

***"This is the peer reviewed version of the following article:*** WHITLEY, R. J., MACINNIS-NG, C. M. O., HUTLEY, L. B., BERINGER, J., ZEPPEL, M., WILLIAMS, M., TAYLOR, D. and EAMUS, D. (2011), Is productivity of mesic savannas light limited or water limited? Results of a simulation study. *Global Change Biology*, 17: 3130–3149.

***which has been published in final form at*** doi:10.1111/j.1365-2486.2011.02425.x

***This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.***"

2  
3 **Is productivity of mesic savannas light limited or water limited? Results**  
4 **of a simulation study**  
5

6 Rhys J. Whitley<sup>1</sup>, Catriona M.O. Macinnis-Ng<sup>1,2</sup>, Lindsay B. Hutley<sup>3</sup>, Jason Berringer<sup>4</sup>,  
7 Melanie Zeppel<sup>1,5</sup>, Mathew Williams<sup>6</sup>, Daniel Taylor<sup>1</sup>, Derek Eamus<sup>1,7</sup>

8 *<sup>1</sup>Plant Functional Biology and Climate Change Cluster, University of Technology Sydney,*  
9 *Australia*

10 *<sup>2</sup>Current address: School of Environment, University of Auckland, New Zealand*

11 *<sup>3</sup>School of Science & Primary Industries, Charles Darwin University, Australia*

12 *<sup>4</sup>School of Geography and Environmental Science, Monash University, Australia*

13 *<sup>5</sup>Current address: Department of Biological Sciences, Macquarie University, Australia*

14 *<sup>6</sup>School of Geosciences, University of Edinburgh, UK*

15  
16 **Keywords:** Savannas, GPP; evapotranspiration; SPA modelling

17 **<sup>7</sup>Corresponding author:** [Derek.Eamus@uts.edu.au](mailto:Derek.Eamus@uts.edu.au); tel +(61) 2 9514 4154; FAX +(61) 2  
18 9514 4079

19  
20 **Running title:** Savanna GPP and evapotranspiration

22

23 **Abstract**

24 A soil-plant-atmosphere model was used to estimate gross primary productivity (GPP) and  
25 evapotranspiration (ET) of a tropical savanna in Australia. This paper describes model  
26 modifications required to simulate the substantial C4 grass understory together with C3 trees.  
27 The model was further improved to include a seasonal distribution of leaf area and foliar  
28 nitrogen through ten canopy layers. Model outputs were compared to a five year eddy  
29 covariance dataset. Adding the C4 photosynthesis component improved the model efficiency  
30 and root-mean-squared error (RMSE) for total ecosystem GPP by better emulating annual  
31 peaks and troughs in GPP across wet and dry seasons. The C4 photosynthesis component had  
32 minimal impact on modelled values of ET. Outputs of GPP from the modified model agreed  
33 well with measured values, explaining between 79–90% of the variance and having a low  
34 RMSE (0.003-0.281 g C m<sup>-2</sup> d<sup>-1</sup>). Approximately 40% of total annual GPP was contributed  
35 by C4 grasses. Total (trees and grasses) wet season GPP was approximately 75-80% of total  
36 annual GPP. Light-use-efficiency (LUE) was largest for the wet season and smallest in the  
37 dry season and C4 LUE was larger than that of the trees. A sensitivity analysis of GPP  
38 revealed that daily GPP was most sensitive to changes in leaf area index (LAI) and foliar  
39 nitrogen (N<sub>f</sub>) and relatively insensitive to changes in maximum carboxylation rate (V<sub>cmax</sub>),  
40 maximum electron transport rate (J<sub>max</sub>) and minimum leaf water potential (ψ<sub>min</sub>). The  
41 modified model was also able to represent daily and seasonal patterns in ET, (explaining 68–  
42 81% of variance) with a low RMSE (0.038-0.19 mm d<sup>-1</sup>). Current values of N<sub>f</sub>, LAI and other  
43 parameters appear to be co-limiting for maximising GPP. By manipulating LAI and soil  
44 moisture content inputs, we show that modelled GPP is limited by light interception rather  
45 than water availability at this site.

46

47 **Introduction**

48 Globally, savannas cover an area larger than that of wet tropical rainforest and contribute  
49 approximately 30% of the gross primary productivity of all terrestrial ecosystems (Kanniah *et*  
50 *al.* 2009). They are continentally and globally important to the C cycle, are major  
51 determinants of regional water budgets and have high conservation, social, cultural and  
52 economic value (Eamus and Prior, 2001). Savannas have a discontinuous tree canopy above a  
53 continuous herbaceous layer, predominantly comprised of C4 grasses.

54

55 Savannas cover approximately 25% of the Australian continent (Hutley *et al.* 2000) and  
56 consequently make a significant contribution to Australia's carbon budget. Savannas of  
57 northern Australia experience a monsoonal climate with a distinct wet season (accounting for  
58 approximately 95% of the rainfall) and a dry season when grasses are absent. Despite this, C4  
59 grasses make a significant contribution to the annual carbon cycle of savannas and  
60 approximately three quarters of the annual carbon flux of north Australian savannas occurs  
61 during the wet season (Chen *et al.* 2003) when the grasses often account for more than half of  
62 the total leaf area index (Eamus *et al.* 2001, Hutley *et al.* 2005). Similarly, stable isotope  
63 analysis suggests that approximately 40% of the annual net primary productivity of a savanna  
64 in Brazil may have originated from C4 grasses, even though the LAI of grasses was only 0.4  
65 and 0.2 for the wet and dry seasons respectively (Miranda *et al.* 1997).

66

67 While there have been many studies using the eddy covariance method to quantify carbon  
68 and water fluxes at savanna sites (Hutley *et al.* 2000, Eamus *et al.* 2001, Hutley *et al.* 2005),

69 there is no widely available detailed mechanistic model currently available to accurately  
70 describe diurnal, seasonal and annual variation in gross primary productivity of ecosystems  
71 comprised of mixed C3 (trees and shrubs) and C4 (grasses) species. Indeed there is an urgent  
72 need to examine the patterns and drivers of savanna productivity because such information is  
73 central to understanding and predicting the response of savannas to climate change; to  
74 improve land and water management practices; and to inform policy initiatives in relation to  
75 C sequestration, woody thickening (Kanniah *et al.* 2009; Macinnis-Ng *et al.* 2010) and fire  
76 management (Beringer *et al.* 2007). The soil-plant atmosphere (SPA) model of Williams *et al.*  
77 *al.* (1996) is one of the most widely and successfully applied land surface exchange models  
78 and has been tested and validated across a range of diverse ecosystems, including Arctic  
79 tundra (Williams *et al.* 2001), Brazilian tropical rainforests (Williams *et al.* 1998; Fisher *et al.*  
80 *al.* 2007) and a temperate Australian woodland (Zeppel *et al.* 2008). The SPA model is a  
81 mechanistic model that predicts, amongst other parameters, carbon and water fluxes, leaf  
82 water relations and changes in soil moisture. However, it has not been applied to savannas  
83 because the productivity sub-model uses only the C3-photosynthesis model of Farquhar *et al.*  
84 (1980) and therefore cannot account for the behaviour of the C4 grass layer. In this paper we  
85 describe the changes required to incorporate C4 metabolism into the SPA model. This  
86 modified SPA model allows us to quantify ecosystem dynamics and to investigate the  
87 physiological mechanisms underlying observed behaviour.

88

89 Seasonality is a significant factor influencing productivity and water use of tropical  
90 ecosystems. For instance, an increase in the soil-root hydraulic resistance during the dry  
91 season caused seasonal reductions in carbon and water fluxes in a Brazillian rain forest  
92 (Williams *et al.* 1998). Wet season productivity in savannas creates a carbon sink of between

93 0.1 and 0.2 mol C m<sup>-2</sup> day<sup>-1</sup>, but photosynthetic activity declines during the dry season and  
94 the ecosystem may become a net source of C at this time (Chen *et al.* 2003). Seasonality in  
95 productivity is often attributed to stomatal closure and leaf loss during the dry season (Eamus  
96 and Prior, 2001) but gas exchange is limited by reduced  $g_s$  in the afternoon in both seasons at  
97 the Howard Springs site used in this study (Eamus *et al.* 1999; 2000). Soil water content and  
98 root access to moisture must be accurately modelled for successful prediction of annual C  
99 fluxes and evapotranspiration because soil water availability and atmospheric water content  
100 interact with  $g_s$  (Thomas and Eamus 1999; Thomas *et al.* 2000; Ju *et al.* 2006). Coupling  
101 between seasonal rainfall patterns (and therefore soil water content) and productivity has  
102 been observed at the leaf (Eamus *et al.* 1999), canopy (Eamus *et al.* 2001) and ecosystem  
103 scales (Chen *et al.* 2003; Eamus 2003). The test of the modified SPA model, therefore, will  
104 be its ability to reflect observed trends in water and carbon flux across seasons. We chose to  
105 model GPP and evapotranspiration because changes in these fluxes in a savanna are strongly  
106 affected by (a) seasonal changes in total site LAI arising (principally) from changes in the  
107 grass understorey; (b) daily changes in soil and atmospheric water content; and (c) hourly  
108 changes in ambient conditions. Consequently modelling these fluxes provides an assessment  
109 of the behaviour of the model across a wide temporal scale.

110

111 The aims of this study were to first, modify the SPA model to incorporate both C3 and C4  
112 photosynthesis; second, validate the modified model with five years of ecosystem GPP and  
113 ET field-data for a savanna site; third investigate intra- and inter-annual variation in GPP of a  
114 savanna; fourth, evaluate the sensitivity of GPP to a number of abiotic and biotic factors, with  
115 particular reference to the question: are the parameter values displayed by this vegetation  
116 optimised for maximising GPP; fifth, present an annual carbon and water budget for the

117 savanna that is disaggregated amongst seasons and C3 and C4 vegetation; and sixth,  
118 determine whether GPP is limited by water availability or energy capture at this site.

119

## 120 **Materials and methods**

### 121 *Study site*

122 Eddy covariance (EC) data spanning five years (2001-2005) were collected near Howard  
123 Springs (131°5'E, 12°30'S), approximately 35 km southeast of Darwin, Northern Territory,  
124 Australia. A full description of the site, species and EC methodologies are contained in  
125 Hutley *et al.* (2000) and Eamus *et al.* (2001). In summary, vegetation at the site is  
126 representative of a mesic open forest savanna with an overstorey dominated by *Eucalyptus*  
127 *tetrodonta* (F.Muell.) and *E. miniata* (Cunn. ex Schauer), forming a discontinuous canopy of  
128 about 50% cover. These two species account for approximately 90% of the tree basal area of  
129 8-10 m<sup>2</sup> ha<sup>-1</sup>. Overstorey LAI varies seasonally because of the presence of brevi- semi- and  
130 fully deciduous species, while the dominant evergreen species maintain canopy fullness  
131 throughout the dry season (Williams *et al.* 1996). The understorey includes semi-deciduous  
132 and deciduous small trees and shrubs but is dominated by C4 grasses such as annual *Sorghum*  
133 spp. and *Sarga* spp. and the perennial grass *Heteropogon triticeus*. Climate is characterised as  
134 wet-dry-tropical with highly seasonal rainfall and distinct wet (November to April inclusive)  
135 and dry (May to October inclusive) seasons. The wet season accounts for approximately 95%  
136 of the average annual rainfall of 1750 mm. Mean daily maximum temperatures remain above  
137 30°C throughout the year, irrespective of season.

138

139

140 *Eddy covariance data*

141 The eddy covariance technique (Baldocchi *et al.* 1988) was used to calculate flux variables at  
142 30 min time intervals. The instruments were mounted on a 23 m flux tower within a plot of  
143 open-forest savanna approximately 340 ha in size. The slope was less than 1° and the fetch  
144 was homogenous in all directions (>1 km). Wind speed and direction was measured with a 3-  
145 D sonic anemometer (Campbell Scientific Inc. model CSAT3, Logan Utah, USA) and CO<sub>2</sub>  
146 and H<sub>2</sub>O fluxes were measured at 10 Hz with an LI-7500 open-path CO<sub>2</sub>/H<sub>2</sub>O analyser (Licor  
147 Inc., Lincoln NE, USA). CO<sub>2</sub> fluxes were corrected for fluctuations in air density due to  
148 sensible and latent heat fluxes (Webb *et al.* 1980). Half-hourly values of rainfall, air  
149 temperature, relative humidity, and net radiation were measured at the same height as the flux  
150 data. Soil moisture at 10 cm depth was measured on a daily time-step. Soil moisture at this  
151 depth is strongly correlated with deeper soil moisture during the wet season and reflects the  
152 decline in soil moisture as the dry season progresses. Soil moisture values are a strong  
153 determinant of canopy gas fluxes in savannas of the Northern Territory (Eamus and Prior  
154 2001). Missing or invalid flux data were gap-filled using either linear interpolation (for gaps  
155 shorter than 3 hrs), or an artificial neural network (ANN) (for extended gaps; Beringer *et al.*  
156 2007).

157 Gross primary production (GPP) was calculated as the sum of net CO<sub>2</sub> flux ( $F_c$ ) and  
158 ecosystem respiration ( $R_e$ ).  $R_e$  was assumed to be equivalent to night-time  $F_c$  under adequate  
159 wind speed conditions (where friction velocity values were greater than 0.15 m s<sup>-1</sup>). Values of  
160  $F_c$  collected under low wind speed conditions were excluded to avoid underestimation of  $R_e$   
161 due to inadequate turbulent mixing (Baldocchi *et al.* 2000, Mäkelä *et al.* 2006, Beringer *et al.*  
162 2007). Using the ANN, daytime values of  $R_e$  were calculated from values of temperature and  
163 soil moisture.



164 *The Soil-Plant-Atmosphere model*

165 The SPA model simulates canopy exchanges of carbon and water at 30 minute resolution for  
166 multiple (up to 10) foliage layers. Model inputs include meteorological data, biophysical  
167 parameters for vegetation and soil characteristics, and are described in Table 1. The model  
168 was used in the form as described by Zeppel *et al.* (2008), and further explanation on the sub-  
169 routines of SPA may be found in Williams *et al.* (1996, 1998, 2001). Modifications have  
170 been made to the calculation of assimilation to include a C4 photosynthesis model, to  
171 describe understorey grass layers. In previous SPA applications a single phenology has been  
172 applied to all canopy layers. In the present study, the seasonal dying and regeneration of  
173 understorey grasses and the largely evergreen overstorey leaf area are dynamic and  
174 independent, as is the allocation of foliar nitrogen to each canopy layer. Both of these  
175 modifications to SPA are described below.

176

177 *C4 photosynthesis model*

178 The simplified C4 photosynthesis model as described by Collatz *et al.* (1992) was used to  
179 determine the C4 net assimilation rate ( $A_n^{C4}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Gross photosynthesis is given as a  
180 function of the incident quantum flux density and  $\text{CO}_2$  intercellular partial pressure, in the  
181 form of two nested quadratic equations. The first quadratic equation describes the flux  
182 determined by Rubisco activity and RuP<sub>2</sub> regeneration, and is given as:

$$\theta_{cj} M^2 - (V_{cmax} + \alpha_{rf} Q_p) M + V_{cmax} \alpha_{rf} Q_p = 0 \quad [1]$$

183

184 where,  $\theta_{cj}$  is a parameter describing the transition between light-limited and Rubisco limited  
185  $\text{CO}_2$  flux,  $\alpha_{rf}$  ( $\mu\text{mol mol}^{-1}$ ) is a combined constant describing the intrinsic quantum yield, and

186 fraction of absorbed photons used by the reaction process,  $V_{cmax}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the  
 187 maximum C4 Rubisco carboxylation rate and  $M$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the  $\text{CO}_2$  flux determined by  
 188 both Rubisco and light-limited photosynthetic capacities and  $Q_p$  is incident quantum flux  
 189 density. Equation 1 is therefore solved for  $M$  as follows:

$$M = \frac{V_{cmax} + \alpha_{rf} Q_p \pm \sqrt{(V_{cmax} + \alpha_{rf} Q_p)^2 - 4\theta_{cj} V_{cmax} \alpha_{rf} Q_p}}{2\theta_{cj}} \quad [2]$$

190

191 Overall net C4 assimilation rate is similarly determined through a quadratic expression,  
 192 which includes the Rubisco and light-limited capacities described above as well as the  $\text{CO}_2$   
 193 limited flux rate, and is expressed as:

$$\beta A_g^2 - (M + C_i k_T) A_g + M C_i k_T = 0 \quad [3]$$

194

195 where  $\beta$  is a parameter describing the co-limitation between light, Rubisco and  $\text{CO}_2$  limited  
 196 flux,  $C_i$  ( $\mu\text{mol mol}^{-1}$ ) is the intercellular  $\text{CO}_2$  concentration of the mesophyll cells,  $k_T = k_p - L/C_i$   
 197 ( $\text{mol m}^{-2} \text{s}^{-1}$ ) and describes the interactions of  $k_p$ , a first-order rate constant for PEP  
 198 carboxylase with respect to the ratio between  $C_i$  and  $L$ ; the amount of  $\text{CO}_2$  leakage from the  
 199 bundle sheath to the intercellular air spaces of the mesophyll.  $A_g$  is the gross C4  
 200 photosynthetic rate, and is found by solving Equation 3 for  $A_g$ , given as:

$$A_g = \frac{M + C_i k_T \pm \sqrt{(M + C_i k_T)^2 - 4\beta M C_i k_T}}{2\beta} \quad [4]$$

201

$$A_n^{C4} = A_g - R_d \quad [5]$$

202

203 Additionally parameters  $V_{cmax}$ ,  $k_T$  and  $R_d$  are all affected by variation in leaf temperature, and  
204 so  $Q_{10}$  temperature functions were used to modify these values accordingly (Collatz *et al.*  
205 1992).

206

### 207 *LAI and foliar nitrogen matrix*

208 The model contains 10 canopy layers. Given the significant contribution of the grass to total  
209 LAI (slightly larger than that of the overstorey LAI during the wet season), we define five of  
210 the layers as grass (C4) and five of the layers as shrubs and trees (C3). Each grass layer was  
211 0.3 m deep (a total height of 1.5 m) and the tree layers were each 2.5 m deep, taking the total  
212 canopy height to 14 m. Seasonal variations in leaf area of each canopy layer were  
213 incorporated into the phenology input file of the model. LAI of the overstorey was measured  
214 each month for a year using the Adelaide technique (O'Grady *et al.* 2000). Understorey LAI  
215 was also measured monthly using a direct harvest method of 21 x 1m<sup>2</sup> quadrats at three  
216 locations at Howard Springs with all grasses and woody saplings sampled. Allometric  
217 relationships were developed for each species of grass and woody sampling describing the  
218 relationship between plant biomass and leaf area to derive LAI (Hutley and Williams, unpub.  
219 data). The understorey leaf area values ranged from 1.1 to 0.05 during the wet and dry  
220 seasons respectively and the overstorey values were between 1.2 and 0.6 (Fig. 1). Measured  
221 ground data were compared to monthly MODIS LAI values for the whole canopy for each of  
222 the sample years. There were some small differences between years in total (overstorey and  
223 understorey) LAI detected in the remote sensing but preliminary analysis showed that the  
224 small changes in LAI caused a less than 2% difference in annual carbon and water fluxes in  
225 the model. For this reason, we used the same LAI matrix for each year and focused on  
226 capturing the seasonal changes in the leaf phenology file, rather than the inter-annual

227 changes. This approach allowed for a realistic distribution of leaf area between the C4 and C3  
228 components of the canopy throughout the year.

229 The majority of the reduction in LAI occurred in the understorey, during the onset of the dry  
230 season (from March onwards). Before rains arrive, the overstorey begins flushing with new  
231 leaves in October and then the grasses return from November (Palmer *et al.* 2008). The  
232 overstorey layers reflect the seasonal patterns of the four phenological types described by  
233 Williams *et al.* (1997). We assigned an evergreen phenology to the top two canopy layers (9  
234 to 11.5 m and 11.5 to 14 m canopy height) because the two dominant tree species are  
235 evergreen. Consequently the LAI of these layers remains reasonably constant throughout the  
236 year, while the bottom three canopy layers of the overstorey (1.5 to 4 m, 4 to 6.5 m and 6.5 to  
237 9 m) incorporated components of the brevi-deciduous, semi-deciduous and fully deciduous  
238 species and the LAI values declined slightly during the dry season, as shown in Williams *et*  
239 *al.* (1997).

240

241 Foliar nitrogen concentrations were determined from the literature for similar sites and  
242 species. Myrtaceous species may typically have a leaf N concentration of  $1.7 \text{ g m}^{-2}$  leaf area  
243 (Prior *et al.* 2004) and the C4 grass *Sorghum bicolor* typically may have a leaf N  
244 concentration of  $1.6 \text{ g m}^{-2}$  leaf area (Ghannoum *et al.* 2005). Based on maximum LAI of 2.35  
245 and assuming the overstorey and understorey values were 1.2 and 1.15 respectively, the  
246 maximum total foliar N concentration was  $3.88 \text{ g m}^{-2}$  ground area. The minimum total foliar  
247 N concentration in the dry season was approximately  $0.7 \text{ g m}^{-2}$  ground area. We incorporated  
248 some seasonal reductions in foliar N on a leaf area basis consistent with Prior *et al.* (2004).  
249 The foliar N matrix for the 10 canopy layers was based on the LAI matrix (Fig. 1b,c).

250

251 *Model performance*

252 For this study we also include several statistical tests in order to analyse the performance of  
253 the SPA model estimates against the measured EC data. In addition to using the coefficient of  
254 determination ( $R^2$ ) and root-mean-square error (RMSE) we have also used model efficiency  
255 (ME), given as:

$$ME = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y}_i)^2} \quad [6]$$

256

257 which estimates the proportion of variance of the EC data explained by the 1:1 line (Medlyn  
258 *et al.* 2005). The ME can range between  $-\infty$  and 1, where a  $ME = 1$  corresponds to a ‘perfect’  
259 match between modelled and measured data, a  $ME = 0$  indicates that the model predictions  
260 are as accurate as the mean of the measured data, and a  $ME < 0$  dictates that the measured  
261 mean is a better predictor than the model.

262 **Results**

263 *Meteorology*

264 Darwin and its environs are characterised by a distinct bi-modal wet season. Ninety five  
265 percent of the annual rainfall occurs between the start of November and the end of March  
266 (Fig. 2). However, there were significant rainfall events in July, 2001, May, 2004, and  
267 October (2001, 2004 and 2005), as is commonly observed in long-term records. There was  
268 also significant inter-annual variability in annual total rainfall for the years 2001 – 2005, with  
269 2003 receiving the most (2467 mm) and 2005 receiving the least (1219 mm). The long-term  
270 average annual rainfall for the site is 1750 mm.

271

272 Maximum solar radiation levels showed little variation between the wet season (typically 900  
273 – 1100 W m<sup>-2</sup>) and dry season (typically about 800 W m<sup>-2</sup>), reflecting the high latitude of the  
274 site and the absence of cloud during the dry season (Fig. 2). Mean daily vapour pressure  
275 deficit peaked in the dry season and was typically between 3.0 and 4.5 kPa at this time (Fig.  
276 2). In the wet season, VPD was generally lower and was predominantly within the range 1 –  
277 2.5 kPa in the absence of rain.

278

### 279 *Seasonal and annual patterns in GPP and ET*

280

281 Values of ecosystem GPP derived from eddy covariance measurements were largest in the  
282 wet season, typically within the range 4.0 – 8.0 gC m<sup>-2</sup> d<sup>-1</sup> (Fig. 3). Only rarely did GPP  
283 decline below 3.0 gC m<sup>-2</sup> d<sup>-1</sup> in the wet season. Day-to-day variation in GPP in the wet season  
284 closely reflected patterns in rainfall and solar radiation. From approximately mid-March  
285 through to September, ecosystem GPP declined approximately exponentially to a minimum  
286 of 1 – 2.0 gC m<sup>-2</sup> d<sup>-1</sup>. The start of the increase in GPP following the dry season minima  
287 generally began between mid-October and the early November (Fig. 3).

288

289 The SPA model was able to replicate the seasonal trends in GPP (Fig. 3). Including C4  
290 photosynthesis greatly improved SPA's ability to simulate wet season GPP (Fig. 3a-b). While  
291 the model underestimated GPP for October to April each year when C3 photosynthesis was  
292 used for all canopy layers (Fig. 3a), incorporating the C4 subroutine for the grass layers  
293 improved congruity between EC and model values (Fig. 3b). This is supported by improved  
294 ME and RMSE values for GPP outputs when the C4 subroutine was active (Table 2). As was  
295 observed in EC derived estimates, maximum GPP occurred in the wet season and ranged

296 between 4 and 8 gC m<sup>-2</sup> d<sup>-1</sup> whilst minimum values of calculated GPP occurred in September.  
297 The SPA model estimated the minimum value of GPP to be approximately 2 gC m<sup>-2</sup> d<sup>-1</sup>.

298

299 Across all five years of study, there was a significant positive relationship between modelled  
300 and observed GPP (Fig. 4, Table 2). The  $R^2$  for the regression ranged from 0.79 (2004) to  
301 0.90 (2002), whilst the model efficiency (ME) ranged from 0.44 (2004) to 0.80 (2002) (Table  
302 2). For large values of GPP (> 6 gC m<sup>-2</sup> d<sup>-1</sup>) modelled values of GPP were over-estimated by  
303 up to 17 % of observed values. In contrast, for small values of GPP (< 3 gC m<sup>-2</sup> d<sup>-1</sup>) the  
304 model tended to underestimate the values derived from EC measurements by up to 20% (Fig.  
305 4). When data for all years were pooled, the regression of SPA *versus* observed GPP yielded  
306 an  $R^2$  of 0.86, a model efficiency of 0.70 and a slope of 0.83 (Fig. 4, Table 2).

307

308 Seasonal and annual patterns of evapotranspiration (ET) closely matched those observed in  
309 GPP (Fig. 3). However, the C4 subroutine made very little difference to congruity between  
310 EC and model values (Fig. 3c-d, Table 2). Maximum rates of ET were observed in the wet  
311 season and ranged from 3 – 7 mm d<sup>-1</sup>, followed by an approximately exponential decline to a  
312 dry season minima of 1- 2 mm d<sup>-1</sup>. SPA was able to replicate these patterns closely; the  $R^2$  for  
313 the regression ranged from 0.67 (2005) to 0.81 (2002), whilst the model efficiency (ME)  
314 ranged from 0.44 (2005) to 0.65 (2002) (Fig. 4, Table 2). When all years were pooled the  
315 regression of SPA *versus* observed ET yielded an  $R^2$  of 0.75, a model efficiency of 0.53 and a  
316 slope of 0.83 (Fig. 4, Table 2).

317

318

319

320

321 *Intra-daily variation in GPP and ET across wet and dry seasons*

322

323 To examine diel patterns of ET and GPP across the year, observed or modelled values of ET  
324 and GPP were binned across all 5 years for each hourly value across each day of the month to  
325 produce a composite 12 month plot (Fig. 5). Clearly apparent are the daily patterns in ET and  
326 GPP, with peak values occurring around midday, and the seasonal decline in maximum  
327 values of ET and GPP as the dry season progresses from April through October. Similar  
328 patterns in hourly ET and GPP were observed for EC and modelled data with modelled  
329 values generally falling within the 95% confidence range of observed data.

330

331

332 *Partitioning total ET and GPP into C3 and C4 components*

333

334 Using SPA model outputs it was possible to partition landscape carbon and water fluxes  
335 between the C3 overstorey and C4 understorey components. During the wet season total GPP  
336 ranged between 2 – 8 gC m<sup>-2</sup> d<sup>-1</sup> and the C3 tree and C4 grass understorey each accounted for  
337 approximately 50% of the total flux (Fig 6; SPA simulation). In contrast, the rate of water use  
338 of the C4 understorey only accounted for approximately 23 – 35% of the total water flux in  
339 the wet season, which exhibited peak values of approximately 5 – 6 mm d<sup>-1</sup>. During the dry  
340 season, when the grasses were absent, all C and water fluxes were accounted for by the C3  
341 component of the vegetation as there was no leaf area or biomass to support any fluxes from  
342 the C4 grasses (Fig 6).

343

344

345



346 *Annual sums of GPP and ET across seasons and across years*

347

348 Annual total GPP and water use values were calculated for the EC data and the SPA outputs  
349 for each year (Fig 7a, b). Total GPP for the EC observations and SPA outputs ranged from  
350 1409 to 1560 gC m<sup>-2</sup> y<sup>-1</sup> and 1440 to 1501 gC m<sup>-2</sup> y<sup>-1</sup> respectively across the 5 years (Fig. 7a).  
351 Wet season GPP accounted for between 74 and 81% (EC data) or 80 to 83% (SPA outputs) of  
352 the annual total. Total annual water use ranged from 1052 mm to 1213 mm (EC data) or 1181  
353 mm to 1352 mm (SPA output) (Fig. 7b). Wet season water use accounted for 73 to 80% (EC  
354 data) or 71 to 76% (SPA) of the annual total.

355

356 It is not possible to partition the carbon and water fluxes between the C3 and C4 components  
357 of the vegetation using EC data. However, our modified SPA is able to generate outputs for  
358 the two vegetation types independently (Fig 7c, d). During the wet season, the proportion of  
359 the total GPP that was accounted for by the C3 component was about 43% across the five  
360 years and about 18% of GPP was contributed by the overstorey in the dry season (Fig. 7c).  
361 During the dry season, there was no active C4 vegetation present therefore the contribution of  
362 C4 grasses to total annual GPP was approximately 38%. Proportions of transpiration for wet  
363 season overstorey, wet season understorey and dry season over storey were 54, 17 and 29%  
364 respectively (Fig. 7d). Therefore, 83% of total annual transpiration was used by overstorey  
365 trees but only 62% of total ecosystem GPP was accounted for by C3 trees (Fig. 7c, d).

366

367 *The relative contribution of changes in soil moisture and LAI to patterns in ET and GPP*

368

369 In order to assess the relative importance of seasonal changes in either LAI or soil moisture  
370 content on carbon and water fluxes, two simulations were used. In the first, LAI was kept

371 constant at the peak wet season value for the entire year and soil moisture fluctuations  
372 occurred as normal in this simulation. In the second, soil moisture content was kept high at  
373 wet season values for the entire year but LAI showed normal seasonal cycles.

374

375 When LAI was kept constant all year both GPP and ET remained high all year, showing no  
376 significant decline in the dry season, despite significant declines in the water content of the  
377 upper soil profile during the dry season (Fig 8a). In contrast, when soil moisture content was  
378 kept artificially high all year and LAI declined as normal in the dry season, the normal dry  
379 season declines in ET and GPP were observed (Fig 8b). There were only very small  
380 differences in the patterns of GPP and ET for the control simulation (normal pattern of  
381 seasonal change in LAI and soil moisture content) and this second simulation.

382

383

#### 384 *Sensitivity analyses of factors affecting GPP and ET*

385

386 GPP and ET are sensitive to many biotic factors, including foliar N concentration, LAI and  
387 many others. Using SPA we doubled and halved the value of many factors and compared  
388 average daily GPP and ET for one representative year (2003; Fig. 9). Of all the factors  
389 examined, seven are presented here. Doubling the foliar N concentration of all layers resulted  
390 in a small increase (about 15%) in GPP and this was apparent for only a small part of the year  
391 (April to July). In contrast, halving the foliar N concentration caused a larger decline (10 – 25  
392 %) for most, but not all, of the year (Fig. 9b). A similar response of GPP was observed when  
393 LAI was halved or doubled, although the magnitude of the decline when LAI was halved was  
394 larger (up to 50% decline) than that when foliar N was reduced (Fig. 9c). When LAI and  
395 foliar N were doubled or halved in tandem (Fig. 9a) GPP increased by between 30% and

396 100% (when doubling the values) or declined by 5% to 30% when foliar N and LAI were  
397 halved. In contrast to these significant responses in GPP to changes in LAI and foliar N,  
398 significant increases in whole plant hydraulic conductance ( $G_{\text{plant}}$ ), minimum leaf water  
399 potential,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  had a very small impact on GPP (Fig. 9d, e, f, g). Halving the value  
400 of these 4 parameter values had a much larger impact on GPP than doubling their values (Fig  
401 9d, e, f, g). ET was less sensitive to variation in these factors than GPP (Fig. 9). Halving or  
402 doubling of foliar N and LAI had no impact on ET (Figs. 9b, a), although ET did decline or  
403 increase when foliar N and LAI values were altered in tandem (Fig. 9a). ET was sensitive to  
404 changes in  $G_{\text{plant}}$  and minimum leaf water potential (Fig. 9d, e) but insensitive to changes in  
405  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (Fig. 9f, g).

406

#### 407 *Micro-meteorological drivers of GPP and ET*

408

409 A comparison of the responses of hourly assimilation ( $A_n$ ) and transpiration ( $E_t$ ) to solar  
410 radiation ( $R_s$ ), vapour pressure deficit (VPD), soil moisture content and LAI in 2003 is  
411 presented in Fig. 10. Data are separated by season and canopy layer for clear interpretation of  
412 the patterns.  $A_n$  increased curvi-linearly with increasing  $R_s$  but there was a significant decline  
413 in maximum values of  $A_n$  in the dry season (Fig 10a, b). Maximum  $E_t$  vales were similar for  
414 wet and dry seasons for C3 canopy layers (Fig. 10c, d). C3 and C4 responses of  $A_n$  to  $R_s$  were  
415 similar in the wet season (Fig. 10a) while C4 canopy layers had a much lower rate of  $E_t$   
416 during the wet season compared to C3 canopy layers (Fig. 10c). Small increases in VPD from  
417 very low levels of VPD resulted in increases in  $A_n$  in the wet season but when VPD exceeded  
418 1 – 2 kPa, any further increase reduced  $A_n$  in both C3 and C4 canopy layers (Fig. 10e). There  
419 was very little response to VPD during the dry season (Fig. 10f). For C3 canopy layers,  $E_t$   
420 increased as VPD increased up to about 1.5 kPa, then  $E_t$  declined when VPD increased

421 further during the wet season (Fig. 10g). The C3 layers had a higher  $E_t$  peak than C4 layers  
422 (Fig. 10g) and  $E_t$  did not peak in the dry season until VPD reached about 2.5 kPa (Fig. 10h).  
423 Soil moisture content did not impact on  $A_n$  nor  $E_t$  for either canopy layer in either season  
424 (Fig. 10i-l), however, as LAI increased during a season,  $A_n$  and  $E_t$  increased to a plateau (Fig.  
425 10m-p) for C3 and C4 canopy layers.

426

427 We used to SPA outputs to estimate water-use-efficiency (WUE) and light-use-efficiency  
428 (LUE) of the C3 overstorey and C4 understorey separately (Table 3). Water-use-efficiency  
429 was always larger in the wet season than the dry season by between 18 and 64%. The WUE  
430 of the understorey was always larger than that of the overstorey, typically by a factor of 2.8 –  
431 3 times. Similarly whole-canopy LUE for the overstorey was always 10 – 26% larger in the  
432 wet season than the dry season and whole-canopy LUE for the understorey was always  
433 approximately 66% larger than the LUE for the overstorey (Table 3).

434

## 435 **Discussion**

### 436 *GPP and the modified SPA model*

437 The initial aim of this work was to successfully incorporate provision for a C4 grass layer  
438 within the SPA model, thereby allowing its application to savannas and other ecosystems  
439 with a significant C4 component. Adding the C4 photosynthetic sub-model and LAI/foiar N  
440 matrix allowed us to significantly improve wet- and dry-season estimates of GPP. Thus, the  
441 slope of the regression of measured and modelled GPP without the C4 capability (excluding  
442 C4 photosynthesis routine and LAI/foiar N matrix) was 1.31 and the model efficiency was  
443 0.29 (data not shown). In contrast, the slope of this regression when the model included the  
444 C4 capability was 0.83 and model efficiency increased to 0.70, indicating a significant

445 improvement in model performance. The RMSE was also significantly improved when the  
446 C4 capability was added (RMSE values 0.0057 and 1.185 with or without C4 and phenology  
447 matrix included, respectively). This improvement was not only because of the incorporation  
448 of the C4 photosynthetic pathway for the grass understorey but also because of the capture of  
449 seasonal dynamics of LAI and foliar N, especially for grass layers. With only a C3  
450 photosynthetic sub-model GPP was underestimated by 25-30 % during the wet season (data  
451 not shown).

452 Variation in the ability of SPA to accurately reflect intra-annual variation (Table 2) may  
453 result from the application of a single common LAI and foliar N dynamic across all years,  
454 rather than having an individual input of LAI and foliar N for each year but preliminary  
455 analysis showed using remotely sensed LAI data specific for each year changed annual fluxes  
456 by no more than 2%. Despite use of a single dynamic for LAI and foliar N for all years, for  
457 most of the range of GPP values ( $1.0$  to  $7 \text{ gC m}^{-2} \text{ d}^{-1}$ ) the difference between observed and  
458 modelled was less than 10%. Similarly good correlations between observed and modelled  
459 hourly values of GPP were obtained in both the wet and dry seasons (Fig 5), further  
460 indicating that at this shorter time-scale the SPA model was able to describe diurnal patterns  
461 in GPP.

462

### 463 *Primary drivers of seasonal changes in GPP*

464 GPP of this savanna site was smallest at the end of the dry season and largest in the mid-and  
465 late wet seasons. There are three principal causes of this variation. First, seasonality of  
466 changes in LAI of the savanna (trees and grasses) was a principle cause of the decline in GPP  
467 observed at the end of the wet season. The annual grasses lose 100% of leaf area by May of  
468 each year and approximately 10% of the woody species present are also dry-season

469 deciduous (Williams *et al.* 1997). A further 15% are dry season semi- or brevi-deciduous  
470 (Williams *et al.* 1997). Second, the decline in soil moisture of the upper soil profile (upper 1  
471 m) that occurs throughout the dry season is associated with a decline in stomatal conductance  
472 and photosynthetic rate of the trees (Prior *et al.* 1997a; Eamus and Cole 1997). This response  
473 is clearly evident in Figs 5 and 7 where peak rates of GPP were up to 60% smaller in the dry  
474 season than the wet season. The third cause of the decline was the increase in vapour pressure  
475 deficit that occurred in the dry season compared to the wet season (Fig. 2). A decline in  
476 stomatal conductance and leaf-scale photosynthesis in response to seasonal increases in VPD  
477 have been observed previously (Prior *et al.* 1997b) at this site. An influence of declining soil  
478 moisture content and diurnal changes in VPD are also present in the wet season but the  
479 magnitude of the impact tends to be smaller in the wet season than the dry season because of  
480 the interactive effect of VPD with soil moisture (Thomas *et al.* 1999). Although some studies  
481 have shown seasonal variations in GPP may be strongly temperature dependent (Mäkelä *et*  
482 *al.* 2006), we found minimal impact of temperature variation on GPP because the range of  
483 daytime temperature change was relatively small at this site.

484

#### 485 *Inter-annual variation of site GPP and contribution of C4 photosynthesis*

486 The savanna at Howard Springs was a net sink for carbon annually across all five years.  
487 Measured annual totals of GPP estimated from eddy covariance ranged from 1409 - 1558 gC  
488 m<sup>-2</sup> yr<sup>-1</sup> (Fig. 7). The equivalent range from the SPA output was 1516 - 1618 gC m<sup>-2</sup> yr<sup>-1</sup>.  
489 Such estimates compare well with remotely sensed estimates of GPP using MODIS GPP  
490 products 4.5 and 4.8 which predicted annual GPP for the same years as the present study to  
491 be in the range 1120 -1780 gC m<sup>-2</sup> yr<sup>-1</sup> (Kanniah *et al.* 2009). Even during the dry season the  
492 savanna maintained a positive carbon balance through having access to deep soil water stores

493 in the profile and regulating water-use through stomatal closure and adjustment of LAI  
494 (Eamus *et al.* 2000; Eamus *et al.* 2001; Kelley *et al.* 2007). Total wet season productivity  
495 contributed approximately 74 - 81% (EC and SPA data) of the total annual productivity  
496 because of the large contribution of the C4 grass layer to total ecosystem LAI and the large  
497 rates of photosynthesis of C4 grasses. C3 vegetation accounted for approximately 62% of the  
498 total annual GPP, despite the C3 vegetation having a substantial LAI for the entire year  
499 whilst the grasses were present for only 6 months of the year.

500

501 One hypothesis to explain inter-annual variation in GPP at this site is the large inter-annual  
502 variation in rainfall, both in terms of the total rainfall and the temporal distribution of rainfall  
503 across the year. However, no relationship was found between any measure of measured or  
504 modelled GPP (for example wet season or annual GPP) and any measure of precipitation (for  
505 example total precipitation, or wet or dry season length ( $P > 0.05$ )). In contrast, Leuning *et al.*  
506 (2005) and Pepper *et al.* (2008), found a positive relationship between rainfall and site  
507 productivity. However, the mean annual rainfall described by Leuning *et al.* (2005) is  
508 approximately one third (~37 %) of that at Howard Springs and in Budyko's terminology  
509 (see Donohue *et al.* 2007 for discussion) would be considered to be a water limited site,  
510 whilst the NT savannas of the present study are energy, and not water, limited (see discussion  
511 below). For energy limited sites, small-to-moderate variations in total rainfall are unlikely to  
512 have significant effects on GPP. Furthermore the error in values of GPP calculated from EC  
513 data are also likely to be of the order  $\pm 150 \text{ gC m}^{-2} \text{ y}^{-1}$  (Hutley *et al.* 2000) which may account  
514 for much of the observed inter-annual variation in GPP.

515 The estimate of annual C4 grass GPP was approximately  $5.7 \text{ tonnes C ha}^{-1} \text{ y}^{-1}$  (Fig 7).

516 Assuming that half of GPP is lost as respiration (a commonly assumed ratio; Waring *et al.*,

517 1998; McMurtrie *et al.*, 2008) and half is sequestered to below-ground biomass, and  
518 assuming that half the dry weight of grass is C, this equates to a total grass dry biomass of  
519 2.85 tonnes ha<sup>-1</sup> y<sup>-1</sup> available for combustion in savanna fires. This compares well with the  
520 range of fine fuel load (including fine woody debris) that accumulates at this site each year  
521 (1.58 – 4.26 t dry mass ha<sup>-1</sup> y<sup>-1</sup>; Beringer *et al.* 2007).

522

### 523 *Light-use-efficiency derived from SPA*

524 Light-use-efficiency of the overstorey canopy was larger in the wet season than the dry  
525 seasons for all years (Table 3) as has been observed in leaf-scale measurements in tropical  
526 woodlands previously (Fordyce *et al.* 1995; Eamus and Cole 1997) and in eddy covariance  
527 data (Hutley *et al.* 2001). The three causes of this response are first, increased VPD in the dry  
528 season, which can both decrease stomatal conductance and hence C flux but also increase  
529 transpiration (Fordyce *et al.* 1995; Eamus and Cole 1997; O'Grady *et al.* 1999; Eamus *et al.*  
530 1999); second, increased leaf temperature to supra-optimal values (Prior *et al.* 1997b); and  
531 third, a decline in soil moisture which causes decreased stomatal conductance. The (C4)  
532 understorey exhibited a much larger (by 66%) LUE than the C3 overstorey, reflecting the  
533 CO<sub>2</sub> concentrating mechanism, high assimilation rate and lower stomatal conductance  
534 typically seen in C4 plants compared to C3 plants (Collatz *et al.* 1992).

535

### 536 *Evapotranspiration and WUE*

537 The strong positive correlation between measured and observed rates of daily ET for all years  
538 (Fig 4, Table 2) indicates that the inclusion of the C4 photosynthetic sub-routine was able to  
539 capture water fluxes of the grass canopy as well as the C fluxes. Similarly the range in



540 estimates of total annual ET from the SPA model (1181 – 1352 mm) was comparable to that  
541 observed in the EC data (1052 - 1213 mm). Wet season ET accounted for 71 – 80% (EC and  
542 SPA data) of the annual total ET and the C3 component of the landscape generally accounted  
543 for 76 – 78% of the wet season total ET. These relativities in GPP and ET for the C3 and C4  
544 components of the landscape resulted in much larger water-use-efficiencies (WUE) for the  
545 grasses (typically more than 3 times larger WUE for the grasses) than the trees (Table 3).  
546 This reflects the smaller stomatal conductance and larger photosynthetic rates of C4 grasses  
547 compared to C3 trees.

548

#### 549 *Sensitivity analysis of model biophysical parameters*

550 A sensitivity analysis on the model's vegetation parameters revealed that GPP was very  
551 sensitive to changes in LAI and total foliar N ( $N_f$ ). Increasing LAI alone, whilst keeping  $N_f$   
552 constant resulted in an asymptotic responses of GPP. As LAI increased and  $N_f$  remained  
553 constant, the concentration of N within each leaf declined (a fixed amount of N was being  
554 spread across an increasingly large leaf area). Consequently net assimilation became limited  
555 through limitation in the rate of RuBP carboxylation. Conversely, when  $N_f$  was increased  
556 with a constant LAI, a similar asymptotic response of GPP was observed as the canopy  
557 became saturated with N and light interception limited GPP. It is noteworthy that the plateau  
558 in GPP occurred at the level of LAI and  $N_f$  corresponding to 100% of the current value. This  
559 suggests that the canopy LAI and  $N_f$  are currently co-limited and hence have reached  
560 optimality. Optimality is defined here as having arisen through evolution such that vegetation  
561 displays parameter values that maximise the C gain for a given investment of resources (for  
562 instance foliar N). This is similar to the definition used by Schymanski *et al.* (2007). The  
563 maximal (wet season) LAI value found to be optimal in our approach was 2.2 – 2.5 which

564 agrees well with the value of 2.5 derived by Schymanski *et al.* (2007, 2008) using a formal  
565 optimality model. The biophysical parameters  $G_{plant}$ ,  $\Psi_{min}$ ,  $V_{cmax}$  and  $J_{max}$ , were also found to  
566 have current values that appear to be optimal, whereby the maximum rate of GPP was  
567 attained at values of these parameters that correspond to the observed (100%) value for each  
568 parameter. Thus, doubling the parameter value did not, in any instance, significantly increase  
569 GPP whilst halving the parameter value caused a small decline in GPP.

570

### 571 *Energy versus water limited savanna productivity*

572 The GPP and ET of arid and semi-arid sites are clearly water limited, whilst those of mesic  
573 sites are energy limited. All catchments can be shown to be somewhere along a continuum  
574 between extremely water limited and extremely energy limited sites (Budyko 1974; Donohue  
575 *et al.* 2007). Budyko (1974) developed a framework for modelling ET based on the  
576 relationship of available water and energy, and constrained by the limits of these two  
577 variables. We have used this conceptual framework to ask: are these savannas energy or  
578 water limited? Given the annual high rainfall and the long dry season without rain, the  
579 answer is not intuitively obvious.

580 When the SPA model was run for one year with a fixed LAI all year (set to wet season values  
581 for both the C3 and C4 components) but with real-time observed variation in soil moisture  
582 and other meteorological drivers, daily values of GPP (and ET) remained high all year at  
583 values closely matching observed wet season values of GPP (Fig 8). Thus dry season declines  
584 in GPP (and ET) were not observed. This is in marked contrast to the alternative scenario,  
585 where a fixed (high) soil moisture content was maintained all year and normal variations in  
586 C3 and C4 LAI were imposed. When this occurred, daily rates of GPP and ET closely  
587 matched the observed values throughout the year. We conclude that this savanna site is

588 limited by the amount of solar radiation intercepted by the canopy. The site is not water  
589 limited, despite the presence of a 6 month dry season every year. This is in contrast to the  
590 generally accepted view that savanna function and productivity are limited by water  
591 availability (Kanniah *et al.* 2009) but is consistent with other findings in this study. The lack  
592 of a relationship between annual GPP and any measure of rainfall at this site described above  
593 indicates the unlikelihood of water limitation. Furthermore, sensitivity analysis revealed that  
594 minimum leaf water potential and whole plant hydraulic conductance (both determinants of  
595 water availability in the plant) had to be reduced to unrealistically low values for there to be  
596 any impact on GPP (Fig. 9) suggesting GPP is unresponsive to water availability. Finally,  
597 seasonal responses of hourly leaf-scale carbon and water fluxes were unresponsive to soil  
598 moisture but were bound by values of radiation, VPD and LAI (Fig. 10).

599 Model outputs unaffected by artificially wet soil and the lack of a relationship between GPP  
600 and rainfall or soil moisture are supported by sapflow measurements of tree transpiration at  
601 the same site. Rates of sap flux remained constant throughout the year, with no seasonal  
602 decline during the dry season (Hutley *et al.* 2000). Furthermore, these trees did not suffer  
603 significant water stress during the dry season as leaf water potentials remained high, despite 6  
604 months without rain (Duff *et al.* 1997). The constant rate of transpiration and lack of extreme  
605 water stress together with late dry season canopy flushing was attributed to deep tree roots  
606 (estimated to be >6m by Cook *et al.* 1998) extracting water from the capillary fringe of the  
607 water table as it declined during the dry season (Hutley *et al.* 2000). The interaction of the  
608 depth of rooting of eucalypts and the large water storage capacity of the soil within the root  
609 zone (Cook *et al.* 1998) provides a consistent water supply for trees when precipitation is  
610 scarce. Finally, Cernusak *et al.* (2011) conclude that leaf-scale photosynthesis of *Eucalyptus*  
611 and *Corymbia* tree species in these north Australian savannas was not light saturated at full  
612 sunlight, which strongly supports our conclusion that the system is light limited.

613 It is noteworthy that the annual grasses at this site are genetically predestined to die each  
614 year, irrespective of soil moisture content (ie the decline in grass LAI is not in response to  
615 declining soil moisture content). It is further noteworthy that irrigation of this savanna into  
616 the dry season had very little impact on the LAI of the overstorey (Myers *et al.* 1998).  
617 However, exclusion of fires for several years causes an increase in tree LAI which results in  
618 an increase in measured GPP due to increased light capture and hence enhanced C uptake  
619 (Williams *et al.* 2004, Beringer *et al.* 2007). Therefore, hydrological (Cook *et al.* 1998) and  
620 ecophysiological (Duff *et al.* 1997, Hutley *et al.* 2000, Beringer *et al.* 2007) data from the site  
621 support the model finding that productivity of the vegetation is not limited by water  
622 availability (as this is available in deep stores throughout the year). We conclude that the  
623 alternative hypothesis, that LAI limits interception of light which limits the maximum GPP,  
624 and that the largest driver of the change in savanna LAI is driven by seasonal change in C4  
625 grass LAI, is supported by the analyses presented and the outputs of the modelling.

626

## 627 **Conclusions**

628

629 Modelling C4 photosynthesis is important if we wish to correctly estimate savanna gas  
630 exchange. Furthermore, it is critical that seasonal variation in LAI and foliar N content of  
631 savanna grasses also be included. The modified SPA model containing an accepted  
632 representation of C4 metabolism was able to capture both wet and dry season fluxes of  
633 carbon and water of a north Australian savanna. The understorey C4 grasses contributed  
634 approximately 38% to total savanna GPP and total wet season GPP accounted for  
635 approximately 80% of total annual GPP. Modelled values of GPP agreed well with the eddy-  
636 covariance derived estimates of GPP, explaining between 80–87% of the variance and having  
637 a low RMSE. Several canopy parameter values (including LAI, foliar N, and  $G_{\text{plant}}$ ) appeared

638 to be co-limiting, such that large increases in allocation of resources to any one of these  
639 attributes did not result in large increases in GPP. Counter-intuitively, we conclude that GPP  
640 at this site is limited by light interception rather than water availability despite a long and  
641 pronounced dry season each year.

642

643 **References**

- 644  
645 Baldocchi DD, Finnigan J, Wilson K, Paw UKT, Falge E (2000) On measuring net  
646 ecosystem carbon exchange over tall vegetation on complex terrain. *Boundary-Layer*  
647 *Meteorology*, **96**, 257-291.
- 648 Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of  
649 biologically related gases with micrometeorological methods. *Ecology*, **69**, 1331-  
650 1340.
- 651 Beringer J, Hutley LB, Tapper NJ Cernusak LA (2007) Savanna fires and their impact on net  
652 ecosystem productivity in North Australia. *Global Change Biology*, **13**, 990-1004.
- 653 Budyko MI, (1974) *Climate and Life*, New York, Academic Press.
- 654 Cernusak LA, Hutley, LB, Beringer J, Holtum, JAM and Turner BL.(2011) Photosynthetic  
655 physiology of eucalypts along a sub-continental rainfall gradient in north Australia.  
656 *Agricultural and Forest Meteorology* (2011). Doi:10.1016/j.agformet.2011.01.006.
- 657 Chen X, Hutley LB, Eamus D (2003) Carbon balance of a tropical savanna of northern  
658 Australia. *Oecologia*, **137**, 405-416.
- 659 Collatz JG, Ribas-Carbo M, Berry JA (1992) Coupled Photosynthesis-Stomatal Conductance  
660 Model for Leaves of C<sub>4</sub> Plants. *Australian Journal of Plant Physiology*, **19**, 519-538.
- 661 Cook PG, Hatton TJ, Pidsley D, Herczeg AL, Held A, O'Grady A, Eamus D (1998) Water  
662 balance of a tropical woodland ecosystem, northern Australia: a combination of  
663 micro-meteorological, soil physical and groundwater chemical approaches. *Journal of*  
664 *Hydrology*, **210**, 161-177.
- 665 Donohue RJ, Roderick ML, McVicar TR (2007) On the importance of including vegetation  
666 dynamics in Budyko's hydrological model. *Hydrology and Earth System Sciences*, **11**,  
667 983-995.
- 668 Duff GA, Myers BA, Williams RJ, Eamus D, O'Grady A, Fordyce IR (1997) Seasonal  
669 patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn

670 water potential in a Northern Australian savanna. *Australian Journal of Botany*, **45**,  
671 211-224.

672 Eamus D (2003) How does ecosystem water balance affect net primary productivity of  
673 woody ecosystems? *Functional Plant Biology*, **30**, 187-205.

674 Eamus D, Cole S (1997) Diurnal and seasonal comparisons of assimilation, phyllode  
675 conductance and water potential of three *Acacia* and one *Eucalyptus* species in the  
676 wet-dry tropics of Australia. *Australian Journal of Botany*, **45**, 275-290.

677 Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: Comparisons  
678 among phenologies. *Advances in Ecological Research*, **32**, 113-197.

679 Eamus D, Hutley LB O'Grady AP (2001) Daily and seasonal patterns of carbon and water  
680 fluxes above a north Australian savanna. *Tree Physiology*, **21**, 977-988.

681 Eamus D, Myers B, Duff G, Williams D (1999) Seasonal changes in photosynthesis of eight  
682 savanna tree species. *Tree Physiology*, **19**, 665-671.

683 Eamus D, O'Grady AP, Hutley L (2000) Dry season conditions determine wet season water  
684 use in the wet-dry tropical savannas of northern Australia. *Tree Physiology*, **20**, 1219-  
685 1226.

686 Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic  
687 CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> Species. *Planta*, **149**, 78-90.

688 Fisher RA, Williams M, Lola da Costa A, Malhi Y, da Costa RF, Almeida S, Meir P (2007)  
689 The response of an Eastern Amazonian rain forest to drought stress: results and  
690 modelling analyses from a throughfall exclusion experiment. *Global Change Biology*,  
691 **13**, 1-18.

692 Fordyce IC, Duff GA, Eamus D (1995). The ecophysiology of *Allosyncarpia ternata* in  
693 northern Australia: tree physiognomy, leaf characteristics and assimilation at  
694 contrasting sites. *Australian Journal of Botany*, **43**, 367-377.

695 Ghannoum O, Evans JR, Chow WS, Andrews TJ, Conroy JP, von Caemmerer S (2005)  
696 Faster rubisco is the key to superior nitrogen-use efficiency in NADP-malic enzyme  
697 relative to NAD-malic enzyme C-4 grasses. *Plant Physiology*, **137**, 638-650.

698 Hutley LB, O'Grady AP, Eamus D (2000) Evapotranspiration from eucalypt open-forest  
699 savanna of northern Australia. *Functional Ecology*, **14**, 183-194.

700 Hutley LB, Leuning R, Beringer J, Cleugh HA (2005) The utility of the eddy covariance  
701 techniques as a tool in carbon accounting: tropical savanna as a case study. *Australian*  
702 *Journal of Botany*, **53**, 663-675.

703 Ju W, Chen JM, Black TA, Barr AG, Liu J, Chen B (2006) Modelling multi-year coupled  
704 carbon and water fluxes in a boreal aspen forest. *Agricultural and Forest*  
705 *Meteorology*, **140**, 136-151.

706 Kanniah KD, Beringer J, Hutley LB, Tapper NJ, Zhu X (2009) Evaluation of collection 4 and  
707 5 of the MODIS GPP product and algorithm improvement at a tropical savanna site in  
708 northern Australia. *Remote Sensing of Environment*, **113**, 1808-1822.

709 Kelley G, O'Grady AP, Hutley LB, and Eamus D (2007) A comparison of tree water use in  
710 two contiguous vegetation communities of the seasonally dry tropics of Australia:  
711 the importance of site water budget to tree hydraulics. *Australian Journal of Botany*,  
712 **55**, 700-708.

713 Leuning R, Cleugh HA, Zegelin SJ, Hughes D (2005) Carbon and water fluxes over a  
714 temperate Eucalyptus forest and a tropical wet/dry savanna in Australia:  
715 measurements and comparison with MODIS remote sensing estimates. *Agricultural*  
716 *and Forest Meteorology*, **129**, 151-173.

717 Macinnis-Ng C, Zeppel M, Williams M, Eamus D (2011) Applying a SPA model to examine  
718 the impact of climate change on GPP of open woodlands and the potential for woody  
719 thickening. *Ecohydrology*, **2**. In Press. DOI 10.1002/eco.138



720 Mäkelä A, Kolari P, Karimäki J, Nikinmaa E, Perämäki M, Hari P (2006) Modelling five  
721 years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest*  
722 *Meteorology*, **139**, 382-398.

723 McKenzie N, Jacquier D, Isbell R, Brown K (2004) *Australian Soils and Landscapes*. CSIRO  
724 Publishing. Melbourne. 416 pp.

725 McMurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM.  
726 2008. Why is plant-growth response to elevated CO<sub>2</sub> amplified when water is  
727 limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis.  
728 *Functional Plant Biology*, **35**: 521–534.

729 Medlyn BE, Robinson A, Clement R, McMurtrie RE (2005) On the validation of models of  
730 forest CO<sub>2</sub> exchange using eddy covariance data: some perils and pitfalls. *Tree*  
731 *Physiology*, **25**, 839-857.

732 Miranda AC, Miranda HS, Lloyd J *et al.* (1997) Fluxes of carbon, water and energy over  
733 Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant Cell*  
734 *and Environment*, **20**, 315-328.

735 Myers BA, Williams RJ, Fordyce I, Duff, GA, Eamus D (1998) Does irrigation affect leaf  
736 phenology in deciduous and evergreen trees of the savannas of northern Australia?  
737 *Australian Journal of Ecology*, **23**, 329–339

738 O’Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season:  
739 patterns of tree water use in eucalypt open-forests of northern Australia. *Tree*  
740 *Physiology*, **19**, 591–598

741 O’Grady AP, Chen X, Eamus D, Hutley LB (2000) Composition, leaf area index and standing  
742 biomass of eucalypt open forests near Darwin in the Northern Territory, Australia.  
743 *Australian Journal of Botany*, **48**, 629-638.

744 Palmer A, Fuentes S, Taylor DT *et al.* (2008) The use of pre-dawn leaf water potential and  
745 MODIS LAI to explore seasonal trends in the phenology of Australian and southern  
746 African woodlands and savannas. *Australian Journal of Botany*, **56**, 557-563.

747 Pepper DA, McMurtrie RE, Medlyn BE, Keith H, Eamus D (2008) Mechanisms linking plant  
748 productivity and water status for a temperate Eucalyptus forest flux site: analysis over  
749 wet and dry years with a simple model. *Functional Plant Biology*, **35**, 493-508.

750 Prior L, Eamus D, Duff GA (1997a) Seasonal and diurnal patterns of carbon assimilation,  
751 stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a  
752 wet-dry savanna in northern Australia. *Australian Journal of Botany*, **45**, 241 - 258.

753 Prior L, Eamus D, Duff GA (1997b) Seasonal trends in carbon assimilation, stomatal  
754 conductance, pre-dawn leaf water potential and growth of *Terminalia ferdinandiana*, a  
755 deciduous tree of northern Australia. *Australian Journal of Botany*, **45**, 53-69.

756 Prior L, Bowman DMJS, Eamus D (2004) Seasonal differences in leaf attributes in Australian  
757 tropical tree species: family and habitat comparisons. *Functional Ecology*, **18**, 707-  
758 718.

759 Schymanski SJ, Roderick ML, Sivapalan M, Hutley LB, Beringer J (2007) A test of the  
760 optimality approach to modelling canopy properties and CO<sub>2</sub> uptake by natural  
761 vegetation. *Plant Cell and Environment*, **30**, 1586-1598.

762 Schymanski SJ, Sivapalan M, Roderick ML, Beringer J, Hutley LB (2008) An optimality-  
763 based model of the coupled soil moisture and root dynamics. *Hydrology and Earth  
764 System Sciences*, **12**, 913-932.

765 Thomas DS, Eamus D (1999) The influence of predawn leaf water potential on stem  
766 hydraulic conductivity and foliar ABA concentrations and on stomatal responses to  
767 atmospheric water content at constant C<sub>i</sub>. *Journal of Experimental Botany*, **50**, 243-  
768 251.

- 769 Thomas DS, Eamus D, Bell D (1999) Optimization theory of stomatal behaviour II. Stomatal  
770 responses of several tree species of north Australia to changes in light, soil and  
771 atmospheric water content and temperature. *Journal of Experimental Botany*, **50**, 393-  
772 400.
- 773 Thomas DS, Eamus D, Shanahan S (2000) Studies on the influence of season, drought and  
774 xylem ABA on stomatal responses to leaf-to-air vapour pressure difference of trees of  
775 the Australian wet-dry tropics. *Australian Journal of Botany*, **48**, 143-153.
- 776 Waring RH, Landsberg JJ, Williams M. 1998. Net primary production of forests: a constant  
777 fraction of gross primary production? *Tree Physiology* **18**: 129–134.
- 778 Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density  
779 effects due to heat and water vapour transfer. *Quarterly Journal of the Royal*  
780 *Meteorological Society*, **106**, 85-100.
- 781 Williams M, Rastetter EB, Fernandes DN *et al.* (1996) Modelling the soil-plant-atmosphere  
782 continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomata  
783 conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and*  
784 *Environment*, **19**, 911-927.
- 785 Williams RJ, Myers BA, Muller WA, Duff GA, Eamus D (1997) Leaf phenology of woody  
786 species in a north Australian tropical savanna. *Ecology* **78**, 2542-2558.
- 787 Williams M, Malhi Y, Nobre A, Rastetter E, Grace J, Pereira M (1998) Seasonal variation in  
788 net carbon exchange and evapotranspiration in a Brazilian rain forest. *Plant Cell and*  
789 *Environment*, **21**, 953-968.
- 790 Williams M, Rastetter EB, Shaver GR, Hobbie JE, Carpino E, Kwiatkowski BL (2001)  
791 Primary production of an arctic watershed: an uncertainty analysis. *Ecological*  
792 *Applications*, **11**, 1800-1816.

793 Williams RJ, Hutley LB, Cook GD, Russell-Smith J, Edwards A, Chen XY (2004) Assessing  
794 the carbon sequestration potential of mesic savannas in the Northern Territory,  
795 Australia: approaches, uncertainties and potential impacts of fire. *Functional Plant*  
796 *Biology*, **31**, 415-422.

797 Zeppel MJB, Macinnis-Ng CMO, Palmer A *et al.* (2008) An analysis of the sensitivity of sap  
798 flux to soil and plant variables assessed for an Australian woodland using a soil-plant-  
799 atmosphere model. *Functional Plant Biology*, **35**, 509-520.

800

801

802 **Tables**

803 **Table 1. Values used in SPA for this study.**

804

805 SPA model input values indicating the name, symbol, units, value used and whether the data

806 were measured or estimated for the study site.

807

<i>Parameter/Variable</i>	<i>Symbol</i>	<i>Units</i>	<i>Value</i>	<i>Source</i>
Ambient atmospheric CO <sub>2</sub> concentration	C <sub>a</sub>	mmol mol <sup>-1</sup>	374	Measured, this study.
Canopy layer capacitance	C <sub>n</sub>		5000	Williams <i>et al.</i> 1996
Canopy hydraulic conductivity	G <sub>plant</sub>	mmol m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup>	3.5	Zeppel <i>et al.</i> 2008
Layer height of soil	H	m	0.2 to 1.6 m depth, then 1.6 to 6.4 m	Site estimate
Leaf Area Index	LAI	m <sup>-2</sup> m <sup>2</sup>	0.6 to 2.35	MODIS LAI product and measured values
Proportion of LAI in top layer	L <sub>top</sub>		0.125	Estimated using Weibull cumulative distribution function
Areal concentration of leaf N	N	g m <sup>-2</sup> ground area	3.84	Prior <i>et al.</i> 2004 and Ghannoum <i>et al.</i> 2005
Proportion of total canopy N in top layer	N <sub>top</sub>		0.125	Estimated, this study
Fine root radius	r <sub>r</sub>	M	0.0001	Measured, this study.
Air temperature	T <sub>a</sub>	°C	Variable	Measured, this study.
Leaf temperature	T <sub>i</sub>	°C	Variable	Measured, this study.
C3 RuBP carboxylation capacity	C3 V <sub>cmax</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	73.6	Zeppel <i>et al.</i> 2008
C3 Maximum electron transport rate	C3 J <sub>max</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	129.8	Zeppel <i>et al.</i> 2008
C4 RuBP carboxylation capacity	C3 V <sub>cmax</sub>	μmol m <sup>-2</sup> s <sup>-1</sup>	47.0	Ghannoum <i>et al.</i> 2005
Transition between light-limited and RuBisCO limited CO <sub>2</sub> flux	θ <sub>cj</sub>	0.83	unitless	Collatz <i>et al.</i> 1992
Intrinsic quantum yield	α <sub>rf</sub>	0.067	mol mol <sup>-1</sup>	Collatz <i>et al.</i> 1992
Co-limitation between light, RuBisCO and CO <sub>2</sub> limited flux	β	0.93	unitless	Collatz <i>et al.</i> 1992
First order rate constant	k <sub>T</sub>	0.7	mol m <sup>-2</sup> s <sup>-1</sup>	Collatz <i>et al.</i> 1992
ΔA/δg <sub>s</sub> threshold for stomatal opening	I	%	1.0007	Williams <i>et al.</i> 1996

Minimum sustainable leaf water potential	$\Psi_{\text{min}}$	MPa	-2.5	Kelley <i>et al.</i> 2007
Soil water potential	$\Psi_s$	MPa	-0.5	Pre-dawn leaf water potential, this study
% soil clay content in top 10 cm		%	5.0	McKenzie <i>et al.</i> 2004
% soil sand content in top 10 cm		%	45.0	McKenzie <i>et al.</i> 2004
Draincheck – field capacity as fraction of total porosity		fraction	0.5	Zeppel <i>et al.</i> 2008
Latitude		°	12°29.712'S	Measured, this study.
Dimension of leaves		m <sup>2</sup>	0.08	Prior <i>et al.</i> 1997a.
Root resistivity		MPa s g mmol <sup>-1</sup>	100	Estimated, this study.
Root biomass		g	1930	Chen <i>et al.</i> 2003
Rooting depth		m	6.4	Chen <i>et al.</i> 2003

808

809

810 Table 2: Model performance for each year and the total dataset for gross primary productivity  
811 and evapotranspiration reported as  $R^2$ , model efficiency (ME), root-mean-square error  
812 (RMSE), slope and y-intercept. Values of ME range from  $-\infty$  to 1, where 1 represents a  
813 perfect match between measured and modelled values. Units of RMSE are  $\text{g C m}^{-2} \text{d}^{-1}$  for  
814 GPP and  $\text{mm d}^{-1}$  for ET.

<b>Simulation</b>								
<b>Type</b>	<b>Year</b>	<b>Output</b>	<b><math>R^2</math></b>	<b>ME</b>	<b>RMSE</b>	<b>Slope</b>	<b>Intercept</b>	
<b>C3 only</b>	2001	GPP	0.86	0.62	0.5788	1.04	0.45556	
		ET	0.78	0.58	0.1843	0.9	0.15756	
	2002	GPP	0.88	0.58	0.7753	1.29	-0.19748	
		ET	0.82	0.65	0.1437	0.86	0.36164	
	2003	GPP	0.88	0.71	0.3870	1.26	-0.50405	
		ET	0.75	0.47	0.0604	0.72	1.00741	
	2004	GPP	0.79	0.43	0.6450	0.88	1.06609	
		ET	0.76	0.50	0.1212	0.73	1.10041	
	2005	GPP	0.88	0.54	0.8887	1.25	0.02909	
		ET	0.69	0.45	0.0221	0.81	0.65499	
	All	GPP	0.85	0.59	0.6550	1.14	0.18159	
		ET	0.76	0.54	0.0336	0.81	0.64933	
	<b>Mixed C3/C4</b>	2001	GPP	0.87	0.67	0.0875	0.75	0.90186
			ET	0.77	0.58	0.1205	0.93	0.13424
2002		GPP	0.90	0.80	0.1124	0.95	0.31099	
		ET	0.81	0.65	0.0656	0.89	0.32019	
2003		GPP	0.88	0.74	0.2806	0.89	0.15795	
		ET	0.73	0.46	0.1309	0.74	0.99381	
2004		GPP	0.79	0.44	0.0025	0.64	1.47203	
		ET	0.76	0.49	0.1929	0.76	1.06808	
2005		GPP	0.87	0.73	0.2248	0.91	0.60362	
		ET	0.67	0.44	0.0500	0.83	0.63642	
All		GPP	0.86	0.70	0.0057	0.83	0.69562	
		ET	0.75	0.53	0.0376	0.83	0.62319	

815

816

**Table 3:** Using SPA outputs, annual and seasonal water and C fluxes, water-use-efficiency and light-use-efficiency have been partitioned between the C3 overstorey and the C4 understorey. ET = Evapotranspiration (other water fluxes are transpiration rates only). Over = Overstorey; Under = understorey. By definition, the grass understorey is absent in the dry season and hence doesn't have C and water flux values.

	Year	Annual				Wet Season				Dry Season			
		ET	Over + under	Over	Under	ET	Over + under	Over	Under	ET	Over + under	Over	Under
Water Use (mm)	2001	1243	805	674	131	926	571	440	131	317	234	234	0
	2002	1352	914	754	160	1021	670	510	160	331	244	244	0
	2003	1181	803	673	130	850	555	425	130	331	248	248	0
	2004	1320	867	727	140	941	591	451	140	378	276	276	0
	2005	1307	881	733	148	968	634	486	148	339	247	247	0
Carbon uptake (gC m <sup>-2</sup> )	2001		1440	869	567		1186	635	567		254	254	0
	2002		1465	902	571		1204	641	571		261	261	0
	2003		1501	942	573		1202	643	573		299	299	0
	2004		1498	943	564		1202	650	564		293	293	0
	2005		1475	909	575		1214	648	575		261	261	0
WUE (mmol CO <sub>2</sub> mol <sup>-1</sup> H <sub>2</sub> O)	2001		2.68	1.93	6.49		3.12	2.15	6.49		1.63	1.63	0
	2002		2.40	1.79	5.35		2.70	1.89	5.35		1.60	1.60	0
	2003		2.80	2.10	6.61		3.25	2.97	6.61		1.81	1.81	0
	2004		2.59	1.95	6.04		3.05	2.16	6.04		1.59	1.59	0
	2005		2.51	1.86	5.83		2.87	2.00	5.83		1.59	1.59	0
LUE (mol CO <sub>2</sub> mol <sup>-1</sup> )	2001		0.2011	0.1640	0.3046		0.2206	0.1807	0.3046		0.1424	0.1424	0



photon)

2002	0.2046	0.1703	0.3068	0.2240	0.1824	0.3068	0.1463	0.1463	0
2003	0.2096	0.1778	0.3078	0.2236	0.1830	0.3078	0.1676	0.1676	0
2004	0.2092	0.1780	0.3030	0.2236	0.1850	0.3030	0.1642	0.1642	0
2005	0.2060	0.1716	0.3089	0.2258	0.1844	0.3089	0.1463	0.1463	0

---

## Figure legends

Figure 1: Seasonal patterns in (a) total leaf area index (LAI); (b) C3 (tree) and C4 (grass) LAI (the same pattern was applied to all years); and (c) the vertical distribution of LAI through the entire savanna canopy during February when LAI was at its peak. Data were derived from MODIS images and on-ground measurements to create smoothed representations of wet and dry season variation in leaf area index.

Figure 2: Meteorological data measured at the eddy-covariance tower at Howard Springs for all years. Values shown are (a) short-wave solar radiation and maximum daily vapour pressure deficit; (b) maximum and minimum air temperatures; (c) soil moisture content and rainfall (vertical bars).

Figure 3: Annual patterns in ecosystem GPP (top panels) and evapotranspiration and transpiration (bottom panels) for the years 2001-2005 for eddy covariance outputs ( $\diamond$ ) and SPA model outputs (+). The shaded sections represent the dry season each year. All EC data represent total landscape fluxes but SPA model outputs are either the original C3-only SPA formulation ((a) and (c)) or the modified model with both C3 (tree) and C4 (grass) photosynthetic pathways incorporated ((b) and (d)).

Figure 4: Comparisons of measured (eddy covariance) and modelled values of evapotranspiration (a-f) and gross primary productivity (GPP, g-l). Each point represents a daily measurement each year or all years combined. Linear regressions and the 1:1 line are displayed in each plot. See Table 2 for  $R^2$  values for each plot.

Figure 5: Hourly patterns in (a) evapotranspiration (ET) and (b) gross primary productivity (GPP) for binned values of the year 2003. For each month, hourly values across each day were binned to demonstrate seasonal changes in diel patterns. Eddy covariance data are represented by circles and SPA model outputs are shown in as a solid black line. The grey shading represents the 95% confidence range of values measured with eddy covariance.

Figure 6: Modelled daily values of (a) gross primary productivity and (b) transpiration for the C3 (tree) canopy (o), and C4 understorey (x) from 2001 to 2005. The shaded region represents the dry season of each year.

Figure 7: Seasonal (wet and dry season) values of (a) gross primary productivity and (b) evapotranspiration for years 2001 to 2005 for eddy covariance and SPA model outputs. Model outputs of GPP and transpiration are also disaggregated into C3 (overstorey) and C4 (understorey) components for wet and dry seasons in (c) and (d).

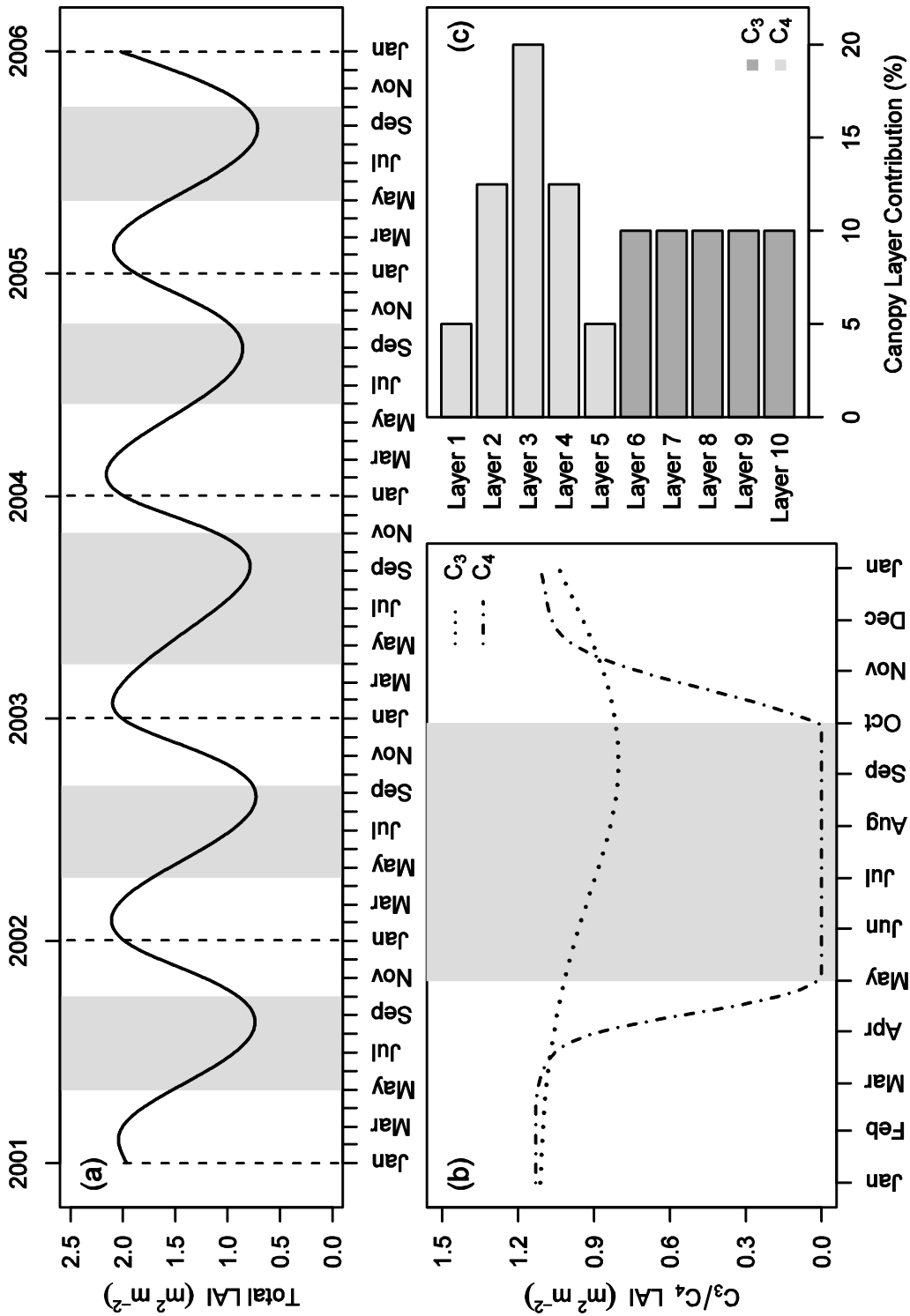
Figure 8: A comparison of model outputs of GPP and transpiration for two contrasting scenarios. In the first scenario, (a) leaf area index (LAI) was kept constant all year and soil water content (SWC) varied seasonally according to observed values in a single (2003) year. In the second scenario (b) soil moisture was kept high throughout the year and LAI showed the standard seasonal decline in the dry season. The grey shading represents the dry season. In both scenarios, model outputs were compared with the output from the “normal simulation” where both LAI and soil moisture content varied seasonally.

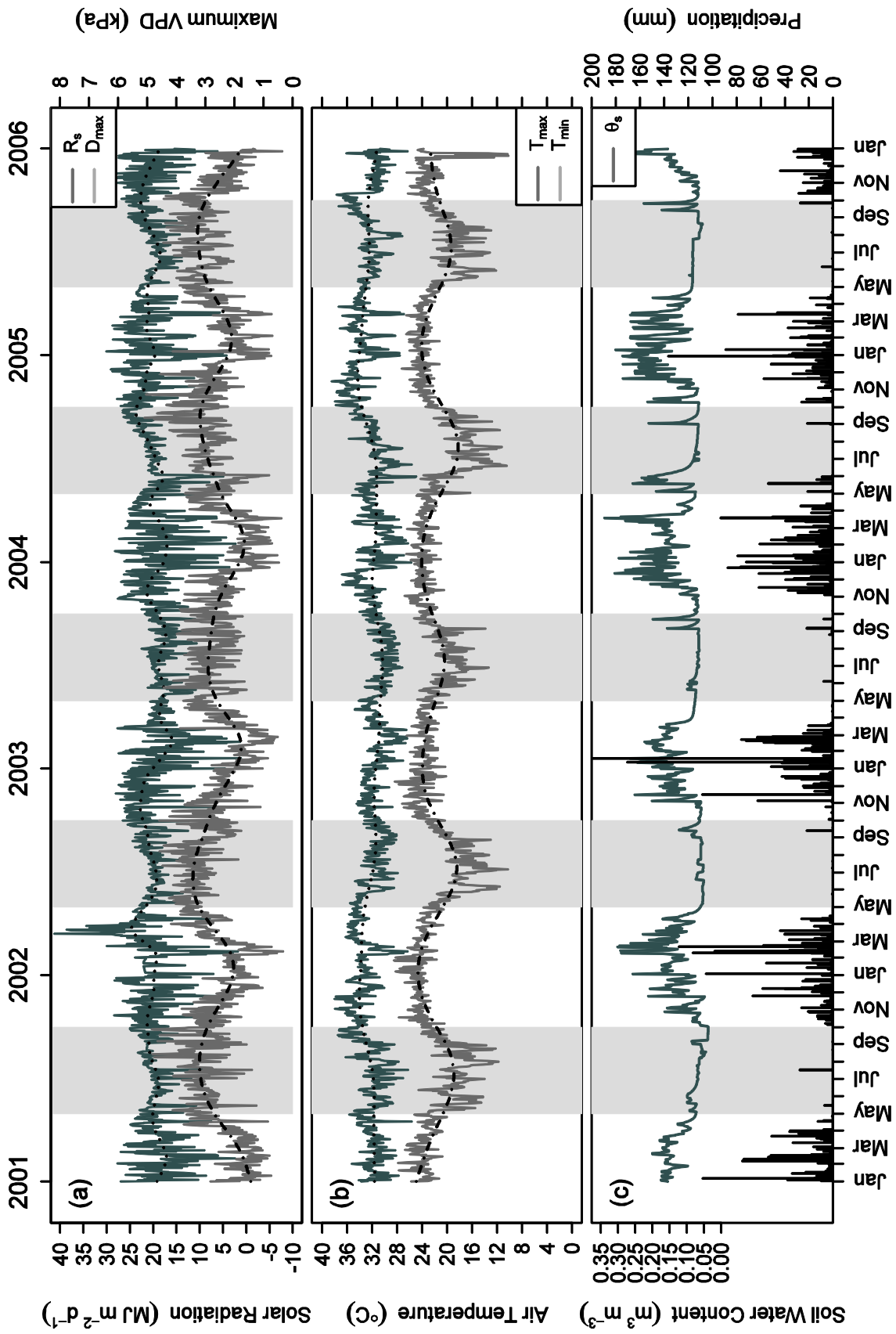
Figure 9: Sensitivity analysis demonstrating the consequence of varying (a) foliar N and leaf area index (LAI) simultaneously; (b) foliar N or (c) LAI separately; (d) whole plant hydraulic conductance ( $G_{\text{plant}}$ ), (e) minimum leaf water potential ( $\psi_{\text{min}}$ ), (f) maximum carboxylation rate ( $V_{\text{cmax}}$ ) and (g) maximum electron transport rate ( $J_{\text{max}}$ ) on daily gross primary productivity (GPP) and evapotranspiration (ET). Values for each parameter were reduced or increased relative to the standard control simulation, defined as 100% (see Table 1 for actual parameter values used in control simulations).

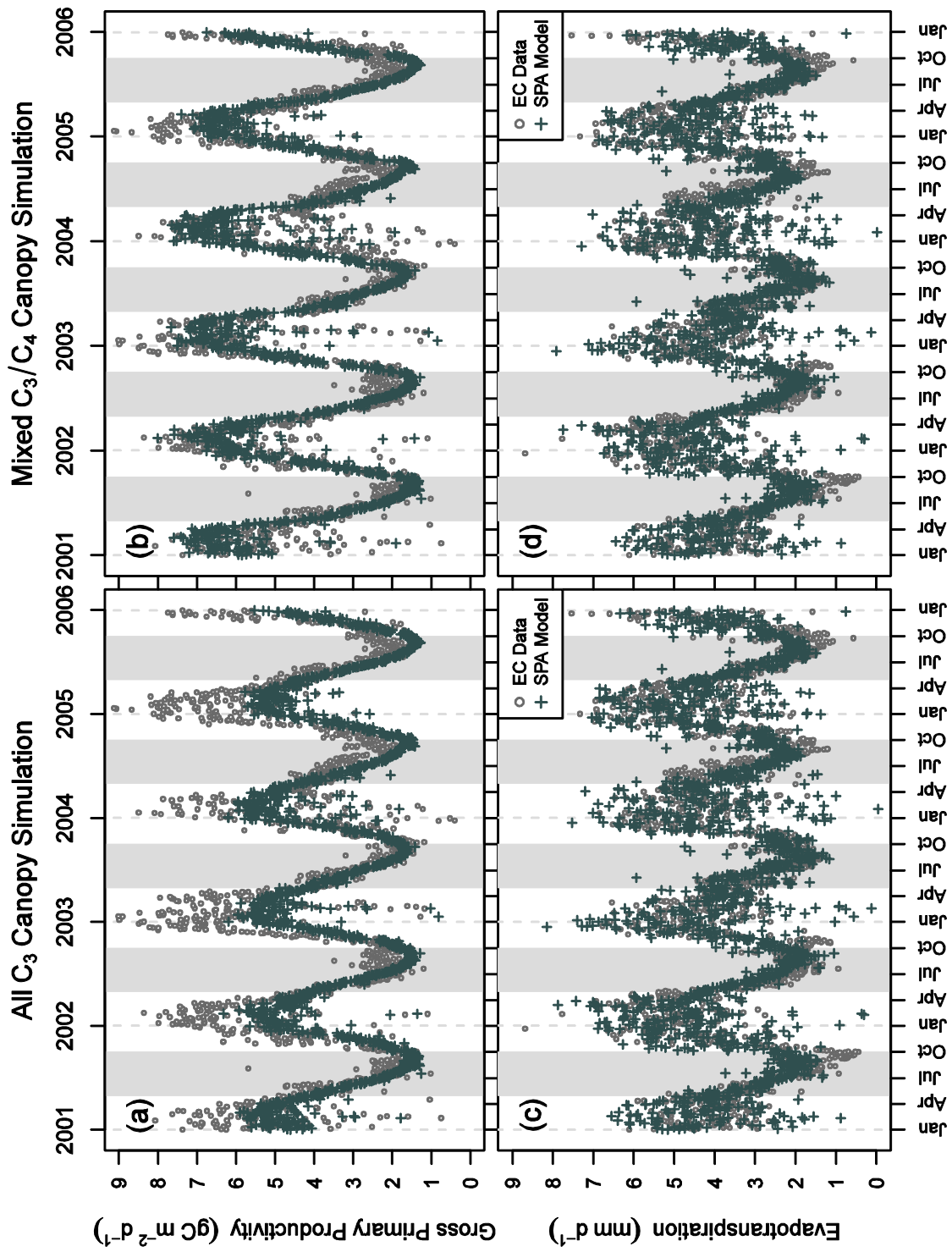
Figure 10: Seasonal responses of hourly values of assimilation ( $A_n$ ) and transpiration ( $E_t$ ) to solar radiation (a-d), vapour pressure deficit (e-h), soil moisture content (i-l) and LAI (m-p) for the wet

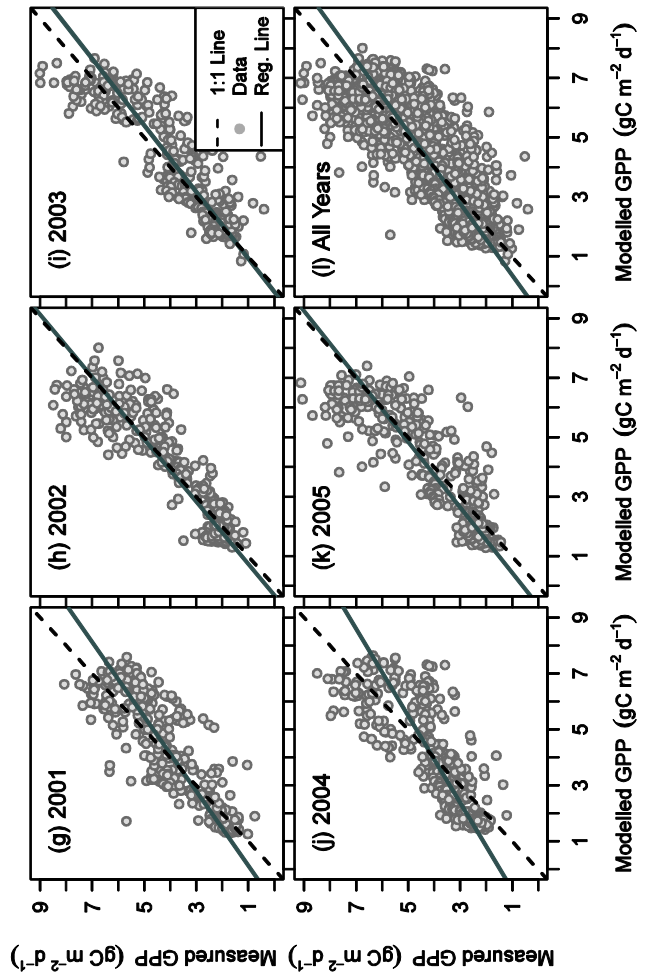
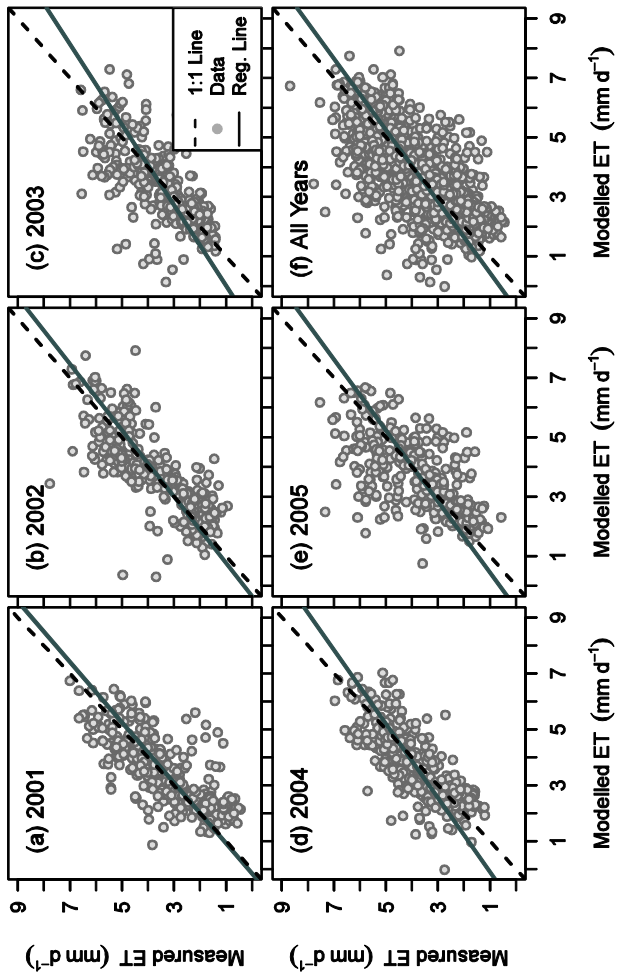
and dry seasons of 2003. Data were separated into C3 (o) and C4 (x) components of the vegetation.

Lines shown are the 95% confidence boundaries for C3 (dashed) and C4 (solid) canopy layers.









Howard Springs, 2003

