The Effect of Drought Stress on the Development of *Pieris macdunnoughii* Feeding on its Native and Non-Native Host Plants

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Ed Program RMBL 2026

Abstract

Pieris macdunnoughii, a montane butterfly species, experiences an evolutionary trap as a result of the introduction of the invasive mustard species *Thlaspi arvense*. *T. arvense* produces similar oviposition stimulants as *Pieris's* native host plants. Caterpillars that hatch may slowly eat the plant but do not survive to pupation. A strange phenomenon has been observed that drought stress of *Thlaspi* allows *Pieris* larvae to eat the plant. In this experiment I measured the development of *P. macdunnoughii* on *T. arvense* plants experiencing different watering treatments. Analysis revealed that the effect of drought on native and non-native host plants had opposite effects. Drought alters the number of days lived for some larvae on *T. arvense*, but ultimately it does not free them from their evolutionary trap. With climate change *P. macdunnoughii*'s relationship with their native and non-native host plants may continue to change.

Introduction

Interactions between native butterfly species and their host plants are changing with warming temperatures. Climate change in the mountains of Colorado is resulting in less snowpack and drier summers (Inouye, 2022). With increasing drought stress, understanding the interactions between plants and butterflies is crucial for understanding montane ecosystems and the trophic relationships that may be affected by these specialized interactions. Drought stress can change the chemicals that mediate specialized interactions between plants and insects, often increasing herbivory (Louda & Collinge, 1992). Understanding the impact of drought on the complex relationship between butterflies and plants will inform us about the future of these species and their populations.

Pieris macdunnoughii (Lepidoptera: Pieridae) is a montane butterfly that is native to the southern Rocky Mountains (Chew & Watt, 2006). They inhabit moist environments near streams and wetlands. Similar to most lepidopteran species, their life cycle starts as an egg, from which they emerge as a larva and go through five instar phases. Within each instar, the larvae eat, grow, and then molt their exoskeletons. They typically molt five times before pupating and then emerge as adult butterflies (Scott, 1997). They feed and lay their eggs on various native mustard plants (Brassicaceae) like *Boechera stricta* and *Cardamine cordifolia*, and have evolved to detoxify glucosinolates (GLS), the defensive secondary compounds produced by plants in this family. Glucosinolate (GLS) expression can be plastic in response to environmental factors such as drought. One hypothesis is that plastic reductions in GLS or other secondary chemical expression under drought could be adaptive because it enables plants to prioritize functions critical to survival (Ben Ammar et al., 2026). Nonnative, invasive mustard plants produce similar glucosinalates to *Pieris*'s native host plants, causing an evolutionary trap (Chew, 1975.): a series of maladaptive interactions between two species resulting in an unreliable relationship (Steward & Boggs, 2020). In this case, *P. macdunnoughii* lay their eggs on *T.arvense*, but larvae that hatch from the eggs do not survive to adulthood (Chew, 1975, Nakajima et al., 2013, Steward & Boggs, 2020).

Despite this, in an experiment at the University of South Carolina that resulted in an accidental wilting of *Thlaspi* due to water and heat stress*, Pieris macdunnoughii* larvae placed on re-watered plants successfully fed and developed to maturity (C. Boggs, Personal

Communication). It is possible that environmental stress may decrease the expression of or change the composition of defense chemicals that previously prevented *P. macdunnoughii* from successfully eating the plant (Steward & Boggs, 2020); however, how *T. arvense* glucosinolate expression responds to drought stress, and the consequences of this for *Pieris* development, are still unknown. Similarly, *B. stricta* plants experiencing experimentally elevated drought stress are more susceptible to herbivory than those experiencing ambient rainfall (Carley et al. 2025), although the underlying chemical responses to drought have not been characterized.

In this study, I examined how drought stress affects the development of *P.macdunnoughii* on its invasive host plant *T. arvense*, and whether changes in response to drought differ in native and non-native host plants. I conducted a lab and field experiment that manipulated drought stress via water withholding and supplemental watering, respectively. Over the course of the experiments, I tracked caterpillar development daily until pupation or death. I hypothesized that *Pieris* caterpillars will live longer on drought stressed *T. arvense* and *B. stricta*.

Methods

Rearing Pieris

We collected 27 female *P. macdunnoughii* between 06/19/2026 and 07/13/2026 from their habitat at a site across the East River from the billy barr Community Center in Gothic. We kept them in cages with the native larval host plant *B. stricta* to allow egg laying. Once *Pieris* laid their eggs, eggs were removed from the stem with a paintbrush and put in a petri dish. The first round of eggs was mostly unsuccessful due to the disturbance of moving them. I then changed my approach so stem sections containing eggs were removed from the cage and put in petri dishes until they hatched (approximately 5-7 days). Upon hatching, caterpillars were assessed to determine whether they had begun feeding on the host plant in the petri dish (indicated by their body color darkening after feeding). Caterpillars that had already consumed *B. stricta* in the petri were assigned to *B. stricta* potted plants. Caterpillars that were still pale (had not eaten) were placed on *T. arvense.* Caterpillars from all the females were randomized across plants in all treatment groups (**Table 1**).

Table 1. Table.Distribution of larvae from female *P. macdunnoughii* across treatment groups.

Butterfly Family ID	**Control *B. stricta***	**Drought *B. stricta***	**Control *T. arvense***	**Drought *T, arvense***
1	0	0	1	2
2	0	0	3	2
5	0	0	15	10
8	2	3	2	6
10	4	7	0	0
22	10	9	0	5
23	1	0	0	0
27	2	4	0	0

Potted Plant Information

The *Boechera* seeds were sourced from three different locations, Brush Creek Trail (BCT), Gothic Townsite (GOT), and Snodgrass Trailhead (SNOD). The *Thlaspi* were from GOT and BCT. All of the plants came from seed collected in August 2025 and grown in the lab beginning in May 2026. Seeds were planted into potting soil (volume per volume: 25% Berger BM2, 25% Berger BM6, 50% Lambert AP LM-3) in cone-tainer pots (Stuewe & Sons, Tangent, OR, USA) and thinned to a single seeding per pot after germination. Pots were watered to saturation every other day and fertilized monthly from the time of planting until the beginning of the experiment.

Lab Experiment

The lab experiment consisted of a drought stress manipulation of *T. arvense* and *B.stricta*. There were four experimental treatment groups: 16 control *B. stricta* plants, 23 drought *B. stricta* plants, 21 control *T. arvense* plants, and 25 drought *T. arvense* plants. These numbers were determined based on how many plants germinated as well as the plants that survived unintentional browsing by mice. The control groups for both species were watered every other day to saturation. The drought treatment groups for both species were dried down and did not receive water, beginning ~1 week before the first round of caterpillars emerged (06/21/2026). Plants experienced a longer drought period for caterpillars that emerged later. Many well watered

plants were turned into drought treatment plants on 07/16/2026 after initial drought plants died. I withheld watering for plants in the drought treatment until plants wilted; however, if all leaves were inedible (wilted or dead), I reinstated watering them to saturation once to ensure there were leaves available for the caterpillars to eat.

To test the effects of water withholding on plant physiological response to drought, I measured stomatal conductance with a porometer (SC-1 Leaf Porometer), indicating stomatal closure in response to drought. Measurements were taken once just before the larvae were put onto the plant, and again a few days later, before all the leaves were eaten. At the time of larval application to each plant, I recorded plant leaf number, and developmental stage (rosette vs. bolting vs. flowering vs. fruiting) as potential covariates influencing larval performance.

Field Experiment

I conducted a field experiment to assess the effects of water availability on the suitability of *T. arvense* as a host plant for *P. macdunnoughii*. I used wild-recruited individuals of *T. arvense* around the Kettle Ponds (**Fig. 1**) to conduct a supplemental watering treatment. I manipulated water availability using supplemental water in the field because, at the outset of the experiment, there was no rain and so rainfall reduction was not possible. The Kettle Pond was completely dried up and the *T. arvense* surrounding the pond varied in developmental stages. I conducted my experiment with plants that were beginning to flower. There were 6 control plots and 6 supplemental watering plots with 1-3 focal plants in each plot; I spread out 3 plots in each treatment on each side of the pond to control for aspect (**Fig. 2**). Control plants were not watered, and experienced ambient environmental conditions. In the supplemental watering group, 6 plots of 1-3 plants received one watering can (1.5 gal) of water every other day starting two weeks before placing larvae on the plant.I applied one caterpillar to each focal *T. arvense* individual in

each plot, and contained it on the host plant in a mesh bag. I applied the supplemental watering treatment at the base of the plant making sure not to disturb the caterpillar. As in the lab experiment, I recorded the head capsule size of the instars, time between instars, and noted herbivory throughout the 2-week life cycle of the caterpillar. I monitored how many made it to pupation and the time to death date of each larva.

Fig 1. The Kettle Pond, located along the Kettle pond trail in Gothic, CO. Located in the Rocky Mountains, southeast of Gothic Mountain.

Fig 2. Six treatment (watered) and 6 control plots of 1-2 *T. arvense* seedlings along the edge of the dried up Kettle Pond.

Measured Variables

In my analyses, the independent variable was drought: we controlled for the amount of water given to the plants. The drought plants received a dry down, and we stopped providing water to them a week before the first round of caterpillars were placed on the plant. The dependent variables I measured regarding caterpillar performance were larval days lived and survival to the end of the experiment. To assess the efficacy of my drought treatment on the host plants, I measured stomatal conductance. To account for potential effects of plant development (unrelated to drought stress) on caterpillar performance, I counted the number of leaves and recorded the plant stage (vegetative, bolting, flowering, or fruiting) when larvae were put on the plants. Finally, to understand the chemical changes occurring in the drought and watered plants, I collected leaf samples from all of the plants, stored the tissue in a 70% methanol solution, and

shipped them to the University of Chicago for analysis of glucosinolate profile and concentration using high-performance liquid chromatography (HPLC).

Data Analysis

I ran one and two-way ANOVA to determine how the response variables days lived and survival responded to my experimental treatments. Because survival outcomes were binomial variables, I tested effects using a generalized linear model. The independent variables were treatment (drought vs. watered), species (*T. arvense* or *B. stricta*), and their interaction. I also analyzed the effect of plant source on days lived for each species separately, and developmental stage (vegetative vs. reproductive) in *T. arvense* only. I used post-hoc tests to assess pairwise significant differences among treatment categories with more than two levels (main effect of source on days lived; interaction of treatment x species interaction on days lived). I determined if my drought treatment was successful by running one way ANOVA models with stomatal conductance round one and two and treatment for both species (*T. arvense* and *B. stricta*).

Results

Physiological effects of laboratory drought treatment

The laboratory drought experiment altered plant physiology for both host plant species, but this effect did not manifest immediately. At the earlier time point (seven days into the drought experiment), average stomatal conductance was slightly lower in plants in the drought treatment for both species (**Fig. 3, a, c)**, but this was not significant for either *T. arvense* ($F_{1,44}$=0.06, P = 0.4417) or *B. stricta* ($F_{1,17}$=0.51 , P = 0.4859). After a longer period of water withholding (<<add number of days after start of treatment, similar to previous sentence>>), stomatal conductance was significantly lower in plants in the drought treatment than plants in the control treatment (**Fig. 3, b, d**) for both *T. arvense* ($F_{1,44}$=10.11, P = 0.003) and *B. stricta* ($F_{1,25}$=4.16, P = 0.04904).

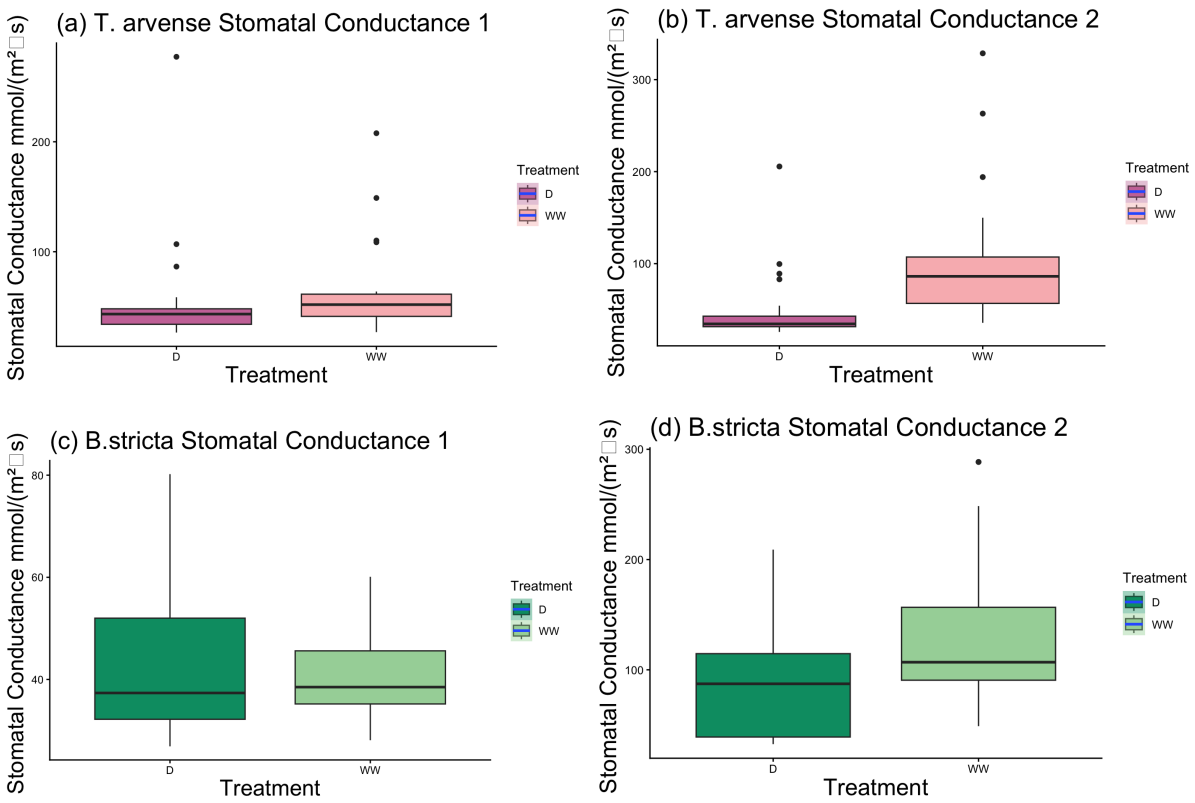


Fig 3. (a) Effect of drought treatment on stomatal conductance in *T. arvense* (a, b) and *B. stricta* (c, d) during the laboratory drought experiment at two time points.

Effect of Stomatal Conductance on Caterpillar Performance

Stomatal conductance taken in both the first round and second round did not have a significant effect on survival or days lived in either species.

Effect of Drought on Caterpillar Performance

The average number of days lived on *B. stricta* was 9.55. The overall average number of days lived on *T. arvense* was 6.19 (**Fig. 4**). Neither treatment nor species had a main effect on the number of days lived, but their interaction was significant (**Fig. 4**; $F_{3, 51} = 3.843$, $P = 0.03$). Post-hoc tests (Tukey HSD) determined that the mean days lived of larvae on well-watered *B. stricta* and well-watered *T. arvense* significantly differed ($P = 0.008$); larvae on well watered *B. stricta* lived the longest, and well watered *T. arvense* lived the fewest days. Days lived on drought-stressed plants did not differ across host species ($P > 0.05$).

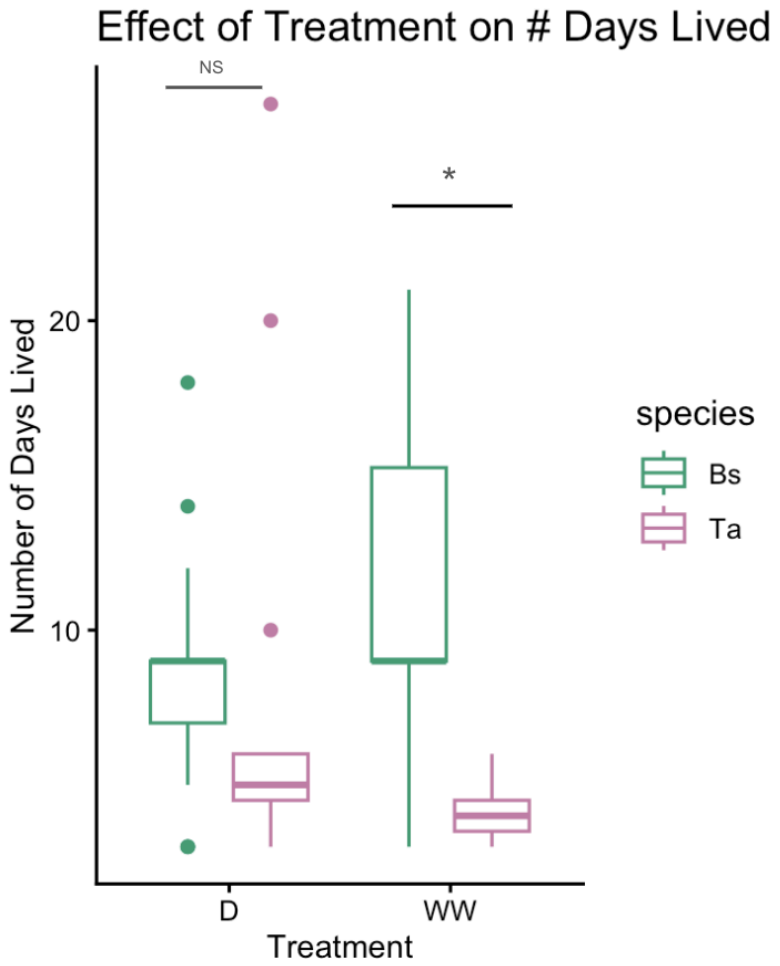


Fig 4. Effect of the laboratory drought treatment on the number of days lived for *P. macdunnoughii* feeding on *B. stricta* (green) and *T. arvense* (pink).

Each larvae was assigned a 1 (survived to pupation) or a 0 (died before pupation) in order to calculate survival. Zero *T. arvense* larvae survived to pupation. On *B. stricta*, there was marginally significant difference between survival in the well watered and drought treatment (χ^2 = 3.45, P = 0.06); larvae on well watered *B. stricta* had higher survival than larvae on the drought-stressed *B. stricta* (**Fig 5**).

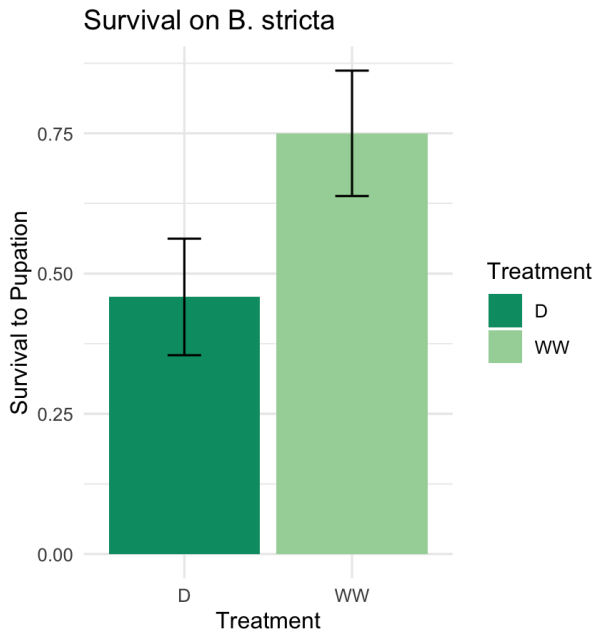


Fig 5. Effect of treatment on survival to end of the experiment for *B. stricta* in drought (dark green) and well watered (light green).

Development Rate of Larvae on *T. arvense* and *B. stricta*

Table 2. Number of larvae that lived to second instar in all treatment and control groups.

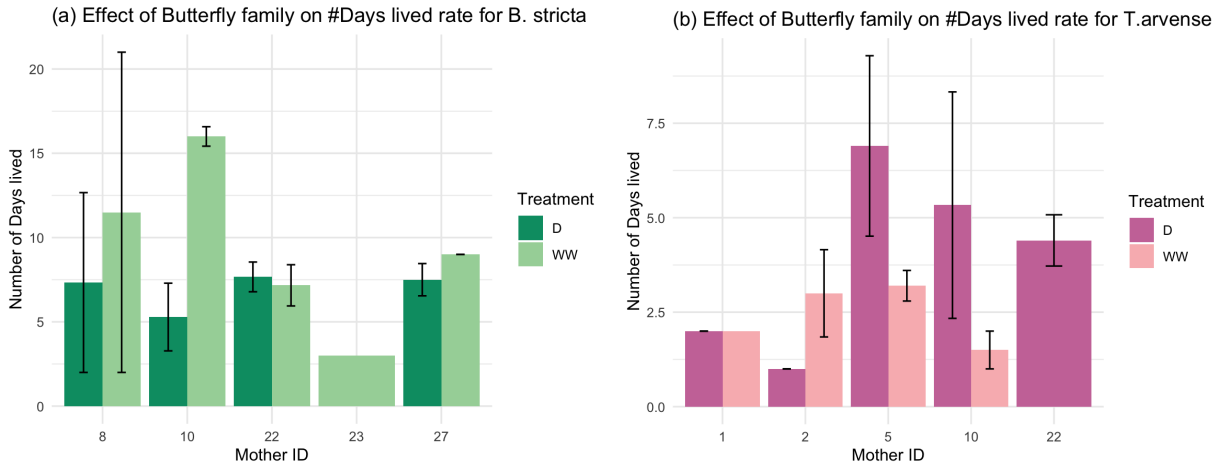
	Control *B. stricta*	Drought *B. stricta*	Control *T. arvense*	Drought *T. arvense*
# of larvae that survived to 2nd instar / total # of larvae	**11**/16	**11**/23	**0**/21	**3**/25

On *T. arvense*, no larvae survived beyond the second instar. The three larvae that survived longer than the average 6 days on *T. arvense* survived to second instar before dying. Conversely, most caterpillars on *B. stricta* at the end of my experiment had survived to the second instar (**Table 2**).

Effect of Butterfly Family on Caterpillar Performance

On *B. stricta* host plants, survival to the end of the experiment was significantly affected by butterfly family ID (F = 4.65, P = 0.009), treatment (F = 12.06, P = 0.0016), and their interaction (F = 2.98, P = 0.05). Larvae on well watered plants had a better chance of surviving, and the average survival rate differed across maternal families (**Fig 6c**). I could not test for effects of butterfly family ID on survival on *T. arvense* because zero larvae survived to pupation.

On *B. stricta* and *T. arvense*, the number of days lived were not significantly affected by butterfly family ID (fig 6a,b). In models excluding maternal lines that were not distributed across both treatments (line 23 on *B. stricta* and line 22 on *T. arvense*), there was no significant interaction between maternal line and drought treatment on days lived for larvae feeding on either host species.



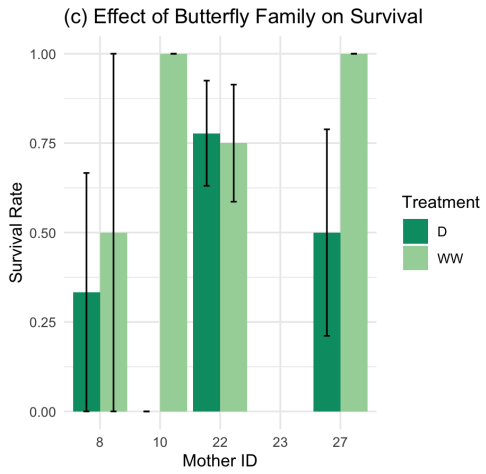


Fig 6. Effect of maternal ID on number of days lived in *B. stricta* (a), drought (dark green) and well watered (light green). Effect of mother ID on number of days lived in *T. arvense* (b) drought (dark pink) and well watered (light pink). Effect of mother ID on survival in *B. stricta* (c) drought (dark green) and well watered (light green).

Effect of Plant Traits on Caterpillar Performance

I analyzed the effects of source population on caterpillar performance separately for the two host species, because the wild populations from which seeds were collected were only partially overlapping.

For *B. stricta*, the source population did not affect the number of days lived. However, the effect of drought treatment was significant ($F = 12.33$, $P = 0.001$), as was the interaction between source and treatment ($F = 4.39$, $P = 0.02$). Larvae on BCT well watered lived longer potentially meaning a slower development.

After running a post- hoc test I determined that larvae feeding on well-watered plants from the BCT population lived significantly longer than those feeding on any other source population or treatment (**Fig. 7a**; pairwise contrasts: BCT drought,$P = 0.02$; GOT drought, $P = 0.004$; SNOD drought, $P = 0.01$; GOT well watered, $P = 0.02$; SNOD well watered, $P = 0.03$). The effect of source on survival is not significant, both with and without treatment.

Plant source did not significantly affect the number of days larvae lived on *T. arvense*, analyzed with and without treatment (**Fig 7b**). I could not quantitatively assess differences in survival on *T. arvense* across treatments because there were no surviving individuals on *T. arvense*.

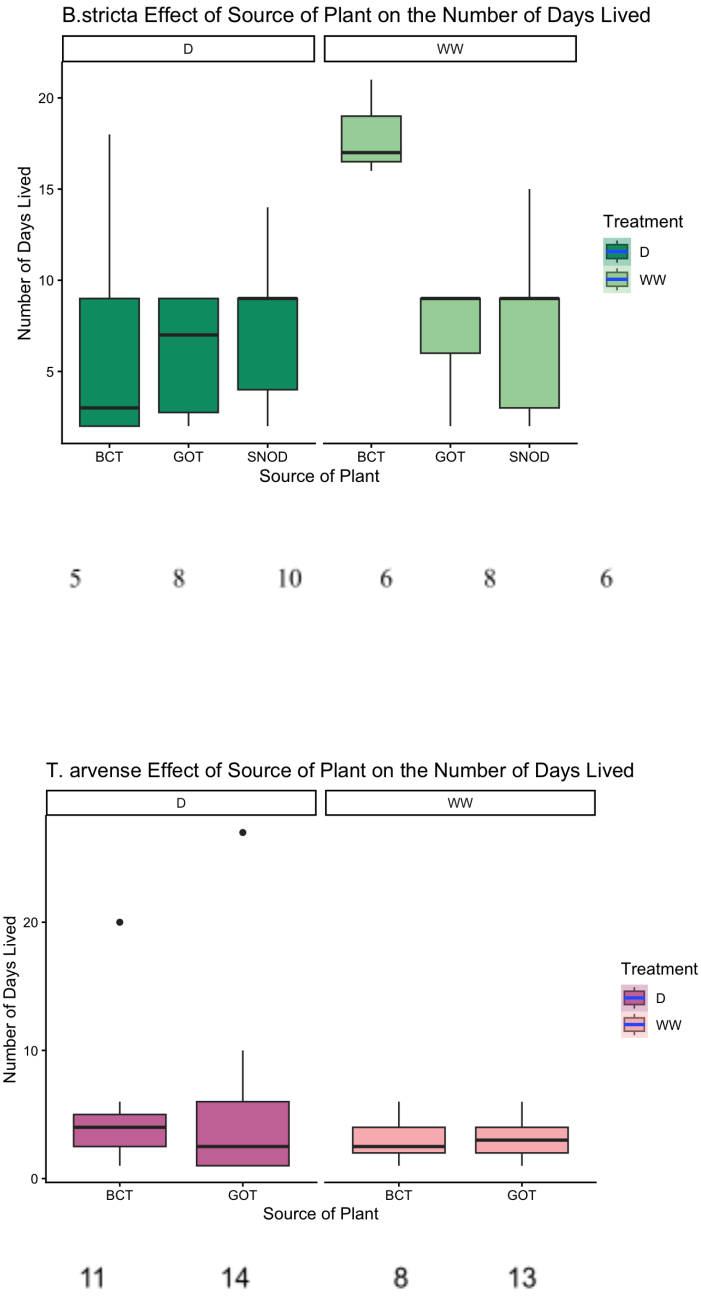


Fig 7. Effect of the source of the plant on the number of days lived in *B. stricta* (a) and *T. arvense* (b), drought and a well watered. Sample size of each source listed underneath.

For *T. arvense*, the phenological stage of the plant when the larva was put on it did not have a significant effect on the number of days lived. I was not able to analyze this in *B. stricta* because the plants were all rosettes.

The number of leaves had a significant effect on the number of days that larvae lived. The species term had a significant effect (**Fig 8 a**; F = 6.48, P = .01). Larvae lived longer on *T. arvense* with more leaves. Conversely, larvae lived fewer days on *B. stricta* with more leaves (**Fig 8a**). The interaction between the number of leaves and species was marginally significant (F = 3.24, P = 0.07). Whether larvae survived to the end of the experiment on *B. stricta* was not affected by the number of leaves.

Analyzed by species, the treatments did not significantly modify the effect of leaf number on days the larvae lived on *B. stricta* or *T. arvense* (**Fig. 8b-c**).

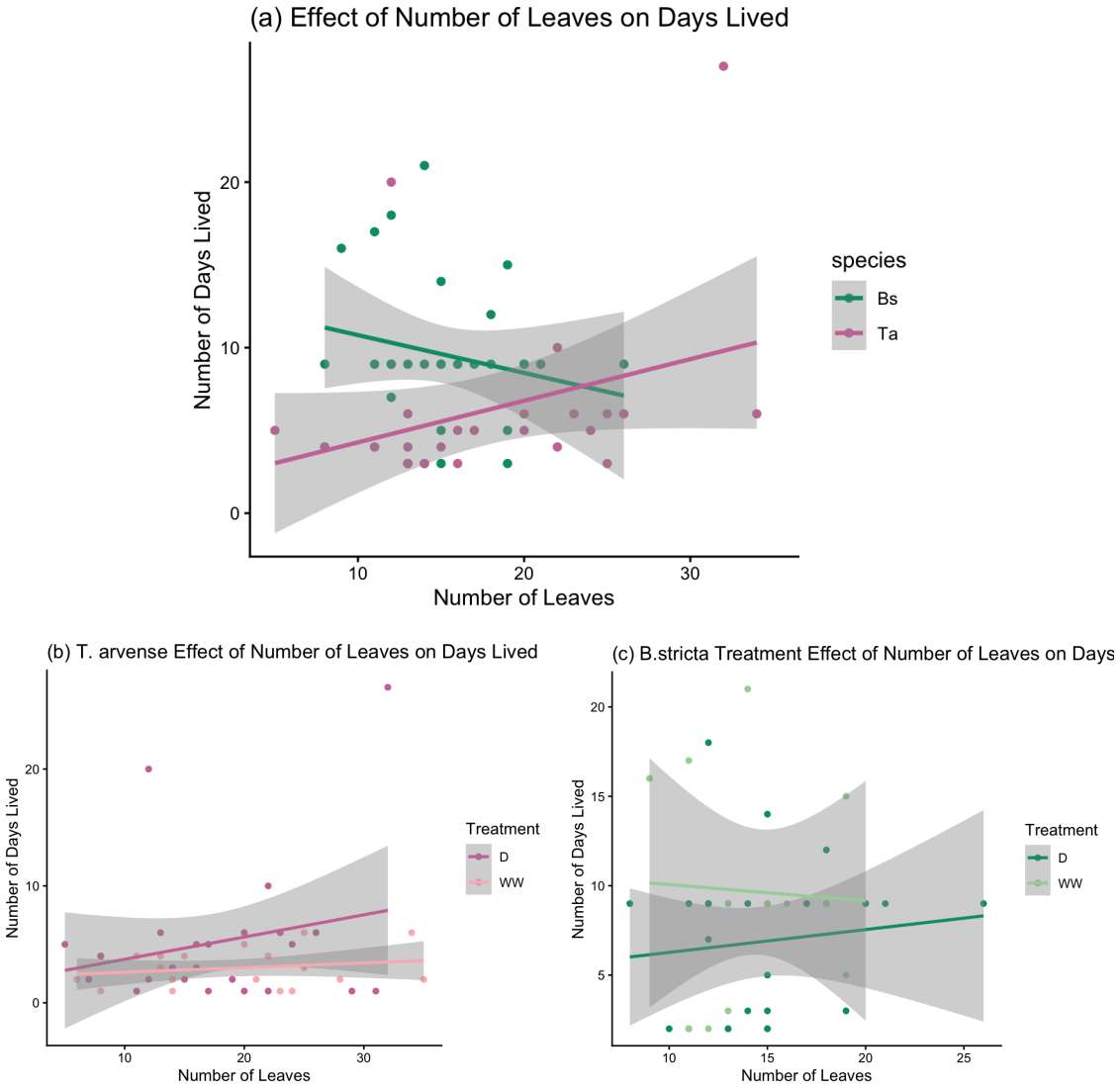


Fig 8. (a) Effect of leaf number on the number of days lived on *B. stricta*,(green) and *T. arvense* (pink). (b-c) Effect of treatment and leaf number on the number of days lived on *T. arvense* and *B. stricta.*

Field Experiment

My field experiment was ineffective because of grazing cow disturbances. I was able to collect 3 days of data on eight caterpillars before many *T. arvense* plots were trampled. Larvae on both the watered and control plants did not eat any of the plant. All caterpillars died after four days due to starvation from not eating and/or trampling.

Discussion

Field Experiment

None of the larvae consumed any of the *T. arvense* at the Kettle Pond. It is possible that none of the plants in the field experienced drought stress to the extent that they did in the lab. I was not able to record porometer data in the field. In the future this could be a good way to ensure the drought treatment in the lab and field resemble each other.

Differing Effects of Drought on Days Lived on Native and Non-Native Host Plants

I compared *P. macdunnoughii* larval performance on both *B. stricta,* a native host, and *T. arvense,* its invasive lethal host plant. With two main response variables–survival to the end of my experiment and the number of days lived–I found that treatment and species significantly interacted to determine the number of days lived. This implies that the drought treatment in *T. arvense* impacted the palatability of the plant, allowing for some of the larvae to consume its leaves. The drought treatment had opposite effects for *B. stricta* and *T. arvense*. For *T. arvense*, some larvae on the plant were able to eat more than those on the watered *T. arvense*. It appears that drought reduced the magnitude of differences in host plant suitability between *B. stricta* and *T. arvense*. This implies that drought may have altered chemical defense expression in *T. arvense*, making the leaf tissue less immediately toxic to the larvae; this hypothesis will be tested with foliar chemical data being generated by collaborators at the University of Chicago. Conversely, in *B. stricta,* some of the drought leaves died and became inedible for the caterpillars, resulting in more caterpillars living longer on well watered *B. stricta*. This suggests that responses to drought in native and non native host plants differ.

For larvae on *T. arvense*, the drought treatment did not significantly impact days lived. However, there were 3 outliers surviving well beyond the average of 6 days on *T. arvense* (10, 20, and 27 days). While these three larvae lived longer than the rest of the larvae on *T. arvense*, I observed

that their development or progression to the next instar stage was slower than larvae on *B. stricta* (personal observation). I was not able to statistically test this due to the small number of larvae surviving beyond the first instar. These outliers most likely exist due to the plants reacting differently to drought stress. In this case slow development is not ideal compared to the fast development on *B. stricta*. Slow development here is a sign of an unhealthy caterpillar. Future glucosinolate analysis will shed light on whether the plants the outliers were on differed in chemistry from the other plants.

Survival on Native and Non-Native Host Plants as a Response to Drought

Larval survival on *T. arvense* was zero percent and on *B. stricta* larval survival to the end of the experiment was 57.5%. This shows that larvae in my experiment were able to develop on their usual host plant, and that death on *T. arvense* was not due to lab conditions, handling, or other extraneous conditions. The *B. stricta* average survival was measured as caterpillars that reached pupation by the end of my experiment on 07/28/2026, and thus may be an underestimate. Species and treatment significantly affected survival, but the interaction did not change the survival outcome. *Pieris macdunnoughii* are still not able to survive to adulthood on *T. arvense,* watered or drought stressed. In some cases drought alters their development time and lengthens their life span, but it does not completely free them from their evolutionary trap. To answer my first question, "How does drought stress affect the development of *P. macdunnoughii* on its native and non-native host plants?" *P. macdunnoughii* had a slower growth rate on drought *T. arvense* but ultimately did not survive. On *B. stricta* there is a higher success rate on well watered plants in comparison to drought plants.

Genetic variation for Host Plant Suitability

The identity of the maternal butterfly affected larval survival to pupation on *B. stricta*, implying genetic variation for development and fitness amongst the *P. macdunnoughii* females. I was not able to test this for *T. arvense,* as none of them survived to pupation.

The sources of the *B. stricta* host plants interacted significantly with drought treatment to impact the number of days the larvae lived. This implies genetic and environmental differences in the quality of the host plant as a good source for this species, depending on population source from which the seeds were collected. Different source populations could be adapted to different abiotic conditions, therefore differing their response to drought in ways that affect larval development. One possible abiotic condition that differs is the geologic make up of the different sites, resulting in different geologic properties of the soil. This may influence water availability

for the plants based on how the soil drains and how much water binds to the soil particles, as well as exposure of the plants to heavy metals and other toxins.

The number of leaves had a significant effect on the number of days lived in both species, but the direction of this effect differed between *B. stricta* and *T. arvense*. *T. arvense* had a positive linear relationship between the number of leaves and the number of days the caterpillars lived. *B. stricta* had a negative linear relationship. More leaves for *T. arvense* may correlate with the age of the plant which may affect the production of secondary metabolites. For *B. stricta* less leaves meant fewer days lived, perhaps due to effects of plant age on glucosinolate production.

In a study looking at *Hypericum perforatum* L., (Radušienė et al., 2012)found that secondary metabolites highly depend on phenological cycle. Metabolites such as chlorogenic acid, rutin, hyperoside, apigenin-7-O-glucoside, quercitrin, and quercetin changed greatly during plant development and the highest levels reached at flowering phase. In my experiment all of the *B. stricta* plants were rosettes and there was not a significant effect on caterpillar performance based on vegetative or reproductive stage of *T. arvense*. In the future having more of a range of *T. arvense* at different phenological stages may change the expression of secondary metabolites, as reflected in the study above.

Conclusions

My main conclusion was that larvae on *T. arvense* had a zero percent survival rate, regardless of treatment. While some larvae survived longer on drought *T. arvense* than on well watered, a larger sample size, more forms of drought manipulation, and examining heat stress is needed to come to a significant conclusion. Drought stress of native and non-native host plants on *P. macdunnoughii* have opposite effects on caterpillar performance. Finally, drought stress does not entirely free *P. macdunnoughii* from its evolutionary trap. The broader implications of these conclusions are that as climate change progresses, drought stress will continue to alter relationships between *P. macdunnoughii* and their host plants, potentially in different ways for native and invasive hosts. Other insect and plant relationships may also follow similar patterns that we observed in this experiment. Montane ecosystems and organisms will continue to shift and evolve with the changing climate.

Future Work

The results from the glucosinolate analysis will tell us whether glucosinolate expression is plastic in response to drought. If this is the case, then we will be able to test whether this is consistent across plant populations and species. The chemical data will also help us understand in more detail the relationship between drought and foliar palatability to *P. macdunnoughii* larvae.

A previous study looking at sinigrin concentrations found that sinigrin in *T. arvense* glucosinolate profile may contribute to plant defense and toxicity to larvae (Steward et al., 2019). Based on this, I expect to see decreased amounts of sinigrin in drought stressed *T. arvense* leaves from the glucosinolate analysis. If this is the case, it will support the hypothesis that sinigrin is the factor determining if caterpillars can survive on *T. arvense*. Sinigrin may not be the only secondary compounds determining if *P. macdunnoughii* larvae are able to eat *T. arvense*. We may find other compounds that contribute to this relationship as well as any compounds that are present in *B. stricta* and not in *T. arvense*.

The original USC accidental wilting experiment was the result of heat and drought stress. Future directions to study this phenomenon may include simulating heat stress as a potential way for *P. macdunnoughii* to escape their evolutionary trap.

Acknowledgements

I would like to thank Dr. Carol Boggs and Dr. Lauren Carley for mentoring me this summer. The Boggs Lab: Laurent Duverglas, Chloe Keck, Maddy Mengel, Jenna Rechsteiner, Maya Faltin, Kenna Bunnell for helping me catch butterflies. The Carley lab: Elsa Godtfredsen, Charlotte Wallsten, Greta Thoresen, Caroline Pollan, Dani Hanson. Genevieve Tostevin, for helping me set up my experiment and prepare the drought treatment. I would also like to thank Dr. Rosemary Smith for helping with water caching and other field logistics. Dr. Jennie Reithel for helping me find a field site and keeping me informed about the cows. Dr. Brad Taylor for lending me a water jug for my field experiment. Dr. Amanda Henderson for helping me with my ArcGIS map. RMBL Admin for lending me a water jug and other field logistics. Finally to my friends and family for constantly supporting me and keeping me sane.

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