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Droughts and the Ecological Future of Tropical Savanna Vegetation

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Abstract

1. Climate change is expected to lead to more frequent, intense and longer droughts in the future, with major implications for ecosystem processes and human livelihoods. The impacts of such droughts are already evident, with vegetation dieback reported from a range of ecosystems, including savannas, in recent years.
2. Most of our insights into the mechanisms governing vegetation drought responses have come from forests and temperate grasslands, while responses of savannas have received less attention. Because the two lifeforms that dominate savannas- C_3 trees and C_4 grasses- respond differently to the same environmental controls, savanna responses to droughts can differ from those of forests and grasslands.
3. Drought-driven mortality of savanna vegetation is not readily predicted by just plant drought-tolerance traits alone, but is the net outcome of multiple factors including drought-avoidance strategies, landscape and neighborhood context, and impacts of past and current stressors including fire, herbivory and inter-lifeform competition.
4. Many savannas currently appear to have the capacity to recover from moderate to severe short-term droughts, although recovery times can be substantial. Factors facilitating recovery include the resprouting ability of vegetation, enhanced flowering and seeding, and post-drought amelioration of herbivory and fire. Future increases in drought severity, length and frequency can interrupt recovery trajectories and lead to compositional shifts, and thus pose substantial threats, particularly to arid and semi-arid savannas.
5. *Synthesis*: Our understanding of, and ability to predict, savanna drought responses is currently limited by availability of relevant data, and there is an urgent need for campaigns quantifying drought-survival traits across diverse savannas. Importantly, these campaigns must move beyond reliance on a limited set of plant functional traits to identifying suites of physiological, morphological, anatomical and structural traits or "syndromes" that encapsulate both avoidance and tolerance strategies. There is also a critical need for a global network of long-term savanna monitoring sites as these can provide key insights into factors influencing both resistance and resilience of different savannas to droughts. Such efforts, coupled with site-specific rainfall manipulation experiments that characterize plant trait–drought response relationships, and modelling efforts, will enable a more comprehensive understanding of savanna drought responses.

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

Introduction

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

This statement is particularly true of the Earth's tropical savannas. Tropical savannas are indeed a curious biome, neither grassland nor forest, but one in which two contrasting lifeforms – C_3 trees and C_4 grasses – compete for dominance in the face of limited resource availability and frequent disturbances such as fire and herbivory. In fact, savannas were long perceived as degraded ecosystems, derived from forests as a result of disturbances, anthropogenic or otherwise (Scholes & Walker 1993, Bond & Parr 2010, Parr et al. 2014, Veldman et al. 2015a, Ratnam et al. 2016). However, tropical savannas are ancient biomes, their origins dating back to the late Miocene and early Pliocene, ~4 - 8 Mya, and the near-synchronous expansion of C_4 grasses around the world (Beerling & Osborne 2006, Osborne 2008, Edwards et al. 2010, Simon & Pennington 2012). This global rise to dominance of C_4 grasses occurred fairly rapidly in geological terms, within about a million years, and represents one of the most dramatic examples of biome assembly in the geological record (Beerling & Osborne 2006, Edwards et al. 2010).

Savannas and grasslands are among the most extensive vegetation types in tropical and sub-tropical regions (Solbrig, Medina & Silva 1996, Scholes & Archer 1997). However, over the last couple of centuries, they have been drastically altered by human activities (Ramankutty & Foley 1999, Lambin, Geist & Lepers 2003, Miles et al. 2006, Murphy, Andersen & Parr 2016, Ratnam et al. 2016, Strassburg et al. 2017). As human populations grow and expand, the remaining savanna habitats are increasingly threatened by a range of anthropogenic activities including land-use transformation, tree plantations for carbon-sequestration initiatives and alterations of fire and herbivory regimes (Bond & Parr 2010, Parr et al. 2014, Veldman et al. 2015b, Bond 2016, Murphy, Andersen & Parr 2016, Ratnam et al. 2016, Abreu et al. 2017, Strassburg et al. 2017, Osborne 2018). Further, global changes in the form of altered precipitation and temperature regimes, elevated atmospheric [CO_2] and atmospheric N and P deposition have emerged as major threats to the ecological integrity of these biomes (Parr et al. 2014, Bond & Midgley 2012, Midgley & Bond 2015), prompting Bond & Midgley (2012) to ask if the rise to dominance of this biome in the Late Miocene is likely to be matched by an equally dramatic decline in the Anthropocene.

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

(Scholes & Archer 1997, Bond, Midgley & Woodward. 2003, Sankaran et al. 2005, Sankaran, Ratnam & Hanan 2008, Buccini & Hanan 2007, Good & Caylor 2011, Lehmann et al. 2014, D'Onofrio et al. 2018), ii) changes in precipitation regimes, coupled with warmer temperatures that increase evaporative demand, are projected to lead to more intense and frequent regional-scale droughts across large parts of the globe, including savanna regions (Dai 2013, IPCC 2014, Mitchell et al. 2014, Trenberth et al. 2014), iii) savannas are expected to be particularly responsive to precipitation changes given the tight coupling between rainfall and production in these systems (Sala et al. 2000, 2012, Knapp & Smith 2001, Xu et al. 2018), and iv) in contrast to forests, the role of droughts in regulating tropical savanna dynamics has received relatively less attention. Importantly, inferring savanna responses based on studies carried out in other ecosystems is not straightforward. Because the two dominant life forms that characterize savanna ecosystems – C_4 grasses and C_3 trees and shrubs – respond differently to the same environmental controls, and because many vegetation traits of tropical savanna trees and grasses differ consistently from those of forests and temperate grasslands (Craine et al. 2005, Hoffmann et al. 2005, Ratnam et al. 2011, Charles-Dominique et al. 2015), savannas are likely to respond to climate change in ways that forests and grasslands may not (Lehmann et al. 2014, Osborne et al. 2018).

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

For the purposes of this review, I use the term drought to broadly refer to periods where lowered rainfall during the growing season reduces plant water availability to levels significantly below average annual conditions (Greenwood et al. 2017, O'Brien et al. 2017). I don't specifically consider how vegetation responses change with drought intensity *per se*, but acknowledge that the magnitude of observed responses will undoubtedly be more pronounced as droughts become more extreme and protracted (Ruppert et al. 2015, Greenwood et al. 2017, Young et al. 2017). I draw on both observational studies that have recorded responses of savanna trees and grasses to droughts, as well as experimental studies that have manipulated plant water availability under controlled conditions. Although experiments allow for clearer attribution of causes (Smith 2011, Greenwood et al. 2017), manipulating water availability for adult savanna trees is challenging given their size and longevity (O'Brien et al. 2017). Consequently, experiments are typically limited to grasses and tree seedlings, and don't capture adult tree responses, which observational studies do.

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

Direct effects of droughts on savanna tree mortality

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

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

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

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

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

The xylem water potentials at which cavitation occurs (cavitation resistance; characterized as the pressure that induces 50% (Ψ_{50})or 88% (Ψ_{88}) loss of xylem hydraulic conductivity) differs between species and is largely determined by xylem anatomical features including the diameter, length, connectivity and density of xylem conduits and the porosity of pit membranes (Choat et al. 2012, 2018, Anderegg et al. 2016). Tree species also differ in the extent to which they regulate their internal water status through the opening and closing of their stomata. Isohydric species, on the one hand, use stomatal regulation to maintain more or less constant midday plant water potentials and avoid cavitation. However, with stomata closed, photosynthesis is curtailed, and these species run the risk of carbon starvation during droughts (McDowell et al. 2008, Zeppel et al. 2011, Konings & Gentine 2017). 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 (McDowell et al. 2008, Zeppel et al. 2011, Konings & Gentine 2017, Konings, Williams & Gentine 2017). The difference between the typical minimum xylem water potential experienced by trees and that which causes xylem dysfunction provides a measure of the 'hydraulic safety margin (HSM)' within which trees operate, and serves as a useful index of the physiological vulnerability of trees to drought induced mortality (Choat et al. 2012, 2018, Anderegg et al. 2016).

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

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

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

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

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

Ultimately, the ability of trees to withstand and survive droughts is the net outcome of interactions between a number of physical, morphological and life-history traits that enable trees to tolerate desiccation stress, or alternately avoid or delay it to the extent possible (O'Brien et al. 2017, Choat et al. 2018). It is becoming increasingly apparent that many easily measurable traits such as wood density and specific leaf area are rarely successful at fully predicting drought mortality patterns in the field by themselves, and extrapolations based on single traits including hydraulic safety margins can often be misleading (Pausas et al. 2016, Adams et al. 2017). For example, high wood density species have been shown to survive better during droughts in some systems, but suffer greater mortality in others (Hoffmann et al. 2011, O'Brien et al. 2017). Similarly, mortality has been reported to be higher in shallow-rooted species in some instances, but greater in deeper-rooted species in others (Rice et al. 2004, Fensham et al. 2015, Chitra-Tarak et al. 2017). It is unlikely that plants have evolved to rely on a single strategy to deal with drought (Anderegg, Berry & Field 2012) and there is thus a need for drought survival to be considered in the context of suites of multiple physiological, morphological, anatomical and structural traits or "syndromes" that encapsulate both avoidance and tolerance strategies. Such an expanded campaign will yield rich dividends and is less unwieldy that it may seem. Many hydraulic and physiological traits appear to covary in a coordinated fashion, suggesting that the complexity of hydraulic traits can be collapsed into one or a few axes of physiological drought tolerance strategies (Mencuccini et al. 2015, Bartlett et al. 2016, Choat et al. 2018). Combining these with axes that similarly capture anatomical, morphological (e.g. rooting characteristics) and avoidance traits can help identify alternate 'syndromes' that plants employ to deal with droughts, and provide insights into how these change across broad environmental gradients.

Direct effects of droughts on savanna grasses

Tropical savanna C_4 grasses typically use water more efficiently, and are more physiologically responsive to intermittent rainfall events, compared to C_3 trees and shrubs (Williams 1998, Ghannoum et al., 2003; Swemmer, Knapp & Smith 2006, Ripley et al. 2007, Ghannoum 2009, Volder, Tjoelker & Briske 2010). However, this greater water use efficiency does not necessarily translate into a greater tolerance for protracted water stress compared to C_3 plants (Ripley et al. 2007, Ripley, Frole & Gilbert 2010, Ghannoum 2009, Taylor et al. 2011, Volder, Tjoelker & Briske 2010). Although they are capable of assimilating large amounts of carbon when soil water is available, this capacity diminishes rapidly as soil water content decreases (Ripley et al. 2007, Ghannoum 2009, Taylor et al. 2011, Volder, Tjoelker & Briske 2010, Connor & Hawkes 2018). Thus, although C_4 grasses may be better able to deal with and recover from low to moderate drought, they may be equally or even more sensitive to periods of severe or protracted water stress when compared to C_3 plants (Walker et al. 1987, Ripley et al. 2007, Ghannoum 2009, Volder, Tjoelker & Briske 2010). Drought impacts on grass mortality in savannas can thus be substantial (Scholes 1985, Walker et al. 1987, Danckwerts & Stuart-Hill 1988, Mott et al. 1992, O'Connor et al. 1994, 1995, Swemmer et al. 2018), with grasses often dying before woody plants (Walker et al. 1987).

Physiological drought tolerance of grasses, assessed based on leaf water potentials at which stomatal conductance falls below critical thresholds for ecological functioning, has been shown to vary nearly 10-fold between grass species, both across and within sites (Craine et al. 2013). Using data from 426 tropical and temperate grass species spanning a range of rainfall, biogeographic and phylogenetic affinities, Craine et al. (2013) showed that physiologically drought tolerant grasses, i.e. those with critical leaf water thresholds below the median value for all species assessed (-4.1 MPa), typically have higher photosynthetic rates and stomatal conductance, and narrower xylem elements consistent with mechanisms of cavitation resistance. Leaf-width also appears to be correlated with drought tolerance with wide-leaved grasses tending to be drought-intolerant and narrow-leaved species displaying a wide range of abilities from tolerance to intolerance (Craine et al. 2013).

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

Drought tolerance also potentially differs between different C_4 grass photosynthetic subtypes, the distributions of which are strongly influenced by rainfall (Ripley et al. 2007, Ripley, Frole & Gilbert 2010, Ghannoum 2009). C_4 grasses are grouped into 3 photosynthetic subtypes based on the major C_4 acid decarboxylation enzyme in their bundle sheaths: NAD-ME (NAD malic enzyme), NADP-ME (NADP malic enzyme) and PCK (phosphoenolpyruvate carboxykinase; Ghannoum 2009). NAD-ME grasses tend to increase in abundance, while NADP-ME grasses decrease, across a gradient of decreasing rainfall (from 900 to 50 mm mean annual precipitation) while the distribution of PCK species does not appear to be strongly correlated with rainfall (Ghannoum 2009 and references therein). Data, albeit from a very limited number of species, suggests that NAD-ME species possess traits better suited to arid conditions and tend to have higher whole-plant water use efficiency under water stress than NADP-ME species (Ghannoum, Von Caemmerer & Conroy 2002, Carmo-Silva et al. 2009, Taylor et al. 2011).

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

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

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

Savannas are complex systems whose structure is ultimately determined by a suite of factors including inter- and intra-lifeform competition between trees and grasses, climate, soils, fire, browsing and grazing (Sankaran & Anderson 2009). Thus, the effects of droughts on savanna structure and function cannot be fully understood by studying responses of the major functional groups, C_3 trees and C_4 grasses, in isolation as net effects can be altered depending on how droughts impact fire and herbivory regimes, as well as the nature and intensity of tree-grass competition.

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

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

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

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

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

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

Factors that attenuate mortality of vegetation during droughts include site characteristics, lowered competition, facilitation, attenuation of stressors and functional trait diversity in communities (Lloret et al. 2012). As discussed, spatial variability in topographic and edaphic factors can generate a heterogeneous abiotic template that can result in a mosaic of drought severity across the landscape, enabling localized persistence of tree and grass populations during droughts and providing a source pool for subsequent recolonization (O’Connor 1995, Lloret et al. 2012). In drier sites, grasses can persist under tree canopies which provide ameliorated conditions and protection from grazing during droughts, even if populations are substantially reduced in tree interspaces (O'Connor 1995). Similarly, heterogeneity in tree densities across the landscape can result in lowered mortality in low density sites as a result of less intense competition for water. There is evidence to suggest that reductions in tree densities following initial mortality can increase available water for surviving individuals, lowering competition and subsequent mortality of trees during later stages of the drought (Lloret et al. 2012, Wonkka et al. 2016). Reductions in grazing and browsing intensity as a result of herbivore die-off or movement during droughts, as well as reductions in fire frequencies and intensities as a result of lowered grass-fuel loads can similarly lower mortality rates in the later stages of droughts. In addition, standing dead grass canopies have also been shown to enhance survival and establishment of juvenile trees during droughts by reducing irradiation and increasing soil moisture, thereby ameliorating abiotic conditions for seedlings (de Dios et al. 2014).

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

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

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

However, despite the existence of such stabilizing mechanisms, frequent, longer and more intense droughts can nevertheless serve to destabilize savannas and lead to structural and compositional shifts in the future. Severe and protracted droughts can significantly depress productivity and elicit widespread mortality of vegetation in savannas (Walker et al. 1987, Fensham, Fairfax & Ward 2009, Ruppert et al. 2015, Swemmer et al. 2018), and can also drive compositional shifts in communities (Cipriotti et al. 2008, Evans et al. 2011). Even if ecosystem productivity is regained quickly following return to normal conditions (Walker et al. 1997, Hoover, Knapp & Smith 2014), compositional shifts in tree and grass communities can have longer term impacts on savanna function. Severe droughts coupled with intense grazing can cause transitions from communities dominated by palatable, perennial grasses to systems composed of unpalatable, annual grasses and forbs (Scholes 1985, O'Connor 1994, 1995, 1998, Fuhlendorf & Smeins 1997, Fuhlendorf et al. 2001, Jin et al. 2018). Such changes in understory composition can be particularly hard to reverse, with recovery times ranging from a few years to over a decade or more, and potentially requiring the provisioning of seeds (Walker et al. 1987, Fuhlendorf & Smeins 1997, O'Connor 1998). Because annual-dominated communities are less resistant to droughts than perennial-dominated ones, i.e. suffer greater reductions in productivity for the same drought intensity, such compositional shifts can also impair the ability of savannas to deal with future droughts (Ruppert et al. 2015).

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

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

A hierarchy of drivers

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

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

Post-drought recovery of biomass, productivity and species composition is similarly a function of multiple factors that govern subsequent colonization, establishment (or re-establishment) and growth of vegetation (Fig 1, Table 2,), with longer recovery times following droughts that are more protracted and severe. The herbaceous layer can generally be expected to recover biomass quicker than the woody layer given their higher growth rates. The rate of recovery of species composition on the other hand depends on the extent to which species are differentially affected by droughts, with recovery times longer in systems where the dominant species are disproportionately impacted and are poor colonizers. However, as droughts become more frequent, or where desertification occurs, it can lead to compositional shifts in savanna understory and woody communities. Such shifts can then feedback to influence the ability of savannas to resist future droughts by altering both the distribution of drought tolerance and avoidance traits as well as species and functional trait diversity in the community.

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

The way ahead

Tropical savannas are highly variable in structure and composition across their distributional range, spanning the gradient from nearly open grasslands to closed woodlands, and differing in the characteristics of the dominant trees (deciduous versus evergreen, broad-leaved vs. fine-leaved trees) and herbaceous vegetation (tall vs short grasses, annual vs. perennial). This variability arises from underlying differences in resource availability (rainfall and soil nutrients), strength of top-down forces (fire and herbivory) and evolutionary history (Scholes & Walker 1993, Scholes & Archer 1997, Sankaran, Ratnam & Hanan 2004, Lehmann et al. 2011, 2014), and can pose challenges when generalizing drought effects across savannas. Understanding how these diverse savannas differ in their resistance and resilience to droughts represents a major task ahead for savanna ecologists; one that requires an integrative approach that combines trait data quantification with observation, experiments and modelling.

Expanded Trait Campaigns:

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

Long-term Savanna Monitoring Plots:

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

As we go forward, a network of long-term savanna monitoring plots where individuals are tagged and monitored over time will be invaluable. Such efforts can provide us with insights into vegetation dynamics and demography that other kinds of studies cannot (Harper 1967). In fact, many of our insights into drought responses of vegetation have come fortuitously from opportunistic studies in forested ecosystems where droughts have occurred during the course of ongoing long-term observational and experimental studies (Breshears et al. 2009, Phillips et al. 2009, Smith 2011, Fensham et al. 2017). However, in contrast to forests, a network of long-term monitoring plots that spans the climatic, edaphic and biotic gradients that characterize savanna ecosystems is currently lacking (Staver 2018). Such long-term efforts are particularly insightful because: i) detailed pre-drought data on vegetation are available, which is useful for understanding the role of previous stressors and past individual performance on drought survival, ii) concurrent data on physiological parameters and water stress metrics are often available, or can be gathered, which can provide us with a more nuanced understanding of drought responses of vegetation, iii) sustained monitoring can provide us with key information on post-drought recovery and factors affecting resilience of vegetation, for which data are currently limited, as well as help understand how repeated droughts impact the resistance and resilience of savanna vegetation, and iv) data are available even when the ecological responses to climatic droughts are not extreme. This last point is critical because in order to effectively predict savanna responses, we need to understand plant traits and site characteristics that confer resistance as well as render vegetation susceptible to droughts (Smith 2011, Breshears et al. 2008, Fensham, Fairfax & Ward 2009, Mitchell et al. 2014).

Targeted Field Experiments:

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

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

Process-based models

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

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

Our understanding of the mechanisms, physiological thresholds and traits that govern vegetation responses to drought, especially trees, has improved substantially in the last decade, thanks largely to a substantial body of recent work emanating from forest ecosystems. However, in order to predict savanna responses to drought this body of knowledge needs to be integrated with a detailed understanding of not just grass responses to droughts, but also feedback effects arising through alterations in herbivory and fire regimes. It is now fairly well-established that savannas on different continents, while structurally similar, differ functionally in their sensitivities and responses to climatic, edaphic and disturbance drivers such as fire and herbivory as a result of their different evolutionary histories (Lehmann et al. 2014). A comprehensive understanding of global savanna responses to drought will therefore require a more detailed understanding of how these different evolutionary histories have shaped the distribution of drought-tolerance and avoidance traits on different continents as well as how feedback effects arising from different fire and grazing regimes influence the resilience of these 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 (Ψ_{50} and Ψ_{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 (Ψ_{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 (Ψ_{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 Ψ_{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

Traits	**Description**
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

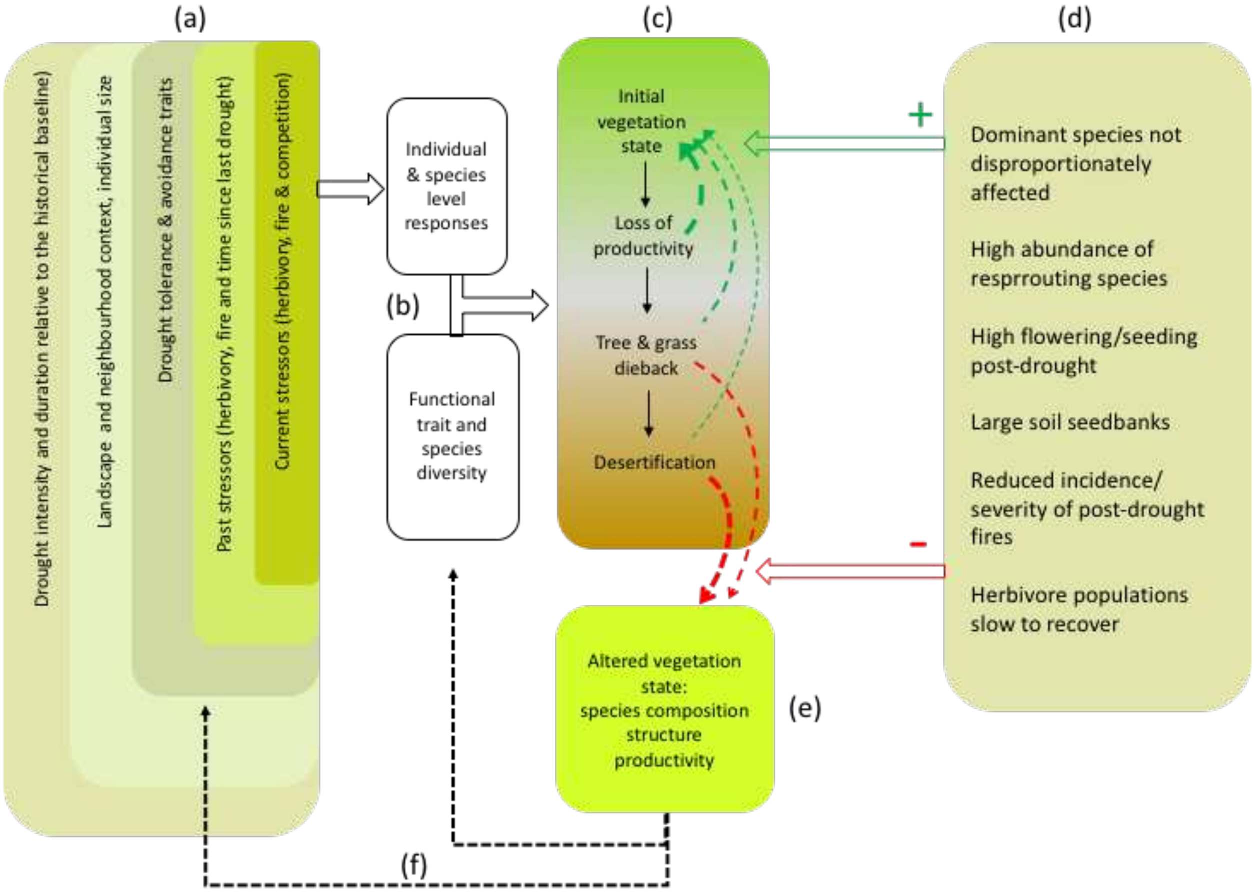
Table 2. Community and ecosystem level determinants of the resistance and resilience of savannas to droughts.

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

Figure legends

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

Figure 1


(a)
Drought intensity and duration relative to the historical baseline)
Landscape and neighbourhood context, individual size
Drought tolerance & avoidance traits
Past stressors (herbivory, fire and time since last drought)
Current stressors (herbivory, fire & competition)
Individual & species level responses
(b)
Functional trait and species diversity
(c)
Initial vegetation state
Loss of productivity
Tree & grass dieback
Desertification
(d)
+
Dominant species not disproportionately affected
High abundance of resprrouting species
High flowering/seeding post-drought
Large soil seedbanks
Reduced incidence/ severity of post-drought fires
Herbivore populations slow to recover
-
Altered vegetation state: species composition structure productivity
(e)
(f)