

**Modelling Seasonal and Inter-annual Variations in Carbon and Water Fluxes in an  
Arid-zone *Acacia* Savanna Woodland, 1981-2012**

**Running head: Modelling Variations in Carbon and Water Fluxes**

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20 **ABSTRACT**

21 Changes in climatic characteristics such as seasonal and inter-annual variability may affect  
22 ecosystem structure and function, hence alter carbon and water budgets of ecosystems. Studies of  
23 modelling combined with field experiments can provide essential information to investigate  
24 interactions between carbon and water cycles and climate. Here we present a first attempt to  
25 investigate the long-term climate controls on seasonal patterns and inter-annual variations in water  
26 and carbon exchanges in an arid-zone savanna-woodland ecosystem using a detailed mechanistic  
27 soil-plant-atmosphere model (SPA), driven by leaf area index (LAI) simulated by an  
28 ecohydrological model (WAVES) and observed climate data during 1981–2012. The SPA was  
29 tested against almost three years of eddy covariance flux measurements in terms of gross primary  
30 productivity (GPP) and evapotranspiration (ET). The model was able to explain 80% and 71% of  
31 the variability of observed daily GPP and ET, respectively. Long-term simulations showed that  
32 carbon accumulation rates and ET ranged from 20.6 g C m<sup>-2</sup> mon<sup>-1</sup> in the late dry season to 45.8 g  
33 C m<sup>-2</sup> mon<sup>-1</sup> in the late wet season, respectively, primarily driven by seasonal variations in LAI and  
34 soil moisture. Large climate variations resulted in large seasonal variation in ecosystem water-use  
35 efficiency (eWUE). Simulated annual GPP varied between 146.4 and 604.7 g C m<sup>-2</sup> yr<sup>-1</sup>. Variations  
36 in annual ET coincided with that of GPP, ranging from 110.2 to 625.8 mm yr<sup>-1</sup>. Annual variations  
37 in GPP and ET were driven by the annual variations in precipitation and vapour pressure deficit  
38 (VPD) but not temperature. The linear coupling of simulated annual GPP and ET resulted in  
39 eWUE having relatively small year-to-year variation.

40 **Keywords:** Gross primary production; Evapotranspiration; Transpiration; Water-use efficiency;  
41 WAVES model; SPA model.

## 42 INTRODUCTION

43 Climate and its variability play an important role in mediating the structure and function of  
44 terrestrial ecosystems because of the close association between the carbon and hydrological cycles  
45 (Baldocchi 1997; Williams and others 2001a). It has been predicted that climate will change at  
46 both regional and globe scales and thus patterns of precipitation, temperature, solar radiation and  
47 vapour pressure deficit (VPD) may vary seasonally (Houghton and others 1996; IPCC 2014).  
48 Year-to-year variability under a future warmer climate is also expected to be larger (Salinger 2005).  
49 These changes in climate are likely to affect terrestrial ecosystem uptake of atmospheric CO<sub>2</sub> and  
50 the hydrological cycle. Understanding the responses of hydrological and plant physiological  
51 processes in terrestrial ecosystem to climate variations is of importance to rangeland and water  
52 resource managers, particularly in arid and semi-arid regions, such as arid-zone savanna  
53 woodlands.

54 Savannas are among the most striking vegetation types, located in tropical and sub-tropical zones  
55 that contain a discontinuous tree canopy with a substantial grass understory (Eamus and Prior  
56 2001). These ecosystems occupy a large proportion of global land area (about 20%) and  
57 significantly contribute to regional and continental-scale carbon and water budgets. Savannas  
58 experience large variations in temperature, moisture availability and sunlight, which are  
59 controlling factors of the ecosystem CO<sub>2</sub> exchange (Baldocchi 2008; Wohlfahrt and others 2008;  
60 Yan and others 2011; Cleverly and others 2013) and water fluxes (Eamus and others 2013b). This  
61 is particularly the case in Australia, the driest permanently inhabited continent on Earth (Eamus  
62 2003), where savannas cover approximately 25% of the continent.

63 Due to the remoteness of Australia's interior, however, studies that investigate the controls exerted

64 by climate on water and carbon dynamics have only recently been undertaken in Australian  
65 arid-zone savannas (Cleverly and others 2013; Eamus and others 2013b). The climate of the region  
66 is characterized by a distinct wet season (Nov–Feb) accounting for 75–80% of annual precipitation  
67 (Eamus and others 2013b), but with a long period (up to four months) of no rainfall in the dry  
68 season. These field experiments were conducted over a period of about 2 years and provided  
69 useful information on carbon and water dynamics in the arid-zone savannas. However, long-term  
70 studies of carbon and water fluxes are needed to understand seasonal and inter-annual relationships  
71 between climate and the exchanges of carbon and water.

72 Detailed process-based simulation models are valuable tools to integrate knowledge of climate,  
73 plant processes and hydrology and scale these processes to stand and ecosystem levels (Williams  
74 and others 1996; Landsberg and Coops 1999; Braswell and others 2005). The  
75 soil-plant-atmosphere (SPA) model is a process-based model that is able to simulate ecosystem  
76 photosynthesis, energy balance and water transport. The model was designed for direct  
77 comparisons with eddy covariance (EC) estimates of carbon and water fluxes and has been  
78 successfully implemented in temperate (Williams and others 1996, 2001a), tropical (Williams and  
79 others 1998) and arctic (Williams and others 2000) ecosystems, including recent applications in  
80 Australian ecosystems (Zeppel and others 2008; Whitley and others 2011; Eamus and others  
81 2013a). In one example from a temperate ecosystem, Schwarz and others (2004) concluded that  
82 SPA was suitable for simulating seasonal and annual responses of gross primary productivity (GPP)  
83 and transpiration (T) to climate variability in seasonally drought-affected Ponderosa pine forests.  
84 Likewise in the present study we applied the SPA model to investigate climatic controls on GPP  
85 and evapotranspiration (ET) in a Mulga-dominated landscape.

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4 86 The SPA model requires daily leaf area index (LAI) as an input. In contrast to the soil, plant  
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6 87 physiological and meteorological parameters, it is difficult to obtain daily LAI for long-term  
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8 88 simulations (e.g. 30 years). The water-atmosphere-vegetation-energy-soil (WAVES) is a model  
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11 89 based on the biophysical processes within the soil-vegetation-atmosphere system (Zhang and  
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13 90 others 1996; Zhang and Dawes 1998). In the model, carbon assimilation, allocation and respiration  
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16 91 are dynamically estimated from empirical relationships with the availability of light, water,  
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18 92 nutrients and ambient CO<sub>2</sub> concentration, which allows LAI to vary with environmental conditions.  
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21 93 Hence, daily LAI was simulated by the WAVES model and was used as an input to the SPA model  
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24 94 in this study.

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26 95 The ecosystem water-use efficiency (eWUE) can be expressed as net ecosystem exchange (NEE)  
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28 96 or GPP to ET (Beer and others 2009; Perez-Ruiz and others 2010; Linderson and others 2012). It is  
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31 97 an important index representing the trade-off between carbon uptake and water loss and provides a  
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34 98 metric for evaluating ecosystem productivity and resilience (Baldocchi 1994; Ponce-Campos and  
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36 99 others 2013). Alternative to eWUE, inherent WUE (IWUE), calculated as the ratio of  $GPP \times VPD$   
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39 100 to ET (Eamus and others 2013b) can be used to examine the intrinsic link between carbon and  
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41 101 water fluxes through stomatal conductance at the ecosystem level. Studies of eWUE and IWUE  
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44 102 have indicated that they respond differently between wet and dry years (Ponce-Campos and others  
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46 103 2013) and wet and dry seasons (Eamus and others 2013b). Thus the work described herein also  
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49 104 examined the responses of eWUE and IWUE to historical climate variations at both seasonal and  
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51 105 inter-annual scales in this savanna woodland ecosystem.

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54 106 The objectives of this study were to: (1) parameterize and validate the SPA model using almost  
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56 107 three years of eddy covariance measurements and LAI simulated by WAVES in a landscape of  
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central Australia dominated by a N-fixing tree, Mulga (*Acacia aneura*); and (2) quantify and explain seasonal and interannual variability of carbon- and water fluxes under historical climate variations, in terms of GPP, ET and WUE. The primary purpose of this study was to test the hypotheses that seasonal variations of GPP, ET and WUE of this mulga-dominated landscape are controlled principally by temperature and VPD, not precipitation considering the fact that precipitation has relatively less seasonal variation with the dominant pattern of summer rainfall (Nov–Feb; Eamus and others 2013b); while the large variations in inter-annual precipitation (Chen and others 2014) affect GPP, ET and eWUE at an inter-annual time scale. As far as it is known to the authors, this is the first attempt to explore seasonal and inter-annual dynamics of carbon and water fluxes for this ecosystem over a long time period (1981–2012). Such information is critical to estimating future changes to carbon sink-source status and hydrological cycles associated with changes in climate in arid-zone Australia.

**MATERIALS AND METHODS**

**Study Site**

The site selected for this study is in central Australia, located approximately 200 km north of Alice Springs, NT (22.283S, 133.249E and a.s.l. 600 m). Climate in this region is characterized by hot summers and warm winters in the arid tropics. In the past 32 years (1981–2012), summer maximal temperature (46.2 °C) occurred in Jan and winter minimal temperature (-4 °C) was reached in Aug in 1994 at the nearest meteorological station (Territory Grape Farm; Eamus and others 2013b). Large variation in inter-annual precipitation occurs here, ranging from 97.4 to 832.9 mm yr<sup>-1</sup>, with an average of 326.0 mm yr<sup>-1</sup>. Precipitation is also highly seasonal, with about 75–80% of rainfall occurring during the wet season (Nov–Apr; Bowman and others 2010). The soil is characterised as

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4 130 a red kandosol. The ecosystem is an Mulga (*Acacia neura*) savanna woodland with an average  
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6 131 canopy height of 6.5 m above an understory dominated by C4 warm-season grasses that is  
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8 132 dependent upon rainfall (Cleverly and others 2013).  
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#### 10 11 133 Experimental Data for Testing the SPA and WAVES Models 12

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14 134 An eddy covariance tower, a member of the OzFlux network (<http://www.ozflux.org.au/>; Cleverly  
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16 135 2011), was located on a flat plain between the Hanson and Woodforde Rivers. Potential fetch is 11  
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18 136 km to the east and 16 km to the south. EC data were initiated on 2 September 2010 and collected  
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20 137 from a 13.7 m tower. The three-dimensional eddy covariance system was mounted 11.6 m above  
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22 138 the ground, facing into the predominant south-east wind direction (Chen and others 1991), and  
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24 139 consisting of a CSAT3 three-dimensional sonic anemometer (Campbell Scientific Australia,  
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26 140 Townsville, QLD, Australia) and a LiCor 7500 open-path infrared gas analyser (John Morris,  
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28 141 Chatswood, NSW, Australia). Air temperature and relative humidity were measured using an  
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30 142 HMP45C (Vaisala, Helsinki, Finland) at the height of 11.6 m above the ground. Four-component  
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32 143 net radiation was measured at 12.2 m above the ground with a CNR1 (Kipp & Zonen, Delft, The  
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34 144 Netherlands). Precipitation was measured with a CS7000 (Hydrologic services, Warwick, NSW,  
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36 145 Australia), centred in a 10 m × 15 m clearing (about 15 m from the eddy covariance tower) at the  
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38 146 top of a 2.5 m mast. Flux measurements were made at frequency of 10 Hz with a 30-minute  
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40 147 covariance interval.  
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49 148 An AMS Soil Core Sampler (The Environmental Collective, Auckland, New Zealand) was used to  
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51 149 extract intact cores (38 mm diameter × 10 cm depth to a maximum depth of 1.4 m) for laboratory  
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53 150 analysis. A fairly uniform soil profile was identified with bulk density varying only slightly from  
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55 151 1.67 g cm<sup>-3</sup> at the surface to 1.86 g cm<sup>-3</sup> at a depth of 1.4 m. A soil column of 4 m was chosen to  
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152 simulate the relatively shallow rooting depth for Mulga at this site.

153 To calibrate the WAVES model, LAI was derived from images acquired with a digital camera

154 (Canon DSLR). Five 100 m long transects were established in the tower footprint (NE to SW). To

155 compute LAI for the canopy (Mulga), images were acquired with the camera oriented toward

156 zenith (to the sky, 0°). These canopy images were analyzed in Matlab (R2012, The Mathworks,

157 Natick, MA, USA) using the method of MacFarlane and others (2007). To compute understory

158 LAI, photographs were oriented toward the soil at an angle of 57.5° from nadir (Weiss and others

159 2004) and analyzed with CANEYE (V6.3, <https://www4.paca.inra.fr/can-eye>), based on the

160 method proposed by MacFarlane and others (2007). Total LAI was calculated as the sum of the

161 canopy and understory components.

162 A more detailed description of field measurements and data processing can be found in Cleverly

163 and others (2013) and Eamus and others (2013b).

164 Forcing Energy Balance Closure

165 The use of flux data to validate biophysically-based models requires that conservation of energy is

166 satisfied as it is defined in the model (Twine and others 2000; Chen and others 2014). To force

167 energy balance closure, energy is generally added into the turbulent term  $[H+\lambda E]$  (where  $H$  and  $\lambda E$

168 are sensible and latent heat fluxes, respectively) of the closure ratio  $D ([H+\lambda E]/[R_n-G-S])$ , where  $R_n$

169 is net radiation,  $G$  is ground heat flux and  $S$  is heat storage) in proportion to the measured Bowen

170 ratio ( $H/\lambda E$ ). In practice, energy in semi-arid regions is returned to  $H$  when  $ET$  is small and into  $\lambda E$

171 during the days following rainfall when  $\lambda E$  is large and  $H$  is limited by cloud cover. In the present

172 study,  $S$  was relatively minor and negligible due to the minimal biomass density of short canopies

173 (Wilson and others 2002). Therefore, the energy balance was closed each half-hourly period by



174 attributing the residual energy to  $H$  and  $\lambda E$  according to the observed Bowen ratio in that half  
175 hourly period.

176 SPA Model

177 The SPA model is a process model (Williams and others 1996) that was designed for direct  
178 comparisons with eddy covariance estimates of carbon and water fluxes (GPP, ET and T) and can  
179 simulate ecosystem photosynthesis, energy balance and water transport at fine temporal and spatial  
180 scales (Williams and others 2001b). The original model has 20 soil layers to simulate root  
181 distribution and soil-water uptake and has 10 canopy layers to simulate C3 vascular plant  
182 processes at a 30-min time step. The ecosystem structure is described by vertical variations among  
183 canopy layers in light absorbing leaf area, photosynthetic capacity, and plant hydraulic properties  
184 (Williams and others 2001a). Because of the significant contribution of C4 grasses to total LAI  
185 during the wet season in tropical savannas, Whitely and others (2011) added a C4 photosynthesis  
186 module to simulate understory grasses. The modified SPA model was used here. Photosynthesis  
187 process for C3 trees is predicted by using the C3-photosynthesis model of Farquhar and others  
188 (1980), and the simplified C4 photosynthesis model as described by Collatz and others (1992) is  
189 used to determine the C4 net assimilation rate. The model contains 10 canopy layers. The model  
190 user can define the layers accounted for by C3 trees and C4 grass based on the contribution of the  
191 tree or grass to total LAI. ET and T are determined by the Penman-Monteith equation (Monteith  
192 and Unsworth 2008), in which surface conductance is derived internally from the optimal stomatal  
193 conductance that is adjusted to maximize daily carbon uptake per unit of foliar nitrogen and  
194 maintain vapour exchange beneath a threshold maximum to avoid cavitation of the hydraulic  
195 system (Williams and others 1996). Water loss is determined by the water potential gradient

196 between leaf and soil, liquid phase hydraulic resistances and the capacitance of the pathway from  
197 soil to leaf. Detailed information on the parameterization of the model is given in Table 1. More  
198 detailed descriptions of the fundamental equations, model logic, algorithms and the development  
199 history of the SPA model were given by Williams and others (1996, 1998, 2001a) and Whitley and  
200 others (2011).

201 SPA is one of the most widely and successfully applied land surface exchange models and has  
202 been tested across a range of diverse ecosystems such as Arctic tundra (Williams and others 2001a)  
203 and Brazilian tropical rainforests (Fisher and others 2007). The model driven by observed LAI has  
204 also been tested and used for simulating carbon and water cycle components in woodland of arid  
205 and semi-arid Australia (Zeppel and others 2008; Whitley and others 2011). These applications of  
206 the SPA model indicate that model simulation can explain at least 60% of the variation in carbon  
207 and water fluxes in these tested areas. However, it is difficult to obtain daily LAI values at  
208 long-time scale, which limits the application of the model for the long-term simulations.

209 WAVES Model

210 WAVES is an ecohydrological model (Dawes and Hatton 1993; Zhang and others 1996) that  
211 adopts a one or two layer canopy representation with a soil layer underneath. In WAVES, the  
212 micrometeorological interactions between canopy and atmosphere are regulated by the omega  
213 coefficient proposed by Jarvis and McNaughton (1986). The model includes estimates of carbon  
214 storage and allocation between leaves, roots and stems as in Running and Coughlan (1988). The  
215 daily carbon assimilation rate is estimated by the maximum carbon assimilation rate and relative  
216 growth rate multiplicatively, the former of which is a species dependent parameter reported for C3  
217 plants by Collatz and others (1991) and C4 by Collatz and others (1992). Assimilation is allocated

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4 218 according to the priorities of maintenance respiration, growth respiration, leaf and root growth, and  
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6 219 stem growth. Leaf area increase is determined by carbon allocated to leaves and specific leaf area,  
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9 220 and root growth is determined by the allocated carbon that is distributed amongst soil nodes  
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11 221 weighted by the availability of soil water and nutrients following the methodology of Wu (1994).  
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14 222 The physiological responses of canopy conductance and assimilation rate are fully coupled with  
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16 223 climatic regulation on stomata and water and nutrients availability to roots, which allows LAI to  
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19 224 vary with different environmental conditions. The WAVES model has been proven to be able to  
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21 225 successfully reproduce vegetation structure (e.g. LAI) from field observations (Zhang and others  
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24 226 1999; Wang and others 2001; Shao and others 2002). However, WAVES is an ecohydrological  
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26 227 model, not a process-based carbon model. It does not explicitly simulate full carbon cycle and nor  
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29 228 does it provide direct GPP estimates, the latter of which is one of the objectives of this study. As  
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31 229 with SPA, ET was estimated by the Penman-Monteith approach (Monteith and Unsworth 2008) in  
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34 230 WAVES. A more detailed description of WAVES is provided in Zhang and others (1996), Dawes  
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36 231 and others (1998) and Zhang and Dawes (1998).  
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39 232 We recently successfully parameterized and tested WAVES for this site (Chen and others 2014),  
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41 233 using the same flux data as used in the present study. Although MODIS reflectance data are often  
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44 234 noisy, LAI modeled with WAVES agreed reasonably well with measured and MODIS LAI,  
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46 235 derived from the MOD15A2 product (8-Day Composite, 1 km wide  $\times$  1 km high) centered on the  
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49 236 coordinate of the tower (<http://daac.ornl.gov/MODIS/>). The model was able to explain about 93%  
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51 237 of the variation in observed understory LAI (0.04 RMSE) and 65% of the variation in the canopy  
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54 238 LAI (0.05 RMSE, Fig. 1). In the simulation, the coefficient of determination of simulated and  
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56 239 measured canopy LAI was smaller than that for the understory (Chen and others 2014), due to  
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240 extreme variability in leaf physiology, water status and responses to moisture and heat stress of  
241 Mulga as a “stress endurer” (Winkworth 1973; O’Grady and others 2009; Cleverly and others  
242 2013; Eamus and others 2013b). This was also because LAI was optimized to maintain a better  
243 match between simulated and measured values of ET. Generally speaking, the calibrated WAVES  
244 model can be used confidently to simulate vegetation growth in the study area. Thus in the present  
245 study, we firstly used the parameterized WAVES model to obtain the dynamics of LAI for the  
246 period of 1981-2012, and then by using the LAI output from WAVES as an input for SPA, the SPA  
247 model was used to quantify the response of water and carbon fluxes to climate variability at this  
248 Mulga site during 1981–2012. The combination of the two models enabled us to estimate carbon  
249 and water fluxes under different climatic and vegetation characteristics by taking the advantages of  
250 each model.

251 The SPA Model Evaluation

252 The EC flux data during 3 Sep 2010–30 Jun 2013 were used to evaluate the performance of the  
253 SPA model in simulating water and carbon fluxes under variable climate conditions in terms of ET  
254 and GPP. We divided these data into two datasets. The data obtained between 3 Sep 2010 and 31  
255 Dec 2011 were used to parameterize the model; those obtained during 1 Jan 2012 and 30 Jun 2013  
256 were used to validate the model. Model inputs and their values and source of this study were  
257 shown in Table 1. Three indices were used to evaluate the performance of the SPA model: i) the  
258 coefficient of determination ( $r^2$ ), describing the proportion of the variance in measured data  
259 explained by the model; ii) the root mean square error (RMSE), providing a measure of the  
260 absolute magnitude of the error; and iii) model efficiency (ME), presenting variation in measured  
261 values accounted for the model. The indices were calculated as follows:

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2} \quad (1)$$

$$\text{ME} = 1 - \frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (O_i - O_{\text{avg}})^2} \quad (2)$$

## Application of the SPA Model for Long-term Simulations

The validated SPA model was then applied to simulate the responses of carbon and water fluxes in the arid-zone *Acacia* savanna woodland to historical climate variability (1981–2012). For application of the SPA model, meteorological data at half-hourly intervals are needed. To meet this requirement for long-term simulation, daily climate data during 1981–2012 at Territory Grape Farm, extracted from SILO (Jeffrey and others 2001; <http://www.bom.gov.au>) were interpolated into half-hourly intervals. To do this, firstly, the half-hourly meteorological data (temperature, solar radiation, rainfall or VPD) during Sep 2010–Jun 2013 measured at an on-site meteorological station were obtained. Secondly, these measured half-hourly meteorological data were examined and fitted to determine the daily climatological cycle of each climate variable at an half-hourly time step, using a fourth-order polynomial regression. Thirdly, the measured half-hourly meteorological data were converted into daily values for each day of the entire period (Sep 2010–Jun 2013) and then these values were averaged to obtain a daily climatology for each climate variable. Finally, the fitted curve of each climate variable obtained in the second step was used to re-scale the 32 years of meteorological data to obtain long-term half-hourly meteorological data, by multiplying the ratio of the daily value during 1981–2012 to the daily average obtained in the third step. Due to the lack of local CO<sub>2</sub> concentration values, global monthly CO<sub>2</sub> concentration values during 1981–2012 were used for each 30 minutes during the corresponding

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282 month of the year. Moreover, the average annual cycle of half-hourly wind speed during the field  
283 experimental period was used for all the 32 years due to unavailability of wind speed data at this  
284 remote meteorological station.

285 **RESULTS**

286 **Model Performance**

287 The comparisons of simulated ET and GPP with the corresponding measurements obtained from  
288 the field experiment during 3 Sep 2010–30 Jun 2013 are shown in Fig. 2. In general, the model  
289 was able to capture periods of very low and peak values of measured daily ET, which ranged from  
290 0.0 to 5.93 mm with an average of 1.15 mm, compared to the simulated ET that ranged from 0.0 to  
291 5.31 mm with an average of 1.29 mm (Fig. 2a). The SPA model was also able to capture periods of  
292 low and peak daily GPP and replicate seasonal and annual patterns of derived GPP closely (Fig. 2b).  
293 Values of GPP derived from EC measurements ranged from 0 to 5.57 g C m<sup>-2</sup> d<sup>-1</sup> with an average  
294 of 1.52 g C m<sup>-2</sup> d<sup>-1</sup>, with maximum values occurring in March and minima in July. Maximal and  
295 minimal GPP simulated by SPA also occurred in March and July, respectively. The modelled GPP  
296 ranged from 0.09 to 5.43 g C m<sup>-2</sup> d<sup>-1</sup> with an average of 1.49 g C m<sup>-2</sup> d<sup>-1</sup>.

297 The model simulated carbon and water fluxes with acceptable accuracy and precision. There was a  
298 significant positive relationship between simulated and observed ET across the field observational  
299 period (Table 2), with r<sup>2</sup> of 0.71 and RMSE of 0.86 mm d<sup>-1</sup>, although the model slightly  
300 overestimated ET by 12.2% due to an overestimation of LAI values (Fig. 1). This overestimation  
301 resulted from maintaining a match between modelled and measured values of ET in WAVES that  
302 has the difficulty in capturing the extreme variability in leaf physiology, water status and responses  
303 to moisture and heat stress of Mulga as a “stress endurer” (Chen and others 2014). The model

explained 80% of the variation in daily GPP, with a RMSE value of  $0.45 \text{ g C m}^{-2} \text{ d}^{-1}$ . The values of ME were close to 1 for both GPP and ET.

### Seasonal Patterns in Carbon and Water Fluxes

The climate at this site is characterized by two distinct seasons: hot-wet summer (Dec–Feb) and warm winter (Jun–Aug; Fig. 3). During the observation period monthly mean temperatures ranged from  $13.6^\circ\text{C}$  in July to  $29.8^\circ\text{C}$  in January (Fig. 3a), while monthly mean solar radiation varied between  $15.9$  in June and  $26.2 \text{ MJ m}^{-2} \text{ d}^{-1}$  in January (Fig. 3b). About 55% of precipitation fell in the three summer months (Dec to Feb, Fig. 3c). VPD in the summer was almost three times larger than in the winter (Jun to Aug; Fig. 3d) as a result of high temperatures that compensated for the large absolute humidity during the summer. The largest total monthly GPP ( $48.5 \text{ g C m}^{-2}$ ) occurred in March (Fig. 4a), reflecting the influence of high (relative to winter values) soil water content arising from summer rainfall coupled with moderate temperature and solar radiation in this month (relative to higher values in January and much lower values in June; Fig. 3). From March through to September, ecosystem GPP declined exponentially to a minimum of  $20.6 \text{ g C m}^{-2} \text{ mon}^{-1}$ . Simulated ET also displayed strong seasonal variations (Fig. 4b). The largest total monthly ET occurred in February ( $46.2 \text{ mm}$ ) due to the effects of summer rainfall, high temperature and high VPD in this month. After reaching maximum values in February, ET showed an approximately exponential decline to a minimum monthly value of  $11.5 \text{ mm}$  in September.

Using the SPA model with LAI outputs from the WAVES model as inputs, landscape carbon and water fluxes for the C3 overstory and C4 understory were disaggregated. During the wet season (Nov to Mar), simulated total monthly GPP ranged between  $23.4$  and  $48.5 \text{ g C m}^{-2}$ , of which the C3 tree overstory accounted for 62–86% and C4 grass understory contributed 14–38% (Fig. 4c).

Over the same period, the water transpired by the C3 overstory accounted for about 66–81% of the total water-use (ET), while C4 understory accounted for approximately 8–23% (Fig. 4d). During the dry season (Jun to Sep), almost all carbon and water fluxes were accounted for by the C3 component of the vegetation (Fig. 4c, d), as there was little C4 leaf area or biomass to support any carbon and water fluxes.

Inter-annual Variability in Water and Carbon Fluxes

Climatic conditions in the last 32 years were highly variable with large fluctuations in precipitation (97.4–832.5 mm yr<sup>-1</sup>; Fig. 5c). Annual mean VPD showed moderate variation, ranging from 1.3 to 2.1 kPa (Fig. 5d). Likewise, variations in annual mean temperature (21.2–23.4 °C) and solar radiation (20.7–23.1 MJ m<sup>-2</sup> d<sup>-1</sup>) were relatively small (Fig. 5a, b). Such inter-annual climate variability resulted in GPP ranging between 146.4 and 604.7 g C m<sup>-2</sup> yr<sup>-1</sup> (standard deviation of 97.6 g C m<sup>-2</sup> yr<sup>-1</sup>) over the 32-year period (Fig. 6a). C3 trees were estimated to contribute more than 75% of total GPP in 85% of 32 simulated years. In contrast, average annual GPP of C4 grass understory accounted for 20% of total GPP due to its short growing season and small LAI. The annual total ET from the *Acacia* savanna woodland was simulated to vary between 110.2 and 625.8 mm yr<sup>-1</sup> over 32 years, with a standard deviation of 114.2 mm yr<sup>-1</sup> (Fig. 6b). Annual patterns of simulated GPP (Fig. 6a) closely matched those in simulated annual ET (Fig. 6b). Simulated T of the C3 overstory ranged from 74.3 to 459.2 mm yr<sup>-1</sup>, accounting for 60–73% of the estimated ET. In contrast, the simulated water transpired by C4 grasses only accounted for 6–17%.

Ecosystem Water-Use-Efficiency and Inherent WUE

We used SPA outputs to estimate water-use-efficiency at the ecosystem scale (eWUE, calculated as GPP/ET; Perez-Ruiz and others 2010) and inherent WUE (IWUE; calculated as GPP\*VPD/ET;



348 Eamus and others 2013b) (Figs. 7, 8), eWUE for C3 trees (C3 WUE, calculated as  $GPP/T$ ) and C4  
 349 grasses (C4 WUE, calculated as  $GPP/T$ ) (Figs. 7, 8). Monthly mean eWUE showed strong  
 350 seasonal variations, with values ranging from  $0.77$  to  $1.88 \text{ g C m}^{-2} (\text{mm water})^{-1}$  with a standard  
 351 deviation of  $0.42 \text{ g C m}^{-2} (\text{mm water})^{-1}$  (Fig. 7). Even larger variation was found for IWUE,  
 352 varying between  $1.26$  to  $3.39 \text{ g C m}^{-2} (\text{mm water})^{-1}$  with a standard deviation of  $0.61 \text{ g C m}^{-2} (\text{mm}$   
 353  $\text{water})^{-1}$ . The average values of eWUE and IWUE were  $1.28$  to  $2.17 \text{ g C m}^{-2} (\text{mm water})^{-1}$ ,  
 354 respectively. The mean monthly WUE of C4 grasses was always larger than that of C3 trees (37%  
 355 on average).

356 Annual mean eWUE varied between  $0.75$  and  $1.59 \text{ g C m}^{-2} (\text{mm water})^{-1}$  during 1981-2012, with  
 357 an average of  $1.17 \text{ g C m}^{-2} (\text{mm water})^{-1}$  (Fig. 8). The lower eWUE usually occurred in wet years  
 358 when VPD was small, and *vice versa*. Thus, due to the effects of inter-annual variability in VPD,  
 359 compared with that of eWUE, inter-annual variations of IWUE were enlarged, in which the range  
 360 increased from  $1.1$  to  $3.3 \text{ g C m}^{-2} (\text{mm water})^{-1}$ . The average value of eWUE ( $1.1 \text{ g C m}^{-2} (\text{mm}$   
 361  $\text{water})^{-1}$ ) was smaller than that for IWUE ( $2.2 \text{ g C m}^{-2} (\text{mm water})^{-1}$ ).

362 The inter-annual variation of eWUE for C3 trees was similar to that of eWUE due to the large  
 363 proportion of annual GPP and T by C3 vegetation (Fig. 8). Compared with eWUE and C3 WUE,  
 364 C4 WUE showed largest inter-annual variability with a range of  $1.11$  to  $3.06 \text{ g C m}^{-2} (\text{mm water})^{-1}$ .

## 365 DISCUSSION

### 366 The Simulation Models and Data Extrapolation

367 Understanding carbon–water relations in arid-zone woodland ecosystems is important for  
 368 improving land and water management within the limitations of the ecohydrologic system. A  
 369 modeling approach is especially effective in examining the patterns and drivers in complex fluxes

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370 across long timescales because conducting field experiments and maintaining a field-based flux  
371 measurement system in remote regions is difficult and expensive. This study presents a first  
372 attempt to explore the long-term temporal dynamics of water and carbon cycles in an arid-zone  
373 savanna-woodland ecosystem by combining an ecohydrological model, WAVES, that simulates the  
374 dynamics of vegetation growth and development, with a detailed mechanistic soil-plant-  
375 atmosphere model, SPA. Land surface exchange models that simulate long-term fluxes usually  
376 require such input variables as LAI (Baldocchi and Wilson 2001), which is difficult to obtain at  
377 fine- and long-time scales. Thus, attempts to model carbon dioxide and water vapour exchange  
378 over decadal time-scales often require linked ecophysiological models that provide information on  
379 parameters related to vegetation growth (especially LAI).

380 The first objective of this study was to parameterize and test SPA against eddy covariance data.  
381 The large ME and small RMSE values for simulated ET and GPP show that the SPA model, driven  
382 by LAI values provided by the WAVES model, is able to reproduce the responses of water and  
383 carbon fluxes of the woodland ecosystem to climate variability. Although experimental data  
384 used to test the model was only over a 3-year period, this time period contained two years  
385 of contrasting rainfall. The first year was wet (>250 mm above average rainfall), while  
386 little precipitation (>100 mm below average) fell during the second year (Cleverly and  
387 others, 2013). As such, we have reason to believe that the parameters calibrated for the  
388 experimental period are suitable to others years. This combination of two process-based  
389 models has the potential to provide answers to questions concerning the role of climate on  
390 ecosystem water and carbon balances. To use the calibrated model to analyse carbon and water  
391 fluxes of the last 32 years, we first interpolated daily climate data for 32 years into half-hour

intervals to meet the requirement of the SPA model. Some interpolation errors may result from the assumption that each climate variable (temperature, solar radiation, precipitation or vapour pressure deficit) had the same daily cycle throughout the study period. In addition, because of a lack of long-term wind speed data, we assumed the 32-year wind speed was the same as the observed half-hour wind speed climatological cycle. Such assumptions are possibly a major source for uncertainty in simulated GPP and ET at half-hour resolution. A sensitivity analysis showed that a 50% of decrease in wind speed would result into about 2% decrease in simulated ET and 2% increase in simulated GPP, while a 50% of increase in wind speed would decrease about 14% of ET and decrease about 17% of GPP. These uncertainties may further affect eWUE (-4% – 5%) at this time scale. However, being restricted by data availability this study aims to make a first attempt to explore seasonal and inter-annual dynamics of carbon and water fluxes for an arid-zone savanna ecosystem in the remoteness of Australia's interior over such a long time period (1981–2012). We argue that our results of simulated GPP and ET at seasonal and inter-annual scales are reliable, despite those uncertainties, as the daily average of interpolated climate variable were still kept the same as the original daily average.

#### Seasonal Fluxes of GPP and ET and the Relative Contributions of C3 Trees and C4 Grasses (1981-2012)

Simulated GPP and ET were smallest at the end of the dry season (Sep) and highest in the wet season (Feb–Mar; Fig. 4). Although showing a similar seasonal cycle, a linear regression fit of temperature, solar radiation and VPD with GPP and ET indicates a low correlation with the coefficient of determination ( $r^2$ ) varying between 0.001 to 0.23 for GPP and 0.19 to 0.70 for ET (Table 3). In contrast, the correlations between GPP and ET with the LAI and the soil water content

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414 were much stronger at a seasonal timescale ( $r^2$  values  $\geq 0.72$ ; Fig. 9). Thus, meteorological  
415 variables are only indirectly related to GPP and ET at the seasonal time-scale. Consequently, our  
416 first hypothesis that temperature and VPD would explain the seasonal variability of GPP and ET  
417 was rejected. We conclude that it is not the direct influence of climate variables on leaf physiology  
418 *per se* that causes seasonal changes in GPP and ET of the savanna ecosystem but variations in LAI  
419 and soil water that are important. Whereas, by contrast, Migliavacca and others (2009) showed that,  
420 during summer, a significant reduction of net productivity of a poplar plantation under peculiar  
421 eco-climatic conditions was mainly driven by high temperature even in absence of marked soil  
422 water stress. Tian and others (2000) found that seasonality in precipitation (but not temperature),  
423 especially the amount received during the drier months, was an important control on net ecosystem  
424 production in the undisturbed ecosystems of the Amazon Basin.

425 Changes in total LAI were found predominantly in the C4 understory, in which physiological  
426 activity is restricted to the summer (Fig. 10). Consequently, despite having a lower contribution to  
427 the total green biomass, the understory plays a significant role in shaping the seasonality of the  
428 LAI. The months of peak LAI in the understory (Jan–Feb) coincided with peaks in temperature,  
429 precipitation and VPD (Chen and others 2014). In contrast, GPP and T peaked in March (Fig. 4)  
430 after precipitation had mostly ceased, temperature and VPD were moderate, and canopy LAI was  
431 near a minimum (Fig. 10). Mulga GPP and T were relatively small during December through  
432 February (Fig. 4) due to extreme high temperature (Nix and Austin, 1973) and VPD (Eamus and  
433 others 2013b). However, they were even smaller during July through September due to low  
434 precipitation and hence reduced soil moisture content. By the end of the winter dry season, soil  
435 moisture content declined to a minimal value, which was associated with a decline in stomatal

conductance and photosynthetic rate of savanna species generally, including Mulga trees (Eamus and Cole 1997; O'Grady and others 2009; Cleverly and others 2013). The combined effects of minimal understory LAI and declining soil moisture content resulted in little ET and GPP towards the end of the dry season, when Mulga growth was also restricted. In brief, seasonal variability of GPP and ET was driven by LAI and soil moisture in this arid-zone Acacia savanna woodland. Simulated wet season productivity accounted for approximately 50% of total annual productivity as a result of the large contribution by C4 grasses to total LAI and wet soil due to summer precipitation control, which were the main factors to affect GPP (Fig. 9). Due to the high water stress tolerance of Mulga trees (O'Grady and others 2009), they remain photosynthetically active in the dry season (although dropping a large percentage of their green leaf area), thus, contributing 5.7 times more to the total annual GPP compared to the annual C4 grasses. Approximately 62% of annual ET occurred in wet seasons, of which T of C3 trees accounted for 66% and that of C4 grasses accounted for 11%. Although C4 grasses contributed a relatively small proportion of ecosystem ET across the wet season, those contributions were disproportionately focused on sub-seasonal periods of wet soils, high temperature and large VPD (Nix and Austin 1973).

Inter-annual Variation of GPP and ET and the Relative Contributions of C3 Trees and C4 Grasses (1981-2012)

Climate in the last 32 years varied with large fluctuations in precipitation, radiation, temperature and VPD due to the effects of the Australian monsoon depressions (Kong and Zhao 2010; Berry and others 2011). Years with large amounts of precipitation also experienced reduced temperature, solar radiation receipt and VPD (Fig. 5), illustrating the control exerted by precipitation and cloud

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cover on temperature and VPD at an annual timescale (Cleverly and others 2013). Correlation analysis showed that variations in annual GPP and ET were significantly related to inter-annual variations of annual precipitation, and to a lesser extent VPD (Fig. 11). Our results therefore showed that inter-annual variability of annual GPP in savanna woodland ecosystem is functionally more dependent on precipitation and VPD than temperature. In other words, inter-annual variability of GPP and ET is driven by differences in precipitation and VPD, as concluded by Eamus and others (2013b). This is in contrast to other cooler ecosystems such as boreal forests, in which annual GPP is positively correlated with mean annual air temperature (Law and others 2002; Nemani and others 2003). This is because mean annual temperature in the present study is higher than the threshold of 20 °C (Fig. 5), above which GPP is generally insensitive (Wang and others 2008). As a result of high inter-annual variability in precipitation (Fig. 5c) and VPD (Fig. 5d), simulated annual ET and GPP differed substantially between dry years (years when precipitation was below 25% of the precipitation percentiles from 1981 to 2012) and wet years (years when precipitation was larger than 75% of the precipitation percentiles from 1981 to 2012; Fig. 12). Simulated annual ET varied between 110.2 to 625.8 mm, which accounted for 74–134% (97% on average) of annual rainfall ranging from 97.4 to 832.5 mm. The over 100% values of the ratio of annual ET to annual rainfall indicate that there was carry-over of water stored in the soil from one year to the next (Fig. 13a, b). Our simulation results showed that this time lagged response happened in 32% of simulated years and could be sustained up to three continuous years (data not shown). Such time lagged responses have previously been demonstrated in semi-arid grasslands and woodlands (Flanagan and others 2011; Raz-Yaseef and others 2012). The use of water that was released from storage in a different year from which it entered was largest when a relatively wet

year was followed by a dry year. Carry-over of soil moisture is possible in this area due to the patchy but extensive hardpan that underlies central Australian red kandosols within rooting depths (Morton and others 2011). The sub-surface hardpan prevents rainfall from generating deep drainage and thereby increases the duration for which water is available to vegetation. As an evergreen “stress endurer” (Winkworth 1973; O’Grady and others 2009; Cleverly and others 2013; Eamus and others 2013b), Mulga can maintain positive rates of photosynthesis and T in drought years by having access to soil moisture that was stored during antecedent wet years.

Studies showed that, in the tropical eucalypt savannas of northern Australia (annual average rainfall of 1750 mm), C3 vegetation accounted for approximately 60% of the total annual GPP and T of C3 trees contributed about 57% of total annual ET, while C4 grasses contributed 40% and 11% to total annual GPP and ET, respectively (Whitley and others 2011). In contrast, in this study C3 trees accounted for 81% and 71% of the total annual GPP and ET in the semi-arid Mulga woodland region during the 32 years of study period (1981–2012), with C4 grasses contributing 19% of total GPP and T of C4 grasses being 11% of annual total ET (Fig. 6). Even though their annual average contributions to GPP and ET are relatively small due to the large variability in rainfall, the contributions by C4 grasses to annual carbon and water budgets should not be ignored because photosynthesis and T in the understory occur during the summer when GPP in the C3 trees is still minimal (Fig. 5).

#### Ecosystem Water-Use Efficiency and Inherent WUE

Determinations of the temporal pattern of the WUE in arid-wood land ecosystem is an important contribution to our understanding of the carbon-water relations of these systems. Whitley and others (2011) discussed the seasonal and inter-annual patterns of ecosystem WUE in mesic

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4 502 savannas for 5-year period. By contrast, we explored seasonal and inter-annual dynamics of  
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6 503 ecosystem WUE over a longer time period (1981–2012) in a semi-arid woodland savanna. Our  
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9 504 results showed that eWUE was much higher (56% increase) in the dry season than the  
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11 505 corresponding value in the wet season (Fig. 7). This is because that the relative magnitude  
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14 506 difference in GPP between wet season and dry season (Fig. 4a) was much smaller than that in ET  
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16 507 between the two seasons (Fig. 4b). This arose because of the maintenance of a modest GPP and a  
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19 508 much reduced ET of the Mulga in the dry season. The smaller eWUE values in the wet season  
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21 509 resulted from higher VPD, higher temperature and relative more precipitation that increased ET  
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24 510 more than GPP.  
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26 511 Both C3 WUE and C4 WUE were larger in the dry season than in the wet season for similar  
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29 512 reasons as those explaining eWUE discussed above. The relative contributions to total GPP and T  
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31 513 by the C3 and C4 components of the landscape resulted in much larger WUE for C4 grasses than  
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34 514 Mulga trees, indicating the smaller stomatal conductance and larger photosynthetic rates of C4  
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36 515 grasses compared with C3 trees. In contrast, the difference in IWUE between wet and dry seasons  
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39 516 was small (Fig. 7) because of the mediating effects of VPD. However, variations in IWUE can be  
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41 517 overridden at annual timescales, which was found in the current study, through fluctuations in  
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44 518 VPD and by compensation in stomatal conductance and GPP to changing conditions (Beer and  
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46 519 others 2009). Such dependences of IWUE on environmental conditions indicate ecosystem  
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49 520 physiology possesses an inherent ability to adaptively respond to environmental changes (Beer and  
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51 521 others 2009).  
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54 522 In this semi-arid savanna woodland, simulated annual GPP followed a similar pattern to annual ET  
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56 523 (Fig. 6), as a result of the intrinsic link between carbon and water fluxes via stomatal conductance  
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(Beer and others 2009; Leuning 1995; Niu and others 2008). This has also been observed in previous studies (Baldocchi 1994; Beer and others 2009). This linear coupling of GPP and ET resulted in relatively small variations in annual eWUE, ranging from between 0.80 and 1.46 g C m<sup>-2</sup> (mm water)<sup>-1</sup> in 94% of simulated years, with an average of 1.17 g C m<sup>-2</sup> (mm water)<sup>-1</sup> (Fig. 8). Although the SPA model has been validated for this site, there may still be many uncertainties in temporal interpolation of climate data and assumptions in wind speeds which may incur some errors on simulated GPP and ET, which therefore may introduce uncertainties into eWUE. However, the estimated annual mean average eWUE is comparable to those observed for other vegetation types. It was slightly larger than the global annual mean WUE for forests (0.95 g C m<sup>-2</sup> (mm water)<sup>-1</sup>), for grasslands (0.93 g C m<sup>-2</sup> (mm water)<sup>-1</sup>) and for deciduous broadleaf forests (0.87 g C m<sup>-2</sup> (mm water)<sup>-1</sup>), but is similar to evergreen conifer forests (1.15 g C m<sup>-2</sup> (mm water)<sup>-1</sup>) (Ponton and others 2006).

Over long-time scales (i.e. years to decades), the IWUE of mesic to wet ecosystems (500–3500 mm yr<sup>-1</sup> precipitation) decreases with declining soil moisture, LAI and maximal leaf-level assimilation (Beer and others 2009). By contrast in the current study, four of the five wettest years were associated with minimal values in both forms eWUE and IWUE (Fig. 5 and Fig. 8) because ET responded more rapidly to increased precipitation than GPP, and consequently, the larger eWUE usually occurred in dry years. Similarly, Eamus and others (2013b) observed a seasonal increase of IWUE as soil moisture declined for this site Mulga woodland. Large inter-annual variations in precipitation and VPD may lead to large inter-annual variations in IWUE. Due to a larger mean VPD in a dry year than in a wet year, the eWUE in the dry year was increased more than in the wet year when it was normalized by VPD (calculation of IWUE). Consequently IWUE

showed larger year-to-year variations than eWUE.

Climate, GPP and ET

The climate in tropical Australia is characterized by strong coupling between precipitation and the Indian Ocean dipole (Saji and others 1999; Ihara and others 2008), which results in highly variable moisture availability (Van Etten 2009; Papalexiou and Koutsoyiannis 2013). Since the mid-1970s, the entire Indian Ocean has been warming, coinciding with a shift in climate regime over the Pacific Ocean (Ihara and others 2008). During the same period, average annual precipitation has increased and the occurrences of extreme precipitation events has increased, half of which occurred during the latter half of the period of this study (data not shown), which explained the increasing trend and larger variability of simulated annual GPP and ET during this study period. With increasing amounts and variability of precipitation, carbon and water fluxes are expected to become larger in response to (1) a larger proportion of years that promote growth of C4 grasses; (2) carry-over of soil moisture storage for use by C3 trees during favorable conditions in dry years; and (3) higher IWUE at the seasonal time-scale and higher ecosystem WUE at the inter-annual timescale.

**CONCLUSIONS**

The modified SPA model successfully reproduced the seasonal evolution and inter-annual variability of measured gross primary productivity and evapotranspiration, by combining with the WAVES model through use of the LAI outputs of WAVES as inputs to SPA. Linking land surface exchange models with eco-physiological models is an effective way to explore ecosystem gas exchanges on decadal to century time-scales and has the potential to investigate possible impacts of future climate change on carbon and water fluxes of terrestrial ecosystems.

The strong seasonal and inter-annual variations in ecosystem carbon uptake and ET were driven by different climate factors. Maximal ecosystem carbon accumulation rates and ET occurred in the late wet season as a result of accumulation of sufficient soil moisture after intensive summer rainfall and the largest LAI. While the lowest GPP and ET occurred in the late dry season when water limitation was maximal and total LAI was minimal. As such we conclude that seasonality in meteorological variables of temperature, solar radiation, rainfall and vapour pressure deficit cause seasonal responses in LAI and soil water, the latter of which drive seasonal patterns of GPP and ET. Simultaneously ecosystem water-use efficiency showed large seasonal variability as a result of the variations in these climate variables. Simulated annual GPP and ET varied substantially between years due to the effects of large inter-annual variability of precipitation and vapour pressure deficit, ranging from 146.4 and 604.7 g C m<sup>-2</sup> yr<sup>-1</sup> for GPP and 110.2 to 625.8 mm yr<sup>-1</sup> for ET. Average annual precipitation and occurrences of extreme precipitation events have increased during the latter half of the period of this study, which resulted in an increasing trend and larger variability of annual GPP and ET during this period. Climate change, especially changes in annual precipitation and vapour pressure deficit, is likely to cause changes in annual budgets for carbon and water fluxes in this savanna ecosystem. The linear coupling of annual GPP to ET resulted in minimal year-to-year variation in ecosystem water-use efficiency.

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## REFERENCES

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590 Baldocchi DD. 1994. A comparative study of mass and energy exchange rates over a closed C3  
591 (wheat) and an open C4 (corn) crop: II. CO<sub>2</sub> exchange and water use efficiency. Agric For  
592 Meteorol 67(3): 291–321.

593 Baldocchi DD. 1997. Measuring and modelling carbon dioxide and water vapour exchange over a  
594 temperate broad-leaved forest during the 1995 summer drought. Plant, Cell Environ 20: 1108.

595 Baldocchi DD. 2008. Breathing of the terrestrial biosphere: lessons learned from a global network  
596 of carbon dioxide flux measurement systems. Aust J Bot 56: 1–26.

597 Baldocchi DD, Wilson KB. 2001. Modeling CO<sub>2</sub> and water vapour exchange of a temperate  
598 broadleaved forest across hourly to decadal time scales. Ecol Model 142(1): 155–184.

599 Barton CVM, Duursma RA, Medlyn BE, Ellsworth DS, Eamus D, Tissue DT, Adams MA, Conroy  
600 J, Crous KY, Liberloo M, Löw M, Linder S, McMurtrie RE. 2011. Effects of elevated  
601 atmospheric [CO<sub>2</sub>] on instantaneous transpiration efficiency at leaf and canopy scales in  
602 Eucalyptus saligna. Global Change Biol 18: 585–595.

603 Beer C, Ciais P, Reichstein MD, Baldocchi D, Law BE, Papale D, Soussana JF, Ammann C,  
604 Buchmann N, Frank D, Gianelle D, Janssens IA, Knohl A, Köstner B, Moors E, Rouspard O,  
605 Verbeeck H, Vesala T, Williams CA, Wohlfahrt G. 2009. Temporal and among-site variability of  
606 inherent water use efficiency at the ecosystem level. Glob Biogeochem Cyc 23(2), GB2018,  
607 doi:10.1029/2008GB003233.

608 Berry G, Reeder MJ, Jakob C. 2011. Physical mechanisms regulating summertime rainfall over  
609 northwestern Australia. J Climate 24: 3705–3717.

610 Bowman D, Brown GK, Braby MF, Brown JR, Cook LG, Crisp MD, Ford F, Haberle S, Hughes J,  
611 Isagi Y, Joseph L, McBride J, Nelson G, Ladiges PY. 2010. Biogeography of the Australian

- monsoon tropics. *J Biogeography* 37: 201–216.
- Chen C, Eamus D, Cleverly J, Boulain N, Cook P. 2014. Modelling vegetation water-use and groundwater recharge as affected by climate variability in an arid-zone *Acacia* savanna woodland. *J Hydrology* 519(2014): 1084–1096.
- Chen XY, Bowler JM, Magee JW. 1991. Aeolian landscapes in central Australia: gypsiferous and quartz dune environments from Lake Amadeus. *Sedimentology* 38(3): 519–538.
- Cleverly J. 2011. Alice Springs Mulga OzFlux site, OzFlux: Australian and New Zealand Flux Research and Monitoring Network, hdl: 102.100.100/8697.
- Cleverly J, Boulain N, Villalobos-Vega R, Grant N, Faux R, Wood C, Cook PG, Yu Q, Leigh A, Eamus D. 2013. Dynamics of component carbon fluxes in a semi-arid *Acacia* woodland, central Australia. *J Geophys Res-Biogeosciences* 118(3): 1168–1185.
- Collatz GJ, Ball JT, Grivet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agric For Meteorol* 54: 107–136.
- Collatz GJ, Ribas-Carbo M, Berry JA. 1992. Coupled photosynthesis-stomatal conductance model for leaves of  $C_4$  plants. *Aus J Plant Physiol* 19: 519–538.
- Dawes W, Hatton TJ. 1993. Topog\_IRM 1. Model description. CSIRO Division of Water Resources, Technical Memorandum 93: 33.
- Dawes WR, Zhang L, Dyce P. 1998. WAVES V3.5 User Manual, CSIRO Land and Water, Canberra, ACT.
- Eamus D. 2003. How does ecosystem water balance affect net primary productivity of woody ecosystems? *Funct Plant Biol* 30: 187–205.

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634 Eamus D, Boulain N, Cleverly J, Breshears DD. 2013a. Global change-type drought-induced tree  
635 mortality: vapour pressure deficit is more important than temperature per se in causing decline in  
636 tree health. *Ecol Evol* 3: 2711–2729.

637 Eamus D, Cleverly J, Boulain N, Grant N, Faux R, Villalobos-Vega R. 2013b. Carbon and water  
638 fluxes in an arid-zone *Acacia* savanna woodland: An analyses of seasonal patterns and responses  
639 to rainfall events. *Agric For Meteorol* 182–183: 225–238.

640 Eamus D, Cole S. 1997. Diurnal and seasonal comparsons of assimilation, phyllode conductance  
641 and water potential of tree *Acaia* and one *Eucalyptus* species in the wet-dry tropics of Australia.  
642 *Aust J Bot* 45: 275–290.

643 Eamus D, Prior L. 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among  
644 phenologies. *Advan Ecol Res* 32: 113–197.

645 Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO<sub>2</sub>  
646 assimilation in leaves of C3 species. *Planta* 149: 78–90.

647 Fisher RA, Williams M, Lola da Costa A, Malhi Y, da Costa RF, Almeida S, Meir P (2007) The  
648 response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses  
649 from a throughfall exclusion experiment. *Glob Change Biol* 13: 1–18.

650 Flanagan LB, Adkinson AC. 2011. Interacting controls on productivity in a northern Great Plains  
651 grassland and implications for response to ENSO events. *Glob Change Biol* 17: 3293–3311.

652 Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K. 1996. Climate  
653 change 1995. The science of climate change. Cambridge University Press, Cambridge pp.572.

654 Ihara C, Kushnir Y, Cane MA. 2008. Warming trend of the Indian Ocean SST and Indian Ocean  
655 dipole from 1880 to 2004. *J Climate* 21: 2035–2046.

- IPCC. 2014. Working Group II contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, United Kingdom.
- Jarvis PG, McNaughton KG. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv Ecol Res* 15: 1–49.
- Jeffrey SJ, Carter JO, Moodie KB, Beswick AR. 2001. Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environ Model Software* 16: 309–330.
- Kong Q, Zhao S. 2010. Heavy rainfall caused by interactions between monsoon depression and middle-latitude systems in Australia: a case study. *Meteor Atmos Phys* 106: 205–226.
- Landsberg JJ, Coops NC. 1999. Modeling forest productivity across large areas and long periods. *Nat Res Model* 12: 383–411.
- Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, Berbigier P, Davis K, Dolman AJ, Falk M, Fuentes JD, Goldstein A, Granier A, Grelle A, Hollinger D, Janssens IA, Jarvis P, Jensen NO, Katul G, Mahli K, Matteucci G, Meyers T, Monson R, Munger W, Oechel W, Olson R, Pilegaard K, Paw UKT, Thorgeirsson H, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S. 2002. Environmental controls over carbon dioxide and water vapour exchange of terrestrial vegetation. *Agric For Meteorol* 113: 97–120.
- Leuning R. 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant Cell Environ* 18(4): 339–355.
- Linderson ML, Mikkelsen TN, Ibrom A, Lindroth A, Ro-Poulsen H, Pilegaard K. 2012. Up-scaling of water use efficiency from leaf to canopy as based on leafgas exchange relationships and the modelled in-canopy light distribution. *Agric For Met* 152: 201–211.

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55  
56  
57  
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59  
60

678 MacFarlane C, Hoffman M, Eamus D, Kerp N, Higginson S, McMurtrie R, Adams M. 2007.  
679 Estimation of leaf area index in eucalypt forest using digital photography. *Agric For Meteorol*  
680 143: 176–188.

681 Migliavacca M, Meroni M, Manca G, Matteucci G, Montagnani L, Grassi G, Zenone T,  
682 Teobaldelli M, Goded I, Colombo R, Seufert G. 2009. Seasonal and interannual patterns of  
683 carbon and water fluxes of a poplar plantation under peculiar eco-climatic conditions. *Agric For*  
684 *Meteorol* 149(9): 1460–1476.

685 Monteith J, Unsworth M. 2008. *Principles of Environmental Physics*. Edward Arnold, London, UK  
686 pp250.

687 Morton SR, Stafford Smith DM, Dickman CR, Dunkerley DL, Friedel MH, McAllister RRJ, Reid  
688 JRW, Roshier DA, Smith MA, Walsh FJ, Wardle GM, Watson IW, Westoby M. 2011. A fresh  
689 framework for the ecology of arid Australia. *J Arid Environ* 75(4): 313–329.

690 Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running  
691 SW. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to  
692 1999. *Science* 300(5625): 1560–1563.

693 Niu SL, Wu MY, Han Y, Xia JY, Li LH, Wan SQ. 2008. Water-mediated responses of ecosystem  
694 carbon fluxes to climatic change in a temperate steppe. *New Phyt* 177: 209–219.

695 Nix HA, Austin MP. 1973. Mulga: a bioclimatic analysis. *Tropic Grassl* 7: 9–20.

696 O'Grady AP, Cook PG, Eamus D, Duguid A, Wischusen JDH, Fass T, Worldege D. 2009.  
697 Convergence of tree water use within an arid-zone woodland. *Oecologia* 160: 643–655.

698 Papalexiou SM, Koutsoyiannis D. 2013. Battle of extreme value distributions: A global survey on  
699 extreme daily rainfall. *Water Res Res* 49: 10.



- 700 Perez-Ruiz ER, Garatuza-Payan J, Watts CJ, Rodriguez JC, Yepez EA, Scott RL. 2010. Carbon  
 701 dioxide and water vapour exchange in a tropical dry forest influenced by the North American  
 702 Monsoon System (NAMS). *J Arid Environ* 74: 556–563.
- 703 Ponce-Campos GE, Moran MS, Huete A, Zhang Y, Bresloff C, Huxman TE, Eamus D, Bosch DD,  
 704 Buda AR, Gunter SA, Scalley TH, Kitchen SG, McClaran MP, McNab WH, Montoya DS,  
 705 Morgan JA, Peters DPC, Sadler JE, Seyfried MS, Starks PJ. 2013. Ecosystem resilience despite  
 706 large-scale altered hydroclimatic conditions. *Nature* 494: 349–352.
- 707 Ponton S, Flanagan LB, Alstad KP, Johnson BG, Morgenstern K, Kljun N, Black TA, Barr AG.  
 708 2006. Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and  
 709 grassland using eddy covariance and carbon isotope techniques. *Global Change Biol* 12:  
 710 294–310.
- 711 Raz-Yaseef N, Yakir D, Schiller G, Cohen S. 2012. Dynamics of evapotranspiration partitioning in  
 712 a semi-arid forest as affected by temporal rainfall patterns. *Agric For Meteorol* 157: 77–85.
- 713 Running SW, Coughlan JC. 1988. A general model of forest ecosystem processes for regional  
 714 applications. 1. Hydrological balance, canopy gas exchange and primary production processes.  
 715 *Ecolo Model* 42: 125-154.
- 716 Saji NH, Goswami BN, Vinayachandran PN, Yamagata T. 1999. A dipole mode in the tropical  
 717 Indian Ocean. *Nature* 401: 360–363.
- 718 Salinger MJ. 2005. Climate variability and change: past, present and future-an overview. *Climatic*  
 719 *Change* 70(1-2): 9–29.
- 720 Schwarz PA, Law BE, Williams M, Irvine J, Kurpius M, Moore D. 2004. Climatic versus biotic  
 721 constraints on carbon and water fluxes in seasonally drought-affected ponderosa pine ecosystems.

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722 Global Biogeochem Cyc 18: 1–17.

723 Shao MA, Huang M, Zhang L, Li YS. 2002. Simulation of field-scale water balance on the Loess

724 Plateau using the WAVES model. ACIAR Mono Ser 84: 48–56.

725 Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich Iii J, Moore Iii B, Vörösmarty CJ.

726 2000. Climatic and biotic controls on annual carbon storage in Amazonian ecosystems. Global

727 Ecol Biogeogr 9(4): 315-335.

728 Twine TE, Kustas WP, Norman JM, Cook DR, Houser PR, Meyers TP, Prueger JH, Starks PJ,

729 Wesley ML. 2000. Correcting eddy-covariance flux underestimates over a grassland. Agric For

730 Meteorol 103: 279–300.

731 Van Etten EJB. 2009. Inter-annual rainfall variability of arid Australia: Greater than elsewhere?

732 Aust Geogr 40: 109–120.

733 Wang H, Zhang L, Dawes WR, Liu C. 2001. Improving water use efficiency of irrigated crops in

734 the North China Plain—measurements and modelling. Agric Water Manage 48(2): 151–167.

735 Wang X, Wang C, Yu G. 2008. Spatio-temporal patterns of forest carbon dioxide exchange based

736 on global eddy covariance measurements. Sci China Ser D: Earth Sci 51: 1129–1143.

737 Weiss M, Baret F, Smith GJ, Jonckheere I, Coppin P. 2004. Review of methods for in situ leaf area

738 index (LAI) determination Part II, Estimation of LAI, errors and sampling. Agric For Meteorol

739 121: 37–53.

740 Whitley RJ, Macinnis-Ng CM, Hutley LB, Beringer J, Zeppel M, Williams M, Taylor D, Eamus, D.

741 2011. Is productivity of mesic savannas light limited or water limited? Results of a simulation

742 study. Glob Change Biol 17(10): 3130–3149.

743 Williams M, Eugster W, Rastetter EB, Mcfadden JP, Chapin Iii FS. 2000. The controls on net

- ecosystem productivity along an Arctic transect: a model comparison with flux measurements. *Glob Change Biol* 6(S1): 116–126.
- Williams M, Law BE, Anthoni PM, Unsworth MH. 2001a. Use of a simulation model and ecosystem flux data to examine carbon-water interactions in Ponderosa pine. *Tree Phys* 21: 287–298.
- Williams M, Rastetter EB, Shaver GR, Hobbie JE, Carpino E, Kwiatkowski B. 2001b. Primary production of an Arctic watershed: an uncertainty analysis. *Ecol Appl* 11 (6): 1800–1816.
- Williams M, Malhi Y, Nobre AD, Rastetter EB, Grace J, Pereira MGP. 1998. Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Plant Cell Environ* 21(10): 953–968.
- Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, Melillo JM, Munger JW, Fan SM, Nadelhoffer KJ. 1996. Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ* 19(8): 911–927.
- Wilson K, Goldstein A, Falge E, Aubinet M, Baldocchi D, Berbigier P, Bernhofer C, Ceulemans R, Dolman H, Field C, Grelle A, Ibrom A, Law BE, Kowalski A, Meyers T, Moncrieff J, Monson R, Oechel W, Tenhunen J, Verma S, Valentini R. 2002. Energy balance closure at FLUXNET sites. *Agric For Meteorol* 113: 223–243.
- Winkworth RE. 1973. Eco-physiology of Mulga (*Acacia aneura*). *Tropic Grassl* 7(1): 43–48.
- Wohlfahrt G, Fenstermaker LF, Arnone JA. 2008. Large annual net ecosystem CO<sub>2</sub> uptake of a Mojave Desert ecosystem. *Glob Change Biol* 14: 1475–1487.
- Wu H, Rykiel Jr EJ, Hatton T, Walker J. 1994. An integrated rate methodology (IRM) for

1  
2  
3  
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766 multi-factor growth rate modelling. *Ecol Model* 73: 97–116.

767 Yan LM, Chen SP, Huang JH, Lin GH. 2011. Water regulated effects of photosynthetic substrate  
768 supply on soil respiration in a semiarid steppe. *Glob Change Biol* 17: 1990–2001.

769 Zeppel M, Macinnis-Ng C, Palmer A, Taylor D, Whitley R, Fuentes S, Yunusa I, Williams M,  
770 Eamus D. 2008. An analysis of the sensitivity of sap flux to soil and plant variables assessed for  
771 an Australian woodland using a soil–plant–atmosphere model. *Funct Plant Biol* 35 (6): 509–520.

772 Zhang L, Dawes WR (Eds). 1998. WAVES-An Integrated Energy and Water Balance Model.  
773 Technical Report No. 31/98, CSIRO Land and Water, Canberra, Australia.

774 Zhang L, Dawes WR, Hatton TJ. 1996. Modelling hydrologic processes using a biophysically  
775 based model application of WAVES to FIFE and HAPEX-MOBILHY. *J Hydrology* 185:  
776 147–169.

777 Zhang L, Dawes WR, Slavich PG, Meyer WS, Thorburn PJ, Smith DJ, Walker GR. 1999. Growth  
778 and ground water uptake responses of lucerne to changes in groundwater levels and salinity:  
779 lysimeter, isotope and modelling studies. *Agric Water Manage* 39(2): 265–282.

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## Figure Legends

Figure 1. Comparison of total leaf area index (LAI) from field measurements, MODIS and simulations (a). Comparison of measured and simulated break down of canopy (b) and understory (c) LAI.

Figure 2. Comparison of measured and simulated daily ET (a) and GPP (b) at Alice Spring flux station from 3 Sep 2010 to 30 Jun 2013.

Figure 3. Monthly mean air temperature (a), monthly mean solar radiation (b), monthly precipitation (c) and monthly mean vapour pressure deficit (VPD) (d) during 1981–2012 at Territory Grape Farm Station obtained from SILO (Jeffrey and others 2001). The error bar indicates the ranges of monthly mean air temperature, mean solar radiation, monthly precipitation or monthly mean VPD during 1981–2012 for each month.

Figure 4. (a) Simulated seasonal dynamics of gross primary productivity (GPP) and (c) the corresponding contributions of tree (C3) and understory (C4); (b) Simulated seasonal dynamics of ecosystem evapotranspiration (ET) and (d) transpiration (T) of C3 and C4 during 1981–2012. The dotted–solid lines represent the mean monthly values averaged over the period 1981–2012. The error bars indicate the range of monthly GPP and ET for each month during 1981–2012.

Figure 5. Mean annual temperature (a), mean annual solar radiation (b), annual precipitation (c) and mean annual vapour pressure deficit (VPD; d) during 1981–2012.

Figure 6. (a) Simulated total annual GPP and the corresponding contributions of C3 and C4; (b) Simulated total annual ET and transpiration (T) of C3 and C4 during 1981–2012.

Figure 7. Simulated mean seasonal variations of ecosystem water-use-efficiency (eWUE), inherent water-use-efficiency (IWUE), WUE for C3 trees (C3 WUE) and WUE for C4 grasses (C4 WUE) during 1981–2012.

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804 Figure 8. Simulated annual mean water-use-efficiency (eWUE), annual mean inherent  
805 water-use-efficiency (IWUE), eWUE for C3 trees (C3 WUE) and eWUE for C4 grasses (C4  
806 WUE) during 1981–2012.

807 Figure 9. The Average monthly (Jan-Dec) GPP (a, c) and ET (b, d) as a function of average  
808 monthly (Jan-Dec) total LAI (upper panel) and soil moisture content (lower panel) during  
809 1981–2012. \*\* indicates  $p < 0.01$ .

810 Figure 10. Simulated monthly mean LAI of the canopy (C3), understory (C4) and their total during  
811 1981–2012, obtained from Chen *et al.* (2014).

812 Figure 11. The linear/curvilinear relationship between annual total GPP (solid line) and ET (dashed  
813 line) and precipitation (a), vapour presser deficit (VPD; b) and temperature (c). \*\* indicates  $p <$   
814  $0.01$ ; \* indicates  $p < 0.05$ .

815 Figure 12. Simulated seasonal dynamics of gross primary productivity (GPP; a) and ecosystem  
816 evapotranspiration (ET; b) in dry (less than 25% of the precipitation percentiles) and wet (higher  
817 than 75% of the precipitation percentiles) years during 1981–2012.

818 Figure 13. The difference between simulated annual ET and precipitation as a function of annual  
819 precipitation during 1981–2012 (a). The difference between simulated annual ET and  
820 precipitation as a function of the previous year's precipitation during 1981–2011 (b). A positive  
821 difference (ET exceeded rainfall) means there was carry-over of water in a given year and this  
822 effect was largest when dry years followed wet years. \*\* indicates  $p < 0.01$ .

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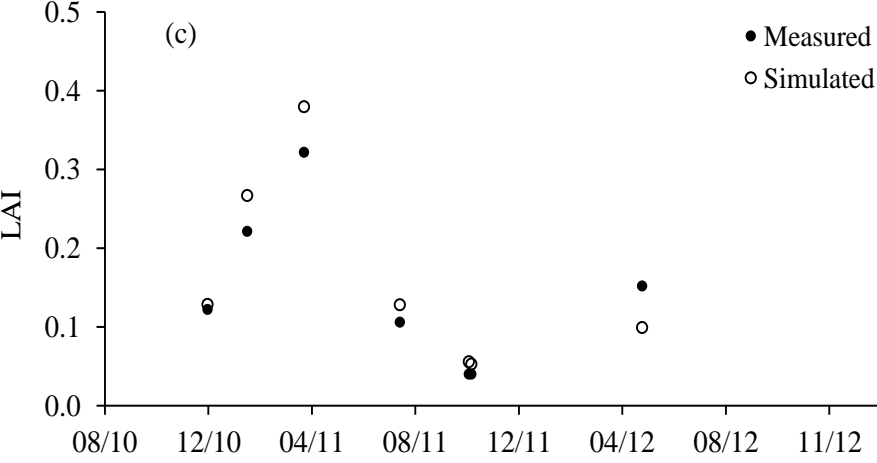
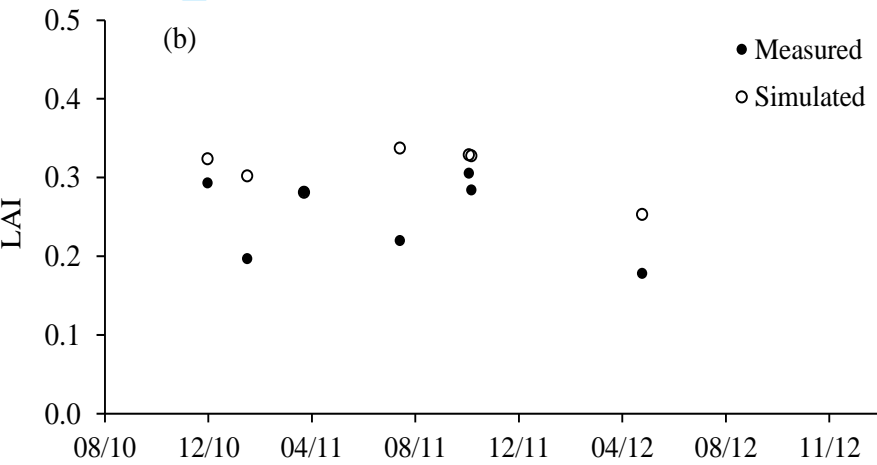
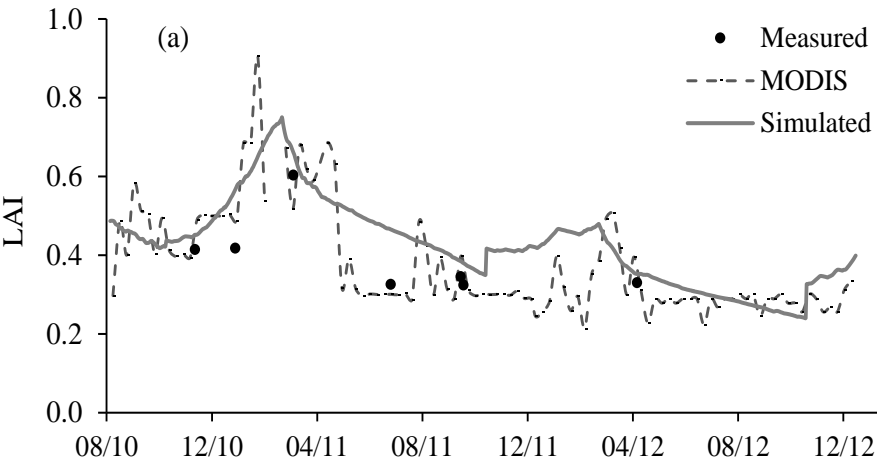
824 **Table Legends**

825 **Table 1:** Parameter/variable values used in soil-plant atmosphere (SPA) for this study.

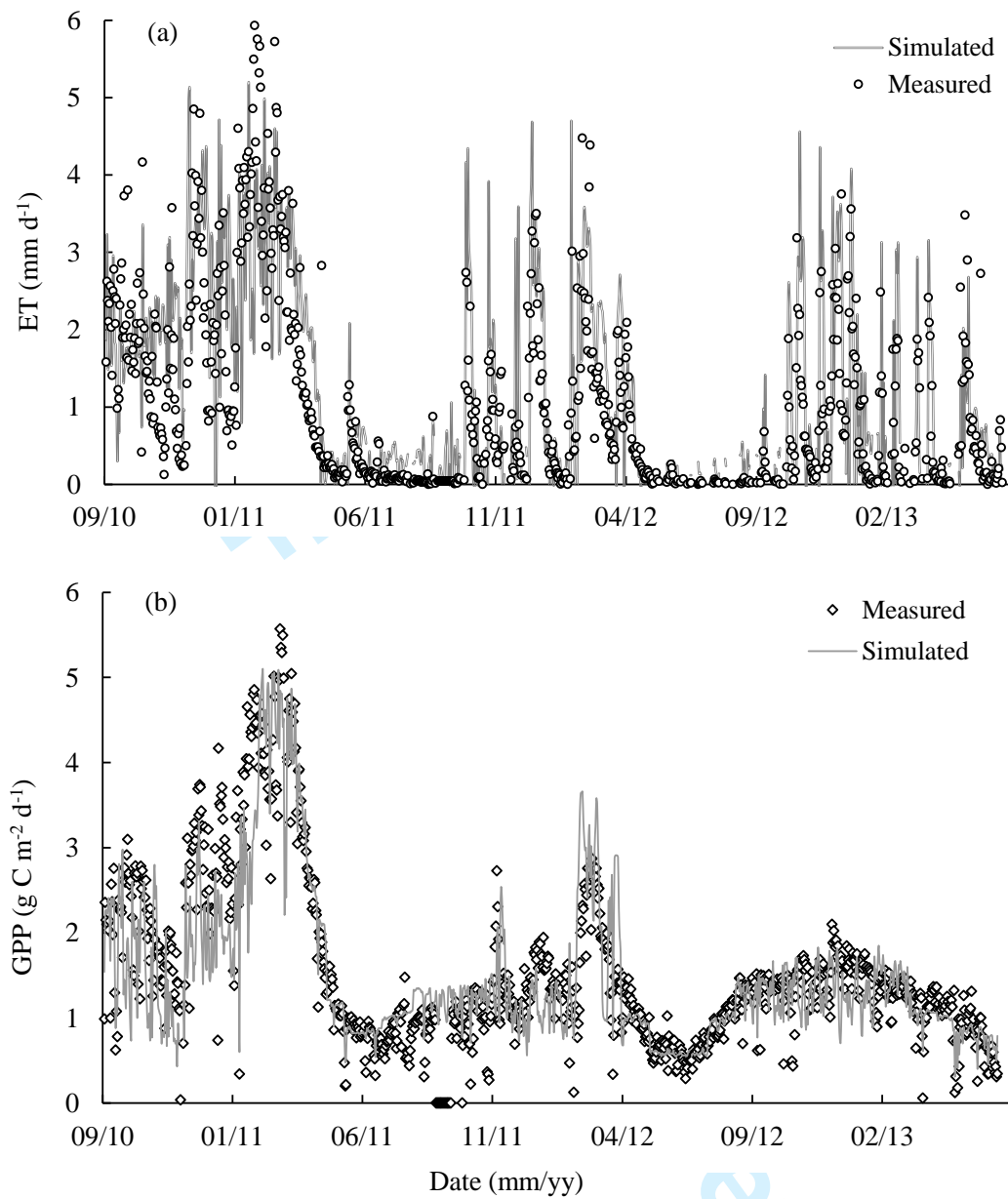
826 **Table 2:** The coefficient of determination ( $r^2$ ), root mean square error (RMSE) and model  
827 efficiency (ME) of simulated ET and GPP.

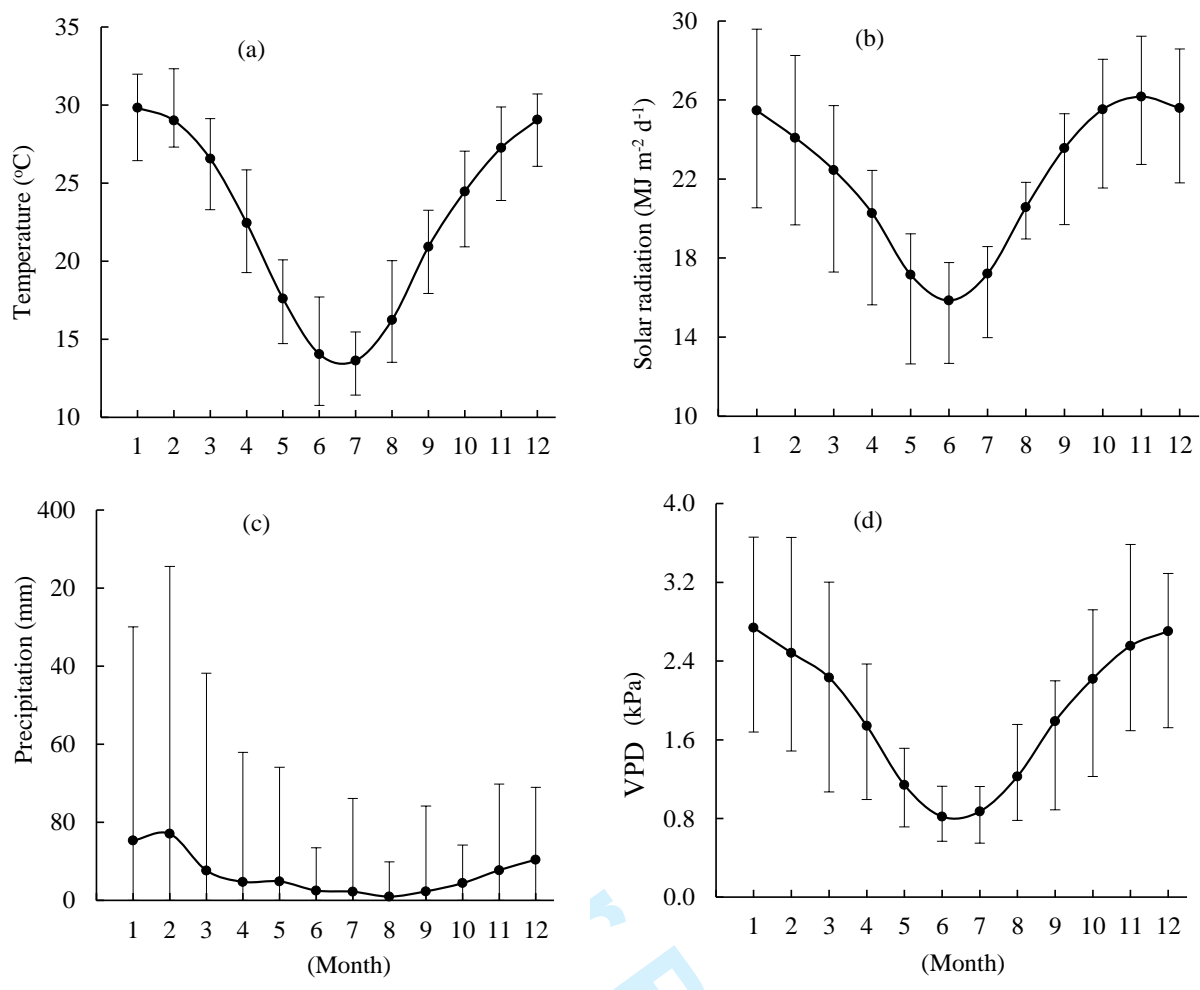
828 **Table 3:** The linear relationship between average monthly gross primary productivity (GPP),  
829 evapotranspiration (ET) and temperature (T), precipitation (P), solar radiation (SR), vapour  
830 pressure deficit (VPD) and the linear relationship between ecosystem water-use efficiency (eWUE)  
831 and T, P, SR, VPD and average total LAI (LAI) and soil water content (SW) during 1981–2012.

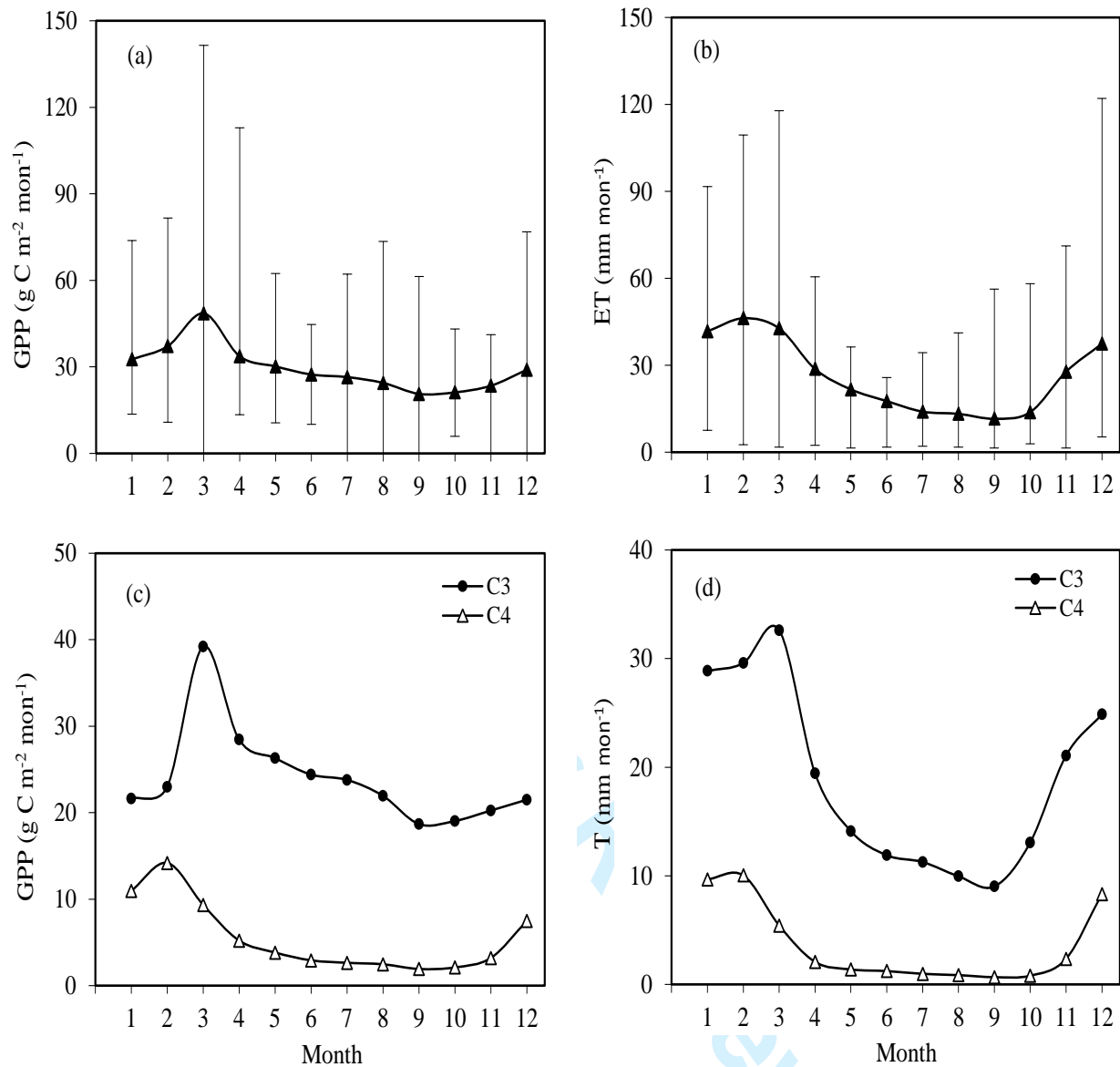
832 \*\* indicates  $p < 0.01$ .



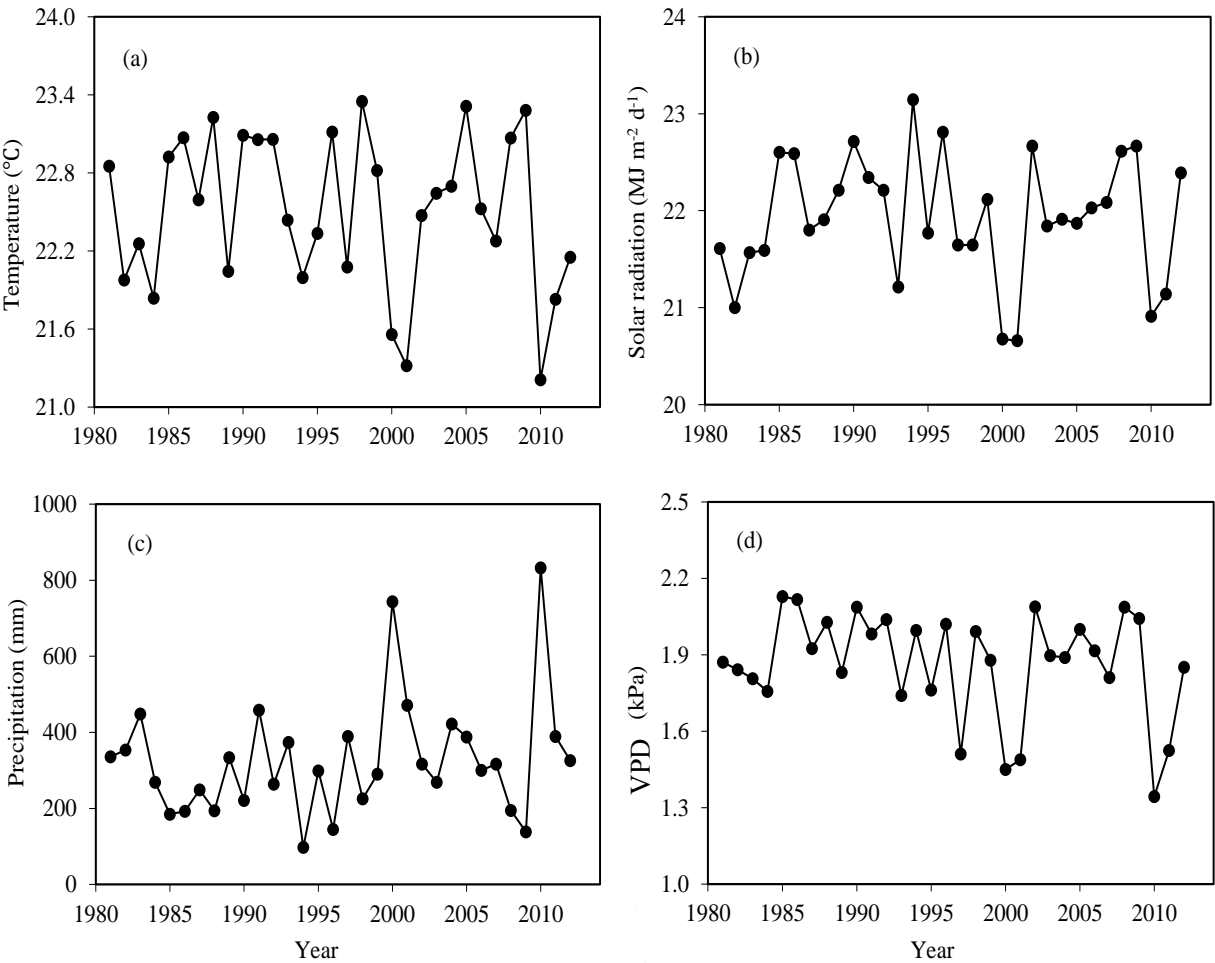




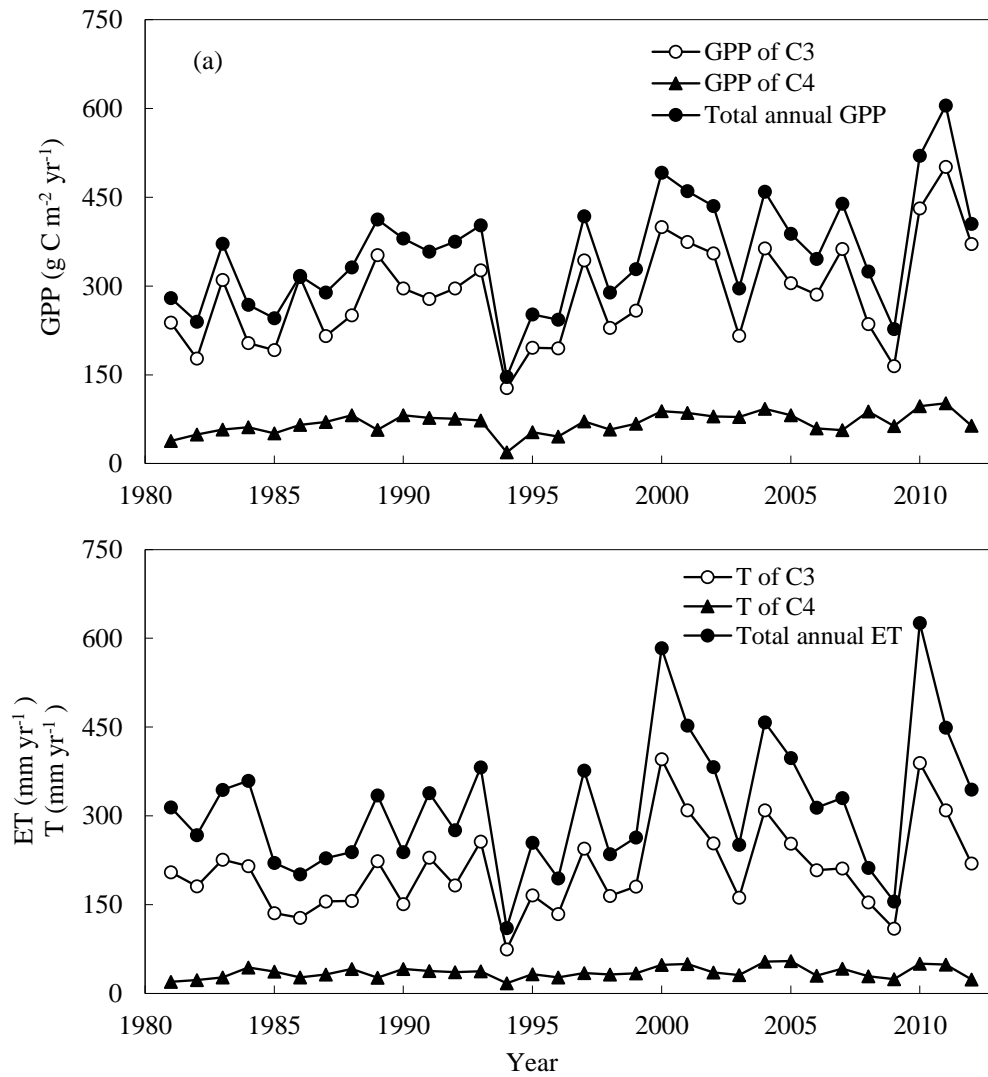


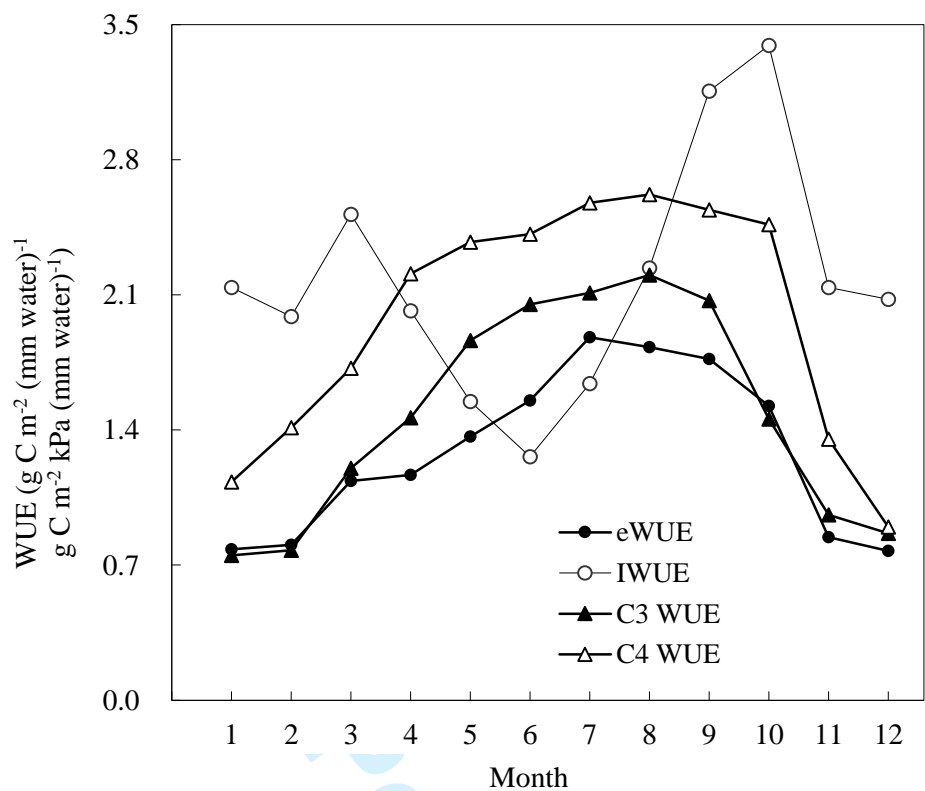


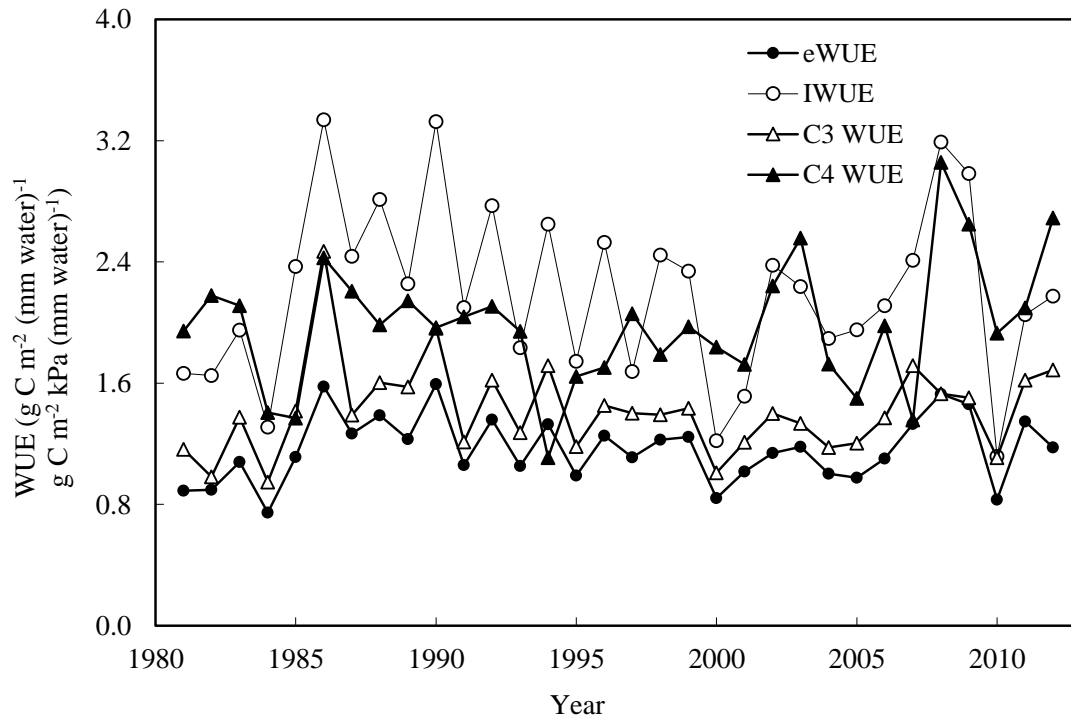
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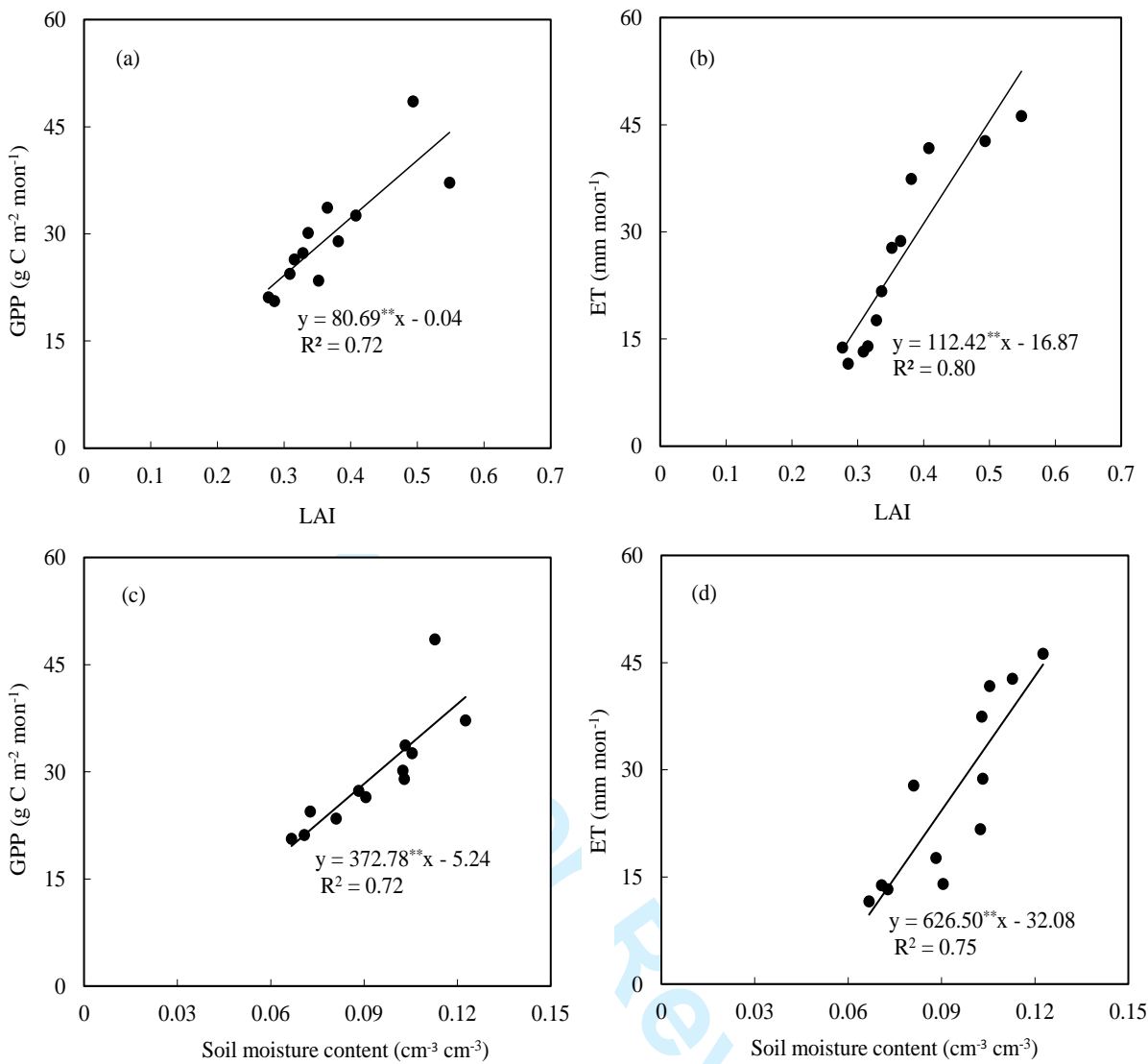


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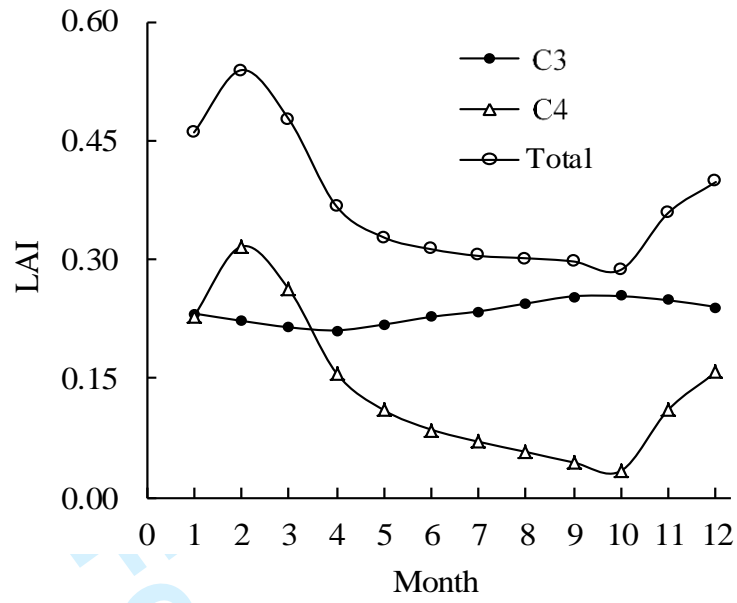


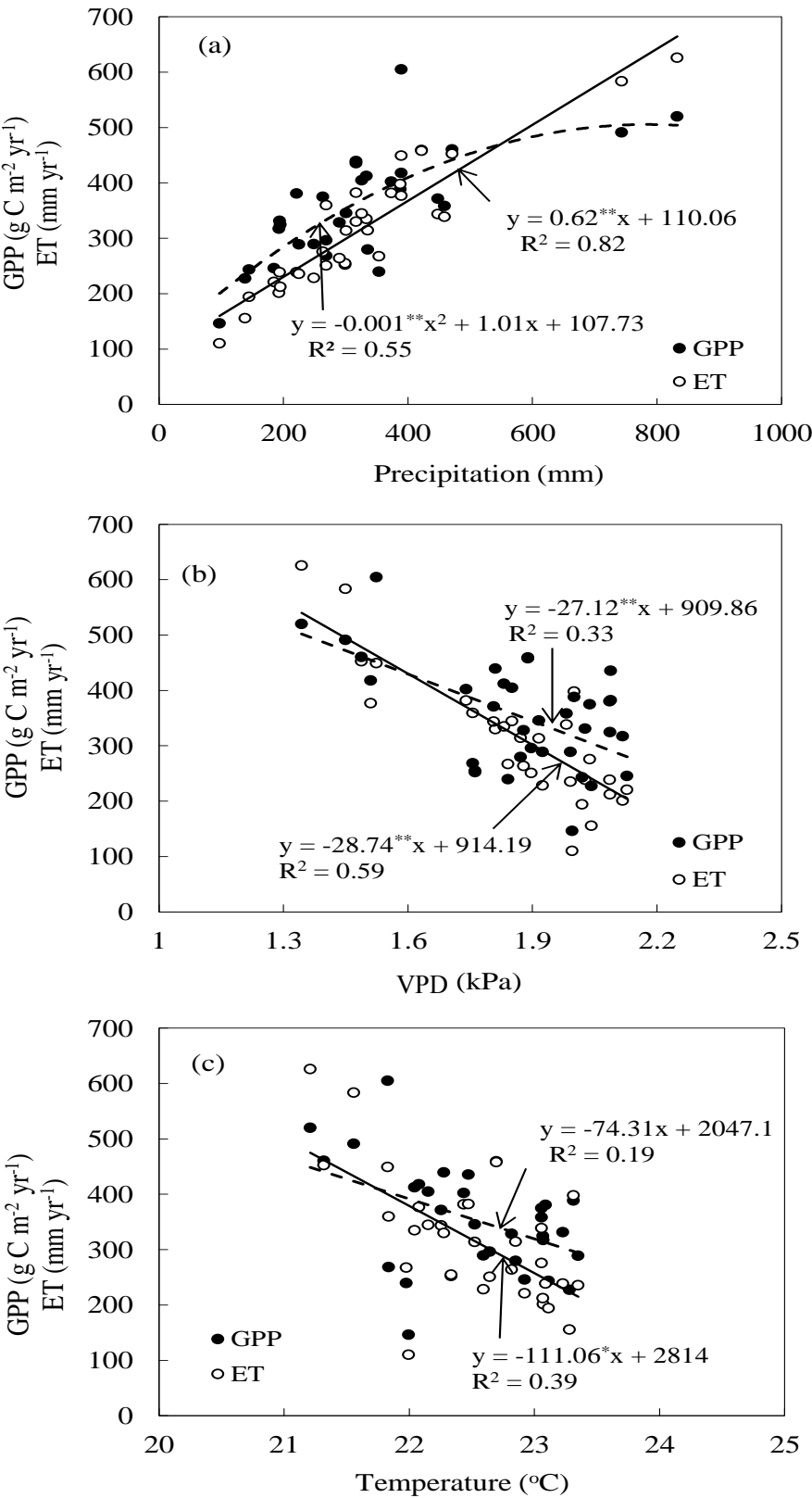


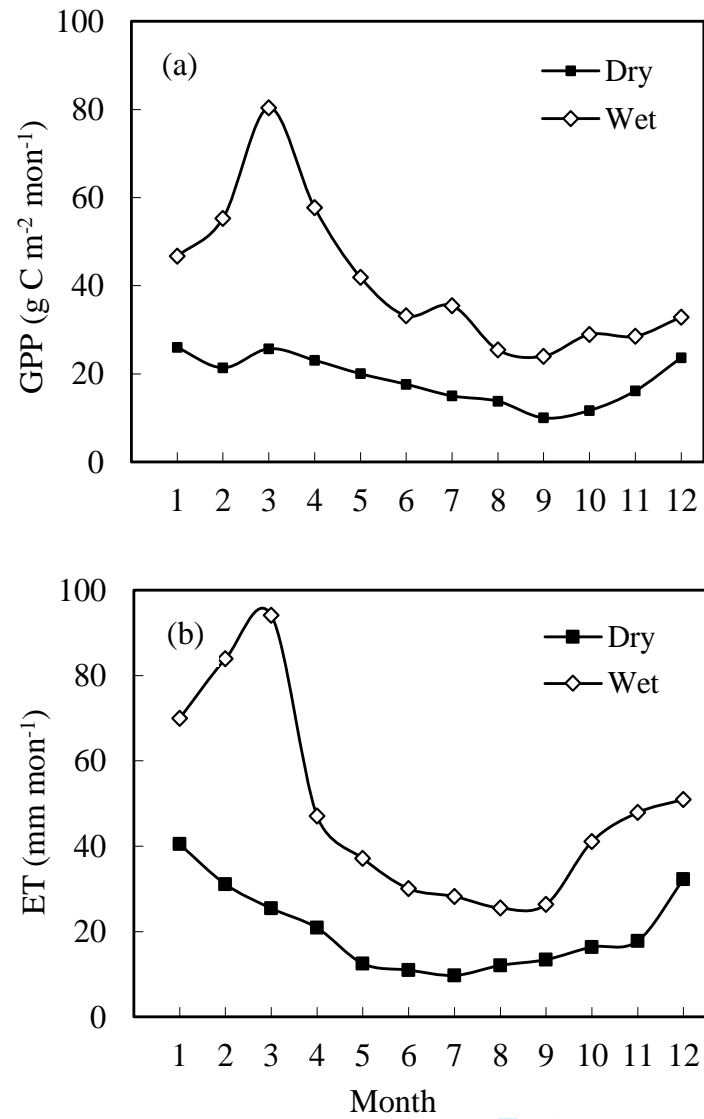


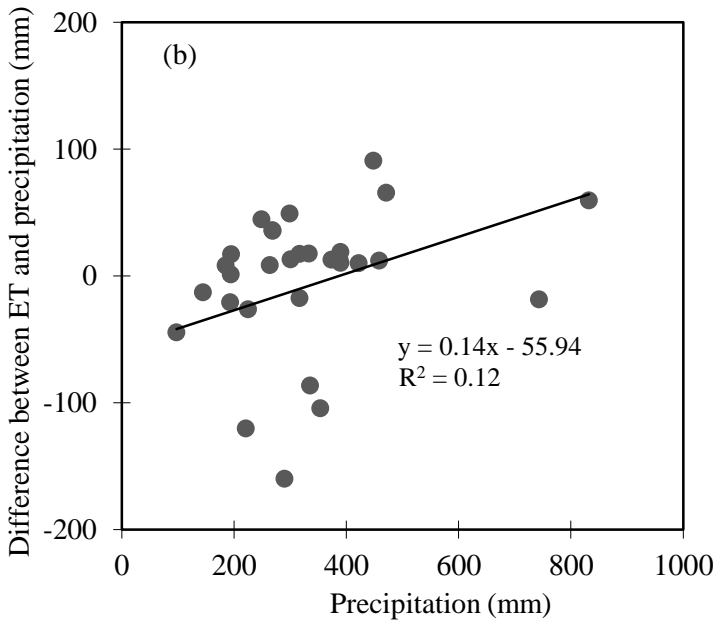
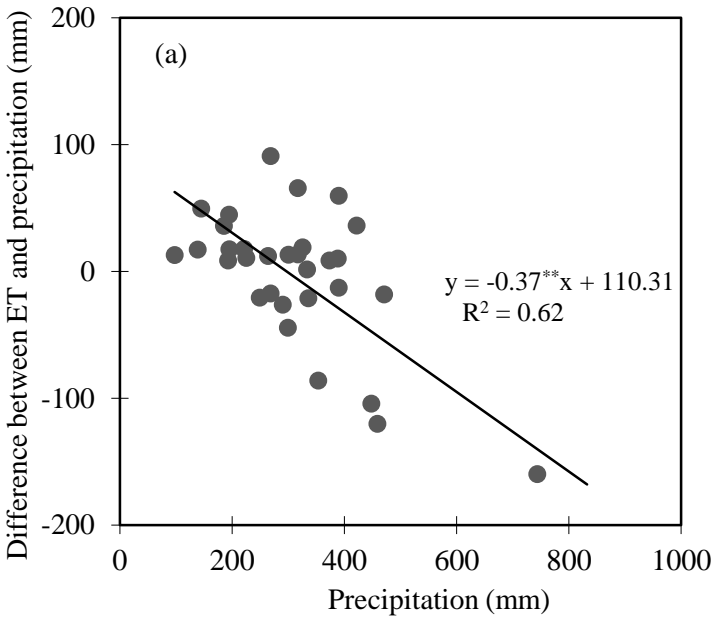












**Table 1:** Parameter/variable values used in SPA

Parameter/variable	Symbol	Units	Value	Source
<b>Meteorology</b>				
Air temperature	$T_a$	$^{\circ}\text{C}$	Variable	Extracted from SILO (Jeffrey <i>et al.</i> , 2001) and measured
Precipitation	P	mm		
Solar radiation	S	$\text{W m}^{-2}$		
Vapour pressure deficit	VPD	hPa		
Photosynthetically active radiation	PAR		Variable	Calculated based on solar radiation
Wind speed	W	m/s	Variable	Measured and estimated
<b>Soil</b>				
Layer height of soil	HS	m	0.1–1.0m, then 1.1–4 m	Site estimated
% soil clay content in top 10 cm		%	15	Measured
% soil sand content in top 10 cm		%	74	Measured
Organic matter content in top 10 cm		%	20	Measured
Soil water potential	$\Psi_s$	MPa	-3	Predawn leaf water potential
Initial soil water content		$\text{cm}^{-3} \text{cm}^{-3}$	Variable	Measured
Root biomass		g	1500	Pressland (1975)
Rooting depth		m	4	Hill and Hill (2003), Anderson <i>et al.</i> (2008) and Barron <i>et al.</i> (2012)
<b>Biophysics</b>				
Canopy layer capacitance	$C_n$	$\text{mmol layer}^{-1} \text{MPa}^{-1}$	5000	Williams <i>et al.</i> (1996)
Canopy hydraulic conductivity	$G_{\text{plant}}$	$\text{mmol m}^{-1} \text{s}^{-1} \text{MP}^{-1}$	3.5	Zeppel <i>et al.</i> (2008)
Leaf area index	LAI	$\text{m}^{-2} \text{m}^{-2}$	0.13–0.97	Simulated by WAVES and measured
Dimension of leaves		$\text{m}^2$	0.08	Prior <i>et al.</i> (1997)
Minimum sustainable leaf water potential	$\Psi_{\text{imin}}$	MPa	-20	Measured

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**Continued: Table 1:** Parameter/variable values used in SPA

Areal concentration of leaf N	N	g m <sup>-2</sup>	2.9	Evans <i>et al.</i> (2000)
Proportion of total canopy N in top layer	N <sub>top</sub>		0.1	Site estimated
Leaf temperature	T <sub>i</sub>	°C	Variable	Extracted from SILO (Jeffrey <i>et al.</i> , 2001) and measured
C3 RuBP carboxylation capacity	C3, V <sub>cmax</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	30.4	Adjusted based on the value
C3 maximum electron transport rate	C3, J <sub>max</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	50.1	in Whitely <i>et al.</i> (2011)
C4 RuBP carboxylation capacity	C4, V <sub>cmax</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	26.3	
δA/δg <sub>s</sub> threshold for stomatal opening	t	%	1.0007	Williams <i>et al.</i> (1996)
Root resistivity		MPa s g mol <sup>-1</sup>	100	Whitely <i>et al.</i> (2011)
Fine root radius	r <sub>r</sub>	m	0.0001	Measured

**Table 2:** The  $r^2$ , RMSE and ME of simulated ET and GPP.

Item	Observed range (mean)	Simulated range (mean)	$r^2$	RMSE	ME
ET (mm d <sup>-1</sup> )	0.0–5.93 (1.15)	0.0–5.31 (1.29)	0.71	0.86	0.90
GPP (g C m <sup>-2</sup> d <sup>-1</sup> )	0–5.57 (1.52)	0.09–5.43 (1.49)	0.80	0.45	0.79

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1    **Table 3:** Relationship between GPP, ET, WUE and climate factors, LAI and SW

Factors	r <sup>2</sup>	Factors	r <sup>2</sup>
GPP-T	0.13	eWUE-T	0.90 <sup>**</sup>
GPP-P	0.23	eWUE-P	0.51 <sup>**</sup>
GPP-SR	0.001	eWUE-SR	0.94 <sup>**</sup>
GPP-D	0.06	eWUE-D	0.96 <sup>**</sup>
ET-T	0.59 <sup>**</sup>	eWUE-LAI	0.14
ET-P	0.70 <sup>**</sup>	eWUE-SW	0.03
ET-SR	0.18		
ET-D	0.42 <sup>**</sup>		

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