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Friend or foe? The role of biotic agents in drought-induced plant mortality

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Abstract Plant mortality is a complex process influenced by both biotic and abiotic factors. In recent decades, widespread mortality events have been attributed to increasing drought severity, which has motivated research to examine the physiological mechanisms of drought-induced mortality, particularly hydraulic failure. Drought-based mortality mechanisms are further influenced by plant interactions with biota such as neighboring plants, insect pests, and microbes. In this review, we highlight some of the most influential papers addressing these biotic interactions and their influence on plant mortality. Plant–plant interactions can be positive (facilitation), neutral, or negative (competition), depending on drought intensity and neighbor identity. For example, stand-scale mortality likely increases with basal area (an index of competition). However, the diversity of forest stands matters, as more diverse forests suffer less mortality from drought than species-poor forests. Dense forest stands also increase bark beetle attack frequency, which can exacerbate drought stress and mortality, particularly for fast-growing species with lower defense allocation. In some cases, however, drought stress can alleviate biotic attack, depending on feedbacks between plant and pest physiology. Finally, plant interactions with beneficial microorganisms can increase drought tolerance, reduce the likelihood of mortality, and even extend plant distributions into drier habitats. Our review suggests more work is needed in natural herbaceous plant communities as well as dry tropical ecosystems where mortality mechanisms are less understood. Overall, relatively few studies directly link biotic interactions with the physiological mechanisms of mortality. Simultaneous manipulations of biotic interactions and measurements of physiological thresholds (e.g., xylem cavitation) are needed to fully represent biotic interactions in predictive models of plant mortality.

Keywords Drought · Plant mortality · Facilitation · Competition · Plant–microbe interactions · Herbivory

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Introduction

The question of how plants die has long puzzled ecologists. Certain species are exceptionally long-lived (e.g., > 2000 years for *Sequoia sempervirens* and *Sequoiadendron giganteum*; Sillett et al. 2015), while others can go dormant for long periods of time only to restart metabolism and growth when optimal environmental conditions return (e.g., resurrection plants, *Selaginella lepidophylla*). An individual plant's progression towards mortality was described by Manion (1991) as a "death spiral" in which certain abiotic and biotic factors predispose, incite, or contribute directly to plant death (Fig. 1). Abiotic factors contributing to mortality include extreme events such as fire, windstorms, heat waves, flooding, and/or drought. Biotic factors can include the physiology, morphology, and life history of the individual plant as well as its interactions with other organisms, such as neighboring plants, herbivores, or microbes.

Recent widespread plant mortality has been attributed to hotter and more severe droughts that are occurring more frequently with climate change (Allen et al. 2010). This has motivated new studies to investigate the physiological mechanisms of drought-induced plant mortality, most of which point to thresholds of xylem cavitation—the formation and spread of minute air bubbles within xylem under extreme negative pressure—as the primary means of mortality (Adams et al. 2017). However, as Manion's

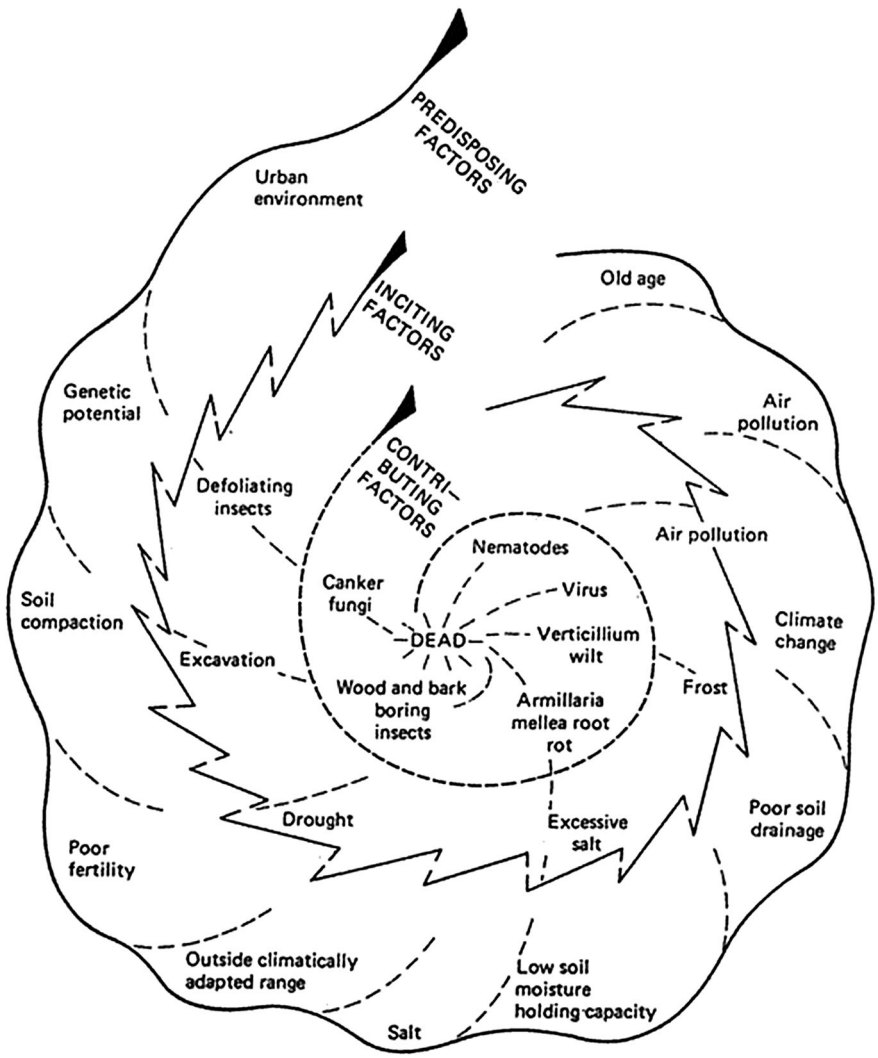

Fig. 1 Original "death spiral" from Manion (1991) describing biotic and abiotic factors leading to plant mortality. Reproduced from Prentice-Hall (Pearson)

"death spiral" suggests, such physiological mechanisms are only one part of a complex path towards mortality. Myriad other ecological interactions throughout an individual plant's life affect its resistance and susceptibility to drought.

In this review, we focus on biotic interactions and highlight some of the most recent influential studies of biotic agents (or mediators) of drought-induced plant mortality (Table 1). Specifically, we summarize how physiological mechanisms of drought-induced mortality may be influenced positively or negatively by plant interactions with (1) neighboring plants (e.g., competition and facilitation), (2) animals (e.g., insect pests), and (3) microbes (e.g., mycorrhizal fungi and endophytes). This review is not an exhaustive list of biotic interactions, but rather highlights the general importance of incorporating biotic interactions into our understanding and predictions of plant mortality.

Plant–plant interactions

Hydraulic failure via xylem cavitation is the principal physiological cause of plant mortality during drought. While the concept of carbon (C) starvation via stomatal closure was posited as a potential cause of drought mortality (McDowell et al. 2008), recent studies have generally not supported this concept as a direct mortality agent (Hartmann et al. 2013), although reduced C reserves sometimes occurs simultaneously with hydraulic dysfunction (Adams et al. 2017). Few studies have assessed how positive and negative interactions between neighboring plants influence those physiological mechanisms. This is surprising given the clear and opposing impacts that competitive (Young et al. 2017) and facilitative (Hisano et al. 2019) interactions can have on drought-induced plant mortality. The predominant effect of biotic interactions in a community (i.e., relative importance of competition vs. facilitation) can shift depending on drought intensity, local environmental conditions, and/or species identity (Sthultz et al. 2007; Ploughe et al. 2019). Understanding this complexity at broad

Table 1 Ten focal papers on the role of biotic agents in drought-induced plant mortality, highlighting their critical contributions to the field

Reference	Biotic interaction	Key contribution
Sthultz et al. (2007)	Plant—plant interactions	Interactions with neighboring plants can alleviate or exacerbate drought-induced mortality depending on species identity, life history stage, and environmental context
Young et al. (2017).	Plant—plant interactions	Competitive interactions may increase drought-induced mortality at a stand scale even under moderate water stress
Hisano et al. (2019).	Plant—plant interactions	Plant diversity reduces tree mortality in response to climate change through facilitative interactions
Gaylord et al. (2013)	Plant—animal interactions	Insect pests exacerbate drought stress and plant mortality, particularly for species with lower defense allocation
Jactel et al. (2012)	Plant—animal interactions	Drought can exacerbate or ameliorate stress caused by natural enemies depending on the pest's reliance on plant performance
He et al. (2017)	Plant—animal interactions	Drought predisposes herbaceous plants to herbivory-associated mortality and herbivory reduces drought resiliency of plants
Gehring et al. (2017).	Plant—microbe interactions	Plant associations with ectomycorrhizal fungi are heritable interactions that can ameliorate drought stress and mortality
Lau and Lennon (2012)	Plant—microbe interactions	Legacy effects of drought pre-condition microbial communities to enhance plant performance during drought
Afkhami et al. (2014)	Plant—microbe interactions	Endophyte infection can improve drought resistance and even extend the geographic distribution of plants into increasingly arid regions
Egerton-Warburton et al. (2007)	Plant—microbe interactions	Plant drought stress and mortality can be alleviated through shared fungal networks that assist in the redistribution of hydraulically lifted water

Papers are grouped by the type of biotic interaction described

spatial and temporal scales is critical to predicting the causes and consequences of plant mortality.

On a local scale, interactions between plants could increase the probability of drought mortality through competition for water, light, or other resources, or decrease drought mortality through facilitative mechanisms like shading or hydraulic lift. The stress-gradient hypothesis (SGH) proposes that positive interactions between plants should be strongest in harsh environments, while negative interactions should be strongest in benign environments (Bertness and Callaway 1994). Sthultz et al. (2007) tested this hypothesis using the interaction between nurse shrubs (*Fallugia paradoxa*) and juvenile piñon pines (*Pinus edulis*), predicting more facilitation at drier high-elevation sites and during periods of drought. While earlier studies tested SGH predictions, the range of environmental and experimental conditions tested by Sthultz et al. (2007) allowed a novel examination of factors driving a shift from competition to facilitation during drought. Sthultz et al. (2007) measured growth and mortality in open areas, under shrubs, and in experimental conditions with complete or above-ground shrub removal at high- and low-stress sites. The results broadly fit SGH predictions: *P. edulis* mortality decreased, and growth increased in the presence of nurse shrubs in a high-stress (i.e., high-elevation) environment, with the strongest positive effect occurring during an intense drought. In a less stressful low-elevation environment, the opposite effect was observed: *P. edulis* growth decreased, and mortality increased in the presence of *F. paradoxa*. There was evidence for both above-ground and below-ground competition, but only for above-ground facilitation, lending support to the role of shading in reducing evaporative water loss rather than hydraulic lift, the process by which deep-rooted plants redistribute water from deeper soil layers to the rooting zone of shallow-rooted species (Egerton-Warburton et al. 2007). In addition, there was stronger facilitation of younger plants. These results confirm that both spatial and temporal variability in environmental conditions can change the interaction between plants from facilitation to competition, which has been confirmed by more recent work (He et al. 2013). However, the relative contributions of local-scale facilitation and competition to plant mortality at ecosystem or landscape scales during drought remains understudied.

Widespread plant mortality due to climate change has prompted more recent studies on the impact of plant–plant interactions on stand-level tree mortality. Young et al. (2017) assessed the influence of competitive interactions on plant mortality during the widespread and extreme drought in California from 2012 to 2015. Plant mortality was assessed using aerial surveys paired with remotely sensed estimates of basal area (an index of competition strength) across forested land in California. Unsurprisingly, tree mortality was highest in areas with high climatic water deficit (CWD), with the most substantial tree mortality occurring within the final two years of drought. Among locations with comparable CWD, however, those with higher basal area suffered greater mortality. This was particularly apparent in intermediate to high basal area stands (> 30 m^2 ha^{-1}) where even modest CWD (> 600 mm) led to substantial tree mortality. This key result indicates that competition for scarce water resources during an extreme drought may have exacerbated tree mortality. Alternatively, the positive association between stand density and mortality rate could be indicative of higher beetle kill as mountain pine beetles prefer denser stands (Fettig et al. 2007). Indeed, much of the mortality observed by Young et al. (2017) occurred in the southern Sierra Mountains, where mortality rates are dominated by pines, and pine beetles preferentially attack larger pines growing in dense forest stands (Stephenson et al. 2019). However, Young et al. (2017) did not measure beetle attack damage nor did they isolate species-specific mortality patterns, highlighting the need for more studies that pair modeling exercises with field surveys. It is possible that a physiological drought response such as constrained capacity to produce defenses (e.g., terpenes and pitch) may have contributed to the higher beetle kill in dense stands, although this was not directly tested. If indeed competition influenced mortality, this contrasts with SGH, which predicts reduced competition and increased facilitation with drought stress, assuming soil moisture is the primary factor determining stress in this ecosystem.

Stand density and competition between neighboring plants are important factors influencing drought-induced plant mortality (Young et al. 2017). However, species diversity of stands is equally important, as demonstrated by Hisano et al. (2019) in their analysis of long-term records of boreal forest tree growth and

mortality. Seminal work in herbaceous-dominated ecosystems has shown that species-poor communities suffer greater declines in net primary productivity (NPP) during drought than species-rich communities (Tilman and Downing 1994; but see Huston 1997) and similar positive diversity effects have been observed in some forests, such as temperate beech and thermophilous deciduous forests (Grossiord et al. 2014). Expanding on this work, Hisano et al. (2019) tested the hypothesis that species-poor forests suffer greater declines in NPP in response to decreased water availability than species-rich forests due to greater tree mortality. Using a 57-years record of NPP from 871 Canadian boreal forest plots (> 200,000 individual trees) varying in species richness (1–7 species ha^{-1}), Hisano et al. (2019) assessed temporal trends in tree growth and mortality while accounting for differences in stand age and site characteristics. Over the past several decades, species-rich plots grew more and experienced less mortality than species-poor plots leading to higher NPP. Furthermore, this diversity effect on mortality was associated with moisture availability.

Unlike the xeric ecosystems studied in Young et al. (2017) and Sthultz et al. (2007), Canadian boreal forests do not experience regular extreme droughts; however, the region has experienced a drying trend and a steady rise in temperature since the 1950s (Hisano et al. 2019). Tree mortality in species-poor forests increased during dry periods while that of species-rich forests remained the same, a finding that Hisano et al. attribute to both positive species interactions and selection effects (i.e., the presence of drought-tolerant species in diverse stands). Drought-induced plant mortality may be avoided or postponed because of facilitative interactions between neighboring plants that alleviate water stress. Such facilitative interactions can involve habitat modification (e.g., canopy shade reduces thermal stress and soil moisture losses), resource enhancement (e.g., hydraulic lift from deep-rooting species), recruitment enhancement (e.g., nurse plants reducing seedling mortality), and/or refuge from competitors (Ploughe et al. 2019). Refuge from competitors is a plausible mechanism in boreal forests where inter-specific competitive intensity is weaker than intra-specific competition (Hisano et al. 2019). How such mechanisms reduce plant mortality in more diverse ecosystems, such as moist tropical forests, remains unresolved, although the lower mortality rates observed in the tropics compared to temperate biomes following drought may be due to higher diversity (McDowell et al. 2018).

Plant–animal interactions

Natural enemies can exacerbate plant mortality during drought, depending on plant investment in defense mechanisms. Certain plant species, such as ponderosa pines (*Pinus ponderosa*), face a genetic trade-off between growth and defense against herbivory (de la Mata et al. 2017), which may increase mortality of fast-growing pines when drought and mountain pine beetle attack occur simultaneously. A shift in selection pressure during ontogeny occurs with fast growth selected for in juvenile pines and slower growth in mature trees, likely due to beetle preference for mature trees and greater allocation to defense in slower growing trees (de la Mata et al. 2017). However, few studies have investigated the role of drought in the context of growth-defense trade-offs or how specific defenses may influence tree mortality following beetle attack during drought. Gaylord et al. (2013) were the first to simulate drought while simultaneously measuring bark beetle attack intensity, tree defense strategies, and tree mortality in piñon-juniper woodlands. Based on observations from previous natural droughts, the authors tested the hypothesis that piñon pine (*P. edulis*) would suffer greater mortality than co-occurring one-seed juniper (*Juniperus monosperma*) due to drought-induced reductions in resin defense mechanisms in piñon. Following three years of experimental drought (45% reduction in ambient precipitation), piñon pine trees experienced more frequent bark and twig beetle attacks and suffered greater mortality than either unstressed piñon or drought-stressed juniper trees. It is noteworthy that juniper trees did not suffer any mortality during this experiment, which the authors attribute to differences in hydraulic strategies (Gaylord et al. 2013). Dead piñon trees also had significantly smaller resin ducts and reduced twig resin flow compared to surviving piñon trees, although resin flow was less associated with piñon mortality than duct density/area. Interestingly, Gaylord et al. (2013) observed a bell-shaped relationship between resin production and radial growth across treatments suggesting that resin production is maximized in moderately stressed trees.

Unstressed trees in the control treatment allocated more resources to growth than defense, while severely drought-stressed trees were unable to supply photosynthate for either resin production or growth.

Overall, the results of Gaylord et al. (2013) suggest drought may predispose piñon, but not juniper trees, to biotic attack and mortality. Piñon and juniper trees are not closely related and their insect herbivores are largely non-overlapping (Gaylord et al. 2013), making it difficult to ascribe any specific mechanism to piñon's comparatively high drought sensitivity. However, the intra-specific comparison of dead vs. surviving piñon suggests resin-based defenses prevent mortality at least during short-term drought. Additionally, the bell-shaped growth-defense trade-off suggests moderately stressed trees may be less susceptible to future beetle attack. While juniper trees were less sensitive to drought treatments, other studies with more intense and prolonged drought have shown increased insect damage and mortality even in juniper (Clifford et al 2013). This confirms work on other conifers which suggests resin-based defenses are effective against small-scale herbivory but less effective during insect outbreaks (Boone et al. 2011).

As demonstrated by Gaylord et al., insect herbivores can intensify the impacts of water stress on plants. However, given that pest populations themselves are impacted by plant performance, there are likely cases in which herbivore damage is ameliorated under drought conditions. This is the premise of the meta-analysis of Jactel et al. (2012), involving 100 comparisons from 40 studies that examined herbivore and pathogen damage on 'control' versus water-stressed trees. The dataset included water manipulations in the field and greenhouse, and observational field studies, mostly in temperate forests of the Northern hemisphere. Pests of interest included 27 insect and 14 fungal species, specializing either on wood or leaf tissue and categorized into several feeding guilds. Importantly, wood pests were further separated into 'primary' and 'secondary' agents, the latter applying only to those pests that are associated with unhealthy trees. Results were variable: the authors found nearly as many studies reporting water stress reduced herbivore impacts as studies reporting drought amplified herbivore damage. For leaf pests, water stress often increased leaf damage, supporting a 'death spiral' scenario of trees succumbing to multiple stress agents (Fig. 1). For primary wood pests, however, damage was significantly greater in control trees experiencing lower water stress. Unsurprisingly, the wood damage effect switched for secondary pests that often occurred on drought-stressed trees. Although the differences in herbivore–drought interactions across tissue types emerges as a general pattern across studies, it leaves open the question of how opposing herbivore impacts on wood and leaves affects mortality, particularly when insects and diseases are at non-epidemic levels. On the other hand, under extreme drought conditions, the results of Jactel et al. suggest many temperate trees will also be heavily impacted by leaf herbivores, which could trigger death for fast-growing species with lower defense allocation (Gaylord et al. 2013; de la Mata et al. 2017).

The impact of non-insect herbivores on drought-induced plant mortality, particularly in herbaceous-dominated ecosystems, is rarely studied. One example of such a study is He et al. (2017), which tracked the impact of crab grazing on salt marsh vegetation die-off before, during, and after a natural drought. They found that drought significantly reduced plant cover, from 80% in pre-drought years to less than 20% in the drought year. In contrast, grazing exclusion alone had little impact on vegetation cover. However, a synergistic effect of grazing and drought resulted in elevated loss of plant cover, leading to ecosystem-level plant die-off with exceptionally low recovery rates. Furthermore, plants that survived drought were less likely to recover from subsequent grazing. These results indicate that drought predisposes herbaceous plants to herbivory-associated mortality and conversely, herbivory reduces the drought resilience of salt marsh plants. Contrary to research on woody species, the role of hydraulic failure as a mechanism of drought-induced mortality in herbaceous plants is not well supported (Ocheltree et al. 2016). Many herbaceous species, and some trees, depend on below-ground meristematic buds for re-sprouting after drought conditions (Ott et al. 2019). Therefore, future research on herbaceous plant mortality should address how biotic interactions influence below-ground carbon reserves and re-sprouting potential.

An additional component of He et al. (2017) was a summary of the global distribution of studies on drought-induced mortality and their associated natural enemies. Our current understanding of drought-herbivore-plant mortality mechanisms primarily stems from research on temperate trees such as pines,

junipers and a few broadleaf species. Even though drought and biotic agents (pathogens and herbivores) are proposed to be important drivers of plant mortality in the tropics (McDowell 2018), more empirical studies are needed from both paleo- and neo-tropical forests to establish the importance of the synergistic impact of these drivers on plant mortality. This is crucial for the dry tropics which have been experiencing higher frequencies of drought as a result of climate change (Allen et al. 2017). In addition to disparities in the biomes studied, research thus far has strongly favored insect herbivores. Mammalian grazers can also influence plant responses to drought by reducing transpirational surface area and indirectly increasing soil moisture (Frank et al. 2018). However, very few studies have empirically tested the impacts of both drought and grazing on plant mortality, and how patterns may vary among ecosystems.

Plant–microbe interactions

Plants react and adapt to drought in association with their microbiota, which includes pathogens, mutualists, and saprotrophic organisms (Compant et al. 2010). Here, we focus primarily on beneficial microbial interactions that are hypothesized to reduce the likelihood of plant mortality, although we recognize the importance of biotic stress induced by plant pathogens. Beneficial microorganisms can ameliorate drought stress (Lau and Lennon 2012), provide a channel by which water physically moves within the soil and between plants (Egerton-Warburton 2007), and in some cases alter plant species ranges (Afkhami et al. 2014). Genetic variation among plant hosts can further influence these effects if genetically different hosts cultivate specific microbial communities that impact plant drought responses (Gehring et al. 2017). Due to the complex diversity and spatial heterogeneity of plant–microbe associations, many questions remain regarding the mechanisms by which microbes contribute to or mediate plant drought stress and mortality and how these effects scale from individuals to ecosystems.

Individual plant genotypes can uniquely structure their microbiomes (Johnson et al. 2012), which can feed back to affect plant drought tolerance in genotype-specific ways. Using a combination of greenhouse experiments and long-term observational field studies, Gehring et al. (2017) tested whether offspring of both drought-tolerant and -intolerant genotypes of piñon pine (*P. edulis*) form distinct ectomycorrhizal fungal (EMF) communities and surveyed the consequences of this for tree survival during drought. Seedlings from drought-tolerant and -intolerant genotypes grew similarly under drought in sterile conditions, but drought-tolerant lines with their associated EMF communities grew 25% larger in the greenhouse and suffered less mortality under natural drought conditions. Additionally, EMF community composition was structured more by seed lines than inoculum source. Together these results indicate that host plant genetics strongly determine EMF communities in this system, which in turn determine plant responses to drought. Furthermore, drought resistant genotypes in the field experienced drastically lower rates of mortality across large areas of the landscape during record climate change-driven drought events of the last several decades (e.g., Sthultz et al. 2009) and EMF colonization and composition are known to vary in natural populations that experienced different degrees of drought stress and mortality (Swaty et al. 2004). This study highlights how plant–fungal associations represent an important mechanism by which a plant might escape the death spiral and recover from drought; it also illustrates how a mismatch between plant genotype and microbial community composition could hinder that recovery.

Plant–microbe interactions can be further influenced by the history of environmental stress experienced by microbes independently of the host. Importantly, microbes may experience their own "death spiral" and their ability to adapt to drought influences where and how the plant and microbe death spirals might intersect. In the landmark experiment of Lau and Lennon (2012), replicated *Brassica rapa* plants and soil microbes were pre-conditioned with either high or low soil moisture treatments for multiple plant generations. Live soil inocula and *B. rapa* seeds from these treatments were used in a reciprocal transplant experiment to test the legacy effects of previous growth conditions on plant responses to wet and dry soil conditions. Overall, plant growth and fitness (e.g., flower and fruit production) increased when grown with microbial communities pre-conditioned for the contemporary soil moisture treatment (i.e., drought-stressed plants growing with drought-conditioned microbes). Moreover, positive plant

responses were primarily driven by changes in microbial community composition rather than adaptive changes in plant traits due to natural selection on plant populations during the multi-generational preconditioning phase. These findings have changed the narrative regarding plant drought tolerance and mortality (Gehring et al, 2017). Rather than plants being bound by their own plasticity or rates of evolution (Goh et al. 2013), rapid shifts in microbial communities below-ground can prime the plant or soil such that drought tolerance is increased at least in the near term (Revillini et al, 2016). Importantly, because *B. rapa* does not form mycorrhizal symbioses, the beneficial microbial effects were due to unidentified rhizosphere organisms that might not be as readily expected to positively affect plant drought tolerance. While Lau and Lennon did not measure plant mortality, their findings suggest that more attention should be given to microbial community responses to drought, especially when assessing potential legacy effects of drought on plant mortality (Anderegg et al. 2013a, b).

Above-ground interactions between plants and non-pathogenic microbes may also affect plant survival during drought. Afkhami et al. (2014) evaluated interactions between plants and fungal endophytes across the geographic distribution of *Bromus laevipes* to test the hypothesis that endophyte-associated (E+) plants are more drought tolerant than endophyte-free (E−) plants, allowing them to occupy more xeric habitats than E− plants. Across 10 common gardens distributed along a precipitation gradient, survivorship of E− plants relative to E+ plants was greater in wet regions, while the opposite was true on the dry end of the gradient. Additionally, survivorship and performance of E+ plants were greater than E− plants in a manipulative drought experiment. These results suggest that leaf endophytes can mediate plant survival during drought and potentially expand the distribution of this species into more arid or drought-prone ecosystems. Using species distribution modeling, Afkhami et al. (2014) show that endophyte infection (E+) broadens the range of *B. laevipes* into drier regions (~20% larger distribution than E−). Additionally, 19-22% of the current geographic range (> 25,000 km) was suitable only for E+ plants, and niche overlap between E+ and E- *B. laevipes* was less than or statistically comparable to the overlap of *B. laevipes* with other *Bromus* species, indicating that the difference in drought tolerance of E+ and E− plants is biologically meaningful. This work was the first to use an integrative approach to establish a relationship between plant–endophyte mutualism, drought tolerance, and geographic range expansion (or contraction in the case of E−) of the host on a broad scale. With dryland ecosystems expanding worldwide (Yao et al. 2020), plant associations with non-pathogenic microbes may be a strong determinant of which species or genotypes will survive or even expand under climate change.

Although the overall effect of plant–endophyte association during water stress was positive, these microbial agents were not beneficial in other environmental contexts (Afkhami et al. 2014) and are not necessarily applicable to other species (Rudgers and Swafford 2009). Future work should investigate the physiological mechanism by which certain endophytes can confer drought tolerance to their hosts, as well as the effect of non-clavicipitaceous (NC) endophytes on drought response in eudicot hosts. Unlike grass or clavicipitaceous endophytes, NC endophytes can be transmitted horizontally between hosts and are not systemic throughout the host, so drought response in eudicots may be less mediated by the response of a single fungus and more by the response of NC fungal communities to drought.

Mutualistic fungal symbionts can also ameliorate drought stress by facilitating resource transfer between plants and fungi. Plants colonized by mycorrhizal fungi have the benefit of potentially forming common mycorrhizal/mycelial networks (CMN), which can expand their access to water during drought. This plant–microbe interaction is particularly important for shallow-rooted species unable to access water in deeper soil layers. Egerton-Warburton et al. (2007) tested the hypothesis that hydraulically lifted water from coast live oak trees (*Quercus agrifolia*) could flow through CMN pathways and alleviate drought stress in nearby conspecific and heterospecific seedlings. Using a drought mesocosm experiment including several arid plant species, Egerton-Warburton et al. (2007) tracked the flow of deuterium-rich water from donor plants (*Q. agrifolia*) to receiver plants that were either connected to or disconnected from a CMN. Deuterium was detected in the transpiration flux of receiver plants that maintained a CMN connection, indicating hydraulically lifted water was transferred from *Q. agrifolia* via a CMN. Fluorescent tracers in the water suggested that this hydraulic transfer

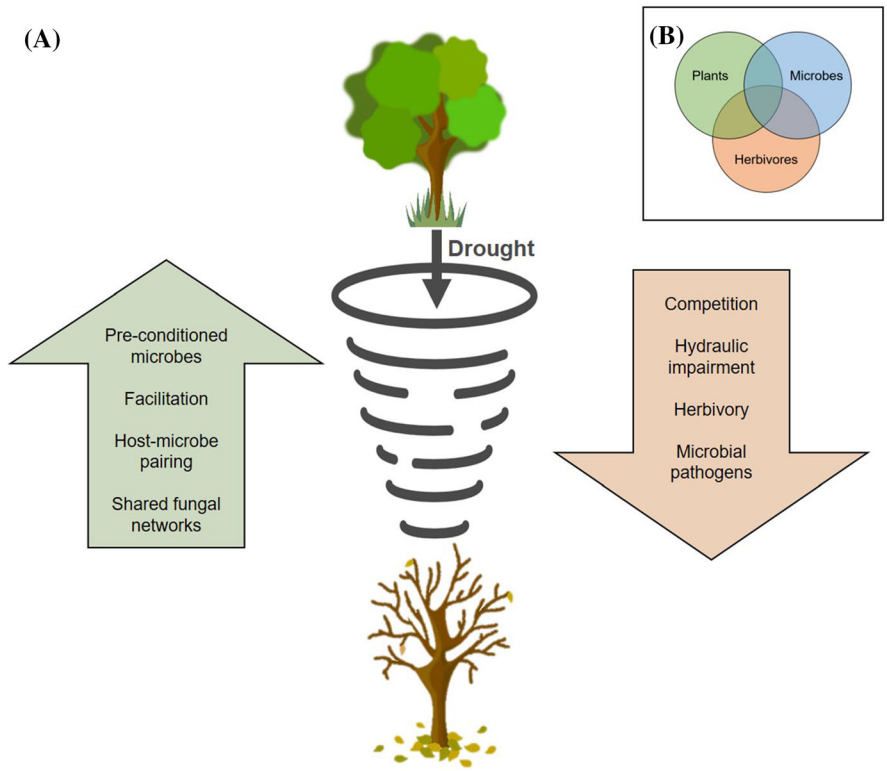

Fig. 2 Reconstruction of Manion's death spiral with factors that either increase (red arrow) or decrease (green arrow) a plant's chances of mortality **(a)**. A healthy plant enters the spiral during drought. Negative biotic interactions (e.g., competition and herbivory) as well as physiological traits (e.g., vulnerability to cavitation) can exacerbate the effect of drought leading to mortality. Positive biotic interactions (e.g., facilitation, host–microbe pairing, and shared fungal networks) and associated legacy effects (e.g., pre-conditioned microbes) can remove the plant from the death spiral thereby avoiding mortality at least temporarily. Importantly, each interacting organism also experiences its own potential "death spiral" as it responds and acclimates to drought. Where and when these separate death spirals intersect (shown here as circles in a Venn diagram) **(b)** may influence mortality of the target plant. For example, the impacts of pests may be exacerbated if the target plant is farther along in its own death spiral, but the interacting pest is just beginning to experience the impacts of drought. Alternatively, microbes may have a larger impact (positive or negative) if they experience drought or adapt to drought more rapidly than their hosts. In other words, the timing of when populations experience drought can influence the extent to which their individual death spirals overlap and the outcome of those interactions

occurred through a relatively small portion of hyphal components within the CMN. Additionally, only plant species with a strong dependence on mycorrhizal fungi consistently joined CMN to receive hydraulically lifted water. Overall, the work of Egerton-Warburton et al. (2007) identifies a mechanism for how fungi may facilitate positive plant–plant interactions to alleviate drought stress (Hisano et al. 2019) and increase the survival and establishment of tree seedlings under drought conditions (Bingham and Simard 2011).

Conclusion

Manion (1991) included drought as an inciting factor of plant mortality (Fig. 1), with many of the biotic interactions described here being contributing or predisposing factors. Our review suggests these pathways towards mortality are more complex (Fig. 2), with multiple routes to escape mortality depending on the nature of the interaction. For example, the presence/absence of plant associations with microbial communities predisposes individuals to certain drought responses. However, this response depends on the history of climatic disturbance experienced by the microbial community (Lau and Lennon 2012).

Insect pests contribute to plant mortality during drought via direct physical damage (Gaylord et al. 2013); whether this causes mortality, however, depends on the degree to which the insect relies on plant performance for its own survival (Jactel et al. 2012). And finally, high plant density increases mortality risk via competitive interactions between neighboring plants (Young et al. 2017), although this depends on the identity of those neighbors and whether they share common fungal networks (Egerton-Warburton 2007).

The complexity of these biotic interactions highlights the need to identify clear physiological linkages between the external biotic agents of mortality and internal plant mechanisms of mortality. Moving forward, we argue that more studies should assess how interactions with microbial communities, herbivores, and/or neighboring plants directly influence plant vulnerability to xylem cavitation and/or the ability to mobilize carbon for metabolic demands, repair, and defense. Recent work has suggested that plants often adopt a riskier water use strategy in response to dehydration in the presence of competing neighbors (Zenes et al. 2020). First principles suggest this would exacerbate mortality risk during extreme drought, although this has not been measured directly in the field. Determining how plant–plant interactions directly influence physiological mechanisms of mortality is difficult as it likely requires knowing how much rooting systems overlap, compete, and share resources.

The studies surveyed here represent key advances in plant mortality research over the last twenty years. They also highlight areas of limited knowledge and potential for future research. Woody plant species, and particularly those in semi-arid ecosystems, have dominated the field of plant mortality research. This is due in part to the economic costs of forest mortality for timber industries (Anderegg et al. 2013), but also to a lack of consensus on definitions of mortality in herbaceous plant physiology literature. In general, data from other ecosystems with a diversity of biotic agents, including mammals, are needed to gain a better understanding of drought-induced plant mortality (He et al. 2017). Of the studies mentioned here, nearly half were conducted in semi-arid woodlands of the American Southwest (Table 1). Although this region is a hotspot for research on drought physiology, it underscores our limited ability to apply our understanding of drought mortality to ecosystems and plant functional types around the world. Finally, future studies should further explore the intersection of separate death spirals of interacting organisms (Fig. 2b). Each interacting organism experiences its own physiological response to drought (e.g., Lau and Lennon 2012) with a characteristic death spiral. Accounting for where and when these separate death spirals intersect is critical if our goal is to better predict plant mortality (Trugman et al. 2021) and scale this concept from individual plants to ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest

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