

Spatiotemporal variation in deer browse and tolerance in a woodland herb

HOLLY R. PRENDEVILLE,^{1,3} JANET C. STEVEN,^{2,4} AND LAURA F. GALLOWAY¹

¹University of Virginia, Department of Biology, Charlottesville, Virginia 22904-4328 USA

²Sweet Briar College, Department of Biology, Sweet Briar, Virginia 24595 USA

Abstract. Herbivory can shape the dynamics of plant populations, including effects on survival and reproduction, and is in turn affected by environmental factors that vary in space and time. White-tailed deer are significant herbivores in North America that have been broadly documented to affect plant reproductive success. If variation in the frequency and impact of herbivory by deer correlates with a broad-scale latitudinal gradient, climatic effects may be important for shaping plant–herbivore interactions. Alternatively, a lack of broad-scale gradients would suggest local factors such as plant community composition and deer densities are affecting herbivory. To investigate broad-scale patterns of deer herbivory, we examined the frequency and reproductive consequences of deer browse over three years in 17 populations of *Campanulastrum americanum* spanning the latitudinal extent of its range. Even though deer are overabundant throughout the range of *C. americanum*, we found spatiotemporal variation in deer browse frequency (0–0.96, mean 0.46) and its effects on plant reproductive success. The four southernmost populations experienced high levels of herbivory, and were responsible for generating a negative relationship between latitude and herbivory. In general, patterns of variation in the frequency and impact of herbivory across the entire latitudinal gradient pointed to the importance of local rather than broad-scale factors. Within a population, deer consumed larger plants. Across many populations and years, average fitnesses of browsed and uneaten plants were similar, suggesting that plants are tolerant to browse. However, since large plants have greater reproductive success and are more likely to be browsed, tolerance may be influenced by plant size. When plant size was accounted for, most populations did not fully compensate for browsing. There was no relationship between browsing intensity and tolerance, suggesting that browsing may be too variable to consistently select for tolerance, or that increases in deer density are too recent for increased tolerance to evolve.

Key words: *Campanula*; *Campanulastrum americanum*; fecundity; herbivory; intraspecific variation; range-wide; tolerance; white-tailed deer.

INTRODUCTION

Herbivory is a common and significant ecological interaction that can have major effects on individual plants, populations, and ecosystems (McGraw and Furedi 2005, Knight et al. 2009, Suzuki et al. 2013, Kalisz et al. 2014). At the plant level, tissue loss from herbivory has been broadly documented to reduce growth, survival, and reproduction (Crawley 1989, Huntly 1991, Bergelson and Crawley 1992, Augustine and Frelich 1998, Russell et al. 2001, Rooney and Waller 2003, Lin and Galloway 2010). The effect of herbivory on plant fitness can vary widely, both because levels of herbivory may differ and because a plant's ability to

mitigate negative effects of tissue loss due to herbivory is variable (Simms 2000).

Tolerance to herbivory is a plant's ability to maintain fitness after being eaten via mechanisms such as compensatory growth or increased photosynthetic rate (Rosenthal and Kotanen 1994, Stowe et al. 2000, Tiffin 2000, Núñez-Farfán et al. 2007). For example, tolerance to apical meristem or main stem removal typically involves growth of shoots from basal meristems and lateral branches from axillary buds (Tiffin 2000, Hawkes and Sullivan 2001, Wise and Abrahamson 2007). Tolerance is predicted to evolve when the probability of being eaten is size dependent or herbivory is severe (Stowe et al. 2000). Plants may instead avoid herbivory by altering apparency or phenology (Brown et al. 1991, Pilon 2000, Tiffin 2000). Because herbivory directly affects fitness components, it has the potential to shape patterns of natural selection on tolerance (Núñez-Farfán et al. 2007, Fornoni 2011) and avoidance. If herbivory and its effects on subsequent growth and reproduction vary among populations, the plant–herbivore relation-

Manuscript received 4 April 2014; revised 14 July 2014; accepted 5 August 2014. Corresponding Editor: G. A. Fox.

³ Present address: Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA.
E-mail: hp8j@virginia.edu.

⁴ Present address: Christopher Newport University, Department of Organismal and Environmental Biology, Newport News, Virginia 23606 USA.

ship may be an important force in shaping population differentiation (Knight et al. 2009).

Herbivory and tolerance could covary with latitudinal or climatic gradients over large areas, but broad-scale patterns are largely unknown (Russell et al. 2001). The prevailing hypothesis is that herbivory is greater at lower latitudes than higher latitudes due to a climatic gradient that affects abundance and intensity of plant–herbivore interactions (Coley and Barone 1996, Pennings et al. 2009). As a consequence, we may expect populations at lower latitudes to have evolved greater defenses or increased tolerance to being eaten. However, current empirical work and meta-analysis do not support a latitudinal gradient in herbivory and plant defense (Moles et al. 2011a, b, Poore et al. 2012). Other work has found variation in tolerance among populations in a limited area (Bergelson and Crawley 1992, Juenger et al. 2000, Banta et al. 2010, Boalt et al. 2010). A range-wide comparison of herbivory and tolerance would reveal whether broad-scale patterns such as climatic gradients shape these factors, or if herbivory and tolerance may be better characterized by a mosaic of variation, indicating the dominance of local factors, such as plant community composition and deer density.

Much of the work investigating the effects of herbivory on plant populations has focused on insects (as reviewed by Coley and Barone 1996, Moles et al. 2011a), therefore it is less known whether generalities, such as latitudinal patterns, are also applicable to mammalian herbivores. White-tailed deer (*Odocoileus virginianus*) are worldwide and cause major ecological impacts through herbivory (Crête 1999, Côté et al. 2004, McGraw and Furedi 2005, Suzuki et al. 2013). In North America, deer are native but have recently become overabundant (McCabe and McCabe 1997). They are selective foragers that browse on trees and herbs (Rooney and Waller 2003, Côté et al. 2004, Kimball et al. 2012), and typically consume larger individuals (Freeman et al. 2003, McGraw and Furedi 2005, Knight et al. 2009). Deer browse reduces population viability (McGraw and Furedi 2005) and modifies abundance and vegetation dynamics (Côté et al. 2004, 2008, DiTommaso et al. 2014, Kalisz et al. 2014, Nuttle et al. 2014). However, broad-scale effects of deer browse on plant populations are unknown.

To explore broad-scale patterns of deer browse and its consequences for reproductive success and differentiation among populations, we surveyed 17 populations of the monocarpic herb *Campanulastrum americanum*. Previous work in a single population found extremely high frequencies of browsing (70–100% of plants eaten) that depended on local light environments and led to substantial reductions in reproductive success (75–94%, Lin and Galloway 2010). However, it is not known how widespread such impacts of deer are across populations or years. In addition, the ability of plants to tolerate herbivory can be influenced by environmental conditions such as light, nutrient, and water availability

(Hawkes and Sullivan 2001, Wise and Abrahamson 2007, Lin and Galloway 2010). Therefore, we conducted this survey in each of three years, addressing the following questions: (1) Does the frequency of deer browse vary across *C. americanum*'s range and is it consistent across years? (2) Do deer prefer larger plants? (3) Are plants tolerant to being browsed? (4) If deer consume larger plants, does deer preference influence our interpretation of tolerance to browsing? (5) Finally, do populations with greater browse frequency show a greater degree of tolerance, suggesting adaptation to browsing pressure?

METHODS

Study system

Campanulastrum americanum (L.) Small (= *Campanula americana* L.), in the Campanulaceae, is an insect-pollinated monocarpic herb that occurs in the central to eastern United States (Appendix: Fig. A1). Habitats of *C. americanum* have well-drained, moist soil and include deciduous forest, limestone outcroppings, and riparian woodland. These habitats are typically disturbed, such as areas adjacent to trails, in and near forest edges, and amid tree-fall gaps. Seeds germinate in the fall or spring. Winter cues reproduction, therefore plants are monocarpic and have an obligately annual (fall germinating) or biennial (spring germinating) life history. Individuals grow as rosettes: bolting starts in the spring and flowering begins in mid-summer and continues through the end of summer. Flowers occur in compact inflorescences at nodes on the main stem and lateral branches. Fruits develop over 5–10 weeks and, when mature, pores thin and open to passively disperse seeds while fruits remain on the plant.

Throughout the *C. americanum* range, deer account for the majority of tissue lost to all herbivores (H. R. Prendeville, J. C. Steven, and L. F. Galloway, unpublished data). White-tailed deer, *Odocoileus virginianus*, rarely browse on *C. americanum* rosettes, instead primarily consuming plants during bolting. Deer typically bite the plant mid-stem, removing ~25% of the apical portion of the bolting stalk prior to flowering (average, post-browse height was 32–48 cm [Lin and Galloway 2010]). They may also consume lateral branches if present. Since fruits are borne along the length of the main stem and lateral branches, deer browse can dramatically reduce reproductive success of *C. americanum* (Lin and Galloway 2010). Plants compensate for browsing through the production of lateral branches with new reproductive nodes.

Survey of deer browse and reproductive success in wild populations

To determine whether the amount and effects of deer browse differ across the *C. americanum* range, we surveyed 17 populations of *C. americanum* along a latitudinal transect over three years (Appendix A: Fig. A1, Table A1). Across the range of *C. americanum*,

latitude was negatively correlated with 50-year averages of mean annual temperature and total annual precipitation (Prendeville et al. 2013). Following methods in Prendeville et al. (2013), we examined the relationship between latitude and climate for the 17 populations in the three years of the study. For each year in this study, latitude was negatively correlated with mean annual temperature and total annual precipitation (temperature $r \leq -0.95$, $P < 0.0001$; precipitation $r \leq -0.96$, $P < 0.0001$). So, on average, northern populations experience a cooler and drier environment than southern populations.

In 2011–2013, we surveyed the 17 populations in late August–September, when most fruits had been initiated and the majority of reproduction had occurred. In 2011, we established 8–29 representative census locations by haphazardly placing 0.5×0.5 m quadrats in each *C. americanum* population. Quadrat number varied among populations (mean 20) because a few low-density populations required more quadrats to achieve an adequate sample size of flowering plants. One site (VA) was excluded in 2011 because it only had three reproductive plants. In 2012 and 2013, additional quadrats were added to replace those with no reproductive plants. For every plant within a quadrat, we recorded the presence or absence of deer browse (indicated by uneven removal of stem tissue as deer have bottom incisors and lack top incisors), measured stem diameter at the base of the plant, and counted the number of fruits and open flowers. Reproductive success was estimated by the total of fruits and flowers. Although not all flowers become fruit, most do, and because herbivory delays reproduction (Lin and Galloway 2010), including flowers in the reproductive estimate reduces bias against eaten plants. On average, only 5% of the reproductive structures we counted were flowers, indicating that the majority of reproduction had occurred and any bias was minimal. There were fewer seeds per fruit on average in eaten (25.8 seeds) than uneaten plants (30.85 seeds, $F_{1,247} = 4.03$, $P = 0.046$); therefore, fruit counts underestimate reproductive success differences due to herbivory. Stem diameter is an index of plant size that does not change after deer browse (J. C. Steven, *unpublished data*). In each population, the number of plants surveyed ranged from 10 to 134 each year, with an overall average of 53 plants.

Statistical analysis

We examined the effects of population, year, and plant stem diameter on the frequency of browse. A general linear model with population and year as fixed effects, plant stem diameter as a covariate, and a binomial error distribution was used to evaluate the presence or absence of deer browse on each flowering plant (PROC GLIMMIX, SAS 9.3 [SAS Institute 2011]). The population, year, and stem diameter three-way interaction was not significant and was removed from the model.

TABLE 1. Analysis of variance examining the effects of stem diameter, a measure of plant size, on the presence or absence of deer browse in 17 *Campanulastrum americanum* populations in three years.

Factor	df	F	P
Population	16	6.22	<0.0001
Stem diameter	1	90.81	<0.0001
Population \times Stem diameter	16	3.89	<0.0001
Year	2	0.00	0.9988
Population \times Year	30	3.80	<0.0001
Stem diameter \times Year	2	1.58	0.2068
Error	2143		

Surveyed populations occur along a latitudinal gradient (Fig. A1). To determine if there was a relationship between browse and latitude, we used a generalized linear model with a beta error distribution to examine the fixed effect of year with latitude as a covariate and the interaction of these factors on population mean browse (PROC GLIMMIX). Since the four southernmost populations experienced high herbivory, we used the same model to investigate the effect of latitude on browse without these populations.

We determined the effects of deer herbivory on plant reproductive success. We examined the effects of browse, population, year, and the interaction of these factors on the reproductive success of individual plants using a generalized linear model with a negative binomial error distribution since the variance exceeded the mean. Plant stem diameter was included as a covariate in order to evaluate whether browsing reduced reproductive success after accounting for plant size. There was a significant interaction between population, year, and browse, so we analyzed the effects of population and browse separately for each year. In addition, we conducted the same analysis without stem diameter as a covariate to understand the relationship between reproductive success and deer browse under conditions in which deer preference for plant size affected reproductive success. We estimated least-square means of reproductive success for each population and year for browsed and uneaten plants from this analysis. Tolerance was indicated if the difference in reproductive success between eaten and uneaten plants was at or above zero. We examined the relationship between the population proportion of deer browse and tolerance by calculating the correlation between the proportion browsed and the difference in mean reproductive success of eaten and uneaten plants.

Least-square means \pm SE are presented unless otherwise noted.

RESULTS

The proportion of *C. americanum* eaten by deer varied among the 17 populations and deer consumed larger plants (Table 1). Across populations and years, the proportion of plants eaten ranged from 0 to 0.96 with almost half of the plants in a population being browsed

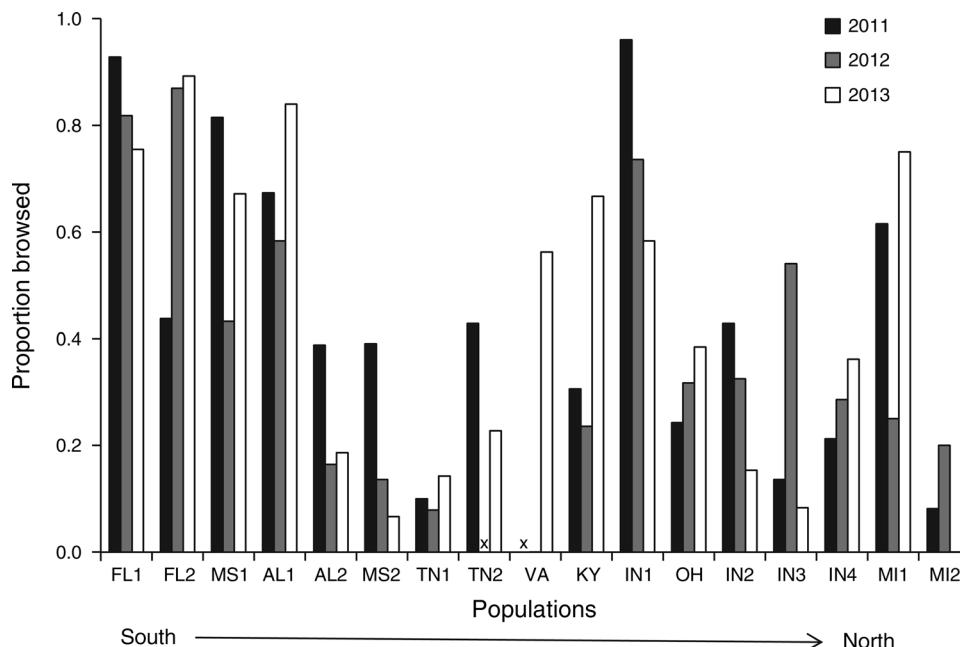


FIG. 1. Proportion of deer browse surveyed in each population of *Campanulastrum americanum* in 2011 (black bars), 2012 (gray bars), and 2013 (white bars). Populations not surveyed in certain years are indicated with an x. Populations are organized by latitude and identifications are the U.S. State abbreviation and site number within a state.

on average (0.46 ± 0.01 ; Fig. 1). The frequency of browse within populations differed among years, although browse levels across years were similar on average (Table 1; Fig. 1). Plants browsed by deer were larger (stem diameter 3.95 ± 0.7 mm) in comparison to uneaten plants (3.32 ± 0.06 mm; Table 1; Fig. 2a–c). The effect of plant size on the probability of being eaten was consistent among years, but varied among plant populations (Table 1; Fig. 2a–c).

Browse levels were greater in southern populations than northern populations and this pattern was consistent among years (Table 2a). The four southernmost populations, which span just more than 1° latitude, experienced a high proportion of deer browse (average across years: 0.64–0.83; Fig. 1). When these populations were removed from the analysis, there was no effect of latitude, year, or the interaction between these factors on the proportion of browse among the remaining 13 populations that span almost 9° latitude (average across years and populations: 0.32; Table 2b).

After removing variation due to plant size, the reproductive success of browsed plants was less (25.39 ± 2.35) than unbrowsed plants (28.84 ± 2.04 ; Table 3). The magnitude of the difference varied among years and populations. However, in two out of three years, reduction in reproductive success due to browsing was similar among populations, when controlling for plant size (though in 2011 the interaction between population and browse was near significance, Table 3; Fig. 2d–f).

Since deer consume larger plants and reproductive success is positively correlated with plant size (uneaten

plants $r = 0.64$, $P < 0.0001$), we examined the effects of browse on reproductive success without controlling for plant size. Here, reproductive success was similar for eaten and uneaten plants in 2011 and 2012, but in 2013, reproductive success of uneaten plants was greater than that of eaten plants (Table 3). Over three years of observation, there were only a few populations where the reproductive success of eaten plants was on average greater than that of uneaten plants (Fig. 3).

The degree of tolerance was not associated with the frequency of browse. The proportion of herbivory experienced by a population did not affect the difference in reproductive success between uneaten and eaten plants ($r = -0.145$, $P = 0.393$; Fig. 3).

DISCUSSION

Throughout the range of *C. americanum*, we found variation among populations in the extent to which plants were browsed by deer. Some of this variation was explained by latitude with plants in southern populations more likely to be browsed than those in the north. However, the pattern was gone without the four southernmost populations, suggesting a regional effect rather than clinal variation. Such local- or regional-scale patterns of deer herbivory may be due to variation in deer abundance and behavior, relative plant apparency, or plant palatability (cf. Miller et al. 2007, Bee et al. 2009, Kimball et al. 2012, Masé and Côté 2013). Thus, our work in conjunction with other recent work (Moles et al. 2011a, Poore et al. 2012), does not support the

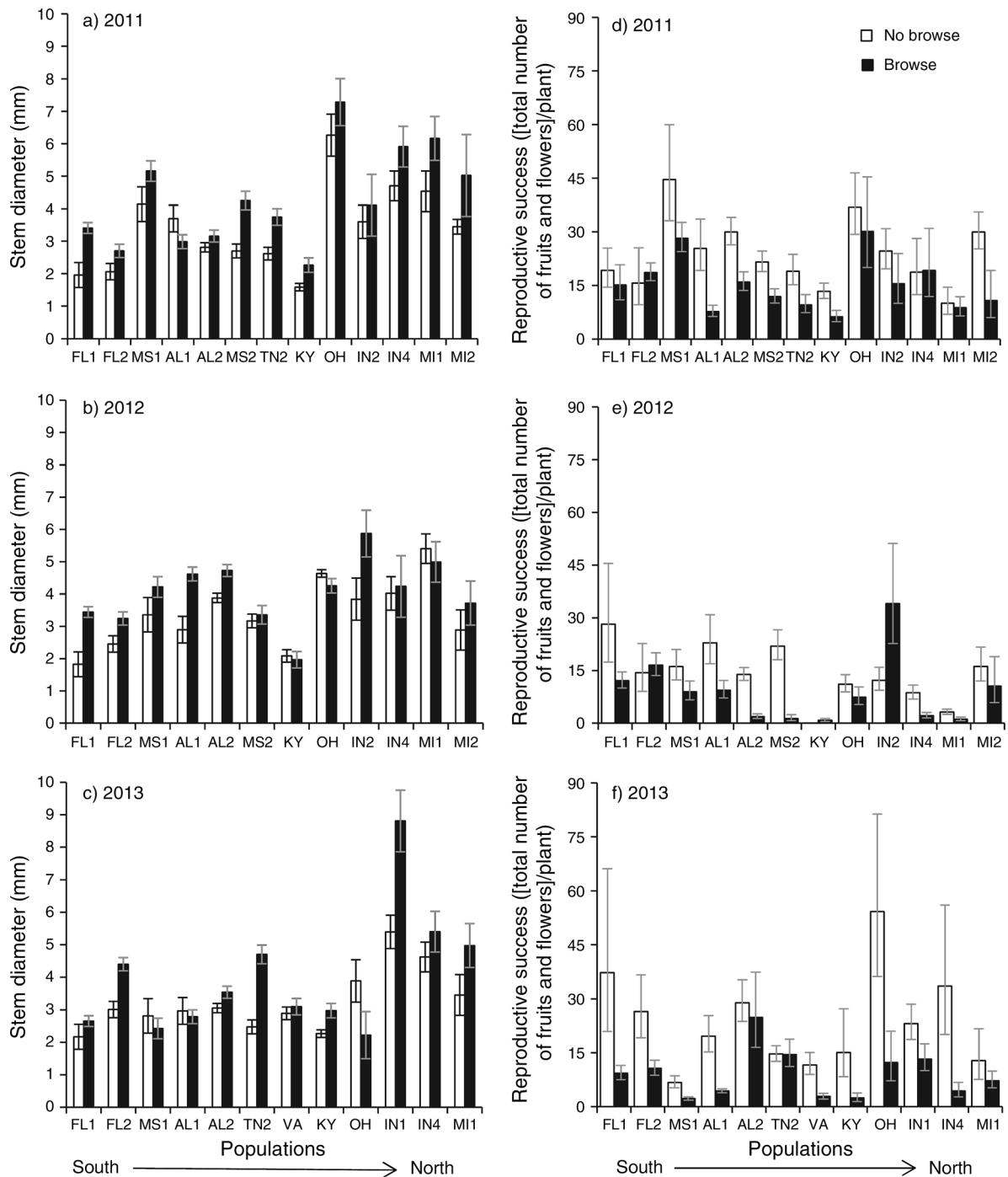


FIG. 2. (a–c) Stem diameter (mean \pm SE) and (d–f) reproductive success (least-square mean \pm SE) with plant stem diameter as a covariate, of plants not eaten by deer (white bars) or eaten by deer (black bars) in each *Campanulastrum americanum* population for 2011, 2012, and 2013. Reproductive success was estimated by the total of fruits and flowers per plant. Least-square means and SE are back transformed. Among years, some populations were excluded due to limited sample size. Populations are organized by latitude and identifications are the U.S. State abbreviation and site number within a state.

hypothesis that there is a broad-scale relationship between latitude and herbivory.

Plants were tolerant to deer browse, but estimates of tolerance from natural populations were affected by

deer selectively consuming larger plants. In wild populations, tolerance is typically measured by comparing the reproductive success of eaten plants to uneaten plants (Strauss and Agrawal 1999). If reproductive

TABLE 2. Analysis of covariance of *Campanulastrum americanum* population mean proportion of deer browse in three years for latitude of (a) all 17 populations and (b) 13 populations, excluding the most southern populations.

Factor	df	F	P
a) 17 populations			
Latitude	1	7.76	0.0081
Year	2	0.14	0.8729
Latitude × Year	2	0.11	0.9004
Error	41		
b) 13 populations			
Latitude	1	1.39	0.2482
Year	2	1.28	0.2930
Latitude × Year	2	1.24	0.3044
Error	29		

success of eaten plants is equivalent to or greater than uneaten plants, then plants are tolerant to herbivory. However, in wild populations under natural levels of herbivory, this definition of tolerance is difficult to interpret. For example, if deer are selective in which plants they browse, reproductive success of the browsed group will be influenced both by the fact that they are browsed and by plant attributes on which the browsing preference was based. As a consequence, estimates of tolerance to herbivory from nature are biased (Stowe et al. 2000). In many populations and years, *C. americana-*

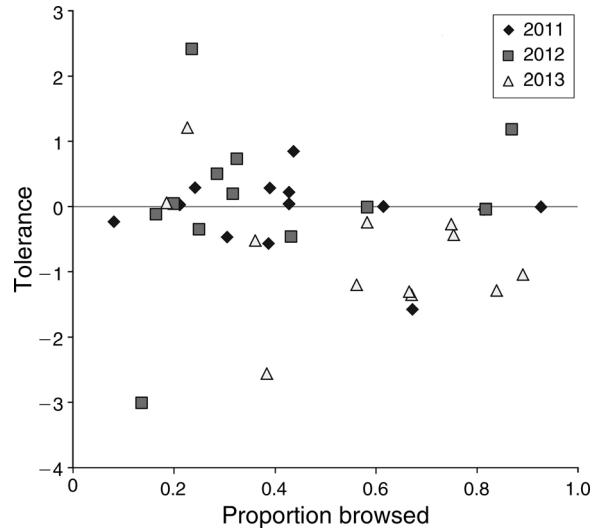


FIG. 3. The proportion of deer browse by tolerance, which was measured as the difference in least-square mean reproductive success of uneaten and eaten plants for each *Campanulastrum americanum* population in 2011 (black diamonds), 2012 (gray squares), and 2013 (white triangles). Mean reproductive success is not adjusted for plant size. Values above zero indicate that eaten plants had greater reproductive success than uneaten plants, while values below zero indicate that the uneaten plants had greater reproductive success than eaten plants. Among years, some populations were excluded due to limited sample size.

TABLE 3. Analysis of variance of reproductive success (the number of fruits and flowers on a plant) from populations of *Campanulastrum americanum* with stem diameter as a covariate and with no covariate (a) across all three years, and for (b) 2011, (c) 2012, and (d) 2013. Among years, some populations were excluded due to limited sample size.

Factor	With covariate			No covariate		
	df	F	P	df	F	P
a) All three years						
Browse	1	76.32	<0.0001	1	6.29	0.0122
Population	14	11.45	<0.0001	14	21.72	<0.0001
Browse × Population	14	2.94	0.0002	14	3.41	<0.0001
Year	2	50.29	<0.0001	2	39.72	<0.0001
Browse × Year	2	5.40	0.0046	2	7.66	0.0005
Population × Year	20	9.30	<0.0001	20	11.64	<0.0001
Browse × Year × Population	20	3.21	<0.0001	20	3.00	<0.0001
Stem diameter	1	745.23	<0.0001			
Error	1834			1867		
b) 2011						
Browse	1	25.45	<0.0001	1	0.66	0.4170
Population	12	10.68	<0.0001	12	33.83	<0.0001
Browse × Population	12	1.68	0.0659	12	3.02	0.0004
Stem diameter	1	572.21	<0.0001			
Error	770			772		
c) 2012						
Browse	1	9.85	0.0018	1	0.20	0.6531
Population	11	11.57	<0.0001	11	15.05	<0.0001
Browse × Population	11	3.94	<0.0001	11	2.32	0.0086
Stem diameter	1	133.75	<0.0001			
Error	514			543		
d) 2013						
Browse	1	33.27	<0.0001	1	10.54	0.0012
Population	11	5.47	<0.0001	11	7.33	<0.0001
Browse × Population	11	1.22	0.2703	11	2.44	0.0056
Stem diameter	1	150.99	<0.0001			
Error	548			552		

num seem to tolerate deer browse. However, as found in other species (Freeman et al. 2003, McGraw and Furedi 2005, Knight et al. 2009), *C. americanum* consumed by deer were larger and larger plants had greater reproductive success. Thus, browsed plants had similar reproductive success to those not eaten due to size differences, and populations appear more tolerant to deer browse when plant size is not controlled. When reproductive success was adjusted for plant size, it was typically lower in eaten plants than uneaten plants, although the magnitude of that reduction, and hence the evidence for tolerance, varied among populations and years.

Deer browse is intense in some populations of *C. americanum*, and these populations are expected to be under selective pressure to avoid or compensate for this herbivory. In *C. americanum*, previous work found sufficient genetic variation in reproductive phenology to allow for substantial evolutionary change after just a few generations of artificial selection (Burgess et al. 2007, Galloway et al. 2009). This variation, together with intense selection by deer, may result in plants that avoid being browsed by delaying bolting until the surrounding community reduces apparency or deer preferences change. In support of this idea, there was a positive relationship between the proportion of deer browse in 2012 and the day of first flower in greenhouse-grown plants from the same populations ($N = 9$, $r = 0.84$, $P = 0.018$; first flower data from Prendeville et al. [2013]) though this relationship does not exist when comparing levels of deer browse in other years. Alternatively, plants may accelerate bolting to have additional time for regrowth and mitigate the negative effects of browse on reproductive success. Such selective pressures imposed by deer browse may explain variation in reproductive phenology observed among populations of *C. americanum*, particularly the day of first flower; unlike many other taxa, the day of first flower in *C. americanum* is not correlated with latitude (Prendeville et al. 2013).

Deer browse can be intense and reduce reproductive success in *C. americanum*, yet many populations are not tolerant to high levels of browsing. In particular, the level of deer browse varied among populations, but populations that experienced greater browsing frequency did not have greater tolerance. Variability over both short and long time scales may contribute to this lack of a relationship. There were substantial year-to-year differences in deer browse, which could lead to variable selection for tolerance and consequently a weak correspondence between browsing and tolerance (also see Strauss and Agrawal 1999). In addition, overabundance of deer is relatively recent, and tolerance levels may not match the current selective environment. However, only controlled experiments, not field observations as presented here, will clarify the role of other factors on selection for tolerance and reproductive success. Regardless, the lack of a strong latitudinal gradient in patterns of browse intensity and tolerance

suggests that relevant environmental factors are likely to be local rather than large-scale climate patterns.

ACKNOWLEDGMENTS

Funding for this work by NSF DEB-1020717 and an ROA supplement; J. C. Steven was supported by a faculty fellowship from Sweet Briar College. We are thankful for assistance in locating and providing access to wild populations by A. Stiles, W. Bailey, Florida Caverns and Torreya State Parks of Florida, M. Alford, S. Threlkeld, C. Potts, Land Trust of North Alabama, R. McCoy, Tennessee State Parks, B. R. Keener, J. Bender, Kentucky State Nature Preserves Commission, B. James, Floraciffs State Nature Preserve, M. Crews, Lincoln State Park of Indiana, M. Becus, Ault Park, C. Bladow, The Nature Conservancy, S. Ross, B. Yankowiak, Little River Wetlands Project, Fernwood Botanical Garden and Nature Preserve, T. Basset, M. Richards, and Fort Custer Training Center. We are grateful for field assistance from Carolyn Beans, Anna Greenlee, Karen Barnard-Kubow, and Rowan Sprague.

LITERATURE CITED

- Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conservation Biology* 12:995–1004.
- Banta, J. A., M. H. H. Stevens, and M. Pigliucci. 2010. A comprehensive test of the “limiting resources” framework applied to plant tolerance to apical meristem damage. *Oikos* 119:359–369.
- Bee, J. N., A. J. Tanentzap, W. G. Lee, R. B. Lavers, A. F. Mark, J. A. Mills, and D. A. Coomes. 2009. The benefits of being in a bad neighbourhood: plant community composition influences red deer foraging decisions. *Oikos* 118:18–24.
- Bergelson, J., and M. J. Crawley. 1992. Herbivory and *Ipomopsis aggregata*: the disadvantage of being eaten. *American Naturalist* 139:870–882.
- Boalt, E., L. Arvanitis, K. Lehtilä, and J. Ehrlén. 2010. The association among herbivory tolerance, ploidy level, and herbivory pressure in *Cardamine pratensis*. *Evolutionary Ecology* 24:1101–1113.
- Brown, V. K., J. H. Lawton, and P. J. Grubb. 1991. Herbivory and the evolution of leaf size and shape. *Philosophical Transactions of the Royal Society B* 333:265–272.
- Burgess, K. S., J. R. Etterson, and L. F. Galloway. 2007. Artificial selection shifts flowering phenology and other correlated traits in an autotetraploid herb. *Heredity* 99: 641–648.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- Côté, S. D., C. Dussault, J. Huot, F. O. Potvin, J.-P. Tremblay, and V. Viera. 2008. High herbivore density and boreal forest ecology: white-tailed deer on Anticosti Island. Pages 154–161 in A. J. Gaston, T. E. Golumbia, J.-L. Martin, and S. T. Sharpe, editors. *Lessons from the islands: introduced species and what they tell us about how ecosystems work*. Canadian Wildlife Service, Environment Canada, Queen Charlotte City, Queen Charlotte Islands, British Columbia.
- Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147.
- Crawley, M. J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34:531–564.
- Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. *Ecology Letters* 2:223–227.
- DiTommaso, A., S. H. Morris, J. D. Parker, C. L. Cone, and A. A. Agrawal. 2014. Deer browsing delays succession by

- altering aboveground vegetation and belowground seed banks. *PLoS ONE* 9:e91155.
- Fornoni, J. 2011. Ecological and evolutionary implications of plant tolerance to herbivory. *Functional Ecology* 25:399–407.
- Freeman, R. S., A. K. Brody, and C. D. Neefus. 2003. Flowering phenology and compensation for herbivory in *Ipomopsis aggregata*. *Oecologia* 136:394–401.
- Galloway, L. F., J. R. Etterson, and J. W. McGlothlin. 2009. Contribution of direct and maternal genetic effects to life-history evolution. *New Phytologist* 183:826–838.
- Hawkes, C. V., and J. J. Sullivan. 2001. The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82:2045–2058.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 22:477–503.
- Juenger, T., T. Lennartsson, and J. Tuomi. 2000. The evolution of tolerance to damage in *Gentianella campestris*: natural selection and the quantitative genetics of tolerance. *Evolutionary Ecology* 14:393–419.
- Kalish, S., R. B. Spigler, and C. C. Horvitz. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *Proceedings of the National Academy of Sciences USA* 11:4501–4506.
- Kimball, B. A., J. H. Russell, and P. K. Ott. 2012. Phytochemical variation within a single plant species influences foraging behavior of deer. *Oikos* 121:743–751.
- Knight, T. M., H. Caswell, and S. Kalisz. 2009. Population growth rate of a common understory herb decreases nonlinearly across a gradient of deer herbivory. *Forest Ecology and Management* 257:1095–1103.
- Lin, S. M., and L. F. Galloway. 2010. Environmental context determines within- and potential between-generation consequences of herbivory. *Oecologia* 163:911–920.
- Masé, A., and S. D. Côté. 2013. Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Canadian Journal of Zoology* 91:252–263.
- McCabe, T. R., and R. E. McCabe. 1997. Recounting whitetails past. Pages 11–26 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- McGraw, J. B., and M. A. Furedi. 2005. Deer browsing and population viability of a forest understory plant. *Science* 307:920–922.
- Miller, A. M., C. McArthur, and P. J. Smethurst. 2007. Effects of within-patch characteristics on the vulnerability of a plant to herbivory. *Oikos* 116:41–52.
- Moles, A. T., S. P. Bonser, A. G. B. Poore, I. R. Wallis, and W. J. Foley. 2011a. Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25:380–388.
- Moles, A. T., et al. 2011b. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist* 191:777–788.
- Núñez-Farfán, J., J. Fornoni, and P. L. Valverde. 2007. The evolution of resistance and tolerance to herbivores. *Annual Review of Ecology, Evolution, and Systematics* 38:541–566.
- Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *Journal of Ecology* 102:221–228.
- Pennings, S. C., C.-H. Ho, C. S. Salgado, K. Wieski, N. Davé, A. E. Kunza, and E. L. Wason. 2009. Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* 90:183–195.
- Pilson, D. 2000. Herbivory and natural selection on flowering phenology in wild sunflower, *Helianthus annuus*. *Oecologia* 122:72–82.
- Poore, A. G., et al. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* 15:912–922.
- Prendeville, H. R., K. Barnard-Kubow, C. Dai, B. C. Barringer, and L. F. Galloway. 2013. Clinal variation for only some phenological traits across a species range. *Oecologia* 173:421–430.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Rosenthal, J. P., and P. M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution* 9:145–148.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1–26.
- SAS Institute. 2011. SAS 9.3. SAS Institute, Cary, North Carolina, USA.
- Simms, E. L. 2000. Defining tolerance as a norm of reaction. *Evolutionary Ecology* 14:563–570.
- Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance and consumer damage. *Annual Review of Ecology, Evolution, and Systematics* 31:565–595.
- Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14:179–185.
- Suzuki, M., T. Miyashita, H. Kabaya, K. Ochiai, M. Asada, and Z. Kikvidze. 2013. Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos* 122:104–110.
- Tiffin, P. 2000. Mechanisms of tolerance to herbivore damage: what do we know? *Evolutionary Ecology* 14:523–536.
- Wise, M. J., and W. G. Abrahamson. 2007. Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *American Naturalist* 169:443–454.

SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-0653.1.sm>