Agricultural and Forest Meteorology 233 (2017) 235–241

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Groundwater facilitated water-use efficiency along a gradient of groundwater depth in arid northwestern China

Bing Liu[a,*], Huade Guan[b], Wenzhi Zhao[a], Yuting Yang[c], Shoubo Li[d]

[a] Linze Inland River Basin Research Station, Laboratory of Heihe River Eco-Hydrology and Basin Science, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000
[b] School of the Environment and National Centre for Groundwater Research and Training, Flinders University, Adelaide, SA 5001, Australia
[c] CSIRO Land and Water, Canberra, ACT 2601, Australia
[d] School of Geography and Remote Sensing, Nanjing University of Information Science and Technology, Nanjing, 210044, China

ARTICLE INFO

Article history:
Received 28 September 2016
Received in revised form
29 November 2016
Accepted 4 December 2016
Available online 9 December 2016

Keywords:
Groundwater
Rainfall
Aboveground net primary production
Water-use efficiency
Groundwater use efficiency
Rain use efficiency

ABSTRACT

Groundwater strongly impacts ecosystem performance in arid regions by driving vegetation structure and species distribution. It is unknown how water use efficiency varies along a gradient of depth to groundwater (*DWT*). In this study, we developed a framework to estimate water use efficiency (*WUE*), groundwater use efficiency (*GUE*), and rain use efficiency (*RUE*), and to examine the contribution of rainfall to transpiration in groundwater-dependent ecosystems (GDEs). The method was applied to an arid region in northwest China with a gradient of groundwater depth from 0.5 to 12 m. The results indicate that the above-ground primary production, evapotranspiration, plant transpiration, *WUE*, and *GUE* decreased significantly from riparian forest, wetland, oasis edge, desert-oasis ecotone, and to sandy desert along a gradient of increasing *DWT*. *RUE* is found to be 0.26 g m^{-2} mm^{-1} at the sandy desert without groundwater contribution where 21% of rainfall is used for transpiration. Water use efficiency increases to 0.85 g m^{-2} mm^{-1} at the riparian site where groundwater is about 0.5 m depth. The fraction of rainfall consumed by plants increases with a decreasing *DWT* from a threshold of 6.3 m, suggesting groundwater enhances rain use efficiency in GDEs.

1. Introduction

Ecosystems are controlled by water availability in semi-arid and arid regions (Rodriguez-Iturbe and Rinaldo, 2001; Hickler et al., 2009; Yang et al., 2014), which occupy approximately 40% of the global land area (Parsons and Abrahams, 1994). In arid regions, annual rainfall is much less than annual potential evapotranspiration (E_p) (Parsons and Abrahams, 1994; Guswa et al., 2004; Newman et al., 2006; Yang et al., 2016a). In addition, the water supply for vegetation from surface flows (e.g., runoff, rivers) is generally very limited. Groundwater therefore becomes an important source of water that greatly affects the spatial and temporal distributions of soil moisture, which in turn affects the distribution of vegetation (Lowry et al., 2011; Naumburg et al., 2005; De Paola and Ranucci, 2012; Dai et al., 2014; Zhu et al., 2015). Along the gradient of groundwater depth, the vegetation community undergoes succession from phreatophytes, which obtain a large fraction of water from near-surface groundwater or the capillary fringe, perennial shrubs, xerophytic species, which depend mostly on rainfall, and to annuals and ephemerals) (Steed and DeWald, 2003; Dwire et al., 2004; Liu et al., 2010, 2011, 2013; Zhao and Liu, 2010; Fan et al., 2014). These ecosystems are highly sensitive to changes in water table, which are characterized as groundwater-dependent ecosystems (*GDEs*) (Eamus et al., 2006; Lowry and Loheide, 2010). The pattern of vegetation cover is primarily controlled by groundwater which determines ecosystem stability and evolvement between oasisization and desertification.

Water availability is a key control of aboveground net primary production (*ANPP*) worldwide (Yahdjian and Sala, 2006; Yang et al., 2015). *ANPP* increases linearly along spatial precipitation gradients from deserts to steppes and grasslands in China, North America, South America, and Africa (Webb et al., 1978; Lauenroth, 1979; Liang et al., 2015; Sala et al., 1989; McNaughton et al., 1993; Paruelo et al., 1998; Yahdjian and Sala, 2006; Bai et al., 2008). However, the impact of groundwater on *ANPP* is seldom documented. As a critical link between water and carbon cycles in terrestrial ecosystems, water-use efficiency (*WUE*), has been identified as an effective integral trait for assessing the response of ecosystem *ANPP* to water

* Corresponding author.
E-mail address: liubing@lzb.ac.cn (B. Liu).

http://dx.doi.org/10.1016/j.agrformet.2016.12.003

availability (Kuglitsch et al., 2008; Beer et al., 2009; Scott et al., 2010). However, the published studies on the WUE response to precipitation variability are sometimes conflicting. For example, the *WUE* and rainfall-use efficiency (*RUE*) have been reported to decrease (Huxman et al., 2004; Scanlon and Albertson, 2004; Bai et al., 2008; Yu et al., 2008) or keep constant (Lauenroth et al., 2000; Niu et al., 2011) with increasing precipitation along a spatial precipitation gradient. For a given ecosystem, a number of studies have shown that ecosystem *WUE* decreases (Lauenroth et al., 2000; Li et al., 2008; Fay et al., 2003) or increases (Bai et al., 2008; Yang et al., 2016b) over time with increasing annual precipitation. These seemingly conflicting spatial and temporal patterns of *WUE* in different ecosystems may be associated with the different scales of the analyses (Wu and Loucks, 1995; Wu et al., 2006).

Groundwater can be a source of soil moisture for plant water uptake to support photosynthesis (York et al., 2002; Yeh and Eltahir, 2005; Fan et al., 2007; Niu et al., 2007; Maxwell and Kollet, 2008; Lowry and Loheide, 2010; Soylu et al., 2014), and increase soil evaporation and plant transpiration (Orellana et al., 2012). With accessible groundwater, ecosystems develop better vegetation coverage, which may enhance rain water use efficiency, i.e., more proportion of rain can be used for transpiration. Meanwhile, groundwater used by ecosystems may also contribute to primary production. However, no research has been done on groundwater-use efficiency (*GUE*). In the present study, we attempted to examine how *WUE*, *GUE*, and *RUE* vary along a gradient of depth to groundwater table, and investigate the contributions of rainfall and groundwater to *ANPP* of the GDEs. The objectives were to answer three questions: (1) How do *WUE* and *GUE* vary in GDEs along a gradient of groundwater table? (2) What are the relative contributions of *WUE* and *GUE* in these ecosystems? (3) What are the water sources for plant transpiration? We hypothesized that (1) both *WUE* and *GUE* would increase with decreasing depth to groundwater table, (2) *GUE* would be greater than *RUE*, and (3) groundwater would increase the proportion of rain being used for transpiration.

2. Theory and hypotheses

The normalized-difference vegetation index (*NDVI*) typically increases with decreasing depth to the water table (*DWT*), but approaches a constant background value determined by the climate when *DWT* is greater than a certain threshold (DWT_0). This relationship can be described by the following empirical equation (Lv et al., 2013):

$$NDVI = NDVI_0 + k_v(DWT - DWT_0)\text{forDWT} <= \text{DWT}_0 \quad (1)$$

where $NDVI_0$ is the *NDVI* of baseline vegetation supported by rainfall without any contribution of groundwater, *DWT* is the depth to the water table, DWT_0 is the threshold depth beyond which there is no groundwater contribution to ecosystem primary production, and k_v is an empirical regression coefficient. In the present study, we assumed that *NDVI* in Gobi desert, an arid region where plants are supported primarily by local rainfall, represented $NDVI_0$, in which *DWT* stabilized at a value deeper than 12 m (CV = 4.5%). As a result, desert plants can't access groundwater in this region throughout the year. We hypothesized that k_v is contributed both by high temporal availability of the groundwater supply and by an increase in the bio-consumptive fraction of rainfall with a shallower groundwater (f_0, proportion of rainfall being used for transpiration).

WUE (g m^{-2} mm^{-1}) is defined as the ratio of *ANPP* (g m^{-2}) to *ET* (mm) (Monclus et al., 2006):

$$WUE = ANPP/ET \quad (2)$$

At a site where $DWT > DWT_0$ and there is no significant surface flow, water loss through evapotranspiration is replenished only by rainfall. Thus, *RUE* (g m^{-2} mm^{-1}) can be obtained as the threshold value of *WUE* (WUE_0), and described as the ratio of the aboveground net primary production without any contribution from groundwater ($ANPP_0$) to the mean annual precipitation (P) (Huxman et al., 2004; Bai et al., 2008; Yang et al., 2010).

$$RUE = ANPP_0/P \quad (3)$$

where *P* is the mean annual precipitation.

At a site where $DWT < DWT_0$, soil moisture loss by ET is replenished by a combination of water from rainfall and groundwater. In this case, *GUE* is calculated as follows:

$$GUE = (ANPP - ANPP_0)/(ET - P) \quad (4)$$

The increase in ANPP from the climatic background value (i.e., ANPP-ANPP0) can be partly due to an increased bio-consumptive fraction of the rainfall in GDEs.

For a site where $DWT > DWT_0$,

$$f_0 = T_P/ET = (P - E)/P \quad (5)$$

where T_P is amount of precipitation being used for plant transpiration (mm) and *E* is soil evaporation (mm).

For a site where $DWT < DWT_0$, we expect to see a larger value of *f* because of increased vegetation cover.

$$f = T_P/P \quad (6)$$

It is expected that

$$f = f_0 + k_w(DWT - DWT_0) \quad (7)$$

where k_w represents the contribution groundwater to enhance *RUE*.

To calculate the ratio of T_P to *P*:

For a site where *DWT* is low («DWT_0), $T_P/P = (1 - [E/ET])$.

For a site where *DWT* is high, (>DWT_0), $T_P/P = (P - E)/P$.

3. Study sites and data collection

3.1. Study sites

Our study area (Fig. 1) is located in the middle reaches of China's Heihe River Basin (between 39°10′ N and 39°40′N, and between 100°02′E and 100°11′E). The region has been described in detail in Liu et al. (2010, 2012, 2014). The study area is dominated by groundwater-dependent ecosystems, which form a spectrum from riparian forest, wetland, oasis edge, a desert-oasis ecotone, sandy desert, and to gobi desert along a gradient of groundwater depths. (Note that in this paper, *gobi* refers to a desert in which the surface is primarily coarse particles in the gravel size categories.) The gradient covers a total length of about 15 km, over which mean precipitation is very similar. The difference in the vegetation types is driven solely by the groundwater gradient. In the riparian forest zone, vegetation is distributed on or near the banks of the Heihe River and is dominated by trees (*Populus alba*, *Elaeagnus angustifolia*, *Salix babylonica*), shrubs (*Tamarix chinensis*), and herbs (*Carex karoi*, *Juncus articulatus*, *Phragmites australis*, *Leymus secalinus*, *Sophora alopecuroides*). This ecosystem has the highest *NDVI* and species richness (Table 1). The wetland ecosystem is primarily wet meadows dominated by shrubs (*T. chinensis*) and halophytic herbs (*P. australis*, *Agropyron cristatum*, *Oxytropis glabra*, *Equisetum ramosissimum*, *Typha orientalis*, *Carex tangiana*). The oasis edge belongs to the shelter forest belt, which is a combination of agricultural land, tree, shrub and grass. It plays an important role in the control of sand dunes and protection of farmland. The soil water mainly comes from the lateral seepage from farmland irrigation and the recharge from shallow groundwater. The desert-oasis ecotone ecosystem is dominated by fixed and semi-fixed dunes that are separated by inter-dune lowlands. Its vegetation comprises desert

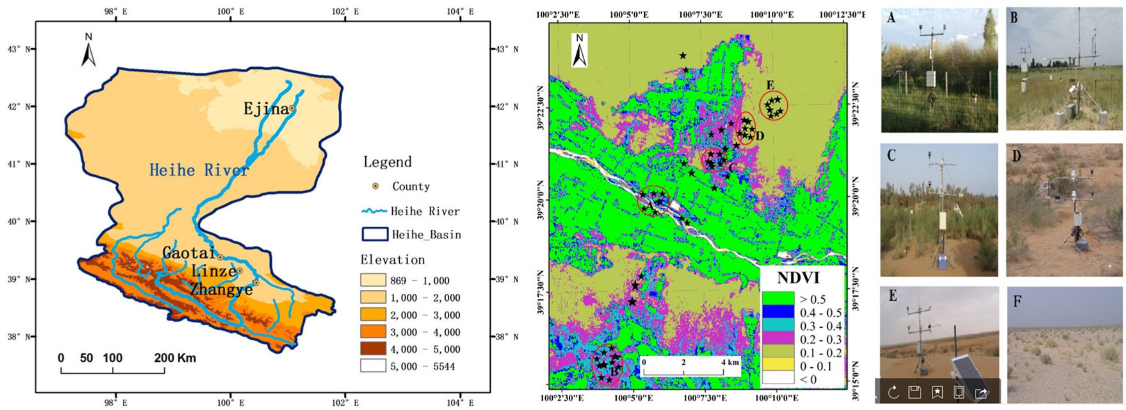

Fig. 1. Map of the study area and its location in China, and distribution of *NDVI* values from 2010 to 2013. The key ecosystems in the study area: (A) riparian forest; (B) wetland; (C) oasis edge; (D) desert-oasis ecotone; (E) sandy desert; (F) gobi desert.

Table 1
Descriptions of the study sites, their geographic coordinates, the dominant plant functional types (PFTs), and depth to water table (*DWT*), vegetation cover, and species richness. Ecosystem types: R, riparian forest; W, wetland; O, oasis edge; E, desert-oasis ecotone; D, sandy desert; and G, gobi desert).

Ecosystem type	Lat. (°N)	Long. (°E)	PFTs	*DWT*	Vegetation cover	Species richness
R	39°15′	100°5′	trees, shrubs, and herbs	0.81 ± 0.13	85.5 ± 14.5%	26 ± 2
W	39°20′	100°6′	shrubs, halophytic herbs	1.00 ± 0.25	65.5 ± 12%	20 ± 1
O	39°21′	100°7′	shrubs, annual herbs	4.37 ± 0.55	25.5 ± 3.5%	10 ± 1
E	39°22′	100°8′	shrubs, annual herbs	5.85 ± 0.46	15.5 ± 1.2%	7 ± 1
D	39°23′	100°10′	annual herbs	6.15 ± 0.31	1.5 ± 0.5%	3 ± 1
G	39°24′	100°7′	shrubs, annual herbs	12.17 ± 0.13	2.5 ± 0.6%	5 ± 1

shrubs (*C. mongolicum*, *Nitraria sphaerocarpa*) on the fixed dunes and in the inter-dune lowlands, and annual herbs similar to those in the oasis edge ecosystem (Liu and Zhao, 2012). The gobi desert ecosystem is dominated by *N. sphaerocarpa* and annual herbs. In the sandy desert ecosystem, there are a few annual and ephemeral plants during the rainy season.

3.2. Data collection

The experiments were conducted along a gradient of groundwater depths from the riparian forest, wetland, oasis edge, desert-oasis ecotone, sandy desert, and to gobi desert ecosystems in August from 2010 to 2013. For each ecosystem, we established five 10 m × 10 m sample plots for trees, shrubs, and sub-shrubs, and 10 quadrats (1 m × 1 m) to sample herbs at each plot. Species were grouped into different plant functional groups according to their life forms: annual herbs, perennial herbs, sub-shrubs, shrubs, and trees. We determined the site locations using a GPS receiver (eTrex Vista Cx, Garmin, U.S. A, http://www.ebay.com/p/Garmin-eTrex-Vista-C-Handheld-GPS-Receiver/48465609), then created a distribution map for each sub-shrub, shrub, and tree in the plots. We measured the basal diameter, height, crown area, canopy cover, number of branches, and branch length for each shrub and tree in the plots in all four years of the experiment.

ANPP was calculated after the vegetation had reached its peak standing biomass (Scurlock et al., 2002). The individual shrubs and trees were cut at ground level in August 2010, and their total fresh weight was obtained in the field using a hanging scale (Goldenlark OEM BT-203), with an accuracy of ±0.1 kg. Fresh subsamples of the wood and of the twigs with leaves attached were collected from five individuals per species, stored in sealed plastic bags, and transported to the laboratory. All samples in 256 points were then oven-dried in a forced-air oven at 75 °C until constant weight and re-weighed to estimate the water content, thereby allowing calculation of the dry weight for each species and the total aboveground biomass for each ecosystem. Based on the method developed by Conti and Díaz (2013) and Conti et al. (2013), we developed a multiple-regression model of aboveground biomass (SB, $kg\,m^{-2}$) for shrubs and trees as a function of their crown area (S, m^{-2}), plant height (H, m) and branch base diameter (D, m), respectively. ($SB = 0.85(H \times S + D^2)^{0.823}$, $R^2 = 0.885$ for trees; $SB = 0.25(H \times S + D^2)^{0.542}$, $R^2 = 0.893$ for shrubs). We then calculated *ANPP* of all shrubs and trees in the plots based on the change in aboveground biomass between years. We also estimated *ANPP* for all herbaceous vegetation in each quadrat by harvesting all plant material at the ground level at August in each year. This allows us calculate the total *ANPP* (woody and herbaceous biomass combined) for all vegetation in each ecosystem (Fig. 2).

NDVI is strongly correlated with the green biomass level (i.e., leaves and green stems of woody vegetation plus aboveground herbaceous biomass) in semiarid landscapes (Huete et al., 2002; Moreno-de las et al., 2012). We therefore used the change in *NDVI* as a function of groundwater depth to determine how *DWT* influenced the vegetation distribution in our study area. To perform this analysis, we used the *NDVI* layers from the Terra-MODIS MOD13Q1 image product (version 005 tile, H12V12, 250-m resolution) with a temporal resolution of 8 days, obtained from the MODIS Subsets gateway for pixels centered on the study sites. The *NDVI* values were estimated from the six vegetation types (riparian forest, wetland, oasis edge, desert-oasis ecotone, sandy desert, and Gobi desert) once every month from 2010 to 2013. To reduce the effect of cloud anomalies in the compiled *NDVI* series, we used the reliability summary layer of the MODIS product and discarded *NDVI* values that did not have the highest quality flag value (i.e., we discarded less than 2% of the data). To reduce the inherent noise in the *NDVI* data series, we smoothed the data using a cubic spline polynomial (Furrer et al., 2011). We performed regression analyses using *NDVI* as the independent variable and *ANPP* as the dependent variable for each vegetation type in August, and developed an empirical model ($ANPP = 27.8\,e^{6.4\,NDVI}$, $R^2 = 0.74$, $n = 250$, $P < 0.001$) to estimate *ANPP* for the six vegetation cover types at a regional scale.

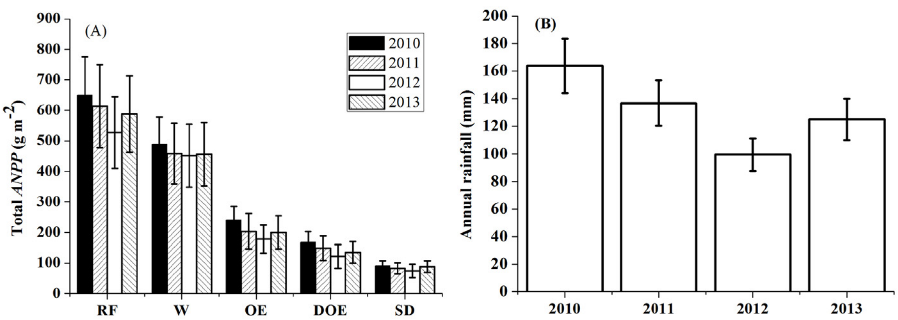

Fig. 2. The annual change of (A) the measured *ANPP* among vegetation types and (B) annual rainfall during growing period. Vegetation types: RF, riparian forest; W, wetland; OE, oasis edge; DOE, desert-oasis ecotone; and SD, sandy desert).

In each ecosystem, we measured soil evaporation (*E*) using micro-lysimeters with a diameter of 30 cm and a depth of 30 cm. We installed 10 micro-lysimeter at each site, and weighed the micro-lysimeters at 19:00 every day using an electronic balance (PL 6001-L, Mettler Toledo Inc., Greifensee, Switzerland) with an accuracy of ±0.1 g. Soil in the micro-lysimeters was replaced every week and after heavy rains. Simultaneously, we measured *DWT* in five randomly located observation wells at each ecosystem type (using 5-cm-diameter PVC pipe) using a water-level sensor (HOBO, Onset Computer Corporation, Bourne, MA, USA).

Meteorological data were measured using an automated weather system (Onset Computer Corporation) at ecosystem type. We used the Bowen ratio energy-balance method to measure ecosystem evapotranspiration (*ET*). The accuracy of the calculated values of the latent and sensible heat fluxes depends on the accuracy of the measurements, and we performed quality control for all measured data to evaluate the measurement consistency by comparison on the premise of independent measurement (Zhao et al., 2016). We completed our quality control using the post-processing steps described by Fischer et al. (2013) and Zhao et al. (2016). After performing this quality control, 20.5% of the total number of Bowen ratio energy-balance data points were eliminated, and the accuracy (based on estimation of the relative error) was greater than 75.5%.

4. Results and discussion

4.1. Variation in NDVI along the gradient of groundwater depths

In all months except April (when the soil was still frozen; Fig. 3A), *NDVI* decreased with increasing *DWT*, while approached a constant value when *DWT* was greater than 6.0 m during the growing season (Fig. 3B–F, 0. 82 < R^2 < 0.87, P < 0.001). However, such a DWT threshold was not observed in Gong et al. (2004), who reported a linear correlation between the *NDVI* and *DWT* based on water table measurement at 28 sites in a Californian mountain meadow ecosystem. Our study showed *NDVI* differed significantly among vegetation cover types (Fig. 3G, F_{5720} = 9.98, P < 0.05), but the difference was not significant between riparian forest and wetland or among the desert-oasis ecotone, sandy desert, and Gobi desert. Zolfaghar et al. (2014) also found that *ANPP* had a significantly larger value when the groundwater level is high. In GDEs, *NDVI* and $NDVI_0$ (the y-intercept) varied between months, with the corresponding maximum value of 0.41 and 0.17 occurring both in August. The slope of the regression (k_v) became more negative from May to August and then increased in September, (Fig. 3B–F). This pattern was basically consistent with the seasonal change of rainfall. Simultaneously, DWT_0 increased from 6.04 m to 6.5 m during the growing season, because groundwater was withdrawn as a result of water consumption by the vegetation. This indicates that the vegetation depended on groundwater only for *DWT* of less than about 6.0 m. McLendon et al. (2008) found that groundwater absorbed by shrub- and grass-dominated communities when DWT fluctuate from 6 m to 8 m in the Owens Valley of California, whereas Lv et al. (2013) considered that when DWT is greater than 10 m at a semi-arid region in China.

4.2. Changes in WUE, GUE, and RUE

ET, *E*, and *T* decreased significantly with increasing *DWT* along the groundwater gradient (Fig. 4, P < 0.05). ET decreased from the riparian forest (550 mm), followed by wetland, (505 mm), oasis edge, (283 mm), desert-oasis ecotone (127 mm), to sandy desert (103 mm) (Fig. 4A). Luo and Sophocleous (2010) also found that ET was linearly correlated with water input for different values of *DWT*. The maximum value of *E* appeared in wetlands, where a wide range of soil salinization leads to a lower vegetation cover. *T* differed significantly among all ecosystems except between the desert-oasis ecotone and the sandy desert (Fig. 4C, P < 0.05). Fig. 4 shows that more water was lost by plant transpiration than evaporation, except for the sandy desert and desert-oasis ecotone.

WUE and *GUE* gradually decreased along the groundwater depth gradient, and the difference was generally significant. *WUE* was highest in the riparian forest (0.85 g m^{-2} mm^{-1}), followed by wetland, (0.82 g m^{-2} mm^{-1}), oasis edge, (0.70 g m^{-2} mm^{-1}), desert-oasis ecotone (0.65 g m^{-2} mm^{-1}), and sandy desert (0.26 g m^{-2} mm^{-1}) (Fig. 5A). This is consistent with the trend for *WUE* in terrestrial ecosystems of the southern United States (Tian et al., 2010) and the New South Wales of Australia (Zolfaghar et al., 2014). *GUE* showed the same trend (Fig. 5B), which can be ascribed to the difference in vegetation composition, distribution of roots, and interspecific competition. For example, the vegetation communities in riparian forest and wetland with a relatively shallow water table are more likely to contain functional groups with niche complementarity between species, which could improve *WUE*. Simultaneously, the main roots of shrubs exceeded 220 cm, which can access the groundwater and increase *GUE* with a shallower water table in riparian forest and wetland. Simultaneously, shrubs can facilitate understorey grass productivity is through hydraulic lift (Bruno et al., 2003; Ludwig et al., 2004), which may be an important water source to promote net primary productivity for neighboring plants, such as herb, and shallow root shrubs, etc (Caldwell et al., 1998; Horton and Hart, 1998).

RUE decreases across biomes as mean annual precipitation increases in almost all terrestrial ecosystems (Huxman et al., 2004; Bai et al., 2008; Yang et al., 2010). The RUE gradually increased along the groundwater gradient, and the value were significantly higher in the desert and desert-oasis ecotone than in the riparian forest, wetland and oasis edge (Fig. 4C, P < 0.05). However, all ecosystems of deserts, grasslands and forests exhibit the same RUE in years when water is most limiting, despite differences in phys-

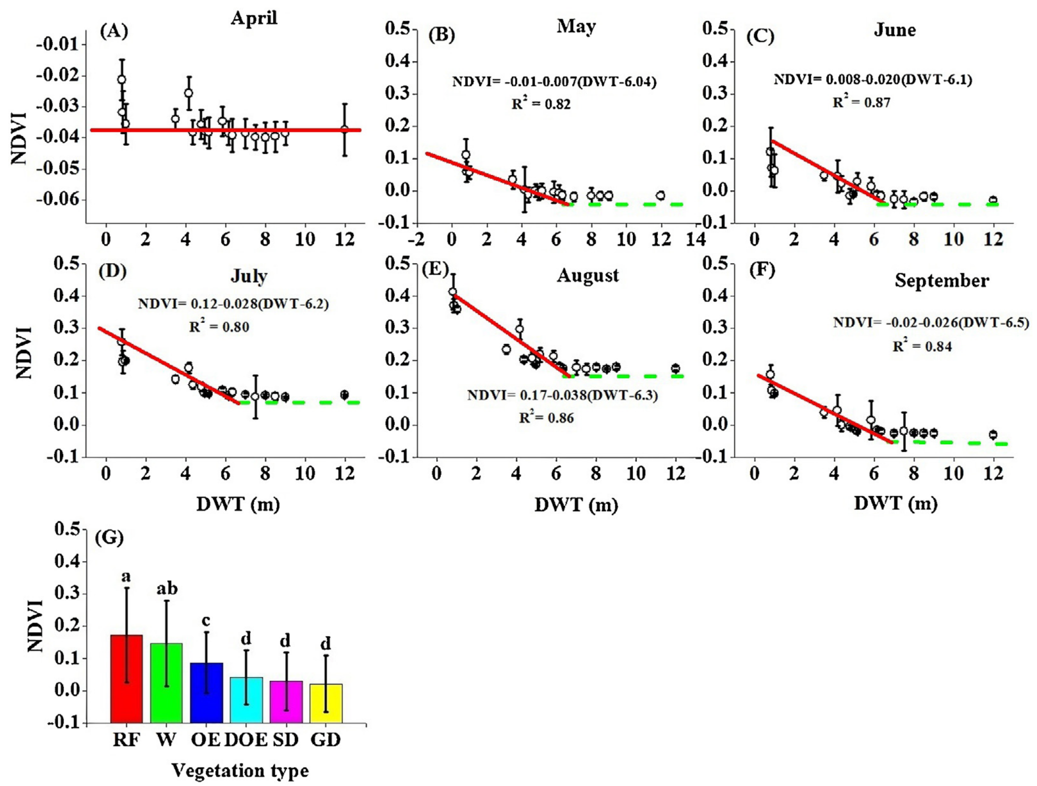

Fig. 3. The change of *NDVI* along a gradient of depth to the water table (*DWT*) during growing period. Vegetation cover types: RF, riparian forest; W, wetland; OE, oasis edge; DOE, desert-oasis ecotone; SD, sandy desert; and GD, gobi desert). Values (means ± SE) labelled with different letters differ significantly (Tukey's HSD, $P<0.05$). The curve regression were made when *DWT* is lower than 7 m. DWT_0 is an intersection between the slopes and the horizontal line that the *NDVI* is almost invariable.

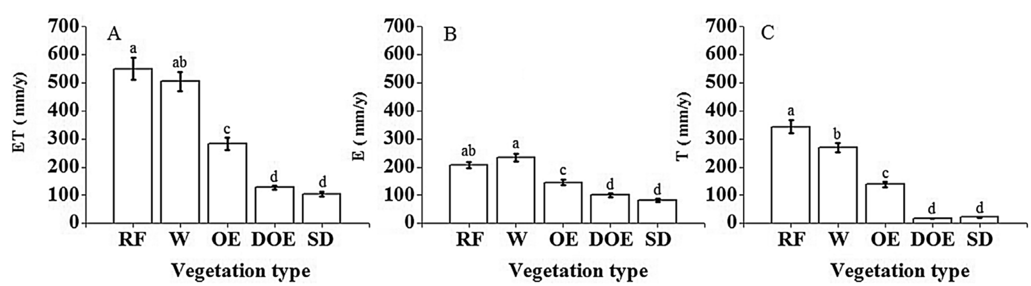

Fig. 4. The average annual (A) evapotranspiration (*ET*), (B) evaporation (*E*), and (C) transpiration (*T*) among vegetation cover types from 2010 to 2013. Values (means ± SE) in a graph followed by different letters differ significantly (Tukey's HSD, $P<0.05$). Vegetation types: RF, riparian forest; W, wetland; OE, oasis edge; DOE, desert-oasis ecotone; and SD, sandy desert).

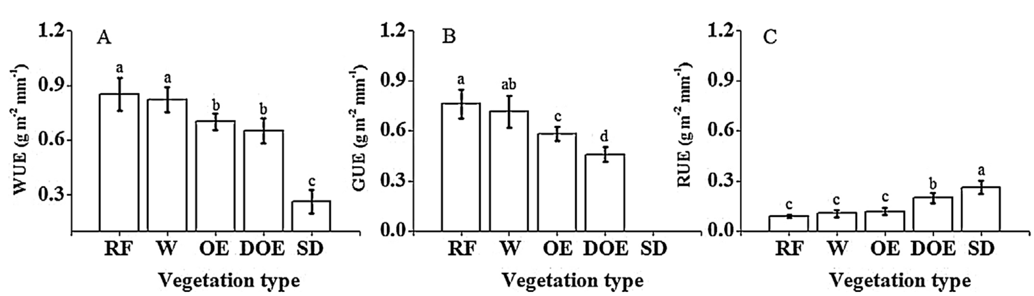

Fig. 5. The changes of the calculated (A) water-use efficiency (*WUE*), (B) groundwater-use efficiency (*GUE*), and (C) rainfall-use efficiency (*RUE*) among the vegetation types along the gradient of water table depth. *ANPP* was obtained from our developed model (for all vegetation types combined, $ANPP = 27.8\,e^{6.4\,NDVI}$, $R^2 = 0.74$, $n = 250$, $P < 0.001$). Vegetation types: RF, riparian forest; W, wetland; OE, oasis edge; DOE, desert-oasis ecotone; and SD, sandy desert.

iognomy and site-level RUE (Huxman et al., 2004). Therefore, *RUE* is a constant value of 0.26 g m^{-2} mm^{-1} at the sandy desert, where the groundwater is too deep to contribute to *ANPP*. This is much smaller than the reported *RUE* of 0.67 g m^{-2} mm^{-1} in arid ecosystems on the Inner Mongolia Plateau (Bai et al., 2008), but does not differ significantly from the value for degraded shrubland (0.27 g m^{-2} mm^{-1}) in western Australia (Holm et al., 2003).

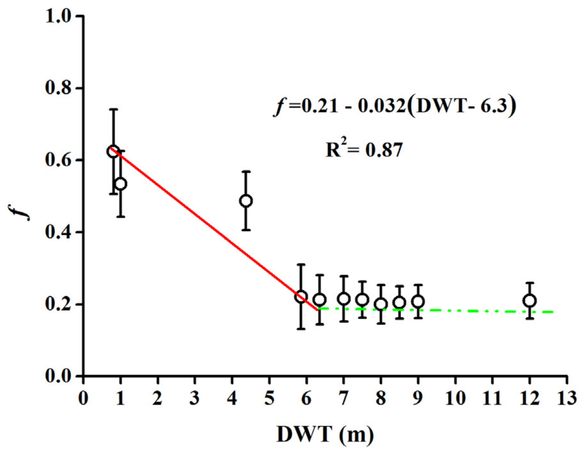

Fig. 6. Changes in the fraction of rainfall consumed by plants (*f*) along the depth of the water table (*DWT*).

4.3. The contribution of rainfall to plant transpiration

The *f* value, which represents the contribution of rainfall to T_P, responded strongly to the groundwater gradient and decreased with increasing *DWT* (Fig. 6, $R^2 = 0.87$, $P < 0.001$), but approached a constant value when *DWT* was greater than DWT_0 (6.3 m). The f_0 value was constant at 0.21, which means that 21% rainfall is used by vegetation for *ANPP* when groundwater is not available. Groundwater supports more vegetation to harvest rainfall for biological consumption where DWT is shallower than 6 m. In previous research, the contribution of rainfall accounted for 20–40% for *ANPP* (Huxman et al., 2004; Sala et al., 2012; Reichmann et al., 2013), but Hsu et al. (2012) found that it accounted for a lower proportion (16%) of the variation of *ANPP* in many terrestrial ecosystems.

5. Conclusions

In this study, we developed a method to estimate *WUE* and *GUE* and the proportion of rainfall used to support plant transpiration in GDEs in an arid region of northwestern China. We found that *the above ground primary production* decreased with increasing *DWT*, but approached a constant value when *DWT* was greater than 6.3 m. *WUE* and *GUE* gradually decreased with increasing *DWT*; *RUE* reached a constant value of 0.26 g m^{-2} mm^{-1} at the sandy desert, where groundwater no longer contributed to *ANPP*. The fraction of rainfall consumed by plants increases with a decreasing *DWT* from a threshold of 6.3 m, suggesting groundwater enhances rain use efficiency in GDEs.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (No. 41471024) and the key project of the National Natural Science Foundation of China (No. 41630861). We gratefully acknowledge funding from the China Scholarship Council and Flinders University, which supported the first author visiting research at Flinders University in Australia.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2016.12.003.

References

Bai, Y., Wu, J., Xing, Q., Pan, Q., Huang, J., Yang, D., Han, X., 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolian plateau. Ecology 89 (8), 2140–2153.

Beer, C., Ciais, P., Reichstein, M., Baldocchi, D., Law, B.E., Papale, D., Soussana, J.F., Ammann, C., Buchmann, N., Frank, D., Gianelle, D., Janssens, I.A., Knohl, A., Köstner, B., Moors, E., Roupsard, O., Verbeeck, H., Vesala, T., Williams, C.A., Wohlfahrt, G., 2009. Temporal and among-site variability of inherent water use efficiency at the ecosystem level. Global Biogeochem. Cycles 23 (2), 4184–4188.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18 (3), 119–125.

Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux for the roots of plants. Oecologia 113 (2), 151–161.

Conti, G., Díaz, S., 2013. Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. J. Ecol. 101 (1), 18–28.

Conti, G., Enrico, L., Casanoves, F., Díaz, S., 2013. Shrub biomass estimation in the semiarid Chaco forest: a contribution to the quantification of an underrated carbon stock. Ann. For. Sci. 70 (5), 515–524.

Dai, Z., Keating, E., Bacon, D., Viswanathan, H., Stauffer, P., Jordan, A., Pawar, R., 2014. Probabilistic evaluation of shallow groundwater resources at a hypothetical carbon sequestration site. Sci. Rep. 4 (6157), 1154–1158.

De Paola, F., Ranucci, A., 2012. Analysis of spatial variability for stormwater capture tank assessment. Irrig. Drain. 61 (5), 682–690.

Dwire, K.A., Kauffman, J.B., Brookshire, E.N.J., Baham, J.E., 2004. Plant biomass and species composition along an environmental gradient in montane riparian meadows. Oecologia 139 (2), 309–317.

Eamus, D., Froend, R., Loomes, R., Hose, G., Murray, B., 2006. A functional methodology for determining the groundwater regime needed to maintain the health of groundwater-dependent vegetation. Aust. J. Bot. 54 (2), 97–114.

Fan, Y., Miguez-Macho, G., Weaver, C.P., Walko, R., Robock, A., 2007. Incorporating water table dynamics in climate modeling: 1. Water table observations and equilibrium water table simulations. J. Geophys. Res. 112 (112), 676–684.

Fan, J.L., Oestergaard, K.T., Guyot, A., Lockington, D.A., 2014. Estimating groundwater recharge and evapotranspiration from water table fluctuations under three vegetation covers in a coastal sandy aquifer of subtropical Australia. J. Hydrol. 519 (PA), 1120–1129.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia 137 (2), 245–251.

Fischer, M., Trnka, M., Kučera, J., Deckmyn, G., Orság, M., Sedlak, P., Žalud, Z., Ceulemans, R., 2013. Evapotranspiration of a high-density poplar stand in comparison with a reference grass cover in the Czech-Moravian Highlands. Agric. For. Meteorol. 118, 43–60.

Furrer, R., Nychka, D., Sain, S., 2011. Smoothing Spline Regression (sreg), in Fields: Tools for Spatial Data, R Package Version 6.5.2. Inst. for Stat. and Math., Vienna, pp. 143–147, Available at http://cran.r-project.org.

Gong, P., Miao, X., Tate, K., Battaglia, C., Biging, G.S., 2004. Water table level in relation to EO-1 ALI and ETM+ data over a mountainous meadow in California. Can. J. Remote Sens. 30, 691–696.

Guswa, A.J., Celia, M.A., Rodriguez-Iturbe, I., 2004. Effect of vertical resolution on predictions of transpiration in water-limited ecosystems. Adv. Water Resour. 27 (5), 467–480.

Hickler, T., Fronzek, S., Araújo, M.B., Schweiger, O., Thuiller, W., Sykes, M.T., 2009. An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models. Glob. Ecol. Biogeogr. 18 (3), 304–313.

Holm, A., Watson, I., Loneragan, A., Adams, M., 2003. Loss of patch-scale heterogeneity on primary productivity and rainfall-use efficiency in Western Australia. Basic Appl. Ecol. 4 (6), 569–578.

Horton, J.L., Hart, S.C., 1998. Hydraulic lift: a potentially important ecosystem process. Trends Ecol. Evol. 13 (6), 232–235.

Hsu, J.S., Powell, J., Adler, P.B., 2012. Sensitivity of mean annual primary production to precipitation. Global Change Biol. 18 (7), 2246–2255.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens. Environ. 83 (1–2), 195–213.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E., Williams, D.G., 2004. Convergence across biomes to a common rain-use efficiency. Nature 429 (10), 651–654.

Kuglitsch, F.G., Reichstein, M., Beer, C., Carrara, A., 2008. Characterisation of ecosystem water use efficiency of European forests from eddy covariance measurements. Biogeosci. Discuss. 5 (2), 4481–4519.

Lauenroth, W.K., Burke, I.C., Paruelo, J.M., 2000. Patterns of production and precipitation use efficiency of winter wheat and native grasslands in the Central Great Plains of the United States. Ecosystems 3 (4), 344–351.

Lauenroth, W.K., 1979. Grassland primary production: North American grasslands in perspective. In: French, N.R. (Ed.), Perspectives in Grassland Ecology. Ecological Studies, vol. 32. Springer-Verlag, New York, pp. 3–24.

Li, S., Eugster, W., Asanuma, J., Kotani, A., Davaa, G., Oyunbaatar, D., Sugita, M., 2008. Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. J. Geophys. Res. 113 (G1), 777–793.

Liang, W., Yang, Y.T., Fan, D.M., Guan, H.D., Zhang, T., Long, D., Zhou, Y., Bai, D., 2015. Analysis of spatial and temporal patterns of net primary production and their climate controls in China from 1982 to 2010. Agric. For. Meteorol. 204, 22–36.
Liu, B., Zhao, W.Z., 2012. Photosynthetic response of two shrubs to rainfall pulses in desert regions of northwestern China. Photosynthetica 50 (1), 109–119.
Liu, B., Zhao, W.Z., Chang, X.X., Li, S.B., Zhang, Z.H., Du, M.W., 2010. Water requirements and stability of oasis ecosystem in arid region, China. Environ. Earth Sci. 59, 1235–1244.
Liu, B., Zhao, W.Z., Jin, B.W., 2011. The response of sap flow in desert shrubs to environmental variables in an arid region of China. Ecohydrology 4 (3), 448–457.
Liu, R., Pan, L.P., Jenerette, G.D., Wang, Q.X., Cieraad, E., Li, Y., 2012. High efficiency in water use and carbon gain in a wet year for a desert halophyte community. Agric. For. Meteorol. 162–163 (6), 127–135.
Liu, B., Zhao, W.Z., Zeng, F.J., 2013. Statistical analysis of the temporal stability of soil moisture in three desert regions of northwestern China. Environ. Earth Sci. 70, 2249–2262.
Liu, B., Zhao, W.Z., Wen, Z.J., Zhang, Z.H., 2014. Response of water and energy exchange to the environmental variable in a desert-oasis wetland of Northwest China. Hydrol. Process. 28 (2), 6098–6112.
Lowry, C.S., Loheide, S.P.I.I., 2010. Groundwater-dependent vegetation: quantifying the groundwater subsidy. Water Resour. Res. 46 (6), 666–669.
Lowry, C.S., Loheide II, S.P., Moore, C.E., Lundquist, J.D., 2011. Groundwater controls on vegetation composition and patterning in mountain meadows. Water Resour. Res. 47 (10), 896–898.
Ludwig, F., Dawson, T.E., Prins, H.H.T., Berendse, F., de Kroon, H., 2004. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. Ecol. Lett. 7 (8), 623–631.
Luo, Y., Sophocleous, M., 2010. Seasonal groundwater contribution to crop-water use assessed with lysimeter observations and model simulations. J. Hydrol. 389 (3), 325–335.
Lv, J.J., Wang, X.X., Zhou, Y.X., Qian, K.Z., Wan, L., Eamus, D., Tao, Z.P., 2013. Groundwater-dependent distribution of vegetation in Hailiutu River catchment, a semi-arid region in China. Ecohydrology 6 (1), 142–149.
Maxwell, R.M., Kollet, S.J., 2008. Interdependence of groundwater dynamics and land-energy feedbacks under climate change. Nature Geosci. 1 (10), 665–669.
McLendon, T., Hubbard, P.J., Martin, D.W., 2008. Partitioning the use of precipitation- and groundwater-derived moisture by vegetation in an arid ecosystem in California. J. Arid Environ. 72 (6), 986–1001.
McNaughton, S.J., Sala, O.E., Oesterheld, M., 1993. Comparative ecology of African and South American arid to subhumid ecosystems. In: Goldblatt, P. (Ed.), Biological Relationships Between Africa and South America. Yale University Press, New Haven, Connecticut, pp. 548–567.
Monclus, R., Dreyer, E., Villar, M., Delmotte, F.M., Delay, D., Petit, J.M., Barbaroux, C., Thiec, D., Bréchet, C., Brignolas, F., 2006. Impact of drought on productivity and water use efficiency in 29 genotypes of *Populus deltoides* × *Populus nigra*. New Phytol. 169 (4), 765–777.
Moreno-de las, M.L.H., Saco, P.M., Willgoose, G.R., Tongway, D.J., 2012. Variations in hydrological connectivity of Australian semiarid landscapes indicate abrupt changes in rainfall-use efficiency of vegetation. J. Geophys. Res.-Biogeosci. 117 (G3), 362–364.
Naumburg, E., Mata-Gonzalez, R., Hunter, R., Mclendon, T., Martin, D., 2005. Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. Environ. Manage. 35 (6), 726–740.
Newman, B.D., Wilcox, B.P., Archer, S.R., Breshears, D.D., Dahm, C.N., Duffy, C.J., McDowell, N.G., Phillips, F.M., Scanlon, B.R., Vivoni, E.R., 2006. Ecohydrology of water-limited environments: a scientific vision. Water Resour. Res. 42 (6), 376–389.
Niu, G.Y., Yang, Z.L., Dickinson, R.E., Gulden, L.E., Su, H., 2007. Development of a simple groundwater model for use in climate models and evaluation with gravity recovery and climate experiment data. J. Geophys. Res. 112 (D7), 277–287.
Niu, S.L., Xing, X.R., Zhang, Z., Xia, J.Y., Zhou, X.H., Song, B., Li, L.H., Wang, S.Q., 2011. Water-use efficiency in response to climate change: from leaf to ecosystem in a temperate steppe. Global Change Biol. 17 (2), 1073–1082.
Orellana, F., Verma, P., Loheide, I.I., Daly, S.P.E., 2012. Monitoring and modeling water–vegetation interactions in groundwater-dependent ecosystems. Rev. Geophys. 50 (3), 185–201.
Parsons, A.J., Abrahams, A.D., 1994. Geomorphology of desert environments. In: Abrahams, A.D., Parsons, A.J. (Eds.), Geomorphology of Desert Environments. CRC Press, Boca Raton, Fla, pp. 1–12.
Paruelo, J.M., Jobbágy, E.G., Sala, O.E., Lauenroth, W.K., Burke, I.C., 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecol. Appl. 8 (1), 194–206.
Reichmann, L.G., Sala, O.E., Peters, D.P.C., 2013. Precipitation legacies in desert grassland primary production occur through previous-year tiller density. Ecology 94 (2), 435–443.
Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A., 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81 (4), 501–505.
Sala, O.E., Gherardi, L.A., Reichmann, L.G., Jobbágy, E.G., Peters, D.P., 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. P. R. Soc. B 367 (1606), 3135–3144.
Scanlon, T.M., Albertson, J.D., 2004. Canopy scale measurements of CO_2 and water vapor exchange along a precipitation gradient in southern Africa. Global Change Biol. 10 (3), 329–341.
Scott, R.L., Hamerlynck, E.P., Jenerette, G.D., Moran, M.S., Barron-Gafford, G.A., 2010. Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. J. Geophys. Res. G: Biogeosci. 115 (G3), 494–494.
Scurlock, J.M.O., Johnson, K., Olson, R.J., 2002. Estimating net primary productivity from grassland biomass dynamics measurements. Glob. Change Biol. 8 (8), 736–753.
Soylu, M.E., Kucharik, C.J., Loheide II, S.P., 2014. Influence of groundwater on plant water use and productivity: development of an integrated ecosystem–variably saturated soil water flow model. Agric. For. Meteorol. 189–190 (6), 198–210.
Steed, J.E., DeWald, L.E., 2003. Transplanting sedges (*Carex* spp.) in southwestern riparian meadows. Restor. Ecol. 11 (2), 247–256.
Tian, H.Q., Chen, G.S., Liu, M.L., Zhang, C., Sun, G., Lu, C.Q., Xu, X.F., Ren, W., Pan, S.F., Chappelka, A., 2010. Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895–2007. For. Ecol. Manag. 259 (7), 1311–1327.
Webb, W., Szarek, S., Lauenroth, W.K., Kinerson, R., Smith, M., 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. Ecology 59 (6), 1239–1247.
Wu, J., Loucks, O.L., 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. Q. Rev. Biol. 70 (4), 439–466.
Wu, J.G., Jones, K.B., Li, H.B., Loucks, O.L., 2006. Scaling and Uncertainty Analysis in Ecology: Methods and Applications. Springer, Dordrecht, The Netherlands.
Yahdjian, L., Sala, O.E., 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. Ecology 87 (4), 952–962.
Yang, Y.H., Fang, J.Y., Fay, P.A., Bell, J.E., Ji, C.J., 2010. Rain use efficiency across a precipitation gradient on the Tibetan Plateau. Geophys. Res. Lett. 37 (15), 78–82.
Yang, Y.T., Long, D., Guan, H.D., Scanlon, B., Simmons, C.T., Jiang, L., Xu, X., 2014. GRACE satellite observed hydrological controls on interannual and seasonal variability of surface greenness over mainland Australia. J. Geophys. Res. Biogeosci. 119, 2245–2260.
Yang, Y.T., Donohue, R.J., McVicar, T.R., Roderick, M.L., 2015. An analytical model for relating global terrestrial carbon assimilation with climate and surface conditions using a rate-limitation framework. Geophys. Res. Lett. 42, 9825–9835.
Yang, Y.T., Donohue, R.J., McVicar, T.R., 2016a. Global estimation of effective plant rooting depth: implication for hydrological modeling. Water Resour. Res. 52, 8260–8276.
Yang, Y.T., Guan, H.D., Batelaan, O., McVicar, T.R., Long, D., Liang, W., Piao, S.L., Liu, B., Jin, Z., Simmons, C.T., 2016b. Contrasting responses of water use efficiency to drought across global terrestrial ecosystems. Sci. Rep. 6, 23284.
Yeh, P.J.F., Eltahir, E.A.B., 2005. Representation of water table dynamics in a land surface scheme, part I: model development. Climate 18 (12), 1861–1880.
York, J.P., Person, M., Gutowski, W.J., Winter, T.C., 2002. Putting aquifers into atmospheric simulation models: an example from Mill Creek Watershed, north-eastern Kansas. Adv. Water Resour. 25 (2), 221–238.
Yu, G.R., Song, X., Wang, Q.F., Liu, Y.F., Guan, D.X., Yan, J.H., Sun, X.M., Zhang, L.M., Wen, X.F., 2008. Water-use efficiency of forest ecosystems in eastern China and its relations to climatic variables. New Phytol. 177 (4), 927–937.
Zhao, W.Z., Liu, B., 2010. The response of sap flow in shrubs to rainfall pulses in the desert region of China. Agric. For. Meteorol 150, 1297–1306.
Zhao, W.Z., Liu, B., Chang, X.X., Yang, Q.Q., Yang, Y.T., Liu, Z.L., Cleverly, J., Eamus, D., 2016. Evapotranspiration partitioning, stomatal conductance, and components of the water balance: a special case of a desert ecosystem in China. J. Hydrol. 538, 374–386.
Zhu, L., Gong, H.L., Dai, Z.X., Xu, T.B., Su, X.S., 2015. An integrated assessment of the impact of precipitation and groundwater on vegetation growth in arid and semiarid areas. Environ. Earth Sci. 74 (6), 5009–5021.
Zolfaghar, S., Villalobos-Vega, R., Cleverly, J., Zeppel, M., Rumman, R., Eamus, D., 2014. The influence of depth-to-groundwater on structure and productivity of *Eucalyptus* woodlands. Aust. J. Bot. 62, 428–437.