Title:

Benefit of Drought on an Herbivore of Herbaceous Plants: Enemy Free Space and Reduced Competition

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Declaration of authorship

PAL, KN, CKH, WPC, and GWF conceived the ideas, designed methodology. PAL and JAO analyzed the data. PAL, CML, and CHS collected the data. PAL, CML, JAO, KN, CKH, WPC, and GWF wrote the manuscript.

Abstract

Drought is known to benefit insect herbivores indirectly through plants in some instances; however, the mechanisms that lead to these benefits remain debated and limited. To understand the impact of drought on the quality of host plants and the interactions of insect herbivores with the arthropod community associated with host plants, we conducted a manipulative field study using a specialist herbivore *Pieris rapae*, and its host plant, *Rorippa indica*, in two populations. We found that drought increased the survival of *P. rapae* on *R. indica*, which was associated with the reduced abundance of other herbivores and natural enemies. Drought decreased the suitability of *R. indica* to most herbivores indicated by reduced abundance in the field and decreased relative growth rate of herbivores when fed with drought stressed *R. indica*. However, the performance of *P. rapae* larvae was not affected by changes in the quality of *R. indica*, suggesting their ability to utilize host plants with variable quality. Our findings showed that drought is beneficial to certain specialist herbivores, and in contrast, detrimental to most other herbivores. The present study highlights the role of the arthropod community associated with plants in determining the impacts of drought on insect herbivores.

Key words

plant quality, environmental heterogeneity, species interaction, water stress, insect herbivore

Introduction

Drought is a prevalent abiotic stress of terrestrial plants. Drought affects individuals, populations, and communities of plants (Schulze, 1986; Bunker & Carson, 2005), and ultimately other organisms (Anderegg, Kane & Anderegg, 2013). An interesting example is the association between drought and outbreaks of insect herbivores (White, 1969; White, 1974; Mattson & Haack, 1987). Although there are seemingly positive impacts of drought on insect herbivores, the cause of such phenomenon remains debated (White, 2009). Disagreements occur partly due to how drought stress is defined and framed. Studies that reported an increased in insect population following drought were usually studied under the climatic context, whereas others studied drought as a physiological state of water deficiency (Waring & Cobb, 1992). These different contexts have accentuated the disagreements and led to the development of several hypothesis (White, 2009). In addition, plant life-form in question also generates another layer of complication and complexity. In a meta-analysis, Waring and Cobb (1992) found that studies on trees usually looked at the impact of environmentally-induced drought on insect herbivores in the field, whereas studies on herbaceous plants usually used experimentally-induced drought in lab settings. Although manipulative lab experiments on herbaceous plants have improved

our understanding regarding impacts of drought on plant physiology and associated insect herbivores (Gutbrodt, Mody & Dorn, 2011; Han *et al.*, 2014), field studies are required to test how well these conclusions hold true under natural settings.

The impacts of drought on herbaceous plants and the associated insect herbivores may seem trivial. Drought stress caused by a shortage of rainfall reduces the productivity, biomass, and survival of herbaceous plants (Garssen, Verhoeven & Soons, 2014). Reduction in food source likely leads to a decrease in the population of insect herbivores (Ehrlich *et al.*, 1980). However, drought stress can be prevalent in herbaceous plants even when climatic conditions are stable (Murren *et al.*, 2020). This may be particularly true in grasslands and urban/agricultural areas, where high light intensity, temperature, and shallow soil depth increases the likelihood of drought. Same magnitude of environmental changes likely causes greater impacts on herbaceous plants that have little capacity to buffer sub-optimal conditions (Alpert & Simms, 2002). Although some studies have shown the importance of small-scale environmental variations on plant-associated arthropod composition (Tack *et al.*, 2010), little attention has focused on drought caused by spatial heterogeneity and how it affects host plant use of insect herbivores.

While many studies aim to understand how drought affects insect populations, a major limitation is the overemphasis on the direct interactions between plants and insects (English-Loeb, Stout & Duffey, 1997). Phenotypic changes induced by drought, not only affect insect herbivores of interest but also other species associated with the plant (Trotter, Cobb & Whitham, 2008). Changes in plant-associated communities following drought, may alter the strength and type of species interactions (Kroes *et al.*, 2016), which affects the fitness of insect herbivores (Jamieson *et al.*, 2012). Changes in species interactions may even contribute more to the overall impacts of abiotic stress than effect of pairwise interactions (Ockendon *et al.*, 2014). However, studies investigating the role of drought on plant-insect interactions across trophic levels remain limited.

To understand the impact of drought on an insect herbivore and its herbaceous host plant, we conducted a manipulative field study using a wild host, *Rorippa indica* (L.) Hiern, of the specialist herbivore, cabbage white butterfly (*Pieris rapae*) from two populations in Taiwan and Japan. *R. indica* is a perennial glabrous herb that is commonly found in highly disturbed areas such as roadsides, gardens, and field margins throughout the main island of Taiwan (Huang, 1994) and also during May to September in most parts of Japan (Jisaburo□ O□i, 1965). *R. indica* individuals with different stress levels and phenotypes are commonly observed in the field due to habitat heterogeneity. By

manipulating water status of *R. indica* in the field, in combination with feeding assays in the lab, we aimed to determine the impact of drought on: (1) preference of adult *P. rapae*, (2) performance and survival of larvae *P. rapae*, (3) quality of *R. indica* to herbivores, and (4) arthropod community associated with the plant. Using this information, we aimed to understand the factors from host plants and other associated organisms that influence survival of *P. rapae* on *R. indica* under different water availability.

Materials and methods

Insect, plant, water treatment and drought quantification

Cabbage white butterflies, *Pieris rapae*, were collected in the experimental field of National Taiwan University (NTU, Taipei, Taiwan) and University of Tsukuba (UT, Ibaraki, Japan), and kept at 14:10 light:dark cycle, 25-27$°C$, on cabbage (*Brassica oleracea* var. capitata) and Komatsuna (*Brassica rapa* var. Perviridis) respectively. Seeds of *Rorippa indica* were collected in the experimental fields. Plants were maintained in semi-closed greenhouse, and grown in 3-inch pots with a mixture of peat moss (Kekkila, Finland): perlite (2-8 mm) (3:1 volume) supplied with fertilizer Osmocote Plus (Everris, Netherland). Plants with 7-8 fully expanded leaves were subjected to two levels of water treatments: (1) well-watered (200 ml day^{-1} pot^{-1}), (2) drought-stressed (10 ml day^{-1} pot^{-1}). Water was

applied daily at 9 a.m. for 7 days. Water status of plants were quantified after the establishment of drought stress (Appendix 1). For field experiments, water status of *R. indica* was maintained by the same procedure, accompanied with daily observation at 12, 2, and 4 p.m. (Appendix 2).

Field experiment: Oviposition preference, survival, and arthropod community

Individual *R. indica* with different water status (in pots) were placed in the experimental field at 7 a.m., 3 meters apart in a square grid (Appendix 3). Ovipositional preferences were determined by recording the number of eggs of *P. rapae* after the first 72 hours. Insect community associated with *R. indica* was determined on the same day by recording all arthropods on plants during 7 a.m.-12 p.m. All morphospecies observed in the field were listed in Appendix 4. Individual plants were kept in the field for an additional 7 days before *P. rapae* larvae were collected. Only larvae older than second instar were collected to ensure that the collected caterpillars came from the recorded eggs. Because *P. rapae* larvae rarely move away from their host even when the host plant was stressed, the survival of *P. rapae* was defined and calculated as: (caterpillar number) (egg number)$^{-1}$. Field experiments took place in Taiwan during April – June 2018, and in Japan during July – September 2018. The experiment was replicated three times in both locations, with one trial in each month, defined as early, middle, and late season. The experimental fields were located within the campus of NTU

(25°00'55.9"N 121°32'25.0"E) and UT (36°06'51.7"N 140°05'59.7"E), and both were at an elevation of about 900 m^2. The natural community of plants in the experimental fields was allowed to grow undisturbed. Each trial contained 20-25 individual *R. indica* from each water treatment (total of 40-50 plants). For more information on field experiment please see Appendix 5.

Host plant quality under different water treatments

We analyzed the relative growth rate (RGR) of larvae to determine the quality of *R. indica* to caterpillars under different water treatments. Larvae of *P. rapae* from both populations were fed with *R. indica* from respective population. Third instar larvae of *P. rapae* were weighed, and placed in 30 c.c. plastic cups with thin layer of 1% agar (5 ml). The larvae were fed with mature leaves of specific water status (either 200 ml day^{-1}, 10 ml day^{-1}, and an additional intermediate drought level: 50 ml day^{-1}). Larvae were weighed after 3 days. The start and end weights were used to calculate RGR using the equation: (end weight – start weight) (end weight + start weight)$^{-1}$ $days^{-1}$ (Felton *et al.*, 1989). Due to the discrepancy between the survival in field and performance of *P. rapae* larvae in RGR assay, we conducted another set of common garden experiment to test the changes in host quality using insects without previous evolutionary history with *R. indica* of both populations. Plants were grown in a greenhouse (University Park, Pennsylvania State University, USA) with 16:8 light cycle at 25°C.

Leaves were collected from two different water treatments (200 ml day^{-1}, 10 ml day^{-1}) from both populations of *R. indica* and fed to third instar larvae of caterpillars from North America, including *P. rapae* (specialist), *Trichloplusia ni* (semi-specialist, cabbage looper), *Helicoverpa zea* (generalist, corn earworm), and *Spodoptera frugiperda* (generalist, fall armyworm) using method as described above.

Statistical analysis

All statistical analyses were conducted in R version 3.5.3 (R-Core-Team, 2017). Univariate response variables were modeled with generalized linear models (GLM) with treatment, population, season and their interaction as fixed effects. We analyzed all count data (egg, caterpillar, herbivore, and natural enemy) with negative binomial GLM (package: *MASS*) (Venables & Ripley, 2013) with biomass of plants as an offset variable. Survival probabilities of *P. rapae* were modeled with binomial GLM as the odds ratio between alive (caterpillar count) and dead (egg count - caterpillar count). We excluded samples with no eggs observed. Dispersion, zero-inflation, residual normality, and homoscedasticity of all model fits were evaluated with simulation-based residual plots (package: *DHARMa*) (Hartig, 2016). Significance of model parameters were tested by Type II rather than Type III Wald's Chi-squared test (package: *car*) (Fox & Weisberg, 2018) to account for unbalanced data (Langsrud, 2003).

To examine whether the variations in survival of *P. rapae* could be attributed to abundance of other arthropods, we pooled samples between treatments and fitted binomial generalized linear mixed-effect models (GLMM, package: *glmmTMB*) (Brooks et al., 2017) with observation-level random effect to improve residuals. Abundances of trophic guilds (herbivore and natural enemy, Fig. 4), and the abundances of individual species (Table 1) were used as fixed effect predictors. Individual GLMM was fitted for each season in each location. We implemented backwards model selection (likelihood ratio tests) until all terms were significant (Zuur *et al.*, 2009). Other model diagnostics are performed as described above. Continuous variables such as water content, biomass, and relative growth rate were analyzed using ANOVA, followed by Tukey HSD. Diagnostic plots were used to check for model assumptions, such as equal variance and normality (Zuur, Ieno & Elphick, 2010).

Results

Drought stress quantification

Different water treatments led to observable differences in phenotype, individuals under drought were smaller and darker in color (Fig. 1a). Leaf number and shape were not affected by drought (Fig. 1b); however, leaf shape differed between populations (Fig. 1c, $F_{1,29} = 13.03$, $P = 0.001$). Fresh weight of shoot of individuals was negatively affected by drought (Fig. 1d, $F_{1,29} = 65.29$, $P < 0.001$) and higher

in the Taiwanese population compared to the Japanese population ($F_{1,29}$ = 22.59, P < 0.001). Dry weight was also negatively affected by drought (Fig. 1e, $F_{1,29}$ = 17.05, P < 0.001) and higher in the Taiwanese population ($F_{1,29}$ = 8.5, P = 0.007). Water content of shoot was reduced by drought (Fig. 1f, $F_{1,28}$ = 105.02, P < 0.001), and higher in Taiwanese population ($F_{1,28}$ = 5.48, P = 0.027). However, the effect of population was only significant under drought, indicated by significant interaction between water and population ($F_{1,28}$ = 5.48, P = 0.027). The biomass of root was not affected by water treatments. However, root biomass was higher in Taiwanese population (Fig. 1g, $F_{1,28}$ = 8.605, P = 0.007). Root: shoot ratio was positively affected by drought (Fig. 1h, $F_{1,28}$ = 88.17, P < 0.001). Volumetric water content (θv) of the soil was negatively affected by drought (Fig. 1i, $F_{1,29}$ = 2238.65, P < 0.001).

Oviposition preference, caterpillar number, and survival

Higher quantities of eggs were observed on well-watered *R. indica* (Fig. 2a, GLM, water: 200 ml day^{-1}, estimate = 1.04, Z = 4.79, P < 0.001). Egg number on *R. indica* was greater in Taiwan than in Japan (GLM, region: Taiwan, estimate = 2.2, Z= 10.21, P < 0.001). In addition, egg number was negatively associated with late season in Taiwan (GLM, season*region: late*Taiwan, estimate = -1.74, Z= -7.11, P < 0.001).

The number of caterpillars on *R. indica* was overall higher in Taiwan (Fig. 2b, GLM, region: Taiwan, estimate = 1.25, Z= 3.57, $P < 0.001$), but lower on well-watered *R. indica* in Taiwan (GLM, water*region: 20 ml day^{-1}*Taiwan, estimate = -0.94, Z= -2.66, $P = 0.008$). The number of caterpillars were negatively associated with late season (GLM, season: late, estimate = -1.72, Z = -4.19, $P < 0.001$), and not affected by water treatment in general.

Survival of *P. rapae* was negatively associated with well-watered *R. indica* (Fig. 2c, GLM, water: 200 ml day^{-1}, estimate = -2.15, Z = -8.79, $P < 0.001$), middle and late seasons (GLM, season: middle, estimate = -0.63, Z = -2.58, $P = 0.01$; season: late, estimate = -3.96, Z = -14.95, $P < 0.001$). However, the pattern was influenced by several interacting factors. Survival of *P. rapae* was positively associate with well-watered *R. indica* in middle and late season (GLM, water*season: 200 ml day^{-1}*middle, estimate = 1.57, Z = 10.1, $P < 0.001$; water*season: 200 ml day^{-1}*late, estimate = 1.31, Z = 6.52, $P < 0.001$), but negatively associated with well-watered *R, indica* in Taiwan (GLM, water*region: 200 ml day^{-1}*late, estimate = -0.53, Z = -2.34, $P = 0.019$). The survival of *P. rapae* was overall lower in Taiwan (GLM, location: Taiwan, estimate = -2.74, Z = -10.81, $P < 0.001$), but significantly higher in late season (GLM, season*location: late*Taiwan, estimate = 4.2, Z = 17.49, $P < 0.001$) and lower in middle season (GLM, season*location: middle*Taiwan, estimate = -0.53, Z = -2.34, $P = 0.019$).

Changes in host quality by drought: Caterpillar performance assays

The relative growth rates (RGR) of *P. rapae* larvae were not affected by drought stressed *R. indica* from same geographic origin (Fig. 3a, b). In contrast, drought-stressed *R. indica* from both populations led to significant decreases in RGR of *P. rapae* from North America (Fig. 3c, $F_{1,141} = 12.96$, $P < 0.001$). Drought negatively affected RGR of generalist caterpillars. RGR of *H. zea* larvae were lower on drought stressed *R. indica* (Fig. 3d, $F_{1,147} = 25.41$, $P < 0.001$). RGR of *T. ni* larvae were lower on drought stressed *R. indica* (Fig. 3e, $F_{1,128} = 8.76$, $P = 0.004$) and *R. indica* from Taiwan ($F_{1,128} = 8.62$, $P = 0.004$). However, the negative impacts of drought were only significant when *T. ni* larvae fed on *R. indica* from Taiwan ($F_{1,128} = 5.2$, $P = 0.024$). *S. frugiperda* completely rejected *R. indica* from Taiwan as food source, and we observed a small amount of feeding on *R. indica* from Japan. The mortality of *S. frugiperda* larvae were significantly lower when *R. indica* from Taiwan was provided as food (Fig. 3f, GLM, 200 ml day^{-1}: estimate = -1.81, $P < 0.001$).

Abundance of herbivore and natural enemy

Herbivore abundance on *R. indica* was positively associated with well-watered *R. indica* (Fig. 4a and Fig. 4i, GLM, water: 200 ml day^{-1}, estimate = 1.43, Z = 4.32, $P < 0.001$), and negatively associated with late season (GLM, season: late, estimate = -2.61, Z = -6.54, $P < 0.001$). The negative association

between herbivore abundance and late season was especially stronger on well-watered *R. indica* (GLM, water*season: 200 ml day^{-1}*late, estimate = -1.45, Z = -3.39, $P < 0.001$), and became positive during late season in Taiwan (GLM, season*location: late*Taiwan, estimate = 2.69, Z = 6.23, $P < 0.001$).

Natural enemy abundance was positively associated with well-water *R. indica* (Fig. 4e and Fig. 4m, GLM, water: 200 ml day^{-1}, estimate = 1.98, Z = 4.21, $P < 0.001$), but negatively associated with middle and late season (GLM, season: middle, estimate = -1.54, Z = -2.28, $P = 0.022$; season: late, estimate = -2.04, Z = -3.26, $P = 0.001$). Natural enemy abundance was lower in Taiwan compared to Japan (GLM, region: Taiwan, estimate = -1.84, Z = -3.24, $P = 0.001$), but increased drastically in middle and late season in Taiwan (GLM, season*location: middle*Taiwan, estimate = 2.51, Z = 5.04, $P < 0.001$; season*location: late*Taiwan, estimate = 4.49, Z = 8.61, $P < 0.001$). For descriptions of qualitative changes in the composition of herbivores and natural enemies please see Appendix 6-9.

Survival of Pieris rapae and arthropod community

We found significant negative associations between the abundance of herbivores and natural enemies with the survival of *P. rapae* during several seasons in both locations (Fig. 4). In Taiwan, abundance of herbivore was negatively associated with the survival of *P. rapae* during early (Fig. 4b, GLMM,

estimate = -1.75, Z = -5.7, $p < 0.001$) and middle season (Fig. 4c, GLMM, estimate = -0.12, Z = -2.41, $p = 0.016$). Abundance of natural enemy was negatively associated with survival of *P. rapae* during early (Fig. 4f, GLMM, estimate = -3.64 Z = -10.11, $p < 0.001$) and late season (Fig. 4h, GLMM, estimate = -0.24, Z = -4.05, $p < 0.001$).

Most of the herbivores observed on *R. indica* showed negative associations with *R. indica* survival (Table 1). For instance, flea beetles (*P. stiolata*) that heavily attacked well-watered *R. indica* were negatively associated with survival of *P. rapae* during early season in Taiwan (GLMM, estimate = -6.50, $p = 0.04$). Two herbivores were found to be positively associated with survival of *P. rapae*, including scarlet shieldbugs (*E. dominulus*) and Cicadellidae during middle and late season in Taiwan respectively (GLMM, estimate = 0.99, $p = 0.08$; GLMM, estimate = 1.31, $p < 0.001$). However, the scarlet shieldbug (*E. dominulus*) had contrasting associations with the survival of *P. rapae* in different month (negative association during late season, GLMM, estimate = -0.95, $p < 0.001$), likely due to the difference in abundance between seasons (Individual plant^{-1}: Middle = 0.136; Late = 0.275). The analysis of morphospecies in Japan revealed some unexpected associations; for example, Lauxaniidae, a parasitic mite of aphids, and Syrphidae (during early season, GLMM, estimate = -0.95, $p = 0.021$; estimate = 0.50, $p = 0.001$; estimate = -0.31, $p = 0.041$).

Discussion

These findings supported the common belief that drought decreases the quality of plants to insect herbivores (Waring & Cobb, 1992; English-Loeb, Stout & Duffey, 1997). Drought reduced the abundance of herbivores on *R. indica* in field, and the RGR of herbivores that fed on these *R. indica,* except for *P. rapae* from Taiwan and Japan. Individuals from these populations were not affected by changes in host plant quality under drought when plants were from the same geographic origin. In contrast, the RGR of the North American *P. rapae* decreased when fed with drought stressed *R. indic*a from either Taiwan or Japan (Fig. 3). This indicated potential local adaptation to deal with variations in host quality caused by drought.

The reduction in other herbivores and natural enemies on drought stressed *R. indica* was likely the most important factor that increases the survival of *P. rapae*, given that quality changes of the host plant under drought did not benefit *P. rapae.* Although we did not explicitly evaluate the level of predation and competition, field observations supported this hypothesis. There were several important morphospecies that either constantly observed to prey on *P. rapae* or caused large amounts of damage to *R. indica* (Appendix 7). In addition, the lack of overall association between abundance of

arthropods and survival of *P. rapae* on *R. indica* in Japan was likely due to overall low abundance of both herbivore and natural enemy, and species that directly interact with *P. rapae*. Another surprising finding was the positive associations between the survival of *P. rapae* with two piercing-sucking herbivores in Taiwan and a species of parasitic mite (Trombidiidae) on aphids in Japan. Although this observation contradicted our overall conclusion that stronger competition on well-watered *R. indica* reduced the survival of *P. rapae*, it reveals potential antagonistic relationships of the defense responses elicited by different herbivores. Piercing-sucking insects in the order Hemiptera induce distinct defense pathways in plants compared to chewing herbivores (De Vos *et al.*, 2005), and may benefit chewing herbivores (Soler *et al.*, 2012; Li *et al.*, 2014; Kroes, Van Loon & Dicke, 2015). The tradeoffs among defenses elicit by different groups of insects was likely due to the antagonistic relationship between phytohormone jasmonic acid (JA) and salicylic acid (SA) mediated defense pathways, which are involved in defense against chewing and piercing-sucking insect herbivores respectively (Pieterse *et al.*, 2012). It has also been shown that the positive impacts of piercing-sucking herbivores took place only under low density (Kroes, Van Loon & Dicke, 2015), which explained the switch in association between survival of *P. rapae* and *E. dominulus* from positive to negative as the density of *E. dominulus* doubled.

Although the RGR of local *P. rapae* was not affected by the changes in host quality under drought, *P. rapae* may still perceive changes in host plants and react accordingly. According to the preference-performance hypothesis (PPH), oviposition of females should match the performance of their offspring (Thompson, 1988; Gripenberg *et al.*, 2010). However, based on the observed decrease in oviposition on drought-stressed *R. indica* in two populations and the lack of performance cost when fed with drought stressed *R. indica*, it seems that the preference-performance relationship predicted by PPH was not observed. It has been shown that the preference of females could be blurred by temporal variation in resource quality (Cronin, Abrahamson & Craig, 2001; Gripenberg *et al.*, 2007), and thus failed to evolve a proper mechanism to perceive these changes in host quality for their offspring. Alternatively, this behavior could also be a passive response of female *P. rapae* due to changes in attractiveness (due to size or chemical cues) of plants under drought. For example, changes in volatile emission patterns are known to be important in determining the attractiveness of plants to insects (Pichersky & Gershenzon, 2002; Orre *et al.*, 2010), and drought stress affects volatile emissions (Copolovici *et al.*, 2014; Scott *et al.*, 2018).

There are some caveats in the present study, since we only recorded the abundance of herbivore and natural enemy once in each field experiment, it was likely that the abundance and composition of

these communities were underestimated. In addition, the time period of the field experiment was shorter than the larval stage of *P. rapae*. Although at the end of 10-day field experiment, the majority of the plants still maintained 50-70% of the biomass, it is unknown whether longer periods in the field would result in complete defoliation. This information can be important for understanding how drought affects the population dynamics of *P. rapae*. Even so, the likelihood of complete defoliation seems very low due to the ability of plants to regrow and potential control by natural enemies under well-watered conditions, and the low quality of plants to other herbivores under drought conditions. The observation that certain herbivores (i.e. *P. rapae*) were not affected by the reduction in host quality pointed out a common limitation in past studies that focus on specific species without incorporating the natural insect community that interacts with the plant in field. From a plant ecology perspective, it could be misleading to look at few selected insect species and groups of defense responses because the evolutionary relationship between the selected defense and the insect herbivore were often assumed. For example, herbivores other than *P. rapae* such as flea beetle in Taiwan may impose strong selection on *R. indica*. As a result, changes under drought might evolve targeting herbivores other than *P. rapae*. Conclusions from these studies may vary based on the choice of

herbivore and plant traits. Hence, care must be taken when drawing conclusions from studies that looked at a few herbivore species or a few plant responses.

In summary, the present study provides insights to the ongoing discussion on how drought influences insect herbivores (Mattson & Haack, 1987; Waring & Cobb, 1992; White, 2009). By studying impact of drought under the context of arthropod community in addition to the direct interaction between plant and insect herbivore, our study revealed one of the potential mechanisms and scenarios in which drought can be beneficial to some insect but detrimental to others. However, the contradicting impacts of drought-stressed *R. indica* on *P. rapae* and other arthropod species, reveals the complexity and context dependency of interactions among abiotic stress, plant and insect. These findings beg the questions of how important environmental heterogeneity affects the ecology and evolution of interactions between herbaceous plants and insect herbivores. Further study is needed to understand how host plant variations caused by environmental heterogeneity affects insect herbivore populations, which will provide useful information on species distribution, dynamics, and provide a better understanding between the interactions of plants and herbivores.

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Data availability statement

Data in this manuscript will be deposited and made available in the Dryad Digital Repository.

References

Alpert P, Simms EL (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evol Ecol* **16,** 285-297.

Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat Clim Change* **3,** 30-36.

Anderson SS, McCrea KD, Abrahamson WG, Hartzel LM (1989) Host genotype choice by the ball gallmaker *Eurosta Solidaginis* (Diptera: Tephritidae). *Ecology* **70,** 1048-1054.

Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* **47,** 817-844.

Backhaus S, Wiehl D, Beierkuhnlein C., Jentsch A, Wellstein C (2014) Warming and drought do not influence the palatability of *Quercus pubescens* Willd. leaves of four European provenances. *Arthropod-Plant Interactions* **8,** 329-337.

Barbosa P, Greenblatt J (1979) Suitability, digestibility and assimilation of various host plants of the gypsy moth *Lymantria dispar* L. *Oecologia* **43,** 111-119.

Berenbaum M (1981) Patterns of furanocoumarin distribution and insect herbivory in the Umbelliferae - plant chemistry and community structure. *Ecology* **62,** 1254-1266.

Bernays EA (1998) Evolution of feeding behavior in insect herbivores. *BioScience* **48,** 35-44.

Bjorkman C (2000) Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia* **123,** 223-231.

Bowers MD, Stamp NE (1993) Effects of plant age, genotype and herbivory on plantago performance and chemistry. *Ecology* **74,** 1778-1791.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* 9:378-400

Bunker DE, Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *J Ecol* **93,** 794-806.

Coley P (1998) Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Clim Change* **39,** 455-472.

Copolovici L, Kännaste A, Remmel T, Niinemets Ü (2014) Volatile organic compound emissions from *Alnus glutinosa* under interacting drought and herbivory stresses. *Enviro Exp Bot* **100,** 55-63.

Craig TP, Itami JK, Craig JV (2007) Host plant genotype influences survival of hybrids between *Eurosta solidaginis* host races. *Evolution* **61,** 2607-2613.

Cronin JT, Abrahamson WG (1999) Host-plant genotype and other herbivores influence goldenrod stem galler preference and performance. *Oecologia* **121,** 392-404.

Cronin JT, Abrahamson WG, Craig TP (2001) Temporal variation in herbivore host-plant preference and performance: constraints on host-plant adaptation. *Oikos* **93,** 312-320.

Crutsinger GM (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313,** 966-968.

De Vos M, Van Oosten VR, Van Poecke RM, Van Pelt JA, Pozo MJ, Mueller MJ, Buchala AJ, Metraux JP, Van Loon LC, Dicke M, Pieterse CM (2005) Signal signature and transcriptome changes of *Arabidopsis* during pathogen and insect attack. *Mol Plant Microbe Interact* **18,** 923-937.

Deane Bowers M, Collinge SK, Gamble SE, Schmitt J (1992) Effects of genotype, habitat, and seasonal variation on iridoid glycoside content of *Plantago lanceolata* (Plantaginaceae) and the implications for insect herbivores. *Oecologia* **91,** 201-207.

Delagrange S, Messier C, Lechowicz MJ, Dizengremel P (2004) Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiol* **24,** 775-784.

Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu Rev Entomol* **40,** 297-331.

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol Evol* **13,** 77-81.

Ehrlich PR, Murphy DD, Singer MC, Sherwood CB, White RR, Brown IL (1980) Extinction, reduction, stability and increase: The responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*, **46,** 101-105.

English-Loeb G, Stout MJ, Duffey SS (1997) Drought stress in tomatoes: changes in plant chemistry and potential nonlinear consequences for insect herbivores. *Oikos* 456-468.

Evans LM, Clark JS, Whipple AV, Whitham TG (2012) The relative influences of host plant genotype and yearly abiotic variability in determining herbivore abundance. *Oecologia* **168,** 483-489.

Felton GW, Donato K, Del Vecchio RJ, Duffey SS (1989) Activation of plant foliar oxidases by insect feeding reduces nutritive quality of foliage for noctuid herbivores. *J Chem Ecol* **15,** 2667-2694

Fox J, Weisberg S (2018) *An R companion to applied regression*. Sage Publications.

Fritz RS, Price PW (1988) Genetic variation among plants and insect community structure: willows and sawflies. *Ecology* **69,** 845-856.

Garssen AG, Verhoeven JTA, Soons MB (2014) Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis. *Freshw Biol* **59,** 1052-1063.

Gottlieb LD (1977) Genotypic similarity of large and small individuals in a natural population of the annual plant *Stephanomeria exigua* ssp. Coronaria (Compositae). *J Ecol* **65,** 127-134.

Grassein F, Till-Bottraud I, Lavorel S (2010) Plant resource-use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. *Ann Bot* **106,** 637-645.

Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecol Lett* **13,** 383-393.

Gripenberg S, Morriën E, Cudmore A, Salminen JP, Roslin T (2007) Resource selection by female moths in a heterogeneous environment: what is a poor girl to do? *J Anim Ecol* **76,** 854-865.

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

Habib H, Fazili KM (2007) Plant protease inhibitors: a defense strategy in plants. *Biotchnol Mol Biol Rev* **2,** 68-85.

Hahn PG, Agrawal AA, Sussman KI, Maron JL (2019) Population variation, environmental gradients, and the evolutionary ecology of plant defense against herbivory. *Am Nat* **193,** 20-34.

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.

Harrison XA (2015) A comparison of observation-level random effect and beta-binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ* **3,** e1114.

Hartig F (2016) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1. 0.

Henriksson J, Haukioja E, Ossipov V, Ossipova S, Sillanpaa S, Kapari L, Pihlaja K (2003) Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds. *Oikos* **103,** 3-16.

Horner JD, Abrahamson WG (1992) Influence of plant genotype and environment on oviposition preference and offspring survival in a gallmaking herbivore. *Oecologia* **90,** 323-332.

Hunter MD, McNeil JN (1997) Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* **78,** 977-986.

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

Jisaburo O i FGM, Egbert HW (1965) Flora of Japan. Smithsonian Institution.

Johnson MT (2008) Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* **89,** 145-154.

Johnson MTJ, Agrawal AA (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* **86,** 874-885.

Johnson MTJ, Lajeunesse MJ, Agrawal AA (2005) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol Lett* **9,** 24-34 .

Mooney KA, Agrawal AA (2008) Plant genotype shapes ant-aphid interactions: implications for community structure and indirect plant defense. *Am Nat* **171,** E195-E205.

Kaplan I, Denno RF (2007) Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol Lett* **10,** 977-994.

Khan M, Ulrichs C, Mewis I (2011) Water stress alters aphid-induced glucosinolate response in *Brassica oleracea* var. italica differently. *Chemoecology* **21,** 235-242.

Khan ZR, Abenes MLP, Fernandez NJ (1996) Suitability of graminaceous weed species as host plants for rice leaffolders, *Cnaphalocrocis medinalis* and *Marasmia patnalis*. *Crop Prot* **15,** 121-127.

Kroes A, Stam JM, David A, Boland W, Van Loon JJA, Dicke M, Poelman EH (2016) Plant-mediated interactions between two herbivores differentially affect a subsequently arriving third herbivore in populations of wild cabbage. *Plant Biol* **18,** 981-991.

Kroes A, Van Loon JJA, Dicke M (2015) Density-dependent interference of aphids with caterpillar-induced defenses in *Arabidopsis*: involvement of phytohormones and transcription factors. *Plant Cell Physiol* **56,** 98-106.

Langsrud Ø (2003) ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Stat Comput* **13,** 163-167.

Larsson S (1989) Stressful times for the plant stress: insect performance hypothesis. *Oikos* **56,** 277-283.

Lawton JH, DR Strong J (1981) Community patterns and competition in folivorous insects. *Am Nat* **118,** 317-338.

Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* **28,** 23-39.

Lenhart P, Eubanks M, Behmer S (2015) Water stress in grasslands: dynamic responses of plants and insect herbivores. *Oikos* **124,** 381-390.

Lenth R (2018) Emmeans: Estimated marginal means, aka least-squares means. *R package version,* **1**.

Li Y, Dicke M, Harvey JA, Gols R (2014) Intra-specific variation in wild *Brassica oleracea* for aphid-induced plant responses and consequences for caterpillar–parasitoid interactions. *Oecologia* **174,** 853-862.

Maddox GD, Root RB (1987) Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*: genetic variation and heritability. *Oecologia* **72,** 8-14.

Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. *Bioscience* **37,** 110-118.

Mattson WJ (1980) Herbivory in relation to plant nitrogen-content. *Annu Rev Ecol Evol* **11,** 119-161.

Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos* **79,** 417-428.

McIntyre PJ, Whitham TG (2003) Plant genotype affects long-term herbivore population dynamics and extinction: Conservation implications. *Ecology* **84,** 311-322.

Mewis I, Khan MAM, Glawischnig E, Schreiner M, Ulrichs C (2012) Water stress and aphid feeding differentially influence metabolite composition in *Arabidopsis thaliana* (L.). *PLoS One* **7,** e48661.

Mody K, Eichenberger D, Dorn S (2009) Stress magnitude matters: different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. *Ecol Entomol* **34,** 133-143.

Moran N (1981) Intraspecific variability in herbivore performance and host quality - a field-study of *Uroleucon caligatum* (Homoptera, Aphididae) and its *Solidago* hosts (Asteraceae). *Ecol Entomol* **6,** 301-306.

Murren CJ, Alt CHS, Kohler C, Sancho G (2020) Natural variation on whole-plant form in the wild is influenced by multivariate soil nutrient characteristics: natural selection acts on root traits. *Am J Bot* ***107****, 319-328*

Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests—general aspects and the pine processionary moth as specific example. *For Ecol Manag* **259,** 831-838.

Ockendon N, Baker DJ, Carr JA, White EC, Almond REA, Amano T, Bertram E, Bradbury RB, Bradley C, Butchart SHM, Doswald N, Foden W, Gill DJC, Green RE, Sutherland WJ, Tanner EVJ,

Pearce-Higgins JW (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Glob Change Biol,* **20,** 2221-2229.

O'Reilly-Wapstra JM, McArthur C, Potts BM (2004) Linking plant genotype, plant defensive chemistry and mammal browsing in a *Eucalyptus* species. *Func Ecol* **18,** 677-684.

Orre GUS, Wratten SD, Jonsson M, Hale RJ (2010) Effects of an herbivore-induced plant volatile on arthropods from three trophic levels in brassicas. *Biol Control* **53,** 62-67.

Pichersky E, Gershenzon J (2002) The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Curr Opin Plant Biol,* **5,** 237-243.

Pieterse C, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees S, Schekman R (2012) Hormonal modulation of plant immunity. *Annu Rev Cell Dev Bi, Vol 28,* **28,** 489-521.

Poorter H, Niinemets Ü, Walter A, Fiorani F, Schurr U (2010) A method to construct dose–response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *J Exp Bot* **61,** 2043-2055.

Price P, Hunter M (2015) Population dynamics of an insect herbivore over 32 Years are driven by precipitation and host-plant effects: testing model predictions. *Environ Entomol* **44,** 463-473.

Price PW, Clancy KM (1986) Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. *Ecol Res* **1,** 1-14.

Price PW (1991) The plant vigor hypothesis and herbivore attack. *Oikos* 244-251.

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Evol* **11,** 41-65.

R-Core-Team (2017) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Vienna, Austria.

Rosenthal GA, Berenbaum MR (2012) Herbivores: their interactions with secondary plant metabolites: ecological and evolutionary processes. Academic Press.

Rudgers JA, Whitney KD (2006) Interactions between insect herbivores and a plant architectural dimorphism. *J Ecol* **94,** 1249-1260.

Scheirs J, De Bruyn L (2002) Integrating optimal foraging and optimal oviposition theory in plant–insect research. *Oikos* **96,** 187-191.

Scheirs J, De Bruyn L (2005) Plant-mediated effects of drought stress on host preference and performance of a grass miner. *Oikos* **108,** 371-385.

Schowalter TD, Lightfoot DC, Whitford WG (1999) Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *Am Midl Nat* **142,** 281-290.

Schulze E (1986) Whole-plant responses to drought. *Func Plant Biol* **13,** 127-141.

Scott ER, Li X, Kfoury N, Morimoto J, Han WY, Ahmed S, Cash SB, Griffin TS, Stepp JR, Robbat A, Orians CM (2018) Interactive effects of drought severity and simulated herbivory on tea (*Camellia sinensis*) volatile and non-volatile metabolites. *Environ Exp Bot* **157**, 283-292

Scriber JM (1977) Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia* **28,** 269-287.

Shen C, Bach C (1997) Genetic variation in resistance and tolerance to insect herbivory in *Salix cordata*. *Ecol Entomol* **22,** 335-342.

Huang TC (1994). Flora of Taiwan (Vol. 2). The Committee.

Smiley J (1978) Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* **201,** 745-747.

Soler R, Badenes-Pérez FR, Broekgaarden C, Zheng SJ, David A, Boland W, Dicke M (2012) Plant-mediated facilitation between a leaf-feeding and a phloem-feeding insect in a brassicaceous plant: from insect performance to gene transcription. *Func Ecol* **26,** 156-166.

Soliveres S, Garcia-Palacios P, Castillo-Monroy A, Maestre F, Escudero A, Valladares F (2011) Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass-shrub interaction in a semi-arid ecosystem. *Oikos* **120,** 710-719.

Stiling P, Rossi AM (1996) Complex effects of genotype and environment on insect herbivores and their enemies. *Ecology* **77,** 2212.

Stireman JO, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ, Ricklefs RE, Gentry GL, Hallwachs W, Coley PD, Barone JA, Greeney HF, Connahs H, Barbosa P, Morais HC, Diniz IR (2005) Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proc Natl Acad Sci USA*, **102,** 17384-17387.

Sumerford D, Abrahamson W, Weis A (2000) The effects of drought on the *Solidago altissima-Eurosta solidaginis*-natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. *Oecologia* **122,** 240-248.

Tack AJM, Ovaskainen O, Pulkkinen P, Roslin T (2010) Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology* **91,** 2660-2672.

Tariq M, Wright D, Rossiter J, Staley J (2012) Aphids in a changing world: testing the plant stress, plant vigour and pulsed stress hypotheses. *Agr Forest Entomol* **14,** 177-185.

Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annu Rev Entomol* **36,** 65-89.

Thompson JN (1983) Selection pressures on phytophagous insects feeding on small host plants. *Oikos* **40,** 438.

Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol Exp Appl* **47,** 3-14.

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

Underwood N, Rausher MD (2000) The effects of host-plant genotype on herbivore population dynamics. *Ecology* **81,** 1565-1576.

Utsumi S, Ando Y, Craig Timothy P, Ohgushi T (2011) Plant genotypic diversity increases population size of a herbivorous insect. *P Roy Soc B-Biol Sci* **278,** 3108-3115.

Venables WN, Ripley BD (2013) Modern applied statistics with S-PLUS. Springer Science & Business Media.

Verdugo J, Sauge M, Lacroze J, Francis F, Ramirez C (2015) Drought-stress and plant resistance affect herbivore performance and proteome: the case of the green peach aphid *Myzus persicae* (Hemiptera: Aphididae). *Physiol Entomol* **40,** 265-276.

Villalpando SN, Williams RS, Norby RJ (2009) Elevated air temperature alters an old-field insect community in a multifactor climate change experiment. *Glob Change Biol* **15,** 930-942.

Walter J, Hein R, Auge H, Beierkuhnlein C, Loffler S, Reifenrath K, Schadler M, Weber M, Jentsch A (2012) How do extreme drought and plant community composition affect host plant metabolites and herbivore performance? *Arthropod-Plant Inte* **6,** 15-25.

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

White TC (1974) A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* **16,** 279-301.

White TC (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* **63,** 90-105.

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.

Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* **18,** 185-197.

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

Yano S, Wakabayashi M, Takabayashi J, Takafuji A (1998) Factors determining the host plant range of the phytophagous mite, *Tetranychus urticae* (Acari: Tetranychidae): a method for quantifying host plant acceptance. *Exp Appl Acarol* **22,** 595-601.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* **1,** 3-14.

Figures

Legends

Fig 1 Quantification of drought on *Rorippa indica*. **(a)** phenotypes after water treatment in a common garden (2 hours after daily water application). (**b**) Box plot of leaf number (n=8, GLM, Poisson). (**c**) Ratio of length and width of mature leaves (n=8). (**d**) Fresh weight of shoot (n=8). (**e**) Dry weight of shoot (n=8). (**f**) Shoot water content (n=8). (**g**) Dry mass of root (n=8). (**h**) Root: shoot ratio (g g^{-1}, dry mass) (n=8). (**i**) Soil volumetric water content (θ_v) (n=8). Dots indicate individual observations. Values indicate mean ± SE. Different letters indicate significant differences between means (ANOVA, Tukey HSD).

Fig 2 Influences of water status (of *Rorippa indica*), population, and season on *Pieris rapae*. (a) Ovipositional preferences. (b) Total caterpillars at the end of field experiment, (c) Survival of *P. rapae* on *R. indica*. Count data were offset by biomass of *R. indica*. Due to higher values of egg, caterpillar, and herbivore count, data were plotted at the log scale. Transparent points indicate individual observations; opaque points and error bars indicate mean ± 95% CI.

Fig 3 Relative growth rates of lepidopteran larvae feeding on *Rorippa indica*. (a) *Pieris rapae* (Taiwan) on *R. indica* (Taiwan) (n=30). (b) *P. rapae* (Japan) on *R. indica* (Japan) (n=35). (c) *P. rapae*

(North America) on *R. indica* from both location (Taiwan and Japan) (n=40). (d) *Helicoverpa zea* (North America) on *R. indica* from both location (Taiwan and Japan) (n=40). (e) *Trichoplusia ni* (North America) on *R. indica* from both location (Taiwan and Japan) (n=40). Values represent means ± SE. Different letters indicate significant differences between means (ANOVA, Tukey HSD). (f) *Spodoptera frugiperda* (North America) on *R. indica* from both location (Taiwan and Japan) (n=40). 1 = dead, 0 = lived. Bar indicated the mean and boxes represent 95% CI (GLM, binomial).

Fig 4 Abundance of herbivore and natural enemy and its associations with water status of *Rorippa indica* and survival of *Pieris rapae*. (a) Abundance of herbivore in Taiwan. (b-d) Association between herbivore abundance and survival of *Pieris rapae* in Taiwan during early, middle, and late season. (e) Abundance of natural enemy in Taiwan. (f-h) Association between natural enemy abundance and survival of *Pieris rapae* in Taiwan during early, middle, and late season. (a) Abundance of herbivore in Japan. (b-d) Association between herbivore abundance and survival of *Pieris rapae* in Japan during early, middle, and late season. (e) Abundance of natural enemy in Japan. (f-h) Association between natural enemy abundance and survival of *Pieris rapae* in Japan during early, middle, and late season. Lines represent model predictions (solid: significant; dashed: non-significant). Grey areas indicate 95% CI. For abundance plots, values indicate estimated mean with 95% CI. All dots indicate

individual observations. Letters indicate significant difference between means (Tukey HSD). * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Fig 5 Summary of relationship between drought-stressed plant and insect herbivore. Female *Peiris rapae* showed ovipositional preferences toward non-stressed *Rorippa indica*. Drought stressed *R. indica* were associated with lower overall abundance of arthropods. The changes in species interactions may contribute to the higher survival of *P. rapae* larvae on drought stressed *R. indica*.

Fig. 1

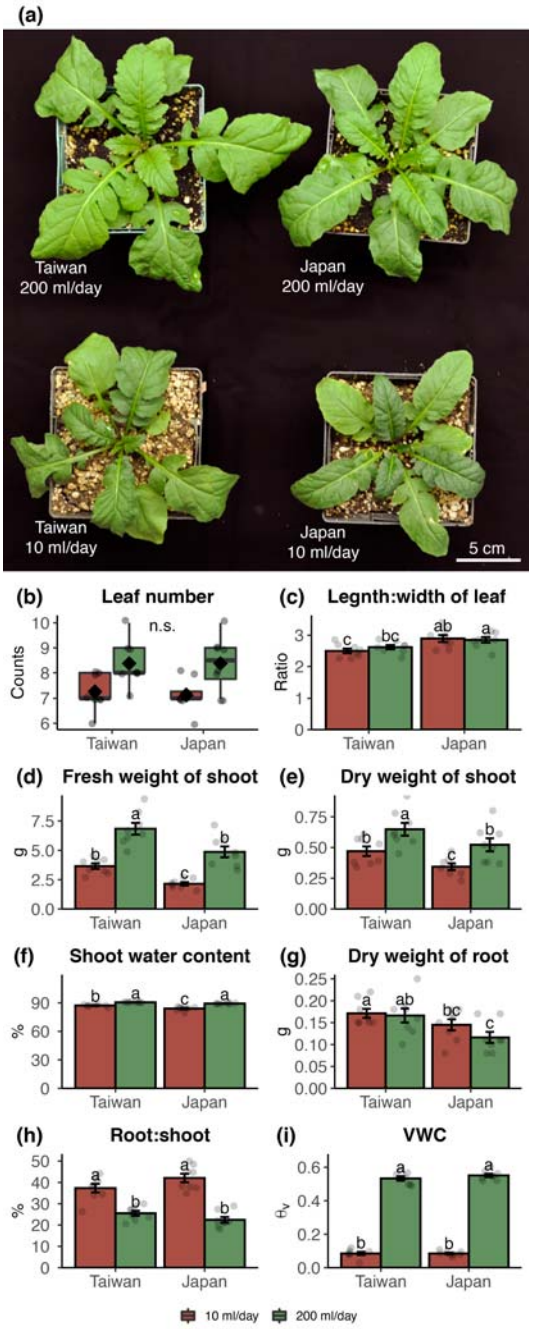

(a)
Taiwan
200 ml/day
Japan
200 ml/day
Taiwan
10 ml/day
Japan
10 ml/day
5 cm
(b) Leaf number
n.s.
Counts
Taiwan
Japan
(c) Legnth:width of leaf
Ratio
(d) Fresh weight of shoot
g
(e) Dry weight of shoot
(f) Shoot water content
%
(g) Dry weight of root
(h) Root:shoot
(i) VWC
10 ml/day
200 ml/day

Fig. 2

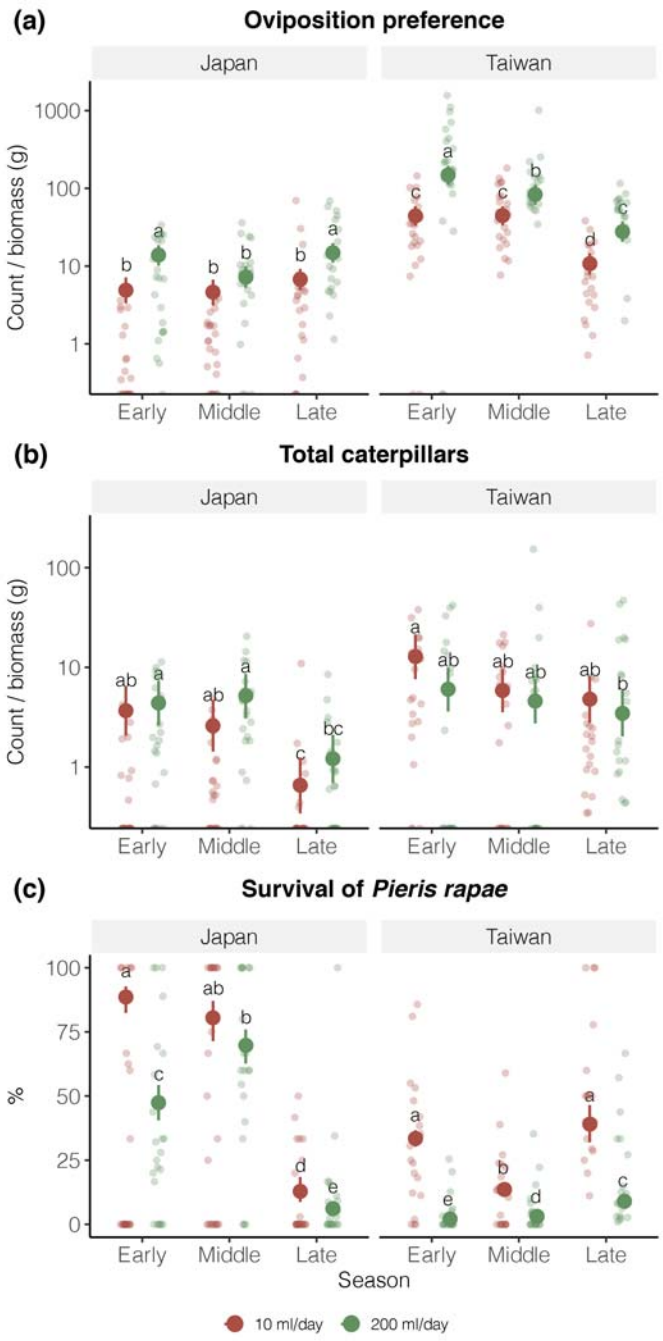

(a)
Oviposition preference
Japan
Taiwan
Count / biomass (g)
1000
100
10
1
Early
Middle
Late
(b)
Total caterpillars
Japan
Taiwan
Count / biomass (g)
100
10
1
Early
Middle
Late
(c)
Survival of Pieris rapae
Japan
Taiwan
%
100
75
50
25
0
Early
Middle
Late
Season
10 ml/day
200 ml/day

Fig. 3

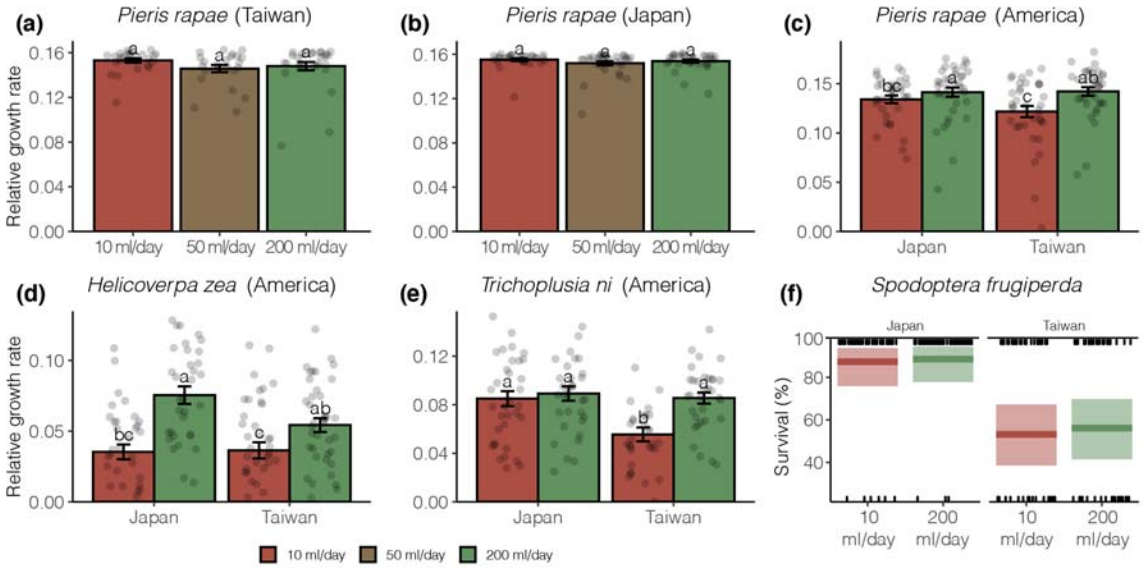

(a)
Pieris rapae (Taiwan)
Relative growth rate
10 ml/day
50 ml/day
200 ml/day
(b)
Pieris rapae (Japan)
(c)
Pieris rapae (America)
Japan
Taiwan
(d)
Helicoverpa zea (America)
(e)
Trichoplusia ni (America)
(f)
Spodoptera frugiperda
Survival (%)

Fig. 4

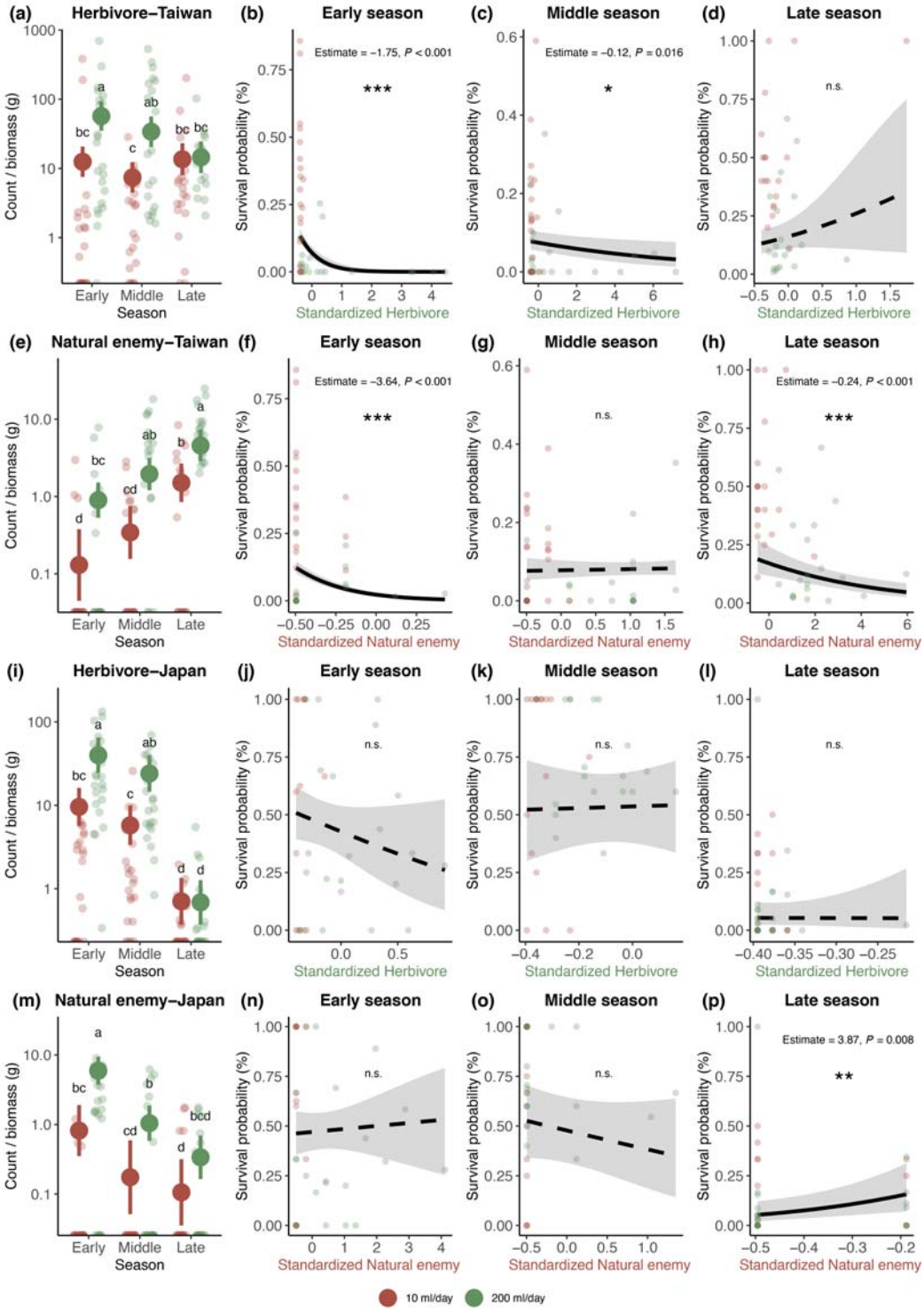
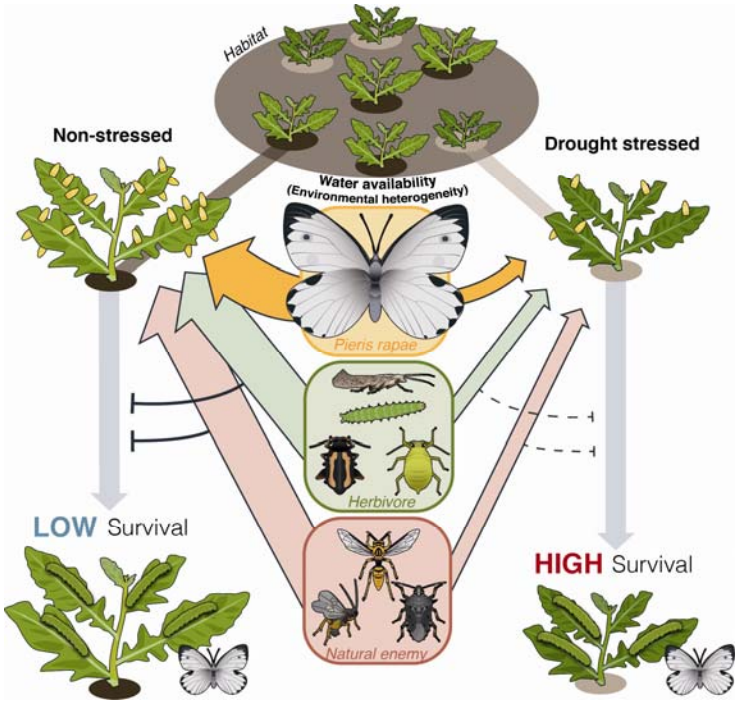

(a) Herbivore–Taiwan
(b) Early season
Estimate = −1.75, P < 0.001
(c) Middle season
Estimate = −0.12, P = 0.016
(d) Late season
(e) Natural enemy–Taiwan
(f) Early season
Estimate = −3.64, P < 0.001
(g) Middle season
(h) Late season
Estimate = −0.24, P < 0.001
(i) Herbivore–Japan
(j) Early season
(k) Middle season
(l) Late season
(m) Natural enemy–Japan
(n) Early season
(o) Middle season
(p) Late season
Estimate = 3.87, P = 0.008
Count / biomass (g)
Survival probability (%)
Early
Middle
Late
Season
Standardized Herbivore
Standardized Natural enemy
n.s.
10 ml/day
200 ml/day

Fig. 5


Habitat
Non-stressed
Drought stressed
Water availability
(Environmental heterogeneity)
Pieris rapae
Herbivore
Natural enemy
LOW Survival
HIGH Survival

Table

Table 1 Model summaries of associations between survival of *Pieris rapae* and morphospecies.

Term	Estimate	SE	Z-value	P-value
Taiwan (Early)				
Intercept	-5.215	1.236	-4.221	<0.001
Phyllotreta	-6.500	3.151	-2.063	0.04
Taiwan (Middle)				
Intercept	-3.544	0.33	-10.729	<0.001
Phyllotreta	-1.049	0.334	-3.141	0.002
Eurydema	0.988	0.374	2.643	0.008
Braconidae	-1.675	0.419	-3.994	<0.001
Tetranychidae	-0.789	0.376	-2.095	0.036
Taiwan (Late)				
Intercept	-1.283	0.171	-7.506	<0.001
Eurydema	-0.953	0.272	-3.503	<0.001
Cicadellidae	1.31	0.29	4.516	<0.001
Eupelmidae	-0.6	0.178	-3.382	0.001
Eocanthecona	-0.441	0.186	-2.371	0.018
Japan (Early)				
Intercept	-0.639	0.194	-3.298	0.001
Lauxaniidae	-0.953	0.412	-2.315	0.021
Trombidiidae	0.499	0.15	3.326	0.001
Japan (Middle)				
Intercept	0.873	0.206	4.238	<0.001
Syrphidae	-0.31	0.151	-2.048	0.041
Japan (Late)				
NA	NA	NA	NA	NA