# Mulga, a major tropical dry open forest of Australia: recent insights to carbon and water fluxes

You may also be interested in:

Intrinsic climate dependency of ecosystem light and water-use-efficiencies across Australian biomes
Hao Shi, Longhui Li, Derek Eamus et al.

Impact of mountain pine beetle induced mortality on forest carbon and water fluxes
David E Reed, Brent E Ewers and Elise Pendall

Estimation of aboveground net primary productivity in secondary tropical dry forests using the Carnegie–Ames–Stanford Approach (CASA) model
S Cao, GA Sanchez-Azofeifa, SM Duran et al.

Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes?
Kara Allen, Juan Manuel Dupuy, Maria G Gei et al.

Modeling Long-term Forest Carbon Spatiotemporal Dynamics With Historical Climate and Recent Remote Sensing Data
Jing M. Chen

Spatio-temporal dynamics of evapotranspiration on the Tibetan Plateau from 2000 to 2010
Lulu Song, Qianlai Zhuang, Yunhe Yin et al.

Satellite observation of tropical forest seasonality: spatial patterns of carbon exchange in Amazonia
Liang Xu, Sassan S Saatchi, Yan Yang et al.

Process contributions of Australian ecosystems to interannual variations in the carbon cycle
Vanessa Haverd, Benjamin Smith and Cathy Trudinger

# Environmental Research Letters

**LETTER**

# Mulga, a major tropical dry open forest of Australia: recent insights to carbon and water fluxes

Derek Eamus[1], Alfredo Huete, James Cleverly, Rachael H Nolan, Xuanlong Ma, Tonantzin Tarin and Nadia S Santini

Terrestrial Ecohydrology Research Group, University of Technology Sydney, Australia
[1]  Author to whom any correspondence should be addressed.

**E-mail:** Derek.Eamus@uts.edu.au

## Abstract

Mulga, comprised of a complex of closely related *Acacia* spp., grades from a low open forest to tall shrublands in tropical and sub-tropical arid and semi-arid regions of Australia and experiences warm-to-hot annual temperatures and a pronounced dry season. This short synthesis of current knowledge briefly outlines the causes of the extreme variability in rainfall characteristic of much of central Australia, and then discusses the patterns and drivers of variability in carbon and water fluxes of a central Australian low open Mulga forest. Variation in phenology and the impact of differences in the amount and timing of precipitation on vegetation function are then discussed. We use field observations, with particular emphasis on eddy covariance data, coupled with modelling and remote sensing products to interpret inter-seasonal and inter-annual patterns in the behaviour of this ecosystem. We show that Mulga can vary between periods of near carbon neutrality to periods of being a significant sink or source for carbon, depending on both the amount and timing of rainfall. Further, we demonstrate that Mulga contributed significantly to the 2011 global land sink anomaly, a result ascribed to the exceptional rainfall of 2010/2011. Finally, we compare and contrast the hydraulic traits of three tree species growing close to the Mulga and show how each species uses different combinations of trait strategies (for example, sapwood density, xylem vessel implosion resistance, phenological guild, access to groundwater and Huber value) to co-exist in this semi-arid environment. Understanding the inter-annual variability in functional behaviour of this important arid-zone biome and mechanisms underlying species co-existence will increase our ability to predict trajectories of carbon and water balances for future changing climates.

## 1. Introduction

Tropical dry forests (TDFs) are globally extensive and widely threatened (Pulla *et al* 2015), representing the first frontier of anthropogenic land-use change (Portillo-Quintero and Sanchez-Azofeifa 2010). Globally, research and conservation efforts for rainforests and tropical moist forests greatly exceed that for TDFs (Pulla *et al* 2015), despite the fact that the loss of TDFs arising from human activities exceeds that for rainforests and moist tropical forests (Miles *et al* 2006), probably because human population densities in TDFs tend to be larger than those in rainforests and moist tropical forests.

Tropical forests represent significant sites of C uptake and storage. In 2011 a global land sink anomaly occurred (Le Quéré *et al* 2014, Poulter *et al* 2014) and this was predominantly the result of increased productivity of southern hemisphere (especially Australian) semi-arid vegetation (Poulter *et al* 2014, Cleverly *et al* 2016a). Given the importance of Australian TDFs (including Mulga and riparian forests) to global atmospheric C dynamics and regional water and C budgets it is timely to provide a synthesis of recent developments in our understanding of the structure, function and behaviour of this biome and to discuss the specifics of the behaviour of Mulga during the land sink anomaly.

TDFs have two key climatic features: they experience warm or hot temperatures all year (mean annual biotemperature $>18\,°C$), and they experience a predictable dry season every year. The former attribute is the same as that for lowland rainforests but distinguishes them from tropical montane forests, which experience lower daytime temperatures because of the effect of altitude on temperature (Eamus *et al* 2016). Unlike many TDFs globally, Australian TDFs, as with most Australian woody ecosystems, are dominated by evergreen species.

In this short synthesis we summarise our current understanding of the ecophysiology and ecohydrology of a large (5500 km$^2$) endorheic semi-arid tropical low open forest in central Australia. In particular we address the following key questions:

(1) What determines the climate of this region?

(2) How does climate influence phenology of this region?

(3) What are the principle drivers of daily, seasonal and inter-annual patterns of carbon (C) and water fluxes?

(4) How did the Mulga forests contribute to the 2010/2011 global land sink anomaly?

(5) How do hydraulic traits of Mulga compare with those of two co-occurring tree species and which traits may be associated with extreme drought resilience?

### 1.1. Mulga: a major dry open forest of tropical Australia

Mulga are comprised of a complex of closely related *Acacia* spp., especially *A. aneura* and *A. aptaneuera* (Maslin and Reid 2012). *Acacia* dominated landscapes grade from low open forests, through woodlands to low shrub lands (Specht and Specht 1999) and cover 20%–25% of the Australian continent (figure 1(a); Nicholas *et al* 2011). They are especially adapted to semi-arid and arid tropical and sub-tropical regions. As with all *Acacias*, Mulga forms symbioses with nitrogen-fixing cyanobacteria. Across the continent forest density (trees per hectare), height and growth form of Mulga trees are highly variable, ranging from relatively short ($<3$ m) to relatively tall ($>10$ m) trees, and ranging from a very open tree canopy to a relatively closed canopy. Mulga occurs on flat terrain and requires significant water storage capacities in the substrate (e.g., clay-rich soils or the presence of a hardpan within several meters of the surface; Pressland 1976), with low rates of drainage past the relatively shallow roots. Mulga usually forms a non-overlapping mosaic with hummock (spinifex) grasslands (figure 1(b); Nicholas *et al* 2011). The boundaries between Mulga and adjacent spinifex grasslands have
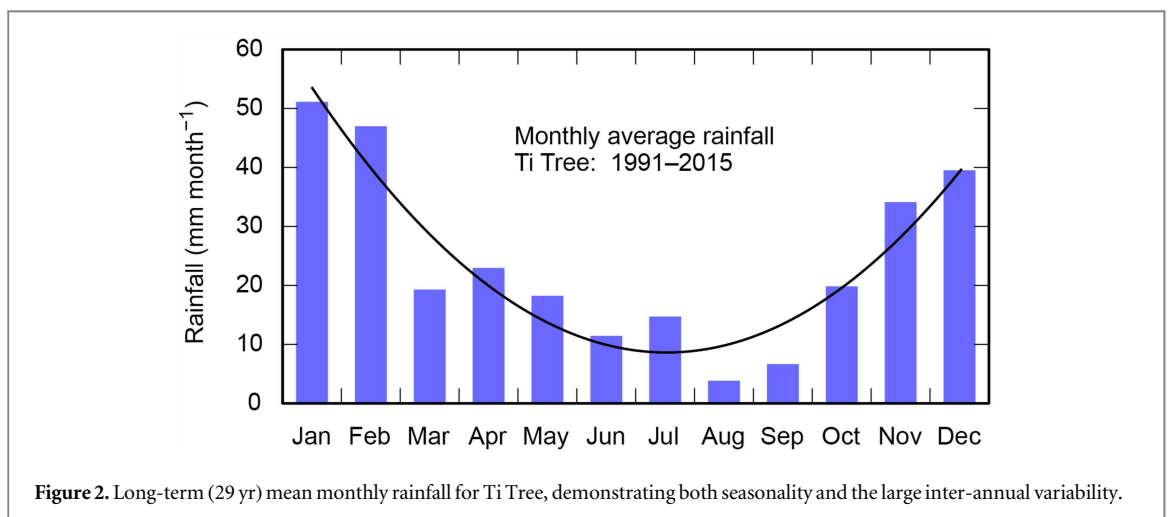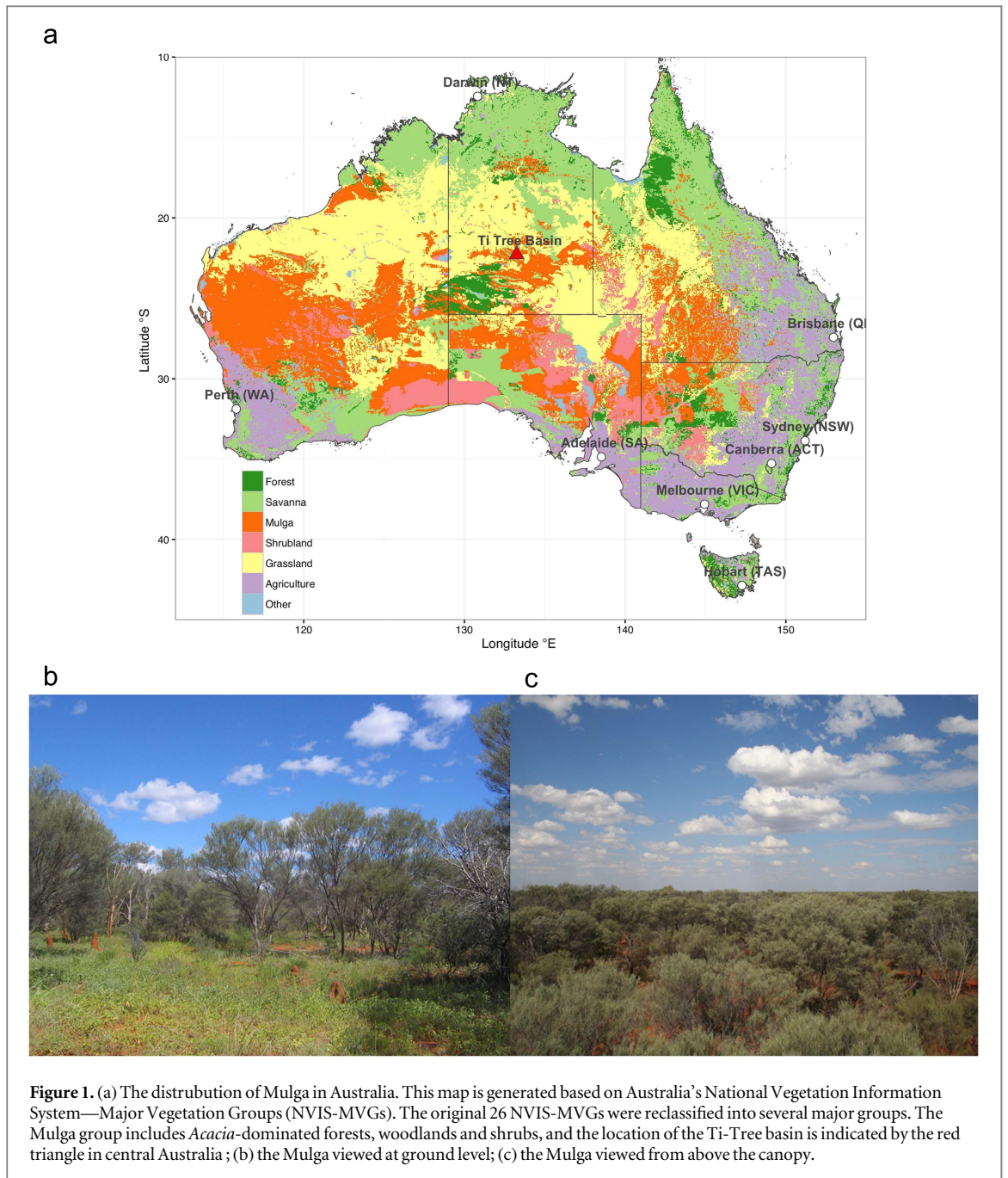
not moved in the past 1000 years (Bowman *et al* 2007), suggesting that they have persisted in roughly the same locations over a possibly large diversity of climatic conditions.

In the Ti Tree basin in central Australia (approximately 22° 14′ S, 133° 17′ E), the site of the studies discussed here, the Mulga canopy is ca. 6.5 m tall with a basal area of 8 m$^2$ ha$^{-1}$ and a stem density of approximately 3300 stems ha$^{-1}$ (figure 1). Dominant understory forbs and herbs include *Psydrax latifolia*, *Eremophila gilesii*, *Eremophila latrobei* ssp *glabra*, *Sida* and *Abutilon* spp., and *Solanum ellipticum*. The dominant grasses form a nearly complete cover when conditions permit and include perennials *Thyridolepis mitchelliana* and *Eragrostis eriopoda*, and annual *Eriachne pulchella* ssp *pulchella*. The Ti Tree basin receives the majority of its annual rainfall (long term (1987–2016) median of 299 mm) in the Austral summer wet season (December to February; figure 2), although rainfall can occur in any month (figure 2). The low level of rainfall received in the months June to September inclusive ($<20$ mm month$^{-1}$) is essentially ineffective in wetting the soil profile to any significant depth: almost all of this rain is intercepted by litter (and shallow roots) and evaporated rapidly back to the atmosphere. In the past 29 years annual rainfall has varied between 97.4 mm (1994) and 750.6 mm (2010).

### 1.2. What determines the climate of central Australia?

The semi-arid climate of central Australia is old. The development of a distinct dry season occurred as much as 35–50 Mya, preceding the separation of Australia and South America from Antarctica which opened the Southern Ocean and changed the world's climate to a cooler and drier regime (Crisp and Cook 2013). The modern climate regime was established by the end of the Pliocene (2.6 Mya), since which time the climate has dried by stages (Martin 2006) and was likely to have become semi-arid ca. 0.5 Mya. By using the term *dried by stages*, Martin (2006) meant that, whilst glacial periods have been drier than during inter-glacial periods, successive glacial and inter-glacial periods have been drier than those that occurred before. Thus, the longest and driest droughts in Australia spanned the most recent glacial period.

The second important feature of the Australian climate is its inter-annual variability in rainfall. Amongst the arid and semi-arid regions of the world, three of the four with the largest variability in rainfall occur along the rim of the Indian Ocean (the Thar Desert in India, Somalia and Australia north of 27 °S; Van Etten 2009). In the Ti Tree basin over just the last 100 years, for example, annual rainfall has been as low as 25 mm yr$^{-1}$ in 1928 and as high as 955 mm yr$^{-1}$ in 1974 (Cleverly *et al* 2016a, 2016b). Together, the ancient and more recent climate histories underscore two critical features that impact the development of

**Figure 1.** (a) The distrubution of Mulga in Australia. This map is generated based on Australia's National Vegetation Information System—Major Vegetation Groups (NVIS-MVGs). The original 26 NVIS-MVGs were reclassified into several major groups. The Mulga group includes *Acacia*-dominated forests, woodlands and shrubs, and the location of the Ti-Tree basin is indicated by the red triangle in central Australia ; (b) the Mulga viewed at ground level; (c) the Mulga viewed from above the canopy.



**Figure 2.** Long-term (29 yr) mean monthly rainfall for Ti Tree, demonstrating both seasonality and the large inter-annual variability.

Australian TDFs: an exceptional amount of inter-annual variability in rainfall and a long-term drying trend.

Three climate drivers have the potential to have a direct influence on continental weather patterns in Australia: El Niño-Southern Oscillation (ENSO) in the equatorial Pacific Ocean, the Indian Ocean dipole (IOD), and the southern annular mode (in the Southern Ocean, SAM). These *climate modes* have been individually related to the occurrence of rainfall, but not to amount (Pui *et al* 2012). However, ENSO, IOD and SAM periodically synchronise their effects on Australia's weather patterns, resulting in extremes of rainfall and drought (Cleverly *et al* 2016a). One such period began in 1999, signalling an increase in extreme weather events like the Millennium Drought at the beginning of the 21st century and widespread flooding in Queensland in 2011.

Our recent analysis (Cleverly *et al* 2016a) has demonstrated that when climate modes synchronise, the general amount of atmospheric moisture formed by ENSO (i.e., dry in Australia during El Niño, wet during La Niña) combines with the strength of the monsoon depression driven by IOD and placement of weather systems by SAM to enhance or prevent rainfall across the continent (Cleverly *et al* 2016a). Facilitated by Australia's flat terrain, a strong monsoon depression can interact with the continental low (which is indirectly influenced by SAM) to generate widespread storms with the intensity of summer rainfall but the large spatial and temporal extent of winter storms (Kong and Zhao 2010, Cleverly *et al* 2013). Alternatively, dry conditions induced by each climate mode individually can combine to further reduce rainfall beyond the effects of any single climate mode, leading to more intense Australian heatwaves (Perkins *et al* 2015). However, these interactions were not apparent in the early part of the measurement record (1982–1998), suggesting that this interaction among climate modes is a periodic feature of regional climate. Thus, these three climate drivers interact in the Indian Ocean region to generate the large degree of rainfall variability observed across Australia.

## 2. How does climate determine phenological patterns of Mulga low open forest?
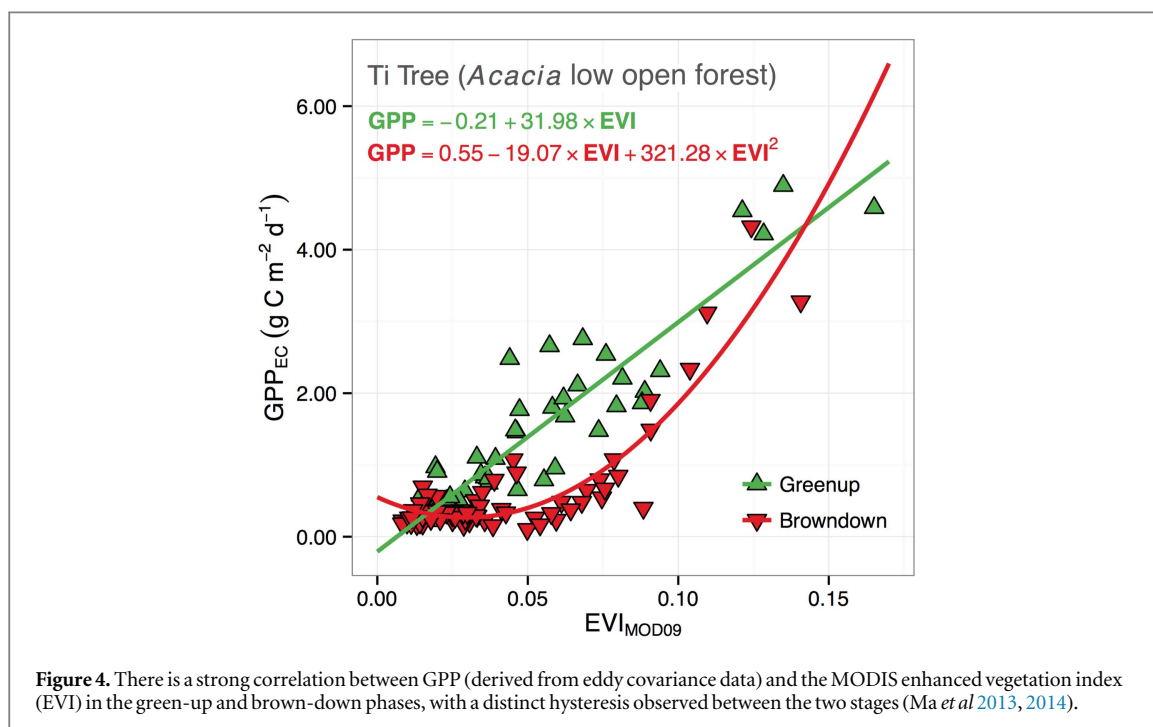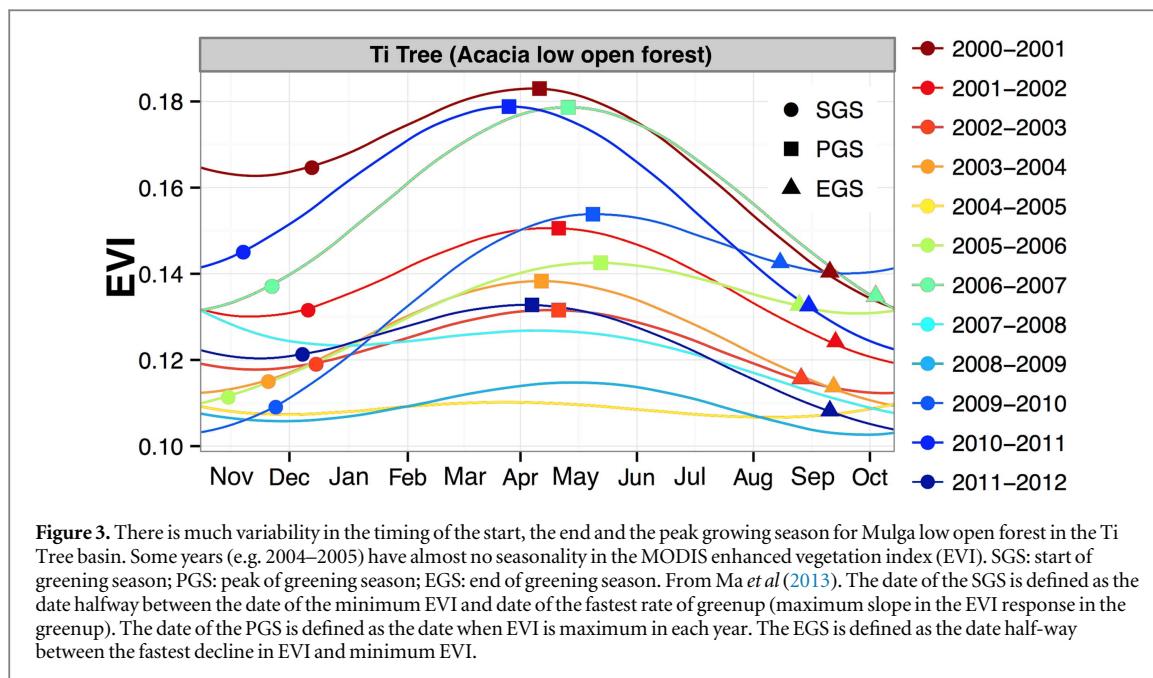
Mulga has a highly variable phenology that is largely rainfall-pulse driven. Key features of this phenological variability include large fluctuations in the dates of start-of-growing season, growing season peak and end-of-growing season, along with season length and the presence of a growing season in a given year (figure 3; Ma *et al* 2013). During very dry years, no detectable growing season occurs (ie there is minimal seasonal variation in the enhanced vegetation index EVI; Ma *et al* 2013), and minimal but non-negligible

amounts of photosynthetic production are restricted to the winter dry season in Mulga (Cleverly *et al* 2016c).

The phenology of Australia's semi-arid ecosystems is very sensitive to extremes of climate such that variance in total annual amount of rainfall alone explains 80% of variation in the length of the growing season (Ma *et al* 2013, 2015). However, uneven distribution of rainfall across the year can inhibit phenological responses in Mulga of central Australia due to the juxtaposition of wet and dry months (Nano and Clarke 2010). Thus, greenness in the vegetation of central Australia as determined from Moderate Resolution Imaging Spectroradiometer (MODIS) EVI is more highly correlated to the synchronised climate signal amongst ENSO, IOD and SAM than to rainfall (Cleverly *et al* 2016a), implying that the suite of meteorological conditions associated with the state of the climate system (e.g., cool and wet or hot and dry) exerts a larger influence on the phenology of Mulga than any individual environmental driver.

Seasonal and inter-annual phenological variation across the landscape is large. Seasonal variations in leaf area index (LAI) and landscape-scale photosynthetic capacity are primarily driven by seasonal variations in understory grasses and forbs (Eamus *et al* 2013a, Ma *et al* 2013). Seasonal changes in LAI of the *Acacia* overstory, in contrast, are relatively minor (Eamus *et al* 2013a). In the understorey of *Acacia* Mulga, annual grasses (such as *Aristida* spp.) green up in response to summer rain (~February) and set seed in autumn (Mott and McComb 1975). In contrast annual forbs, such as species of *Helichrysum* spp. and *Helipterum* spp. germinate in response to rain in early winter (May–June) (Mott and McComb 1975), and perennial grasses green up into the summer monsoon periods (Flora of Australia 2002). Collectively, these different phenological patterns of understorey in *Acacia* low open forests enable a long greening period (figure 3) at the community scale during the wet periods and are observable by satellite sensors (Ma *et al* 2013).

Despite the principal control of rainfall on phenology, the response of Mulga to rainfall can be inhibited during the summer wet season by canopy temperatures that exceed *Acacia's* 38 °C thermal limit for growth (Nix and Austin 1973, Cleverly *et al* 2016b). Thus, growing-season phenology and canopy structure of this low open forest are strongly related to its physiological phenology (e.g., the seasonal and annual cycle of ecosystem productivity and light use efficiency; Migliavacca *et al* 2015), which provides a basis for the strong relationships amongst gross primary production and EVI during the green-up phase and hysteresis during autumnal brown-down (figure 4; Ma *et al* 2013, 2014). Hysteresis means that the relationships between GPP and EVI during greenup differs from that during browndown. In Mulga the lower GPP for a given EVI during browndown presumably

**Figure 3.** There is much variability in the timing of the start, the end and the peak growing season for Mulga low open forest in the Ti Tree basin. Some years (e.g. 2004–2005) have almost no seasonality in the MODIS enhanced vegetation index (EVI). SGS: start of greening season; PGS: peak of greening season; EGS: end of greening season. From Ma *et al* (2013). The date of the SGS is defined as the date halfway between the date of the minimum EVI and date of the fastest rate of greenup (maximum slope in the EVI response in the greenup). The date of the PGS is defined as the date when EVI is maximum in each year. The EGS is defined as the date half-way between the fastest decline in EVI and minimum EVI.



**Figure 4.** There is a strong correlation between GPP (derived from eddy covariance data) and the MODIS enhanced vegetation index (EVI) in the green-up and brown-down phases, with a distinct hysteresis observed between the two stages (Ma *et al* 2013, 2014).

reflects a loss of photosynthetic potential in the canopy during browndown.

Although direct empirical relationships between photosynthetic activity, ecosystem productivity and MODIS vegetation indices have been observed in various temperate and tropical ecosystems, MODIS vegetation products have been less successful in capturing seasonality of productivity in many Australian evergreen forests and sclerophyll woodlands (Restrepo-Coupe *et al* 2016). This prompted a re-evaluation of the connection between satellite observations and various flux productivity measures with the expectation that satellite greenness products constituted a combined measurement of ecosystem structure (e.g. LAI)

and function (e.g. leaf level photosynthetic assimilation capacity), rather than productivity *per* se. Restrepo-Coupe *et al* (2016) showed the lowest correlations between MODIS vegetation products and productivity at locations where meteorological variables (drivers) and vegetation phenology were asynchronous, as in Mediterranean ecosystems (schelophyll forests). In contrast, the largest correlations were observed at locations where synchrony across meteorological variables and vegetation phenology was apparent, as observed in the Mulga TDF. They concluded that remote sensing products would not follow productivity when: either phenology is asynchronous with key meteorological drivers, and productivity is

therefore driven by one or more meteorologic drivers over different times of the year; or when phenology is relatively aseasonal, and productivity is solely driven by meteorology (especially solar radiation, air temperature, soil water availability, VPD, or different combinations).

## 3. Drivers of seasonal and annual patterns of C and water flux

The environmental drivers associated with patterns of C and water flux are closely related to those driving phenology in Australia (Ma *et al* 2014). In this section, we will address how patterns of rainfall, soil moisture content and meteorological drivers affect dynamics in C and water fluxes during a drier-than-average year (hydrologic year 2012–2013) and two years with average amounts of rainfall (2013–2014 and 2014–2015). Evaluation of drivers in this section will begin with a comparison of rainfall, evapotranspiration (ET) and net ecosystem productivity (NEP) between a drier-than-average year (2012–2013) and the subsequent year with average rainfall (2013–2014; Cleverly *et al* 2016c).

### 3.1. Comparing a drier-and wetter-than average year

Mulga shows a disproportionate response to extremely high inputs of rainfall (e.g. during the global land sink anomaly; Cleverly *et al* 2013, Eamus *et al* 2013a). This is driven by a tropical-extra-tropical connection in the Great Australian Bight which creates a regular pattern of storm-interstorm intervals (Berry *et al* 2011) and thereby provides periods of high light, soil moisture content and humidity during wetter-than-average years that are highly favourable for photosynthesis (Cleverely *et al* 2013). By contrast, inter-storm periods during dry-to-average years are hot and VPD is large, exceeding Mulga's thermal tolerance of 38°C (Cleverly *et al* 2016b). In this section, we explore these issues more fully.

Rainfall in hydrologic years 2012–2013 (193 mm) and 2013–2014 (295 mm) was approximately 65% and 99% of the long-term average (median 299 mm), respectively. As is typical of this site, rainfall predominantly occurred in the summer wet season. Rates of ET are extremely responsive to pulses of rain (Cleverly *et al* 2016c). After rains have concluded, however, ET declines rapidly (and exponentially) to zero (Eamus *et al* 2013a, Cleverly *et al* 2016c). Peak rates of daily ET in the wet season range between three and four millimetres, whilst cumulative ET in the two years was 150 and 250 mm, or 50% and 84% of average annual rainfall (figure 5).

Over these two years, the Mulga low open forest oscillated across the seasons between being a C sink and C source (figure 6). During the winter and early spring, the Mulga was a small sink (positive values of NEP ranged from 0.1 to 0.3 gC m$^{-2}$ d$^{-1}$). The largest sink activity during this two-year period (2012–2014) occurred in late summer/early autumn of 2014 when temperatures, vapour pressure deficit and soil moisture content were optimal for NEP. Source activity in the Mulga occurred in pulses during the summer/autumn of 2013 and the summer of 2014 (figure 6). On a hydrological annual time-scale, the Mulga was a small source in the drier-than-average hydrologic year (−26 gC m$^{-2}$ d$^{-1}$ in 2012–2013) and a small sink in the average year (12 gC m$^{-2}$ d$^{-1}$ in 2013–2014). It was not until the wet summer of the second hydrologic year that Mulga became a moderate-to-strong sink. Importantly, rainfall in the first hydrologic year (193 mm) was significantly less than in the second hydrologic year (295 mm), thereby revealing the importance of the amount of rainfall received as a determinant of productivity of this semi-arid tropical ecosystem.

Different combinations of rainfall, temperature, solar radiation and vapour pressure deficit are the principle determinants of NEP and GPP (van Dijk *et al* 2005, Baldocchi 2008, Kanniah *et al* 2010, Baldocchi and Ryu 2011, Zha *et al* 2013). It is apparent that inter-annual differences in rainfall are the principle causes of inter-annual differences in sink strength for the Mulga (table 1), in strong agreement with multiple other arid and semi-arid biomes (Huxman *et al* 2004, Flanagan and Adkinson 2011, Barron-Gafford *et al* 2012, Ma *et al* 2012, Chen *et al* 2014) but in marked contrast to boreal, tropical montane, temperate mesic deciduous forests and tropical mesic savannas, where temperature, solar radiation and the length of the growing season are the principal drivers of variation in NEP (Luyssaert *et al* 2007, Whitley *et al* 2011, Ma *et al* 2013, Zha *et al* 2013, Keenan *et al* 2014). However, this does not mean that these other drivers are not important for explaining inter-annual variation in NEP; instead, the environmental drivers are themselves related to rainfall in a series of complexities which we will now discuss.

### 3.2. The importance of wet season rainfall distribution in driving patterns of NEP

Cleverly *et al* (2016b) compared NEP during two years with near-average annual rainfall (2013–2014 and 2014–2015) but with different temporal patterns to evaluate the impact of differences in the distribution of precipitation within the wet season. Each wet season received about 280 mm, but it was distributed more evenly across the wet season of 2013–2014 than that of 2014–2015. In 2014–2015 most of the rainfall had accumulated by mid-January, and the site received very little rainfall for months afterward (figure 7). These differences had significant effects on summer and autumn patterns of soil moisture content and hence the response of NEP across these two years. In the summer wet season 2013–2014, there was a
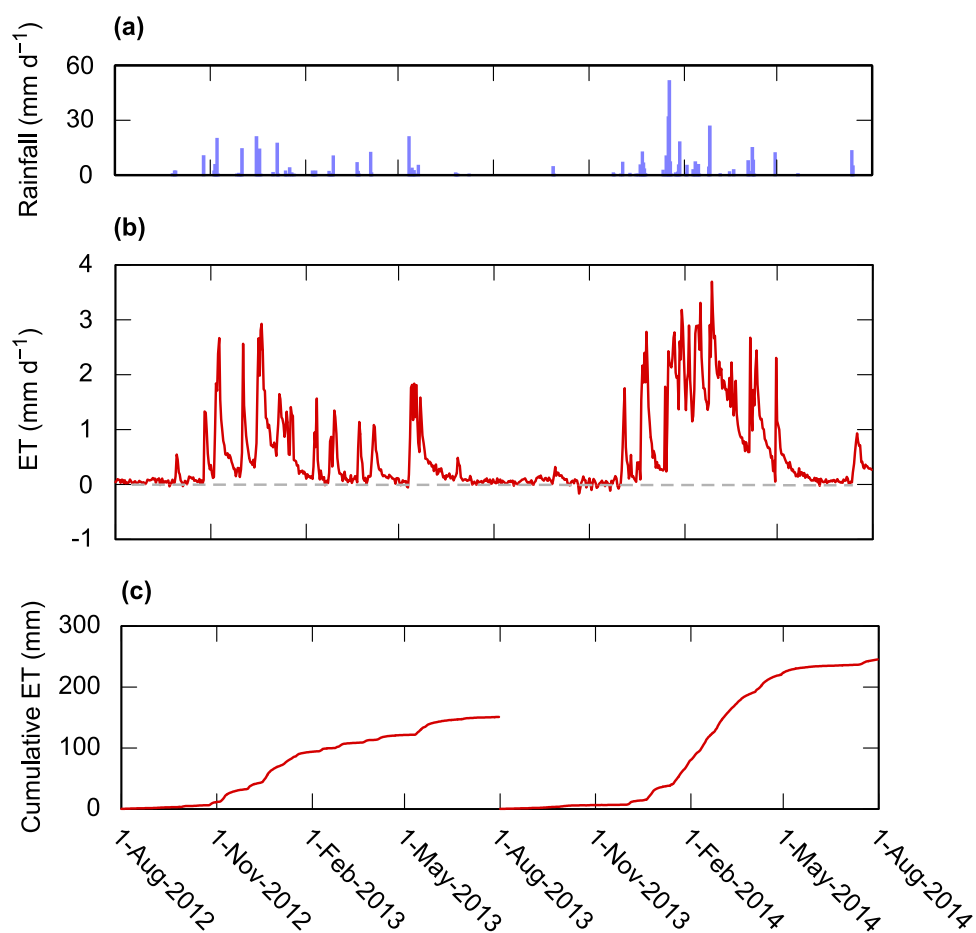
**Figure 5.** Patterns of rainfall and evapotranspiration (ET, daily and cumulative), August 2012–July 2014. Redrawn from Cleverly *et al* (2016c).
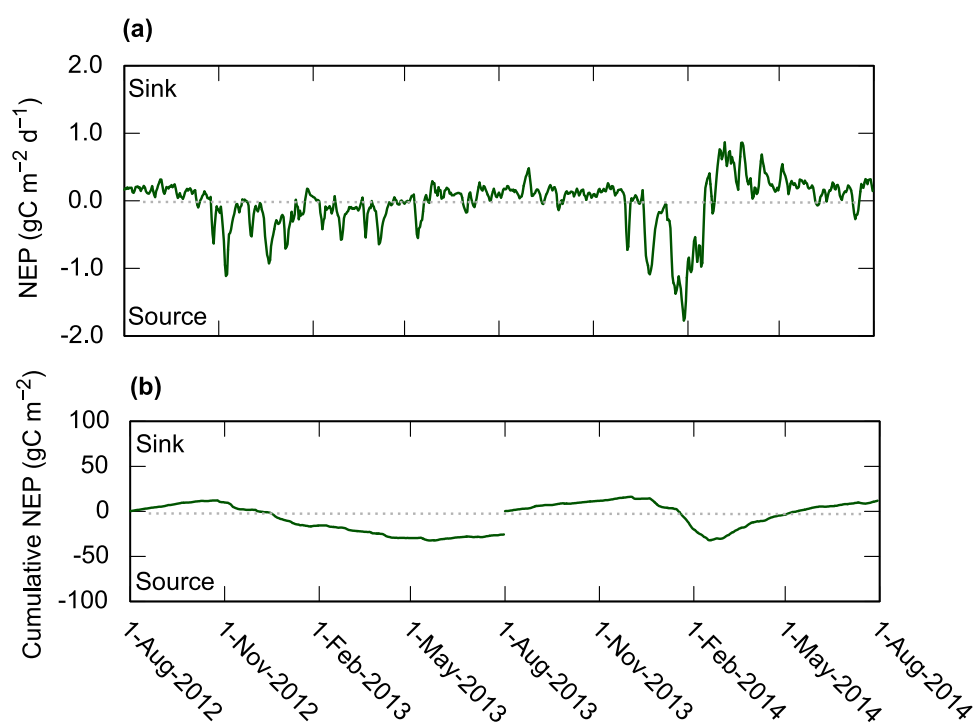


**Figure 6.** Patterns of net ecosystem productivity (NEP, daily and cumulative), August 2012–July 2014. Redrawn from Cleverly *et al* (2016c).

Table 1. Annual rainfall, net ecosystem productivity (NEP) and evapotranspiration (ET) in the Mulga low open forest across the measurement period.

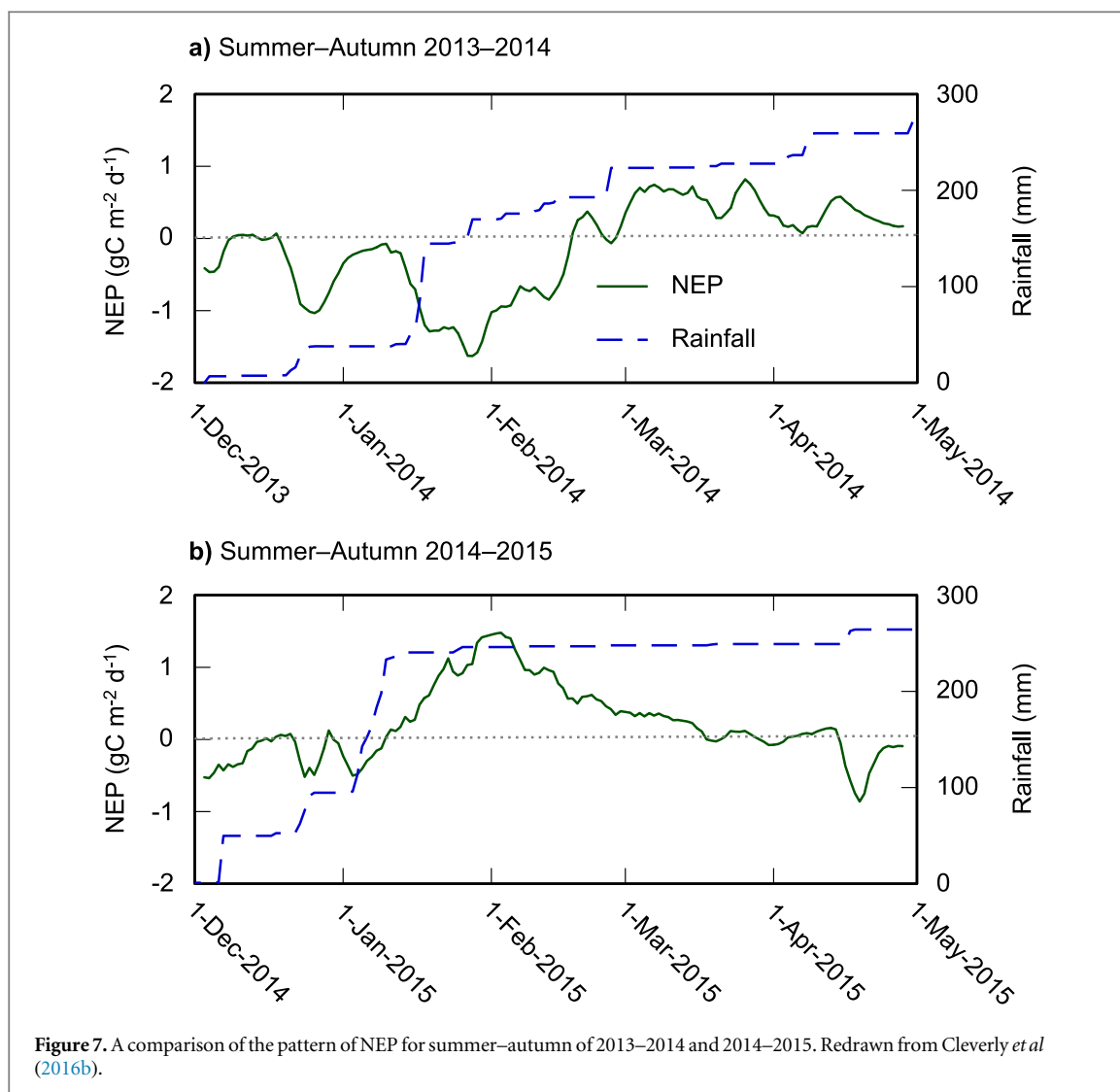| Year | Rainfall (mm y$^{-1}$) | NEP (g C m$^{-2}$ yr$^{-1}$) | | ET (mm yr$^{-1}$) |
| --- | --- | --- | --- | --- |
| 2010–2011 | 565 | 259 | (sink) | 518 |
| 2011–2012 | 184 | −4 | (source) | 204 |
| 2012–2013 | 193 | −25 | (source) | 151 |
| 2013–2014 | 295 | 12 | (sink) | 248 |
| 2014–2015 | 302 | 34 | (sink) | 245 |

substantial delay (six weeks) in the response of NEP to the rainfall that began in late December 2013 and fell through February 2014. Sink activity was not recorded until late February, and this was maintained through to the end of April 2014. The delayed stimulation of NEP in early 2014 was the result of environmental stress, in particular large temperatures and VPDs and a lack of soil moisture in mid and late summer of 2014. This resulted in the Mulga canopy experiencing conditions that exceeded the thermal tolerance of the phyllodes. It was not until cooler temperatures, a smaller VPD and the positive impact of transpirational cooling on canopy temperature (once soil moisture levels were sufficient) were evident, that NEP became positive in late February and March 2014. In contrast, rain in December 2014–January 2015 produced a positive response in NEP almost immediately, and a large C sink was maintained throughout January and February of 2015. Cooler air temperatures and sufficient soil moisture above the hard pan to allow transpirational canopy cooling resulted in positive NEP in mid-January to mid-March 2015, much earlier than during the previous year.

We will now demonstrate how differences in soil moisture content were formed due to differences in the weekly-to-monthly pattern of rainfall in the Mulga TDF.

Soil moisture content measured at a point approximately 1 m below the ground surface is highly dependent upon the (i) amount, timing and intensity of rainfall and (ii) the presence of a subsurface hardpan at this site (Cleverly *et al* 2013, 2016b, 2016c). The siliceous hardpan is buried below the surface and prevents drainage of water to the regional water table, which is 49 m deep at this site (Cleverly *et al* 2016c). Soil moisture content in the hardpan is 0.05 m$^3$ m$^{-3}$ and has shown only minor fluctuations since measurements began in 2010. Conversely, soil moisture content in the unconsolidated loamy sand above the hardpan has fluctuated between ca. 0.08 m$^3$ m$^{-3}$ and 0.35 m$^3$ m$^{-3}$ (saturated) since 2010 (Cleverly *et al* 2013, 2016b). The fluctuations in soil moisture content in the unconsolidated soil above the hardpan relate strongly to the amount and pattern of rainfall, hence providing a link for responses of NEP to rainfall (Cleverly *et al* 2016b).

With the hardpan acting as a barrier to drainage, rainfall that delivers water in excess of that which is required by the vegetation can be stored and carried-over to other seasons or years. The importance of inter-seasonal and inter-annual carry-over of rainfall to sustaining NEP is well documented in arid and semi-arid ecosystems globally (Flanagan and Adkinson 2011). Even during a drier-than-average year (2011–2012, 184 mm of rainfall), drawdown of the storage reservoir in the unconsolidated soil above the hardpan (from 0.10 m$^3$ m$^{-3}$ to 0.08 m$^3$ m$^{-3}$) was associated with maintenance of gross primary production at low but non-negligible levels (Cleverly *et al* 2013). The reservoir was then rapidly re-filled and maintained soil moisture content of ca. 0.10 m$^3$ m$^{-3}$ across the following autumn-winter (Cleverly *et al* 2013). We have found that Mulga trees have a small but significant proliferation of roots near the top of the hardpan where this soil moisture reservoir accumulates (Cleverly *et al* 2016b), and these roots are likely to remain active during all seasons because of the consistent elevation of soil moisture content in the reservoir relative to the hardpan (Cleverly *et al* 2013, 2016b). Whereas carry-over of soil moisture appeared to be an important feature of the site water budget in a drier-than-average year, it wasn't until the first year with average rainfall in the study (2014–2015) when soil moisture content increased substantially (>0.2 m$^3$ m$^{-3}$) such that delayed increases in NEP were associated with carry-over of that soil moisture (figure 7).

In comparing the summer wet season during two years with average rainfall (2013–2014 versus 2014–2015), it became apparent that the pattern of rainfall distribution affected the degree to which soil moisture storage filled to capacity in the unconsolidated soil above the hardpan (Cleverly *et al* 2016b). During the summer-autumn of 2013–2014, soil moisture content increased to 0.26 m$^3$ m$^{-3}$ following several weeks of rainfall (150 mm of rainfall by mid-January, figure 8), including one storm which delivered 105 mm of rainfall over six days (Cleverly *et al* 2016b). By contrast, in the summer-autumn of 2014–2015, rainfall was 250 mm by mid-January with 145 mm delivered over 12 days; soil moisture content increased to saturation (which is 0.35 m$^3$ m$^{-3}$ in this soil) immediately thereafter; and NEP responded immediately and was positive by mid-January 2015. Saturation of the upper soil profile (top 1 m) in January 2015 resulted in the formation of a perched, ephemeral water table located in the unconsolidated soil above the hardpan (figure 8). These results are consistent with the threshold-delay model of Ogle and Reynolds (2004) whereby a pulse of rain that is insufficient to fill the 'bucket' (i.e., the soil moisture storage reservoir containing roots) causes a delay in the response of NEP, whereas sufficient rain to fill the bucket induces a rapid response in NEP (i.e., inhibition of the delay).

**Figure 7.** A comparison of the pattern of NEP for summer–autumn of 2013–2014 and 2014–2015. Redrawn from Cleverly *et al* (2016b).
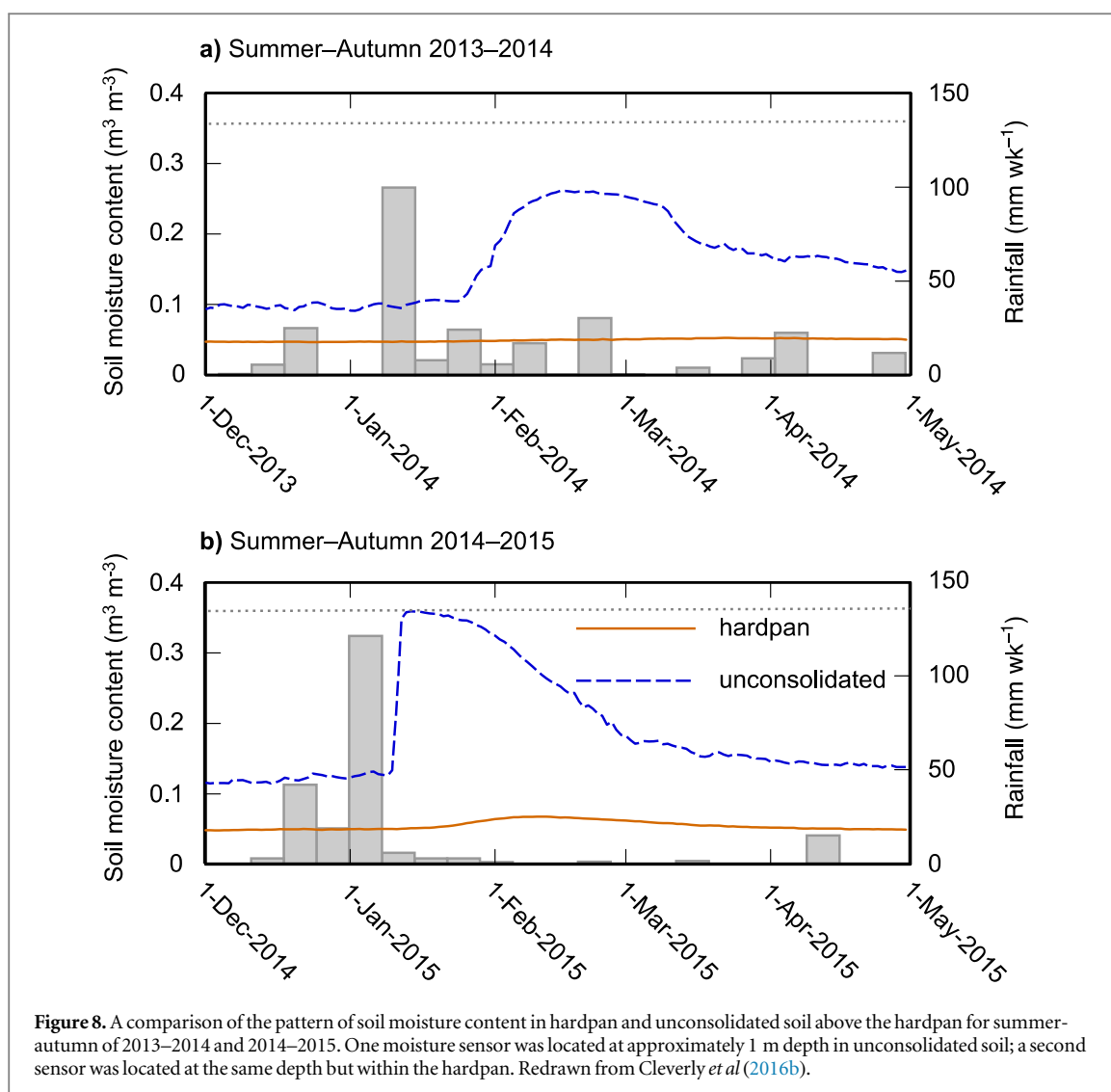
When stomatal conductance is large, transpiration and transpirational cooling proceed at rates that exceed those observed when conductance is low. When the bucket was not filled during summer of 2013–2014 and NEP was delayed, transpiration would have been minimised; therefore, incoming solar radiation would have been partitioned into sensible heat flux instead of latent heat flux, thereby minimising transpirational cooling (Cleverly *et al* 2016b). In contrast, in the summer of 2014–2015 when NEP was positive and large rates of transpiration were occurring, less partitioning to sensible heat flux would be expected. In agreement with this is the observation that sensible heat flux in January–February 2014 was 307.1 W m$^{-2}$ but in the same period in 2015, sensible heat flux was smaller (270.4 W m$^{-2}$). Using imagery obtained from an unmanned drone with a thermal camera in March 2014 (i.e., during the autumn following the delay in NEP), it was revealed that a large fraction of the Mulga canopy still exceeded the 38 °C thermal optimum for this species (Cleverly *et al* 2016b), further suggesting that a soil moisture reservoir that is not full is insufficient to provide the

resources for transpirational cooling until the heat of the summer has passed.

### 3.3. Interactions of soil moisture content with temperature and VPD as drivers of variation in NEP

Having established the importance of the timing of rainfall as a determinant of the response of NEP, we extend this analysis to examine in detail the interactions among soil moisture content, VPD and solar radiation as determinants of NEP. Thus we evaluate meteorological drivers and NEP across a wide range of soil moisture contents during a very wet year (2010–2011) and the subsequent drier-than-average year (2011–2012). The effects of air and soil temperature, VPD and solar radiation on NEP were closely related to variations in soil moisture content as a consequence of correlations between these drivers and rainfall (Cleverly *et al* 2013). For example, the temperature at which peak NEP occurred and the reduction of NEP at high temperature were dependent upon soil moisture content (figure 9). Similarly, the VPD at which NEP was maximised depended upon soil moisture, as was the response of NEP to light intensity.
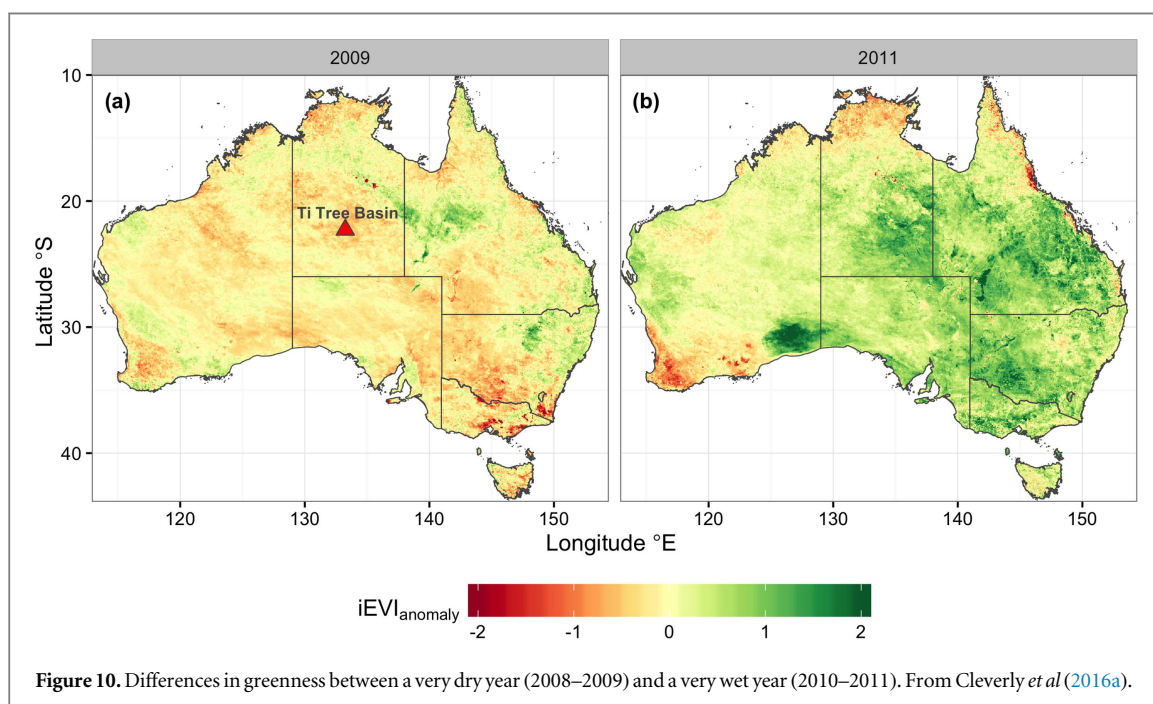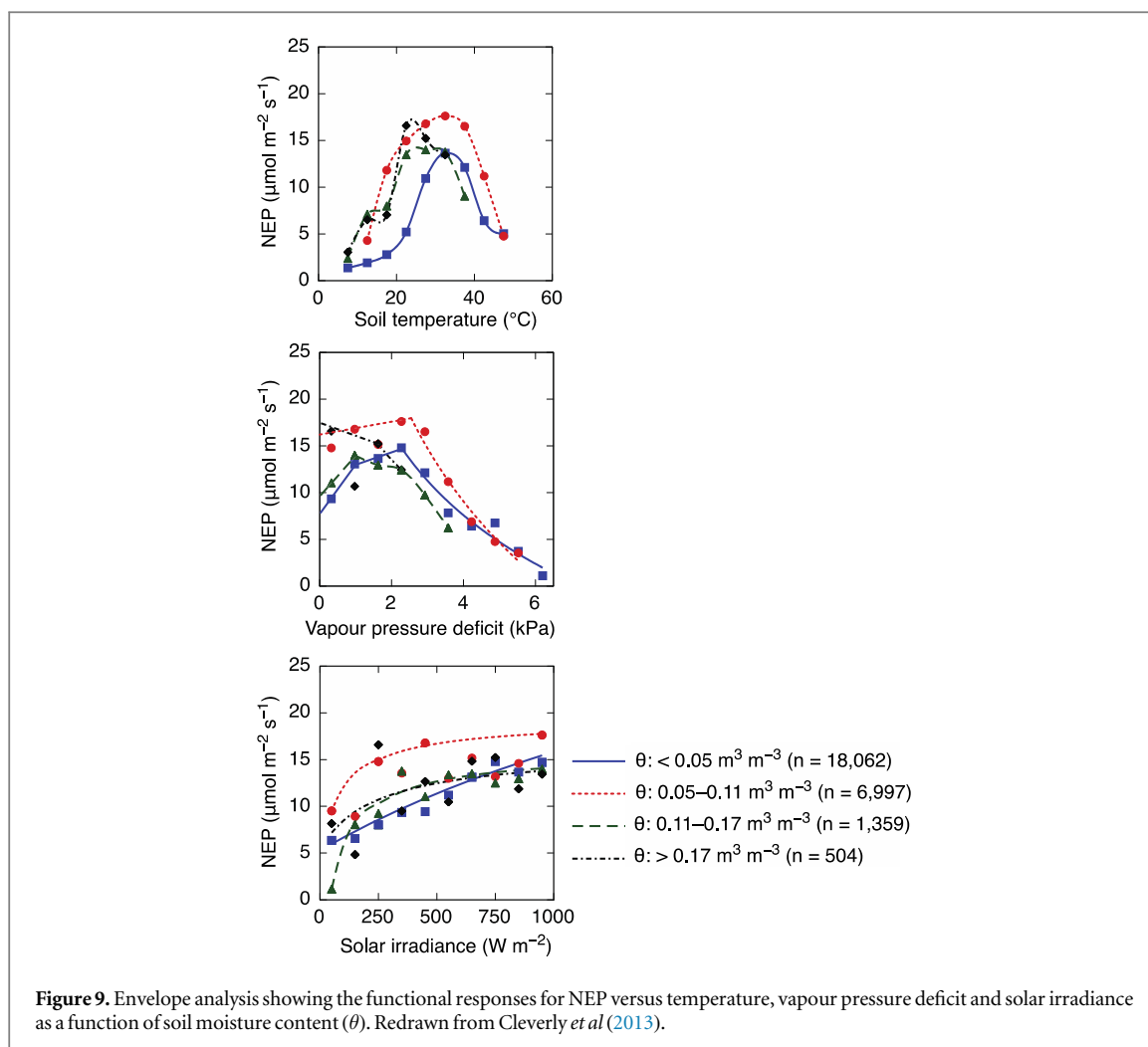
**Figure 8.** A comparison of the pattern of soil moisture content in hardpan and unconsolidated soil above the hardpan for summer-autumn of 2013–2014 and 2014–2015. One moisture sensor was located at approximately 1 m depth in unconsolidated soil; a second sensor was located at the same depth but within the hardpan. Redrawn from Cleverly *et al* (2016b).

The thermal responses of NEP to soil moisture content in Mulga were not dissimilar to those of *Eucalyptus* leaves as a function of $[CO_2]$, although NEP in Mulga appears to be more limited at low temperature than for leaf photosynthesis in *Eucalyptus* (Eamus *et al* 1995). Furthermore, the responses of NEP to VPD in Mulga imply a close link to ET via canopy conductance (as assimilation is linked to transpiration via stomatal conductance in leaves; Duursma *et al* 2014). Thus in Mulga, ecosystem inherent water-use efficiency (IWUE, the ratio of [NEP $\times$ VPD] to ET) is highly dependent upon soil moisture content during wet and dry seasons (Eamus *et al* 2013a), illustrating the coordinated control of NEP and ET by soil moisture, VPD and temperature.

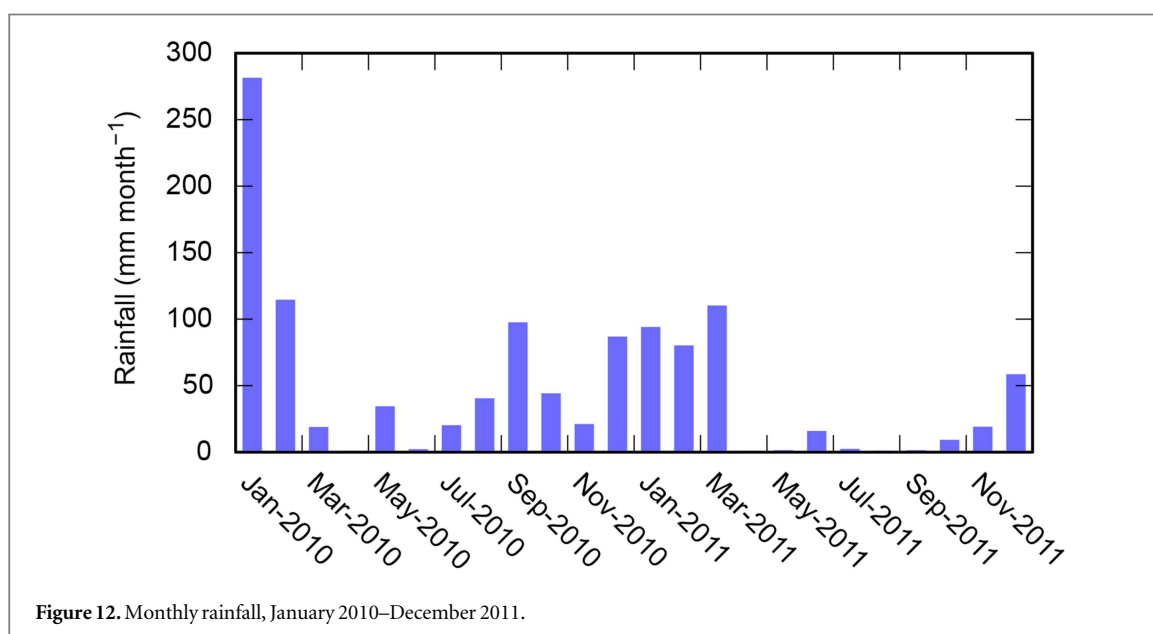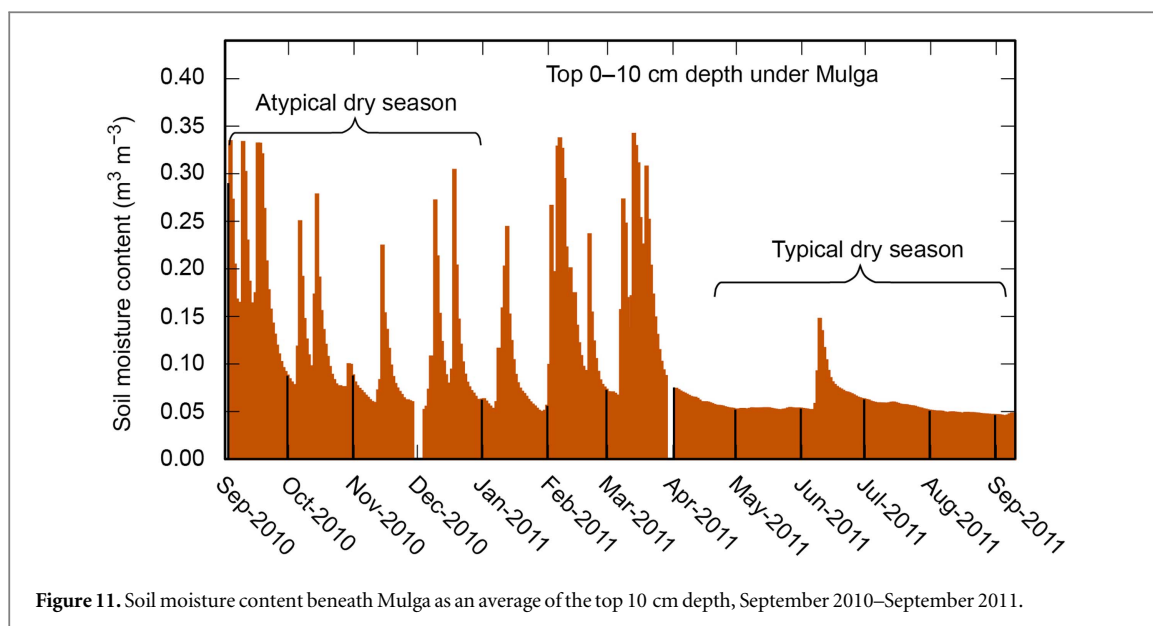## 4. The global land sink anomaly and Mulga

Having established general relationships among rainfall (timing and amount), temperature, VPD and NEP we now discuss the specific case of the 2010/2011 global land sink anomaly and Mulga.

Le Quéré *et al* (2014) identified the 2011 global land sink anomaly whereby global rates of C uptake increased from a decadal average of 2.8 GtC $yr^{-1}$ (2003–2012) to 4.0 GtC $yr^{-1}$. Poulter *et al* (2014) used a combination of remote sensing and biogeochemical modelling to establish that this global land sink anomaly was driven by an upsurge in growth of vegetation in semi-arid regions. In particular they identified the Southern Hemisphere as being the main location of this enhancement in growth, with 60% of the enhancement occurring in Australia. The cause of this C sink anomaly was a strong monsoon depression (negative IOD), deep continental low (negative SAM) and the strongest sustained La Niña since 1917 (Cleverly *et al* 2016a). The massive increase in rainfall resulted in a drop in global mean sea level of about 5 mm, and remote sensing established a dramatic greening of eastern and central Australia (figure 10). The Gravity Recovery and Climate Experiment satellites also recorded significant increases in the mass of water stored across Australia in 2011 (Boening *et al* 2012, Xie *et al* 2016). Furthermore, Fasullo *et al* (2013) demonstrated that

**Figure 9.** Envelope analysis showing the functional responses for NEP versus temperature, vapour pressure deficit and solar irradiance as a function of soil moisture content ($\theta$). Redrawn from Cleverly *et al* (2013).



**Figure 10.** Differences in greenness between a very dry year (2008–2009) and a very wet year (2010–2011). From Cleverly *et al* (2016a).

Australia maintained a positive water mass anomaly in 2012, meaning that a significant fraction of the extra water received in 2011 in Australia remained detectable after the conclusion of the global land sink anomaly and suggesting that increased C uptake in arid Australia *may* have persisted beyond the 2010/

**Figure 11.** Soil moisture content beneath Mulga as an average of the top 10 cm depth, September 2010–September 2011.



**Figure 12.** Monthly rainfall, January 2010–December 2011.

2011 global sink anomaly. We now address the question: was there an observed response in C uptake for the Mulga during the 2010/2011 global land sink anomaly?

During the hydrologic year 2010–2011 rainfall in the Ti Tree basin was 565 mm, or 75% larger than the long-term average. Furthermore, a large fraction of this rainfall was received in the dry season of 2010, as is reflected in the repeated recharge of soil moisture in September–November 2010 (figure 11). Indeed the wet season for this hydrologic year was eight months long (figure 12) rather than the usual three or four months (Ma *et al* 2013).

The response of ET and NEE to this unusual pattern and amount of rainfall is shown in figure 13. Large rates of ET were maintained for the unseasonably wet dry season of 2010 through to the early autumn of 2011. By the winter of 2011, however, ET

had declined to zero except for a brief increase in response to rain in June 2011. Across the 372-day study, total ET was 430.6 mm (76% of rainfall). The exponential decline in ET following rainfall exhibited a half-time of decay of 5.2 days, whilst a threshold amount of rainfall had to be exceeded (3.0 mm) for transpiration to increase. This half-time is similar to that observed in semi-arid grasslands and shrublands of central New Mexico (half-time approximately 2 days; Kurc and Small 2004) but shorter than the range in half-times observed across 15 sites of North America, Europe, Afric and New Zealand (15–35 days) by Teuling *et al* (2006). Interestingly, despite large differences across sites, there were no significant differences within sites across multiple years, and longer half-times were observed at sites experiencing seasonal droughts or at sites with woody vegetation. Our much shorter half-times
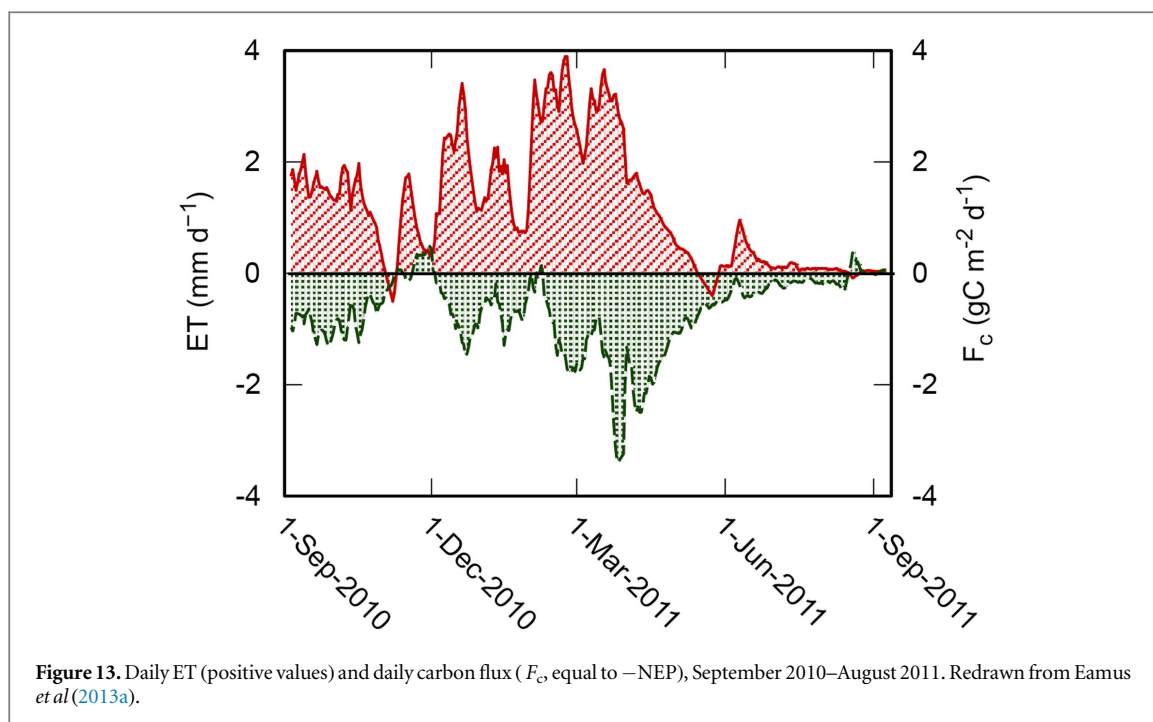
**Figure 13.** Daily ET (positive values) and daily carbon flux ($F_c$, equal to −NEP), September 2010–August 2011. Redrawn from Eamus *et al* (2013a).

may reflect the sandy soils, the impact of the very shallow roots of Mulga and Mulga's rapid phenological response to precipitation when conditions are favourable (Cleverly *et al* 2016b).

The large rates of ET in the winter of 2010 and the late summer and autumn of 2011 were mirrored by large rates of C uptake (figure 13). The half-time of the decay in C uptake following rain was 7.2 days (Eamus *et al* 2013a). Unlike ET, which increased immediately following rain, C uptake showed a 1–3 day delay.

The large rates of C uptake sustained from September 2010 through to June 2011 are in marked contrast to the short duration of C uptake in figure 7 and in contrast to the annual totals for years 2011–2015 (table 1), and reflect the impact of large and sustained increase in soil moisture content during the 2010/2011 La Niña event. If we assume that all Australia's Mulga behave the same as the Mulga in the Ti Tree and all received similar increases in rainfall, it is possible to estimate the contribution of Australia's Mulga to the NEE anomaly quantified in Poulter *et al* (2014). Mulga covers approximately 33% of the 70% of Australia that is semi-arid. The anomalous increase in C uptake by the Ti Tree Mulga was 247 gC m$^{-2}$ yr$^{-1}$ (the difference between uptake in 2010–2011 and uptake in a 2013–2014 when rainfall was average). This represents 0.435 Pg C yr$^{-1}$ for the entire Mulga estate, which accounts for about 50%–70% of the anomaly identified by Poulter *et al* (2014) as originating in Australia (0.6–0.9 Pg C yr$^{-1}$). However, tree density of Mulga in the Ti Tree is larger than that of most Mulga in Australia and the contribution of all Mulga is therefore likely to range from 30% to 40% of the total anomaly.

## 5. Ecosystem C and water budgets: an ecosystem services perspective

Ecosystem services are the goods and services provided by ecosystems that are of benefit to humans (Eamus *et al* 2005). Examples of ecosystem services include erosion control, regulation of local and regional climate, C sequestration and the regulation of water flows (surface, sub-surface and groundwater recharge). For terrestrial ecosystems, the provision of ecosystem services is dependent on neutral or positive C and water budgets. A neutral or positive C budget means no net loss or an accumulation of C within the catchment. A neutral or positive water budget means that there is not a net export of water from the catchment; for example, by over-extraction of groundwater (by human extraction). This raises the question: over what timeframe should C and water budgets be determined? It is clear that seasonally, Mulga can oscillate between being a net sink or a net source of C. Similarly, at an annual time-scale, Mulga can be a net sink or source of C. Mulga in the Ti Tree basin has undoubtedly persisted for more than 50 yr, and probably for considerably longer. Table 1 shows how widely NEP and ET can vary across just four years of study. Interestingly, a regression of NEP versus rainfall using data in table 1 shows that when annual rainfall exceeded a threshold of 233 mm ($R^2 = 0.95$), Mulga was a sink but when rainfall is <233 mm Mulga was a source. This is smaller than the thresholds of 275–350 mm identified for several semi-arid ecosystems in south-western USA (Scott *et al* 2015), but, is consistent with the approximately 100 mm difference between the threshold rainfall and the long-term average rainfall observed by Scott *et al* (2015). We

estimate that this offset of 100 mm ensures that a positive C balance will be maintained in approximately 70% of years (because only about 30% of years have rainfall less than this threshold).

In a recent analysis of the Ti Tree Mulga, Chen *et al* (2014) concluded that annual vegetation water use varied between 64 and 601 mm for the period 1981–2012. Most importantly (from an ecosystem services perspective), groundwater recharge (noting that the Ti Tree basin may become a significant source of potable groundwater for industrial, irrigation and domestic uses in central Australia) varied between 0 and 48 mm yr$^{-1}$ but significant rates of recharge were very rare events, highlighting the need to extract groundwater at sustainable rates for the long-term preservation of this important resource.

It is clear that short-term (<5 years) studies of C balances for TDFs are unlikely to be adequate to provide sufficient information to determine whether particular locations are in a negative, neutral or positive C balance. This is because TDFs tend to have much larger variability in the timing, intensity and amount of rainfall than tropical rainforests and other mesic biomes. This large degree of variability is reflected in the large fluctuations between sink and source strength. Furthermore, large inter-annual variability in rainfall and hence ET impacts on the provision of water resources (surface and groundwater), and this should inform management decisions on the timing and volume of water resource extraction. The size and magnitude of changes in C storage pools (aboveground and below ground, biotic and abiotic) and the role of disturbance (for example fire and prolonged drought) in C and water balances remain poorly documented for much of the arid and semi-arid regions of Australia.

## 6. Mulga traits versus traits of co-occurring tree species

The Ti Tree basin contains three major ecosystems. The first is Mulga, dominated by *Acacia* spp., the second is riparian forest that follows the ephemeral rivers. The riparian forest is dominated by large *Eucalyptus camaldulensis* trees. Whilst the majority of tree species across the basin are evergreen (including Mulga and *Eucalyptus camaldulensis*), patches of the deciduous *Erythrina vespertilio* occur in paleochannels (a remnant of an inactive river or stream that has been subsequently infilled by younger sediment; Shanafield *et al* 2015) and along ephemeral rivers. Ecohydrological niche separation theory (Silvertown *et al* 2015) predicts that co-occurring species should partition water resources through variation in traits related to the uptake and transport of water. Table 2 summarises some hydraulic traits of these three contrasting species. Comparisons of traits amongst these species contribute to our understanding of niche separation

and also to our understanding of how some species in semi-arid regions, such as Mulga, are so resilient. The third ecosystem in the Ti Tree is a sparse *Corymbia* savanna which we do not discuss further.

Mulga is shallow rooted (<2 m), evergreen and located above a shallow hard pan (Cleverly *et al* 2016b). Consequently it experiences very low phyllode water potentials, both pre-dawn and midday (the limit of our pressure chamber was 10 MPa, hence we can only state that midday water potentials were lower than −10 MPa). Several predictions can be made about the traits that should be associated with such low water potentials. A key prediction is that Mulga should exhibit a high resistance to xylem embolism to avoid catastrophic loss of the ability to transport water to the canopy (Sperry and Tyree 1988). A high resistance to embolism requires thick walled xylem conduits, which in turn results in a large wood density, coupled with a small sapwood conductive area and a concomitant small sapwood hydraulic conductivity. Similarly, we would predict a large resistance to vessel implosion (Hacke *et al* 2001). Finally, we would predict a large water-use-efficiency, as indicated by an enrichment (closer to zero) of $\delta^{13}C$ of leaves. It is clear that Mulga does possess this suite of traits (table 2), and this contributes to the ability of this species to persist through multi-year periods of low annual rainfall and the dry season that occurs each year. These traits also confer a low rate of tree water-use, as has been previously observed (O'Grady *et al* 2009). Low rates of tree water use are also the result of the large Huber values ($H_v$, ratio of sapwood area to leaf area; Eamus and Prior 2001) exhibited in Mulga (table 2). For every m$^2$ of sapwood, only about 880 m$^2$ of phyllode area is supported. This is much smaller than the 1800–2000 m$^2$ of leaf area supported by 1 m$^2$ of sapwood in *Eucalyptus camaldulensis* and *Erythrina vespertilio*. Changes in $H_v$ in response to changes in soil water availability are a common adaptive strategy to differences in water availability (Togashi *et al* 2015, Zolfaghar *et al* 2015).

A high resistance to xylem embolism and the very low leaf potentials experienced by Mulga are also associated with the lowest water potential at zero turgor of the three species discussed herein. Low water potential at zero turgor in Mulga is indicative of the accumulation of chemically inert compounds that confer protection from water stress, and these osmoprotective compounds are known to occur in Mulga as nitrogen-rich compounds such as proline and glycine betaine (Erskine *et al* 1996). This is an important trait for shallow rooted evergreen species in semi-arid regions growing without access to groundwater. The maintenance of positive turgor is required to drive cell growth and maintain open stomata, thereby allowing photosynthesis to occur during periods of low soil moisture availability.

By contrast, *Eucalyptus camaldulensis* and *Erythrina vespertilio* exhibit markedly different strategies

**Table 2.** Trait comparisons of three contrasting tree species in the Ti Tree basin. From Santini *et al* (2016).

| Trait | *Acacia aneura* (Mulga) | *Eucalyptus camaldulensis* (River Red Gum) | *Erythrina vespertilio* |
|---|---|---|---|
| Phenology | Evergreen | Evergreen | Deciduous |
| Groundwater dependent or not | Not | Highly | Confined to paleochannels which act as sites of run-on and possible short-lived perched shallow water table |
| Pre-dawn/midday leaf water potential March/April 2014 (MPa) | $-7.2/<-10.0$ | $-1.0/-2.4$ | $-0.5/-0.9$ |
| Branch sapwood density (g cm$^{-3}$) | 0.95 | 0.65 | 0.4 |
| Fibre wall thickness ($\mu$m) | 4.01 | 3.31 | 2.80 |
| Vessel implosion resistance $(t/b)^2$ | 0.059 | 0.0237 | 0.0096 |
| Conductive area (mm$^2$ mm$^{-2}$) | 0.098 | 0.258 | 0.249 |
| Theoretical hydraulic conductivity (kg mm$^{-1}$ MPa$^{-1}$ s$^{-1}$) | 0.109 | 0.328 | 0.383 |
| Huber value | 0.001696 | 0.00049 | 0.000554 |
| Water potential at turgor loss | $-2.51$ | $-1.13$ | $-1.02$ |
| $\delta^{13}$C of leaves/WUE | $-26.96/82.38$ | $-29.89/47.89$ | $-27.45/75.26$ |

from Mulga for persistence in this semi-arid environment. *Eucalyptus camaldulensis* has access to groundwater and thus does not experience the very low pre-dawn and midday water potentials that occur in Mulga. *Eucalyptus camaldulensis* is highly groundwater dependent and occurs predominantly as riparian forest above shallow unconfined groundwater (<6 m depth). Because it is less reliant on rainfall, with yearlong access to groundwater, this species does not experience low leaf water potentials, and thus does not require thick xylem cell walls to resists xylem embolism. Consequently the sapwood density and vessel implosion resistance (Hacke *et al* 2001) are smaller in *Eucalyptus camaldulensis* than in Mulga (table 2). This easy access to groundwater and large conductive sapwood area support much larger rates of transpiration than observed in Mulga, despite high canopy water potential (relative to Mulga; O'Grady *et al* 2009). To maintain a large rate of transpiration and high canopy water potential requires a large sapwood hydraulic conductivity, as is observed (table 2). Furthermore, *Eucalyptus camaldulensis* has a larger (closer to zero) water potential at zero turgor than Mulga because it experiences much larger canopy water potentials than Mulga. Finally, the $\delta^{13}$C of its leaves are much larger than those of Mulga, reflecting its relatively low WUE: the value recorded is close to that observed for leaves of Eucalypts growing in regions receiving >1500 mm rain per year. However, it does possess the capacity for a reduction in leaf area as a mechanism for adjusting water use during prolonged dry periods (O'Grady *et al* 2009), and mortality can occur in small trees during extended dry periods (Horner *et al* 2009).

*Erythrina vespertilio* has a similar strategy to *Eucalyptus camaldulensis* for surviving semi-arid conditions, but with one important difference. Like *Eucalyptus camaldulensis*, *Erythrina vespertilio* does not experience low canopy water potentials and therefore

has a low wood density, narrow fibre walls and a very low vessel implosion resistance. It also possesses large cross-sectional areas of parenchyma, indicative of a large capacity for water storage. Similarly, it has a large theoretical hydraulic conductivity (table 2). However, it has ephemeral access to groundwater, occurring in paleochannels which are sites of small amounts of run-on from precipitation and which contain perched shallow water tables for short periods of time. Consequently the $\delta^{13}$C of leaves of *Erythrina vespertilio* (and hence WUE) is intermediate between Mulga and *Eucalyptus camaldulensis*, and its H$_v$ is also intermediate between these two species. However, the key trait exhibited by this species is its deciduous habit. By being an obligate deciduous species its canopy entirely avoids periods of low soil and atmospheric water content. Consequently it never experiences low canopy water potential and therefore its water potential at zero turgor is very high (close to zero)—a trait that is associated with deciduous and mesic species.

# 7. Conclusions and future directions

TDFs experience warm/hot temperatures and a predictable dry season. However, as we have shown for our Mulga site in central Australia and in agreement with most other semi-arid and arid ecosystems, rainfall is extremely variable in terms of the amount and timing of precipitation. This has major impacts on phenological behaviour and concomitant productivity of such ecosystems. Mulga in this climate zone can oscillate repeatedly between being approximately C neutral to being large C sinks and large C sources. Contrary to widely held expectations the behaviour of semi-arid ecosystems can impact significantly on global C and water cycles. An important feature of arid and semi-arid regions is the importance of

groundwater and associated terrestrial groundwater dependent ecosystems both to human well-being and the health and functioning of these landscapes. This synthesis has reiterated the importance of field ecophysiology, remote sensing and modelling to the generation of an in-depth understanding of the behaviour and functioning of these regions (Eamus *et al* 2016).

Future work is required to examine the above-and below ground C storage pools and how these change at annual and decadal time-scales and to determine the resilience, sensitivities and and tipping-points of Mulga in the face of a changing climate. Since 1940, mean annual temperature in Alice Springs (200 km south) has increased by approximately 1.5 °C, with associated increases in VPD during all except the wettest years. Since increased VPD and temperature increase the likelihood of forest mortality, (Eamus *et al* 2013b), the probability of mortality of Mulga is likely to also increase, thereby exerting a significant impact on regional C and water budgets and global productivity (Poulter *et al* 2014), especially during droughts in the Southern Hemisphere. Although mortality and drought are not unusual for Mulga, which was found to experience up to 40% mortality during the 1964–1966 drought (Cunningham and Walker 1973), thus far, Mulga has shown resilience to drought and high temperatures, thereby maintaining a neutral carbon balance through drier-than-average years. Determining the climate thresholds that induce mortality (and recruitment; Mulga is a masting species, producing large seed crops only after exceptionally high rainfall years) and determining how these events might change in the future remains a significant research challenge.

Recent studies have found semi-arid ecosystems (including Mulga) to be particularly sensitive to hydroclimatic variability and are thus vulnerable to future climatic extremes (Ma *et al* 2015). Such sensitivity suggests that maintaining ecosystem services and functioning of Mulga may be threatened in the future. Further studies are needed to examine the impact of climatic extremes on Mulga ecosystems to better understand climate thresholds of this important Australian TDF. Finally, further investigations of the mechanisms underpinning ecohydrological niche separation within these biomes is required to inform land surface models and global dynamic vegetation models, which are increasingly used in ecological and ecohydrological studies of TDFs.

## Acknowledgments

## References

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

Baldocchi D D 2011 A synthesis of forest evaporation fluxes—from days to years—as measured with eddy covariance *Forest Hydrology and Biogeochemistry: Synthesis of Past Research and Future Directions* ed D F Levia *et al* (Dordrecht: Springer) pp 101–16

Barron-Gafford G A, Scott R L, Jenerette G D, Hamerlynck E P and Huxman T E 2012 Temperature and precipitation controls over leaf- and ecosystem-level $CO_2$ flux along a woody plant encroachment gradient *Glob. Change Biol.* **18** 1389–400

Berry G, Reeder M J and Jakob C 2011 Physical mechanisms regulating summertime rainfall over northwestern Australia *J. Clim.* **24** 3705–17

Boening C, Willis J K, Landerer F W, Nerem R S and Fasullo J 2012 The 2011 La Niña: so strong, the oceans fell *Geophys. Res. Lett.* **39** L19602

Bowman D, Boggs G S, Prior L D and Krull E S 2007 Dynamics of *Acacia aneura-Triodia* boundaries using carbon ($^{14}$C and $\delta^{13}$C) and nitrogen ($\delta^{15}$N) signatures in soil organic matter in central Australia *Holocene* **17** 311–8

Chen C, Eamus D, Cleverly J, Boulain N, Cook P, Zhang L, Cheng L and Yu Q 2014 Modelling vegetation water-use and groundwater recharge as affected by climate variability in an arid-zone *Acacia* savanna woodland *J. Hydrol.* **519** 1084–96

Cleverly J, Boulain N, Villalobos-Vega R, Grant N, Faux R, Wood C, Cook P G, Yu Q, Leigh A and Eamus D 2013 Dynamics of component carbon fluxes in a semi-arid *Acacia* woodland, central Australia *J. Geophys. Res.* **118** 1168–85

Cleverly J, Eamus D, Luo Q, Restrepo Coupe N, Kljun N, Ma X, Ewenz C, Li L, Yu Q and Huete A 2016a The importance of interacting climate modes on Australia's contribution to global carbon cycle extremes *Sci. Rep.* **6** 23113

Cleverly J *et al* 2016b Soil moisture controls on phenology and productivity in a semi-arid critical zone *Sci. Total Environ.* **568** 1227–37

Cleverly J *et al* 2016c Productivity and evapotranspiration of two contrasting semiarid ecosystems following the 2011 global carbon land sink anomaly *Agric. Forest Meteorol.* **220** 151–9

Crisp M D and Cook L G 2013 How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective *Annu. Rev. Ecol. Evol. Syst.* **44** 303–24

Cunningham G M and Walker P J 1973 Growth and survival of mulga (*Acacia aneura* F. Muell. ex Benth.) in western New South Wales *Tropical Grasslands* **7** 69–77

Duursma R A, Barton C V M, Lin Y S, Medlyn B E, Eamus D, Tissue D T, Ellsworth D S and McMurtrie R E 2014 The peaked response of transpiration rate to vapour pressure deficit in field conditions can be explained by the temperature optimum of photosynthesis *Agric. Forest Meteorol.* **189** 2–10

Eamus D, Boulain N, Cleverly J and Breshears D D 2013b Global change-type drought-induced tree mortality: vapor pressure deficit is more important than temperature per se in causing decline in tree health *Ecol. Evol.* **3** 2711–29

Eamus D, Cleverly J, Boulain N, Grant N, Faux R and Villalobos-Vega R 2013a Carbon and water fluxes in an arid-zone *Acacia* savanna woodland: An analyses of seasonal patterns and responses to rainfall events *Agric. Forest Meteorol.* **182–183** 225–38

Eamus D, Duff G A and Berryman C A 1995 Photosynthetic responses to temperature, light flux density, $CO_2$ concenrtation and vapour pressure deficit in *Eucalyptus tetrodonta* under $CO_2$ enrichment *Environ. Pollut.* **90** 41–9

Eamus D, Huete A and Yu Q 2016 *Vegetation Dynamics: A Synthesis of Plant Ecophysiology, Remote Sensing and Modelling* (New York: Cambridge University Press) 518pp

Eamus D, Macinnis-Ng C M O, Hose G C, Zeppel M J B, Taylor D T and Murray B R 2005 Ecosystem services: an ecophysiological examination *Aust. J. Bot.* **53** 1–19

Eamus D and Prior L 2001 Ecophysiology of trees of the seasonally dry tropics: comparisons among phenologies *Adv. Ecol.Res.* **31** 113–97

Erskine P D, Stewart G R, Schmidt S, Turnbull M H, Unkovich M and Pate J S 1996 Water availability—a physiological constraint on nitrate utilization in plants of Australian semi-arid mulga woodlands *Plant Cell Environ.* **19** 1149–59

Fasullo J T, Boening C, Landerer F W and Nerem R S 2013 Australia's unique influence on global sea level in 2010–2011 *Geophys. Res. Lett.* **40** 4368–73

Flanagan L B and Adkinson A C 2011 Interacting controls on productivity in a northern Great Plains grassland and implications for response to ENSO events *Glob. Change Biol.* **17** 3293–311

Flora of Australia 2002 vol 43 (Canberra: CSIRO Publishing and Australian Biological Resources Study) p 172 & p 216

Hacke U G, Sperry J S, Pockman W T, Davis S D and McCulloh K A 2001 Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure *Oecologia* **126** 457–61

Horner G J, Baker P J, Mac Nally R, Cunningham S C, Thomson J R and Hamilton F 2009 Mortality of developing floodplain forests subjected to a drying climate and water extraction *Glob. Change Biol.* **15** 2176–86

Huxman T E, Snyder K A, Tissue D, Leffler A J, Ogle K, Pockman W T, Sandquist D R, Potts D L and Schwinning S 2004 Precipitation pulses and carbon fluxes in semiarid and arid ecosystems *Oecologia* **141** 254–68

Kanniah K D, Beringer J and Hutley L B 2010 The comparative role of key environmental factors in determining savanna productivity and carbon fluxes: a review, with special reference to Northern Australia *Prog. Phys. Geogr.* **34** 459–90

Keenan T F et al 2014 Net carbon uptake has increased through warming-induced changes in temperate forest phenology *Nat. Clim. Change* **4** 598–604

Kong Q and Zhao S 2010 Heavy rainfall caused by interactions between monsoon depression and middle-latitude systems in Australia: a case study *Meteorol. Atmos. Phys.* **106** 205–26

Kurc S A and Small E 2004 Dynamics of evapotranspiration in semi-arid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico *Water Resour. Res.* **40** W09305

Le Quéré C et al 2014 Global carbon budget 2013 *Earth Syst. Sci. Data* **6** 235–63

Luyssaert S et al 2007 $CO_2$ balance of boreal, temperate, and tropical forests derived from a global database *Glob. Change Biol.* **13** 2509–37

Ma X, Huete A, Moran S, Ponce-Campos G and Eamus D 2015 Abrupt shifts in phenology and vegetation productivity under climate extremes *J. Geophys. Res.* **120** 2036–52

Ma X, Huete A, Yu Q, Restrepo-Coupe N, Beringer J, Hutley L B, Kanniah K D, Cleverly J and Eamus D 2014 Parameterization of an ecosystem light-use-efficiency model for predicting savanna GPP using MODIS EVI *Remote Sens. Environ.* **154** 253–71

Ma J, Zheng X J and Li Y 2012 The response of $CO_2$ flux to rain pulses at a saline desert *Hydrol. Process.* **26** 4029–37

Ma X et al 2013 Spatial patterns and temporal dynamics in savanna vegetation phenology across the North Australian Tropical Transect *Remote Sens. Environ.* **139** 97–115

Martin H A 2006 Cenozoic climatic change and the development of the arid vegetation in Australia *J. Arid Environ.* **66** 533–63

Maslin B R and Reid J B 2012 A taxanomic revision of Mulga (*Acacia aneura* and its close relatives: Fabaceae) in Western Australia *Nuytsia* **22** 129–267

Migliavacca M et al 2015 Influence of physiological phenology on the seasonal pattern of ecosystem respiration in deciduous forests *Glob. Change Biol.* **21** 363–76

Miles L et al 2006 A global overview of the conservation status of tropical dry forests *J. Biogeogr.* **33** 491–505

Mott J J and McComb A J 1975 The role of photoperiod and temperature in controlling the phenology of three annual species from an arid region of Western Australia *J Ecol.* **63** 633–41

Nano C E M and Clarke P J 2010 Woody-grass ratios in a grassy arid system are limited by multi-causal interactions of abiotic constraint, competition and fire *Oecologia* **162** 719–32

Nicholas A M M, Franklin D C and Bowman D M J S 2011 Floristic uniformity across abrupt boundaries between *Triodia* hummock grassland and *Acacia* shrubland on an Australian desert sandplain *J. Arid Environ.* **75** 1090–6

Nix H A and Austin M P 1973 Mulga: a bioclimatic analysis *Tropical Grasslands* **7** 9–20

O'Grady A P, Cook P G, Eamus D, Duguid A, Wischusen J D H, Fass T and Worldege D 2009 Convergence of tree water use within an arid-zone woodland *Oecologia* **160** 643–55

Ogle K and Reynolds J F 2004 Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays *Oecologia* **141** 282–94

Perkins S E, Argueso D and White C J 2015 Relationships between climate variability, soil moisture, and Australian heatwaves *J. Geophys. Res.: Atmos.* **120** 8144–64

Portillo-Quintero C A and Sanchez-Azofeifa G A 2010 xtent and conservation of tropical dry forests in the Americas *Biol. Conserv.* **143** 144–55

Poulter B et al 2014 Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle *Nature* **509** 600–3

Pressland A J 1976 Effect of stand density on water-use of mulga (*Acacia aneura* F. Muell) woodlands in southwestern Queensland *Aust. J. Bot.* **24** 177–91

Pui A, Sharma A, Santoso A and Westra S 2012 Impact of the El Nino-southern oscillation, Indian Ocean dipole, and southern annular mode on daily to subdaily rainfall characteristics in East Australia *Mon. Weather Rev.* **140** 1665–82

Pulla S, Ramaswami G, Mondal N, Chitra-Tarak R, Suresh H S, Dattaraja H S, Vivek P, Parthasarathy N, Ramesh B R and Sukumar R 2015 Assessing the resilience of global seasonally dry tropical forests *Int. Forestry Rev.* **17** 91–113

Restrepo-Coupe N, Huete A, Davies K, Cleverly J, Beringer J, Eamus D, van Gorsel E, Hutley L B and Meyer W S 2016 MODIS vegetation products as proxies of photosynthetic potential: a look across meteorological and biologic driven ecosystem productivity *Biogeosciences* **13** 5587–608

Santini N S, Cleverly J, Faux R, Lestrange C, Rumman R and Eamus D 2016 Xylem traits and water-use efficiency of woody species co-occurring in the Ti Tree basin arid zone *Trees* **30** 295–303

Scott R L, Biederman J A, Hamerlynck E P and Barron-Gafford G A 2015 The carbon balance pivot point of southwestern U.S. semiarid ecosystems: insights from the 21st century drought *J. Geophys. Res.: Biogeosci.* **120** 2612–24

Shanafield M, Cook P G, Gutierrez-Jurado H A, Faux R, Cleverly J and Eamus D 2015 Field comparison of methods for estimating groundwater discharge by evaporation and evapotranspiration in an arid-zone playa *J. Hydrol.* **527** 1073–83

Silvertown J, Araya Y and Gowing D 2015 Hydrological niches in terrestrial plant communities: a review *J. Ecol.* **103** 93–108

Specht R A and Specht A 1999 Australian plant communities (Melbourne: Oxford University Press) pp 492

Sperry J S and Tyree M T 1988 Mechanisms to water stress-induced xylem embolism *Plant Physiol.* **88** 581–7

Teuling A J M, Seniviratne S I, Williams C and Troch P A 2006 Observed time-scales of evapotranspiration response to soil moisture *Geophys. Res. Lett.* **33** L23403

Togashi H F, Prentice I C, Evans B J, Forrester D I, Drake P, Feikema P, Brooksbank K, Eamus D and Taylor D 2015 Morphological and moisture availability controls of the leaf area-to-sapwood area ratio: analysis of measurements on Australian trees *Ecol. Evol.* **5** 1263–70

van Dijk A, Dolman A J and Schulze E D 2005 Radiation, temperature, and leaf area explain ecosystem carbon fluxes in

boreal and temperate European forests *Glob. Biogeochem. Cycles* **19** GB2029

Van Etten E J B 2009 Inter-annual rainfall variability of arid Australia: greater than elsewhere? *Aust. Geogr.* **40** 109–20

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 *Glob. Change Biol.* **17** 3130–49

Xie Z, Huete A, Restrepo-Coupe N, Ma X, Devadas R and Caprarelli G 2016 Spatial partitioning and temporal evolution of Australia's total water storage under extreme hydroclimatic impacts *Remote Sens. Environ.* **183** 43–52

Zha T S, Li C Y, Kellomaki S, Peltola H, Wang K Y and Zhang Y Q 2013 Controls of evapotranspiration and $CO_2$ fluxes from Scots pine by surface conductance and abiotic factors *PloS One* **8** e69027

Zolfaghar S, Villalobos-Vega R, Zeppel M and Eamus D 2015 The hydraulic architecture of Eucalyptus trees growing across a gradient of depth to groundwater *Funct. Plant Biol.* **42** 888–98