



A carcass of an elephant that succumbed to drought is seen under a tree in Hwange National Park, in Zimbabwe, on 12 November 2019.

REVIEW

Hanging by a thread? Forests and drought

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Trees are the living foundations on which most terrestrial biodiversity is built. Central to the success of trees are their woody bodies, which connect their elevated photosynthetic canopies with the essential belowground activities of water and nutrient acquisition. The slow construction of these carbon-dense, woody skeletons leads to a slow generation time, leaving trees and forests highly susceptible to rapid changes in climate. Other long-lived, sessile organisms such as corals appear to be poorly equipped to survive rapid changes, which raises questions about the vulnerability of contemporary forests to future climate change. The emerging view that, similar to corals, **tree species have rather inflexible damage thresholds, particularly in terms of water stress, is especially concerning. This Review examines recent progress in our understanding of how the future looks for forests growing in a hotter and drier atmosphere.**

No tree species can survive acute desiccation. Despite this unambiguous constraint, predicting the death of trees during drought is complicated by the process of evolution, whereby the fitness of tree species may benefit equally from traits that either increase growth or enhance drought resilience. Complexity arises because improving either of these two beneficial states often requires the same key traits to move in opposite directions, which leads to important trade-offs in adaptation to water availability. This conflict promotes strategic diversity in different species' adaptations to water availability, even within ecosystems. Understanding how the diversity of tree species will be affected by future droughts requires a detailed knowledge of how the functions of different species interact with their environment. Temperature and atmospheric CO₂ concentration are fundamental elements that affect the water relations of all tree species, and the rapid rise in both of these

potent environmental drivers has the potential to markedly change the way trees behave during drought. **The future of many forest systems will be dictated by how these atmospheric changes interact with tree function.**

Is rising CO₂ good for trees?

A primary example of conflicting selection pressures on trees can be seen in the basic operation of photosynthesis. Achieving a higher photosynthetic rate requires higher leaf porosity to CO₂, but a higher leaf porosity causes a parallel increase in water loss, which is detrimental during an environmental water shortage. This trade-off plays a fundamental role in structuring terrestrial plant evolution and ecology (1), emphasizing the potential for rising CO₂ levels and temperatures to affect forests during drought conditions. There has been a change in perspective over the past 10 years, from expectations of enhanced forest growth under enriched atmospheric CO₂ to the more sobering prospect of damage or decimation of standing forest caused by an increase in the drying rates of leaves and soil in a hotter climate (2).

Early discussions of plant responses to rising atmospheric CO₂ (3) focused largely on CO₂ fertilization, a concept that refers to the potentially beneficial effects of atmospheric CO₂ en-

richment on plant growth. Under controlled conditions, elevated CO₂ can theoretically increase plant growth by stimulating photosynthesis or by increasing the water use efficiency (WUE) of plants (the ratio of carbon intake to water lost by leaves). Both of these behaviors depend on the active response of stomata (microscopic valves on the leaf surface that regulate gas exchange) to CO₂ (4). Long-term studies of tree growth under artificially enhanced atmospheric CO₂ suggest that improved photosynthetic performance at elevated CO₂ can translate into increased growth (5, 6), but there is little evidence of any CO₂-associated growth enhancement in natural forest conditions (7, 8). This is thought to be either because of colimiting resources for plant growth, such as water and nitrogen (9–11), or because stomatal closure in response to rising CO₂ increases WUE (12, 13) at the cost of enhanced assimilation and growth. Controversially, it has been suggested that the impacts of future drought stress may be ameliorated by higher atmospheric CO₂ if WUE is sufficiently enhanced (14, 15). The validity of this concept depends largely on the effects of rising temperature on WUE and plant survival during extended rainfall deficits.

Rising temperature and drought

Ultimately, the impact of elevated CO₂ on forest trees is likely to come down to the intensity of the CO₂-associated temperature rise and its effect on trees' water use. This is because the distributions of tree species, in terms of water availability, broadly reflect their intrinsic tolerance of water stress (16–18). **In other words, species from rainforests to arid woodlands face similar exposure to stress or damage during periods of drought (19). Hence, any increase in the rate of soil drying caused by elevated temperatures is likely to lead to increasing damage to standing forests during drought.**

Improved tree WUE could ameliorate the temperature effect, but this argument remains highly debatable because most reports of improvements in tree WUE with rising atmospheric CO₂ refer to intrinsic WUE, a value that converts to real plant water use only with a knowledge of leaf temperature and atmospheric humidity (20). Thus, rising atmospheric temperature and the associated increase in evaporative demand is likely to reverse the improvements in tree WUE that are proposed to result from higher CO₂. Recent evidence suggests that this is the case, with observations of reduced global tree growth and vegetation health associated with enhanced evaporative gradients and warming temperatures (21, 22).

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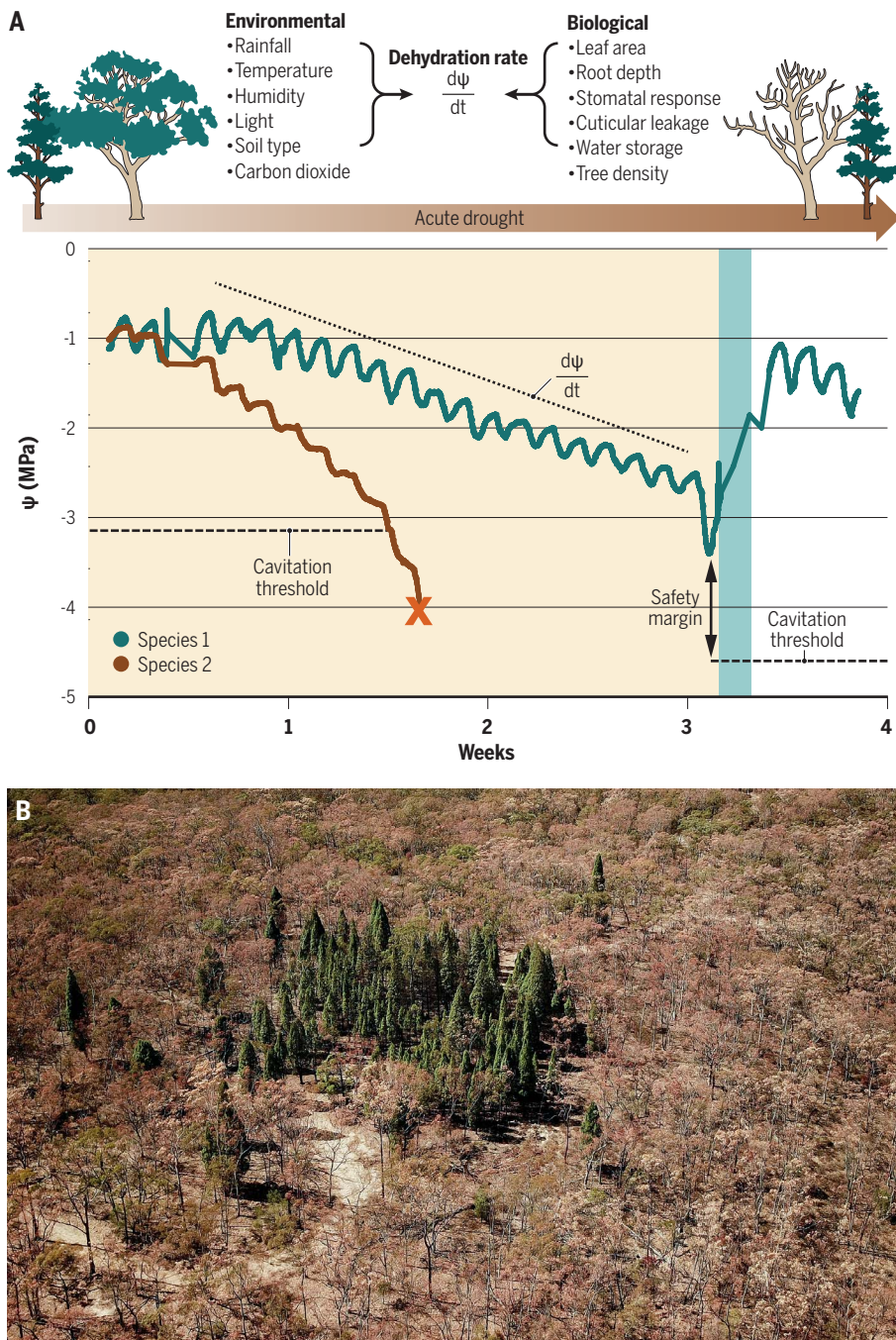


Fig. 1. Theoretical and observed impacts of drought on co-occurring tree species. (A) A representation of the impact of drought on two tree species with different thresholds for drought-induced vascular damage. Different xylem cavitation thresholds determine the water potential (Ψ : water stress intensifies as water potential becomes more negative) causing tree mortality. Two lines indicate the oscillating water stress between day and night as the two species (indicated by small tree icons) dehydrate after the cessation of rainfall (data are from two trees from a dry forest site in Tasmania, Australia). The cavitation threshold and the rate of drying ($d\Psi/dt$) both determine how many days into an acute drought each species will die. The taller species, which is more vulnerable to cavitation and faster drying, dies (indicated by an orange X) in week 2, whereas the shorter species survives until rainfall (indicated by the blue rectangle in week 3), enabling the tree to recover hydration. The proximity between the cavitation threshold and the lowest water potential during drought is known as the hydraulic safety margin. The dehydration rate is a product of a set of environmental and biological factors, many of which interact. Increasing temperature increases the rate of drying both directly and by interaction with biological factors, whereas CO_2 has the potential to reduce dehydration by its biological interaction with stomata and the photosynthetic rate. **(B)** Recent (2019) drought-induced mortality of native forest in eastern Australia. Large-scale mortality of *Eucalyptus* trees (seen as recently killed dry canopies) contrast with the more cavitation-resistant conifer species (*Callitris*). The observed pattern of mortality can be explained by the processes described in (A).

In combination with the size and allometry of trees, the dynamic behavior of stomata and their regulation of water loss from tree canopies largely dictates the course of plant and soil dehydration. During atmospheric or soil water deficit, stomatal closure limits transpiration, preserving water content in the soil and tree (23). However, this well-characterized behavior becomes unpredictable when leaf temperatures are substantially elevated, with stomata permitting greater water loss than expected during both day (24, 25) and night (26–28). Additionally, plants continue to lose some residual water after the stomatal valves are closed, and this residual leakiness also appears to increase with elevated temperatures (29–31). Herein lies perhaps the greatest threat for forests subjected to warming atmospheric temperature, because warmer plants not only consume water faster when soils are hydrated, but they also have a diminished capacity to restrict water loss during drought, thereby exhausting soil water reserves.

Tree mortality is most commonly observed when drought and high temperature are combined (32–34), likely owing to the compounding effects of the increased evaporative gradient and the increased porosity of leaves at high temperature. The inevitable rise in the intensity and/or frequency of such events as global temperatures climb (35) has already been associated with an increase in tree mortality globally (36), especially in larger trees (37), which raises a grave concern about the capacity of existing forests to persist into the future. Establishing the magnitude of this threat is an important challenge that requires a fundamental understanding of how water deficit leads to tree mortality.

Much research has focused on the possible mechanisms behind tree death during drought. Possible mechanisms primarily include vascular damage, carbon starvation, and enhanced herbivory (38–42). These studies reveal the complex nature of tree death, where the moment of death is difficult to pinpoint or even define (43). Although it remains difficult to connect cause and effect at the point where drought injury becomes lethal, strong and consistent correlational data from trees suffering mortality or growth inhibition across the globe point unequivocally to the plant water transport system as a fundamental axis dictating the long-term survival of trees (44–47).

Forests on a thread

The massive woody structure of trees provides mechanical support for their photosynthetic crowns; however, the matrix of microscopic threads of water that is housed within the porous woody cells of the xylem is even more fundamental to tree survival. These liquid threads provide a highly efficient mechanism to transport large quantities of water over

long distances under tension, from the roots to the leaves. Relying on this passive pathway to replace the water transpired by leaves has the major drawback that the internal water column in trees becomes increasingly unstable during times of water stress, as the tension required to draw water from the soil increases. Rising xylem water tension (conventionally described as an increasingly negative water potential) during intensifying soil water deficit exposes a universal vulnerability in trees to xylem cavitation during drought (48). This occurs when the water potential in the xylem becomes sufficiently negative to draw minute bubbles through the cell wall into the lumen of the xylem cells, at which point the small bubbles trigger a very rapid formation of voids (in a process termed xylem cavitation), which subsequently become air bubbles or embolisms that block water flow. The vulnerability of a species to cavitation is conventionally quantified as a P50, which is the water potential that causes 50% of the xylem to cavitate. The most extreme form of xylem damage occurs when a feedback develops, as increasing xylem water tension caused by soil water deficit leads to xylem cavitation and blockage, further exacerbating the tension in the xylem, and ultimately killing the plant by completely severing the connection between soil and leaves. This process is likely to occur under acute water shortage (49, 50), killing plants (51) before the return of rainfall. Although this type of acute drought-induced mortality may not describe all instances of tree death during water shortage, the existence of quantifiable biophysical thresholds defining specific survival limits for different tree species has greatly enabled our capacity to understand tree mortality and distribution (42) and provides a robust basis for modeling future effects of drought (52, 53). Many aspects of the xylem cavitation process remain uncertain because of difficulties associated with measuring water flow in a system that operates under high tension (54); however, new methods are providing more clarity and confidence to our understanding of the critical sensitivity of plant vascular systems to damage under water stress (55, 56).

The water transport system in plants lies at the center of interactions between rainfall, soil water, carbon uptake, and canopy dehydration, which makes xylem hydraulics an obvious focus for understanding and predicting the thresholds between tree death or survival during exposure to drought and heat stress. Xylem vulnerability to cavitation varies markedly among species (19), not only indicating sensitivity to water deficit but also enabling the quantification of functional impairment if trees are not immediately killed by drought (43, 50). Although a knowledge of cavitation thresholds informs the triggering of tree damage, the rate of tree dehydration indicates

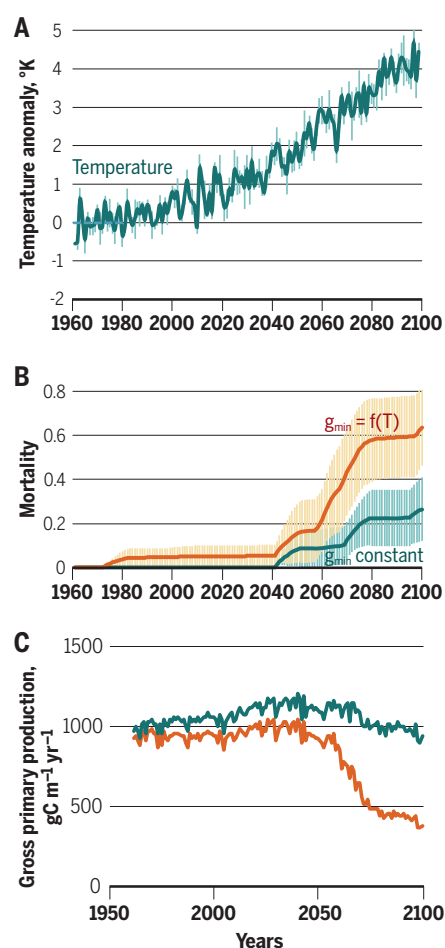


Fig. 2. A mechanistic hydraulic model of future drought-induced tree mortality. (A to C) Sensitivity of a process-based hydraulic model to predict tree mortality and gross primary production (GPP) under the representative concentration pathway (RCP) 8.5 climatic scenario. The model was parametrized with data for a population of a typical temperate coniferous tree, displaying a Gaussian distribution of cavitation resistance (mean xylem vulnerability of P50 = −3.5 MPa, variance = 0.3). Daily climatic data from five Eurocode climate models were used to simulate tree transpiration, soil water content, xylem water tension, and xylem cavitation. The lethal threshold of cavitation was set to 88%. The model forecasts an increase in tree mortality with the rise of temperature caused by predicted climate change. The predicted collapse of the tree population and forest GPP was more drastic when a more realistic temperature-dependent increase in the cuticular leakage (g_{min}) (108) was implemented in the model [$g_{min} = f(T)$; orange line] compared with a static cuticular leakage [g_{min} constant (gC); green line]

how quickly that damage threshold is approached during drought. The characteristics of tree species that are classically associated with adaptation to water availability—such as rooting depth, water storage, stomatal behavior, root and canopy area, and leaf phenology—can be predictably integrated to determine how

plant water content will respond to environmental conditions. The combination of environmental conditions with biological attributes results in a highly tractable framework (Fig. 1) for understanding the dynamics of mortality or survival during slow dehydration (57).

Despite the existence of sharp xylem cavitation thresholds, post-drought legacies of damage and mortality of trees are often protracted over months or years after peak drought intensity (58), which implies that more-complex interactions between plant water and carbon status are also important in the recovery process. Post-drought rainfall enables trees that have not suffered catastrophic xylem failure to replace drought-damaged xylem by woody regrowth (50), but this is highly costly and can lead to rapid depletion of tree carbon reserves (59), leaving them vulnerable to insect attack [although insect interactions remain unpredictable (60)] unless conditions remain favorable. Recovering, drought-damaged trees may invest disproportionately in new leaves rather than xylem growth (61), potentially making them more sensitive to subsequent water shortage because of reduced xylem water delivery. Although much remains to be learned about the physiology of plant hydraulics, the principles of hydraulic failure provide a solid framework for understanding and predicting mortality, damage, and recovery under a diversity of drought scenarios.

Modeling forest mortality in the future

Diverse approaches have been employed to predict how forests are likely to respond to hotter and potentially drier and more-variable conditions in the future. Progress toward understanding the mechanisms that lead to tree mortality has seen a movement away from traditional correlative niche models (62) in favor of more process-based modeling. Incorporation of theoretically derived mortality modules into dynamic vegetation models has the potential to capture drought mortality, but these models are currently rather unsophisticated and unreliable, particularly when applied outside the domain of calibration (63, 64). At the more functional end of the modeling spectrum are recent attempts to explicitly model drought mortality triggered by hydraulic failure (or associated carbon starvation) (52). In particular, the combination of tree hydraulics with the principles of stomatal optimization (assuming that stomatal behavior regulates assimilation and transpiration to achieve a maximum difference between photosynthetic gain and the risk of hydraulic damage) is emerging as a promising structure for models of land surface gas exchange (65–67). Although the mathematical rendering of physiological processes to predict forest productivity and tree survival provides a powerful approach for modeling the performances of species or genotypes in a range

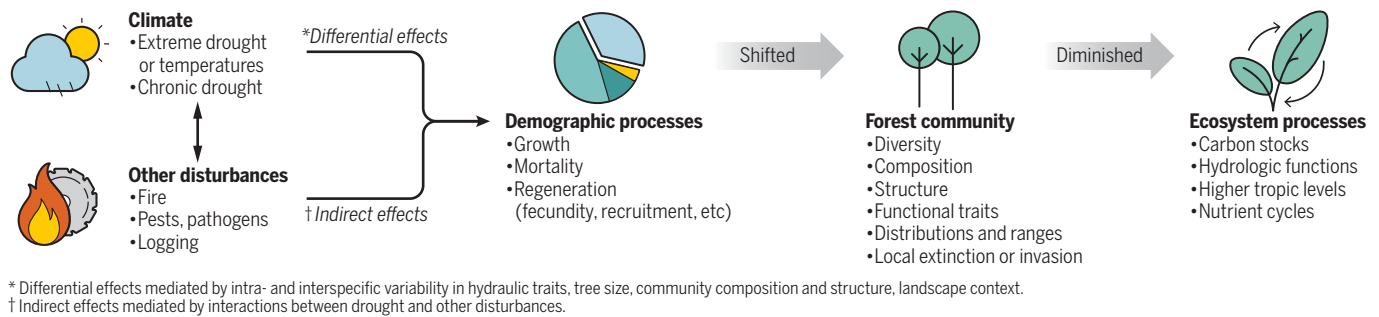


Fig. 3. Interactions between climate and forest community. Schematic of how climatic variability interacts with disturbance to affect tree demographic processes, which may result in shifted community diversity and species distributions as well as ecosystem processes.

of future climates, a limitation in using these mechanistic formulations is that relatively small changes in parameterization or biological assumption can substantially change predictions (Fig. 2). To capture this uncertainty, recent studies have spanned a range of assumptions, particularly with regard to how trees might acclimate to drought, in order to reveal a range of possible scenarios (15, 68).

Modeling provides the most credible view of how forests may cope with different intensities of future global warming, with most models suggesting large-scale mortality, range contraction, and productivity loss through this century under the current warming trajectories (Fig. 2). Greater precision as to the nature and pace of forest change is urgently needed, requiring dedicated work on key knowledge gaps (69) that limit model precision accuracy. These gaps are apparent in even the basic physiological processes of trees, such as stomatal behavior, tree water acquisition (70), and interactions between water and carbon stores in trees (67). Critical components such as the dynamic connection between trees and the soil are highly simplified in models owing to a lack of knowledge about water transfer and storage in the roots under conditions of water stress. The triggering of mortality is also highly oversimplified because the negative feedbacks likely to operate during acute tree stress are difficult to capture in a model. Avoiding this complexity, a commonly used proxy for lethal water stress is the point of 50% xylem cavitation in stems (Fig. 2). Although this threshold is not strictly correct (because trees can survive with a 50% impairment of water transport capacity), it does provide a readily measurable indication of rapid vascular decline incipient to complete failure of the vascular connection between roots and leaves. More-precise understanding of the post-drought transition to recovery or tree death is needed to accurately represent the legacy effects of drought in large-scale models.

Acclimation of forest in situ

The long generation time and slow growth of trees present a formidable challenge to survival in the face of rapid environmental change, particularly increases in aridity and the fre-

quency of extreme-drought events. Avoidance of local extinction (extirpation) in tree species is possible by two non-mutually exclusive mechanisms: (i) migration tracking the ecological niches to which they are adapted or (ii) adaptation and acclimation to novel climate conditions and persistence within their current range. Species distribution models based on climatic envelopes have predicted pronounced range shifts in tree populations over the next century; however, this mechanism of survival is contingent on the capacity of species to achieve rapid migration (71), and few tree species are likely to disperse rapidly enough to keep pace with the current rate of climate warming (72). The persistence of tree populations exposed to increased aridity in their current range will depend on adaptation and acclimation to higher intensities of plant water stress. Given the rapid pace of climate change, adaptation of organisms with such long generation times appears unlikely to enable persistence in most species.

The potential for rates of adaptation to keep pace with environmental change depends on a number of factors, including the levels of genetic diversity present in critical traits, differentiation between leading and trailing edge populations, and gene flow between populations. Very few studies have examined the genetic diversity present in important plant hydraulic traits, with the most-comprehensive studies focused on temperate deciduous and conifer species (73–75). The results of these studies suggest that genetic diversity of traits, such as cavitation resistance, is low in pine species (74) but may be higher in temperate angiosperms such as beech (73, 76). Overall, genetic diversity in hydraulic traits appears to be limited relative to the changes in intensity of water stress that are expected over the coming decades. This lack of genetic diversity across populations may limit the capacity for adaptation to increasing aridity in current distributions.

Acclimation by means of phenotypic plasticity presents another mechanism by which trees may adjust to novel climate regimes (77). Acclimation is dependent on trait plasticity in individuals and may occur over much shorter time scales than evolutionary processes such as adaptation. The acclimation of some phys-

iological and morphological traits in response to changes in temperature and drought stress is well documented. This includes the acclimation of photosynthesis, respiration, and leaf thermal tolerance to temperature (24, 71) and changes in resource allocation, such as sapwood-to-leaf ratio (78). For example, leaf shedding allows trees to rapidly reduce the leaf surface area available for transpiration and is a primary mechanism limiting water loss during drought. Studies examining intraspecific variation across precipitation gradients have shown that populations adjust to greater aridity through increasing sapwood-to-leaf ratios (79–81), increasing hydraulic capacity relative to leaf area deployed.

Acclimation in physiological traits related to drought tolerance is less well studied. However, the available data suggest that there is limited plasticity in key mechanistic traits. This is borne out in common-garden and reciprocal transplant experiments as well as throughfall exclusion experiments and studies of natural populations growing across aridity gradients (80, 82, 83). Low plasticity in hydraulic safety has also been observed with tree size (84), although the behavior of seedlings remains unknown. Pine species exhibit particularly low variation in cavitation resistance, with available evidence suggesting canalization of hydraulic traits, which constrains the capacity of pines to acclimate or adapt to drier conditions (74). Common-garden studies suggest that traits associated with hydraulic safety (Fig. 1) appear to be under strong genetic control (16, 81). This may be one reason why partial leaf shedding is a commonly observed response to drought, because higher plasticity in leaf area may assist trees in maintaining levels of water stress within the functional limits set by inflexible hydraulic failure thresholds. However, reducing leaf area comes at the cost of lowered productivity and growth rates, and it may adversely affect survival in trailing edge populations exposed to intense interspecific competition.

Communities and consequences

Although hydraulic failure may be sudden and pronounced, predicting the consequences of drought for tree populations and communities is more challenging than simply extrapolating

from models of hydraulic processes. This is because drought may also affect demographic processes beyond tree mortality and may interact with other disturbances. Stand-level interactions among individuals and species may attenuate or exacerbate drought impacts, and landscape-scale variations in topography, edaphic conditions, or forest-patch characteristics can modulate drought effects (Fig. 3). Moreover, current forest communities are responding to both extreme events, such as El Niño–Southern Oscillation (ENSO)–related droughts (85), and to directional changes in rainfall, such as decadal-long decreases in rainfall (86). What does seem certain is that these changes in forest composition and tree species distributions will have important consequences for the diversity and structure (69), hydrologic function (87), and carbon-storage potential (88) of future forests.

Interspecific variation in hydraulic and other traits is clearly linked to differential damage and mortality rates during extreme drought (47, 89, 90). However, other demographic processes or life history stages—such as fecundity, seedling recruitment, and tree growth—may also be affected, and species- or functional group-specific responses to drought may change community composition and functional traits over decadal time scales or even result in shifts among biomes, such as forests being replaced by shrublands (91). Regeneration dynamics are especially critical in mediating shifts between vegetation types or biomes (91), but, at this point, the data are too limited to generalize about how the likelihood of such shifts differs among forest types. For example, an extreme drought during the 2015 ENSO reduced seed rain of drought-deciduous tree species relative to evergreen trees and lianas in a seasonally dry tropical forest in Costa Rica (92). By contrast, in a semimoiest tropical forest in Panama, a 30-year record of leaf and fruit production showed elevated seed production during ENSO years that mirrors seasonal patterns, suggesting that the sunnier conditions that accompany ENSO favor fruit over leaf production (93).

Predicting or modeling the impacts of drought on forest communities is also complicated by interactions between changes in climate and interactions with other disturbance agents, such as fire (94), insects and pathogens (95), or logging (96). The catastrophic wildfires that have affected Australia in 2019 and 2020, after years of extreme drought, is just one such example of drought-fire interactions. Such interactions are also affecting forests in North America (97), Amazonia (94), and elsewhere (98). Increases in vapor-pressure deficit and temperature during drought dry out fuel, thereby increasing fire activity and the area that is burned (97). Drought-fire interactions may also cause tipping points and shifts among vegetation types in areas such as the southwestern Amazon (94). There, tree mortality is elevated during intense

fires experienced in drought years (94), resulting in altered microclimatic conditions and grass invasion into the understories, which further increases flammability and fire risk (94).

The identification of which trees and species within stands are most vulnerable to drought (37, 99) and of the factors that render certain stands within landscapes more susceptible to changing climates (100, 101) may inform both basic science and management strategies (69). Meta-analysis and theoretical models suggest that large trees are more likely than smaller trees to die during and after drought (37, 59). However, simple predictions of which size classes of trees die during drought may not hold in mixed-species forests, where different sizes of drought-weakened trees experience different levels of attack by host-specific bark beetles in idiosyncratic ways (102). Additional knowledge of community composition beyond tree size—i.e., size-species distributions—may help bridge predictions from the individual to the stand scale (69). Forest density may be an indication of competition for water, and trees growing at low densities may experience lower mortality rates (101) and less-pronounced reductions in growth during drought compared with those in higher density stands (103).

Advances in the remote sensing of proxies of plant stress, like canopy water content, may help us to monitor and map patterns at coarse geographic scales (104). These findings may guide silvicultural actions, such as selective thinning to reduce vulnerability to drought in managed forests (103). Finally, the diversity of hydraulic traits in forests has emerged as a property that helps explain ecosystem responses to climatic variability (105). Ecosystem fluxes inferred from eddy covariance measurements of forests with higher trait diversity of hydraulic traits appear more buffered against changes in soil water and vapor-pressure deficit compared with forests with low trait diversity (105), presumably because catastrophic failures of canopy dominants (Fig. 1B) are reduced. This underscores the idea that building large databases of hydraulic traits, rather than morphological traits such as specific leaf area and wood density, is a high priority to advance our understanding of forest vulnerability to drought (106).

Outlook

Drought is a natural phenomenon that plays a major role in limiting the distributions of species. However, the extremely rapid pace of climate change appears to be introducing enormous instability into the mortality rates of global forests (107). Instability and unpredictability are intrinsic aspects of the physiological processes that are linked to the drought-induced mortality process, whereby vascular damage is prone to failure and positive feedback, leading to tree death. Most models predict major damage to forests in the next century if current climate

trajectories are not ameliorated. Debate still remains as to the magnitude of stabilizing forces, such as tree acclimation and positive CO₂-associated effects on water use, but most observational data suggest that forest decline is well under way. Future improvements in physiological understanding and dynamic monitoring are needed to improve the clarity of future predictions; however, changes in community structure and ecology are certain, as are extinctions of tree species by the direct or indirect action of drought and high temperatures.

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