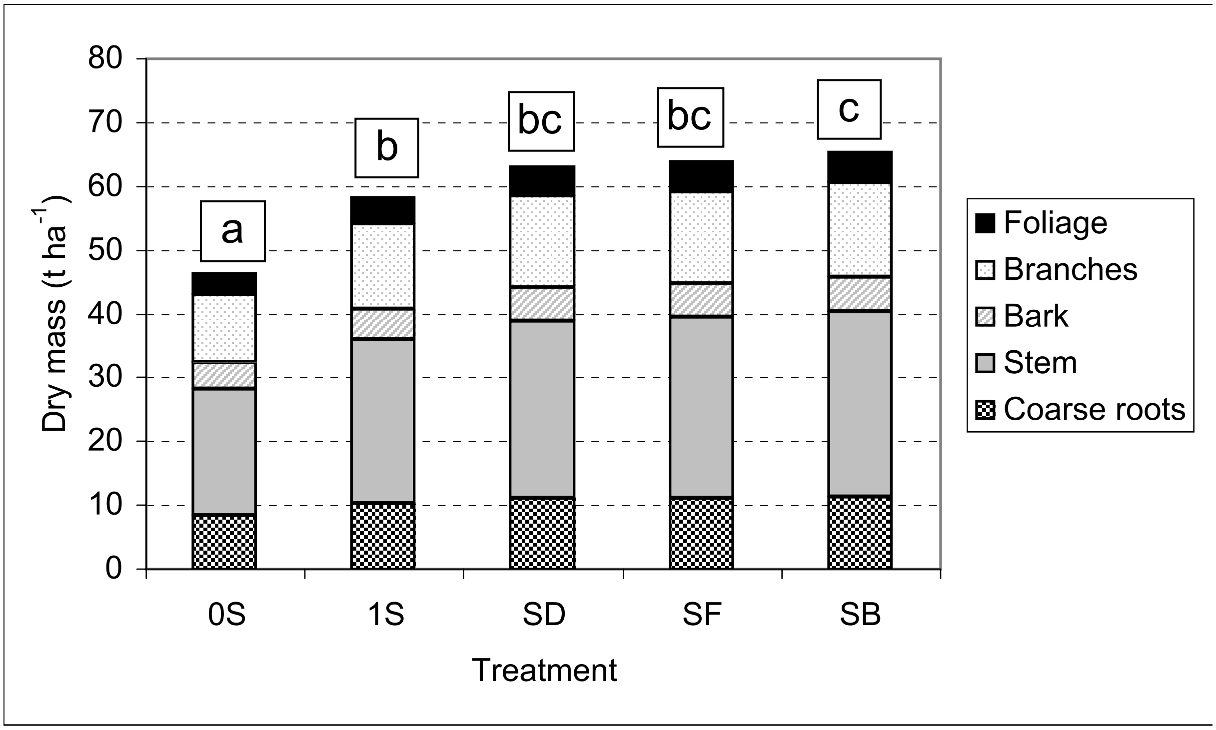
## Figure captions

Figure 1. Development of utilizable stem volume from 0 to 3.0 years of age. Values more closely spaced than the vertical bars are not significantly different ($p$=0.05).

Figure 2. Biomass distribution in various stand components. Columns headed by the same letter code are not significantly different at $p<0.05$.

**Figure**


0S
1S
SB
SD
SF
100
80
60
40
20
0
Volume ($m^3$ $ha^{-1}$)
0.5
1
1.5
2
2.5
3
Stand age (years)


80
70
60
50
40
30
20
10
0
Dry mass (t ha$^{-1}$)
a
b
bc
bc
c
0S
1S
SD
SF
SB
Treatment
■ Foliage
▨ Branches
▨ Bark
▨ Stem
▨ Coarse roots

ge
ches

n
rse roots