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Impacts of elevated CO_2, climate change and their interactions on water budgets in four different catchments in Australia

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SUMMARY

Future water availability is affected directly by climate change mainly through changes in precipitation and indirectly by the biological effects of climate change and elevated atmospheric CO_2 concentration (eCO_2) through changes in vegetation water use. Previous studies of climate change impact on hydrology have focused on the direct impact and little has been reported in the literature on catchment-scale the indirect impact. In this study, we calibrated an ecohydrological model (WAVES) and used this model to estimate the direct and indirect effects and the interactive effect between climate change and eCO_2 on water availability in four different catchments in Australia with contrasting climate regime and vegetation cover. These catchments were: a water-limited forest catchment and an energy-limited forest catchment, a water-limited grass catchment and an energy-limited grass catchment. The future meteorological forcing was projected from 12 GCMs representing a period centred on 2050s and future CO_2 concentration was set as 550 ppm. Modelling experiments show that impacts of eCO_2 and projected climate change on vegetation growth, evapotranspiration (ET) and runoff were in the same magnitude but opposite directions in all four catchments, except for the effects on runoff in the energy-limited grass catchment. Predicted responses of runoff to eCO_2 indicate that eCO_2 increased runoff in the energy-limited forest catchment by ~2% but decreased runoff in other three catchments from 1% to 18%. This study indicates that rising CO_2 increases ecosystem water use efficiency but it does not necessarily result in increased runoff because elevated CO_2 also stimulates vegetation growth and increases ET. Elevated CO_2 was proved to have greater impacts on runoff than climate change in the forest catchments. Modelling experiments also suggest that interactive effects between climate and CO_2 are important, especially for predicting leaf area index (LAI) and ET in grassland catchments or runoff in water-limited catchments, where interactive effects were 1–6%. It implies that the assumption that linear combination of individual effects in most of previous studies is not appropriate. This study highlights the importance of considering elevated CO_2 in assessing climate change impacts on catchment-scale water balance and failure to account for direct eCO_2 effect or its interactive effects can lead to large bias in the predictions of future water budgets, especially for the water-limited catchments in Australia.

1. Introduction

Climate change is predicted to shape new hydroclimatic regimes in many regions of the world (Ramanathan et al., 2001; Dore, 2005; Dai, 2013), and will have significant impacts on water availability (Milly et al., 2005; Bates et al., 2008; Milly et al., 2008). Recent observational studies have shown that elevated atmospheric CO_2 concentration (denoted as eCO_2) may have significant implications for water availability through its physiological effects on plant function associated with the increased water-use-efficiency (WUE) (Eamus, 1991; Field et al., 1995; O'Grady et al., 2011). Modelling results at both plot and global scales have shown that changes in WUE may lead to a discernible increase in water availability or runoff (Gedney et al., 2006; Betts et al., 2007; Cao et al., 2010; Warren et al., 2011). Potential increase in water availability under eCO_2 may be particularly important for water-limited regions (Wullschleger et al., 2002), such as Australia (Eamus et al., 2006). However, the physiological effects of eCO_2 on water budget at catchment scales have rarely been addressed (Bates et al., 2008).

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At the leaf scale, eCO_2 trends to reduce stomatal conductance and consequently lower transpiration rate per unit leaf area. This is a water saving effect. Thus, if all other factors remain unchanged, eCO_2 should increase water availability. This leaf-scale effect has been observed in many experimental studies (Eamus and Jarvis, 1989; Norby et al., 1999; Medlyn et al., 2001; Ainsworth and Long, 2005). Several modelling studies showed that runoff increased significantly caused by this leaf-scale physiological effect of eCO_2 (e.g., Aston (1984), Gedney et al. (2006) and Cao et al. (2010)). At stand or regional scales, however, the physiological processes associated with eCO_2 can increase canopy leaf area index (LAI) via two mechanisms. One is via direct CO_2 fertilization effects (Field et al., 1995; Körner et al., 2007; De Kauwe et al., 2014); the other is indirectly via increased water availability resulting from reduced stomatal conductance (Wullschleger et al., 2002; Morgan et al., 2011). Increased LAI may offset the effect of the leaf-scale increased WUE on ecosystem water availability and result in little or no change in ecosystem water budgets (Levis et al., 2000). The net effect of eCO_2 on regional water budgets therefore depends on both responses of stomatal conductance and feedbacks of canopy LAI. The magnitude of the feedbacks of LAI is a key determinant of whether eCO_2 will increase runoff and by how much because leaves are the primary interface of among energy, water and carbon (Woodward, 1990; Cowling and Field, 2003; Piao et al., 2007; Bounoua et al., 2010; Norby and Zak, 2011). How the physiological effects of eCO_2 will manifest at catchment scale is poorly understood and likely to vary across different climate regimes and ecosystems (Ainsworth and Long, 2005; McMurtrie et al., 2008; Leakey et al., 2012).

Future changes in precipitation, temperature and evaporative demand (determined by radiation, humidity, wind speed and temperature) are direct drivers of catchment water yield (Bates et al., 2008). Increased evaporative demand can enhance regional evapotranspiration and decrease runoff. However, both evapotranspiration (ET) and runoff can increase if precipitation increases. Similarly, canopy LAI may be altered by climate change directly by the changes in meteorological forcing on growth (Cowling and Field, 2003) and indirectly through the influence of climate change on regional soil water availability (Knapp et al., 2002; Gerten et al., 2008a). Changes in canopy LAI induced by climate change can also exert indirect influences on regional water budgets through changes in partitioning of ecosystem transpiration and evaporation water use (Zhang et al., 2001; Puma et al., 2013). Future climate change is projected to vary spatiotemporally in both magnitude and direction (IPCC, 2007), thus sensitivities of both vegetation and water budget to climate change may be markedly different across space and time (Milly et al., 2005; Hyvönen et al., 2007; Bonan, 2008). In addition, complex interactions among the influences of both eCO_2 and climate change on canopy LAI and water budget can dampen or amplify the impacts of either individual factor (Cramer et al., 2001; Gerten et al., 2005), because physiological effects of eCO_2 at regional scale depend on both canopy LAI and meteorological conditions. However, the effects of the interactions between climate change and eCO_2 on canopy LAI and water budget have rarely been considered. In those studies that considered such effects, a linear combination of these effects caused by eCO_2 and other environmental drivers was routinely assumed (e.g., Betts et al. (1997), Gedney et al. (2006) and Piao et al. (2007)). Sellers et al. (1996) showed that nonlinear interactions between physiological and radiative effects of double CO_2 on plant growth were noticeable and differed across latitudinal gradients. Luo et al. (2008) demonstrated that interactions among changes in temperature, CO_2 and precipitation on carbon and water dynamics are not consistent among different ecosystems. However, whether nonlinear interactions between climate and CO_2 on plant growth and their impacts on the water availability are important has rarely been quantified across different ecosystems.

Quantifying the changes in future water yield due to either eCO_2 and climate change remains a challenge (Huntington, 2008; Luo et al., 2011), and whether interactive effects between eCO_2 and climate change on both canopy LAI and water budgets are negligible in different climatic and vegetation condition needs further investigation. Model simulations are a useful approach to elucidate and predict the physiological effects of eCO_2 and their interactions with climate change since physiological effects of eCO_2 at regional scale were poorly understood and atmospheric CO_2 content is projected to rise beyond our observation (Luo et al., 2011). General circulation models with sophisticated land surface models have been used to study the eCO_2 effects on water availability globally (e.g., Sellers et al. (1996), Betts et al. (1997), Gedney et al. (2006), Piao et al. (2007), Betts et al. (2007), Gerten et al. (2008b), Cao et al. (2010)), however the results of these studies are inconclusive due to their differences in modelling methodology including physiological processes of eCO_2, model structure and underlying assumptions (Gerten et al., 2008b; Bounoua et al., 2010; De Kauwe et al., 2013) and poor hydrological performances (Zhou et al., 2012). At catchment scales, previous modelling experiments have consistently predicted an increase in runoff in response to eCO_2 with a relative response ranging from less than 10% (Eckhardt and Ulbrich (2003), Kruijt et al. (2008), and Leuzinger and Körner (2010)) to about 90% (Aston, 1984). Many previous studies of eCO_2 at catchment scale suffer from two weaknesses. First, physiological processes and hydrological processes were loosely coupled in those models (e.g. Eckhardt and Ulbrich (2003)). As a result, interactions between canopy LAI and soil hydrology under eCO_2 cannot be studied systematically (Gerten et al., 2004; De Kauwe et al., 2013). Secondly, modelling was usually carried out for specific climate regime and vegetation cover. Thus results from those studies may not be applicable to other regions (Wullschleger et al., 2002; McMurtrie et al., 2008).

In this study, a coupled water-carbon ecohydrological model WAVES (WAter Vegetation Energy and Solute modelling, see Zhang et al. (1996)) was used to investigate the effects of eCO_2 and their interactions with future climate change on canopy LAI and the water budget. Four small catchments in Australia were selected with contrasting vegetation cover (i.e. forest versus grass) and climate regimes (i.e. water-limited versus energy-limited). Water-limited climate represents a dry climatic condition where mean annual precipitation is less than mean annual potential evaporation. While, energy-limited climate regime refers to a wet climatic condition where mean annual precipitation is larger than mean annual potential evaporation. The four selected catchments included a water-limited forest catchment and an energy-limited forest catchment as well as a water-limited grass catchment and an energy-limited grass catchment. The future meteorological forcing representing 2050s was projected from 12 GCMs of IPCC AR4 with emission scenario A2, and then downscaled to the study catchments. The future CO_2 concentration under emission scenario A2 (i.e., eCO_2) at 2050s is projected to be 550 ppm. In particular, this study has four objectives: (1) to demonstrate whether a water-carbon coupled model can capture the physiological impacts of both eCO_2 and climate change on canopy LAI and their hydrological impacts on catchment water budgets in different typical ecosystems; (2) to assess effects of eCO_2 on canopy LAI and catchment water yield under different climate regimes and vegetation cover in Australia; (3) to estimate whether impacts of eCO_2 on water budgets in vegetated catchments are small enough to be ignored in comparison to the impacts of future climate change; (4) to investigate whether the interactions between eCO_2 and changes in climate forcing are negligible in predicting future canopy LAI and water yield.

2. Method

2.1. Ecohydrological model: WAVES

In WAVES, available energy is partitioned between canopy and soil available energy using the Beer's law. Daily transpiration is calculated by a 'big-leaf' application of the Penman-Monteith formula. Leaf g_s is calculated by the equation developed by Leuning (1995) and this is then scaled up to canopy scale using the method proposed by Sellers et al. (1992). The vegetation canopy and the atmosphere are coupled in the WAVES model and the feedback between canopy and atmosphere is estimated using the omega coefficient proposed by Jarvis and McNaughton (1986). The daily carbon assimilation rate is estimate by the maximum carbon assimilation rate and relative growth rate multiplicatively. The maximum carbon assimilation rate is a model parameter, which represents the maximum growth rate under optimum condition. It was set as a constant for each vegetation type. The relative growth rate varies between 0 and 1 to represent the availability of different resources for growth using an Integrated Rate Method (IRM) developed by Wu et al. (1994) based on saturation rate kinetics. The WAVES model use in this study coded CO_2 as a variable in the canopy conductance (g_c) module as in Eq. (1) and daily assimilation (A_i) module using IRM approach as in Eq. (2).

$$g_c = g_0 LAI + \frac{g_1 A_i}{(C_{si} - \Gamma)(1 + D_{ci}/D_{co})} \frac{1 - \exp(-kLAI)}{k} \quad (1)$$

where g_0 is the residual stomatal conductance, g_1 is an empirical coefficient, A_i is the daily carbon assimilation rate, C_{si} is the CO_2 mole fraction of the air at the canopy surface, Γ is the CO_2 compensation point, D_{ci} is the vapour pressure deficit at the canopy surface, D_{co} is an empirical coefficient, LAI is the canopy leaf area index, k is the attenuation coefficient for light. The g_0, C_{si}, D_{co} and Γ were constant and the same for all catchments, while g_1 and k were calibrated within their physical meaning recommended by Zhang and Dawes (1998).

$$A_i = A_{\max} \frac{1 + W_2 + W_3 + W_4}{\frac{1}{m_1 x_1} + \frac{W_2}{x_2} + \frac{W_3}{x_3} + \frac{1}{m_4 x_4}} \quad (2)$$

where $A_{\max}$ is the maximum carbon assimilation rate; W_2, W_3 and W_4 are the weighting factor for water, nutrients and CO_2 relative to light, respectively; x_1, x_2, x_3 and x_4 are normalized availability of photosynthesis active radiation, water, nutrients and CO_2, respectively; m_1 is the temperature modifier, and m_4 is the vapour pressure modifier. Stresses from light, water and nutrient on the growth are integrated into weighting factors and normalized relative availability. Eq. (2) combines four limiting factors on growth into a single scalar. Level of water stress on growth is depend on several factors including transpiration demand, availability of soil water (depth-weighted integral of the soil matric and osmotic potentials in the root zone), species-specific maximum available water potential and salinity. Nutrient stress is simply measured by a prescribed constant (i.e. x_3 in Eq. (2)). All the weighting factors and normalized availabilities were calibrated against both LAI and observed streamflow records within the ranges as recommended by Zhang and Dawes (1998).

Three carbon pools (or compartments) of leaves, roots and stems are set for respiration and allocation as in Running and Coughlan (1988). Assimilation is allocated according to the priorities as in Running and Gower (1991): (1) maintenance respiration, (2) growth respiration, (3) leaf and root growth, and (4) stem growth. The ratio of leaf/root allocation reflects growth stress and smaller ratio indicates that more carbon is allocated to roots to acquire nutrients or water for growth. Carbon allocated to leaves is assumed to increase leaf area by an amount determined by the specific leaf area and the carbon allocated to roots is distributed amongst soil nodes weighted by the availability of soil water and nutrients. So, the physiological responses of canopy conductance and assimilation rate in WAVES are fully coupled with climatic regulation on stomata and both water and nutrients availability to roots, which allows LAI to vary with different environmental conditions.

The infiltration of net rainfall and soil water movement along the soil profile is simulated using a fully finite difference numerical solution of the Richards equation (Ross, 1990; Dawes and Short, 1993). For each soil type, an analytical soil model proposed by Broadbridge and White (1988) is employed to describe the relationships amongst water potential, volumetric water content and hydraulic conductivity. Overland flow (i.e., surface flow) can be generated from the infiltration excess rainfall and rainfall over saturated area. Lateral flow (i.e., subsurface flow) can be generated via the saturated water table and is simulated by Darcy's law if non-zero slope is specified. Water can leak out of soil column if it is set in the model. The availability of soil water that can be extracted by roots for transportation is estimated according to the distributions of both roots density and soil water content as in Ritchie et al. (1986). A more detailed modelling strategy and descriptions of WAVES are provided in Zhang et al. (1996) and Zhang and Dawes (1998).

The capability of WAVE model for simulating coupled water and carbon processes has been demonstrated against a number of experimental datasets including field observed ET (Zhang et al., 1996), LAI (Wang et al., 2001), soil water content and groundwater (Zhang and Dawes, 1998), isotope concentrations (Zhang et al., 1999). Recently, WAVES model has been applied to the FACE experiments to investigate the ecohydrological impacts of elevated CO_2 (Cheng et al., 2014). The advantages of the WAVES model used in this study are: (1) dynamically linking hydrological processes with vegetation growth at fine spatial scale so that it can accurately simulate development of LAI, canopy transpiration, rooting dynamics and soil water stress on both transpiration and growth at plot or small catchment scale; (2) accurate representation of soil moisture dynamics in saturated and unsaturated zones using the Richards equation; (3) consistent level of complexity in representing hydrological and physiological processes with appropriate feedbacks incorporated; (4) integrated representation of multiple limiting factors on vegetation growth, retaining complex mechanism of chemical and mechanical controls.

2.2. Catchments and data

The four catchments selected were all small with the dominant vegetation cover was either forest or grass. The locations of the four catchments are shown in Fig. 1. The energy-limited forest catchment used in this study is a tributary of Bellinger River in the northeast of New South Wales (NSW) with an area about 150 km^2. Mean annual precipitation is 1830 mm, and aridity index (ratio of mean annual potential evapotranspiration and mean annual rainfall. If the value is smaller than 1.0, it indicates an energy-limited or wet environment. If the value is larger than 1.0, it indicates a water-limited or dry environment) is about 0.7 (Chiew et al., 2009). More than 90% of the catchment area is covered by forest identified from the National Vegetation Information System (NVIS, http://www.environment.gov.au/erin/nvis/index.html). The energy-limited grass catchment used in this study is the Fisher River, upstream of Lake Mackenzie in the north of Tasmania (TAS) with an area of 37.5 km^2. Mean annual precipitation is 1860 mm, and aridity index is about 0.25 (CSIRO, 2009). The vegetation in the Fisher River is dominated by native grass (*ca.* 60%) and sparse shrub and woodlands (30%) (Brown et al., 2006). The topography is plateau with many rock outcrops and chains of lakes. The

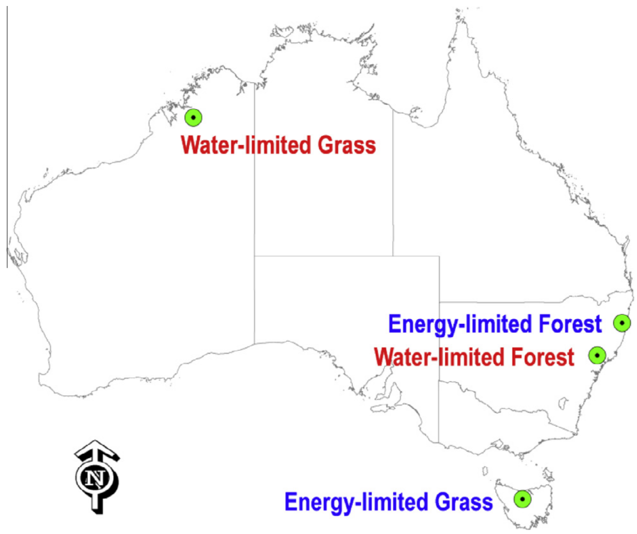

Fig. 1. A schematic map showing the locations of four different ecosystems studied.

water-limited forest catchment selected for this study is West Brook upstream of Glendon Brook River in the south-east of the NSW, with an area of 73 km^2. Mean annual precipitation is 750 mm and aridity index is about 1.7 (Zhang et al., 2011). The vegetation cover identified from NVIS is eucalypt tall open forests (41.5%) and eucalypt open forests (58.5%); however, the forests are not dense. The topography of the West Brook is a ridge and valley complex and moderately steep hill slopes, with a mean slope about 6°. The water-limited grass catchment chosen for this study is the Fletcher River at Dromedary of Fitzroy River in the north-west coast of West Australia (WA), with an area of 68.2 km^2. Mean annual precipitation is 1000 mm, and the aridity index is about 2.2. The catchment is completely covered by Hummock Grasslands (100%) identified from NVIS (Department of the Environment and Water Resources, 2007). The detailed descriptions of the climatic, geological and vegetation characteristics of each catchment are presented as following and the basic information are summarized in Table 1.

The soil information for each catchment were identified from the Australian Soil Resources Information System (ASRIS, http://www.asris.csiro.au/index_other.html), including soil types, texture, horizons and thickness McKenzie et al. (2000). The depth of different layers was determined by averaged thickness of different horizons. Based on the ASRIS, two soil layers were identified for all the four catchments but with different thickness. The upper and lower layer were 0.3 m and 0.6 m for the energy-limited forest catchment; 0.2 m and 1.0 m for the energy-limited grass catchment; 0.4 m and 0.4 m for the water-limited forest catchment; and 0.4 m and 0.5 m for the water-limited grass catchment. Another clay layer was set underlying these two layers. The total depth of soil column was up to 5.0 m in the two forest catchments and 3.0 m in the two grass catchments. The dominant soil type of each layer was also identified from ASRIS. This dominant soil type was used to determine the initial soil parameters.

The meteorological data needed to run the WAVES model included daily precipitation, daily maximum and minimum temperature, daily vapour pressure deficit, daily rainfall duration, and daily solar radiation. Daily precipitation, daily maximum and minimum temperature were obtained from the "SILO Data Drill" of the Queensland Department of Natural Resources and Water (http://www.longpaddock.qld.gov.au/silo/) (Jeffrey et al., 2001). The daily vapour pressure deficit and solar radiation are estimated according to daily temperature measurements following Kimball et al. (1997) and Thornton and Running (1999). Observed streamflow data and leaf area index (LAI) data of each catchment was collected to calibrate the model. The LAI was obtained from MODIS Land Product Subsets (MOD15A2, Collection 5) (http://daac.ornl.gov/MODIS/modis.shtml) with a quadrate of 7 × 7 km on the centre of catchment. The Savitzky–Golay filtering method was employed to smooth the raw LAI derived from MOD15A2 combined with quality control data using TIMESET 3.1 (Jönsson and Eklundh, 2004; Eklundh and Jönsson, 2011). The smoothed mean LAI time series of each catchment from 2000 to 2005 is shown Fig. 4.

2.3. Future meteorological forcing data

The 12 GCMs used in this study are listed in Table S1 in the auxiliary material. These GCMs were selected because projections of them performed better than others compared with historical climate of Australia (Crosbie et al., 2011; Vaze et al., 2011). Four meteorological variables were projected to represent future climatic conditions centred on 2050 (2040–2060) including precipitation, daily maximum temperature (T_{max}), daily minimum temperature (T_{min}), and solar radiation. The constant scaling method proposed by Santer et al. (1990) (also called the delta or

Table 1
Key features of the four catchments selected in this study.

		Energy-limited		Water-limited	
		Forest	Grass	Forest	Grass
State	–	NSW	TAS	NSW	WA
Latitude(S)	Degree	30.34	41.70	32.46	17.09
Longitude(E)	Degree	152.53	146.42	151.28	125.04
Catchment area	km^2	150	37.5	72.9	68.2
Mean slope	Degree	12	1	5.5	2.5
Mean elevation	m	300	1140	250	247
Mean annual precipitation	mm	1830	1860	750	1020
Aridity index	mm/mm	0.7	0.25	1.7	2.16
Mean annual temperature	°C	12.5	5.9	17.8	26.8
Photosynthesis pathway	–	C3	C3	C3	C4
Vegetation growth type	–	Perennial	Perennial	Perennial	Annual
Leaf area index (maximum)	m^2/m^2	6.0	1.25	2.5	1.25
Vegetation layers	–	2	1	2	1
Modelled soil depth	m	5.0	3.0	5.0	3.0
Soil types	–	3	3	3	3
Number of soil nodes	–	25	25	25	25
Runoff records		1995–2005	1995–2005	1995–2005	1995–1999
Baseline CO_2 concentration	ppm	370	370	370	370

perturbation method) was used to downscale GCM outputs to future daily time series for the study catchments. This method generates future climate time series by scaling observed historical time series with constant scaling factors, which are estimated from the historical observed time series and projected time series. Constant scaling factors of each variable were estimated at seasonal time-scales of each GCM. Three global warming scenarios (low, median, and high), which indicate different rate of climate change, were applied to provide a range of possibilities of future change.

Future precipitation and radiation at a specific day (x'_n) were estimated using Eq. (3a), and future daily maximum and minimum temperature at a specific day (x'_n) were estimate in terms of Eq. (3b).

$$x'_n = x_n(1 + t_k f_{i,j}/100) \tag{3a}$$

$$x'_n = x_n + t_k f_{i,j} \tag{3b}$$

where x_n and x'_n are observed and projected climatic variables at a specific date n; t_k (°C) is waring temperature of k-th global warming scenario ($1 \leqslant k \leqslant 3$, i.e., low, median and high); $f_{i,j}$ is constant scaling factor of i-th season ($1 \leqslant i \leqslant 4$, i.e., spring, summer, autumn and winter) of j-th GCM ($1 \leqslant j \leqslant 12$), $f_{i,j}$ is in %/°C (percentage change per degree Celsius of global warming) for precipitation and radiation and in °C/°C (degree Celsius increases per degree Celsius of global warming) for maximum and minimum temperature. According to the IPCC projections (CSIRO and BoM, 2007), low, median and high global warming scenarios were 0.84 °C, 1.4 °C and 2.24 °C, respectively. Thus, 36 scenarios are assembled for each catchment and daily pattern of scaled time series were kept the same as observed series.

The seasonal scaling factors (or changes) of four meteorological variables from 12 GCMs are shown in Fig. S1 in auxiliary materials. The climatic changes derived in this study are all in close agreement with previous estimates by CSIRO and BoM (2007). Assemble mean change in precipitation and potential evaporation estimated as in Priestley and Taylor (1972) are shown in Fig. 2 in terms of the four projected meteorological variables. Precipitation was projected to increase in the water-limited forest catchment only about 1.0%. Precipitation decreased by about 1.5%, 5% and 1% in energy-limited forest catchment, energy-limited grass catchment and water-limited grass catchment, respectively. Potential evaporation was increased in all the four catchments. It increased about 5% in the energy-limited grass catchment and approximately 2% in other three catchments.

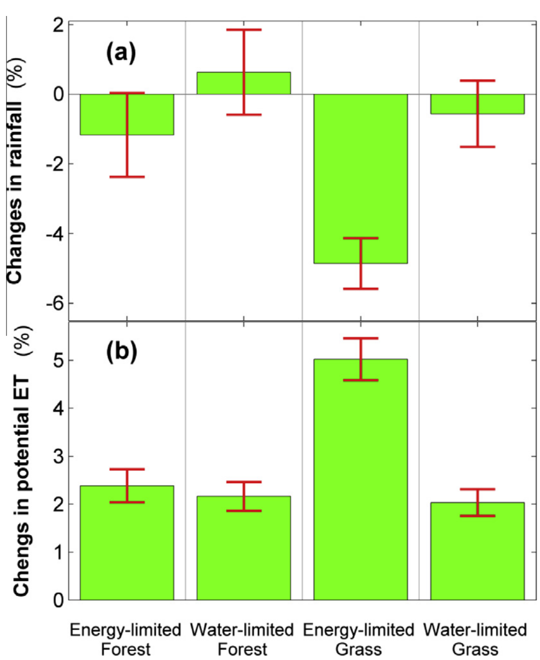

Fig. 2. Average changes of all assembled scenarios in (a) precipitation and (b) potential evaporation (PET) in different catchments. The error bars show standard error of all assembled scenarios ($n = 36$).

2.4. Parameter estimation

For the two forested catchments, both overstorey and understorey were considered. The overstorey layer is dominated by tall eucalyptus trees at two sites. The understorey layer includes grass and/or liana, and it was treated as a perennial C3 grass layer. For the two grass catchments, only one vegetation layer was considered. The vegetation was set as C3 perennial grass in the energy-limited catchment and as C4 annual grass in the water-limited grass catchments. For each vegetation type, there are 26 vegetation parameters used representing the physiological and phenological processes of plant growth in WAVES. The vegetation parameters include canopy albedo, soil albedo, rainfall interception coefficient, light extinction coefficient, maximum plant available soil water potential, *etc.*

Some vegetation parameters and all the soil parameters were optimised by minimizing the differences between modelled and observed streamflow data and smoothed MODIS LAI data together using the shuffled complex evolution (SCE-UA) method (Duan et al., 1992). The calibrated vegetation parameters include rainfall interception coefficients, maximum carbon assimilation rate, specific leaf area, respiration coefficient of leaf and root, leaf mortality rate and aerodynamic resistance. Previous study found that all these parameters have significant influences on the simulated plant-water interactions in WAVES (Zhang and Dawes, 1998). All the calibrated parameters were allowed to vary within their ranges as recommended by Dawes et al. (1998). Both bias and Nash–Sutcliffe coefficient (Nash and Sutcliffe, 1970) were incorporated into the objective function of the SCE-UA method as in Viney et al. (2009) to quantify the dynamic and systematic differences between simulated and observed streamflow and LAI series to identify optimal soil and vegetation parameters.

2.5. Modelling experiments

For a catchment, runoff (R) is influenced by climate (M) and atmospheric CO_2 (C):

$$R = f(M, C) \tag{4}$$

Using Taylor approximation, changes in runoff at catchment scales under future climate (ΔR_M) or increased CO_2 (ΔR_C), or both climate and increased atmospheric CO_2 (ΔR_{MC}) can be expressed as:

$$\Delta R_M \approx \frac{\partial f}{\partial M}\Delta M + \frac{1}{2!}\frac{\partial^2 f}{\partial M^2}\Delta M^2 + \cdots + \frac{1}{n!}\frac{\partial^n f}{\partial M^n}\Delta M^n \tag{5a}$$

$$\Delta R_C \approx \frac{\partial f}{\partial M}\Delta C + \frac{1}{2!}\frac{\partial^2 f}{\partial M^2}\Delta C^2 + \cdots + \frac{1}{n!}\frac{\partial^n f}{\partial M^n}\Delta C^n \tag{5b}$$

$$\Delta R_{MC} \approx \Delta R_M + \Delta R_C + \underbrace{\frac{1}{2!}\frac{\partial^2 f}{\partial C \partial M}\Delta C \Delta M + \cdots}_{\text{interactions}} \tag{5c}$$

where ΔM is change in climate and ΔC is change in CO_2. The first two terms in Eq. (5c), which are Eqs. (5a) and (5b), represent sensitivities of runoff to changes in climate forcing and CO_2, respectively. The rest of the terms in Eq. (5c) represent interactions between M

Table 2
A summary of the four scenarios considered in this study.

No.	Climate	CO_2	Descriptions
Expt1	Observed	Current (370 ppm)	The model was run with observed daily meteorological data, current ambient CO_2 concentration, and optimised model parameter values. Results of Experiment 1 represent water balance under current climatic and CO_2 conditions. Experiment 1 provides the reference for assessing the impact of climate change and CO_2 concentration on water balance
Expt2	Observed	Elevated (eCO_2, 550 ppm)	The same as Experiment 1, except the CO_2 concentration was elevated to 550 ppm. Experiment 2 was designed to estimate the impact of elevated CO_2 under current climate condition. It is similar as FACE experiments
Expt3	Projected	Current (370 ppm)	The same as Experiment 1, except future climate forcing projected from GCMs were considered. Experiment 3 is designed to estimate impact of future climate change on water balance without considering impact of CO_2 and to separate the impacts of changing climate and CO_2 concentration
Expt4	Projected	Elevated (eCO_2, 550 ppm)	The model was run with future climate forcing obtained from GCMs, elevated CO_2 concentration, and optimised model parameter values. Experiment 4 was designed to investigate the effect of changes in both climatic variables and CO_2 concentration on water balance

and *C*. Changes in evapotranspiration (ET) and LAI can also be estimated using equations similar to (5) as they are both influenced by climatic and CO_2.

Four modelling experiments with different climate forcing and CO_2 were designed to investigate the impacts exerted by future climate change (ΔM) and eCO_2 (ΔC). Basic descriptions of the modelling experiments are listed in Table 2.

As shown in Table 2, Experiment 1 (Expt1) was used as the baseline for assessing the impacts of changes in climate and atmospheric CO_2 concentration on canopy LAI and catchment water budget. Baseline is defined as the period from 1995 to 2005 and is the same for all four catchments. Experiment 2 (Expt2) was the same as Expt1 except CO_2 concentration was increased to 550 ppm, a level close to most FACE experiments. Experiment 3 (Expt3) was designed to quantify the impact of climate change. Experiment 4 (Expt4) considers the effects of both future atmospheric CO_2 concentration and climatic conditions. The differences between Expt2 and Expt1 represent the sensitivity to eCO_2, which stands for ΔR_C (namely Eq. (5b) and the second approximation term in Eq. (5c)). The differences between Expt3 and Expt1 represent the sensitivities to future climate change, which corresponds to ΔR_M (namely Eq. (5a) and the first approximation term in Eq. (5c)). The differences between Expt4 and Expt1, which stands for ΔR_{MC}, include not only the sensitivities to both climate change and eCO_2 but also interactions between two drivers (i.e. interaction terms in Eq. (5c)).

In summary, Expt2 is similar to FACE experiments for investigating the ecohydrological sensitivity to elevated CO_2. Expt3 is similar to most studies of climate change impact on water resources, which failed to consider the changes in vegetation water use due to changes in both CO_2 and climate. Expt4 provides a more comprehensive assessment of future climate change on runoff by considering changes in both meteorological variables and CO_2 concentration.

3. Results

3.1. Model calibration over baseline period: results of Expt1

The WAVES model was calibrated over the baseline period using observed daily streamflow and 8-day MODIS LAI. Model simulations, i.e. Expt1, are for current CO_2 and climate conditions (1995–2005). Modelled monthly runoff agrees well with the observations for all four catchments using the optimised parameters (see Fig. 3). The slope between modelled and observed monthly runoff is not statistically significant different from 1 for the two grassland catchments and wet forest catchment, but is greater than 1 for the dry forest catchment. Therefore our model tends to overestimate the monthly runoff for the dry forest catchment. Nash–Sutcliffe efficiencies of simulated monthly streamflow with optimal parameters were 0.89, 0.66, 0.74 and 0.70, and biases of water balance were −12.4%, −1.2%, −0.3%, and −2.4% for energy-limited forest, water-limited forest, energy-limited grass, and water-limited grass catchments, respectively.

Fig. 4 shows that the 8-day variation of canopy LAI modelled by WAVES agree reasonably well the MODIS LAI, but with smaller amplitude than the MODIS LAI for all four catchments. The Nash–Sutcliffe efficiencies were 0.67, 0.36, 0.34 and 0.82, and biases were −0.1%, −0.03%, 1.0%, and −0.9% for LAI for energy-limited forest, water-limited forest, energy-limited grass, and water-limited grass catchments, respectively. The above results indicated that WAVES is capable for simulating both streamflow and LAI variations in catchments across different climatic regime and vegetation types.

3.2. Sensitivities of LAI, ET and runoff to eCO_2 and climate change

The mean of ensemble sensitivities in percentage of LAI, ET and runoff to eCO_2 (i.e., Expt2) or projected climate change (i.e., Expt3) are shown in Fig. 5. Modelling results of Expt2 show that the eCO_2 increased canopy LAI in all four catchments, and it also increased evapotranspiration, but decreased runoff in all catchments except the energy-limited forest catchment, which showed a reduction in ET and an increase in runoff. Predicted increase in LAI was smallest (1.8%) in the energy-limited forest catchment and largest (21.2%) in the water-limited grass catchment due to eCO_2. Modelled LAI increases were 12.7% and 14.7% in water-limited forest catchment and energy-limit grass catchment, respectively (Fig. 5a). Predicted evapotranspiration changed −1.4% (−14.7 mm), 0.6% (3.9 mm), 3.9% (15.8 mm) and 10.1% (65.6 mm) and runoff changed 1.8% (14.6 mm), −2.9% (−2.2 mm), −1.1% (−15.7 mm) and −18.2% (−63.0 mm) due to eCO_2 (i.e., Expt2) in the energy-limited forest catchment, water-limited forest catchment, energy-limited grass catchment and water-limited grass catchment, respectively (Fig. 5b and c). Modelling results indicated that vegetation in water-limited environments would exhibit stronger response to elevated CO_2 in terms of LAI. Water saving effect of elevated CO_2 on stomatal conductance resulted in an increase in runoff for the energy-limited forest catchment. However, the effect was offset by increased LAI under elevated CO_2 in the remaining catchments.

Under climate change scenario (i.e., Expt3), modelled canopy LAI decreased in all four catchments (Fig. 5a). Evapotranspiration was predicted to increase in energy-limited forest catchment but decrease in other three catchments (Fig. 5b). Catchment runoff was predicted to decrease in the energy-limited catchments, but to increase in the water-limited catchments (Fig. 5c). The decrease in canopy LAI simulated by the model was smallest (2.7%) in the energy-limited catchment and largest (25.5%) in the water-limited grass catchment. Predicted changes in ET were 0.5% (5.1 mm), −0.3% (−2.0 mm), −2.0% (−8.2 mm) and −8.4% (−54.6 mm), and changes in runoff were −1.4% (−11.4 mm), 3.4% (2.5 mm), −5.8%

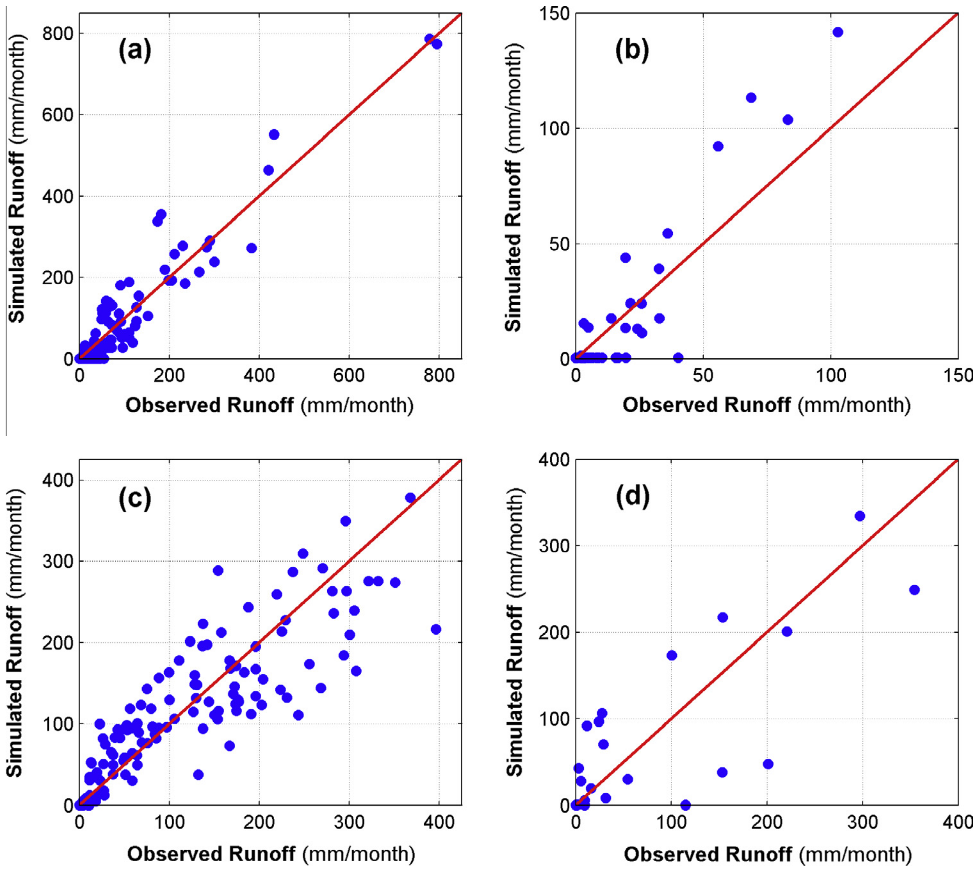

Fig. 3. Scatter plots comparing the observed and simulated monthly total streamflow in (a) energy-limited forest catchment, (b) water-limited forest catchment, (c) energy-limited grass catchment, or (d) water-limited grass catchment.

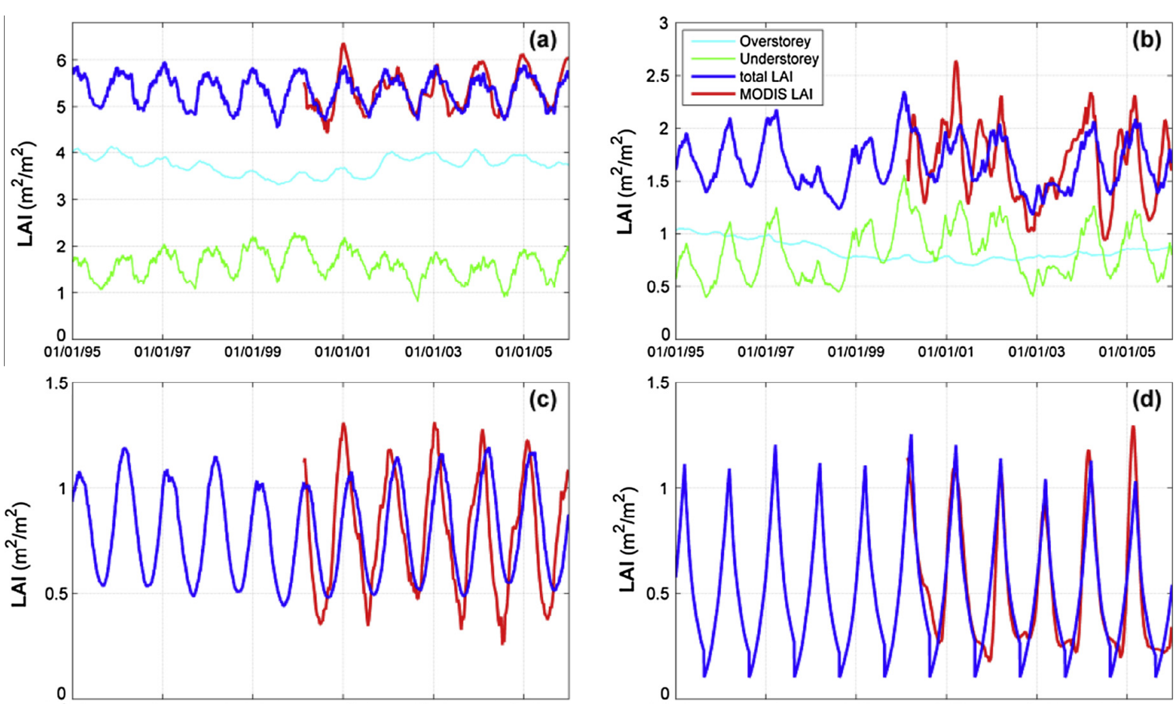

Fig. 4. Comparison of simulated daily LAI variations during baseline period of (a) energy-limited forest catchment, (b) water-limited forest catchment, (c) energy-limited grass catchment, or (d) water-limited grass catchment.

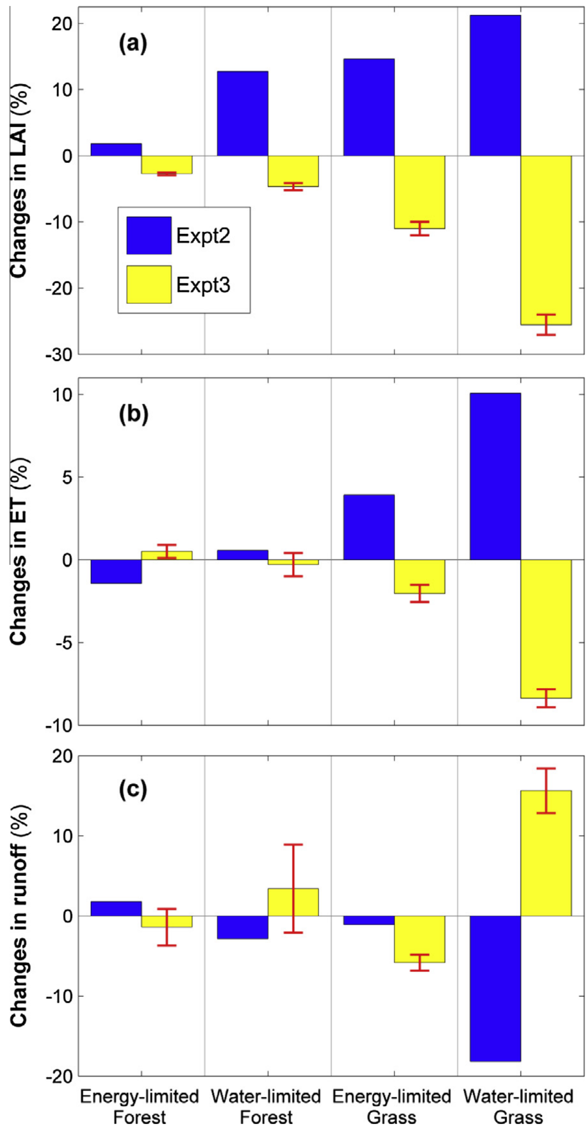

Fig. 5. The sensitivities of the (a) LAI, (b) ET and (c) runoff to elevated CO_2 (i.e., Expt2, blue bar) and climate change (i.e., Expt3, yellow bar). The bars and error bars represent assemble mean ($n = 36$) and standard error of all assembled scenarios, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

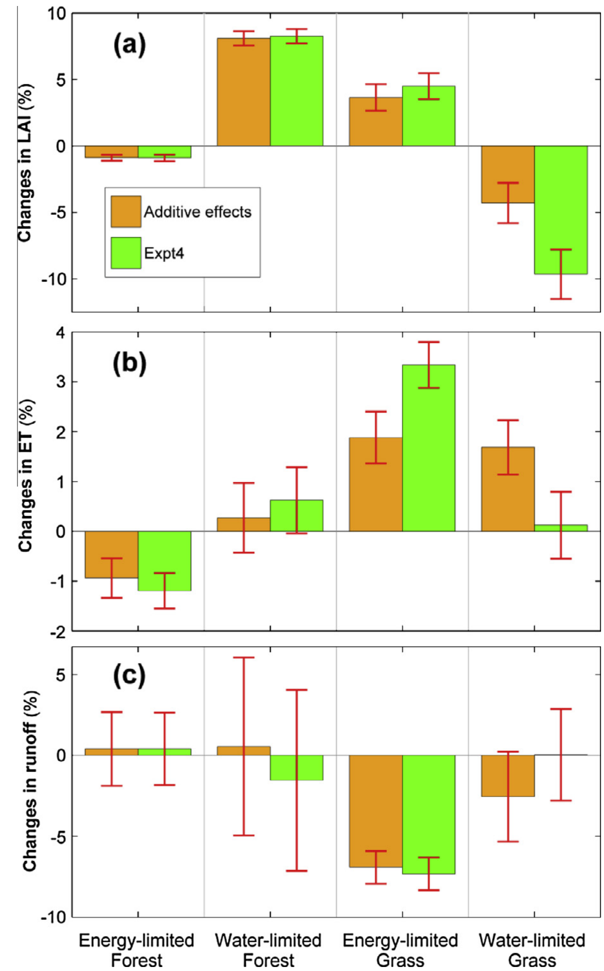

Fig. 6. Changes in the (a) LAI, (b) ET and (c) runoff in Expt4 (green bars). The orange bars show the additive impacts of the climate change and eCO_2 (i.e., sum up of Expt2 and Expt3 in Fig. 5). The meaning of bars and error bars is the same as that in Fig. 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(−84.0 mm) and 15.6% (54.2 mm) in energy-limited forest catchment, water-limited forest catchment, energy-limited grass catchment and water-limited grass catchment, respectively (Fig. 5b and c). Compared with elevated CO_2, climate change was predicted to result in changes in LAI, ET and runoff that are approximately equivalent in magnitude but in opposite directions. The exception was the energy-limited grass catchments, where both elevated CO_2 and climate change let to reductions in runoff.

3.3. Interactive effects of the eCO_2 and climate change on LAI, ET and runoff

The additive effects of eCO_2 and climate change (i.e., sum of changes in Expt2 and Expt3 as expressed by Eqs. (5a) and (5b)) and combined effects (i.e., relative changes in Expt4 as expressed by Eq. (5c)), which include additive effects and interactive effects of both eCO_2 and climate change, are shown in Fig. 6. Under "real future" climate scenario (i.e., Expt4), the combined effects on LAI, ET, and runoff are not necessarily in the same direction and magnitude as the individual effects of climate change or CO_2 in all four catchments. These modelling results indicate that the relative importance of climate change and elevated CO_2 varies across the catchments. When both climate change and elevated CO_2 are considered, simulated LAI changed −0.9%, 8.3%, 4.5%, and −9.6%, ET changed −1.2% (−12.2 mm), 0.6% (4.3 mm), 3.3% (13.4 mm), and 0.12% (0.8 mm), and runoff changed 0.4% (3.2 mm), −1.5% (−1.2 mm), −7.3% (−105.6 mm), and 0.04% (0.1 mm) in energy-limited forest catchment, water-limited forest catchment, energy-limited grass catchment and water-limited grass catchment, respectively (Fig. 6). The combined effect on LAI is in the same direction as the effect of elevated CO_2 in the water-limited forest catchment and energy-limited grass catchment, indicating dominance of elevated CO_2 over climate change. Similarly, elevated CO_2 was predicted to exert greater effects on runoff in the forested catchments.

The interactive effect represented by the third term in Eq. (5c) was taken as the difference between the combined effect and additive effect. The interactive effect on LAI in the forest catchments was small (<0.2%), but larger in the grass catchments (e.g. −5.4% in the water-limited grass catchment). The interactive effect on ET was −0.2%, 0.4%, 1.5% and −1.6% in energy-limited forest catchment, water-limited forest catchment, energy-limited grass catchment and water-limited grass catchment, respectively. The interactive effect on runoff was small (<0.5%) in the energy-limited catchments and larger (i.e. over 2%) in the water-limited catchments. Results in Fig. 6 indicate that the interactive effect was significant (⩾1%) for LAI and ET in the grass catchments and significant for runoff in the water-limited catchments. Modelling results indicate that the assumption that linear combination of individual effects is very unlikely to apply to predictions of LAI and ET in either of the two grassland catchments and runoff in either of the two water-limited catchments. Furthermore, additive effects and combined effects (i.e., Expt4) on runoff were in opposing directions in the two water-limited catchments. These modelling results suggest that prediction of runoff in two water-limited catchments was not only biased but also may in opposite direction, if interactive effects between eCO_2 and climate were neglected.

4. Discussion

4.1. Plant growth responses to elevated CO_2 and climate change

WAVES predicted increases in LAI under the elevated CO_2 scenario due to increased supply of carbon for photosynthesis. As can be seen in Eq. (2) that carbon assimilation rate in WAVES is considered to be positively correlated with CO_2 concentration and hence elevated CO_2 would mean more biomass production and higher LAI. However, the response of LAI to eCO_2 is not identical in all four catchments. For a given vegetation cover, WAVES predicted larger increase in LAI in water-limited catchments, while for a given climate grass catchments showed higher sensitivity in LAI (Fig. 5a). The modelling results are consistent with previous studies, such as Luo et al. (2008) and Piao et al. (2007). LAI of water-limited catchments was more sensitive to elevated CO_2 because the indirect water effect of eCO_2 on plant growth (i.e., via increased soil moisture content arising from reduced stomatal conductance) is larger. It has been observed that plant growth in water-limited environment is dominated by available water in comparison with other resources (Wullschleger et al., 2002; Eamus and Palmer, 2007; Macinnis-Ng et al., 2011) and this is reflected in the WAVES model with a larger relative weight of water (Zhang and Dawes, 1998). Thus, indirect water effect of CO_2 is more pronounced and resulted in greater increase in LAI in water-limited region. Previous studies also indicated that vegetation growth in water-limited region under eCO_2 condition can be stimulated by both direct fertilization effects of eCO_2 (Eamus and Jarvis, 1989; Woodward, 1990), and indirect water effects of eCO_2, which reduce water use and thus can ameliorate water stress under water-limited condition (Wullschleger et al., 2002; Gerten et al., 2005; Crosbie et al., 2012). Larger increases in LAI in water-limited regions under eCO_2 have also been observed in field experiments (Morgan et al., 2004; Morgan et al., 2011). Norby and Zak (2011) showed that stands with low LAI had a larger response of LAI to eCO_2 than did stands with high LAI among different forest FACE experiments, which is consistent with the simulated gradient in responses of LAI in this study from water-limited catchment to energy-limited catchment. However, predicted responses of LAI to CO_2 in this study may relate to the carbon allocation mechanisms parameterized in the WAVES model. De Kauwe et al. (2014) demonstrated that differences in allocation schemes in different models can result in a wide range (*c.a.* 2–20%) of predicted responses of LAI to eCO_2. It highlights the importance of reducing the uncertainties in carbon allocation mechanisms for capturing the impact of eCO_2 on LAI and its consequences in water use.

LAI was predicted to decrease under projected future climate change in all catchments and the reductions in LAI were principally associated with rising temperature. In WAVES model, the impacts of climate change on LAI were determined by relative responses of assimilation and respiration. Assimilation increases with increasing temperature to some optimum temperature, and then declines. Respiration monotonically increases with temperature. Although increase in temperature may have positive effect on the LAI, simulated decreases in LAI in all four catchments indicated that increase in temperature had larger effects on respiration than on assimilation. This is because the calibrated optimal temperatures for growth were already close to mean daily temperature during the growing season in all four catchments and any increases in temperature would be sub-optimal for plant growth. Increasing temperature also has indirect negative effects on plant growth in WAVES via aggravating water stress because rising temperature is associated with increases in potential ET (Fig. 2b). Predicted responses of vegetation growth in this study agreed well with previous assessments that climate change may influence vegetation growth detrimentally (Gerten et al., 2005; Fischlin et al., 2007; Luo et al., 2008). Predicted decrease in LAI in the water-limited grass catchment was consistent with the observed growth decline in the southern Spain induced by rapid climate change (Jump et al., 2006).

Under "real" future scenario (i.e., Expt4), both changes in climate and CO_2 can influence plant growth. For instance, rising temperature can pose positive or negative impacts on plant growth depending on climatic regimes and vegetation conditions (Fischlin et al., 2007; Bonan, 2008), meanwhile it can also affect both direct fertilization effects and indirect water effects of eCO_2 on plant growth (Leuzinger et al., 2011; O'Grady et al., 2011). The eCO_2 can enhance plant growth, at the same time, it can also modulate the impact of climate change on plant growth by altering WUE (Crosbie et al., 2012). Predicted changes in LAI in Expt4 indicates that growth were more sensitive to climate change in the energy-limited forest catchment and water-limited grass catchment, but more sensitive to eCO_2 in the other two catchments in term of the direction of additive effects on LAI (Fig. 6a). It is clear that the relative control of elevated CO_2 on plant growth is dependent on degree of climate change (e.g. changes in rainfall) and vegetation type. This study demonstrated that both changes in climate and CO_2 can have significant impacts on the LAI and it is important to take both factors into account to predict change in future water availability. However, it should also be acknowledged that the LAI responses reported here may be site-specific in terms of the vegetation type and degree of the projected changes in both climate and CO_2 concentration.

4.2. Shift of water budgets due to elevated CO_2 and climate change

The physiological effects of eCO_2 on catchment water budgets operate directly through reductions in canopy transpiration and indirectly through changes in canopy LAI (Katul et al., 2012). Our modelling results show that eCO_2 induced reductions in ET and increases in runoff only occurred in the energy-limited forest catchment (i.e., Expt2, Fig. 5b and c). Decreased ET in this catchment resulted from decreases in stomatal conductance, which reduced canopy transpiration and outweighed any increase in water consumption associated with increased LAI (~2%, Fig. 5a), resulting in increased runoff in this catchment. For the other three catchments, predicted increase in ET is related to the significant increase in LAI under eCO_2 conditions, which transpired more water and outweighed the effect of stomatal closure.

The projected climate changes indicated increases in potential ET in the four catchments (Fig. 2b). In the energy-limited forest catchment, WAVES predicted a slight increase in ET and decrease in runoff and this is likely caused by increase in potential ET. However, the energy-limited grass catchment showed reduction in ET when the potential ET was increased, opposite to what is expected. It appears that a greater rainfall reduction projected for this catchment may have offset the effect of increased potential ET, resulting in reduction in ET. Under the future climate change scenarios, ET was predicted to decrease in the water-limited catchments. A close examination showed that increased temperature was indirectly responsible for the reductions in ET through its impact on plant growth (i.e. LAI). Runoff was predicted to increase in the water-limited environment. However, the cause of the change was different depending on the vegetation type. For forest catchment, increased rainfall was mainly responsible for the increase in runoff, while increased temperature was the main cause for the grass catchment as it reduced plant growth (i.e., LAI) and in turn increased runoff. Runoff was predicted to decrease in the energy-limited catchments mainly due to projected rainfall reduction. It is clear that climate change can influence water budgets directly though changes in climate forcing including precipitation and temperature, and indirectly via impacts on plant growth.

When changes in both CO_2 and climate are considered (i.e. Expt4), the direction of predicted changes in ET in all the catchments was the same as the direction of the effect of CO_2 alone (i.e. Epxt2). This suggests that eCO_2 is more dominant than climate change in controlling ET in these vegetated catchments. For the forest catchments, the effect of CO_2 on runoff was greater than that of climate change, but the trend was opposite for the grass catchments. However, it should be noted that the relative CO_2 effect on catchment scale ET and runoff will depend on vegetation characteristics and projected climate change. Because forest and grass showed different sensitivities to CO_2 and climate change and there was apparent trend among three global warming scenarios. Simulated changes in ET and runoff have wider variation ranges, which were mainly determined by the degree of projected future climate change by different GCMs. Basically, the assembled mean changes in runoff under "real" future were about 0.5% to −8%, which can be smaller than uncertainty of the prediction of many models. Therefore, predictions in this study may be site-specific and depend on the vegetation coverage and characteristics, degree of future climate change and even the model itself. Our modelling results suggest that incorporating the impact of eCO_2 on water budgets is important for predicting future water availability of vegetated land and failure to account for the impact may lead to large uncertainty in the predictions.

4.3. Interactive effects between climate change and eCO_2

Modelling results in this study show that interactive effects of climate change and eCO_2 on LAI and ET can be neglected (<0.5%) in the forest catchments but important in the grass catchments (2–2.6%, Fig. 6a) because forest has greater rooting depth that can utilize more available soil water than grasslands (Zhang et al., 2001; Troch et al., 2009; Cheng et al., 2011). For runoff, interactive effects between CO_2 and climate change are important in two water-limited catchments, where ecosystem structure and function are mainly constrained by water (Eamus et al., 2006) and have higher rain-use efficiency (Huxman et al., 2004; Troch et al., 2009). So, small interactive effects on plant water use can result in significant differences in runoff (Cramer et al., 2001; Wullschleger et al., 2002; Bounoua et al., 2010). That is why interactive effects on runoff in water-limited catchments cannot be neglected.

It can be noted that the magnitude of the combined effects of climate change and eCO_2 were much smaller than the magnitude of climate change or eCO_2 alone. This is due to the fact that predicted effects of climate change were in the same magnitude but opposite direction of the eCO_2 effects (Fig. 5), except for runoff in the water-limited grass catchment where the effects of climate change and eCO_2 were in the same direction. These findings are consistent with the conclusion of Luo et al. (2008) from a modelling study and Wu et al. (2011) from multiple manipulated experiments in that future changes in meteorological forcing and rising CO_2 have compensatory effects on growth and water yield. As a result, predict interactive effects are important compared with combined effects. Therefore, the assumption that the effects of climate change and eCO_2 are linearly addictive is not appropriate, especially for changes in LAI and ET in grassland catchments or runoff in water-limited catchments, where interactive effects of eCO_2 and climate change cannot be neglected.

5. Conclusions

In this study, impacts of elevated CO_2 (eCO_2) on canopy leaf area index (LAI) and water budget (evapotranspiration (ET) and runoff) were investigated using an ecohydrological model (WAVES). Future climate changes were considered and interactions between eCO_2 and climate change were estimated in four different ecosystems in Australia with contrasting climate regime and vegetation cover. Modelling experiments show that impacts of eCO_2 and projected climate change on vegetation growth, ET and runoff were in same magnitude but opposite direction in the selected catchments, except for the effects on runoff in the energy-limited grass catchment. Predicted responses of runoff to eCO_2 indicate that eCO_2 increased runoff in the energy-limited forest catchment by about 2% but decreased runoff in other three catchments from 1% to 18%. This study indicates that rising CO_2 increases ecosystem water use efficiency but it does not necessarily result in increased runoff because elevated CO_2 stimulates vegetation growth and increases ET. Elevated CO_2 was proved to have greater impacts on runoff than climate change in the forest catchments. Modelling experiments also suggest that interactive effects between climate and CO_2 are important, especially for predicting LAI and ET in grassland catchments or runoff in water-limited catchments. It implies that the assumption that linear combination of individual effects in most of previous studies is not appropriate. This study highlights the importance of considering elevated CO_2 in assessing climate change impacts on catchment-scale water balance and failure to account for direct eCO_2 effect or its interactive effects can lead to large bias in the predictions of future water budgets, especially for the water-limited catchments in Australia.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jhydrol.2014.09.020.

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