

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

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21 **ABSTRACT**

22
23 Groundwater-dependent ecosystems (GDEs) are at risk globally due to unsustainable levels
24 of groundwater extraction, especially in arid and semi-arid regions. In this review, we
25 examine recent developments in the ecohydrology of GDEs with a focus on three knowledge
26 gaps: (1) how do we locate GDEs, (2) how much water is transpired from shallow aquifers
27 by GDEs and (3) what are the responses of GDEs to excessive groundwater extraction? The
28 answers to these questions will determine water allocations that are required to sustain
29 functioning of GDEs and to guide regulations on groundwater extraction to avoid negative
30 impacts on GDEs.

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

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

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

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

53

54 **1 Introduction**

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

66 About two fifths of the world's terrestrial surface area is arid or semi-arid and more than 38
67 % of the world's population lives there. Managing groundwater resources sustainably is
68 therefore a major global social and economic priority (Glazer and Likens 2012). Whilst
69 about 40 % of global groundwater abstraction occurs in these regions, the scarcity of rain
70 means that only 2 % of groundwater recharge occurs there (Wada et al., 2010). Water is
71 increasingly becoming a geopolitical and strategic resource. Disputes between neighbouring
72 states are increasing as demands for groundwater increase. Because of the close relationship
73 between crop yield and water supply, diminishing availability of groundwater in arid and
74 semi-arid regions has immediate and severe impacts on food supplies, food prices and
75 concomitant social unrest. Recent estimates suggest that between 10 and 25 % of the food
76 produced in China and India (home to 2.5 billion people) is at risk because of groundwater
77 depletion (Seckler et al., 1999; Brown 2007).

78 Over extraction of groundwater stores can create several problems. These include: loss of
79 discharge from groundwater to wetlands, springs and streams/rivers, which results in loss of
80 ecosystem structure and function and the associated loss of ecosystem services (Eamus et al.,

81 2006a; Murray et al., 2006); increased depth of groundwater, thereby reducing its availability
82 within the root zone of terrestrial groundwater-dependent vegetation; reduced availability of
83 groundwater for direct human consumption; and reduced availability of groundwater for
84 commercial use, including irrigation, stock watering and other industrial applications.

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

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

100

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

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

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

107 Application of this simple classification scheme assists managers in identifying the correct
108 techniques for assessing GDE structure, function and management regime (Eamus et al.,
109 2006b), and this classification scheme was recently adopted in the Australian National Atlas
110 of Groundwater-Dependent Ecosystems.

111

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

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

- 120 2. How much groundwater is used by a GDE? If we don't know how much groundwater
121 is used, we cannot allocate an appropriate quantity of the resource.
122 3. What are the likely responses of GDEs to over extraction of groundwater? Without
123 knowing what to measure, we cannot regulate groundwater extraction in ways that do
124 not negatively impact on GDEs.
125

126 **2 Identifying groundwater dependent vegetation**

127 Identifying the location of GDEs is the first requisite step to managing them. However,
128 identifying their location across a landscape is difficult, time-consuming, expensive and
129 requires a high level of technical expertise. In this section, a range of new techniques that can
130 be used to assist in this are discussed.
131

132 **2.1 Methods to identify GDEs: indirect inference**

133 Early assessments of groundwater dependency generally relied on inference (Eamus et al.,
134 2006a; Clifton and Evans 2001). Recent applications of inferential techniques to springs,
135 wetland, rivers and lakes can be found in Brown et al., (2011) and to springs, wetlands and
136 streams reliant on baseflow in Howard and Merrifield (2010) and are not further discussed
137 here.
138

139 **2.2 Direct methods**

140 *2.2.1 Satellite based approaches*

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

149 A key concept in the development of RS applications for identifying the location of GDEs is
150 that of "green islands" (Everitt and DeLoach, 1990; Everitt et al., 1996; Neale, 1997;
151 Akasheh et al., 2008), which began with the airborne observations of desert oases and
152 riparian corridors. In this model the structure or function of one pixel in an RS image is
153 compared to that of another pixel located nearby. If one pixel contains a GDE but the other
154 does not, the hypothesis that the structure and function of vegetation in the two pixels will
155 diverge during extended dry periods can be tested. The underlying assumption is that
156 vegetation with access to groundwater will not be subject to the same degree of soil water

157 deficit as vegetation that does not have access to groundwater, thus the spectral signature of
158 the two pixels will diverge over time. By comparing vegetation structure or function across
159 contrasting periods (e.g., comparisons across “wet” and “dry” periods) or across landscapes
160 (e.g., comparisons from riverside to upland pixels), green islands within a sea of browning
161 vegetation can be identified (Contreras et al., 2011)

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

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

180

181 Fig 1 here

182

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

196 Geological, hydrological and ecological data can be used to define areas that have common
197 physical and climatic profiles. These regions are expected to have similar vegetation cover
198 (assuming no management has induced significant changes), thus such areas are expected to
199 have a similar RS signature. Dresel et al., (2010) applied this approach for individual regions
200 in South Australia by developing a correlation analysis using Landsat summer NDVI and
201 MODIS enhanced vegetation index (EVI) as surrogate measures of productivity. EVI is
202 effective for scaling productivity across the range of global ecosystem types (Campos et al.,
203 2013). MODIS EVI images were used to identify regions displaying a consistent
204 photosynthetic activity throughout the year. Landsat NDVI images were then used to locate
205 areas displaying large inter-annual variation in photosynthetic activity across wet and dry
206 years, which were identified by aridity thresholds that were calculated from the Thornthwaite
207 index. Finally, they used an unsupervised classification of Landsat spectral data to locate
208 pixels with similar spectral signatures of areas corresponding to known groundwater-
209 dependent ecosystems. Species-specific differences in spectral signatures have been
210 identified previously (Nagler et al., 2004). By combining all three sources of information
211 (geological, hydrological and ecological) within a GIS, Dresel et al., (2010) identified all
212 pixels across a catchment that had a very high probability of being a GDE. Critical for
213 providing assurance of accurate mapping, ground reconnaissance (“truthing”) was used to
214 validate these findings.

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

231

232 2.2.2 *Fluctuations in groundwater depth*

233 When rooting depth is sufficient, vegetation can directly access the water table via the
234 capillary zone of shallow unconfined aquifers. In some circumstances groundwater uptake by
235 vegetation can be seen as a diel fluctuation in the depth-to-groundwater (Miller et al., 2010),
236 as first identified in groundwater hydrographs by Walter White (1932). These daily

237 fluctuations in depth-to-groundwater cease when the water table falls below the rooting zone
238 (Butler et al., 2007) or when vegetation is dormant (Lautz, 2008; Martinet et al., 2009; Miller
239 et al., 2010). However, changes in the density of water with temperature can cause expansion
240 and contraction of an aquifer (Post and von Asmuth, 2013), leading to the erroneous
241 conclusion that the vegetation is accessing groundwater. Additionally, when the water table
242 is very shallow direct evaporation from groundwater via bare soil can be substantial (1–10
243 mm d⁻¹) (Thorburn et al., 1992) and this may also be misinterpreted. Thus, groundwater
244 dependency generally requires supporting confirmation from multiple indicators and cannot
245 be identified definitively from the "White method" alone. Further elaboration of the White
246 method is given in section 3.5.1 and described in detail in Orellana et al., (2012).

247 2.2.3 Stable isotope analysis

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

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

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

273

274 Table 1 here

275

276 **3 Quantifying water requirements of GDEs**

277 **3.1 A primer on remote sensing derived values of rates of water flux**

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

283 The energy balance equation for land surfaces is:

284
$$LE + H = R_n - G \quad (1)$$

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

290

291 Table 2 here

292

293 Li and Lyons (1999) compared three methods that use surface temperatures to estimate ET.
294 In two methods, differences in surface and air temperature were used to estimate ET,
295 although the two methods differed in the details of the aerodynamic resistance functions. The
296 third model combined NDVI, surface temperature and a soil-adjusted vegetation index that
297 required the four extreme values of surface temperature and NDVI to be located
298 simultaneously within the study area (i.e., patches of dry bare soils; wet bare soil; wet, fully
299 vegetated patches; and dry, water stressed, fully vegetated surfaces). This can make its
300 application problematic. Two methods used the energy balance equation to estimate ET,
301 whereas ET was estimated in a third by using RS data to estimate the Priestley-Taylor factor
302 that scales between ET and potential ET (ET_p). They concluded that the simplest first and
303 second models produced better estimates of ET and that inclusion of the soil index improved
304 the estimates of ET from native (i.e., non-agricultural) vegetation. Likewise, Nagler et al.,
305 (2005a) found that estimates of ET from riparian corridors using RS were improved with the
306 incorporation of a soil index.

307

308 **3.2 Estimating groundwater use by remote sensing**

309 Quantifying the water balance of arid and semi-arid landscapes and aquifers is important to
310 sustainably manage water resources. Accurate and spatially distributed estimates of discharge

311 through vegetation are difficult to obtain through field measurements. Recently, RS methods
 312 have been calibrated against Penman-Monteith estimates of ET (Glenn et al., 2010; Nagler et
 313 al., 2013; Doody et al., 2014), which requires only standard weather data (net radiation, wind
 314 speed and vapour pressure deficit) and thus increases the coverage of calibration sites.
 315 Because ET in GDEs is generally not limited by soil moisture when groundwater is of high
 316 quality (i.e. not saline), it is assumed that actual ET rates are equivalent to the ET of a
 317 reference grass crop (i.e., reference ET, ET_0), as computed following FAO-56 (Allen et al.,
 318 1998). Then, normalised VIs, either EVI^* or $NDVI^*$, can be used like crop coefficients to
 319 estimate the spatial distribution of ET_a from ET_0 on a per-pixel basis. Nagler et al., (2013)
 320 used an exponential scaling function of EVI^* to estimate ET_a :

321

$$322 \quad ET_a = ET_0 \left(a \left[1 - e^{-b EVI^*} \right] - c \right) \quad (4)$$

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

328

$$329 \quad NDVI^* = (NDVI - NDVI_z) / (NDVI_m - NDVI_z) \quad (5)$$

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

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

$$346 \quad ET_a^* = (ET_a - \text{rainfall}) / (ET_0 - \text{rainfall}) \quad (6)$$

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

350

$$351 \quad ET_a \text{ (estimated)} = (ET_0 - \text{rainfall}) NDVI^* + \text{rainfall} \quad (7)$$

352

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

358

359 3.2.1 Up-scaling from point to larger-scale estimates of ET

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

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

$$377 \quad ET = a \left(1 - e^{-b \text{EVI}^*}\right) \left(c \left/ \left[1 + e^{-\{T_a - d\}/e}\right] \right. \right) + f \quad (\text{Middle Rio Grande}) \text{ and} \quad (2)$$

$$378 \quad ET = a \left(1 - e^{-b \text{EVI}^*}\right) (LST - c) + d \quad (\text{both rivers}) \quad (3)$$

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

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

394

395 **3.3 Gravity recovery and climate experiment (GRACE) for detecting changes in** 396 **total terrestrial water storage**

397 In addition to remote sensing measures of ET anomalies or NDVI green islands, there are
398 also new satellite sensors and techniques that provide estimates of groundwater fluctuations
399 and soil moisture storage changes that are of value to the study of GDE's (Brunner et al.,
400 2007). The twin satellites known as the Gravity Recovery and Climate Experiment (GRACE)
401 were launched in 2002 for the purpose of making detailed measurements of Earth's gravity
402 field (Tapley et al., 2004). Although Earth's gravity variations tend to be relatively constant
403 over long time intervals, more dynamic, time-variable gravity fields can be detected and these
404 have been related to land surface moisture, ground water fluctuations, sea ice, sea level rise,
405 and deep ocean currents. GRACE's ability to monitor changes in such "unseen water
406 reserves" from space are a significant new addition to hydrological studies that can
407 substantially improve our knowledge of below- and aboveground water resources and
408 associated changes to vegetation functioning and GDE's.

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

418 In most cases, soil moisture becomes the sole component that must be removed from the
419 gravity data to estimate groundwater changes, since variability of snow and surface water is
420 relatively insignificant to total water storage variability. By subtracting the soil moisture

421 contribution, the remaining time-variable change in GRACE's measure of total water storage
422 will be due to changes in groundwater. Thus:

$$423 \quad \Delta TWS = \Delta SW + \Delta SM + \Delta GW \quad (8)$$

424

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

426 Many studies have compared changes in groundwater storage obtained from GRACE data
427 with in situ data for validating the accuracy of GRACE data at either regional or continental
428 scales (Henry et al., 2011; Leblanc et al., 2009 ; Rodell et al., 2009, 2007; Scanlon et al.,
429 2012a,b; Syed et al., 2009).

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

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

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

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

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

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

465

466 *3.3.1 Downscaling*

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

478

479 *3.3.2 Groundwater depletion studies*

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

492

493 Fig 2 here

494

495

496 3.3.3 Remote sensing limitations and challenges in GDE studies

497

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

503

504 Regardless of the application, there will be certain limitations in the use of remote sensing
505 that need to be considered. Other geospatial data sources will often need to be integrated to
506 make the best use of remote sensing, including climate, soils, landscape morphology, and
507 ecologic data layers that will enable potential areas for GDEs to be delineated (Bertand et al.,
508 2012). Multiple sensors and image data sets are best suited for studies of GDEs because of
509 the inherent spectral-spatial-temporal limitations of single sensor systems. For example the
510 use of fine spatial resolution Landsat (30 m) and high temporal frequency MODIS data (1-2
511 day) allow us to identify potential GDE vegetation patches (Landsat) and track changes in
512 their seasonal and inter-annual dynamics (MODIS spectral vegetation indices, VIs). Thus,
513 vegetated areas that maintain high VI ‘greenness’ values during extended dry periods can be
514 flagged as ‘*high GDE potential*’, under the premise that GDEs exhibit low seasonality in
515 greenness and ET between dry and wet seasons and low inter-annual variability across years.

516

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

532

533 It should be noted that although remote sensing is a useful diagnostic tool and proxy for the
534 detection and sensing of GDE’s, most detection and mapping is done by inference and careful
535 user interpretation. Remote sensing often cannot directly ascertain causes and mechanisms
536 for GDEs and much remains to be done to assess GDE influences on the water balance, their
537 sensitivity to changing water availability, and responses to stress conditions. Future sensor
538 systems planned for launch in the next few years include follow-on GRACE twin satellite

539 missions with improved sensing capabilities allowing more detailed analyses groundwater,
540 soil moisture, and surface water distributions and trends. The soil moisture active passive
541 (SMAP) mission, launched in 2014, provides improved soil moisture retrievals which will
542 improve upon the detection and differentiation of soil-moisture induced vegetation dynamics
543 from those associated with groundwater use.

544

545 **3.4 Hydrological modelling**

546 *3.4.1 Conceptual water balance approaches*

547 **A spreadsheet tool**

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

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

555

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

$$563 \quad ET_a = (P - ET_p) \left/ \left(P^n + [ET_p]^n \right)^{1/n} \right. \quad (9)$$

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

569

570 Figure 3 here

571

572 The model is run using historical monthly rainfall and estimated ET. Pan evaporation rates
 573 can be used instead of ET_p , in which case $ET_p = 0.75E_{pan}$. Modest agreement between
 574 modelled and observed rates of groundwater discharge was found in two Australian studies
 575 where ET exceeded rainfall in the Wattle Range by 2 to 440 $mm\ y^{-1}$ (Benyon and Doody
 576 2004), although the range of estimated groundwater discharge rates was large: 107 to 671
 577 $mm\ y^{-1}$ (Benyon and Doody 2004) and 380–730 $mm\ y^{-1}$ (Benyon et al., 2006).

578 As an alternative method to the risk assessment just described, Leaney et al., (2011) applied
 579 Eagleson's theory of ecological optimality (Eagleson 1978). This proposes that the LAI of a
 580 site is maximised according to long-term rainfall and soil water holding capacity such that
 581 productivity is maximised whilst minimising the development of water stress. In this
 582 hypothesis, native vegetation is assumed to be at equilibrium with the local hydrological
 583 regime (Nemani and Running 1989). Ellis and Hatton (2008) have shown that the LAI of a
 584 site is proportional to a climate wetness index ($CWI = P/ET_p$), whilst Eamus et al., (2001)
 585 used the Baldocchi-Meyers index (foliar [N] x P/E_{eq} , where foliar [N] is the concentration of
 586 nitrogen in leaves and E_{eq} is equilibrium evapotranspiration) and found a strong ($R^2 = 0.95$
 587 for 16 sites globally) curvilinear relationship with LAI, supporting the essentials of
 588 Eagleson's optimality theory. Similarly, Zeppel (2013) examined multiple species across sites
 589 in Australia and found strong convergence in daily rates of tree water-use and leaf area across
 590 five evergreen sclerophyllous genera. In the Eagleson optimality method of Leaney et al.,
 591 (2011), the relationship between LAI and the CWI of Ellis and Hatton (2008) is used:

592

$$593 \quad LAI = (3.31 \cdot CWI) - 0.04 \quad (10)$$

594

595 In GDEs, groundwater discharge combines with precipitation to supply ET (O'Grady et al.,
 596 2011), thus:

$$597 \quad CWI_g = (P + GW) / ET_p \quad (11)$$

598

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

$$602 \quad ET / ET_p = 1 + (P / ET_p) - \left(1 + [P / ET_p]^w\right)^{1/w} \quad (\text{Zhang et al., 2004}) \quad \text{and} \quad (12)$$

$$603 \quad (ET / ET_p)_g = 1 + ([P + GW] / ET_p) - \left(1 + \{[P + GW] / ET_p\}^w\right)^{1/w} \quad (\text{O'Grady et al., 2011})$$

604 (13)

605 Within zones of the same CWI, sites with access to shallow groundwater maintain a larger
606 LAI than sites without access to groundwater (O'Grady et al., 2011). To determine GW, the
607 pairs of equations (CWI , CWI_g ; ET/ET_p , $[ET/ET_p]_g$) were optimised by obtaining the
608 difference in rainfall required to attain a given LAI with a known CWI value (O'Grady et al.,
609 2011).

610

611 3.4.2 Groundwater flow and variable saturation models: MODFLOW and HYDRUS

612 Two models, MODFLOW and HYDRUS, are commonly used to investigate the hydrologic
613 state of the coupled surface water–groundwater–soil–vegetation system (McDonald and
614 Harbaugh, 1988; Doble et al., 2006; Shah et al., 2007; Lowry and Loheide, 2010; Loheide
615 and Booth, 2011; Ajami et al., 2012). HYDRUS applies Richard's equation to simulate water,
616 heat and solute movements in soil, whereas MODFLOW is fully distributed and coupled
617 hydrologic model of groundwater flow (Orellana et al., 2012). Hydrologic models that apply
618 Richard's equation in a soil medium of variable saturation are important for evaluating the
619 mechanisms that generate groundwater hydrographs and flow. MODFLOW can also perform
620 spatial scaling of ET as a function of depth-to-groundwater, although the form of ET depends
621 upon parameterisation of the model. Often, ET is determined as ET_p or ET_0 , but
622 measurements of ET_a from eddy covariance can also be used. In one example, Wilcox et al.,
623 (2007) estimated ET from Cleverly et al., (2002) to evaluate the interaction between riparian
624 ET and surface water–groundwater interactions.

625 Variable saturation models have improved our understanding of the interactions between
626 groundwater and soil moisture in the vadose zone. Root water uptake (RWU) creates soil
627 moisture deficits in the vadose zone and the capillary fringe, thereby causing vadose zone
628 water content to fluctuate with depth-to-groundwater (Nachabe et al., 2005; Shah et al., 2007;
629 Logsdon et al., 2010). Using HYDRUS 1-D, Lowry and Loheide (2010) integrated ET_g and
630 RWU from the vadose zone by estimating the groundwater subsidy as the difference between
631 RWU from the shallow groundwater and RWU from free drainage. Further complicating the
632 relationship between groundwater and soil moisture, hydraulic redistribution of moisture
633 from deep in the soil column to the surface (i.e., hydraulic lift) can reduce the amplitude of
634 fluctuations in depth-to-groundwater, increase the amount of ET_g that is lost to groundwater
635 evaporation, and decrease the nocturnal recovery in depth-to-groundwater (Orellana et al.,
636 2012).

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

645 and vegetation effects on ET have been thoroughly described, we will focus on the regional
646 aquifer effects on ET_g here.

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

659

660 **3.5 Field based measurements**

661 *3.5.1 Sub-daily fluctuation in groundwater depth*

662 An idealised representation of the “White method” in a shallow unconfined aquifer is shown
663 in Figure four.

664

665 Figure 4 here

666

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

675

$$676 \quad ET_g = S_y (24r + s) \quad (14)$$

677

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

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

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

701 Several modifications to the White method were evaluated in a study by Fahle and Dietrich
702 (2014), in which they compared errors in estimation of S_y , recovery and ET_g . No model
703 outperformed the others in each of these error benchmarks, thus illustrating that errors in the
704 estimation of S_y are compensated by errors in the estimation of recovery (Fahle and Dietrich,
705 2014). The methods that provided the best estimates for recovery of the groundwater used
706 approaches to estimate sub-daily rates of ET_g and recovery (Gribovszki et al., 2008; Loheide
707 and Ii, 2008). In both methods, recovery was estimated from the previous and following
708 nights, although application to other methods might require site-specific parameterisation of
709 the time period that is most representative for their study conditions (e.g., 18.00–6.00; Fahle
710 and Dietrich, 2014). In the method of Gribovszki et al., (2008), recovery was estimated from
711 the time rate of change in depth-to-groundwater, and this important upgrade reduced the error
712 of recovery estimates (Gribovszki et al., 2010; Fahle and Dietrich, 2014).

713 Groundwater hydrographs include the impact of regional fluctuations in the aquifer that are
714 not associated with local changes arising from ET of vegetation (Engel et al., 2005). A
715 regional effect that can cause problems with the White method occur when tides from nearby
716 water bodies generate two daily peaks in the groundwater hydrograph (Miller et al., 2010),
717 thereby requiring measurements of the water body that is causing the effect. After
718 accounting for the regional hydrograph, soil moisture content in the vadose zone can still
719 affect the correlation between sap flow measurements of ET_g and groundwater fluctuations
720 (Engel et al., 2005). This was consistent with the modelling results of Loheide et al., (2005),
721 who found that daily fluctuations were dampened by root water uptake from the vadose zone

722 alone. Spectral methods (e.g., windowed Fourier decomposition) are effective at identifying
723 break points in the daily signal like those associated with regional groundwater and soil
724 moisture effects, although variations in ET_g can result in loss of amplitude, consequently
725 rendering spectral analysis unsuitable for quantitative analysis without an adequate scaling
726 factor (Schilling and Zhang, 2012; Soylu et al., 2012).

727

728 *3.5.2 Using stable isotopes to estimate rates of groundwater use*

729 Estimates of the proportion of total vegetation water use derived from groundwater can be
730 determined from stable isotope analyses (Querejeta et al., 2007; Maguas et al., 2011; Feikema
731 et al., 2010; Kray et al., 2012; McLendon et al., 2008). Two types of information are
732 required to quantitatively partition ET_g from ET . The first is an independent estimate of ET_0
733 or ET_a as derived from eddy covariance (Kelliher et al., 1992; Baldocchi and Vogel, 1996;
734 Baldocchi and Ryu, 2011), sapflow (Cook and O'Grady, 2006; O'Grady et al., 2006; Zeppel,
735 2013) or RS techniques (Nagler et al., 2009; Nagler et al., 2013). The second is the stable
736 isotope composition of water in soil, groundwater and xylem. Upon determination of the
737 proportion of ET that is due to ET_g (Section 3.2), the amount of ET_g , for example in $mm\ d^{-1}$,
738 is the product of that proportion and ET .

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

749 Stable isotope composition varies with depth (Table 1; Querejeta et al., 2007). Consequently
750 taking an average value to represent the entire rooting depth can lead to errors. Whilst use of
751 two independent isotopes allows the relative contribution of three sources to be determined,
752 obtaining independence of both isotopes is very difficult. As an alternative, Cook and
753 O'Grady (2006) developed a model that estimates the relative water uptake by vegetation
754 from different soil depths. This model is based upon the following axioms: the rate of water
755 uptake is determined by (a) the gradient in water potential between bulk soil and leaves; (b)
756 root distribution through the soil profile; and (c) a lumped hydraulic conductance parameter.
757 Soil isotopic composition as a function of depth and of xylem water is used to constrain root
758 distributions within the model. This has the advantage over end-member analyses (an analytic
759 tool to determine the relative contributions of soil water and groundwater to transpiration;
760 Phillips and Gregg 2003) because: (i) it produces a quantitative estimation of the proportion
761 of water extracted from multiple depths (including groundwater); (ii) it doesn't require

762 distinct values of isotope composition for end-member analyses and therefore can deal with
763 the more typical grading of isotope composition observed through the soil profile; and (iii) it
764 is based on simple ecophysiological principles. Cook and O’Grady (2006) applied this
765 model and demonstrated that two co-occurring species obtained 7–15 % of their
766 transpirational water from the water table, a third species accessed 100 % from the water
767 table, and a fourth species derived 53–77 % from groundwater.

768

769 **4 Functional responses of GDEs to changes in GW depth**

770 **4.1 Effects of groundwater on growth and dendrochronological traits**

771 A reduced growth rate in response to declining water availability is a universally observed
772 plant response (Kelliher et al., 1980; Osmond et al., 1987; Oberhuber et al., 1998; Sarris et
773 al., 2007). In most GDEs rainfall and groundwater provide important supplies of water, and
774 the ratio of rainfall to groundwater uptake varies spatially and temporally. Consequently,
775 increases in groundwater depth may be expected *a priori* to have the potential to affect plant
776 growth. Dendrochronology (the study of growth in tree rings) has a long history in ecological
777 research spanning many decades (Drew and Downes 2009; McCarroll and Loader, 2004).
778 However, its application to the study of GDEs is much more recent (e.g. Giantomasi et al.,
779 2012). Similarly, recording point dendrometers, which are sensitive stem gauges that
780 monitor growth increment at hourly time-scales, recently have been used for expanding
781 applications. In this section we briefly review some of the insights gained from
782 dendrochronology and dendrometry in the study of GDEs.

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

797 The timing of groundwater dependence can influence the presence of a climate signal in tree
798 rings: climate signals can be weaker during formation of late wood, when growth rates are
799 small (Oberhuber et al., 1998); or during the dry season, when precipitation rates are
800 negligible and growth is supported by groundwater (Drake and Franks, 2003). Thus, analysis
801 of tree ring chronologies can provide an insight into the importance of access to groundwater

802 on plant growth. Individual events can be identified in the tree ring growth record (Hultine et
803 al., 2010), as can long-term trends in depth-to-groundwater (Bogino and Jobbagy, 2011). In
804 riparian cottonwood trees and willows, Hultine et al., (2010) identified rapid, large and
805 reversible responses of tree ring width to draining and refilling of a reservoir (Fig. 5).

806

807 Figure 5 here

808 Longer-term trends in depth-to-groundwater have impacted dendrochronologies in both
809 directions, toward lower growth rates with groundwater extraction (Lageard and Drew, 2008)
810 and toward increasing growth rates with decreasing depth-to-groundwater, except in response
811 to root anoxia arising from flooding (Bogino and Jobbagy, 2011). However, specific
812 responses depend upon depth-to-groundwater and individual differences amongst functional
813 types; for example, riparian cottonwood trees (*P. fremontii*) responded to rewetting with
814 growth that was larger and faster than the response of co-occurring willow (*S. exigua*), a
815 small-stature, thicket-forming shrub that is restricted to streamside areas with very shallow
816 groundwater (Scurlock, 1998; Rood et al., 2011). From an understanding of the relationships
817 between tree growth and depth-to-groundwater, historical periods of sensitivity to
818 hydrological drought (i.e., affecting groundwater levels) *versus* meteorological drought (i.e.,
819 below-average precipitation) can be identified (Potts and Williams, 2004; Adams and Kolb,
820 2005; Coccozza et al., 2011). Such insights have value in developing a long-term
821 understanding of the relationships amongst GDEs, climate and groundwater depth.

822 Wood formed during drought is enriched in ^{13}C , reflecting decreases in stomatal conductance
823 relative to photosynthesis and the consequential ratio of $[\text{CO}_2]$ within and outside of the leaf
824 (C_i/C_a) (McCarroll and Loader, 2004; Coccozza et al., 2011) (Horton et al., 2001, Maguas et
825 al., 2011). Interpretation of $\delta^{13}\text{C}$ in tree rings can be complicated by the effects of phloem
826 loading (Gessler et al., 2009) and by photosynthetic re-fixation in the bark (Cernusak et al.,
827 2001), although with independent confirmation, xylem $\delta^{13}\text{C}$ can explain differences in
828 groundwater use and water stress in groundwater-dependent trees. In one such comparison,
829 $\delta^{13}\text{C}$ was constant across xylem from *Populus* along a perennial stream (thereby implying
830 access to groundwater) but changed with moisture conditions in an intermittent reach (Potts
831 and Williams, 2004). Likewise, changes in ring width over time were reflected by $\delta^{13}\text{C}$
832 from leaves (Hultine et al., 2010), such that less negative values of $\delta^{13}\text{C}$ indicated increased
833 water-use-efficiency when the supply of water was reduced.

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

842 found that increased groundwater supply (actual or simulated) resulted in increased stem
843 increment, sapflow and xylem water potential.

844

845 **4.2 Two case studies**

846 *4.2.1 The Gngangara Mound*

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

856 To determine long-term floristic changes associated with groundwater abstraction, a series of
857 transect studies were initiated in 1988. A 2.2 m increase in depth-to-groundwater coupled to
858 higher-than-normal summer temperatures resulted in further adult mortality of overstorey
859 species by as much as 80 %; additionally, 64 % mortality was recorded in understory species
860 2 years after the start of groundwater abstraction (Groom et al., 2000). Increased rates of
861 mortality were not observed at control sites that were not subject to groundwater pumping.

862 Large inter-specific differences in rates of mortality were observed in these Gngangara studies.
863 Consequently, a further study examined the vulnerability of individual species to increased
864 depth-to-groundwater (Froend and Drake 2006; Canham et al., 2009). Using xylem
865 embolism vulnerability curves as a measure of sensitivity to water stress, Froend and Drake
866 (2006) compared three *Banksia* and one *Melaleuca* species. They found that xylem
867 vulnerability reflected the broad ecohydrological distribution of species across a topographic
868 gradient, and they identified a threshold leaf water potential below which increased mortality
869 was likely. Similarly Canham et al., (2009) examined Huber values (the ratio of sapwood to
870 leaf area), leaf-specific hydraulic conductivity (k_l) and xylem vulnerability of two obligate
871 phreatophytes and two facultative phreatophytes. At sites where depth-to-groundwater was
872 shallow there were no inter-specific differences in vulnerability to water stress. However, by
873 comparing across a topographic gradient, Canham et al., (2009) showed that two facultative
874 phreatophytes (but not the obligate phreatophytes) were more resistant to xylem embolism at
875 the upper slope (larger depth-to-groundwater) than the lower slope.

876 It is not only aboveground tissues that adapt to changes in groundwater depth. Differences in
877 root growth also respond to changes in depth-to-groundwater. Thus Canham et al., (2012)
878 found that root growth varied with depth within the soil column: at the surface, root growth
879 responded to seasonality and microclimate; at depth, root growth occurred all year and was
880 dependent upon soil aeration (i.e., roots elongated rapidly followed a declining water table

881 during the summer and died back in the following winter as the groundwater rebounded).
882 These results are consistent with the increases in ET following groundwater decline that were
883 observed by Cleverly et al., (2006). The ability to rapidly increase root depth during the (dry)
884 summer is a critical attribute of phreatophytes occupying sites with seasonally dynamic
885 depth-to-groundwater.

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

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

910

911 4.2.2 *Riparian forest vegetation in the southwestern USA*

912 In the southwestern USA, the majority of GDEs are riparian or littoral, where a shallow
913 aquifer is formed by runoff from snowmelt in the mountainous headwaters. Much of the
914 agriculture in the region is found along the rivers due to the large amount of surface water
915 that flows past. The focus of irrigation to the riparian corridors has placed intense
916 competition between water resources for people *versus* the environmental flows that are
917 required to maintain shallow aquifers and associated GDEs. Of further risk to riparian GDEs
918 and agriculture, groundwater extraction and land use change threaten riparian ecosystems
919 (Scott et al., 1999; Nippert et al., 2010; Pert et al., 2010). Thus, many studies have been
920 undertaken over several decades to investigate the water use of GDEs in southwestern North

921 America (van Hylckama, 1970; Gay and Fritschen, 1979; Sala et al., 1996; Devitt et al.,
922 1998; Goodrich et al., 2000a; Cleverly et al., 2002; Scott et al., 2004; Nagler et al., 2005b).

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

935 In southwestern North America, vegetation in riparian corridors and adjacent rangelands or
936 shrublands is classified by reliance upon access to groundwater (i.e., obligate or facultative
937 phreatophyte; Smith et al., 1998) or plant functional type (obligate wetland, shallow-rooted or
938 deep-rooted riparian, transitional riparian, or upland; Pockman and Sperry, 2000; Baird and
939 Maddock, 2005; Baird et al., 2005). The result of groundwater depletion has distinct effects
940 on the vegetation in each functional type. Shallow-rooted, obligate phreatophytes (e.g.,
941 cottonwood, *Populus* spp.) can be very sensitive to groundwater decline, resulting in
942 reductions of ET, productivity and canopy conductance as a consequence of increases in
943 vapour pressure deficit that are correlated with depth-to-groundwater (Gazal et al., 2006;
944 Kochendorfer et al., 2011). Branch sacrifice, partial crown dieback and mortality commonly
945 occur in *Populus* following substantial groundwater drawdown (Mahoney and Rood, 1991;
946 Kranjcec et al., 1998; Scott et al., 1999; Rood et al., 2000; Cooper et al., 2003; Rood et al.,
947 2003). However, stomatal closure and crown dieback in *Populus* can prevent total hydraulic
948 failure, and thereby minimise mortality rates, by maintaining favourable xylem water
949 potentials within the remainder of the crown (Amlin and Rood, 2003).

950 Decreased baseflow and drawdown of groundwater levels has been associated with a shift in
951 dominance to xerophytic species in the American Southwest at the expense of forbs and
952 obligate phreatophytes (Stromberg et al., 1996; Stromberg et al., 2006; Stromberg et al.,
953 2007; Stromberg et al., 2010). Xerophytes in the riparian corridors of the American
954 Southwest include deep-rooted phreatophytes (e.g., *Proposis*, *Tamarix*) and upland species
955 (e.g., *Chrysothamnus*), any of which may be opportunistic users of groundwater or
956 groundwater-independent. Stress tolerance, opportunistic use of groundwater and use of
957 multiple water sources (e.g., soil moisture) have contributed to the invasive success of
958 *Tamarix* (Busch et al., 1992; Cleverly et al., 1997; Di Tomaso, 1998; Nippert et al., 2010).
959 Consequently, *Tamarix* inhabit sites with variable depth-to-groundwater (Lite and Stromberg,
960 2005), which results in an amount of ET that is equivalently variable in time and space
961 (Cleverly et al., 2002; Cleverly, 2013).

962 The effective area of riparian vegetation has historically increased in the American Southwest
963 due to expansion of deep-rooted phreatophytes like *Tamarix* and *Prosopis* (Hultine and Bush,
964 2011). The upland vegetation that previously occupied riverine upper terraces and grasslands
965 supported small rates of ET (Shafroth et al., 2005; Hultine and Bush, 2011), thus expansion
966 of phreatophytes into these areas has resulted in an increase in ET losses (Scott et al., 2006b;
967 Cleverly, 2013) and thereby has placed a potential strain on groundwater resources. In the
968 case of expansion by *Tamarix*, groundwater extraction may result in enhancement of ET
969 (Cleverly et al., 2006), contrasting with post-extraction reductions in ET by native, shallow-
970 rooted phreatophytes such as *Populus* (Cooper et al., 2006; Gazal et al., 2006) and thus
971 representing a shift in the ecohydrology of riparian corridors throughout the semi-arid regions
972 of south western North America.

973

974 **4.3 Integrating multiple-scale responses**

975 *4.3.1 Multiple traits across leaf, branch, whole-tree and stand*

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

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

998

999 Table 3 here

1000 In a recent comprehensive, three-year study, Zolfaghar (2014) examined leaf, branch, tree
1001 and stand-scale functional and structural attributes of woodlands across a gradient of depth-
1002 to-groundwater (2.4 m to 37.5 m) in mesic Australia. She examined eighteen traits, including
1003 stand-scale basal area and tree height, leaf turgor loss point, sapwood hydraulic conductivity,
1004 sensitivity to xylem embolism and above ground net primary productivity. An increase in
1005 depth-to-groundwater across these sites was hypothesised to result in:

- 1006 1. reduced standing biomass;
- 1007 2. adjustment of leaf-, tree- and plot-scale plant traits with associated repercussions on
1008 plant water relations;
- 1009 3. increased drought tolerance; and
- 1010 4. increased water-use-efficiency.

1011
1012 Fig 6 here

1013
1014 Figure seven provides a summary of the observed responses of each trait to increasing depth-
1015 to-groundwater. Refer to Table four for the abbreviations used in Figure seven.

1016
1017
1018 Fig 7 here.

1019
1020
1021 Table 4 here

1022
1023 It is clear from Figure seven that increased depth-to-groundwater was associated with
1024 declines in basal area, tree height and LAI, and hence light interception, of native woodlands.
1025 As a consequence, aboveground net primary productivity was reduced as groundwater
1026 availability declined. Increased drought tolerance, as indicated by increased water-use-
1027 efficiency, increased Huber value and reduced water potential at turgor loss and solute
1028 potential at full turgor, supported the principle over-arching hypothesis that increasing depth-
1029 to-groundwater results in a suite of leaf-branch and tree-scale adaptations that increase tree
1030 tolerance to reduced water supply.

1031 A key aspect of this research was to develop an ecosystem-scale response function for depth-
1032 to-groundwater. Zolfaghar (2014) normalised the responses (0 to 1) such that a response of 1
1033 indicates no effect of differences in depth-to-groundwater and 0.5 indicates a 50 %
1034 decline/increase in the maximal/minimum value of a particular trait. The normalised response
1035 function is presented in Figure eight. Despite the large number of traits and species across the

1036 seven sites, the standard error of the ecosystem-scale average for each data point was
1037 remarkably small, indicating significant convergence in normalised responses to differences
1038 in depth-to-groundwater. Convergence of functional variations in traits across sites and
1039 species is increasingly observed with respect to rainfall or other climatic variables (Wright et
1040 al., 2004; Kattge et al., 2011). Indeed, identification of plant functional types (PFTs) is a
1041 practical means for models of land surface-atmosphere interactions across biomes to integrate
1042 the physiology of vegetation. Similarly, improved accuracy can be obtained from dynamic
1043 global vegetation models (DGVMs) through the construction of large datasets (cf. Wright et
1044 al., 2004, Kattge et al., 2011) that include a representation of groundwater-dependent
1045 ecosystems.

1046 A second feature apparent in the response function of Fig. 8 is the large R^2 of the sigmoidal
1047 regression, reflecting the relatively high degree of confidence in this threshold response. The
1048 response curve further suggests that extraction of groundwater beyond 7 – 9 m depth is likely
1049 to result in significant changes in ecosystem structure and function. Although we cannot
1050 pinpoint the exact break point with precision, it is clearly apparent that a breakpoint does
1051 occur in the data. Furthermore, two recent reviews based on water balance concluded that
1052 groundwater uptake ceased when depths exceeded 7.5 m (Benyon et al., 2006) or 8 – 10 m
1053 (O’Grady et al., 2010), whilst Cook et al., (1998) established a limit of approximately 8 m for
1054 a Eucalypt savanna. Finally, Kath et al., (2014) identified thresholds of groundwater depth
1055 across 118 sites in SE Australia for two tree species ranging from 12.1 m to 26.6 m further
1056 supporting our identification of a breakpoint in the responses of trees to groundwater depth.
1057 Such a strong response, consistent across multiple traits, should provide a strong management
1058 signal to guide future groundwater abstraction.

1059

1060 Figure 8 here

1061 4.3.2 *Co-ordination across traits*

1062 Some plant traits are a better indicator of plant sensitivity to water stress than others. Leaf
1063 water potential at turgor loss is recognised as a physiological measure of plant sensitivity to
1064 water stress (McDowell et al., 2008). Similarly, measurements of vulnerability to xylem
1065 cavitation and safety margins are critical determinants of drought tolerance (Markesteijn et
1066 al., 2011; Sperry et al., 2008). Safety margins are equal to the difference between minimum
1067 daily branch water potential and PLC_{50} (Meinzer et al., 2008; Sperry et al., 2008). A strong
1068 linear correlation between these two traits (Fig. 9) in the Kangaloon study (Zolfaghar 2014)
1069 reveals co-ordination in the response of leaf (cell traits) and xylem (branch trait) anatomy, as
1070 has been observed previously in a study of eight tropical dry forest species (Brodrribb et al.,
1071 2003). This relationship indicates that as depth-to-groundwater increased, sensitivity to
1072 drought at both leaf cell and branch-scale decreased (lower leaf water potential is needed to
1073 reach turgor loss point and PLC_{50} declined).

1074

1075 Figure 9 here

1076

1077 **5 Concluding remarks**

1078 The existence of GDEs has been known for several centuries. The ecological, social, cultural
1079 and economic importance of GDEs, however, has only been understood more recently.
1080 Whilst inferential methods were the main means for determining the presence/location of
1081 GDEs for many decades these have now been replaced by more direct methodologies which
1082 include the use of stable isotopes and hourly direct measurements of fluctuations in shallow
1083 groundwater depth. The most revolutionary recent development has, perhaps, been the
1084 application of remote sensing techniques to identify the location of GDEs but also to reveal
1085 key features of their functional behaviour.

1086 Increasing frequencies, spatial and temporal extent and severity of drought and resulting
1087 drought-induced mortality of forests have been recorded extensively (Dai 2011; Eamus et al.,
1088 2013) in the past two decades. Climate-change-induced changes in rainfall distribution and
1089 amounts pose a new stress to both groundwater resources and associated GDEs. For the first
1090 time, remotely sensed information on both the structure (e.g LAI) and functioning (e.g. rates
1091 of water-use and primary productivity) of GDEs are now available across several decades.
1092 The challenge now is to use this long history of remotely sensed and meteorological data as a
1093 unique natural experiment to determine response functions of multiple GDEs to changes in
1094 climate (and groundwater depth) globally to inform both the science of ecology and the
1095 practical needs of water and land resource managers into the future.

1096

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1098

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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 $\delta^2\text{H}$ values (‰) 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 $\delta^2\text{H}$ 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			
<i>M. argentea</i>	< 0.25		-44	-43 to -48	-43
<i>B. acutangula</i>	3		-80	-46 to -40	-45
<i>C. bella</i>	> 15		-56 to -91	-59 to -71	Not available to roots

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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
$ET_a^* = (ET_a - \text{rainfall}) / (ET_o - \text{rainfall})$ ET_a linearly correlated with NDVI* $ET_g = (ET_o - \text{rainfall}) \cdot NDVI^*$	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 $PET \cdot \text{crop factor}$ and crop factor is derived from EVI	Estimate ET at 1 km spatial resolution	Guerschman et al., 2009

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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

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1868 **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

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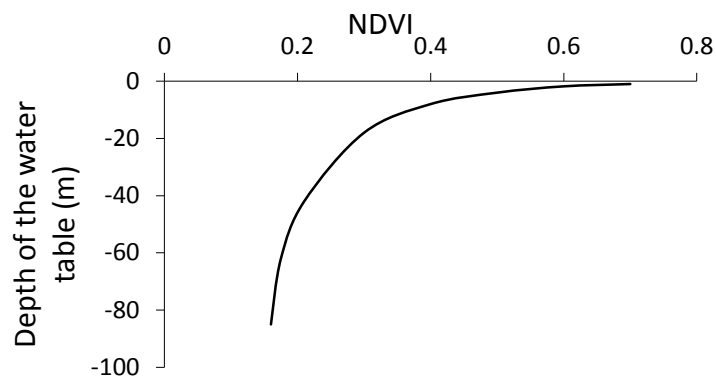
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1879 **Figure 1:** The relationship between NDVI and depth to the water table for the Hailiutu
 1880 River catchment in northern China. Redrawn from Lv et al. (2012).

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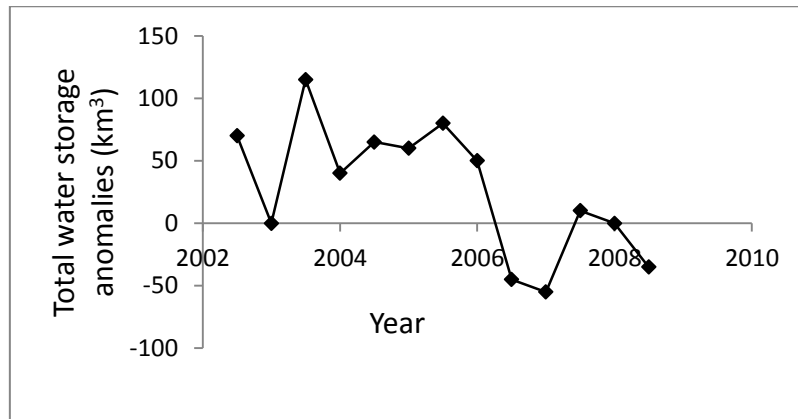
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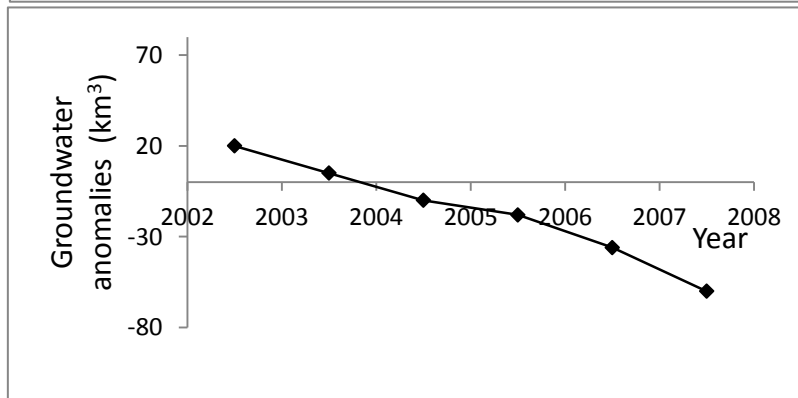
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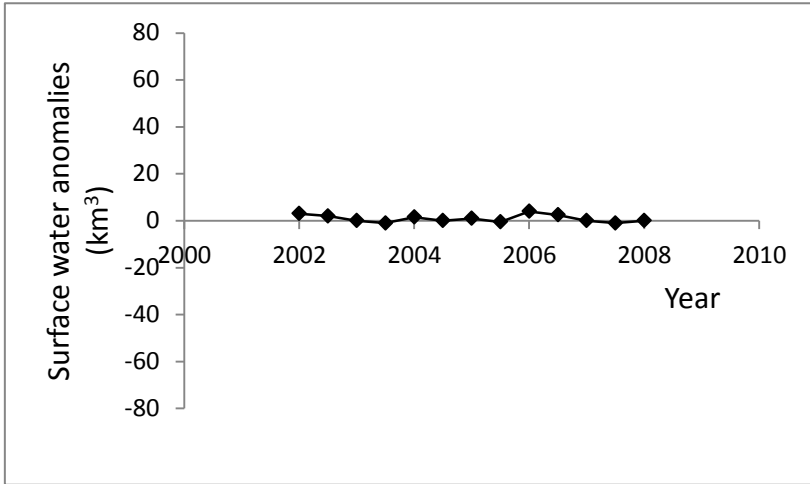
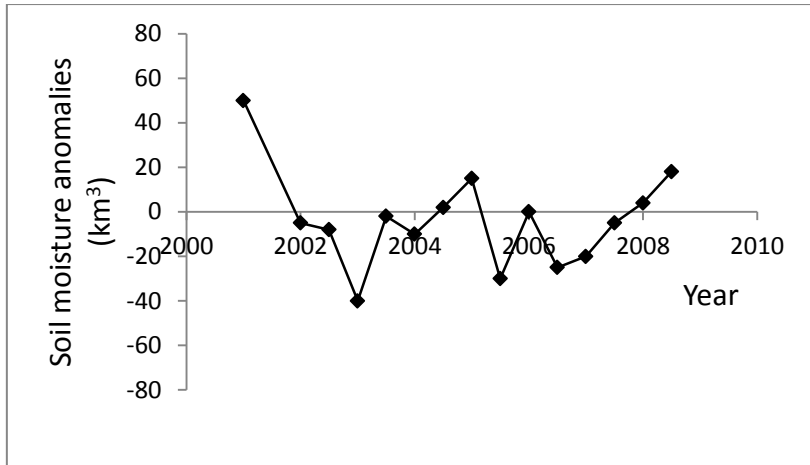
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1891 **Figure 2:** Change of (a) total water storage anomalies; (b) groundwater anomalies; (c) soil
 1892 moisture storage anomalies; and (d) surface water anomalies relative to the mean of
 1893 the Murray-Darling Basin during the multiyear drought. Redrawn from Leblanc et al.
 1894 (2009).

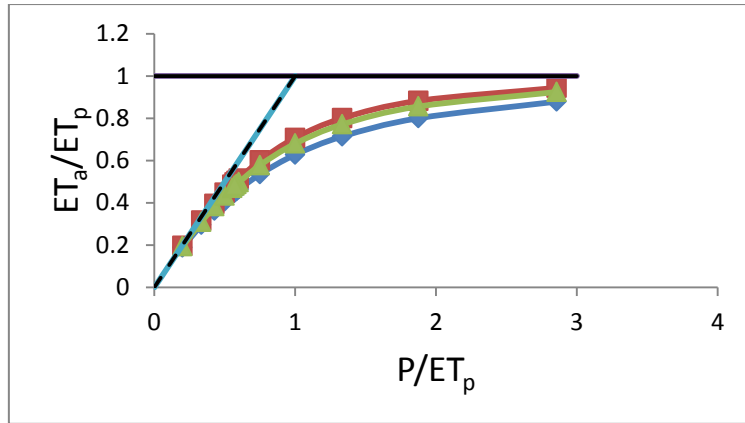
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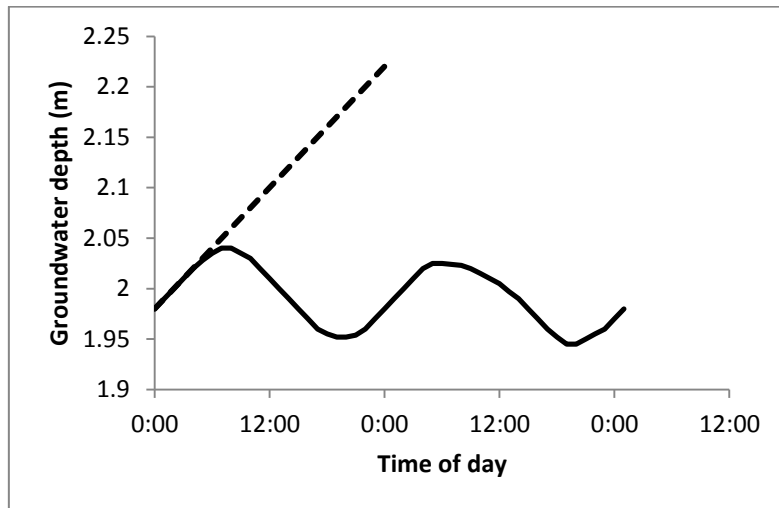
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1902 **Figure 3:** A representation of the Budyko formulation using the Choudhury-Yang
 1903 formulation with three different values of n (from 1.5 to 2.0). Redrawn from
 1904 Leaney et al., (2011).

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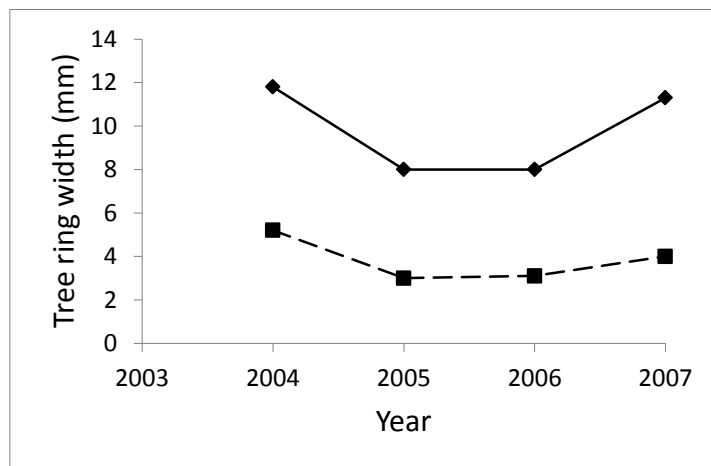


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1909 **Figure 4:** An idealised representation of changes in depth-to-groundwater over a
 1910 48 h period. The water table declines (depth increases) during the day
 1911 because of transpiration by vegetation but increases (depth decreases)
 1912 at night when transpiration tends to zero and recharge exceeds loss.
 1913 The dashed line represents the trajectory of overnight recharge in the

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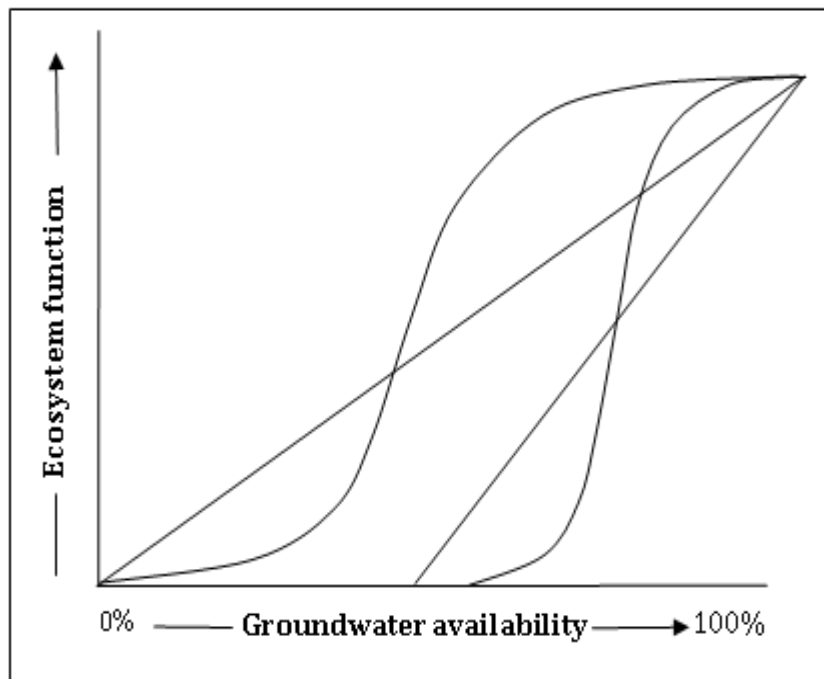
absence of transpiration on the following day. See text for further discussion of this.



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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).

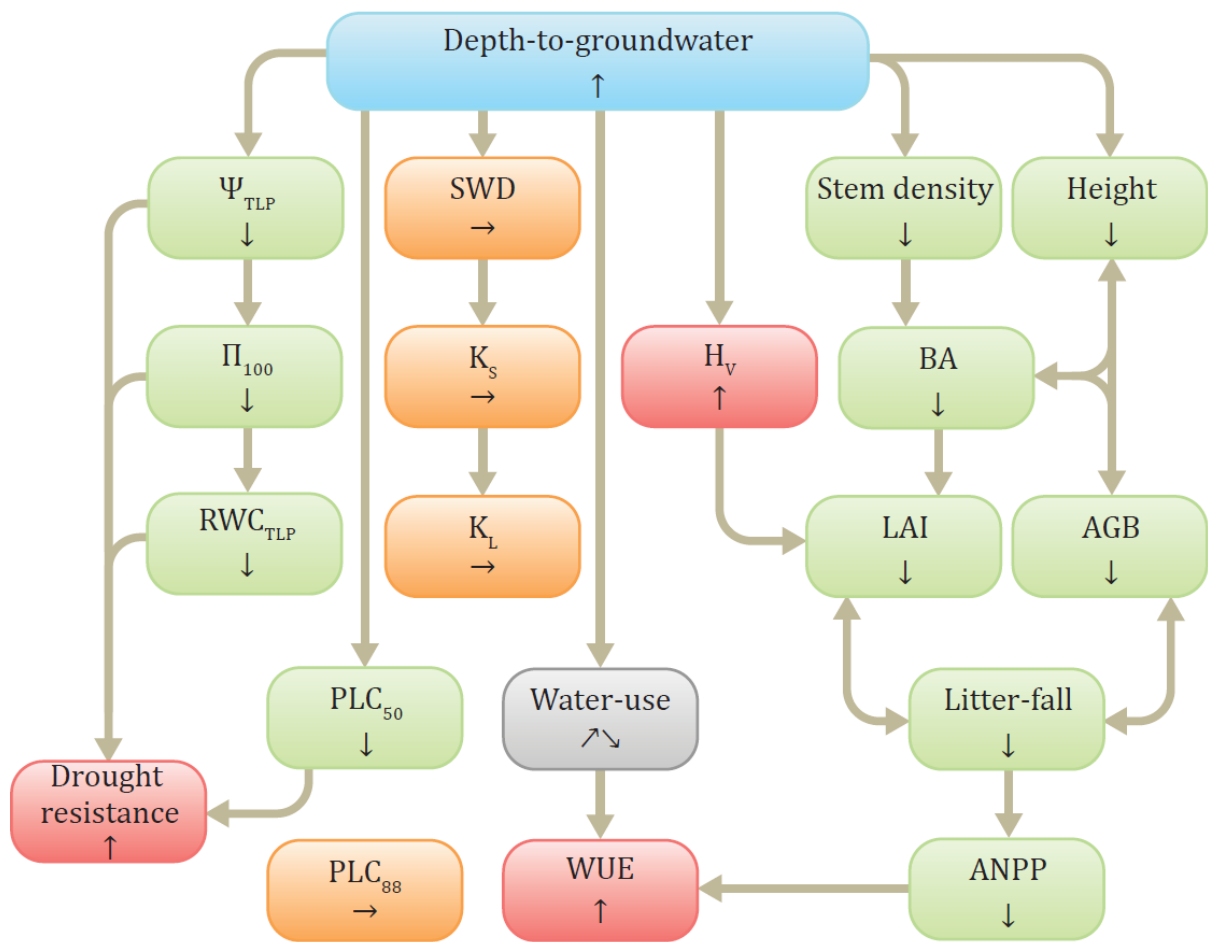
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1942 **Figure 6:** Hypothetical response functions for ecosystem function to differences
1943 groundwater availability. From Eamus *et al.* (2006).

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1955 **Figure 7:** A summary of the traits examined and the general trend in response of those
1956 traits to increased depth-to-groundwater along a natural topographic gradient.
1957 Upward/downward pointing arrows within a coloured text box indicate
1958 increasing/decreasing values of the plant trait as depth-to-groundwater
1959 increases. Horizontal arrows indicate no change. Table four provides the
1960 definition of all abbreviations used in this figure.
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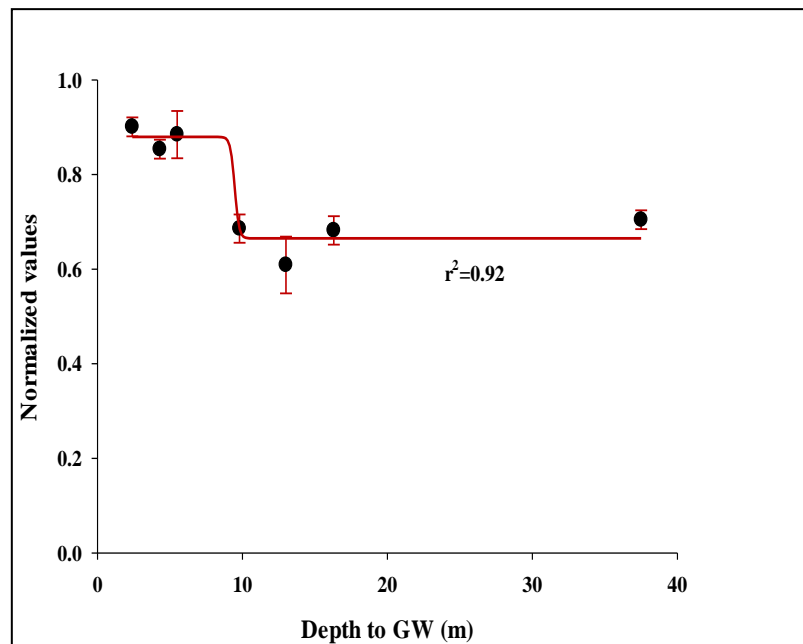
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1973 **Figure 8:** Ecosystem response to increase in depth-to-groundwater, fitted with 4
1974 parameter sigmoidal function. From Zolfaghar (2014).

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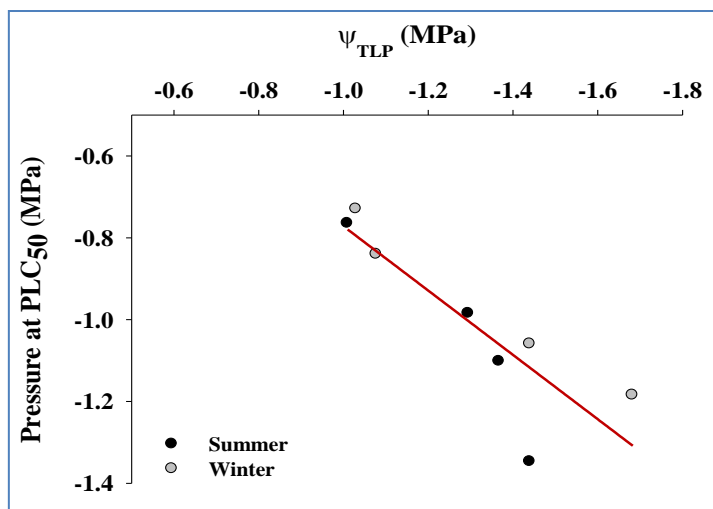


Figure 9: Co-ordination in the response of a leaf-scale and branch-scale trait and drought sensitivity. From Zolfaghar (2014).