

# Satellite-derived estimates of forest leaf area index in southwest Western Australia are not tightly coupled to interannual variations in rainfall: implications for groundwater decline in a drying climate

KEITH R. J. SMETTEM\*, RICHARD H. WARING†, JOHN N. CALLOW‡, MELISSA WILSON\* and QIAOZHEN MU§

\*Centre for Ecohydrology, School of Environmental Systems Engineering, University of Western Australia, Nedlands, WA 6009, Australia, †Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR 97331-5704, USA, ‡School of Earth and Environment, University of Western Australia, Nedlands, WA 6009, Australia, §Numerical Terradynamics Simulation Group, University of Montana, Missoula, MT 59812, USA

## Abstract

There is increasing concern that widespread forest decline could occur in regions of the world where droughts are predicted to increase in frequency and severity as a result of climate change. The average annual leaf area index (LAI) is an indicator of canopy cover and the difference between the annual maximum and minimum LAI is an indicator of annual leaf turnover. In this study, we analyzed satellite-derived estimates of monthly LAI across forested coastal catchments of southwest Western Australia over a 12 year period (2000–2011) that included the driest year on record for the last 60 years. We observed that over the 12 year study period, the spatial pattern of average annual satellite-derived LAI values was linearly related to mean annual rainfall. However, interannual changes to LAI in response to changes in annual rainfall were far less than expected from the long-term LAI-rainfall trend. This buffered response was investigated using a physiological growth model and attributed to availability of deep soil moisture and/or groundwater storage. The maintenance of high LAIs may be linked to a long-term decline in areal average underground water storage and diminished summer flows, with an emerging trend toward more ephemeral flow regimes.

**Keywords:** baseflow, climate change, ecohydrology, evapotranspiration, leaf area index, water balance

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## Introduction

In regions of the world where droughts are predicted to increase in incidence and severity as a result of climate change, there is increasing concern over the potential for widespread forest decline (Choat *et al.*, 2012). It has been widely reported that southern Australia is experiencing an extended period of drought, with southwest Western Australia experiencing significant declines in rainfall since the mid-1970s (Power *et al.*, 2005; Murphy & Timbal, 2007; Bates *et al.*, 2008).

There has been an observed decrease in both the frequency of daily precipitation and wet-day amounts. This decline in regional precipitation is strongly associated with a marked decrease in moisture content in the lower troposphere, an increase in regionally averaged sea level pressure in the first half of the season, and intraseasonal changes in the regional north–south sea level pressure gradient (Bates *et al.*, 2010). Runoff into Perth's surface water supply catchments (20 km inland

from the coast, directly inland from Perth, Western Australia) has decreased by 50% (since 1975) following a 16% reduction in rainfall (Silberstein *et al.*, 2012).

Across the forested water supply catchments of the Darling Plateau, declining rainfall has led to a shift from perennial to ephemeral streams (Bari & Smettem, 2004). A decrease in the annual runoff coefficient (runoff/rainfall) in the last decade suggests that a new hydrologic regime has developed with important implications for future surface water supply to Perth (Petrone *et al.*, 2010; Hughes *et al.*, 2012). The identified synoptic influences on declining rainfall have a regional extent, so forested catchments across the entire southwest of Western Australia may also experience declining rainfall and hence, declines in runoff. Modeled scenarios using input from 15 Global Climate Change Models (GCMs) are also projecting further declines in surface runoff (Silberstein *et al.*, 2012) and lower groundwater levels for forested catchments by 2030 (Ali *et al.*, 2012).

At intermediate spatial scales ( $\approx 1000 \text{ km}^2$ ) when the dominant limitation to plant growth is water, the leaf

Correspondence: Keith R. J. Smettem, tel. +61864881692, fax +61864881015, e-mail: smettem@sese.uwa.edu.au

area of native vegetation is tightly coupled to moisture availability and adjusts in a dynamic fluctuation with it (Nemani & Running, 1989). This suggests a 'steady-state' or ecohydrologically optimal condition in undisturbed ecosystems supporting perennial vegetation (Eagleson, 1982, 2002). This is an integrated response to the processes that affect the availability of water (Donohue *et al.*, 2007), with the canopy size adjusted to relative mean soil water concentration (Eagleson & Tellers, 1982). Indeed, it is common for ecologists to map the distribution of biomes, vegetation cover, and types on the basis of mean annual rainfall (MAR) and mean annual temperature (Bonan, 2002).

Leaf Area Index (LAI) is defined as the projected (one-sided) leaf area ( $\text{m}^2$ ) per unit ground area ( $\text{m}^2$ ) and is the main determinant of light interception and transpiration by vegetation (Landsberg & Waring, 1997). In support of ecological optimality, Palmer *et al.* (2010) related maximum LAI as measured by the Moderate Resolution Imaging Spectroradiometer (MODIS; collection 5 product) with the aridity index (UNEP, 1997) (calculated as long-term average annual rainfall divided by long-term class 'A' pan evaporation). Earlier, Ellis & Hatton (2008) showed that the average long-term LAI is also related to the aridity index. O'Grady *et al.* (2011) demonstrated that LAI is elevated for terrestrial ecosystems with access to fresh groundwater (groundwater-dependent ecosystems). In effect, the amount by which the LAI overshoots the established LAI to climate index relationship of Ellis & Hatton (2008) can be considered as an indicator of groundwater or stored soil moisture used by native ecosystems.

The dry sclerophyll evergreen forests of southwest Western Australia cover an area of about 1.6 Mha. The climate is Mediterranean, with dominant winter rainfall (about 78% of annual rainfall occurs between April and September) followed by hotter and drier summers. Hopper (1979) reports that in the high rainfall zone (800–1400 mm MAR), the dominant overstorey species are Jarrah (*Eucalyptus marginata*), Karri (*E. diversicolor*), and Marri (*E. Calophylla*). Relative to other eucalypt forests, it is low in many nutrients, especially N and P (Grierson & Adams, 2000) and has a particularly deep-rooted habit, with maximum root depths of over 30 m for some species (Canadell *et al.*, 1996). Water uptake by deep roots over the dry summer period may significantly buffer LAI response to interannual variations in rainfall. However, maintenance of high LAI by accessing water sources other than annual rainfall (i.e., groundwater and deep unsaturated zone soil moisture stores) is not sustainable. This may lead to diminishing baseflow and more ephemeral summer flows in a drying climate at a multiannual to decadal timescale. Over

the longer term, when the water source sustaining the high LAI is exhausted, there must be an adjustment to a lower value. In some cases, the adjustment to lack of water supply can occur dramatically as 'drought death' (Allen *et al.*, 2010). Harper *et al.* (2009) showed that deaths in bluegum (*E. globulus*) plantations were associated with 'mining' and then exhaustion of legacy soil water stores created by historically elevated recharge under pastures prior to plantation establishment. The response of these silvicultural systems may provide an analog for the potential response in native ecosystems.

In this article, we derived data from the MOD16 algorithm of Mu *et al.* (2011) at a resolution of ca.  $1 \text{ km}^2$  to investigate the extent to which interannual variations of LAI across a number of forested catchments along the southwest coast of Western Australia are coupled to annual variations in rainfall over the period 2000–2011. We then use the forest growth model 3PG (Landsberg & Waring, 1997; Landsberg *et al.*, 2003) to investigate the sensitivity of long-term monthly evapotranspiration to available water storage. Finally, we comment on the possible link between forest transpiration and observed declines in summer baseflows from these catchments.

## Materials and methods

### Preparation of spatial datasets

The study area included six, gauged and extensively forested catchments in southwest Western Australia, spanning the 600–1200 mm annual rainfall zone (Fig. 1). Proportion clearing (%) reported in Table (1) was calculated using a composite Landsat 7 mosaic from 2000 for southwest Western Australia, classified to a remnant vegetation coverage using a density slicing approach (Bennett, 1987; Johnston & Barson, 1993). For one of the catchments (Warren River), the area of cleared farmland in the upper catchment was excised. Using three gauging stations (two cleared upstream tributaries [Western Australian Department of Water (DoW) Stn: 607004 & 607007] and one downstream [DoW Stn: 607220]), we calculate monthly runoff (mm) from streamflow data (DoW, unpublished results) for the forested area only, along with the other five forested catchments. Monthly rainfall data (Bureau of Meteorology, unpublished data) for open stations in this region were converted into a spatial dataset via regularized splines, produced at the same  $1 \text{ km}^2$  grid as the Moderate Resolution Imaging Spectroradiometer (MODIS) evapotranspiration products. Leaf Area Index (LAI) and predicted plant evapotranspiration (AET) were derived from the improved (2011) MOD16 Global Terrestrial Evapotranspiration Data Set of Mu *et al.* (2007, 2011).

For each catchment, the spatially mapped water balance components over the study period 2000–2011 (Rainfall, MODIS LAI and MODIS ET) were analyzed by sampling and then 'binning' and averaging of point raster values using automated Python scripts utilizing the ArcGIS10 GeoProcessor



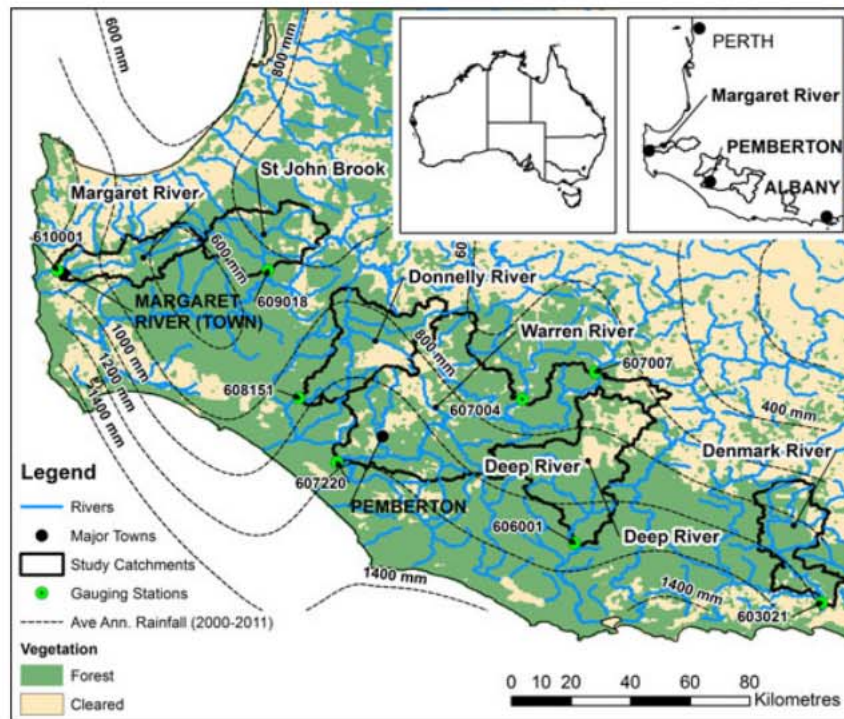


Fig. 1 Location of study catchments and gauging stations in southwest Western Australia.

Table 1 Characteristics of the study catchments

	Area (km <sup>2</sup> )	Percent forest (%)	Mean annual rainfall (2000–2011) (mm)	Mean annual runoff (2000–2011) (mm)	Rain runoff (mm)	Runoff coefficient
Denmark river	663.2	80.6	887.5	50.1	837.4	0.056
Deep river	983.1	80.5	879.3	23.8	855.5	0.027
Warren river*	2394.9	78.8	867.7	54.7	813.0	0.063
Donnelly river	782.1	77.9	712.5	75.3	637.2	0.106
Margaret river	443.0	67.8	789.6	114.5	675.1	0.145
St John's brook	552.3	84.0	659.1	44.3	614.8	0.067

\*Forested reach only.

Toolbox. For the Warren River forested section, MODIS LAI was also stratified by rainfall zone (600–800, 800–1000, and 1000–1200 mm), with monthly LAIs obtained from averages of about 800, 1 km<sup>2</sup> grid values per zone.

#### Structure and parameterization of the 3-PG stand growth model

To evaluate the central hypothesis that the LAI approaches a balance with the availability of soil water in drought-prone areas, we utilized a process-based model, 3-PG (Physiological Processes Predicting Growth) developed by Landsberg & Waring (1997). 3-PG, like other process-based models, is driven by a common suite of climatic variables and environmental constraints placed on photosynthesis, water use, and nutrient cycling associated with soil properties, and ecosystem

structure (see reviews by Mäkelä *et al.*, 2000; Constable & Friend, 2000; Nightingale *et al.*, 2004).

The model contains a number of simplifying assumptions that have emerged from studies conducted over a wide range of forest types. One of the most controversial but useful simplifications is that plant (autotrophic) respiration is assumed to be ca. 50% of gross photosynthesis (Landsberg & Waring, 1997; Waring *et al.*, 1998; Law *et al.*, 2001).

The model works as follows: each month, absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation and modeled predictions of leaf area index (LAI). The product of APAR and light-conversion (quantum) efficiency of photosynthesis represents the upper limit on gross photosynthesis. The utilized portion of APAR, however, is usually less than the potential, so in modeling, APAR is generally reduced by an amount determined by a series of

environmental modifiers that take values between 0 (system 'shutdown') and 1 (no constraint) that reflect the degree to which gas exchange via canopy stomatal conductance is limited (Landsberg & Waring, 1997).

For environments that do not experience freezing, the monthly modifiers are as follows: (i) averaged daytime atmospheric humidity deficits; (ii) soil water deficits; and (iii) deviation from suboptimal temperature defined for a particular taxon. Drought limitations are imposed as a function of soil properties and a simple water balance that calculates when the available soil water is less than transpiration estimated with the Penman Monteith equation. Each month, the most limiting climatic variable on photosynthesis is selected, based on departure from conditions that are optimum. The fraction of production not allocated to roots is partitioned among foliage, stem, and branches based on allometric relationships and knowledge of annual leaf turnover (Landsberg *et al.*, 2003). The fraction of production going to roots ranges from 25% on the most fertile soils to 80% on the least fertile. Rooting depth is not a parameter in the model, which permits estimates of maximum available water storage capacity (max ASW) to vary widely unless soils are very shallow. Sharma (1984) reports that native eucalyptus forest in the wettest part of our study area has rooting depths of at least 6 m.

The outputs from 3-PG can be either monthly or annual values. In this study, we restrict our analysis with 3-PG to assess max ASW required to generate ET that matches the average monthly values of MODIS ET after a slight monthly adjustment (13%) to match the MAR-runoff (2000–2011) for the forested section of the Warren River catchment. We used this catchment as a test case because the long-term meteorological station at Pemberton is located within the catchment. We then proceed to match MODIS-derived estimates of averaged annual LAI for climatic conditions characteristic of different parts of the Warren River Catchment where mean annual precipitation from 2000 to 2011 averaged 700, 900, and 1100 mm. To match average annual LAI values acquired from MODIS for the three values of annual precipitation, we adjusted the values of soil fertility (FR) and canopy quantum efficiency in each model run over a narrow range (Table 2). As mentioned in the introduction, native soils in this region are generally very infertile, particularly when compared with intensively managed plantations (Stape *et al.*, 2004). The midpoint alpha ( $0.034 \text{ mol mol}^{-1} \text{ PAR}$ ) is the same value applied across a wide array of native eucalyptus forests in eastern Australia by Coops *et al.* (1998).

We parameterized 3-PG for *E. globulus* based largely on values derived by Sands & Landsberg (2002) (Table 2). We recognize that *E. globulus* does not grow naturally in Western Australia, but native species in this region have yet to be adequately parameterized for the model (ref: Paul *et al.*, 2007). The Sands and Landsberg parameterization of 3-PG, developed for short-lived plantation trees, required modification in the allometric equations to maintain a stable average LAI characteristic of native forests grown under similar climatic conditions for long periods (Waring, 1983; Coops *et al.*, 1998). We also increased the LAI at which maximum canopy conductance is attained from 3.3 to 5.0, based on data presented by Granier *et al.* (2000).

**Table 2** 3-PG parameters for *Eucalyptus globulus* follow those described by Sands and Landsberg (2002) except for foliage stem partitioning ratios and LAI at maximum canopy conductance

Parameters	Units	Values
Allometric relationships and partitioning		
Foliage : stem partitioning ratio @ diameter = 2 cm		0.8
Foliage : stem partitioning ratio @ diameter = 20 cm		0.5
Constant in the stem mass vs. diam. relationship		0.095
Power in stem mass vs. diam. relationship		2.4
Litterfall and root turnover		
Maximum fraction of NPP to roots		0.8
Minimum fraction of NPP to roots		0.25
Maximum litterfall rate	1 month <sup>-1</sup>	0.027
Average monthly root turnover rate	1 month <sup>-1</sup>	0.015
NPP and conductance modifiers		
Soil fertility for clay loam as fraction of maximum		0.10 0.15
Minimum temperature for photosynthesis	°C	8
Optimum temperature for photosynthesis	°C	16
Maximum temperature for photosynthesis	°C	40
Soil moisture ratio deficit when uptake = 0.5 max		0.5
Power of moisture ratio deficit		5
Canopy structure and processes		
Specific leaf area	m <sup>2</sup> kg <sup>-1</sup>	4
Maximum canopy conductance	m s <sup>-1</sup>	0.02
Leaf area index at maximum canopy conductance	m s <sup>-1</sup>	5.0
Canopy boundary layer conductance	m s <sup>-1</sup>	0.2
Canopy quantum efficiency	mol C per mol PAR	0.027 0.040
Production and respiration		
Ratio NPP/GPP		0.47
Stemwood density	Mg m <sup>-3</sup>	0.45

In the simulations, we assigned an average soil texture of clay loam, estimated from regional soil hydrology groups documented by Moore *et al.* (1998). The soils were also classified as infertile (Grierson & Adams, 2000), receiving a rank between 0.1 and 0.15 of that applied to the most fertile intensively managed plantation sites (Stape *et al.*, 2006). In a direct coupling of FR to canopy quantum efficiency, we varied the latter from 0.027 to  $0.04 \text{ mol C mol}^{-1} \text{ photon}$  (1.48 2.2



g C/MJ APAR) to be representative of native forests (Landsberg & Waring, 1997). Litterfall rates were set as a constant 0.027 per month ( $0.33 \text{ yr}^{-1}$ ) of the total LAI, which is close to values recorded by Pook (1984); we recognize that in few months, the rates will greatly exceed this value (Pook, 1984), and would, if predictable, improve model performance (Siqueira *et al.*, 2006).

#### *Climatic data used for 3PG simulations*

We chose Pemberton, WA (BoM Station No. 9295) as a representative weather station for the wetter part of the Warren River Basin and averaged monthly mean temperature extremes and means as well as precipitation for the decade 2000–2010 (Table 3). Monthly mean solar radiation data for Pemberton were obtained from a website: <http://www.energymatters.com.au/>. We compared these against modeled values based on monthly variation in temperature for a given latitude and elevation and found near 1 : 1 correspondence (Coops *et al.*, 2000; but see Almeida & Landsberg, 2003). Mean monthly vapor pressure deficits (VPD) were calculated by assuming that dew point was reached at the minimum temperature and that the average deficit was 50% of the deficit at the maximum temperature. This is a conservative estimate, first because dewpoint may not be reached at the minimum temperature in months with low precipitation, and secondly, because the deficit during daylight hours when stomata are most sensitive is closer to 2/3th of the maximum value than to half (Almeida & Landsberg, 2003).

To determine whether there was an upward trend in vpd as precipitation decreased, we compared mean monthly values recorded at 15:00 hours at Pemberton ( $1186 \text{ mm yr}^{-1}$ ), Bridgetown ( $824 \text{ mm yr}^{-1}$ ), and Rocky Gully ( $691 \text{ mm yr}^{-1}$ ) and found no trend (Average SD =  $0.054 \text{ kPa}$ ), with values for Pemberton falling consistently between those of the other two stations.

A rainfall anomaly plot for the Pemberton weather station is shown in Fig. 2. In the first 35 years of the record, there

were 62% positive anomalies, but this declined to 43% over the last 35 years. Furthermore, there were six positive anomalies greater than 20% prior to 1975 and only one post 1975.

Since 1941, there has been a weak but significant decline in rainfall described by linear regression as:

$$\text{Annual Rf (mm)} = -2.91x + 6947 \quad (r^2 = 0.10 \quad P = 0.008) \quad (1)$$

where  $x$  is calendar year.

Decline in rainfall at Pemberton since 1975 is about 8%, which is only half of that reported by Silberstein *et al.* (2012) for the more northerly Darling Range catchments.

The 10 year running mean (Fig. 2) indicates that the declining trend was most pronounced from the mid-1950s to mid-1980s, but has recovered somewhat to more average conditions since that time.

#### *Analysis of low summer flows over time*

Baseflow refers to the portion of streamflow discharged from shallow groundwater, in a nonrecharge period (Brutsaert & Sugita, 2008). It can also be called low flow, sustained flow, dry-weather flow, or fair-weather flow.

An initial screening of annual dry season (January–April) flows over time was performed for each catchment. For the Warren catchment, we used the forested reach only. Trends were identified by linear regression, with  $P$  values determined at 95% confidence. The Jarque Bera (JB) test was used to test for normality of the regression residuals (Hill *et al.*, 2011). The test uses skewness,  $s$ , and kurtosis,  $k$ , to test the hypothesis that the residuals are from a normal distribution

$$JB = \frac{n}{6} s^2 + \frac{1}{4} (k - 3)^2 \quad (2)$$

In the case of a normal distribution, the JB statistic asymptotically has a chi-squared distribution with two degrees of freedom.

**Table 3** Mean monthly climatic data (2000–2010) derived from weather station No. 9592 at Pemberton, WA (Lat.  $34.4^\circ\text{S}$ , Long.  $116.0^\circ\text{E}$ , Elev. 174 m)

Month	Precip. mm	% annual precip.	Tmax $^\circ\text{C}$	Tmin $^\circ\text{C}$	Tav. $^\circ\text{C}$	Vapor pressure deficits mBar	Rad. MJ $\text{m}^{-2} \text{ day}^{-1}$
Jan	24.3	2.1	25.9	13.2	19.6	9.1	26.2
Feb	19.5	1.7	26.5	13.8	20.1	11.7	23.1
Mar	34.5	2.9	25.4	12.8	19.1	10.9	19.0
Apr	82.0	7.0	21.8	11.2	16.5	7.9	12.9
May	130.4	11.1	19.6	10.1	14.8	6.5	9.8
Jun	175.9	14.9	16.7	8.0	12.3	5.2	8.2
Jul	190.8	16.2	15.7	7.2	11.5	4.8	8.6
Aug	175.3	14.9	16.1	7.4	11.8	5.0	11.4
Sep	161.6	13.7	17.0	8.1	12.6	5.3	15.1
Oct	76.9	6.5	19.1	9.3	14.2	6.4	19.7
Nov	69.2	5.9	22.3	10.9	16.6	8.6	24.6
Dec	38.3	3.3	24.1	11.8	18.0	10.1	26.8
Sum or Average	<b>1178.7</b>	<b>100</b>	<i>20.9</i>	<i>10.3</i>	<i>15.5</i>	<i>7.6</i>	<b>6239</b>

Average values are in *italics* and sum of values are in **bold**.

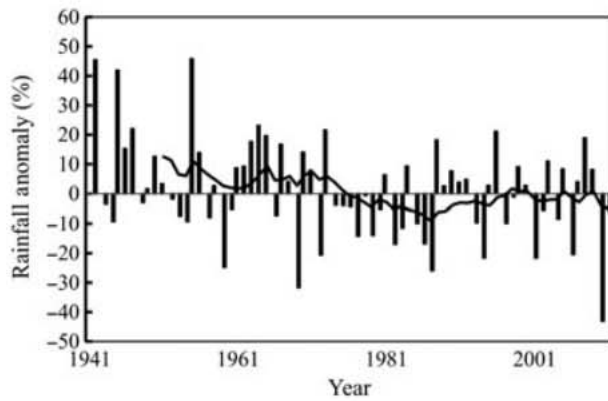


Fig. 2 Rainfall anomaly plot for Pemberton using a base 1961–1990 average. Solid line is the 10 year moving average.

Changes to the annual baseflow trend over time can be used to derive the trend in areal average underground storage ( $S$ ) in a catchment using (Brutsaert, 2012)

$$S = Ky \quad (3)$$

where  $K$  is a characteristic drainage timescale, also referred to as the storage coefficient,  $y = Q/A$ , the rate of flow of the stream per unit catchment area [ $\text{LT}^{-1}$ ],  $Q = Q(t)$ , the volumetric rate of flow in the stream [ $\text{L}^3\text{T}^{-1}$ ], and  $A$  is the area of the basin [ $\text{L}^2$ ].

To provide a robust measure for  $y$  that best reflects the annual value for basin storage, Brutsaert (2008, 2012) proposed use of the lowest 7 days daily mean flow,  $y_{L7}$ . Brutsaert (2012) provides detailed justification for setting  $K = 45$  days and we adopt this operational value in this study. As noted by Brutsaert (2012), it is the sign and significance of the trends that are of significance and not their exact values.

## Results

### MODIS LAI trends

A map of average MODIS LAI values over the study period is shown in Fig. 3.

Leaf Area Index values for the forested region decline away from the coast, following the rainfall gradient. There is also a slight decline in the more westerly catchments of Margaret River and St John's Brook that have lower MARs (Table 1). Measured LAI values for the southwest forests (Hill *et al.*, 2006) are within the range of the MODIS data reported here (Table 4).

Average annual rainfall for each of the three rainfall zones in the Warren River catchment over the study period is shown in Fig. 4. There is no evidence of rainfall decline over this period, but there is high interannual variability. In the 1000–1200 mm zone, the highest annual rainfall was 1350 mm in 2008 and the lowest was 663 mm in 2010.

The monthly patterns for MODIS LAI presented in Fig. 5 show no overlap between the three precipitation zones. The two drier zones, however, are more sensitive to variation in annual precipitation than in the wettest zone, particularly during droughts in April 2001, July 2007, and April 2010 followed by the recovery associated with increasing precipitation in 2011. If interannual LAI response was tightly coupled to annual rainfall, then for the drought year of 2010 (663 mm annual rainfall in the 1000–1200 mm rainfall zone), the maximum LAI in the 1000–1200 mm zone might be

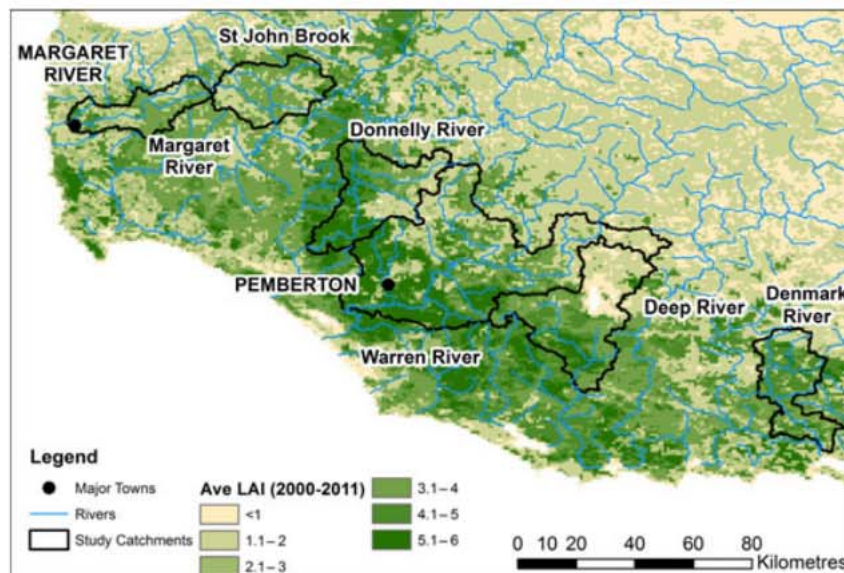


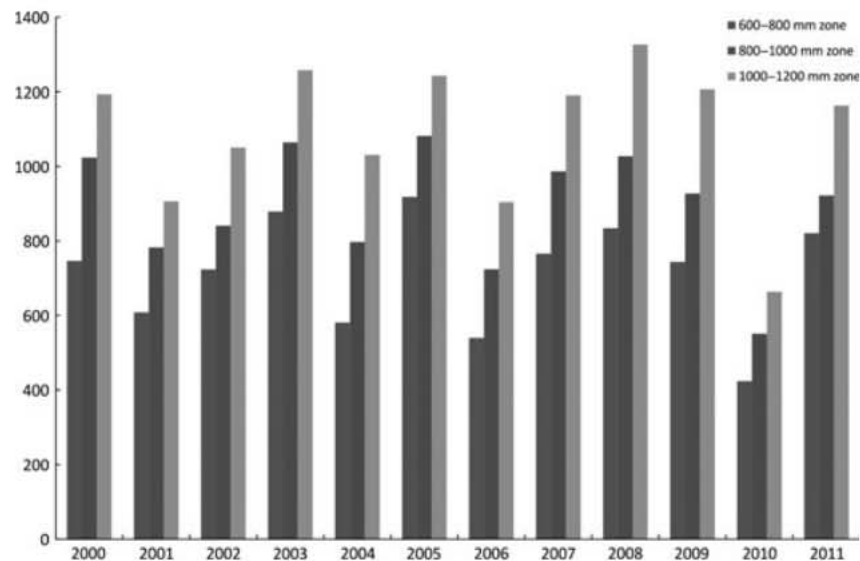
Fig. 3 Average Annual Moderate Resolution Imaging Spectroradiometer leaf area index (MODIS LAI) over the study period (2000–2011).



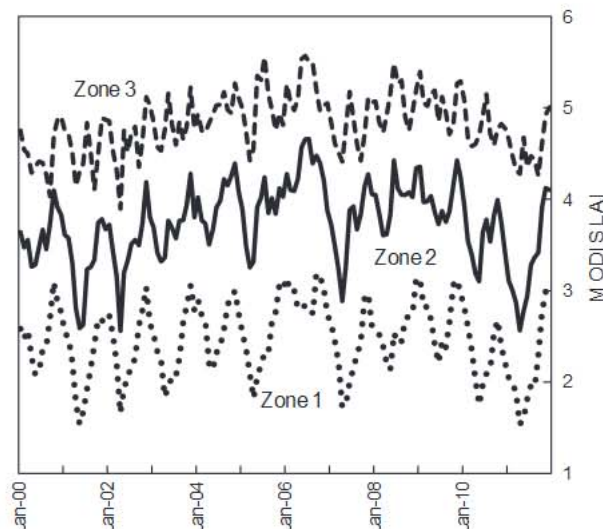
**Table 4** Summary of studies with measured leaf area index (LAI) in southwest WA Forests and Plantations (Hill *et al.*, 2006) compared with Average MODIS LAI (2000–2011) at these locations

Location	Species	Measured LAI	MODIS LAI*
Pemberton	<i>Eucalyptus Diversicolor</i> , <i>E. calophylla</i>	4.2	5.1 (4.1–5.5)
Manjimup	<i>E. globulus</i> 1991–1993	2.7–3.8	3.8 (3.4–4.3)
Hilton	<i>E. globulus</i>	2.7–4.6	3.2 (2.5–3.7)
Bunbury	<i>E. globulus</i> (6–8 years old)	2.3–5.3	3.2 (2.5–3.7)

\*Values in parentheses are (moderate resolution imaging spectroradiometer) MODIS<sub>max</sub> and MODIS<sub>min</sub>, respectively.



**Fig. 4** Annual rainfall over the three rainfall zones in the Warren River Catchment.



**Fig. 5** Monthly moderate resolution imaging spectroradiometer leaf area index (MODIS LAI) averaged across all grid cells in each mean annual rainfall zone in the Warren River Catchment. Zone 1: 600–800 mm; Zone 2: 800–1000 mm; Zone 3: 1000–1200 mm.

expected to decline to the maximum value observed in the 600–800 mm zone, but this does not occur (Fig. 5). The 2010 average LAI in the highest rainfall zone was 4.78, which is considerably higher than the long-term regional average LAI of 3.85 for the 600–800 mm zone. SE bars (not shown) typically average  $\pm 0.6$  LAI, largely reflecting the procedure of averaging over 200 mm rainfall classes.

In Fig. 5, the 1100 mm isobar of annual precipitation, equivalent to an equilibrium LAI of 4.8, is the most buffered of the three cases in response to interannual variation in precipitation and has an apparent second flush in greenness in most years, which can occur under nonwater limiting conditions in eucalypts exhibiting indeterminate growth. The 900 and 700 mm isobar classes have progressively lower LAI values and a more distinct seasonal leaf turnover, characterized by the difference between the LAI<sub>max</sub> and LAI<sub>min</sub> values each year. For the 11 years of record, average annual values of LAI<sub>ave</sub>, LAI<sub>max</sub>, and LAI<sub>min</sub> were stratified into 100 mm rainfall classes across all the forested catchments. These long-term average LAIs exhibit a linear

relation to rainfall, from 600 mm up to about 1150 mm and then appear to plateau (Fig. 6).

Linear regression of the average annual MODIS LAI (2000–2011), (denoted MODIS<sub>average</sub> LAI) vs. MAR (Fig. 6) gives

$$\text{MODIS}_{\text{average}}\text{LAI} = 0.003 \text{ MAR} + 1.86 \quad (r^2 = 0.98) \quad (4)$$

where MAR is the mean annual rainfall (2000–2011).

The lack of a strong LAI response to interannual changes in rainfall is a good indication that the forests are accessing deep moisture reserves or groundwater to buffer the water deficit (Thompson *et al.*, 2011). We investigate this further using 3PG.

### 3-PG Simulations

Initially, we ran the 3-PG model using climatic data presented in Table 3 for the weather station at Pemberton, WA with the parameters listed in Table 2. We reduced the MAR of 1178.7 mm at Pemberton to the value reported for the Warren River forested section (867.7 mm in Table 1) and reduced average monthly values by a similar proportion. We then varied the values of maximum available soil water storage capacity (ASW) over a wide range from 200 to 1000 mm to determine what value produced monthly estimates of evapotranspiration (ET) that most closely corresponded to monthly ET derived from MODIS, after slight scaling to match the recorded precipitation and stream-gauged runoff for the forested reach of the Warren River from 2000–2011 (Fig. 7).

We applied the same approach to estimating max ASW for eucalyptus forests that fell within the three broad bands of mean annual precipitation (1100, 900,

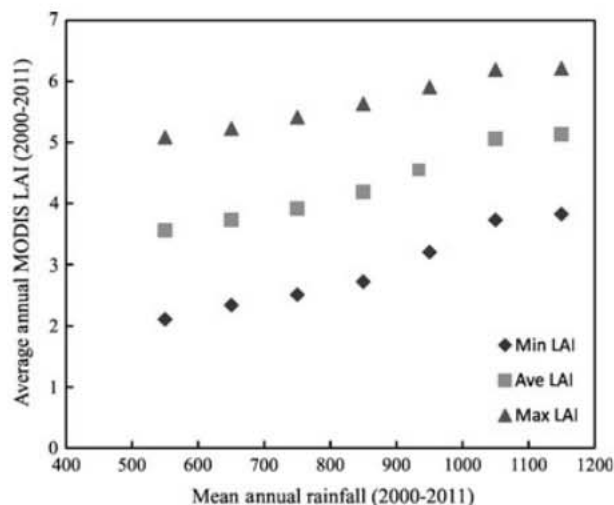


Fig. 6 Average values of moderate resolution imaging spectroradiometer leaf area index (MODIS LAI)<sub>ave</sub> □; LAI<sub>max</sub> △; and LAI<sub>min</sub> ◇ across all forested catchments for 100 mm rainfall zone stratification.

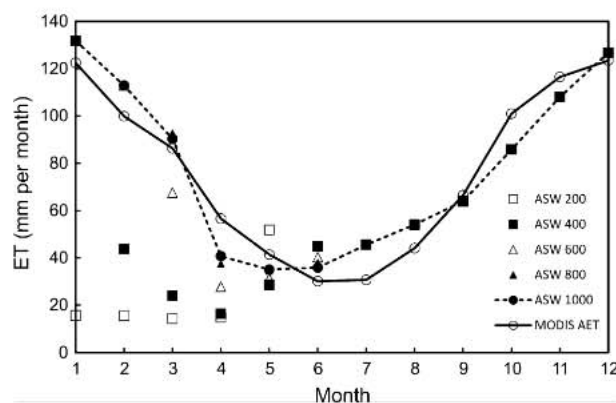


Fig. 7 Simulated evapotranspiration (ET) using 3PG with different values of maximum available soil water storage capacities (ASW) compared with moderate resolution imaging spectroradiometer (MODIS AET) for the Warren river forested section.

and 700 mm) with corresponding mean average MODIS LAI values. All simulations were initiated with seedlings planted at a density of 1000 stems ha<sup>-1</sup> and run for a period of 20 years. At this planting density, LAI approached a plateau within 5 years. The self-thinning routine was turned off, as was an age constraint related to hydraulic restrictions as trees slow in height growth (Waring & Landsberg, 2011).

To assess the extent that FR and canopy quantum efficiency (alpha) might vary across the precipitation gradient, we set max ASW to 1000 mm, representing essentially unlimited water supply, and reduced FR and alpha proportionally from that assumed for 1100 mm (i.e., 0.15 and 0.04, respectively, in Table 2 with an average LAI of 4.8) for the 900 and 700 mm precipitation zones to match satellite-derived mean annual LAI values (i.e., 3.7 and 2.5, respectively).

Figure 8 indicates that in the wettest zone where annual precipitation averages 1100 mm yr<sup>-1</sup>, the 3-PG model produces the closest agreement between predicted and derived monthly values of average ET when max ASW is set at 1000 mm, indicative that trees have continued access to deep soil moisture stores and/or groundwater. To evaluate possible differences in FR and photosynthetic efficiency (alpha), we set max ASW at 1000 mm for all three precipitation zones and adjusted FR and alpha proportionately to match mean LAI values for the two drier zones (Table 5). With these derived values, we reran the model to estimate the max ASW values, which averaged 700 and 550 mm, respectively, for the 900 and 700 mm yr<sup>-1</sup> rainfall zones.

### Analysis of summer flows

An example of the declining trend in summer (January–April) flows is shown in Fig. 9 for the Donnelly



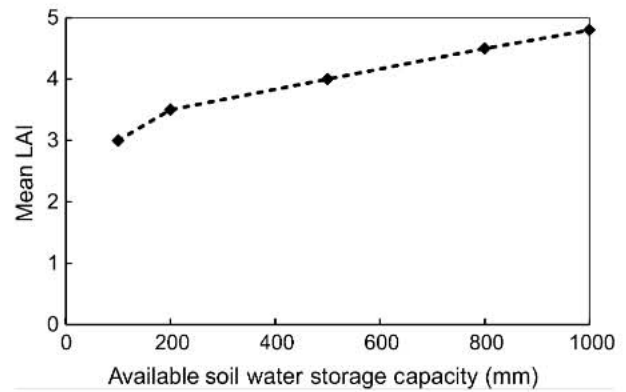
**Table 5** Simulations with the 3-PG Model to estimate maximum available soil water storage (max ASW) with varying mean annual precipitation (PR), and mean leaf area index (LAI) values: (1) with Max ASW set at 1000 mm and soil fertility (FR) and canopy quantum efficiency (alpha) adjusted (15% and 23%) to obtain mean LAI values for PR of 900 and 700 mm, and (2) Max ASW required to match LAI values with the adjustments

Mean PR	LAI	Run No	FR	Alpha	Max ASW
1100	4.8	1	0.15	0.04	1000
1100	4.8	1	0.15	0.04	1000
900	3.7	1	0.128	0.034	1000
900	3.7	2	0.128	0.034	700
700	2.5	1	0.1	0.027	1000
700	2.5	2	0.1	0.027	550

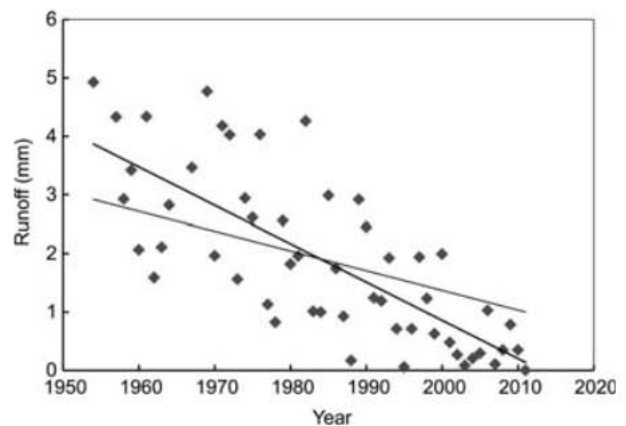
River, which has the longest continuous record of the rivers in this study. The trend is statistically significant ( $P < 0.01$ ), with normally distributed residuals (JB test). The regression line for the Warren River obtained from the period of record (1971–2011) is also shown for comparison. Decadal declines of annual dry season flows obtained from linear regression are summarized in Table 6. Residuals from the regression tests were normally distributed and the declining trends were significant for four of the five rivers listed in Table 6. The trend for the Deep River was not significant, but in comparison with the other four rivers, it has very low summer flow volumes at the start of the record (Table 6) and interannual variability is high. The Denmark River was excluded from this analysis as summer flow increased from 1962 to 2000 as a consequence of earlier land clearing. Since 2000, summer flow (January–April) in the Denmark River has stabilized at about 100 Ml yr<sup>-1</sup>.

#### Changes to annual terrestrial storage

The lowest 7 days daily mean flows,  $y_{L7}$ , were averaged for each decade and used to calculate average annual interdecadal rates of decline. An example of the declining trend is presented for the Donnelly River in Fig. 10. For the decade of the 1950s, the annual lowest terres-



**Fig. 8** Modeled available soil water storage capacity (mm) required to sustain a mean leaf area index (LAI) of 4.8 for a mean rainfall of 1100 mm in southwest Western Australia.



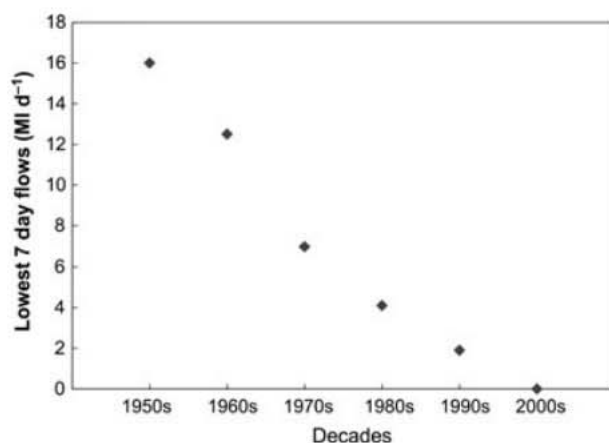
**Fig. 9** Donnelly River. January–April runoff (mm). The regression line (solid) shows a significant declining trend (Runoff =  $-0.065x + 132$ ;  $R^2 = 0.57$ ;  $P < 0.01$ ). Also shown is the projected regression line for the Warren River forested section since the first recording in 1971 (dotted line:  $R^2 = 0.2$ ;  $P < 0.05$ ).

trial storage,  $S$ , (Eqn 2) was 0.9 mm ( $\pm 0.2$  mm), but this had declined to 0 by the 2000s. The rate of decline,  $dS/dt$  was  $-0.02$  mm d<sup>-1</sup> yr<sup>-1</sup> between the 1950s and 1960s, increasing to  $-0.0387$  mm d<sup>-1</sup> yr<sup>-1</sup> by the 1970s and declining to  $-0.0137$  mm d<sup>-1</sup> yr<sup>-1</sup> by 2000, after which it is effectively zero as the river is now ephemeral. Prior to the 1980s, there were no years with zero 7 days daily mean flows. The decades of 1980s

**Table 6** Declines of annual dry season (January–April) river flows

	Start of record	Flow at start of record (Ml)*	Decadal decline (Ml)	Decadal decline (mm)	Significance level ( $P$ )
Deep river	1976	40	8.5	0.01	ns
Warren river	1971	5500	850	0.35	0.05
Donnelly river	1953	3000	500	0.64	0.01
Margaret river	1971	150	37.5	0.08	0.01
St John's brook	1984	160	44.0	0.08	0.01

\*Taken from the regression line at the start of the record.



**Fig. 10** Donnelly River decadal averages of annual lowest 7 days flows per year. In the 2000s, only 2 years that recorded perennial flow.

and 1990s each had 1 year with zero flow for more than 7 days, but in the 2000s, this had increased to 8 years in which a period of no flow >7 days was recorded.

Mean annual terrestrial storage of each catchment for the first decade on record is reported in Table 7, together with decadal rates of decline and the proportion of years since 2000 with more than 7 days of zero flow. The Deep River was ephemeral from the start of recording and so returned  $y_{L7}$  values of zero for the entire period. Margaret River has been ephemeral since the 1980s and although St John's Brook is still perennial, the rate of terrestrial storage decline has doubled over the last two decades. If terrestrial storage continues to decline, then St John's Brook will become ephemeral in the near future.

If groundwater discharge exceeds recharge, there will be a general decline in terrestrial storage over time without forests actively using groundwater to meet transpiration demand. Hughes *et al.* (2011) suggest that in the Darling Ranges, a MAR threshold of about 1050–1400 mm needs to be exceeded for increased ground-

water storage to occur. The lack of significantly greater than (long-term, pre-1975) average rainfall years since 1975, the buffered response of forest LAIs to interannual variations in rainfall (particularly in 2010, which was the driest year on record at Pemberton) and the high ASWs required to support the observed LAIs suggest that the forests are using any annual carry-over of moisture reserves from wetter years.

## Discussion

In Fig. 4, the 1100 mm isobar of annual precipitation in the Warren River catchment, equivalent to an average LAI of 4.8, is the most buffered of the three cases in response to interannual variation in precipitation. The 900 and 700 mm band, although lower in LAI values, show more variability because they are more dependent on recharge of water in the rooting zone and have less access to deep moisture reserves or groundwater during periods of drought (max ASW = ca. 500 mm vs. 1000 mm for the wettest zone).

In this study, we modeled average LAI for the period 2000–2011. This analysis did not provide precise estimates of seasonal or interannual variation in LAI, but the general trends are reasonable. We conclude that MAR, soil depth, and access to differential amounts of deep soil moisture and/or groundwater likely account for major differences in mean LAI across the catchments. Although we could induce a significant drop in LAI by imposing a year of drought (i.e., 30 mm month<sup>-1</sup> precipitation), the pattern was much less than that indicated in Fig. 6, this buffered response is a result of the assumption that monthly litterfall remains a twelfth of the annual value. Under stable climatic conditions where litterfall varies predictably by season, the appropriate values may be programmed into the model (Siqueira *et al.*, 2006). For more dynamic situations shown in Fig. 5 and in field studies by Pook (1984), additional refinements are required in the model to set threshold soil water deficits, and their durations that causes partial to

**Table 7** Mean annual terrestrial storage,  $S$ , for the first decade of record, subsequent interdecadal rates of storage decline and % of years with mean annual 7 days low flows of zero since 2000

	First decade of record	Mean annual S for first decade (mm)	Mean annual -dS/dt (mm d <sup>-1</sup> yr <sup>-1</sup> ) per decade										% of years since 2000 with no $y_{L7}$ flow
			1950s	1960s	1960s	1970s	1970s	1980s	1980s	1990s	1990s	2000s	
Deep river	1970s	0					0		0		0	100	
Warren river	1970s	0.33					0.004		0.0038		0.0038	0	
Donnelly river	1950s	0.90	0.02		0.0387		0.0137		0.0137		0	80	
Margaret river	1970s	0.008					0.0006		0		0	100	
St John's brook	1980s	0.076							0.0019		0.0041	0	



complete defoliation. We propose to consider constructing a more dynamic model of canopy LAI with the availability of site-specific leaf litter collections. It is difficult to obtain estimates of ET across large catchments where precipitation, LAI, and soil properties all vary. Results from satellite imagery, as shown in Fig. 5, can provide detailed seasonal variation in LAI, and an associated MODIS product is ET. This ET estimate, however, does not include limitations imposed by ASW. Thus, in this study, setting max ASW to 1000 mm gives a close fit to MODIS-derived monthly ET values across all precipitation and LAI zones (not shown) and also matches well with ET estimated from the Warren River forested section water balance as average MODIS ET scaled by matching to annual average Rainfall–Runoff. The fact that MODIS-derived ET is unconstrained by the availability of soil water (being based only on the evaporative demand and constraints imposed by VPD on canopy stomatal conductance) provides an opportunity to assess a gradient in soil properties, as shown in Table 5. By inverting the model with reasonable estimates of soil properties, it is possible to obtain estimates of max ASW by matching predicted with observed LAI. This general approach has been recognized in estimating max ASW in the Amazon (Nepstad *et al.*, 2004) and the Pacific Northwest (Coops *et al.*, 2012).

If rainfall continues to decline, then ultimately, the forest LAIs may adjust to a new equilibrium, as indicated by the LAI vs. rainfall gradient shown in Fig. 6, but unless there are substantially wetter than average years, the terrestrial storage and summer flows are likely to continue to decline. Kinal & Stoneman (2011) have also shown that under current climatic conditions, even substantial thinning of forests could not reverse the continued decline in groundwater levels in this region. This raises the possibility that a hydrologic transition from perennial to ephemeral flow regimes could be the harbinger of a future biome shift to progressively more open woodlands.

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## References

- Ali R, McFarlane D, Varma S, Dawes W, Emelyanova I, Hodgson G, Charles S (2012) Potential climate change impacts on groundwater resources of south western Australia. *Journal of Hydrology*, **475**, 456–472.
- Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology & Management*, **259**, 660–684.
- Almeida AC, Landsberg JJ (2003) Evaluating methods of estimating global radiation and vapor pressure deficits using a dense network of automatic weather stations in coastal Brazil. *Agricultural & Forest Meteorology*, **118**, 237–250.
- Bari M, Smettem KRJ (2004) Modelling monthly runoff generation processes following land use changes: groundwater surface runoff interactions. *Hydrology and Earth System Sciences*, **8**, 903–922.
- Bates B, Hope P, Ryan B, Smith I, Charles S (2008) Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change*, **89**, 339–354.
- Bates BC, Chandler RE, Charles SP, Campbell EP (2010) Assessment of apparent non stationarity in time series of annual inflow, daily precipitation, and atmospheric circulation indices: a case study from southwest Western Australia. *Water Resources Research*, **46**, W00H02, doi: 10.1029/2101WR009509
- Bennett MWA (1987). *Rapid Monitoring of Wetland Water Status Using Density Slicing. Proceedings of the 4th Australasian Remote Sensing Conference*, pp. 682–691. Surveying and Spatial Sciences Institute, Adelaide, SA.
- Bonan GB (2002) *Ecological Climatology*. Cambridge University Press, New York.
- Brutsaert W (2008) Long term groundwater storage trends estimated from stream flow records: climatic perspective. *Water Resources Research*, **44**, W02409, doi: 10.1029/2007WR006518
- Brutsaert W (2012) Are the North American deserts expanding? Some climate signals from groundwater storage conditions. *Ecology*, **93**, 541–549.
- Brutsaert W, Sugita M (2008) Is Mongolia's groundwater increasing or decreasing? The case of the Kherlen River basin. *Hydrological Sciences Journal*, **53**, 1221–1229.
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E D (1996) Maximum rooting depths of vegetation types at the global scale. *Oecologia*, **108**, 583–595.
- Choat B, Jansen S, Brodribb SJ *et al.* (2012) Global convergence in the vulnerability of forests to drought. *Nature*, **491**, 752–755.
- Constable J, Friend AL (2000) Suitability of process based growth models for addressing tree response to climate change. *Environmental Pollution*, **110**, 47–59.
- Coops NC, Waring RH, Landsberg JJ (1998) Assessing forest productivity in Australia and New Zealand using a physiologically based model driven with averaged monthly weather data and satellite derived estimates of canopy photosynthetic capacity. *Forest Ecology and Management*, **104**, 113–127.
- Coops NC, Waring RH, Moncrieff J (2000) Estimating mean monthly incident solar radiation on horizontal and inclined slopes from mean monthly temperature extremes. *Journal of Biometeorology*, **44**, 204–211.
- Coops NC, Waring RH, Hilker T (2012) Prediction of soil properties using a process based forest growth model to match satellite derived estimates of leaf area index. *Remote Sensing of Environment*, **126**, 160–173.
- Donohue RJ, Roderick ML, McVicar TR (2007) On the importance of including vegetation dynamics in Budyko's hydrological model. *Hydrology & Earth System Sciences*, **11**, 983–995.
- Eagleson PS (1982) Ecological optimality in water limited natural soil vegetation systems 1: theory and hypothesis. *Water Resources Research*, **18**, 325–340.
- Eagleson PS (2002) *Ecology: Darwinian Expression of Vegetation Form and Function*. Cambridge University Press, New York.
- Eagleson PS, Tellers TE (1982) Ecological optimality in water limited soil vegetation systems 2. Tests and applications. *Water Resources Research*, **18**, 341–354.
- Ellis TW, Hutton TJ (2008) Relating leaf area index of natural eucalypt vegetation to climate variables in southern Australia. *Agricultural Water Management*, **95**, 743–747.
- Granier A, Biron P, Lemoine D (2000) Water balance, transpiration and canopy conductance in two beech stands. *Agricultural Forest Meteorology*, **100**, 291–308.
- Grierson PF, Adams MA (2000) Plant species affect acid phosphatase, ergosterol and microbial P in Jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in south western Australia. *Soil Biology and Biochemistry*, **32**, 1817–1827.
- Harper RJ, Smettem KRJ, Carter JO, McGrath JF (2009) Drought deaths in *Eucalyptus globulus* (Labill.) plantations in relation to soils, geomorphology and climate. *Plant and Soil*, **324**, 199–207.
- Hill MJ, Senarath U, Lee A, Zeppel M, Nightingale JM, Williams RJ, McVicar TM (2006) Assessment of the MODIS LAI product for Australian ecosystems. *Remote Sensing & Environment*, **101**, 495–518.
- Hopper SD (1979) Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics*, **10**, 399–422.
- Hughes JD, Petrone KC, Silberstein RP (2011) Drought, groundwater storage and stream flow decline in southwestern Australia. *Geophysical Research Letters*, **39**, L03408, doi: 10.1029/2011GL050797

- Hughes JD, Petrone KC, Silberstein RP (2012) Drought, groundwater storage and streamflow decline in southwestern Australia. *Geophysical Research Letters*, **39**, L03408, doi: 10.1029/2011GL050797
- Johnston RM, Barson MM (1993) Remote sensing of Australian wetlands: an evaluation of Landsat TM data for inventory and classification. *Australian Journal of Marine & Freshwater Research*, **44**, 235–252.
- Kinal J, Stoneman GL (2011) Hydrological impact of two intensities of timber harvest and associated silviculture in the jarrah forest in south western Australia. *Journal of Hydrology*, **399**, 108–120.
- Landsberg JJ, Waring RH (1997) A generalized model of forest productivity using simplified concepts of radiation use efficiency, carbon balance and partitioning. *Forest Ecology & Management*, **95**, 209–228.
- Landsberg JJ, Waring RH, Coops NC (2003) Performance of the forest productivity model 3PG applied to a wide range of forest types. *Forest Ecology & Management*, **172**, 199–214.
- Law BE, Goldstein AH, Anthoni PM *et al.* (2001) Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology*, **21**, 299–308.
- Mäkelä A, Landsberg J, Alan R *et al.* (2000) Process based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology*, **20**, 289–298.
- Moore G, Hall D, Russell J (1998) Soil water. In: *Soilguide. A Handbook for Understanding and Managing Agricultural Soils* (ed. Moore G), pp. 80–93. Agriculture Western Australia, Perth, Western Australia. Bulletin No. 4343.
- Mu Q, Heinsch FA, Zhao M, Running SW (2007) Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. *Remote Sensing of Environment*, **111**, 519–536.
- Mu Q, Zhao M, Running SW (2011) Improvements to a MODIS global terrestrial evapotranspiration algorithm. *Remote Sensing of Environment*, **115**, 1781–1800.
- Murphy BF, Timbal B (2007) A review of recent climate variability and climate change in southeastern Australia. *International Journal of Climatology*, **28**, 859–879.
- Nemani RR, Running SW (1989) Testing a theoretical climate soil leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agricultural & Forest Meteorology*, **44**, 245–260.
- Nepstad D, Lefebvre P, Lopes da Silva U *et al.* (2004) Amazon drought and its implications for forest flammability and tree growth: a basin wide analysis. *Global Change Biology*, **10**, 704–717.
- Nightingale JM, Phinn SR, Held AA (2004) Ecosystem process models at multiple scales for mapping tropical forest productivity. *Progress in Physical Geography*, **28**, 241–281.
- O'Grady AP, Carter JL, Bruce J (2011) Can we predict groundwater discharge from terrestrial ecosystems using existing eco hydrological concepts? *Hydrology and Earth System Sciences*, **15**, 3731–3739.
- Hill RC, Griffiths WE, Lim MA (2011) *Using Excel for Principles of Econometrics*. John Wiley & Sons, New York.
- Palmer AR, Fuentes S, Taylor D, Macinnis Ng C, Zeppel M, Yanusa I, Eamus D (2010) Towards a spatial understanding of water use of several land cover classes: an examination of relationships amongst pre dawn leaf water potential, vegetation water use, aridity and MODIS LAI. *Ecophysiology*, **3**, 1–10.
- Paul KI, Booth TH, Jovanovic T, Sands PJ, Morris JD (2007) Calibration of the forest growth model 3 PG to eucalypt plantations growing in low rainfall regions of Australia. *Forest Ecology & Management*, **243**, 237–247.
- Petrone KC, Hughes JD, Van Niel TG, Silberstein RP (2010) Streamflow decline in southwestern Australia, 1950–2008. *Geophysical Research Letters*, **37**, L11401.
- Pook EW (1984) Canopy dynamics of *Eucalyptus maculata* Hook. II. Canopy leaf area balance. *Australian Journal of Botany*, **32**, 405–413.
- Power S, Sadler B, Nicholls N (2005) The influence of climate science on water management in western Australia: lessons for climate scientists. *Bulletin of the American Meteorological Society*, **86**, 839–844.
- Sands PJ, Landsberg JJ (2002) Parameterisation of 3 PG for plantation grown *Eucalyptus globulus*. *Forest Ecology & Management*, **163**, 273–292.
- Sharma ML (1984) Evapotranspiration from a Eucalyptus community. *Agricultural Water Management*, **8**, 41–56.
- Silberstein RP, Aryal SK, Durrant J *et al.* (2012) Climate change and runoff in south western Australia. *Journal of Hydrology*, **475**, 441–455.
- Siqueira MB, Katul GG, Sampson DA, Stoy PC, Juang J-Y, McCarthy HR, Oren R, (2006) Multiscale model intercomparisons of CO<sub>2</sub> and H<sub>2</sub>O exchange rates in a maturing southeastern US pine forest. *Global Change Biology*, **12**, 1189–1207.
- Stape JL, Ryan MG, Binkley D (2004) Testing the 3 PG process based model to simulate Eucalyptus growth with an objective approach to the soil fertility rating parameter. *Forest Ecology & Management*, **193**, 219–234.
- Stape JL, Binkley D, Jacob WS, Takahashi EN (2006) A twin plot approach to determine nutrient limitation and potential productivity in *Eucalyptus* plantations at landscape scales in Brazil. *Forest Ecology & Management*, **223**, 358–362.
- Thompson SE, Harman CJ, Konings AG, Sivapalan M, Neal AM, Troch PA (2011) Comparative hydrology across AmeriFlux sites: the variable roles of climate, vegetation, and groundwater. *Water Resources Research*, **47**, W00J07, doi: 10.1029/2010WR009797
- UNEP (1997) *World Atlas of Desertification*. United Nations Environmental Programme, New York.
- Waring RH (1983) Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research*, **13**, 327–354.
- Waring RH, Landsberg JJ (2011) Generalizing plant water relations to landscapes. *Journal of Plant Ecology*, **4**, 101–113.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.