Water availability and plant-herbivore interactions

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Highlight

Water availability strongly influences the interactions between plants and herbivores. This review highlights recent findings, general patterns, and context dependency of water-plant-herbivore interactions.

Abstract

Water is essential to plant growth and drives plant evolution and interactions with other organisms, such as herbivores. However, water availability fluctuates, and these fluctuations are intensified by climate change. How plant water availability influences plant-herbivore interactions in the future is an important question in basic and applied ecology. Here we summarize and synthesize the recent discoveries on the impact of water availability on plant antiherbivore defense ecology and the underlying physiological processes. Water deficit tends to enhance plant resistance and escape traits (i.e., early phenology) against herbivory but negatively affects other defense strategies, including indirect defense and tolerance. However, exceptions were sometimes observed in specific plantherbivore species pairs. We discuss the effect of water availability on species interactions associated with plants and herbivores from individual to community levels and how these interactions drive plant evolution. Although water stress and many other abiotic stresses are predicted to increase in intensity and frequency due to climate change, we identify a significant lack of study on the interactive impact of additional abiotic stressors on water-plant-herbivore interactions. This review summarizes critical knowledge gaps and informs future studies of possible research directions in water-plant-herbivore interactions.

Keywords

Plant defense; insect herbivore; pest; drought; water stress; water deficit; climate change; plant volatile; abiotic stress; resource availability.

1. What do we know about water-plant-herbivore interactions?

Water availability is one of the most important abiotic factors for plant growth and has a long history of research, especially regarding drought (Davies et al., 1986; Hsiao, 1973; Mattson and Haack, 1987; Turner, 1982; Turner, 1986). Drought is defined as a decrease in water input in a given system that leads to feedback from the system (Crausbay et al., 2017; Gilbert and Medina, 2016). Drought can lead to a water deficit when plant water loss is greater than the input (Gilbert and Medina, 2016) and is detrimental to plant growth and development. Regional average of water availability drives the evolution of many constitutive and inducible plant traits (Chaves et al., 2003; Hsiao, 1973; Kumagai and Porporato, 2012; Lombardini and Rossi, 2019; Mundim and Pringle, 2018; Rodrigues et al., 2019; Turner, 1986; Verslues and Juenger, 2011; Volaire, 2018). Constitutive traits include specialized plant habits, such as succulents in arid areas (Danin, 1991; Lombardini and Rossi, 2019), specialized root structures that prevent suffocation in habitats that tend to flood (Armstrong et al., 1994; Srikanth et al., 2016), photosynthesis pathways that preserve water (e.g., C4 and CAM) (Ehleringer and Monson, 1993; Ghannoum, 2008; Gowik and Westhoff, 2011), and rapid growth rate and early phenology in drought-prone areas (Franks et al., 2007; Metz et al., 2020; Volaire, 2018). These adaptations allow plants to grow and develop under the specific water availability in their habitats and are crucial to plant survival (Volaire, 2018). However, temporal changes in water availability can drastically differ from the regional average (Diaz et al., 1989). To deal with short-term water availability fluctuations, plants have evolved many inducible traits, such as stomatal closure/open, growth cessation, and secondary metabolite accumulation (Gupta et al., 2020). These inducible responses are essential parts of plant adaptation to short-term suboptimal water availability (Gupta et al., 2020; McDowell et al., 2008; Rodrigues et al., 2019) and can alter plant responses to other stresses, such as herbivory (Anzano et al., 2022; Gely et al., 2020; Huberty and Denno, 2004; Jamieson et al., 2012; Mattson and Haack, 1987; Nguyen et al., 2016b; Waring and Cobb, 1992).

The influence of water availability on plant-herbivore interactions is especially well-studied due to the observation that drought is often associated with outbreaks of insect herbivores (Mattson and Haack, 1987; Torode et al., 2016; Van Bael et al., 2004; Xu et al., 2019). Many following studies aim to investigate the links between drought and increased herbivore population and have led to several influential theories predicting the impact of water deficit on herbivore performance and population dynamics, including the Plant Stress Hypothesis (White, 1969), Plant Vigor Hypothesis (Price, 1991), and Pulse-Stress Hypothesis (Huberty and Denno, 2004). These early hypotheses have served as foundations that facilitate our understanding of water-plant-insect interactions. Especially regarding how an increase in primary metabolites (e.g., proteins, amino acids, other nutrients) influence plantherbivore interactions (for a detailed review, see (Huberty and Denno, 2004; White, 2009)). While much evidence exists in support of each hypothesis, it is now known that the outcomes of plantherbivore interactions (e.g., changes in performance, fitness, and population) under stress are usually dependent on factors such as species combination (of plants and herbivores), plant habit, stress severity, herbivore feeding guild, and multitrophic interactions (Gely et al., 2020; Guyer et al., 2018; Guyer et al., 2021; Hamann et al., 2020; Huberty and Denno, 2004; Jamieson et al., 2012; Nguyen et al., 2016b; Waring and Cobb, 1992).

In contrast to a focus on herbivore responses, a separate line of research has provided insights into the role of water availability on plant antiherbivore defenses (Stamp, 2003). Especially relevant is the

Growth-Differentiation Balance Hypothesis, which describes the tradeoffs between growth and differentiation-related (e.g., defense) processes in plants (Herms and Mattson, 1992). It predicts that environmental factors that limit growth more than photosynthesis will allow the plants to allocate more resources to differentiation-related processes, such as defense (Stamp, 2004). A mild water deficit falls into this resource tradeoff scenario and might lead to higher defense allocation (Herms and Mattson, 1992). It is well-established that plants growing under mild water deficit show reduced photosynthesis/growth, changes in biomass allocation, and enhanced investment in secondary metabolites (Driesen et al., 2020; Gupta et al., 2020; Lim et al., 2015; Lin et al., 2021b; Mundim and Pringle, 2018; Nguyen et al., 2016b; Rodrigues et al., 2019; Siqueira et al., 2021). Secondary metabolites are multifunctional (Erb and Kliebenstein, 2020) and are involved in distinct antiherbivore defense strategies, including direct defense (i.e., the defense that does not involve other trophic levels), indirect defense (i.e., the defense that relies on other trophic levels), or both (Zhou and Jander, 2022). Water deficit often triggers secondary metabolites accumulation in ways that favor direct defense (Gely et al., 2020; Nguyen et al., 2016b; Rai et al., 2018) over indirect defenses (Câmara et al., 2021; Han et al., 2015; Hassani-Kakhki et al., 2019) (for exceptions, see (Weldegergis et al., 2015)(Fig. 1).

As shown by the recent IPCC report (IPCC, 2021), climate changes and anthropogenic activities will likely lead to increases in concurring environmental stresses, such as drought and herbivory (Hamann et al., 2020; Zandalinas et al., 2021a). One of the primary goals of understanding how water availability influences plant-herbivore interactions is to gather sufficient knowledge to predict and prevent the potentially catastrophic effects of these stresses on ecosystem functions and human society. However, our pace in understanding these processes is slower than the rapid increases in severity and frequency of these stresses (Zandalinas et al., 2021a). In an endeavor to facilitate such research, we summarize some of the most recent findings on water-plant-herbivore interactions and synthesize current knowledge for general patterns of water-plant-herbivore interactions in light of their context dependency. In the following sections, we first summarize current knowledge on how water availability influence plant defense strategies. In addition to the focus on non-volatile compounds, we review the emerging role of plant volatiles in water-plant-herbivore interactions. Water availability modifies plant volatile traits and can influence volatile-mediated biotic interactions and likely contribute to community-level changes. However, how water availability influences populational/community-level interactions is generally understudied. We highlight current studies on how water availability influences biotic interactions, community, and evolution of plants and herbivores. With the exacerbation of climate change, water-plant-herbivore interactions are increasingly influenced by fluctuation of other abiotic factors. We discuss the interactive effect of water availability and other abiotic factors on plant-herbivore interactions. Since changes in precipitation and water availability can have a major impact on natural ecosystems and human society, we also synthesize the potential applied values of knowledge regarding water-plantherbivore interactions in dealing with the negative impacts of our changing climate. We further identify some of the important knowledge gaps that will help us understand the complex interactions between water, plants, and herbivores and search for general patterns.

2. Plant antiherbivore defense under changing water availability

2.1. Altering defense strategies: resistance, tolerance, and escape

The physiological changes caused by water stress are well-documented (Anzano et al., 2022; Gupta et al., 2020; Zandalinas and Mittler, 2022) and can influence the expression of plant resistance traits against herbivory (Anzano et al., 2022; Gely et al., 2020; Jamieson et al., 2012; Leybourne et al., 2021; Nguyen et al., 2016b) (Fig. 2). Water deficit causes an accumulation of abscisic acid (ABA) and low transpiration due to stomatal closure (Lim et al., 2015), which is linked to reductions in photosynthesis and growth (Rodrigues et al., 2019). Water deficit also changes other phytohormones, including an increase in jasmonic acid (JA) and salicylic acid (SA), and a decrease in gibberellins (for comprehensive reviews, see (Jogawat et al., 2021; Ullah et al., 2018). Water deficit triggers accumulations of secondary metabolites, such as flavonoids, terpenoids, alkaloids, glucosinolates, cyanogenic glucosides, and amino acid derivatives that are also involved in plant response to herbivory (Erb and Kliebenstein, 2020; Habib and Fazili, 2007; Jamieson et al., 2017; Jogawat et al., 2021; Mundim and Pringle, 2018; Nguyen et al., 2022; Zandalinas et al., 2022; Zhou and Jander, 2022) (Fig. 2). Additionally, water deficit also triggers modification of plant surface traits, such as increased trichomes (Atala and Gianoli, 2009) and wax layer (Gong et al., 2010) which are associated with both drought tolerance and herbivore resistance. However, the impacts of drought on secondary metabolisms are not all positive. Photosynthesis inhibition due to water deficit can lead to an overall decrease in secondary metabolism (Matt et al., 2002). Whether drought inhibits or enhances secondary metabolite accumulation likely depends on the type of metabolites and severity of drought (Gutbrodt et al., 2011; Kansman et al., 2022). Stress severity can influence plant responses in a hormetic way (Agathokleous et al., 2018), which is also observed in the metabolic responses of plants growing under different water deficit levels (Asiyeh Notghi Moghadam et al., 2022; Erb et al., 2011; Gutbrodt et al., 2011; Kansman et al., 2022; Sconiers et al., 2020). However, studies that investigate across varying water availability levels remain scarce. An additional point to consider it that herbivory causes localized drought responses, for instance attacks by chewing herbivores (Peschiutta et al., 2016) and some sap feeding insects that lead to excessive water loss (Shannag, 2007) or trigger drought-related physiological responses of plant, e.g., ABA accumulation (Hillwig et al., 2016). . It is therefore likely that responses against chewing herbivores and drought stress are tightly linked, as shown in studies suggesting the role of ABA in defenses against chewing herbivores (Thaler and Bostock, 2004).

As mentioned before, water deficit often enhances the accumulation of secondary metabolites. Although secondary metabolite accumulation might confer higher resistance against different herbivores, the adaptation of specific herbivores to plant defenses can alter the correlation between enhanced secondary metabolites and higher resistance (Dobler *et al.*, 2012; Rivas-Ubach *et al.*, 2014; Wittstock *et al.*, 2004; Xia *et al.*, 2021). In support of this argument, when plant resistance is evaluated by the response of the entire herbivore community (i.e., herbivore abundance), enhanced resistance (e.g., reduced overall herbivore abundance) is usually observed under water deficit (Lin *et al.*, 2021a; Pepi *et al.*, 2021; Trotter *et al.*, 2008). An emerging pattern is that plant responses against water deficit and herbivory, specifically direct defense, can be somewhat similar and perhaps synergistic in some ways (Erb *et al.*, 2012). A particularly interesting case is glucosinolates which is generally known as antiherbivore compounds in Brassicaceae plants. These aliphatic glucosinolates have also been found to play a critical role in stomatal regulation and drought resistance (Salehin *et* al., 2019). The multifunctionality of secondary metabolite suggests and strong synergism between plant responses against water deficit and herbivory. It is noteworthy that some forest pests (Van Bael et al., 2004; Xu et al., 2019) and piercing-sucking pests in the agricultural system (Santamaria et al., 2018) respond positively to plants under water deficit and do not fit well with this pattern due to their specific interactions with plants. This is likely due to the specific interactions plants and herbivore has. For instance, resin of conifers is an important resistant trait against bark beetles, and resin can be strongly inhibited by short-term drought (Rissanen et al., 2021; Sopow et al., 2015). Therefore, although drought enhances resistant traits (e.g., monoterpenes) of conifers (Suárez-Vidal et al., 2019; Turtola et al., 2003), changes in overall defense syndrome may failed to defend against the attack of certain herbivores (Sopow et al., 2015; Suárez-Vidal et al., 2019). Coincidentally, some of the herbivores that are positively affected by drought (e.g., bark beetle) can inflict tremendous damage to plants, and therefore has been a primary research focus in water-plant-herbivore interactions, which lead to the conclusion that drought can be beneficial to insect herbivore (see for more discussion (Gely et al., 2020; Sopow et al., 2015). Phytohormones that regulate biotic interactions are also involved in plant responses to drought stress (Jogawat et al., 2021). For instance, SA (Khan et al., 2019) and JA (Sheteiwy et al., 2018) applications enhance drought resistance. In addition to phytohormones, other secondary metabolites have also been shown to play critical roles in both drought resistance and direct antiherbivore defenses, for instance, glucosinolates (Bennett and Wallsgrove, 1994; Salehin et al., 2019), terpenoids (Mundim et al., 2021; Peñuelas and Staudt, 2010; Zhou and Jander, 2022), flavonoids (Hernández et al., 2006; Li et al., 2022b), and protease inhibitors (Fan et al., 2019; Lin et al., 2021b; Nguyen et al., 2016a; Zhang et al., 2008). Contrary to the speculated synergism between drought resistance and antiherbivore defenses, a negative correlation between percentage biomass loss under herbivory and water deficit across accessions of Arabidopsis has been reported, suggesting a lack of synergisms (Davila Olivas et al., 2017). However, plant drought resistance can be categorized into different strategies, such as drought tolerance, drought avoidance, and drought escape (Kooyers, 2015; Touchette et al., 2007). Growth inhibition is one of the traits associated with drought avoidance (Kooyers, 2015). This study provides valuable insights into the association of different stress responses and informs us of the importance of considering different plant drought resistance strategies. While much evidence suggests synergisms between drought resistance and antiherbivore defenses, the links between specific strategies of drought resistance and antiherbivore deference remain to be investigated.

In addition to water deficit, excessive precipitation leads to flooding and can also influence the direct defense of plants against herbivores. However, flooding has distinct effects on plants compared to water deficits (Wang and Komatsu, 2022). For example, flooding does not induce JA accumulation and suppresses the expression of many genes otherwise upregulated by water deficit (Nguyen *et al.*, 2016a). Similarly, flooding triggers ethylene accumulation in rice (*Oryza sativa*) which lowers JA levels and suppresses plant volatile emissions (Mujiono *et al.*, 2020). Flooding decreases the resistance of dogwood (*Cornus florida*) toward ambrosia beetle (*Xylosandrus germanus*), likely due to ethanol accumulation in flooded trees (Ranger *et al.*, 2013). Notably, the number of studies investigating excessive water on plant-herbivore interactions is much less than those investigating water deficit. Additionally, physical contact with raindrops can directly affect smaller herbivores (Chen *et al.*, 2019; Lin *et al.*, 2016). Since it is increasingly understood that physical touch can trigger significant plant physiological responses (Markovic *et al.*, 2019; Szechyńska-Hebda *et al.*, 2022), these studies highlighted the potential importance of physical contact by rain in water-plant-

herbivory interactions. As climate change increases precipitation frequency and intensity in many parts of the world, it would be essential to understand the impact of excessive water on plantherbivore interactions.

The influence of water availability on plant tolerance to herbivory is slightly more complicated due to how plant tolerance is estimated (Agrawal, 2007; Wise and Abrahamson, 2007) (Fig. 1). Unlike resistant traits that are either chemical or structural (Agrawal, 2007), plant tolerance is defined by the percentage of fitness changes between plants under herbivory and a reference state, which is undamaged plants (Strauss and Agrawal, 1999). Higher herbivory tolerance is defined by a lower fitness gap between herbivory and undamaged reference condition. With this definition, it has been found that water deficit could either increase (Gassmann, 2004) or decrease (Levine and Paige, 2004; Lin et al., 2021b) plant tolerance to herbivory. However, the traditional definition of tolerance does not consider the impact of abiotic factors on individual fitness within the plant population (Strauss and Agrawal, 1999). This is problematic due to the inherent fitness gap between plants growing under suboptimal abiotic conditions regardless of herbivory (Wise and Abrahamson, 2007). To highlight the interactive effect of abiotic and biotic factors on plant tolerance to herbivory, a helpful definition of herbivory tolerance is the fitness gap between plants (under any abiotic condition and herbivory) to an optimal reference state within a plant population which is a condition that has no-herbivory and optimal abiotic conditions. Plants under suboptimal abiotic conditions have lower herbivory tolerance due to lower fitness than the reference state, even without herbivory. This view of herbivory tolerance provides a conceptual basis for comparing plant tolerance under interacting abiotic stress and herbivory. By including the influence of abiotic factors on plant fitness, this definition also links different conceptual theories that focus on the tradeoff between growth and defense with theories that focus on tolerance and resistance that did not consider abiotic factors initially (Stamp, 2003; Strauss and Agrawal, 1999).

An essential but seldom investigated antiherbivore strategy in the context of water-plant-herbivore interactions is the ability of plants to escape herbivores by adjusting their life-history traits to separate themselves temporally or spatially from herbivores (Bont *et al.*, 2020; Stowe *et al.*, 2000) (Fig. 1). Very little is known about how abiotic factors influence the escape defense strategy. Still, recent evidence has shown that drought and climate change have caused plants to evolve toward early flowering in both manipulative experiments and natural plant populations (Anderson *et al.*, 2012; Franks *et al.*, 2007; Metz *et al.*, 2020; Rauschkolb *et al.*, 2022). The influence of changes in phenology on herbivory and how herbivory may also contribute to the evolution of such traits remain unclear.

2.2. Herbivore-induced plant volatiles and their multifunctionality

Changes in non-volatile secondary metabolites under different water availability have been a major focus in water-plant-herbivore interactions (but see (Pagadala Damodaram *et al.*, 2021; Scott *et al.*, 2019; Weldegergis *et al.*, 2015). However, plant volatiles also play crucial roles in antiherbivore defenses (Turlings and Erb, 2018). For instance, Herbivore-induced plant volatiles (HIPVs) serve as cues that modulate the interaction between plants and natural enemies and, therefore, an essential trait associated with indirect defense (Pearse *et al.*, 2020; Turlings and Erb, 2018) (Fig. 3). In general, mild water deficit enhances plant volatile emission, whereas severe water deficit inhibits volatile emission (Niinemets *et al.*, 2004; Peñuelas and Staudt, 2010). Similarly, mild water deficit also

increases HIPV emission and decreases HIPV emission as drought severity increases (Gouinguené and Turlings, 2002; Scott et al., 2019; Tariq et al., 2013). In addition to the well-known role of HIPV in natural enemy attraction, HIPVs can also function as direct defenses by repelling (Conboy et al., 2020; Gaffke et al., 2020; Stratton et al., 2019) or being toxic to herbivores (Chen et al., 2021; Veyrat et al., 2016). Similar to other direct defense traits, recent studies found that plant volatile emission under water deficit tends to change in a way that favors direct defense over indirect defenses (Lin et al., 2022; Martini and Stelinski, 2017; Tarig et al., 2013). Although we speculate that ecological and evolutionary tradeoffs might exist between resistance and other defense strategies, such as tolerance and indirect defenses under abiotic stress, this hypothesis remains to be investigated. Additionally, recent studies have highlighted the role of plant volatiles, especially HIPVs, in plantplant interactions, as they can be perceived as warning cues by neighboring plants (Brosset and Blande, 2022). While most cases were reported for plant-herbivore interactions (Brosset and Blande, 2022), it seems that plant volatiles can also serve as warning signals for plants to prepare for abiotic stresses (Cofer et al., 2018). For instance, maize seedlings exposed to (Z)-3-hexenyl acetate have enhanced cold tolerance compared to unexposed seedlings (Cofer et al., 2018). In contrast, volatiles induced by polyethylene glycol (i.e., simulated drought) has been shown to decrease drought resistance (Jin et al., 2021). These results suggested that these plant stress-related volatiles serve multiple biological functions in plant response toward biotic and abiotic stresses (Erb, 2018). It is increasingly evident that a multifunctionality perspective might be necessary to understand plant volatiles' adaptive values.

3. Water availability and species interactions across scales

3.1. Changing water availability and associated species interactions

Besides direct interactions between plants and herbivores, the influence of water availability on plant-herbivore interactions has also been studied in the context of other species interactions, such as competition (Fig. 4). Recent evidence has suggested that plant-plant interactions play a vital role in the outcome of water-plant-herbivore interactions. In a manipulative experiment using birch, oak, and pine, birch (*Betula pendula*) tended to have lower direct defenses (e.g., phenolics and condensed tannins) and receive more herbivory when they were grown next to different species, but only under water deficit conditions (Castagneyrol *et al.*, 2018). While the mechanisms underlying these observed herbivory patterns remain unknown, it is clear that competition or other interspecific interactions modulate water-plant-herbivore interactions (Castagneyrol *et al.*, 2018). Changes in water availability also potentially change the competitive interactions between herbivores. Water deficit ameliorates the competitive interactions of aphids, for instance, *Metopolophium festucae* and *Rhopalosiphum padi* on wheat (*Triticum aestivum*) (Foote *et al.*, 2017) and *Acyrthosiphon pisum* and *Therioaphis maculata* on alfalfa (*Medicago sativa*) (Barton and Ives, 2014).

Interactions with microbes also modulate water-plant-herbivore interactions. Feeding on host plants growing under water deficit changes the gut microbial community of the Finnish Glanville fritillary butterfly (*Melitaea cinxia*), which was also linked to better performance (Rosa *et al.*, 2019). In addition, water availability influences the interactions between herbivore and their pathogens. Higher than average rainfall is linked to a decrease in the hemlock woolly adelgid (*Adelges tsugae*) population in Carolina and eastern hemlock (*Tsuga caroliniana* and *T. canadensis*) in the Eastern United States (Chandler *et al.*, 2022). It was hypothesized that this decrease in herbivores might be

associated with a higher incidence of the fungal pathogen during wetter climates. Plant-associated microbes are also affected by water availability and potentially have an indirect impact on plantherbivore interactions (Lozano et al., 2021). For instance, mycorrhizal fungi altered the growthdefense pattern of plants under different water availability by lowering the defense investment of plants under lower water availability (Orine et al., 2022) The potential outcomes of drought events for vector-borne pathogens requires an understanding of the effects of drought on the performance and behavior of the vector organism, as well as the ability of the host plant to coordinate its responses to three stress agents simultaneously: herbivore, pathogen, and water stress (Discussed in detail in Szczepaniec and Finke (2019). Herbivores on water-limited plants feed for less time and are less effective at transmitting plant pathogens that require long bouts of feeding (Kansman et al., 2020; Nachappa et al., 2016). However, pathogens that are acquired by the plant quickly after stylet contact show increased transmission on water-limited hosts due to increased vector movement between plants (Krugner and Backus, 2014). Vector density also affects the vulnerability of a plant to pathogens, but while many pathogen-transmitting herbivores experience performance declines on water-limited hosts (Huberty and Denno, 2004; Leybourne et al., 2021), the presence of a pathogen either within the herbivore or in the host-plant can counteract this effect leaving the herbivore unaffected by water limitation (Davis et al., 2015; Nachappa et al., 2016) or improve herbivore performance (Davis et al., 2015). It is unclear if this outcome is a consequence of antagonistic plantstress responses to abiotic and biotic stressors (Gely et al., 2020) or due to a virus-driven change within the herbivore itself (Mauck et al., 2016). Pollinators (e.g., Lepidoptera and Hymenoptera) that feed on plant reproductive tissues are also affected by water availability (Glenny et al., 2018; Salman et al., 2022). Water deficit changes foraging cues for pollinators, including floral visual traits (e.g., size) (Kuppler et al., 2021) and volatile emissions. For instance, terpene synthase genes are upregulated under osmotic stress in rose flowers (Yan et al., 2022). However, the outcome of water availability on plant-pollinator interactions is variable. In general, water deficit tends to negatively affect pollinator attraction (Glenny et al., 2018; Salman et al., 2022), but changes in floral traits due to water availability have been associated with either decreased or increased pollinator visits (Grant et al., 2017).

3.2. Community-wide effect of changing water availability

Water availability determines plant community composition (Batbaatar *et al.*, 2022; Franklin *et al.*, 2016). Lower water availability is generally associated with lower plant diversity (Barnett and Facey, 2016; Bunker and Carson, 2005; López-Rubio *et al.*, 2022; Prugh *et al.*, 2018) as well as the diversity of associated-herbivore community (Lin *et al.*, 2021a; Trotter *et al.*, 2008) However, recent studies have shown the resilience of plant communities to changes in water availability in some ecosystems (López-Rubio *et al.*, 2022). For instance, a four-year drought (55% growing season precipitation) decreases above-ground net primary production of grassland in the early years but increases primary productivity in the fourth year more than ambient precipitation treatment. Plant species composition also changes across the years but does not change species richness or evenness. The results suggest that temperate grassland is relatively resistant to multi-year decreases in precipitation (Batbaatar *et al.*, 2022). While plant diversity can be influenced by water availability, plant diversity itself has crucial implications for drought resilience (Grossiord, 2020). Additionally, while water deficit is known to cause shifts in the microbiome associated with plants (Santos-Medellín *et al.*, 2021), higher plant diversity enhances the resilience of soil microbial communities to drought (Li *et al.*, 2022). These findings suggest the importance of biodiversity and communities to

structure in plant stress resilience and reveal a lack of understanding regarding community-wide interaction under variable water availability.

Herbivore outbreaks under drought are well-known in water-plant-herbivore interactions (Mattson and Haack, 1987; White, 1969). In contrast to the outbreak of specific herbivore species, the herbivore community usually responds negatively to water deficits. For example, reduced precipitation treatment is linked to reduced arthropod abundance and diversity in the mixed-grass prairie (Prather et al., 2020), herbaceous plant (Lin et al., 2021a), wheat (Kansman et al., 2021), and pine (Trotter et al., 2008). However, when focusing on specific species of herbivores, drier and warmer climates can sometimes be associated with outbreaks of insect herbivores, especially those associated with trees, such as Ormiscodes (Lepidoptera, Saturniidae) (Paritsis and Veblen, 2011) and bark beetles on ponderosa pines in the Western United States (Negrón et al., 2009). Droughtassociated herbivore outbreaks are usually not observed in agricultural systems (except for mites, see (Santamaria et al., 2018) for more discussion), perhaps due to the herbaceous or grassy nature of many crops and their specific interactions with herbivores. In addition to insect abundance, insect assemblages were found to be significantly influenced by aridity, with more generalist herbivores in dryer areas than wetter areas across the Caatinga dry forest of northeast Brazil (Santos-Neto et al., 2022). Whether the changes in herbivore assemblage can be observed in other natural ecosystems and agroecosystems, remain to be investigated. Understanding insect assemblage changes under different water availability may have important conservation and pest management values.

Water deficit can also decrease herbivore abundance by influencing herbivores' interactions with their natural enemies. Field studies have revealed that water deficit tends to reduce the aboveground natural enemies of herbivores, in the case of variable leaf watercress (*Rorippa indica*) (Lin *et al.*, 2021a), wheat (Kansman *et al.*, 2021) and pine (Trotter *et al.*, 2008). In contrast, decreased soildwelling predatory ants due to enhanced rainfall were linked to an increased abundance of ranchman's tiger moth, *Platyprepia virginali*, under increased precipitation (Karban *et al.*, 2017). A similar increase in predatory ants under low water availability was also observed in maize (Guyer *et al.*, 2018). Although water deficit generally decreases overall natural enemies associated with plants, further investigation is needed to test this hypothesis and identify special cases. These types of data are especially lacking in agricultural systems.

Interestingly, drought can positively affect the conservation of rare species. Drought during 2013-2015 in California was found to promote the persistence of rare species and decrease dominant species across the taxa of species (e.g., plants, arthropods, reptiles, and mammals) (Prugh *et al.*, 2018). Whether this is commonly observed elsewhere remains unknown, but this finding suggests that fluctuation in water availability might contribute to the maintenance of biodiversity.

3.3. Evolution under variable water availability

Water availability influences the evolution of plant traits, such as flowering time, stomatal behavior, and drought resistance (Anderson *et al.*, 2012; Anstett *et al.*, 2021; Franks *et al.*, 2016; Franks *et al.*, 2007; Yang *et al.*, 2021), as well as antiherbivore traits (López-Goldar *et al.*, 2020). It has been shown that abiotic factors such as precipitation are linked to variation in plant volatile profile among populations of California sagebrush (*Artemisia californica*). Populations in southern drier areas typically have higher concentrations of total terpene and monoterpene than populations from

northern wetter areas (Pratt *et al.*, 2014). This finding suggests that abiotic factors play an essential role in plant volatile trait evolution, and terpenes might be associated with abiotic tolerance. However, studies investigating the populational variation of defensive traits across regions with variable water availability remain scarce, and how these defensive traits are also influenced by herbivory remains unclear.

Animals also evolved according to their abiotic environments (Grant *et al.*, 2017), such as the beak size evolution of Darwin's ground finches (*Geospiza spp.*) under drought (Grant and Grant, 2006). Abiotic factors can influence herbivore evolution indirectly via changes in their host plants. English grain aphid (*Sitobion avenae*) from arid areas perform better on wheat seedlings under mild water deficit (leaf water potential: – 0.2 to – 0.6 MPa), suggesting these aphids adapted to drought-stressed host plants (Liu *et al.*, 2018). Additionally, water availability influences the host plant specificity of herbivores. Lepidopteran herbivores in less stressful areas feed on a lower number of host plants, likely due to decreased plant quantity and quality (López-Carretero *et al.*, 2018). Similarly, it was found that generalist herbivores became more specialized on host plants when they grow in serpentine soil, which has low water availability. This observation suggests that upon water limitation, most plants become more resistant to herbivory (i.e., less suitable) and can influence the host choice of herbivores (Robinson and Strauss, 2020). These findings highlight the role of water deficit in influencing food web structure and host specificity evolution by affecting herbivore diet breadth.

4. Interactive effect of water availability and other abiotic factors on plant-herbivore interactions

Plants are usually challenged by multiple environmental stresses, and anthropogenic changes have increased the frequency of concurrent stresses (Zandalinas *et al.*, 2021a). Although there are sometimes synergistic relationships between different stress responses, such as water deficit and herbivory (Erb and Reymond, 2019; Jogawat *et al.*, 2021), general tradeoffs seem to exist between plants' ability to cope with different stresses (Langley *et al.*, 2022). A recent report documented the negative effects of multifactorial stresses (e.g., acidity, heavy metal, heat stress, salt stress, oxidative stress) on plant fitness and survival (Zandalinas *et al.*, 2021b). Although the above study did not consider biotic stresses, such as herbivory, this emerging concept necessitate a better understanding of plant responses to concurrent biotic and abiotic stresses.

4.1. Atmospheric factors

The increase in CO_2 concentration in the atmosphere can lead to a beneficial effect on plant growth, known as CO_2 fertilization (Wang *et al.*, 2020), which can sometimes ameliorate the negative impact of water deficit on plants (Domec *et al.*, 2017; Medina *et al.*, 2016) and lead to increase soil water availability (Morgan *et al.*, 2001). CO_2 fertilization can negate the effect of water deficit in enhancing plant defenses (Casteel *et al.*, 2012), which influences herbivores positively (Rosenblatt *et al.*, 2017) or have minimal impacts on water-plant-herbivore interactions (Guyer *et al.*, 2021; Xing *et al.*, 2003). For mites that usually benefit from plants under water deficit, CO_2 fertilization further increases mite performance (Sinaie *et al.*, 2019). CO_2 fertilization and water deficit have also been found to decrease the survival of some natural enemies (e.g., entomopathogenic nematodes) under elevated temperatures but do not affect other natural enemies in short-term assays (Doan *et al.*, 2021). Ozone (O₃) is one of the most damaging air pollutants, which has been found to disturb plant development and growth (Tai *et al.*, 2014). Many ozone-triggered plant responses are associated with plant responses to water deficit, including stomatal closure and enhanced volatile emission (Brosset *et al.*, 2020; Kask *et al.*, 2021; Li *et al.*, 2017; Papazian *et al.*, 2016). Interestingly, drought has also been found to lead to increased O₃ pollution (Solberg *et al.*, 2008; Wang *et al.*, 2017), e.g., tropospheric O₃, which is created by chemical reactions between oxides of nitrogen and volatile organic compounds. (Vicente-Serrano *et al.*, 2020). Few studies have investigated the interactive effects of combined ozone and water stress. Ozone has been linked to drought-associated susceptibility of pine trees to bark beetle attacks (Eatough Jones *et al.*, 2004). Although many plant volatiles responsive to ozone are also involved in plant-herbivore interactions (Kask *et al.*, 2021; Palmer-Young *et al.*, 2015), the interactive effects of ozone and water stress of ozone and water stress on plant-herbivore interactions (Kask *et al.*, 2021; Palmer-Young *et al.*, 2015), the interactive effects of ozone and water stress on plant-herbivore interactions remain to be investigated.

Chemical composition in the atmosphere can lead to physical changes in the atmosphere, such as warming (IPCC, 2021). The elevated temperature often co-occurs with water deficit by enhancing transpiration in both soil and plants (Yuan *et al.*, 2019). The interactive effect of elevated temperature and water deficit is relatively well studied in natural- and agricultural ecosystems (Querejeta *et al.*, 2021; Zandalinas and Mittler, 2022). Water deficit has been demonstrated to be a more deterministic factor than warming on plant-herbivore interactions (Orians *et al.*, 2019; Scherber *et al.*, 2013) and plant volatile emission (Trowbridge *et al.*, 2019). However, warming and water deficit can have a positive synergistic effect on the performance of herbivores, such as scale insects (Dale and Frank, 2017).

Warming increases vapor pressure deficit (VPD) (Yuan *et al.*, 2019). VPD has been found to have important implications for plant stomatal behavior, physiological responses, and plant growth from individual to ecosystem levels (Yuan *et al.*, 2019). VPD can contribute to and exacerbate plant water deficit (Dannenberg *et al.*, 2022). However, how VPD might influence plant-herbivore interactions remains unclear. VPD's impact on stomatal behavior and photosynthesis will likely lead to changes in plant volatile emission and volatile-mediated biotic interactions. In addition to VPD, air movement (i.e., wind) also determine the speed of plant water loss and contributes to the development of water deficit. It has been shown that in addition to the influence of wind on plant growth inhibition, wind exposure also enhances the defenses of black mustard (*Brassica nigra*) and the development time of two specialist caterpillars (*Pieris brassicae* and *Plutella xylostella*) (Chen *et al.*, 2018).

An interesting recent study shows that stress-induced plant monoterpene emission enhances the formation of secondary organic aerosols, which act as cloud condensation nuclei, potentially increasing precipitation (Holopainen *et al.*, 2022). This study suggests that plant volatiles are involved in organism-level interactions and play essential roles in the hydrological cycle, which significantly influences water-plant-herbivore interactions (Fig. 3).

4.2. Soil abiotic factors

Water is essential for dissolving mineral nutrients and plant absorption of nutrients such as nitrogen (for other nutrients, we refer the reader to (Hu and Schmidhalter, 2005). Water deficit antagonizes the positive effect of nitrogen enrichment in short-term or greenhouse experiments but not in long-term or field experiments (Guo *et al.*, 2022). In the context of plant-herbivore interactions, nitrogen/water deficit generally lower herbivore performances in the tomato system (Han *et al.*, 2016; Han *et al.*, 2014). Inadequate nitrogen fertilization levels and water deficit interact to compromise natural enemy attraction (Olson *et al.*, 2009). In some cases, water deficit has a much more significant impact than nitrogen on natural enemies (Dong *et al.*, 2018).

Silicon (Si) is closely linked with enhanced antiherbivore defenses in some plants (e.g., Poaceae) (Acevedo *et al.*, 2021; Debona *et al.*, 2017; Waterman *et al.*, 2020). Enhanced Si availability has also been found to lessen the negative effect of water deficit on plants (Debona *et al.*, 2017). In collard plants (*Brassica oleracea*), Si application enhances plant growth, plant water content, and secondary metabolite accumulation, as well as herbivore resistance indicated by a decreased caterpillar (*Plutella xylostella*) performance (Teixeira *et al.*, 2020). Additionally, Si fertilization influences the availability and accumulation of other nutrients in maize (Greger *et al.*, 2018). Si seems essential in enhancing plant defense against water deficit and herbivory and plant nutritional balance.

4.3. Multifactorial stress and water-plant-herbivore interactions

Although an increasing number of studies has investigated the interactive impacts of one or two additional abiotic stress with water deficit on plant-herbivore interaction, the amount of research effort falls far behind the importance of stresses combination on plant resilience to abiotic and biotic stresses (Zandalinas and Mittler, 2022). Many stress combinations remain poorly investigated. Given the known context-dependency of water-plant-herbivore interactions, it is important to fill these knowledge gaps by investigating more plant species under different stress combinations. However, there are major empirical challenges to conducting such studies investigating multiple stress interactions on plants. Depending on the focal abiotic or biotic factors, much equipment might be needed to create suitable and comparable stress treatments (e.g., CO_2 or O_3 system, irrigation system, gas exchange measuring device, etc.). It will be increasingly difficult as the stress combinations increase. The need to investigate different stress severities exacerbate this empirical difficulty, and traditional empirical methods are often inadequate for studying the responses of plants and associated herbivores to multi-stress combinations. Major technical breakthroughs, such as high throughput systems/devices that allow testing for multiple stresses, are needed for the study of multi-stress interactions, which will facilitate the development of multi-stress resilient plants and more reliable models of insect outbreaks in future climatic scenarios (Correia et al., 2022; Hall et al., 2022; Strock et al., 2022).

5. Applied aspects of water-plant-herbivore interactions

Changes in herbivore populations due to water availability fluctuation can have profound impact on their associated ecosystems. For instance, the well-known association between drought and some species of forest pest outbreaks (Mattson and Haack, 1987; Van Bael *et al.*, 2004; Xu *et al.*, 2019). Therefore, one of the goals of water-plant-herbivore interactions is to generate knowledge that allows for better forest pest management (Jaworski and Hilszczański, 2013). In contrast to the forest system, water stress in the agricultural system does not lead to outbreaks of herbivores but

significantly impacts productivity (Bodner et al., 2015). Breeding drought resistant cultivars are, therefore, a major goal for most crop species (Hu and Xiong, 2014). Although evidence suggests that plant responses toward water deficit and herbivory are often similar (see Section 2, Fig. 2), whether there are links between resilient traits against these two stresses across plant genotypes is poorly understood. Studies comparing traits against biotic and abiotic stresses are particularly useful to address this question. For example, drought resistant cultivars of spring wheat (Triticum aestivum) do not seem to influence plant resistance to aphid herbivory. It was found that leaf traits (e.g., trichomes and cell junction cuticle thickness) are better parameters that predict plant resistance to aphids among the six spring wheat cultivars tested (Saska et al., 2021). While these types of studies remain scarce, future studies should focus on identifying the existence (or lack) of such linkage across different plants and the underlying biochemical and physiological links between drought resistance and antiherbivore defense (Saska et al., 2022). Additionally, many plant volatiles, such as isoprenoids (e.g., monoterpene, sesquiterpenes) can act as antioxidants in plants directly protecting plants from oxidative stresses triggered by different stresses (Vickers et al., 2009), which could be a promising trait that can be used for future breeding programs for resilient plants against multiple stresses.

Recent findings suggest that drought-stressed plants are usually less attractive to natural enemies of herbivores and have been associated with a reduced natural enemy community in some systems (Doan *et al.*, 2021; Guyer *et al.*, 2018; Guyer *et al.*, 2021; Kansman *et al.*, 2021; Lin *et al.*, 2021a; Trotter *et al.*, 2008). Based on the above observations, we speculate that the temporal and spatial variations of water availability in the agroecosystem might influence the effectiveness of biological controls on pest herbivores. Related to this hypothesis is that agricultural practices that enhance plant diversity also often lead to more soil coverage, less evaporation, and better water availability (Murrell, 2017). Interestingly, these agricultural practices are often associated with a higher number of natural enemies and lower pest damages (González-Chang *et al.*, 2019). While enhanced habitat complexity is believed to contribute to such beneficial effects, it is likely that better plant quality due to enhanced water availability also plays a role in contributing to better natural enemy communities (Kansman *et al.*, 2021; Lin *et al.*, 2021a; Trotter *et al.*, 2008). However, different natural enemies might be influenced by changes in water availability and multiple trophic interactions might provide essential knowledge to integrate pest management and water management.

One of the most critical steps in the current integrated pest management program is to accurately predict the outbreak of pests and facilitate the decision-making of necessary pest management measures which is increasingly challenging under climate change (Ziska and McConnell, 2016). Since changes in water availability influence herbivore population dynamics, it is likely that these climatic or abiotic parameters, such as water availability, will serve as an essential parameter for future pest monitors and prediction. For example, landscape and precipitation influence the population dynamics of potato psyllids (*Bactericera cockerelli*) in agroecosystems. Including these environmental factors in the modeling procedure can lead to better prediction and more effective pest management (Gutiérrez Illán *et al.*, 2020).

6. Conclusion and future directions

The interactions between water availability, plants, and herbivores are complicated and difficult to generalize (Gely et al., 2020; Hamann et al., 2020; Huberty and Denno, 2004; Jamieson et al., 2012; Waring and Cobb, 1992). The limitation of empirical studies on the number of species and the level of water availability investigated have created much of the observed context-dependency of waterplant-herbivore interactions. However, we do start to see some patterns emerging from the accumulating number of studies. For instance, Plants enhance antiherbivore defenses under water deficit (Kansman et al., 2022; Lin et al., 2021b), leading to increased resistance (i.e., direct defense), and have also been shown to evolve early phenology (Metz et al., 2020). These defense strategies are potentially caused by the limitation of other available defense strategies such as tolerance (Lin et al., 2021b) and indirect defense (Kansman et al., 2021; Lin et al., 2022; Trotter et al., 2008). Recent findings underscore the importance of plant volatiles in responses against water deficit and herbivory (Lin et al., 2022; Peñuelas and Staudt, 2010; Tarig et al., 2013; Zhou and Jander, 2022). Studies of specific species pairs will be most valuable in elucidating the underlying mechanisms of water-plant-herbivore interactions. However, it is noteworthy that the pattern might change when specific species are studied. For instance, plant volatiles that are generally repellent to insect herbivores might be used by specialized herbivores or natural enemies as foraging cues. An additional limitation was that past studies focus primarily on selected tree and crop species. There is a general lack of study on plants outside of these model systems. This pattern is the same for herbivores species for most studies focused mainly on certain pests. There is also considerable publication bias due to positive effect of drought on herbivores being more readily observable (i.e., outbreak) than negative impacts (i.e., decrease in insect numbers), this tendency has no doubt led to the previous belief that drought is beneficial for insect herbivores. It is therefore necessary to expand the number of studied species in water-plant-herbivore interactions. Another perhaps more efficient way of addressing the above limitation, is to use a combination of studies on specific species (Kansman et al., 2020) and community response (Kansman et al., 2021). Community-level studies will be necessary since they incorporate a wide range/network of biotic interactions associated with plants. Community-level studies will therefore be an important future research direction, especially in agricultural systems. We believe that as studies of water-plant-herbivore interactions accumulate in number (more species combinations and water availability scenarios), clearer patterns of water-plant-herbivore interactions will likely emerge. An additional aspect that is essential in the search for general patterns of water-plant-herbivore interactions is the proper quantification of plant water status and the inclusion of multiple water availability levels (Gormally et al., 2020; Jones, 2007). Different water availability levels (or stress severity) can trigger different plant responses and lead to distinct outcomes of plant-herbivore interactions, sometimes in a nonlinear way (Gutbrodt et al., 2011; Kansman et al., 2022; Lin et al., 2021b; Saska et al., 2022). It is also important to include at least three levels of water availability due to the hormetic response of plants to stresses (Li et al., 2022a). As the importance of multiple dimensions of drought (i.e., duration, timing, and severity) on plant resilience is being uncovered (Song et al., 2022), investigating the impact of these dimensions is key to a comprehensive understanding of water-plant-herbivore interactions and an important area of future study.

Climate changes have increased the frequency and severity of many abiotic stresses (e.g., drought), which will likely co-occur in nature (Zandalinas *et al.*, 2021a). Other abiotic factors likely affected the outcome of water-plant-herbivore interactions and therefore provide another layer of challenges to

search for general patterns in water-plant-herbivore interactions. A priority for future study is therefore to understand how concurrent stresses influence water-plant-herbivore interactions. Although not directly linked to plant-herbivore interactions, recent studies have shown that specific plant traits can be associated with resilience against different stresses, such as low availability of both water and phosphate (Oliveira *et al.*, 2019). The synergisms between different plant stress responses suggest that many of these stress responses are potentially not just an adaptation to specific stress. Arguably, most plant stress responses evolved under multifactorial stress conditions. Many plant stress responses likely serve multiple functions in plant resilience against stresses. Thus, the multifunctionality of stress responses will be an essential aspect in future studies of water-plant-herbivore interactions. However, a primary challenge of multifactorial stress studies is the technical difficulties in controlling different abiotic factors as the number of stresses increases. Methodological advancements, such as devices/systems that can control multiple abiotic factors simultaneously, are necessary to facilitate the research on multifactorial stresses.

Furthermore, we identify three additional aspects that require research attention. First, changes in water availability have long been studied under the context of precipitation changes, especially drought (Hamann et al., 2020). While the importance of drought on plant-herbivore interactions is undisputable, water availability can change due to other factors such as soil property (e.g., soil depth and soil type) (Haruna and Nkongolo, 2013; Mastrotheodoros et al., 2020). Water availability changes due to spatial heterogeneity within a habitat are common and likely lead to plants with distinct water statuses within a habitat (Haruna and Nkongolo, 2013). Still, they are often overlooked in studies of water-plant-herbivore interactions. How changes in water availability due to environmental heterogeneity affect the ecology and evolution of plant-herbivore interactions remains unclear and could serve as an essential factor that drives plants defensive strategies. Second, plant stress from flooding and oversaturation is a significant environmental concern and results in different outcomes from water deficit stress, despite receiving less attention (Ngumbi and Ugarte, 2021; Rai et al., 2018). Though both conditions result in negative effects for herbivores and plants, in the same system water saturation increases plant vulnerability to pathogen infection while water deficit reduces infection (Nachappa et al., 2016). Third, the studies of water-plant-herbivore interactions came from many parts of the world. However, like most academic disciplines, a disproportionate number of studies are coming from temperate regions (e.g., the Global North (Dados and Connell, 2012)). Fewer studies have come from subtropical and tropical areas (e.g., the Global South (Dados and Connell, 2012)), which are predicted to experience more severe climate change impacts (Blicharska et al., 2017). The observation that contrast effects of drought on plantherbivore interactions in temperate and tropic regions further necessitate the comparison between different climatic regions (Gely et al., 2020). An important future goal will be filling this knowledge gap by investigating how water availability in different climatic regions influences plant-herbivore interactions.

Decades of water-plant-herbivore interactions have led to advances in our knowledge of these complex interactions and created more challenges, questions, and novel hypotheses regarding the ecology and evolution of plant-herbivore interactions under variable water availability. These challenges and undesirable fluctuations in water availability due to climate changes necessitate further investigations of the ecology and evolution of water-plant-herbivore interactions for both scientific and applied purposes. For instance, advancing our knowledge of how different plant traits

contribute to plant resilience to abiotic stress has created opportunities for crop breeding. Bioengineering and gene modification of specific cell types such as stomata and phloem will help produce crops resilient to climate change and biotic stress (e.g., herbivory and pathogen) (Drincovich and Maurino, 2022). To facilitate the development of plants that can cope with multiple stresses, a better understanding of the underlying mechanisms is crucial. High-throughput phenotyping regarding stress resilience will be a helpful step to expedite this process. (Correia *et al.*, 2022). We believe the overall efforts in understanding water-plant-herbivore interactions, will eventually allow us to move toward the goal to better predict potential anthropogenic disturbance, promote plant resilience and ecosystem resilience to changes in water availability, and ultimately protect agricultural ecosystems, natural ecosystems, and the well-being of humans (Hernández-Blanco *et al.*, 2022).

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8. Author contribution

PAL: conceptualization, writing, and visualization. JK: writing and review. WPC: writing and review. CR: writing and review. ME; writing, review, and providing funding. GF: writing and review.

9. Conflicts of Interest

We declare no conflict of interest.

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Figure legends

Fig. 1 Influences of water availability on plant antiherbivore defenses strategies and their impacts on herbivores. Water deficit generally increases plant resistance to herbivores and compromises plant indirect defenses, such as natural enemy attraction. Water deficits reduce plant ability to tolerate herbivory. In addition to the plasticity of these defense strategies, plants evolve better herbivory escape traits (e.g., early phenology) under low water availability. Plant volatiles organic compounds (VOCs) are a group of secondary metabolites that are increasingly known to involve in water-plant-herbivore interactions, especially via their role in indirect defenses and resistance. Solid arrows indicate stronger relationships; dashed arrows indicate weaker or compromised relationships. Question marks indicate unknown aspects. Plus/minus signs indicate the positive/negative impacts of defense strategy changes on herbivores under different water availability. The size of the signs indicates the frequency of effects reported. HIPVs: herbivore-induced plant volatiles.

Fig. 2 Similarities between physiological responses triggered by herbivory and water deficit. Both stresses trigger similar phytohormonal responses with enhanced ABA, JA, and SA accumulation and decreased GA. Both herbivory and water deficit enhance secondary metabolites accumulation and an overall decrease in stomatal conductance, photosynthesis, and growth. However, an important knowledge gap is the role of water availability levels (i.e., stress severity) on these responses. Question marks indicate unclear relationships.

Fig. 3 Functions of plant volatiles in water-plant-herbivore interactions. Plants release distinct blends of volatiles under different stresses. Herbivore-induced plant volatiles (HIPVs) are well-known for their roles in plant defenses against herbivores and can be perceived by neighboring plants (receivers) as warning signals that prime or trigger defense responses. The role of drought-induced plant volatiles (DIPVs) is less clear. However, it has been shown that many of these volatiles act as antioxidants that protect plants from oxidative damage under abiotic stress. Fumigation of these volatiles leads to better abiotic stress tolerance. These biogenic VOCs (BVOCs) are also involved in atmospheric processes that indirectly influence water availability or the emission of plant VOCs. Plant VOCs, therefore, are likely involved in water-plant-herbivore interactions from all levels of biological organizations. Solid arrows and question marks indicate clear relationships; dashed arrows and question marks indicate unclear relationships.

Fig. 4 Influence of low water availability on species interactions and community structure. Low water availability has been shown to influence intraspecific interactions such as competition between plants and herbivores and interactions between plants, herbivores, natural enemies, and pollinators. These changes in interactions lead to alteration in community structures and dynamics, which in turn influences the biological interactions within the community. Plus/minus signs indicate the positive/negative influences of low water availability on each factor; each sign's size indicates the frequency of the observed effects. Question marks indicate unclear relationships.



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