

Intrinsic climate dependency of ecosystem light and water-use-efficiencies across Australian biomes

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Received 11 February 2014, revised 19 August 2014

Accepted for publication 26 August 2014

Published 3 October 2014

Abstract

The sensitivity of ecosystem gross primary production (GPP) to availability of water and photosynthetically active radiation (PAR) differs among biomes. Here we investigated variations of ecosystem light-use-efficiency (eLUE: GPP/PAR) and water-use-efficiency (eWUE: GPP/evapotranspiration) among seven Australian eddy covariance sites with differing annual precipitation, species composition and temperature. Changes to both eLUE and eWUE were primarily correlated with atmospheric vapor pressure deficit (VPD) at multiple temporal scales across biomes, with minor additional correlations observed with soil moisture and temperature. The effects of leaf area index on eLUE and eWUE were also relatively weak compared to VPD, indicating an intrinsic dependency of eLUE and eWUE on climate. Additionally, eLUE and eWUE were statistically different for biomes between summer and winter, except eWUE for savannas and the grassland. These findings will improve our understanding of how light- and water-use traits in Australian ecosystems may respond to climate change.

 Online supplementary data available from stacks.iop.org/ERL/9/104002/mmedia

Keywords: ecosystem light- and water-use-efficiencies, temporal scales, biomes, climate, spatial pattern

1. Introduction

Climate imposes important but often contrasting limitations on productivity in most vegetated biomes (Churkina and Running 1998). Among climate factors, solar radiation

provides the energy source for photosynthesis, while water availability alters leaf-scale photosynthesis via modulations of plant stomatal conductance (Beer *et al* 2009) and canopy-scale photosynthesis via changes in leaf area index (Eamus *et al* 2001). Ecosystem light-use-efficiency (eLUE) and water-use-efficiency (eWUE) are two critical traits of terrestrial ecosystems that characterize the sensitivity of biomass production to solar irradiance and water supply (Beer *et al* 2007, Hu *et al* 2008, Ponton *et al* 2006, Turner *et al* 2003). eLUE and eWUE differ substantially in range and



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vary with environmental stress and vegetation structure within and across biomes (Farquhar *et al* 1989, Law *et al* 2002, Schwalm *et al* 2006). The values of both eLUE and eWUE exhibit time-scale dependence in the sense that their primary environmental controls vary temporally (Campos *et al* 2013, Schwalm *et al* 2006, Turner *et al* 2003).

Historically, eLUE (ϵ) has been defined as the ratio of net primary production (NPP, aboveground or total, ϵ_n) or gross primary production (GPP, ϵ_g) to incident photosynthetically active radiation (PAR) or absorbed PAR (APAR) (Gower *et al* 1999). Based upon evolutionary and physiological theory, ϵ_n and ϵ_g are expected to converge across biomes (Goetz and Prince 1999). However, values of each are dependent on plant function type (Gower *et al* 1999, Schwalm *et al* 2006, Turner *et al* 2003). The biophysical, biochemical and meteorological controls of eLUE among biomes at multiple temporal time-scales are not well understood, resulting in imprecise estimates of NPP and GPP and uncertainties in the responses of eLUE to climate change (Kanniah *et al* 2011). For example, daily ϵ_g decreased with increasing APAR but was poorly correlated with vapor pressure deficit (VPD) or air temperature (T_a), while the relative values of ϵ_g across biomes were influenced by relative nitrogen availability (Turner *et al* 2003). In contrast, Schwalm *et al* (2006) observed that changes in daily ϵ_g were driven by variation in light and temperature with no correlation to water availability or foliar nitrogen, while annual ϵ_g varied across biomes as a function of mean annual temperature (MAT) and leaf area index (LAI). Additionally, annual ϵ_g can increase with increasing total annual precipitation and decreasing potential evapotranspiration (Polley *et al* 2011) or MAT (Lafont *et al* 2002).

eWUE reflects a trade-off between carbon gain and water loss from leaves and ecosystems (Baldocchi 1994), and is important for ecosystem productivity and resilience (Campos *et al* 2013, Huxman *et al* 2004). At the leaf-scale, eWUE is expressed as the ratio of net photosynthesis to transpiration but at the ecosystem-scale, eWUE is defined as the ratio of either NEE or GPP to ET or canopy transpiration (Beer *et al* 2009, Niu *et al* 2011). To quantify the role of water limitation on above-ground NPP, rain-use-efficiency (RUE, the ratio of above-ground NPP to rainfall) is widely used (Huxman *et al* 2004). Alternatively, inherent water-use-efficiency (IWUE, $GPP \cdot VPD/ET$) can be used to normalize the effect of VPD on ET (Beer *et al* 2009, Eamus *et al* 2013). Daily eWUE is negatively correlated with VPD during the time of peak GPP activity (Ponton *et al* 2006) and so is monthly eWUE across a large range of biomes (Law *et al* 2002). In contrast, annual eWUE tends to be similar across biomes except for tundra vegetation (Law *et al* 2002). Across a grassland transect in China, LAI is considered as the primary determinant of seasonal eWUE (Hu *et al* 2008). Annual eWUE of grasslands may decrease (Li *et al* 2008) or increase (Niu *et al* 2011) with increasing annual precipitation whilst eWUE may differ between wet and dry years (Campos *et al* 2013, Huxman *et al* 2004) or wet and dry seasons (Eamus *et al* 2013), and varies with soil moisture and LAI (Beer *et al* 2009).

The lack of consensus on the relative importance of different controlling factors of eLUE and eWUE across biomes at multiple temporal scales reflects the complexity of interactions between terrestrial ecosystems and climate. Therefore, a key issue to resolve is the relationships of eLUE and eWUE to climatic drivers. The eddy covariance (EC) technique provides an opportunity to examine the potential relationships due to simultaneous measurements of solar radiation, carbon and water fluxes, VPD and soil water content (SWC), thereby generating an extensive time series of eLUE and eWUE from hourly to multi-annual time-scales. Concurrent measurement of meteorological variables with fluxes can be used to quantify limitations on eLUE and eWUE and the interaction of climate variables as determinants of eLUE and eWUE. Thus, the current study used EC data from seven contrasting ecosystems in Australia for examining the magnitude, spatial patterns, and environmental regulation of eLUE and eWUE at multiple time-scales (hourly, daily, eight-day, monthly, and yearly). These seven EC sites encompass a range of biomes along a large precipitation, species compositional and temperature gradient, thereby providing further insights into coupling between ecosystems and climate. We aimed to identify variations in eLUE and eWUE of Australian major ecosystems over different time-scales and their key climatic drivers among biomes. This will allow for a better understanding of the coupling of carbon and water cycles and the effects of climate change on ecosystem carbon budgets and water use.

2. Methods

2.1. Sites and data processing

Seven sites were selected for this study in Australia. Individual site names, details, statistics and plots are given in the supplementary information (see supplementary information available at stacks.iop.org/ERL/9/104002/mmedia). These sites include four contrasting savannas (Savn, AU-Ade, AU-Asm, AU-Dry and AU-How sites), two different evergreen broadleaf forests (EBF, AU-Tum and AU-Wac sites), and one grassland (Grass, AU-Stp site) (supplementary table S1; supplementary figure S1). Bioclimatic classifications of these sites range from tropical wet-dry in northern Australia, through tropical semi-arid in central Australia to cool temperate mesic in southeastern. Mean annual precipitation is smallest in central Australia and largest in far northern monsoonal Australia. All sites show seasonal patterns in precipitation, temperature and VPD that interact with large fluctuations in water availability. Seasonal variability in temperature and PAR was larger at the two forests in southeastern Australia than at the grassland and savanna sites. Conversely, seasonal variability in VPD and rainfall was larger in the northern and central sites, where a distinct dry season occurs during Australian winter (supplementary figure S1).

At each site, LAI data were derived from the space-borne MODIS (Moderate Resolution Imaging Spectroradiometer)

sensor (500 m spatial resolution and eight day temporal resolution). The MODIS images are spatially similar to the footprint size of the EC data used. A central 3 × 3 window was used to extract the flux tower LAI time series. This sampling strategy can effectively reduce the error due to the scale mismatch between the tower footprint and MODIS pixels (Rahman *et al* 2005, Xiao *et al* 2005). Then the LAI data series were smoothed using the TIMESAT tool (Jönsson and Eklundh 2004). Mean maximum LAI (LAI_{max}) for each site were aggregated at eight-day, monthly and yearly scales. Half-hourly meteorological data, water and CO₂ fluxes were measured using an EC system and associated meteorological sensors installed at each site. All data were processed through OzFlux standard methods (see supplementary information).

2.2. Wavelet aggregation method

Half-hourly eLUE and eWUE were defined as ratios of GPP to PAR and GPP to ET, respectively. For eLUE, using incident PAR as the denominator instead of APAR can couple carbon and energy budgets directly at the ecosystem level rather than merely focusing on the biological mechanisms that drive photosynthesis (Schwalm *et al* 2006). When large disturbances occurred (for example, fire or extensive insect-induced defoliation), flux and LAI data were excluded from all analyses to minimize the introduction of bias arising from the inclusion of short-term episodic large-scale fluctuations in these data. To analyze multi-scale interactions between eLUE/eWUE and forcing variables, measured carbon and water fluxes, meteorological variables, SWC and LAI were resolved using the wavelet transformation (Ding *et al* 2013, Stoy *et al* 2005, Torrence and Compo 1998). The wavelet transformation can be used to analyze time series such as EC fluxes (Scanlon and Albertson 2001) that contain non-stationary power at different frequencies (Daubechies 1990). Here a continuous wavelet transformation with the Morlet basis was employed. Half-hourly carbon and water fluxes and environmental factors were transformed, reconstructed and then aggregated at hourly, daily, eight-day, monthly, seasonal and yearly time-scales, respectively. eLUE and eWUE were concurrently calculated at each time-scale. The detailed description of the Morlet wavelet transformation and an example of the reconstruction at the Howard Springs site were given in supplementary material (supplementary figure S2).

3. Results

3.1. GPP responses to PAR and ET

Figure 1 shows the multi-temporal (i.e. at daily to yearly time-scales) responses of GPP to variations in PAR and ET across the various ecosystems. GPP and PAR were significantly correlated only at the two temperate forest sites ($R^2 = 0.88\text{--}0.97$, $p < 0.001$ and $R^2 = 0.67\text{--}0.98$, $p < 0.001$ at AU-Tum and AU-Wac, respectively) (figure 1). Generally, GPP exhibited a significant linear correlation with ET (R^2 from 0.48 to 0.96, $p < 0.001$) at all sites across daily to

monthly time-scales. Across the three biomes, average eLUE and eWUE were largest in forests, intermediate in savannas, and smallest in the grassland. Among the savannas, eLUE and eWUE were largest at AU-How and AU-Ade (tropical savannas) and smallest at AU-Asm (semi-arid savanna).

3.2. Relationships of eLUE and eWUE with climate

eLUE was significantly correlated with air temperature and PAR, and eWUE was significantly correlated with PAR. However, these correlations across biomes became much weaker at shorter time-scales, especially at the hourly time-scale and in the summer when light is less limiting (table 1). PAR explained less variation in eLUE than VPD at all time-scales, and air temperature was less correlated with eWUE than VPD at all time-scales except the hourly time-scale. Henceforth, of climate factors we mainly focus on the relationships between eLUE/eWUE and VPD, but this does not mean the effects of PAR on eLUE and air temperature on eWUE were not important. Across all sites, eLUE and eWUE followed a negative logarithmic relationship with VPD (table 1; figure 2). The goodness-of-fit increased as the time-scale increased. However, within a given ecosystem, a significant relationship between eLUE or eWUE and meteorology was, on occasion, absent. For example, at the AU-How site, eWUE was very weakly or not correlated with VPD (figure 2). Likewise at the AU-Asm site, eLUE was very weakly or not correlated with VPD (figure 2). This suggests that the factors driving eLUE and eWUE can differ within and across biomes.

3.3. Relationships of eLUE and eWUE to SWC and LAI

Significant positive correlations between eLUE/eWUE and SWC were observed across all time-scales (table 1; figure 3). The strength of these correlations increased with increasing time-scale. SWC showed a slightly better relationship with eLUE at hourly time-scale than VPD (table 1), while at other time-scales, the influence of SWC was consistently and slightly weaker than VPD. Across all time-scales, SWC was less correlated with eWUE than VPD. Specifically, SWC explained much less compared to VPD in variation of eLUE in summer. Considering the seven ecosystems together, a spatial pattern emerged whereby ecosystems with high annual average SWC also had large eLUE and eWUE. This was consistent with the response of eLUE/eWUE to VPD because of the inverse relationship between SWC and VPD. However, the relationships between eLUE/eWUE and SWC varied from site to site. Notably, at the AU-How site, eLUE increased with SWC whereas eWUE appeared to decrease as SWC increased (figure 3).

There were significant positive correlations between eLUE or eWUE and LAI_{max} at eight-day, monthly and annual time-scales (table 1; supplementary figure S3). These relationships were much weaker than those between eLUE/eWUE and VPD. Specifically, in winter, eLUE and eWUE were moderately or weakly correlated with LAI_{max} . In

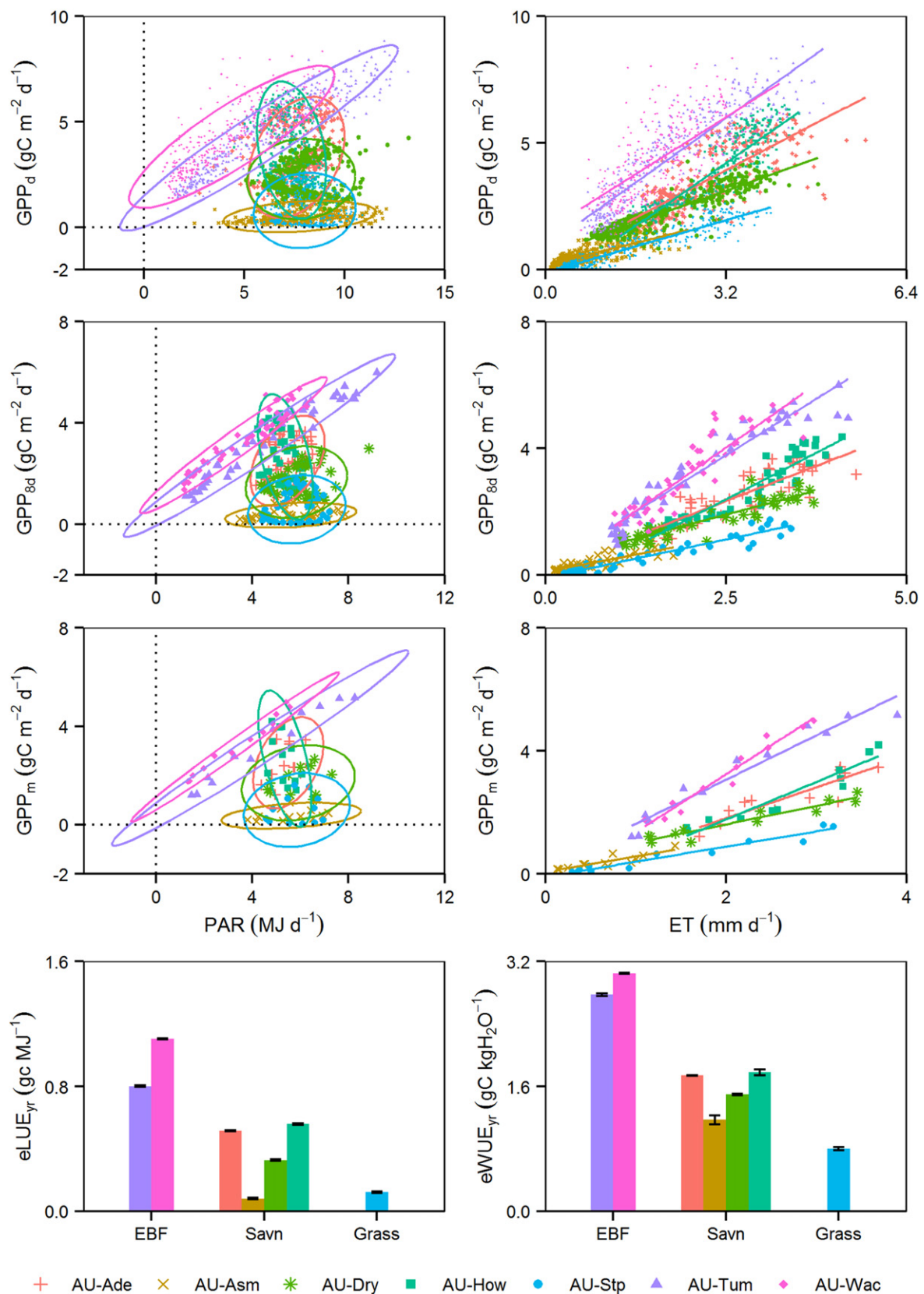


Figure 1. Relationships between (left) daily (GPP_d), eight day (GPP_{8d}), monthly (GPP_m) GPP and PAR and between (right) GPP and ET for seven sites. Ellipses (left) indicate 95% confidence boundaries of GPP. Bars indicate annual standard deviations of eLUE or eWUE at each site. Also shown is the linear fit between GPP and ET (right). Annual eLUE(eLUE_{yr}) and eWUE(eWUE_{yr}) were calculated from annual GPP, PAR and ET.

Table 1. Coefficients of determination (R^2) between LUE, WUE and T_a , PAR, VPD, SWC or LAI_{max} by logarithmic/exponential (Log/exp) and linear (Lin) fitting, respectively. ***, **, *, and NULL indicates significant relationship at $p < 0.001$, 0.01, 0.05 and not significant, respectively. Monthly(S) and Monthly(W) indicate monthly variables in summer (December, January, and February) and winter (June, January, and August).

Scale	Model	Hourly		Daily		Eight-day		Monthly		Monthly(S)		Monthly(W)		Annual	
		Log/exp	Lin	Log/exp	Lin	Log/exp	Lin	Log/exp	Lin	Log/exp	Lin	Log/exp	Lin	Log/exp	Lin
eLUE	T_a	0.34***	0.35***	0.41***	0.41***	0.43***	0.43***	0.44***	0.44***	0.38**	0.39**	0.52***	0.51**	0.59*	0.56
	PAR	0.20***	0.21***	0.52***	0.43***	0.46***	0.39***	0.46***	0.41***	0.40**	0.35**	0.77***	0.70***	0.82**	0.84**
	VPD	0.43***	0.34***	0.71***	0.62***	0.76***	0.71***	0.78***	0.75***	0.90***	0.83***	0.76***	0.74***	0.89**	0.94***
	SWC	0.59***	0.49***	0.63***	0.67***	0.63***	0.74***	0.64***	0.76***	0.63***	0.61***	0.65***	0.84***	0.70*	0.84**
	LAI_{max}					0.48***	0.33***	0.53***	0.38***	0.81***	0.58***	0.36**	0.20*	0.83**	0.68*
eWUE	T_a	0.52***	0.52***	0.62***	0.63***	0.62***	0.65***	0.64***	0.67***	0.65***	0.67***	0.63***	0.59***	0.75*	0.71*
	PAR	0.05***	0.11***	0.51***	0.46***	0.44***	0.41***	0.46***	0.44***	0.22*	0.19*	0.73***	0.69***	0.82**	0.85**
	VPD	0.49***	0.34***	0.71***	0.57***	0.74***	0.65***	0.78***	0.72***	0.83***	0.69***	0.79***	0.78***	0.95***	0.96***
	SWC	0.44***	0.45***	0.50***	0.56***	0.53***	0.62***	0.55***	0.66***	0.51***	0.60***	0.60***	0.77***	0.70*	0.81**
	LAI_{max}					0.50***	0.47***	0.55***	0.52***	0.82***	0.73***	0.49***	0.36**	0.84**	0.80**

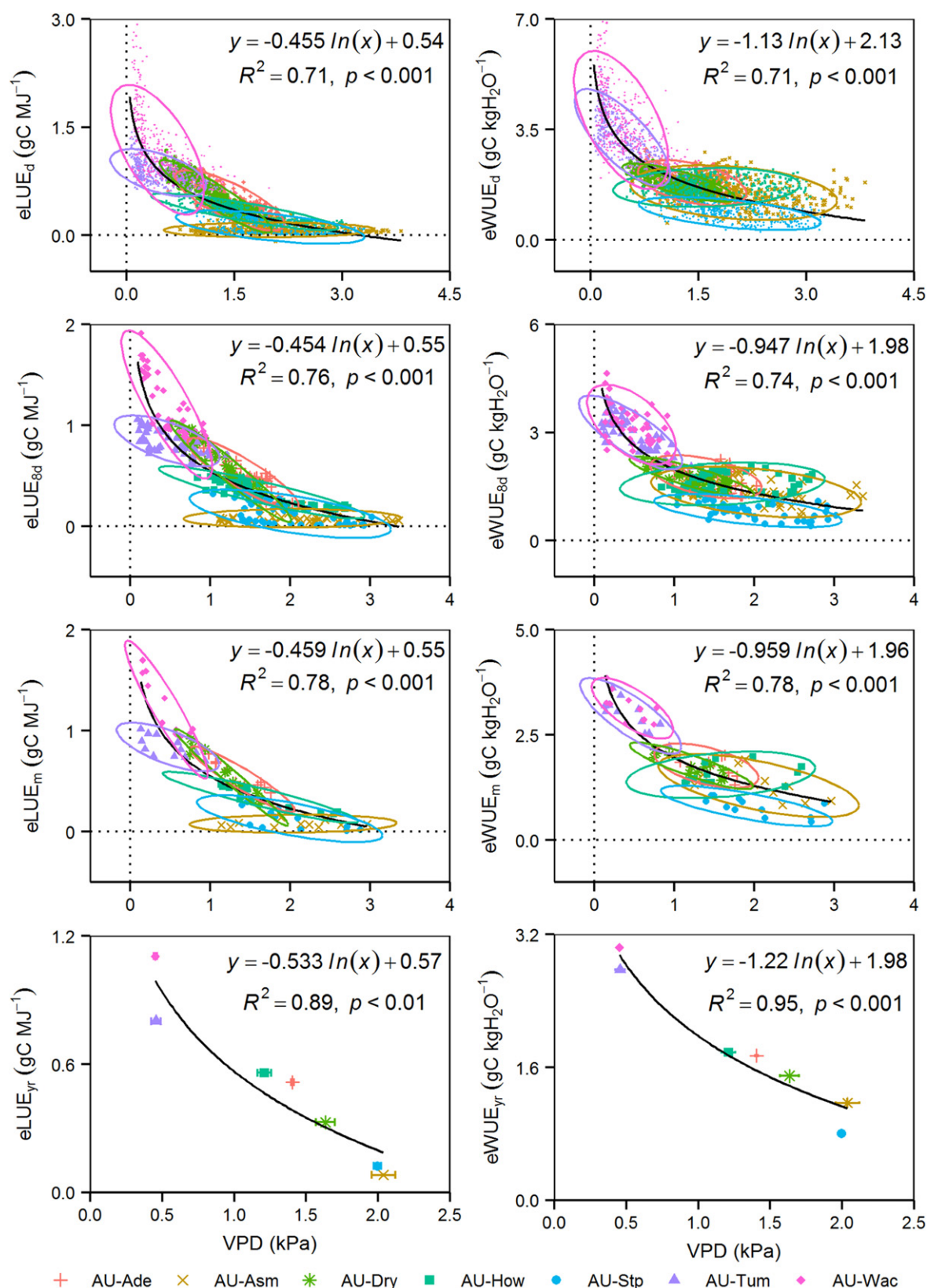


Figure 2. Relationships between (left) daily (eLUE_d), eight day (eLUE_{8d}), monthly (eLUE_m) eLUE and VPD and between (right) daily (eWUE_d), eight day (eWUE_{8d}), monthly (eWUE_m) eWUE and VPD for seven sites. Ellipses indicate 95% confidence boundaries of eLUE and eWUE. Bars indicate annual standard deviations of eLUE, eWUE or VPD at each site. Also shown are logarithmically fitted functions, coefficients of determination (R^2) and p values.

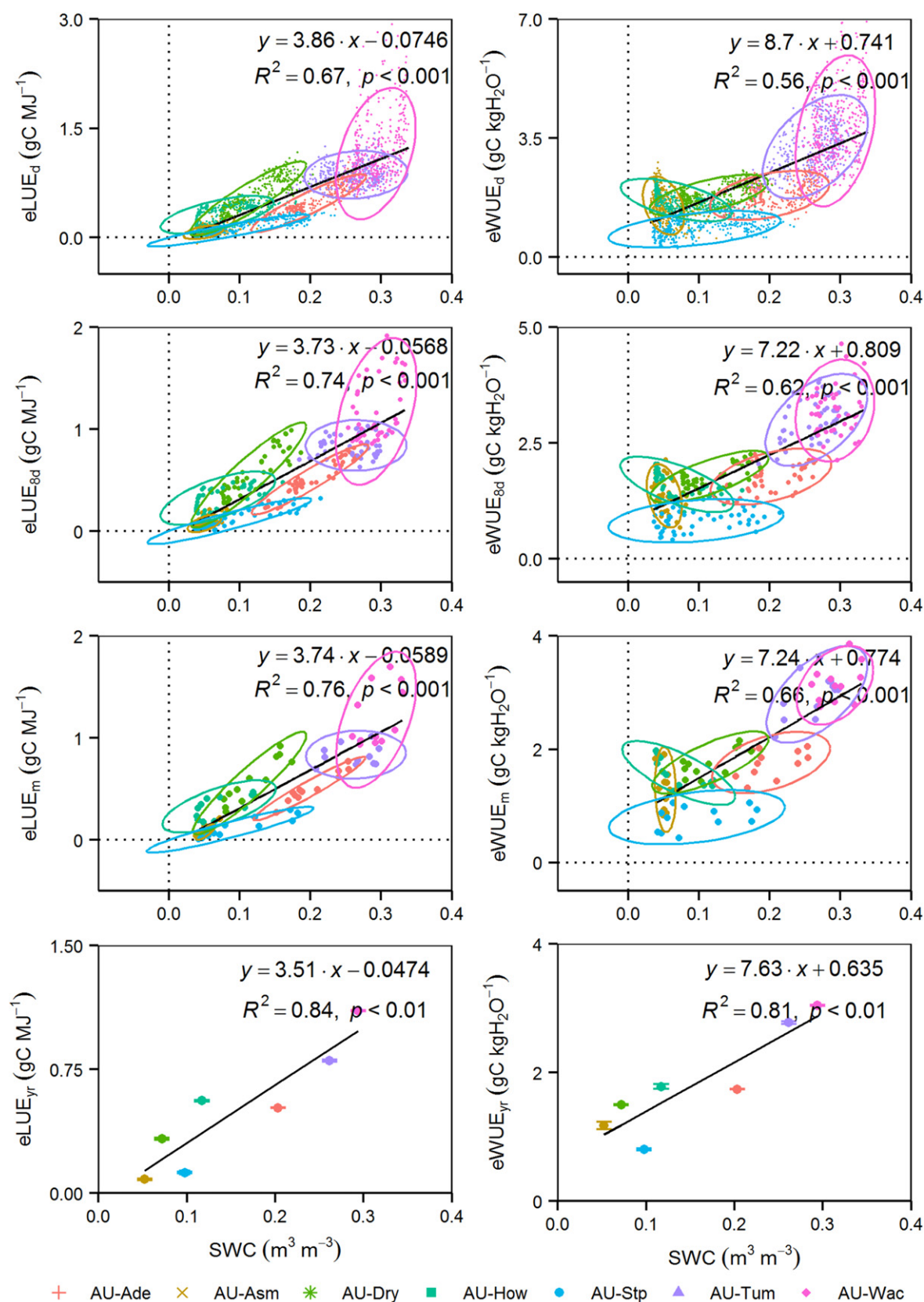


Figure 3. Relationships between (left) daily ($eLUE_d$), eight day ($eLUE_{8d}$), monthly ($eLUE_m$) eLUE and SWC and between (right) daily ($eWUE_d$), eight day ($eWUE_{8d}$), monthly ($eWUE_m$) eWUE and SWC for seven sites. Ellipses indicate 95% confidence boundaries of eLUE and eWUE. Bars indicate annual standard deviations of eLUE, eWUE or SWC at each site. Also shown are logarithmically fitted functions, coefficients of determination (R^2) and p values.

contrast, eLUE and eWUE in summer showed strong correlation with LAI_{max}.

3.4. Behavior of eLUE and eWUE in summer and winter

Monthly eLUE and eWUE in summer and winter showed responses to climate variables consistent with the daily/eight-day to annual time-scales (table 1; figure 4) but the correlation between eLUE/eWUE versus SWC in summer became relatively weak compared with VPD and LAI (table 1). During summer, the VPD dependence of eLUE and eWUE were more apparent than dependence on other climate variables and SWC (table 1). By contrast in winter, variations in eLUE and eWUE were less sensitive to VPD (i.e. the fitted slopes in figure 4). Notably, SWC explained slightly more variability in eLUE during winter, than climatic variables in summer, suggesting different controlling factors and/or mechanisms regulating eLUE in contrary hydrothermal conditions.

Seasonal eLUE differed between summer and winter at all sites except three savannas sites (figure 4). Notably, difference of eLUE between summer and winter was significantly large ($p < 0.001$) at the AU-How savannas site. Contrary to AU-How and the grassland, the two EBF sites showed higher eLUE in winter. There was no significant difference of seasonal eWUE at biome scale except EBF. Similar to eLUE, eWUE at the two EBF sites was lower in summer than that in winter.

4. Discussion

4.1. Relationships between GPP, PAR and ET

Canopy photosynthesis can be linearly related with PAR (McMurtrie and Wang 1993) or show a hyperbolic response function (Ramier *et al* 2009). Hyperbolic responses of canopy photosynthesis to PAR are expected in biomes with low photosynthetic capacity or low LAI (Baldocchi and Amthor 2001), where self-shading within canopies is relatively small, in contrast to biomes with large LAI where light saturation of photosynthesis does not occur so frequently in the lower canopy. Thus, the significant linear correlation of GPP with PAR at EBF sites can be explained by their relatively large LAI (supplementary table S1; figure 1). Thus, these sites are primarily light limited and were not light saturated during the period of measurement. In savannas and the grassland, GPP was not correlated with variations in PAR at these northern tropical sites (figure 1) due to relatively small intra-annual variations in daily average PAR (lower latitude) (supplementary figure S1; figure 1). Seasonal variation in GPP primarily responded to large changes in LAI arising from senescence of the grassy understory as driven by seasonal monsoonal rainfall (Whitley *et al* 2011). Thus it is light interception rather than light supply that limits GPP at these sites.

Coupling of GPP to ET has been observed in many studies (Baldocchi 1994, Beer *et al* 2009), and stems from the intrinsic link between carbon and water fluxes via stomatal

conductance at the leaf level (Beer *et al* 2009). In contrast to reported convergence of annual eWUE across multiple biomes (except for tundra vegetation) (Law *et al* 2002), we only observed similar eWUE values (that is, functional convergence of eWUE) within the savannas (figure 1). Similarly, Ponton *et al* (2006) identified differing eWUE among Douglas-fir forest, aspen forest and grassland within a growing season. However, it is worth noting that the regression slope of GPP against ET in savannas during the dry season (when ET is minimal) was similar to that of forests (figure 1). This is likely to be because ET is driven by C3 trees in the dry season following senescence of the annual grasses. At larger rates of ET during the wet season, C4 grasses dominate the understory and have a larger WUE than C3 plants. Thus, there is some evidence that the eucalypt species examined across temperature and tropical biomes in the current study converged to a common WUE. This result is consistent with the results of O'Grady *et al* (2009), who observed convergence of rates of tree water use within an arid-zone woodland in Australia. Apparent divergence of eWUE between seasons in wet-dry tropical biomes is therefore driven by changes in the relative contributions of upper (C3) and lower (C4) canopies to ET and GPP, rather than changes in functional behavior of the biomes *per se*.

4.2. Climate dependence of eLUE and eWUE among biomes

Variations of eLUE were best explained by VPD and SWC while variations of eWUE were best explained by VPD across all time-scales but also well correlated with SWC (table 1). This suggested that VPD co-varied with SWC and water availability was the most influential factor for eLUE/eWUE. Rapid ecosystem transitions that include changes in ecosystem productivity, structure and water cycling can result from long-term climate variations, such as variability in inter-annual precipitation and seasonality of precipitation (Grimm *et al* 2013). Over northern savannas and the grassland, rainfall is the primary environmental controlling factor such that vegetation structure (i.e. tree height and LAI) has adapted to the available resources (Cook *et al* 2002). In contrast, PAR, VPD and air temperature which usually strongly co-vary, were the major drivers of variation in ecosystem productivity in the two temperate forests (Cleverly *et al* 2013, Kanniah *et al* 2011, van Gorsel *et al* 2013). Therefore, climate variables are critical factors that essentially regulate eLUE and eWUE through their long-term influence on ecosystem structure and functioning. Consequently, our results showed a robust intrinsic dependence of eLUE and eWUE on climate across all time-scales.

Several explanations exist for the strong link between eLUE/eWUE and climate. Generally, climatic control of ET and GPP lies somewhere along a continuum between either severe water or energy limitation (Budyko 1974, Whitley *et al* 2011), although temperature also limits productivity in many ecosystems (Churkina and Running 1998). Deficits of radiation, temperature or water that cause a decrease in GPP will lead to lower canopy conductance and ET (Beer *et al* 2009). Most sites in the present study, and particularly

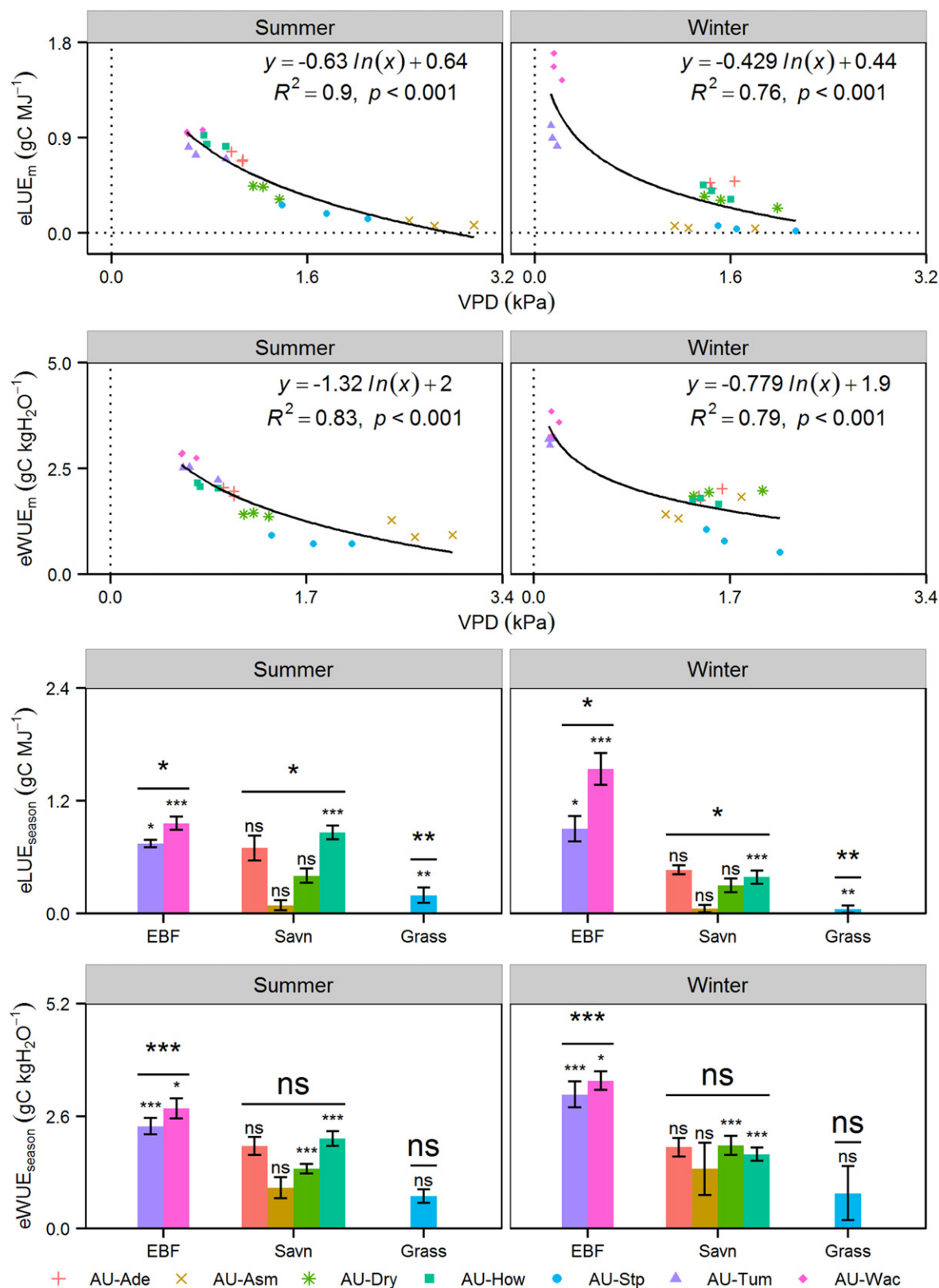


Figure 4. Logarithmical relationships between (top two) monthly LUE (eLUE_m) and VPD and between monthly WUE (eWUE_m) and VPD in summer and winter, respectively. Comparisons of (bottom two) average seasonal eLUE (eLUE_{season}) and eWUE (eWUE_{season}) for seven sites are also shown in summer and winter, respectively. Error bars indicate the standard deviations of seasonal eLUE or eWUE at each site. '***', '**', and '*' above the error bars of each site indicate significance at 0.001, 0.01, and 0.05 levels, while 'ns' represents not significant, based on *t*-test statistics, and these symbols above the horizontal lines represent significance at biome level.

the tropical ones that experience a distinct dry season, did not show evidence of energy supply limitation (as inferred from PAR) at any temporal scales because the range in daily PAR was too small (figure 1). VPD can represent atmospheric evaporative demand and is responsive to patterns of water availability. Increasing VPD leads to reduced GPP through smaller stomatal conductance (Beer *et al* 2009), hence eLUE and eWUE decline with increasing VPD because at low and moderate values of VPD, increasing VPD causes increased ET (Eamus *et al* 2008, Thomas and Eamus 1999, Wharton *et al* 2009) but reduced GPP (table 1; figure 4).

4.3. Seasonal patterns of eLUE and eWUE across biomes

eLUE and eWUE showed significant difference between summer and winter at several sites (figure 4). Seasonal changes in climate variables, SWC and vegetation structure (e.g. LAI_{max}) can explain these seasonal similarity or difference. At the EBF sites during winter, GPP increased with PAR. During winter neither temperature nor VPD were supra-optimal for GPP. In contrast, in the summer, increasing PAR was accompanied by either temperature or VPD attaining supra-optimal values, thereby limiting the response of GPP to increased PAR and leading to a smaller eLUE in summer. A similar phenomenon was also found in eWUE. At the EBF sites, both GPP and ET decreased in winter. However, in summer, high VPD and temperature imposed larger limiting effects on GPP than ET, which caused a smaller eWUE in summer. This limiting effect was especially obvious at the AU-Wac site because VPD became increasingly important for GPP during summer compared to winter (Kilinc *et al* 2013). Meanwhile, since both GPP and LAI_{max} at AU-Wac were larger in summer whereas the corresponding eLUE was relatively smaller ($p < 0.01$), eLUE was negatively correlated with LAI_{max} (supplementary figure S3) as with VPD. At the grassland site, dry winter (supplementary figure S1) caused SWC and LAI to decline significantly compared to summer (data not shown), which decreased canopy photosynthesis and transpiration and further decreased eLUE substantially but not significantly affected eWUE. At AU-How, as a combination of trees and seasonal grass, savannas have larger LAI in summer resulting in a larger GPP. Meanwhile, PAR in winter at AU-How was comparable to that in summer. Consequently, eLUE in summer at this site was larger than that in winter ($p < 0.001$). Similarly, both GPP and ET in winter significantly decreased resulting from senescence of C4 grass and effects of meteorological variables, but the decrease in GPP was stronger than the decrease in ET at AU-How, leading to a smaller eWUE. Contrarily, at AU-Dry the decrease in ET exceeded the decrease in GPP resulting in a larger eWUE in winter. This asynchronous response of GPP and ET to climatic variables or LAI and thus variations of eWUE are in good agreement with previous findings in China (Yu *et al* 2008).

5. Conclusions

Climate drivers are critical in regulating water cycling (and consequently SWC) and LAI through their long term influences on ecosystem structure and functioning (Kanniah *et al* 2011). Understanding the spatial patterns of eLUE and eWUE at multiple time-scales and their underlying environmental control mechanisms is of great significance for estimating ecosystem carbon budgets and water carrying capacity under changing hydrothermal conditions (i.e., climate change) (Yu *et al* 2008). In this study, we investigated the relationships between eLUE and eWUE versus climate factors, SWC and vegetation dynamics across diverse climatic regimes with environmental gradients. Across biomes, eLUE and eWUE were tightly and coherently correlated with climate drivers, particularly VPD (and consequently SWC), at multiple time-scales. For any specific biome, eLUE and eWUE were significantly different between summer and winter except eWUE for savannas and the grassland. LAI played an important role in influencing eLUE and eWUE in summer season. Our results provide valuable information for predicting the spatial pattern of eLUE and eWUE at multiple time-scales across Australian biomes. Also this study improves understanding of the responses of ecosystem functional traits to gradients in water availability and temperature, which in turn enables improvements of estimating carbon and water fluxes on a large spatial scale.

Acknowledgements

This research was supported by an Australian Research Council Discovery Early Career Research Award (project number DE120103022).

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