

Population-level Consequences of Herbivory Timing in *Trillium grandiflorum*

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ABSTRACT.—The timing of herbivory may have important consequences to components of plant fitness as well as the growth rate and persistence of plant populations. Specifically, this study examines whether the timing of herbivory by white-tailed deer (*Odocoileus virginianus*) affects the population dynamics of the long-lived herb, *Trillium grandiflorum*. This study combines results from a clipping experiment with demographic matrix modeling in four different *T. grandiflorum* populations to determine how both the frequency and timing of herbivory alter the population growth rate. Herbivory early, but not late in the season, increased the probability that reproductive plants fail to reproduce in the next year. Both early and late season herbivory resulted in a complete loss of reproductive success in the current year. Because the growth rates of these populations were sensitive to changes in the fate of reproductive plants, but insensitive to changes in annual fecundity, early season herbivory was more detrimental to population growth rates than late season herbivory. Plant persistence may depend as much on the timing of herbivory as it does its frequency.

INTRODUCTION

The persistence of a population depends in part on the strengths of its interactions with other members of the community. Herbivores often play a strong role in determining plant abundance (*e.g.*, Bastrenta *et al.*, 1995; Ehrlén, 1995). There has been much focus on the role that the frequency and intensity of herbivory has on aspects of plant fitness, such as survival, growth and reproduction (reviewed in Huntly, 1991; Stowe *et al.*, 2000), and on plant population dynamics, such as the population growth rate (Bastrenta *et al.*, 1995; Ehrlén, 1995; Rooney and Gross, 2003; Knight, 2004; Rooney and Millam, 2005). However, in a seasonal environment, effects of herbivory on plant fitness may depend on its timing. While many studies have examined the effects of herbivory timing on plant fitness (Maschinski and Whitham, 1989; Gedge and Maun, 1992; Marquis, 1992; Lennartsson *et al.*, 1998; Tiffin, 2002; Garcia and Ehrlén, 2002; Knight, 2003a; Anderson and Frank, 2003; Gustafsson, 2004; Hester *et al.*, 2004; Marshall *et al.*, 2005), few have incorporated these results into demographic matrix models to determine how herbivory timing may influence the population growth rate (but *see* Garcia and Ehrlén, 2002).

The effect of herbivory timing on components of plant fitness may depend on whether or not the plant can compensate for herbivory in the same growing season in which it is consumed. For plant species that can compensate within the growing season, herbivory early in the season has been shown to be less detrimental to fitness than herbivory late in the season (Maschinski and Whitham, 1989; Gedge and Maun, 1992; Lennartsson *et al.*, 1998; Tiffin, 2002). In these species, partial defoliation early in the season was less detrimental because it allowed more time for re-growth before reproduction. However, when compensation for defoliation occurs in the following growing season, the loss of photosynthetic tissue early in the season has been shown to be more detrimental than the loss of tissue later in the season (Marquis, 1992; Garcia and Ehrlén, 2002; Knight, 2003a; Gustafsson, 2004).

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It is possible that large changes in components of fitness may lead to insignificant changes in the population growth rate (λ), if the growth rate of the population is insensitive to those fitness components (Crone, 2001). When demographic matrix models are constructed for a plant population, the effects of herbivory on vital rates can be incorporated into those models, and λ can be assessed (Bastrenta *et al.*, 1995; Ehrlén, 1995; Garcia and Ehrlén, 2002; Rooney and Gross, 2003; Knight, 2004). Further, perturbation analyses, such as sensitivities and elasticities (Caswell, 2001), can elucidate how sensitive λ is to changes in particular vital rates, including those that are affected by herbivory. The population-level effect will depend on both the magnitude by which the vital rates (*e.g.*, survival, fecundity) are affected by herbivory, and the sensitivity of the population growth rate to changes in those vital rates. Garcia and Ehrlén (2002) found that early season defoliation (via clipping) more strongly reduced λ than late season herbivory because it caused a larger decrease in the size of reproductive plants, a demographic change that λ was highly sensitive to.

In this study, I consider the effects of herbivory timing on the population growth rate of the perennial herb, *Trillium grandiflorum*. Previous work on this species has shown that: (1) herbivores, specifically white-tailed deer (*Odocoileus virginianus*), primarily consume large reproductive plants (Augustine and Frelich, 1998; Knight, 2003a), (2) the timing of herbivory varies across individuals and populations (Knight, 2003a) and (3) the timing of herbivory differentially influences some aspects of plant fitness. Plants consumed early and late in the season both lose all female reproductive success for that season, but plants consumed early are more likely to retrogress to a non-reproductive stage in the next growing season, whereas plants consumed late are not (Knight, 2003a). Finally, matrix models of *Trillium grandiflorum* have shown that λ is more sensitive to changes in the fates of reproductive plants than in changes in annual fecundity (Rooney and Gross, 2003; Knight, 2004). This leads to the prediction that early season herbivory will cause a larger decrease in λ than late season herbivory.

In 2000 I experimentally clipped reproductive plants early and late in the season in four *Trillium grandiflorum* populations and compared the stage transitions of these plants to unclipped control plants in 2001 (Knight, 2003a). The objectives of this study are to: (1) create a demographic projection matrix for each population, and comparing the population growth rates of plants clipped early and late, (2) simulate how different frequencies and timings of herbivory by white-tailed deer should affect the persistence of these four *Trillium grandiflorum* populations and (3) conduct elasticity analyses, to examine the sensitivity of λ to the vital rates influenced by herbivory and examine how these sensitivities vary with different frequencies and timing of herbivory.

METHODS

STUDY SYSTEM

Trillium grandiflorum (Melanthiaceae) is a long-lived herb that occurs in deciduous forests throughout the eastern United States and Canada. Individuals persist in a dormant state during autumn and winter, and leaves appear above ground early in the spring (mid-April), before the forest canopy leaf-out. Leaf senescence occurs in late summer, and the plants enter the dormant stage until the following spring (Case and Case, 1997). Reproductive plants produce a single, hermaphroditic, white flower and are primarily bumble-bee pollinated (Irwin, 2000; Knight, 2003b; Steven *et al.*, 2003). Seeds develop within a single fruit and are ant dispersed (Kalisz *et al.*, 1999). Seeds germinate below ground in their first year, and a single cotyledon leaf appears above ground in their second year. If plants survive to their third year, a single true leaf is present. These plants are non-clonal, and are easily

classified into 6 stage classes: germinant (below-ground germinated seed), seedling (a single cotyledon appears above ground), 1-leaf, small 3-leaf (leaf length <5 cm), large 3-leaf (leaf length >5 cm) and reproductive. Plants can remain in the 1-leaf, 3-leaf and reproductive stage classes for multiple years. *Trillium grandiflorum* individuals have been shown to take at least 17 y to reach maturity in forests (Hanzawa and Kalisz, 1993) and can live over 70 y (Jules, 1998).

White-tailed deer preferentially consume reproductive *Trillium grandiflorum*, and defoliation generally results in the loss of all above ground leaves and reproductive structures (Augustine and Frelich, 1998; Knight, 2003a). After consumption, plants will not re-emerge until the following growing season. While herbivory by deer does not usually kill these plants, it does increase the probability that they will retrogress to a non-reproductive stage (Lubber and Lechowicz, 1989; Anderson, 1994; Knight, 2003a).

The populations used in this study occurred in mature beech and maple forests in northwestern Pennsylvania, USA. I use a two-letter code to refer to each population, which corresponds to its location or property owner: Deezik creek (DC), R. Higgin's property (RH), Tryon Webber Woods (TW) and Whitehill Road (WH). Population TW is owned by the Western Pennsylvania Conservancy and all other populations were located on private property. In these four populations of *Trillium grandiflorum*, herbivory naturally occurs both early and late in the growing season (Knight, 2003a). Because herbivory generally occurs before fruit maturation, both early and late season herbivory result in a complete loss of female reproductive success for that growing season; plants eaten by deer produce no seeds. However, early season herbivory was more unfavorable to the future size and stage of reproductive plants.

I conducted a clipping experiment in 2000 on reproductive plants in these four populations. Plants were in one of three treatments (N=30 plants per treatment per population): clipped early in the season (May 1), clipped late (June 30) or control (not clipped). The clipping simulated herbivory by white-tailed deer; the stem of the plant was cut, which removed all three leaves and the flower (or developing fruit). Plants clipped early in the season were 2.5 times more likely to retrogress in stage in the next year (2001) than late clipped and control plants (Fig. 1, see also Knight, 2003a). The effects of natural herbivory on reproductive plants matched that of the experimental herbivory and, thus, the clipping experiments effectively simulate natural herbivory (Knight, 2003a).

DEMOGRAPHIC MATRIX MODEL

To estimate the stage-specific vital rates (*e.g.*, survival, fecundity), I established permanent 1-m² plots in each population in 1998 (except for population WH, in which plots were established in 1999). The number of plots depended on density of population and ranged from 5–27; the goal was to sample at least 40 individuals in each stage class at each population. In all populations except TW, the plots were located along a single transect running through the population and plots were separated by at least 30 m. In TW, 9 transects and 27 plots were necessary to achieve adequate sample size. In April of 1998 (or 1999 for population WH), I tagged and classified all plants within each plot by stage: seedling, 1-leaf, small 3-leaf, large 3-leaf and reproductive. In addition, I tagged plants in rare stages (usually seedlings and/or reproductive plants) in extra plots, until either sample sizes of 40 were reached for each stage or until all plants of a stage in that population were tagged. In 1999, 2000, 2001 and 2002 I conducted a census of all plots to document the stage and size (leaf length) of each tagged plant and to tag new seedlings. Censuses were always done in late April, when the plants first emerged, and before deer consumed any. In total, 1583 plants were monitored in these plots.

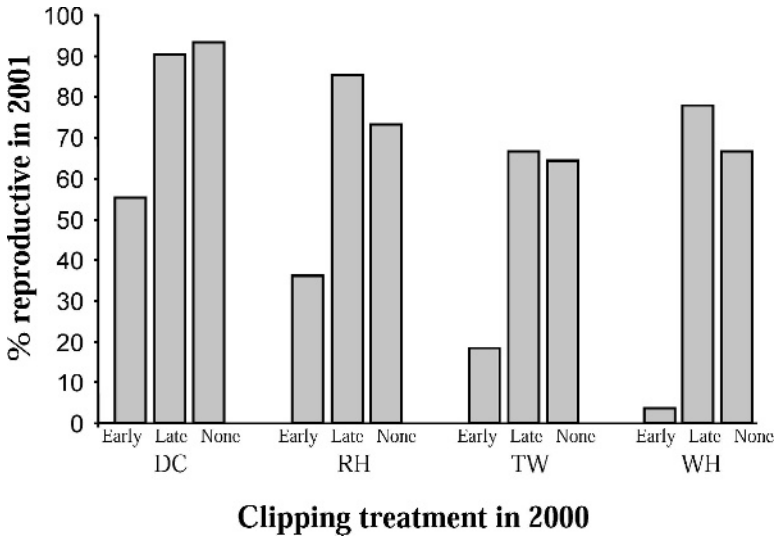


FIG. 1.—Effects of experimental clipping on the proportion of plants flowering in the following year in *Trillium grandiflorum* populations. Clipping treatments simulated herbivory by white-tailed deer early (1 May 2000) and late (30 June 2000) in the season at four populations (DC, RH, TW, WH). All plants were reproductive in 2000, and the y-axis shows the percent of plants that were still in the reproductive stage class in 2001. The remaining plants retrogressed to a non-reproductive stage class. No mortality was observed in this experiment

To estimate the annual fecundity for each population, I collected fruits from reproductive plants in each of the observed plots and from randomly selected reproductive plants outside of the plots. For all reproductive plants not consumed by deer, I averaged the number of seeds produced per plant in each population in 1999, 2000 and 2001. The zero values of plants that failed to set fruit were included in these averages.

Seed germination rate was estimated at each population by placing sieved soil from the site and 30 seeds in 25-cm³ seed baskets (1-mm mesh fiberglass screening) in 1999. Twenty seeds baskets were set up in each population except TW. This population had so few reproductive plants with mature fruits, that only 10 seed baskets could be established. I collected half of the seed baskets in May of 2000, sieved them and counted the number of germinants. This allowed me to calculate the average proportion of seeds that survived 1 y for each population (*i.e.*, the germination rate). I found no evidence for seed dormancy; seeds either germinated or died in their first year. In 2001 I counted the number of seedlings that emerged from the remaining half of the seed baskets and calculated the average proportion of seeds that survived 2 y. I estimated the rate at which germinated seeds survive to the seedling stage (*i.e.*, seedling emergence rate) as

Seedling emergence rate = (proportion of seeds that survived two years) / (germination rate)

I constructed a 6-stage demographic projection matrix (**A**) with 13 matrix elements (a_{ij}), which represent 1-y stage transitions (matrix elements are the non-zero values in Table 1). The matrix elements are averages of transition probabilities observed over four time intervals (1998–1999, 1999–2000, 2000–2001, 2001–2002). The reproductive to germinant matrix element (a_{16}) is the product of fecundity and germination rate, since both occur within the 1-y time interval. The values determined in the clipping experiment were used as

TABLE 1.—Projection matrices for four *Trillium grandiflorum* populations (DC, RH, TW and WH) from one year to the next. Stage classes are: germinant (Germ), seedling (SL), 1-leaf (1L), small 3-leaf (S3L), large 3-leaf (L3L) and reproductive (Rep). Matrix elements are averages over all years observed (1998–2002 for populations DC, RH and TW; 1999–2002 for population WH). The matrix elements corresponding to reproductive plants at time t depend on the frequency and timing of herbivory by white tailed deer at time t . f_N , f_E , and f_L are the frequencies by which reproductive plants are not eaten, eaten early, and eaten late in the season, respectively

Stage at time t+1	Stage at time t					
	Germ	SL	1L	S3L	L3L	Rep
Population DC						
Germ	0	0	0	0	0	(f_N) (13.16)
SL	0.194	0	0	0	0	0
1L	0	0.238	0.650	0.022	0	0
S3L	0	0	0.063	0.810	0.102	0
L3L	0	0	0	0.081	0.662	$1 - [(f_N)(0.993) + (f_E)(0.552) + (f_L)(0.903)]$
Rep	0	0	0	0	0.236	$(f_N)(0.993) + (f_E)(0.552) + (f_L)(0.903)$
Population RH						
Germ	0	0	0	0	0	(f_N) (11.69)
SL	0.273	0	0	0	0	0
1L	0	0.417	0.633	0.035	0	0
S3L	0	0	0.157	0.822	0.104	0
L3L	0	0	0	0.113	0.553	$1 - [(f_N)(0.733) + (f_E)(0.360) + (f_L)(0.852)]$
Rep	0	0	0	0	0.343	$(f_N)(0.733) + (f_E)(0.360) + (f_L)(0.852)$
Population TW						
Germ	0	0	0	0	0	(f_N) (7.99)
SL	0.506	0	0	0	0	0
1L	0	0.328	0.612	0.037	0	0
S3L	0	0	0.268	0.815	0.269	0
L3L	0	0	0	0.111	0.678	$1 - [(f_N)(0.643) + (f_E)(0.185) + (f_L)(0.667)]$
Rep	0	0	0	0	0.053	$(f_N)(0.643) + (f_E)(0.185) + (f_L)(0.667)$
Population WH						
Germ	0	0	0	0	0	(f_N) (13.73)
SL	0.398	0	0	0	0	0
1L	0	0.289	0.528	0.018	0	0
S3L	0	0	0.107	0.701	0.123	0
L3L	0	0	0	0.148	0.778	$1 - [(f_N)(0.667) + (f_E)(0.037) + (f_L)(0.778)]$
Rep	0	0	0	0	0.089	$(f_N)(0.667) + (f_E)(0.037) + (f_L)(0.778)$

estimated for two matrix entries: (1) the proportion of reproductive plants that remain reproductive (a_{66}) and (2) the proportion of reproductive plants that retrogress to the large 3-leaf stage class (a_{56}). These two matrix elements sum to 1; there was no detectable mortality of plants in the reproductive stage class. All of the transitions of reproductive plants (reproductive-germinant, reproductive-large 3 leaf, reproductive-reproductive) depend on the frequency and timing of herbivory (Table 1). I simulated different frequencies of herbivory on reproductive plants from 0 to 100%, at 10% intervals.

I projected the population growth rate and elasticity matrix using standard demographic techniques (Caswell, 2001) in MATLAB (2000). The population growth rate, λ , is the dominant eigenvalue of \mathbf{A} . λ provides a critical borderline between population persistence

($\lambda \geq 1$) and extinction ($\lambda < 1$). However, because this model does not incorporate demographic or environmental stochasticity, it is likely an overestimate of the true growth rate for these populations (Morris and Doak, 2002). Elasticities (e_{ij}), are proportional sensitivities, indicating how a proportional change in each element would effect λ (de Kroon *et al.*, 1986; Caswell, 2001).

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})}$$

All values in the elasticity matrix sum to 1 (Caswell, 2001). For each population, I varied the frequency of early and late season herbivory on reproductive plants from 0 to 100%, at 10% intervals, and calculated λ . At each frequency of herbivory, I used paired t-test to determine if λ of plants eaten early differed from λ of plants eaten late. Each pair represented a single population, for a total of four pairs. I summed the elasticities of the two stage transitions of reproductive plants (e56 and e66), to describe the elasticities of λ to the 'fate of reproductive plants'. I graphed the elasticities of the fate of reproductive plants along a gradient of herbivory frequency for both timings of herbivory (early, late) and all four populations. I also made the same graphs for the elasticities of λ to fecundity.

RESULTS

Trillium grandiflorum individuals were found to have low survival rates when in smaller stage classes, but no detectable mortality once they reach the large 3-leaf and reproductive stage classes (Table 1). The stage transitions of reproductive plants depend on the frequency and timing of herbivory. Results from a clipping experiment indicate that reproductive plants clipped early in the season were less likely to be reproductive in the following year than reproductive plants clipped late in the season or not at all (Fig. 1; *see also* Knight, 2003a). The reproductive to germinant stage transition is a function of the frequency of plants not eaten by deer (since those eaten early and late produce no seeds), the average number of seeds produced per reproductive plant and the germination rate of seeds (Table 1).

Not surprisingly, λ decreased as the frequency of herbivory increased. However, λ was also significantly affected by the timing of herbivory; λ is lower when herbivory occurs early rather than late in the season (Fig. 2, Table 2). Herbivory affects both fates of reproductive plants (a56 and a66) and fecundity (a16). λ was sensitive to changes in the fates of reproductive plants and relatively insensitive to changes in fecundity. Elasticity values for the fates of reproductive plants ranged from 0.02 to 0.72 (Fig. 3), whereas elasticity values for fecundity ranged from 0 to 0.04 (Fig. 4). The elasticity of λ to the fates of reproductive plants and to fecundity decreased with the frequency of herbivory (Figs. 3, 4). When deer consumption was early in the season, the relationship between the elasticity of λ to the fates of reproductive plants and the herbivory was a decelerating curve; the slope was greater at lower frequencies of herbivory than at higher frequencies of herbivory.

DISCUSSION

Both the frequency and timing of herbivory have dramatic affects on λ of *Trillium grandiflorum*. For one population, DC, the frequency of herbivory that allowed persistence of the population ($\lambda > 1$) was twice as high when the herbivory was late in the season than when the herbivory was early in the season. Thus, when considering the critical threshold of herbivory that a plant population can withstand, it is critical to consider the timing in which that herbivory occurs.

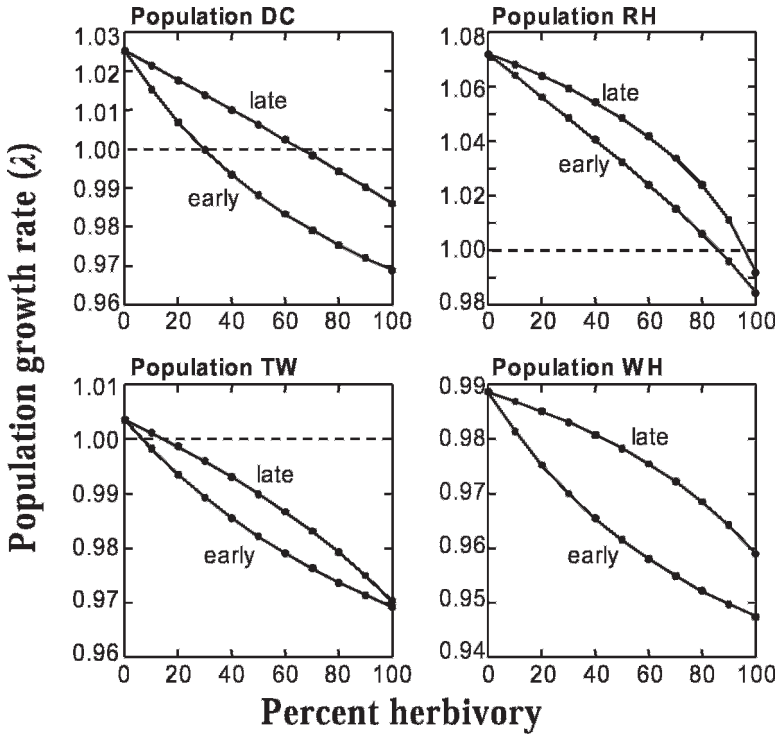


FIG. 2.—The population growth rate for plants consumed early and late along a gradient of herbivory frequency. A separate graph is shown for each *Trillium grandiflorum* population. The dotted line shows the critical value for population persistence ($\lambda=1$)

TABLE 2.—Results from paired t-tests examining the difference in the population growth rates of plants consumed early and late in the season (see Fig. 2 for population growth rates). The tests used demographic information from four populations of *Trillium grandiflorum*, and in each case there is 3 degrees of freedom. Significant *p* values indicate that the population growth rate was greater for plants consumed late in the season at a given frequency of herbivory

Frequency of herbivory	t	P
10	6.48	<0.01
20	6.69	<0.01
30	6.74	<0.01
40	6.61	<0.01
50	6.31	<0.01
60	5.87	<0.05
70	5.34	<0.05
80	4.75	<0.05
90	4.04	<0.05
100	2.74	0.07

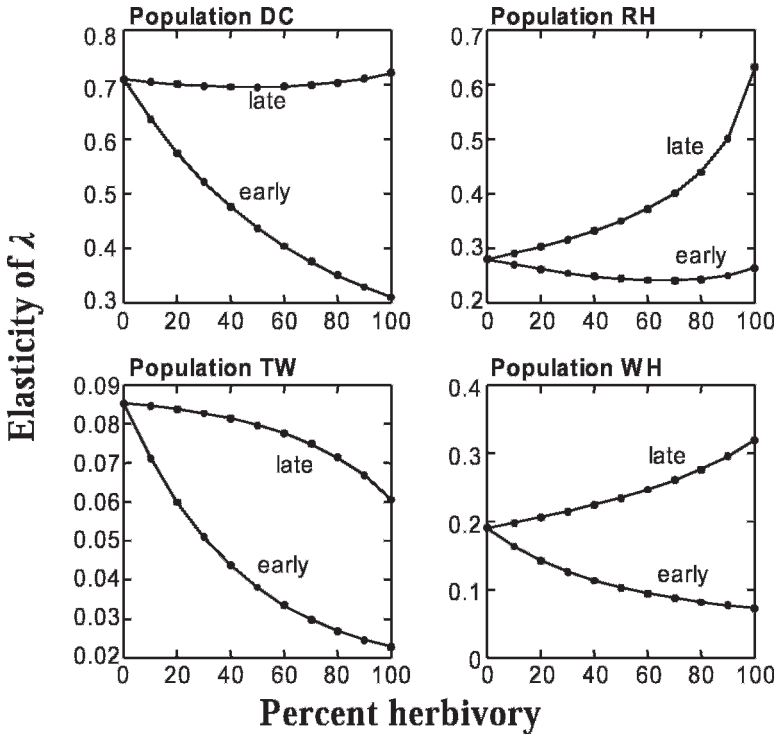


FIG. 3.—The elasticity of the population growth rate to changes in the fates of reproductive plants along a gradient of herbivory frequency and at two different timings of herbivory (early and late in the season). A separate graph is shown for each *Trillium grandiflorum* population

The elasticities of λ to the fate of reproductive plants decreased with the frequency of early season herbivory. Early season herbivory causes more reproductive plants to retrogress to a non-reproductive stage class. This, in turn, causes the population to become more dominated by non-reproductive plants at stable stage distribution. λ is more sensitive to changes in the matrix elements corresponding to more common stage classes, and as a result, λ becomes less sensitive to changes in the fates of reproductive plants and to fecundity as the frequency of herbivory increases.

The timing in which a species of herbivore attacks individuals and entire populations will often vary throughout the growing season. For example, many herbivores forage on a plant species throughout the growing season such that some individuals will be eaten early, and others late, as in the white-tailed deer-*Trillium grandiflorum* system. In addition, variation among populations of a plant species, such as their location in the surrounding plant community, or in surrounding patches within the landscape, may cause different populations to be vulnerable to herbivores at different times of the year (e.g., Bailey *et al.*, 1996; Hanley, 1997; Augustine and McNaughton, 1998). Further, different species of herbivores are active at different times of the growing season and will vary in the seasonal timing of herbivory they impose on perennial plants. For example, Ehrlén (1995) found that mollusk herbivory occurred early in the season, whereas vertebrate herbivory occurred later in the season in a population of *Lathyrus vernus*. In addition to variation in the timing of herbivory

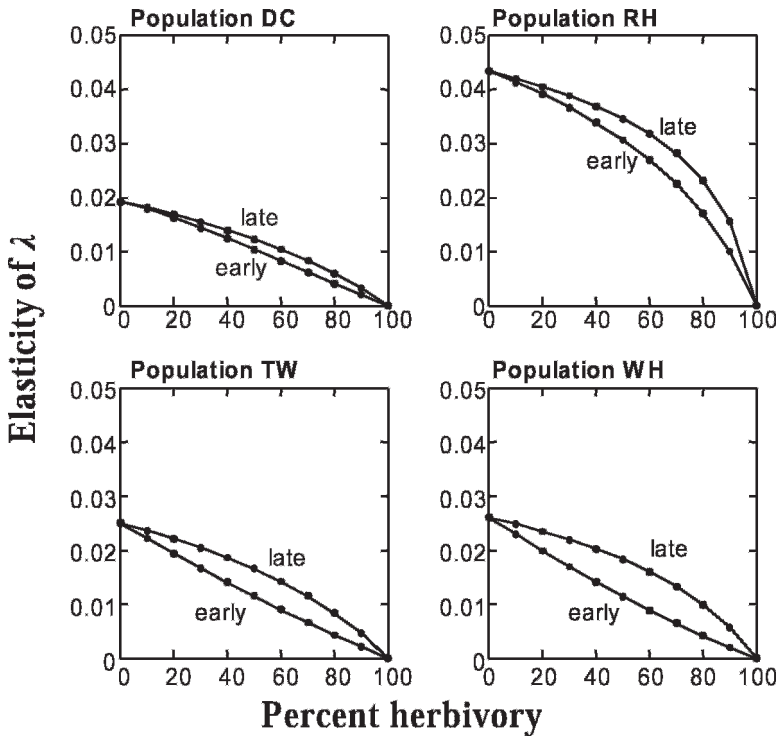


FIG. 4.—The elasticity of the population growth rate to changes in the annual fecundity (number of seeds produced per reproductive plant) along a gradient of herbivory frequency and at two different timings of herbivory (early and late in the season). A separate graph is shown for each *Trillium grandiflorum* population

being a common occurrence, I also suggest that perennial plants are likely to respond to variation in the timing of herbivory in a similar way to *Trillium grandiflorum*. Specifically, early season herbivory may often be more detrimental to plant population growth rates than late season herbivory in perennial plants (e.g., Marquis, 1992; Garcia and Ehrlén, 2002).

In an experimental study exploring the effects of several factors on the population growth rate of *Primula veris*, Garcia and Ehrlén (2002) found that removing leaf tissue early in the growing season had a greater effect on population growth rate than removing leaf tissue later in the growing season. Similar to *Trillium grandiflorum*, *P. veris* is a long-lived perennial that is sensitive to changes in the stage transitions of reproductive plants, and early season clipping decreased the proportion of reproductive plants that remained in the reproductive stage. In fact, many long-lived perennials have a life cycle similar to *Trillium grandiflorum*; mortality is greater at early stages of the life cycle, and once plants are in the reproductive stage, they experience low mortality and have many opportunities to reproduce. The population growth rate of perennials is typically more sensitive to changes in the stage transitions of reproductive plants than it is to changes in annual fertility rates (Silvertown *et al.*, 1993; Crone, 2001). If early season herbivory generally has a greater effect on the stage transitions of reproductive plants than late season herbivory in other perennial plants, then it will likely also have a greater effect on λ .

Studying the strengths of interspecific interactions allows for the understanding of how populations persist (or do not persist) in a given environment. Further, as anthropogenic influences alter habitats and the densities of the interacting species, our knowledge of these effects will be critical for the protection and management of populations. However, studying interaction strength among organisms has been a complicated and contentious issue (Laska and Wootton, 1998; Berlow *et al.*, 1999; Abrams, 2001). My study highlights two often overlooked, but potentially very important aspect of studying the strengths of interspecific interactions. First, short-term effects of interspecific interactions on components of fitness such as fecundity or survival, may poorly translate into the effects on lifetime fitness and population dynamics of species with stage or age-structured populations (*see* also Crone, 2001). Second, studies of the interactions between predators and prey typically assume that the strength of that interaction is static both spatially and temporally. However, this study shows that interaction strength can vary due to seasonal variation in the interaction between predators and prey. Because prey can vary in their developmental or physiological state through time, the timing in which they are eaten in a seasonal environment may often play a large role in both the individual and population levels responses to their predator. This study provides evidence that in a seasonal environment, the timing of herbivory can be as important to the population growth rate as the magnitude of herbivory.

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