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Tree Physiology review

Not all droughts are created equal: translating meteorological drought into woody plant mortality

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Widespread drought-induced mortality of woody plants has recently occurred worldwide, is likely to be exacerbated by future climate change and holds large ecological consequences. Yet despite decades of research on plant–water relations, the pathways through which drought causes plant mortality are poorly understood. Recent work on the physiology of tree mortality has begun to reveal how physiological dysfunction induced by water stress leads to plant death; however, we are still far from being able to predict tree mortality using easily observed or modeled meteorological variables. In this review, we contend that, in order to fully understand when and where plants will exceed mortality thresholds when drought occurs, we must understand the entire path by which precipitation deficit is translated into physiological dysfunction and lasting physiological damage. In temperate ecosystems with seasonal climate patterns, precipitation characteristics such as seasonality, timing, form (snow versus rain) and intensity interact with edaphic characteristics to determine when and how much water is actually available to plants as soil moisture. Plant and community characteristics then mediate how quickly water is used and seasonally varying plant physiology determines whether the resulting soil moisture deficit is physiologically damaging. Recent research suggests that drought seasonality and timing matter for how an ecosystem experiences drought. But, mortality studies that bridge the gaps between climatology, hydrology, plant ecology and plant physiology are rare. Drawing upon a broad hydrological and ecological perspective, we highlight key and underappreciated processes that may mediate drought-induced tree mortality and propose steps to better include these components in current research.

Keywords: climate change, drought seasonality, ecohydrology, tree death.

Introduction

Owing to human-induced climate change, the global hydrological cycle of the coming century is likely to differ significantly from that of the last 100 years. The global distribution of precipitation is likely to shift, with high latitudes generally becoming wetter and subtropics and poleward fringes of the subtropics becoming drier (Zhang et al. 2007). In addition to regional shifts in precipitation quantity, precipitation form will shift the balance of snow versus rain towards less snow in many areas. Decreases in snowpack and earlier runoff dates have already been detected in the western USA and are expected to accelerate with climate change (Mote et al. 2005, Adam et al. 2009), potentially changing the timing and availability of soil moisture independent of changes in precipitation quantity. Moreover, precipitation is expected to become more intense but less frequent, resulting in larger runoff and longer dry spells (Trenberth et al. 2003, Sun et al. 2007). While regional downscaling of precipitation projections remains difficult, it is reasonably clear that the temporal availability of water is going to shift, even in places with no directional trend in mean climatology.

Beyond shifts in mean precipitation, perhaps the most ecologically important hydrological change over the coming century will be an increase in the variance in precipitation, leading to extreme hydrological events such as drought (Figure 1) (Jentsch et al. 2007). Climate change has already likely amplified the hydrological cycle, increasing latent heat fluxes and the frequency of precipitation extremes (Huntington 2006). This amplification is predicted to grow stronger in the future, expanding climate variability in most parts of the world (Seager et al. 2012), but particularly in the southwestern USA (Diffenbaugh et al. 2008), where warming trends are predicted to exacerbate future droughts (Gutzler and Robbins 2011). While our ability to predict individual droughts is currently constrained by our ability to model sea surface temperature anomalies, such as the El Niño-Southern Oscillation, there is significant model agreement that the increased atmospheric demand will increase the spatial extent and severity of drought (Figure 2, Dai 2010). Even in regions with no directional trend in mean precipitation, the frequency and intensity of droughts will likely increase (IPCC 2007, Dai 2010). The area under extreme and severe drought (< -4.3 and < -3.3 value on the Palmer Drought Severity Index (PDSI), respectively) are both predicted to triple by 2090 (Burke et al. 2006), and the frequencies of short-term (4–6 months duration) and long-term droughts (>12 months duration) are expected to double and triple, respectively (Sheffield and Wood 2008). Moreover, an increase in inter-annual precipitation variability has non-linear effects on the inter-annual distribution of mean soil moisture that could drastically alter the ecohydrology of some semi-arid locations even without the influence of extreme droughts (D'Odorico et al. 2000).

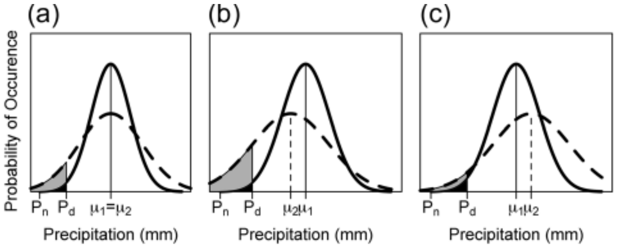

Figure 1. Climate change has and will continue to amplify the hydrological cycle, resulting in greater inter-annual climate variability. For precipitation, this will qualitatively result in a shift from the solid historical distribution to the dotted future distribution (shown here as normal distributions for ease of illustration, but typically fit or modeled using different distributions, e.g., Guttman 1999, Rodriguez-Iturbe and Porporato 2004). (a) In areas with no change in mean precipitation ($\mu_1 = \mu_2$), increased variability will result in more droughts (gray area to the left of critical drought point p_d), as well as droughts of novel extremity (gray area to left of novel precipitation point p_n). (b) For areas experiencing a decrease in mean precipitation ($\mu_1 > \mu_2$) such as the American southwest (see Seager et al. 2007, Seager and Vecchi 2010), this will result in drastically more frequent droughts and droughts of novel severity. (c) Even for locations with positive shifts in mean precipitation ($\mu_1 < \mu_2$), this could still result in more frequent and more extreme droughts (see Trömel and Schönwiese 2007 for winter precipitation in Germany). Modified after Jentsch et al. (2007).

Recent widespread forest mortality associated with drought and/or temperature stress, documented on all vegetated continents, has raised concern over forests' vulnerability to future climate change (Logan et al. 2003, Allen et al. 2010). Because trees structure many ecosystems, tree death is a fundamental process critical to many fields of basic and applied ecology (Franklin et al. 1987). Thus, recent and future forest mortality can potentially affect biodiversity, risk of wildfire, nutrient cycling, hydrology, land–atmosphere interactions and ecosystems services supplied to humans on a regional to global scale (Anderegg et al. 2013*b*). Because forests store over 45% of the carbon found in terrestrial ecosystems (Bonan 2008) and can turn from carbon sinks to carbon sources due to climate-related mortality (Kurz et al. 2008*a*, Schwalm et al. 2012), forest mortality could also result in a positive feedback on climate warming (Breshears and Allen 2002) and can affect climate policy (Kurz et al. 2008*b*). In addition, recent forest mortality suggests that many of the climate change-induced vegetation shifts that have been widely predicted (Sitch et al. 2008) may be the rapid repercussions of extreme events rather than gradual changes in climate (Allen and Breshears 1998, Allen et al. 2010, but see Fellows and Goulden 2012).

Forest mortality has received increasing attention in the scientific literature (Allen et al. 2010), and there has been a concerted effort to understand the physiology behind drought-induced tree death (Sala et al. 2010, Hartmann 2011, McDowell et al. 2011). Yet, most work on drought and plant mortality to date has underappreciated the context of how and why a plant becomes water stressed in determining whether that stress causes what we term 'physiological damage'. We define 'physiological damage' as drought-induced changes, be they physical damage to tissues or disruption of physiological processes, which results in physiological dysfunction (impaired or abnormal functioning) beyond the duration of water stress. For example, cavitation fatigue (increased xylem element vulnerability to cavitation following previous embolism, Hacke et al. 2001) is a lasting physiological damage, while dial cavitation and refilling of leaf petioles (Zufferey et al. 2011) are not. As illustrated by the recent literature exploring the consequences of the amplification of the hydrologic cycle (Box 1), not all rain is ecologically, nor we contend, physiologically equal. In this perspective, we argue that considering the full ecohydrological context of how meteorological drought translates into tree death will greatly improve our understanding of and ability to predict woody plant mortality. This ecohydrological context includes the meteorological context (i.e., timing/seasonality of drought), ecological context (i.e., community processes that mediate how much, when, and where soil moisture is available) and physiological context (timing/seasonality of processes such as growth, repair and evapotranspiration (ET)).

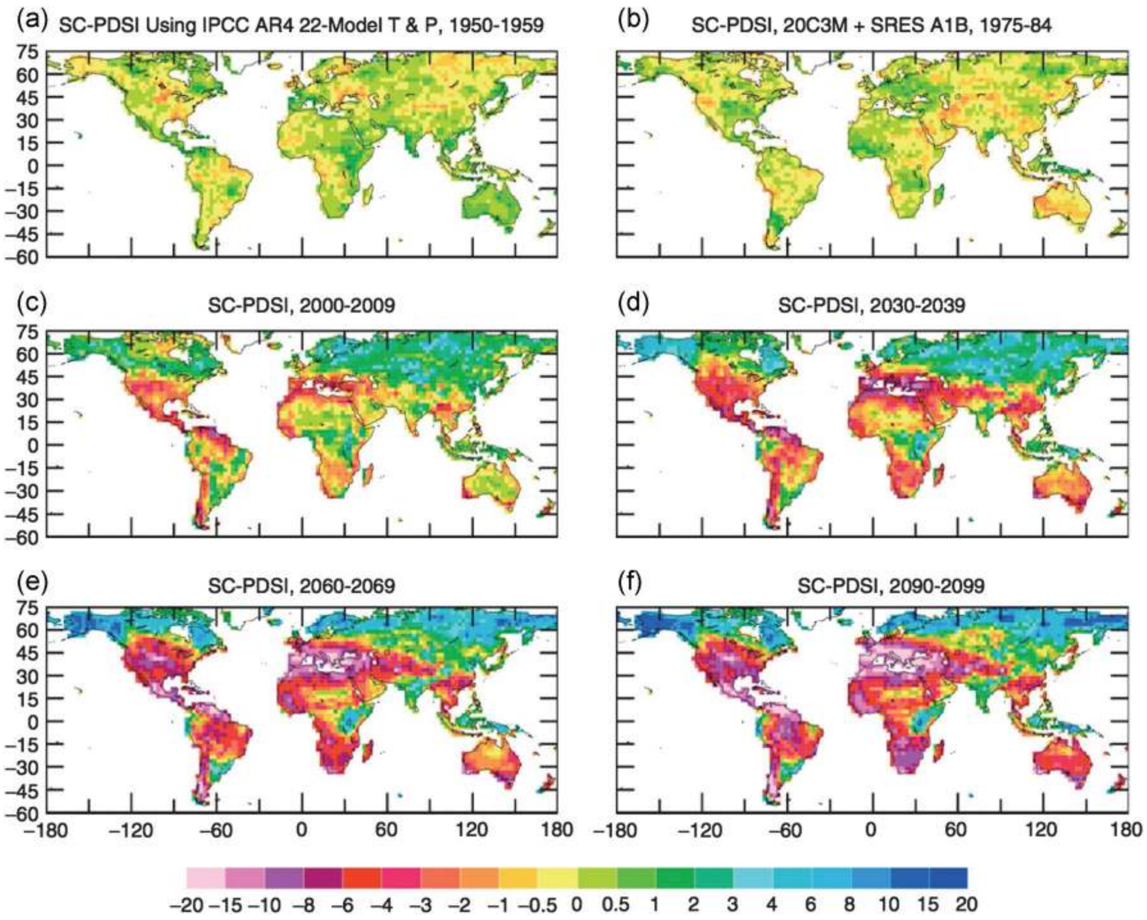

Figure 2. Mean annual self-calibrated Palmer Drought Severity Index (sc-PDSI) for years (a) 1950–59, (b) 1975–84, (c) 2000–09, (d) 2030–39, (e) 2060–69 and (f) 2090–99 calculated using the 22-model ensemble-mean surface air temperature, precipitation, humidity, net radiation and wind speed used in the IPCC AR4 from the 20th century and SRES A1B 21st century simulations. Red to pink areas are extremely dry (severe drought) conditions while blue colors indicate wet areas relative to the 1950–79 mean (reprinted with permission from Dai 2010, copyright 2010 John Wiley & Sons).

Box 1. Consequences of hydrological regime amplification.

In addition to increasing climate variability and drought frequency and severity, climate change-related amplification of the hydrologic cycle will also result in an increase in storm intensity accompanied by a decrease in storm frequency (Knapp et al. 2008). The ecological implications of this effect have been explored both theoretically (Knapp et al. 2008) as well as, at least in grasslands, observationally (Nippert et al. 2006, Ross et al. 2012) and experimentally (Heisler-White et al. 2009, Robertson et al. 2009, 2010, Robinson and Gross 2010). The emerging message from these studies is that precipitation variability results in ecologically significant variations in soil moisture even without changes in net precipitation, though the magnitude and ecological effect of the soil moisture changes vary between systems (particularly grassland versus woodland/forest) and locations. For instance, Knapp et al. (2008) predict that extreme rainfall regimes will result in increased water stress in mesic ecosystems due to longer periods between rains, but decreased water stress in xeric systems due to decreased evaporative water loss during larger rain events. Heisler-White et al. (2009) found that even along a precipitation gradient in Central Plains grasslands, a wet site experienced a reduction in annual net primary production due to increased precipitation regime severity, while an intermediate and a dry site both increased annual net primary production. Meanwhile, Ross et al. (2012) found that woody FLUXNET sites showed decreases in gross primary production and net ecosystem productivity with increasing rainfall intermittency, and that these effects were most pronounced at arid sites. In essence, not all rains are ecologically equal, though they may be identical in total amount.

While it has long been acknowledged by scientists studying plant adaptation and acclimation to arid environments that the context of water stress matters (Hsiao 1973, Turner and Kramer 1980), this knowledge has generally not been applied to the study of drought-induced forest mortality. Moreover, while much arid and semi-arid ecological theory (e.g., responses to pulsed resource availability) can fruitfully be applied to understand drought-induced tree mortality, forest mortality has already been documented and will likely occur in the future beyond arid or semi-arid regions (Allen et al.

2010). We review here the effect of drought seasonality on water stress-induced mortality as an important example of the context-dependent nature of drought mortality physiology. We then walk through the entire path by which precipitation deficit is translated into plant physiological damage (Figure 3), and discuss how to explore and incorporate drought mortality's ecohydrological context (a context that is changing with climate change) into future physiological research.

Drought timing and its ramifications for plants

In locations that exhibit seasonal weather patterns, first principles of plant–water relations suggest that the effects of precipitation on plant water status and physiology are not equal at all times of the year. In any ecosystem where the soil freezes during the winter or where winter precipitation falls as snow, seasonal precipitation varies drastically in its rate and time of infiltration, loss to evaporation, and the availability at different depths in the soil column. Thus, the timing or seasonality of drought influences both the temporal and spatial availability of soil moisture relative to the timing of plant water use, which may itself shift due to climate change. Additionally, due to seasonal variation in photosynthesis, growth and senescence patterns, available soil moisture is more critical to plants at certain times of the year than others for processes such as growth, repair and reproduction. Lastly, plant stress responses and the physiological pathways through which they occur depend on the time course of water stress (length, severity, time of peak stress, etc.).

How much do precipitation timing and seasonality matter? A rich literature has examined the effects of precipitation seasonality (typically winter versus summer) and timing (when in a season precipitation falls) on carbon uptake in grassland and desert ecosystems via water addition and exclusion experiments (Chou et al. 2008, Aanderud et al. 2010, Chimner et al. 2010). In many of these systems, but not all, precipitation seasonality has strong effects on net primary production, biomass and carbon uptake (Bates et al. 2006, Chimner et al. 2010). For instance, increased spring water availability led to increases in herbaceous species' growth, biomass, density and reproduction in a sagebrush steppe, but increased winter precipitation had no effects (Bates et al. 2006). In arid communities in the Chihahuan Desert, interannual increases in winter precipitation were associated with changes in species richness, while total annual precipitation led to changes in plant density (Robertson et al. 2009, 2010). Together, these studies indicate that the seasonality of precipitation mediates the ecological significance of precipitation, particularly for annual and herbaceous plants that exhibit relatively rapid and easily monitored growth and population responses to water availability as well as discrete intervals of water use for different life cycle stages. However, most grassland studies monitor ecosystem function or grassy/herbaceous plant population dynamics (some species of which actually benefit from drought mortality, i.e., Tilman 1996) rather than woody plant stress physiology or mortality (Bates et al. 2006, Chou et al. 2008, Miranda et al. 2009, Robertson et al. 2009, 2010, Aanderud et al. 2010, Chimner et al. 2010). They therefore yield relatively little information about the effects of drought seasonality on woody plants, which are long lived, inertia laden and contingency dependent (Franklin et al. 1987, Manion 1991, Miao et al. 2009).

Currently, experimental studies linking drought seasonality to mortality physiology are lacking, though there is significant correlational evidence that drought seasonality influences tree mortality (stemming mainly from retrospective dendrochronological analyses such as Villalba and Veblen 1998, Guarin and Taylor 2005, Bigler et al. 2007). Using tree ring analysis in a montane conifer forest in the western USA, Bigler et al. (2007) found that *Picea engelmannii* Perry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. exhibited lagged mortality following early season (Jan–July) drought. Meanwhile, both *P. engelmannii* and *A. lasiocarpa* showed more rapid mortality after late season drought, suggesting different mortality mechanisms at work. Similarly, in Argentina the conifer *Austrocedrus chilensis* (D. Don) Flor. et Boult. exhibited significant mortality after particularly dry springs and summers (Villalba and Veblen 1998).

However, the correlation between (and assumed vulnerability to) drought seasonality and mortality appears to vary between systems. Leveraging the spatial variation in the severity of a single drought event, McAuliffe and Hamerlynck (2010) assessed regional mortality of perennial shrub communities in the Mojave and Sonoran deserts. The only significant predictor of vegetation mortality across the region was the 60-month SPI (Standard Precipitation Index, a well-used drought index, see below). No indicators of shorter term or cold-season/warm-season drought were associated with mortality. Meanwhile, a similar analysis that examined the mortality of trembling aspen (*Populus tremuloides* Michx.) forests to the same severe drought found that 1-year summer temperature anomalies and summer surface soil moisture deficits best explained mortality patterns across the State of Colorado (Anderegg et al. 2013*a*).

These links between seasonality and mortality as well as the variation between the strength of these links in different systems could derive from two possible sources. The first are the seasonality-mediated differences in soil moisture abundance, with seasonal moisture varying in both the actual percentage of precipitation that becomes available to plants and the distribution of that moisture in the soil column. Depending on the rooting structure and rooting plasticity of the woody plant in question, this alone could cause a plant to become water stressed during some droughts and not during others

(Schwinning et al. 2005*a*). The second (and non-mutually exclusive) source is the temporal vulnerability of plant physiology to water stress, such as periods required for xylem element construction.

Unfortunately, the physiology underlying most of the above correlations has yet to be fully explored. The robust literature on plant water stress physiology (which has been sustained by a desire to create more drought resistant crops) recognized long ago that stress responses such as stomatal regulation (Ludlow 1980), regulation of root and shoot growth (Davies and Zhang 1991) and dissipation of excess radiation (Chaves et al. 2003) are dependent on the context and time course of the inciting water stress. Much early research in this area was performed on herbaceous plants, but there is evidence that the same is true for woody plants as well (Chaves et al. 2002). The most obvious example is the relationship between water stress and stem growth increment, which in many conifers is sensitive to both early and late summer water stress, while in many hardwoods is sensitive only to early season water stress (Hanson and Weltzin 2000, Hanson et al. 2001).

However, historic water stress physiology research focused principally on how drought-adapted plants survive water stress rather than why plants (both arid and mesic) die during drought. Thus, there is little known about what happens to most physiological processes (signaling pathways, carbon and nutrient allocation to growth versus reserves, etc.) when plants face extreme water deficits that exceed their ability to avoid or acclimate. In other words, most plant–water relations research has studied normal physiological responses and regulation (Chaves et al. 2003) rather than extreme physiological damage. Due in part to this difference in motivating question (how plants survive drought versus why plants die), the link between drought seasonality and physiological damage is relatively unexplored in the current plant mortality literature (i.e., McDowell et al. 2011). Yet, we contend that two key points emerge from historic drought literature: (i) water stress regulates a number of physiological processes besides transpiration and (ii) most of these processes such as fine root growth and stem xylem formation display seasonal phenology.

One of the best examples of the physiological repercussions of seasonal water stress on woody plants comes from the arid southwestern USA. Using a suite of water potential, photosynthesis, morphological and isotopic analyses, Schwinning et al. (2005*a*, 2005*b*) examined the effects of winter versus summer water exclusion on three desert species (two shrubs and one perennial grass) with different rooting depths. Winter drought influenced branch growth of both woody species, because growth took place primarily in the late winter/spring and used mostly carbon fixed during the fall through spring. Summer drought, while reducing photosynthesis, did not drastically influence growth or flowering, but severely affected plant water status of all species, regardless of rooting depth. Thus, in this cold desert system, carbon limitations to growth were imposed principally by winter drought, while summer drought placed severe stress on the hydraulic system (e.g., stress that could potentially lead to hydraulic failure). While it is unlikely that this seasonal dichotomy is broadly generalizable, particularly to non-water-limited systems, these results highlight the temporal context of water stress physiology.

Taken together, these initial studies begin to reveal the complex interactions between drought timing and plant physiological damage. We posit that hysteresis and timing dependence of drought impacts on plants are likely general phenomena within seasonal ecosystems, both because stress responses are temporally dependent on their initiating cause and also because many normal processes such as fine root growth, phloem growth and xylem repair are seasonal and thus likely have windows of vulnerability.

Vegetation mortality during drought: incorporating the ecohydrological context

As suggested by recent drought seasonality research, the context of drought matters for our understanding of drought-induced mortality. This point is particularly important, given that the hydrological as well as physiological context in which plants are living will change over the next century. In order to better understand drought-related plant mortality in an era of changing climate, we must explore a variety of hydrological, ecological, and physiological processes and interactions that are currently poorly understood. We present below a heuristic diagram that highlights underappreciated processes and potentially critical unknowns in the translation of meteorological drought to plant health and plant mortality (Figure 3). We argue that better inclusion of the hydrological and ecological contexts of drought can inform the physiological processes leading to mortality. Almost all recent theoretical work on the physiology of mortality has assumed a type of 'steady-state' plant, a plant that does not have specific periods of growth, senescence or repair (McDowell et al. 2008, 2011, Sala et al. 2010), which has in turn shaped many of the experimental investigations of drought mortality (Adams et al. 2009, Anderegg et al. 2012*b*). To our knowledge, no studies have recreated in detail the soil moisture dynamics that led to recent mortality events, nor analyzed how those dynamics interact with plant physiology. The considerable literature on probabilistic modeling of soil moisture dynamics may be of use in this regard, particularly for contextualizing and defining the extremity of soil moisture excursion during droughts of interest (see Rodriguez-Iturbe and Porporato 2004). While current research strives towards defining the physiological thresholds that induce woody plant mortality, if we hope to regionally or globally model plant mortality, we must be able to translate climate inputs into physiologically relevant outputs, and must therefore consider the entire path rather than merely the endpoint.

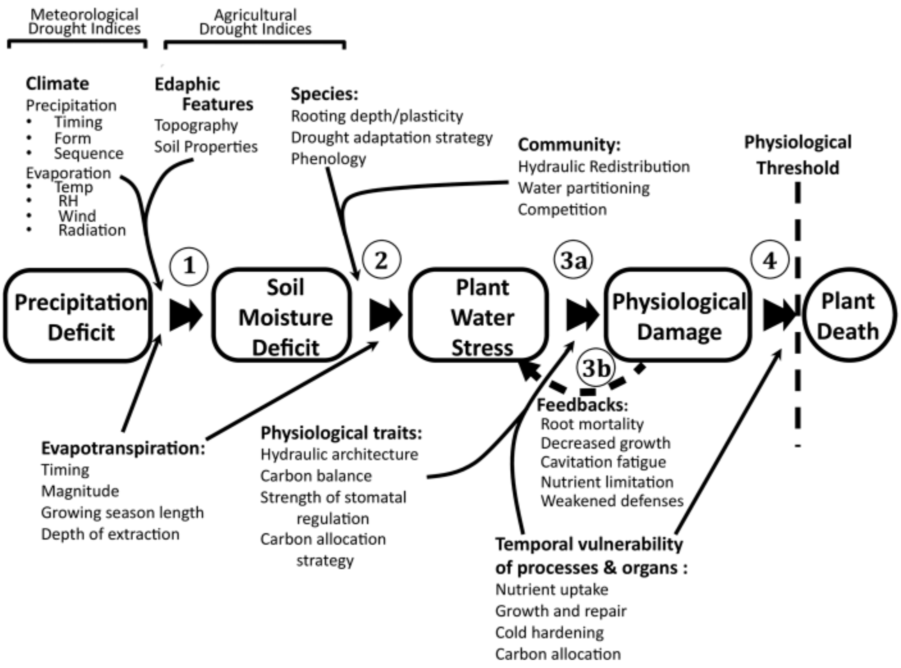

Figure 3. Conceptual diagram outlining how precipitation deficit is translated into plant physiological damage and ultimately plant mortality. Large numbered arrows represent the transition from one box to another and are discussed in the text, while small arrows indicate factors that influence large arrows. Meteorological drought (lack of precipitation) is translated into soil moisture deficit mediated by abiotic factors (climatic and edaphic factors influencing soil infiltration and evaporative demand) and biotic evapotranspirative withdrawal. Depending on plant and community characteristics and plant evapotranspirative demands, this soil moisture deficit can then cause plant water stress. The ways in which plant water stress are translated into physiological damage (defined as anything that results in physiological dysfunction even when water stress is alleviated) are then mediated by a number of physiological characteristics, processes and feedbacks that are temporally variable and vulnerable, and which are dependent on the characteristics (seasonality, duration, etc.) of the plant water stress. If a plant accumulates sufficient physiological damage, it cannot recover physiological function and dies.

We orient our discussion on a continuum from precipitation deficit to physiological damage (lasting physiological dysfunction) that eventually crosses a threshold leading to vegetation mortality (Figure 3). This continuum likely represents a transition from processes that are system or region specific to processes that are often species or even individual specific.

Evaluating the impacts of drought begins quantitatively with an assessment of meteorological drought, the precipitation deficit of a given period compared with the historical levels. Meteorological drought can be assessed over many time intervals. For instance, SPI calculates this anomaly compared with at least a 30-year climatological period (fit to a gamma distribution and transformed to a normal distribution), and the anomaly period can be assessed over time periods of 1 month to multiple years (McKee et al. 1993). Although regional downscaling remains difficult, all current climate models simulate precipitation and can thus be used to project precipitation deficit as a meteorological foundation for modeling drought effects.

How meteorological water deficit translates into soil water deficit must then be considered (Figure 3, arrow 1). This translation involves both an abiotic component (the nature of the precipitation supply, edaphic features and evaporative demand), and a biotic component (the nature of the evapotranspirative demand). Many agricultural drought indices, such as the PDSI (Palmer 1965; Alley 1984), build on precipitation anomalies to model soil water deficit by incorporating the effects of soil properties and, critically, estimates of vegetation ET based on temperature, radiation, humidity and wind. While these estimates of soil water deficit are useful for informing ecological impacts of drought, they often show significant regional biases and are not particularly well-suited to many ecosystems, especially forest ecosystems. The ET estimates are often based on well-watered agricultural fields in the midwestern USA and may not be particularly accurate in more arid or seasonal ecosystems (Alley 1984). Topographical effects on runoff and infiltration, especially in mountainous areas, are seldom included in these indices. Many of the indices, including PDSI, do not account for snowfall in an accurate manner, leading to large overestimates of ET and runoff during the winter. Meanwhile, seasonal growth of many temperate ecosystems, particularly deciduous systems, can lead to little ET during cold months and large ET during spring and summer months. Additionally, differences in functional rooting depths and plasticity in water source use between plants in various systems influences from where in the soil column water is extracted, which in turn can influence soil moisture infiltration and movement dynamics (Rodriguez-Iturbe and Porporato 2004, Schwinning et al. 2005*a*).

Thus, extant second-order drought indices—indices that build on meteorological drought to model water availability for purposes such as agriculture or water management (e.g., PDSI, Palmer Hydrological Drought Index)—cannot be assumed a priori to be indicative of the soil moisture deficit experienced by woody plants. We argue that estimates of soil water deficit for ecological measures of drought will need to go beyond agricultural drought indices to account for seasonality, timing and sequence of precipitation, the timing of plant ET and plant water uptake characteristics (Figure 3, arrows leading into 1). In systems with limited topography where there is no vertical partitioning of soil water by plant species or plant functional types, a simple parameterized bucket model such as a modified PDSI may be sufficient for regional approximations of an 'ecological' drought index. However, in topographically complex systems and/or systems with vertically partitioned water acquisition strategies, more complex (and computationally intense) hydrological models with multiple soil layers such as the Variable Infiltration Capacity (VIC) model (Liang and Xie 2001) must serve as the hydrological basis for an accurate ecological drought index, which can then be modified to account for biotic water use factors. Because most of these biotic processes are often described at the ecological community or 'plant functional type' scale (e.g., Sitch et al. 2008), it could be possible to develop an ecological parameterization of ET based on average values for large-scale cover types combined with vegetation-type rooting depth data from global databases (e.g., Jackson et al. 1996).

Further translating soil water deficits into meaningful plant water stress (Figure 3, arrow 2) is a challenging and largely unstudied area, especially with regard to woody ecosystems and at regional scales. Many plant species characteristics as well as plant community characteristics are likely to mediate whether a plant actually 'experiences' water stress at a given level and spatial distribution of soil moisture deficit. Root depth as well as plasticity of root depth and growth again are likely to be very important in determining a plant's vulnerability to moisture deficit (Jackson et al. 1996, Rodriguez-Iturbe and Porporato 2004). Species and systems that have adapted to growing season drought by developing deep roots (particularly groundwater-dependent ecosystems, Eamus and Froend 2006) or communities where vertical hydraulic redistribution is important should withstand similar levels of surface soil water deficit better than those communities with shallow rooting depths. However, deep-rooted plants often use groundwater to sustain ET during drought but require shallow moisture for growth (Miller et al. 2010) and may be susceptible to sustained and multiyear drought that depletes deep water supplies (or drought and overexploitation of groundwater, Froend and Drake 2006). Meanwhile, shallow rooted communities may be most vulnerable to severe summer drought, but less susceptible to protracted but moderate drought due to their ability to capitalize on smaller water pulses. Drought adaptation strategies (e.g., stomatal response, hydraulic architecture) and phenology (e.g., dormancy) also play a role in mediating drought stress (Allen et al. 2010).

Because individual and species characteristics increasingly mediate the final steps in the continuum (Figure 3, arrows 2, 3a/b and 4), forest mortality is fundamentally species specific. However, when and to what extent plant community interactions influence the translation of soil moisture deficit to plant water stress is a major area of uncertainty that warrants future research. In systems with strong water resource partitioning, plant water stress must be considered on a species, or at least functional type basis. In systems with less resource partitioning, a community-based approach may be more feasible.

For example, in systems in which vertical hydraulic redistribution is prevalent, the water status of many shallow rooted species may be entirely dependent on the dominant tree species that performs the hydraulic lift (Dawson 1993). Meanwhile, in plant communities that do not partition water, water status of one species during drought may be heavily influenced by competition with other species. Competition can vary by time and water resource (Ryel et al. 2008), such that abundant shallow water following significant precipitation could be rapidly taken up by multiple species and used for growth and nutrient uptake, while deeper soil water used to sustain function during drought might be used less competitively.

The next step from water stress to physiological damage that can ultimately lead to mortality (Figure 3, arrows 3a and 4) is currently an active area of research. Yet we suggest that, because not all water stress is created equal, research into the mechanisms of drought-induced mortality could be informed by an understanding of the temporal context of water deficit and therefore temporal and spatial soil moisture dynamics (things that influence arrows 1 and 2). Timing and severity of water stress could significantly mediate processes such as carbon allocation between growth and carbohydrate reserves (Galvez et al. 2013), as well as hydraulic processes such as vessel cavitation and refilling (McDowell et al. 2011). For species that are accustomed to withstanding drought such as the piñon pine (*Pinus edulis* Engelm.) in the southwestern USA, how water stress translates into accumulated physiological damage may be more than a question of drought length. Mortality causing droughts for arid-adapted plants are likely to be multi-year events that involve cycles of damage and repair, seasonal xylem and root growth, bud and foliage growth or cold hardening. On the other hand, for less drought-adapted species, drought mortality may be more a matter of what processes and tissues are vulnerable when acute drought strikes (Galvez et al. 2013).

Moreover, feedbacks of physiological damage to increase plant water stress, particularly over multiple years, may prove critical to explaining some recent mortality events (Figure 3, arrow 3b). For example, inhibition of new xylem growth (Anderegg and Callaway 2012), xylem cavitation fatigue (Hacke et al. 2001, Anderegg et al. 2013*c*) or increased fine root mortality (Anderegg et al. 2012*b*) may leave a tree more vulnerable to drought the following year. In particular, damage that limits a plant's ability to make use of water or nutrients when they briefly become available again could interact with multi-year drought, infestation dynamics or other stressors to cause system failure, akin to Manion's slow decline framework (Manion 1991), but not well-captured in a carbon starvation and hydraulic failure framing (Anderegg et al. 2012*a*). Finally, the accumulated physiological damage crosses some threshold or thresholds that initiate plant mortality (Figure 3, arrow 4). We suggest, however, that because long-lived woody plants are inherently memory- and inertia-laden (Franklin et al. 1987, Manion 1991, Suarez et al. 2004), drought characteristics and history may in fact influence these thresholds via accumulated physiological damage.

Conclusions

Future research at all stages along the continuum between meteorological drought and plant die-off is necessary in order to develop a stronger understanding of how drought kills plants. We address below, however, several underappreciated and promising areas in which research is needed. The first is in the species and community characteristics that mediate the translation of soil moisture deficit to plant water stress (Figure 3, arrow 2). Before we may generalize important processes to the regional or global level, there is a significant need for information on the basic functional characteristics such as rooting depth and rooting plasticity of vulnerable plant species and in generalizing what communities are likely to exhibit various interspecies interactions (hydraulic redistribution, resource partitioning, resource competition, etc.) as well as the relative strength of those interactions. Considerable effort has already been spent in understanding root distributions (e.g., Jackson et al. 1996), but there remain large unknowns about plant and community behavior at the extremes of plant water stress. Critically, it is unknown whether most observations of plant rooting depth and plasticity measured under normal conditions remain true under severe water stress.

A closely related area of uncertainty is the role of adaptation and acclimation to spatially varying climatic conditions in determining a plant's vulnerability to drought. Relatively plastic traits such as tree height, root/shoot or root/leaf area index ratios allow trees to acclimate to water stress over long time periods, and community characteristics such as stand density can alter the net evapotranspirative demand. But how finely tuned are most trees and communities to their environment? Do these acclimations prepare a tree for drought extremes, or merely for differences in mean climate? One way to explore such questions as well as many others would be to install rainout experiments at multiple sites across the geographic distribution of a species and a precipitation gradient. For example, the monsoonal to non-monsoonal hydrological gradient examined by Williams and Ehleringer (2000) would provide an opportunity to study the drought responses of the same species adapted to different hydrological regimes. This approach would be most effective if also combined with a technique that is prevalent in current extreme event ecology (e.g., Kreyling et al. 2008, Jentsch et al. 2009) but not as yet in most forest mortality experiments: tailoring precipitation manipulation to the long-term distribution of precipitation at the particular site. Rather than excluding an arbitrary percentage of rainfall (e.g., 45%, Pangle et al. 2012; 50%, Anderegg et al. 2012*b*; 33%, Hanson et al. 2001), rainfall manipulations recreating a specific drought type (i.e., 100-year return interval summer drought) could make experimental results directly relevant to regional projections of future climate even before we fully understand the physiology of drought-induced mortality.

While difficult to undertake, large rainfall manipulations have previously yielded rich insights into tree response to drought (Hanson 2000, Limousin et al. 2009), particularly tree growth and the susceptibility of different species to drought (Hanson et al. 2001, Ogaya and Penuelas 2007). A widely geographically replicated precipitation manipulation would likely be labor and funding intensive, but would allow quantification of the strength of community, morphological and physiological traits that mediate much of the translation of precipitation deficit into plant physiological damage (Figure 3, arrows 1, 2 and 3a). It would also give us an estimate of the plasticity of such traits across a landscape, and thus an indication of what processes we can expect to drive the spatial variation in future mortality events—whether such variation is due to spatial differences in climatic conditions with respect to historic distributions or to fundamental plant physiological limits, and whether plant community, morphological and physiological acclimation are important mediators of this variation. Some of these questions, such as the role of drought severity relative to mean climate versus fundamental physiological limits, may be addressable in more tractable experiments such as carefully controlled greenhouse experiments on trees grown under different watering regimes or common garden experiments that out-plant identically grown trees into different environments.

Taxonomic focus of such research should be placed either on species currently undergoing die-off or foundational plant species that define large ecotypes and whose mortality would hold large ecological consequences. Geographically, emphasis might be placed on systems that have already demonstrated susceptibility to drought-induced mortality and/or areas that are predicted to increase in aridity (Figure 2) as regional precipitation modeling becomes more accurate. As illustrated by Figure 1b, drying areas are likely to experience disproportionately more and more severe droughts than other areas during the coming century due to the increase in temporal climate variation.

A second promising research area is the physiological mechanisms underlying the associations between the temporal context of water stress and tree mortality. As demonstrated by some of the drought seasonality literature, retrospective time-of-death dendrochronological studies can be extremely useful for identifying drought characteristics that are associated with mortality (Bigler et al. 2007). And, in species that do not lend themselves to dendrochronological work, analyses of the spatial variation in death can serve the same function (McAuliffe and Hamerlynck 2010, Anderegg et al. 2013*a*). However, in addition to being relatively rare, such studies have yet to be put to productive use in guiding physiological investigation. Such information can and should help formulate testable hypotheses about the time-course of water stress and the physiological mechanisms of mortality, both in the oft-discussed role of drought length and severity (McDowell et al. 2008, Allen et al. 2010) and in the role of drought seasonality. For instance, what little evidence exists suggests that spring and/or summer drought are associated with mortality in many species (Villalba and Veblen 1998, Schwinning et al. 2005*a*, Bigler et al. 2007, Anderegg et al. 2013*a*), except those most drought adapted (McAuliffe and Hamerlynck 2010). This suggests that processes such as early season stem xylem and fine root growth, as well as mycorrhizal activity, might be highly susceptible to water stress, or produce particularly large physiological consequences when curtailed. There is therefore a need to both expand research relating drought characteristics to extant mortality (time-resolved remote sensing studies that indicate not just where trees die but when they die could be particularly useful) and apply this research to the growing number of greenhouse drought physiology experiments (Zeppel et al. 2011). Additionally, as we gain an appreciation for the ubiquity of lagged and multi-year mortality events (Anderegg et al. 2013*c*), there is increasing need to explore feedback mechanisms that may drive mortality even after normal conditions have returned (Figure 3 arrow 3b). This will require prolonging the monitoring of in situ or greenhouse manipulations, as well as explicitly monitoring changes to hydraulic capacities, root growth and mortality, nutrient uptake and defensive capabilities in a subset of trees that have been re-watered following drought manipulation.

Future research into the translation of meteorological drought into plant physiological damage is necessary to improve existing models of how plants will respond to climate change. Current dynamic global vegetation models generally lack mechanistic detail in simulating mortality (McDowell et al. 2011), and are far from incorporating complex dynamics involving drought characteristics and vegetation. This greatly restricts their ability to predict vegetation shifts due to rapid drought-related mortality. While climate envelope models can often include variables of precipitation seasonality (e.g., Rehfeldt et al. 2009), they too are limited in their treatment of many processes that may define species responses to climate change, such as rapid mortality due to climate extremes (as opposed to climate means) (Pearson and Dawson 2003, Thuiller et al. 2008).

We argue here that forthcoming changes in drought due to climate change as well as evidence of drought effects in recent widespread vegetation mortality highlight the need for a more nuanced understanding of how drought affects plants. The seasonality, form, timing and sequence of precipitation that determine available soil water, as well as the responses of plant species to soil water deficit, are all critical components of an ecologically meaningful measure of drought stress. We emphasize that the flow of information about various processes need not move along the continuum only in the direction of the arrows in Figure 1, which represent merely the translation of precipitation deficit into physiological stress. For instance, physiological work could find that hydraulic redistribution does not play a significant role in certain systems during extreme drought, and thus help define what processes to include in hydrological models. Future research in this area will require interdisciplinary collaboration between climatologists, hydrologists, ecologists and plant biologists. Nonetheless, this understanding could be critical in projecting ecological drought impacts and managing ecosystems for climate change.

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Conflict of interest

None declared.

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