Groundwater-dependent ecosystems: recent insights from satellite and field-based studies

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ABSTRACT

Groundwater-dependent ecosystems (GDEs) are at risk globally due to unsustainable levels of groundwater extraction, especially in arid and semi-arid regions. In this review, we examine recent developments in the ecohydrology of GDEs with a focus on three knowledge gaps: (1) how do we locate GDEs, (2) how much water is transpired from shallow aquifers by GDEs and (3) what are the responses of GDEs to excessive groundwater extraction? The answers to these questions will determine water allocations that are required to sustain functioning of GDEs and to guide regulations on groundwater extraction to avoid negative impacts on GDEs.

We discuss three methods for identifying GDEs: (1) techniques relying on remotely sensed information; (2) fluctuations in depth-to-groundwater that are associated with diurnal variations in transpiration; and (3) stable isotope analysis of water sources in the transpiration stream.

We then discuss several methods for estimating rates of GW use, including direct measurement using sapflux or eddy covariance technologies, estimation of a climate wetness index within a Budyko framework, spatial distribution of ET using remote sensing, groundwater modelling and stable isotopes. Remote sensing methods often rely on direct measurements to calibrate the relationship between vegetation indices and ET. ET from GDEs is also determined using hydrologic models of varying complexity, from the "White method" to fully coupled, variable saturation models. Combinations of methods are typically

employed to obtain clearer insight into the components of groundwater discharge in GDEs, such as the proportional importance of transpiration *versus* evaporation (e.g., using stable isotopes) or from groundwater *versus* rainwater sources.

Groundwater extraction can have severe consequences on structure and function of GDEs. In the most extreme cases, phreatophytes experience crown dieback and death following groundwater drawdown. We provide a brief review of two case studies of the impacts of GW extraction and then provide an ecosystem-scale, multiple trait, integrated metric of the impact of differences in groundwater depth on the structure and function of eucalypt forests growing along a natural gradient in depth to groundwater. We conclude with a discussion of a depth-to-groundwater threshold in this mesic GDE. Beyond this threshold, significant changes occur in ecosystem structure and function.

1 Introduction

Water stored belowground in the saturated zone (groundwater) is the largest global store of liquid freshwater, accounting for about 96 % of all liquid freshwater (Shiklomanov 2008). Whilst readily accessed by humans for millennia at naturally occurring springs/oases and as baseflow discharge into rivers, it has only been during the past 100 years that exploitation of groundwater resources has become of global concern (Gleick and Palaniappan 2010). The rate of groundwater use of three (Pakistan, Iran and Saudi Arabia) of the seven largest users of groundwater (India, the USA, Pakistan, China, Iran, Mexico and Saudi Arabia) use groundwater at an annual rate that exceeds the renewable resource volume (Giordano 2009). Only three of the top 10 users are OECD members, reflecting the large reliance on groundwater of less developed nations, which are often located in arid and semi-arid climates where surface water stores are generally low.

About two fifths of the world’s terrestrial surface area is arid or semi-arid and more than 38 % of the world’s population lives there. Managing groundwater resources sustainably is therefore a major global social and economic priority (Glazer and Likens 2012). Whilst about 40 % of global groundwater abstraction occurs in these regions, the scarcity of rain means that only 2 % of groundwater recharge occurs there (Wada et al., 2010). Water is increasingly becoming a geopolitical and strategic resource. Disputes between neighbouring states are increasing as demands for groundwater increase. Because of the close relationship between crop yield and water supply, diminishing availability of groundwater in arid and semi-arid regions has immediate and severe impacts on food supplies, food prices and concomitant social unrest. Recent estimates suggest that between 10 and 25 % of the food produced in China and India (home to 2.5 billion people) is at risk because of groundwater depletion (Seckler et al., 1999; Brown 2007).

Over extraction of groundwater stores can create several problems. These include: loss of discharge from groundwater to wetlands, springs and streams/rivers, which results in loss of ecosystem structure and function and the associated loss of ecosystem services (Eamus et al., 2006a; Murray et al., 2006); increased depth of groundwater, thereby reducing its availability within the root zone of terrestrial groundwater-dependent vegetation; reduced availability of groundwater for direct human consumption; and reduced availability of groundwater for commercial use, including irrigation, stock watering and other industrial applications.

In a recent wide-ranging review of GDEs, Orellana et al., (2012) identified quantification of the water used by GDEs and an understanding of the physiology of GDEs as major unresolved problems. Naumburg et al., (2005) provide a review of the impact of both declining and increasing depth to the water table on phreatophytic vegetation in arid zones and provide two conceptual models describing ecosystem responses to these changes in depth. They note that information on root depth and the impact this may have on responses to changes in depth-to-groundwater as a key knowledge gap. In this current review we discuss application of remote sensing techniques to quantify rates of water use of GDEs. We present ecophysiological responses of vegetation to differences in groundwater availability in two case studies plus the results of a four year ecophysiological study of eucalypt woodlands across a natural gradient in depth-to-groundwater in a mesic environment. From this last study we produce an integrated response metric for the response of these woodlands to differences in groundwater depth.

Whilst Hatton and Evans (1998) recognised five classes of ecosystem dependency on groundwater, we use the simplified classification system proposed by Eamus et al., (2006b):

(Class I) *Aquifer and cave ecosystems where stygofauna reside*. This class also includes the hyporheic zones of rivers and floodplains.

(Class II) *Ecosystems reliant on the surface expression of groundwater*. This includes springs, estuarine seagrasses, and base-flow rivers, streams and wetlands.

(Class III) *Ecosystems reliant on sub-surface presence of groundwater within the rooting depth of the ecosystem* (usually via the capillary fringe).

Application of this simple classification scheme assists managers in identifying the correct techniques for assessing GDE structure, function and management regime (Eamus et al., 2006b), and this classification scheme was recently adopted in the Australian National Atlas of Groundwater-Dependent Ecosystems.

In this review, we focus on the ecohydrology of groundwater-dependent ecosystems rather than on groundwater resources *per se*. This is because we feel that environmental allocations of groundwater have generally received less attention than allocations to human demands and because we identify three important knowledge gaps to the sustainable management of groundwater for environmental allocations. These are:

1. How do we know where a groundwater-dependent ecosystem (GDE) is in the landscape? If we don’t know where they are, we can’t manage them and allocate groundwater resources appropriately.

2. How much groundwater is used by a GDE? If we don’t know how much groundwater is used, we cannot allocate an appropriate quantity of the resource.
3. What are the likely responses of GDEs to over extraction of groundwater? Without knowing what to measure, we cannot regulate groundwater extraction in ways that do not negatively impact on GDEs.

2 Identifying groundwater dependent vegetation

Identifying the location of GDEs is the first requisite step to managing them. However, identifying their location across a landscape is difficult, time-consuming, expensive and requires a high level of technical expertise. In this section, a range of new techniques that can be used to assist in this are discussed.

2.1 Methods to identify GDEs: indirect inference

Early assessments of groundwater dependency generally relied on inference (Eamus et al., 2006a; Clifton and Evans 2001). Recent applications of inferential techniques to springs, wetland, rivers and lakes can be found in Brown et al., (2011) and to springs, wetlands and streams reliant on baseflow in Howard and Merrifield (2010) and are not further discussed here.

2.2 Direct methods

2.2.1 Satellite based approaches

In recent years remote sensing (RS) of land surfaces and vegetation structure (e.g. phenology, LAI) and function (e.g. ET, gross primary productivity) has become increasingly sophisticated (Glenn et al., 2010; Yuan et al., 2010; Jung et al., 2011; Rossini et al., 2012; Kanniah et al., 2013; Ma et al., 2013; Nagler et al., 2013) and increasingly applied to real-world applications of water resource management (Scott et al., 2008; Glenn et al., 2010; Barron et al., 2014; Doody et al., 2014). Remote sensing (RS) provides a robust and spatially explicit means to assess not only vegetation structure and function but also relationships amongst these and climate variables.

A key concept in the development of RS applications for identifying the location of GDEs is that of “green islands” (Everitt and DeLoach, 1990; Everitt et al., 1996; Neale, 1997; Akasheh et al., 2008), which began with the airborne observations of desert oases and riparian corridors. In this model the structure or function of one pixel in an RS image is compared to that of another pixel located nearby. If one pixel contains a GDE but the other does not, the hypothesis that the structure and function of vegetation in the two pixels will diverge during extended dry periods can be tested. The underlying assumption is that vegetation with access to groundwater will not be subject to the same degree of soil water deficit as vegetation that does not have access to groundwater, thus the spectral signature of the two pixels will diverge over time. By comparing vegetation structure or function across contrasting periods (e.g., comparisons across “wet” and “dry” periods) or across landscapes (e.g., comparisons from riverside to upland pixels), green islands within a sea of browning vegetation can be identified (Contreras et al., 2011)

Munch and Conrad (2007) used Landsat imagery to identify the presence/absence of wetlands across three catchments in South Africa. They combined this with GIS terrain modelling to determine whether GDEs could be identified using a landscape “wetness potential” for class II GDEs (those reliant on a surface expression of groundwater). They concluded that RS data could be used to classify landscapes by comparing the attributes of potential GDEs to the attributes of surrounding land covers during three periods: in July when rains started at the end of a dry year; in August during the winter of a wet year; and at the end of a dry summer. When this was combined with a GIS model using landscape characteristics, they were able to produce a regional-scale map of the distributions of GDEs.

Plant density is often correlated with water availability, especially in arid and semi-arid regions. Thus, plant density tends to be larger when groundwater is available than in nearby vegetation that does not have access to groundwater. Lv et al., (2012) used a remotely sensed vegetation index (normalised difference vegetation index; NDVI; 300 m resolution) to examine changes in depth-to-groundwater within a small region in northern China. NDVI is a reliable measure of the chlorophyll content (“greenness”) in leaves and vegetation cover (Gamon et al., 1995; Carlson and Ripley, 1997; Huete et al., 2002). Using a 25 m resolution digital elevation model and groundwater bore data, the resultant relationship between NDVI and depth-to-groundwater was obtained (Fig. 1).

Fig 1 here

Similar in shape to the relationship between LAI and NDVI, the largest values of NDVI occurred at sites with shallow groundwater and declined curvi-linearly as depth-to-groundwater increased. In that study, a cut-off of approximately 10 m depth-to-groundwater was identified below which vegetation cover was relatively insensitive to further increase in groundwater depth. In contrast, the threshold was about 4.4 m depth-to-groundwater in the Ejina area of NW China (Jin et al., 2011). In their study, which included part of the Gobi desert where annual rainfall was about 40 mm, vegetation was absent in regions where groundwater depth exceeded 5.5 m. They also used NDVI and 13 groundwater bores, from which relationships between NDVI and groundwater depth for three vegetation classes (grassland, woodland and scrubland) were established. Maximal values of NDVI occurred at sites with intermediate (2.5 – 3.5 m) depth-to-groundwater rather than at sites with shallower groundwater, a result often ascribed to the effect of anoxia arising from root flooding when the water table is too shallow (Naumburg et al., 2005).

Geological, hydrological and ecological data can be used to define areas that have common physical and climatic profiles. These regions are expected to have similar vegetation cover (assuming no management has induced significant changes), thus such areas are expected to have a similar RS signature. Dresel et al., (2010) applied this approach for individual regions in South Australia by developing a correlation analysis using Landsat summer NDVI and MODIS enhanced vegetation index (EVI) as surrogate measures of productivity. EVI is effective for scaling productivity across the range of global ecosystem types (Campos et al., 2013). MODIS EVI images were used to identify regions displaying a consistent photosynthetic activity throughout the year. Landsat NDVI images were then used to locate areas displaying large inter-annual variation in photosynthetic activity across wet and dry years, which were identified by aridity thresholds that were calculated from the Thornthwaite index. Finally, they used an unsupervised classification of Landsat spectral data to locate pixels with similar spectral signatures of areas corresponding to known groundwater-dependent ecosystems. Species-specific differences in spectral signatures have been identified previously (Nagler et al., 2004). By combining all three sources of information (geological, hydrological and ecological) within a GIS, Dresel et al., (2010) identified all pixels across a catchment that had a very high probability of being a GDE. Critical for providing assurance of accurate mapping, ground reconnaissance ("truthing") was used to validate these findings.

Mapping of groundwater discharge zones (that is, discharge through transpiration and to the ground surface) provides an alternative approach to finding GDEs. Discharge of groundwater has a large effect on local ecology. To define the spatial extent of discharge, information is required about the geology, hydrology, ecology and climate of a site (Tweed et al., 2007). By using thermal, Landsat optical and MODIS NDVI data coupled to digital elevation models and depth-to-groundwater data, Leblanc et al., (2003a, b), located discharge areas in semi-arid Lake Chad basin in Africa. Similarly Tweed et al., (2007) examined discharge (and recharge) of the Glenelg-Hopkins catchment in SE Australia. Discharge occurred through direct evaporation from the water table (i.e., groundwater evaporation); groundwater transpiration; and discharge to the ground surface at landscape depressions, rivers, wetlands and break-of-slope localities. Importantly, they observed low variability of vegetation activity across wet and dry periods (seasons or years) using the NDVI as a measure of vegetation. In this case, the variability in NDVI was correlated with locations where groundwater was supporting vegetation activity. One possible limitation to this method is that it tends to be most accurate in more xeric locations, where rainfall is more likely to limit vegetation function, except during extended droughts.

2.2.2 Fluctuations in groundwater depth

When rooting depth is sufficient, vegetation can directly access the water table via the capillary zone of shallow unconfined aquifers. In some circumstances groundwater uptake by vegetation can be seen as a diel fluctuation in the depth-to-groundwater (Miller et al., 2010), as first identified in groundwater hydrographs by Walter White (1932). These daily fluctuations in depth-to-groundwater cease when the water table falls below the rooting zone (Butler et al., 2007) or when vegetation is dormant (Lautz, 2008; Martinet et al., 2009; Miller et al., 2010). However, changes in the density of water with temperature can cause expansion and contraction of an aquifer (Post and von Asmuth, 2013), leading to the erroneous conclusion that the vegetation is accessing groundwater. Additionally, when the water table is very shallow direct evaporation from groundwater via bare soil can be substantial (1–10 mm d^{-1}) (Thorburn et al., 1992) and this may also be misinterpreted. Thus, groundwater dependency generally requires supporting confirmation from multiple indicators and cannot be identified definitively from the "White method" alone. Further elaboration of the White method is given in section 3.5.1 and described in detail in Orellana et al., (2012).

2.2.3 Stable isotope analysis

Direct evidence that vegetation is using groundwater can be obtained by comparing the stable isotope composition of groundwater, soil water, surface water (if relevant) and xylem water (Thorburn et al., 1993; Zencich et al., 2002; Lamontagne et al. 2005; O'Grady et al., 2006a, b; Kray et al., 2012; Busch et al., 1992; Ehleringer and Dawson, 1992; Smith et al., 1998). This method is very effective in semi-arid regions where groundwater is derived from snowmelt or winter precipitation (which is isotopically lighter than summer precipitation) (Ehleringer and Dawson, 1992; Smith et al., 1998; Jobbagy et al., 2011). When sufficient differences in isotopic composition exist among sources of water, the dominant source used by different species at different times of year can be identified (Zencich et al., 2002).

An example of deuterium isotope analysis of water collected from xylem, soil, river and groundwater is shown in Table one. Species growing close to groundwater (*Melaleuca argentea*) have xylem isotope compositions close to that of groundwater but species growing further upslope away from the river had xylem isotope compositions close to that of soil water isotope. Further examples include: a) identification of soil and surface water use by juvenile riparian plants, in contrast to groundwater use by mature trees (Dawson and Ehleringer, 1991); and b) determination of the mountainous source of groundwater and opportunistic use of that groundwater by riparian trees (Chimner and Cooper, 2004).

Mixed-member models (i.e., "Keeling plots") can be applied to allow estimation of the relative contribution of multiple sources of water to the water absorbed by roots (Phillips and Greg 2003). While it is possible for a linear mixing model to distinguish more than two potential sources of water, such an application requires the fractionation of ^{2}H or ^{18}O to be independent of each other, which is often not the case. At a minimum, the use of stable isotopes can provide information about spatial and temporal variation in groundwater dependency across species and ecosystems. Application of stable isotope analyses to quantify the rate of water use is discussed later (Section 3.5.2).

Table 1 here

3 Application of remote sensing to the study of GDEs

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3.1 A primer on remote sensing derived values of rates of water flux

Before discussing the application of RS techniques to estimate rates of groundwater use by vegetation, we will provide a simple summary of the principles of using RS to estimate ET more broadly. For a detailed and comprehensive evaluation of these methods, refer to Glenn et al., (2007). Table 2 provides examples of recent studies that have used RS in the study of GDEs.

The energy balance equation for land surfaces is:

$$LE + H = R_n - G \qquad (1)$$

where LE is latent energy flux (ET), H is sensible heat flux. R_n is net radiation and G is soil heat flux. Differences in temperature between air temperature and canopy temperature have been used to estimate sensible heat flux (Glenn et al., 2010). Using the reasonable assumption that G averages out to zero over any single 24-hour period and R_n is either measured or derived from remote sensing data, then LE (that is, ET) can be calculated by difference.

Table 2 here

Li and Lyons (1999) compared three methods that use surface temperatures to estimate ET. In two methods, differences in surface and air temperature were used to estimate ET, although the two methods differed in the details of the aerodynamic resistance functions. The third model combined NDVI, surface temperature and a soil-adjusted vegetation index that required the four extreme values of surface temperature and NDVI to be located simultaneously within the study area (i.e., patches of dry bare soils; wet bare soil; wet, fully vegetated patches; and dry, water stressed, fully vegetated surfaces). This can make its application problematic. Two methods used the energy balance equation to estimate ET, whereas ET was estimated in a third by using RS data to estimate the Priestley-Taylor factor that scales between ET and potential ET (ET_p). They concluded that the simplest first and second models produced better estimates of ET and that inclusion of the soil index improved the estimates of ET from native (i.e., non-agricultural) vegetation. Likewise, Nagler et al., (2005a) found that estimates of ET from riparian corridors using RS were improved with the incorporation of a soil index.

3.2 Estimating groundwater use by remote sensing

Quantifying the water balance of arid and semi-arid landscapes and aquifers is important to sustainably manage water resources. Accurate and spatially distributed estimates of discharge through vegetation are difficult to obtain through field measurements. Recently, RS methods have been calibrated against Penman-Monteith estimates of ET (Glenn et al., 2010; Nagler et al., 2013; Doody et al., 2014), which requires only standard weather data (net radiation, wind speed and vapour pressure deficit) and thus increases the coverage of calibration sites. Because ET in GDEs is generally not limited by soil moisture when groundwater is of high quality (i.e. not saline), it is assumed that actual ET rates are equivalent to the ET of a reference grass crop (i.e., reference ET, ET_0), as computed following FAO-56 (Allen et al., 1998). Then, normalised VIs, either EVI* or NDVI*, can be used like crop coefficients to estimate the spatial distribution of ET_a from ET_0 on a per-pixel basis. Nagler et al., (2013) used an exponential scaling function of EVI* to estimate ET_a:

$$ET_a = ET_0\left(a\left[1 - e^{-b\ EVI^*}\right] - c\right) \qquad (4)$$

Similarly, Groeneveld and Baugh (2007) found that this methodology is particularly applicable to arid and semi-arid vegetation underlain by a shallow water table. In arid and semi-arid regions, annual rainfall is low and often erratic. Consequently, the presence of a shallow water table results in a relatively consistent supply of water to roots. NDVI* was calculated from summer peak season NDVI (Groeneveld and Baugh 2007):

$$NDVI^* = \left(NDVI - NDVI_z\right) \big/ \left(NDVI_m - NDVI_z\right) \qquad (5)$$

where $NDVI_z$ and $NDVI_m$ are the NDVI values for zero vegetation cover and NDVI at saturation, respectively. Although selection of the values for $NDVI_z$ and $NDVI_m$ can introduce uncertainty, Groeneveld and Baugh (2007) found significant convergence in the NDVI by removal of non-systematic scatter in the data. Calibration of ET in the field is not required to apply this method but it is necessary to define $NDVI_m$. This requires highly verdant pixels in the RS images, arising either from irrigation or the presence of, for example, riparian vegetation that maintains a large LAI. At mesic sites, defining $NDVI_z$ may also be difficult. Despite these problems, Groeneveld and Baugh (2007) were able to disaggregate the influence of groundwater supply from that of recent rainfall.

Groeneveld et al., (2007) applied this NDVI* methodology to three arid sites in the US where annual ET_a values were available through the availability of Bowen ratio or eddy covariance measurements. A significant linear relationship ($R^2 = 0.94$) was found between measured annual ET_a and mid-summer NDVI*, despite very different vegetation composition and structure across those sites. However, the regression of ET_a/ET_0 *versus* NDVI* did not pass through the origin and would introduce an offset error if NDVI* were used to estimate ET_a. To overcome this, Groeneveld et al., (2007) transformed ET_a to ET_a*:

$$ET_a{}^* = \left(ET_a - \text{rainfall}\right) \big/ \left(ET_0 - \text{rainfall}\right) \qquad (6)$$

The resulting regression of ET_a* *versus* NDVI* yielded a slope of 0.97, an intercept of zero and an R^2 of 0.96. They concluded that NDVI* was a reliable indicator of ET_a*. Re-arranging the equation above and substituting NDVI* for ET_a*, they demonstrated that:

$$ET_a\left(\text{estimated}\right) = \left(ET_0 - \text{ rainfall}\right)\text{NDVI}* + \text{rainfall} \qquad (7)$$

They estimated the amount of groundwater transpired (ET_g) by deducting annual rainfall from annual ET_a. That is, ET_g = (ET_0 – rainfall) NDVI*. The average error in ET_g was estimated to be about 12 %, which in the absence of field measurements is a very valuable estimate of rates of groundwater use. Further application of the Groeneveld et al., (2007) method can be found in Groeneveld (2008).

3.2.1 Up-scaling from point to larger-scale estimates of ET

Riparian vegetation is often reliant on groundwater (either through bank recharge or direct access to the shallow water table), especially in arid and semi-arid regions. Rates of ET are enhanced by groundwater use in dry environments (Cleverly 2013), where riparian ET is a large component of the water balance (Dahm et al., 2002; Scott et al., 2008). However, measurement of the riparian ET component depends upon the physical characteristics of the riparian corridor. If a riparian corridor is sufficiently wide, eddy covariance can be used to directly measure ET (Cleverly 2013). Where the corridor is insufficiently wide, tree-scale sapflow techniques can be used (O'Grady et al., 2006)(Goodrich et al., 2000b). Combinations of both methods (Moore et al., 2008; Oishi et al., 2008) can be used to partition transpiration from evapotranspiration (Scott et al., 2006a), thereby estimating the proportion of ET due to transpiration from groundwater with the condition that groundwater evaporation is negligible.

RS methods are used to expand from measurements of ET at discrete locations to the large-scale that is required by resource managers. In two studies, (Nagler et al., 2005a; Nagler et al., 2005b)MODIS EVI and maximum daily air temperatures (from MODIS land surface temperature LST) were used to derive an empirical estimate of riparian ET for the San Pedro River and Middle Rio Grande of the USA (Nagler et al., 2005a; Nagler et al., 2005b). Their equations for daily ET were:

$$ET = a\left(1 - e^{-b\ \text{EVI}*}\right)\left(c \big/ \left[1 + e^{-\left\{T_a - d/e\right\}}\right]\right) + f \qquad \text{(Middle Rio Grande) and} \qquad (2)$$

$$ET = a\left(1 - e^{-b\ \text{EVI}*}\right)\left(\text{LST} - c\right) + d \qquad \text{(both rivers)} \qquad (3)$$

where a, b, c, d, e and f are regression constants derived by regression analysis, T_a is air temperature derived from MODIS LST retrievals, and EVI was normalised to obtain EVI* .

Strong correlations between EVI*, T_a and ET were observed and used to provide scaled estimates for larger areas of vegetation. Despite this being an empirically derived equation from a single study, the form of the equation appears to be relatively robust across catchments (Nagler et al., 2005b). Similarly, Scott et al., (2008) and Nagler et al., (2009) applied these equations (Nagler et al., 2005a; Nagler et al., 2005b) in which they used MODIS-derived nocturnal surface temperature and daily maximal air temperature, respectively. In the regression between ET derived from RS and EC methods, the coefficient of determination (R^2) was larger than 0.93 during all three years of study and across three vegetation types (grassland, shrubland and woodland), thereby indicating the broad applicability of this method. Thus, this method has the ability to (a) scale from point measurements using individual EC towers to much larger areas; and (b) estimate the difference between annual rainfall and ET and, where ET > rainfall, estimate vegetation groundwater use.

3.3 Gravity recovery and climate experiment (GRACE) for detecting changes in total terrestrial water storage

In addition to remote sensing measures of ET anomalies or NDVI green islands, there are also new satellite sensors and techniques that provide estimates of groundwater fluctuations and soil moisture storage changes that are of value to the study of GDE's (Brunner et al., 2007). The twin satellites known as the Gravity Recovery and Climate Experiment (GRACE) were launched in 2002 for the purpose of making detailed measurements of Earth's gravity field (Tapley et al., 2004). Although Earth's gravity variations tend to be relatively constant over long time intervals, more dynamic, time-variable gravity fields can be detected and these have been related to land surface moisture, ground water fluctuations, sea ice, sea level rise, and deep ocean currents. GRACE's ability to monitor changes in such "unseen water reserves" from space are a significant new addition to hydrological studies that can substantially improve our knowledge of below- and aboveground water resources and associated changes to vegetation functioning and GDE's. However, GRACE is not able to estimate rates of actual groundwater-use by GDEs.

Comment [u2]: New text to explain GRACE is NOT about estimating rates o water use by GDEs

Technically, the GRACE satellites detect changes in the Earth's gravity field by monitoring the changes in distance between the two spacecraft as they orbit Earth. The relative distance will change in response to variations in the Earth's mass, including changes in mass of both above- and below-ground water reservoirs (groundwater, soil moisture, snow, ice, and surface waters). The GRACE satellite data directly measures changes in total water storage (TWS) and not changes of the individual hydrologic components (e.g., surface water, soil moisture, and groundwater). Groundwater storage changes from GRACE are thus inferred by isolating and removing the contributions of all other TWS components, using either independent hydrologic datasets and/or land surface models.

In most cases, soil moisture becomes the sole component that must be removed from the gravity data to estimate groundwater changes, since variability of snow and surface water is relatively insignificant to total water storage variability. By subtracting the soil moisture contribution, the remaining time-variable change in GRACE’s measure of total water storage will be due to changes in groundwater. Thus:

$$DTWS = DSW + DSM + DGW \qquad (8)$$

Where ΔTWS, ΔSW, ΔSM and ΔGW are changes in total water store, soil moisture,

Many studies have compared changes in groundwater storage obtained from GRACE data with in situ data for validating the accuracy of GRACE data at either regional or continental scales (Henry et al., 2011; Leblanc et al., 2009 ; Rodell et al., 2009, 2007; Scanlon et al., 2012a,b; Syed et al., 2009).

GRACE is not a way to measure exact water storage amounts from space and cannot be used to measure how much water is stored in a river basin at a particular instant in time. Instead, gravity information is used to assess relative changes in water storage over large areas at monthly, seasonal or annual time steps. Seasonal changes in water storage may be the easiest to detect using the GRACE technique because such changes tend to be large.

In general, GRACE data are more accurate for large areas over long time intervals. For example, GRACE can detect seasonal and annual changes in water storage over large areas- and can detect month-to-month changes over entire river basins (of the order of millions of square kilometers). Presently, GRACE can confidently detect water storage changes in areas larger than 200,000 square kilometers.

Rodell and Famiglietti (2001) showed that GRACE data can estimate annual groundwater change over the High Plains, USA within about 8.7 mm of their actual value. This level of accuracy may not always be an improvement for well-sampled and instrumented aquifers, but for most places in the world, estimates of water levels within a centimeter or less are extremely valuable and will help reveal groundwater depletion in areas of the world where such measurements are not systematically recorded.

Despite these coarse scales, such information can be extremely useful for water resource managers, especially as GRACE data continues to be refined to provide improved estimates of groundwater fluctuations and depletion. Regional monitoring of groundwater levels is limited by the lack of ground-based measurements and the lack of a sufficiently extensive network of monitoring wells. Thereby, the GRACE technique offers an objective, unbiased method for monitoring water storage changes at large scales.

Although many advances in TWS monitoring have been made using GRACE data, the practical application of GRACE data for local water resources management has been limited by the low spatial (>150,000 km^2) and temporal (>10 days) resolution of GRACE measurements and by difficulties in disaggregating the various TWS components (Rodell et al., 2007). There is a trade-off between coarse spatial resolution and accuracy, and it remains to be determined whether better spatial resolutions can be achieved without degrading or increasing the uncertainties. However, Houborg et al., (2012) show the potential value of

GRACE data to significantly improve drought prediction capacity through assimilation of these data into the Catchment Land Surface Model using ensemble Kalman smoother and forcing data from North American and Global Land Data Assimilation Systems Phase 2 (NLDAS-2). Similarly, Sun et al., (2012) imposed GRACE observations as constraints when recalibrating a regional-scale groundwater model, further highlighting the value of GRACE data to the study of groundwater and GDEs.

3.3.1 Downscaling of GRACE

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To fully realize the potential of GRACE data for hydrological applications, downscaling, both in space and time are required. This will enable better predictions of changes in groundwater level (Houborg et al., 2012). Sun et al., (2013) explored various downscaling techniques for GRACE data for useful predictions of changes in water level. They developed artificial neural network (ANN) model schemes to predict such changes directly by using a gridded GRACE product and other publicly available hydrometeorological data sets. Their statistical downscaling approach can be readily integrated into local water resources planning activities, especially in the absence of continuous in situ groundwater observations. They noted that downscaled GRACE data could potentially fill the gap created by the declining coverage of in situ groundwater monitoring networks and ‘index’ wells used to gauge the wellbeing of aquifers.

3.3.2 Groundwater depletion studies and GRACE

Comment [u4]: Added some words
to clarify

GRACE satellite data have been used to estimate groundwater depletion associated with severe droughts in Europe, U.S., China, and India (LeBlanc et al., 2009; Rodell et al., 2009). Groundwater pumping of aquifers often increases during severe droughts for urban, agriculture, livestock, and industry needs. This results in the decline of groundwater levels and the decrease of ground-water discharge to springs, surface water bodies and riparian zones (Peters et al., 2003). Leblanc et al., (2009) attempted to attribute groundwater loss during the recent drought in Murray-Darling Basin in Australia to groundwater pumping. However, they found that the pumping rate represented only less than 10% of the decline rate in groundwater storage as observed by GRACE from 2003 to 2008 (Fig. 2). They concluded that the observed decline is mostly be explained by reductions of groundwater recharge and the vast amount of groundwater transpired during the drought by the widespread presence of deep rooted trees (GDEs) as well as capillary rise from the saturated to the unsaturated zone.

Fig 2 here

3.4 Remote sensing limitations and challenges in studies of GDEs

Comment [u5]: Heading numbering changed

Remote Sensing applications in studies of GDEs vary greatly, from basic detection, mapping, and monitoring of GDEs to more complex and quantitative measurements of ET, functioning, and energy and water balance. In most cases, mapping of GDE locations at appropriate management scales is prerequisite to more detailed studies, such as groundwater assessments that may require accurate estimates of ET (Gou et al., 2015).

Regardless of the application, there will be certain limitations in the use of remote sensing that need to be considered. Other geospatial data sources will often need to be integrated to make the best use of remote sensing, including climate, soils, landscape morphology, and ecologic data layers that will enable potential areas for GDEs to be delineated (Bertand et al., 2012). Multiple sensors and image data sets are best suited for studies of GDEs because of the inherent spectral-spatial-temporal limitations of single sensor systems. For example the use of fine spatial resolution Landsat (30 m) and high temporal frequency MODIS data (1-2 day) allow us to identify potential GDE vegetation patches (Landsat) and track changes in their seasonal and inter-annual dynamics (MODIS spectral vegetation indices, VIs). Thus, vegetated areas that maintain high VI 'greenness' values during extended dry periods can be flagged as '*high GDE potential*', under the premise that GDEs exhibit low seasonality in greenness and ET between dry and wet seasons and low inter-annual variability across years.

However, many ecosystems may contain trees and shrubs that are non-GDE yet also exhibit weak seasonality and inter-annual variation due to their evergreen phenologies. In these mixed tree- grass landscapes, seasonal variability follows the very dynamic herbaceous grass layer that is strongly coupled to rainfall rather than groundwater availability. The stronger seasonality present in the grass layer can readily mask GDE signals from the tree layer and confuse GDE detection. This "mixed-pixel" problem restricts many remote sensing applications, particularly when the matrix background of an area with GDEs has insufficient thermal or greenness contrast to enable GDE detection. The detection of 'cool' thermal patches (transpiring GDE trees) from relatively warmer backgrounds (soil) will be a function of the size and magnitude of the cold patch relative to the pixel area. The 'greener' and 'cooler' signals from a groundwater dependent tree may be averaged out by the non-GDE plants present in the same pixel and a stressed GDE tree can gradually fade into the warmer soil background matrix. Spatial heterogeneity may overwhelm detection. Finer resolution imagery will improve detection capabilities but temporal information is then made poorer, due to inherent sensor resolution trade-off's.

It should be noted that although remote sensing is a useful diagnostic tool and proxy for the detection and sensing of GDE's, most detection and mapping is done by inference and careful user interpretation. Remote sensing often cannot directly ascertain causes and mechanisms for GDEs and much remains to be done to assess GDE influences on the water balance, their sensitivity to changing water availability, and responses to stress conditions. Future sensor systems planned for launch in the next few years include follow-on GRACE twin satellite missions with improved sensing capabilities allowing more detailed analyses groundwater, soil moisture, and surface water distributions and trends. The soil moisture active passive (SMAP) mission, launched in 2014, provides improved soil moisture retrievals which will improve upon the detection and differentiation of soil-moisture induced vegetation dynamics from those associated with groundwater use.

4 Hydrological modelling of water-use by GDEs

Comment [u6]: Number level chang heading title altered

4.1 Conceptual water balance approaches

Comment [u7]: Number level chang

A spreadsheet tool

O'Grady and co-workers have developed a simple but useful first-order approximation to estimate groundwater use of vegetation in an Excel spreadsheet tool (Leaney et al., 2011; http://www.csiro.au/products/recharge-discharge-estimation-suite). This toolbox includes three methods to estimate rates of groundwater discharge by vegetation:

1. Groundwater Risk Model
2. Ecological Optimality Model
3. Groundwater Discharge Salinity Model (not described here)

The groundwater risk model uses historical monthly rainfall and evaporation data for a site to produce a water balance. Soil texture is used to estimate soil moisture characteristics in each layer of the model, and groundwater uptake by vegetation is assumed to occur when ET exceeds rainfall, when also accounting for soil water storage for each month. ET is estimated from total evaporation using the Budyko framework (Budyko 1974; Donohue et al., 2007; Yang et al., 2008; Roderick and Farquhar 2009). The risk model in Leaney et al., (2011) uses the Choudhury-Yang formulation of the Budyko equation:

$$ET_a = \left(P\ ET_p\right) / \left(P^n + \left[ET_p\right]^n\right)^{1/n} \qquad (9)$$

where P is rainfall and n is a fitting parameter that determines the shape of the curve. Determining the value of n is difficult, but a close approximation can be derived from the climate wetness index (CWI = P/ET_p). When the CWI > 0.3, n is approximately equal to CWI and when CWI < 0.3, n is approximately 1.8 (Leaney et al., 2011). The influence of variation in *n* and the Budyko formulation is shown in Figure 3.

Figure 3 here

The model is run using historical monthly rainfall and estimated ET. Pan evaporation rates can be used instead of ET_p, in which case $ET_p = 0.75E_{pan}$. Modest agreement between modelled and observed rates of groundwater discharge was found in two Australian studies where ET exceeded rainfall in the Wattle Range by 2 to 440 mm y^{-1} (Benyon and Doody 2004), although the range of estimated groundwater discharge rates was large: 107 to 671 mm y^{-1} (Benyon and Doody 2004) and 380–730 mm y^{-1} (Benyon et al., 2006).

As an alternative method to the risk assessment just described, Leaney et al., (2011) applied Eagleson's theory of ecological optimality (Eagleson 1978). This proposes that the LAI of a site is maximised according to long-term rainfall and soil water holding capacity such that productivity is maximised whilst minimising the development of water stress. In this hypothesis, native vegetation is assumed to be at equilibrium with the local hydrological regime (Nemani and Running 1989). Ellis and Hatton (2008) have shown that the LAI of a site is proportional to a climate wetness index ($CWI = P / ET_p$), whilst Eamus et al., (2001) used the Baldocchi-Meyers index (foliar [N] x P/E_{eq}, where foliar [N] is the concentration of nitrogen in leaves and E_{eq} is equilibrium evapotranspiration) and found a strong ($R^2 = 0.95$ for 16 sites globally) curvilinear relationship with LAI, supporting the essentials of Eagleson's optimality theory. Similarly, Zeppel (2013) examined multiple species across sites in Australia and found strong convergence in daily rates of tree water-use and leaf area across five evergreen sclerophyllous genera. In the Eagleson optimality method of Leaney et al., (2011), the relationship between LAI and the CWI of Ellis and Hatton (2008) is used:

$$\mathrm{LAI} = \left(3.31 \times \mathrm{CWI}\right) - 0.04 \qquad (10)$$

In GDEs, groundwater discharge combines with precipitation to supply ET (O'Grady et al., 2011), thus:

$$\mathrm{CWI}_g = \left(\mathrm{P} + \mathrm{GW}\right) / \mathrm{ET}_p \qquad (11)$$

where CWI_g is the climate wetness index that includes the groundwater component (GW). Likewise, the Budyko curve can be modified to include the contribution of groundwater discharge to ET:

$$\mathrm{ET} / \mathrm{ET}_p = 1 + \left(\mathrm{P} / \mathrm{ET}_p\right) - \left(1 + \left[\mathrm{P} / \mathrm{ET}_p\right]^w\right)^{1/w} \text{ (Zhang et al., 2004) and} \qquad (12)$$

$$\left(\mathrm{ET} / \mathrm{ET}_p\right)_g = 1 + \left(\left[\mathrm{P} + \mathrm{GW}\right] / \mathrm{ET}_p\right) - \left(1 + \left[\left\{\mathrm{P} + \mathrm{GW}\right\} / \mathrm{ET}_p\right]^w\right)^{1/w} \text{ (O'Grady et al., 2011)}$$

(13)

Within zones of the same CWI, sites with access to shallow groundwater maintain a larger LAI than sites without access to groundwater (O'Grady et al., 2011). To determine GW, the pairs of equations (CWI, CWI_g; ET/ET_p, $[ET/ET_p]_g$) were optimised by obtaining the difference in rainfall required to attain a given LAI with a known CWI value (O'Grady et al., 2011).

4.2 Groundwater flow and variable saturation models: MODFLOW and HYDRUS

Two models, MODFLOW and HYDRUS, are commonly used to investigate the hydrologic state of the coupled surface water–groundwater–soil–vegetation system (McDonald and Harbaugh, 1988; Doble et al., 2006; Shah et al., 2007; Lowry and Loheide, 2010; Loheide and Booth, 2011; Ajami et al., 2012). HYDRUS applies Richard's equation to simulate water, heat and solute movements in soil, whereas MODFLOW is fully distributed and coupled hydrologic model of groundwater flow (Orellana et al., 2012). Hydrologic models that apply Richard’s equation in a soil medium of variable saturation are important for evaluating the mechanisms that generate groundwater hydrographs and flow. MODFLOW can also perform spatial scaling of ET as a function of depth-to-groundwater, although the form of ET depends upon parameterisation of the model. Often, ET is determined as ET_p or ET_0, but measurements of ET_a from eddy covariance can also be used. In one example, Wilcox et al., (2007) estimated ET from Cleverly et al., (2002) to evaluate the interaction between riparian ET and surface water–groundwater interactions.

Variable saturation models have improved our understanding of the interactions between groundwater and soil moisture in the vadose zone. Root water uptake (RWU) creates soil moisture deficits in the vadose zone and the capillary fringe, thereby causing vadose zone water content to fluctuate with depth-to-groundwater (Nachabe et al., 2005; Shah et al., 2007; Logsdon et al., 2010). Using HYDRUS 1-D, Lowry and Loheide (2010) integrated ET_g and RWU from the vadose zone by estimating the groundwater subsidy as the difference between RWU from the shallow groundwater and RWU from free drainage. Further complicating the relationship between groundwater and soil moisture, hydraulic redistribution of moisture from deep in the soil column to the surface (i.e., hydraulic lift) can reduce the amplitude of fluctuations in depth-to-groundwater, increase the amount of ET_g that is lost to groundwater evaporation, and decrease the nocturnal recovery in depth-to-groundwater (Orellana et al., 2012).

One of the goals of ecohydrological modelling in GDEs is the prediction of vegetation state based upon groundwater regime (Loheide and Booth, 2011). Likewise, the principle drivers of water use by vegetation in GDEs were aquifer attributes (S_y, regional groundwater flow), meteorology (solar radiation, vapour pressure deficit), environmental stress, and vegetation attributes (LAI, species composition) (Cleverly et al., 1997; Perkins and Sophocleous, 1999; Dahm et al., 2002; Cleverly et al., 2006; Butler et al., 2007; Lautz, 2008; Abudu et al., 2010). In general, these controls are observed in the wider literature on the controls of vegetation water use (Eamus et al., 2006b; Whitley et al., 2009). As the meteorological, environmental and vegetation effects on ET have been thoroughly described, we will focus on the regional aquifer effects on ET_g here.

One geomorphologic attribute of the aquifer that controls the flow of groundwater and thereby affects the distribution of groundwater-dependent vegetation depends upon whether the aquifer is gaining (i.e., water flows into the aquifer from its surroundings) or losing (i.e., an area where groundwater is lost to adjacent unsaturated soils) (Cleverly, 2013). A larger ET_g can lead to contrasting effects on seepage from streams to aquifers, depending upon whether along a losing or gaining reach (Ajami et al., 2011). Similarly, fluctuations in depth-to-groundwater can differ between gaining and losing reaches, of which the occurrence of the latter is where groundwater inflow might be insufficient to support large recovery rates in depth-to-groundwater (Schilling, 2012). The relationships between plant water use, aquifer dynamics, and seasonality (e.g., Logsdon et al., 2010; Ajami et al., 2011) are influenced by the rooting patterns and groundwater depth–ET_g relationships of the specific plant functional types that inhabit the GDE (Baird and Maddock, 2005).

5 Field based measurements of water-use by GDEs

Comment [u8]: New heading level

5.1 Sub-daily fluctuation in groundwater depth

An idealised representation of the "White method" in a shallow unconfined aquifer is shown in Figure four.

Figure 4 here

In Figure four the oscillating curve represents the cycle of groundwater drawdown arising from evapotranspiration (ET) during the day followed by a "rebound" of the water table when ET returns to zero at night. The dashed straight line (with slope = r) provides an estimate of the recovery rate, which is how fast the water table rises in the absence of groundwater use (Butler et al., 2007). After accounting for recovery, the daily drawdown of the water table is scaled by the effective specific yield (S_y), or the volume of water (per unit surface area of an unconfined aquifer) released from the soil pores with a given change in depth-to-groundwater (White, 1932):

$$ET_g = S_y\left(24r + s\right) \qquad (14)$$

where *s* is the change in aquifer storage and is determined from the 24-hr change in depth-to-groundwater. This approach has been successfully applied in the Okavango Delta in

Botswana (Bauer et al., 2004), an upland grassland catchment in central Argentina (Engel et al., 2005), an oak/grassland site on the Great Hungarian Plain of eastern Hungary (Nosetto et al., 2007), the Sopron Hills of western Hungary (Gribovszki et al., 2008), the Gobi Desert of northwest China (Wang et al., 2014), and various sites in the USA (Butler et al., 2007; Lautz et al., 2008; Martinet et al., 2009).

The White method tends to over-estimate ET_g (Loheide et al., 2005; Martinet et al., 2009). A major source of error is estimation of S_y, to which this method is very sensitive (Loheide et al., 2005; Gribovszki et al., 2008; Lautz, 2008; Logsdon et al., 2010; Miller et al., 2010). Furthermore, representative measurements of the readily available S_y are difficult to make and are complicated by capillary flux, trapped air, hysteresis, and departure of the soil–water ecosystem from an equilibrium (Logsdon et al., 2010). The value of S_y is dependent upon soil texture (Loheide et al., 2005), thus Martinet et al., (2009) applied a value of S_y that varied with the soil texture in contact with the capillary fringe of the water table. With a measure of ET_g (e.g., from eddy covariance), the White equation can be inverted to investigate the variation in Sy (Miller et al., 2010). Using an inversion of the White method, estimates of S_y account for spatial heterogeneity in soil texture and scaling effects on S_y, but further studies are required before comprehensive predictions of S_y can be obtained without independent measurements of ET_g. Alternatively, Nachabe et al., (2005) used a more direct estimate of S_y in the soil column by combining measured fluctuations of depth-to-groundwater and soil moisture across the vadose (i.e., unsaturated) zone. In either case, additional instrumentation to measure ET_g or soil moisture profiles improved the estimation of S_y.

Several modifications to the White method were evaluated in a study by Fahle and Dietrich (2014), in which they compared errors in estimation of S_y, recovery and ET_g. No model outperformed the others in each of these error benchmarks, thus illustrating that errors in the estimation of S_y are compensated by errors in the estimation of recovery (Fahle and Dietrich, 2014). The methods that provided the best estimates for recovery of the groundwater used approaches to estimate sub-daily rates of ET_g and recovery (Gribovszki et al., 2008; Loheide and Ii, 2008). In both methods, recovery was estimated from the previous and following nights, although application to other methods might require site-specific parameterisation of the time period that is most representative for their study conditions (e.g., 18.00–6.00; Fahle and Dietrich, 2014). In the method of Gribovszki et al., (2008), recovery was estimated from the time rate of change in depth-to-groundwater, and this important upgrade reduced the error of recovery estimates (Gribovszki et al., 2010; Fahle and Dietrich, 2014).

Groundwater hydrographs include the impact of regional fluctuations in the aquifer that are not associated with local changes arising from ET of vegetation (Engel et al., 2005). A regional effect that can cause problems with the White method occur when tides from nearby water bodies generate two daily peaks in the groundwater hydrograph (Miller et al., 2010), thereby requiring measurements of the water body that is causing the effect. After accounting for the regional hydrograph, soil moisture content in the vadose zone can still affect the correlation between sap flow measurements of ET_g and groundwater fluctuations (Engel et al., 2005). This was consistent with the modelling results of Loheide et al., (2005), who found that daily fluctuations were dampened by root water uptake from the vadose zone alone. Spectral methods (e.g., windowed Fourier decomposition) are effective at identifying break points in the daily signal like those associated with regional groundwater and soil moisture effects, although variations in ET_g can result in loss of amplitude, consequently rendering spectral analysis unsuitable for quantitative analysis without an adequate scaling factor (Schilling and Zhang, 2012; Soylu et al., 2012).

5.2 Using stable isotopes to estimate rates of groundwater use

Estimates of the proportion of total vegetation water use derived from groundwater can be determined from stable isotope anlyses (Querejeta et al., 2007; Maguas et al., 2011; Feikema et al., 2010; Kray et al., 2012; McLendon et al., 2008). Two types of information are required to quantitatively partition ET_g from ET. The first is an independent estimate of ET_0 or ET_a as derived from eddy covariance (Kelliher et al., 1992; Baldocchi and Vogel, 1996; Baldocchi and Ryu, 2011), sapflow (Cook and O'Grady, 2006; O'Grady et al., 2006; Zeppel, 2013) or RS techniques (Nagler et al., 2009; Nagler et al., 2013). The second is the stable isotope composition of water in soil, groundwater and xylem. Upon determination of the proportion of ET that is due to ET_g (Section 3.2), the amount of ET_g, for example in mm d^{-1}, is the product of that proportion and ET.

Three generalities can be identified in the results of stable isotope studies of GDEs. First, multi-species comparisons at a common site generally confirm niche separation (spatially or temporally) in patterns of water uptake, thereby minimising competition for water (Lamontagne et al., 2005; Querejeta et al., 2007; Kray et al., 2012). Second, increased depth-to-groundwater results in a declining proportion of groundwater use (O’Grady et al., 2006), although this can vary amongst different vegetation communities (McLendon et al., (2008). Finally, as time since last rain increases, the proportion of groundwater used by vegetation usually increases (McLendon et al., 2008), but not always (Kray et al., 2012). Consequently seasonality of groundwater use may occur when rainfall is highly seasonal and groundwater availability is maintained throughout the dry season (O’Grady et al., 2006).

Stable isotope composition varies with depth (Table 1; Querejeta et al., 2007). Consequently taking an average value to represent the entire rooting depth can lead to errors. Whilst use of two independent isotopes allows the relative contribution of three sources to be determined, obtaining independence of both isotopes is very difficult. As an alternative, Cook and O’Grady (2006) developed a model that estimates the relative water uptake by vegetation from different soil depths. This model is based upon the following axioms: the rate of water uptake is determined by (a) the gradient in water potential between bulk soil and leaves; (b) root distribution through the soil profile; and (c) a lumped hydraulic conductance parameter. Soil isotopic composition as a function of depth and of xylem water is used to constrain root distributions within the model. This has the advantage over end-member analyses (an analytic tool to determine the relative contributions of soil water and groundwater to transpiration; Phillips and Gregg 2003) because: (i) it produces a quantitative estimation of the proportion of water extracted from multiple depths (including groundwater); (ii) it doesn’t require distinct values of isotope composition for end-member analyses and therefore can deal with the more typical grading of isotope composition observed through the soil profile; and (iii) it is based on simple ecophysiological principles. Cook and O'Grady (2006) applied this model and demonstrated that two co-occurring species obtained 7–15 % of their transpirational water from the water table, a third species accessed 100 % from the water table, and a fourth species derived 53–77 % from groundwater.

6 Functional responses of GDEs to changes in GW depth

Comment [u9]: New heading level

6.1 Effects of groundwater on growth and dendrochronological traits

Comment [u10]: New heading level

A reduced growth rate in response to declining water availability is a universally observed plant response (Kelliher et al., 1980; Osmond et al., 1987; Oberhuber et al., 1998; Sarris et al., 2007). In most GDEs rainfall and groundwater provide important supplies of water, and the ratio of rainfall to groundwater uptake varies spatially and temporally. Consequently, increases in groundwater depth may be expected *a priori* to have the potential to affect plant growth. Dendrochronology (the study of growth in tree rings) has a long history in ecological research spanning many decades (Drew and Downes 2009; McCarroll and Loader, 2004). However, its application to the study of GDEs is much more recent (e.g. Giantomasi et al., 2012). Similarly, recording point dendrometers, which are sensitive stem gauges that monitor growth increment at hourly time-scales, recently have been used for expanding applications. In this section we briefly review some of the insights gained form dendrochronology and dendrometry in the study of GDEs.

Tree rings represent the history of past growth events, which are often but not always annual (Prior et al., 2012). Quantification of growth rates from tree rings can be used to reconstruct fluctuations in the supply water from precipitation and groundwater (Oberhuber et al., 1998; Bogino and Jobbagy, 2011; Perez-Valdivia and Sauchyn, 2011; Xiao et al., 2014). In mountainous regions where the regional water supply is derived from snowmelt, tree growth and groundwater depth are correlated with precipitation during the year prior to growth because much of the snow received in the winter melts in the year after it fell (Oberhuber et al., 1998; Perez-Valdivia and Sauchyn, 2011). Likewise, tree ring growth and groundwater fluctuations are correlated to the dominant climate driver in an area (e.g., the Pacific decadal oscillation and El Niño–Southern Oscillation in California, USA) (Hanson et al., 2006). In some circumstances, the effect of groundwater can be disentangled from climate through the use of spectral analysis (Bogino and Jobbagy, 2011), but in other cases depth-to-groundwater was not found to be a significant factor in explaining differences in either ring width of basal area increment (Stock et al., 2012).

The timing of groundwater dependence can influence the presence of a climate signal in tree rings: climate signals can be weaker during formation of late wood, when growth rates are small (Oberhuber et al., 1998); or during the dry season, when precipitation rates are negligible and growth is supported by groundwater (Drake and Franks, 2003). Thus, analysis of tree ring chronologies can provide an insight into the importance of access to groundwater on plant growth. Individual events can be identified in the tree ring growth record (Hultine et al., 2010), as can long-term trends in depth-to-groundwater (Bogino and Jobbagy, 2011). In riparian cottonwood trees and willows, Hultine et al., (2010) identified rapid, large and reversible responses of tree ring width to draining and refilling of a reservoir (Fig. 5).

Figure 5 here

Longer-term trends in depth-to-groundwater have impacted dendrochronologies in both directions, toward lower growth rates with groundwater extraction (Lageard and Drew, 2008) and toward increasing growth rates with decreasing depth-to-groundwater, except in response to root anoxia arising from flooding (Bogino and Jobbagy, 2011). However, specific responses depend upon depth-to-groundwater and individual differences amongst functional types; for example, riparian cottonwood trees (*P. fremontii*) responded to rewetting with growth that was larger and faster than the response of co-occurring willow (*S. exigua*), a small-stature, thicket-forming shrub that is restricted to streamside areas with very shallow groundwater (Scurlock, 1998; Rood et al., 2011). From an understanding of the relationships between tree growth and depth-to-groundwater, historical periods of sensitivity to hydrological drought (i.e., affecting groundwater levels) *versus* meteorological drought (i.e., below-average precipitation) can be identified (Potts and Williams, 2004; Adams and Kolb, 2005; Cocozza et al., 2011). Such insights have value in developing a long-term understanding of the relationships amongst GDEs, climate and groundwater depth.

Wood formed during drought is enriched in ^{13}C, reflecting decreases in stomatal conductance relative to photosynthesis and the consequential ratio of [CO_2] within and outside of the leaf (C_i/C_a) (McCarroll and Loader, 2004; Cocozza et al., 2011) (Horton et al., 2001, Maguas et al., 2011). Interpretation of δ^{13}C in tree rings can be complicated by the effects of phloem loading (Gessler et al., 2009) and by photosynthetic re-fixation in the bark (Cernusak et al., 2001), although with independent confirmation, xylem δ^{13}C can explain differences in groundwater use and water stress in groundwater-dependent trees. In one such comparison, δ^{13}C was constant across xylem from *Populus* along a perennial stream (thereby implying access to groundwater) but changed with moisture conditions in an intermittent reach (Potts and Williams, 2004).   Likewise, changes in ring width over time were reflected by $\delta\ ^{13}$C from leaves (Hultine et al., 2010), such that less negative values of δ^{13}C indicated increased water-use-efficiency when the supply of water was reduced.

On small time-scales (hourly-to-daily), incremental stem growth (and shrinkage) is measured using precision dendrometers that contain linear-variable-displacement transducers (Zweifel et al., 2005, Drew et al., 2008, Drew and Downes 2009). Changes in maximum daily trunk shrinkage arising from reduced water availability occur earlier and stronger than changes in stomatal conductance, stem water potential or transpiration (Ortuno et al., 2006, Conejero et al., 2007, 2011, Galindo et al., 2013).   Nonetheless, rates of sapflow declined with maximum daily stem shrinkage, both of which responded exponentially to changes in depth-to-groundwater (Ma et al., 2013).   Similarly February et al., (2007) and Drake et al., (2013) found that increased groundwater supply (actual or simulated) resulted in increased stem increment, sapflow and xylem water potential.

7.0 Two case studies

Comment [u11]: New heading level

Two case studies are now presented, one from Australia and one from the USA. These case studies serve several purposes. First, they provide examples of the multiple approaches required in the study of GDEs (physiological, remote sensing, ecological). Second, they provide a valuable bridge between sections 2 – 6 (water-use, remote sensing, modelling) and section 8 (vegetation response trajectories to changes in groundwater depth). Finally, they integrate the results of many years of concentrated study in two diverse ecosystems.

Comment [u12]: New paragraph of text.

7.1 The Gnangara Mound

The Gnangara Mound is a shallow unconfined aquifer of the Swan Coastal Plain in Western Australia. Increased depth-to-groundwater has occurred over the past several decades as the result of long-term declines in annual rainfall, increased human abstraction and increased discharge arising from the development of a plantation industry in the region (Elmahdi and McFarlane, 2012). The impacts of groundwater abstraction on woodlands have been documented in this region (Groom et al., 2000; Canham et al., 2009; Canham et al., 2012; Stock et al., 2012). In 1985 large rates of summer abstraction in this Mediterranean climate was associated with increased and widespread mortality of native woodlands (up to 80 % mortality close to abstraction bores; Mattiske and Associated 1988).

To determine long-term floristic changes associated with groundwater abstraction, a series of transect studies were initiated in 1988. A 2.2 m increase in depth-to-groundwater coupled to higher-than-normal summer temperatures resulted in further adult mortality of overstorey species by as much as 80 %; additionally, 64 % mortality was recorded in understory species 2 years after the start of groundwater abstraction (Groom et al., 2000). Increased rates of mortality were not observed at control sites that were not subject to groundwater pumping.

Large inter-specific differences in rates of mortality were observed in these Gnangara studies. Consequently, a further study examined the vulnerability of individual species to increased depth-to-groundwater (Froend and Drake 2006; Canham et al., 2009). Using xylem embolism vulnerability curves as a measure of sensitivity to water stress, Froend and Drake (2006) compared three *Banksia* and one *Melaleuca* species. They found that xylem vulnerability reflected the broad ecohydrological distribution of species across a topographic gradient, and they identified a threshold leaf water potential below which increased mortality was likely. Similarly Canham et al., (2009) examined Huber values (the ratio of sapwood to leaf area), leaf-specific hydraulic conductivity (k_l) and xylem vulnerability of two obligate phreatophytes and two facultative phreatophytes. At sites where depth-to-groundwater was shallow there were no inter-specific differences in vulnerability to water stress. However, by comparing across a topographic gradient, Canham et al., (2009) showed that two facultative phreatophytes (but not the obligate phreatophytes) were more resistant to xylem embolism at the upper slope (larger depth-to-groundwater) than the lower slope.

It is not only aboveground tissues that adapt to changes in groundwater depth. Differences in root growth also respond to changes in depth-to-groundwater. Thus Canham et al., (2012) found that root growth varied with depth within the soil column: at the surface, root growth responded to seasonality and microclimate; at depth, root growth occurred all year and was dependent upon soil aeration (i.e., roots elongated rapidly followed a declining water table during the summer and died back in the following winter as the groundwater rebounded). These results are consistent with the increases in ET following groundwater decline that were observed by Cleverly et al., (2006). The ability to rapidly increase root depth during the (dry) summer is a critical attribute of phreatophytes occupying sites with seasonally dynamic depth-to-groundwater.

The development of ecosystem response trajectories for the impact of groundwater abstraction is an important resource management imperative. Froend and Sommer (2010) examined a rare, 40-year vegetation survey dataset from the Gnangara Mound. Whilst the long-term average (1976–2008) rainfall was 850 mm, the annual average for the recent past was about 730 mm and depth-to-groundwater has increased by 1 m in the past 50 years. Depth-to-groundwater fluctuates about 0.5–3 m seasonally, and maximal depth occurs at the end of summer. Two transects were compared: a “control” where gradual increases in depth-to-groundwater (9 cm y^{-1}) have occurred as a result of the decline in annual rainfall; and an “impacted” transect where large rates of increase in depth-to-groundwater have occurred (50 cm y^{-1}). Principal component analyses were used to identify three vegetation communities: those associated with down-slope, mid-slope and upper-slope positions. Species having a high reliance on consistent water supplies (mesic species) were dominant at the down-slope site while xeric species dominated the upper-slope sites.

On the control transect it was hypothesised that groundwater decline would result in a replacement of the mesic by the xeric species. However, this hypothesis was not supported. Indeed, most of the compositional and structural attributes of the three communities remained unchanged. The principle community-scale response was a change in the abundance of mesic and xeric species rather than complete replacement of one species for another. In contrast to the results of Shatfroth et al., (2000), mesic species at sites with shallow groundwater were not more sensitive to increases in depth-to-groundwater than xeric species. By contrast, changes in composition on the impacted transect were far more pronounced, and mass mortality was observed across all classes (mesic to xeric) species. This study emphasises the importance of the rate of change in depth-to-groundwater as a determinant of the response of species and communities.

7.2 Riparian forest vegetation in the southwestern USA

In the southwestern USA, the majority of GDEs are riparian or littoral, where a shallow aquifer is formed by runoff from snowmelt in the mountainous headwaters. Much of the agriculture in the region is found along the rivers due to the large amount of surface water that flows past. The focus of irrigation to the riparian corridors has placed intense competition between water resources for people *versus* the environmental flows that are required to maintain shallow aquifers and associated GDEs. Of further risk to riparian GDEs and agriculture, groundwater extraction and land use change threaten riparian ecosystems (Scott et al., 1999; Nippert et al., 2010; Pert et al., 2010). Thus, many studies have been undertaken over several decades to investigate the water use of GDEs in southwestern North America (van Hylckama, 1970; Gay and Fritschen, 1979; Sala et al., 1996; Devitt et al., 1998; Goodrich et al., 2000a; Cleverly et al., 2002; Scott et al., 2004; Nagler et al., 2005b).

Sunlight is plentiful in the southwestern USA, thus riparian GDEs are strong carbon sinks (Kochendorfer et al., 2011). However, seasonal variability in surface water discharge and aquifer recharge can create cycles of hypoxia and drought stress (Lowry et al., 2011), both of which act to reduce production (Shah and Dahm, 2008). Often existing between these two states of stress, riparian vegetation can transpire substantial amounts of water, reaching near the theoretical maximum (ca. 12 mm d^{-1}) (Cleverly, 2013). This general release from limitations due to energy, moisture and stress results in rates of latent heat flux that exceed precipitation (i.e., $ET / P > 1$) (Scott et al., 2000; Cleverly et al., 2006; Scott et al., 2006b) and net radiation (Devitt et al., 1998). Even when little or no groundwater use can be identified in the vegetation (e.g., in *Sporobolis*), ET losses from the riparian corridor can exceed precipitation inputs (Scott et al., 2000), implying that soil moisture in the vadose zone can be recharged by groundwater and that riparian GDEs need not use the groundwater directly.

In southwestern North America, vegetation in riparian corridors and adjacent rangelands or shrublands is classified by reliance upon access to groundwater (i.e., obligate or facultative phreatophyte; Smith et al., 1998) or plant functional type (obligate wetland, shallow-rooted or deep-rooted riparian, transitional riparian, or upland; Pockman and Sperry, 2000; Baird and Maddock, 2005; Baird et al., 2005). The result of groundwater depletion has distinct effects on the vegetation in each functional type. Shallow-rooted, obligate phreatophytes (e.g., cottonwood, Populus spp.) can be very sensitive to groundwater decline, resulting in reductions of ET, productivity and canopy conductance as a consequence of increases in vapour pressure deficit that are correlated with depth-to-groundwater (Gazal et al., 2006; Kochendorfer et al., 2011). Branch sacrifice, partial crown dieback and mortality commonly occur in *Populus* following substantial groundwater drawdown (Mahoney and Rood, 1991; Kranjcec et al., 1998; Scott et al., 1999; Rood et al., 2000; Cooper et al., 2003; Rood et al., 2003). However, stomatal closure and crown dieback in *Populus* can prevent total hydraulic failure, and thereby minimise mortality rates, by maintaining favourable xylem water potentials within the remainder of the crown (Amlin and Rood, 2003).

Decreased baseflow and drawdown of groundwater levels has been associated with a shift in dominance to xerophytic species in the American Southwest at the expense of forbs and obligate phreatophytes (Stromberg et al., 1996; Stromberg et al., 2006; Stromberg et al., 2007; Stromberg et al., 2010). Xerophytes in the riparian corridors of the American Southwest include deep-rooted phreatophytes (e.g., *Proposis*, *Tamarix*) and upland species (e.g., *Chrysothamnus*), any of which may be opportunistic users of groundwater or groundwater-independent. Stress tolerance, opportunistic use of groundwater and use of multiple water sources (e.g., soil moisture) have contributed to the invasive success of *Tamarix* (Busch et al., 1992; Cleverly et al., 1997; Di Tomaso, 1998; Nippert et al., 2010). Consequently, *Tamarix* inhabit sites with variable depth-to-groundwater (Lite and Stromberg, 2005), which results in an amount of ET that is equivalently variable in time and space (Cleverly et al., 2002; Cleverly, 2013).

The effective area of riparian vegetation has historically increased in the American Southwest due to expansion of deep-rooted phreatophytes like *Tamarix* and *Prosopis* (Hultine and Bush, 2011). The upland vegetation that previously occupied riverine upper terraces and grasslands supported small rates of ET (Shafroth et al., 2005; Hultine and Bush, 2011), thus expansion of phreatophytes into these areas has resulted in an increase in ET losses (Scott et al., 2006b; Cleverly, 2013) and thereby has placed a potential strain on groundwater resources. In the case of expansion by Tamarix, groundwater extraction may result in enhancement of ET (Cleverly et al., 2006), contrasting with post-extraction reductions in ET by native, shallow-rooted phreatophytes such as *Populus* (Cooper et al., 2006; Gazal et al., 2006) and thus representing a shift in the ecohydrology of riparian corridors throughout the semi-arid regions of south western North America.

8 Integrating multiple-scale responses

Comment [u13]: New heading level

8.1 Multiple traits across leaf, branch, whole-tree and stand

Comment [u14]: New heading level

The responses of vegetation to differences in depth-to-groundwater have been examined extensively at leaf, tree, canopy and population scales. Rates of leaf-scale photosynthesis, stomatal conductance, whole plant hydraulic conductance, tree- and canopy-scale transpiration and plant density are known to decline in response to reduced supply of groundwater (Table 3). Similarly, increased Huber value, crown dieback and mortality in response to reduced supply of groundwater have been observed (Table 3). Consequently, response functions for individual traits are readily apparent; examples include changes with depth-to-groundwater in rates of photosynthesis (Horton et al., 2001), plant cover (Elmore et al., 2006), NDVI (Lv et al., 2012) and crown dieback (Horton et al., 2001). However, few studies have examined *multiple traits* across *multiple scales* and then provided an integrated "ecosystem-scale" response function to differences in groundwater availability. Integrated ecosystem-scale responses to changes in groundwater availability have been hypothesised to be linear (Fig. 6), curvi-linear or a step function with which minimal damage occurs until a threshold is reached (Leffler and Evans, 1999; Eamus et al., 2006).

Information on how vegetation adapts to differences in water supply is critical for predicting vegetation survival, growth and water-use, which have important impacts on site hydrology (McDowell et al., 2008; Carter and White, 2009). The development of integrated response curves to reduced groundwater availability would significantly enhance our understanding of water requirements and lead to the identification of response thresholds. Such thresholds could be used to identify the limits of reduction in water-source availability, a useful parameter for characterising water requirements for resource and conservation management (Froend and Drake, 2006).

Table 3 here

In a recent comprehensive, three-year study, Zolfaghar (2014) examined leaf, branch, tree and stand-scale functional and structural attributes of woodlands across a gradient of depth-to-groundwater (2.4 m to 37.5 m) in mesic Australia. She examined eighteen traits, including stand-scale basal area and tree height, leaf turgor loss point, sapwood hydraulic conductivity, sensitivity to xylem embolism and above ground net primary productivity. An increase in depth-to-groundwater across these sites was hypothesised to result in:

1. reduced standing biomass;
2. adjustment of leaf-, tree- and plot-scale plant traits with associated repercussions on plant water relations;
3. increased drought tolerance; and
4. increased water-use-efficiency.

Fig 6 here

Figure seven provides a summary of the observed responses of each trait to increasing depth-to-groundwater. Refer to Table four for the abbreviations used in Figure seven.

Fig 7 here.

Table 4 here

It is clear from Figure seven that increased depth-to-groundwater was associated with declines in basal area, tree height and LAI, and hence light interception, of native woodlands. As a consequence, aboveground net primary productivity was reduced as groundwater availability declined. Increased drought tolerance, as indicated by increased water-use-efficiency, increased Huber value and reduced water potential at turgor loss and solute potential at full turgor, supported the principle over-arching hypothesis that increasing depth-to-groundwater results in a suite of leaf-branch and tree-scale adaptations that increase tree tolerance to reduced water supply.

A key aspect of this research was to develop an ecosystem-scale response function for depth-to-groundwater. Zolfaghar (2014) normalised the responses (0 to 1) such that a response of 1 indicates no effect of differences in depth-to-groundwater and 0.5 indicates a 50 % decline/increase in the maximal/minimum value of a particular trait. The normalised response function is presented in Figure eight. Despite the large number of traits and species across the seven sites, the standard error of the ecosystem-scale average for each data point was remarkably small, indicating significant convergence in normalised responses to differences in depth-to-groundwater. Convergence of functional variations in traits across sites and species is increasingly observed with respect to rainfall or other climatic variables (Wright et al., 2004; Kattge et al., 2011). Indeed, identification of plant functional types (PFTs) is a practical means for models of land surface-atmosphere interactions across biomes to integrate the physiology of vegetation. Similarly, improved accuracy can be obtained from dynamic global vegetation models (DGVMs) through the construction of large datasets (cf. Wright et al., 2004, Kattge et al., 2011) that include a representation of groundwater-dependent ecosystems.

A second feature apparent in the response function of Fig. 8 is the large R^2 of the sigmoidal regression, reflecting the relatively high degree of confidence in this threshold response. The response curve further suggests that extraction of groundwater beyond 7 – 9 m depth is likely to result in significant changes in ecosystem structure and function. Although we cannot pinpoint the exact break point with precision, it is clearly apparent that a breakpoint does occur in the data. Furthermore, two recent reviews based on water balance concluded that groundwater uptake ceased when depths exceeded 7.5 m (Benyon et al., 2006) or 8 – 10 m (O’Grady et al., 2010), whilst Cook et al., (1998) established a limit of approximately 8 m for a Eucalypt savanna. Finally, Kath et al., (2014) identified thresholds of groundwater depth across 118 sites in SE Australia for two tree species ranging from 12.1 m to 26.6 m further supporting our identification of a breakpoint in the responses of trees to groundwater depth. Such a strong response, consistent across multiple traits, should provide a strong management signal to guide future groundwater abstraction.

Figure 8 here

8.2 Co-ordination across traits

Some plant traits are a better indicator of plant sensitivity to water stress than others. Leaf water potential at turgor loss is recognised as a physiological measure of plant sensitivity to water stress (McDowell et al., 2008). Similarly, measurements of vulnerability to xylem cavitation and safety margins are critical determinants of drought tolerance (Markesteijn et al., 2011; Sperry et al., 2008). Safety margins are equal to the difference between minimum daily branch water potential and PLC_{50} (Meinzer et al., 2008; Sperry et al., 2008). A strong linear correlation between these two traits (Fig. 9) in the Kangaloon study (Zolfaghar 2014) reveals co-ordination in the response of leaf (cell traits) and xylem (branch trait) anatomy, as has been observed previously in a study of eight tropical dry forest species (Brodribb et al., 2003). This relationship indicates that as depth-to-groundwater increased, sensitivity to drought at both leaf cell and branch-scale decreased (lower leaf water potential is needed to reach turgor loss point and PLC_{50} declined).

Figure 9 here

9 Concluding remarks

Comment [u15]: New heading level

The existence of GDEs has been known for several centuries. The ecological, social, cultural and economic importance of GDEs, however, has only been understood more recently. Whilst inferential methods were the main means for determining the presence/location of GDEs for many decades these have now been replaced by more direct methodologies which include the use of stable isotopes and hourly direct measurements of fluctuations in shallow groundwater depth. The most revolutionary recent development has, perhaps, been the application of remote sensing techniques to identify the location of GDEs but also to reveal key features of their functional behaviour.

Increasing frequencies, spatial and temporal extent and severity of drought and resulting drought-induced mortality of forests have been recorded extensively (Dai 2011; Eamus et al., 2013) in the past two decades. Climate-change-induced changes in rainfall distribution and amounts pose a new stress to both groundwater resources and associated GDEs. For the first time, remotely sensed information on both the structure (e.g LAI) and functioning (e.g. rates of water-use and primary productivity) of GDEs are now available across several decades. The challenge now is to use this long history of remotely sensed and meteorological data as a unique natural experiment to determine response functions of multiple GDEs to changes in climate (and groundwater depth) globally to inform both the science of ecology and the practical needs of water and land resource managers into the future.

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Table 1: Deuterium analysis of xylem, soil, river water and groundwater in a study of three species growing in the Northern Territory of Australia. The δ^2H values (%o) of soil became more negative as distance from groundwater increased due to enrichment during surface evaporation. At shallow sites (*Melaleuca argentea*) the groundwater is near the surface and xylem water δ^2H values match soil water and groundwater. As depth-to-groundwater increased (because of local topography: the site slopes up from the river) xylem water isotope composition was increasingly more negative than groundwater because groundwater was unavailable to the roots. From Lamontagne *et al.* (2005).

	Depth-to-groundwater (m)	River water	Soil water	Xylem water	Groundwater
Daly River	0	-44			
M. argentea	< 0.25		-44	-43 to -48	-43
B. acutangula	3		-80	-46 to -40	-45
C. bella	> 15		-56 to -91	-59 to -71	Not available to roots

Table 2: Some examples of the application of remote sensing to the study of groundwater dependent ecosystems.

Notes on methods	**Application**	**Reference**
eVI (MODIS) + MODIS land surface temp + water balance equation	Calibrated, empirical model of riparian ET; groundwater use quantified from $ET_g = ET - (P - \Delta S)$	Scott et al., 2008
eVI (MODIS) + empirical relationship of ET, eVI and ET_o	Calibrated, empirical model of riparian ET; groundwater use quantified	Tillman et al., 2012
"Green island method": Calculate standard deviation in NDVI across 14 y pixel by pixel	Identifying location of GDEs by determining where veg activity shows minimal seasonal variation	Tweed et al., 2007
"Green island method": Calculate standard deviation in eVI across years and seasonally	Identifying location of GDEs by determining where veg activity shows minimal seasonal/inter annual variation	Dresel et al., 2010
"Green island method": Calculate LAI for adjacent pixels ; find regions with larger LAI with GW access	Identifying location of GDEs by determining larger LAI	Colvin et al., 2007
NDVI (MODIS) + groundwater depth from bore data	Relationship between GW depth and vegetation cover	Jin et al., 2011

NDVI (MODIS) + groundwater depth from bore data	Relationship between GW depth and vegetation cover	Lv et al., 2012
Surface energy balance (SEBAL) + Landsat surface temp; LAI derived from MODIS	Estimating ET from GDEs at pixel-by-pixel resolution	Yang et al., 2008; 2011
SEBAL + NDVI (MODIS)	Estimating ET at 90 m resolution	Bindhu et al., 2013
SEBAL + MODIS	Estimating ET	Tang et al., 2013
SEBAL + SWAT model (hydrology)	Estimating groundwater recharge	Githui et al., 2012
SEBAL + LANDSAT images	Estimating arid zone shallow aquifer discharge	Matic et al., 2011
Penman-Monteith equation with RS estimates of LAI, NDVI and used to estimate land surface conductance	km-scale estimates of ET	Cleugh et al., 2007
EVI + surface temperature + canopy fractional cover	Partitions ET into vegetation and soil components	Mu et al., 2007
ET_a* = ET_a – rainfall)/(ET_o – rainfall) ET_a linearly correlated with NDVI* ET_g = ET_0 –rainfall)NDVI*	Estimated GW use (ET_g) rather than ET_a	Groeneveld 2008
MODIS veg indices compared; PM equation used to find G_c and regress G_c against MODIS veg indices	Estimate ET_a and G_c	Yebra et al., 2013
MODIS reflectance + residual moisture index (from eVI) + Global veg moisture index Actual ET calculated from PET*crop factor and crop factor is derived from EVI	Estimate ET at 1 km spatial resolution	Guerschman et al., 2009

Table 3: A summary of some of the recent literature documenting the response of vegetation, across multiple scales, to reduced availability of groundwater.

Process/trait	Response to reduced availability of groundwater and range of depths	References
Leaf-scale photosynthesis	Decreased (zero to -9 m DGW);	Horton et al., 2001
Stomatal conductance	Decrease (zero to -9 m DGW); Decreased (zero to >-1 m DGW increased) ; Stomatal resistance increased from 38.8 to 112.5 (zero to >-3 m DGW) Decreased (-7 to -23 m DGW) Decreased (-2 to -4 m DGW)	Horton et al., 2001 Cooper et al., 2003 Zunzunegui et al., 2000 Gries et al., 2003 Kochendorfer et al., 2011
Canopy conductance	Decreased (-1.5 to >-5 m DGW) Decreased (-2 to -4 m DGW)	Carter and White 2009b Kochendorfer et al., 2011
Leaf and stem water potential	Ψ_{pd} decrease from -0.5 to -1.7 MPa (zero to -9 m); Ψ_{pd} decreased from 0.2-0.4 to -0.4 to -0.8 MPa (zero to >-1 m DGW increased) ; Decreased from -0.79 to -2.55 MPa (<-2 to >-20 m DGW);	Horton et al., 2001 Cooper et al., 2003 Froend and Drake 2006 Zunzunegui et al., 2000 Gries et al., 2003

	Decreased from -1.85 to -3.99 (zero to >-3 m DGW) Ψ_{midday} decreased (-7 to -23 m DGW)	
Transpiration rate	Total Et decreased 32% (-0.9 to -2.5 m DGW); Et decreased (-2 to -4 m DGW) E decreased from 966 to 484 mm (-1.1 to -3.1 m DGW) Annual E decreased (zero to -8 m DGW)	Cooper et al., 2006 Kochendorfer et al., 2011 Gazal et al., 2006 Ford et al., 2008
Resistance to xylem embolism	Increased (-1.5 to -30 m DGW); PLC_{50} decreased from -1.07 to -3.24 MPa (<-2 to >-20 m DGW)	Canham et al., 2009 Froend and Drake 2006
Growth rate	Decreased (zero to >-1 m DGW increased); Decreased (-7 to -23 m DGW)	Scott et al. 1999 Gries et al. 2003
Leaf area index	Decreased from 3.5 to 1.0 (-1.5 to >-5 m DGW) Decreased Decreased from 2.5 to 0.66 (zero to ->3 m DGW) Decreased from 2.7 to 1.7 (-1.1 to -3.1 m DGW)	Carter and White 2009b O'Grady et al. 2011 Zunzunegui et al. 2000 Gazal et al., 2006
Huber value (SWA/ LA)	Increased from 3.3 to 4.7 (-1.1 to -3.1 m DGW) No change (-1.5 to -30 m DGW) increased from 3.4 to 4.3 x10^{-4} (-1.5 to >-5 m DGW)	Gazal et al., 2006 Canham et al., 2009 Carter and White 2009b
Plant density	Vascular species number decreased; Species composition changed (-0.9 to -2.5 m DGW); plant cover type changed (-1.1 to -2.5 m DGW); vegetation cover and diversity decreased (-1 to – 110 m DGW)	Zinko et al., 2005 Cooper et al., 2006 Merritt and Bateman 2012 Lv et al., 2013
NDVI	Decreased (-1 to – 110 m DGW); Decreased (zero to -1.5 m DGW increased) Decreased (-1.8 to -3.5 m DGW)	Lv et al., 2013 Aguilar et al., 2012 Wang et al., 2011
Crown die-back	Increased between <40% to >50% (zero to -9 m); Leaf loss 34% (zero to >-1 m DGW increased)	Horton et al., 2001 Cooper et al., 2003
Mortality	Increased (>-2.2 DGW increased); Increased (zero to >-1 m DGW increased) Increased (-0.4 to -5 m DGW)	Groom et al., 2000 Scott et al., 1999 González et al., 2012

Table 4: The meaning of the abbreviations/ traits used in Figure 7.

Abbreviation	**Explanation/definition**
Ψ_{TLP}	The water potential of leaves at which turgor is zero
Π_{100}	The solute potential at a relative water content of 100 %
RWC_{TLP}	The relative water content at which leaf turgor is zero
SWD	The saturated water content of wood
K_s	Sapwood-specific hydraulic conductivity of branch xylem
K_L	Leaf-specific hydraulic conductivity of branch xylem
PLC_{50}	The water potential at which 50 % of the hydraulic conductivity is lost
PLC_{88}	The water potential at which 88 % of the hydraulic conductivity is lost
H_v	Huber value: the ratio of leaf area to sapwood area
BA	Total basal area of trees within a plot
LAI	Leaf area index of a stand of trees
AGB	Above-ground biomass
ANPP	Above-ground net primary productivity

WUE	Water-use-efficiency; calculated as the ratio of ANPP/stand water-use
Height	Average height of the trees in a plot
Water-use	Rates of stand water-use; up-scaled from sapflow measurements
Stem density	The number of trees per hectare
Litterfall	Rates of annual litterfall within a plot

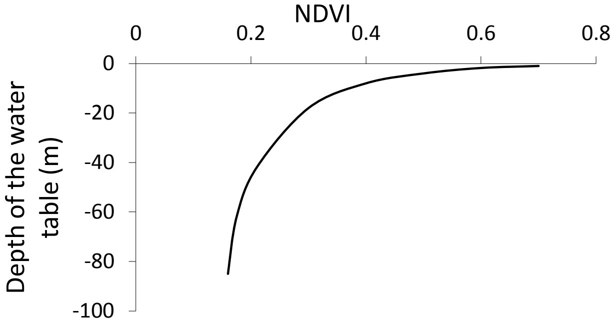
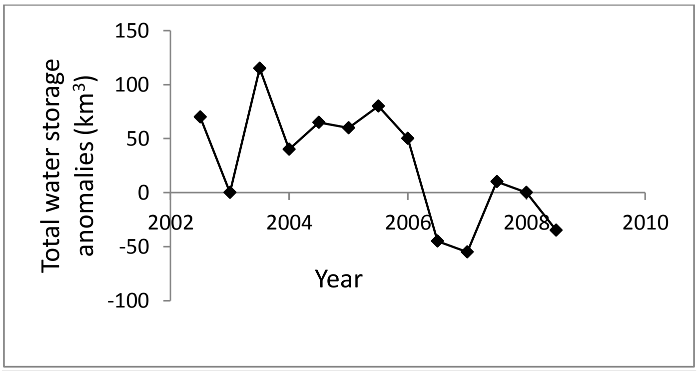
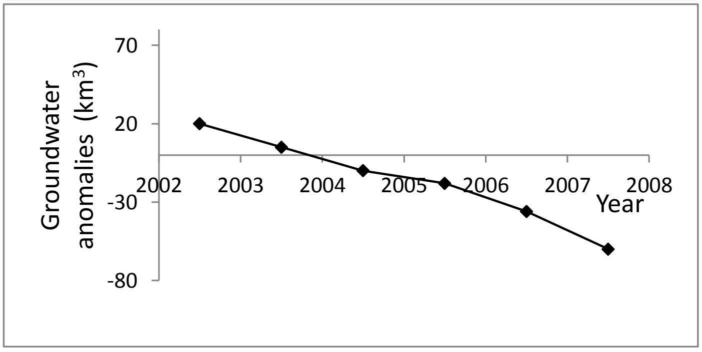


Figure 1: The relationship between NDVI and depth to the water table for the Hailiutu River catchment in northern China. Redrawn from Lv et al. (2012).


Total water storage anomalies (km³)
150
100
50
0
-50
-100
2002
2004
2006
2008
2010
Year


Groundwater anomalies (km³)
70
20
-30
-80
2002
2003
2004
2005
2006
2007
2008
Year

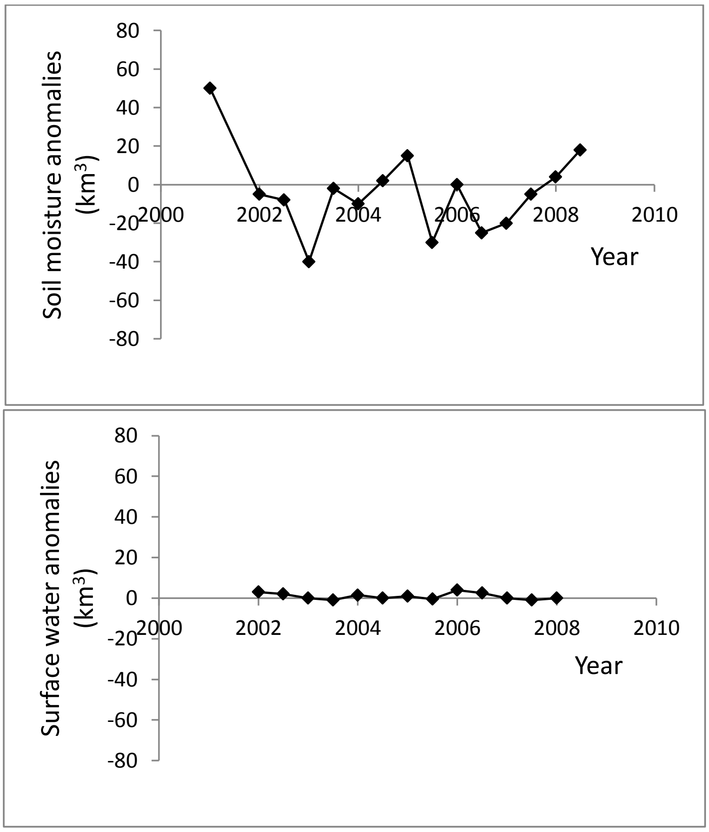


Figure 2: Change of (a) total water storage anomalies; (b) groundwater anomalies; (c) soil moisture storage anomalies; and (d) surface water anomalies relative to the mean of the Murray-Darling Basin during the multiyear drought. Redrawn from Leblanc et al. (2009).

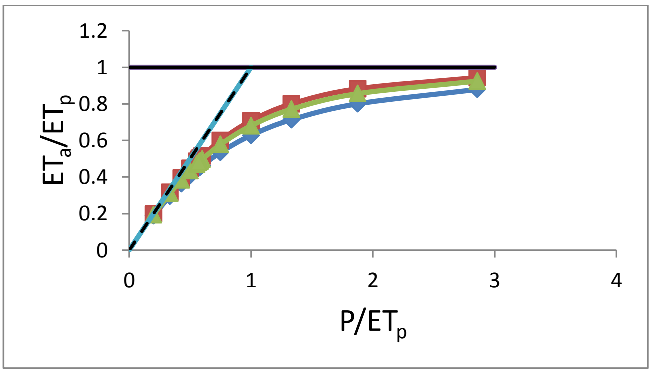


Figure 3: A representation of the Budyko formulation using the Choudhury-Yang formulation with three different values of n (from 1.5 to 2.0). Redrawn from Leaney et al., (2011).

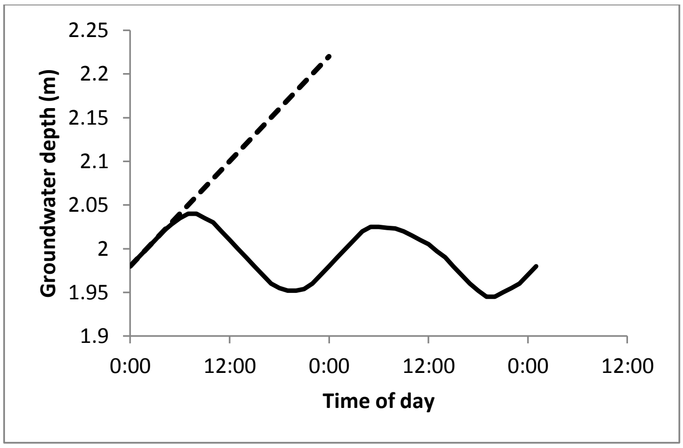


Figure 4: An idealised representation of changes in depth-to-groundwater over a 48 h period. The water table declines (depth increases) during the day because of transpiration by vegetation but increases (depth decreases) at night when transpiration tends to zero and recharge exceeds loss. The dashed line represents the trajectory of overnight recharge in the

absence of transpiration on the following day. See text for further discussion of this.

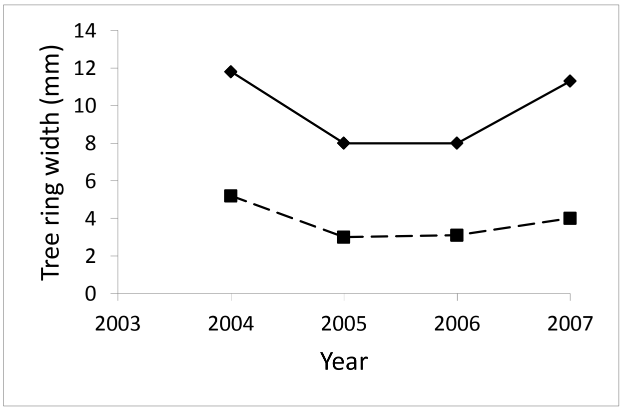


Figure 5: Change in tree ring width of cottonwood (solid line, diamonds) and willow (dashed line, squares) before (2004) during (2005 – 2006) and after draining the reservoir (early 2005) and refilling (mid 2006). Redrawn from Hultine et al. (2010).

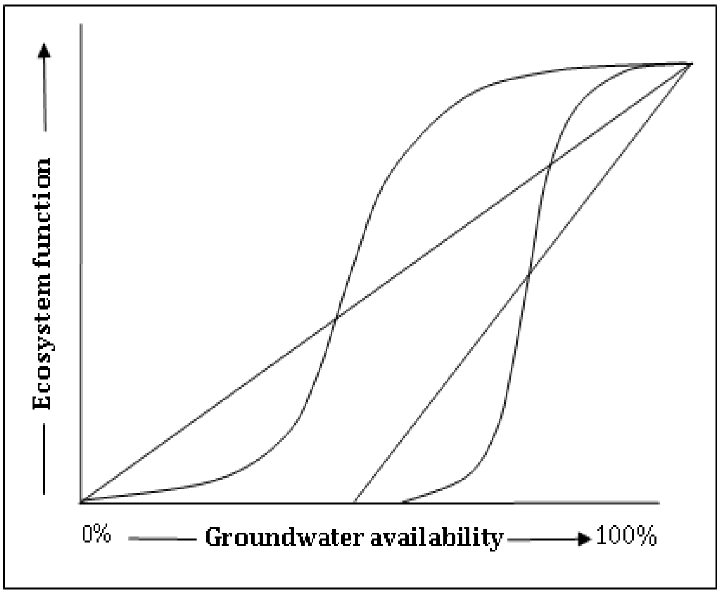


Figure 6: Hypothetical response functions for ecosystem function to differences groundwater availability. From Eamus *et al.* (2006).

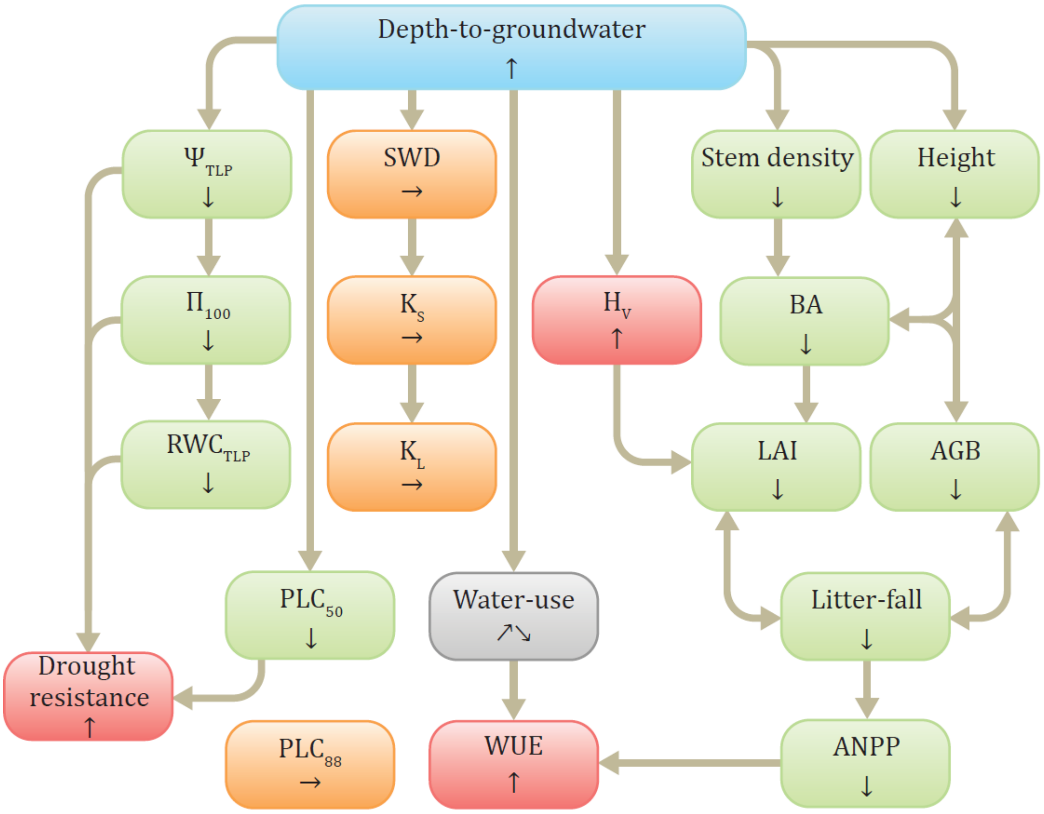

Depth-to-groundwater ↑
Ψ_TLP ↓
SWD →
Stem density ↓
Height ↓
Π_100 ↓
K_S →
H_V ↑
BA ↓
RWC_TLP ↓
K_L →
LAI ↓
AGB ↓
PLC_50 ↓
Water-use ↗↘
Litter-fall ↓
Drought resistance ↑
PLC_88 →
WUE ↑
ANPP ↓

Figure 7: A summary of the traits examined and the general trend in response of those traits to increased depth-to-groundwater along a natural topographic gradient. Upward/downward pointing arrows within a coloured text box indicate increasing/decreasing values of the plant trait as depth-to-groundwater increases. Horizontal arrows indicate no change. Table four provides the definition of all abbreviations used in this figure.

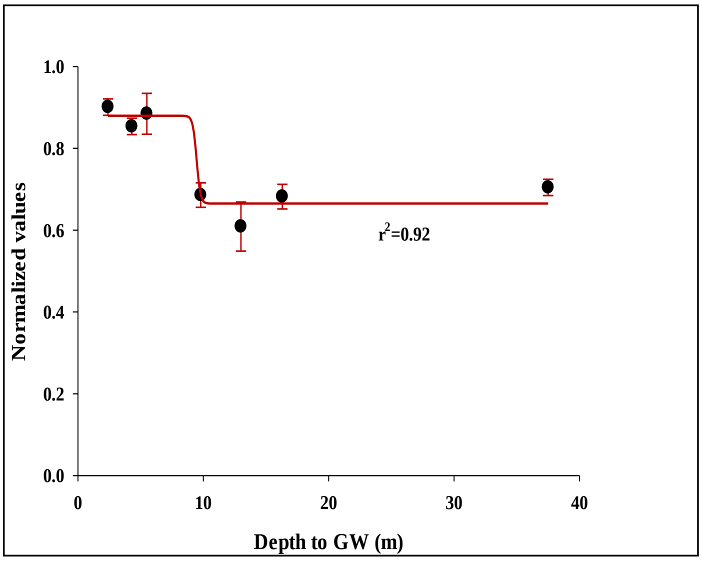


Figure 8: Ecosystem response to increase in depth-to-groundwater, fitted with 4 parameter sigmoidal function. From Zolfaghar (2014).

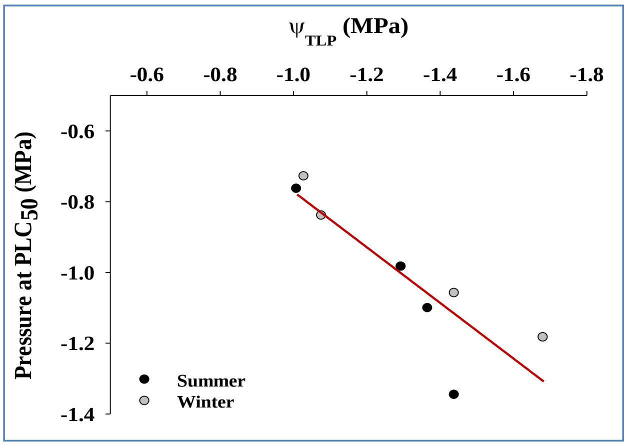


Figure 9: Co-ordination in the response of a leaf-scale and branch-scale trait and drought sensitivity. From Zolfaghar (2014).