

## Research Article

**Cite this article:** Lamb R, Keller J, and Shea K (2024). Competition reduces structural defense in an invasive thistle in the field. *Invasive Plant Sci. Manag.* doi: [10.1017/inp.2023.33](https://doi.org/10.1017/inp.2023.33)

Received: 4 September 2023

Revised: 3 December 2023

Accepted: 18 December 2023

**Associate Editor:**

Guillaume Fried, ANSES

**Keywords:**

*Carduus nutans*; competition; phenotypic plasticity; prickles; structural defense

**Corresponding author:**

Joseph Keller; Email: [jak573@psu.edu](mailto:jak573@psu.edu)

# Competition reduces structural defense in an invasive thistle in the field

Rachel Lamb<sup>1</sup>, Joseph Keller<sup>2</sup>  and Katriona Shea<sup>3</sup> 

<sup>1</sup>Undergraduate Researcher, Department of Biology, Pennsylvania State University, University Park, PA 16802, USA;

<sup>2</sup>Graduate Fellow, Department of Biology, Pennsylvania State University, University Park, PA 16802, USA and

<sup>3</sup>Professor of Biology and Alumni Professor in the Biological Sciences, Department of Biology, Pennsylvania State University, University Park, PA 16802, USA

### Abstract

Invasive thistles reduce the productivity of pastures and rangelands because their structural defenses make them unpalatable to grazing livestock. However, plants potentially alter their growth patterns, including their allocation of resources to defense, in response to the presence of competing vegetation. Understanding the effects of competition on the structural defense of problematic pasture weeds can inform management plans that reduce the economic harm caused by these pests. We grew musk thistle (*Carduus nutans* L., also commonly called nodding thistle) in a fully crossed factorial field experiment in a single abandoned pasture in 2017 with two experimental factors: the level of thistle infestation (1 thistle or 5, resulting in densities of 4 or 20 plants m<sup>-2</sup>) and the presence or absence of grazing (simulated by weekly trimming of competing vegetation). We assessed the effects of treatments on defense by counting prickles >3-mm long on leaves. Our analysis included leaf age and leaf size as covariates. Competition reduced the number of prickles present on leaves. Regression analysis showed that an increase from, for example, 50 g to 200 g of competing vegetation within 50 by 50 cm study plots reduced the expected average number of prickles on intermediate-aged leaves with average length 25.5 cm by 76.9 prickles per leaf, or 41%. This pattern was similar for leaves of all ages, although the oldest leaves generally had fewer prickles than younger leaves. We did not observe differences in defense structures between plants neighbored by conspecifics and those neighbored by other competitors. *Carduus nutans* has been previously managed using high densities of grazers, and this practice may be more likely to damage less-defended individuals such as those we observed in our treatments with competition. This finding suggests that maintaining competition in pastures may increase *C. nutans* vulnerability to grazing.

### Introduction

Invasive weeds cause enormous economic harm in rangelands in pastures, where they interfere with grazing livestock (DiTomaso 2000). Some invasive weeds reduce livestock productivity because their structural defenses against herbivory make them unpalatable, and they occupy space that would otherwise support more profitable forage species (Duncan et al. 2004; Hanley et al. 2007). Despite these plants' defenses, grazing livestock may be used in control efforts aimed at these weeds (Huwer et al. 2005). Managers can alter the type of livestock, the timing of grazing, and density of livestock to encourage feeding on otherwise unpalatable weeds (Popay and Field 1996). The success of such efforts, however, may depend on the level of defense present among targeted weeds, which may vary substantially depending on a variety of environmental conditions. Plants may vary their investment in long-lasting, constitutive defenses based on a variety of environmental factors, including soil fertility, light conditions, and temperature (Fine et al. 2006; Lynds and Baldwin 1998; Zhang et al. 2012).

The presence or absence of neighboring plants, and the identities of neighboring plants, may have large effects on optimal allocation of resources to defense. Some neighbors may lend plants associational resistance, reducing herbivory with their presence (Barbosa et al. 2009). This reduction in herbivory may have many causes: well-defended neighbors may repel herbivores, palatable neighbors may draw herbivores away from a focal plant, and other neighbors may reduce herbivores' physical access to focal plants or prevent herbivores from detecting focal plants. Reduced herbivory alters the balance of the trade-off between defense and other uses of resources, favoring reduced allocation toward defense (Zangerl and Bazzaz 1992). Neighboring plants also compete with focal plants for resources. Competition between plants and their neighbors has the potential to further affect the trade-off between defense and growth. The cost of defense may be greater under strong competition, because investing in defense rather than growth reduces individuals' ability to compete (de Vries et al. 2017).

We investigated the extent to which the presence and identity of neighboring vegetation affected structural defense on leaves of musk thistle (*Carduus nutans* L., also commonly called nodding thistle). This weed is an invasive species with highly spinescent leaves that deter grazing

© The Author(s), 2024. Published by Cambridge University Press on behalf of Weed Science Society of America. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.



### Management Implications

Many invasive pasture pests cause economic harm because they are unpalatable to grazing livestock and take up resources that might otherwise contribute to the growth of more beneficial plants. Oftentimes, structural defenses against herbivory drive livestock's aversion: spines, thorns, and prickles can all deter grazing. To build these defenses, however, weeds must allocate resources to the construction of defensive structures rather than to growth or reproduction. When plants are stressed, for example, by the presence of competing vegetation, they may alter their growth, reducing defenses and thereby potentially increasing their palatability to grazers. We tested the influence of competing vegetation on the growth and structural defense of the invasive pasture pest *Carduus nutans* (musk thistle) in a field experiment in Pennsylvania, USA. We found that when individuals were grown with competing vegetation, they grew to smaller sizes and produced fewer prickles on leaf margins. This suggests that the maintenance of competing vegetation in pastures can have multiple payoffs: *C. nutans* individuals will be smaller and also potentially more palatable to livestock. Crash grazing programs, in which grazers are introduced in high density over short periods of time could aim to exploit this pattern, but will need to be tailored to local conditions. By maintaining competing vegetation and controlling the timing and intensity of grazing, managers may be able to substantially increase herbivory on *C. nutans* and thereby limit population growth.

livestock (Desrochers et al. 1988). Lost grazing productivity is a primary cause of *C. nutans* economic impact (Kelly and Popay 1985). Prior work has shown plasticity in *C. nutans* prickle density in response to experimental warming in the field, indicating that this trait may vary in response to other environmental factors (Zhang et al. 2012). We grew thistle rosettes in 50 by 50 cm (0.25-m<sup>2</sup>) plots and manipulated two factors in a fully factorial design: the level of thistle infestation (1 thistle or 5, resulting in densities of 4 or 20 plants m<sup>-2</sup>) and the presence or absence of grazing (simulated by weekly trimming of competing vegetation). Because conspecifics share the same resource requirements, we anticipated that the impact of neighboring conspecifics may be greater than that of other neighboring vegetation (Adler et al. 2018). Additionally, for *C. nutans*, conspecific vegetation would also bear prickles, potentially lending neighbors associational resistance (Barbosa et al. 2009). Our research therefore addressed two questions:

1. How does the presence of competing vegetation affect *C. nutans* structural defense?
2. Do different types of competing vegetation (conspecifics vs. other naturally occurring competitors) have differing effects on *C. nutans* structural defense?

Understanding the influence of competition on structural defense in this widespread invasive species can inform managers as they develop grazing plans and weed control programs.

## Materials and Methods

### Study Species

*Carduus nutans* is an herbaceous plant native to Eurasia (Desrochers et al. 1988). Invasive populations have been documented in North

America, South America, Australia, and New Zealand (Desrochers et al. 1988; Jessep 1990; Popay and Medd 1990). Individuals produce wind-dispersed seeds, typically in summer (Smith and Kok 1984). Seeds germinate in summer, fall, and spring and form low-lying rosettes. Once rosettes grow large enough, they bolt in spring, extending one or more upright stems, flowering, releasing seed, and then dying. *Carduus nutans* is a monocarpic perennial; ranging from annual, through biennial, to even longer-lived in some settings, but reproducing only once.

*Carduus nutans* leaves are pinnately lobed, and each lobe ends in a prickle (Desrochers et al. 1988; Rhoades and Block 2007). Bolting individuals also have spinescent wings on stems. Leaf prickles are effective in protecting individuals from being damaged by large, grazing herbivores (Lee and Hamrick 1983). *Carduus nutans* is unpalatable to livestock, and it reduces productivity in infested rangelands and pastures and is therefore widely considered a noxious invader (USDA-NRCS 2023). A prior field experiment demonstrated that experimental elevated temperature in the field via open-top chamber reduced prickle density on *C. nutans* leaves, demonstrating that structural defenses can depend on local environmental conditions in this species (Zhang et al. 2012).

### Field Experiment

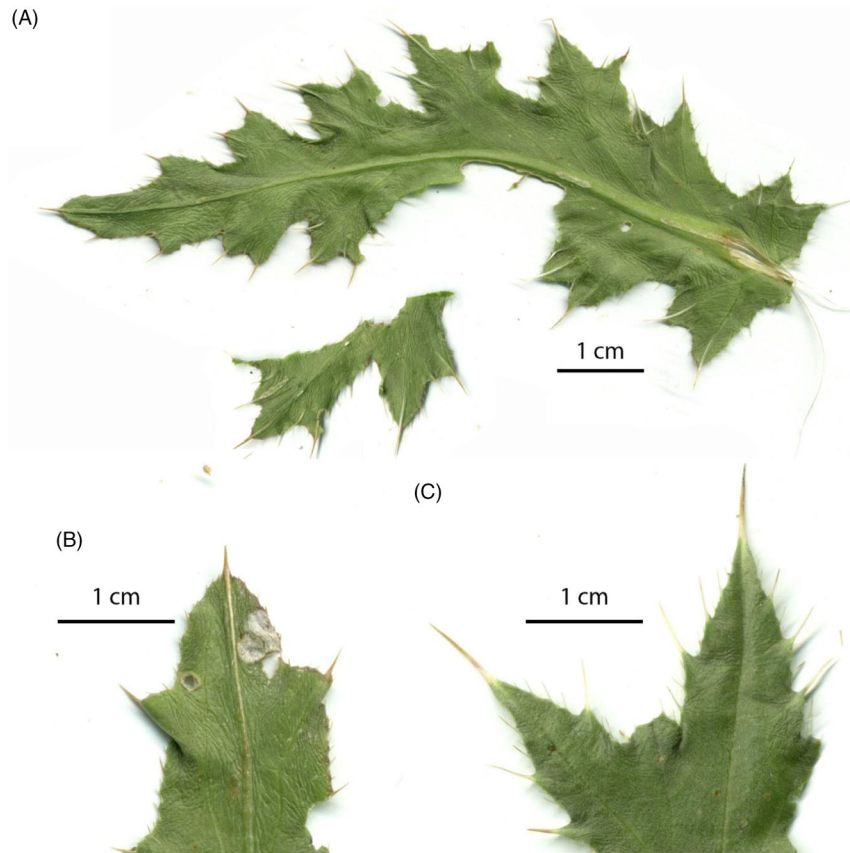
We conducted our field experiment in an abandoned pasture at the Russell E. Larson Agricultural Research Farm in Rock Springs, PA (40.711°N, 77.944°W). The soil type at the experiment site was Hagerstown silt loam (fine, mixed, semiactive, mesic Typic Hapludalfs). Temperatures at this location range from an average minimum of -6.7 C in January to an average maximum of 28.1C in July (Nord et al. 2010). On average, the site receives 933 mm of precipitation annually (Nord et al. 2010). Experimental plots were tilled 4 d before starting the experiment to disturb the soil and remove all aboveground vegetation.

We collected seed from a single invasive population in Carlisle, PA, in July 2016. Seeds from multiple plants were mixed and sifted to remove nonviable achenes. We planted seeds in MetroMix 360 (SunGro Horticulture, Agawam, MA, USA 01001) soil in the greenhouse in late April, 2017. Plants were held in the greenhouse under ambient light and temperature and watered daily for 25 d after planting. Established rosettes were then transplanted to the field.

We laid out 16 replicate blocks, each containing four 50 by 50 cm plots. Plots were separated by 1 m. A single focal thistle was planted in the center of each plot. We crossed two experimental factors: the level of thistle infestation and the removal of other competing vegetation to simulate grazing (Supplementary Figure S1). Within each block, each plot was randomly allocated to one of four treatments:

1. low thistle density (1 individual), grazed (competing vegetation removed);
2. high thistle density (5 individuals), grazed;
3. low thistle density, ungrazed (all competing vegetation left intact); and
4. high thistle density, ungrazed

In plots with high thistle density, we planted four additional thistles 10 cm away from the focal thistle at the corners of a square. This density mimicked heavily infested pasture. In plots assigned to have simulated grazing, all vegetation except transplanted thistles



**Figure 1.** Scanned images showing the adaxial surface of *Carduus nutans* leaves. (A) Leaves were dissected when necessary to ensure that the full leaf margin was visible within the image. (B and C) Differences between a leaf with few, small prickles (B) and a leaf with many, large prickles (C). Note that postharvest wilting, fading, and compression in the scanner has affected the leaves' appearance; see Supplementary Figure S1 for images of the experimental plants in the field.

was clipped down to the soil surface weekly. This frequent clipping mimicked high grazing pressure. In ungrazed plots, we allowed resprouting and newly germinating vegetation to grow unchecked. Common species at the study site included tall oatgrass (*Arrhenatherum elatius* L.), orchardgrass (*Dactylis glomerata* L.), quackgrass (*Elymus repens* L.), timothy (*Phleum pratense* L.), butter and eggs (*Linaria vulgaris* Mill.), plantain (*Plantago* spp.), dandelion (*Taraxacum* spp.), clover (*Trifolium* spp.), and bedstraw (*Galium* spp.). At the end of the growing season, all aboveground biomass in each plot was harvested, dried, and weighed. Focal thistles, competing thistles, and other competing vegetation were weighed separately.

Eight weeks after transplanting thistles, we collected leaves from three positions on the focal thistle rosette in each plot. These positions were: (1) touching the soil (the oldest leaves), (2) directly above leaf 1 (intermediate leaves), and (3) closest to the center of the rosette with leaf length >5 cm (youngest leaves). All leaves were harvested from the same cardinal direction.

Each leaf was scanned alongside a ruler using an GT-1500 (Epson America Inc. Los Alamitos, CA, USA 90720) scanner to create a 1,200 dpi image (Figure 1). To prevent overlapping portions of the leaf from obscuring other leaf parts, we dissected leaves to ensure they laid flat. We used the Java-based image processing program [ImageJ] to measure the length of each prickle (Schneider et al. 2012). We also measured the length of each leaf. To quantify the number of prickles present on leaves, we counted the number of prickles that were >3 mm long (per the protocol in Zhang et al. 2012).

### Statistical Analysis

We developed a generalized linear mixed-effects model to predict prickle count using the package GLMMTMB in R (Magnusson et al. 2017; R Core Team 2017). We used a negative binomial error structure with a log link function. We included leaf length, leaf position, aboveground dry biomass of conspecific competing vegetation, aboveground dry biomass of other competing vegetation, and the interactions between these terms as fixed effects in the full model. We included nested random effects for plants within blocks to account for the sampling structure in our data. We fit the full model and evaluated all models containing subsets of these predictors using the *dredge* function from the MUMIN package (Bartón 2022). We selected the simplest model with AICc, the small-sample equivalent of the Akaike information criterion (Brewer et al. 2016), within 2 of the lowest value. Model assumptions were validated by inspecting residuals using the DHARMA package in R (Hartig 2022). We assessed whether any points were exceedingly influential by calculating Cook's distance and found no issues.

We used a similar approach to analyze the aboveground biomass of focal thistles. We fit a generalized linear model with gamma error structure and log link function using GLMMTMB (Magnusson et al. 2017). This error structure accounts for the fact that biomass cannot be negative. We included aboveground biomass of competing *C. nutans*, aboveground biomass of other competing vegetation, and their interaction as fixed effects. Block was included as a random effect. Again, we fit all models with

**Table 1.** Aboveground biomass of competing vegetation in experimental plots, listing least-squares mean estimates based on regression and the 95% confidence interval for the mean in brackets.

Competition treatment	Conspecific competition	Other competition	Total competition
	$g$		
None	0	0	0
Interspecific only	0	65.0 [21.8, 108.2]	65.0 [21.8, 108.2]
Intraspecific only	79.3 [69.1, 89.6]	0	79.3 [69.1, 89.6]
Both	59.3 [49.1, 69.6]	42.2 [25.9, 58.5]	101.5 [83.74, 119.25]

subsets of these predictors and selected the simplest model with AICc within 2 of the lowest and verified model assumptions by inspecting residuals using DHARMA. We identified one plant with large influence, an outlier with very high competing biomass due to the presence of large milkweeds (*Asclepias* spp.) within the plot (Cook's distance > 1). This point was excluded from analysis.

## Results and Discussion

Experimental treatments resulted in differing amounts of competing vegetation. Generally, plots with high *C. nutans* density and no simulated grazing had higher amounts of total aboveground competing biomass (Table 1). Plots with low *C. nutans* density and simulated grazing had no competing vegetation by design. Plots with the other two treatments had intermediate amounts of competition.

The number of prickles on leaves was affected by leaf length, leaf position on the rosette (which correlates with leaf age), the amount of interspecific competition, and the amount of intraspecific competition (Table 2). As the amount of competing vegetation increased, the average number of prickles declined (Figure 2). The identity of the competing vegetation (conspecifics or not) had no apparent effect on the impact of competition on *C. nutans* structural defense. The fitted slope with respect to aboveground biomass of interspecific competition ( $-0.00349$  on the link scale) was not significantly different from the slope with respect to aboveground biomass of intraspecific competition ( $-0.00342$  on the link scale, two-sided two-sample  $z$ -test  $P = 0.95$ ).

Competing vegetation also influenced aboveground biomass of focal thistles (Table 3). Individuals growing with more competing vegetation had lower biomass than those facing less competition (Figure 3). Again, we found no evidence that the identity of the competing vegetation (interspecific or intraspecific) altered the impact on a focal thistle's aboveground biomass. The fitted slopes for these two types of competition were not significantly different (two-sided two-sample  $z$ -test  $P = 0.32$ ).

The presence of competition, therefore, resulted in smaller rosettes that were less defended by prickles. This finding aligns with other cases in which no trade-off between growth and defense was found (e.g., Messina et al. 2002; Ridenour et al. 2008; Siemens et al. 2002).

Prickle density varied with leaf age. Young leaves from the center of rosettes generally had more prickles than older leaves from the outer portions of rosettes. This finding concurs with widespread observations showing that investment in defense varies across plants' life cycles, and the trend toward increased defense on later-developing (younger) tissue corresponds to typical patterns in other herbaceous plants (Barton and Koricheva 2010). In our

**Table 2.** Fitted regression parameters for the generalized linear mixed-effects model for prickle counts per leaf on *Carduus nutans* leaves.<sup>a</sup>

	Prickle count	
	Negative binomial error, log link	
Leaf 1	1.471***	(0.353)
Leaf 2	4.959***	(0.196)
Leaf 3	4.242***	(0.277)
Leaf length (cm)	0.080***	(0.010)
Interspecific competition aboveground biomass (g)	$-0.003500^{**}$	(1.300)
Intraspecific competition aboveground biomass (g)	$-0.003420^{***}$	(0.788)
Leaf 2 $\times$ leaf length (cm)	$-0.068^{***}$	(0.012)
Leaf 3 $\times$ leaf length (cm)	$-0.004$	(0.031)
Number of observations	192	
Number of blocks	16	
SD (block)	0.00011	
Number of plants	64	
SD (plant:block)	0.350	
Pseudo-R <sup>2</sup>	0.70	

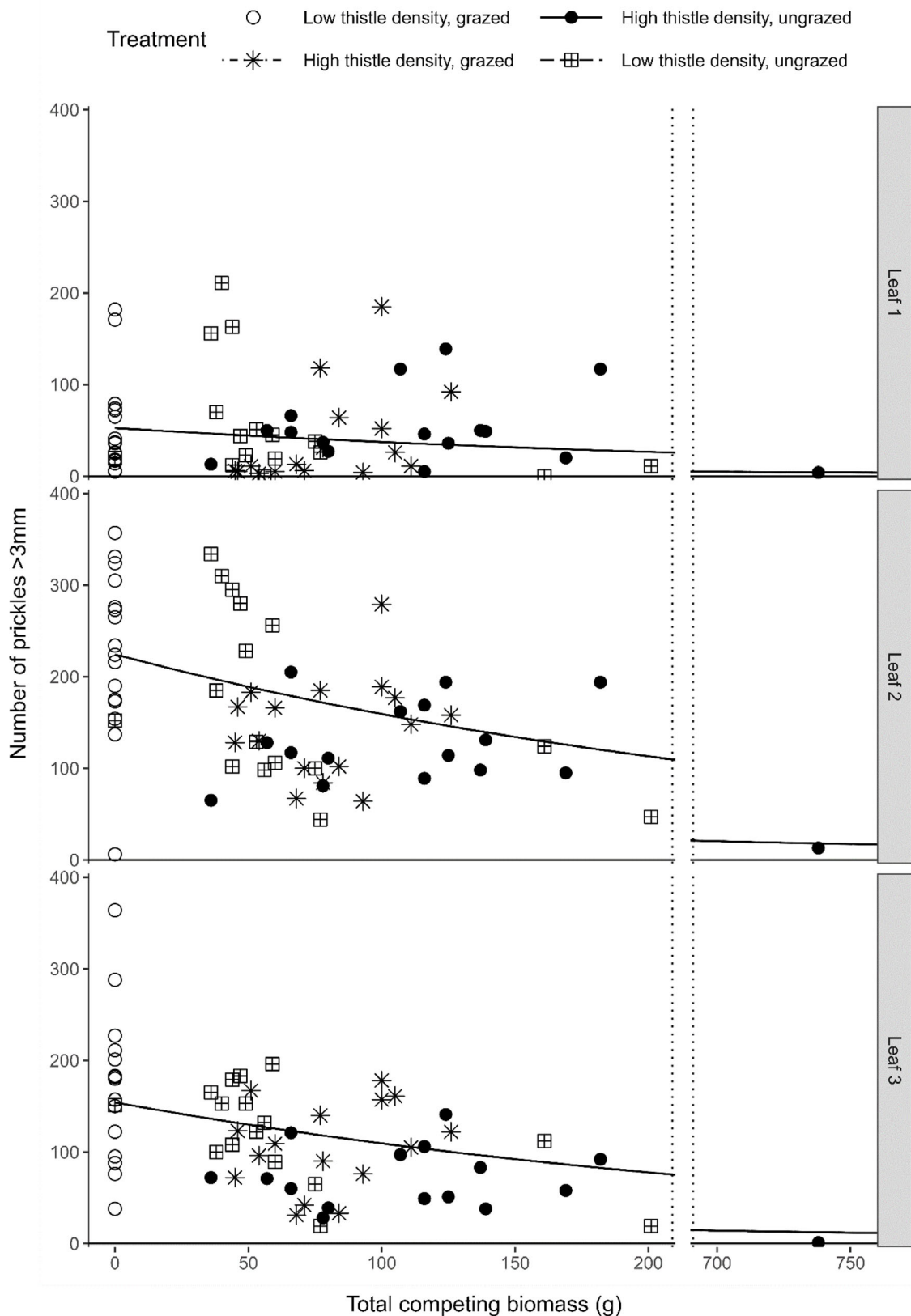
<sup>a</sup>Predictors included leaf position (categorical, Leaf 1 on the ground, Leaf 2 intermediate, and Leaf 3 near rosettes' centers), leaf length, the amount of aboveground non-thistle competing biomass, the amount of aboveground conspecific thistle competing biomass, and the interaction between leaf position and leaf length. Standard errors for fitted regression parameters are in parentheses. Due to the log link employed in this model, coefficients listed here represent the expected differences in the log prickle count associated with each covariate.

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

study plots, the amount of vegetation in our competition treatments increased over time, making direct assessments of the influence of age on defense difficult. Immediately after being transplanted, individuals in all treatments faced relatively little competition. Over time, though, plants growing in our treatments experienced substantially different conditions as background vegetation germinated and resprouted and as neighboring thistles grew large enough to interfere with focal thistles. The trend toward larger differences in defense for later-appearing leaves may therefore have been caused in part by temporal patterns in competition in our experiment. Future work transplanting *C. nutans* individuals into areas with established competing vegetation may help to resolve whether ontogeny or the amount and/or timing of competition causes differences in defense between young and old leaves (Wright and McConnaughay 2002).

Our experiment, though highly replicated at our study site, was not repeated in multiple years or at multiple locations. This decision was made based on the targeted nature of our research questions and logistical constraints on our ability to adequately suppress competing vegetation across multiple sites. Care should thus be taken in interpreting the results of this study. Prior work has shown that *C. nutans* growth patterns and demography can vary substantially across its cosmopolitan range (Jongejans et al. 2008). The patterns observed in temperate Pennsylvania, USA, are unlikely to be identical in Australia, for example, where seasonal precipitation patterns strongly influence *C. nutans* life cycle and performance (Shea et al. 2006). Our main conclusion (that both growth and structural defense were enhanced when competing vegetation was suppressed), though, has been noted in other



**Figure 2.** Prickle counts on *Carduus nutans* leaves grown in plots with differing amounts of competing vegetation. Plants were grown in four treatments: low-density infestation with simulated grazing (open circles), high-density infestation with simulated grazing (asterisks, dot-dashed line), low-density infestation with no grazing (crossed squares, dashed line), and high-density infestation with no grazing (filled circles, solid line). Each panel shows results for leaves collected from different positions on rosettes: Leaf 1 was touching the soil (the oldest leaves), Leaf 2 was directly above Leaf 1 (intermediate leaves), and Leaf 3 was closest to the center of the rosette with leaf length >5 cm (youngest leaves). Fitted regression lines were estimated using the average leaf length for each leaf position. The fitted line for the treatment including both intra- and interspecific competition was evaluated with the total biomass made up of 64% other thistles, as this was the average proportion in those plots. Note that the x axis includes a break, marked with vertical dotted lines. Also note that distinct lines for each treatment (except the treatment with no competition, which has no variation along the x axis) are drawn in each panel, but they overlay one another and are difficult to distinguish visually.

**Table 3.** Fitted regression parameters for the generalized linear mixed-effects model for focal thistle aboveground dry biomass.<sup>a</sup>

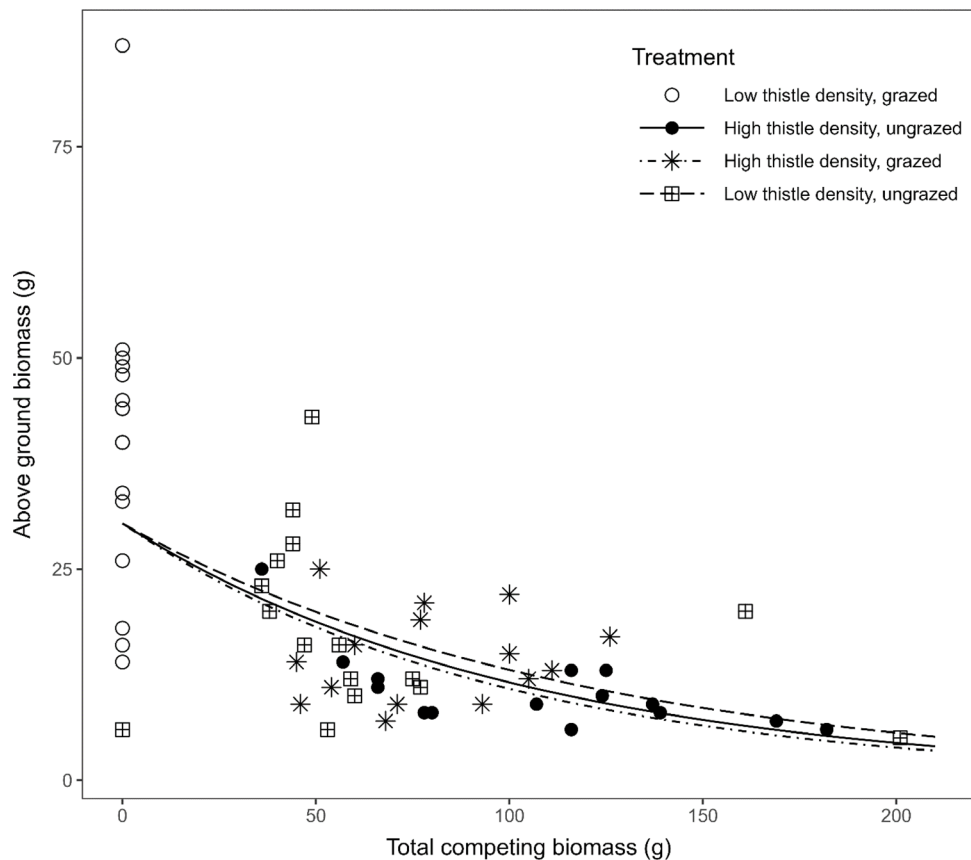
	Aboveground dry biomass g plant <sup>-1</sup>
	Gamma error, log link
Intercept	-3.495*** (0.097)
Non-thistle competition aboveground biomass (g)	-0.008444*** (0.001323)
Other thistle competition aboveground biomass (g)	-0.010326*** (0.001387)
Number of observations	62
Number of blocks	16
SD (block)	0.174
Pseudo-R <sup>2</sup>	0.60

<sup>a</sup>Standard errors for regression coefficients are shown in parentheses. Due to the log link employed in this model, coefficients listed here represent the expected differences in log biomass associated with each covariate.

\*\*\*P < 0.001.

systems (Messina et al. 2002; Ridenour et al. 2008; Siemens et al. 2002). Additional experiments in other parts of *C. nutans*' range may address the generality of our findings for this species: questions relating to the interactions between climatic conditions and competition effects on *C. nutans* defense are beyond the scope of the present study. Similarly, the influence of individual competing species (other than conspecific *C. nutans*, which were experimentally manipulated here) cannot be discerned based this study, and sites with differing communities of competing plants may have differing outcomes. Future work expanding on the results presented here would certainly be valuable. Experiments testing, for example, whether drought or warmed conditions alter the observed relationship between competition and *C. nutans* defense could improve recommendations for how growers might best suppress this weed in different regions and in future climates.

Prickles are but one of several anti-herbivore defenses exhibited by *C. nutans*. While structural defense by prickles is known to vary with environmental factors (Zhang et al. 2012), investment in these other defenses may vary as well, and individuals may trade off between constructing different defenses. *Carduus nutans* leaves also contain anthocyanins, which may act as a defense against herbivores (Close and Beadle 2003). Leaves also vary in the number



**Figure 3.** Aboveground biomass of *Carduus nutans* rosettes grown in plots with differing amounts of competing vegetation. Plants were grown in four treatments: low-density infestation with simulated grazing (open circles), high-density infestation with simulated grazing (asterisks, dot-dashed line), low-density infestation with no grazing (crossed squares, dashed line), and high-density infestation with no grazing (filled circles, solid line). Fitted regression lines for intraspecific competition (100% competing vegetation made up of *C. nutans*), interspecific competition (0% of competing vegetation made up of *C. nutans*), and both (64% of competing vegetation made up of *C. nutans*) are shown. Results from a plot with far more competing biomass (0.73 kg) are not shown.

and size of trichomes present. Some leaves are densely pubescent, while others are glabrous (Desrochers et al. 1988). Trichomes may be especially effective against insect herbivores, including the thistle specialist tortoise beetle (*Cassida rubiginosa* Müller 1776), which has been shown to have reduced survival when feeding on *Cirsium* species with dense trichomes compared with *Cirsium* species with less dense trichomes (Cripps et al. 2015). *Carduus nutans* leaves may also contain silica, which wears herbivores' mouthparts and thus contributes to defense (Massey and Hartley 2009). Understanding how plant–plant interactions influence resource allocation to these other defenses in addition to prickle defense may lead to a more complete conceptualization of how total allocation to defense is controlled.

Interactions with herbivores are also likely to contribute to *C. nutans*' allocation of resources toward defenses. In our experiment, we allowed naturally occurring invertebrate herbivores to feed on plants without obstruction, and we observed approximately equal herbivory across all competition treatments. Future work explicitly investigating the interacting influences of herbivores and vegetative competition could potentially find interesting patterns that we did not investigate in this experiment.

Plants can exert diverse effects on their neighbors. They compete for nutrients and for access to sunlight, exchange chemical signals via volatile compounds and root exudates, and influence microclimate, including temperature and moisture conditions. Prior work shows that *C. nutans* individuals generally tolerate intraspecific competition well, reaching approximately the same sizes when facing high densities of conspecifics as they do when grown at reduced densities or even without competition (Rauschert and Shea 2012). Overshadowing by taller vegetation, however, strongly reduces *C. nutans* performance, and this species does not frequently survive in forest understory or in dense vegetation (Desrochers et al. 1988). While we saw similar outcomes regardless of the identity of neighboring vegetation, our experimental design did not allow us to distinguish between the many potential effects of competition on *C. nutans* performance and morphology. Distinguishing these potentially interacting effects would be extremely difficult, as competing vegetation's myriad effects co-occur in nature. Future studies that independently vary the total amount of competing biomass and the identity of competing plants may help to partially resolve this question.

Understanding how competition affects *C. nutans*' investment in defense may have direct application for farmers and land managers working to control this invasive weed. Crash grazing, wherein high densities of grazers are confined in an area to encourage grazing on less-preferred forage, is one approach managers use to control *C. nutans* (Shea et al. 2006). Even at high densities, though, grazers may avoid well-defended, prickly *C. nutans* individuals. Our results suggest that preserving competing vegetation may reduce *C. nutans* prickle defense and potentially thereby increase palatability to grazing herbivores. By maintaining competing vegetation in pastures, managers may be able to reduce *C. nutans* performance before grazing and also increase susceptibility to crash grazing. Maintaining competing vegetation is already recommended as a tool to reduce the germination and establishment of *C. nutans*, and this work expands that finding to show continuing benefits of competition throughout rosettes' growth (Wardle et al. 1992). Future work to explore the interaction between competition and *C. nutans*' palatability to grazers should test this hypothesis.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2023.33>

**Acknowledgments.** This work was made possible by a 2017 Erickson Discovery Grant. Thanks to Caitlin Mroz and Tala Attia for field assistance. We also thank Corey Dillon and the farm managers at the Russell E. Larson Agricultural Research Center for assistance setting up the field experiment. Financial support also came from National Institute of Food and Agriculture, U.S. Department of Agriculture award number 2016-67011-24710 to JK. Any opinions, findings, and conclusions or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the USDA.

No competing interests have been declared.

## References

- Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, Meiners JM, Tredebeck AT, Veblen KE (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecol Lett* 21:1319–1329
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu Rev Ecol Evol Syst* 40:1–20
- Barton KE, Koricheva J (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *Am Nat* 175:481–49
- Bartoń K (2022) MuMin: Multi-Model Inference. R Package Version 1.47.1. <https://CRAN.R-project.org/package=MumIn>. Accessed: March 10, 2023
- Brewer MJ, Butler A, Cooksley SL (2016) The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. *Methods Ecol Evol* 7:679–692
- Close DC, Beadle CL (2003) The ecophysiology of foliar anthocyanin. *Bot Rev* 69:149–161
- Cripps MG, Jackman SD, Rostas M, Van Koten C, Bourdot G W (2015) Leaf traits of congeneric host plants explain differences in performance of a specialist herbivore. *Ecol Entomol* 40: 237–246
- de Vries J, Evers JB, Poelman EH (2017) Dynamic plant–plant–herbivore interactions govern plant growth–defence integration. *Trends Plant Sci* 22:329–337
- Desrochers AM, Bain JF, Warwick SI (1988) The biology of Canadian weeds: 89. *Carduus nutans* L. and *Carduus acanthoides* L. *Can J Plant Sci* 68:1053–1068
- DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Sci* 48:255–265
- Duncan CA, Jachetta JJ, Brown ML, Carrithers VF, Clark JK, DiTomaso JM, Lym RG, McDaniel KC, Renz MJ, Rice PM (2004) Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. *Weed Technol* 18:1411–1416
- Fine PV, Miller ZJ, Mesones I, Irazuzta S, Appel HM, Stevens MHH, Sääksjärvi I, Schultz JC, Coley PD (2006) The growth–defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87:S150–S162
- Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. *Perspect Plant Ecol Evol Syst* 8:157–178
- Hartig F (2022) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMA>
- Huwer RK, Briese DT, Dowling PM, Kemp DR, Lonsdale WM, Michalk DL, Neave MJ, Sheppard AW, Woodburn TL (2005) Can an integrated management approach provide a basis for long-term prevention of weed dominance in Australian pasture systems? *Weed Res* 45:175–192
- Jessep CT (1990) Aspects of the biology of nodding thistle (*Carduus nutans* L.) in Canterbury, New Zealand. *NZ J Agric Res* 33:173–183
- Jongejans E, Shea K, Skarpaas O, Kelly D, Sheppard AW, Woodburn TL (2008) Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. *J Ecol* 96:687–697
- Kelly D, Popay AI (1985) Pasture production lost to unsprayed thistles at two sites. *Proc 38th NZ Weed Pest Control Conf* 38:115–118
- Lee JM, Hamrick JL (1983) Demography of two natural populations of musk thistle (*Carduus nutans*). *J Ecol* 71:923–936

- Lynds GY, Baldwin IT (1998) Fire, nitrogen, and defensive plasticity in *Nicotiana attenuata*. *Oecologia* 115:531–540
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler, van Benthem K, Bolker B, Brooks MM (2017) Package ‘glmmTMB’. R Package Version 0.2.0. <https://CRAN.R-project.org/package=MuMIn>. Accessed: March 10, 2023
- Massey FP, Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *J Anim Ecol* 78:281–291
- Messina FJ, Durham SL, Richards JH, McArthur DE (2002) Trade-off between plant growth and defense? A comparison of sagebrush populations. *Oecologia* 131:43–51
- Nord AN, Mortensen DA, Rauschert ESJ (2010) Environmental factors influence early population growth of Japanese stiltgrass (*Microstegium vimineum*). *Invasive Plant Sci Manag* 3.1: 17–25
- Popay AI, Medd RW (1990) The biology of Australian weeds. 21. *Carduus nutans* L. ssp. *nutans*. *Plant Prot Q* 5:3–13
- Popay I, Field R (1996) Grazing animals as weed control agents. *Weed Technol* 10:217–231
- Rauschert ESJ, Shea K (2012) Invasional interference due to similar inter- and intraspecific competition between invaders may affect management. *Ecol Applic* 22:1413–1420
- R Core Team (2017) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org>
- Rhoads AF, Block TA (2007) The Plants of Pennsylvania: An Illustrated Manual. Philadelphia: University of Pennsylvania Press. 1056 p
- Ridenour WM, Vivanco JM, Feng Y, Horiuchi JJ, Callaway RM (2008) No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecol Monogr* 78:369–386
- Schneider CA, Rasband W, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods*, 9(7), 671–675. doi: [10.1038/nmeth.2089](https://doi.org/10.1038/nmeth.2089)
- Shea K, Sheppard A, Woodburn T (2006) Seasonal life-history models for the integrated management of the invasive weed nodding thistle *Carduus nutans* in Australia. *J Appl Ecol* 43:517–526
- Siemens DH, Garner SH, Mitchell-Olds T, Callaway RM (2002) Cost of defense in the context of plant competition: *Brassica rapa* may grow and defend. *Ecology* 83:505–517
- Smith LM, Kok LT (1984) Dispersal of musk thistle (*Carduus nutans*) seeds. *Weed Sci* 32:120–125
- [USDA-NRCS] U.S. Department of Agriculture–Natural Resources Conservation Service (2023) The PLANTS Database. Greensboro, NC: National Plant Data Team. <http://plants.usda.gov>. Accessed: August 30, 2023
- Wardle DA, Nicholson KS, Rahman A (1992) Influence of pasture grass and legume swards on seedling emergence and growth of *Carduus nutans* L. and *Cirsium vulgare* L. *Weed Res* 32:119–128
- Wright SD, McConnaughay KD (2002) Interpreting phenotypic plasticity: the importance of ontogeny. *Plant Species Biol* 17:119–131
- Zangerl AR, Bazzaz FA (1992) Theory and pattern in plant defense allocation. Pages 363–391 in Fritz RS, Sims EL, eds. *Plant Resistance to Herbivores and Pathogens*. Chicago: University of Chicago Press
- Zhang R, Leshak A, Shea K (2012) Decreased structural defence of an invasive thistle under warming. *Plant Biol* 14:249–252