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Applying a SPA model to examine the impact of climate change on GPP of open
woodlands and the potential for woody thickening

Catriona Macinnis-Ng¹, Melanie Zeppel¹, Mathew Williams³, Derek Eamus^{1,2}

¹ University of Technology, Sydney, PO Box 123, Broadway, Sydney, NSW, 2007, Australia

² Corresponding author (email Derek.Eamus@uts.edu.au)

³ School of GeoSciences, University of Edinburgh, Edinburgh, UK

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ABSTRACT

Woody thickening is a global phenomenon that influences landscape C density, regional ecohydrology and biogeochemical cycling. The aim of the work described here is to test the hypothesis that increased atmospheric CO₂ concentration, with or without photosynthetic acclimation, can increase GPP and that this can explain woody thickening. We examine mechanisms underlying the response of GPP and highlight the importance of changes in soil water content by applying a detailed soil-plant-atmosphere model. Through this model we show that CO₂ enrichment with decreased or increased D and photosynthetic acclimation, results in decreased canopy water use because of reduced g_s . The decline in water use coupled with increased photosynthesis, resulted in increased GPP, water-use-efficiency and soil moisture content. This study shows that there is a valid mechanism for GPP increase due to CO₂ enrichment coupled with either a decrease or an increase in D, in water limited environments. We also show that a large increase in LAI could be sustained in the future as a result of the increased soil moisture content arising from CO₂ enrichment and this increase was larger if D decreases rather than increases in the future. Large-scale predictions arising from this simple conceptual model are discussed and found to be supported in the literature. We conclude that woody thickening in Australia and probably globally, can be explained by changes in landscape GPP and soil moisture balance arising principally from an increased atmospheric CO₂ concentration.

INTRODUCTION

Woody thickening (also called vegetation thickening, woody weed increase and woody re-growth; Gifford and Howden, 2001) is herein defined as the increase in woody standing biomass in a landscape already containing woody biomass. This differentiates it from woody encroachment, (also called woody plant invasion; Jackson *et al.*, 2002) herein defined as the movement of woody species into a landscape that *presently* does not contain woody species (either through management of the landscape or through other factors). Both woody thickening and woody plant invasion are global phenomena that are commonly observed in arid and semi-arid regions, including Australia (Bowman *et al.* 2001; Burrows *et al.*, 2002; Asner *et al.*, 2003; Fensham *et al.*, 2005; Scott *et al.*, 2006; Witt *et al.*, 2009). They are also observed in tropical rainforests of Central and South America (Phillips *et al.*, 1998) and temperate forests globally (Birdsey *et al.*, 1993). Evidence for woody thickening can be observed using time-series analyses of aerial photographs (Bowman *et al.*, 2001; Fensham *et al.*, 2005; Witt *et al.*, 2009), long-term monitoring sites (Watson *et al.*, 2000) or satellite-based remote sensing (Lucas *et al.*, 2008).

The impact of woody thickening and woody invasion on biogeochemical cycling (McCulley *et al.*, 2004), C stocks (Gifford and Howden, 2001; Burrows *et al.*, 2002) and ecohydrology (Huxman *et al.*, 2005; Scott *et al.*, 2006) is regionally substantial and globally significant (Pacala *et al.*, 2001; Foley *et al.*, 2005). For example, Scholes and Hall (1996) estimate that the conversion of grasslands to closed woodlands would represent a terrestrial sink of 94.3 PgC. Whilst the cause of woody invasion has been attributed principally to changes in land-use practice, including changes in fire regime and grazing pressure (Archer *et al.*, 1995; van Langevelde *et al.*, 2003) and the cessation of clearing and abandonment of formerly managed

grass and cropland (Schimel *et al.*, 2001; Gifford and Howden, 2001; Jackson *et al.*, 2002), the cause of woody thickening remains debated. A role for changes in fire regime and grazing intensity is clearly apparent (Scholes and Archer, 1997) but there is an increasing awareness of potential roles for climate and changes in atmospheric CO₂ concentration in causing woody thickening (and woody invasion) (Fensham *et al.*, 2005; Berry and Roderick, 2006; Davis *et al.*, 2007; Sankaran *et al.*, 2008).

Eamus and Palmer (2007) postulated that climate change (in particular, increased atmospheric CO₂ concentration and declining evaporative demand) may explain the global phenomenon of woody thickening. In particular, they proposed a purely conceptual model based around six key observations. These are (1) the concentration of atmospheric CO₂ has increased since the industrial revolution (Keeling *et al.*, 1995); (2) this increase accelerates the rate of photosynthesis (Eamus *et al.*, 1995; Eamus and Jarvis, 1989) and this increase is larger in C3 plants (that is, trees) than C4 grasses (Medlyn *et al.*, 1999); (3) stomatal conductance declines in response to elevated concentrations of CO₂ in the atmosphere (Medlyn *et al.*, 2001); (4) the growth rate of young trees and shrubs is enhanced by CO₂ enrichment (Berryman *et al.*, 1993; Duff *et al.*, 1994) and the proportional stimulation of growth is larger in xeric than mesic sites (Eamus and Ceulemans, 2001); (5) pan evaporation rates have declined globally (Roderick and Farquhar, 2002; 2004); and (6) because of (3) and (5) above, there is increased water availability in the short-to-medium term which can support a larger standing biomass of woody species, that is, woody thickening.

A widely applied model of vegetation function is the soil-plant-atmosphere (SPA) model of Williams *et al.* (1996a). This has been tested and validated across a range of diverse ecosystems, including Arctic tundra (Williams *et al.*, 2000), Brazilian tropical rainforests

(Williams *et al.*, 1998; Fisher *et al.*, 2006) and temperate Ponderosa pine forests (Williams *et al.*, 2001). The SPA model is a mechanistic model which predicts, amongst other parameters, gross primary productivity, canopy water use, stomatal conductance and leaf-scale photosynthetic rate. We have recently successfully applied it to describe the functioning of a temperate open woodland in Australia (Zeppel *et al.*, 2008). As such it provides a methodology for testing the conceptual model of Eamus and Palmer (2007).

In the present paper we address the following questions: (1) can CO₂ enrichment and reduced atmospheric vapour pressure deficit, singly and in combination, significantly enhance GPP; (2) does photosynthetic acclimation or reduced foliar N content negate any stimulation of GPP arising from CO₂ enrichment; (3) is there an enhancement of soil moisture content under conditions of CO₂ enrichment and decreased vapour pressure deficit (D); (4) can an increase in LAI which may arise from increased GPP, be supported in a landscape without additional rainfall? Specifically, we examine the response of GPP and stand water use of a typical Australian woodland using the recently parameterised soil-plant-atmosphere (SPA) model (Zeppel *et al.*, 2008). The impact of reduced foliar N and photosynthetic acclimation of V_{cmax} and J_{max} are investigated because such acclimation is almost universally observed in FACE studies of tree responses to CO₂ enrichment (Ainsworth and Long 2005).

MATERIALS AND METHODS

Study site and weather data

The study site was located in a remnant Cumberland Plains woodland, near Richmond in western Sydney, New South Wales, Australia (33° 39' S, 150° 46' E, elevation 32 m).

Vegetation at the site consisted of a steady-state open woodland, with an average height of 14 m, dominated by *Angophora bakeri* (E.C.Hall), (narrow-leaved apple) and *Eucalyptus*

parramattensis C.A.Hall (Parramatta Red Gum). These two dominant species account for approximately 80% of tree basal area at the site. Mean tree basal area for the site was $12.3 \pm 3.2 \text{ m}^2 \text{ ha}^{-1}$ with $85.5 \pm 6.5 \text{ stems ha}^{-1}$ and leaf area index of the tree canopy varied from 1.3 to 1.9 throughout the 12 month study period, measured using the digital image method of MacFarlane *et al.* (2007). The understorey was dominated by shrubs and grasses including *Pultenaea elliptica*, *Cryptandra amara* and *Melaleuca thymifolia*. Soils at the site are duplex with a very sandy upper profile to 0.8 m overlying a deep (> 10 m) weakly pedal orange heavy clay (Macinnis-Ng *et al.*, 2010). The climate is warm temperate, with mean maximum winter (July) and summer temperatures (Jan) in 2006 of 17.2 and 29.3°C respectively. Mean annual rainfall is 729 mm and is usually slightly summer dominant (http://www.bom.gov.au/climate/averages/tables/cw_067105.shtml, accessed 21st January 2010) but this was not the case during the study period (see below), which started on August 28, 2006 and finished 365 days later.

Weather data (air temperature, solar radiation, vapour pressure deficit (*D*), and rainfall) were gathered at half-hourly intervals for the study period with an on-site meteorological station. We estimated ambient CO₂ concentration through use of a portable IRGA and calculated photosynthetically active radiation from solar radiation (where PAR= 2.3*solar radiation when solar radiation is measured in W m⁻² and PAR is calculated in μmol m⁻² s⁻¹). These data defined the ambient conditions (control, or scenario one).

Model application

We applied the Soil-Plant-Atmosphere (SPA) model to the Cumberland Plains woodland site. The SPA model is a multi-layered model, having multiple soil and canopy layers. It takes as

inputs weather data, soil and plant-specific data (see below) and quantifies, amongst other variables, water and carbon fluxes at leaf and canopy scales, a soil water balance, GPP, stomatal conductance and leaf water potential. For a full description see Williams *et al.* (1996a).

We recently parameterised and tested SPA for this site using multiple independent data sets (Zeppel *et al.*, 2008). Sapflow measured with the heat ratio method and sapflow modelled with SPA over a 115 day period agreed well. For half-hourly values of observed *versus* modelled sapflow, regression analysis r^2 values were 0.80 for spring and 0.73 for summer, while slopes were 0.91 and 1.04 respectively (Zeppel *et al.*, 2008). For the year long dataset used in the present study, there were 286 days of sapflow data available (due to equipment failure, power loss and animal attack). We divided these data into 2 datasets of alternate days. One was deemed the training dataset (used to parameterise the model) and the second was the testing dataset (used to validate the model). For the training dataset, the R^2 and root mean squared error (RMSE) were 0.61 and 0.029 mm d⁻¹ respectively and for the testing dataset, they were 0.59 and 0.030 mm d⁻¹ respectively. The overall R^2 across the 286 days was 0.60. The only input changed for this sample period (compared to that of Zeppel *et al.*, 2008) was the minimum leaf water potential which was decreased from -2.8 MPa to -3.2 MPa to allow greater sapflow during dry periods. Both values of leaf water potential were within the measured limits (data not shown).

The site-specific parameters used for model parameterisation were soil physical characteristics (including particle size analysis and organic matter content analysis), root biomass distribution, soil moisture content at 10, 40 and 70 cm depths at the start of the study period, the annual cycle of leaf area index, minimum leaf water potential, whole plant

hydraulic conductance, maximum rates of carboxylation and electron transport, mean foliar nitrogen concentration and hourly meteorological data. Full details of the model parameterisation can be found in Zeppel *et al.* (2008). Table one provides a list of model inputs and their values and their source.

Climate manipulations – single factor studies

To examine the impact of climate change on vegetation function, we began by varying individual parameters; thus we varied atmospheric CO₂ concentration from 80% to 200% of current values and kept all else constant, or varied D from 75% to 125% of current values (ie we multiplied each half-hourly value by 0.75 or 1.25 respectively), and kept all else constant. These ranges were chosen to encompass the recent past (post-industrialisation) and the near future range of values for D and CO₂ concentration. Preliminary analysis showed that increasing temperature by 4°C with D and CO₂ unchanged from nominal values decreased the annual sum of sapflow by only 0.2% and increased annual GPP by only 1%, so the effect of temperature was not considered further in this analysis. Similarly we have not addressed changes in rainfall distribution and intensity in this analysis, as this is the subject of on-going work and local predictions for changes in these variables are not available at such fine spatial and temporal resolution. The annual rainfall for our study year was 13% larger than the long-term average (Fig. 1) so we did a sensitivity analysis in SPA and found that a 10% decrease in annual rainfall for this year results in a 2.8% decrease in annual sapflow and a 1% decrease in annual GPP. Because the impacts on annual sapflow and GPP were far smaller than the 10% decline in rainfall, we assumed having a slightly larger rainfall for our study was acceptable. Furthermore, using a slightly larger annual rainfall for this analysis would

produce conservative estimate of CO₂ elevation impacts because CO₂ effects are more apparent when water is more scarce (McMurtrie *et al.*, 2008).

The values of sapflow, gross primary production, water use efficiency, stomatal conductance (g_s), assimilation rate and soil water content resulting from changes in CO₂ concentration and D were assessed on annual, seasonal and daily scales. All values were produced directly by the model, except for WUE which was calculated as GPP divided by total sapflow for each day and expressed as gC m⁻¹.

Photosynthetic acclimation in response to elevated CO₂

Increasing atmospheric concentrations of CO₂ causes photosynthetic acclimation, leading to declines in maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) (Medlyn *et al.*, 1999; Kirschbaum, 2004). Acclimation through reductions in V_{cmax} and J_{max} alone or through reductions in foliar N and V_{cmax} and J_{max} are the two mechanisms by which downward acclimation of photosynthesis occurs (Ainsworth and Long, 2005). While some studies have found little or no photosynthetic acclimation (Ainsworth and Rogers, 2007), the down-regulation of photosynthesis has been linked to leaf longevity (Rogers and Ellsworth, 2002) where the photosynthetic apparatus of longer-lived leaves shows a larger acclimation response to elevated CO₂. Leaves at the present site are relatively long-lived in the whole canopy (1.6-1.9 y Wright and Cannon, 2001) so we assumed that they would perform like the longer lived leaves in the Rogers and Ellsworth (2002) study and photosynthetic acclimation would occur and ran model scenarios to determine the influence of photosynthetic down-regulation on ecosystem function. Downward acclimation has been observed in Australian tropical tree species (Eamus *et al.*, 1995; Goodfellow *et al.*, 1997). We partition downward

acclimation equally to a decrease in foliar N (5% decrease) and decreased V_{cmax} and J_{max} (5% decrease). This is equivalent to a 10% decline in V_{cmax} and J_{max} if foliar N remains unchanged and these values are similar to the averages recorded in 15 y of free air CO₂ enrichment studies (Ainsworth and Long, 2005). Preliminary investigations showed that further decreases in foliar N, V_{cmax} and J_{max} cause a proportional reduction in GPP in the model (data not shown).

It was assumed that J_{max} varied in proportion to V_{cmax} (Wullschleger, 1993; Medlyn *et al.*, 1999; Medlyn *et al.*, 2002; Kirschbaum, 2004) and that both V_{cmax} and J_{max} values varied proportionally in response to CO₂ concentration changes. Therefore, for CO₂ treatments at 80, 150 and 200% of present day values, we used foliar N, V_{cmax} and J_{max} values at 102, 95 and 90% of present day, equating to up or downregulation of 104, 90 and 80% respectively.

Four climate scenarios compared

In addition to examining the impact of changes in CO₂ concentration or D applied singly, we also compared the impact of four climate scenarios. In the first, (control), ambient conditions were maintained. In the second (past scenario), atmospheric CO₂ concentration was decreased to 75% of current levels and a 25% increase in D was imposed. In the third (future scenario), atmospheric CO₂ concentration was increased to 150% of current levels and a 10% photosynthetic acclimation (expressed as a 5% decline in foliar N, J_{max} and V_{cmax}) and a 25% reduction in D was imposed. The fourth scenario was identical to the third but an increased LAI was imposed. The magnitude of the increase in LAI was chosen specifically so that annual canopy water use in scenario three was identical to that observed under current (control) conditions. The level of increase in LAI required to bring water use in scenario three

to control levels was 30%. Concentrations of CO₂ were chosen to reflect atmospheric conditions approximately 100 years in to the past and future respectively (consistent with values used in FACE experiments across the globe, e.g. Körner *et al.*, 2005, Norby *et al.*, 2005 and many others). 150% equates to an increase of approximately 180 ppm. Current increases are about 1.5 ppm CO₂ per year so this is representative of a 100 year period which will be reached this century according to the midrange of the IPCC projections (Fig. 3.11, <http://www.ipcc.ch/ipccreports/tar/wg1/pdf/TAR-03.PDF>). D was increased in the past scenario and increased in the future scenario because of the evidence that pan evaporation rates have declined globally, despite a warming trend (Roderick and Farquhar, 2002, 2004).

Comparing GPP on cloudy and clear days

In order to determine the influence of cloud cover on gross primary production (GPP), the meteorological data set was mined for adjacent days with contrasting light conditions. Low light conditions (generally below 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were classed as overcast and those days with high light conditions (above 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the middle of the day) were classed as clear. Adjacent overcast and clear days were used to so that soil moisture conditions would be similar. Only days with temperatures reaching above 20°C (to eliminate low temperature as a confounding factor) and having no rainfall (to eliminate wet canopies as a confounding factor) were used. A paired t-test was used for the comparison between GPP values for cloudy and clear days and regression analysis was used to demonstrate the effect of photosynthetic acclimation. We used SPSS (v. 14.0, SPSS Inc., 2005) for all statistical analyses.

RESULTS

Weather

Maximum daily solar radiation, average daily temperature and maximum vapour pressure deficit (D) peaked in summer (December and January) whilst minima were observed in winter (July and August; Fig. 1). Solar radiation, temperature and D ranged from 180 to 1200 W m^{-2} , 5 to 30°C and 0.4 to 6 kPa respectively. Rainfall was winter dominant with large (> 30 mm) rainfall events occurring in the latter half of the study period but not the first half (Fig. 1). Annual rainfall for the study period was 827 mm which is 13% larger than the long-term average of 729 mm. We do not believe there was a significant change in D due to the larger than average rainfall. Bureau of Meteorology data from the nearest monitoring station (about 6 km from the site) showed the annual rainfall in 2006 was 525 mm while in 2007, it was 1020 mm. Despite there being almost twice as much rainfall in 2007 as 2006, there was very little difference between the mean daily evaporation values for each year (3.5 and 3.6 mm for 2006 and 2007 respectively).

The impact of single factor manipulations on fluxes of water and CO₂

Annual sapflow was sensitive to both increasing CO₂ concentration and increasing D. Thus as the atmospheric concentration of CO₂ increased from 80% of current values to 200% of current values, annual sapflow declined by approximately 10% (Fig 2). This decline in sapflow was due to the decline in stomatal conductance (g_s) that occurred in response to CO₂ enrichment (data not shown). The impact of photosynthetic acclimation (through reduced V_{cmax} and J_{max} and foliar N) on the response of sapflow to CO₂ enrichment was minimal at all but the largest value of CO₂ enrichment. However, when D increased from 75% of current values to 125% of current values, sapflow increased by approximately 18%; this was despite

a decline in g_s of almost 50% (data not shown). In contrast to these trends, GPP increased by 28% (with photosynthetic acclimation) or 44% (with acclimation) with increasing atmospheric CO₂ concentrations but declined by approximately 10% when D increased (Fig. 2) from sub-ambient to supra-ambient values.

As a result of the relative changes in sapflow and GPP, water-use-efficiency (WUE), expressed as the ratio of annual GPP to annual sapflow, increased by approximately 55% (from 4500 gC m⁻¹ to approximately 7000 gC m⁻¹; equivalent to approximately 6.8 and 10.5 mmol C mol H₂O⁻¹ respectively), with increasing atmospheric CO₂ concentration (Fig. 2). The impact of photosynthetic acclimation on WUE was not detectable for any level of CO₂ enrichment. In contrast, WUE declined by approximately 50% as D increased (Fig. 2). A 10% reduction in V_{cmax} alone (but in combination with CO₂ enrichment to 150% of current levels) resulted in a 4.5% decline in GPP whilst a 10% reduction in J_{max} alone (but in combination with CO₂ enrichment) on GPP was negligible (less than a 0.5% reduction in annual GPP; Fig. 3). In contrast, and when both J_{max} and V_{cmax} were reduced by 10%, GPP declined by 4.8% (Fig. 3).

Reducing foliar N by 10% without any changes in J_{max} and V_{cmax} resulted in a 5% reduction in annual GPP, a value almost identical to the 4.5% reduction in GPP arising from a 10% decline in J_{max} . Similarly, a 5% reduction in foliar N, J_{max} and V_{cmax} resulted in a 4.8% reduction in annual GPP (Fig 3), a value identical to that observed for a 10% reduction in both J_{max} and V_{cmax} . For all scenarios with CO₂ enrichment (with and without acclimation) daily GPP ranged between 0.8 and 8 gC m⁻² d⁻¹ (Fig. 3).

The cause of the increase in annual GPP observed in response to CO₂ enrichment was an increase in leaf-scale assimilation rate (A) (data not shown) and the stimulation of A was largest when photosynthetic acclimation was absent (75% increase in A) compared to when acclimation was present (50% increase in A). When photosynthetic acclimation was present A approached an asymptotic value more rapidly than when acclimation was absent.

Comparing four climate scenarios on gas fluxes

Four climate scenarios were examined in this study. In the first, (control), ambient conditions were maintained. In the second, the atmospheric CO₂ concentration was decreased to 75% of current levels and D was increased to 125% of current levels to simulate past conditions. In the third, the atmospheric CO₂ concentration was increased to 150% of current levels (with a 10% photosynthetic acclimation expressed as a 5% decline in foliar N, J_{max} and V_{cmax}) and D was reduced to 75% of current levels to simulate future conditions. In the fourth, an increased LAI was adopted which increased annual canopy water use to a level equivalent to that observed under current (control) conditions. The level of increase in LAI required to bring water use in scenario four to control levels was 30%.

In scenario two, annual sapflow increased 7% from 400 mm y⁻¹ to 427 mm y⁻¹ (Table 2) and GPP decreased 19% from 1485 to 1210 gC m⁻² y⁻¹). This increase in water use and decrease in productivity was associated with a decline in WUE when projecting into the past. These changes in annual sapflow, GPP and WUE were seen in a representative period of daily (Fig. 4) and hourly (Fig. 5) outputs from the model in both summer and winter periods.

In scenario three (atmospheric CO₂ concentration enriched to 150% of current values with photosynthetic acclimation and a decline in D to 75% of current ambient levels), annual

sapflow declined by almost 11% from 400 mm y⁻¹ to 357 mm y⁻¹ when projecting into the future (Table 2). By definition, sapflow for scenario four was the same as that for scenario one (control) as this was the objective for increasing the LAI (see discussion). The decline in annual sapflow in scenario three compared with scenario one was the result of a decline in daily sapflow (Fig. 4) and 15% decline in mean daily g_s (Fig. 5). Increasing the LAI by 30% (scenario four) further reduced mean daily g_s and this accounted for the decline in mean daily A for scenario three compared to scenario two (Fig. 5).

Under scenario three conditions annual GPP increased by 16% (Table 2). This increase was the result of a 30% increase in mean daily A (Fig. 5). When LAI was increased by 30% in scenario four, GPP was further increased by 6% above that of scenario three (Table 2). This increase in GPP was not reflected in increased leaf-scale A, as mean daily A was reduced below scenario three levels (Fig. 5) when LAI was increased, most likely as a result of increased self-shading.

Water-use-efficiency increased 43% (from about 4700 to about 6800 gC m⁻¹) in scenario three compared to control conditions because of the increase in GPP and the decline in sapflow observed in scenario three. Similarly, WUE remained enhanced in scenario four compared to scenario one (Table 2) despite the 30% increase in LAI of scenario three.

Seasonal changes in soil moisture, sapflow, GPP and WUE

The total sum of soil moisture in the upper 70 cm of the soil profile (which contains more than 70% of root biomass) was consistently lower in the first 170 days of the study compared to the second half of the study (Fig. 6), reflecting the relative distributions of rainfall between

the two periods. During the first 160 days, soil moisture ranged from 60 mm to 110 mm. However, following the 100 mm rainfall that was received on days 168 and 169 of the study period, total soil moisture in the second half of the study ranged from 125 mm to 275 mm (Fig. 6). For almost the entire study period the amount of water in the soil profile was larger under scenarios three and four than under scenario one (ambient) conditions, resulting in a larger soil moisture sum across the year (Table 2). Similarly, soil moisture was reduced in scenario two in comparison to scenario one and this pattern is consistent with more soil water availability as the climate changes over time. Soil moisture content was consistently larger under scenario three than scenarios one or four. In the second half of the study period the increase in soil moisture content for scenario three was up to 10 mm of water (days 240 – 280). In the first half of the study period, the difference was typically 5 mm of water (Fig. 6).

Daily patterns in A and g_s

Daily patterns in A and g_s are shown for representative days in winter and summer in Fig. 5 to assist in interpreting the functional response of the canopy to climate change under contrasting local conditions. In both summer and winter, rates of leaf-scale photosynthesis (A) were increased by 50 – 100% in scenario three (future) compared to scenario one (ambient) and they were decreased in scenario two (past) compared to scenario one. The slightly earlier peak in photosynthesis in the morning under ambient (scenario one) conditions was mirrored in the earlier peak for g_s observed for scenario one, especially in the summer (Fig. 5). The increase in LAI of 30% of scenario four reduced leaf-scale A compared to scenario three although it remained increased compared to scenario one. The reduction in leaf-scale photosynthesis in scenario four compared to scenario three evident in Fig. 5 mirrors that observed in the daily mean values of photosynthesis and g_s presented in Fig. 4 and

reflects the increased self-shading (within the canopy of a single tree) arising from a 30% increase in LAI. A role for diffuse beam *versus* direct beam radiation was evident in the comparison of mean daily GPP for clear and overcast conditions for 21 pairs of consecutive days having clear or overcast days in each pair (Fig. 7). During overcast days mean daily GPP was significantly higher (by 8%) than on clear days. These data refer to ambient conditions only but serve to highlight the fact that even under ambient conditions, self-shading was a limiting factor on A and that reduced shading (through increased diffuse beam radiation on overcast days) increased A.

DISCUSSION

Woody thickening is a globally observed phenomenon (Birdsey *et al.*, 1993; Phillips *et al.*, 1998; Gifford and Howden, 2001; Fensham *et al.*, 2005; Scott *et al.*, 2006). Although there have been extensive discussions of the relative importance of changes in fire regime, grazing intensity and nitrogen deposition (Walker *et al.*, 1981; Scholes and Archer, 1997; Kochy and Wilson, 2001) as potential causes of thickening, the impact of climate change is now receiving increasing attention. Thus, a possible role for CO₂ enrichment in enhanced regrowth of juvenile trees following disturbance (Bond and Midgely, 2000) has been proposed, whilst enhanced root growth (Derner *et al.*, 2003), and differential responses of C3 trees compared to C4 grasses to climate change (Stock *et al.* 2005; Morgan *et al.*, 2007) have been explored. The recent analyses of Berry and Roderick (2002) have shown an increase in the evergreen component of Australia's vegetation over the past 200 years and they conclude that this is a result of CO₂ enrichment. However, most recently, Eamus and Palmer (2007) proposed a conceptual model that provides a synthesis of four observations to explain woody thickening. This paper uses the soil-plant-atmosphere model of Williams *et al.* (2002) to

examine the mechanisms underlying their conceptual model and briefly examines predictions arising from the model.

There are four key requirements for the Eamus and Palmer (2007) model to be accepted. The first is for an increase in leaf-scale photosynthesis in response to CO₂ enrichment. The stimulation in mean daily photosynthesis (*A*) as a result of CO₂ enrichment (to 150% of ambient levels) in the present modelling study was 26%. With photosynthetic acclimation the enhancement of *A* was 21% (Fig. 2). In the absence of photosynthetic acclimation the stimulation of photosynthesis was much larger and was maintained to larger levels of CO₂ enrichment. However, since down regulation (photosynthetic acclimation) is expected in evergreen trees (Rogers and Humphries, 2000) and routinely observed in tree FACE experiments (Ainsworth and Long, 2005) we do not consider this scenario (that is, no photosynthetic acclimation) any further. Enhancement of photosynthesis in response to CO₂ enrichment (with photosynthetic acclimation present) is generally observed in C3 plants (Eamus and Jarvis, 1989; Ainsworth and Long, 2005); the observed stimulation in this simulation was close to the average of 25% observed in trees in a meta-analysis of published data (Medlyn *et al.*, 1999). We also found that a 25% reduction in *D* alone also resulted in a stimulation of photosynthesis of 15%, because of increased stomatal opening (Fig. 2). Increases in rates of photosynthesis in response to decreased *D* have been observed previously (Prior *et al.*, 1997; Baligar *et al.*, 2008). In combination, CO₂ enrichment and reduced *D* (scenario three) with photosynthetic acclimation caused an enhancement of mean daily photosynthesis of 25% (Fig. 4), thereby supporting the foundation of the Eamus and Palmer (2007) model.

The second requirement for the conceptual model to be accepted is a reduced stomatal conductance. When CO₂ concentration was increased alone (with photosynthetic acclimation) or in combination with increased D (scenario three), mean daily stomatal conductance (g_s) was reduced; the reduction of approximately 20% when CO₂ concentration was enriched to 150% of ambient and photosynthetic acclimation was present (Fig. 2) is close to the mean decline of 20% observed in a recent meta-analysis of published conductance data (Medlyn *et al.*, 2001) and similar to that observed by Eamus *et al.* (1995) in their study of a tropical eucalypt species.

The third requirement is for an increase in soil moisture availability under conditions of CO₂ enrichment. As a result of declines in g_s arising from CO₂ enrichment alone or combined with increased D, there was a decline in average daily and annual sums of sapflow (Figs 2 & 4). Because of this the soil water store was larger for the future climate scenario than ambient conditions (45.7 m vs. 43.8 m sum for the year respectively, Table 2). Annual water savings in response to CO₂ enrichment have been observed under a range of FACE experiments (Wullschleger *et al.*, 2002a; Raison *et al.*, 2008). Although the difference between scenario one and three was generally only 3 – 6 mm on any given day (but was as large as 10 mm on many days; Fig. 6) the presence of this offset for most of the year is likely to be sufficient to allow a significant increase in LAI of a woodland site. To test whether this offset was sufficient to support a larger LAI, we increased the LAI of the canopy until the annual sum of water use with the increased LAI was equal to the annual water use of the canopy under ambient (control) conditions. It was found that an increase of 30% of the LAI (if D decreased) could be sustained under current rainfall conditions and CO₂ enrichment of a 15 % increase could be sustained (with increased D). We therefore conclude that the observed water savings arising from reduced sapflow in scenario three could support a larger LAI.

Increasing LAI with increasing availability of water is a consistently observed phenomenon across aridity gradients (Williams *et al.*, 1996b; Schulze *et al.* 1998) and for changes in soil water availability (Benyon *et al.*, 2006).

In the field an increase in LAI through increased soil moisture availability can be achieved either through larger trees or an increase in tree density; either constitute woody thickening. However, it is clear that the water savings observed in scenario three were not sufficient for the canopy to always maintain a higher rate of sapflow. Although rates of sapflow in scenario three were generally higher than under ambient conditions in the first half of the study (summer), in the second half of the study period (winter), rates of sapflow in scenario three were generally lower than for ambient (scenario one) conditions, despite the larger soil moisture contents for all scenarios in winter compared to summer. Clearly the larger water contents of the soil in scenario three and four were sufficient to support larger rates of sapflow in summer, but not in winter, despite the larger absolute values of soil water content that were observed in winter compared to summer. Concomitant with this pattern in sapflow was the larger stimulation of GPP occurring in the summer than in winter in response to climate change (Fig. 8). A differential response to CO₂ enrichment in the response of soil moisture, g_s and leaf water potential has been observed between seasons previously (Eamus *et al.*, 1995; Wullschleger *et al.*, 2002b; Cech *et al.*, 2003).

There is some evidence that D is increasing on a local scale (rather than decreasing) as the climate changes (Pearce *et al.*, 2007). To investigate the role of D in the combined scenarios, we ran a new scenario with 150% CO₂, 10% photosynthetic acclimation and a 3% increase in D. Such an increase is in the mid-range of possible increases in D (reduced atmospheric moisture) from a range of global circulation models for the mid-to-late 21st century in eastern Australia (Pearce *et al.*, 2007). The total annual sapflow was 378 mm under this scenario

(compared to 400 and 357 mm for ambient and future scenarios respectively). Therefore the increase in D decreased water savings. However, despite this decrease in water savings compared to decreased D, we did find that an LAI of 15% more than the current values could still be supported by the same amount of rainfall. Therefore even if D is increasing into the future, the third requirement of Eamus and Palmer (2007) would still be met.

The final requirement for the Eamus and Palmer (2007) model to be accepted is that GPP and hence NPP increase in response to CO₂ enrichment and a decline in D. As water availability increases from arid through to semi-arid zones, changes in vegetation structure are observed through changes in species composition, increased tree density, increased bole volume and increased leaf area index (Schulze *et al.*, 1998; Eamus *et al.* 2000; Kelley *et al.*, 2007). Whilst the SPA model predicts GPP, we feel it is realistic to assume that an increased annual GPP will be reflected in NPP and hence biomass at a site (Makela and Valentine, 2001). For an open semi-arid site such as the one modelled in the present study, the ratio of NPP to GPP is likely to be larger than that of a mesic site (Zhang *et al.*, 2009) and therefore the potential increase in NPP arising from our observed increased GPP will be larger for our open semi-arid site than more mesic sites (Zhang *et al.*, 2009). In a meta-analysis of the responses of patterns of allocation of biomass to CO₂ enrichment, Poorter and Nagel (2000) found that enhanced CO₂ supply did not significantly alter the pattern of biomass allocation and therefore we conclude that increased NPP arising from increased CO₂ supply will be reflected in increased above and below-ground biomass; that is, woody thickening.

GPP was increased, typically by 15%, in response to CO₂ enrichment alone, reduced D alone or in combination (scenario three; Figs 2 & 4). This is in modest agreement with the 23% stimulation of NPP observed across a range of biomes having FACE experiments (Norby *et*

et al., 2005). Using the generally accepted ratio of NPP:GPP of 0.5 (Waring *et al.*, 1998; Norby *et al.*, 2006; McMurtrie *et al.*, 2008) this corresponds to an increase in NPP of approximately 0.2 to 0.4 gC m⁻² d⁻¹ (or 0.73 to 1.46 tC ha⁻¹ y⁻¹). If this ratio is larger, as seems likely for our site (Zhang *et al.*, 2009) the increase in NPP will be correspondingly larger. The scale of increase in NPP arising in the present study is comparable to an estimated increase of 0.38 tonnes of biomass accumulated per hectare of sweetgum forest for a water saving of 20 mm per year arising from CO₂ enrichment (Wullschleger and Norby, 2001). The increased NPP predicted from the results presented in the current study represents an increase when it occurs every year and when it is noted that annual NPP for savannas, drought deciduous woodlands and tropical rainforest ranges between approximately 4 and 16 tC ha⁻¹ y⁻¹ (Chen *et al.*, 2003).

Predictions arising from the conceptual model

Two large-scale and long-term predictions emerge from the conceptual model of Eamus and Palmer (2007). First, water-use-efficiency should increase in response to CO₂ enrichment and a decreased D and this should be apparent in long-term trends for forests and woodlands globally. Short-term (daily and seasonal) enhancement of WUE was observed in the model's outputs and long-term (decades or more) increased WUE has been observed for tropical woody species in Brazil (Hietz *et al.*, 2005) and forests in Siberia (Saurer *et al.*, 2004) and Austria (Leal *et al.*, 2008); laboratory and open-top chamber studies on tree seedlings and young trees have also shown an increase in WUE under enriched CO₂ concentrations (Hättenschwiler *et al.*, 1997; Tognetti *et al.*, 2000; Körner *et al.*, 2005). Second, the model predicts that in the short-to-medium term (that is, until a new, larger, equilibrium LAI is attained at a site), soil moisture content should increase and therefore run-off (principally sub-surface) should increase. In the short-term, the model predicted increased soil moisture

content in the upper 70 cm of the soil profile (where most root biomass is found). This result corresponds with the frequent observation of increased soil moisture content in CO₂ enrichment studies (Eamus *et al.*, 1995; Tognetti *et al.*, 2000; Wullschleger *et al.*, 2002b) and in the longer-term, increased continental-scale run-off may be increasing (Labat *et al.*, 2004; Gedney *et al.*, 2006). Interestingly, soil moisture content has increased in the past 35 y in non-woody playa in New Mexico but decreased on woody playa where LAI has increased, exactly as would be expected from the conceptual model (Eamus and Palmer, 2007).

How much increase in LAI could be supported by this climate change scenario?

A conceptual framework for the mechanisms of woody thickening driven by climate change is shown in Fig. 8. The feedback causing increased biomass accumulation (woody thickening) continues until resources (assumed to be water at our water-limited site) are exhausted. In the long-term, when a new, larger standing biomass and hence LAI has been established, we would expect annual water use in the new vegetation structure to approach ecohydrological equilibrium (Eagleson and Tellers, 1982; Hatton *et al.*, 2004; Eamus *et al.*, 2006). Assuming no change in the amount nor timing of rainfall in the new climate, an increase in LAI of 30% could be supported through the increase in CO₂ supply and decreased D associated with the new climate. The current structure of the stand appears to be at an approximate optimum in terms of maximising GPP because when LAI for the current stand was increased or decreased under current climate conditions, GPP declined (data not shown). When LAI increased, self-shading is likely to be increased, reducing GPP and when LAI decreased, APAR (absorbed photosynthetically active radiation) and hence GPP decreased. Similarly, with a new equilibrium vegetation with the new climate, the increase in LAI required to attain ecohydrological equilibrium was also an optimum for GPP because any

decline or increase in LAI resulted in a decreased GPP once again. The influence of increased shading with the 30% increase in LAI can be inferred by examining the differential effect of direct and diffuse beam radiation on GPP (Fig. 7). Under clear conditions and a larger direct beam and small diffuse beam component and a larger absolute amount of light available to the canopy, GPP was significantly smaller (by 8%) than under overcast and hence mostly diffuse beam conditions. Increased productivity with increased diffuse beam fraction has been noted previously in large-scale reviews of eddy covariance data (Law *et al.*, 2002).

CONCLUSIONS

Through use of a globally applicable SPA model we were able to demonstrate that in a CO₂ enriched atmosphere with decreased D and photosynthetic acclimation of the canopy, decreased water use by the canopy occurred because of a decline in g_s . The decline in canopy water use coupled with increased leaf-scale photosynthesis, resulted in increased GPP, increased WUE and increased soil moisture content for most of the year. The observed increase in GPP, when translated into NPP, can increase stand woody biomass and the water requirements of the stand with an increase in LAI of 30% could be maintained with the current rainfall regime. This study shows that there is a valid mechanism for GPP increase due to an increase in CO₂, and a decrease in D in a water limited stand like the one in this study. Large-scale predictions arising from this simple conceptual model were also supported in the literature and the results provide a valid mechanism for the conclusion of Berry and Roderick (2002) that evergreen vegetation has increased across Australia over the past 200 years as a result of CO₂ enrichment.

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Figure legends

Figure 1: Meteorological conditions measured during the study period (September 2006 to August 2007) at a Cumberland Plains Woodland near Richmond NSW.

Figure 2: The influence of changing CO₂ and D on annual sapflow and GPP and daily average and standard error of WUE across the year. For the CO₂ plots, data are shown with (open circles) and without (closed circles) photosynthetic down-regulation. Measured annual sapflow is shown with a star.

Figure 3: Influence of photosynthetic acclimation and foliar N concentration on daily GPP (gC m⁻² d⁻¹), shown with regression analysis between GPP values for elevated CO₂ concentrations with and without photosynthetic acclimation and reduction in foliar N. Each point represents one daily GPP value. The panels show V_{cmax} reduced by 10% (a), J_{max} reduced by 10% (b), V_{cmax} together with J_{max} reduced by 10% (c), reduced foliar N reduced by 10% (d) and foliar N reduced by 5% with V_{cmax} and J_{max} both reduced by 5%. All R² values were greater than 0.98 and the dotted line shows the 1:1 line.

Figure 4: Daily values of Sapflow, GPP and WUE for representative periods of summer and winter. Climate change conditions were CO₂ 75%, D 125% for past scenario, CO₂ 150%, D 75%, foliar N 95% and V_{cmax} and J_{max} both 95% of current values for future scenario. Increased LAI was 130% of current values, the proportional increase which would be allowed if current annual sapflow was maintained.

Figure 5: Daily values of A and g_s for representative days in summer and winter. On day 339 D remained below 2 and for day 96 D peaked above 6 MPa (under ambient conditions). Climate change conditions were CO₂ 75%, D 125% for past scenario, CO₂ 150%, D 75%, foliar N 95% and V_{cmax} and J_{max} both 95% of current values. Increased LAI was 130% of current values, the proportional increase which would be allowed if current annual sapflow was maintained.

Figure 6: Soil water content in the top 70 cm of the soil profile for each day of the one year study period under ambient, climate change and climate change with increased LAI conditions. Climate change involved CO₂ elevation to 150%, reduction in D to 75% and 10% photosynthetic down-regulation (foliar N, V_{cmax} and J_{max} all 95% of current values).

Figure 7: Mean daily GPP for clear and overcast conditions. A total of 21 pairs of adjacent days with contrasting clear and overcast skies were used for the analysis. Five of these pairs had larger GPP values on the clear day, while the remainder had larger GPP values on the overcast day. The difference between the GPP values for different light conditions was significant (p = 0.013) and the average difference between the pairs was 0.33 gC m⁻² d⁻¹.

Figure 8: Conceptual mechanism for the role of climate change in woody thickening.

Table 1. Values used in SPA for this study.

SPA model input values indicating the name, symbol, units, value used and whether the data were measured or estimated for the study site.

<i>Parameter/Variable</i>	<i>Symbol</i>	<i>Units</i>	<i>Value</i>	<i>Source</i>
Ambient atmospheric CO ₂ concentration	C _a	mmol mol ⁻¹	374 (ambient)	Varied as a model input
Canopy layer capacitance	C _n		5000	Williams <i>et al.</i> , 1996
Canopy hydraulic conductivity	G _p	mmol m ⁻¹ s ⁻¹ MPa ⁻¹	3.5	Measured for this site, Zeppel <i>et al.</i> 2008
Layer height of soil	H	m	0.1 to 0.8 m depth, then 0.2 to 3.2 m	Measured for this site, Zeppel <i>et al.</i> 2008
Leaf Area Index	L	m ⁻² m ²	1.3 to 1.9	Measured for this site, Zeppel <i>et al.</i> 2008
Proportion of LAI in top layer	L _{top}		0.125	Estimated using Weibull cumulative distribution function
Fine root length per m ² ground area; total/layer	l _R /l _r		1930/3450	Measured for this site, Zeppel <i>et al.</i> 2008
Saturated hydraulic conductivity of clay	L _{clay}	mm h ⁻¹	0.66	Measured for this site, Zeppel <i>et al.</i> 2008
Saturated hydraulic conductivity of sand	L _{sand}	mm h ⁻¹	124.2	Measured for this site, Zeppel <i>et al.</i> 2008
Areal concentration of leaf N	N	g m ⁻² ground area	2.7	Measured for this site, Zeppel <i>et al.</i> 2008
Proportion of total canopy N in top layer	N _{top}		0.125	Measured for this site, Zeppel <i>et al.</i> 2008
Fine root radius	r _r	M	0.0001	Measured for this site, Zeppel <i>et al.</i> 2008
Air temperature	T _a	°C	Variable	Measured for this site, Zeppel <i>et al.</i> 2008
Leaf temperature	T _i	°C	Variable	Measured for this site, Zeppel <i>et al.</i> 2008
RuBP carboxylation capacity	V _{cmax}	μmol g ⁻¹ s ⁻¹	73.6	Measured for this site, Zeppel <i>et al.</i> 2008 and varied as model input

Maximum electron transport rate	J_{\max}	$\mu\text{mol g}^{-1} \text{s}^{-1}$	129.8	Measured for this site, Zeppel <i>et al.</i> 2008 and varied as model input
$\delta A/\delta g_s$ threshold for stomatal opening	ι	%	1.0007	Williams <i>et al.</i> , 1996
Minimum sustainable leaf water potential	Ψ_{imin}	MPa	-3.2	Measured for this site, Zeppel <i>et al.</i> 2008
Soil water potential	Ψ_s	MPa	-0.5	Measured for this site, Zeppel <i>et al.</i> 2008
% soil clay content in top 10 cm		%	9.79	Measured for this site, Zeppel <i>et al.</i> 2008
% soil sand content in top 10 cm		%	85.62	Measured for this site, Zeppel <i>et al.</i> 2008
Draincheck – field capacity as fraction of total porosity		fraction	0.5	Measured for this site, Zeppel <i>et al.</i> 2008
Latitude		°	33	Zeppel <i>et al.</i> 2008
Dimension of leaves		m^2	0.08	Estimated
Root resistivity		MPa s g mmol^{-1}	100	Estimated
Root mass		g	3450	Measured for this site, Zeppel <i>et al.</i> 2008
Rooting depth		m	3.2	Estimated.

Table 2: Total annual sapflow and GPP values and mean daily WUE across the year for the four climate change scenarios.

Scenario	Total annual sapflow (mm y ⁻¹)	Total annual GPP (gC m ⁻² y ⁻¹)	Mean daily WUE (x10 ³ gC m ⁻¹)	Total soil water in the top 70 cm (m y ⁻¹)
Ambient	400	1485	4.7 ± 0.2	43.8
Past, pre-industrialisation (CO ₂ 275 ppm, D 125% of present)	427	1210	3.5 ± 0.1	42.5
Future climate change (CO ₂ 561 ppm, D 75% of present, 10% photosynthetic acclimation)	357	1727	6.8 ± 0.4	45.7
Future climate change with LAI increased 30%	398	1811	6.3 ± 0.3	44.7

Figures

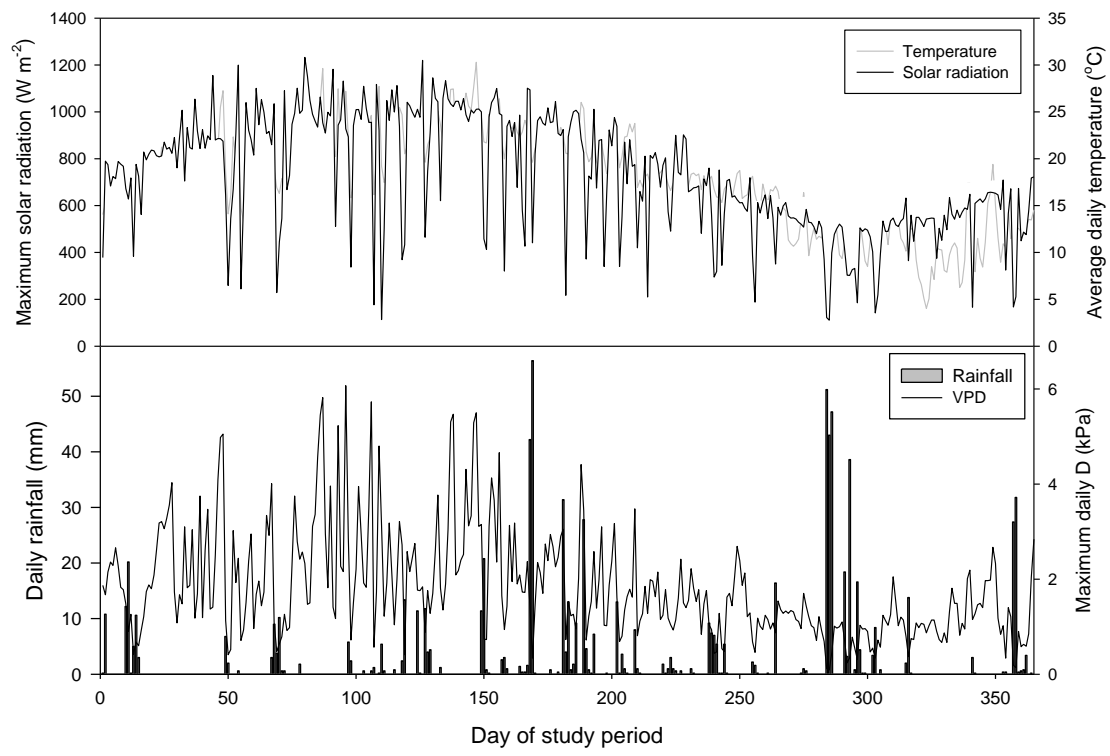


Fig 1

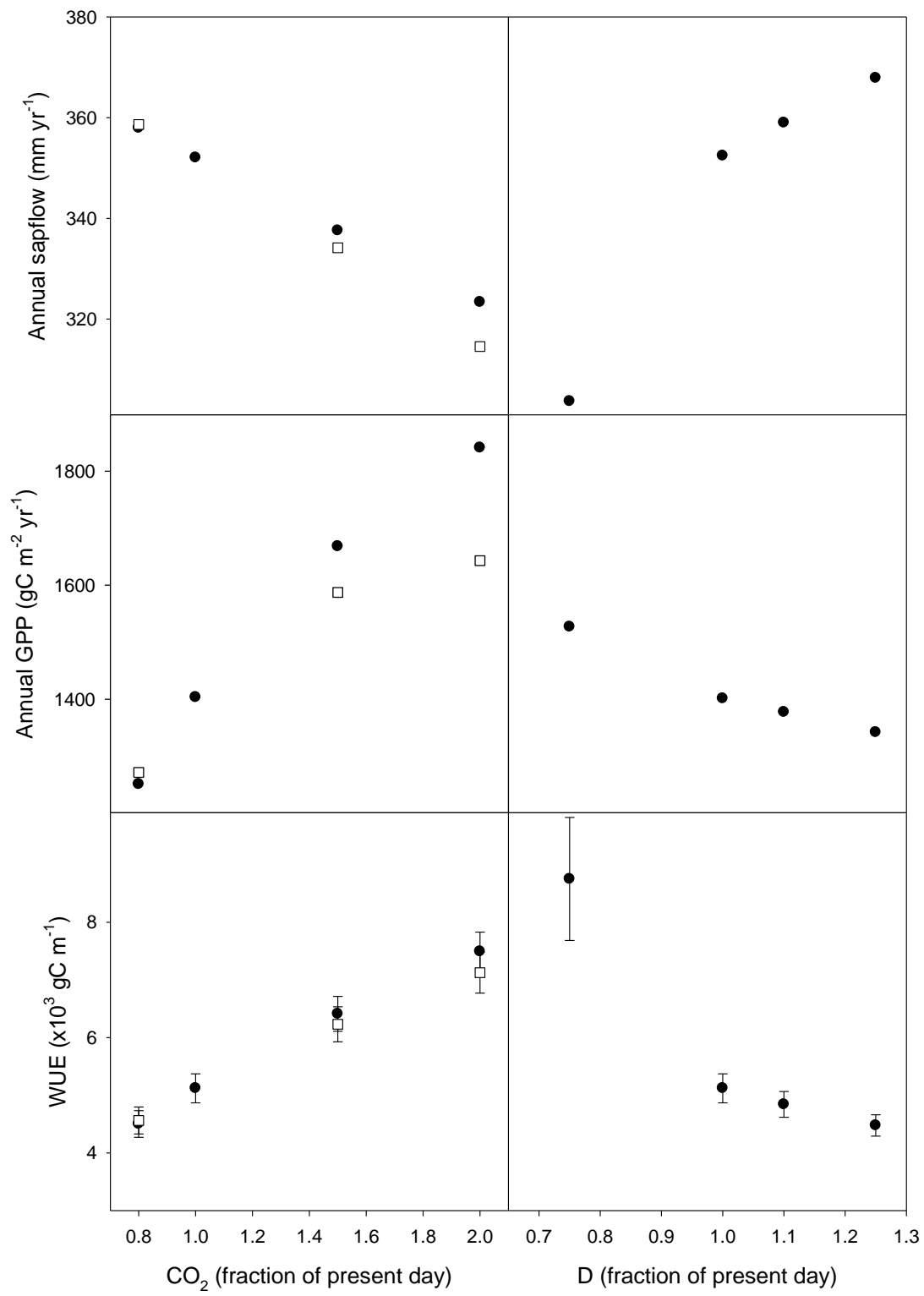


Fig 2

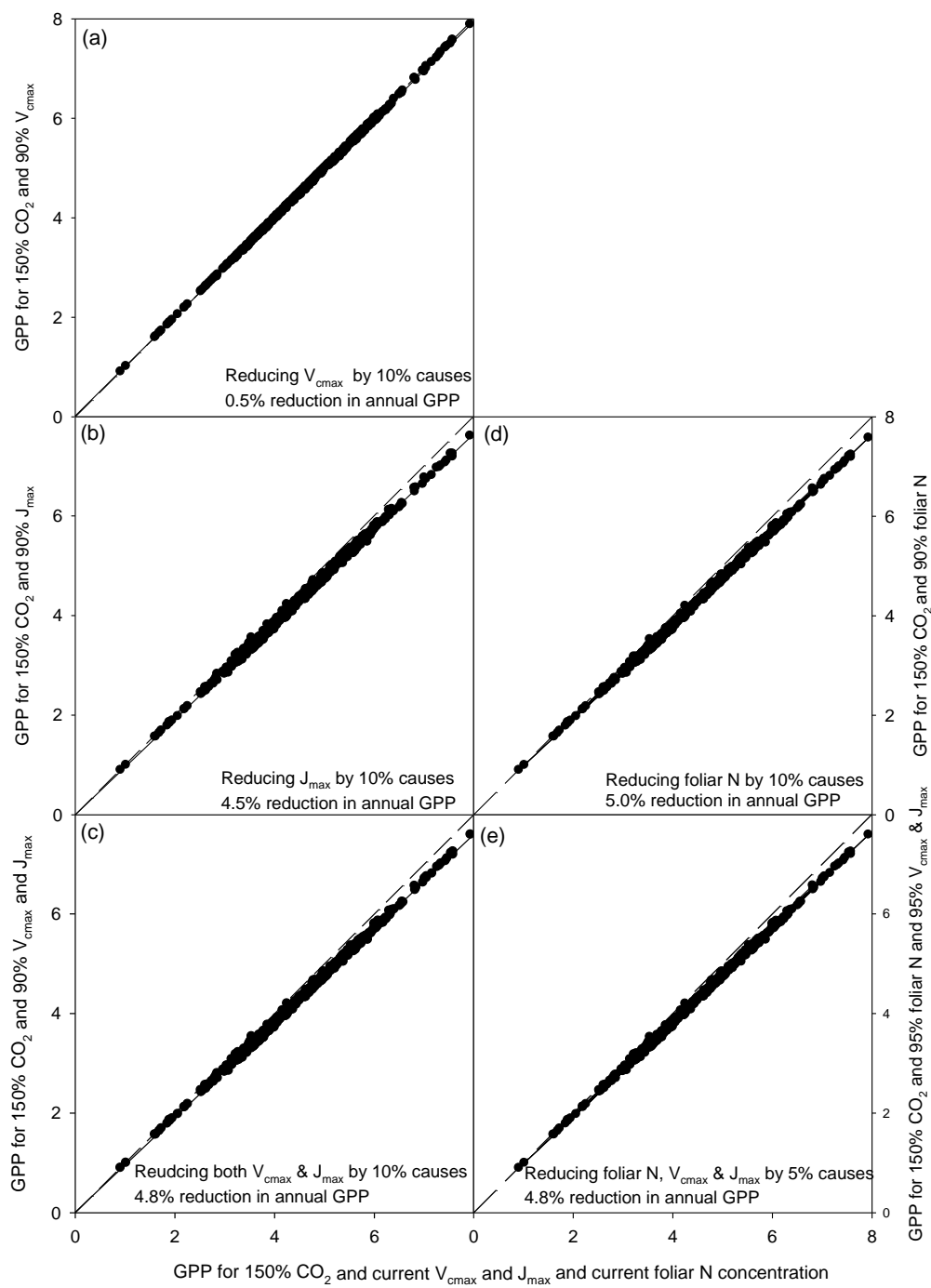


Fig 3

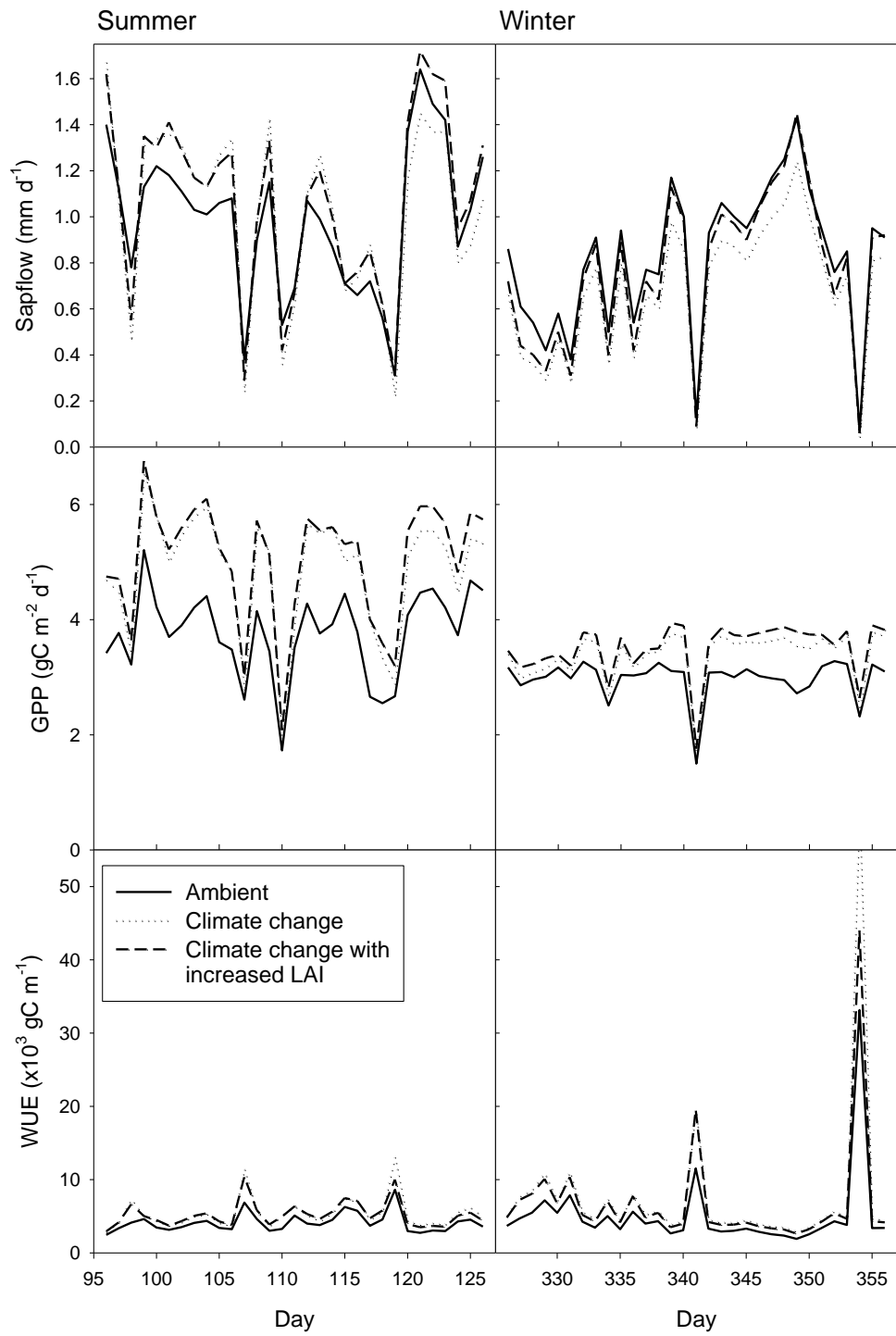


Fig 4

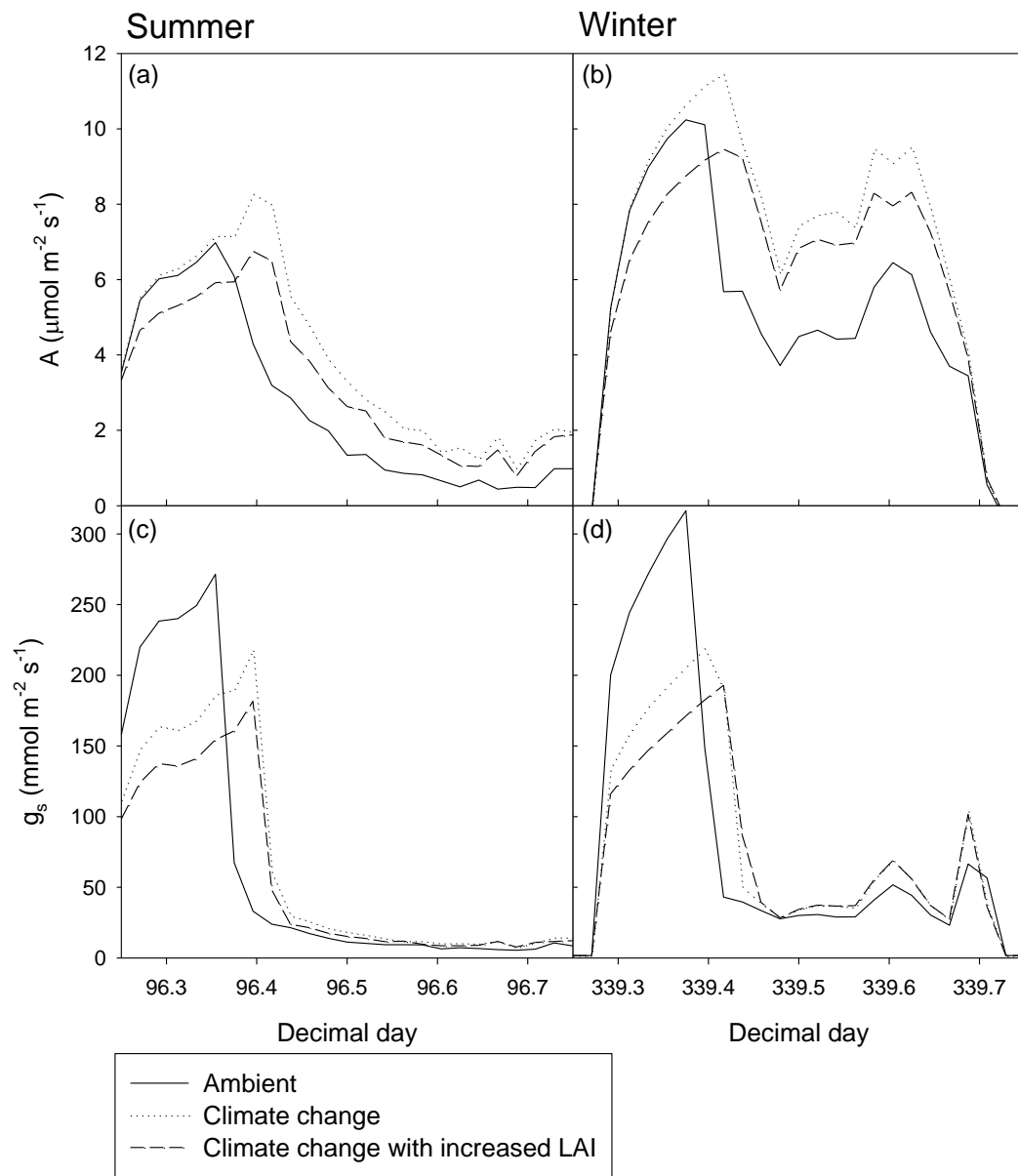


Fig 5

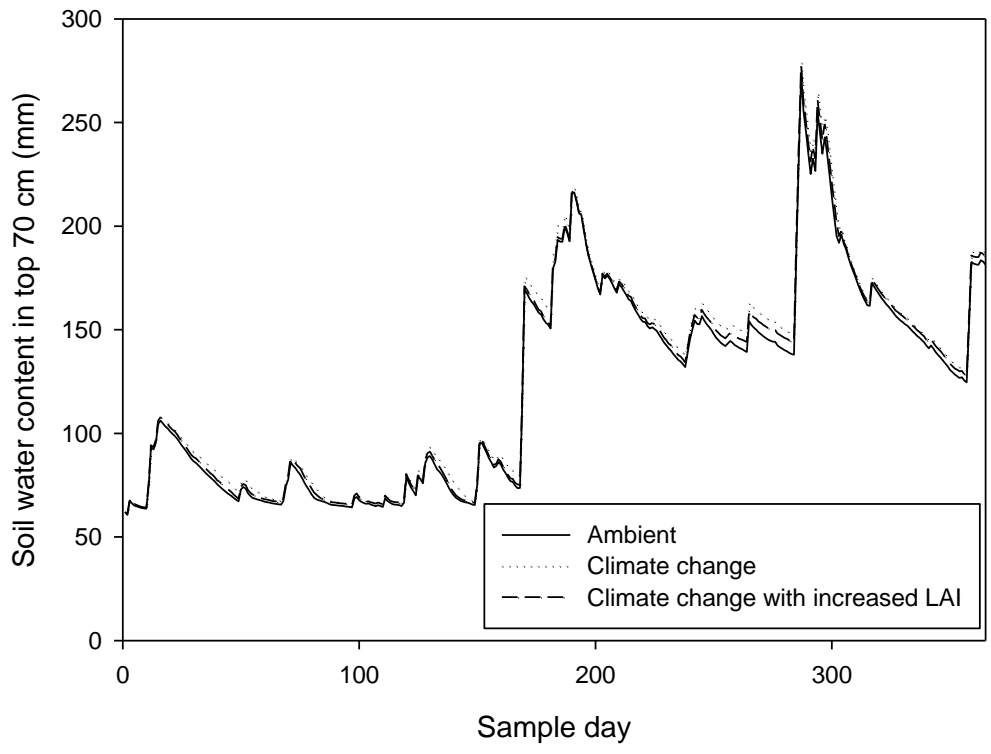


Fig 6

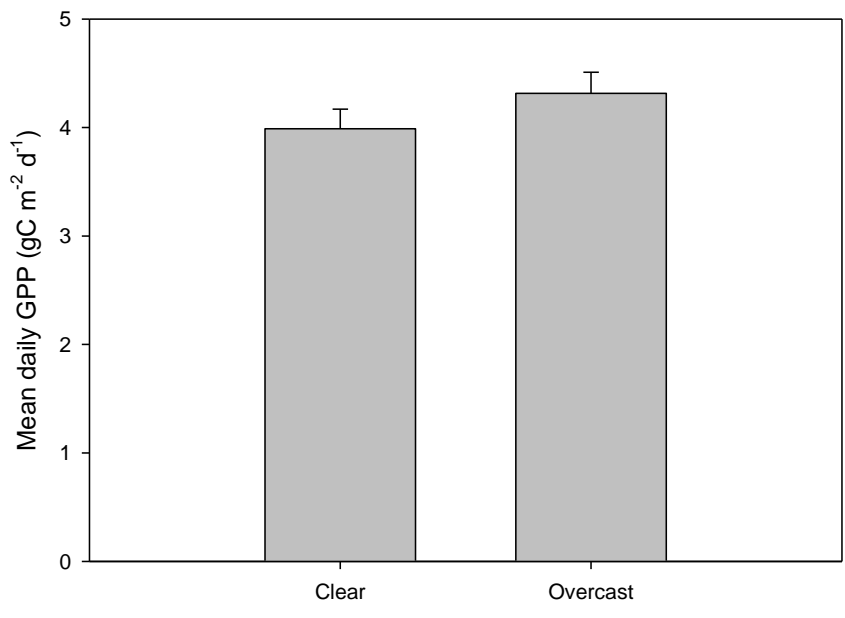


Fig 7

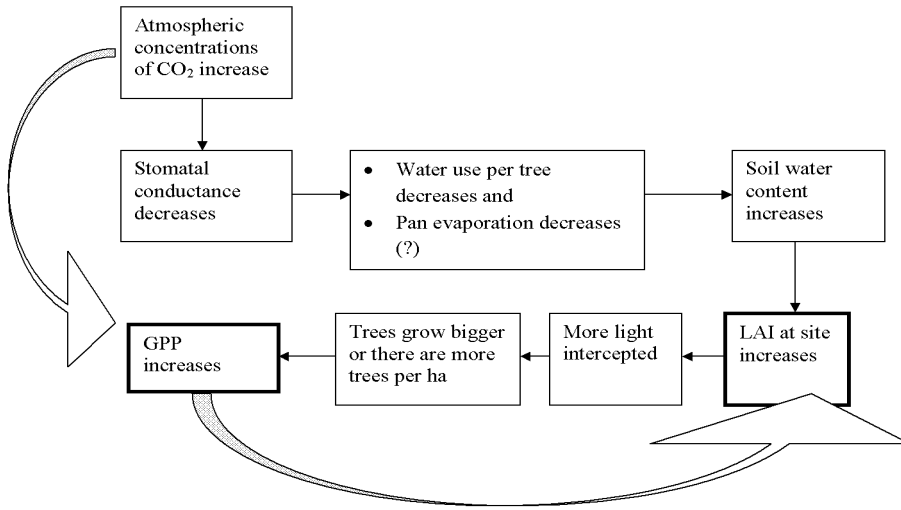


Fig 7