The land sink anomaly of 2011 was very short-lived in semi-arid Australia

An *Acacia* woodland returned to carbon neutrality post-2011

An open *Corymbia* savanna was a very large carbon source post-2011

Access to groundwater by *Corymbia* in the savanna was inferred from leaf $^{13}C$

Groundwater contributed to evapotranspiration excess in a year of average rainfall
Productivity and evapotranspiration of two contrasting semiarid ecosystems following the 2011 carbon land sink anomaly

James CLEVERLY\textsuperscript{a,b}, Derek EAMUS\textsuperscript{a,b}, Eva VAN GORSEL\textsuperscript{c}, Chao CHEN\textsuperscript{a,1}, Rizwana RUMMAN\textsuperscript{a}, Quying LUO\textsuperscript{d}, Natalia RESTREPO COUPE\textsuperscript{d}, Longhui LI\textsuperscript{a}, Natascha KLJUN\textsuperscript{a}, Ralph FAUX\textsuperscript{a}, Qiang YU\textsuperscript{a} and Alfredo HUETE\textsuperscript{d}

\textsuperscript{a} School of Life Sciences, University of Technology Sydney, PO Box 123, Broadway, NSW, 2007, Australia

\textsuperscript{b} Australian Supersite Network, Terrestrial Ecosystem Research Network, University of Technology Sydney, PO Box 123, Broadway, NSW, 2007, Australia

\textsuperscript{c} CSIRO Marine and Atmospheric Research, Pye Laboratory, Clunies Ross Street, Acton, ACT 2600, Australia

\textsuperscript{d} Climate Change Cluster, University of Technology Sydney, PO Box 123, Broadway, NSW, 2007, Australia

\textsuperscript{e} Department of Geography, Swansea University, Singleton Park, Swansea SA2 8PP, UK

*Correspondence: James.Cleverly@UTS.edu.au, +61 (02) 9514 8405, +61 (02) 9514 4079 (FAX)

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\textsuperscript{1} Present address: CSIRO Agriculture Flagship, PMB 5, PO Wembley, WA, 6913, Australia
Global carbon balances are increasingly affected by large fluctuations in productivity occurring throughout the semiarid regions. Recent analyses found a large C uptake anomaly in 2011 in arid and semiarid regions of the southern hemisphere. Consequently, we compared the C and water fluxes of two distinct woody ecosystems (a Mulga (*Acacia*) woodland and a *Corymbia* savanna) between August 2012 and August 2014 in semiarid central Australia, demonstrating that the 2011 anomaly was short-lived in both ecosystems. The Mulga woodland was approximately C neutral but with periods of significant uptake within both years. The extreme drought tolerance of *Acacia* is presumed to have contributed to this. By contrast, the *Corymbia* savanna was a very large net C source (130 and 200 g C m\(^{-2}\) yr\(^{-1}\) in average and below average rainfall years, respectively), which is likely to have been a consequence of the degradation of standing, senescent biomass that was a legacy of high productivity during the 2011 anomaly. The magnitude and temporal patterns in ecosystem water-use efficiencies (WUE), derived from eddy covariance data, differed across the two sites, reflecting differences in the relative contributions of respiration to net C fluxes across the two ecosystems. In contrast, differences in leaf-scale measures of WUE, derived from \(^{13}\)C stable isotope analyses, were apparent at small spatial scales and may reflect the different rooting strategies of *Corymbia* and *Acacia* trees within the *Corymbia* savanna. Restrictions on root growth and infiltration by a siliceous hardpan located below *Acacia*, whether in the Mulga woodland or in the Mulga patches of the *Corymbia* savanna, impedes drainage of water to depth, thereby producing a reservoir for soil moisture storage under *Acacia* while acting as a barrier to access of groundwater by *Corymbia* trees in Mulga patches, but not in the open *Corymbia* savanna.
1. Introduction

Inter-annual variability in atmospheric concentrations of CO$_2$ is large (Le Quéré et al., 2014), and much of this variability is driven by fluctuations in the source/sink strength of terrestrial ecosystems (Cox et al., 2013). During the latter half of the twentieth century, global net primary productivity (NPP) may have increased (Nemani et al., 2003), resulting in a potential increase in uptake of 0.05 Pg C per year (Ballantyne et al., 2012). Then, global NPP was reduced by 0.55 Pg C during the period 2000–2009, a result ascribed to large-scale drought in the southern hemisphere (Zhao and Running, 2010). Thereafter, Le Quéré et al. (2014) identified the 2011 land sink anomaly, which was a year of exceptional productivity, and Poulter et al. (2014) confirmed this anomaly by using a combination of modelling and remote sensing approaches. This land sink anomaly was driven by growth in semiarid vegetation of the southern hemisphere, with almost 60% occurring in Australia (Poulter et al., 2014). We have previously shown, using field observations of landscape fluxes of CO$_2$, that one of the dominant ecosystems of semiarid central Australia was indeed a large sink for C over almost all of the 12 months between October 2010 and October 2011 (Cleverly et al., 2013a; Eamus et al., 2013). Large fluctuations in productivity, evapotranspiration (ET) and ecosystem water-use efficiency (eWUE) across these semiarid regions reflect the very high ecosystem resilience of vegetation (Campos et al., 2013), which can have large effects on global C relations and consequently drive events such as the land sink anomaly of 2011.

Globally, dryland regions (arid, semiarid, and subhumid) cover 41% of the land area (Reynolds et al., 2007). Within these regions, arid and semiarid environments are characterised by chronic water shortages. Thus, productivity and ET are closely dependent upon the timing, frequency and amount of precipitation (Huxman et al., 2004), through which plant water availability is mediated by local hydrology (Breshears et al.,
Terrain, soil texture, vegetation and precipitation intensity influence runoff (Ludwig et al., 2005), while soil moisture responses to precipitation pulses can depend upon runoff patterns, soil structure, rooting dynamics, the spatial distribution of vegetation, and infiltration versus evaporation from topsoil (Breshears et al., 2009; Ludwig et al., 2005; Martinez-Meza and Whitford, 1996). Variation in local moisture availability is dependent upon rainfall pulses such that the amount of precipitation required to induce a response in semiarid and arid vegetation is dependent upon soil moisture storage capacity and run-off versus infiltration patterns (Huxman et al., 2004; Ludwig et al., 2005; Ogle and Reynolds, 2004; Schwinning et al., 2004). Together, these hydrologic factors influence the occurrence and timing of respiratory pulses (one day following precipitation), pulses of productivity (3–4 days, if present), and the exponential decline of ET following rainfall (Eamus et al., 2013; Huxman et al., 2004). A detailed understanding of the variations in ecohydrology within these regions is thus required to predict the source/sink strengths of water-limited ecosystems.

The semiarid regions of Australia are dominated by three major biomes along a woodland-savanna-grassland continuum: (1) Mulga woodlands (Acacia spp.), which cover approximately 20–25% of the continental land area (Bowman et al., 2008), and (2) Corymbia savanna over a hummock grass (Triodia spp.) understorey that grades into (3) treeless hummock grasslands. Mulga trees range in height (2–10 m) and ground cover (10–70%) (Nix and Austin, 1973), and they are preferentially located where storage of soil moisture occurs near the surface in sand dunes, clay-rich soil or over the siliceous hardpans that are common across semiarid Australia (Bowman et al., 2007; Ludwig et al., 2005; Maslin and Reid, 2012; Nano and Clarke, 2010; Nix and Austin, 1973; Thiry et al., 2006; Tongway and Ludwig, 1990). In contrast, tree density (stems per hectare) and cover
in *Corymbia* savannas are very low, and tree height ranges from 5–15 m. *Corymbia opaca* is deep-rooted (8–20 m), and tends to be groundwater dependent in semiarid areas (Cook and O'Grady, 2006; O'Grady et al., 2006a; O'Grady et al., 2006b). The understory in the *Corymbia* savanna is characterised by a continuous cover of perennial hummock grasses (*Triodia* spp.), which are widespread throughout Australia and cover an additional 20–25% of the continental land area (Bowman et al., 2008; Nano and Clarke, 2010; Reid et al., 2008).

The aim of this study was to investigate fluctuations in the fluxes of C and water from iconic Australian semiarid vegetation in response to reductions in precipitation subsequent to the 2011 land sink anomaly. In this manuscript we compare and contrast the behaviour of two disparate arid-zone tropical ecosystems (Mulga woodland and *Corymbia* savanna) in central Australia to address four over-arching questions: (a) did the 2011 anomaly persist into 2012/2013/2014 in either biome; (b) do these two contrasting ecosystems respond similarly to almost identical weather patterns; (c) how do ecosystem water-use efficiencies compare across ecosystems; and (d) at small spatial scales within the *Corymbia* savanna, how do leaf-scale water-use efficiencies across the two tree species (*Acacia* and *Corymbia*) differ?

### 2. Materials and Methods

#### 2.1. Site descriptions

This study was located on Pine Hill cattle station in the Ti Tree catchment of central Australia and was co-located with several previous hydrological, ecological and ecophysiological studies (Calf et al., 1991; Cleverly et al., 2013a; Eamus et al., 2013; Harrington et al., 2002; Ma et al., 2013; O'Grady et al., 2009; Scanlon et al., 2006). The Ti Tree catchment is an enclosed basin that covers 5,500 km$^2$ and contains two main
ecosystems: Mulga woodlands and *Corymbia* savanna (Harrington et al., 2002).

Measurements were collected from two locations: one in the Mulga woodland and one in the *Corymbia* savanna. An eddy covariance tower was located in each ecosystem, separated by 40 km at the same latitude ([22.3 °S 133.25 °E] and [22.3 °S 133.65 °E]).

A full description of the soil, floristics, leaf area index (LAI), energy balance and C relations of the Mulga woodland can be found in Cleverly et al. (2013a) and Eamus et al. (2013). Briefly, the Mulga woodland is characterised by a discontinuous canopy of short (3–7 m), evergreen *Acacia* trees (*A. aptaneura* and *A. aneura*) with an understorey of shrubs, herbs and grasses (C₃ and C₄) that are conditionally active depending upon moisture availability and season (Cleverly et al., 2013a). The cover of *Acacia* is 74.5 % of the land area in the Mulga woodland; *C. opaca* is essentially absent from the Mulga woodland (one tree within the EC footprint, cf. Section 2.2). The basal area of *Acacia* within the woodland is 8 m² ha⁻¹ (Eamus et al., 2013).

The second eddy covariance site contains two species of trees: widely spaced and tall *Corymbia opaca* trees above a matrix of hummock grass (*Spinifex, Triodia schinzii*) and small patches of Mulga (*A. sericophylla, A. melleodora* and *A. aptaneura*) that contain an understorey of herbs and tussock grasses (*Aristida* spp., *Eremophila latrobei* subsp. *gabra, Eragrostis eriopoda* subsp. *red earth, Paraneurachne muelleri* and *Psydrax latifolia*). Although the distribution of *T. schinzii* does not substantially overlap with Mulga, *C. opaca* trees were present in both habitats. Representing only 0.4 % cover (basal area of 0.21 m² ha⁻¹), *C. opaca* are found predominantly in the open savanna, although they are found occasionally in the isolated small Mulga patch close to the EC tower within in the *Corymbia* savanna. Soil texture is sandier in the *Corymbia* savanna (loamy sand) than in the Mulga woodland (sandy loam). Soil organic matter is less than 1% at both sites. In the *Corymbia* savanna, the energy balance ratio \((H + LE)/(R_n - G)\)
was 0.97 ± 0.005 (January 2013–July 2014), wherein $H$ is sensible heat flux, $LE$ is latent heat flux, $R_n$ is net radiation and $G$ is ground heat flux. Over the same period in the Mulga woodland, the energy balance ratio was 0.89 ± 0.005. The Bowen ratio ($H/LE$) was large at both sites: 37.5 (range 0.78–408) in the Mulga woodland and 37.9 (0.23–511) in the Corymbia savanna.

Long-term annual average precipitation (1987–2014) at the nearest meteorological station (Territory Grape Farm, 18 km due south of the Corymbia savanna site) is 320.7 mm (http://www.bom.gov.au). The monsoon tropics of Australia are defined by the receipt of 85% of annual precipitation during the November–April monsoon season (Bowman et al., 2010), which places these sites within the monsoon zone on average (Cleverly et al., 2013a). However, during the first 16 months of this study (August 2012–November 2013), very little rain was received and there was consequently negligible grassy understorey, in contrast to the extensive understorey that was present during the land sink anomaly of 2011 (Eamus et al., 2013).

2.2. Eddy covariance data

Eddy covariance analyses of net ecosystem photosynthesis (NEP) and evapotranspiration (ET) were used as measures of net C uptake and ecosystem water use. In the eddy covariance method, ET is determined from the covariance between vertical wind speed ($w$) and specific humidity ($q$): $ET = \langle w'q' \rangle / \rho w$, where $\langle \rangle$ represents an average in time and the prime operator represents the deviation from a mean: $q' = \langle q \rangle - q_i$. Similarly, NEP was taken to be the negative covariance between $w$ and $[CO_2]$ (c): $NEP = -\langle w'c' \rangle$. By this definition, NEP is positive during C uptake (i.e., photosynthesis, C sink) and negative for net C emissions (C source). The trade-off between C uptake and ET was represented by eWUE, which was calculated as the ratio of NEP and ET. Because
of non-linearity at very small values of ET, eWUE was determined only when ET was larger than 0.2 mm d\(^{-1}\).

Both tower sites are part of the OzFlux Network (Cleverly, 2011; Cleverly, 2013). The 90% flux footprint (Kljun et al., 2004) under turbulent conditions extended 200–300 m to the southeast of either tower, although variability in roughness length across the *Corymbia* savanna interferes with the reliability of footprint estimates at that site. In the *Corymbia* savanna, approximately 25% of the flux footprint covered the *Corymbia* savanna, while the remaining 75% of the footprint was located over the small Mulga patch that included *Acacia*, *Corymbia* and tussock grasses. The trees nearest the tower in the open *Corymbia* savanna are *Acacia* with a canopy height of 4.85 m, in contrast to the 6.5 m tall *Acacia* in the Mulga woodland. Thus, measurements were made over the *Corymbia* savanna at a slightly lower height (9.85 m) than above the Mulga woodland (11.6 m, Cleverly et al., 2013a). Where possible, the instruments on each tower were the same (e.g., Campbell Scientific CSAT3) or only different in the model of sensor (e.g., Kipp & Zonen CNR1 v. CNR4, Li-Cor 7500 v. 7500A), in which the newer models were used in the *Corymbia* savanna.

All estimates of error were determined as the standard error (s.e. = \(\sigma/n^{0.5}\), where \(\sigma\) is the standard deviation and \(n\) is sample size).

### 2.2.1. Quality control, corrections and gap-filling

Quality control of meteorological and flux measurements (QA/QC) was performed on both towers as described in Eamus et al. (2013). Briefly, QA/QC procedures included spike detection and removal, range checks that include rejection of measurements when the wind was from a 90° arc behind the sonic anemometer (CSAT3) and tower (10% of observations, only during the passage of frontal systems that generate advection and
negative fluxes of LE; Beringer and Tapper, 2000), and filtering for bad measurements of
humidity from the IRGA in comparison to a slow-response sensor. Corrections included
2-dimensional coordinate rotation (Wesely, 1970), frequency attenuation correction for
time averaging and sensor displacement (Massman and Clement, 2004), conversion of
virtual to actual sensible heat flux (Campbell Scientific Inc., 2004; Schotanus et al., 1983),
correction for flux-density effects (WPL; Webb et al., 1980) and storage of heat in the soil
above the ground heat flux plates. Corrections and QA/QC steps were performed using
OzFluxQC and the OzFluxQC Simulator, both in version 2.8.5 and available online (e.g.,
Cleverly and Isaac, 2015). Gaps in fluxes were filled using a self-organising linear output
(SOLO) that was trained on a self-organising feature map (SOFM) of meteorological (net
radiation, air temperature, vapour pressure deficit, specific humidity) and soil
measurements (G, soil temperature, soil moisture content at the surface) (Eamus et al.,
2013). SOLO is a statistical artificial neural network (ANN) and was chosen for its
resistance to overtraining (Hsu et al., 2002), ability to simulate fluxes (Abramowitz et al.,
2006), and small RMSE relative to feed forward ANNs (Eamus et al., 2013).
In contrast to gaps in the flux measurements, two types of gaps were identified in
the meteorological data: those that were due to measurement over-ranging on the
datalogger and those that occurred during system maintenance. Over-ranging was
identified in the measurement of solar radiation during periods when reflection from a
cloud face generated large (> 1200 W m$^{-2}$) radiant fluxes. To avoid underestimation bias
in these cases, gaps in 30-minute solar ($R_s$) and net ($R_n$) radiation were filled from the
measured value in each minute that did not report an over-ranging error (26–29 one-
minute values). These gaps first occurred during the summer 2012–2013 at the Corymbia
savanna site, after which modifications to the datalogger prevented re-occurrence of solar
spike gaps.
System maintenance gaps were typically 30–300 minutes and did not coincide among sites. Filling of gaps in the meteorological variables that were used as predictors for gap filling of fluxes was performed using several methods: 1) linear interpolation, 2) replacement of measurements from the companion tower, and 3) SOLO-SOFM trained on measurements from the paired tower. Gaps in meteorological measurements were filled using the method that produced the smallest disjunction at gap boundaries.

2.3. Trends in satellite derived enhanced vegetation index (EVI) for the two sites

The moderate resolution imaging spectroradiometer (MODIS) enhanced vegetation index (EVI) is sensitive to vegetation “greenness” (i.e., chlorophyll content) and structural properties (e.g., LAI, canopy type, plant physiognomy, canopy architecture) (Huete et al., 2002). Thus, the satellite product MODIS EVI was used in this study to assess structural and functional responses of the vegetation. The MOD13Q1 product was retrieved from the satellite at a temporal resolution of 16 days and a spatial resolution of 250 m, and then the values were composited into a single $9 \times 9$ pixel centred on each tower (2.25 km resolution, only pixels that passed QA at 100% were used). The MODIS satellite was launched in 2000, and we present the entire record to provide context for the ecosystem dynamics observed over this two-year study.

2.4. $^{13}$C foliar stable isotopes

To compare leaf-scale intrinsic WUE ($WUE_i$) at small spatial scales within the Corymbia savanna, leaf samples were collected in September 2013 for analysis of the stable isotope ratio of C ($\delta^{13}C$). Mature leaves of Corymbia opaca and Acacia trees were collected from three habitats within the Corymbia savanna. The first habitat was from the Corymbia savanna per se; the second habitat was the small Mulga patch close to the EC
tower within the *Corymbia* savanna; the third habitat was the transition between the small Mulga patch and the *Corymbia* savanna. For comparison with *Acacia* sampled within the *Corymbia* savanna, $\delta^{13}C$ of bulk leaf tissue was also measured in the Mulga woodland from two replicate branches of three replicate trees of *Acacia*.

In *Corymbia*, three leaves from different branches were collected. Each leaf was ground and subsampled to obtain three representative independent values per tree. Likewise, *Acacia* phyllodes were sampled from three different branches, although several phyllodes were combined from each branch due to their small size. The C isotopic composition was measured using a Picarro G2121-i Analyser for Isotopic CO$_2$ (Picarro Inc., Santa Clara CA USA). Atropine and acetanilide were used as internal reference standards and calibrated against international measurement standards sucrose (IAEA-CH-6, $\delta^{13}C_{VPDB} = -10.45\%$), cellulose (IAEA-CH-3, $\delta^{13}C_{VPDB} = -24.72\%$) and graphite (USGS24, $\delta^{13}C_{VPDB} = -16.05\%$). Values of $\delta^{13}C$ in bulk leaf samples represent an integrated value of $C_l/C_a$ (i.e., the ratio of internal leaf and atmospheric CO$_2$ density) during the entire age of the leaf.

### 3. Results

#### 3.1. Water fluxes: daily, seasonal and annual precipitation

Daily rainfall across the two-year period showed minimal differences between the Mulga woodland and *Corymbia* savanna sites (Fig. 1a, b). Rainfall in both years was concentrated between November and early May, although both sites received about 12 mm of rain in July 2014. During the first year of this study (2013–2014), rainfall during the monsoon season (November–April) was 71 and 74% of total annual rainfall for that year in the Mulga woodland and *Corymbia* savanna, respectively. In the following year, rainfall during the monsoon season was 92% of total annual rainfall at both sites.
Although these sites are within the monsoon zone on average (Cleverly et al., 2013a), the monsoon did not penetrate inland to the location of these sites in the first year of the present study (August 2012–July 2013). Due to the proximity between sites, annual rainfall did not differ in either of the two years of the present study. Likewise, due to cross-correlation between precipitation versus temperature (maximum, mean, minimum), solar radiation and vapour pressure deficit (Cleverly et al., 2013a), meteorological conditions were equivalent across sites (data not shown).

In the 2010–2011 hydrological year (August–July), annual rainfall (565 mm) was significantly larger than the long-term average of 320.7 mm (Table 1). In contrast, annual rainfall was smaller than average in hydrological years 2011–2013 (Table 1). During the first year of this study (August

<table>
<thead>
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<th>Year</th>
<th>Rainfall (mm y⁻¹)</th>
<th>NEP (g C m⁻² y⁻¹)</th>
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<tr>
<td>2010–2011</td>
<td>565</td>
<td>259</td>
</tr>
<tr>
<td>2011–2012</td>
<td>184</td>
<td>−4</td>
</tr>
<tr>
<td>2012–2013</td>
<td>193</td>
<td>−25</td>
</tr>
<tr>
<td>2013–2014</td>
<td>295</td>
<td>12</td>
</tr>
</tbody>
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Figure 1. Daily (a, b) and cumulative (c) precipitation in the Mulga woodland (a, solid line c) and the Corymbia savanna (b, broken line c).
2012–July 2013), annual rainfall was approximately 40% less than the long-term average (192.8 and 190.6 mm in the Mulga woodland and Corymbia savanna, respectively). In the second year of this study (2013–2014), rainfall was 294.6 and 289.8 mm in the Mulga woodland and Corymbia savanna, respectively (approximately 8% below the long-term average). Monthly patterns and cumulative annual (August–July) rainfall in the first year of study were almost identical at the two sites (Fig. 1c). In contrast there was more rain earlier in the second hydrologic year (November 2013–February 2014) at the Corymbia savanna than the Mulga woodland, although annual totals for the two sites did not differ.

3.2. Water fluxes: evapotranspiration

Patterns in daily ET were similar across the two-year study at both sites (Fig. 2a) and closely followed those observed for rainfall. Daily ET at both sites was negligible during those periods when daily rainfall was zero for more than two weeks (e.g., August

![Figure 2. Daily (a) and cumulative (b) evapotranspiration (ET) in the Mulga woodland (solid line) and the Corymbia savanna (broken line).](image-url)
maximum rates of daily ET from the *Corymbia* savanna were either equal to or frequently larger (by up to approximately 80%) than those from the Mulga woodland (Fig. 2a). Summer total and maximum daily rates of ET were larger in the second summer than the first at both sites. As with rainfall, 73 and 88% of ET was lost from the Mulga woodland during the first and second monsoon seasons, respectively. Likewise in the *Corymbia* savanna, 71 and 91% of ET was lost during the respective monsoon seasons.

In both hydrologic years (August 2012–July 2014), patterns of cumulative ET were broadly similar at the two sites, but with a consistent difference in the total amount of ET (Fig. 2b). Moreover, the annual sum of ET was smaller for the Mulga woodland than the *Corymbia* savanna in both years. The annual total ET for the *Corymbia* savanna was 96 and 110% of annual rainfall in each year (2012–2013 and 2013–2014, respectively), but in the Mulga woodland the annual sum of ET was approximately 80% of total rainfall in both years (cf. Figs. 1c and 2b). Immediately following precipitation, there were larger pulses of ET from the *Corymbia* savanna than from the Mulga woodland (cf. Figs. 1c and 2a). These short imbalances were more prominent in the second year, when ET was 110% of precipitation in the *Corymbia* savanna.

**3.3. Carbon fluxes: net productivity and water-use efficiency**

In contrast to the very similar patterns in daily ET at both sites, patterns in daily NEP differed substantially between the two sites (Fig. 3a). During the winter and early spring (August–October) of 2012, the Mulga woodland was a small sink (NEP = 0.1 to 0.3 g C m\(^{-2}\) d\(^{-1}\)), but the *Corymbia* savanna was a moderate source for C (NEP = −0.6 to −0.3 g C m\(^{-2}\) d\(^{-1}\)). This pattern was repeated in the second winter/early spring (June–August 2013). The *Corymbia* savanna remained a moderate-to-strong source (NEP = −1.75 to 1.1 g C m\(^{-2}\) d\(^{-1}\)) in the second year.
−0.5 g C m⁻² d⁻¹) between November 2012 and January 2014, with the exception of a short period during June 2013 when the *Corymbia* savanna became C neutral (uptake equalled release) (Fig. 3a). The *Corymbia* savanna was a sink for C (maximum daily NEP = 1.5 g C m⁻² d⁻¹) for approximately 6 weeks in the summer of 2014 (late January to early March). The Mulga was a moderate-to-large C source for the spring and early summer of 2014 and became a moderate sink (maximum NEP = 0.75 g C m⁻² d⁻¹) in late summer and autumn of 2014 (Fig. 3a).

During summer in the *Corymbia* savanna, the pulse of productivity was rapid and large following the largest storm in the two years of study (> 100 mm in January 2014; cf. Figs. 1 and 3a), and this was due to the dominant cover of C₄ grasses (90%). By contrast in the Mulga woodland, productivity was limited during the summer, acting as a source for several weeks until late summer and early autumn of 2014 (Fig. 3a). In contrast, both sites were a C source in January 2013 (Fig. 3a). During this time, ecosystem respiration at

Figure 3. Daily (a) and cumulative annual (b) net ecosystem productivity (NEP) in the Mulga woodland (solid line) and the *Corymbia* savanna (broken line). Daily values are shown as the 3-day running average. Values of NEP that are larger than zero (dashed line) represent carbon uptake.
night was similarly small in the Mulga woodland and *Corymbia* savanna (Fig. 4).

However, during the sunlit hours, NEP diverged between the two sites. Even though the Mulga woodland was a net C source, small rates of NEP were observed in the morning before declining well before sundown (Fig. 4). By contrast, NEP declined during sunlit hours in the *Corymbia* savanna, illustrating that C losses were enhanced in the daytime (Fig. 4).

Cumulative annual NEP in both hydrologic years showed the *Corymbia* savanna to be a strong source (cumulative NEP = −197 and −131 g C m\(^{-2}\) y\(^{-1}\) for the first and second years, respectively; Fig. 3b). In contrast, the Mulga woodland was a small source (−26 g C m\(^{-2}\) y\(^{-1}\)) in the first hydrologic year but a small sink (12 g C m\(^{-2}\) y\(^{-1}\)) in the second year. It wasn’t until the occurrence of a wet summer that the Mulga woodland again became a moderate-to-strong sink (0.9 g C m\(^{-2}\) d\(^{-1}\)), although annual C uptake was considerably less than that observed in the 2010–2011 anomaly (12 versus 259 g C m\(^{-2}\) y\(^{-1}\)), reflecting the non-linear response of NEP to total annual rainfall in this system. The trend in cumulative NEP at the two sites diverged in early March 2014, with the *Corymbia* savanna reverting to a source for the remaining five months of the study and the Mulga continuing as a net sink (Fig. 3b).

In the *Corymbia* savanna, eWUE was negative (negative because respiratory loss exceeded photosynthetic C gain) for most of the two years of study (Fig. 5) and was more...
negative in the first hydrologic year than the second. Periods of very small positive or
slightly negative eWUE for the Corymbia coincided with the rainfall of November 2012–February 2013, May 2013 and January–March 2014. In contrast, the Mulga woodland
maintained near-zero values of eWUE in both years. In the Mulga woodland, eWUE
increased with time since rainfall during each year's autumn (March–May, Fig. 5).

3.4. Trends in enhanced vegetation index and foliar $^{13}$C stable isotope contents

MODIS EVI peaked at the study sites in five of 13 years since the launch of the
satellite: March 2000, April 2001, April 2007, March 2010 and March 2011 (Fig. 6). In a
given year, neither ecosystem
consistently responded to precipitation
with more production of green tissue
than the other (Fig. 6). While MODIS
EVI was generally larger in the Mulga
woodland than the Corymbia savanna,
two periods (2004 and 2010) when this
pattern was reversed are apparent (Fig.
6). Note that during the first year of this study (2012–2013), MODIS EVI values were the smallest on record for the Mulga woodland and as small as previous minima in the Corymbia savanna (2008, 2009).

In Acacia phyllodes, $\delta^{13}C$ values averaged $-27.9\%$ and did not differ substantially across the two sites and in the three habitats sampled within the Corymbia savanna. By contrast, $\delta^{13}C$ in Corymbia opaca leaves declined substantially across habitats (Fig. 7). Leaf $\delta^{13}C$ of the Corymbia trees declined in the sequence: Corymbia trees in the Mulga patch within the Corymbia savanna > Corymbia trees in the transition between the Acacia patch and open Corymbia savanna > Corymbia trees in the extensive open savanna (Fig. 7). Leaf $\delta^{13}C$ in Corymbia was less negative than in Acacia phylloide in the Mulga patch (Fig. 7).

4. Discussion

4.1. The 2011 anomaly and beyond

Although measurements were not initiated in the Corymbia savanna until after the conclusion of the land sink anomaly, C fluxes in subsequent years can only be explained within the context of the land sink anomaly. Several lines of field-based evidence support the conclusion (Le Quéré et al., 2014; Poulter et al., 2014) that Australian semi-arid vegetation had a major role in the large global land sink anomaly of 2011. First, our field-based studies of CO$_2$ fluxes in central Australia (Table 1; Eamus et al., 2013)
demonstrated that the Mulga woodland was indeed a large sink for C (2.6 t C ha$^{-1}$ y$^{-1}$, 259 g C m$^{-2}$ y$^{-1}$, Table 1) during that year (September 2010–August 2011; Eamus et al., 2013). This sink formed in response to a disproportionate increase in gross primary production (GPP, 7.9 t C ha$^{-1}$ y$^{-1}$, 793 g C m$^{-2}$ y$^{-1}$) relative to the moderate increase in ecosystem respiration (Cleverly et al., 2013a). Second, the largest value of EVI since 2000 was observed in hydrologic year 2010–2011 (Ma et al., 2013), which suggests as large a C sink in the *Corymbia* savanna as in the Mulga woodland due to the close correlation between EVI and GPP across Australia (Donohue et al., 2014; Ma et al., 2013; Ma et al., 2014). Third, 2010–2011 was identified as having the largest rates of ET in the Ti Tree basin since 1981 (Chen et al., 2014). Finally, the Gravity Recovery and Climate Experiment satellite data recorded significant increases in the amount of water stored across the Australian landmass in 2011 (Boening et al., 2012), coincident with the extremely large La Niña conditions that dominated weather across Australia in that year.

During the land sink anomaly of 2011, rainfall at our sites was almost double the long-term average (565 mm *versus* 320.7 mm, 1987–2014), resulting in very large rates of ecosystem productivity in the Mulga woodland (Eamus et al., 2013) and the *Corymbia* savanna (Fig. 6). Across a range of biomes, different combinations of rainfall, temperature, solar radiation and vapour pressure deficit are the principle determinants of NEP and GPP (Baldocchi, 2008; Baldocchi and Ryu, 2011; Kanniah et al., 2010; van Dijk et al., 2005; Zha et al., 2013). It is apparent that inter-annual differences in rainfall are the principle causes of interannual differences in sink strength for the Mulga woodland (Table 1), in strong agreement with multiple other arid and semiarid biomes (Barron-Gafford et al., 2012; Chen et al., 2014; Flanagan and Adkinson, 2011; Huxman et al., 2004; Ma et al., 2012) but in marked contrast to boreal forests, tropical montane forests, temperate mesic deciduous forests and tropical mesic savannas, where temperature, solar radiation and the
length of the growing season are the principal factors limiting NEP (Baldocchi, 2008; Dunn et al., 2007; Keenan et al., 2014; Luyssaert et al., 2007; Ma et al., 2013; Whitley et al., 2011; Zha et al., 2013). We now discuss the question: did this anomaly persist into 2012–2014 for our two study sites?

The productivity pulse of 2011 did not persist in either ecosystem following the conclusion of the land sink anomaly. Productivity declined in the Mulga woodland by July 2011, which was four months following the end of the summer rains (Cleverly et al., 2013a; Eamus et al., 2013), and the Mulga woodland was effectively C neutral (i.e., near zero within the limits of measurement uncertainty) in the three following years (2012–2014). The ratio of GPP to ecosystem respiration fell between 2011 and 2012, reflecting a two-fold decline in annual GPP (Cleverly et al., 2013a) and a four-fold decline in the seasonal peak of daily GPP (Ma et al., 2013). Similarly, there was little evidence of productivity in the Corymbia savanna during the first nine months of the current study (August 2012–May 2013). In pyrophytic landscapes such as the Corymbia savanna, large amounts of fuel can accumulate following very wet periods (King et al., 2013; Schlesinger et al., 2013). However, large rates of C loss from this biome during subsequent dry years imply a rapid loss of fuel load via photodegradation. Thus, Corymbia savannas that do not burn in the first few years following very wet conditions are less likely to burn thereafter.

4.2. Corymbia savanna versus Mulga woodland

In this section, we address the question: how do current behaviours of the Mulga woodland (in terms of CO₂ and water fluxes) compare to those of an adjacent, floristically different, Corymbia savanna?
Some of the ET excess in the *Corymbia* savanna in the second year of study (ET = 110% of precipitation) arose from precipitation that fell during the first year but contributed to second-year ET, while the remainder may illustrate the opportunistic use of groundwater by *Corymbia* trees in the open savanna during short periods of cloud cover, cool temperatures, and low VPD that accompany rainfall. What was perhaps surprising was the continued ET deficit in the Mulga woodland (about 80% of annual rainfall) in the very wet (2011) year (Eamus et al., 2013) and the subsequent the dry years, with little apparent use of water that was carried-over in soil storage. However, the abundant sunshine and soil moisture availability during the summer of 2013–2014 may suggest that ET was limited by stomatal responses to high temperature and large VPD (Cleverly et al., 2013b) rather than energy or water availability. Thus, recharge and discharge of soil moisture storage (and the ratio of ET to precipitation) vary on longer timescales than the scope of our measurements, in contrast to the intra-annual carry-over of water from the wet season into the cool season observed in North American drylands (Hastings et al., 2005).

The interplay between drought tolerance and resilience resulted in a near-neutral annual C balance in the Mulga woodland (Fig. 3 and Cleverly et al., 2013a), whereas the C cycle in the *Corymbia* savanna was dominated by large C losses (Fig. 3). Two reasons may be postulated to explain the difference in C balance of the two sites. First, *Acacia* has a suite of traits that are indicative of a high degree of drought tolerance compared to *Corymbia*: larger wood density, smaller specific leaf area (SLA, ratio of leaf area to leaf dry mass) and larger Huber value (ratio of sapwood cross-sectional area to leaf area) (O’Grady et al., 2009). Large wood densities are strongly correlated with enhanced resistance to xylem embolism, reduced soil-to-leaf hydraulic conductance and small transpiration rates (Wright et al., 2006; Zhang et al., 2009), while a small SLA correlates
with an ability to tolerate lower (more negative) canopy water potentials. As a result, small rates of productivity in the Mulga woodland were sufficient for maintaining C neutrality. Second, woody plants dominate the Mulga woodland, whereas the contribution of *Acacia* and *Corymbia* to the cover, basal area and LAI of the *Corymbia* savanna is small relative to the extensive C₄ grasses. We propose that the large amount of standing dead biomass in the *Corymbia* savanna (accumulated during the 2011 anomaly) was subject to physical fragmentation by photodegradation (i.e., in the presence of light, e.g. Fig. 4, and absence of soil moisture; Rutledge et al., 2010; Vanderbilt et al., 2008).

### 4.3. Ecosystem-scale water use efficiency (eWUE) and small-scale differences in foliar WUE (WUEᵢ)

By delaying production until the autumn of 2014, eWUE in the Mulga woodland was larger than in the *Corymbia* savanna. In addition to the traits of drought tolerance, which are correlated to large WUE, the large foliar N content of the nitrogen fixing *Acacia* allows for significant resource substitution, whereby larger-than-expected rates of photosynthesis can be sustained in arid environments through preferential allocations of nitrogen to Rubisco (Taylor and Eamus, 2008). When stomatal conductance and transpiration rates decline in response to large VPD, resource substitution results in large eWUE. Further, spatial variability in soil properties (especially the distribution of the hardpan) restricts soil moisture availability (Chen et al., 2014) and contributes to large values of eWUE in the Mulga woodland.

It is important to note that the eWUE of the Mulga woodland consistently showed that photosynthetic C uptake exceeded respiratory loss per unit ET during the early or late summer and autumn of both years, as previously observed by Eamus et al. (2013). The very low values of eWUE in the *Corymbia* savanna imply that C source strength was
maintained regardless of moisture status, thus eWUE became much more negative during dry periods than eWUE in the Mulga woodland (Fig. 5). These predominantly large, negative values of eWUE (respiration exceeds C gain per unit ET) in the Corymbia savanna are further symptomatic of photodegradation. Despite the differences in eWUE between ecosystems and the plants that co-exist in them, eWUE in the Mulga woodland and the Corymbia savanna showed large fluctuations between wet and dry periods that reflected differences in the moisture requirements of photosynthesis, autotrophic and microbial respiration and photodegradation.

In leaves of Corymbia across all three habitats, declining leaf $\delta^{13}C$ represents increased access to water and declining WUE$_i$ (Leffler and Evans, 1999; Zolfaghar et al., 2014) and has been previously used to infer access to groundwater (Zolfaghar et al., 2014). We interpret this as reflecting an increasing rooting depth of Corymbia trees within the Corymbia savanna when moving into the extensive open savanna from the Mulga patch. The potential for groundwater access by deeply rooted Corymbia in the extensive savanna, where groundwater depth is approximately 8 m, is presumably large and may explain the lower WUE$_i$ of Corymbia, while the presence of an inferred hardpan within the Mulga patch prevents access to the water table and hence an increased WUE$_i$ for Corymbia within the Mulga patch. The absence of any significant change in phyllode $\delta^{13}C$ for the Acacia at any of the three locations within the Corymbia savanna reflects the shallow rooting habit of Acacia (Pressland, 1975). More importantly, there was no difference in foliar $^{13}C$ content of Acacia sampled from the Mulga woodland where groundwater depth is known to exceed 50 m, further supporting the conclusion that access to groundwater by Mulga within the Corymbia savanna is not occurring. The low values of $\delta^{13}C$ in Acacia phyllodes are consistent with their anisohydric stomatal responses to soil
drying; that is, their stomata remain open even at very low water potentials (O'Grady et al., 2009; Winkworth, 1973).

5. Conclusions

We have demonstrated that the large 2011 anomaly in terrestrial C uptake was short-lived in the arid zone of central Australia. In the Mulga woodland, storage of soil moisture within the root zone contributed to C neutrality (i.e., C sources were equivalent to sinks) in the subsequent drier-than-average years by facilitating the delayed response of productivity to precipitation. We also demonstrated that productivity in the Mulga woodland was larger than that of the Corymbia savanna in the drier-than-average years of the study and attributed this to the multiple drought tolerant attributes and the larger potential for resource substitution of Acacia compared to Corymbia. Drought tolerance in the Mulga woodland further restricted ET to 80% of precipitation in each year since 2010, indicating that variations in soil moisture storage occur over very long timescales. In contrast, ET from the Corymbia savanna was larger than precipitation in the near-average rainfall year, illustrating that groundwater use by Corymbia occurred opportunistically during wet periods. However, the Corymbia savanna was a strong source of CO₂ in drier-than-average and near-average years due to photodegradation of the extensive grassy understorey. Finally, we demonstrated that ecosystem water-use efficiency was larger in the Mulga woodland than in the Corymbia savanna, while differences in leaf/phyllode δ¹³C between Acacia and Corymbia reflected differential access to groundwater and the different rooting characteristics of these two tree species.
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7. References


8. Legends

Table 1. Summary of rainfall and net ecosystem productivity (NEP) for four years of study at the Mulga woodland. Data for 2010–2012 from Eamus et al. (2013) and Cleverly et al. (2013a).

Figure 1. Daily (a, b) and cumulative (c) precipitation in the Mulga woodland (a, solid line c) and the Corymbia savanna (b, broken line c).

Figure 2. Daily (a) and cumulative (b) evapotranspiration (ET) in the Mulga woodland (solid line) and the Corymbia savanna (broken line).

Figure 3. Daily (a) and cumulative annual (b) net ecosystem productivity (NEP) in the Mulga woodland (solid line) and the Corymbia savanna (broken line). Daily values are shown as the 3-day running average. Values of NEP that are larger than zero (dashed line) represent carbon uptake.

Figure 4. Daily cycle of NEP. Values represent hourly average ± standard error (s.e.) during January 2013.

Figure 5. Daily ecosystem water use efficiency (eWUE). Values were determined as NEP/ET and shown for days when ET > 0.2 mm d⁻¹. Values above zero (dashed line) represent photosynthetic eWUE, while increasingly negative values of eWUE represent increasing values of respiratory eWUE.

Figure 6. MODIS enhanced vegetation index (EVI) as a four-month running average.

Figure 7. Carbon stable isotope ratio (δ¹³C) of Acacia (squares) and C. opaca (circles) leaves in the Mulga woodland and across three habitats (Mulga patch, open savanna, transition) within the Corymbia savanna. Symbols show mean ± s.e.