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Short Communication

Plant water limitation and its impact on the oviposition preferences of the monarch butterfly (Lepidoptera: Nymphalidae)

Aramee C. Diethelm[1,2,*], Konnor E. Kost[1], Elizabeth G. Pringle[1,2]

[1]Department of Biology, University of Nevada, Reno, NV, USA, [2]Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV, USA *Corresponding author, mail: adiethelm@unr.edu

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Intensifying drought conditions across the western United States due to global climate change are altering plant–insect interactions. Specialist herbivores must find their host plants within a matrix of nonhosts, and thus often rely upon specific plant secondary chemistry for host location and oviposition cues. Climate-induced alterations to plant chemistry could thus affect female selection of larval food plants. Here, we investigated whether host-plant water limitation influenced oviposition preference in a threatened invertebrate: the monarch butterfly (*Danaus plexippus*). We found that females deposited more eggs on reduced-water than on well-watered narrowleaf milkweed plants (*Asclepias fascicularis*), but we could not attribute this change to any specific change in plant chemistry. Specialist herbivores, such as the monarch butterfly, which are tightly linked to specific plant cues, may experience shift in preferences under global-change conditions. Understanding oviposition preferences will be important to directing ongoing habitat restoration activities for this declining insect.

Key words: Asclepias fascicularis, drought, , milkweed, phytochemistry, plant–insect interaction

Introduction

Increased periods of drought across the Western United States may change plant–insect interactions (Cook et al. 2015). Water limitation induces plastic changes to plant chemical traits (Chaves et al. 2002), increasing concentrations of both primary and secondary metabolites (Mundim and Pringle 2018). Higher primary metabolites may attract insects and stimulate feeding behavior (Mattson and Haack 1987; but see, e.g., Huberty and Denno 2004). Secondary metabolites can be attractants or deterrents, depending on their toxicity and the herbivores' degree of specialization (Gutbrodt et al. 2011). Specialist herbivores often use particular secondary metabolites to detect their host plants (Schoonhoven et al. 2005).

Climate-induced changes in plant chemistry could thus affect female insects' choice of larval food plants, particularly among specialists. Oviposition selection relies on olfactory, visual, and physical cues (Schoonhoven et al. 2005). Olfactory cues, in particular, may change with plant chemistry (Conchou et al. 2019). Oviposition preferences then affect offspring development and survival, particularly when larvae have initially low mobility (Gripenberg et al. 2010), and can go on to affect adult traits such as wing loading and fecundity (Soule et al. 2020). Indeed, ovipositing females are expected to prefer plant traits that favor higher offspring performance (i.e., the Preference-Performance Hypothesis; Jaenike 1978), although, in actuality, females frequently choose to oviposit on plants with suboptimal larval conditions (Mayhew 2001). For example, females may select plants for oviposition that have more adult food resources, whether or not those plants improve larval performance (Gripenberg et al. 2010). Climate-induced changes in plant chemistry may thus create or widen disconnects between female preference and offspring performance.

Here we evaluated the effect of water limitation on the oviposition preferences of a threatened specialist herbivore, the western monarch butterfly (*Danaus plexippus*). A recent population decline has prompted restoration activities for the monarch's larval food plants: milkweeds in the genus *Asclepias* (Pelton et al. 2019). Milkweeds have numerous secondary metabolites, including flavonol glycosides and cardenolides, which are oviposition cues for monarchs (Haribal and Renwick 1996, Agrawal et al. 2021). Water limitation can change the concentrations of these compounds in plant tissues (Diethelm et al. 2022), suggesting that climatic stress could alter female preference via changes in secondary metabolites (McCluney et al. 2012). Here, we hypothesized that water limitation would affect monarch oviposition preferences. In particular, we predicted that females would prefer low-water plants over well-watered plants due to an upregulation of leaf flavonol glycosides under water limitation (Diethelm et al. 2022).

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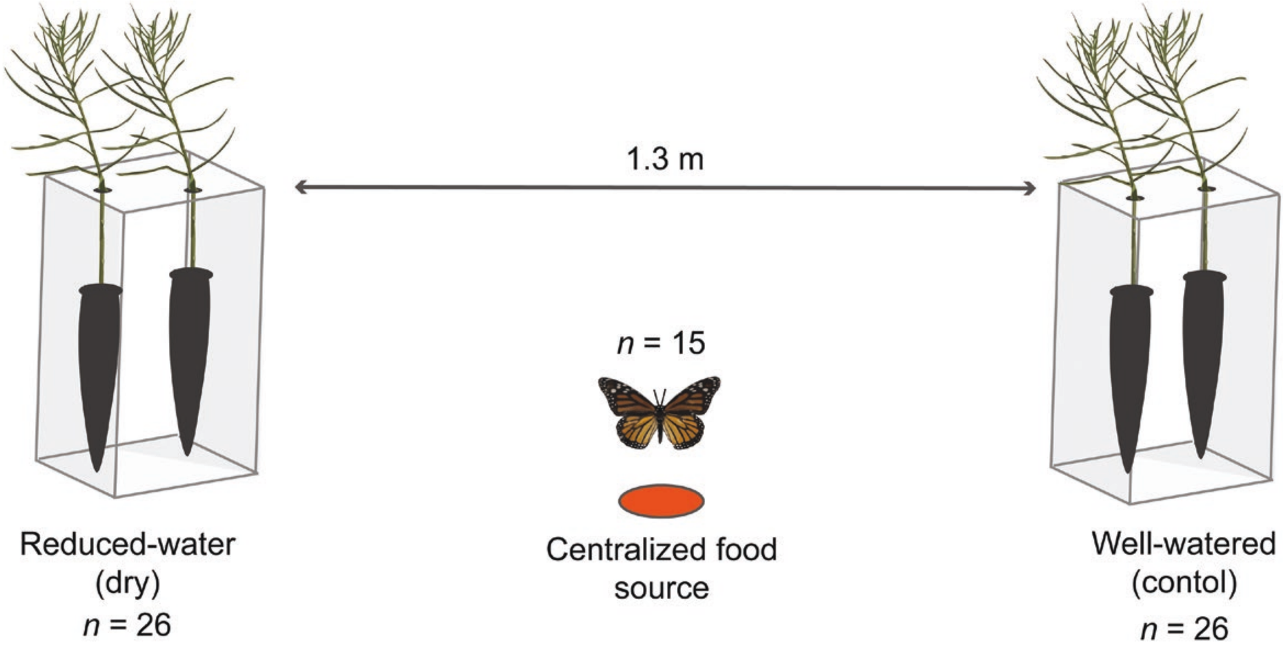

Fig. 1. Diagram of the oviposition preference trials with *Danaus plexippus* on *Asclepias fascicularis.* At the start of the trial, gravid females (*n* = 15) were placed the center of the 20 m^3 flight cage and allowed to feed ad libitum using a cotton pad soaked in a 1:1 ratio of red Gatorade:deionized. Two plants per treatment (well-watered = 70% soil field capacity or reduced-water = 30% soil field capacity) were kept in acrylic boxes (14 × 14 × 24 cm) with the top 10 cm of the plant exposed to the females. Boxes were randomly assigned to the north or south position in each trial and placed 0.65 m from the food source.

Materials and Methods

Experimental Design

To determine if plant water status affects plant selection by females, we conducted an oviposition choice experiment using *D. plexippus* and *Asclepias fascicularis* (narrowleaf milkweed), one of the most widely distributed milkweed species in the Western United States. *Asclepias fascicularis* is an important food species for the western monarch (Dilts et al. 2019).

Seeds of *A. fascicularis* were collected from Reno, NV (39.49361, −119.85459) in 2018 and 2019 and germinated in May 2020. Plants were grown in 164 ml treepots with 50% peat moss: 34% vermiculite: 16% perlite. To manipulate water availability, soil saturation was maintained at 70% field capacity in control (well-watered) plants and at 30% in reduced-water plants for 1–3 wk using a gravitational dry-down method following Diethelm et al. (2022). The variation in dry-down time is due to initially high dieback in the reduced-water group, which led us to add more plants to that treatment group, with the treatment maintained for ≥1 wk. The 70% control level reflects what plants typically experience at agricultural field edges, whereas 30% represents a dry treatment that does not induce wilting (Diethelm et al. 2022). We avoided wilting because females may discriminate against wilted plants, independent of plant chemistry (Aikins et al. 2023).

To allow female monarchs to select a mate, each female was initially kept in a mesh caging (40 cm × 40 cm × 61 cm) with 3 male butterflies and 2 other females. Male–female pairs that were observed mating were moved, still linked, to separate cages, and mated females were isolated the following day. Once males were observed to mate twice, they were removed from the study. Each oviposition preference trial presented a single, mated female butterfly (*n* = 15) with a choice between one control and one reduced-water plant box within a flight cage. In an attempt to isolate the effects of plant chemistry and account for potential oviposition bias toward larger plants (Cohen and Brower 1982), we selected experimental plants of similar size and presented only the top 10 cm of the stem to the butterflies (Fig. 1). Each oviposition trial occurred in a 20 m^3 flight cage for 3 h between 9:30 AM and 6:30 PM. To allow females to eat ad libitum, a cotton pad of 1:1 ratio of red Gatorade:deionized water was placed at the middle of the flight cage. After each trial, the exposed biomass of milkweeds per treatment was clipped, the number of monarch eggs per treatment was recorded before eggs were removed, and the plant section was weighed. All but two of the females were used twice, with trials > 6 d apart. At the end of each 3 h trial, the exposed sections of the plants were transferred to a −80 °C freezer for storage until chemical analysis. For additional methods see Supplementary Appendix S1: Methods S1.

To investigate how our water treatments affected plant secondary metabolites, we performed a non-targeted analysis of UV-absorbent metabolites following Diethelm et al. (2022). We estimated the concentration of each metabolite using ultrahigh-performance liquid chromatography (Waters Corporation, Milford, MA). To calculate the concentrations of plant secondary compounds in digitoxin equivalents, we used a digitoxin internal standard (Sigma Chemical Company, St. Louis, MO) and corrected peak areas by sample dry mass and the 0.15 mg/ml concentration of the digitoxin standard. We also calculated metabolite diversity, using the exponential term of the Shannon index (q = 1; Chao et al. 2014). For additional methods see Supplementary Appendix S1: Methods S2.

Statistical Analysis

For female choice response variables, we used generalized linear mixed models with Gaussian or negative binomial distributions from the *glmmTMB* R package (Brooks et al. 2017) in R version 3.6.1 (R Core Team 2021). For secondary chemistry response variables, we modeled the data with linear regressions. We report beta coefficients (β) with standard errors as effect sizes (Bischl et al. 2017). Marginal

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Table 1. Model selection results for female oviposition preferences from the global GLMM. Parameters in the model (*K*), degrees of freedom error (DF), Aikaike's information criterion for small sample sizes (AIC$_c$), the difference in AIC (dAIC), and variance of the random intercept terms are shown. All models included a random effect of the trial number nested within monarch identity. Only models with dAIC$_c$ < 2.5 are shown. Marginal (fixed effects only; R^2_M) and conditional (fixed + random effects; R^2_C) R^2 values are also shown

						Random effect		
Model	Fixed effects	*K*	DF (*N*)	AIC$_c$	dAIC	Female ID/trial code	R^2_M	R^2_C
Number of eggs ~	Water availability	5	47	263.3	0.0	0.045	0.05	0.50
	Water + flavonoid concn	6	46	265.2	1.9	0.046	0.07	0.52
	None	4	48	265.3	2.0	0.042	0.00	0.41

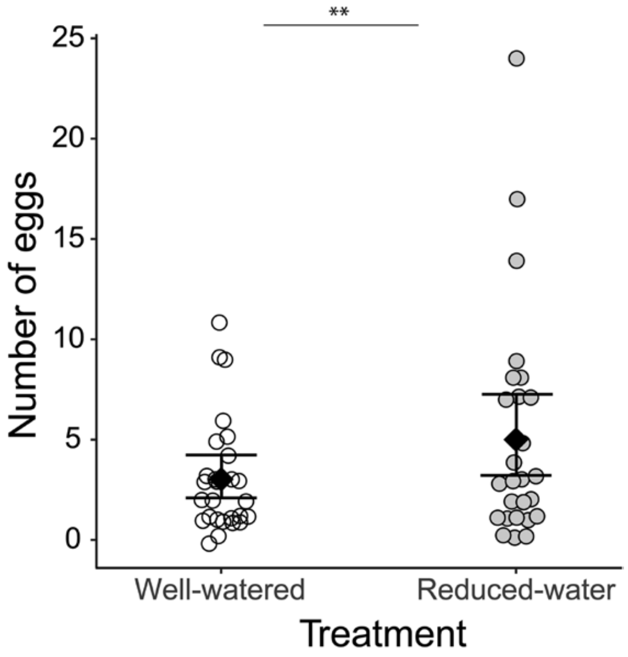

Fig. 2. Eggs laid on *Asclepias fascicularis* by *Danaus plexippus* (n = 15) on control (70% soil field capacity) and reduced-water (30% soil field capacity) treatment plants during 3 h preference trials. Points represent individual trials, black diamonds represent means, and bars represent SE. Asterisks ** denote $P < 0.03$ from the generalized linear mixed model.

and conditional R^2 values were calculated in the *MuMIn* R package (Barton 2009).

To establish the predictors of the number of monarch eggs, we started with a saturated model treating water and the concentration of flavonol glycosides as fixed effects and the number of leaves, female age, time since female mated, and female identity as covariates (Table 1). We included both flavonol glycosides and water treatment as fixed effects in the model because preliminary tests suggested that the water treatment did not affect chemistry (t = −0.5, df = 50, P = 0.6). To account for repeated trials of a given female, we included female identity as a random intercept effect. To control for nonindependence between plants within a single trial, the trial number was also as a random intercept effect, nested within female identity. We then used backward selection (Zuur et al. 2009) in *MuMIn*, and the best-fit model was selected based on the Akaike information criterion (AIC$_c$). Marginal predictors were evaluated using log-likelihood ratio tests in *lmtest* (Zeileis and Hothorn 2002). To evaluate the predictors of plant secondary metabolites, including the total concentration of UV-absorbent metabolites, the concentration of flavonol glycosides, and the exponential of Shannon's entropy index (q = 1) for metabolite diversity, we modeled water as a fixed effect and the duration of dry-down as a covariate. To measure the strength of the relationship between total concentration and the concentration of flavonol glycosides, we calculated a Pearson's correlation value.

Results

Gravid monarchs preferred reduced-water plants, leaving an average of ~40% more eggs on dry plants than on control plants (β_{water} = 0.46 ± 0.21, z = 2.19, P < 0.03; Fig. 2). Based on the corrected Akaike Information Criterion for k-means and likelihood ratio tests, none of our selected covariates improved the model fit for oviposition preferences (Table 1). Females typically explored both plants in each trial and displayed postalighting discriminatory behavior (Supplementary Appendix S1: Video S1).

We isolated 32 unique UV-absorbent metabolites in the plants (Supplementary Appendix S2). We did not detect any cardiac glycosides (cardenolides) in our experimental plants. Two flavonol glycosides—quercetin-glucoside-rhamnoside and isorhamnetin-glucoside-rhamnoside—were present in all plant samples. The value of total concentration was strongly driven by the concentration of flavonols (r = 0.94). The presence of benzoylated pregnane glycosides was highly variable (ranging from 2 to 8 compounds per plant). Neither the total concentration of UV-absorbent secondary metabolites, nor flavonol glycoside content, nor the diversity of metabolites differed between water treatments (β_{water} = −1.18 ± 2.18, z = −0.54, P = 0.6; β_{water} = −0.95 ± 1.83, z = −0.52, P = 0.6, β_{water} = 0.06 ± 0.17, z = 0.34, P = 0.7).

Discussion

Here we show that gravid monarch butterflies preferred to deposit their eggs on reduced-water plants. Counter to our prediction, however, our reduced-water treatment did not induce higher concentrations of flavonol glycosides or alter chemical diversity. Given that we also controlled for plant size and wilting, it is not clear what signal caused observed preference between plants of different water stress. However, our observation that females explored plants from both treatments suggests that oviposition preferences were based on plant quality (Baur et al. 1998).

Although we did not uncover any probable causal mechanism for female preference of low-water plants, our results suggest that the females were able to detect differences between the water treatment groups. Our results warrant further investigation into the mechanism behind monarch oviposition preferences for low-water plants. For example, *Asclepias syriaca* can increase foliar nitrogen levels under water-limited conditions (Couture et al. 2015, but see Hahn and Maron 2018), which could alter female preferences based

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on nutritional quality (C/N levels) of the plant tissue. Similarly, water limitation could induce a change in the volatile organic compound omitted by the plant or perhaps change leaf surface characteristics such as foliar water content (Mundim and Pringle 2018, Conchou et al. 2019). Understanding the traits used by females in larval-host plant selection will be important to targeted conservation efforts. To verify whether the preferences observed in this experiment remain consistent in field conditions, additional oviposition trials should be conducted in outdoor common gardens where females experience a more realistic suite of abiotic and biotic conditions. Because *A. fascicularis* is being used in habitat restoration activities for monarchs across the aridifying West, successful conservation will require consideration of female oviposition preferences and the effect that those preferences may have on the fitness of the offspring generation.

Female preference for low-water plants could have a positive impact on larval performance if low-water plants are less defended or more nutritious. Monarch larvae tend to gain more weight on water-limited than on well-watered milkweed in another species, the common milkweed *A. syriaca* (Couture et al. 2015, Hahn and Maron 2018), suggesting that larval performance could improve if females oviposit on drier plants. However, *A. fascicularis* has different defense strategies, including a different chemical profile, than *A. syriaca* (Agrawal and Fishbein 2006, 2008). *Asclepias fascicularis* is also morphologically different than *A. syriaca*, with thinner leaves that could result in larvae needing to move more frequently and thus expend more energy to consume the same amount of leaf tissue.

Alternatively, whatever the plant's condition, larvae developing among a higher density of eggs and larvae could be disadvantaged. For example, an increased density of monarch offspring is correlated to a higher rate of infection by the protozoan parasite *Ophryocystis elektroscirrha*, which decreases larval survival and hinders adult flight performance (Bartel et al. 2011). In addition, higher densities of monarch larvae may reduce both larval and adult size and survival rates (Flockhart et al. 2012). Typically, monarch butterflies deposit a solitary egg on each milkweed ramet (Prysby and Oberhauser 2004), although field studies have documented cases in which as many as ten eggs were discovered (Zalucki and Kitching 1982). We observed that a small number of females depositing more than 10 eggs over the course of the trial (Fig. 2). Our high values could be a result of females responding to limited host plants by egg dumping (Aikins et al. 2023). Regardless, females in this trial exhibited plant investigation behaviors and postalighting preferences for water-limited milkweeds.

By investigating the oviposition preferences of gravid monarch butterflies under water-limited conditions, our study demonstrates the potential for climate change to disrupt the relationship between specialist herbivores, like the monarch butterfly, and the cues they rely on from their host plants. Understanding exactly which plant traits produced the oviposition preferences seen here could benefit conservation efforts and promote the reproductive success of this iconic butterfly species. Moreover, future work should investigate larval development and survival on milkweeds with low-water milkweeds. Higher larval performance given higher female preference is by no means assured (Jones and Agrawal 2019). Our findings emphasize the need for comprehensive conservation strategies that consider not only the availability of host plants but also the intricate cues and mechanisms that guide the behavior of herbivores in decline.

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Author Contributions

Aramee Diethelm (Conceptualization [Equal], Data curation [Lead], Formal analysis [Equal], Investigation [Lead], Project administration [Lead], Writing – original draft [Lead], Writing – review & editing [Lead]), Konnor Kost (Data curation [Supporting], Formal analysis [Supporting], Investigation [Supporting], Methodology [Equal], Writing – review & editing [Supporting]), and Elizabeth Pringle (Conceptualization [Equal], Formal analysis [Equal], Funding acquisition [Lead], Writing – original draft [Supporting], Writing – review & editing [Supporting])

Data Availability

All data and corresponding R code are archived in Dryad (DOI: 10.5061/dryad.bcc2fqzjc).

Supplementary Material

Supplementary material is available at *Journal of Insect Science* online.

References

Agrawal AA, Böröczky K, Haribal M, Hastings AP, White RA, Jiang R-W, Duplais C. Cardenolides, toxicity, and the costs of sequestration in the coevolutionary interaction between monarchs and milkweeds. *Proc Natl Acad Sci.* **2021**:118(16):e2024463118. https://doi.org/10.1073/pnas.2024463118

Agrawal AA, Fishbein M. Plant defense syndromes. *Ecology*. **2006**:87(7 Suppl):S132–S149, S166. https://doi.org/10.1890/0012-9658(2006)87[132:pds]2.0.co;2

Agrawal AA, Fishbein M. Phylogenetic escalation and decline of plant defense strategies. *Proc Natl Acad Sci.* **2008**:105(29):10057–10060. https://doi.org/10.1073/pnas.0802368105

Aikins C, Altizer S, Sasaki T. Neither copy nor avoid: no evidence for social cue use in monarch butterfly oviposition site selection. *J Insect Behav.* **2023**:36(1):33–44. https://doi.org/10.1007/s10905-023-09817-8

Bartel RA, Oberhauser KS, de Roode JC, Altizer SM. Monarch butterfly migration and parasite transmission in eastern North America. *Ecology.* **2011**:92(2):342–351. https://doi.org/10.1890/10-0489.1

Barton K. MuMIn: multi-model inference. R Package Version 0.12.2/r18. **2009**. [accessed 2020 Oct 09]. https://CRAN.R-project.org/package=MuMIn.

Baur R, Haribal M, Renwick JAA, Städler E. Contact chemoreception related to host selection and oviposition behaviour in the monarch butterfly, *Danaus plexippus*. *Physiol Entomol.* **1998**:23(1):7–19. https://doi.org/10.1046/j.1365-3032.1998.2310007.x

Bischl B, Lang M, Bossek J, Horn D, Richter J, Surmann D. BBmisc: miscellaneous helper functions for B. Bischl. R Package Version 1.13. **2017**. [accessed 2020 Oct 09]. http://cran.r-project.org/web/packages/BBmisc/index.html.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **2017**:9(2):378–400.

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Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr.* **2014**:84(1):45–67. https://doi.org/10.1890/13-0133.1

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho I, Faria T, Pinheiro C. How plants cope with water stress in the field. Photosynthesis and growth. *Ann Bot*. **2002**:89 Spec No(7):907–916. https://doi.org/10.1093/aob/mcf105

Cohen JA, Brower LP. Oviposition and larval success of wild monarch butterflies (Lepidoptera: Danaidae) in relation to host plant size and cardenolide concentration. *J Kans Entomol Soc*. **1982**:55(2):343–348. https://www.jstor.org/stable/25084295.

Conchou L, Lucas P, Meslin C, Proffit M, Staudt M, Renou M. Insect odorscapes: from plant volatiles to natural olfactory scenes. *Front Physiol.* **2019**:10(972). https://doi.org/10.3389/fphys.2019.00972

Cook BI, Ault TR, Smerdon JE. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Sci Adv.* **2015**:1(1):e1400082. https://doi.org/10.1126/sciadv.1400082

Couture JJ, Serbin SP, Townsend PA. Elevated temperature and periodic water stress alter growth and quality of common milkweed (*Asclepias syriaca*) and monarch (*Danaus plexippus*) larval performance. *Arthropod Plant Interact*. **2015**:9(2):149–161. https://doi.org/10.1007/s11829-015-9367-y

Diethelm AC, Reichelt M, Dilts TE, Farlin JP, Marlar A, Pringle EG. Climatic history, constraints, and the plasticity of phytochemical traits under water stress. *Ecosphere*. **2022**:13(8):e4167.

Dilts TE, Steele MO, Engler JD, Pelton EM, Jepsen SJ, McKnight SJ, Taylor AR, Fallon CE, Black SH, Cruz EE, *et al*. Host plants and climate structure habitat associations of the Western monarch butterfly. *Front Ecol Evol.* **2019**:7(258). https://doi.org/10.3389/fevo.2019.00188

Flockhart DTT, Martin TG, Norris DR. Experimental examination of intraspecific density-dependent competition during the breeding period in monarch butterflies (*Danaus plexippus*). Walker S, ed. *PLoS One.* **2012**:7(9):e45080. https://doi.org/10.1371/journal.pone.0045080

Gripenberg S, Mayhew PJ, Parnell M, Roslin T. A meta-analysis of preference–performance relationships in phytophagous insects. *Ecol Lett.* **2010**:13(3):383–393. https://doi.org/10.1111/j.1461-0248.2009.01433.x

Gutbrodt B, Mody K, Dorn S. Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos*. **2011**:120(11):1732–1740. https://doi.org/10.1111/j.1600-0706.2011.19558.x

Hahn PG, Maron JL. Plant water stress and previous herbivore damage affect insect performance: abiotic and biotic effects on insect performance. *Ecol Entomol.* **2018**:43(1):47–54. https://doi.org/10.1111/een.12468

Haribal M, Renwick JAA. Oviposition stimulants for the monarch butterfly: flavonol glycosides from *Asclepias curassavica*. *Phytochem.* **1996**:41(1):139–144. https://doi.org/10.1016/0031-9422(95)00511-0

Huberty AF, Denno RF. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology.* **2004**:85(5):1383–1398. https://doi.org/10.1890/03-0352

Jaenike J. On optimal oviposition behavior in phytophagous insects. *Theor Popul Biol.* **1978**:14(3):350–356. https://doi.org/10.1016/0040-5809(78)90012-6

Jones PL, Agrawal AA. Beyond preference and performance: host plant selection by monarch butterflies, *Danaus plexippus*. *Oikos*. **2019**:128(8):1092–1102. https://doi.org/10.1111/oik.06001

Mattson WJ, Haack RA. The role of drought in outbreaks of plant-eating insects. *BioScience*. **1987**:37(2):110–118. https://doi.org/10.2307/1310365

Mayhew PJ. Herbivore host choice and optimal bad motherhood. *Trends Ecol Evol.* **2001**:16(4):165–167. https://doi.org/10.1016/s0169-5347(00)02099-1

McCluney KE, Belnap J, Collins SL, González AL, Hagen EM, Nathaniel Holland J, Kotler BP, Maestre FT, Smith SD, Wolf BO. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biol Rev.* **2012**:87(3):563–582. https://doi.org/10.1111/j.1469-185X.2011.00209.x

Mundim FM, Pringle EG. Whole-plant metabolic allocation under water stress. *Front Plant Sci.* **2018**:9(852). https://doi.org/10.3389/fpls.2018.00852

Pelton EM, Schultz CB, Jepsen SJ, Black SH, Crone EE. Western monarch population plummets: status, probable causes, and recommended conservation actions. *Front Ecol Evol*. **2019**:7(258). https://doi.org/10.3389/fevo.2019.00258

Prysby M, Oberhauser K. The monarch butterfly: biology and conservation. In: Solensky MJ, Oberhauser KS, editors. *Temporal and geographic variation in monarch densities: citizen scientists document monarch population patterns*. Ithaca (NY): Comstock Publishing Associates; **2004**. p. 009–020.

R Core Team. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; **2021**. [accessed 2020 Oct 01]. https://www.R-project.org.

Schoonhoven LM, van Loon JJA, Dicke M. *Insect-plant biology*. 2nd ed. Oxford (UK): Oxford University Press; **2005**.

Soule AJ, Decker LE, Hunter MD. Effects of diet and temperature on monarch butterfly wing morphology and flight ability. *J Insect Conserv.* **2020**:24(6):961–975. https://doi.org/10.1007/s10841-020-00267-7

Zalucki MP, Kitching RL. Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, Asclepias. *J Zool.* **1982**:198(1):103–116. https://doi.org/10.1111/j.1469-7998.1982.tb02063.x

Zeileis A, Hothorn T. Diagnostic checking in regression relationships. *R News*. **2002**:2(3):7–10.

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

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