Water availability and plant-herbivore interactions

Po-An Lin, poanlin@ntu.edu.tw, Department of Entomology, National Taiwan University, Taipei, Taiwan

Jessica Kansman, kansmanj@psu.edu, Department of Entomology, the Pennsylvania State University, University Park, USA

Wen-Po Chuang, wenpo@ntu.edu.tw, Department of Agronomy, National Taiwan University, Taipei, Taiwan

Christelle Robert, christelle.robert@ips.unibe.ch, Institute of Plant Science, University of Bern, Bern, Switzerland.

Matthias Erb, mattias.erb@ips.unibe.ch, Institute of Plant Science, University of Bern, Bern, Switzerland.

Gary W. Felton, gwf10@psu.edu, Department of Entomology, the Pennsylvania State University, University Park, USA

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 plant-herbivore 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 plant-herbivore 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 plant-herbivore 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-plant-herbivore 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 plant-herbivore 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; Tariq *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 plant-plant 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 inter-specific 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 plant-herbivore interactions (Lozano *et al.*, 2021). For instance, mycorrhizal fungi altered the growth-defense 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 plant-stress 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.*, 2022c). These findings suggest the importance of biodiversity and community 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). Drought-associated 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 above-ground 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 soil-dwelling 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 of tropical forests feed on higher numbers of host plants. In contrast, herbivores in 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).

Additionally, CO_2 fertilization has been shown to influence plants with distinct photosynthetic pathways differentially (e.g., C3, C4, CAM; for details, see (Leegood, 2002)). How these physiological differences affect the interactions between CO_2, water availability, and herbivory remains unclear.

Ozone (O_3) 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 O_3 pollution (Solberg *et al.*, 2008; Wang *et al.*, 2017), e.g., tropospheric O_3, 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 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 in distinct ways (Guyer *et al.*, 2018). A better understanding of the links between 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 water-plant-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; Tariq *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 non-linear 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 plant-herbivore 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).

7. Acknowledgment

We thank the editors for the invitation to submit this review.

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.

10. Funding Statement

The work of Dr. Christelle Robert was supported by the Swiss National Science Foundation, grant #310030_189071.

References

Acevedo FE, Peiffer M, Ray S, Tan C-W, Felton GW. 2021. Silicon-Mediated Enhancement of Herbivore Resistance in Agricultural Crops. Frontiers in Plant Science **12**.

Agathokleous E, Kitao M, Calabrese EJ. 2018. Emission of volatile organic compounds from plants shows a biphasic pattern within an hormetic context. Environmental Pollution **239**, 318-321.

Agrawal AA. 2007. Macroevolution of plant defense strategies. Trends in Ecology & Evolution **22**, 103-109.

Anderson JT, Inouye DW, McKinney AM, Colautti RI, Mitchell-Olds T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of the Royal Society B: Biological Sciences **279**, 3843-3852.

Anstett DN, Branch HA, Angert AL. 2021. Regional differences in rapid evolution during severe drought. Evolution Letters.

Anzano A, Bonanomi G, Mazzoleni S, Lanzotti V. 2022. Plant metabolomics in biotic and abiotic stress: a critical overview. Phytochemistry Reviews **21**, 503-524.

Armstrong W, Brändle R, Jackson MB. 1994. Mechanisms of flood tolerance in plants. Acta Botanica Neerlandica **43**, 307-358.

Asiyeh Notghi Moghadam S, Sadeghi-Namaghi H, Moodi S. 2022. Plant-mediated effects of water-deficit stress on the performance of the jujube lace bug, Monosteira alticarinata Ghauri (Hemiptera: Tingidae) on Jujube tree. Journal of Asia-Pacific Entomology, 101917.

Atala C, Gianoli E. 2009. Effect of water availability on tolerance of leaf damage in tall morning glory, *Ipomoea purpurea*. Acta Oecologica **35**, 236-242.

Barnett KL, Facey SL. 2016. Grasslands, Invertebrates, and Precipitation: A Review of the Effects of Climate Change. Frontiers in Plant Science **7**.

Barton BT, Ives AR. 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. Ecology **95**, 486-494.

Batbaatar A, Carlyle CN, Bork EW, Chang SX, Cahill JF. 2022. Multi- year drought alters plant species composition more than productivity across northern temperate grasslands. Journal of Ecology **110**, 197-209.

Bennett RN, Wallsgrove RM. 1994. SECONDARY METABOLITES IN PLANT DEFENSE-MECHANISMS. New Phytologist **127**, 617-633.

Blicharska M, Smithers RJ, Kuchler M, Agrawal GK, Gutiérrez JM, Hassanali A, Huq S, Koller SH, Marjit S, Mshinda HM, Masjuki HH, Solomons NW, Staden JV, Mikusiński G. 2017. Steps to overcome the North–South divide in research relevant to climate change policy and practice. Nature Climate Change **7**, 21-27.

Bodner G, Nakhforoosh A, Kaul H-P. 2015. Management of crop water under drought: a review. Agronomy for Sustainable Development **35**, 401-442.

Bont Z, Pfander M, Robert CAM, Huber M, Poelman EH, Raaijmakers CE, Erb M. 2020. Adapted dandelions trade dispersal for germination upon root herbivore attack. Proceedings of the Royal Society B: Biological Sciences **287**, 20192930.

Brosset A, Blande JD. 2022. Volatile-mediated plant–plant interactions: volatile organic compounds as modulators of receiver plant defence, growth, and reproduction. Journal of Experimental Botany **73**, 511-528.

Brosset A, Saunier A, Mofikoya AO, Kivimäenpää M, Blande JD. 2020. The Effects of Ozone on Herbivore-Induced Volatile Emissions of Cultivated and Wild Brassica Rapa. Atmosphere **11**, 1213.

Bunker DE, Carson WP. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. Journal of Ecology **93**, 794-806.

Câmara T, Reis DQDA, Arnan X, Oliveira FMP, Arruda ECP, Leal IR. 2021. Drought- induced reductions in plant defenses: Insights from extrafloral nectaries in the Caatinga dry forest. Biotropica.

Castagneyrol B, Jactel H, Moreira X. 2018. Anti-herbivore defences and insect herbivory: Interactive effects of drought and tree neighbours. Journal of Ecology **106**, 2043-2057.

Casteel CL, Niziolek OK, Leakey ADB, Berenbaum MR, Delucia EH. 2012. Effects of elevated CO2 and soil water content on phytohormone transcript induction in Glycine max after Popillia japonica feeding. Arthropod-Plant Interactions **6**, 439-447.

Chandler JL, Elkinton JS, Orwig DA. 2022. High Rainfall May Induce Fungal Attack of Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Leading to Regional Decline. Environmental Entomology **51**, 286-293.

Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought—from genes to the whole plant. Functional Plant Biology **30**, 239-264.

Chen C, Biere A, Gols R, Halfwerk W, Van Oers K, Harvey JA. 2018. Responses of insect herbivores and their food plants to wind exposure and the importance of predation risk. Journal of Animal Ecology **87**, 1046-1057.

Chen C, Chen H, Huang S, Jiang T, Wang C, Tao Z, He C, Tang Q, Li P. 2021. Volatile DMNT directly protects plants against Plutella xylostella by disrupting peritrophic matrix barrier in midgut. eLife **10**, e63938.

Chen C, Harvey JA, Biere A, Gols R. 2019. Rain downpours affect survival and development of insect herbivores: the specter of climate change? Ecology **100**.

Cofer TM, Engelberth M, Engelberth J. 2018. Green leaf volatiles protect maize (Zea mays) seedlings against damage from cold stress. Plant, Cell & Environment **41**, 1673-1682.

Conboy NJA, McDaniel T, George D, Ormerod A, Edwards M, Donohoe P, Gatehouse AMR, Tosh CR. 2020. Volatile Organic Compounds as Insect Repellents and Plant Elicitors: an Integrated Pest Management (IPM) Strategy for Glasshouse Whitefly (Trialeurodes vaporariorum). Journal of Chemical Ecology.

Correia PMP, Cairo Westergaard J, Da Silva AB, Roitsch T, Carmo-Silva E, Da Silva JM. 2022. High-throughput phenotyping of physiological traits for wheat resilience to high temperature and drought stress. Journal of Experimental Botany.

Crausbay SD, Ramirez AR, Carter SL, Cross MS, Hall KR, Bathke DJ, Betancourt JL, Colt S, Cravens AE, Dalton MS, Dunham JB, Hay LE, Hayes MJ, McEvoy J, McNutt CA, Moritz MA, Nislow KH, Raheem N, Sanford T. 2017. Defining Ecological Drought for the Twenty-First Century. Bulletin of the American Meteorological Society **98**, 2543-2550.

Dados N, Connell R. 2012. The Global South. Contexts **11**, 12-13.

Dale AG, Frank SD. 2017. Warming and drought combine to increase pest insect fitness on urban trees. PLOS ONE **12**, e0173844.

Danin A. 1991. Plant adaptations in desert dunes. Journal of Arid Environments **21**, 193-212.

Dannenberg MP, Yan D, Barnes ML, Smith WK, Johnston MR, Scott RL, Biederman JA, Knowles JF, Wang X, Duman T, Litvak ME, Kimball JS, Williams AP, Zhang Y. 2022. Exceptional heat and atmospheric dryness amplified losses of primary production during the 2020 U.S. Southwest hot drought. Global Change Biology.

Davies WJ, Metcalfe J, Lodge TA, da Costa AR. 1986. Plant Growth Substances and the Regulation of Growth Under Drought. Functional Plant Biology **13**, 105-125.

Davila Olivas NH, Kruijer W, Gort G, Wijnen CL, Loon JJA, Dicke M. 2017. Genome- wide association analysis reveals distinct genetic architectures for single and combined stress responses in Arabidopsis thaliana. New Phytologist **213**, 838-851.

Davis TS, Bosque-Pérez NA, Foote NE, Magney T, Eigenbrode SD, Cadotte M. 2015. Environmentally dependent host-pathogen and vector-pathogen interactions in the Barley yellow dwarf virus

pathosystem. Journal of Applied Ecology **52**, 1392-1401.

Debona D, Rodrigues FA, Datnoff LE. 2017. Silicon's Role in Abiotic and Biotic Plant Stresses. Annual Review of Phytopathology **55**, 85-107.

Diaz HF, Bradley RS, Eischeid JK. 1989. Precipitation fluctuations over global land areas since the late 1800's. Journal of Geophysical Research **94**, 1195.

Doan C, Pfander M, Guyer AS, Zhang X, Maurer C, Robert CAM. 2021. Natural enemies of herbivores maintain their biological control potential under short- term exposure to future CO 2 , temperature, and precipitation patterns. Ecology and Evolution **11**, 4182-4192.

Dobler S, Dalla S, Wagschal V, Agrawal AA. 2012. Community-wide convergent evolution in insect adaptation to toxic cardenolides by substitutions in the Na,K-ATPase. Proceedings of the National Academy of Sciences **109**, 13040-13045.

Domec J-C, Smith DD, McCulloh KA. 2017. A synthesis of the effects of atmospheric carbon dioxide enrichment on plant hydraulics: implications for whole-plant water use efficiency and resistance to drought. Plant, Cell & Environment **40**, 921-937.

Dong YC, Han P, Niu CY, Zappala L, Amiens-Desneux E, Bearez P, Lavoir AV, Biondi A, Desneux N. 2018. Nitrogen and water inputs to tomato plant do not trigger bottom-up effects on a leafminer parasitoid through host and non-host exposures. Pest Manag Sci **74**, 516-522.

Driesen E, Van Den Ende W, De Proft M, Saeys W. 2020. Influence of Environmental Factors Light, CO2, Temperature, and Relative Humidity on Stomatal Opening and Development: A Review. Agronomy **10**, 1975.

Drincovich MF, Maurino VG. 2022. Adjustments of carbon allocation and stomatal dynamics by target localized strategies to increase crop productivity under changing climates. Journal of Plant Physiology **272**, 153685.

Eatough Jones M, Paine TD, Fenn ME, Poth MA. 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. Forest Ecology and Management **200**, 67-76.

Ehleringer JR, Monson RK. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics **24**, 411-439.

Erb M. 2018. Volatiles as inducers and suppressors of plant defense and immunity—origins, specificity, perception and signaling. Current Opinion in Plant Biology **44**, 117-121.

Erb M, Kliebenstein DJ. 2020. Plant Secondary Metabolites as Defenses, Regulators, and Primary Metabolites: The Blurred Functional Trichotomy. Plant Physiology **184**, 39-52.

Erb M, Köllner TG, Degenhardt J, Zwahlen C, Hibbard BE, Turlings TCJ. 2011. The role of abscisic acid and water stress in root herbivore- induced leaf resistance. New Phytologist **189**, 308-320.

Erb M, Meldau S, Howe GA. 2012. Role of phytohormones in insect-specific plant reactions. Trends in Plant Science **17**, 250-259.

Erb M, Reymond P. 2019. Molecular interactions between plants and insect herbivores. Annual Review of Plant Biology **70**, 527-557.

Fan Y, Yang W, Yan Q, Chen C, Li J. 2019. Genome-Wide Identification and Expression Analysis of the Protease Inhibitor Gene Families in Tomato. Genes **11**, 1.

Foote NE, Davis TS, Crowder DW, Bosque-Pérez NA, Eigenbrode SD. 2017. Plant Water Stress Affects Interactions Between an Invasive and a Naturalized Aphid Species on Cereal Crops. Environmental Entomology **46**, 609-616.

Franklin J, Serra-Diaz JM, Syphard AD, Regan HM. 2016. Global change and terrestrial plant community dynamics. Proceedings of the National Academy of Sciences **113**, 3725-3734.

Franks SJ, Kane NC, O'Hara NB, Tittes S, Rest JS. 2016. Rapid genome- wide evolution in Brassica rapa populations following drought revealed by sequencing of ancestral and descendant gene pools. Molecular Ecology **25**, 3622-3631.

Franks SJ, Sim S, Weis AE. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci U S A **104**, 1278-1282.

Gaffke AM, Sing SE, Millar JG, Dudley TL, Bean DW, Peterson RKD, Weaver DK. 2020. An Herbivore-Induced Plant Volatile From Saltcedar (Tamarix spp.) Is Repellent to Diorhabda carinulata (Coleoptera: Chrysomelidae). Environmental Entomology.

Gassmann AJ. 2004. Effect of photosynthetic efficiency and water availability on tolerance of leaf removal in *Amaranthus hybridus*. Journal of Ecology **92**, 882-892.

Gely C, Laurance SGW, Stork NE. 2020. How do herbivorous insects respond to drought stress in trees? Biological Reviews of the Cambridge Philosophical Society **95**, 434-448.

Ghannoum O. 2008. C4 photosynthesis and water stress. Annals of Botany **103**, 635-644.

Gilbert ME, Medina V. 2016. Drought Adaptation Mechanisms Should Guide Experimental Design. Trends in Plant Science **21**, 639-647.

Glenny WR, Runyon JB, Burkle LA. 2018. Drought and increased CO2 alter floral visual and olfactory traits with context-dependent effects on pollinator visitation. New Phytologist **220**, 785-798.

Gong P, Zhang J, Li H, Yang C, Zhang C, Zhang X, Khurram Z, Zhang Y, Wang T, Fei Z, Ye Z. 2010. Transcriptional profiles of drought-responsive genes in modulating transcription signal transduction, and biochemical pathways in tomato. Journal of Experimental Botany **61**, 3563-3575.

González-Chang M, Tiwari S, Sharma S, Wratten SD. 2019. Habitat Management for Pest Management: Limitations and Prospects. Annals of the Entomological Society of America **112**, 302-317.

Gormally BMG, Romero LM, Angelier F. 2020. What are you actually measuring? A review of techniques that integrate the stress response on distinct time- scales. Functional Ecology **34**, 2030-2044.

Gouinguené SP, Turlings TCJ. 2002. The Effects of Abiotic Factors on Induced Volatile Emissions in Corn Plants. Plant Physiology **129**, 1296-1307.

Gowik U, Westhoff P. 2011. The Path from C3 to C4 Photosynthesis. Plant Physiology **155**, 56-63.

Grant PR, Grant BR. 2006. Evolution of Character Displacement in Darwin's Finches. Science **313**, 224-226.

Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. 2017. Evolution caused by extreme events. Philosophical Transactions of the Royal Society B: Biological Sciences **372**, 20160146.

Greger M, Landberg T, Vaculík M. 2018. Silicon Influences Soil Availability and Accumulation of Mineral Nutrients in Various Plant Species. Plants **7**, 41.

Grossiord C. 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytologist **228**, 42-49.

Guo X, Liu H, Ngosong C, Li B, Wang Q, Zhou W, Nie M. 2022. Response of plant functional traits to nitrogen enrichment under climate change: A meta-analysis. Science of the Total Environment, 155379.

Gupta A, Rico-Medina A, Cano-Delgado AI. 2020. The physiology of plant responses to drought. Science **368**, 266-269.

Gutbrodt B, Mody K, Dorn S. 2011. Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. Oikos **120**, 1732-1740.

Gutiérrez Illán J, Bloom EH, Wohleb CH, Wenninger EJ, Rondon SI, Jensen AS, Snyder WE, Crowder DW. 2020. Landscape structure and climate drive population dynamics of an insect vector within intensely managed agroecosystems. Ecological Applications **30**.

Guyer A, Hibbard BE, Holzkämper A, Erb M, Robert CAM. 2018. Influence of drought on plant performance through changes in belowground tritrophic interactions. Ecology and Evolution **8**, 6756-6765.

Guyer A, Van Doan C, Maurer C, Machado RAR, Mateo P, Steinauer K, Kesner L, Hoch G, Kahmen A, Erb M, Robert CAM. 2021. Climate Change Modulates Multitrophic Interactions Between Maize, A Root Herbivore, and Its Enemies. Journal of Chemical Ecology.

Habib H, Fazili KM. 2007. Plant protease inhibitors: a defense strategy in plants. Biotechnology and Molecular Biology Reviews **2**, 68-85.

Hall RD, D'Auria JC, Silva Ferreira AC, Gibon Y, Kruszka D, Mishra P, Van De Zedde R. 2022. High-throughput plant phenotyping: a role for metabolomics? Trends in Plant Science.

Hamann E, Blevins C, Franks SJ, Jameel MI, Anderson JT. 2020. Climate change alters plant–herbivore interactions. New Phytologist.

Han P, Desneux N, Michel T, Le Bot J, Seassau A, Wajnberg E, Amiens-Desneux E, Lavoir A-V. 2016. Does Plant Cultivar Difference Modify the Bottom-Up Effects of Resource Limitation on Plant-Insect Herbivore Interactions? Journal of Chemical Ecology **42**, 1293-1303.

Han P, Dong Y, Lavoir AV, Adamowicz S, Bearez P, Wajnberg E, Desneux N. 2015. Effect of plant nitrogen and water status on the foraging behavior and fitness of an omnivorous arthropod. Ecol Evol **5**, 5468-5477.

Han P, Lavoir AV, Le Bot J, Amiens-Desneux E, Desneux N. 2014. Nitrogen and water availability to tomato plants triggers bottom-up effects on the leafminer Tuta absoluta. Sci Rep **4**, 4455.

Haruna SI, Nkongolo NV. 2013. Variability of Soil Physical Properties in a Clay-Loam Soil and Its Implication on Soil Management Practices. ISRN Soil Science **2013**, 1-8.

Hassani-Kakhki M, Karimi J, El Borai F, Killiny N, Hosseini M, Stelinski LL, Duncan L. 2019. Drought Stress Impairs Communication Between Solanum tuberosum (Solanales: Solanaceae) and Subterranean Biological Control Agents. Annals of the Entomological Society of America.

Herms DA, Mattson WJ. 1992. The Dilemma of Plants: To Grow or Defend. The Quarterly Review of Biology **67**, 283-335.

Hernández I, Alegre L, Munné-Bosch S. 2006. Enhanced oxidation of flavan-3-ols and proanthocyanidin accumulation in water-stressed tea plants. Phytochemistry **67**, 1120-1126.

Hernández- Blanco M, Costanza R, Chen H, Degroot D, Jarvis D, Kubiszewski I, Montoya J, Sangha K, Stoeckl N, Turner K, Van 'T Hoff V. 2022. Ecosystem health, ecosystem services, and the well- being of humans and the rest of nature. Global Change Biology.

Hillwig MS, Chiozza M, Casteel CL, Lau ST, Hohenstein J, Hernandez E, Jander G, MacIntosh GC. 2016. Abscisic acid deficiency increases defence responses against Myzus persicae in Arabidopsis. Molecular Plant Pathology **17**, 225-235.

Holopainen E, Kokkola H, Faiola C, Laakso A, Kühn T. 2022. Insect herbivory caused plant stress emissions increases the negative radiative forcing of aerosols. Journal of Geophysical Research: Atmospheres.

Hsiao TC. 1973. Plant responses to water stress. Annual review of plant physiology **24**, 519-570.

Hu H, Xiong L. 2014. Genetic Engineering and Breeding of Drought-Resistant Crops. Annual Review of Plant Biology **65**, 715-741.

Hu Y, Schmidhalter U. 2005. Drought and salinity: A comparison of their effects on mineral nutrition of plants. Journal of Plant Nutrition and Soil Science **168**, 541-549.

Huberty AF, Denno RF. 2004. Plant water stress and its consequences for herbivorous insects: A new synthesis. Ecology **85**, 1383-1398.

IPCC. 2021. Climate Change 2021: The Physical Science Basis. *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*: IPCC.

Jamieson MA, Burkle LA, Manson JS, Runyon JB, Trowbridge AM, Zientek J. 2017. Global change effects on plant–insect interactions: the role of phytochemistry. Current Opinion in Insect Science **23**, 70-80.

Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. Plant Physiology **160**, 1719-1727.

Jaworski T, Hilszczański J. 2013. The effect of temperature and humidity changes on insects development their impact on forest ecosystems in the expected climate change. Forest Research Papers **74**, 345-355.

Jin J, Zhao M, Gao T, Jing T, Zhang N, Wang J, Zhang X, Huang J, Schwab W, Song C. 2021. Amplification of early drought responses caused by volatile cues emitted from neighboring tea plants. Horticulture Research **8**.

Jogawat A, Yadav B, Chhaya, Lakra N, Singh AK, Narayan OP. 2021. Crosstalk between phytohormones and secondary metabolites in the drought stress tolerance of crop plants: A review. Physiologia Plantarum **172**, 1106-1132.

Jones HG. 2007. Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. Journal of Experimental Botany **58**, 119-130.

Kansman J, Nalam V, Nachappa P, Finke D. 2020. Plant water stress intensity mediates aphid host choiceand feeding behaviour. Ecological Entomology.

Kansman JT, Basu S, Casteel CL, Crowder DW, Lee BW, Nihranz CT, Finke DL. 2022. Plant Water Stress Reduces Aphid Performance: Exploring Mechanisms Driven by Water Stress Intensity. Frontiers in Ecology and Evolution **10**.

Kansman JT, Crowder DW, Finke DL. 2021. Primacy of plants in driving the response of arthropod communities to drought. Oecologia.

Karban R, Grof- Tisza P, Holyoak M. 2017. Wet years have more caterpillars: interacting roles of plant litter and predation by ants. Ecology **98**, 2370-2378.

Kask K, Kaurilind E, Talts E, Kännaste A, Niinemets Ü. 2021. Combined Acute Ozone and Water Stress Alters the Quantitative Relationships between O3 Uptake, Photosynthetic Characteristics and Volatile Emissions in Brassica nigra. Molecules **26**, 3114.

Khan N, Bano A, Babar MDA. 2019. Metabolic and physiological changes induced by plant growth regulators and plant growth promoting rhizobacteria and their impact on drought tolerance in Cicer arietinum L. PLOS ONE **14**, e0213040.

Kooyers NJ. 2015. The evolution of drought escape and avoidance in natural herbaceous populations. Plant Science **234**, 155-162.

Krugner R, Backus EA. 2014. Plant Water Stress Effects on Stylet Probing Behaviors of Homalodisca vitripennis (Hemiptera: Cicadellidae) Associated With Acquisition and Inoculation of the Bacterium Xylella fastidiosa. Journal of Economic Entomology **107**, 66-74.

Kumagai TO, Porporato A. 2012. Strategies of a Bornean tropical rainforest water use as a function of rainfall regime: isohydric or anisohydric? Plant, Cell & Environment **35**, 61-71.

Kuppler J, Wieland J, Junker RR, Ayasse M. 2021. Drought-induced reduction in flower size and abundance correlates with reduced flower visits by bumble bees. AoB PLANTS **13**.

Langley JA, Grman E, Wilcox KR, Avolio ML, Komatsu KJ, Collins SL, Koerner SE, Smith MD, Baldwin AH, Bowman W, Chiariello N, Eskelinen A, Harmens H, Hovenden M, Klanderud K, McCulley RL, Onipchenko VG, Robinson CH, Suding KN. 2022. Do trade- offs govern plant species' responses to different global change treatments? Ecology.

Leegood RC. 2002. C4 photosynthesis: principles of CO2 concentration and prospects for its introduction into C3 plants. Journal of Experimental Botany **53**, 581-590.

Levine M, Paige K. 2004. Direct and indirect effects of drought on compensation following herbivory in scarlet gilia. Ecology **85**, 3185-3191.

Leybourne DJ, Preedy KF, Valentine TA, Bos JIB, Karley AJ. 2021. Drought has negative consequences on aphid fitness and plant vigor: Insights from a meta- analysis. Ecology and Evolution **11**, 11915-11929.

Li S, Harley PC, Niinemets Ü. 2017. Ozone-induced foliar damage and release of stress volatiles is highly dependent on stomatal openness and priming by low-level ozone exposure in Phaseolus vulgaris. Plant, Cell & Environment **40**, 1984-2003.

Li S, Li H, Wang J, Chen C, Hao D. 2022a. Hormetic response and co-expression of cytochrome P450 and cuticular protein reveal the tolerance to host-specific terpenoid defences in an emerging insect pest, Pagiophloeus tsushimanus (Coleoptera: Curculionidae). Journal of Pest Science.

Li X, Zhang J, Lin S, Xing Y, Zhang X, Ye M, Chang Y, Guo H, Sun X. 2022b. (+)-Catechin, epicatechin and epigallocatechin gallate are important inducible defensive compounds against Ectropis grisescens in tea plants. Plant, Cell & Environment **45**, 496-511.

Li Y, Jiang W, Shen C, Wang J, Singh BK, Ge Y. 2022c. Plant diversity improves resistance of plant biomass and soil microbial communities to drought. Journal of Ecology.

Lim C, Baek W, Jung J, Kim J, Lee S. 2015. Function of ABA in Stomatal Defense against Biotic and Drought Stresses. International Journal of Molecular Sciences **16**, 15251-15270.

Lin M, Vasseur L, Yang G, Gurr GM, You M. 2016. Avoidance, escape and microstructural adaptations of the tea green leafhopper to water droplets. Scientific Reports **6**, 37026.

Lin PA, Liu CM, Ou JA, Sun CH, Chuang WP, Ho CK, Kinoshita N, Felton GW. 2021a. Changes in arthropod community but not plant quality benefit a specialist herbivore on plants under reduced water availability. Oecologia **195**, 383-396.

Lin PA, Paudel S, Afzal A, Shedd NL, Felton GW. 2021b. Changes in tolerance and resistance of a plant to insect herbivores under variable water availability. Environmental and Experimental Botany **183**, 104334.

Lin PA, Paudel S, Bin Zainuddin N, Tan CW, Helms A, Ali JG, Felton GW. 2022. Low water availability enhances volatile-mediated direct defences but disturbs indirect defences against herbivores. Journal of Ecology **n/a**.

Liu D, Dai P, Li S, Ahmed SS, Shang Z, Shi X. 2018. Life-history responses of insects to water-deficit stress: a case study with the aphid Sitobion avenae. BMC Ecology **18**.

Lombardini L, Rossi L. 2019. Ecophysiology of Plants in Dry Environments. In: D'Odorico P, Porporato A, Wilkinson Runyan C, eds. *Dryland Ecohydrology*. Cham: Springer International Publishing, 71-100.

López-Carretero A, Díaz-Castelazo C, Boege K, Rico-Gray V. 2018. Temporal variation in structural properties of tropical plant-herbivore networks: The role of climatic factors. Acta Oecologica **92**, 59-66.

López- Goldar X, Zas R, Sampedro L. 2020. Resource availability drives microevolutionary patterns of plant defences. Functional Ecology.

López- Rubio R, Pescador DS, Escudero A, Sánchez AM. 2022. Rainy years counteract negative effects of drought on taxonomic, functional, and phylogenetic diversity: resilience in annual plant communities. Journal of Ecology **n/a**.

Lozano YM, Aguilar- Trigueros CA, Roy J, Rillig MC. 2021. Drought induces shifts in soil fungal communities that can be linked to root traits across 24 plant species. New Phytologist **232**, 1917-1929.

Markovic D, Colzi I, Taiti C, Ray S, Scalone R, Gregory Ali J, Mancuso S, Ninkovic V. 2019. Airborne signals synchronize the defenses of neighboring plants in response to touch. Journal of Experimental Botany **70**, 691-700.

Martini X, Stelinski LL. 2017. Drought stress affects response of phytopathogen vectors and their parasitoids to infection- and damage-induced plant volatile cues. Ecological Entomology **42**, 721-730.

Mastrotheodoros T, Pappas C, Molnar P, Burlando P, Manoli G, Parajka J, Rigon R, Szeles B, Bottazzi M, Hadjidoukas P, Fatichi S. 2020. More green and less blue water in the Alps during warmer summers. Nature Climate Change **10**, 155-161.

Matt P, Krapp A, Haake V, Mock H-P, Stitt M. 2002. Decreased Rubisco activity leads to dramatic changes of nitrate metabolism, amino acid metabolism and the levels of phenylpropanoids and nicotine in tobacco antisense RBCS transformants. The Plant Journal **30**, 663-677.

Mattson WJ, Haack RA. 1987. The Role of Drought in Outbreaks of Plant-Eating Insects. Bioscience **37**, 110-118.

Mauck KE, De Moraes CM, Mescher MC. 2016. Effects of pathogens on sensory-mediated interactions between plants and insect vectors. Current Opinion in Plant Biology **32**, 53-61.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist **178**, 719-739.

Medina S, Vicente R, Amador A, Araus JL. 2016. Interactive Effects of Elevated [CO2] and Water Stress on Physiological Traits and Gene Expression during Vegetative Growth in Four Durum Wheat Genotypes. Frontiers in Plant Science **7**.

Metz J, Lampei C, Bäumler L, Bocherens H, Dittberner H, Henneberg L, Meaux J, Tielbörger K. 2020. Rapid adaptive evolution to drought in a subset of plant traits in a large- scale climate change experiment. Ecology Letters **23**, 1643-1653.

Morgan JA, Lecain DR, Mosier AR, Milchunas DG. 2001. Elevated CO2 enhances water relations and productivity and affects gas exchange in C3 and C4 grasses of the Colorado shortgrass steppe. Global Change Biology **7**, 451-466.

Mujiono K, Tohi T, Sobhy IS, Hojo Y, Ho NT, Shinya T, Galis I. 2020. Ethylene functions as a suppressor of volatile production in rice. Journal of Experimental Botany **71**, 6491-6511.

Mundim FM, Pringle EG. 2018. Whole-Plant Metabolic Allocation Under Water Stress. Frontiers in Plant Science **9**.

Mundim FM, Vieira- Neto EHM, Alborn H, Bruna EM. 2021. Disentangling the influence of water limitation and simultaneous above and belowground herbivory on plant tolerance and resistance to stress. Journal of Ecology **109**, 2729-2739.

Murrell EG. 2017. Can agricultural practices that mitigate or improve crop resilience to climate change also manage crop pests? Current Opinion in Insect Science **23**, 81-88.

Nachappa P, Culkin CT, Saya PM, Han J, Nalam VJ. 2016. Water Stress Modulates Soybean Aphid Performance, Feeding Behavior, and Virus Transmission in Soybean. Frontiers in Plant Science **7**.

Negrón JF, McMillin JD, Anhold JA, Coulson D. 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. Forest Ecology and Management **257**, 1353-1362.

Ngumbi EN, Ugarte CM. 2021. Flooding and Herbivory Interact to Alter Volatile Organic Compound Emissions in Two Maize Hybrids. Journal of Chemical Ecology.

Nguyen D, D'Agostino N, Tytgat TO, Sun P, Lortzing T, Visser EJ, Cristescu SM, Steppuhn A, Mariani C, Dam NM. 2016a. Drought and flooding have distinct effects on herbivore- induced responses and resistance in Solanum dulcamara. Plant, Cell & Environment.

Nguyen D, Rieu I, Mariani C, van Dam NM. 2016b. How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory. Plant Molecular Biology **91**, 727-740.

Nguyen TH, Goossens A, Lacchini E. 2022. Jasmonate: A hormone of primary importance for plant metabolism. Current Opinion in Plant Biology **67**, 102197.

Niinemets U, Loreto F, Reichstein M. 2004. Physiological and physicochemical controls on foliar volatile organic compound emissions. Trends in Plant Science **9**, 180-186.

Oliveira RS, Costa FRC, Baalen E, Jonge A, Bittencourt PR, Almanza Y, Barros FDV, Cordoba EC, Fagundes MV, Garcia S, Zilza, Hertel M, Schietti J, Rodrigues- Souza J, Poorter L. 2019. Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro- topographic gradients. New Phytologist **221**, 1457-1465.

Olson DM, Cortesero AM, Rains GC, Potter T, Lewis WJ. 2009. Nitrogen and water affect direct and indirect plant systemic induced defense in cotton. **49**, 239-244.

Orians CM, Schweiger R, Dukes JS, Scott ER, Müller C. 2019. Combined impacts of prolonged drought and warming on plant size and foliar chemistry. Annals of Botany.

Orine D, Defossez E, Vergara F, Uthe H, Van Dam NM, Rasmann S. 2022. Arbuscular mycorrhizal fungi prevent the negative effect of drought and modulate the growth- defence trade- off in tomato plants. Journal of Sustainable Agriculture and Environment.

Pagadala Damodaram KJ, Gadad HS, Parepally SK, Vaddi S, Ramanna Hunashikatti L, Bhat RM. 2021. Low moisture stress influences plant volatile emissions affecting herbivore interactions in tomato,

Solanum lycopersicum. Ecological Entomology **46**, 637-650.

Palmer-Young EC, Veit D, Gershenzon J, Schuman MC. 2015. The Sesquiterpenes(E)-ß-Farnesene and (E)-α-Bergamotene Quench Ozone but Fail to Protect the Wild Tobacco Nicotiana attenuata from Ozone, UVB, and Drought Stresses. PLOS ONE **10**, e0127296.

Papazian S, Khaling E, Bonnet C, Lassueur S, Reymond P, Moritz T, Blande JD, Albrectsen BR. 2016. Central metabolic responses to ozone and herbivory affect photosynthesis and stomatal closure. Plant Physiology **172**, 2057-2078.

Paritsis J, Veblen TT. 2011. Dendroecological analysis of defoliator outbreaks on Nothofagus pumilio and their relation to climate variability in the Patagonian Andes. Global Change Biology **17**, 239-253.

Pearse IS, LoPresti E, Schaeffer RN, Wetzel WC, Mooney KA, Ali JG, Ode PJ, Eubanks MD, Bronstein JL, Weber MG. 2020. Generalising indirect defence and resistance of plants. Ecology Letters **23**, 1137-1152.

Peñuelas J, Staudt M. 2010. BVOCs and global change. Trends in Plant Science **15**, 133-144.

Pepi A, Holyoak M, Karban R. 2021. Altered precipitation dynamics lead to a shift in herbivore dynamical regime. Ecology Letters **24**, 1400-1407.

Peschiutta ML, Bucci SJ, Scholz FG, Goldstein G. 2016. Compensatory responses in plant-herbivore interactions: Impacts of insects on leaf water relations. Acta Oecologica **73**, 71-79.

Prather RM, Castillioni K, Welti EAR, Kaspari M, Souza L. 2020. Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. Ecology **101**.

Pratt JD, Keefover-Ring K, Liu LY, Mooney KA. 2014. Genetically based latitudinal variation inArtemisia californicasecondary chemistry. Oikos **123**, 953-963.

Price PW. 1991. The Plant Vigor Hypothesis and Herbivore Attack. Oikos **62**, 244-251.

Prugh LR, Deguines N, Grinath JB, Suding KN, Bean WT, Stafford R, Brashares JS. 2018. Ecological winners and losers of extreme drought in California. Nature Climate Change **8**, 819-824.

Querejeta JI, Ren W, Prieto I. 2021. Vertical decoupling of soil nutrients and water under climate warming reduces plant cumulative nutrient uptake, water use efficiency and productivity. New Phytologist.

Rai B, Klein AM, Walter J. 2018. Chronic dryness and wetness and especially pulsed drought threaten a generalist arthropod herbivore. Oecologia **188**, 931-943.

Ranger CM, Reding ME, Schultz PB, Oliver JB. 2013. Influence of flood-stress on ambrosia beetle host-selection and implications for their management in a changing climate. Agricultural and Forest Entomology **15**, 56-64.

Rauschkolb R, Li Z, Godefroid S, Dixon L, Durka W, Májeková M, Bossdorf O, Ensslin A, Scheepens JF. 2022. Evolution of plant drought strategies and herbivore tolerance after two decades of climate change. New Phytologist.

Rissanen K, Hölttä T, Bäck J, Rigling A, Wermelinger B, Gessler A. 2021. Drought effects on carbon allocation to resin defences and on resin dynamics in old-grown Scots pine. Environmental and Experimental Botany, 104410.

Rivas-Ubach A, Gargallo-Garriga A, Sardans J, Oravec M, Mateu-Castell L, Perez-Trujillo M, Parella T, Ogaya R, Urban O, Penuelas J. 2014. Drought enhances folivory by shifting foliar metabolomes in Quercus ilex trees. New Phytologist **202**, 874-885.

Robinson ML, Strauss SY. 2020. Generalists are more specialized in low-resource habitats, increasing stability of ecological network structure. Proceedings of the National Academy of Sciences **117**, 2043-2048.

Rodrigues J, Inzé D, Nelissen H, Saibo NJM. 2019. Source–Sink Regulation in Crops under Water Deficit. Trends in Plant Science **24**, 652-663.

Rosa E, Minard G, Lindholm J, Saastamoinen M. 2019. Moderate plant water stress improves larval development, and impacts immunity and gut microbiota of a specialist herbivore. PLOS ONE **14**, e0204292.

Rosenblatt AE, Smith-Ramesh LM, Schmitz OJ. 2017. Interactive effects of multiple climate change variables on food web dynamics: Modeling the effects of changing temperature, CO2, and water availability on a tri-trophic food web. Food Webs **13**, 98-108.

Salehin M, Li B, Tang M, Katz E, Song L, Ecker JR, Kliebenstein DJ, Estelle M. 2019. Auxin-sensitive Aux/IAA proteins mediate drought tolerance in Arabidopsis by regulating glucosinolate levels. Nature Communications **10**, 4021.

Salman INA, Cna'ani A, Tzin V, Seifan M. 2022. Bumblebee attraction to *Matthiola livida* flowers is altered by combined water stress and insect herbivory. Entomologia Experimentalis et Applicata.

Santamaria ME, Diaz I, Martinez M. 2018. Dehydration Stress Contributes to the Enhancement of Plant Defense Response and Mite Performance on Barley. Frontiers in Plant Science **9**.

Santos-Medellín C, Liechty Z, Edwards J, Nguyen B, Huang B, Weimer BC, Sundaresan V. 2021. Prolonged drought imparts lasting compositional changes to the rice root microbiome. Nature Plants **7**, 1065-1077.

Santos-Neto PE, Arnan X, Ribeiro-Neto JD, Wirth R, Leal IR. 2022. Aridity, but not disturbance, reduces the specialization and modularity of plant–insect herbivore interaction networks in Caatinga dry forest. Journal of Insect Conservation **26**, 175-189.

Saska P, Skuhrovec J, Platková H, Kosová K, Tylová E, Tuan S-J, Vítámvás P. 2022. Response of the spring wheat–cereal aphid system to drought: support for the plant vigour hypothesis. Journal of Pest Science.

Saska P, Skuhrovec J, Tylová E, Platková H, Tuan S-J, Hsu Y-T, Vítámvás P. 2021. Leaf structural traits rather than drought resistance determine aphid performance on spring wheat. Journal of Pest Science **94**, 423-434.

Scherber C, Gladbach DJ, Stevnbak K, Karsten RJ, Schmidt IK, Michelsen A, Albert KR, Larsen KS, Mikkelsen TN, Beier C, Christensen S. 2013. Multi-factor climate change effects on insect herbivore performance. Ecology and Evolution **3**, 1449-1460.

Sconiers WB, Rowland DL, Eubanks MD. 2020. Pulsed drought: The effects of varying water stress on plant physiology and predicting herbivore response. Crop Science **60**, 2543-2561.

Scott ER, Li X, Kfoury N, Morimoto J, Han W-Y, Ahmed S, Cash SB, Griffin TS, Stepp JR, Robbat A, Orians CM. 2019. Interactive effects of drought severity and simulated herbivory on tea (*Camellia sinensis*) volatile and non-volatile metabolites. Environmental and Experimental Botany **157**, 283-292.

Shannag HK. 2007. Effect of black bean aphid, Aphis fabae, on transpiration, stomatal conductance and crude protein content of faba bean. Annals of Applied Biology **151**, 183-188.

Sheteiwy MS, Gong D, Gao Y, Pan R, Hu J, Guan Y. 2018. Priming with methyl jasmonate alleviates polyethylene glycol-induced osmotic stress in rice seeds by regulating the seed metabolic profile. Environmental and Experimental Botany **153**, 236-248.

Sinaie S, Sadeghi-Namaghi H, Fekrat L. 2019. Effects of elevated CO2 and water stress on population growth of the two-spotted spider mite, Tetranychus urticae Koch (Acari: Tetranychidae), on sweet pepper under environmentally controlled conditions. Journal of Asia-Pacific Entomology **22**, 96-102.

Siqueira JA, Oliveira De Oliveira H, Nunes-Nesi A, Araújo WL. 2021. Guard cell regulation: pulling the strings behind the scenes. Trends in Plant Science **26**, 1093-1095.

Solberg S, Hov Ø, Søvde A, Isaksen ISA, Coddeville P, De Backer H, Forster C, Orsolini Y, Uhse K. 2008. European surface ozone in the extreme summer 2003. Journal of Geophysical Research **113**.

Song Y, Sterck F, Sass- Klaassen U, Li C, Poorter L. 2022. Growth resilience of conifer species decreases with early, long- lasting and intense droughts but cannot be explained by hydraulic traits. Journal of Ecology.

Sopow S, Bader M, Brockerhoff E. 2015. Bark beetles attacking conifer seedlings: picking on the weakest or feasting upon the fittest? Journal of Applied Ecology **52**, 220-227.

Srikanth S, Lum SKY, Chen Z. 2016. Mangrove root: adaptations and ecological importance. Trees **30**, 451-465.

Stamp N. 2003. Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology **78**, 23-55.

Stamp N. 2004. Can the growth-differentiation balance hypothesis be tested rigorously? Oikos **107**, 439-448.

Stowe KA, Marquis RJ, Hochwender CG, Simms EL. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics **31**, 565-595.

Stratton CA, Hodgdon E, Rodriguez-Saona C, Shelton AM, Chen YH. 2019. Odors from phylogenetically-distant plants to Brassicaceae repel an herbivorous Brassica specialist. Scientific Reports **9**.

Strauss SY, Agrawal AA. 1999. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology & Evolution **14**, 179-185.

Strock CF, Schneider HM, Lynch JP. 2022. Anatomics: High-throughput phenotyping of plant anatomy. Trends in Plant Science.

Suárez-Vidal E, Sampedro L, Voltas J, Serrano L, Notivol E, Zas R. 2019. Drought stress modifies early effective resistance and induced chemical defences of Aleppo pine against a chewing insect herbivore. Environmental and Experimental Botany **162**, 550-559.

Szczepaniec A, Finke D. 2019. Plant-Vector-Pathogen Interactions in the Context of Drought Stress. Frontiers in Ecology and Evolution **7**.

Szechyńska-Hebda M, Lewandowska M, Witoń D, Fichman Y, Mittler R, Karpiński SM. 2022. Aboveground Plant-to-Plant Electrical Signaling Mediates Network Acquired Acclimation. The Plant Cell.

Tai APK, Martin MV, Heald CL. 2014. Threat to future global food security from climate change and ozone air pollution. Nature Climate Change **4**, 817-821.

Tariq M, Wright DJ, Bruce TJ, Staley JT. 2013. Drought and root herbivory interact to alter the response of above-ground parasitoids to aphid infested plants and associated plant volatile signals. PLOS ONE **8**, e69013.

Teixeira NC, Valim JOS, Oliveira MGA, Campos WG. 2020. Combined effects of soil silicon and drought stress on host plant chemical and ultrastructural quality for leaf- chewing and sap- sucking insects. Journal of Agronomy and Crop Science **206**, 187-201.

Thaler J, Bostock R. 2004. Interactions between abscisic-acid-mediated responses and plant resistance to pathogens and insects. Ecology **85**, 48-58.

Torode MD, Barnett KL, Facey SL, Nielsen UN, Power SA, Johnson SN. 2016. Altered Precipitation Impacts on Above- and Below-Ground Grassland Invertebrates: Summer Drought Leads to Outbreaks in Spring. Frontiers in Plant Science **7**.

Touchette BW, Iannacone LR, Turner GE, Frank AR. 2007. Drought tolerance versus drought avoidance: A comparison of plant-water relations in herbaceous wetland plants subjected to water withdrawal and repletion. Wetlands **27**, 656-667.

Trotter R, Cobb N, Whitham T. 2008. Arthropod community diversity and trophic structure: a comparison between extremes of plant stress. Ecological Entomology **33**, 1-11.

Trowbridge AM, Stoy PC, Adams HD, Law DJ, Breshears DD, Helmig D, Monson RK. 2019. Drought supersedes warming in determining volatile and tissue defenses of piñon pine (Pinus edulis). Environmental Research Letters **14**, 065006.

Turlings TCJ, Erb M. 2018. Tritrophic Interactions Mediated by Herbivore-Induced Plant Volatiles: Mechanisms, Ecological Relevance, and Application Potential. Annual Review of Entomology **63**, 433-452.

Turner N. 1982. The role of shoot characteristics in drought resistance of crop plants. Drought resistance in crops with emphasis on rice, 115-134.

Turner NC. 1986. Adaptation to water deficits: a changing perspective. Functional Plant Biology **13**, 175-190.

Turtola S, Manninen AM, Rikala R, Kainulainen P. 2003. Drought stress alters the concentration of wood terpenoids in Scots pine and Norway spruce seedlings. Journal of Chemical Ecology **29**, 1981-1995.

Ullah A, Manghwar H, Shaban M, Khan AH, Akbar A, Ali U, Ali E, Fahad S. 2018. Phytohormones enhanced drought tolerance in plants: a coping strategy. Environmental Science and Pollution Research **25**, 33103-33118.

Van Bael SA, Aiello A, Valderrama A, Medianero E, Samaniego M, Wright SJ. 2004. General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest. Journal of Tropical Ecology **20**, 625-633.

Verslues PE, Juenger TE. 2011. Drought, metabolites, and Arabidopsis natural variation: a promising combination for understanding adaptation to water-limited environments. Current Opinion in Plant Biology **14**, 240-245.

Veyrat N, Robert CAM, Turlings TCJ, Erb M. 2016. Herbivore intoxication as a potential primary function of an inducible volatile plant signal. Journal of Ecology **104**, 591-600.

Vicente-Serrano SM, Quiring SM, Peña-Gallardo M, Yuan S, Domínguez-Castro F. 2020. A review of environmental droughts: Increased risk under global warming? Earth-Science Reviews **201**, 102953.

Vickers CE, Gershenzon J, Lerdau MT, Loreto F. 2009. A unified mechanism of action for volatile isoprenoids in plant abiotic stress. Nature Chemical Biology **5**, 283-291.

Volaire F. 2018. A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. Global Change Biology **24**, 2929-2938.

Wang S, Zhang Y, Ju W, Chen JM, Ciais P, Cescatti A, Sardans J, Janssens IA, Wu M, Berry JA, Campbell E, Fernández-Martínez M, Alkama R, Sitch S, Friedlingstein P, Smith WK, Yuan W, He W, Lombardozzi D, Kautz M, Zhu D, Lienert S, Kato E, Poulter B, Sanders TGM, Krüger I, Wang R, Zeng N, Tian H, Vuichard N, Jain AK, Wiltshire A, Haverd V, Goll DS, Peñuelas J. 2020. Recent global decline of CO₂ fertilization effects on vegetation photosynthesis. Science **370**, 1295-1300.

Wang X, Komatsu S. 2022. The Role of Phytohormones in Plant Response to Flooding. International Journal of Molecular Sciences **23**, 6383.

Wang Y, Xie Y, Dong W, Ming Y, Wang J, Shen L. 2017. Adverse effects of increasing drought on air quality via natural processes. Atmospheric Chemistry and Physics **17**, 12827-12843.

Waring GL, Cobb NS. 1992. The impact of plant stress on herbivore population dynamics. Insect-plant interactions **4**, 167-226.

Waterman JM, Hall CR, Mikhael M, Cazzonelli CI, Hartley SE, Johnson SN. 2020. Short- term resistance that persists: Rapidly induced silicon anti- herbivore defence affects carbon- based plant defences. Functional Ecology.

Weldegergis B, Zhu F, Poelman E, Dicke M. 2015. Drought stress affects plant metabolites and herbivore preference but not host location by its parasitoids. Oecologia **177**, 701-713.

White TCR. 1969. An Index to Measure Weather-Induced Stress of Trees Associated With Outbreaks of Psyllids in Australia. Ecology **50**, 905-909.

White TCR. 2009. Plant vigour versus plant stress: a false dichotomy. Oikos **118**, 807-808.

Wise MJ, Abrahamson WG. 2007. Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. American Naturalist **169**, 443-454.

Wittstock U, Agerbirk N, Stauber EJ, Olsen CE, Hippler M, Mitchell-Olds T, Gershenzon J, Vogel H. 2004. Successful herbivore attack due to metabolic diversion of a plant chemical defense. Proceedings of the National Academy of Sciences **101**, 4859-4864.

Xia J, Guo Z, Yang Z, Han H, Wang S, Xu H, Yang X, Yang F, Wu Q, Xie W, Zhou X, Dermauw W, Turlings TCJ, Zhang Y. 2021. Whitefly hijacks a plant detoxification gene that neutralizes plant toxins. Cell.

Xing G, Zhang J, Liu J, Zhang X, Wang G, Wang Y. 2003. Impacts of atmospheric CO2 concentrations and soil water on the population dynamics, fecundity and development of the bird cherry-oat aphidRhopalosiphum padi. Phytoparasitica **31**, 499-514.

Xu BB, Hicke JA, Abatzoglou JT. 2019. Drought and Moisture Availability and Recent Western Spruce Budworm Outbreaks in the Western United States. Forests **10**.

Yan Y, Li M, Zhang X, Kong W, Bendahmane M, Bao M, Fu X. 2022. Tissue-Specific Expression of the Terpene Synthase Family Genes in Rosa chinensis and Effect of Abiotic Stress Conditions. Genes **13**, 547.

Yang YJ, Bi MH, Nie ZF, Jiang H, Liu XD, Fang XW, Brodribb TJ. 2021. Evolution of stomatal closure to optimise water use efficiency in response to dehydration in ferns and seed plants. New Phytologist.

Yuan W, Zheng Y, Piao S, Ciais P, Lombardozzi D, Wang Y, Ryu Y, Chen G, Dong W, Hu Z, Jain AK, Jiang C, Kato E, Li S, Lienert S, Liu S, Nabel JEMS, Qin Z, Quine T, Sitch S, Smith WK, Wang F, Wu C, Xiao Z, Yang S. 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Science Advances **5**, eaax1396.

Zandalinas SI, Balfagón D, Gómez-Cadenas A, Mittler R. 2022. Responses of plants to climate change: Metabolic changes during abiotic stress combination in plants. Journal of Experimental Botany.

Zandalinas SI, Fritschi FB, Mittler R. 2021a. Global Warming, Climate Change, and Environmental Pollution: Recipe for a Multifactorial Stress Combination Disaster. Trends in Plant Science.

Zandalinas SI, Mittler R. 2022. Plant responses to multifactorial stress combination. New Phytologist **234**, 1161-1167.

Zandalinas SI, Sengupta S, Fritschi FB, Azad RK, Nechushtai R, Mittler R. 2021b. The impact of multifactorial stress combination on plant growth and survival. New Phytologist.

Zhang X, Liu S, Takano T. 2008. Two cysteine proteinase inhibitors from Arabidopsis thaliana, AtCYSa and AtCYSb, increasing the salt, drought, oxidation and cold tolerance. Plant Molecular Biology **68**, 131-143.

Zhou S, Jander G. 2022. Molecular ecology of plant volatiles in interactions with insect herbivores. Journal of Experimental Botany **73**, 449-462.

Ziska LH, McConnell LL. 2016. Climate Change, Carbon Dioxide, and Pest Biology: Monitor, Mitigate, Manage. Journal of Agricultural and Food Chemistry **64**, 6-12.

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.

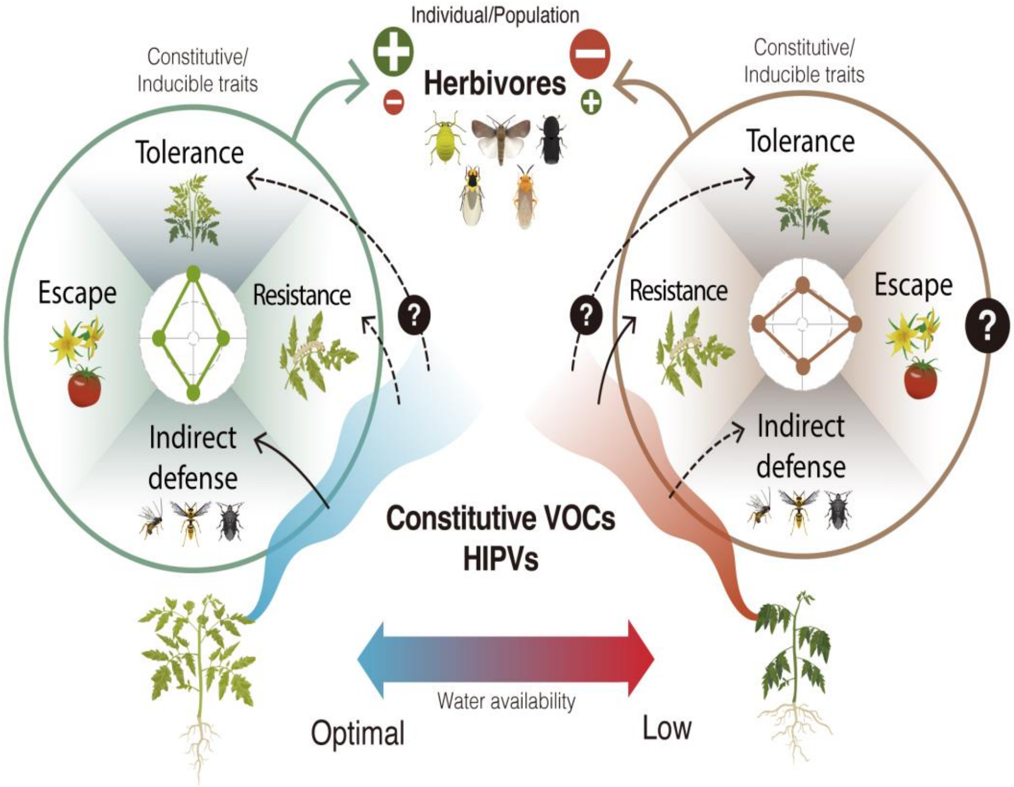

Fig. 1 Influences of water availability on plant antiherbivore defenses strategies and their impacts on herbivores. Water deficit generally increases plant resistance to herbivores and compromises plant indirect defenses, such as natural enemy attraction. Water deficits reduce plant ability to tolerate 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.

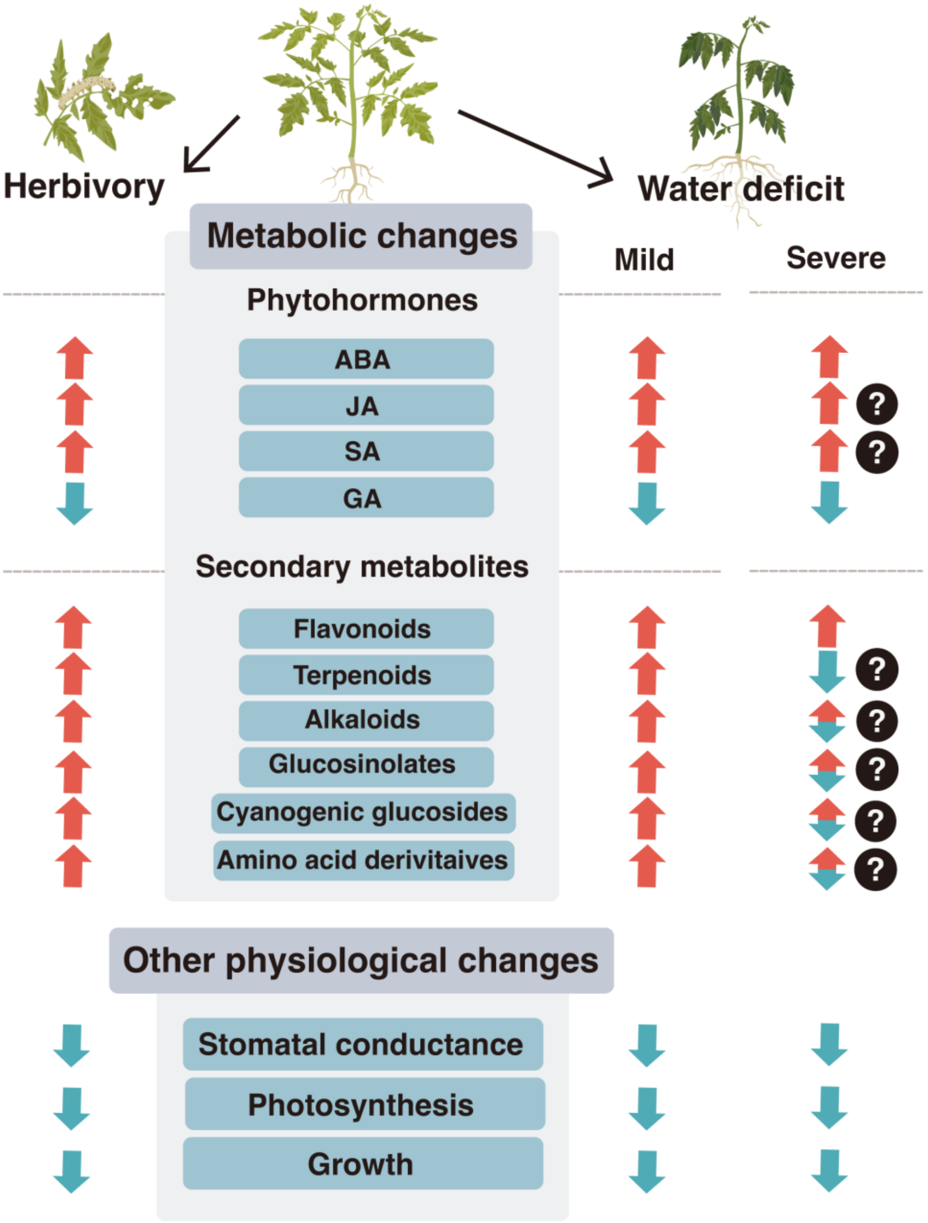

Fig. 2 Similarities between physiological responses triggered by herbivory and water deficit. Both stresses trigger similar phytohormonal responses with enhanced ABA, JA, and SA accumulation and decreased GA. Both herbivory and water deficit enhance secondary metabolites accumulation and an overall decrease 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.

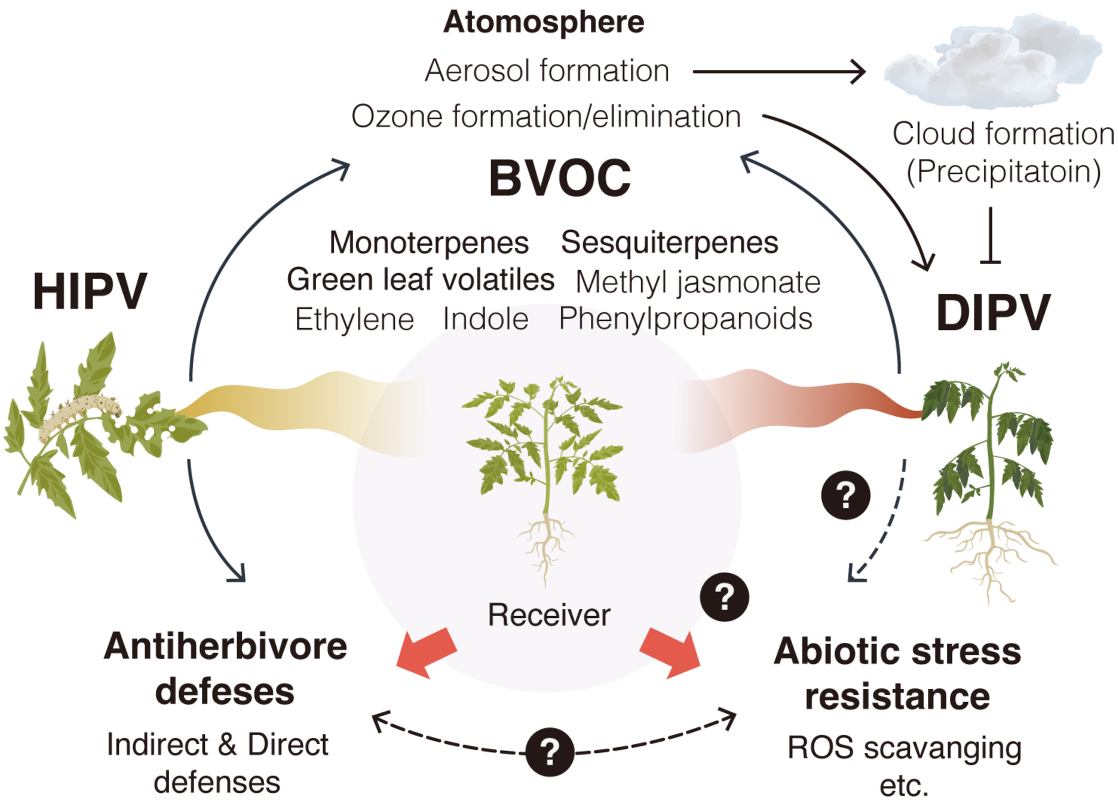

Fig. 3 Functions of plant volatiles in water-plant-herbivore interactions. Plants release distinct blends of volatiles under different stresses. Herbivore-induced plant volatiles (HIPVs) are well-known for their roles in plant defenses against herbivores and can be perceived by neighboring plants (receivers) 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.

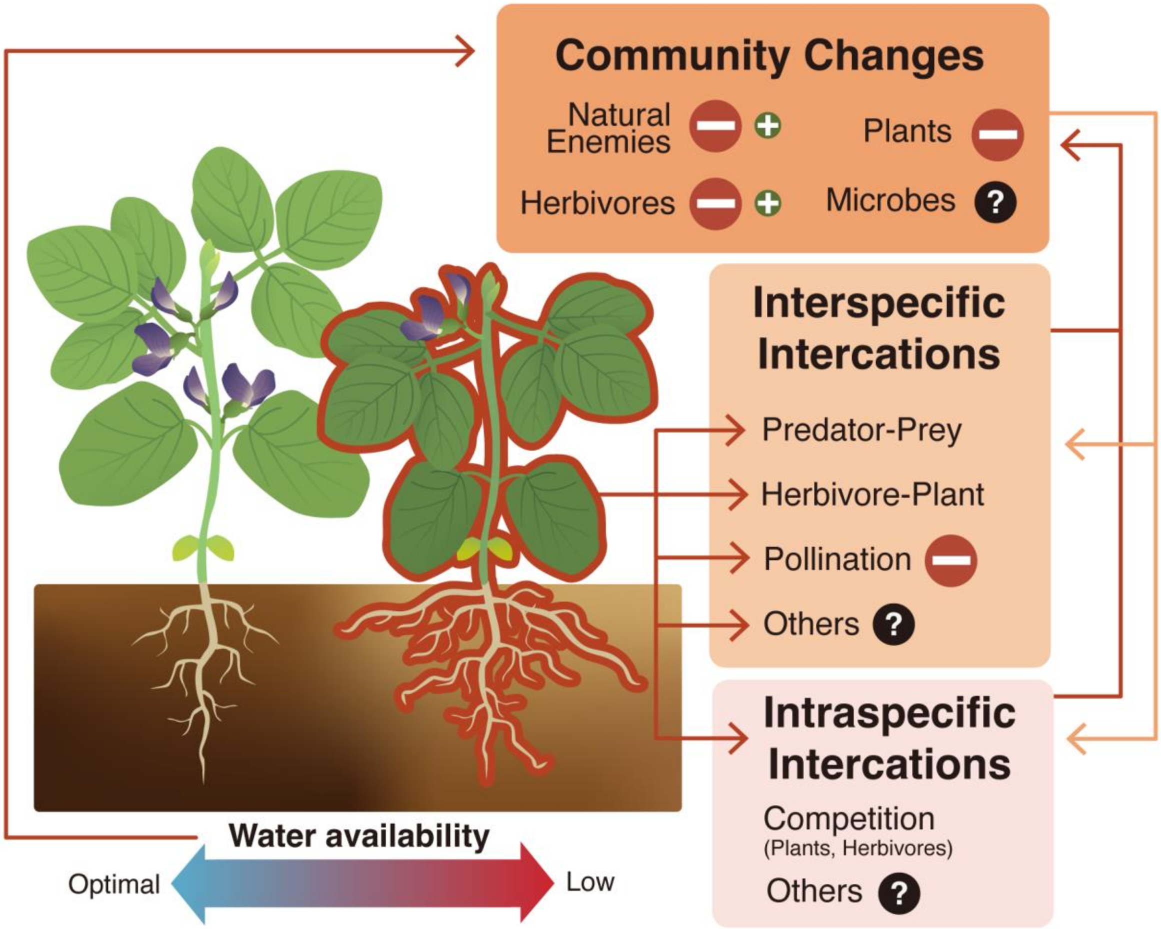

Fig. 4 Influence of low water availability on species interactions and community structure. Low water availability has been shown to influence intraspecific interactions such as competition between plants and herbivores and interactions between plants, herbivores, natural enemies, and pollinators. These 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.