

Environmental context determines within- and potential between-generation consequences of herbivory

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Abstract Plant tolerance to herbivory may depend on local environmental conditions. Models predict both increased and decreased tolerance with increasing resources. Transgenerational effects of herbivory may result in cross-generation tolerance. We evaluated within- and potential between-generation consequences of deer browsing in light-gap and understory habitats in the forest-edge herb, *Campanulastrum americanum*. Plants were assigned to deer-browsed, simulated-herbivory, and control (undamaged) treatments in the two light environments. In light gaps, plants were eaten earlier, more frequently, and had less vegetative recovery relative to uneaten plants than in the understory. As a result, browsed light-gap plants had a greater reduction in flowers and fruit than understory plants. This reduced tolerance was in part because deer browsing damaged plants in light gaps more than those in the understory. However, in the simulated herbivory treatment, where damage levels were similar between light habitats, plants growing in high-resource light gaps also had reduced tolerance of herbivory relative to those in the forest understory. *C. americanum*'s reproductive phenology was delayed by reduced light and the loss of the apical meristem. As a result, deer-browsed plants in the light gap flowered slightly later than uneaten plants in the understory. *C. americanum* has a polymorphic life history and maternal

flowering time influences the frequency of annual and biennial offspring. The later flowering of deer-browsed plants in light gaps will likely result in a reduced frequency of high-fitness annual offspring and an increase in lower fitness biennial offspring. Therefore, additional between-generation costs of herbivory are expected relative to those predicted by fruit number alone.

Keywords Deer · Flowering phenology · Maternal effects · Plasticity to light · Tolerance

Introduction

Plants differ in their tolerance to herbivory. Some show limited tolerance and are not capable of compensating for losses they sustain from herbivores. In particular, consumption of entire leaves, stems, flowers and fruits by large mammalian herbivores has been shown to jeopardize survival and reproductive success (Crawley 1989; Whigham 1990; Bergelson and Crawley 1992; Augustine and Frelich 1998; Russell et al. 2001; Rooney and Waller 2003). Other plants demonstrate high levels of tolerance, compensating or, in some cases, overcompensating for tissue loss with increased vegetative biomass and seed production (McNaughton 1983; Wallace et al. 1985; Paige and Whitham 1987; Bullock et al. 1994; Lennartsson et al. 1997). Environmental conditions have been shown to affect a plant's ability to tolerate herbivore damage (reviewed in Hawkes and Sullivan 2001; Wise and Abrahamson 2007, 2008). Models of the influence of environmental conditions on tolerance predict varied outcomes including increased tolerance in high-resource conditions (compensatory continuum hypothesis, Maschinski and Whitham 1989), increased tolerance in limited-resource conditions (growth rate model, Hilbert

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et al. 1981), and increased or decreased tolerance depending on whether the environmental difference represents a limiting resource and whether herbivore damage affects the acquisition of that resource (limiting resource model, Wise and Abrahamson 2005). A recent review of the literature suggests that the more detailed limiting resource model has a stronger predictive ability than the other more general models (Wise and Abrahamson 2007). However, most studies were conducted with simulated herbivory under controlled conditions; data to evaluate model predictions are needed from natural populations to complement this review.

Changes to growth, phenology, resource allocation and the expression of defensive compounds as a consequence of herbivory may affect an individual's offspring. The effects of maternal herbivory may alter the expression of offspring traits through a number of mechanisms. Most simply, changes in resource allocation associated with herbivory may alter seed size, and seed size often determines timing of germination and offspring growth rate (Crawley and Nachapong 1985; Agrawal 2001; Pilon and Decker 2002; Mueller et al. 2005). Herbivory has also been found to elicit transgenerational effects, resulting in offspring with increased resistance to herbivore damage (Agrawal et al. 1999) or enhanced defensive traits (Lammerink et al. 1984; Holeski 2007). Finally, herbivory may affect offspring quality by altering the maternal mating system (Steets and Ashman 2004). However, few studies examining the possible effects of maternal herbivory have been conducted under natural conditions. Therefore, we have little knowledge of potential transgenerational effects of herbivory in relevant ecological environments or whether their expression varies across resource levels.

We evaluate the importance of environmental context to damage from deer browsing in a woodland herb. White-tailed deer (*Odocoileus virginianus*) are native herbivores of particular interest because of their increase in abundance in understory habitats throughout much of eastern and central North America (McShea et al. 1997; Augustine and Frelich 1998; Russell et al. 2001; Virginia Department of Game and Inland Fisheries 2007; Thiemann et al. 2009). Increases in deer populations have major ecological implications because they are selective browsers (Cote et al. 2004). Recent studies on American ginseng (McGraw and Furedi 2005) and *Trillium grandiflorum* (Knight 2004) found that deer browsing is so intense that without more long-term management of deer populations, these and other understory herbs are likely to be pushed toward extinction. Given this concern, understanding the extent to which environmental conditions influence the frequency and tolerance of deer herbivory is critical.

We focus on effects of deer browsing in an understory herb with a polymorphic life history. In *Campanulastrum*

americanum, fall-germinating individuals grow as annuals while spring-germinating seeds are biennials (Baskin and Baskin 1984). In the absence of herbivory, *C. americanum*'s light environment indirectly determines the offspring life history schedule by altering flowering time. Light-gap plants grow faster and initiate flowering earlier than their shaded counterparts (Galloway and Etterson 2009). Earlier flowering leads to earlier seed production, and earlier dispersed seeds are more likely to germinate in the fall as annuals (Galloway and Burgess 2009). Consequently, by influencing flowering time, the maternal light environment promotes the production of annual offspring in light-gap habitats and biennials in the shaded understory (Galloway 2002, 2005). Browsing has been shown to alter phenology in other plant species (Lennartsson et al. 1998; Tiffin 2000; Freeman et al. 2003; Huhta et al. 2009). If deer herbivory likewise affects the temporal components of flowering in *C. americanum*, browsed plants may be biased towards the production of either annual or biennial offspring.

Given the importance of light habitat for *C. americanum*'s life history and fitness, we explore whether the frequency and response to deer browsing depend on the local light environment. We evaluate within- and potential between-generation impacts of deer herbivory on *C. americanum* by first addressing whether deer are selective when they browse:

1. In particular, does light environment influence the probability of a plant being eaten?
2. If so, does it influence when a plant is eaten?

We then determine whether light environment influences response to herbivory:

3. Specifically, do survival and regrowth differ between light-gap and understory habitats?
4. Are there potential transgenerational effects of herbivory due to effects on reproductive phenology?
5. Finally, are there within- and potential between-generation costs of herbivory and do these depend on the light environment?

To address these questions, we determined herbivory rate and timing as well as growth, phenology and reproduction on deer-browsed, experimentally clipped and uneaten plants in understory and light-gap locations in a natural population.

Materials and methods

Study system

Campanulastrum americanum (Campanulaceae) Small (= *Campanula americana* L.) is a predominately outcrossing

(Galloway et al. 2003) woodland herb found throughout deciduous forests of eastern North America. Individuals are monocarpic, growing either as annuals or biennials, because vegetative rosettes require a cold period before initiating reproduction. The study population is located on Bean Field Mountain near the Mountain Lake Biological Station on Route 613, Giles County, Virginia, USA. In this population, plants overwinter as rosettes and bolt when temperatures warm in early May. Bolting continues for an average of 65 days until flowering begins in July (B. P. Haggerty and L. F. Galloway, in review). Browsing by white-tailed deer is most intense midway through *C. americanum*'s bolting period (personal observation, see "Results"); rosettes are rarely eaten. All bolting plants that survive flower, therefore browsing may alter the magnitude, but not the probability of reproduction. Browsing typically removes the apical portion of the bolting shoot. In large branched plants, the ends of individual branches may also be removed. In this site, deer herbivory results in substantially greater tissue loss than herbivory by invertebrates for *C. americanum* (Yang 2008).

Campanulastrum americanum have a preference for partial sun and populations inhabit both understory and light-gap areas of wood margins near road cuts, streams and tree falls. Plants in light gaps are typically phenologically accelerated, bolting and flowering before those in the understory (Kilkenny and Galloway 2008; Galloway and Etterson 2009). In addition, germination conditions in light-gap habitats result in more annuals while those under the forest canopy produce more biennials (Galloway and Etterson 2007). The study population is located on a steep slope with a number of tree-fall light gaps.

Experimental design

Prior to the onset of deer herbivory in the spring, a total of 260 individuals were haphazardly selected from light-gap ($n = 151$) and shaded understory ($n = 109$) areas of the study population. Distances between plants ranged from ~ 0.5 m to the extent of the population, ~ 100 m. Plants within each light environment were subject to one of three herbivory treatments: deer-browsed, simulated herbivory or control. Approximately one-third of the plants in each light environment were designated as controls and were individually protected from deer herbivory with wire-mesh enclosures (understory $n = 31$, light gap $n = 41$). The remaining plants were unprotected. Whenever a plant was browsed, the date was recorded and the plant was assigned to the deer-browsed treatment (understory $n = 42$, light gap $n = 81$). On that date, an undamaged plant from the same light environment, relatively near the browsed plant, was assigned to the simulated-herbivory treatment (understory $n = 32$, light gap $n = 24$). The top 18 cm of stem was

removed when plants were assigned to the simulated-herbivory treatment, an amount comparable to herbivory-induced tissue loss (see "Results"). Wire-mesh enclosures were placed around plants assigned to deer-browsed and simulated-herbivory treatments to protect them from future browsing. The simulated-herbivory treatment was designed to test for the consequences of biomass removal independent of other browsing effects, i.e., stimulatory effects of deer saliva and/or trampling, and it also permits evaluation of response to biomass removal in random plants in contrast to those deer select to browse.

To evaluate patterns of herbivory, we scored browsing damage and plant size at regular intervals. Height was measured on all individuals at the start of the experiment and uneaten plants every third day until flowering to estimate plant size prior to being browsed. After observing the first deer-browsed plant on 13 June, plants were checked for deer herbivory and survival every third day until all plants had initiated flowering. Following an herbivory event, the height of the deer-eaten stem was recorded. We estimated the amount of stem consumed by comparing the height of the remaining stem to the most recent measurement from the height census.

Response to the loss of vegetative tissue in deer-browsed and simulated-herbivory plants was tracked by measuring branch number and length. These measurements were taken on all plants every third day from the date of first herbivory until all plants flowered. Every third day we also recorded newly flowering plants (date of first flower) and the number of open flowers. We harvested plants when flowering was finished, dried them, and counted the number of fruits and determined above-ground biomass for each individual.

Statistical analysis

Initially, patterns of deer browsing were analyzed. A χ^2 test was used to evaluate whether the probability of being browsed differed between light environments. Deer preference associated with plant size was determined using logistic regression with whether or not a plant was eaten as the dependent variable and initial size as the independent variable. The timing of herbivory in light-gap and understory regions was compared using a *t*-test. Analysis of covariance (ANCOVA) was employed to determine whether the difference in the timing of herbivory in the two light environments was influenced by differences in plant size; initial size was used to allow for a comparison among all individuals. The absolute and relative amount of tissue loss due to browsing was compared between the light environments with ANCOVA including light as a fixed effect and height prior to being eaten as the covariate.

Survival and growth of browsed, clipped and uneaten plants were then compared. To determine whether survival of deer-browsed plants differed between light environ-

ments, we conducted a log-linear analysis with light as a categorical factor and size prior to herbivory and after herbivory as continuous variables. Recovery from herbivory was estimated by total branch length at the initiation of flowering. This was square-root transformed and analyzed using ANOVA with light environment, herbivory treatment and their interaction as factors. A repeated-measures ANOVA on total branch length measured at 3-day intervals was also conducted with these same factors to evaluate whether the pattern of branch growth varied among light environments or herbivory treatments. Final plant size was estimated with harvest biomass (ln-transformed) and analyzed with ANOVA using light, herbivory, and their interaction as factors.

Phenological traits (date of first flower, average flower day and flowering duration) and the fitness correlate (fruit number) were analyzed with ANOVA using light, herbivory, and a light-by-herbivory interaction term as factors. If there was a significant light environment by herbivory treatment interaction, the herbivory treatments within in each light environment were compared with ANOVA. We estimated flowering duration as the number of days from initiation of flowering to when the last flower was observed. We also calculated average flower day to evaluate differences in seasonal patterns of flower production. Average flower day estimates the day the mean flower was produced and was calculated by weighting each of the repeated flower counts by the census date on which the count was made (Nuismer and Cunningham 2005). Fruit number (ln + 1 transformed) includes plants that died as zero so it reflects both the survival and fecundity components of fitness.

All analyses were conducted using SAS (SAS Institute 2005), light environment and herbivory treatments were treated as fixed effects, and traits were transformed as indicated to meet the assumptions of ANOVA. SEs are reported throughout except where indicated.

Results

Patterns of deer herbivory

Light environment affected the likelihood that a plant would be browsed. Plants in light gaps were more likely to be foraged upon by deer than their understory counterparts ($\chi^2_1 = 27.86$, $n = 141$, $P < 0.001$). All unprotected light-gap plants were browsed, while browsing occurred on only 70% of the understory plants (Fig. 1). Since all the unprotected plants in the light gaps were eaten, it was not possible to determine whether deer exhibited a preference for larger plants. However, in the understory, deer were selective with respect to the size of the plants that they chose to browse

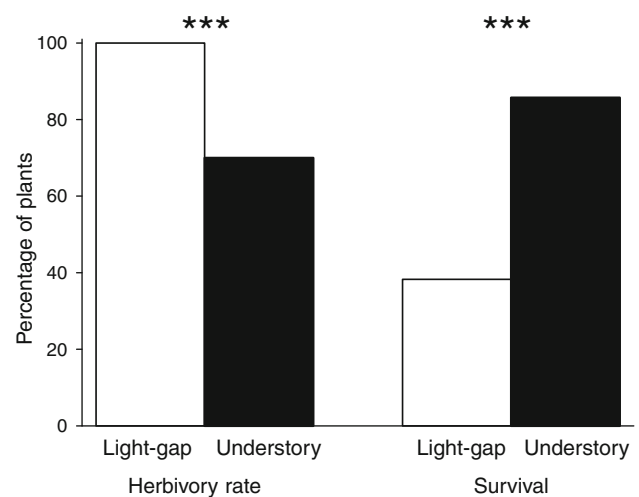


Fig. 1 The rate of herbivory, measured as the percentage of plants eaten, and percentage survival for deer-browsed *Campanulastrum americanum* growing in light-gap and understory environments. *** $P < 0.001$ (comparison between light-gap and understory habitats, see text for details)

($\chi^2_1 = 4.89$, $n = 60$, $P = 0.027$). Larger plants were more likely to be eaten; the mean initial height of eaten plants was 48.5 ± 1.9 cm and of uneaten plants 40.25 ± 2.8 cm. Light-gap plants were on average larger than understory plants ($t = 8.89$, $df = 258$, $P < 0.001$; initial height: light gap 62.5 ± 2.4 cm, understory 46.0 ± 1.3 cm), and this difference in size may underlie the greater herbivory in light gaps.

Light environment also affected when plants were browsed. Light-gap plants were intensely browsed over a short period of time early in the study (~1 week), while deer damage in the understory occurred over a longer time scale (~6 weeks). On average, plants in light gaps were browsed 2 weeks earlier than plants in the understory habitat ($t = 6.51$, $df = 41$, $P < 0.001$; mean date of browsing: light gaps 19 June ± 0.34 days, understory 2 July ± 2.01 days). Deer browsed larger plants earlier than smaller plants ($r^2 = -0.281$, $n = 121$, $P = 0.002$). However, this relationship was due to the fact the larger plants occurred within light gaps. Plant size did not explain when plants were browsed once light environment was taken into account (initial height: $F_{1,119} = 0.06$, $P = 0.814$) and the relationship between initial height and timing of herbivory did not differ between light environments (light \times initial height: $F_{1,119} = 0.09$, $P = 0.764$).

On average, deer-browsed plants in light gaps lost 14.64 ± 2.17 (SD) cm of stem while those in the understory lost 14.56 ± 2.14 (SD) cm of stem. The range of tissue removed was also similar between habitats, from near 0 to 52 cm (light gap) and 56 cm (understory). Deer may have consumed slightly more tissue than this, however, because mean height increased in the 3 days between

Table 1 ANOVA for branch length at flowering, above-ground biomass, day of first flower, average flower day, flowering duration and fruit number for *Campanulastrum americanum* that experienced three

levels of herbivory and were grown in understory and light-gap regions of their natural population

Source	df	Branch length	Biomass	Day of first flower	Average flower day	Flowering duration	Fruit number
Herbivory	2	4.53*	13.39***	85.15***	69.60***	32.57***	78.97***
Light	1	32.34***	112.31***	79.55***	39.54***	53.97***	30.68***
Herbivory × light	2	10.96***	7.82***	2.20	1.34	0.37	13.89***
Error df		245	147	159	160	160	220

F-statistics are shown

* $P < 0.05$, *** $P < 0.001$

measurements 4.76 ± 2.59 (SD) in light gaps and 1.92 ± 2.00 (SD) in the understory. Larger plants lost more vegetative tissue when browsed ($F_{1,119} = 26.20, P < 0.001$). However, relative tissue loss, measured as the ratio of plant height before and after herbivory, was not related to plant size ($F_{1,119} = 0.55, P = 0.46$). The amount of stem removed, both in absolute and relative terms, did not depend on the light environment after accounting for plant size (light, absolute loss, $F_{1,119} = 0.15, P = 0.23$; relative loss, $F_{1,119} = 0.12, P = 0.73$). However, deer tended to remove more tissue on larger understory plants than light-gap plants while plant size did not affect the relative loss across light habitats (light × height, absolute loss, $F_{1,119} = 3.81, P = 0.05$; relative loss, $F_{1,119} = 1.15, P = 0.29$).

Response to herbivory

Survival of deer-browsed plants differed between the two light environments. Understory plants were much more likely to survive browsing events than light-gap plants ($\chi^2_1 = 18.83, n = 123, P < 0.001$; Fig. 1). Survival did not depend on plant size before ($\chi^2_1 = 0.00, n = 123, P = 0.99$) or after ($\chi^2_1 = 0.14, n = 123, P = 0.71$) herbivory. All control plants survived through reproduction.

Of the plants that did survive, recovery of damaged plants, measured as changes in branch length, depended on both light and herbivory treatments (Table 1; Fig. 2; repeated measures analysis time × light × herbivory interaction $F_{1,1940} = 13.52, P < 0.001$). In the understory, there was no difference in branch growth between deer-browsed and simulated-herbivory plants. Whereas in light gaps, branches grew more quickly on simulated-herbivory plants than deer-browsed plants. As a consequence at flowering, uneaten and simulated-herbivory plants had longer branches than those that were deer-browsed in the light-gap environment. While in the understory, uneaten plants had shorter branches than the deer-browsed and simulated-herbivory treatment plants (Fig. 2). Overall, light-gap plants had longer branches than their understory counterparts (Fig. 2). The effect of herbivory on final biomass also depended on the light environment (Table 1). Biomass of

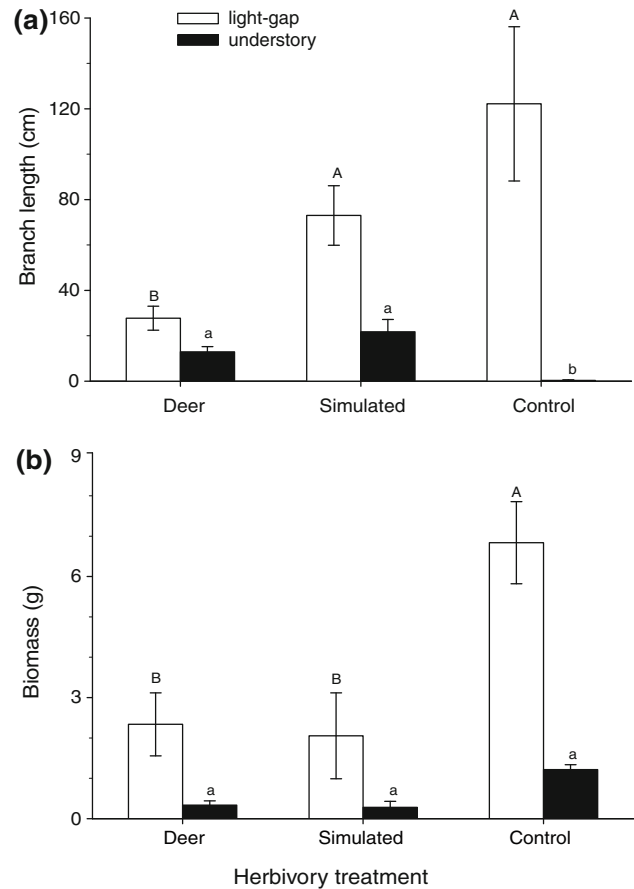


Fig. 2 Mean **a** branch length and **b** final above-ground biomass (\pm SE) for *C. americanum* plants that experienced deer browsing, simulated herbivory or no herbivory growing in light-gap and understory environments. Means of the herbivory treatments were compared within each light environment due to significant light × herbivory interactions (Table 1). Means different at $\alpha = 0.05$ within each light environment are indicated by different letters

understory plants was similar regardless of the herbivory treatment ($F_{2,77} = 2.84, P < 0.06$). In contrast, in light gaps control plants were significantly heavier than those that experienced deer browsing or simulated herbivory ($F_{2,70} = 17.13, P < 0.001$; Fig. 2).

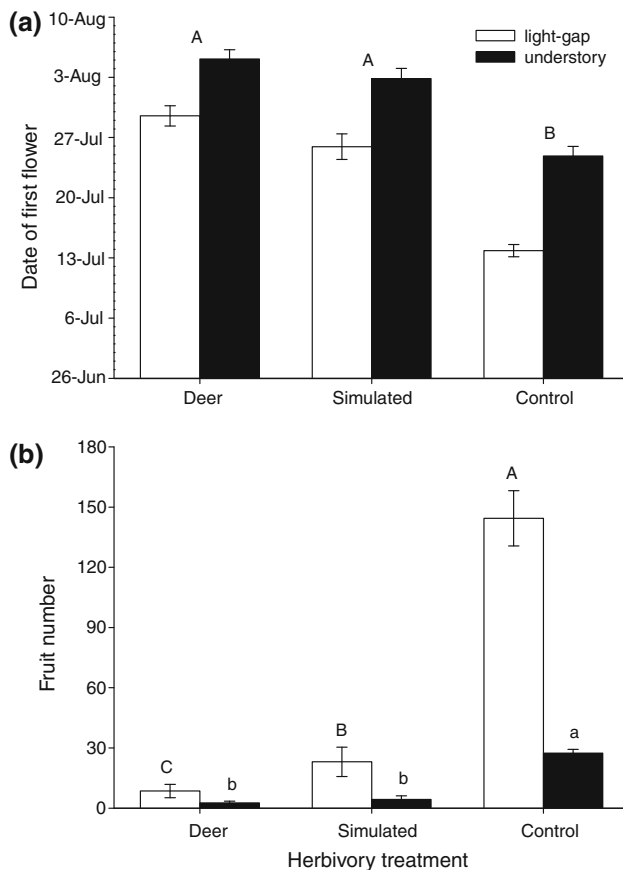


Fig. 3 Mean (\pm SE) **a** date of first flower and **b** fruit number for *C. americanum* plants that experienced deer browsing, simulated herbivory and no herbivory growing in light-gap and understory environments. Means different at $\alpha = 0.05$ are indicated by different letters. For fruit number comparisons were made within each light environment due to a significant light \times herbivory interaction (Table 1)

The light environment and herbivory treatment both influenced reproductive phenology. Plants that experienced vegetative tissue loss flowered later than control plants (Table 1; Fig. 3). Understory plants also initiated flowering later than light-gap plants. However, changes in flowering initiation in response to herbivory were similar across light environments. Corresponding to these differences in the day of first flower, flowers were produced earlier in the season on uneaten plants and on plants growing in light gaps (Fig. 4). Average flower day summarizes differences in these floral deployment curves. The average flower day was strongly correlated with date of first flower ($r = 0.88$, $n = 165$, $P < 0.001$) and was earlier for light-gap plants and uneaten plants (Table 1; Fig. 4). Flowering duration is longer for plants growing in light gaps and for uneaten plants (Table 1; Fig. 4).

Light environment and herbivory treatment jointly influenced fruit production (Table 1). In the understory fruit production of control plants was larger than that of plants

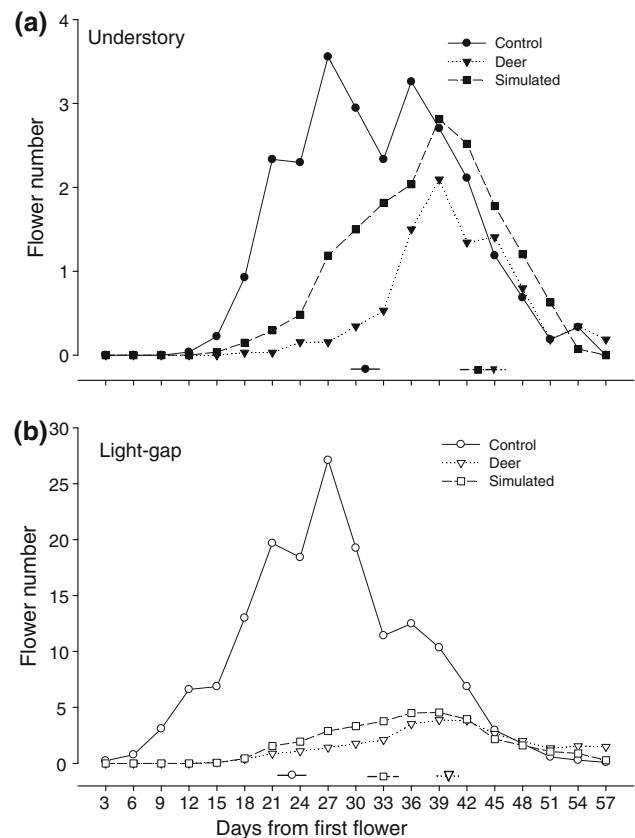


Fig. 4 Mean number of flowers open at 3-day intervals throughout the reproductive season for *C. americanum* plants that experienced deer browsing, simulated herbivory or no herbivory growing in **a** understory and **b** light-gap environments. Plants without flowers, i.e., that had not yet initiated reproduction or had finished blooming, were scored as zero. Symbols above the x-axis indicate the average flower day (SE) for a given treatment. Note the scale of the y-axis differs between light environments

that had lost tissue ($F_{2,94} = 15.96$, $P < 0.001$; Fig. 3). In light gaps, fruit production was greatest in control plants followed by simulated-herbivory and then deer-browsed plants ($F_{2,126} = 79.65$, $P < 0.001$).

Discussion

Deer herbivory had a dramatic impact on the survival, recovery and reproduction of *C. americanum* and this impact was not equivalent within the two light environments. First, the rate of herbivory differed between light environments. Light-gap plants were more likely to be eaten and were eaten earlier than understory plants. Both results suggest deer have a preference for light-gap plants. Although our work does not take into consideration the habitat preference of deer, under-canopy areas are a central component of their habitats (Tufto et al. 1996) where they spend the majority of their time (Lesage et al. 2002;

L. F. Galloway, personal observation), suggesting increased herbivory in light gaps is not simply due to increased herbivore presence. Instead, this preference may be due to plant size. Initial height of light-gap plants was 36% greater than that of understory plants and greater growth rates (results not shown) amplified this difference such that the final biomass of uneaten light-gap plants was 6 times larger than that of understory plants (see also Kilkenny and Galloway 2008). The differences in size are not surprising as light gaps represent higher resource habitats that receive, on average, 10 times more radiation than understory regions in this population (Galloway and Ettersson 2007). Alternatively, greater preference for light-gap plants may be due to unknown differences in shoot chemistry or physiology (e.g., Muth et al. 2008). Further work is necessary to evaluate whether differences in herbivory between the light environments are due to potential differences in resistance to browsing or to size-related differences in apparency.

Second, the survival of browsed plants differed between light habitats. Deer-browsed plants were over 4 times more likely to die in light gaps than in the understory. In contrast, tree seedlings have been shown to have lower survival in response to clipping or mammalian browsing in understory habitats in many species (Blundell and Peart 2001; Milbrath 2008; Norghauer et al. 2008) but not all (Husheer et al. 2006). The difference in survival found here was caused by disparities in the extent of deer-inflicted damage to light-gap and understory plants. Light-gap plants not only had their apical meristems removed but most were also trampled, which, not surprisingly, dramatically reduced survival. In contrast, we did not record a single incident of trampling amongst deer-browsed understory plants. Trampling also explained most of the difference in survival between simulated-herbivory and deer-browsed plants; there was no survival difference between browsed and simulated-herbivory plants in the understory where there was no trampling ($\chi^2_1 = 0.47$, $n = 73$, $P = 0.49$), but in light gaps browsed plants had lower survival ($\chi^2_1 = 12.90$, $n = 100$, $P < 0.001$). Therefore, differences in survival between the light habitats reflect differences in damage, outside of the amount of tissue removed by deer.

Third, recovery from herbivory measured by changes in branch length and final plant size differed between the light environments. Under the forest canopy, branches were largely limited to plants that had lost their apical meristem. In contrast, uneaten and simulated-herbivory light-gap plants had longer branches than deer-browsed plants. The branch length of the simulated-herbivory plants that did not experience trampling was the same as that of uneaten plants in light gaps but smaller under the forest canopy revealing that release from apical dominance is only relevant under limited-light conditions. Overall greater branch length in the light gap than the understory supports the disparity in

resource availability between the habitats. Despite reduced resource levels, understory plants compensate for herbivory in final plant size (although not fitness, see below) whereas there was no evidence for compensation in the higher resource light gaps where uneaten plants were substantially larger than either deer-browsed or simulated herbivory plants. In contrast, in tree seedlings, where apical dominance does not differ between habitats, greater vegetative recovery was found under high-light conditions (Häsler et al. 2008).

Finally, fitness of browsed plants, measured by fruit production, was less than that of uneaten plants across both light environments but the difference was greater in light gaps than in the understory. Uneaten plants in light gaps produced approximately 17 times more fruit than deer-browsed plants. In contrast, in the understory uneaten plants had only about 4 times the reproductive output of deer-browsed plants. Because fruit number includes all plants, regardless of whether they survived, it is possible that the greater fitness cost of herbivory in light gaps is due to trampling. However, this is not the only explanation because when trampled plants were not included in the analysis, changes in fruit number among the herbivory treatments still differed between the light environments ($F_{2,185} = 5.58$, $P < 0.004$). Although without the trampled plants, the pattern of response was more similar to the understory where there was no difference in fruit production between the simulated-herbivory and the deer-browsed treatments.

These results indicate that unlike some other monocarpic plants that are browsed while bolting (e.g., Paige and Whitham 1987; Irwin and Aarssen 1996; Lennartsson et al. 1997), there is no evidence for compensation in fitness in *C. americanum*. In addition, tolerance of herbivory is less in light gaps than under the forest canopy. However, as a consequence of trampling, we cannot use the pattern of response to deer browsing to evaluate which model of the effect of resource availability on tolerance best fits the observed data. This is because deer browsing damages light-gap plants more than understory plants, and the models assume that the level of damage is consistent across resource treatments (Wise and Abrahamson 2007). In contrast, levels of simulated herbivory are the same across light environments and they approximate the amount of tissue lost to deer browsing. Therefore, this treatment is appropriate for evaluating whether the response of plants to tissue loss from deer browsing depends on the environment. A statistical comparison of the control and simulated-herbivory plants found the reduction in fruit production due to simulated herbivory differed between the light environments ($F_{1,106} = 5.99$, $P < 0.016$), with light-gap plants having a 84% loss in fruit production while understory plants had only a 47% reduction.

The fitness loss due to simulated browsing of light-gap plants was almost twice that of understory plants. Reduced tolerance in high-resource light gaps is not predicted by the compensatory continuum hypothesis (Maschinski and Whitham 1989). Differences in plant size, growth rate, and fitness, indicate light is a limiting resource for *C. americanum*. When herbivore damage reduces the acquisition of a limiting resource, as in the loss of leaf tissue here, the limiting resource model predicts lower tolerance in the low-resource environment (Wise and Abrahamson 2007). Therefore, our results are also not predicted by the limiting resource model. Rather tolerance to herbivory in *C. americanum* is better explained by the growth rate model which predicts that the increased growth rate necessary for compensation is more readily achieved in slow-growth environments than those where growth is already rapid (Hilbert et al. 1981). This conclusion supports the results of a meta-analysis that found dicot herbs tend to have greater tolerance under low-resource conditions (Hawkes and Sullivan 2001).

It is surprising that our results were not predicted by the limiting resource model as a recent survey found 95% of studies are consistent with this model (Wise and Abrahamson 2007). One possibility is that meristem number is a limiting resource, and the release from apical dominance due to herbivory ameliorates fitness loss to different degrees in the two habitats (Irwin and Aarssen 1996; Rautio et al. 2005; Wise and Abrahamson 2008). Differences in branch length between meristem-removal treatments and the control reveal that apical dominance limits growth under the canopy but not in light-gap habitats. This leads to the prediction that tolerance should be similar in both environments (Wise and Abrahamson 2008). While this yields a closer match to the data than the limiting resource model, the prediction still does not match the results. Another possibility is that we estimated damage using the wrong currency. Deer browsing removes the apical portion of the bolting shoot. In this section of the shoot, nodes are clustered together, not yet fully elongated. Because light-gap plants become taller than understory plants, they may have more nodes with their associated leaves, in a similar length section of the shoot. Therefore, the simulated-herbivory treatment (as well as deer browsing) may remove more nodes, and therefore compromises future growth more, in light gaps than in the understory. Additional work is needed to evaluate this possibility. In conclusion, despite the increased explanatory value of the limiting resource model, tolerance of tissue loss due to deer browsing in *C. americanum* is better predicted by the growth rate model. However, as this discussion makes clear, applying these models to plants with natural patterns of herbivory and environmental variation is at best approximate because they rarely conform to the model assumptions.

Reproductive phenology was also shaped by herbivory and light environment but in contrast to growth and reproductive output, responses were similar between light environments. In both light environments, deer-browsed plants flowered later than undamaged plants. The delay in flowering was approximately 2 weeks, regardless of light environment. A previous study similarly showed that snipping apical meristems in potted *C. americanum* resulted in delayed flowering (L. Guarinello, unpublished data). Later flowering of damaged plants is not surprising as most flowers were produced on side branches that grew after the loss of the apical meristem, and indeed is found in a number of species (e.g., Lennartsson et al. 1998; Tiffin 2000; Freeman et al. 2003; Huhta et al. 2009). However, because understory plants flower on average 11 days after light-gap plants (see also Galloway and Etterson 2009), this delay resulted in deer-browsed plants in light gaps initiating flowering slightly after uneaten plants in the understory. Average flower date and flowering duration had comparable responses to light and herbivory as date of first flower, indicating that patterns of flower production were similar between the treatments, therefore any differences found in initiation of flowering were carried through the reproductive phenology.

Timing of flowering influences whether the next generation of *C. americanum* grow as annuals or biennials. Previous work has shown that the initiation of flowering is tightly associated with when fruit mature, and the timing of fruit maturation and seed dispersal determines whether offspring adopt an annual or biennial growth form (Galloway 2002; Galloway and Burgess 2009). Indeed, these three phenological stages (flowering time, fruit maturation time, germination time) are so tightly associated that flowering phenology can be used to predict offspring life history form (Galloway and Burgess 2009). As a consequence, earlier flowering in light gaps and later flowering under the forest canopy leads to a greater number of annuals in light gaps and biennials in the understory (Galloway and Etterson 2009). However, herbivory-induced delays in flowering are expected to shift the ratio of annuals to biennials in light gaps to be more similar to that in the understory. As a result, browsing by deer is expected to increase the frequency of biennials in this *C. americanum* population. These potential transgenerational effects are a consequence of changes in timing of reproduction rather than seed quality (L. Guarinello, unpublished data). Previous work has found that annuals have greater fitness in light gaps and biennials under the forest canopy (Galloway and Etterson 2007). Therefore, potential changes in the frequency of life history schedule due to transgenerational effects of deer browsing are likely maladaptive. The potential for indirect transgenerational effects of herbivory that we show here may be common as browsing frequently delays reproduction,

and delaying reproduction may alter abiotic and biotic factors during seed development, dispersal and germination.

In summary, deer browsing has substantial within- and potential between-generation fitness costs. Although tolerance is greater for understory plants, the population growth rate of these plants is less than 20% that of light-gap plants (Galloway and Etterson 2007). Therefore, the different patterns of tolerance between understory and light-gap habitats may alter patterns of population growth and habitat usage. In addition, potential changes in the life history schedule of the population due to transgenerational effects of browsing could change population growth rates beyond that predicted by changes in fruit production alone (e.g., Steets et al. 2007). To fully understand the long-term consequences of these within- and between-generation effects of deer browsing will require a demographic approach (e.g., Knight 2004).

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