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The effect of fertilization on sap flux and canopy conductance in a *Eucalyptus saligna* experimental forest

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Abstract

Land devoted to plantation forestry (50 million ha) has been increasing worldwide and the genus *Eucalyptus* is a popular plantation species (14 million ha) for its rapid growth and ability to grow well on a wide range of sites. Fertilization is a common silvicultural tool to improve tree growth with potential effects on stand water use, but the relationship between wood growth and water use in response to fertilization remains poorly quantified. Our objectives in this study were to determine the extent, timing and longevity of fertilization effects on water use and wood growth in a non-water limited *Eucalyptus saligna* experimental forest near Hilo, HI. We evaluated the short- and long-term effects of fertilization on water use by measuring sap flux per unit sapwood area, canopy conductance, transpiration per unit leaf area and water-use efficiency in control and fertilized stands. Short-term effects were assessed by comparing sap flux before and after fertilizer application. Long-term effects were assessed by comparing control plots and plots that had received nutrient additions for 5 years.

For the short-term response, total water use in fertilized plots increased from 265 to 487 mm yr^{-1} during the 5 months following fertilization. The increase was driven by an increase in stand leaf area accompanied by an increase in sap flux per unit sapwood area. Sap flux per unit leaf area and canopy conductance did not differ during the 5 months following fertilizer additions. For the last 2 months of our short-term measurements, fertilized trees used less water per unit carbon gain (361 compared with 751 kg H_2O kg C^{-1} in control stands). Trees with 5 years of fertilization also used significantly more water than controls (401 vs. 302 mm yr^{-1}) because of greater leaf area in the fertilized stands. Sap flux per unit sapwood area, sap flux per unit leaf area, and canopy conductance did not differ between control and fertilized trees in the long-term plots. In contrast to the short-term response, the long-term response of water use per unit wood growth was not significant. Overall, fertilization of *E. saligna* at our site increased stand water use by increasing leaf area. Fertilized trees grew more wood and used more water, but fertilization did not change wood growth per unit water use.

Keywords: growth, nutrients, sap flow, stomatal conductance, transpiration, water use

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Introduction

Land area devoted to plantation forestry (50 million ha; Nielson, 2000) has been increasing worldwide in response to increased demand for wood products and concerns regarding preservation of old growth forests. The genus *Eucalyptus* is a popular plantation tree (14 million ha globally; Nielson, 2000) because of its rapid growth, wood and fiber quality and because many countries are establishing *Eucalyptus* plantations on deforested land to generate carbon credits for the Kyoto protocol (e.g. Fung *et al*., 1997). In some areas,

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such as South Africa, replacement of low water use vegetation (grasslands) with high water use tree species has raised concerns about the effects of this land use change on local and regional long-term water supply (Scott, 1999). Determining the best management strategies and understanding the role these plantations play in regional and global carbon and water cycling requires a detailed understanding of the effects of climate and management on the growth and water use of these forests.

Fertilization is a common practice in plantation forestry and is implemented to increase growth, shorten rotation times and maximize profits. We know that fertilization increases growth and leaf area, but its effects on total stand water use are not well understood because most of our knowledge about fertilization effects on water use comes from agricultural studies (e.g. Hatfield *et al.*, 2001; Howell, 2001). Although there is a growing body of literature of fertilization effects on water use in conifer plantations (e.g. Myers & Talsma, 1992; Ewers *et al.*, 1999, 2000; Phillips *et al.*, 2001), studies examining fertilization effects for other genera are sparse.

Fertilization can have large impacts on water use by changing allocation to transpirational and absorptive tissues. Increased leaf area is one of the most common effects of fertilization (Myers & Talsma, 1992; Teskey & Sheriff, 1996; Harrington *et al.*, 2001; Giardina *et al.*, 2003). In general, higher leaf area is associated with increased water use (Meinzer & Grantz, 1991; Myers & Talsma, 1992; Sala *et al.*, 1996) although increases after canopy closure may be minimal (e.g. Kelliher *et al.*, 1990; Granier *et al.*, 2000). Increased leaf area may reduce the average canopy stomatal conductance per unit leaf area if boundary layer resistance increases (e.g. Culler *et al.*, 1976; Jarvis & McNaughton, 1986) or if higher leaf area results in increased shading of foliage in the lower canopy (Myers & Talsma, 1992). Increased leaf area has also been shown to increase interception losses (Myers & Talsma, 1992) possibly leading to decreased site water availability. Improved nutrition of forest stands may also reduce belowground carbon allocation (Fabião *et al.*, 1995; Gower *et al.*, 1992; Haynes & Gower, 1995; Albaugh *et al.*, 1998; Giardina *et al.*, 2003), which might have the potential to limit water uptake capacity.

For a given set of environmental conditions, canopy transpiration will be determined by how stomata balance the liquid and vapor phase transport through the soil–atmosphere continuum and fertilization has the potential to affect both of these processes. Liquid water transport is dependent on the ratio of leaf area to sapwood area ($A_l : A_s$), the conductivity of the pathway from soil to leaf, and the difference in leaf and soil water potentials ($\Delta\Psi$) (Whitehead *et al.*, 1984). Fertilization (especially in the short term) may change $A_l : A_s$ by increasing leaf area and wood growth disproportionately. Long-term improvements in nutrition may also increase overall xylem conductivity. If new wood growth produces xylem conduits of larger diameter and similar length, canopy transpiration will increase if $\Delta\Psi$ remains unchanged. Fertilization may also affect vapor phase conductances. For example, if fertilization increases photosynthetic capacity, internal CO_2 concentration may decline, resulting in increased stomatal conductance (Mitchell & Hinckley, 1993). If this results in higher average canopy stomatal conductance, stand water use may increase.

Water loss through stomata is a necessary consequence of plant carbon uptake. Understanding changes in the amount of water required to support growth increases induced by fertilization is important to understand from both management and ecological perspectives. Where water limits plant production, fertilization may be a less attractive silvicultural tool if it significantly increases stand water use, or alters the ratio of carbon gain to water use (water-use efficiency, WUE), (Lajtha & Getz, 1993; Powers & Reynolds, 1999; Clearwater & Meinzer, 2001). Little information on the effects of fertilization on stand water use or WUE is available for broadleaf forests because most studies have focused on agricultural crops (Olesen *et al.*, 2000) or leaf level (Mitchell & Hinckley, 1993; Weih, 2001) responses.

The complex interactions between water availability, climatic variation, and fertilization challenge efforts to decipher cause and effect relationships between fertilization and stand water use. The northeast coast of Hawaii is characterized by evenly distributed, large annual precipitation inputs ($\sim$4000 mm yr^{-1}) and low atmospheric moisture deficits making it an ideal site to examine the effects of fertilization on water use without the confounding effects of limited water availability. A long-term study examining the role of nutrients in age-related stand productivity decline provided the framework for our experiments (Binkley & Resh, 1999; Giardina *et al.*, 2003; Ryan *et al.*, in press).

Our objective in this study was to examine the effects of fertilization on stand water use and WUE in a fast growing *Eucalyptus* experimental forest. Short-term effects were assessed by a comparing control and treatment plots 3 months before, and 5 months following fertilization. Long-term effects were assessed for 3 months by comparing control plots with treatment plots that had been fertilized for the previous 5 years. Using whole tree sap flux instrumentation, we designed an experiment to answer three basic questions: (i) does fertilization increase stand level water use and if so, what is the timing, magnitude, and duration of the increase; (ii) are changes in stand water use associated changes in transpiration per unit per unit sapwood area, transpiration per unit leaf area, canopy conductance, or some combination of the above; and (iii) how does fertilization affect short- and long-term stand WUE?

Methods

Our study site is a 2.5 ha experimental forest of fast growing *Eucalyptus saligna* on the windward side of the island of Hawaii (19°50′28.1″N, 155°7′28.3″W). Elevation for the site is 350 m, and annual precipitation averages 4000 mm (Binkley *et al.*, 1992). Soils are deep (>2 m) and classified as thixotropic, isothermic Typic Hydrudands in the Kaiwiki series. The research site was cropped with sugarcane from ca. 1910 to 1993, 1 year prior to forest establishment. Routine management of sugarcane included biannual applications of 85 kg N ha^{-1}, 75 kg P ha^{-1}, and 11 kg K ha^{-1}, and, after 1955, biannual applications 700 kg ha^{-1} of lime (Binkley & Resh, 1999).

As part of a larger study examining age-related decline in productivity (Giardina & Ryan 2002; Giardina *et al.* 2003; Ryan *et al.*, in press), 18 30 m × 30 m plots, organized into three completely randomized blocks, were planted in May 1994 with seedlings of *E. saligna* at either a 1 m × 1 m or a 3 m × 3 m spacing. Measurements were conducted on 15 m × 15 m interior plots for the 3 m × 3 m spacing plots and on 10 m × 10 m interior plots for the 1 m × 1 m spacing. All plots received the current recommendation in Hawaii for operational plantations on sites of moderate quality (Schubert & Whitesell, 1985): 310 kg N ha^{-1}, 130 kg P ha^{-1}, 260 kg K ha^{-1}, 125 kg Ca ha^{-1}, 58 kg S ha^{-1}, 23 kg Mg ha^{-1}, and 10 kg ha^{-1} micronutrients (5% Mn, 5% Zn, 5% Fe, 5% S, 1.5% Cu, and 0.5% B). Half of the fertilizer was applied in holes adjacent to seedlings at planting and the other half was applied 7 months later with a broadcast spreader. Following the second application of fertilizer in December 1994, six of the 18 plots (long-term fertilization treatment) continued to receive quarterly additions of fertilizer, while the remaining 12 plots were managed without fertilizer until April of 1998. At this time, one randomly preassigned plot at either planting density in each block (short-term fertilization treatment) began receiving quarterly applications of fertilizer that equaled the continuous fertilization treatment. For this study, we used three control plots, three short-term fertilization plots and three long-term fertilization plots, all with 3 m × 3 m spacing.

Environmental measurements

We collected standard meteorological data at a weather station approximately 100 m from our study site. We measured air temperature and relative humidity (CS500, Campbell Scientific, Logan, UT, USA), wind speed (014A, Met One, Grants Pass, OR, USA) and photosynthetically active radiation (PAR, LI-19OSB, LICOR, Inc., Lincoln, NE, USA) and collected 15 min averages over the course of our experiment.

Sap flux measurements

Short- and long-term effects of fertilization on sap flux (J_s, mmol H_2O cm^{-2} s^{-1}) were assessed using the constant heat method of Granier (1987) during 1998 and 1999, respectively. In 1998, we measured sap flux in one control plot (nine trees) and one short-term fertilization plot (nine trees). Average tree diameters in the control and short-term fertilization plots were 14.9 and 18.3 cm, respectively (Table 1). In 1999, we measured sap flux on eleven trees each in one control and one short-term fertilization plot. Average tree diameters in the control and long-term fertilization plot were 19.6 and 22.0 cm, respectively (Table 1). Sap flux probes were inserted on the north (to prevent solar heating of the measurement point) side of the tree at 2 m above the ground. Trunks of these trees were uniform and data from another study at our site indicated that sap flux did not differ by more than 11% with circumference (Barnard & Ryan, 2003). Sapwood thickness averaged 2.5 cm (± 0.2, 95% confidence interval) in 49 trees harvested during 1998 and 1999 from the borders of the control and fertilized plots. We used 2 cm long probes for our sap flux

Table 1 Number of trees instrumented (*n*) and average diameter and sapwood area at 2 m

	Control			Fertilized		
	n	Diameter (cm)	Sapwood area (cm^2)	*n*	Diameter (cm)	Sapwood area (cm^2)
Short-term plots	9	14.9 (1.5)	86.1 (12.8)	9	18.3 (1.6)	117.7 (16.3)
Long-term plots	11	19.6 (1.3)	130.3 (9.9)	11	22.0 (1.6)	158.0 (17.3)

Values in parentheses are standard errors of the mean.

measurements and assumed a uniform water flow across the sapwood cross-sectional area. Probes were insulated 0.5 m above and below the measuring point to ensure stable, uniform temperatures and we attached plastic sheeting to each stem using silicone caulk to prevent stem flow from influencing probe temperatures. Sap flux was recorded every 15 s and stored as 15 min means using a Campbell 21 × datalogger (Campbell Scientific, Logan, UT, USA). In 1998, we began our measurements on Julian day 25 and completed them on Julian day 231 for a total of 206 measurement days. We collected 75 days of pretreatment data and on Julian day 100, we fertilized the treatment plots as described above. In 1999, we began our measurements on Julian day 163 and ended measurements on day 235.

We estimated average monthly J_s for control and treatment plots (both short- and long-term fertilization plots) and used this value to scale sap flux to the plot level using sapwood area of all trees in each of the nine 15 m × 15 m plots used in this study (three treatments with $n = 3$ per treatment). We assumed that average J_s in the sap flux measurement plots applied to the other control and treatment plots. Sapwood area for all trees was estimated from a non-linear regression-relating diameter to sapwood area developed at our site ($1.14 \times \text{diameter}^{1.59}$, $R^2 = 0.98$). For each tree in the plot, we estimated diameter at 2 m from quarterly diameter breast height measurements and then estimated sapwood area (cm^2) at the measuring point based on this diameter. Canopy transpiration (E_c) was calculated as the product of J_s and sapwood area. We assumed that the effect of capacitance was negligible based on analysis in a separate study of water use between mature and young stands at our site (Barnard & Ryan, 2003).

We estimated monthly transpiration per unit leaf area (E_L) as the quotient of E_c and plot leaf area. Leaf area in each plot was derived using a LAI-2000 (Li-Cor Inc., Lincoln, NE, USA) leaf area meter. The LAI-2000 underestimates actual leaf area because of clumping at branch and tree scales (Gower & Norman, 1991; Chen, 1996). Our LAI measurements were corrected for clumping using an actual leaf area measurement from two separate biomass harvests at our site. The details of the LAI measurements and the corrections are given in (Giardina *et al.*, 2003; Ryan *et al.*, in press).

Water-use efficiency

WUE provides useful information regarding the trade-offs between production and transpiration. We estimated WUE as

$$\mathrm{WUE} = C/E_c \qquad (1)$$

where C is wood aboveground net primary production (ANPP, kg C m^{-2} yr^{-1}) and E_c is expressed in kg of water. Quarterly measurements of wood ANPP were used to estimate carbon gain. Details of these measurements are given in Giardina *et al.* (2003) and Ryan *et al.* (in press). We assumed linear wood growth between quarterly measurements.

Canopy conductance

We estimated canopy conductance (G_t mmol m^{-2} leaf area s^{-1}) under high light (PAR $>800\,\mu$mol m^{-2} s^{-1}), during the final 2 months of the short- and long-term fertilization treatments as

$$G_t = E_L/D \qquad (2)$$

where D is air saturation deficit in partial pressure units (kPa/kPa) and E_L is canopy transpiration per unit leaf area (Whitehead *et al.*, 1996). G_t represents the total canopy conductance and consists of both aerodynamic g_a and canopy g_c components (Köstner *et al.*, 1992). We assumed that these Eucalypt canopies were well coupled to the atmosphere with $g_a \gg g_c$. We did not collect the data necessary to measure the decoupling coefficient (Ω) (Jarvis & McNaughton, 1986); however, we examined the extent that wind speed (u) influenced J_s at high light (PAR $>800\,\mu$mol m^{-2} s^{-1}). We assessed the difference in J_s at low wind (u average <2.5 m s^{-1} for 15 min) and high wind (u average ≥ 2.5 m s^{-1} for 15 min) assuming that transpiration in a well-coupled canopy would be relatively unaffected by increased wind speed.

Statistical analysis

Differences in the short-term response of E_c, WUE, and E_L were assessed using a repeated measures analysis with the plot ($n = 3$) as our sampling unit. Differences in J_s between treatments were also assessed with a repeated measures analysis, with the individual measurement tree as our sampling unit. Differences in G_t were analyzed by estimating a *t*-value, and comparing fertilization and control treatment plots ($n = 3$) by 0.25D classes (Ramsay & Silverman, 1997). Long-term responses for the above variables were evaluated using an independent samples *t*-test ($n = 3$ plots) for the 3 months of measurements.

Results

Sort-term response

Sap flux per unit sapwood area (J_s), increased following fertilization from 0.07 to 0.10 mmol m^{-2} s^{-1} ($P = 0.04$,

Fig. 1) and the ratio of sap flux per unit sapwood for control and fertilized trees increased steadily after fertilization (0.9–1.3, $P < 0.01$, Fig. 1). Sap velocities for the 5 months following fertilization averaged 4.3 and $5.3\,\mathrm{cm\,h^{-1}}$ in control and fertilized plots, respectively. These rates are similar to but slightly lower than those found for *E. regnans* (Dunn & Connor, 1993; Vertessy *et al.*, 1995) and *E. Globulus* (Zang *et al.*, 1996).

For the 2 months prior to fertilizer application, total monthly water use was similar for the control and treatment plots, but began to increase shortly after fertilization. Water use almost doubled during the 5 months following fertilization increasing from 265 to $488\,\mathrm{mm\,yr^{-1}}$ ($P < 0.01$, Fig. 2). Over the same 5-month period, there was also a slight increase in water use by control trees, perhaps because of low rainfall during the prefertilization period. However, water use in the short-term fertilization plots averaged about 33% higher than control plots during the 5 months following fertilization.

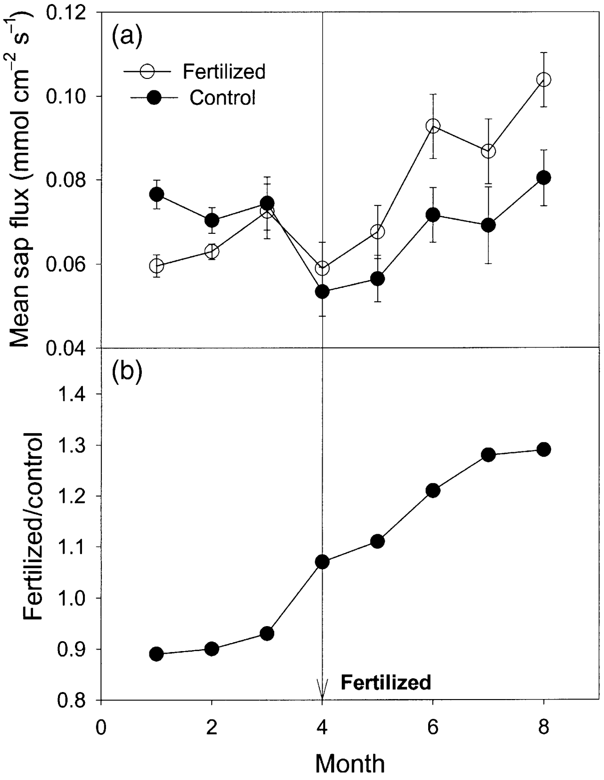

Fig. 1 Sap flux per unit sapwood area (a) and the ratio of control to short-term fertilization treatments (b). Means are for nine instrumented trees in each treatment. Sap flux per unit sapwood area increased significantly in short-term fertilization treatments ($P = 0.04$) and the ratio of sap flux per unit sapwood area in control and short-term fertilization treatments increased significantly over the course of the experiment ($P < 0.01$).

Despite the increase in J_s and E_c, E_L was similar for the control and short-term fertilization plots during the course of our short-term measurements ($P = 0.23$, Fig. 3). Average monthly E_L ranged from 5.4 to $7.5\,\mathrm{kg\,month^{-1}\,m^{-2}}$ leaf area and 5.2 to $9.4\,\mathrm{kg\,month^{-1}\,m^{-2}}$ leaf area for control and fertilized plots, respectively. Leaf area index increased substantially with fertilization increasing from 3.5 just before fertilization to 6.0 5 months after fertilizer application ($P < 0.01$, Fig. 4).

Coincident with a lack of change in E_L, G_t was similar between short-term fertilization and control treatments ($P = 0.3$, Fig. 5). We examined differences in G_t under high light ($> 800\,\mathrm{\mu mol\,m^{-2}\,s^{-1}}$) during the months of

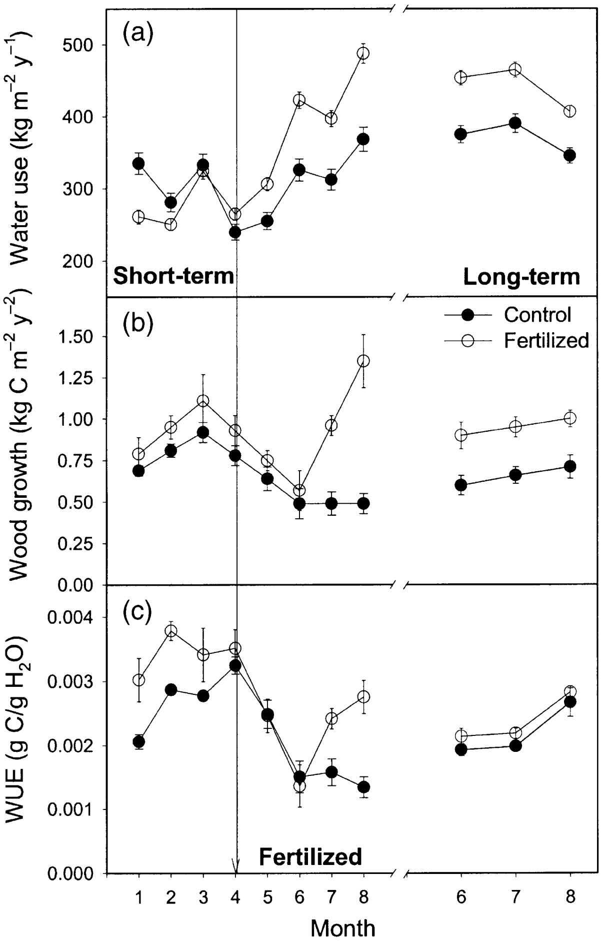

Fig. 2 Stand level water use (a), wood growth (b), and water use efficiency (c) in short-term fertilization plots from January through August, 1998 and in long-term fertilization plots from June through August 1999. Fertilization in short-term plots occurred on the tenth of April. Fertilization caused a significant increase ($P < 0.01$) in wood growth, and water use in both short- and long-term fertilization treatments. WUE was significantly higher in short-term fertilized treatments in July and August 1998 ($P < 0.01$) but not in long-term fertilization treatments.

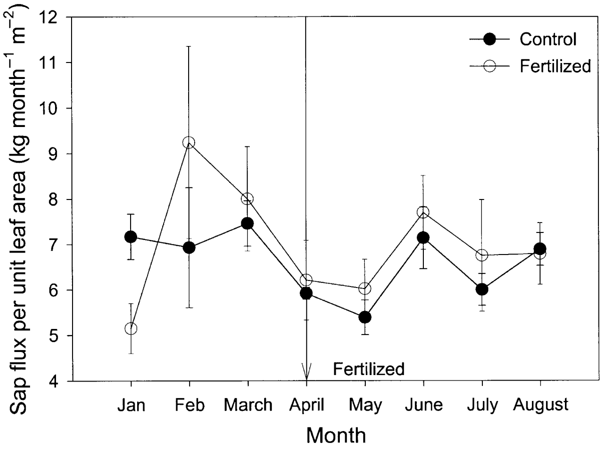

Fig. 3 Sap flux per unit leaf area from January through August 1998 in control and short-term fertilization treatments. Data points are means of three plots for each treatment. There was no significant difference between control and fertilized treatments ($P = 0.23$).

July and August to isolate the time when fertilization would have its largest effect. G_t did not differ for any D class over the range of D we observed during this time period (0.25–1.25). G_t was 71.3 and 85.7 mmol m^{-2} s^{-1} for control and fertilized trees, respectively, at low D and declined at high D to 41.5 for control trees and 37.6 mmol m^{-2} s^{-1} for fertilized trees. G_t decreased with increased D in both control and fertilized stands and values at low and high D are within the range of those reviewed by Oren *et al.* (1999) for numerous other species. Canopies of control and fertilized plots were reasonably well coupled to the atmosphere according to our wind speed analysis. J_s increased from low to high wind speeds by 20% and 10% for control and fertilized treatments, respectively, indicating control and treatment canopies were reasonably well coupled. Consequently, we suggest that our assumption of $g_a \gg g_c$ was valid for these canopies.

During the final 2 months of our short-term measurements, treatment plots showed a decrease in the amount of carbon gained per unit water use. WUE increased from 0.0014 to 0.0028 during July and August ($P<0.01$, Fig. 2). Much of this increase was driven by the large increase in aboveground woody annual increment increase (Fig. 2). WUE was similar between control and short-term fertilization plots before fertilization and for the first 2 months after fertilization.

Long-term response

Total water use in the long-term fertilization plots was substantially higher (401 kg m^{-2} yr^{-1}) than in control plots (301 kg m^{2} yr^{-1}), ($P<0.01$, Fig. 2). Aboveground wood NPP was also higher in the fertilized plots (Fig. 2). In contrast to our short-term measurements, J_s ($P = 0.34$) and WUE ($P = 0.13$) were not significantly different between control and fertilized treatments. We also found no difference in E_L and/or G_t between control and fertilized plots ($P = 0.11$ and 0.42, respectively).

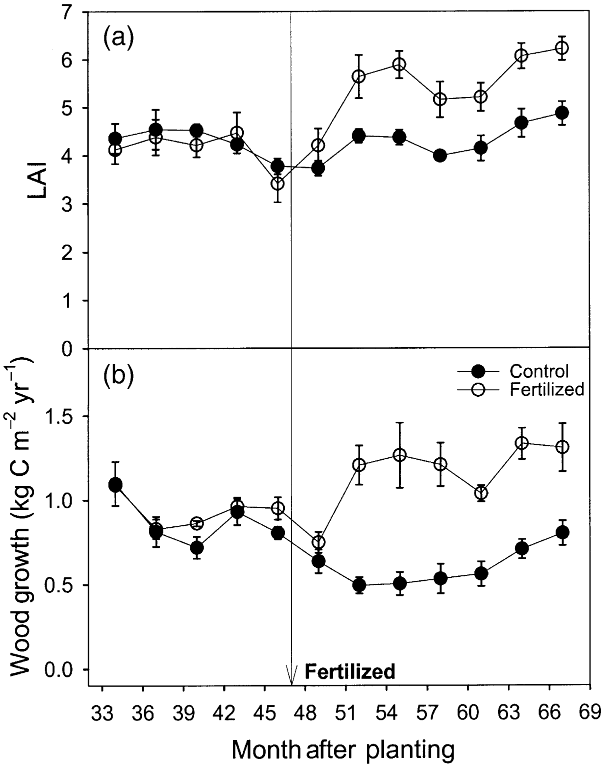

Fig. 4 Leaf area index (a) and above ground wood growth (b) for 72 months of growth in control and short-term fertilization treatments. Data points are means of three plots per treatment. Both leaf area index and wood growth increased significantly following fertilization ($P<0.01$).

Discussion

Fertilization caused a rapid and substantial increase in water use for *E. saligna* stands at our research site. J_s increased immediately (weeks) following fertilization (Fig. 1) and water use in controls averaged 28% lower than fertilized plots for the 5 months following fertilization. When we compared control and long-term fertilization plots, we found similar results with control stands using approximately 33% less water per year than fertilized stands (Fig. 2, 1999 data), indicating fertilization causes a sustained increase in stand water use. The increase was driven by a large increase in leaf area in the fertilized stands. Furthermore, because leaf area was higher and J_s was not significantly different in

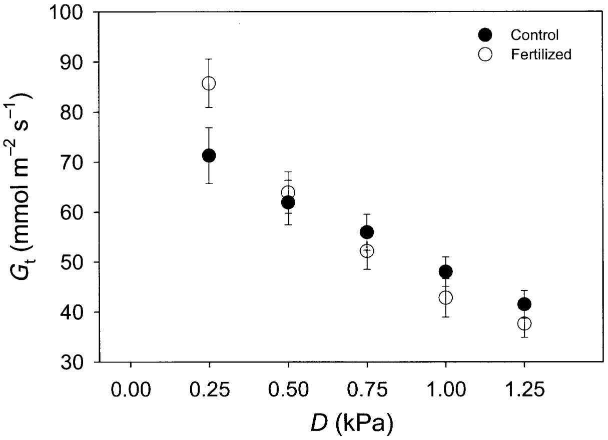

Fig. 5 Canopy conductance (G_t) by air saturation deficit (D) classes. Data are for July and August 1998 only. Data points represent the mean of three plots per treatment. G_t did not differ with fertilization in these stands ($P = 0.3$).

long-term fertilization vs. control treatments, leaf area to sapwood ratios had likely stabilized.

Studies examining the effects of fertilization on water use of *Eucalyptus* species are few, and mostly limited to the application of sewage effluents. Myers *et al.* (1996) found *E. grandis* trees irrigated with effluent used approximately 12% more water than irrigated controls. Because the increase was much smaller than what we observed in this study, *E. grandis* trees may have been more water than nutrient limited. Although they did not evaluate total stand or tree water use directly, Clearwater & Meinzer (2001) found that fertilization increased leaf area, sapwood area and photosynthetic capacity in *E. grandis* trees, indicating a possible increase in water use.

Overall, water use in our control and fertilized stands was lower (0.84–1.33 mm d^{-1}, respectively) than rates reported elsewhere for *Eucalyptus* species. For example, White *et al.* (2002) found that when planted in contour belts, average rates for *E. platypus*, *E. camaldulensis*, *E. leucoxylon*, and *E. saligna* were 0.87, 1.01, 1.24, and 1.43 mm d^{-1}, respectively. Other direct measurements of water use in *Eucalyptus* species range from 0.96 to 3.8 mm d^{-1} for *E. camaldulensis* (Salama *et al.*, 1994; Mahmood *et al.*, 2001) and 0.81 to 1.86 mm d^{-1} for 50- and 230-year-old stands of *E. regnans*, respectively (Dunn & Connor, 1993). Lower transpiration rates at our site probably result from lower air saturation deficits (average daytime = 0.49 kPa) compared with other studies.

The rapid increase in water use caused by fertilization was the result of structural rather than physiological changes. Fertilization caused a rapid increase in leaf area, followed by an increase in wood NPP, and increased stand water use was directly proportional to increased leaf area in the fertilized stands ($R^2 = 0.85$, data not shown). Because J_s increased so rapidly following fertilization, it is possible that water transport capacity for these *Eucalyptus* trees is in excess of that required for a given amount of leaf area. This may be because these trees rarely experience significant water stress such that growth constraints on vessel diameter are not driven by significant and/or frequent cavitation events.

In contrast to observed changes in structure, physiological adjustments, as measured by G_t and E_L, were not detectable and varied little between control and short-term fertilization treatments (Fig. 5). Our long-term fertilization comparisons likewise indicated that physiological adjustments were negligible in response to fertilization. Clearwater & Meinzer (2001) also reported no difference in G_t between control and fertilized treatments in a *E. grandis* plantation. In contrast to our results, changes in G_t in response to fertilization are not uncommon in other species. Ewers *et al.* (2001) found the magnitude and direction of a G_t response to fertilization in *Picea abies* and *Pinus taeda* was dependent upon if irrigation was added to the fertilization treatment. Phillips *et al.* (2001) reported lower G_s in fertilized treatments but the magnitude of change was low enough to not significantly influence stand level transpiration on a ground area basis. Hence, fertilization effects and their interactions on factors influencing liquid and vapor phase transport in forest stands are likely site and species specific.

Water use and wood growth were closely linked in this study and fertilization did not change the quantity of water used per unit wood growth over the long term. WUE increased after 2 months of fertilization (Fig. 2, 1998 data). However, we found no significant difference in WUE between controls and the long-term fertilization plots (Fig. 2, 1999 data). Long-term data may better reflect the influence of fertilization on WUE because wood growth and leaf area have become stabilized compared with shortly after fertilization.

Although WUE did not vary in response to fertilization, it is possible that the power of our statistical test was not sufficient (i.e. small sample size of three plots) to detect the long-term changes in WUE. Therefore, we examined the 'efficiency' of water use and carbon gain from a slightly different perspective. Because we found no difference in water use per unit leaf area, we reasoned that growth efficiency (wood growth per unit leaf area) should follow the same pattern as WUE (i.e. little response to fertilization). We analyzed 3 years of growth per unit leaf area for the control and long-term fertilization plots. Although not significant ($P = 0.19$), wood growth per unit leaf area was generally higher in

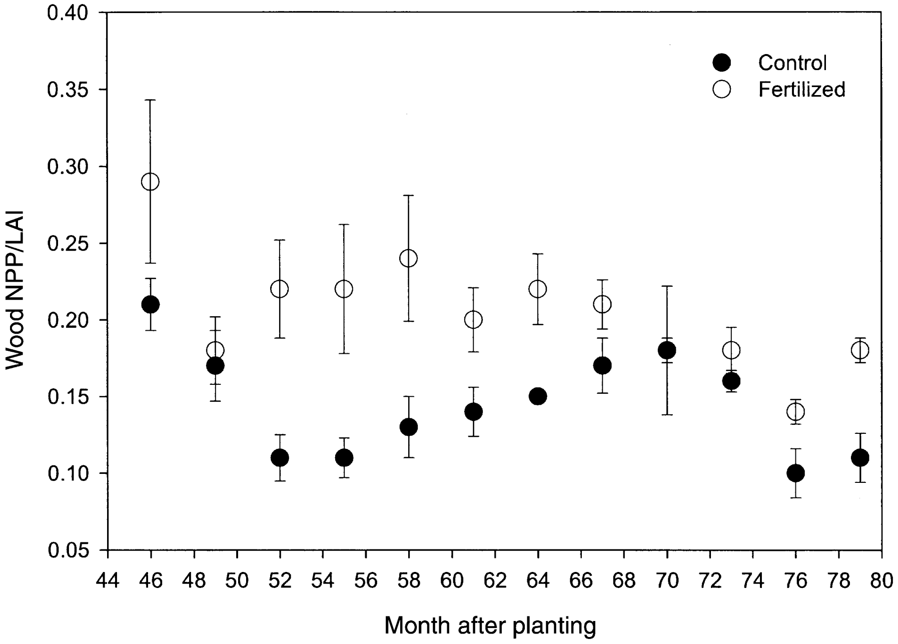

Fig. 6 Wood production per unit leaf area index for 1998, 1999, and 2000 averaged 0.21 and 0.15 for controls and long-term fertilization plots, respectively. Differences were not significant ($P = 0.19$).

the fertilized stands (Fig. 6); the same general pattern as WUE.

While we cannot conclude that fertilization decreases WUE, our data and data in the literature suggest that at the very least, fertilization will not result in *less* carbon gain per unit water use. Clearwater & Meinzer (2001) reported WUE increased with fertilization in *E. grandis*. In addition, Stape (2002) showed that higher productivity *Eucalyptus* stands in Brazil were the most water-use efficient; however, precipitation covaried among his sites so our results are not directly comparable.

The global land area dedicated to plantation forestry is significant and has been increasing dramatically over the past two decades (FAO, 1999). As technology continues to develop for *Eucalyptus* wood products, *Eucalyptus* plantation area will also likely continue to increase (Nielson, 2000). The tight link between growth and water use found in our study suggests that in areas where regional water supply exceeds demand, fertilization is a valuable, cost effective, silvicultural tool to improve yields (recognizing potential tradeoffs with groundwater quality, energy usage, etc.). Although higher wood growth and yield is typically the ultimate goal in plantation forestry, there may be tradeoffs between higher yields from fertilization and increased water use in more arid areas. For example, South Africa has >600 000 ha devoted to *Eucalyptus* plantations, (FAO, 1999) and there are now concerns in that country that afforestation of grass and pasture land with higher water use species like *Eucalyptus* may decrease watershed level stream flow (Smith & Scott, 1992; Scott & Lesch, 1997). Large-scale fertilization in these stands may exacerbate stream flow reductions depending on fertilization effects on allocation and canopy conductance.

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