



Primacy of plants in driving the response of arthropod communities to drought

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Abstract

Drought threatens arthropod communities worldwide. Water limitation affects the quantity and quality of plants available to herbivores as food, and can also affect higher trophic-level consumers through variability in prey quality and reduced availability of suitable habitats. Our study assessed the response of an arthropod community to water limited wheat (*Triticum aestivum* L.) in a field setting. We used rainout shelters to exclude precipitation, irrigated raised bed plots to create three levels of water availability, and monitored arthropod community development over 8 weeks. First, we compared arthropod communities in habitats with different levels of water limitation and found that community composition was reliant on the magnitude of the water stress. This difference was largely due to the loss of piercing–sucking herbivores and predators in high-stress environments. Next, we focused on aphids and their natural enemies to investigate the underlying mechanisms driving community responses using structural equation modeling (SEM). Aphid abundance was negatively affected by water limitation, and this response was primarily associated with stress-induced plant physiological changes and not plant biomass or natural enemy abundance. Natural enemy abundance was also reduced in water-limited habitats, but natural enemies responded to plant biomass and not prey availability. These effects were exacerbated as water stress increased. The absence of natural enemy effects on aphids indicates that top–down predation effects were dampened by strong bottom–up effects of plant water limitation. This study revealed the importance of considering water stress intensity when predicting outcomes of droughts for arthropod communities.

Keywords Aphids · Tritrophic interactions · Habitat complexity · Plant stress · Structural equation modeling

Introduction

Climate change has increased the frequency and intensity of drought events worldwide (Coumou and Rahmstorf 2012; Prein et al. 2017). More extreme and variable precipitation can have widespread impacts on plant productivity, species interactions, and ecosystem processes (Knapp et al. 2008; Eigenbrode et al. 2015; Barnett and Facey 2016). Understanding such impacts is critical to predict how altered precipitation patterns may affect the provisioning of ecosystem services.

Water availability can be a significant driver of arthropod abundance and species composition within natural and agroecosystems. Broad assessments of natural systems suggest that low water availability reduces species diversity and decreases the prevalence of leaf herbivory (Suttle et al. 2007; Trotter et al. 2008; Moreira et al. 2015). However, manipulative field studies produce a wide array of arthropod responses to drought (Frampton et al. 2000; Lee et al.

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Plant water stress affects the whole community, but different trophic groups are responding to different bottom-up traits.

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2014; Zhu et al. 2014; Torode et al. 2016). Disparities in these results may be due differences in the intensity of water stress across systems. Models suggest that drought intensity should be important, with slight water limitation increasing herbivory and predation, but higher stress decreasing community diversity and reducing predation (McCluney et al. 2012). Furthermore, trophic-level differences in insect responses to water stress intensity can lead to outbreaks of drought-tolerant herbivore pest species that are unchecked by predators (Barton and Ives 2014). Thus, to make predictions about the outcomes of droughts for arthropod communities, manipulative field studies that explore a variety of drought intensities are necessary.

Drought stress leads to dynamic shifts in plant physiology and morphology that are important for herbivorous arthropods. Plant responses to abiotic stress conditions modify plant nutritional quality, anti-herbivore defenses, morphology, and biomass (Showler 2013). These stress-induced changes in plant traits have significant consequences for herbivores, but the outcome is dependent on the feeding guild of the herbivore and the intensity of plant water stress (Huberty and Denno 2004; Mody et al. 2009; Tariq et al. 2012). Piercing–sucking herbivores often experience declines in performance on stressed hosts, which is predicted to be driven by reduced phloem pressure and increased plant defensive chemistry (Hale et al. 2003; Johnson et al. 2011; Kansman et al. 2020; Xie et al. 2020). In contrast, chewing herbivores may be more tolerant of plant water limitation, especially specialist herbivores that are less affected by increased plant defensive chemistry (Huberty and Denno 2004; Gutbrodt et al. 2011). In addition to these traits, drought leads to reduced plant biomass, and therefore food quantity, which has the potential to affect herbivore performance across feeding guilds.

Plant water limitation has direct and indirect effects on third trophic-level consumers. Natural enemy abundance may respond directly to changes in the quality and availability of their herbivore prey (Banfield-Zanin and Leather 2015; Ahmed et al. 2017; Wade et al. 2017). However, drought stress may also influence the foraging success of natural enemies by altering plant volatiles that are used as prey finding cues or plant biomass that influences the complexity of the habitat (Tariq et al. 2013; Weldegergis et al. 2015; Martini and Stelinski 2017). Natural enemies often take refuge in complex habitats where microclimate is moderated and vulnerability to their own enemies is reduced (Langellotto and Denno 2004). Therefore, direct effects of plant water limitation could be a major driver of natural enemy abundance in drought-stressed agroecosystems in addition to indirect effects mediated by prey condition.

In this study, we examined the effects of plant water limitation on the arthropod community associated with wheat (*Triticum aestivum* L.). Our study is notable in that

we simulated three precipitation scenarios in an open field setting from the time plants were seedlings until seed production. Our first goal was to quantify the response of the arthropod community to plants experiencing different levels of water stress intensity and to identify which taxa were most sensitive to changes in water availability. Given the duration of the study and the open plot design, the abundance and composition of the community were a function of immigration and emigration, individual performance, and species interactions. Overall, we predicted arthropod abundance would decline on stressed plants. We predicted that plant water stress would alter the composition of the community as species more vulnerable to environmental perturbations are eliminated and tolerant species remain. Additionally, we predicted that piercing–sucking herbivores would be associated with well-watered conditions, and chewing herbivores would be less influenced by changing water relations and not associated with any particular water treatment. Our second goal was to investigate the mechanisms underlying the arthropod community response to drought. To do this, we narrowed our focus to only the most abundant herbivore and examined the direct and indirect effects of water limitation on plants, aphids, and aphid natural enemies using structural equation modeling (SEM). Using this model, we were able to test predictions of whether arthropod abundance was more affected by stress-induced changes in plant quantity or quality. By identifying the driving forces behind the responses of arthropods to drought stress in a field setting, this work contributes to the body of knowledge predicting how arthropod communities will be affected by changing climate.

Materials and methods

Field design

The experiment took place from June to September 2017 at the Hinkson Valley Farm, University of Missouri, MO, USA. All experimental plots were located under two rain-excluding shelters (11 × 16 m) located within 20 m of each other. Each shelter was covered with a tarp roof that was rolled down to shield the plots from rain and rolled up to allow full sun exposure (Fig. S1A and B). The plots were surrounded by a soybean (*Glycine max* L.) field and a wooded lot.

Experimental plots were raised beds constructed using large storage tubs (45 Gal. Sterlite, Townsend, MA) drilled with holes to allow water drainage. Tubs were filled with topsoil from an adjacent field comprised of 50% sand, 38.5% silt, and 12.5% clay (Mahmoud et al. 2018). Three tubs placed side by side were considered one plot (18 plots = 54 tubs). Each plot was ~ 1.5 × 1 m and separated from other plots by a minimum of 2 m. The experimental design included six replications of three water treatments in

a randomized complete block, with treatments assigned to plots (Fig. S1C). Wheat plants (Coker 9553, AgriPro, Syngenta) were grown from seed at the Ashland Road Greenhouse Facility (University of Missouri, Columbia, MO, USA) and fertilized once (All Purpose Plant Food, Scott's Miracle Gro, Marysville, OH) prior to transplanting. Each plot received 180 wheat transplants (7 days old), 60 per tub, and plants were replaced if they did not establish in the first week. The plants were watered ad libitum for 3 weeks (1 week in greenhouse, 2 weeks in the field) prior to water manipulations.

Watering methods

A soaker hose irrigation system was used to create differences in water availability across plots. Identical irrigation systems were established under each rainout shelter. Each system was connected to a water pump fixed with a canister filter (RAINDRIP Inc., Fresno, CA, USA) and water pressure regulator (Peaceful Valley Farm Supply Inc.) to ensure consistent water flow. Each plot had a coupling valve (Drip Depot Inc., White City, OR, USA) to manually control the flow of water to six 1.27-cm soaker hoses (Mr. Soaker Hose, Peaceful Valley Farm Supply Inc., Grass Valley, CA, USA), which were arranged with two hoses per tub. The standard baseline irrigation rate for each day followed recommendations based on the evapotranspiration rate over the previous 24 h ($T = D \times A \times 43550 / (96.3 \times Q \times E)$), where T = time, D = evapotranspiration rate, A = area (acres), Q = irrigation flow rate, E = system efficiency, Washington State University Extension; [http://irrigation.wsu.edu/Content/Calculator/General/Set Times.php](http://irrigation.wsu.edu/Content/Calculator/General/Set%20Times.php)). The evapotranspiration rate was acquired from a nearby weather station (Sanborn Field, University of Missouri, Columbia, MO, USA). This calculation provided a recommended amount of time that a plot should be watered each day, and the amount of time changed daily based on the evapotranspiration rate. For three water availability treatments, plots were watered to 100% (well-watered), 75% (mild-stress), or 50% (high stress) of the time recommended by the calculation. Water was added to the plots by opening the valves at each plot for the indicated amount of time. Treatments were applied 10 days before arthropod surveys began.

Plant response to water limitation

The physiological stress response of the plants was inferred using whole plant water potential measurements. Water potential is a physiological measurement of the energy potential of the water within the plant, and is commonly used to quantify plant water deficit (Taiz and Zeiger 2015). A lower water potential measurement corresponds to a higher plant stress response. Midday water potential measurements

were taken on weeks 1, 3, and 6 of arthropod surveys by randomly selecting 3 plants per plot (Scholander pressure bomb, Model 670, PMS Instrument Company, Albany, OR, USA).

The effects of water stress on plant growth, reproduction, and morphology were assessed by collecting all of the above and belowground plant material from the plots at the end of the study. Plant material was dried on a greenhouse bench for at least 30 days. Once completely dry, above and belowground biomass, number of seed heads, and tillers per plant were evaluated.

Arthropod sampling methods

Weekly visual surveys were conducted to assess the arthropod community response to water limitation. After 10 days of initial watering treatment application, the plots were subsampled each week for 8 weeks by randomly selecting one of the three tubs for 10 min of observation, which resulted in an exhaustive sample of all arthropods present. The sampling began with an overview of the top of the plant canopy, followed by manipulating the plants to check stems and the mid canopy, and finishing with a survey of the soil surface. Arthropods were identified to the lowest taxonomic unit possible, commonly family.

Statistical methods

Water potential was evaluated using repeated measures mixed models with block as a random factor (PROC MIXED, SAS v. 9.4, SAS institute, Cary, NC) to confirm that distinct plant water stress treatments were achieved over time. Effects of the water stress treatments on aboveground plant biomass, belowground biomass, average tillers per plant, and number of seed heads per plot were also evaluated using linear mixed models with block as a random factor.

Arthropod community composition and abundance

Effects of plant water stress on the overall abundance of the arthropod community were assessed using linear mixed models with block as a random factor. To compare the arthropod community composition across the water treatments, we used non-metric multidimensional scaling (NMS) with a Sørensen (Bray Curtis) distance matrix (PC ORD v.6, (McCune and Mefford 2011)). Arthropod abundance in each plot ($n = 18$) was summed across the 8-week observation. Families that only appeared twice, or groups that could not be identified to family, were not included. A two-dimensional solution was selected for the final ordination based on the stress value (< 25) and significance of Monte Carlo randomization test (PC ORD v.6, (McCune and Mefford 2011)). Visual differences in the composition of the

arthropod community across watering treatments were confirmed statistically using multi-response permutation procedure (MRPP; PC ORD v.6). An indicator taxon analysis was performed to assess associations between arthropod families and water treatments (PC ORD v.6).

Aphids and their natural enemies

Effects of water treatments on the abundance of aphids and their natural enemies across the whole sampling period were assessed using linear mixed models with block as a random factor (PROC MIXED, SAS 9.4). The data met the assumptions of parametric procedures. To elucidate the mechanisms underlying these responses, a structural equation modeling approach (SEM) was used (Scheiner and Gurevitch 2001). SEM tests a priori predictions about hypothesized casual relationships between measured variables using a series of regressions. Our SEM incorporated the measured variables of plant water potential, aboveground plant biomass, aphid abundance, and natural enemy abundance. By including water potential and biomass as separate predictors, we were able to disentangle the effects of plant quantity (biomass)

from other stress-induced plant physiological responses (water potential) on aphid and natural enemy abundance. Arthropod survey data from weeks when naturally occurring aphid populations were present (weeks 6–8) were used in the analysis. One of the three tubs per plot was visually sampled each week; thus, aphid and natural enemy count data corresponded to the plant aboveground biomass and average water potential for the specific tub sub-sampled. Aphid abundance was assessed with a negative binomial distribution based on the variability in the count data.

Our a priori predictions for the SEM were translated into regression equations (Figs. 1a, S2). First, we predicted water limitation would reduce plant water potential and biomass (Taiz and Zeiger 2015). We predicted that aphid abundance would decline in response to reduced plant biomass, but aphids would be more strongly influenced by stress-induced changes plant quality and physiology and not biomass (Huberty and Denno 2004). We also predicted aphids would respond positively to reduced natural enemy abundance due to relaxed predation, but their abundance would be influenced more strongly by plant condition than predation. Additionally, we predicted

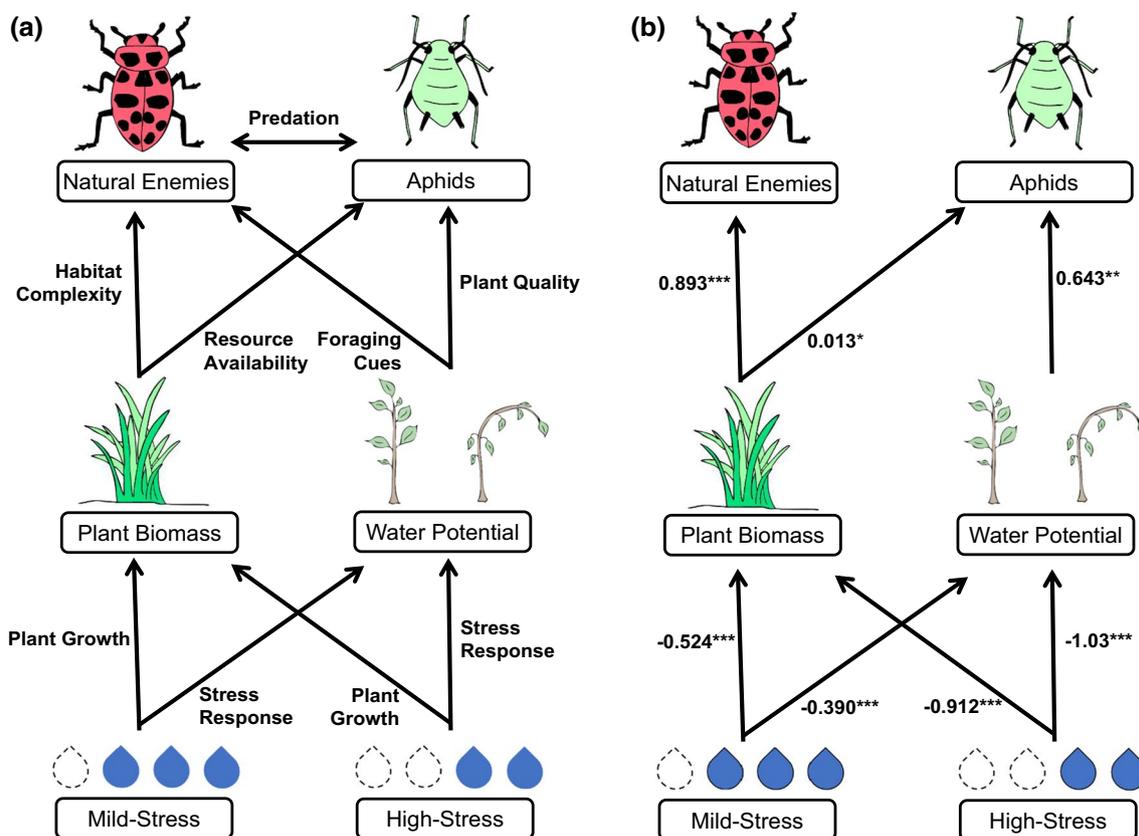


Fig. 1 **a** A priori predictions of direct effects of mild- and high-water limitation on plant biomass, plant water potential, aphid abundance, and natural enemy abundance in the structural equation model. **b** The supported model (Fisher's $C=6.913$, $P=0.94$, $df=14$), where partial

regression coefficients accompany arrows, and positive or negative effects are indicated with \pm . Number of asterisks designate level of significance (* $P<0.1$, ** $P<0.05$, *** $P<0.01$)

that natural enemies would respond negatively to reduced plant biomass due to a reduction in habitat complexity, but may also be affected by reduced water potential since plant stress can affect foraging cues like plant volatiles. We predicted natural enemy abundance would respond more strongly to aphid abundance as an indirect consequence of plant stress compared to changes in plant condition directly. Finally, we predicted that the magnitude of the effects of stress on plants and arthropods would be greater for high-stress conditions compared to mild-stress conditions. We compared the magnitude of the effects of stress conditions using indicator variables for high and mild stress, such that the mild- and high-stress predictors in the model represent the magnitude of effects of the two plant treatments relative to well-watered conditions. The use of indicator variables to represent a categorical variable is useful within SEM models to show effects of each level of a categorical treatment (Lefcheck 2016; Jones et al. 2019). The SEM was analyzed using *piecewiseSEM* (Lefcheck 2016), and the partial regression coefficients associated with each explanatory factor represent the strength of the direct effects. Non-significant links were removed from the model. A Fisher's *C* test was used to determine the goodness-of-fit of the model, where non-significant *p* values indicated a good overall model fit. Indirect effects of mild- and high-water limitation for aphids and natural enemies were calculated by multiplying partial regression coefficients along the path of each effect (plant biomass and water potential) and taking the sum (Fig. S2).

Results

Plant response

Plant water potential was reduced when access to water was limited ($F_{2,40}=223.41$, $P<0.0001$), and the watering treatments created distinct ranges of water potential (Fig. 2a). Water limitation also negatively affected aboveground plant biomass ($F_{2,10}=24.06$, $P=0.0002$; Fig. 2b). Tillers per plant and seed heads per plot declined as water stress increased (tillers: $F_{2,10}=20.51$, $P=0.0003$; seed heads: $F_{2,10}=5.18$, $P=0.029$, Figs. S3–4). Belowground biomass was not affected by mildly stressed conditions, showing a slight non-significant increase, but declined under highly stressed conditions ($F_{2,10}=5.10$, $P=0.03$, Fig S5).

Arthropod community composition and abundance

Overall, 42 arthropod families were identified in plots (Table S1). Plant water limitation decreased arthropod abundance, with 75% lower abundance in highly stressed compared to well-watered plots ($F_{2,10}=9.50$, $P<0.005$; Fig. 3a). Arthropod community composition was affected by water treatment (MRPP, $A=0.14$, $P=0.002$; Fig. 3b), but only in the high-stress plots (well-watered vs. high stress, $A=0.21$, $P=0.001$; mild stress vs high stress, $A=0.08$, $P=0.29$). The two-dimensional solution had a final stress of 7.11 (Monte Carlo randomization test, 250 runs, $P=0.024$). The indicator taxon analysis identified herbivore families Aphididae and Cicadellidae, and predator families Anthocoridae, Carabidae, Coccinellidae, and Linyphiidae as being strongly

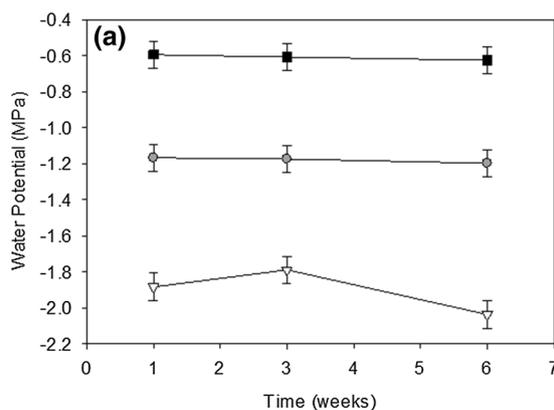
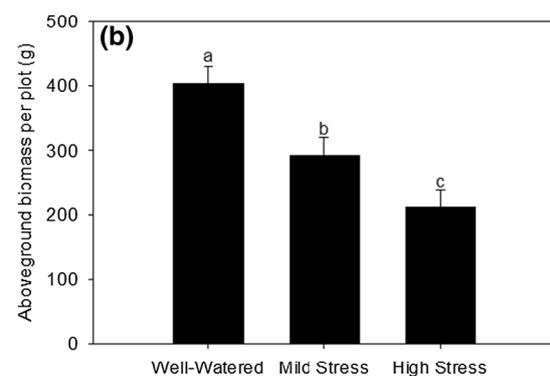


Fig. 2 a Average whole plant water potential (LSmeans \pm SE) of wheat subjected to either well-watered, mildly stressed, or highly stressed conditions on survey weeks 1, 3, and 6 (well-watered: square, mild-stress: circle, high stress: triangle). Water potential is a negative pressure measurement (MPa = megapascals), so more negative values indicate higher drought stress ($F_{2,40}=223.41$, $P<0.0001$).



b Effect of the watering treatment on average dried aboveground biomass per plot (LSmeans \pm SE) collected at the end of the study (week 8). Means with different letters are significantly different at $P<0.05$. Water limitation reduced plant aboveground biomass ($F_{2,10}=24.06$, $P=0.0002$)

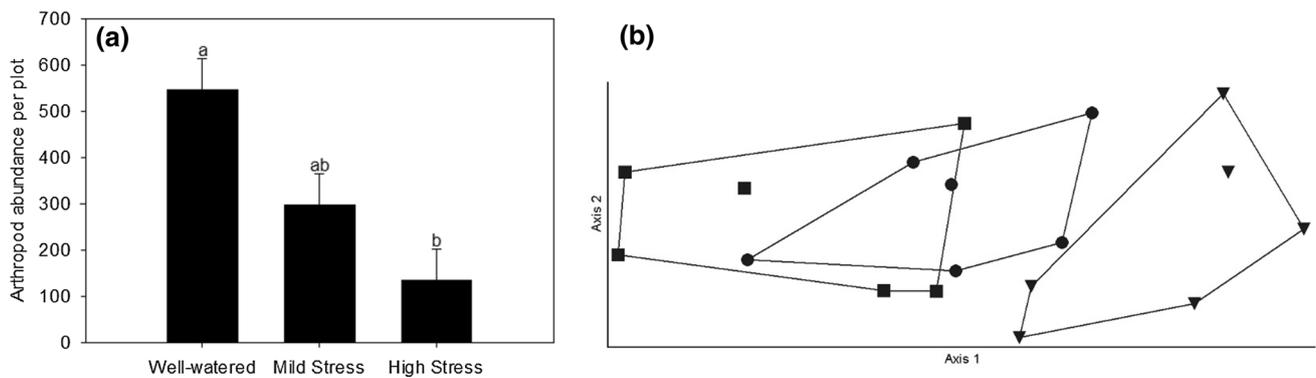


Fig. 3 **a** The effect of watering treatment on cumulative arthropod abundance per plot over the 8-week field season ($F_{2,10}=9.50$, $P<0.005$). **b** The final NMS ordination visualizing the effect of the watering treatment on the arthropod community composition (well-

watered: square, mild-stress: circle, high stress: triangle). Distinct communities do not overlap, and the high-stress community composition was distinct from both the well-watered and mild-stress community (MRPP, $A=0.14$, $P=0.002$)

Table 1 Indicator taxon analysis of arthropod family associations with plots assigned to water treatments

Order	Family	Treatment association	Indicator value	<i>p</i>
Coleoptera	Carabidae	Well Watered	42.2	0.01
Coleoptera	Coccinellidae	Well Watered	40.3	0.01
Coleoptera	Staphylinidae	Well Watered	37.2	0.10
Coleoptera	Chrysomelidae	Well Watered	38.1	0.14
Coleoptera	Phalacridae	Mild Stress	39.7	0.47
Coleoptera	Lampyridae	Well Watered	22.6	0.91
Coleoptera	Melyridae	Mild Stress	24.7	1.00
Coleoptera	Scarabaeidae	Well Watered	20.0	1.00
Diptera	Syrphidae	Well Watered	28.5	0.13
Diptera	Chloropidae	Well Watered	42.2	0.36
Orthoptera	Acrididae	Well Watered	19.6	0.73
Hemiptera	Cicadellidae	Well Watered	41.9	<0.01
Hemiptera	Anthocoridae	Well Watered	37.8	0.02
Hemiptera	Aphididae	Well Watered	46.5	0.04
Hemiptera	Nabidae	Well Watered	26.0	0.09
Hemiptera	Miridae	Well Watered	44.9	0.18
Hemiptera	Blissidae	High Stress	25.8	0.81
Hemiptera	Geocoridae	Well Watered	36.8	0.88
Hemiptera	Pentatomidae	Well Watered	22.2	1.00
Hymenoptera	Formicidae	Well Watered	35.8	0.58
Lepidoptera	Noctuidae	High Stress	39.7	0.33
Neuroptera	Chrysopidae	Well Watered	34.3	0.40
Thysanoptera	Aeolothripidae	Well Watered	40.4	0.31
Thysanoptera	Thripidae	Well Watered	38.3	0.91
Araneae	Linyphiidae	Well Watered	37.0	<0.01
Araneae	Thomisidae	Mild Stress	20.8	0.30
Araneae	Lycosidae	Well Watered	24.4	0.48
Araneae	Salticidae	Well Watered	22.2	1.00

associated with the well-watered habitat (Table 1). Neither the mild-stress or high-stress habitat had any significant associations with arthropod families.

Aphids and their natural enemies

Aphid abundance (primarily *Sitobion avenae* Fabricius) declined when plants were water stressed ($F_{2,10}=4.38$,

$P=0.043$; Fig. 4a). Lady beetles (primarily *Coleomegilla maculata* Degeer), minute pirate bugs (*Orius* sp.), big-eyed bugs (*Geocoris* sp.), and damsel bugs (*Nabis* sp.) were the main natural enemies of aphids in this system. Aphid natural enemy abundance also declined under plant water stress ($F_{2,10}=13.13$, $P=0.0016$; Fig. 4b).

The structural equation model was a good fit to the data (Fisher's $C=6.91$, $P=0.94$, $df=14$) and separated out mechanisms underlying the negative responses of aphids and their natural enemies to declining water availability (Fig. 1b). Plant water potential and biomass both responded negatively to water limitation. Aphid abundance was strongly associated with plant water potential, weakly associated with plant biomass, and unaffected by natural enemy abundance. Natural enemy abundance was strongly associated with plant biomass, but was unaffected by plant water potential or aphid abundance. Although the nature of the direct and indirect effects of water limitation on aphids and their natural enemies was similar across treatments, the magnitude of water stress significantly affected the magnitude of the response. Reducing water availability from mild water limitation to high-water limitation doubled the size of the indirect effect on aphids (mild-stress -0.26 , high stress -0.68) and nearly doubled the indirect effect on natural enemies (mild-stress -0.47 , high stress -0.81).

Discussion

Climate change models predict increasingly extreme precipitation patterns worldwide, resulting in a reduction in soil moisture and less water available for plants despite frequent heavy rainfall events (Knapp et al. 2008; Easterling et al. 2017). Plant water limitation can have direct and indirect effects on multiple trophic levels, resulting in major consequences for insect community structure (Barnett and Facey

2016). In this study, we demonstrated that stress-induced changes in plant quality and quantity reduced the abundance of aphids and their natural enemies, with cascading effects on the composition and abundance of the arthropod community. Our study provides novel insight into how plant water stress can impact entire communities through both direct and indirect effects on plants, herbivores, and natural enemies.

Arthropod communities were sensitive to the intensity of water limitation. Although plant biomass and plant water potential were significantly different across all water treatments, the response of the arthropod community was more variable. A mild reduction of water availability by 25% decreased overall arthropod abundance, but did not change the composition of the community. However, when the intensity of water limitation was increased to 50%, taxonomic changes across the community became evident. Aphids and leafhoppers (Cicadellidae) were abundant piercing–sucking herbivores and both strongly associated with well-watered conditions. In contrast, caterpillars (particularly, *Spodoptera* sp.) were more resilient to changes in water availability, with a slight increase in abundance on stressed hosts (Gutbrodt et al. 2011; Hahn and Maron 2018). A substantial number of predator families were associated with habitats that received ample water, including web-building spiders (Linyphiidae), small ground beetles (Carabidae), lady beetles (primarily *Coleomegilla maculata* Degeer), and minute pirate bugs (*Orius* sp.). Although not significantly associated with a particular habitat, several families that were present in well-watered and mild-stress conditions were not found in the high-stress habitats, including damsel bugs (*Nabis* sp.), crab spiders (Thomisidae), diurnal fireflies (likely *Ellychina* sp.), and hover flies (Syrphidae). Increased predator association with well-watered habitats could be due to the increased plant biomass and habitat complexity facilitating greater prey capture for some predators. This may be the case for web-building Linyphiidae spiders, as high

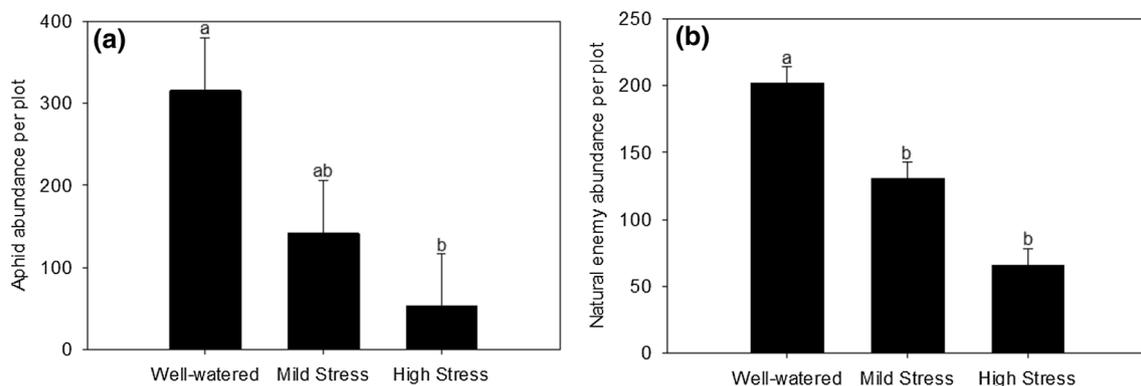


Fig. 4 The effect of the watering treatment on **a** cumulative aphid abundance and **b** cumulative aphid natural enemy abundance across the 8-week field season. LS means \pm SEM are shown, and means

with different letters are significantly different at $P<0.05$. Water limitation reduced aphid and natural enemy abundance (aphid: $F_{2,10}=4.38$, $P=0.043$; natural enemy: $F_{2,10}=13.13$, $P=0.0016$)

structural complexity allows for more attachment sites for webbing (Rypstra et al. 1999). Thus, it appears that differences in arthropod composition in high-stress habitats are largely driven by reduced populations of piercing–sucking herbivores and several key predator families.

The structural equation model approach confirmed predictions that aphids are more affected by stress-mediated plant traits than natural enemies. However, aphids did not respond to all plant traits equally. Plant water potential had a much larger effect on aphid abundance than plant biomass, suggesting aphids were sensitive to changes in plant quality rather than quantity. This is consistent with results from short-term laboratory studies that document negative effects of water limitation on aphid performance (Hale et al. 2003; Ahmed et al. 2017; Xie et al. 2020). Water potential is directly linked to phloem turgor pressure, and low turgor pressure can negatively affect aphid feeding (Auclair 1963). Additionally, aphids are challenged with increased plant defensive chemistry (Showler 2013), increased phloem viscosity (Sevanto 2018), and/or higher osmoregulation demands (Lemoine et al. 2013) on stressed host plants. Reducing water availability from 75% of the recommended watering rate to 50% more than doubled the negative response of aphid populations to both plant water potential and biomass. This suggests some aspects of plant quality decline rapidly as water stress increases, and thus more work is needed to isolate the specific traits that result in deleterious consequences for aphids.

We predicted that natural enemies would be negatively affected by reductions in prey availability and quality in stressed environments. However, plant biomass was the only factor to which natural enemies responded. Natural enemies often aggregate in high biomass, complex structured habitats (Langellotto and Denno 2004). Habitat complexity may provide refuge for natural enemies and reduce the likelihood of antagonistic interactions with other predators. For example, predators are less vulnerable to intraguild predation, and more capable of suppressing prey populations, in complex structured habitats (Finke and Denno 2006). Complex habitats also offer increased protection against abiotic conditions, such as shade from high temperature (Langellotto and Denno 2004). Although we did not see a strong association between natural enemies and plant water potential, laboratory studies have shown that stress-induced changes in plant volatile cues impact natural enemy attraction to stressed host plants (Tariq et al. 2013; Martini and Stelinski 2017). This highlights the need to study the implications of changing plant conditions for third trophic-level consumers in field conditions, as some cues that natural enemies respond to in the lab may be less relevant in a field environment.

Interestingly, the responses of aphids and their natural enemies to environmental change were dominated by the condition of the plant, and not the interaction between predators and prey. This result supports findings where predatory

insect abundance was unaffected by changes in herbivore abundance under decreased precipitation scenarios (Zhu et al. 2014). Many studies have documented suppression of aphids by natural enemies, which both respond to and affect aphid abundance (Toft 2005). However, the generalist predators observed in this study may be less likely to form such a numerical response to any one specific type of prey (Hassell and May 1986). It is possible that the predators were responding to alternative prey sources in the system; however, aphids were by far the most abundant prey item in the habitat. The lack of association between aphid and natural enemy abundance showcases the important role of plants in mediating arthropod community interactions. An ongoing question is whether herbivores are more affected by bottom-up changes in plant resources or top–down effects of natural enemies, and when the two may interact (Hunter and Price 1992; Denno et al. 2002). In this study, we found that bottom-up forces driven by changes in plant water availability were much stronger than top–down effects of predation.

Understanding how arthropods respond to altered precipitation is critical for predicting ecosystem responses to climate change, but our ability to predict these responses is limited by the fact that many field studies only incorporate one level of water stress (Larsson 1989). Here, we demonstrated that the magnitude of plant water stress affects arthropod abundance and composition. This shift was largely driven by piercing–sucking herbivores and predator families, which were more commonly associated with well-watered plots. The structural equation model elucidated that the factors driving aphid and enemy response to water stress varied, and the plant-mediated effects of water limitation had a stronger effect on the insects than changes in their relative abundance. This study highlights the importance of considering community responses to drought conditions beyond the narrow consequences for herbivores and simplified food webs.

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Author contribution statement JK and DF formulated the study and designed experiments. JK performed experiments. DC provided assistance with statistical analysis. JK and DF wrote the manuscript with insight from DC.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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