

# Hydrological niches in terrestrial plant communities:

## A review

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## 1 **Summary**

2 1. Despite the fundamental significance of water to plants and the persisting question  
3 of how competing species coexist, this is the first review of hydrological niches. We  
4 define hydrological niche segregation (HNS) as: (i) partitioning of space on fine-scale  
5 soil-moisture gradients, (ii) partitioning of water as a resource, and/or (iii) partitioning  
6 of recruitment opportunities among years caused by species specializing on particular  
7 patterns of temporal variance of water supply (the storage effect).

8 2. We propose that there are three types of constraint that lead to the trade-offs that  
9 underlie HNS. (i) An edaphic constraint creates a trade-off between the supply to  
10 roots of O<sub>2</sub> on the one hand vs. water and nutrients on the other. (ii) A biophysical  
11 constraint governs gas exchange by leaves, leading to a trade-off between CO<sub>2</sub>  
12 acquisition vs. water loss. (iii) A structural constraint arising from the physics of  
13 water-conducting tissues leads to a safety vs. efficiency trade-off.

14 3. Significant HNS was found in 43/48 field studies across vegetation types ranging  
15 from arid to wet, though its role in coexistence remains to be proven in most cases.  
16 Temporal partitioning promotes coexistence through the storage effect in arid plant  
17 communities, but has yet to be shown elsewhere. In only a few cases is it possible to  
18 unequivocally link HNS to a particular trade-off.

19 5. *Synthesis.* The field and experimental evidence make it clear that HNS is  
20 widespread, though it is less clear what its precise mechanisms or consequences are.  
21 HNS mechanisms should be revealed by further study of the constraints and trade-offs  
22 that govern how plants obtain and use water and HNS can be mechanistically linked

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23 to its consequences with appropriate community models. In a changing climate, such  
24 an integrated programme would pay dividends for global change research.

25 **Key-words:** coexistence, eco-hydrology, global change, hydrological niche, plant  
26 community ecology, plant population and community dynamics, stable isotopes

27 **Introduction**

28 Terrestrial plants use water for just about every function imaginable. It is used  
29 structurally to provide cell turgor, as a raw material, a solvent, a transport medium  
30 and a coolant. Transpiration of water is the source of motive power in the xylem and  
31 the photolysis of water provides hydrogen atoms for the biosynthetic reactions of  
32 photosynthesis. Plants also require a flux of water in order to take up nutrients. Water  
33 is so obviously essential to physiological functions that it is arguable that ecologists  
34 have overlooked the more subtle importance of water to plant community structure,  
35 except in habitats where it is clearly in short supply. Part of the reason for this  
36 oversight must be that water, like light, O<sub>2</sub>, CO<sub>2</sub> and the major nutrients N, P and K, is  
37 an essential resource for all plants and there just don't seem to be enough ways for  
38 species to partition these into the hundreds of niches required for stable coexistence in  
39 the most species-rich plant communities (Silvertown 2004).

40 The problem of coexistence in plant communities and its potential solutions have been  
41 recently reviewed by Wilson (2011). The idea embodied in neutral theory that niches  
42 are unnecessary or irrelevant to plant coexistence (Hubbell 2001), looks increasingly  
43 untenable in the light of recent studies (Levine & HilleRisLambers 2009; Adler *et al.*  
44 2010; Clark 2010; Purves & Turnbull 2010) . It is therefore timely to ask how  
45 important hydrological niches might be to plant community structure, particularly  
46 since hydrology is expected to be altered by climate change and therefore this  
47 information is of practical, predictive value (Bartholomeus *et al.* 2011; Strom *et al.*  
48 2012).

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49 Fan *et al.*(2013) estimate that the water table lies near to the surface in nearly a third  
50 of the Earth's land area, indicating the global importance of groundwater hydrology to  
51 plant communities, but hydrological niches are not confined to such areas. The  
52 evidence is growing that across the full range of water availability from arid habitats  
53 to wetlands (Webb *et al.* 2012), even closely related species differ in their tolerance of  
54 water deficit or excess and how these conditions vary over time (Parolin *et al.* 2010;  
55 West *et al.* 2012; Craine *et al.* 2013). These differences among species frequently  
56 manifest themselves in the segregated distribution of species along gradients.

57 For the purposes of this review, terrestrial plant communities include 'wetlands' that  
58 may be temporarily flooded, but not those that are fully aquatic. The physical scale of  
59 the soil-moisture gradient affecting plant community composition may range from the  
60 geographical to the highly local. Moeslund *et al.* (2013b) surveyed vegetation  
61 composition and variation at spatial resolutions from 2 m–250 m across 43,000 km<sup>2</sup> in  
62 Denmark. They found that topographically-related soil wetness was the primary  
63 determinant of habitat type. The same variable determined variation among grassland  
64 habitat types (Moeslund *et al.* 2013a). Also working at a geographic scale, Schietti *et*  
65 *al.* (2014) found that 82% of the variance in plant composition among plots in  
66 Amazon terra firme forest could be accounted for by the depth to water table.

67 In temperate forest in France, soil-water balance was a better predictor of tree species  
68 distribution than Potential Evapotranspiration (PET) derived from climatic variables  
69 (Piedallu *et al.* 2013). This result underlines the point that plants react to local soil  
70 moisture availability and that this must ultimately be responsible for their segregation  
71 on gradients at large, as well as fine, physical scales. For this reason, the soil-moisture  
72 responses of species can be expected to show correlations across spatial scales. Such a

73 correlation between drought tolerance and distribution at geographic and more local  
74 scales is commonly found among tropical tree species (Comita & Engelbrecht 2013).

75 In this review, we focus mainly on the fine spatial scale relevant to  $\alpha$ -diversity and the  
76  $\alpha$ -niche because it is fundamental both to coexistence (Silvertown 2004) and to  
77 processes determining distribution at larger scales. Following Araya *et al.* (2011), we  
78 define hydrological niche segregation (HNS) as "(i) partitioning of space on fine-scale  
79 soil-moisture gradients (fine-scale being defined as a distance sufficiently small for  
80 species to compete for the same resources), or (ii) partitioning of water as a resource  
81 through different strategies of water acquisition such as different phenologies or  
82 different rooting depths." To this pair of definitions we now add a third that logically  
83 belongs with them, which is (iii) partitioning of recruitment opportunities among  
84 years caused by species specializing on particular patterns of temporal variance of  
85 water supply. This can promote coexistence through the temporal storage effect  
86 (Chesson *et al.* 2004).

87 In this review, we firstly consider the theoretical requirements for hydrological niche  
88 segregation, then we survey the field evidence for the existence of HNS within  
89 communities and finally we discuss these field-survey results in the light of  
90 experimental and other evidence.

## 91 **Hydrological niche segregation**

### 92 **Coexistence mechanisms**

93 Chesson (2000) distinguished between coexistence mechanisms that equalize  
94 interspecific competitive abilities, for example as in the neutral model (Hubbell  
95 2001), and those that stabilize communities through frequency dependence. The

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96 essential condition for a mechanism to be stabilizing is that it should cause any  
97 species to increase when rare. A community of two competing species can satisfy this  
98 condition if each is limited more by intraspecific competition than by interspecific  
99 competition. Niche segregation has this effect because as population density  
100 increases, the impact of intraspecific competition rises and the impact of interspecific  
101 competition falls, thus relieving rare species from competitive pressure by other  
102 species.

103 The temporal instability of soil moisture, which can be very variable from year to year  
104 (Terradas *et al.* 2009), is a feature of hydrological niches not shared by other resource  
105 gradients such as light or nutrients that tend to change gradually. Seedlings are  
106 typically more vulnerable to drought than are mature plants with deeper roots and  
107 hence plants may have different strategies of survival in the regeneration and the later  
108 phases of the life cycle (Grubb 1977). This decoupling between the conditions  
109 required for recruitment, for example through the release of seeds from dormancy,  
110 and for adult survival is a pre-condition for the temporal storage effect. Established  
111 plants (or seeds) that are resistant to drought are "stored" over periods that are too dry  
112 for seedling recruitment.

113 The temporal storage effect in which species depend for recruitment on different  
114 patterns of temporal variance in water availability, needs to be distinguished from  
115 other hydrological niche dimensions with which it is likely to be correlated such as  
116 the amount or the depth of the water resource. For example, temporary water bodies  
117 such as vernal pools often have their own specialized flora of ephemeral species (Deil,  
118 2005) and while it is clear that these communities occupy a  $\beta$  (habitat) niche that is  
119 characterized by a fluctuating water supply, it is less clear whether the coexistence of

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120 species within the pool also depends upon fluctuation. The species are typically zoned  
121 from the pool margin to its interior so the zone of a species defines its  $\alpha$  niche, but in  
122 any particular zone the amount of soil water, the duration of the drought as the pool  
123 dries up, the depth of water and the duration of inundation are all correlated so it is  
124 impossible to tell without experimental manipulation whether the pattern of temporal  
125 variance *per se* is an important dimension of the  $\alpha$  niche.

126 Nygaard & Ejrnaes (2009) factorially manipulated nutrients, water-table depth and  
127 degree of water-level variance in mesocosms sown with a standard mixture of 23  
128 wetland species. Both nutrient and water-level treatments influenced the resulting  
129 community, with the infertile, dry treatment containing the largest number of species.  
130 However, water-level variance had no main or interactive effect on the plant  
131 community, implying the absence of temporal niche separation.

132 The presence of niche differences between species is not in itself sufficient evidence  
133 that niche segregation is the actual mechanism of coexistence (Silvertown, 2004), but  
134 it is a necessary first step towards testing whether this is the case. Confirmation  
135 requires either experimental manipulation of resources to demonstrate that  
136 coexistence depends upon the presence of niche differences, or parameterization of  
137 community models that can then be manipulated to determine which processes  
138 stabilize community composition (Rees *et al.* 1996; Silvertown & Wilson 2000;  
139 Groeneveld *et al.* 2002; Levine & HilleRisLambers 2009).

### 140 **Trade-offs**

141 Niche segregation arises when trade-offs force species to specialize in the zone of  
142 niche space where they grow best (Chase & Leibold 2003). Silvertown *et al.* (1999)



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143 demonstrated a trade-off between species' tolerances of aeration stress and tolerances  
144 of soil drying stress in English meadows where the presence of HNS was supported  
145 by field data. An identical pattern was later discovered in fynbos habitats, strongly  
146 suggesting that the trade-off in question is fundamental and arises from compromises  
147 inherent in the physiology of plant water relations (Araya et al., 2011). In Sonoran  
148 desert annuals, Angert *et al.* (2009) found that coexistence depended on a trade-off  
149 among species between water-use efficiency and relative growth rate.

150 We propose that there are three overlapping types of physiological constraint that  
151 contribute to the overall pattern of trade-offs, none of them mutually exclusive (Fig.  
152 1).

153 Fig.1. here

154 First is the edaphic constraint that is imposed by the soil environment and which  
155 affects the supply of O<sub>2</sub>, water and nutrients to roots. This derives from the fact that  
156 soil-pore space may contain water (and dissolved nutrients) or air, but if pores are  
157 predominantly filled by water, plants' roots may be deprived of oxygen and if  
158 predominantly filled by air, they may be deprived of water and nutrients. This edaphic  
159 constraint presumably explains why below-ground competition is so important to  
160 hydrological niche segregation (Bartelheimer *et al.* 2010; Silvertown *et al.* 2012).

161 The interactive effects of water and nitrogen in soil were neatly shown in a mesocosm  
162 experiment by Nygaard & Ejrnaes (2009). The response of individual species to  
163 water regime in this experiment was strongly influenced by nutrient availability and  
164 overall species richness was determined primarily by the interactive effects of the  
165 water and nutrient treatments. Araya *et al.* (2012a) demonstrated a direct mechanism

166 by which water-regime controlled nitrogen availability, thereby revealing how water-  
167 regime can control RGR even when water is itself a non-limiting resource.

168 Both intrinsic water-use efficiency (WUE: the amount of carbon fixed per unit of  
169 water consumed) and nitrogen-use efficiency (NUE; the amount of carbon fixed per  
170 unit of nitrogen taken up) are highly phenotypically plastic and exhibit a trade-off at  
171 the leaf-level (Patterson *et al.* 1997). A WUE/NUE trade-off has also been found at  
172 species-level in trees and shrubs (Field *et al.* 1983) and grasses (Chen *et al.* 2005;  
173 Gong *et al.* 2011) where differences in species' relative performance on the trade-off  
174 correlate with their distribution on soil moisture and nutrient gradients. The cause of  
175 the WUE/NUE trade-off may be the dependence of nutrient acquisition on water  
176 uptake.

177 Second is the biophysical constraint that governs gas exchange by leaves. This arises  
178 from the fact that stomata regulate both CO<sub>2</sub> acquisition and loss of water through  
179 transpiration. Other things being equal, the biophysical constraint means that closing  
180 stomata to limit water loss incurs a cost in CO<sub>2</sub> uptake. This constraint is inherent in  
181 the equation for intrinsic water use efficiency,  $W_g = A/g_s$  which is the ratio of net  
182 assimilation ( $A$ ) of CO<sub>2</sub> to the stomatal conductance of water ( $g_s$ ) (Seibt *et al.* 2008).  
183 In drought, plants commonly increase  $W_g$  by closing stomata (decreasing  $g_s$ ), but the  
184 degree to which this happens varies both between (Cernusak *et al.* 2007) and within  
185 species (Edwards *et al.* 2012). We propose that this variation provides the biophysical  
186 basis for hydrological niche segregation at the drier end of the soil-moisture gradient  
187 where plants must conserve water (Moreno-Gutierrez *et al.* 2012). Heritable variation  
188 in  $W_g$ , which is typically high, is potentially the basis for ecological speciation. Koziol  
189 *et al.* (2012) found that selection during the domestication of sunflowers resulted in a

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190 decrease in drought tolerance and an increase in growth rate as a result of a trade-off  
191 between these traits.

192 Third is the structural constraint that arises from the physics of water-conducting  
193 tissues. The rate at which water moves through a plant is often the determinant of its  
194 gas-exchange rate, its photosynthetic rate and thus its relative growth rate (RGR)  
195 (Zimmerman 1983). To compete effectively with its neighbours, it may therefore be  
196 important for a plant to maximise its transpirational flux through its xylem system.  
197 High water fluxes require either steep gradients in water potential and/or wide xylem  
198 vessels with high hydraulic conductivity, both of which increase the risk of embolism  
199 (Sperry & Tyree 1988). Given this understanding, specialised xylem structure has  
200 long been postulated as another possible trade-off with respect to water economy.  
201 The topic was being discussed as far back as 1918 (Bailey & Tupper 1918) and its  
202 development has been neatly reviewed by (Tyree *et al.* 1994), who undertook a meta-  
203 analysis of twenty earlier studies to demonstrate a trade-off between hydraulic  
204 efficiency and safety existed. Smaller xylem conduits especially those characterised  
205 by thicker walls, fewer pits and specialized pit membranes (Lens *et al.* 2013) can  
206 tolerate low water potentials without embolizing, giving the plant a margin of safety  
207 when conducting water up to its leaves at close to its maximal rate, even if the  
208 atmosphere is very dry (Manzoni *et al.*, 2013). Larger vessels on the other hand  
209 provide longer, wider conduits with more pits or complete perforations in their walls.  
210 These provide higher hydraulic conductivity and therefore greater efficiency, allowing  
211 them to conduct an equivalent amount of water without requiring such a steep  
212 gradient. However, they are at greater risk of cavitation at a given water potential.

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213 This safety versus efficiency trade-off is discussed by Manzoni (2013), who  
214 demonstrated that trees operate at close to their maximum rates of transpiration, and  
215 thus are frequently prone to embolism. The authors showed that maximal rates of  
216 transpiration were relatively constant within a given environment, but the means by  
217 which species achieved them could differ greatly. Some, notably those that tolerate  
218 harsh conditions (e.g. many coniferous trees) use fine conducting elements  
219 (tracheids), which deliver a low efficiency of water transmission, but provide a high  
220 resistance to failure. Deciduous angiosperm trees in contrast tend to produce larger  
221 xylem elements (vessels) that provide higher efficiency of water transport when water  
222 potentials are high, but which are more vulnerable to cavitation when water potentials  
223 fall (Maherali *et al.* 2004). However, these angiosperms appear able to operate at  
224 closer to their maximum transpiration rates because they also display a greater  
225 ability to repair cavitated vessels (Johnson *et al.* 2012). Water-conducting tissues in  
226 trees have been shown to operate at close to their embolism threshold across all  
227 biomes, with angiosperms generally displaying a narrower safety margin than  
228 gymnosperms (Choat *et al.* 2012).

229 This safety versus efficiency trade-off has been linked to species-distribution patterns  
230 in forest. Markesteijn *et al.* (2011) postulated that species' hydraulic architecture  
231 would be a major driver of their partitioning along soil-moisture gradients. They  
232 measured hydraulic traits in 40 species in a stand of tropical dry forest and found  
233 large differences among species and a strong trade-off between efficiency and safety.  
234 They clearly showed the trait that best characterized trees in resource poor areas  
235 (whether shaded or dry) was high density of wood (i.e. small xylem element size), as  
236 described above, and concluded that hydraulic capacity is integrally linked to niche  
237 differentiation.

**238 The field evidence for hydrological niche segregation**

239 We conducted a survey of the literature on the use of water by coexisting plant  
240 species in the field using the Web of Knowledge to identify papers that cited  
241 foundational studies by Davis & Mooney (1986), Manning & Barbour (1988),  
242 Ehleringer *et al.* (1991) and Silvertown *et al.* (1999). All papers cited by the citing  
243 papers were then evaluated and so on iteratively until no new studies of relevance  
244 were found. This search was limited to papers published before March 2013 and we  
245 identified 48 studies in which water utilization or distribution on soil-moisture  
246 gradients had been statistically compared for at least two coexisting species. The  
247 modal species number per study was only 3 (10 studies) and the median was 5  
248 species. These numbers are low, but many of the species studied were actually the  
249 dominants in their communities and therefore the differences in their hydrological  
250 niches are of particular significance.

251 The 48 studies have been grouped according to the three mechanisms of hydrological  
252 niche segregation mentioned in the introduction. Studies of species growing on a soil-  
253 moisture gradient are summarized in Table 1 (studies #1 - #11), those where  
254 partitioning of water as a resource was tested are shown in Table 2 (studies #12 - #43)  
255 and tests of the temporal storage effect are grouped in Table 3 (studies #44 - #48).

256 Studies are ranked within each table by the average annual amount of precipitation  
257 occurring at the study site. We recognize that this ignores variation in  
258 evapotranspiration rates and also groundwater as a source, but these limitations do not  
259 obscure the fact shown by the data that plants segregate on hydrological gradients in a  
260 remarkably wide range of terrestrial environments ranging from arid to wet. Forty-  
261 three of the 48 studies listed reported evidence of significant HNS. An attempt was

262 made to cross-classify the three groups of studies by the three trade-off types in  
 263 Fig.1., but very few of the source papers contained enough relevant information to  
 264 make this possible. Those where clear trade-offs have been demonstrated are singled  
 265 out for mention below.

266 **Species growing on a soil-moisture gradient**

267 Table 1 here

268 Although only 11 instances of such studies were found by our search methodology  
 269 (Table 1), there is a mostly older literature containing many similar cases (Rutter  
 270 1955; Boedeltje & Bakker 1980; Grootjans *et al.* 1988; Wierda *et al.* 1997; Kotowski  
 271 *et al.* 1998). Three field experiments are included in Table 1. Reynolds *et al.* (1997)  
 272 reciprocally transplanted 3 annuals that occupied soil patches with different soil water  
 273 content, finding that each did better on its home patch. In an experiment that altered  
 274 soil moisture in a perennial grassland community on shallow limestone soil, Fridley *et*  
 275 *al.* (2011) (#11) found that 13 of the 25 species investigated showed soil-depth  
 276 affinities and that the majority of these moved along the soil-depth gradient in  
 277 response to climate change treatments that directly or indirectly changed soil  
 278 moisture.

279 Another experiment on a community where species segregated on parallel gradients  
 280 of soil depth and soil-moisture content showed that soil moisture was the driving  
 281 variable in the segregation of the two competing annuals *Sedum smallii* and *Minuartia*  
 282 *uniflora* that occupy zones of different soil depth in depressions in granite outcrops  
 283 (#10). Clear examples are reported of biophysical trade-offs in a mediterranean  
 284 shrubland (#2) and of edaphic trade-offs in fynbos (#3) and floodplain meadows (#8)

285 (Table 1). A structural trade-off may be the basis of different drought tolerances and  
 286 coexistence in two species of *Adenostoma* in S. California (#4).

287 **Water partitioning among species**

288 Table 2 here

289 The majority of studies (32/48) surveyed fell into this category (Table 2). Most were  
 290 descriptive rather than experimental in approach and used stable isotopes to compare  
 291 the different sources from which co-occurring species drew their water. Twenty-eight  
 292 studies out of 32 found significant evidence of HNS, but there was negative evidence  
 293 in five cases (#24, 29,30,31, 36, Table 2). In two of them (#29, 30), sampling was  
 294 conducted at a time of year when water might be expected to be least limiting. Liu *et*  
 295 *al.*(2011) conducted their study comparing two subalpine shrubs in Sichuan, China  
 296 during the monsoon season (#29). In a study of savanna shrubs in Texas (#30), stable  
 297 isotopes sampled during the season of greatest rainfall showed no differences among  
 298 species in the depth of water sources utilized, although rooting depth profiles were  
 299 different. In another study of two evergreen savanna trees *Quercus fusiformis* and  
 300 *Juniperus ashei* growing in a karst region in Texas (#31), the species also had  
 301 indistinguishable isotopic signatures of water source during and after drought.  
 302 However, these species are known to have different water-use strategies, with needle-  
 303 leaved *J. ashei* able to tolerate drought and sustain gas exchange during water  
 304 shortage while broad-leaved *Q. fusiformis* does not and a recent study found that there  
 305 is a phenological dimension to HNS between these species (Kukowski et al., 2013).

306 Five studies compared overlap in use of water sources over more than one season. In  
 307 three studies the overlap was least in the season of greatest scarcity (#13, 17, 32,

308 Table 2), as would be expected if HNS is driven by resource competition for water  
 309 when it is most limiting. In another study, Verheyen *et al.* (2008) (#27) found that  
 310 total evapotranspiration was greater in mixtures of species than in the best performing  
 311 monocultures, providing evidence of niche complementarity for water use under  
 312 normal conditions. This effect disappeared in conditions of drought. The fifth study  
 313 (#33) also found that, in three subalpine woody plants, species that utilized different  
 314 water sources when rainfall was available were constrained to all use the same source  
 315 in dry conditions. The critical issue required to interpret all these results is how  
 316 relative population growth rates among the coexisting species are affected by water  
 317 availability (Verhulst *et al.*, 2008). If most or all species cease growth in drought, then  
 318 it is HNS at times of greater water availability that is important to coexistence and not  
 319 how species use water when it is most scarce. Drought-induced mortality may still  
 320 differ between species of course.

321 Trade-offs were investigated surprisingly rarely among these studies, given how large  
 322 the sample was. From the evidence of structural trade-offs among tropical trees  
 323 already discussed (Markestijn *et al.* 2011), one might guess that they underlie the  
 324 differentiation among tree species in rooting depth (#42) and degree of dry-season  
 325 deciduousness (#43) found in seasonally dry forest at Barro Colorado in Panama.

### 326 **Temporal storage effect**

327 Table 3

328 Although only five studies were found in this category, three of them demonstrated  
 329 that the temporal storage effect promoted coexistence. In a community of Sonoran  
 330 Desert annuals, Angert *et al.* (2009) (#45) found that the decoupling of reproductive



331 success between species that is required by the temporal storage effect was in part  
332 caused by the biophysical trade-off between relative growth rate (RGR) and intrinsic  
333 water use efficiency (WUE). Species with low RGR and high WUE were able to  
334 exploit small, but frequent rainfall events, while species with high RGR and low  
335 WUE did best under large, infrequent rainfall events. Temporal niche separation  
336 caused by different responses to the size of variable rainfall events was also found  
337 between two desert shrubs in the Chihuahua desert (Verhulst *et al.* 2008) (#46), and  
338 among three dominant prairie grasses in Kansas (Adler *et al.*, 2006) (#48). In both of  
339 these cases models demonstrated that the temporal niche differences that were  
340 observed did actually promote coexistence. The two remaining studies in Table 3  
341 found that species of steppe communities in Patagonia (#44) and N.W. China (#47)  
342 differed in their response to rainfall in a fashion that would suggest temporal niche  
343 segregation, although the effect of this on coexistence was not tested.

## 344 **Discussion**

345 This is the first review of hydrological niches in plant communities and it has revealed  
346 that niche segregation is widespread, occurring in at least 43 out of the 48 studies  
347 examined. It is possible that our survey methodology contained a bias in favour of  
348 finding positive results, but this would not alter the conclusion that HNS has been  
349 found in vegetation types ranging from arid to wet environments and from arctic  
350 alpine to tropical forest.

351 We divided the 48 cases into three groups, depending upon whether the niche  
352 segregation investigated was on a soil moisture gradient (i.e. spatial) (Table 1),  
353 involved partitioning of water resources by, for example, different rooting depths  
354 (Table 2), or tested temporal differences between species (Table 3). Very unequal

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355 numbers of studies fell into the three categories, but we attach little biological  
356 significance to this because sample sizes are influenced to an unknown degree by  
357 sampling error and the cost and availability of methods for investigating different  
358 mechanisms. For example, measuring water partitioning using stable isotopes has  
359 become routine and inexpensive (Dawson *et al.* 2002) (Table 2, n = 32), compared to  
360 the labour-intensive, long-term surveys that are required to evaluate spatial (Araya *et*  
361 *al.*, 2011) (Table 1, n = 11), or temporal (Angert *et al.*, 2007) (Table 3, n = 5) HNS.

362 One clear pattern that may be of biological significance is the predominance of arid  
363 communities among the studies of the temporal storage effect (Table 3). All five  
364 studies were of communities with low precipitation values that lay below the median  
365 for the sample as a whole 588 mm (n = 48). All the studies demonstrated temporal  
366 HNS and three of the five showed that this was sufficient to promote coexistence. Is  
367 the temporal storage effect confined to arid communities? It is too early to say, but we  
368 believe that there is no reason why it should be. Flooding, as well as rainfall, can be  
369 very variable from year-to-year and there is ample evidence among the studies in  
370 Table 1 and elsewhere that plants differ in how they respond to this. To our  
371 knowledge, the storage effect has not yet been tested in plant communities subject to  
372 flooding, but this is an area ripe for investigation.

373 The majority of the field studies surveyed were observational, but 11 of the 43 studies  
374 where HNS was found involved field experiments that manipulated soil moisture  
375 and/or plant-plant interactions. The mechanisms generating HNS require further field  
376 investigation, but mesocosm experiments have implicated the importance of soil  
377 nutrient availability, soil microbial composition, oxygen availability, water deficit and  
378 interspecific competition below-ground. The experimental investigation of

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379 hydrological niches began with the now classic lysimeter experiments performed by  
380 Heinz Ellenberg in the 1950s (Ellenberg 1953; Hector *et al.* 2012) in which he grew  
381 meadow grasses in monocultures and in mixtures along a soil-moisture gradient  
382 created by a gradient of soil depth. There was an almost complete overlap of the  
383 fundamental niches among the six monocultures (94%), but a much reduced overlap  
384 of realized niches in conditions of interspecific competition (72%). Although there  
385 was still substantial overlap of hydrological niches in the mixture, the reduction of  
386 22% caused by interspecific competition was highly significant ( $P < 0.001$ )  
387 (Silvertown *et al.* 1999).

388 Ellenberg's experiment was a powerful, early investigation of the existence of  
389 hydrological niches among meadow grasses. However, the experimental design used  
390 in the 1950s was unreplicated and did not take account of possible spatial  
391 autocorrelation along the gradient or the covariation of water-table depth with soil  
392 volume. All these limitations can be overcome by the use of mesocosms, which are  
393 soil containers that permit the independent, replicated manipulation of water-table  
394 depth and other variables for plants growing in an outdoor environment (Araya *et al.*  
395 2010).

396 In a mesocosm competition experiment with two species of *Senecio*, one native to  
397 wet- and the other to dry grassland, Bartelheimer *et al.* (2010) found that below  
398 ground interspecific competition with the roots of grasses was responsible for limiting  
399 the growth of the dry-habitat species in wet conditions, where without root  
400 competition it could grow quite successfully. A meta-analysis of 38 experiments  
401 found that this may be a common phenomenon, with competition below ground often

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402 more important than competition above, especially in competition with grasses and in  
403 conditions of low fertility (Kiær *et al.* 2013).

404 Using mesocosms, Vivian-Smith (1997) demonstrated the importance of  
405 microtopography, showing that segregation occurred among wetland species  
406 establishing from seed on hummocks and hollows that were only 10–30 mm different  
407 in height. Soil-moisture content, air-filled pore space and nitrogen availability are all  
408 greatly influenced by the depth of the water table beneath the soil surface and any or  
409 all three could be responsible for the observed effect of microtopography.

410 Water displaces air from soil pores, reducing oxygen availability and altering the  
411 composition of the microbial community, which also segregates on soil-moisture  
412 gradients ( Wolfe *et al.* 2006; Cavender-Bares *et al.* 2009; Araya *et al.* 2012a; Lennon  
413 *et al.* 2012). Nitrification in soil depends upon an aerobic microbial community,  
414 whilst nitrate ions are consumed by an anaerobic community, so waterlogged soils are  
415 low in plant-available nitrogen as well as in oxygen (Patrick & Wyatt 1964). Though  
416 the availabilities of water, oxygen and nitrogen covary, they can be decoupled  
417 experimentally to determine the relationships among the variables. Araya *et al.*  
418 (2012a) manipulated air-filled pore space independently of soil-water content and  
419 found that nitrogen mineralization was greatly inhibited at values of air-filled pore  
420 space less than 10%. The same effect is seen when soil-water content reduces air-  
421 filled pore space below this percentage. In the field, nitrogen-mineralization rate  
422 showed an optimum at 40 cm water-table depth, decreasing either side of this value  
423 when at shallower depths there was an oxygen deficit and at deeper levels water  
424 deficit limited microbial decomposition. The absolute value of the optimum depth is

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425 likely to vary widely according to the pore-size distribution and microbial respiration  
426 rate of the soil.

427 The combination of field and experimental evidence that we have assembled in this  
428 review paints a picture of a field that is ripe for synthesis, but that at present lacks  
429 some important components. We believe that it is clear that HNS is widespread, but  
430 less clear what the precise mechanisms or their consequences are. The starting point  
431 for uncovering HNS mechanisms should be the study of the constraints and trade-offs  
432 that govern how plants obtain and use water. The three constraints that we identified  
433 (Fig.1) are unlikely to be the only ones operating, but the field evidence at present is  
434 frustratingly sparse.

435 The consequences of HNS also need further investigation. In a few cases already  
436 mentioned it is clear that HNS is responsible for coexistence and in a larger number  
437 we can at least say that HNS influences community assembly. More studies need to  
438 use appropriate community models so that HNS can be mechanistically linked to its  
439 consequences. This is important not least because improving our understanding of  
440 hydrological niches is needed to predict the consequences of environmental change.

441 Global warming is expected to increase the variability of precipitation patterns (Allan  
442 & Soden 2008) which is likely to have a greater impact on the composition of  
443 vegetation communities than the change in temperature regime itself (Reyer *et al.*  
444 2013). Many plant species have such wide latitudinal ranges and exhibit such a broad  
445 tolerance of temperature regime that the climatic envelope approach is unlikely to be  
446 able to resolve future distributions at anything finer than a regional scale (Zelazowski  
447 *et al.* 2011). In contrast, the sensitivity of species in terms of their preferred  
448 hydrological niche is acute (Silvertown *et al.* 1999) and plants are phenotypically

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449 plastic in response to changes in soil moisture (von Arx *et al.* 2012) as well as stresses  
450 such as flooding (Bailey-Serres & Voesenek 2008).

451 Bartholomeus *et al.* (2011) modelled the effects of future climate scenarios on the  
452 stresses (both drought and aeration) that grassland plants could be exposed to in  
453 future. Their conclusions were that due to increased variability in precipitation, the  
454 main impact would be an expansion in the number of sites that experience a  
455 combination of both stresses in different seasons of the year. They showed that rare  
456 species of conservation importance tend to be absent from such sites and therefore it  
457 is this group that would be disproportionately affected by climate-change in the  
458 future. They emphasise the point that in order to predict vegetation change, you need  
459 to consider the soil moisture regime in detail, because the interaction of the two  
460 stresses (lack of soil oxygen and lack of soil water) cannot be easily generalized.

461 Implicit in their argument is the need to characterize the realized hydrological niche  
462 of each species and to build process-based models. Such models now exist for the  
463 Netherlands (Witte *et al.* 2012) and are emerging elsewhere (Robinson *et al.* 2008;  
464 Seneviratne *et al.* 2010; Maclean *et al.* 2012; Orellana *et al.* 2012). However, there is  
465 much still to do. Methods in eco-hydrology are not standardized, even for recording  
466 variables as basic as the effects on vegetation of manipulating precipitation (Vicca *et*  
467 *al.* 2012). Cross-correlation is needed between the stable isotope methods used to  
468 measure water use by so many studies and direct measurements of plant-available  
469 water. The accumulating evidence for hydrological niches in plants now shows that  
470 the field merits the attention of an integrated programme linked to global change  
471 research.

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475 **Literature Cited**

- 476 Adler, P. B., Ellner, S. P. & Levine, J. M. (2010) Coexistence of perennial plants: an  
 477 embarrassment of niches. *Ecology Letters*, **13**, 1019-1029.
- 478 Adler, P. B., HilleRisLambers, J., Kyriakidis, P. C., Guan, Q. F. & Levine, J. M.  
 479 (2006) Climate variability has a stabilizing effect on the coexistence of prairie  
 480 grasses. *Proceedings of the National Academy of Sciences of the United States*  
 481 *of America*, **103**, 12793-12798.
- 482 Allan, R. P. & Soden, B. J. (2008) Atmospheric warming and the amplification of  
 483 precipitation extremes. *Science*, **321**, 1481-1484.
- 484 Angert, A. L., Huxman, T. E., Barron-Gafford, G. A., Gerst, K. L. & Venable, D. L.  
 485 (2007) Linking growth strategies to long-term population dynamics in a guild  
 486 of desert annuals. *Journal of Ecology*, **95**, 321-331.
- 487 Angert, A. L., Huxman, T. E., Chesson, P. & Venable, D. L. (2009) Functional  
 488 tradeoffs determine species coexistence via the storage effect. *Proceedings of*  
 489 *the National Academy of Sciences of the United States of America*, **106**,  
 490 11641-11645.
- 491 Araya, Y. N., Gowing, D. J. & Dise, N. (2010) A controlled water-table depth system  
 492 to study the influence of fine-scale differences in water regime for plant  
 493 growth. *Aquatic Botany*, **92**, 70-74.
- 494 Araya, Y. N., Gowing, D. J. & Dise, N. (2012a) Does soil nitrogen availability  
 495 mediate the response of grassland composition to water regime? *Journal Of*  
 496 *Vegetation Science*, n/a-n/a.
- 497 Araya, Y. N., Silvertown, J., Gowing, D. J., McConway, K. J., Linder, H. P. &  
 498 Midgley, G. (2012b) Do niche-structured plant communities exhibit  
 499 phylogenetic conservatism? A test case in an endemic clade. *Journal of*  
 500 *Ecology*, **100**, 1434-1439.
- 501 Araya, Y. N., Silvertown, J., Gowing, D. J., McConway, K. J., Peter Linder, H. &  
 502 Midgley, G. (2011) A fundamental, eco-hydrological basis for niche  
 503 segregation in plant communities. *New Phytologist*, **189**, 253-258.
- 504 Bailey, I. W. & Tupper, W. W. (1918) Size variation in tracheary cells. I. A  
 505 comparison between the secondary xylems of vascular cryptogams,

## ESSAY REVIEW

- 506 gymnosperms and angiosperms. *Proceedings of the American Academy of*  
507 *Arts and Sciences*, **54**, 149-204.
- 508 Bailey-Serres, J. & Voesenek, L. A. C. J. (2008) Flooding stress: Acclimations and  
509 genetic diversity. *Annual Review of Plant Biology*, **59**, 313-339.
- 510 Bartelheimer, M., Gowing, D. J. & Silvertown, J. (2010) Explaining hydrological  
511 niches: the decisive role of below-ground competition in two closely related  
512 *Senecio* species. *Journal of Ecology*, **98**, 126-136.
- 513 Bartholomeus, R. P., Witte, J. P. M., van Bodegom, P. M., van Dam, J. C. & Aerts, R.  
514 (2011) Climate change threatens endangered plant species by stronger and  
515 interacting water-related stresses. *Journal of Geophysical Research-*  
516 *Biogeosciences*, **116**.
- 517 Beatty, S. W. (1987) Spatial distributions of *Adenostema* species in Southern  
518 California chaparral - an analysis of niche separation. *Annals of the*  
519 *Association of American Geographers*, **77**, 255-264.
- 520 Boedeltje, G. & Bakker, J. P. (1980) Vegetation, soil, hydrology and management in a  
521 Drenthian brookland (The Netherlands). *Acta Botanica Neerlandica*, **29**, 509-  
522 522.
- 523 Cavender-Bares, J., Izzo, A., Robinson, R. & Lovelock, C. E. (2009) Changes in  
524 ectomycorrhizal community structure on two containerized oak hosts across  
525 an experimental hydrologic gradient. *Mycorrhiza*, **19**, 133-142.
- 526 Cernusak, L. A., Aranda, J., Marshall, J. D. & Winter, K. (2007) Large variation in  
527 whole-plant water-use efficiency among tropical tree species. *New*  
528 *Phytologist*, **173**, 294-305.
- 529 Chase, J. M. & Leibold, M. A. (2003) *Ecological niches*. Chicago University Press,  
530 Chicago.
- 531 Chen, S. P., Bai, Y. F., Zhang, L. X. & Han, X. G. (2005) Comparing physiological  
532 responses of two dominant grass species to nitrogen addition in Xilin River  
533 Basin of China. *Environmental and Experimental Botany*, **53**, 65-75.
- 534 Cheng, X., An, S., Li, B., Chen, J., Lin, G., Liu, Y., Luo, Y. & Liu, S. (2006) Summer  
535 rain pulse size and rainwater uptake by three dominant desert plants in a  
536 desertified grassland ecosystem in northwestern China. *Plant Ecology*, **184**, 1-  
537 12.
- 538 Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review*  
539 *of Ecology and Systematics*, **31**, 343-366.
- 540 Chesson, P., Gebauer, R. L. E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.  
541 S. K., Sher, A., Novoplansky, A. & Weltzin, J. F. (2004) Resource pulses,  
542 species interactions, and diversity maintenance in arid and semi-arid  
543 environments. *Oecologia*, **141**, 236-253.



## ESSAY REVIEW

- 544 Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.  
545 J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F.,  
546 Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J.,  
547 Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I.  
548 J. & Zanne, A. E. (2012) Global convergence in the vulnerability of forests to  
549 drought. *Nature*, **491**, 752-755.
- 550 Clark, J. S. (2010) Individuals and the Variation Needed for High Species Diversity in  
551 Forest Trees. *Science*, **327**, 1129-1132.
- 552 Comita, L. S. & Engelbrecht, B. M. J. (2013) Drought as a driver of tropical tree  
553 species regeneration dynamics and distribution patterns. *Forests and Global*  
554 *Change* (eds D. A. Coomes, D. F. R. P. Burslem & W. D. Simonson).  
555 Cambridge University Press.
- 556 Cook, P. G. & O'Grady, A. P. (2006) Determining soil and ground water use of  
557 vegetation from heat pulse, water potential and stable isotope data. *Oecologia*,  
558 **148**, 97-107.
- 559 Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel,  
560 S. W. & Fargione, J. E. (2013) Global diversity of drought tolerance and  
561 grassland climate-change resilience. *Nature Clim. Change*, **3**, 63-67.
- 562 Davis, S. D. & Mooney, H. A. (1986) Water use patterns of four co-occurring  
563 chaparral shrubs. *Oecologia*, **70**, 172-177.
- 564 Dawson, T. E. (1990) Spatial and physiological overlap of three co-occurring alpine  
565 willows. *Functional Ecology*, **4**, 13-25.
- 566 Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H. & Tu, K. P. (2002)  
567 Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*,  
568 **33**, 507-559.
- 569 Deil, U. (2005) A review on habitats, plant traits and vegetation of ephemeral  
570 wetlands - a global perspective. *Phytocoenologia*, **35**, 533-705.
- 571 Dodd, M. B., Lauenroth, W. K. & Welker, J. M. (1998) Differential water resource  
572 use by herbaceous and woody plant life- forms in a shortgrass steppe  
573 community. *Oecologia*, **117**, 504-512.
- 574 Douda, J., Doudova-Kochankova, J., Boublik, K. & Drasnarova, A. (2012) Plant  
575 species coexistence at local scale in temperate swamp forest: test of habitat  
576 heterogeneity hypothesis. *Oecologia*, **169**, 523-534.
- 577 Drake, P. L. & Franks, P. J. (2003) Water resource partitioning, stem xylem hydraulic  
578 properties, and plant water use strategies in a seasonally dry riparian tropical  
579 rainforest. *Oecologia*, **137**, 321-329.
- 580 Dwire, K. A., Kauffman, J. B. & Baham, J. E. (2006) Plant species distribution in  
581 relation to water-table depth and soil redox potential in Montane riparian  
582 meadows. *Wetlands*, **26**, 131-146.

## ESSAY REVIEW

- 583 Edwards, C. E., Ewers, B. E., McClung, C. R., Lou, P. & Weinig, C. (2012)  
584 Quantitative Variation in Water-Use Efficiency across Water Regimes and Its  
585 Relationship with Circadian, Vegetative, Reproductive, and Leaf Gas-  
586 Exchange Traits. *Molecular Plant*, **5**, 653-668.
- 587 Ehleringer, J. R., Phillips, S. L., Schuster, W. S. F. & Sandquist, D. R. (1991)  
588 Differential utilization of summer rains by desert plants. *Oecologia*, **88**, 430-  
589 434.
- 590 Ellenberg, H. (1953) Physiologisches und ökologisches Verhalten derselben  
591 Pflanzenarten. *Berichte der Deutschen Botanischen Gesellschaft*, **65**, 350-361.
- 592 Fan, Y., Li, H. & Miguez-Macho, G. (2013) Global Patterns of Groundwater Table  
593 Depth. *Science*, **339**, 940-943.
- 594 Field, C., Merino, J. & Mooney, H. A. (1983) Compromises between water-use  
595 efficiency and nitrogen-use efficiency in 5 species of California evergreens.  
596 *Oecologia*, **60**, 384-389.
- 597 Filella, I. & Penuelas, J. (2003) Partitioning of water and nitrogen in co-occurring  
598 Mediterranean woody shrub species of different evolutionary history.  
599 *Oecologia*, **137**, 51-61.
- 600 Flanagan, L. B., Ehleringer, J. R. & Marshall, J. D. (1992) Differential uptake of  
601 summer precipitation among co-occurring trees and shrubs in a pinyon-juniper  
602 woodland. *Plant, Cell & Environment*, **15**, 831-836.
- 603 Fridley, J. D., Grime, J. P., Askew, A. P., Moser, B. & Stevens, C. J. (2011) Soil  
604 heterogeneity buffers community response to climate change in species-rich  
605 grassland. *Global Change Biology*, **17**, 2002-2011.
- 606 Gong, X. Y., Chen, Q., Lin, S., Brueck, H., Dittert, K., Taube, F. & Schnyder, H.  
607 (2011) Tradeoffs between nitrogen- and water-use efficiency in dominant  
608 species of the semiarid steppe of Inner Mongolia. *Plant and Soil*, **340**, 227-  
609 238.
- 610 Groeneveld, J., Enright, N. J., Lamont, B. B. & Wissel, C. (2002) A spatial model of  
611 coexistence among three *Banksia* species along a topographic gradient in fire-  
612 prone shrublands. *Journal of Ecology*, **90**, 762-774.
- 613 Grootjans, A. P., Vandiggelen, R., Wassen, M. J. & Wiersinga, W. A. (1988) The  
614 effects of drainage on groundwater quality and plant-species distribution in  
615 stream valley meadows. *Vegetatio*, **75**, 37-48.
- 616 Grubb, P. J. (1977) The maintenance of species richness in plant communities: The  
617 importance of the regeneration niche. *Biological Reviews*, **52**, 107-145.
- 618 Hasselquist, N. J., Allen, M. F. & Santiago, L. S. (2010) Water relations of evergreen  
619 and drought-deciduous trees along a seasonally dry tropical forest  
620 chronosequence. *Oecologia*, **164**, 881-890.

## ESSAY REVIEW

- 621 Hector, A., von Felten, S., Hautier, Y., Weilenmann, M. & Bruelheide, H. (2012)  
622 Effects of Dominance and Diversity on Productivity along Ellenberg's  
623 Experimental Water Table Gradients. *PLoS One*, **7**, e43358.
- 624 Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography*.  
625 Princeton University Press, Princeton.
- 626 Jackson, P. C., Cavelier, J., Goldstein, G., Meinzer, F. C. & Holbrook, N. M. (1995)  
627 Partitioning of water resources among plants of a lowland tropical forest.  
628 *Oecologia*, **101**, 197-203.
- 629 Jackson, P. C., Meinzer, F. C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.  
630 W., Caldas, L., Iglar, E. & Causin, F. (1999) Partitioning of soil water among  
631 tree species in a Brazilian Cerrado ecosystem. *Tree Physiology*, **19**, 717-724.
- 632 Johnson, D. M., McCulloh, K. A., Woodruff, D. R. & Meinzer, F. C. (2012)  
633 Hydraulic safety margins and embolism reversal in stems and leaves: Why are  
634 conifers and angiosperms so different? *Plant Science*, **195**, 48-53.
- 635 Kiær, L. P., Weisbach, A. N. & Weiner, J. (2013) Root and shoot competition: A  
636 meta-analysis. *Journal of Ecology*, n/a-n/a.
- 637 Kotowski, W., Van Diggelen, R. & Kleinke, J. (1998) Behaviour of wetland plant  
638 species along a moisture gradient in two geographically distant areas. *Acta*  
639 *Botanica Neerlandica*, **47**, 337-349.
- 640 Kowaljow, E. & Fernandez, R. J. (2011) Differential utilization of a shallow-water  
641 pulse by six shrub species in the Patagonian steppe. *Journal Of Arid*  
642 *Environments*, **75**, 211-214.
- 643 Koziol, L., Rieseberg, L. H., Kane, N. & Bever, J. D. (2012) Reduced drought  
644 tolerance during domestication and the evolution of weediness results from  
645 tolerance-growth trade-offs. *Evolution*, no-no.
- 646 Kray, J. A., Cooper, D. J. & Sanderson, J. S. (2012) Groundwater use by native plants  
647 in response to changes in precipitation in an intermountain basin. *Journal Of*  
648 *Arid Environments*, **83**, 25-34.
- 649 Kukowski, K. R., Schwinning, S. & Schwartz, B. F. (2013) Hydraulic responses to  
650 extreme drought conditions in three co-dominant tree species in shallow soil  
651 over bedrock. *Oecologia*, **171**, 819-830.
- 652 Lamont, B. B. & Bergl, S. M. (1991) Water relations, shoot and root architecture, and  
653 phenology of 3 co-occurring *Banksia* species - no evidence for niche  
654 differentiation in the pattern of water-use. *Oikos*, **60**, 291-298.
- 655 Leng, X., Cui, J., Zhang, S. T., Zhang, W. G., Liu, Y. H., Liu, S. R. & An, S. Q.  
656 (2013) Differential water uptake among plant species in humid alpine  
657 meadows. *Journal Of Vegetation Science*, **24**, 138-147.

## ESSAY REVIEW

- 658 Lennon, J. T., Aanderud, Z. T., Lehmkuhl, B. K. & Schoolmaster, D. R. (2012)  
659 Mapping the niche space of soil microorganisms using taxonomy and traits.  
660 *Ecology*, **93**, 1867-1879.
- 661 Lens, F., Tixier, A., Cochard, H., Sperry, J. S., Jansen, S. & Herbette, S. (2013)  
662 Embolism resistance as a key mechanism to understand adaptive plant  
663 strategies. *Current Opinion in Plant Biology*, **16**, 287-292.
- 664 Leroux, X., Bariac, T. & Mariotti, A. (1995) Spatial Partitioning of the Soil-Water  
665 Resource Between Grass and Shrub Components in a West-African Humid  
666 Savanna. *Oecologia*, **104**, 147-155.
- 667 Levine, J. M. & HilleRisLambers, J. (2009) The importance of niches for the  
668 maintenance of species diversity. *Nature*, **461**, 254-U130.
- 669 Lin, G., Phillips, S. L. & Ehleringer, J. R. (1996) Monsoonal Precipitation  
670 Responses of Shrubs in a Cold Desert Community on the Colorado Plateau.  
671 *Oecologia*, **106**, 8-17.
- 672 Liu, W. J., Liu, W. Y., Li, P. J., Duan, W. P. & Li, H. M. (2010) Dry season water  
673 uptake by two dominant canopy tree species in a tropical seasonal rainforest of  
674 Xishuangbanna, SW China. *Agricultural and Forest Meteorology*, **150**, 380-  
675 388.
- 676 Liu, Y. H., Xu, Z., Duffy, R., Chen, W. L., An, S. Q., Liu, S. R. & Liu, F. D. (2011)  
677 Analyzing relationships among water uptake patterns, rootlet biomass  
678 distribution and soil water content profile in a subalpine shrubland using water  
679 isotopes. *European Journal of Soil Biology*, **47**, 380-386.
- 680 Maclean, I. M. D., Bennie, J. J., Scott, A. J. & Wilson, R. J. (2012) A high-resolution  
681 model of soil and surface water conditions. *Ecological Modelling*, **237**, 109-  
682 119.
- 683 Maherali, H., Pockman, W. T. & Jackson, R. B. (2004) Adaptive variation in the  
684 vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184-2199.
- 685 Mamolos, A. P., Veresoglou, D. S., Noitsakis, V. & Gerakis, A. (2001) Differential  
686 drought tolerance of five coexisting plant species in Mediterranean lowland  
687 grasslands. *Journal of Arid Environments*, **49**, 329-341.
- 688 Manning, S. J. & Barbour, M. G. (1988) Root systems, spatial patterns, and  
689 competition for soil moisture between two desert subshrubs. *American  
690 Journal of Botany*, **75**, 885-893.
- 691 Manzoni, S., Vico, G., Katul, G., Palmroth, S., Jackson, R. B. & Porporato, A. (2013)  
692 Hydraulic limits on maximum plant transpiration and the emergence of the  
693 safety-efficiency trade-off. *New Phytologist*, **198**, 169-178.
- 694 Maricle, B. R., Zwenger, S. R. & Lee, R. W. (2011) Carbon, nitrogen, and hydrogen  
695 isotope ratios in creekside trees in western Kansas. *Environmental and  
696 Experimental Botany*, **71**, 1-9.

## ESSAY REVIEW

- 697 Markesteyn, L., Poorter, L., Bongers, F., Paz, H. & Sack, L. (2011) Hydraulics and  
698 life history of tropical dry forest tree species: coordination of species' drought  
699 and shade tolerance. *New Phytologist*, **191**, 480-495.
- 700 Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, N. M., Cavelier, J. & Wright,  
701 S. J. (1999) Partitioning of soil water among canopy trees in a seasonally dry  
702 tropical forest. *Oecologia*, **121**, 293-301.
- 703 Meissner, M., Kohler, M., Schwendenmann, L. & Holscher, D. (2012) Partitioning of  
704 soil water among canopy trees during a soil desiccation period in a temperate  
705 mixed forest. *Biogeosciences*, **9**, 3465-3474.
- 706 Midwood, A. J., Boutton, T. W., Archer, S. R. & Watts, S. E. (1998) Water use by  
707 woody plants on contrasting soils in a savanna parkland: assessment with delta  
708 H-2 and delta O-18. *Plant and Soil*, **205**, 13-24.
- 709 Moeslund, J., Arge, L., Bøcher, P., Dalgaard, T., Ejrnæs, R., Odgaard, M. &  
710 Svenning, J.-C. (2013a) Topographically controlled soil moisture drives plant  
711 diversity patterns within grasslands. *Biodiversity and Conservation*, 1-16.
- 712 Moeslund, J. E., Arge, L., Bøcher, P. K., Dalgaard, T., Odgaard, M. V., Nygaard, B.  
713 & Svenning, J.-C. (2013b) Topographically controlled soil moisture is the  
714 primary driver of local vegetation patterns across a lowland region. *Ecosphere*,  
715 **4**, art91.
- 716 Moreno-Gutierrez, C., Dawson, T. E., Nicolas, E. & Querejeta, J. I. (2012) Isotopes  
717 reveal contrasting water use strategies among coexisting plant species in a  
718 Mediterranean ecosystem. *New Phytologist*, **196**, 489-496.
- 719 Nippert, J. B. & Knapp, A. K. (2007a) Linking water uptake with rooting patterns in  
720 grassland species. *Oecologia*, **153**, 261-272.
- 721 Nippert, J. B. & Knapp, A. K. (2007b) Soil water partitioning contributes to species  
722 coexistence in tallgrass prairie. *Oikos*, **116**, 1017-1029.
- 723 Nordbakken, J. F. (1996) Plant niches along the water-table gradient on an  
724 ombrotrophic mire expanse. *Ecography*, **19**, 114-121.
- 725 Nygaard, B. & Ejrnaes, R. (2009) The impact of hydrology and nutrients on species  
726 composition and richness: evidence from a microcosm experiment. *Wetlands*,  
727 **29**, 187-195.
- 728 Orellana, F., Verma, P., Loheide, S. P. & Daly, E. (2012) Monitoring and modelling  
729 water-vegetation interactions in groundwater-dependent ecosystems. *Reviews*  
730 *of Geophysics*, **50**.
- 731 Parolin, P., Lucas, C., Piedade, M. T. F. & Wittmann, F. (2010) Drought responses of  
732 flood-tolerant trees in Amazonian floodplains. *Annals of Botany*, **105**, 129-  
733 139.

## ESSAY REVIEW

- 734 Patrick, W. H. & Wyatt, R. (1964) Soil nitrogen loss as a result of alternate  
735 submergence and drying. *Soil Science Society of America Journal*, **28**, 647-  
736 653.
- 737 Patterson, T. B., Guy, R. D. & Dang, Q. L. (1997) Whole-plant nitrogen- and water-  
738 relations traits, and their associated trade-offs, in adjacent muskeg and upland  
739 boreal spruce species. *Oecologia*, **110**, 160-168.
- 740 Piedallu, C., Gégout, J.-C., Perez, V. & Lebourgeois, F. (2013) Soil water balance  
741 performs better than climatic water variables in tree species distribution  
742 modelling. *Global Ecology and Biogeography*, **22**, 470-482.
- 743 Purves, D. W. & Turnbull, L. A. (2010) Different but equal: the implausible  
744 assumption at the heart of neutral theory. *Journal of Animal Ecology*, **79**,  
745 1215-1225.
- 746 Querejeta, J. I., Estrada-Medina, H., Allen, M. F. & Jimenez-Osornio, J. J. (2007)  
747 Water source partitioning among trees growing on shallow karst soils in a  
748 seasonally dry tropical climate. *Oecologia*, **152**, 26-36.
- 749 Redtfeldt, R. A. & Davis, S. D. (1996) Physiological and morphological evidence of  
750 niche segregation between two co-occurring species of *Adenostoma* in  
751 California Chaparral. *Ecoscience*, **3**, 290-296.
- 752 Rees, M., Grubb, P. J. & Kelly, D. (1996) Quantifying the impact of competition and  
753 spatial heterogeneity on the structure and dynamics of a four-species guild of  
754 winter annuals. *American Naturalist*, **147**, 1-32.
- 755 Reyer, C. P. O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante,  
756 A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoude, R., Klein, T., Kuster,  
757 T. M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P.,  
758 de Dato, G., Francois, L., Menzel, A. & Pereira, M. (2013) A plant's  
759 perspective of extremes: terrestrial plant responses to changing climatic  
760 variability. *Global Change Biology*, **19**, 75-89.
- 761 Reynolds, H. L., Hungate, B. A., Chapin, F. S. & Dantonio, C. M. (1997) Soil  
762 heterogeneity and plant competition in an annual grassland. *Ecology*, **78**,  
763 2076-2090.
- 764 Robinson, D. A., Binley, A., Crook, N., Day-Lewis, F. D., Ferre, T. P. A., Grauch, V.  
765 J. S., Knight, R., Knoll, M., Lakshmi, V., Miller, R., Nyquist, J., Pellerin, L.,  
766 Singha, K. & Slater, L. (2008) Advancing process-based watershed  
767 hydrological research using near-surface geophysics: a vision for, and review  
768 of, electrical and magnetic geophysical methods. *Hydrological Processes*, **22**,  
769 3604-3635.
- 770 Rutter, A. J. (1955) Composition of wet heath vegetation in relation to the water table.  
771 *Journal of Ecology*, **43**, 507-543.
- 772 Schachtschneider, K. & February, E. C. (2010) The relationship between fog, floods,  
773 groundwater and tree growth along the lower Kuiseb River in the hyperarid  
774 Namib. *Journal Of Arid Environments*, **74**, 1632-1637.

## ESSAY REVIEW

- 775 Schietti, J., Emilio, T., Rennó, C. D., Drucker, D. P., Costa, F. R. C., Nogueira, A.,  
776 Baccaro, F. B., Figueiredo, F., Castilho, C. V., Kinupp, V., Guillaumet, J.-L.,  
777 Garcia, A. R. M., Lima, A. P. & Magnusson, W. E. (2014) Vertical distance  
778 from drainage drives floristic composition changes in an Amazonian  
779 rainforest. *Plant Ecology & Diversity*, **7**, 241-253.
- 780 Schwinning, S. (2008) The Water Relations of Two Evergreen Tree Species in a Karst  
781 Savanna. *Oecologia*, **158**, 373-383.
- 782 Seibt, U., Rajabi, A., Griffiths, H. & Berry, J. (2008) Carbon isotopes and water use  
783 efficiency: sense and sensitivity. *Oecologia*, **155**, 441-454.
- 784 Seneviratne, S. I., Corti, T., Davin, E. L., Hirschi, M., Jaeger, E. B., Lehner, I.,  
785 Orłowsky, B. & Teuling, A. J. (2010) Investigating soil moisture–climate  
786 interactions in a changing climate: A review. *Earth-Science Reviews*, **99**, 125-  
787 161.
- 788 Sharitz, R. R. & McCormick, J. F. (1973) Population dynamics of two competing  
789 annual plant species. *Ecology*, **54**, 723-740.
- 790 Silvertown, J. (2004) Plant coexistence and the niche. *Trends in Ecology & Evolution*,  
791 **19**, 605-611.
- 792 Silvertown, J., Araya, Y. N., Linder, H. P. & Gowing, D. J. (2012) Experimental  
793 investigation of the origin of fynbos plant community structure after fire.  
794 *Annals of Botany*, **110**, 1377-1383.
- 795 Silvertown, J., Dodd, M. E., Gowing, D. & Mountford, O. (1999) Hydrologically-  
796 defined niches reveal a basis for species-richness in plant communities.  
797 *Nature*, **400**, 61-63.
- 798 Silvertown, J. & Wilson, J. B. (2000) Spatial interactions among grassland plant  
799 populations. *The geometry of ecological interactions* (eds U. Dieckman, R.  
800 Law & H. Metz), pp. 28-47. Cambridge University Press, Cambridge.
- 801 Sperry, J. S. & Tyree, M. T. (1988) Mechanism of water-stress induced xylem  
802 embolism. *Plant Physiology*, **88**, 581-587.
- 803 Stokes, C. J. & Archer, S. R. (2010) Niche differentiation and neutral theory: an  
804 integrated perspective on shrub assemblages in a parkland savanna. *Ecology*,  
805 **91**, 1152-1162.
- 806 Stratton, L. C., Goldstein, G. & Meinzer, F. C. (2000) Temporal and spatial  
807 partitioning of water resources among eight woody species in a Hawaiian dry  
808 forest. *Oecologia*, **124**, 309-317.
- 809 Strom, L., Jansson, R. & Nilsson, C. (2012) Projected changes in plant species  
810 richness and extent of riparian vegetation belts as a result of climate-driven  
811 hydrological change along the Vindel River in Sweden. *Freshwater Biology*,  
812 **57**, 49-60.

## ESSAY REVIEW

- 813 Terradas, J., Penuelas, J. & Lloret, F. (2009) The Fluctuation Niche in Plants.  
814 *International Journal of Ecology*, **2009**, 1-5.
- 815 Tyree, M. T., Davis, S. D. & Cochard, H. (1994) Biophysical perspectives of xylem  
816 evolution - is there a tradeoff of hydraulic efficiency for vulnerability to  
817 dysfunction. *Iawa Journal*, **15**, 335-360.
- 818 Verheyen, K., Bulteel, H., Palmborg, C., Olivie, B., Nijs, I., Raes, D. & Muys, B.  
819 (2008) Can complementarity in water use help to explain diversity-  
820 productivity relationships in experimental grassland plots? *Oecologia*, **156**,  
821 351-361.
- 822 Verhulst, J., Montana, C., Mandujano, M. C. & Franco, M. (2008) Demographic  
823 mechanisms in the coexistence of two closely related perennials in a  
824 fluctuating environment. *Oecologia*, **156**, 95-105.
- 825 Vicca, S., Gilgen, A. K., Serrano, M. C., Dreesen, F. E., Dukes, J. S., Estiarte, M.,  
826 Gray, S. B., Guidolotti, G., Hoepfner, S. S., Leakey, A. D. B., Ogaya, R., Ort,  
827 D. R., Ostrogovic, M. Z., Rambal, S., Sardans, J., Schmitt, M., Siebers, M.,  
828 Linden, L. v. d., Straaten, O. v. & Granier, A. (2012) Urgent need for a  
829 common metric to make precipitation manipulation experiments comparable.  
830 *New Phytologist*, **195**, 518-522.
- 831 Vivian-Smith, G. (1997) Microtopographic heterogeneity and floristic diversity in  
832 experimental wetland communities. *Journal of Ecology*, **85**, 71-82.
- 833 von Arx, G., Archer, S. R. & Hughes, M. K. (2012) Long-term functional plasticity in  
834 plant hydraulic architecture in response to supplemental moisture. *Annals of*  
835 *Botany*, **109**, 1091-1100.
- 836 Webb, J. A., Wallis, E. M. & Stewardson, M. J. (2012) A systematic review of  
837 published evidence linking wetland plants to water regime components.  
838 *Aquatic Botany*, **103**, 1-14.
- 839 Weltzin, J. F. & McPherson, G. R. (1997) Spatial and temporal soil moisture resource  
840 partitioning by trees and grasses in a temperate savanna, Arizona, USA.  
841 *Oecologia*, **112**, 156-164.
- 842 West, A. G., Dawson, T. E., February, E. C., Midgley, G. F., Bond, W. J. & Aston, T.  
843 L. (2012) Diverse functional responses to drought in a Mediterranean-type  
844 shrubland in South Africa. *New Phytologist*, **195**, 396-407.
- 845 West, A. G., Hultine, K. R., Burtch, K. G. & Ehleringer, J. R. (2007) Seasonal  
846 variations in moisture use in a pinon-juniper woodland. *Oecologia*, **153**, 787-  
847 798.
- 848 Wierda, A., Fresco, L. F. M., Grootjans, A. P. & Vandiggelen, R. (1997) Numerical  
849 assessment of plant species as indicators of the groundwater regime. *Journal*  
850 *of Vegetation Science*, **8**, 707-716.



## ESSAY REVIEW

- 851 Wilson, J. B. (2011) The twelve theories of co-existence in plant communities: the  
852 doubtful, the important and the unexplored. *Journal Of Vegetation Science*,  
853 **22**, 184-195.
- 854 Witte, J. P. M., Runhaar, J., van Ek, R., van der Hoek, D. C. J., Bartholomeus, R. P.,  
855 Batelaan, O., van Bodegom, P. M., Wassen, M. J. & van der Zee, S. E. A. T.  
856 M. (2012) An ecohydrological sketch of climate change impacts on water and  
857 natural ecosystems for the Netherlands: bridging the gap between science and  
858 society. *Hydrology and Earth System Sciences*, **16**, 3945-3957.
- 859 Wolfe, B. E., Weishampel, P. A. & Klironomos, J. N. (2006) Arbuscular mycorrhizal  
860 fungi and water table affect wetland plant community composition. *Journal of*  
861 *Ecology*, **94**, 905-914.
- 862 Xu, Q., Li, H., Chen, J. Q., Cheng, X. L., Liu, S. R. & An, S. Q. (2011) Water use  
863 patterns of three species in subalpine forest, Southwest China: the deuterium  
864 isotope approach. *Ecohydrology*, **4**, 236-244.
- 865 Yang, H., Auerswald, K., Bai, Y. F. & Han, X. G. (2011) Complementarity in water  
866 sources among dominant species in typical steppe ecosystems of Inner  
867 Mongolia, China. *Plant and Soil*, **340**, 303-313.
- 868 Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. & Fisher, J. B. (2011) Changes  
869 in the potential distribution of humid tropical forests on a warmer planet.  
870 *Philosophical Transactions of the Royal Society a-Mathematical Physical and*  
871 *Engineering Sciences*, **369**, 137-160.
- 872 Zimmerman, M. H. (1983) *Xylem structure and the ascent of sap*. Springer-Verlag,  
873 Berlin.
- 874 Zou, C. B., Barnes, P. W., Archer, S. & McMurtry, C. R. (2005) Soil moisture  
875 redistribution as a mechanism of facilitation in Savanna tree-shrub clusters.  
876 *Oecologia*, **145**, 32-40.

877 **Tables**

878 **Table 1**

879 Table 1. Studies of hydrological niche segregation through the partitioning of space on fine-scale soilmoisture gradients. Any differences among  
 880 species are those found to be statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
1	Alpine tundra	Alberta, Canada	~25	3 <i>Salix</i> spp.	Species occupied distinct though overlapping zones along a topographic and soil moisture gradient. Species position on the gradient correlated with physiological measures of water relations, indicating the likely role of HNS.	(Dawson 1990)
2	Mediterranean shrubland	Spain	288	1 grass and 9 coexisting shrub species of various size	Based upon stable isotope analysis, the ten species segregated along a gradient of water use characteristics from low stomatal conductance ( $g_s$ ) and high WUE to high $g_s$ and low WUE. The ranking of	(Moreno-Gutierrez <i>et al.</i> 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
					species on the gradient was unaffected by differences in rainfall between years.	
3	Fynbos	Western Cape, South Africa	350 - 1400	Restionaceae and fynbos community as a whole separately analysed	Distributions in SEV niche space tested against null models showed HNS among Restionaceae in 7 of 10 sites and for the entire community in 9 out of 10 sites.	(Araya <i>et al.</i> 2011, 2012b)
4	chaparral	S. California, USA	403	2 co-occurring shrubs <i>Adenostoma fasciculatum</i> and <i>A. sparsifolium</i>	<i>A. sparsifolium</i> had much deeper roots than <i>A. fasciculatum</i> but the latter species was more resistant to xylem embolism caused by water stress than the former. Redtfeldt & Davis(1996) made this comparison between adjacent plants, but Beatty (1987) found that the species usually occupied different microsites and were only rarely found as nearest neighbours.	(Beatty 1987), (Redtfeldt & Davis 1996)
5	Temperate swamp forest	Budějovická, Czech Republic	575	3 mosses, 11 perennial herbs, a fern, a floating	Distribution of 9 of 17 species varied significantly across a water table depth gradient of about a metre in vertical	(Douda <i>et al.</i> 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				aquatic and a tree	range.	
6	serpentine annuals	California, USA	589	3 annuals <i>Calycadenia multiglandulosum</i> , <i>Plantago erecta</i> , and <i>Lasthenia californica</i>	Soil water content varied among patches dominated by the 3 different species. A reciprocal sowing experiment among patches showed a home-site advantage for all 3 species.	(Reynolds <i>et al.</i> 1997)
7	riparian meadow	Oregon, USA	650	18 species of sedge, rush, grass and forb	Median water table depths varied among the 18 species over a 50cm range, but with widely overlapping ranges.	(Dwire <i>et al.</i> 2006)
8	floodplain meadow	England, UK	680	2 communities containing 83 species of herbaceous meadow plants	Community-wide segregation found in niche space defined by axes of SEVa and SEVd in both communities.	(Silvertown <i>et al.</i> 1999)
9	mire	SE Norway	800	24 species including 9 vascular plants, 5	Along a water table gradient of 0–25cm depth, all 24 species exhibited some degree of 'preference' for a particular	(Nordbakken 1996)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>Sphagnum</i> spp., 6 hepatics and 4 lichens	depth to water table (DWT). The full range of preferences (0–25cm median DWT) was found among the 9 vascular plant species, with species in each of the other 3 groups showing medians between 0–15cm DWT.	
10	rock outcrop	Georgia, USA	~1,000	Annuals <i>Sedum smallii</i> and <i>Minuartia uniflora</i>	Coexisting annuals shown experimentally to partition the rock depressions in which they grow by soil depth because of the effect this has on soil moisture, favouring <i>M. uniflora</i> in deeper soil that holds more soil moisture and <i>S. smallii</i> in shallow, drier soil.	(Sharitz & McCormick 1973)
11	limestone grassland	Derbyshire, UK	1, 300	25 species of grass and forb	13 species segregated on gradients of soil depth and 9 migrated along these in response to experimental watering and drought treatments.	(Fridley <i>et al.</i> 2011)

882 **Table 2**

883 Table 2. Studies of hydrological niche segregation through different strategies of water acquisition such as different phenologies or different  
 884 rooting depths. Any differences among species are those found to be statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
12	Dry desert	Namibia	12	3 common trees <i>Acacia erioloba</i> , <i>Tamarix usneoides</i> and <i>Faidherbia albida</i>	Stable isotopes were used to partition water sources between fog, ground water, and soil depths 0 - 1m or 1.5 - 3.0m depth. None used fog water. For adult trees in the dry season, > 50% was obtained from deep soil in <i>A. erioloba</i> & <i>T. usneoides</i> , but the spp. accessed different amounts from shallow soil (6% & 17%). <i>F. albida</i> used mainly ground water (52%) and deep water (30%).	(Schachtschneider & February 2010)
13	Desert	Utah, USA	119	5 annuals, 7 herbaceous perennials, 13 woody perennials	Stable isotope analysis indicated that there was no difference among life forms in their exploitation of different water sources in spring, but that differences did	(Ehleringer <i>et al.</i> 1991; Lin <i>et al.</i> 1996)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				and a succulent perennial	occur both within and between life forms in summer. Experimental rainfall additions in summer confirmed that species exploit this water source to different degrees.	
14	Desert	California, USA	144	Co-dominant shrubs <i>Haplopappus cooperi</i> and <i>Chrysothamnus teretifolius</i>	Species had different rooting depths. Experimental removal of <i>C. teretifolius</i> (rooting depth 40cm) improved the water status ( $\Psi$ ) of <i>H. cooperi</i> (rooting depth 20cm), but not vice-versa.	(Manning & Barbour 1988)
15	Intermountain desert basin	Colorado, USA	178	Grasses: <i>Sporobolus airoides</i> and <i>Distichlis spicata</i> ; shrubs: <i>Sarcobatus vermiculatus</i> and <i>Ericameria nauseosa</i>	Experimental rainfall treatments and stable isotope analysis demonstrated that the grasses used surface water while the shrubs used ground and surface water. The shrubs differed from each other in their response to variation in surface water availability.	(Kray <i>et al.</i> 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
16	Savanna	Arizona, USA	202	A dominant tree <i>Quercus emoryi</i> and a co-occurring dominant C-4 grass <i>Trachypogon montufari</i>	Stable isotope analysis demonstrated that established trees and grass utilized different water sources. However, 2 month old tree seedlings obtained water from above the zone exploited by the grass, competed in the same depth zone at ages 1 and 2, and then penetrated to deeper soil when older.	(Weltzin & McPherson 1997)
17	Pinyon- Juniper woodland	Utah, USA	232	<i>Pinus edulis</i> and <i>Juniperus osteosperma</i>	Sap flux and stable isotopes were used to determine the relative use of water by the two species in the two zones 5 - 45cm and > 45cm soil depth. <i>P. edulis</i> depended on summer rain near the surface while <i>J. osteosperma</i> did not. At other times of year the species had similar water utilization to each other.	(West <i>et al.</i> 2007)
18	Woodland	Utah, USA	319	2 trees <i>Juniperus osteosperma</i> & <i>Pinus edulis</i> & 2 shrubs <i>Artemisia</i>	Stable isotope analysis indicated that <i>C. nauseosus</i> depended on ground water while the other 3 species used both precipitation and groundwater, but to	(Flanagan <i>et al.</i> 1992)



#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>tridentate</i> & <i>Chrysothamnus nauseosus</i>	varying degrees.	
19	Shortgrass steppe	Colorado, USA	321	A C-4 grass <i>Bouteloua gracilis</i> , a shrub <i>Atriplex canescens</i> , and a tree <i>Populus sargentii</i>	Stable isotopes indicated that <i>P. sargentii</i> depended exclusively on ground water during the growing season, while <i>B. gracilis</i> depended exclusively on rainfall from near the soil surface. <i>A. canescens</i> probably used both sources, but mainly rainfall obtained from deeper soil. The effects of experimental removal, separately and in combination, of the grasses & shrubs increased soil water content in different soil layers in a manner consistent with the species' patterns of utilization.	(Dodd <i>et al.</i> 1998)
20	Steppe	Inner Mongolia, China	341	C-3 Grasses: <i>Stipa grandis</i> , <i>Agropyron cristatum</i> , <i>Leymus chinensis</i> ; C-4 grass: <i>Cleistogenes</i>	Stable isotopes showed that the shrub <i>Caragana microphylla</i> used only deep soil water, the C4 grass <i>Cleistogenes squarrosa</i> used only summer rainfall, and the C3 grass species used both sources of	(Yang <i>et al.</i> 2011)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>squarrosa</i> ; shrub: <i>Caragana microphylla</i> .	water according to availability.	
21	Mediterranean grassland	Greece	364	Two C-3 grasses <i>Poa bulbosa</i> and <i>Anthoxanthum odoratum</i> , two C-4 grasses <i>Chrysopogon gryllus</i> and <i>Cynodon dactylon</i> , and the C-3 forb <i>Rumex acetosella</i> .	Biomass production was shown to be water-limited in all 5 species. Phenology differed between the C-3 grasses that peaked early in the year, the C-4 grasses that grew later and <i>R. acetosella</i> that peaked in biomass between the two groups of grasses.	(Mamolos <i>et al.</i> 2001)
22	Mediterranean shrubland	Spain	450	Shrubs: pre-Mediterranean <i>Quercus coccifera</i> , <i>Arbutus unedo</i> , <i>Pistacia lentiscus</i> ; Mediterranean <i>Erica multiflora</i> ,	Stable isotope analysis indicated differences in use of water sources between species with different evolutionary history (pre-Mediterranean vs. Mediterranean) and between some species in the time of day when different sources were exploited.	(Filella & Penuelas 2003)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>Globularia alypum</i>		
23	Tropical	Lana'i, Hawaii	500	2 dominant and 5 other tree species and a stem succulent	Stable isotopes indicated that most species including the two most abundant trees utilized shallow water sources and were drought tolerant, while an evergreen that is dominant in wetter Hawaiian forests and a stem succulent were drought avoiders and used deeper water. Among the subordinate trees using shallow water, one species was separated from other trees by a much larger distance than expected, suggesting competition might influence its spatial distribution.	(Stratton <i>et al.</i> 2000)
24	Kwongan	Western Australia	531	3 congeneric shrubs: <i>Banksia hookeriana</i> , <i>B. attenuata</i> and <i>B. menziesii</i>	Water relations did not differ among the 3 species during the dry season. Shoot phenology and root distributions were also the same.	(Lamont & Bergl 1991)
25	riparian	Kansas, USA	586	3 creekside trees	None of the 3 species showed signs of	(Maricle <i>et al.</i>

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
	woodland			<i>Lonicera tatarica</i> , <i>Morus alba</i> and <i>Celtis occidentalis</i>	water stress during soil drying. Stable isotopes indicated that <i>C. occidentalis</i> obtained water from a shallower depth than the other two species, even though this species had the deepest roots.	2011)
26	old growth temperate broadleaf forest	northern Thuringia, Germany	590	3 co-dominant trees <i>Fagus sylvatica</i> , <i>Tilia sp.</i> , <i>Fraxinus excelsior</i>	Stable isotopes were used to estimate depth of water sources from the soil profile for species growing in single-species clusters and in 3-spp mixtures. Overlap was greater among single species than in mixtures due to <i>Fraxinus</i> altering its source depth in mixture.	(Meissner <i>et al.</i> 2012)
27	Experimental grassland	Umeå, Sweden	600	Up to 12 grassland species sown in plots containing 1, 2, 4, 8 or 12 species	Community evapotranspiration and biomass production showed over-yielding in control mixtures compared to monocultures, but this was absent in a drought treatment, suggesting complementary use of soil moisture under normal conditions.	(Verheyen <i>et al.</i> 2008)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
28	Alpine meadow	Mt. Balang, China	710	3 herbs <i>Caltha palustris</i> , <i>Veratrum nigrum</i> , <i>Stellera chamaejasme</i>	Stable isotopes showed that the 3 species used water from 4 soil depth zones differently.	(Leng <i>et al.</i> 2013)
29	sub-alpine	Sichuan, China	711	2 co-dominant shrubs <i>Quercus aquifolioides</i> and <i>Salix luctuosa</i>	Stable isotopes used to measure use of water from 6 depth horizons in the monsoon month of August. The two species were very similar in their use of water from different depths, both matching relative amounts used to relative amounts of water present in the top 50cm of soil.	(Liu <i>et al.</i> 2011)
30	savanna	Texas, USA	720	2 shrubs <i>Prosopis glandulosa</i> (overstorey), <i>Zanthoxylum fagara</i> (understorey) and up to 8 other woody understorey	Rooting depth profiles were different among the species (especially <i>P. glandulosa</i> and <i>Z. fagara</i> ), but stable isotopes sampled during the season of greatest rainfall (late summer - fall) showed no differences among species in the depth of water sources utilized. Hydraulic lift and recruitment around	(Midwood <i>et al.</i> 1998), (Zou <i>et al.</i> 2005), (Stokes & Archer 2010)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				species	nurse plants produce positive interactions among species.	
31	Karst savanna	Texas, USA	800	Two dominant evergreen trees <i>Juniperus ashei</i> and <i>Quercus fusiformis</i>	$\psi_p$ lower in <i>J. ashei</i> than <i>Q. fusiformis</i> , suggesting that the roots of the former are shallower than those of the latter species. However, stable isotopes of co-occurring trees of the two species showed that both utilized the same water source during drought.	(Schwinning 2008)
32	Tallgrass prairie	Kansas, USA	835	7 species including 3 dominant C-4 grasses and 4 C-3 forbs and shrubs	Stable isotopes and $\Psi$ measurements showed all species used water from surface (0 - 25cm) soil in the wet summer season. In the dry season C-4 grasses continued to use this source, while C-3 species used predominantly deeper water	(Nippert & Knapp 2007a, 2007b)
33	Sub-alpine forest	SW China	884	Dominant tree <i>Abies faxoniana</i> , mid-storey tree <i>Betula utilis</i> and	Stable isotopes showed that <i>A. faxoniana</i> depends throughout the year mainly on ground water, while the other two species depend mainly on rainfall, except when	(Xu <i>et al.</i> 2011)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				understory bamboo <i>Bashania fangiana</i>	this is scarce.	
34	Seasonally dry forest	Yucatan, Mexico	1, 000	3 evergreen <i>Brosimum alicastrum</i> , <i>Talisia olivaeformis</i> , <i>Ficus cotinifolia</i> , 3 deciduous <i>Cedrela odorata</i> , <i>Spondias purpurea</i> , <i>Enterolobium cyclocarpum</i> and 1 semi-deciduous <i>Cordia dodecandra</i> tree species	Stable isotopes sampled in the peak of the dry season were used to estimate the % water used that was derived from three soil depth zones and from ground water. None of the species used ground water for more than 11% of their supply. 3 species <i>F. cotinifolia</i> <i>S. purpurea</i> <i>C. dodecandra</i> used water mainly from the soil surface (0 - 15cm) and the other 3 from deep bedrock (70 - 300cm) <i>E. cyclocarpum</i> <i>B. alicastrum</i> <i>T. olivaeformis</i> with differing utilizations of water from the zone between 15 - 70cm.	(Querejeta <i>et al.</i> 2007)
35	chaparral	S. California, USA	1,000	4 coexisting shrubs: <i>Quercus durata</i> , <i>Heteromeles arbutifolia</i> , <i>Adenostoma fasciculatum</i> ,	Water use patterns suggested that <i>Q. durata</i> accessed water from a depth of $\geq$ 2m, <i>H. arbutifolia</i> and <i>A. fasciculatum</i> from 0.75m and <i>R. californica</i> from 0.5m.	(Davis & Mooney 1986)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>Rhamnus californica</i>		
36	savanna	Côte d'Ivoire, W. Africa	1, 210	Shrubs and bunch grasses	Root distributions and stable isotopes indicate that shrubs and grasses both obtain water from near the surface and do not exploit water from substantially different depth zones.	(Leroux <i>et al.</i> 1995)
37	Woodland	N. Queensland, Australia	1, 400	4 dominant trees <i>Corymbia clarksoniana</i> , <i>Lophostemon suaveolens</i> , <i>Eucalyptus platyphylla</i> and <i>Melaleuca viridiflora</i>	Stable isotopes sampled towards the end of the dry season for one individual of each species suggested that <i>C. clarksoniana</i> obtained all of its water from ground water, <i>M. viridiflora</i> obtained 53–77% from this source and <i>L. suaveolens</i> and <i>E. platyphylla</i> obtained between 0% and 15% from ground water.	(Cook & O'Grady 2006)
38	Tropical, seasonal rainforest	SW China	1, 487	2 dominant, canopy trees <i>Pometia tomentosa</i> and	In the dry season <i>G. subaequalis</i> utilized water mainly from shallow soil (< 60cm) and <i>P. tomentosa</i> from deeper soil (>	(Liu <i>et al.</i> 2010)



#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>Gironniera subaequalis</i>	60cm). Seedlings of the latter species also acquired significant amounts of water from fog.	
39	Savanna	Brasilia, Brazil	1, 550	5 deciduous and 5 evergreen woody species	Stable isotope analysis during the dry season divided the species into a group of 5 mainly evergreen species that exploited water in the top 170cm of the soil, a group of 4 mainly deciduous species obtaining water from below 250 cm and one deciduous species that was intermediate between the two groups.	(Jackson <i>et al.</i> 1999)
40	Seasonal tropical forest	Yucatan, Mexico	1, 650	3 evergreen trees <i>Coccoloba diversifolia</i> , <i>Esenbeckia pentaphylla</i> , <i>Vitex gaumeri</i> and 3 drought-deciduous trees <i>Caesalpinia gaumeri</i> , <i>Lonchocarpus</i>	In early but not in late successional forest, stable isotopes indicated that the 3 evergreen species accessed deeper water than the 3 deciduous species.	(Hasselquist <i>et al.</i> 2010)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				<i>castilloi</i> , <i>Lysiloma latisiliquum</i>		
41	riparian tropical rainforest	NE Australia	1, 680	Co-dominant canopy species, tree species: <i>Doryphora aromatica</i> , <i>Argyrodendron trifoliolatum</i> , <i>Castanospora alphandii</i> and climbing palms <i>Calamus australis</i> and <i>C. caryotoides</i>	In the dry season, stable isotopes indicated that two of the trees depended on stream water while the other three species drew water from a zone above the water table.	(Drake & Franks 2003)
42	Tropical	Barro Colorado Island nature monument, Panama	2, 600	9 species of deciduous and evergreen broadleaf tree, one palm, one liana, and 5 species of small trees and shrubs	Stable isotope analysis during the dry season indicated a high degree of vertical partitioning of soil water, especially among evergreen trees and shrubs.	(Jackson <i>et al.</i> 1995)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
43	tropical forest	Barro Colorado Island, Panama	2,600	17 spp. of forest trees ranging from evergreen to varying degrees of dry season deciduousness	Stable isotope and water use measurements made during the dry season demonstrated that smaller diameter trees sourced deeper water than larger ones. Ability to maintain sap flow during the dry season varied with leaf phenology, with evergreen species tapping increasingly deeper water as the dry season progressed.	(Meinzer <i>et al.</i> 1999)

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886

887 **Table 3**

888 Table 3. Studies of hydrological niche segregation in time (temporal storage effect). Any differences among species are those found to be  
 889 statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
44	Steppe	Patagonia, Argentina	174	6 shrubs <i>Anarthrophyllum rigidum</i> , <i>Adesmia volckmanni</i> , <i>Berberis heterophylla</i> , <i>Mulinum spinosum</i> , <i>Schinus poligamus</i> and <i>Senecio filaginoides</i>	Species varied greatly in their uptake of an experimentally-applied pulse of rainfall applied at the beginning of a dry summer, from 0% use of rainfall to 29%.	(Kowaljow & Fernandez 2011)
45	Desert	Sonoran desert, Arizona, USA	250	10 species of winter annual	Differences among species in how germination and fecundity respond to year-to-year variability in rainfall creates a storage effect that facilitates coexistence. Species' specialization into temporal	(Angert <i>et al.</i> 2007, 2009)

					(hydrological) niches is the result of a trade-off between relative growth rate and water use efficiency.	
46	Desert	Chihuahua, Mexico	270	2 shrub species: <i>Atriplex acanthocarpa</i> and <i>A. canescens</i>	<i>A. canescens</i> was more resistant to drought than <i>A. acanthocarpa</i> , but this relationship was reversed for growth response to rainfall, suggesting that year-to-year variation in rainfall/ drought could aid coexistence.	(Verhulst <i>et al.</i> 2008)
47	Steppe	NW China	380	3 dominant species: perennial grass <i>Stipa bungeana</i> , a shrub <i>Artemisia ordosia</i> , and a herb <i>Cynanchum komarovii</i>	Using stable isotopes, differences among the three species were found in how they utilized water from summer rainfall events of different size.	(Cheng <i>et al.</i> 2006)
48	Prairie	Kansas, USA	580	3 dominant perennial grasses ( <i>Bouteloua curtipendula</i> , <i>Bouteloua hirsuta</i> , and <i>Schizachyrium scoparium</i> )	Long-term monitoring of the grasses was used to build models of the response of each population to climate. The models showed that a positive population growth rate at low density depended on climate variability in 2 of the 3 species.	(Adler <i>et al.</i> 2006)



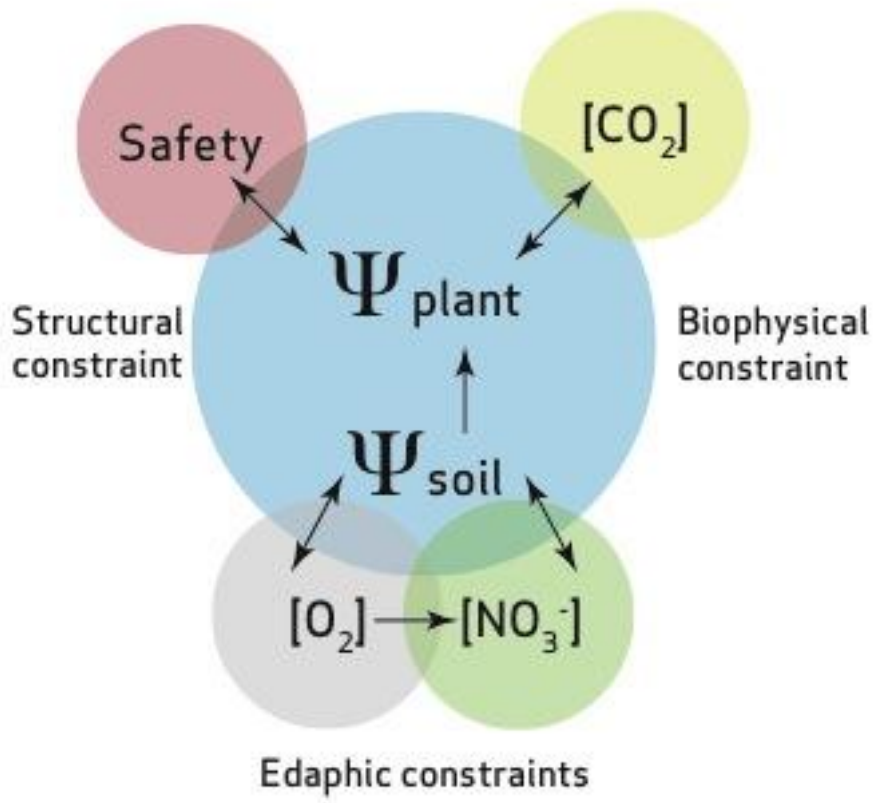
892 **Figure legend**

893 Fig.1. A Venn diagram of the relationship between plant ( $\psi_{\text{plant}}$ ) and soil ( $\psi_{\text{soil}}$ ) water  
894 potentials and the ability of plants to take up  $\text{CO}_2$ ,  $\text{O}_2$ ,  $\text{NO}_3^-$  and to resist failure of the  
895 vascular system (safety). Double-headed arrows indicate trade-offs and the single-  
896 headed arrows indicate the positive relationships between  $\psi_{\text{plant}}$  and  $\psi_{\text{soil}}$  and between  
897 aerobic conditions and the availability of nitrate in soils.

898

899 **Figure**

900 Fig.1.



901