Mechanisms linking plant productivity and water status for a temperate *Eucalyptus* forest flux site: analysis over wet and dry years with a simple model

David A. Pepper^{A,E}, Ross E. McMurtrie^A, Belinda E. Medlyn^B, Heather Keith^C and Derek Eamus^D

^ASchool of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

^BDepartment of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.

^CThe Fenner School of Environment and Society, Australian National University, Canberra, ACT 0200, Australia.

^DInstitute for Water and Environmental Resource Management and Department of Environmental Sciences, University of Technology, Sydney, NSW 2007, Australia.

^ECorresponding author. Email: d.a.pepper@unsw.edu.au

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Abstract. A simple process-based model was applied to a tall *Eucalyptus* forest site over consecutive wet and dry years to examine the importance of different mechanisms linking productivity and water availability. Measured soil moisture, gas flux (CO_2 , H_2O) and meteorological records for the site were used. Similar levels of simulated H_2O flux in ‘wet’ and ‘dry’ years were achieved when water availability was not confined to the first 1.20 m of the soil profile, but was allowed to exceed it. Although the simulated effects of low soil and atmospheric water content on CO_2 flux, presumably via reduction in stomatal aperture, also acted on transpiration, they were offset in the dry year by a higher vapour-pressure deficit. A sensitivity analysis identified the processes that were important in wet versus dry years, and on an intra-annual timeframe. Light-limited productivity dominated in both years, except for the driest period in the dry year. Vapour-pressure deficit affected productivity across more of each year than soil moisture, but both effects were larger in the dry year. The introduction of a reduced leaf area tended to decrease sensitivity in the dry year. Plant hydraulic architecture that increases plant available water, maximises productivity per unit water use and achieves lower sensitivity to low soil moisture levels should minimise production losses during dry conditions.

Additional keywords: CO_2 flux, drought, evapotranspiration, water flux, water use.

Introduction

The pattern of precipitation in Australia has changed considerably over the past three decades (Lavery *et al.* 1997) and is forecast to change further in the future (Pittock 2003; CSIRO and Australian Bureau of Meteorology 2007). In south-eastern Australia, the drought frequency and potential evaporation rate are predicted to increase, and annual average rainfall is predicted to decrease by 7.5–10% relative to the 1990 level by the year 2070 (CSIRO and Australian Bureau of Meteorology 2007). Water availability is a strong determinant of growth in Australian forests, which are dominated by evergreen and broadleaved tree species (Fitzpatrick and Nix 1970), unlike many forest sites studied in the northern hemisphere (e.g. Hughes 2003). Understanding the mechanisms linking Australian forest productivity and site water status will enhance our capacity to manage forest and other natural resources (Ladiges 1974; Davidson and Reid 1989; Oren *et al.* 1999) for a future with less reliable rainfall, and this understanding is

important for predicting the effects of environmental change on water budgets and carbon sequestration (Zhang *et al.* 2001, 2004; Eamus 2003).

In this paper we describe a modelling analysis of a tall, cool temperate *Eucalyptus* forest using records of soil moisture and eddy-covariance flux measurements of water vapour and CO_2 taken at the Tumbarumba flux station (Leuning *et al.* 2005). This flux site is situated within the Bago State Forest, which is located in the highlands of south-eastern New South Wales, Australia, and receives a moderate level of annual precipitation that has fluctuated over the past several decades by approximately $\pm 20\%$. The site has undergone other empirical (Leuning *et al.* 2005) and modelling analyses (Kirschbaum *et al.* 2007) that complement our study, but which differ considerably in model structure and approach. Our strategy (cf. Kirschbaum *et al.* 2007) is to apply a simple ecosystem model (Dewar 1997) to the *Eucalyptus* forest at the Tumbarumba flux site and to focus on the effects of variation

in soil and atmospheric moisture content on productivity using measurements of soil water together with CO₂ and water-vapour fluxes taken in consecutive 'wet' and 'dry' years. The model integrates small-scale, process-level phenomena into a description of ecosystem function (e.g. Hanson *et al.* 2004). The relatively simple process-based model of daily light use, carbon dynamics and their interaction with site water availability provides a mechanistic framework to apply to the forest ecosystem, and to use with UNCSIM software procedures (Brun *et al.* 2001) to evaluate the importance of ecosystem processes under variable environmental conditions. Nutrient cycling has been omitted from the model to focus solely on the effects of soil and atmospheric water content on productivity over a relatively short term with respect to net changes in the nutrient balance in the Bago State Forest. Simulated forest light use and therefore net primary production is negatively impacted by both a dry atmosphere and a dry soil (e.g. Schulze *et al.* 1994; Ciais *et al.* 2005). Both agreement and discrepancy between the simulated output and their corresponding measurements have been used to improve our understanding of key mechanisms at work in wet versus dry years for this particular system. Therefore, our approach uses the model framework as a probe into the system rather than as a test of the predictive capacity of the model.

Leuning *et al.* (2005) concluded that CO₂ fluxes at the Tumbarumba flux site are more strongly constrained by available water than by temperature because net negative monthly CO₂ fluxes (net CO₂ uptake by the forest) were lowest during the dry autumn (April 2003), when mean air temperature (T_a) was 8.0°C and soil moisture stored in the top 1.20 m fell to 260 mm, compared with the wet, cold winter (August 2001), when mean T_a fell to 0.2°C and stored soil moisture was greater than 350 mm. However, Leuning *et al.* (2005) noted that the forest was able to maintain transpiration during the dry summer of 2002–2003 and suggested that this occurred because tree roots had access to water stored deep (>3 m) in the soil (McKenzie and Ryan 1999). Leuning *et al.* (2005) found that night-time CO₂ efflux from the forest was strongly related to soil temperature, but not to soil moisture. The modelling analysis described below will seek a mechanistic understanding of lower annual CO₂ uptake in the dry year compared with that in the wet year, even though annual water flux was similar in the 2 years (Fig. 1).

The present study has two main aims. The first aim is to use a simple model framework to improve our understanding of carbon and water dynamics in a tall *Eucalyptus* forest over wet and dry years. Using the model framework we wanted to assess whether there were any moisture-related effects on productivity (e.g. Eamus 2003; Rascher *et al.* 2004; Whitehead and Beadle 2004) at this site or whether these effects were negligible because of access to deep water sources (e.g. Meinzer *et al.* 1999; Leuning *et al.* 2005). For this aim, we take a strategic approach to model parameterisation. Thus, we investigate the relative impacts of variation in soil and atmospheric moisture content on carbon dynamics, and determine whether the model successfully fits daily measurements of multiple forest variables. The second aim is to identify which processes in the model differ between wet and dry years, and when they become important on an intra-annual timeframe, by using the calibrated model to undertake a

sensitivity analysis of the key parameters. This approach uses parameters in the model related to mechanisms linking productivity and site water status (Calder 1992; Honeysett *et al.* 1992, 1996; Eamus 2003; Rascher *et al.* 2004; Whitehead and Beadle 2004). These mechanisms include: stomatal responses to vapour-pressure deficit and soil water (Pereira *et al.* 1987; White *et al.* 1996; Thomas and Eamus 1999); hydraulic conductance (White *et al.* 1998; Eamus *et al.* 2001); biomass allocation to roots and leaves (e.g. Li and Wang 2003); variations in canopy leaf area and/or specific leaf area (Whitehead and Beadle 2004); and variations in respiration (Turnbull *et al.* 2001).

Materials and methods

Site description and measurements

The Tumbarumba site (35°39'S, 148°09'E; elevation 1200 m a.s.l.) is located within the Bago State Forest in south-eastern New South Wales, Australia. The Bago State Forest is part of a 50 000 ha native forest that has been managed for wood production for over 100 years. The site is a moderately open, wet sclerophyll forest composed of mixed-aged trees ranging up to 90 years and 40 m tall. The overstorey is dominated by *Eucalyptus delegatensis* R.T. Baker and *Eucalyptus dalrympleana* Maiden tree species, and has a leaf area index (LAI) of ~1.4. The understorey comprises shrubs and grasses with an estimated LAI of ~1.0 (Leuning *et al.* 2005). The soil is ~2 m deep, classified as an acidic, eutrophic, red dermosol, overlays a weathered C horizon (H. Keith, unpubl. data), and has moderate levels of stored carbon and nutrients (McKenzie and Ryan 1999).

Mean annual precipitation (1 July–30 June) for the period 1887–2007, recorded at Tumbarumba Post Office, which is located 40 km south of the site, was 978 ± 204 mm (mean $\pm$ s.d.). From mid-winter 2001 to mid-winter 2002 the precipitation measured at the study site was 1090 mm ('wet' year), but in the following year the precipitation was ~20% below average (785 mm; 'dry' year), owing mainly to an extended dry period from October 2002 to April 2003 (from approximately day 640 to 850 in Fig. 1). The average T_a ranged from 0 to 18°C and the daytime humidity deficit ranged from 1.5 to 16.4 mmol mol⁻¹, and both were higher in the dry year (July 2002–June 2003).

Fluxes of water vapour and CO₂ were measured and logged hourly (Leuning *et al.* 2005). Soil moisture content was measured using time domain reflectometry (Zegelin and White 1989) at 0.15-m depth intervals from the surface to 1.20 m and logged hourly. Full details of the instrumentation, flux-data processing and soil moisture measurements are provided by Leuning *et al.* (2005) and references therein. The hourly soil moisture and flux data were used in the present study to derive daily and daytime totals that corresponded to outputs from our daily time-step model. Some litterfall data have been collected for the site (H. Keith, unpubl. data, Kirschbaum *et al.* 2007), and these were used to add variation in LAI for use in the sensitivity analysis.

Model description

The model of light and water use simulates daily carbon and water balance. A light-use efficiency approach is used to simulate

Fig. 1. Measured (grey line) and simulated (black line) variables at the Tumbarumba, NSW, Australia, flux site over wet and dry years. (a) Plant-available water in the 0–0.15 m (upper) and 0–1.20 m (lower) soil layers; (b) water vapour flux (F_w) and variable leaf area index (LAI) (inset is the cumulative F_w); and (c) CO_2 flux (F_c) (inset is the cumulative F_c). Day 1 corresponds to 1 January 2001.

productivity. Transpiration and productivity are related by water-use efficiency. The effects of soil moisture and vapour-pressure deficit on carbon productivity and transpiration are represented using relatively simple functions that act to reduce light-use efficiency. Temperature effects act to increase light-use efficiency. Surface evaporation from the soil and the canopy

are also incorporated into the water flux calculation. Model inputs include daily meteorological data collected for the site: total solar radiation (TSR ; $\text{MJ m}^{-2} \text{ day}^{-1}$), maximum and minimum air temperature (T_{max} and T_{min} , respectively; $^{\circ}\text{C}$), daytime average vapour-pressure deficit (D ; kPa), precipitation (P ; mm), and average soil temperature at a depth of 2 cm (T_s ; $^{\circ}\text{C}$). The

model outputs include daily CO₂ flux, water flux and soil moisture storage in the 0–0.15 m and 0–1.20 m layers of soil. Definitions for all symbols are listed in Table 1.

Carbon balance

Daily CO₂ flux (F_c ; g C m⁻² day⁻¹) is modelled as the difference between gross primary productivity (GPP) and ecosystem respiration (RE),

$$F_c = \text{GPP} - \text{RE}, \quad (1)$$

where GPP is approximated as net primary productivity divided by carbon-use efficiency (CUE) (GPP = NPP/CUE), where it is assumed that autotrophic respiration is a constant fraction of GPP (e.g. Gifford 1992, 2003; Waring *et al.* 1998; Dewar *et al.* 1999), and RE is simulated with a site-derived function depending on soil temperature, but not soil moisture (Leuning *et al.* 2005),

$$\text{RE} = ae^{bT_s}, \quad (2)$$

where $a = 0.46 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $b = 0.132^\circ\text{C}^{-1}$, and RE in units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was converted to g C m⁻² day⁻¹. The RE simulated by Eqn 2 is considerably lower than that estimated by van Gorsel *et al.* (2007). Further analysis of CO₂ flux is currently in progress, particularly in relation to representing processes that determine the net difference between GPP and RE. Although the use of Eqn 2 will have a qualitative effect on the results of the sensitivity analysis it will have a negligible effect on the comparison between wet and dry years. Our modelling analysis is based on the RE estimates of Leuning *et al.* (2005) (Eqn 2).

Net primary productivity is assumed to be proportional to the absorbed photosynthetically active radiation (APAR; MJ m⁻² day⁻¹), with three modifying functions, f_D , f_W and f_T , representing the effects of relative atmospheric water vapour-pressure deficit, soil water content and temperature on NPP, respectively.

$$\text{NPP} = \varepsilon \text{ APAR } f_D f_W f_T, \quad (3)$$

where ε represents the maximum light-use efficiency (g DW MJ⁻¹); we held the carbon fraction of the dry weight biomass constant (0.48 g C g DW⁻¹). APAR depends on LAI and incident radiation (PAR₀) in a Beer's Law formulation simulating light extinction through the canopy,

$$\text{APAR} = \text{PAR}_0 (1 - e^{-k \text{ LAI}}), \quad (4)$$

where k is the light-extinction coefficient. The vapour-pressure deficit modifier f_D decreases linearly from 1 to 0 as the vapour-pressure deficit increases from a minimum point ($D_{\min}$), at which D begins to affect NPP, to a maximum point ($D_{\max}$) when f_D reaches zero,

$$\begin{aligned} f_D &= (D_{\max} - D)/(D_{\max} - D_{\min}) \text{ if } D_{\min} < D < D_{\max} \\ &= 1 \text{ if } D \leq D_{\min} \\ &= 0 \text{ if } D \geq D_{\max}. \end{aligned} \quad (5)$$

For example, if $D_{\max} = 4 \text{ kPa}$ and $D_{\min} = 1 \text{ kPa}$, then as D increases from 0 kPa, f_D plateaus at 1 and then decreases to 0 (at $D = 4 \text{ kPa}$) and then plateaus at 0; f_D fluctuates with changes in

D between 1 and 4 kPa (D in the present study is $< 4 \text{ kPa}$). The f_D attempts to simulate stomatal closure in response to D , and accounts for days when D is high and transpiration is fast, leading to a reduction in stomatal conductance even when soil moisture levels are not low.

Soil-water-limited NPP is simulated through the soil-water factor, f_W , which is represented by a ramp function similar to that in Corbeels *et al.* (2005),

$$\begin{aligned} f_W &= (Q/Q_{\max} - F_{\text{wpmin}})/(F_{\text{wpmax}} - F_{\text{wpmin}}) \\ &\text{if } 0 \leq Q/Q_{\max} < F_{\text{wpmax}} \\ &= 1 \text{ if } Q/Q_{\max} \geq F_{\text{wpmax}}, \end{aligned} \quad (6)$$

where F_{wpmax} is the critical fraction of maximum plant-available water capacity $Q_{\max}$ below which plant-available water Q affects NPP. Plant available water is equivalent to the soil moisture fraction between the soil moisture levels at wilting point and maximum field capacity. The temperature factor f_T was simulated with an empirical function associating biological activity with temperature (e.g. Parton *et al.* 1987; Comins and McMurtrie 1993; Eliasson *et al.* 2005),

$$f_T = a + bT^c - (T/d)^e, \quad (7)$$

where $a = 1$, $b = 0.00251$, $c = 1.65$, $d = 41.75$ and $e = 7.19$ so that f_T scaled between 1 and 1.62 (at 33°C). Incorporation of f_T acknowledges that the temperature effects on productivity are independent of the temperature effects on respiration in Eqn 1.

Water balance

Soil water balance was simulated on a daily basis. A simple soil water balance model calculates water storage in the soil root zone. Soil water storage capacity in the root zone is represented as a fixed 'bucket' volume, with provision for 0–0.15 m, 0–1.20 m and a deeper layer. Soil water level in the top layer (0–0.15 m) affects evaporation from the soil surface (E). Soil water level in the total bucket affects drainage (D) and transpiration (T). The daily change in plant available soil water level (ΔQ ; mm) is calculated as,

$$\Delta Q = P - I - E - T - D, \quad (8)$$

where P , I , E , T and D represent daily values of precipitation, canopy interception loss, evaporation from the soil surface, transpiration and drainage, respectively. Water loss from canopy interception (I) is simulated as (McMurtrie *et al.* 1990):

$$I = \min(I_{\max}, P), \quad (9a)$$

where

$$I_{\max} = z \text{ LAI}, \quad (9b)$$

and z is a proportionality constant. Evaporation from the soil surface is driven by incident solar radiation, but is limited by the available water in the top soil layer. The available energy for soil water evaporation is related to the fraction of net radiation reaching the forest floor,

$$E = R_N e^{-r \text{ LAI}} (e/\lambda(1 + e)) f_{\text{Wtop}}, \quad (10)$$

where r is an energy extinction coefficient from Ritchie (1972) and λ is the latent heat of vaporisation (2.47 MJ kg⁻¹) from

Table 1. Model symbols and their descriptions

Symbol	Units	Description	Value
a, b	...	Coefficients in Eqn 2	0.46, 0.132
$albedo$	...	Reflection coefficient for solar radiation of natural surfaces	0.2
APAR	$\text{MJ m}^{-2} \text{ day}^{-1}$	Photosynthetically active radiation absorbed by the canopy	
CUE	...	Carbon-use efficiency	0.5
c	...	Constant in s/γ equation (Eqn 14)	250300
D	kPa (1 kPa = 10 mb)	Daytime vapour-pressure deficit	Input
d	...	Constant in s/γ equation (Eqn 14)	17.269
$D_{\max}, D_{\min}$	kPa	Maximum and minimum parameters in Eqn 5	7.45, 1.0
E	mm day^{-1}	Soil evaporation	
e	...	s/γ (Eqn 14)	
$f1, f2$	...	Fraction of transpiration extracted from 0–0.15 m and 0–1.20 m soil layers	0.1, 0.5
F_c	$\text{g C m}^{-2} \text{ day}^{-1}$	CO ₂ flux	Output
f_D	...	Vapour-pressure deficit multiplier of net primary productivity	
f_w	...	Soil water multiplier of net primary productivity	
F_w	mm day^{-1}	Water flux	Output
F_{wpmax}	...	Fraction of $Q_{\max}$ below which $f_w < 1$	0.3
F_{wpmin}	...	Adjusts slope of f_w v. Q	–0.5
f_{wtop}	...	Soil water multiplier of soil evaporation from the top layer	
GPP	$\text{g C m}^{-2} \text{ day}^{-1}$	Gross primary productivity	
h	...	Constant in s/γ equation (Eqn 14)	6.46
I	mm day^{-1}	Canopy interception	
k	...	Light-extinction coefficient	0.5
m	...	Constant in R_L equation (Eqn 12)	0.0036
n	...	No. differences calculated for each drying cycle (Table 2)	
NPP	$\text{g C m}^{-2} \text{ day}^{-1}$	Net primary productivity	Output
P	mm day^{-1}	Precipitation	Input
p	...	Constant in R_L equation (Eqn 12)	12
PAR	$\text{MJ m}^{-2} \text{ day}^{-1}$	Photosynthetically active radiation	
PAR_0	$\text{MJ m}^{-2} \text{ day}^{-1}$	Incident photosynthetically active radiation	Input
q	...	Constant in R_L equation (Eqn 12)	107
$Q, Q1, Q2$	mm	Plant-available water in the root zone, top 0–0.15 m layer and 0–1.20 m layer	Output
q_0	$\text{g C kPa m}^{-2} \text{ mm}^{-1}$	Intrinsic water-use efficiency	1.8
$Q1, Q1_{\max}$	mm	Plant-available water in the 0–0.15 m soil layer, maximum	Output, 44.1
$Q2, Q2_{\max}$	mm	Plant-available water in the 0–1.20 m soil layer, maximum	Output, 170
$Q_{\max}$	mm	Maximum plant-available water	350
r	...	Energy extinction coefficient (Eqn 10)	0.398
RE	$\text{g C m}^{-2} \text{ day}^{-1}$, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Ecosystem respiration from Leuning <i>et al.</i> (2005)	
R_L	$\text{MJ m}^{-2} \text{ day}^{-1}$	Long-wave radiation	
R_N	$\text{MJ m}^{-2} \text{ day}^{-1}$	Net radiation	
s	Pa K^{-1}	Slope of the curve relating water vapour saturation and temperature	
SWC	mm	Soil water content (Table 2)	
t	day	Time step	
T	mm day^{-1}	Transpiration	
T_a	°C	Average daily air temperature	
T_d	°C	Average daytime air temperature	
T_K	Kelvin	Absolute temperature	
$T_{\max}, T_{\min}$	°C	Maximum and minimum daily air temperature	Input
T_s	°C	Average soil temperature at 2 cm depth	Input
TSR	$\text{MJ m}^{-2} \text{ day}^{-1}$	Total solar radiation	Input
u	...	Constant in s/γ equation (Eqn 14)	0.006
z	mm day^{-1}	Canopy storage of precipitation	0.5
γ	Pa K^{-1}	Psychrometer constant	
ΔQ	mm day^{-1}	Change in plant-available moisture content per time step	
ϵ	g dry wt MJ^{-1}	Maximum light-use efficiency	0.34
λ	MJ kg^{-1}	Latent heat of vaporisation	2.47

McMurtrie *et al.* (1990), both are assumed to be constant. Net radiation R_N is calculated as a fraction of total solar radiation (R_{TOTAL}) unreflected by surfaces minus long-wave radiation,

$$R_n = R_{TOTAL}(1 - albedo) - R_L, \quad (11)$$

where the surface reflectance factor (*albedo*) is assumed to be constant. Long-wave radiation R_L is calculated as a function of the average temperature in daylight hours (T_d),

$$R_L = mp(q - T_d), \quad (12)$$

where m , p and q are constants. The average T_d is calculated using temperature maximum (T_{max}) and minimum (T_{min}) values in a Taylor expansion formulation,

$$T_d = (T_{max} + T_{min})/2 + (T_{max} - T_{min})/3\pi. \quad (13)$$

This daytime temperature is used to calculate the energy terms involved in soil evaporation: the increase of latent heat content per increase of sensible heat content of saturated air at ambient temperature, the ratio of the slope of the curve relating water vapour saturation and temperature (s) and the psychrometer constant (γ),

$$e = s/\gamma = c \exp(dT_d/T_K)/(h + uT_d)T_K^2, \quad (14)$$

where c , d , h and u are constants, and the temperature is in Kelvin. The factor f_{wtop} in Eqn 10 is a modifier that depends on the water content of the top layer of soil,

$$f_{wtop} = (Q1/Q_{max} - F_{wpm})/(F_{wpm} - F_{wpm}), \quad (15)$$

where f_{wtop} decreases from 1 towards 0 as the plant-available water in the top layer ($Q1$) declines from the threshold F_{wpm} , denoting the maximum fraction of $Q1_{max}$, the maximum plant-available water in the top layer, where F_{wpm} and F_{wpm} are the same parameters used in Eqn 6. The plant-available water in the upper 1.20 m of the soil profile, denoted $Q2$, was also simulated so it could be compared with the measurements.

Daily transpiration is simulated using a water-use efficiency formulation (Dewar 1997),

$$T = NPP D/q_0, \quad (16)$$

where q_0 is the intrinsic water-use efficiency ($g C kPa mm^{-1}$). Daily transpiration extracts soil water from the 0–0.15 m and 0–1.20 m layers and from the deeper total root zone. The fractions of water uptake from the 0–0.15 m and 0–1.20 m layers are $f1$ and $f2$, respectively; if the sum of $f1$ and $f2$ is less than 1 then transpiration extracts water partly from a soil layer deeper than 1.20 m. Daily water flux F_w was calculated as,

$$F_w = T + E + I, \quad (17)$$

For simplicity, the plant biomass components (leaves, fine roots and woody components) are held constant.

Model parameterisation

In this section we describe how the measured values of F_c , F_w and soil moisture were used with the meteorological data to estimate the parameters for the model. Hourly data were available for derivations of daily and daytime totals. These empirical data were

investigated for evidence of relationships represented in the model framework. In particular, we were interested in examining whether variation in vapour-pressure deficit and soil water affected productivity. Overall parameters were estimated from plots of empirical data or by fitting the model to multiple forest variables, or they were taken from the literature, as described in the following subsections.

Effects of vapour-pressure deficit and soil moisture

The rationale in the model is that when the vapour-pressure deficit is large the water loss from leaves may exceed the water supply to the leaves, even under high to moderate levels of soil moisture, and this could reduce leaf water potentials and, hence, stomatal conductance (e.g. Fuchs and Livingston 1996). To establish whether or not the vapour pressure modifier (f_D) in Eqn 5 was relevant to this site, we isolated CO_2 flux measurements (F_c) when $D > 1$ kPa and when soil water content in the 0–1.20 m layer exceeded 299 mm. This was done to see if there was any relationship between F_c and D when the soil water content was not low. We also examined this relationship after normalising F_c by dividing it by TSR ($MJ m^{-2} day^{-1}$) because light can dominate control of stomatal conductance at different times of the day (e.g. Oren *et al.* 1999). Thus, daily CO_2 flux measurements were filtered and used to estimate the maximum (D_{max}) and minimum (D_{min}) parameter values in Eqn 5; hence, the effect of D on NPP was incorporated in the model through Eqn 5 by setting D_{max} and D_{min} values.

We looked for evidence of any soil water limitation on CO_2 flux measurements rather than on H_2O flux measurements to avoid water evaporation from surfaces interfering with the canopy conductance signal. This was done simply by plotting F_c against the soil water content in the 0–1.20 m layer. CO_2 flux measurements normalised by dividing F_c by TSR and then plotted against soil water content in the 0–1.20 m layer were also examined. In addition, we examined the rate of water extraction during drying cycles. In essence, soil moisture drying cycles were isolated from the data series, and the rate of soil water extraction was estimated with linear regression. Drying cycles were isolated using negative soil moisture differences occurring over consecutive days. Mean differences (and their s.d.) were calculated and the first difference at the beginning of each drying cycle was compared with the mean. If this initial extraction rate was more than 2 s.d. faster than the mean for the entire drying cycle then it was denoted as being significantly different from the mean. There were several cases where a significant difference occurred, so initial extraction rates in all cases were not included in the linear regression estimations of mean extraction rate. Linear regressions were only fitted to soil moisture measurements made over the drying cycle periods and the slope was taken to be an estimate of the extraction rate ($mm day^{-1}$). Extraction rates were normalised by dividing by the vapour-pressure deficit.

The effect of variation in soil water content on NPP was incorporated into the model via Eqn 6 by setting the parameters, maximum plant available water (Q_{max}) and the fraction of maximum soil water at which soil water begins to affect NPP (F_{wpm}).

Effect of temperature

Early in the parameterisation procedure, when the temperature effect was set at 1 (no effect), measured CO₂ flux lagged simulated CO₂ flux. A plot of TSR and temperature together versus time revealed that the temperature tended to lag the solar radiation. This was the motivation for including f_T in the model.

Water balance, light-use efficiency and water-use efficiency

Effective precipitation, daily precipitation minus canopy interception ($P - I$), flows into the soil root zone; I was simulated by setting the z parameter in Eqn 9b constant (Table 1). Daily transpiration (T) is the other component of F_w , as represented in Eqn 17, and the f_l parameter adjusts what fraction of T is taken from the top soil layer. Evaporation from soil is a function of f_{wtop} (Eqn 15), which depends on soil moisture in the top soil layer.

The maximum plant-available water in the upper 1.20 m of soil, denoted $Q2_{max}$, was estimated from measurements of soil water (to a depth of 1.20 m) as the maximum soil water level (454 mm) minus the lowest soil water level (245 mm). The maximum plant-available water in the uppermost 0.15 m ($Q1_{max}$) was similarly estimated.

Estimates of other parameter values involved fitting the model to multiple forest variables. We calculated RE from Eqn 2, daily GPP from Eqn 1 and measurements of F_c and daily net primary productivity (NPP') by assuming CUE = 0.5 (Gifford 1992, 2003; Dewar *et al.* 1998, 1999; Waring *et al.* 1998; NPP' = 0.5GPP). The maximum light-use efficiency parameter ϵ was estimated as the maximum slope of a plot of NPP' versus APAR (cf. Medlyn *et al.* 2003), where NPP' was derived as GPP $\times$ CUE and APAR was simulated using Eqn 4. The intrinsic water-use efficiency parameter q_0 was estimated after ϵ by changing q_0 until a reasonable simulation was obtained for measurements (daily values) of F_c , F_w and soil moisture in the 0–0.15 m and 0–1.20 m layers. Both q_0 and ϵ were held constant over wet and dry years.

The maximum plant-available water (Q_{max}) was increased above $Q2_{max}$ to achieve simulations of F_w that were equivalent in wet and dry years, but simulations of F_c that were diminished in the dry year, and simulated soil moisture for the 0–0.15 m and 0–1.20 m layers so that all four model outputs (F_w , F_c , $Q1$ and $Q2$) were reasonable fits to their measured records. This implied that the forest had access to water deeper than 1.20 m.

Leaf area index

Leaf area index (LAI) was reported by Leuning *et al.* (2005) as 1.4 for overstorey and 1.0 for understorey so LAI was set constant at 2.4 for simulating the daily F_c , F_w , $Q1$ and $Q2$ corresponding to the daily totals from the hourly measurements. Variation in rates of litterfall suggests that there may have been variation in LAI between wet and dry years, but variation in rates of litterfall and LAI do not always correlate well, especially because of leaf retention in evergreen species. It is known that drought and storm events can have marked effects on the rates of monthly litterfall, but have little impact on LAI (Dye *et al.* 2004). We held LAI constant for simulations across wet and dry years because this supported our strategy of keeping the modelling analysis simple

and transparent. We did, however, want to test the sensitivity of the modelled system to variable LAI so we added LAI variability into the sensitivity analysis.

Sensitivity analysis

The UNCSIM software package (<http://www.uncsim.eawag.ch>, version 1.1c, accessed 5 April 2005) (Brun *et al.* 2001; Reichert 2006) was interfaced with the model and used to calculate the sensitivity indices described below.

This sensitivity analysis assumes that the vector of model results $y = (y_1, \dots, y_n)^T$ is a deterministic function of the model parameters $\theta_M = (\theta_1, \dots, \theta_M)^T$: $y_M(\theta_M)$, where M indicates the model. In a local neighbourhood of a particular choice of parameter values, θ_M^* , the model equations can be approximated linearly,

$$y_M(\theta_M) \approx y_M(\theta_M^*) + \partial y_M / \partial \theta_M^T (\theta_M - \theta_M^*). \quad (18)$$

The CALCLOSENS routine of UNCSIM calculates the sensitivity as the derivative ($\partial y_{M,i} / \partial \theta_{M,j}^T$) of the model results $y_{M,i}$ with respect to the parameter $\theta_{M,j}$ evaluated at the parameter value θ_M^* . The derivatives are calculated approximately by a finite difference approximation with user-specified parameter increments. Sensitivity $s_{i,j}$ is computed as,

$$s_{i,j} = \Delta \theta_{M,j} / s_{c,i} (\partial y_{M,i} / \partial \theta_{M,j}^T), s_j = (s_{1,j}, \dots, s_{n,j})^T, \quad (19)$$

where $\Delta \theta_{M,j}$ represents the *a priori* uncertainty range in the parameter $\theta_{M,j}$ (Brun *et al.* 2001), and $s_{c,i}$ is a scaling factor that represents a typical order of magnitude for the output variable $y_{M,i}$. The sensitivity measure δ_j^{msqr} , computed and used to rank sensitivities of parameters, is defined as,

$$\delta_j^{msqr}(\theta) = \sqrt{\frac{1}{n} \sum_{i=1}^n s_{ij}^2}. \quad (20)$$

The *a priori* parameter value uncertainty $\Delta \theta_{M,j}$ was set to $\theta_M^* \pm 0.2 \times \theta_M^*$. In the CALCLOSENS routine, this meant that the parameter values (θ_M^*) were all increased by 20%, one-by-one, to determine the sensitivity of the model output. In the present study we used δ_j^{msqr} as a measure of sensitivity on an inter-annual timeframe, and $s_{i,j}$ was used to investigate the sensitivity on an intra-annual timeframe (Pepper *et al.* 2007). We determined the sensitivity of the modelled GPP to the CUE parameter, and of the modelled NPP to 12 other key model parameters that productivity was sensitive to.

To add variability in LAI into the sensitivity analysis we ran the sensitivity analysis with constant LAI and then repeated it with variable LAI. Instead of changing LAI by 20%, like the model parameters, we derived a variable record of LAI and input this into the model. The variable record of LAI was based on variation found in measured litterfall. Litterfall data were collected on an approximately monthly basis (H. Keith, unpubl. data; Kirschbaum *et al.* 2007). These data were converted to daily rates of litterfall and interpolated linearly as constant rates between collection dates. We calculated the quotient of these rates at similar times of the year as, rate(dry year)/rate(wet year), which represented dry-year rates in proportion to wet-year rates; that is, a dry-year quotient of the preceding year. We assumed that LAI was constant at 2.4 under the pattern of wet-year litterfall

rates and we used 2.4 divided by our quotient to generate variability in LAI over the dry year. We fully acknowledge that the LAI variation is unrealistic, which is why its use has been confined to the sensitivity analysis alone. Litterfall is often assumed to be proportional to canopy biomass (e.g. Comins and McMurtrie 1993; Dye *et al.* 2004), but this treatment implies that increased litterfall associated with water stress in the dry year leads to reduced LAI (e.g. Rascher *et al.* 2004).

Results

First, we present results from the analyses of the data because these were an important step in the model parameterisation procedure. This procedure provided a model calibrated to the Tumbumba flux site, which was used in our sensitivity analysis. Estimated parameters are listed in Table 2. Results from the sensitivity analysis with constant LAI, and then repeated with variable LAI, are presented in the second part of this section.

Model parameterisation

Effects of vapour-pressure deficit and soil moisture

The approach taken with parameter estimation revealed evidence of water-related effects on productivity. Slight negative relationships between F_c versus D (slope not significantly different from zero, $P=0.104$) and F_c versus D/TSR (slope was significantly different from zero, $P=0.027$) were found (Fig. 2a). F_c decreases by ~30% over the range 1–3 kPa, so $D_{\max}$ in Eqn 5 would be ~7.45 kPa and $D_{\min}$ would be set at 1 kPa, so that f_D scales from 1 at 1 kPa down to $(1-0.3)=0.7$ at 3 kPa (and down to 0 at 7.45 kPa). To incorporate this D effect into the model via Eqn 5 we set the maximum to 7.45 kPa and the minimum to 1 kPa (Table 2).

There was some structure to the CO_2 flux versus soil moisture plots. Weak evidence of an effect of soil water on F_c was strengthened using the F_c measurements that were normalised to TSR (data not shown), and this evidence was similar for rates of soil water extraction. As the soil moisture content increased from ~245 mm the uppermost normalised F_c data tended to increase. Thus, a limitation to F_c became apparent as soil moisture in the 0–1.20 m layer drops below ~320 mm. Because this could have resulted from a soil moisture effect on respiration or on GPP (Eqn 1), we checked a plot of night-time CO_2 flux measurements against soil moisture and there was no relationship, which is consistent with Leuning *et al.* (2005).

Extraction rates estimated from drying cycles ranged from close to 1.1 mm day^{-1} up to nearly 4.8 mm day^{-1} (Table 3; Rate); extraction rates normalised to the vapour-pressure deficit ($\text{mm kPa}^{-1} \text{ day}^{-1}$) ranged from approximately 0.01 to $0.1 \text{ mm kPa}^{-1} \text{ day}^{-1}$ (Fig. 2b). High normalised extraction rates seemed to be constrained by soil moisture levels below 320 mm approximately to the minimum of 245 mm (Fig. 2b). There were more of these drying cycles in the dry year in spring and autumn, but the rates of extraction were similar in both years (Table 3).

Effects of temperature

Incorporating a temperature effect on NPP into the model improved the simulated F_c (Fig. 1) by reducing the lag observed between the measured and simulated F_c without the temperature effect (i.e. f_T held at 1) and therefore dominated by solar radiation.

Water balance, light-use efficiency and water-use efficiency

Maximum light-use efficiency (ϵ) was estimated as the maximum slope (0.34) of the NPP' versus APAR plot (data not shown). The parameter z in Eqn 9b for maximum canopy interception ($I_{\max}$) was set at 0.5 after McMurtrie *et al.* (1990). Intrinsic water-use efficiency (q_0) was estimated after ϵ , after k was set at 0.5. The f_1 parameter describing the fraction of transpiration taken from the top (0–0.15 m) soil layer was estimated after ϵ and q_0 to simulate soil water in the top layer. The estimated parameter values are provided in Table 2.

Maximum plant-available water ($Q_{\max}$) was an interesting result. To obtain a reasonable fit to the measured records of F_c , F_w , Q_2 and Q_1 , and to simulate reasonable annual values of F_c and F_w in both wet and dry years, we needed to set $Q_{\max}$ greater than Q_2 . This implies that substantial water in addition to that available in the first 1.20 m depth of soil was probably available to the trees. We examined this further using measured records, and calculated the annual water input as the sum of the measured precipitation and the change in measured plant-available water in the 1.20 m layer ($P + \Delta Q_2$) for wet and dry years and compared this to the annual water output (F_w). We found that annual input exceeded annual output in the wet year by ~50%, but in the dry year they were almost equal. Similarly, we calculated water input and water output, both expressed as 7-day running means with a daily time step, and water output exceeded water input 155 days in the wet year compared with 220 days in the dry year.

Table 2. Model parameters estimated using soil moisture, gas flux and meteorological measurements

Symbol	Units	Description	Value
ϵ	g DW MJ^{-1}	Maximum light-use efficiency	0.34
$D_{\max}, D_{\min}$	kPa	Maximum and minimum parameters in Eqn 5	7.45, 1.0
$Q_{\max}$	mm	Maximum plant-available water	350
$Q_1_{\max}$	mm	Maximum plant-available water in the 0–0.15 m soil layer	44.1
$Q_2_{\max}$	mm	Maximum plant-available water in the 0–1.20 m soil layer	170
$F_{w\text{pmax}}$	...	Fraction of $Q_{\max}$ below which $f_w < 1$	0.3
$F_{w\text{pmin}}$	...	Adjusts slope of f_w versus Q	–0.5
f_1, f_2		Fraction of transpiration extracted from the 0–0.15 m and 0–1.20 m soil layers	0.1, 0.5
q_0	$\text{g C kPa m}^{-2} \text{ mm}^{-1}$	Intrinsic water-use efficiency	1.8
albedo	...	Reflection coefficient for solar radiation of natural surfaces	0.2

Fig. 2. (a) Linear regression on CO_2 flux (F_c) measurements versus vapour-pressure deficit (D) (open diamonds) and on F_c normalised to total solar radiation (TSR) versus D (closed squares) using F_c when $D > 1$ kPa and soil water content > 299 mm. (b) Normalised soil water extraction rates at different soil moisture levels. Soil water extraction rates were estimated as the slope of the linear regressions on soil moisture observations over drying cycles (time intervals comprised consecutive days without rainfall). Extraction rates were normalised by dividing by D. The line indicates possible soil moisture constraints on soil water extraction.

On an annual basis, water supply adequately matched water use, but on a weekly basis water use often exceeded the water available from precipitation and storage in the upper 1.20 m, and this occurred more often in the dry year.

Overall, reasonable simulations of Q_1 , Q_2 , F_w and F_c were achieved (Fig. 1) with the estimated parameter set (Table 2). Simulations of water flux were similar for wet and dry years, but simulations of CO_2 flux were lower in the dry year (Fig. 1b, c). It is interesting to note that there was a discrepancy between the modelled and measured Q_1 and Q_2 for considerable periods (weeks) in both wet and dry years.

Leaf area index

The variation that was generated in LAI to reflect variation in litterfall rates relative to the wet year resulted in a LAI that changed abruptly after each collection date in the dry year, increasing to as high as 4.5 and decreasing to as low as 1.42 (Fig. 1b). The introduction of this variability resulted in lower LAI

averaged over the growing season or over the entire dry year. This crude estimate of LAI with abrupt changes was favoured for the sensitivity analysis and was used deliberately to increase the detection of any effect of LAI on CO_2 flux, productivity or water use. Simulated F_c and NPP were positively affected by the variation in LAI, but simulated F_w was little affected.

Sensitivity analysis

Inter-annual sensitivity (with constant LAI)

The 13 model parameters to which productivity was most sensitive are listed in Table 4. Maximum light-use efficiency (ϵ) was ranked the highest and *albedo* was the lowest out of the 13 parameters. This sensitivity was based on δ^{msqr} calculated (Eqn 20) across both wet and dry years. There were also differences in the sensitivities between wet and dry years based on δ^{msqr} calculated for each year. For example, productivity was more sensitive to variation in ϵ , the light extinction coefficient (k) and CUE in the wet year, but the other parameters listed in Table 4 were more important in the dry year. Light-use efficiency is a key parameter in the model (Eqn 3) linking absorbed light and productivity. The light-extinction coefficient affects the fraction of incident light that is absorbed by the canopy (Eqn 4). These three parameters (ϵ , k , CUE) were more important in the wet year because water-limiting effects on productivity were smaller in the wet year compared with the dry year. Maximum plant available water (Q_{max}) and water-use efficiency (q_0) were not important at all in the wet year, but became substantially more important in the dry year. Maximum plant available water Q_{max} (Eqn 6) has an important influence on the soil-water factor f_w because f_w begins to decrease once the Q/Q_{max} fraction drops below its critical value (F_{wpmx}). Thus, the soil-water factor f_w became more important in the dry year because a 20% increase in Q_{max} meant that the Q/Q_{max} fraction spent more time below its critical value F_{wpmx} . Water-use efficiency (q_0) had an important influence on productivity in the dry year because a 20% increase in q_0 reduced transpiration (Eqn 16), which led to increased plant-available water and a diminished soil-water effect in the dry year. The parameters D_{max} and D_{min} in Eqn 5 determine how the vapour-pressure deficit effect (f_D) scales with changes in D. These parameters were more important in the dry year, which was warmer and less humid, because D was higher more often compared with the wet year. The remaining parameters listed in Table 4 all had a negligible effect on productivity in the wet year compared with the dry year. The parameters F_{wpmx} and F_{wpmn} in both Eqns 6 and 15 determine how f_w and f_{wtop} scale with changes in Q and Q_1 , respectively. These parameters were also more important in the dry year because plant-available water (Q , Q_1) was lower compared with the wet year. Maximum plant-available water in the top soil layer (Q_{1max}) was not very important overall, but became more important in the dry year because it effectively reduced the loss of plant-available water, which led to reductions in f_{wtop} and soil water evaporation (Eqn 10). The parameter governing the fraction of transpiration extracted from the top soil layer (f_1) was also of minor importance, but became more important in the dry year for similar reasons; it resulted in less water being removed by surface evaporation from the top soil layer and thus in a small positive gain to the pool of plant-available

Table 3. Mean $\pm$ s.d. of soil moisture differences between consecutive days within each drying cycle (see Fig. 1a) *n*, the number of differences calculated for each drying cycle; Rate, the soil water extraction rate estimated as the slope of the linear regression fitted to soil water content measurements in each drying cycle; Initial SWC, the soil water content at the beginning of each drying cycle; Season, indicates the season in the southern hemisphere

Day	Mean (mm day ⁻¹)	s.d.	<i>n</i> (day)	Significance (mean $- 2 \times$ s.d.)	Rate (mm day ⁻¹)	Initial SWC (mm)	Season
200	-1.38	0.850	4	ns	-1.387	396	Winter
208	-1.22	0.243	4	ns	-1.246	388	Winter
269	-1.49	0.834	4	sig	-1.067	396	Spring
323	-2.51	1.123	4	ns	-2.748	404	Spring
343	-1.48	1.004	4	ns	-1.763	385	Summer
348	-1.45	0.844	8	ns	-1.610	379	Summer
362	-1.42	0.993	4	ns	-1.410	362	Summer
373	-2.03	0.708	6	sig	-1.777	344	Summer
405	-1.87	1.250	5	ns	-1.986	377	Summer
424	-3.28	1.980	9	ns	-3.447	372	Summer
434	-5.03	4.785	4	ns	-4.794	344	Autumn
439	-2.84	1.172	4	ns	-2.599	330	Autumn
454	-2.68	3.434	4	ns	-3.910	339	Autumn
460	-1.32	0.310	4	ns	-1.285	337	Autumn
508	-2.13	1.268	14	sig	-1.802	372	Autumn
556	-2.78	1.613	6	sig	-2.244	384	Winter
601	-1.86	1.004	4	ns	-1.778	366	Winter
618	-2.95	1.726	5	sig	-2.255	370	Spring
646	-1.31	0.412	4	ns	-1.373	345	Spring
654	-1.97	0.940	6	ns	-2.046	350	Spring
664	-1.83	0.925	9	ns	-1.927	337	Spring
675	-1.35	0.668	13	ns	-1.271	317	Spring
709	-3.56	0.891	5	sig	-3.270	331	Summer
718	-4.08	3.313	6	sig	-2.801	325	Summer
732	-5.30	2.357	5	sig	-4.150	324	Summer
739	-1.95	1.160	11	ns	-2.239	297	Summer
753	-2.09	1.668	6	ns	-1.766	276	Summer
772	-4.60	2.397	4	sig	-3.3909	282	Summer
791	-2.56	1.073	5	sig	-2.3144	302	Autumn
800	-2.19	0.939	4	sig	-1.7749	291	Autumn
810	-3.21	1.678	6	sig	-2.5254	303	Autumn
823	-3.99	2.461	4	sig	-2.7541	300	Autumn
836	-2.77	2.799	10	sig	-1.8045	318	Autumn
850	-2.09	0.371	5	sig	-1.9259	306	Autumn

water. Small variations to canopy-intercepted water loss or net radiation reaching the soil surface, simulated via *z* or *albedo* variation, respectively, had minor effects only in the dry year.

Inter-annual sensitivity (with variable LAI)

When variable LAI was incorporated into the sensitivity analysis, the sensitivity of productivity decreased for parameters ranked 10 or above (Table 4). Thus, variable LAI tended to increase the difference in sensitivity between wet and dry years for ϵ , *k* and CUE, but decrease the difference for the other 'moisture-related' parameters (Table 4). The ranking changed only slightly, in positions 11 and 12, when the sensitivity of *albedo* decreased proportionally more than it did for *z*.

Intra-annual sensitivity (with constant LAI)

The daily values of sensitivity (s_{ij} ; Eqn 19) shown in Fig. 3 provide additional information to that summarised in the δ^{msqr} values presented in Table 4. Fig. 3 highlights when parameters

and their related processes became important with respect to productivity at different times of the year, over both the wet and dry years. For most of the time, productivity, GPP or NPP was very sensitive to CUE or ϵ and *k*, respectively (Fig. 3a), but NPP sensitivity to both the 'light-related' parameters ϵ and *k* was diminished almost completely when plant-available water became low in the second year and productivity became sensitive to maximum water availability (Q_{max}); a 20% increase in Q_{max} had a very important impact on NPP when soil moisture was lowest. Increases in D_{max} and D_{min} decreased the effect of *D* on NPP, except during the driest period of the dry year. Fig. 3c shows that NPP was frequently impacted by the vapour-pressure deficit in the middle and second half of the growing season when *D* was high. Understandably, NPP was sensitive to processes related to soil moisture at times of the year when the plant-available water was lowest. An increase in the maximum plant-available water had the greatest impact on NPP during the driest period occurring over the entire 2 years (Fig. 3a, b). This was also the case for water-use efficiency

Table 4. Inter-annual sensitivity of simulated productivity (net primary productivity or gross primary productivity in the case of carbon-use efficiency (CUE)) to parameter variation, first using a constant leaf area index (LAI) and then using a variable LAI based on the δ^{msqr} sensitivity measure (Eqn 20) for wet and dry years and for wet + dry years (the latter has been used to rank the sensitivity of the parameters)

δ^{msqr} was calculated for the first 233 days of each growing season (days 187–419 and days 554–786 in Fig. 1) to avoid the period of discrepancy between the modelled and measured soil moisture values in the latter part of the dry year. A value of zero indicates that productivity was insensitive to variation in the particular parameter under the prevailing environmental conditions

Inter-annual sensitivity with constant LAI				
Rank	Parameter	Wet	Dry	Wet + dry
1	ε	1.0449	0.9882	1.0169
2	k	0.5403	0.5111	0.5259
3	CUE	0.5081	0.3725	0.4455
4	Q_{max}	0	0.5074	0.3588
5	q_0	0	0.4489	0.3174
6	D_{min}	0.0655	0.1412	0.1101
7	D_{max}	0.0867	0.1119	0.1001
8	F_{wpmax}	0	0.1326	0.0938
9	$Q1_{max}$	0	0.0678	0.0480
10	F_{wpmin}	0	0.0670	0.0474
11	$f1$	0	0.0196	0.0138
12	$albedo$	0	0.0167	0.0118
13	z	0	0.0089	0.0063

Inter-annual sensitivity with variable LAI				
Rank	Parameter	Wet	Dry	Wet + dry
1	ε	1.0449	0.8482	0.9516
2	k	0.5403	0.4654	0.5043
3	CUE	0.5081	0.3696	0.4442
4	Q_{max}	0	0.3218	0.2276
5	q_0	0	0.2790	0.1973
6	D_{min}	0.0655	0.1187	0.0959
7	D_{max}	0.0867	0.0956	0.0913
8	F_{wpmax}	0	0.1196	0.0845
9	$Q1_{max}$	0	0.0533	0.0377
10	F_{wpmin}	0	0.0161	0.0114
11	$f1$	0	0.0124	0.0088
12	z	0	0.0028	0.0020
13	$albedo$	0	0.0013	0.0009

(q_0), the parameters (F_{wpmax} , F_{wpmin}) of the water factor (f_w) and for the parameters influencing processes affecting soil moisture in the top layer; processes that led to increased soil moisture in the top layer also led to increased evaporation from the soil surface and to a diminution in plant-available water.

Intra-annual sensitivity (with variable LAI)

When LAI variability was incorporated into the sensitivity analysis the sensitivity results changed little except for the delayed onset of the importance of the water factor parameters (F_{wpmax} and F_{wpmin}), maximum plant-available water (Q_{max} and $Q1_{max}$), water-use efficiency (q_0), canopy storage of precipitation (z) and surface heat flux ($albedo$) by days 21–23 days in the driest part of the dry year, and LAI variability shortened the duration of this importance by 10 days, or lengthened it by 39 days in the case of D_{max} and D_{min} (Fig. 4).

Discussion

The application of a simple model framework to a *Eucalyptus* forest flux site over wet and dry years allowed us to identify the processes that became important as determinants of productivity when site moisture declined, on both inter-annual and intra-annual timeframes. Insights have emerged from both the model parameterisation approach and the sensitivity analysis. We discuss these methods and insights below.

Parameterisation

The simple model defined a minimal set of assumptions about the forest ecosystem, and about the processes that might be active in that system. It also influenced how we used the data; we used the available dataset in two ways: first to estimate the model parameter values or their ranges and second to investigate whether or not processes incorporated in the simple model had relevance to the site. In particular, we assessed whether there were any moisture-related effects on productivity at this site or whether they were negligible owing to access to deep available water sources. The simple framework has made this approach very transparent.

We found that variations in atmospheric and soil water content probably play a significant part in the carbon and water dynamics of this *Eucalyptus* forest. We found a negative correlation between F_c/TDR and D for $D > 1$ kPa, even when soil moisture was adequate. Parameters were set so that the model would simulate this effect of D on F_c with reasonable accuracy, and so it would be included in the sensitivity analysis. F_c plotted against soil moisture revealed the possibility that a soil-moisture effect was active at this site. Analysis of the normalised soil water extraction rates (divided by D) during drying cycles also supported this possibility (Fig. 2b). From this evidence, we concluded that there were probably soil-moisture effects on productivity, and we parameterised the model to reflect this, and so it would be included in the sensitivity analysis.

There were three indicators of plant-available water in the model. Plant-available water in the 0–0.15 m ($Q1$) and 0–1.20 m ($Q2$) soil layers were two of these indicators used in comparisons with their corresponding measurements to estimate parameters related to the site water balance. The third indicator in the model was the overall plant-available water (Q), which we could only estimate indirectly because there were no measurements of soil water below a depth of 1.20 m. However, to obtain reasonable simulations of all four variables, $Q1$, $Q2$, F_w and F_c , particularly in the dry year, we needed to increase the maximum plant-available water (Q_{max}) to a level well above the maximum for the 0–1.20 m soil layer ($Q2_{max}$). Thus, we gained confidence in the estimate of Q_{max} because it was the result of using multiple constraints to inform the model. This is consistent with Leuning *et al.* (2005), who hypothesised that the tall *Eucalyptus* trees must have access to deep sources of water to explain similar annual water flux in wet and dry years. It is also consistent with our calculations of water output exceeding water input on a weekly basis, using the measured records of precipitation and soil water content.

The cumulative water and CO_2 fluxes in the Fig. 1b, c insets, respectively, clearly show that simulated CO_2 flux was reduced in the dry year, even though water flux was similar in both wet and dry years. Although water was available to the plant throughout

Fig. 3. Daily sensitivity (s_{ij}) of simulated productivity (net primary productivity (NPP) or gross primary productivity (GPP) in the case of carbon-use efficiency (CUE)) to small changes in the 13 parameter values listed in Table 4 using a constant leaf area index.

the driest period, low soil and atmospheric moisture content acted to reduce simulated NPP. These dry conditions reduced f_D and f_W (Eqn 3), which led to a reduction in NPP (in Eqn 16), simulating reduced whole-tree conductance to water and stomatal conductance to CO_2 , but higher D in the dry year offset reduced whole-tree conductance and led to the annual water flux in the dry year being similar to that in the wet year. This phenomenon has also been found for trees in seasonally dry savanna in north Australia (O'Grady *et al.* 1999) and for forests in Panama (Meinzer *et al.* 1999), which were able to exploit progressively deeper sources of soil water during the dry season and maintain constant and even increased rates of water use.

The discrepancy between the modelled and measured $Q1$ may, in part, reflect a buffering effect in the measured $Q1$ because of connections with moisture in the deeper adjacent soil layer. Simulated $Q1$ reflects water dynamics in the top soil layer like a 'bucket' that is isolated from the adjacent layers and, therefore, reflects infiltration into the top layer from precipitation events minus simulated water use extracted from the top layer. Measurements of soil moisture in the top layer were, however, taken with a probe at a depth of 0.15 m (Zegelin and White 1989; Leuning *et al.* 2005) and may reflect moisture levels influenced by moisture movement between layers in addition to inputs from infiltration and outputs associated with transpiration and soil surface evaporation. Hydraulic lift (Caldwell and Richards 1989; Caldwell *et al.* 1998; Jackson *et al.* 2000) is also

possible and may help to explain the major discrepancy observed between the measured and modelled soil moisture levels in the 0–1.20 m soil layer in the weeks after day 786 in Fig. 1a.

Sensitivity analysis

The inter-annual sensitivity results indicated that modelled productivity, NPP or GPP was most sensitive to maximum light-use efficiency (ϵ), light-extinction coefficient (k) or CUE, respectively. These three parameters played an important role in both wet and dry years, albeit a diminished role in the dry year (Table 4). The intra-annual sensitivity showed that the ϵ and k parameters were important in both years, except during a relatively narrow period of time when soil moisture levels were lowest. The parameter k relates to canopy light absorption and ϵ relates to the conversion of absorbed light into plant productivity. Thus, the forest's capacities to absorb light and to convert it into production were very important in both wet and dry years, except during the period with lowest soil moisture availability, which occurred in the second half of the growing season (early autumn) in the dry year. During this relatively narrow period of time, the importance of maximum plant-available water ($Q_{\max}$) and water-use efficiency (q_0) increased because $Q_{\max}$ determines the amount of stored water available and q_0 affects water use (or water saved) and, thus, they both affect the amount of water available to the forest to function

Fig. 4. Daily sensitivity (s_{ij}) of simulated productivity (net primary productivity (NPP) or gross primary productivity (GPP) in the case of carbon-use efficiency (CUE)) to small changes in the 13 parameter values listed in Table 4 using a variable leaf area index.

through the whole year, including the driest times of the year. When dry times occur during the growing season when production is high, $Q_{\max}$ and q_0 may become very important to productivity, depending on the level of decline in the fraction of maximum plant-available water ($Q/Q_{\max}$) the forest is subjected to. The $F_{\text{wpm max}}$ parameter defining the critical $Q/Q_{\max}$ point at which plant-available water begins to limit productivity (i.e. $f_w < 1$) is also most important at the driest times. Thus, we conclude that the hydraulic architecture above and below the ground that increases root depth and $Q_{\max}$, uses water conservatively with respect to the accumulation of biomass (q_0) and is less sensitive to the plant-available water fraction (has lower $F_{\text{wpm max}}$) will equip the forest to minimise the loss of productivity arising from dry periods.

In the dry year, variability in LAI tended to decrease the sensitivity of productivity to important parameters. The variability introduced into LAI resulted in an overall reduction in LAI. This LAI reduction tended to reduce the sensitivity of NPP to the light-related (ϵ and k) and the water-related (q_0 , $Q_{\max}$ and $Q1_{\max}$, $F_{\text{wpm max}}$ and $F_{\text{wpm in}}$, $D_{\max}$ and $D_{\min}$) parameters in the dry year. Reduction in LAI affects light extinction through the canopy and thus APAR, and its conversion to productivity (ϵ). This LAI reduction had less of an impact on F_w , particularly when the maximum plant-available water was allowed to exceed the maximum plant-available water in the first 1.20 m (i.e. $Q_{\max} > Q2_{\max}$). This is consistent with leaf area reduction experiments that have very little effect on sapflow (or

transpiration) until large leaf area reductions (up to 50%) have been made (Pataki *et al.* 1998; Oren *et al.* 1999), owing to stomatal compensation in the remaining leaves.

This analysis has provided some insights into the mechanisms linking productivity and site water status (Calder 1992; Honeysett *et al.* 1992, 1996; Eamus 2003; Rascher *et al.* 2004; Whitehead and Beadle 2004). The response of stomatal conductance to variation in vapour-pressure deficit and soil water content (Pereira *et al.* 1987; White *et al.* 1996; Thomas and Eamus 1999) was simulated through the multiplicative effect of f_w and f_D . The effect of vapour pressure (f_D) was important during the middle and second half of the growing seasons in both wet and dry years, but it overlapped with the effect of soil water (f_w) to produce a stronger multiplicative effect in the dry year until the soil water effect dominated in the driest part of the dry year (Fig. 3b, c). The stronger multiplicative effect is consistent with stomatal conductance becoming more sensitive to D with increasing drought, as has been observed previously (Thomas and Eamus 1999). The allocation of biomass to roots and leaves (Li and Wang 2003) was represented by maximum soil water availability ($Q_{\max}$). This was the most important parameter through the driest months of the dry year. Hydraulic conductance (White *et al.* 1998; Eamus *et al.* 2001) in the ecosystem may limit water flow along the soil–plant–atmosphere pathway. Transpiration is a function of hydraulic conductance and is driven by osmotic gradients, including D. To prevent a large decline in leaf water potential

and to prevent stomatal closure and even xylem embolism, hydraulic conductance must be sufficient to supply adequate water to the leaves. The effect of soil water content (f_w), in part, represents a reduction in hydraulic conductance in the soil–plant pathway. This effect on productivity became very important in the driest part of the dry year (Fig. 3b). The mechanism of a direct change in canopy leaf area or in specific leaf area that leads to a change in leaf area (Whitehead and Beadle 2004) was represented by the introduction of variation in LAI. On an inter-annual timeframe the overall reduction in LAI reduced the sensitivity of productivity to all 13 parameters. This effectively increased the contrast between wet and dry years with respect to the forest's capacities to absorb light (k) and to convert it into production (ϵ). However, it reduced the importance of the moisture-related parameters under dry conditions. Thus, the mechanism of an adjustment in the LAI had a widespread effect, exacerbating the effect of the dry-year conditions on the light-related processes and alleviated the effect on the moisture-related processes compared with the wet year.

Lastly, on mechanisms linking productivity and site water, we attempted to represent variation in RE (Turnbull *et al.* 2001; Ciais *et al.* 2005) through the CUE parameter. Productivity (GPP) was consistently very sensitive to this parameter in both the wet and dry years and thus provided limited insight. An alternative representation of this last mechanism might be through light-use efficiency (Eqn 3). For example, under dry conditions with low humidity, where f_w and f_D were <1 , light-use efficiency would decrease, leading to a decreased conversion of absorbed light into productivity. This effectively simulates an increase in autotrophic respiration under dry conditions. The sensitivity of productivity to ϵ and to the parameters associated with f_w and f_D is difficult to evaluate from this analysis. Even if we only consider ϵ and the parameters associated with f_w , the importance of ϵ decreases under dry conditions and the importance of the parameters associated with f_w ($Q_{\max}$, F_{wpmax} and F_{wpmmin}) increase. However, because NPP was insensitive to the parameters associated with f_w in the wet year (Table 4), but was sensitive in the dry year, we could infer that the ϵf_w combination or the combined parameter set (ϵ , $Q_{\max}$, F_{wpmax} and F_{wpmmin}) was more important in the dry year. This would imply that respiration (increased under dry conditions; Turnbull *et al.* 2001; *cf.* Ciais *et al.* 2005) could be a mechanism linking productivity and site water status at the study site, but this remains inconclusive from this analysis.

We assumed that CUE was constant in the model, and that GPP was proportional to NPP over the wet and dry years, to represent autotrophic respiration in a simple way, which is supported by empirical results at other sites and by modelling analyses (Gifford 1992, 2003; Dewar *et al.* 1998, 1999; Waring *et al.* 1998; DeLucia *et al.* 2007). However, there is also evidence that CUE can be higher in young trees and possibly under conditions of abundant nutrients or water (e.g. Mäkelä and Valentine 2001; DeLucia *et al.* 2007; Keeling and Phillips 2007). Therefore, incorporating autotrophic respiration into the model so that it varies with moisture availability appropriately could advance the analyses undertaken in the present study.

The δ^{msqr} values presented in Table 4 allow a robust comparison of the same parameters between wet and

dry years. However, the ranking between different parameters is less robust because of the protocol of varying each parameter value by 20% rather than by a small fraction of an accurate range of uncertainty, which is likely to vary considerably across the parameter set even for this simple model (Brun *et al.* 2001). Nevertheless, the δ^{msqr} values do provide some measure of the importance of the different parameters, particularly the further apart they are ranked. For example, the top four parameters in Table 4 could be of similar importance, but compared with the last four parameters in Table 4 they would be considered to be more important. The same problem arises if one attempts to compare the difference between wet and dry years across different parameters. For instance, $Q_{\max}$ and q_0 are much more sensitive in the dry year, and F_{wpmax} and F_{wpmmin} are also much more sensitive in the dry year (Table 4), but it is more difficult to say whether an increase in the first pair is more important than an increase in the second pair. A graphical representation of daily sensitivity may provide a better view to judge the relative importance of different parameters and their related processes across wet and dry years. Although such a comparison between parameters will not be truly robust either, it is qualitatively useful.

Conclusions

A simple ecosystem model can provide a mechanistic explanation for lower annual CO_2 uptake in a dry year compared with a wet year, even when annual water flux is similar in the 2 years. The effect of lower soil moisture content presumably leading to reduced canopy conductance and lower CO_2 uptake in the dry year was offset by higher vapour-pressure deficits driving water use in the dry year. Consequently, water use in the dry year was similar to water use in the wet year. The hydraulic architecture of the trees (both above and below the ground) at the study site was very important for productivity in the dry year. For instance, plant-available water and, thus, adequate root depth was an important determinant of CO_2 uptake at this site in the dry year, specifically during the driest months of the dry year. Above the ground, water-use efficiency was also very important in these months. The effect of vapour-pressure deficit on productivity was important in both the wet and dry years during the middle and second half of the growing season, but not during the driest months of the dry year. Low intrinsic sensitivity (lower F_{wpmax}) to the plant-available water fraction $Q/Q_{\max}$ benefited productivity through the driest months. The stomatal responses to vapour-pressure deficit and soil water content and hydraulic conductance were important during the dry year, but plant-available water $Q_{\max}$ and water-use efficiency were most important during the driest months of the study period.

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