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# **Droughts and the Ecological Future of Tropical Savanna Vegetation**

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1 **Abstract**

- 2 1. Climate change is expected to lead to more frequent, intense and longer droughts in the  
3 future, with major implications for ecosystem processes and human livelihoods. The  
4 impacts of such droughts are already evident, with vegetation dieback reported from a  
5 range of ecosystems, including savannas, in recent years.
- 6 2. Most of our insights into the mechanisms governing vegetation drought responses have  
7 come from forests and temperate grasslands, while responses of savannas have  
8 received less attention. Because the two lifeforms that dominate savannas- C<sub>3</sub> trees and  
9 C<sub>4</sub> grasses- respond differently to the same environmental controls, savanna responses  
10 to droughts can differ from those of forests and grasslands.
- 11 3. Drought-driven mortality of savanna vegetation is not readily predicted by just plant  
12 drought-tolerance traits alone, but is the net outcome of multiple factors including  
13 drought-avoidance strategies, landscape and neighborhood context, and impacts of past  
14 and current stressors including fire, herbivory and inter-lifeform competition.
- 15 4. Many savannas currently appear to have the capacity to recover from moderate to  
16 severe short-term droughts, although recovery times can be substantial. Factors  
17 facilitating recovery include the resprouting ability of vegetation, enhanced flowering  
18 and seeding, and post-drought amelioration of herbivory and fire. Future increases in  
19 drought severity, length and frequency can interrupt recovery trajectories and lead to  
20 compositional shifts, and thus pose substantial threats, particularly to arid and semi-arid  
21 savannas.
- 22 5. *Synthesis*: Our understanding of, and ability to predict, savanna drought responses is  
23 currently limited by availability of relevant data, and there is an urgent need for  
24 campaigns quantifying drought-survival traits across diverse savannas. Importantly,  
25 these campaigns must move beyond reliance on a limited set of plant functional traits to  
26 identifying suites of physiological, morphological, anatomical and structural traits or  
27 “syndromes” that encapsulate both avoidance and tolerance strategies. There is also a  
28 critical need for a global network of long-term savanna monitoring sites as these can  
29 provide key insights into factors influencing both resistance and resilience of different  
30 savannas to droughts. Such efforts, coupled with site-specific rainfall manipulation  
31 experiments that characterize plant trait–drought response relationships, and modelling  
32 efforts, will enable a more comprehensive understanding of savanna drought responses.

33 **Keywords:** avoidance, hydraulic safety margins, tolerance, resistance, resilience

34

35

36

37 **Introduction**

38 *"In environments in which there is a recurrence of natural hazards, populations may spend most of their*  
39 *time recovering from the hazards...."* Harper (1967)

40 This statement is particularly true of the Earth's tropical savannas. Tropical savannas are  
41 indeed a curious biome, neither grassland nor forest, but one in which two contrasting  
42 lifeforms – C<sub>3</sub> trees and C<sub>4</sub> grasses – compete for dominance in the face of limited resource  
43 availability and frequent disturbances such as fire and herbivory. In fact, savannas were long  
44 perceived as degraded ecosystems, derived from forests as a result of disturbances,  
45 anthropogenic or otherwise (Scholes & Walker 1993, Bond & Parr 2010, Parr et al. 2014,  
46 Veldman et al. 2015a, Ratnam et al. 2016). However, tropical savannas are ancient biomes,  
47 their origins dating back to the late Miocene and early Pliocene, ~4 - 8 Mya, and the near-  
48 synchronous expansion of C<sub>4</sub> grasses around the world (Beerling & Osborne 2006, Osborne  
49 2008, Edwards et al. 2010, Simon & Pennington 2012). This global rise to dominance of C<sub>4</sub>  
50 grasses occurred fairly rapidly in geological terms, within about a million years, and represents  
51 one of the most dramatic examples of biome assembly in the geological record (Beerling &  
52 Osborne 2006, Edwards et al. 2010).

53 Savannas and grasslands are among the most extensive vegetation types in tropical and sub-  
54 tropical regions (Solbrig, Medina & Silva 1996, Scholes & Archer 1997). However, over the last  
55 couple of centuries, they have been drastically altered by human activities (Ramankutty & Foley  
56 1999, Lambin, Geist & Lepers 2003, Miles et al. 2006, Murphy, Andersen & Parr 2016, Ratnam  
57 et al. 2016, Strassburg et al. 2017). As human populations grow and expand, the remaining  
58 savanna habitats are increasingly threatened by a range of anthropogenic activities including  
59 land-use transformation, tree plantations for carbon-sequestration initiatives and alterations of  
60 fire and herbivory regimes (Bond & Parr 2010, Parr et al. 2014, Veldman et al. 2015b, Bond  
61 2016, Murphy, Andersen & Parr 2016, Ratnam et al. 2016, Abreu et al. 2017, Strassburg et al.  
62 2017, Osborne 2018). Further, global changes in the form of altered precipitation and  
63 temperature regimes, elevated atmospheric [CO<sub>2</sub>] and atmospheric N and P deposition have  
64 emerged as major threats to the ecological integrity of these biomes (Parr et al. 2014, Bond &  
65 Midgley 2012, Midgley & Bond 2015), prompting Bond & Midgley (2012) to ask if the rise to  
66 dominance of this biome in the Late Miocene is likely to be matched by an equally dramatic  
67 decline in the Anthropocene.

68 Changes in savanna structure, composition and function as a result of ongoing and future  
69 climate change can have major implications for human wellbeing and ecosystem processes  
70 (Midgley & Bond 2015, Osborne et al. 2018). Here, I focus on the effects of altered rainfall  
71 regimes, specifically droughts, on savanna dynamics. My focus on drought is prompted by the  
72 recognition that: i) water availability is a key determinant of savanna structure and function

73 (Scholes & Archer 1997, Bond, Midgley & Woodward. 2003, Sankaran et al. 2005, Sankaran,  
74 Ratnam & Hanan 2008, Buccini & Hanan 2007, Good & Caylor 2011, Lehmann et al. 2014,  
75 D’Onofrio et al. 2018), ii) changes in precipitation regimes, coupled with warmer temperatures  
76 that increase evaporative demand, are projected to lead to more intense and frequent  
77 regional-scale droughts across large parts of the globe, including savanna regions (Dai 2013,  
78 IPCC 2014, Mitchell et al. 2014, Trenberth et al. 2014), iii) savannas are expected to be  
79 particularly responsive to precipitation changes given the tight coupling between rainfall and  
80 production in these systems (Sala et al. 2000, 2012, Knapp & Smith 2001, Xu et al. 2018), and iv)  
81 in contrast to forests, the role of droughts in regulating tropical savanna dynamics has received  
82 relatively less attention. Importantly, inferring savanna responses based on studies carried out  
83 in other ecosystems is not straightforward. Because the two dominant life forms that  
84 characterize savanna ecosystems – C<sub>4</sub> grasses and C<sub>3</sub> trees and shrubs – respond differently to  
85 the same environmental controls, and because many vegetation traits of tropical savanna trees  
86 and grasses differ consistently from those of forests and temperate grasslands (Craine et al.  
87 2005, Hoffmann et al. 2005, Ratnam et al. 2011, Charles-Dominique et al. 2015), savannas are  
88 likely to respond to climate change in ways that forests and grasslands may not (Lehmann et al.  
89 2014, Osborne et al. 2018).

90 Tropical savannas are characterized by highly seasonal rainfall, with pronounced dry seasons  
91 ranging anywhere from 3 to 8 months (Scholes & Walker 1993). The high irradiance and heat  
92 that characterize these habitats creates a high evaporative demand, with the result that most  
93 savannas are in water deficit for large parts of the year, including the wet season (Scholes &  
94 Walker 1993). In addition, inter-annual rainfall variability is also a defining feature of the  
95 savanna biome, typically increasing with decreasing mean annual rainfall (Knapp & Smith 2001,  
96 Fensham, Fairfax & Ward 2009, Sala et al. 2012). Thus, multiple consecutive years with below  
97 average rainfall are not uncommon in most savannas (Fensham, Fairfax & Ward 2009).  
98 Although savanna vegetation has evolved a diverse range of strategies to cope with such  
99 variability (O’Brien et al. 2017), extreme and/or protracted periods of rainfall deficit, especially  
100 when coupled with warmer temperatures, can nevertheless result in the widespread mortality  
101 of both savanna grasses (Walker et al. 1987, Swemmer et al. 2018, Staver, Wigley-Coetsee &  
102 Botha 2018) and trees (Fensham, Fairfax & Ward 2009, Fensham, Laffineur & Allen 2019).  
103 Here, I primarily focus on the effects of such extreme droughts on savanna vegetation.

104 For the purposes of this review, I use the term drought to broadly refer to periods where  
105 lowered rainfall during the growing season reduces plant water availability to levels significantly  
106 below average annual conditions (Greenwood et al. 2017, O’Brien et al. 2017). I don’t  
107 specifically consider how vegetation responses change with drought intensity *per se*, but  
108 acknowledge that the magnitude of observed responses will undoubtedly be more pronounced  
109 as droughts become more extreme and protracted (Ruppert et al. 2015, Greenwood et al. 2017,

110 Young et al. 2017). I draw on both observational studies that have recorded responses of  
111 savanna trees and grasses to droughts, as well as experimental studies that have manipulated  
112 plant water availability under controlled conditions. Although experiments allow for clearer  
113 attribution of causes (Smith 2011, Greenwood et al. 2017), manipulating water availability for  
114 adult savanna trees is challenging given their size and longevity (O'Brien et al. 2017).  
115 Consequently, experiments are typically limited to grasses and tree seedlings, and don't  
116 capture adult tree responses, which observational studies do.

117 I begin by considering the independent direct effects of droughts on the survival of savanna  
118 trees and grasses, and the traits that govern their ability to tolerate or alternately avoid  
119 droughts (tolerance vs. avoidance). I then look at how increasing water stress can influence  
120 tree-grass interactions, both directly by altering their competitive dynamics, as well as indirectly  
121 by mediating changes in the strength and intensity of top-down drivers such as fire and  
122 herbivory, with implications for the ability of the vegetation to withstand change (resistance) as  
123 well as recover following droughts (resilience; Smith 2011, Lloret et al. 2012, Vicente-Serrano et  
124 al. 2013, Hoover, Knapp & Smith 2014). Finally, I synthesize findings to provide a framework to  
125 assess drought effects in savannas, highlight data gaps and identify research priorities to enable  
126 us to better understand and predict savanna responses to future droughts.

127

## 128 **Direct effects of droughts on savanna tree mortality**

129 Increasing drought stress, particularly when coupled with warmer temperatures, can render  
130 trees more susceptible to mortality, with major implications for the land carbon sink (Phillips et  
131 al 2009, Schwalm et al, 2017). Warmer temperatures increase evaporative demand and  
132 thereby exacerbate drought stresses, leading to earlier and more widespread mortality in trees  
133 (Zeppel, Adams & Anderegg 2011). There is already evidence for episodes of enhanced tree  
134 mortality in response to drought across many parts of the globe, ranging from modest increases  
135 above background levels to regional scale die-offs, with a marked increase in the number of  
136 such documented events since the 2000s (McDowell et al. 2008, 2011, Allen 2009, Fensham,  
137 Fairfax & Ward 2009, Phillips et al. 2009, 2010, Breshears et al. 2009, Adams et al. 2010, Allen  
138 et al. 2010, Anderegg, Kane & Anderegg 2012, Anderegg et al. 2015, 2016, Greenwood et al.  
139 2017, amongst others).

140 The most well documented and dramatic examples of tree die-offs come from forested  
141 ecosystems, where as many as 300 million trees are estimated to have died in some drought  
142 events (Allen 2009; Allen et al., 2010; Anderegg, Kane & Anderegg 2012, Choat et al. 2018).  
143 However, there are also reports of significant drought related tree die-back in savannas  
144 (Scholes 1985, Viljoen 1995, Fensham 1998, Fensham & Holman 1999, MacGregor & O'Connor

145 2002, Rice et al. 2004, Fensham & Fairfax 2007, Fensham, Fairfax & Ward 2009, Fensham et al.  
146 2015, Twidwell et al. 2014, Wonkka et al. 2016, Swemmer et al. 2018, Fensham, Laffineur &  
147 Allen 2019). These cases come from a diverse array of savanna types across multiple  
148 continents, but a common theme emerging from these studies, consistent with work from  
149 other systems, is that the extent to which meteorological droughts translate to physiological  
150 droughts, i.e. water stress experienced by an individual leading to mortality, varies spatially  
151 within landscapes, amongst different species within sites, and across different life history stages  
152 within species.

153 Drought-induced tree mortality in savannas, and indeed other ecosystems, is typically spatially  
154 variable across the landscape in ways that are not just related to patchiness in rainfall, but also  
155 to topography, local edaphic features, patterns of tree density and composition, local  
156 disturbances and management history (Scholes 1985, Viljoen 1995, Fensham & Fairfax 2007,  
157 Fensham 1998, Fensham & Holman 1999, O'Connor 1998, MacGregor & O'Connor 2002, Rice et  
158 al. 2004, Twidwell et al. 2014, O'Brien et al. 2017, Fan et al. 2017, Swemmer et al. 2018).  
159 Topographic and edaphic features drive drainage and infiltration influencing both surface soil  
160 water availability and water table depth and in turn, rooting depths (Fan et al. 2017). Such  
161 variability across the landscape (e.g. between upslope and foot slope locations in savanna  
162 landscapes; Scholes & Walker 1993) can lead to differences in the extent of water-stress, and in  
163 turn mortality, experienced by different individuals during droughts (McDowell et al. 2008, Fan  
164 et al. 2017, Hartmann et al. 2018). Patchiness in mortality can also result from underlying  
165 differences in tree densities across the landscape, with higher density sites typically suffering  
166 greater mortality, potentially a result of more intense competition for limited water in these  
167 sites during drought (MacGregor & O'Connor 2002, Fensham & Fairfax 2007, Dwyer et al. 2010,  
168 Fensham et al. 2017, Young et al. 2017).

169 Tree species also differ inherently in their ability to withstand and recover from droughts  
170 (Viljoen 1995, O'Connor 1998, Rice et al. 2004, Fensham & Fairfax 2007, Breshears et al. 2009,  
171 Fensham et al. 2015, O'Brien et al. 2017, Greenwood et al. 2017). Tree mortality during  
172 droughts can arise from one or more non-exclusive mechanisms including hydraulic failure and  
173 loss of vascular transport capacity as a result of xylem cavitation, carbon starvation as a result  
174 of depletion of carbohydrate reserves, and increased susceptibility to herbivore and pathogen  
175 attacks (McDowell et al. 2008, Breshears et al. 2009, Anderegg, Berry & Field 2012, Anderegg et  
176 al. 2015, 2016, Choat et al. 2018). Hydraulic failure occurs when droughts are particularly  
177 severe, causing the xylem and rhizosphere to cavitate (become filled with air-pockets),  
178 impeding water flow and eventually resulting in desiccation and death (McDowell et al. 2008,  
179 Hartmann et al. 2018). When droughts are less severe but more protracted, stomatal closure  
180 by trees to prevent hydraulic failure can limit carbon fixation, resulting in carbon-starvation in

181 the long-term as trees are unable to meet their continued metabolic demand for carbohydrates  
182 (McDowell et al. 2008, Hartmann et al. 2018).

183 The xylem water potentials at which cavitation occurs (cavitation resistance; characterized as  
184 the pressure that induces 50% ( $\Psi_{50}$ ) or 88% ( $\Psi_{88}$ ) loss of xylem hydraulic conductivity) differs  
185 between species and is largely determined by xylem anatomical features including the  
186 diameter, length, connectivity and density of xylem conduits and the porosity of pit membranes  
187 (Choat et al. 2012, 2018, Anderegg et al. 2016). Tree species also differ in the extent to which  
188 they regulate their internal water status through the opening and closing of their stomata.  
189 Isohydric species, on the one hand, use stomatal regulation to maintain more or less constant  
190 midday plant water potentials and avoid cavitation. However, with stomata closed,  
191 photosynthesis is curtailed, and these species run the risk of carbon starvation during droughts  
192 (McDowell et al. 2008, Zeppel et al. 2011, Konings & Gentine 2017). Anisohydric species, on the  
193 other hand, allow plant water potentials to drop as soil water potentials drop, both diurnally  
194 and seasonally, and so potentially run a greater risk of hydraulic failure during droughts  
195 (McDowell et al. 2008, Zeppel et al. 2011, Konings & Gentine 2017, Konings, Williams & Gentine  
196 2017). The difference between the typical minimum xylem water potential experienced by  
197 trees and that which causes xylem dysfunction provides a measure of the 'hydraulic safety  
198 margin (HSM)' within which trees operate, and serves as a useful index of the physiological  
199 vulnerability of trees to drought induced mortality (Choat et al. 2012, 2018, Anderegg et al.  
200 2016).

201  
202 Recent studies attempting to link patterns of drought-induced mortality of forest trees to  
203 underlying plant traits suggest that species with low cavitation resistance, low hydraulic safety  
204 margins, low wood density and high specific leaf area typically suffer greater mortality during  
205 droughts (Phillips et al. 2010, Anderegg et al. 2016, Greenwood et al. 2017, O'Brien et al. 2017).  
206 However, compared to forests, there are only a few studies at present linking tree traits to  
207 drought related mortality in tropical savannas, largely limited to inferring relationships between  
208 rooting characteristics, species growth rates and storage allocation patterns on mortality.  
209 Results from these studies, although varied, are broadly consistent with those observed in  
210 other ecosystems and suggest that species with higher root densities, slower growth rates and  
211 greater allocation to storage typically experience lower mortality during droughts (Fensham &  
212 Fairfax 2007, Fensham et al. 2015, 2017). In addition, resprouting ability, a common feature of  
213 many savanna trees, has also been linked to higher survival during droughts, presumably a  
214 consequence of the greater allocation to roots and higher stores of non-structural  
215 carbohydrates in resprouting compared to non-resprouting species (Zeppel et al. 2015, but also  
216 see Pausas et al. 2016). It is also plausible that the multi-stemmed nature of resprouting species

217 allows them to better compartmentalize hydraulic failure in stems and branches during  
218 droughts, although explicit tests of this are currently lacking.

219 Low physiological drought tolerance capability, however, does not necessarily always mean  
220 higher mortality in the field during droughts. In addition to tolerance, trees also employ a  
221 range of different strategies to avoid or delay desiccation stress during droughts (avoidance)  
222 including leaf shedding, internal water storage, reduced leaf area and greater allocation to  
223 deeper roots that provide access to the water table, amongst others (Table 1; Eamus 1999,  
224 Choat et al. 2012, 2018). Such avoidance strategies can be quite effective, and there is  
225 evidence from savannas to suggest that ‘avoiders’, despite being more vulnerable to drought-  
226 induced cavitation, suffered lower mortality than ‘tolerators’ during droughts as a consequence  
227 of their deep-rootedness which allowed them to access deep soil water during droughts (Rice et  
228 al. 2004). Similarly, available data across a range of different ecosystem types including some  
229 Southern African savannas suggest no consistent differences in the levels of mortality  
230 experienced by deciduous species (avoiders) when compared to evergreen species (tolerators)  
231 during droughts (Anderegg et al. 2016, Greenwood et al. 2017).

232 Just as all species are not equally susceptible to drought, individuals within species also vary in  
233 the extent to which they suffer mortality during droughts. Across forested ecosystems,  
234 susceptibility is often skewed towards the smallest and/or largest size classes (McDowell et al.  
235 2008, Phillips et al. 2010, Bennett et al. 2015, O’Brien et al. 2017, Greenwood et al. 2017, Choat  
236 et al. 2018, Giardina et al. 2018). Seedlings and young individuals have poorly developed root  
237 and vascular systems and limited carbohydrate reserves, while larger individuals may be more  
238 vulnerable because of their greater overall water requirements, greater inherent vulnerability  
239 to hydraulic stress, or because of the greater cumulative effects of earlier exogenous stressors  
240 such as fires, herbivory, pathogens and competition in larger, older individuals (Rice et al. 2004,  
241 Zhang et al. 2009, Allen et al. 2010, Anderegg, Berry & Field 2012, Bennett et al. 2015).  
242 However, tree size is often a poor proxy for age in savannas. In savannas, frequent fires ‘top-  
243 kill’ small individuals, but mortality as a result of fire is often low (Higgins, Bond & Trollope  
244 2000, Bond 2008, Grady & Hoffmann 2012). Most individuals typically resprout from  
245 belowground reserves and can persist for decades in a ‘fire trap’ of repeated top-kill and  
246 resprouting (Higgins, Bond & Trollope 2000, Bond & Midgley 2001, Grady & Hoffmann 2012).  
247 Chronic browsing can similarly restrict the height of individual trees, maintaining them within a  
248 ‘browse trap’ for extended periods (Bond 2008, Sankaran, Augustine & Ratnam 2013, Staver &  
249 Bond 2014). It is therefore not surprising that size is not a consistent predictor of drought-  
250 induced mortality in savannas. Mortality appears unrelated to size for some species (Fensham  
251 1998, Fensham & Holman 1999, Rice et al. 2004, Fensham et al. 2015), is higher in the large-size  
252 classes for some (Rice et al. 2004, Twidwell et al. 2014, Fensham et al. 2015), while smaller  
253 stems suffer greater mortality in others (Fensham 1998, Fensham & Holman 1999, O’Connor

254 1998, Dwyer et al. 2010, Fensham et al. 2015). These divergent responses across species likely  
255 arise from variation in a) size-related changes in rooting strategies, carbon allocation patterns,  
256 carbohydrate reserves, hydraulic architecture, gas exchange and vulnerability to cavitation  
257 (Rice et al. 2004, Zhang et al. 2009, Bennett et al. 2015, Fensham et al. 2017), and b) the actual  
258 levels of water stress experienced during droughts by small versus large individuals.  
259 Differences in mortality can arise even in the absence of any size-related differences in drought  
260 tolerance *per se* if different sized individuals ‘experience’ droughts to different degrees. For  
261 example, larger individuals with access to the water table might not ‘experience’ droughts to  
262 the same extent as smaller, shallow rooted individuals, and vice versa (Chitra-Tarak et al 2017,  
263 Giardina et al. 2018).

264 Several physiological, morphological and anatomical traits have been identified that provide  
265 measurable indices of the vulnerability of tree species to drought-induced mortality (Table 1;  
266 also see Table 1 in O’Brien et al. (2017) and Table S1 in Choat et al. (2018)). Unfortunately,  
267 information on many of these traits, particularly hydraulic traits and safety margins, are  
268 currently lacking for most savanna species (O’Brien et al. 2017), with available data largely  
269 restricted to a few easily measurable traits such as wood density and specific leaf area. These  
270 traits, although reflective of hydraulic architecture and plant-water relations (Bucci et al. 2004,  
271 2008, Franco et al. 2005, Markesteijn et al. 2011, Anderegg et al. 2016), are not directly  
272 mechanistically related to drought tolerance *per se*, and thus only explain a limited amount of  
273 variability in observed drought mortality responses of species (Anderegg et al. 2016, O’Brien et  
274 al. 2017, Greenwood et al. 2017, Adams et al. 2017). Given that the majority of tree species  
275 globally are estimated to be operating with narrow hydraulic safety margins and potentially  
276 vulnerable to drought induced mortality (Choat et al. 2012), there is an urgent need for  
277 campaigns that quantify, in the first instance, hydraulic traits and safety margins of savanna  
278 trees.

279 Ultimately, the ability of trees to withstand and survive droughts is the net outcome of  
280 interactions between a number of physical, morphological and life-history traits that enable  
281 trees to tolerate desiccation stress, or alternately avoid or delay it to the extent possible  
282 (O’Brien et al. 2017, Choat et al. 2018). It is becoming increasingly apparent that many easily  
283 measurable traits such as wood density and specific leaf area are rarely successful at fully  
284 predicting drought mortality patterns in the field by themselves, and extrapolations based on  
285 single traits including hydraulic safety margins can often be misleading (Pausas et al. 2016,  
286 Adams et al. 2017). For example, high wood density species have been shown to survive better  
287 during droughts in some systems, but suffer greater mortality in others (Hoffmann et al. 2011,  
288 O’Brien et al. 2017). Similarly, mortality has been reported to be higher in shallow-rooted  
289 species in some instances, but greater in deeper-rooted species in others (Rice et al. 2004,  
290 Fensham et al. 2015, Chitra-Tarak et al. 2017). It is unlikely that plants have evolved to rely on a

291 single strategy to deal with drought (Anderegg, Berry & Field 2012) and there is thus a need for  
292 drought survival to be considered in the context of suites of multiple physiological,  
293 morphological, anatomical and structural traits or “syndromes” that encapsulate both  
294 avoidance and tolerance strategies. Such an expanded campaign will yield rich dividends and is  
295 less unwieldy than it may seem. Many hydraulic and physiological traits appear to covary in a  
296 coordinated fashion, suggesting that the complexity of hydraulic traits can be collapsed into  
297 one or a few axes of physiological drought tolerance strategies (Mencuccini et al. 2015, Bartlett  
298 et al. 2016, Choat et al. 2018). Combining these with axes that similarly capture anatomical,  
299 morphological (e.g. rooting characteristics) and avoidance traits can help identify alternate  
300 ‘syndromes’ that plants employ to deal with droughts, and provide insights into how these  
301 change across broad environmental gradients.

302

### 303 **Direct effects of droughts on savanna grasses**

304 Tropical savanna C<sub>4</sub> grasses typically use water more efficiently, and are more physiologically  
305 responsive to intermittent rainfall events, compared to C<sub>3</sub> trees and shrubs (Williams 1998,  
306 Ghannoum et al., 2003; Swemmer, Knapp & Smith 2006, Ripley et al. 2007, Ghannoum 2009,  
307 Volder, Tjoelker & Briske 2010). However, this greater water use efficiency does not necessarily  
308 translate into a greater tolerance for protracted water stress compared to C<sub>3</sub> plants (Ripley et  
309 al. 2007, Ripley, Frole & Gilbert 2010, Ghannoum 2009, Taylor et al. 2011, Volder, Tjoelker &  
310 Briske 2010). Although they are capable of assimilating large amounts of carbon when soil  
311 water is available, this capacity diminishes rapidly as soil water content decreases (Ripley et al.  
312 2007, Ghannoum 2009, Taylor et al. 2011, Volder, Tjoelker & Briske 2010, Connor & Hawkes  
313 2018). Thus, although C<sub>4</sub> grasses may be better able to deal with and recover from low to  
314 moderate drought, they may be equally or even more sensitive to periods of severe or  
315 protracted water stress when compared to C<sub>3</sub> plants (Walker et al. 1987, Ripley et al. 2007,  
316 Ghannoum 2009, Volder, Tjoelker & Briske 2010). Drought impacts on grass mortality in  
317 savannas can thus be substantial (Scholes 1985, Walker et al. 1987, Danckwerts & Stuart-Hill  
318 1988, Mott et al. 1992, O’Connor et al. 1994, 1995, Swemmer et al. 2018), with grasses often  
319 dying before woody plants (Walker et al. 1987).

320 Physiological drought tolerance of grasses, assessed based on leaf water potentials at which  
321 stomatal conductance falls below critical thresholds for ecological functioning, has been shown  
322 to vary nearly 10-fold between grass species, both across and within sites (Craine et al. 2013).  
323 Using data from 426 tropical and temperate grass species spanning a range of rainfall,  
324 biogeographic and phylogenetic affinities, Craine et al. (2013) showed that physiologically  
325 drought tolerant grasses, i.e. those with critical leaf water thresholds below the median value  
326 for all species assessed (-4.1 MPa), typically have higher photosynthetic rates and stomatal

327 conductance, and narrower xylem elements consistent with mechanisms of cavitation  
328 resistance. Leaf-width also appears to be correlated with drought tolerance with wide-leaved  
329 grasses tending to be drought-intolerant and narrow-leaved species displaying a wide range of  
330 abilities from tolerance to intolerance (Craine et al. 2013).

331 As in the case of trees, the ability to physiologically tolerate droughts is not always reflective of  
332 grass mortality patterns in the field, which is also contingent on other factors including  
333 allocation patterns, life history attributes and drought avoidance strategies (Table 1). Species  
334 with deep roots and those that allocate more to roots and less in reproductive structures have  
335 been shown to fare better under conditions of repeated water stress (Swemmer, Knapp &  
336 Smith 2006, Nippert & Holdo 2015). Maximum rooting depth is generally considered a good  
337 indicator of the ability of species to withstand protracted dry periods, but factors such as root  
338 morphology, root biomass allocation with depth, functional plasticity in water uptake in  
339 relation to availability, variation in water transport capabilities and symbiotic associations with  
340 arbuscular mycorrhizal fungi (AMF) are also important (Nippert & Holdo 2015, Petipas et al.  
341 2017). Grass species also show a range of drought avoidance strategies including leaf folding  
342 and rolling, rapid leaf shedding and large amounts of cuticular wax that can help delay the  
343 onset of physiological droughts (Bolger et al. 2005).

344 Drought tolerance also potentially differs between different C<sub>4</sub> grass photosynthetic subtypes,  
345 the distributions of which are strongly influenced by rainfall (Ripley et al. 2007, Ripley, Frole &  
346 Gilbert 2010, Ghannoum 2009). C<sub>4</sub> grasses are grouped into 3 photosynthetic subtypes based  
347 on the major C<sub>4</sub> acid decarboxylation enzyme in their bundle sheaths: NAD-ME (NAD malic  
348 enzyme), NADP-ME (NADP malic enzyme) and PCK (phosphoenolpyruvate carboxykinase;  
349 Ghannoum 2009). NAD-ME grasses tend to increase in abundance, while NADP-ME grasses  
350 decrease, across a gradient of decreasing rainfall (from 900 to 50 mm mean annual  
351 precipitation) while the distribution of PCK species does not appear to be strongly correlated  
352 with rainfall (Ghannoum 2009 and references therein). Data, albeit from a very limited number  
353 of species, suggests that NAD-ME species possess traits better suited to arid conditions and  
354 tend to have higher whole-plant water use efficiency under water stress than NADP-ME species  
355 (Ghannoum, Von Caemmerer & Conroy 2002, Carmo-Silva et al. 2009, Taylor et al. 2011).

356 At present, there are only a few studies that have quantified drought tolerance traits of grasses,  
357 and data are currently available only for a restricted number of savanna species. There is a  
358 clear need for more rigorous efforts to characterize drought tolerance and avoidance traits for  
359 a greater number of savanna grasses across a broader range of climatic conditions. As in the  
360 case of trees, such efforts should focus on identifying drought survival syndromes that  
361 encapsulate both tolerance and avoidance traits of species.

362

363 **Droughts, tree-grass interactions and the feedback effects of fire and herbivory**

364 *“It may be argued, therefore, that the essential qualities which determine the ecology of a*  
365 *species may only be detected by studying the reaction of its individuals to their neighbours and*  
366 *that the behaviour of individuals of the species in isolation may be largely irrelevant to*  
367 *understanding their behaviour in the community.” Harper 1964*

368 Savannas are complex systems whose structure is ultimately determined by a suite of factors  
369 including inter- and intra-lifeform competition between trees and grasses, climate, soils, fire,  
370 browsing and grazing (Sankaran & Anderson 2009). Thus, the effects of droughts on savanna  
371 structure and function cannot be fully understood by studying responses of the major  
372 functional groups, C<sub>3</sub> trees and C<sub>4</sub> grasses, in isolation as net effects can be altered depending  
373 on how droughts impact fire and herbivory regimes, as well as the nature and intensity of tree-  
374 grass competition.

375 Grazing, browsing and fire are integral components of savannas that play key roles in regulating  
376 the growth and survival of both trees and grasses in savannas (Archibald et al. 2005, Staver et  
377 al. 2009, Staver & Bond 2014, Staver, Botha & Hedin 2017). Droughts can alter the extent and  
378 intensity with which these drivers act to influence mortality and growth of vegetation, with  
379 these effects varying both spatially and temporally over the course of the drought. Intense  
380 grazing can suppress grass biomass and productivity during drought years, increasing grass  
381 mortality and reducing grass basal area (Walker et al. 1987, Augustine & McNaughton 2006,  
382 Swemmer et al. 2018), with such effects being particularly pronounced closer to permanent  
383 sources of surface water which the herbivores rely on (Walker et al. 1987). When grazers move  
384 out of droughted areas, they can also extend the ecological impacts of droughts into non-  
385 droughted regions which subsequently suffer higher levels of defoliation and reductions in  
386 grass biomass (Staver, Wigley-Coetsee & Botha 2018). Browsers can similarly significantly  
387 suppress tree growth during droughts, particularly of individuals in smaller-size classes  
388 (Augustine & McNaughton 2004). Intense browsing during droughts, when coupled with  
389 lowered plant photosynthetic rates, can also reduce and prevent the replenishment of starch  
390 reserves in woody plants (Schutz, Bond & Cramer 2011, Pausas & Keeley 2014, Zeppel et al.  
391 2015), with potential longer-term consequences for survival of individuals. Other forms of  
392 damage such as bark stripping of trees by elephants have also been shown to increase during  
393 droughts, which can further compound tree mortality (Walker et al. 1987). Because widespread  
394 herbivore mortality typically occurs only in the later stages of the drought (Walker et al. 1987),  
395 browser and grazer effects on mortality of vegetation are likely to be particularly pronounced  
396 during the early stages, with effects weakening in the later stages of drought following  
397 herbivore die-off.

398 Like herbivory, the importance of fire as an agent of savanna woody plant mortality can also  
399 change over the course of the drought. Because fuel loads can carry over from year to year, the  
400 extent and intensity of fires in any given year are not just contingent on current-year rainfall  
401 but also rainfall in the preceding wet-season or two (Balfour & Howison 2002, Archibald et al.  
402 2009, Sala et al. 2012). Fires that occur early in the drought, particularly when droughts are  
403 preceded by periods of above-average rainfall, are therefore likely to be more widespread and  
404 intense than those that occur later in the drought. Such intense wildfires as a result of hotter  
405 and drier conditions during droughts can significantly enhance tree mortality (Breshears et al.  
406 2016, Twidwell et al. 2016), particularly in wet sites with low grazing pressure where grass  
407 biomass is high. In contrast, during the later stages of drought where fuel loads are low, either  
408 because of the cumulative negative effects of droughts on grass productivity, or in sites  
409 supporting significant grazer populations, fire effects can be minimal because of reductions in  
410 the frequency and intensity of fires. There is evidence to indicate that both size of individual  
411 burns and total area burnt tend to be lower, and fire return intervals longer, during dry phases  
412 when compared to wet phases (Balfour & Howison 2002).

413 The net effects of droughts and disturbances such as fire and herbivory on savanna structure  
414 and function is ultimately contingent on the extent to which grass biomass and productivity are  
415 suppressed relative to woody plants, which determines both the intensity of tree-grass  
416 competition for limited soil moisture as well as the nature of feedback effects arising through  
417 changes in fire regimes. Grasses are indeed formidable competitors for soil moisture, and there  
418 is ample evidence to suggest that grasses can suppress growth of adult and especially juvenile  
419 trees in savannas (Scholes & Archer 1997, Sankaran, Ratnam & Hanan 2004, Bond 2008, Riginos  
420 2009, February et al. 2013, Ward, Weigand & Getzin 2013, Cambell & Holdo 2017, Morisson et  
421 al. 2018). When droughts do not significantly impact grass productivity and biomass, mortality  
422 rates of tree seedlings, often vulnerable to grass competition, may be exacerbated. In contrast,  
423 when grass productivity and biomass are significantly depressed, droughts can benefit the  
424 survival and growth of woody plants both directly by reducing grass competition for limited soil  
425 moisture, as well as indirectly by reducing the frequency and intensity of grass-fueled fires  
426 (Scholes & Archer 1997, Higgins, Bond & Trollope 2000, February et al. 2013, Morrison et al.  
427 2019). The extent to which tree seedlings are suppressed by grasses also appears to differ  
428 between species, with tree species with higher photosynthetic rates suffering greater  
429 reductions in biomass in the presence of grasses (Campbell & Holdo 2017). Droughts can  
430 therefore differentially favor survival and establishment of fast-growing savanna trees,  
431 potentially leading to longer-term compositional shifts in adult tree communities. Thus,  
432 although savanna tree cover and basal area typically increase with rainfall over broad gradients  
433 (Sankaran et al. 2005, Lehmann et al. 2014), reduced rainfall during droughts can paradoxically  
434 facilitate tree establishment, contingent on drought intensity and its relative effects on grasses  
435 (Scholes & Archer 1997, February et al. 2013).

436 Site history also plays an important role in regulating the extent to which these different  
437 stressors impact growth and mortality of savanna vegetation during droughts. A long history of  
438 heavy grazing can 'precondition' sites for enhanced tree dieback during droughts (MacGreggor  
439 & O'Connor 2002). Loss of perennial herbaceous cover and increased cover of bare patches as  
440 a consequence of overgrazing can accelerate erosion leading to increased run-off and  
441 decreased infiltration in patches, enhancing soil water stresses and tree mortality during  
442 droughts compared to light or moderately grazed sites that retain herbaceous cover  
443 (MacGreggor & O'Connor 2002). Similarly, over-browsing can predispose sites to higher  
444 mortality during droughts by reducing starch reserves of trees (Schutz, Bond & Cramer 2011,  
445 Zeppel et al. 2015). In contrast, drought-related tree mortality could potentially be lower in  
446 sites with a history of frequent burning. Frequent fires reduce tree densities which can result in  
447 lowered competition for limiting water, and in turn lowered mortality, during droughts when  
448 compared to unburned or less frequently burned sites that support higher tree densities.

449

#### 450 **Long-term effects of droughts on savannas: stabilizing and destabilizing processes**

451 There is growing concern that increases in the frequency and intensity of extreme events can  
452 potentially trigger abrupt shifts in vegetation in the future (Allen & Breshears 1998, Smith 2011,  
453 Lloret et al. 2012, Breshears et al. 2016). At present, instances of abrupt vegetation shifts  
454 following extreme droughts are rare, and most studies thus far seem to suggest that savannas  
455 and many grassland communities have the capacity to recover from periodic droughts,  
456 although recovery times can be substantial in some cases (Walker et al. 1987, Fuhlendorf &  
457 Smeins 1997, Fuhlendorf, Briske & Smeins 2001, Lloret et al. 2012, Hoover, Knapp & Smith  
458 2014, Breshears et al. 2016, Swemmer et al. 2018, Fensham, Laffineur & Allen 2019). Several  
459 stabilizing processes underlie this inertia to abrupt vegetation change, including those that  
460 serve to attenuate mortality of trees and grasses during droughts (resistance), and factors that  
461 contribute to foster recovery of productivity and species composition following droughts  
462 (resilience; Lloret et al. 2012, Table 2).

463

464 Factors that attenuate mortality of vegetation during droughts include site characteristics,  
465 lowered competition, facilitation, attenuation of stressors and functional trait diversity in  
466 communities (Lloret et al. 2012). As discussed, spatial variability in topographic and edaphic  
467 factors can generate a heterogeneous abiotic template that can result in a mosaic of drought  
468 severity across the landscape, enabling localized persistence of tree and grass populations  
469 during droughts and providing a source pool for subsequent recolonization (O'Connor 1995,  
470 Lloret et al. 2012). In drier sites, grasses can persist under tree canopies which provide  
471 ameliorated conditions and protection from grazing during droughts, even if populations are

472 substantially reduced in tree interspaces (O'Connor 1995). Similarly, heterogeneity in tree  
473 densities across the landscape can result in lowered mortality in low density sites as a result of  
474 less intense competition for water. There is evidence to suggest that reductions in tree  
475 densities following initial mortality can increase available water for surviving individuals,  
476 lowering competition and subsequent mortality of trees during later stages of the drought  
477 (Lloret et al. 2012, Wonkka et al. 2016). Reductions in grazing and browsing intensity as a result  
478 of herbivore die-off or movement during droughts, as well as reductions in fire frequencies and  
479 intensities as a result of lowered grass-fuel loads can similarly lower mortality rates in the later  
480 stages of droughts. In addition, standing dead grass canopies have also been shown to enhance  
481 survival and establishment of juvenile trees during droughts by reducing irradiation and  
482 increasing soil moisture, thereby ameliorating abiotic conditions for seedlings (de Dios et al.  
483 2014).

484  
485 Plant species richness and functional diversity are also likely to be important determinants of  
486 the resistance and resilience of savanna ecosystem processes to droughts. It is well established  
487 that the productivity of grasslands with higher plant species richness and functional diversity  
488 declines less, and recovers sooner, following droughts (Tilman, Reich & Knops 2006, Bloor &  
489 Bardgett 2012, Isbell et al. 2015). Similarly, the functional diversity of woody plant hydraulic  
490 traits (hydraulic safety margins and cavitation resistance) has been shown to be an important  
491 determinant of the extent to which land-atmosphere fluxes of water, carbon and energy in  
492 forests are altered during droughts, with more functionally diverse communities buffered to a  
493 greater extent during periods of water stress (Anderegg et al. 2018). However, unlike forests,  
494 most savannas tend to be species poor (with the exception of the mesic savannas of S. America  
495 and the Miombo woodlands of southern Africa), and dominated by one of a few families of  
496 woody plants (Bond & Parr 2010, Sankaran & Ratnam 2013, Lehmann et al. 2014, Murphy et al.  
497 2016). Such low phylogenetic diversity can be a potential cause for concern, particularly if  
498 drought-tolerance traits tend to be phylogenetically conserved. At present it is unclear how  
499 diversity of drought-tolerance traits is related to phylogenetic diversity in savanna species, but  
500 it is possible that drought traits, like those related to fire-tolerance, are phylogenetically over-  
501 dispersed in savanna species (Simon & Pennington 2012, Cianciaruso et al. 2012). Although  
502 detailed information from savanna ecosystems are lacking, available data from across different  
503 vegetation types suggest that for both trees and grasses, physiological drought tolerance ability  
504 (cavitation resistance) as well as variation in vulnerability to cavitation across species (i.e. a  
505 measure of hydraulic trait diversity) increases with decreasing rainfall, with the greatest range  
506 of variability observed between ~250 and 1000 mm MAP, i.e. the rainfall regime that  
507 characterize savannas (Choat et al. 2012, Craine et al. 2013). These results are indicative of the  
508 potential for high functional trait diversity in savannas, and suggest that most savannas are

509 likely to contain some species that are adapted to, and can tolerate and recover from, droughts  
510 (Choat et al. 2012, Craine et al. 2013).

511 Indeed, many savannas appear surprisingly resilient to moderate and even severe short-term  
512 droughts, capable of regaining productivity of both the herbaceous and woody strata within a  
513 year or two (Walker et al. 1987, Ruppert et al. 2015, Zeppel et al. 2015, Swemmer et al. 2018,  
514 Fensham, Laffineur & Allen 2019). Although droughts drastically reduce aboveground  
515 production of the grass layer, belowground biomass and production tend to be less affected,  
516 allowing for post-drought recovery (Koerner & Collins 2014, Ruppert et al. 2015). Similarly,  
517 resprouting ability, a common feature of many savanna trees, allows trees to re-establish  
518 quickly following disturbances compared to non-resprouters that need to establish from seed  
519 (Zeppel et al. 2015). Many resprouters have been shown to recoup much of their lost leaf area  
520 within a year following droughts (Zeppel et al. 2015), although some delay resprouting until  
521 after the first summer rains following drought (Viljoen 1995). Many savanna species also flower  
522 profusely following droughts (Viljoen 1995). Resultant increases in seed availability, when  
523 coupled with reduced competition following adult tree die-off and reduction in herbaceous  
524 cover, can compensate for adult tree mortality by enhancing post-drought recruitment (Lloret  
525 et al. 2012). Such enhanced post-drought recruitment can even occur several years following  
526 the drought, as has been reported for Sahelian woodlands (Hiernaux et al. 2009, Lloret et al.  
527 2012).

528 Changes in herbivory and fire regimes can also serve to facilitate post-drought vegetation  
529 recovery in savannas. Lowered herbivore populations as a result of movement, widespread  
530 mortality and reduced and delayed calving success during droughts (Walker et al. 1987, Ellis &  
531 Swift 1988, Augustine 2010, Ogutu et al. 2010) can reduce post-drought pressure on  
532 vegetation, allowing vegetation to recover before herbivore populations build up again.  
533 Similarly, drought-induced reductions in grass biomass, and thus fuel loads, can result in fewer,  
534 smaller and less intense fires immediately following droughts (Balfour & Howison 2002,  
535 Archibald et al. 2009), benefitting woody communities in both the short and longer term by  
536 providing a window of opportunity for savanna tree saplings to grow and establish by escaping  
537 the 'fire trap'.

538 However, despite the existence of such stabilizing mechanisms, frequent, longer and more  
539 intense droughts can nevertheless serve to destabilize savannas and lead to structural and  
540 compositional shifts in the future. Severe and protracted droughts can significantly depress  
541 productivity and elicit widespread mortality of vegetation in savannas (Walker et al. 1987,  
542 Fensham, Fairfax & Ward 2009, Ruppert et al. 2015, Swemmer et al. 2018), and can also drive  
543 compositional shifts in communities (Cipriotti et al. 2008, Evans et al. 2011). Even if ecosystem  
544 productivity is regained quickly following return to normal conditions (Walker et al. 1997,

545 Hoover, Knapp & Smith 2014), compositional shifts in tree and grass communities can have  
546 longer term impacts on savanna function. Severe droughts coupled with intense grazing can  
547 cause transitions from communities dominated by palatable, perennial grasses to systems  
548 composed of unpalatable, annual grasses and forbs (Scholes 1985, O'Connor 1994, 1995, 1998,  
549 Fuhlendorf & Smeins 1997, Fuhlendorf et al. 2001, Jin et al. 2018). Such changes in understory  
550 composition can be particularly hard to reverse, with recovery times ranging from a few years  
551 to over a decade or more, and potentially requiring the provisioning of seeds (Walker et al.  
552 1987, Fuhlendorf & Smeins 1997, O'Connor 1998). Because annual-dominated communities are  
553 less resistant to droughts than perennial-dominated ones, i.e. suffer greater reductions in  
554 productivity for the same drought intensity, such compositional shifts can also impair the ability  
555 of savannas to deal with future droughts (Ruppert et al. 2015).

556 Of greater concern possibly is that protracted droughts have been shown to lead to  
557 desertification, i.e. increases in the cover of bare ground relative to vegetated patches (Walker  
558 et al. 1987, Vicente-Serrano et al. 2012, Wonkka et al. 2016). For example, during a severe 4-  
559 year drought in a semi-arid savanna in west Central Texas, USA, tree mortality did not change  
560 after the initial period of death (2 years), but continued drought led to the loss of herbaceous  
561 vegetation and increases in the extent of bare ground (Wonkka et al. 2016). There is  
562 substantial evidence, both empirical and theoretical, to suggest that increased cover of bare  
563 ground can cause arid and semi-arid systems to switch to an alternate stable state  
564 characterized by low water infiltration and high run-off, where original plant communities  
565 cannot re-establish without human intervention (Rietkerk & van de Koppel 1997, van de  
566 Koppel, Rietkerk & Weissing 1997, Rietkerk et al. 2004).

567 Projected increases in the frequency of droughts potentially pose the biggest threat for  
568 savannas, with the ability to impact both the resistance and resilience of these ecosystems to  
569 future droughts. Cumulative physiological damage and cavitation fatigue, i.e. increased  
570 vulnerability to cavitation as a result of previous damage, can render individuals more  
571 susceptible to mortality during future droughts (Anderegg, Berry & Field 2012, Hartmann et al.  
572 2018). Recovery can also be slowed if frequent droughts diminish the capacity of individuals to  
573 replenish stored reserves, which can impact vegetation recovery through resprouting, or when  
574 it reduces seed production, impacting recovery through recolonization (Ruppert et al. 2015,  
575 Hartmann et al. 2018). Recurrent droughts can also increase the likelihood of directional shifts  
576 in understory and woody species composition when droughts recur before vegetation has  
577 recovered, particularly where dominant species are disproportionately affected by droughts.  
578 During successive droughts in the 1990's and 2000's, dominant Eucalypts in semi-arid  
579 Australian savannas suffered greater mortality than sub-dominant species (Fensham & Holman  
580 1999, Fensham et al. 2015). Importantly, tree mortality patterns did not change between  
581 successive droughts and seedling to adult ratios of the dominants following droughts was low,

582 suggesting that the cumulative effects of recurrent droughts could drive an eventual shift in  
583 adult tree community composition in this system (Fensham et al. 2015).

584

### 585 **A hierarchy of drivers**

586 The extent to which meteorological droughts translate into physiological droughts to influence  
587 the growth and survival of individual trees and grasses in savannas is thus determined by a  
588 range of factors that operate at different spatial and temporal scales, and levels of organization  
589 (Figure 1). At the broadest level, drought effects on the survival and growth of vegetation are a  
590 function of the severity and length of drought relative to what has been historically experienced  
591 by the community. i.e. historical baseline (Smith 2011). It is well recognized that all extreme  
592 events including droughts do not necessarily elicit extreme ecological responses (Smith 2011).  
593 The magnitude of the ecological responses elicited in any site depends on both the severity and  
594 duration of drought relative to the historical baseline, as well as vegetation and edaphic  
595 properties. Where meteorological droughts translate to physiological droughts, the extent to  
596 which any individual 'experiences' the drought then depends on the landscape context within  
597 which it exists (e.g. topographic position) as well as its neighborhood context (e.g. tree  
598 densities) and size. For individuals that do experience significant physiological droughts, the  
599 ability to cope with drought is then determined by their drought tolerance and avoidance  
600 strategies. However, additional risk factors can further predispose individuals to suffer greater  
601 reductions in growth and increased mortality during droughts, including past stressors (e.g.  
602 previous history of drought exposure, past damage by herbivores and fire) as well as those that  
603 operate during the drought (increased inter-life form competition, herbivory and fire).

604 The extent to which such individual-level effects then scale up to influence biomass,  
605 productivity and other processes at the ecosystem level depends on how different species and  
606 size-classes are differentially impacted by the drought. Community-wide reductions in biomass  
607 and productivity are likely to be more pronounced when the dominant species and large size  
608 classes of individuals are more negatively impacted. Greater species and functional trait  
609 richness can buffer these impacts to some extent by increasing the probability of species being  
610 present in the community that can cope with droughts. As droughts become more severe  
611 and/or protracted, loss of productivity becomes more pronounced as large-scale grass and tree  
612 dieback occurs, potentially leading to desertification in arid and semi-arid regions.

613 Post-drought recovery of biomass, productivity and species composition is similarly a function  
614 of multiple factors that govern subsequent colonization, establishment (or re-establishment)  
615 and growth of vegetation (Fig 1, Table 2,), with longer recovery times following droughts that  
616 are more protracted and severe. The herbaceous layer can generally be expected to recover

617 biomass quicker than the woody layer given their higher growth rates. The rate of recovery of  
618 species composition on the other hand depends on the extent to which species are  
619 differentially affected by droughts, with recovery times longer in systems where the dominant  
620 species are disproportionately impacted and are poor colonizers. However, as droughts  
621 become more frequent, or where desertification occurs, it can lead to compositional shifts in  
622 savanna understory and woody communities. Such shifts can then feedback to influence the  
623 ability of savannas to resist future droughts by altering both the distribution of drought  
624 tolerance and avoidance traits as well as species and functional trait diversity in the community.

625 The relative roles of these different factors, and in turn the resistance and resilience of savanna  
626 communities, can change across rainfall gradients. Mesic savannas experience less inter-annual  
627 variability and have historically been exposed to fewer extreme droughts, and so may be  
628 expected to be less resistant to longer and more intense future droughts (Greenwood et al.  
629 2017). However, post-drought recovery of productivity in these systems may be faster (i.e.  
630 resilience higher) given the higher growth rates of vegetation. In contrast, arid and semi-arid  
631 savannas display greater inter-annual rainfall variability and experience more extreme droughts  
632 compared to mesic systems, but also characterized by flora that have evolved to deal with  
633 protracted periods of water stress and may thus be expected to be more resistant to droughts  
634 (McDowell et al. 2008, Knapp & Smith 2001, Fensham, Fairfax & Ward 2009, Vicente-Serrano et  
635 al. 2013, O'Brien et al. 2017). When damage occurs though, recovery of productivity typically  
636 tends to be slower in arid savannas (Schwalm et al. 2012, Vicente-Serrano et al. 2013). The  
637 likelihood of drought-induced desertification is also greater in arid and semi-arid sites (IPBES  
638 2018), particularly those with high abundance of livestock, which can further undermine  
639 recovery following severe droughts. In many arid and semi-arid savannas, native herbivore  
640 assemblages have been replaced by domestic livestock that are maintained at artificially high  
641 densities, and also buffered against mortality during droughts, as a result of supplemental  
642 provisioning of water and forage by humans, and predator and disease control (Hempson,  
643 Archibald & Bond 2015, 2017). The 'sedentarization' of livestock has also resulted in grazing  
644 and browsing regimes being more 'chronic' in these systems, with significant negative  
645 consequences for the ability of vegetation to both withstand droughts, as well as recover from  
646 them. These arid and semi-arid rangelands are potentially at the greatest risk of drought-driven  
647 shifts in vegetation structure and composition in the future.

648

## 649 **The way ahead**

650 Tropical savannas are highly variable in structure and composition across their distributional  
651 range, spanning the gradient from nearly open grasslands to closed woodlands, and differing in  
652 the characteristics of the dominant trees (deciduous versus evergreen, broad-leaved vs. fine-

653 leaved trees) and herbaceous vegetation (tall vs short grasses, annual vs. perennial). This  
654 variability arises from underlying differences in resource availability (rainfall and soil nutrients),  
655 strength of top-down forces (fire and herbivory) and evolutionary history (Scholes & Walker  
656 1993, Scholes & Archer 1997, Sankaran, Ratnam & Hanan 2004, Lehmann et al. 2011, 2014),  
657 and can pose challenges when generalizing drought effects across savannas. Understanding  
658 how these diverse savannas differ in their resistance and resilience to droughts represents a  
659 major task ahead for savanna ecologists; one that requires an integrative approach that  
660 combines trait data quantification with observation, experiments and modelling.

661 *Expanded Trait Campaigns:*

662 There is an urgent need to move beyond reliance on one or a few easily measurable traits to  
663 considering drought-survival as the collective outcome of different combinations of tolerance  
664 and avoidance traits, i.e. syndromes. Initial efforts should aim to characterize these syndromes,  
665 and identify representative tolerance and avoidance traits that encapsulate these strategies,  
666 which can then serve as the basis for extended trait data collection campaigns in savannas. In  
667 particular, traits regulating responses of understory species to droughts have received relatively  
668 less attention thus far compared to the woody component, but are a prerequisite to predicting  
669 savanna responses to droughts.

670 *Long-term Savanna Monitoring Plots:*

671 *“Measures of population turnover can only be obtained by the detailed observation of*  
672 *individuals—they are totally obscured by vegetational study and revealed by population studies*  
673 *only if plants are marked for repeated observations”*. Harper 1967

674 As we go forward, a network of long-term savanna monitoring plots where individuals are  
675 tagged and monitored over time will be invaluable. Such efforts can provide us with insights  
676 into vegetation dynamics and demography that other kinds of studies cannot (Harper 1967). In  
677 fact, many of our insights into drought responses of vegetation have come fortuitously from  
678 opportunistic studies in forested ecosystems where droughts have occurred during the course  
679 of ongoing long-term observational and experimental studies (Breshears et al. 2009, Phillips et  
680 al. 2009, Smith 2011, Fensham et al. 2017). However, in contrast to forests, a network of long-  
681 term monitoring plots that spans the climatic, edaphic and biotic gradients that characterize  
682 savanna ecosystems is currently lacking (Staver 2018). Such long-term efforts are particularly  
683 insightful because: i) detailed pre-drought data on vegetation are available, which is useful for  
684 understanding the role of previous stressors and past individual performance on drought  
685 survival, ii) concurrent data on physiological parameters and water stress metrics are often  
686 available, or can be gathered, which can provide us with a more nuanced understanding of  
687 drought responses of vegetation, iii) sustained monitoring can provide us with key information  
688 on post-drought recovery and factors affecting resilience of vegetation, for which data are

689 currently limited, as well as help understand how repeated droughts impact the resistance and  
690 resilience of savanna vegetation, and iv) data are available even when the ecological responses  
691 to climatic droughts are not extreme. This last point is critical because in order to effectively  
692 predict savanna responses, we need to understand plant traits and site characteristics that  
693 confer resistance as well as render vegetation susceptible to droughts (Smith 2011, Breshears  
694 et al. 2008, Fensham, Fairfax & Ward 2009, Mitchell et al. 2014).

695 *Targeted Field Experiments:*

696 There is a large body of experimental work that has provided us with a wealth of understanding  
697 on the responses of temperate grasslands to changes in precipitation patterns, including  
698 extreme drought (Fay et al. 2003, Knapp et al. 2008, Heisler-White, Knapp & Kelly 2008, Heisler-  
699 White et al. 2009, Thomey et al. 2011, Cherwin & Knapp 2012 and others). However, rainfall  
700 manipulation studies in savannas are currently very limited (but see February et al. 2013,  
701 Manea & Leishman 2015). Experimental manipulations in the field can be logistically  
702 challenging, particularly in the presence of fire and mega-herbivores such as elephants, but are  
703 needed to better understand how changes in the intensity, duration and timing of droughts  
704 influence vegetation responses across diverse savanna types. Experimental manipulations that  
705 impose droughts on large trees will also be needed (Choat et al. 2018) for a more  
706 comprehensive understanding of drought effects in savannas.

707 Importantly, all these efforts, from trait data collection to monitoring and experiments, must  
708 span the rainfall, soil fertility, fire and herbivory gradients, as well as the diversity of tree and  
709 grass functional types that characterize the diverse savannas on different continents. Savannas  
710 on different continents differ in the extent to which they are dominated by different functional  
711 groups (evergreen vs deciduous, fine-leaved N-fixers vs broadleaved non-fixers). African and  
712 Asian savannas are dominated by deciduous trees, S. American savannas are largely evergreen  
713 while Australian savannas are characterized by a mix of evergreen, deciduous, semi-deciduous  
714 and brevi-deciduous species (Eamus 1999, Bowman & Prior 2005). Few studies have explicitly  
715 considered how drought tolerance and the mechanisms driving mortality differ between  
716 deciduous and evergreen savanna trees, but it could be argued that evergreen species are  
717 under greater risk of mortality through cavitation during severe droughts, while deciduous  
718 species that shed leaves are under greater risk of carbon starvation as droughts get longer.  
719 Similarly, dominance by N-fixing species also differs between continents; N-fixers are more  
720 abundant in African and Asian savannas compared to S. America and Australia, and tend to  
721 dominate in arid, eutrophic sites while non-fixers dominate in mesic, dystrophic sites (Scholes &  
722 Walker 1993, Pelligrini et al. 2016). Few studies have evaluated differences in drought tolerance  
723 abilities of N-fixing and non N-fixing savanna species, but evidence from other systems suggests  
724 that the high tissue N and water-use efficiencies of N-fixing species might help them survive  
725 and compete better during prolonged droughts (Wurzburger & Miniat 2014, Liao et al. 2017).

726 *Process-based models*

727 Finally, data from experiments, observational studies and trait campaigns need to feed into  
728 process-based vegetation models to better predict future savanna responses to droughts.  
729 Process based models offer some of the most promising approaches for predicting future  
730 vegetation responses to drought, and can also capture spatial variability in mortality patterns  
731 (Anderegg et al. 2015). However, mechanisms of drought-induced mortality are currently  
732 poorly represented in most dynamic vegetation models, and they do not always successfully  
733 predict observed patterns of drought induced mortality (Anderegg et al. 2015, Choat et al.  
734 2018, and references therein). A more comprehensive understanding of how trait variability  
735 across species and plant functional types in savannas influences mortality and demographic  
736 outcomes during droughts can help refine model parameterization and greatly improve their  
737 forecasting ability (Anderegg et al. 2015, Choat et al. 2018).

738 Moving forward, there are several key questions that need addressing: What are the drought  
739 characteristics (severity, length and frequency) that elicit ecological responses in savannas, and  
740 how do these vary across the rainfall gradient from arid to mesic savannas? How do drought-  
741 survival syndromes change across rainfall gradients, and do they differ between dominant plant  
742 functional types in savannas? What is the role of evolutionary history in determining drought  
743 tolerance trait distribution patterns across different savannas of the world, i.e. are some traits  
744 phylogenetically conserved while others over-dispersed within local flora, and are these  
745 patterns consistent across savannas on different continents? How are resistance traits  
746 correlated with resilience traits? Is there a trade-off between traits that confer drought  
747 resistance with those that allow savanna vegetation to persist in the face of other disturbances  
748 such as fire and herbivory, or deal with future global changes?

749 Our understanding of the mechanisms, physiological thresholds and traits that govern  
750 vegetation responses to drought, especially trees, has improved substantially in the last decade,  
751 thanks largely to a substantial body of recent work emanating from forest ecosystems.  
752 However, in order to predict savanna responses to drought this body of knowledge needs to be  
753 integrated with a detailed understanding of not just grass responses to droughts, but also  
754 feedback effects arising through alterations in herbivory and fire regimes. It is now fairly well-  
755 established that savannas on different continents, while structurally similar, differ functionally  
756 in their sensitivities and responses to climatic, edaphic and disturbance drivers such as fire and  
757 herbivory as a result of their different evolutionary histories (Lehmann et al. 2014). A  
758 comprehensive understanding of global savanna responses to drought will therefore require a  
759 more detailed understanding of how these different evolutionary histories have shaped the  
760 distribution of drought-tolerance and avoidance traits on different continents as well as how  
761 feedback effects arising from different fire and grazing regimes influence the resilience of these  
762 different communities.

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## Data Accessibility

Not applicable.

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Table 1. Representative tolerance (a) and avoidance traits (b) that influence growth and survival of trees and grasses during droughts (resistance). The letters T and G in brackets at the start of the description indicate whether the traits are typically quantified for trees or grasses, respectively. For a more detailed description of these traits and their quantification, also see Holloway-Phillips & Brodribb (2011), Craine et al. (2013), O'Brien et al. (2017) and Choat et al. (2018) and references therein.

a) Tolerance traits

Traits	Description
Cavitation or embolism resistance ( $\Psi_{50}$ and $\Psi_{88}$ )	(T,G) Xylem pressure that induces 50% or 88% loss of xylem hydraulic conductivity. Species with more negative values can tolerate drier conditions before cavitation occurs
Xylem conduit dimensions and connectivity	(T,G) Xylem anatomical features that determine vulnerability to cavitation. Species with narrower and shorter xylem elements and lower connectivity are less vulnerable to cavitation
Pit membrane thickness and porosity	(T,G) Determines vulnerability to cavitation. Species with larger pores are more susceptible to cavitation
Minimum leaf water potential ( $\Psi_{min}$ )	(T) Typical minimum xylem water potential experienced by trees under normal conditions. Isohydric species regulate stomata to maintain more or less constant midday plant water potentials to avoid cavitation, but run the risk of carbon starvation. Anisohydric species, on the other hand, allow plant water potentials to drop as soil water potentials drop, both diurnally and seasonally, and so potentially run a greater risk of hydraulic failure during droughts
Leaf water potential corresponding to stomatal closure ( $\Psi_{crit}$ )	(G) Leaf water potentials at which stomatal conductance falls below critical values. Lower values indicate greater drought tolerance.
Hydraulic safety margins (HSM)	(T, G) Difference between the typical minimum xylem water potential experienced by trees and that which causes xylem dysfunction. For grasses, commonly estimated as the difference between leaf water potentials at 95% stomatal closure and $\Psi_{50}$ . Species with greater HSMs fare better during droughts.
Leaf turgor loss point	(T,G) Leaf water potential at which wilting occurs. Species with lower values can maintain gas exchange and growth at lower soil moisture levels, i.e. better tolerate droughts
Non-structural carbohydrate reserves (stem, root & leaf)	(T,G) Species with greater stores of carbohydrate reserves fare better under droughts

Root:shoot ratios	(T,G) Species that allocate relatively more to roots perform better under droughts
Leaf: sapwood area ratio	(T) Species with low leaf:sapwood ratios have a greater capacity to supply water to leaves
Resprouting ability	(T) Resprouting species have greater allocation to roots and higher stores of non-structural carbohydrates which can confer greater drought-tolerance compared to non-resprouters
Wood density	(T) Soft wooded species (low wood density) typically suffer greater mortality during droughts
Specific leaf area	(T, G) Species with high specific leaf area typically suffer greater mortality during droughts
Leaf width	(G) Wide leaved grasses tend to be more drought tolerant, while narrow leaved species show a range of tolerance levels
C4 Photosynthetic pathway (NADP-ME, NAD-ME, PCK)	(G) NAD-ME species have higher whole-plant water use efficiency under water stress and are potentially more drought tolerant
Associations with symbionts (AMF)	(T, G) Drought-tolerance of both trees and grasses can also be enhanced by associations with AMF that facilitate water acquisition

b) Avoidance traits

<b>Traits</b>	<b>Description</b>
Deep roots	(T, G) Provides access to deep soil water and/or water table
Leaf shedding	(T, G) Reduces transpirational loss, water use and lowers vulnerability to cavitation
Internal water storage	(T) Reduces reliance on soil water
Leaf rolling	(G) Reduces water loss
Cuticular wax	(G) Reduces water loss

Table 2. Community and ecosystem level determinants of the resistance and resilience of savannas to droughts.

	Resistance	Resilience
Woody stratum	<p>Neighbourhood tree densities</p> <p>Species and functional trait diversity within the community</p> <p>Extent to which browsing intensity is altered during droughts as a result of browser mortality and movement</p> <p>Extent to which frequency and intensity of fires are altered during droughts</p> <p>Past stressors including previous browsing and fire management, extent of desertification, past history of droughts, and time since last drought</p>	<p>High representation of species with the ability to resprout</p> <p>Increased post-drought flowering and seeding by surviving trees</p> <p>Large soil seedbanks</p> <p>Reduced competition from grasses following droughts</p> <p>Lowered fire frequencies immediately following droughts</p> <p>Reduced browsing pressure post-drought</p> <p>Colonization ability of dominant species</p>
Understory	<p>Species and functional trait diversity within the community</p> <p>Relative abundance of unpalatable grasses</p> <p>Extent to which grazing intensity is altered during droughts as a result of grazer mortality and movement</p> <p>Extent to which frequency and intensity of fires are altered during droughts</p> <p>Distance to permanent sources of surface water</p> <p>Past stressors including previous grazing and fire management, extent of desertification, past history of droughts, and time since last drought</p>	<p>Large soil seedbanks</p> <p>Increased post-drought flowering and seeding by surviving grasses</p> <p>Low extent of desertification (increase in bare ground) as a result of the drought</p> <p>Reduced competition from trees following droughts</p> <p>Reduced grazing pressure post-drought</p> <p>Colonization ability of dominant species</p>

## Figure legends

766 Figure 1. A conceptual representation of the factors influencing the resistance and resilience of  
767 savanna ecosystems to droughts. (a) A range of factors operating at different spatial scales and  
768 levels of organization collectively determine the extent to which meteorological droughts  
769 influence productivity and mortality of individuals. Note that these are not nested factors that  
770 operate at increasingly finer spatial scales, e.g. stressors such as fire and herbivory can operate  
771 at scales larger than the landscape, and even extend beyond drought impacted areas. (b) The  
772 extent to which such effects then translate to impact savanna vegetation state and ecosystem  
773 productivity (depicted in (c)) is contingent on both individual responses as well as the species  
774 and functional trait diversity within the community. (c) As droughts become more severe and  
775 extended (moving from top to bottom, i.e. from green to brown), vegetation responses become  
776 increasingly pronounced from an initial loss of productivity to widespread tree and grass  
777 dieback and potentially desertification in arid and semi-arid savannas, i.e. return to the initial  
778 state (green curved and dashed arrows) becomes progressively harder with these transitions  
779 (as depicted by the decreasing width of the arrows), and is contingent on a range of different  
780 factors (d) that collectively determine savanna resilience. When these are met (positive; green  
781 block arrow), vegetation is resilient. However, when conditions in (d) are not met (negative;  
782 red block arrow), and when droughts are particularly severe, it can lead to compositional shifts  
783 (e) in vegetation. Such compositional shifts in turn can feedback (f) to influence the ability of  
784 savannas to deal with future droughts by altering both the presence and diversity (i.e.  
785 functional diversity) of drought-tolerance and avoidance traits in the community (dashed  
786 arrows).

Figure 1

