

## THE EFFECTS OF HERBIVORY AND POLLEN LIMITATION ON A DECLINING POPULATION OF *TRILLIUM GRANDIFLORUM*

TIFFANY M. KNIGHT<sup>1</sup>

Department of Biological Sciences, University of Pittsburgh, Pennsylvania 15260 USA

**Abstract.** In long-lived organisms, it is often difficult to determine which environmental factors will have the largest effects on population dynamics. In this study, I incorporated the results of short-term experiments and observations into a demographic matrix model to determine the effects of both herbivory and pollen limitation on the dynamics of a declining population of the perennial herb *Trillium grandiflorum*. While pollen supplementation experiments in both 1999 and 2000 revealed that plants produce fewer seeds as a result of pollen limitation, this pollen limitation had almost no effect on the growth rate of the population. White-tailed deer (*Odocoileus virginianus*) consumed nearly half of the reproductive plants in this population in 2000 and 2001. Herbivory causes reproductive and large nonreproductive plants to regress in stage and have lower fecundity. In the absence of herbivory, demographic projections suggest that the population would shift from declining to growing, the proportional representation of new recruits would rise, and plants in larger stage classes would have higher reproductive values. Such shifts in the reproductive values and stable stage distribution result in shifts in elasticities. A life table response experiment demonstrated that, while herbivory affected six vital rates, two of these contributed disproportionately to the change in the population growth rate: reproductive plants remaining reproductive and large nonreproductive plants remaining nonreproductive. In this population, herbivores contribute more to its decline than pollinators. Thus, active long-term management of deer populations appears necessary for the conservation of understory herbs such as *Trillium grandiflorum*.

**Key words:** demography; herbivory; life table response experiment; *Odocoileus virginianus*; pollen limitation; population growth rate; simulation; *Trillium grandiflorum*; white-tailed deer.

### INTRODUCTION

The persistence of a plant population in a given habitat will depend, at least in part, on the strengths of its interactions with other species. Plants are negatively affected by antagonists such as herbivores and positively affected by mutualists such as pollinators. Thus, both herbivores and pollinators may be expected to influence the dynamics of a plant population, such as the growth rate. While many studies have examined the effects of both herbivores (reviewed in Huntly 1991, Stowe et al. 2000) and pollinators (reviewed in Burd 1994, Wilcock and Neiland 2002) on aspects of plant fitness, few have linked these biotic interactions to plant population growth rates (but see Bierzychudek 1982, Calvo and Horvitz 1990, Bastrenta et al. 1995, Ehrlen 1995, Ehrlen and Eriksson 1995, Parker 1997, Garcia and Ehrlen 2002, Rooney and Gross 2003). To date, none have explored the simultaneous effects of different types of biotic interactions on the population growth rate.

Many measures of plant fitness (e.g., survival, seed production) may poorly predict the population dynam-

ics of long-lived plants with stage structured populations (McGraw and Caswell 1996, Crone 2001). The population-level effects of an interacting species depend on three primary factors: (1) which vital rates (e.g., stage-specific rates of fecundity, survival) are affected, (2) the magnitude of change in those vital rates, and (3) the sensitivity of the population growth rate to changes in those vital rates (Caswell 2001). With these factors in hand, ecologists can understand the role of the interactor on the population growth rate of the focal species (e.g., Ehrlen and Eriksson 1995, McPeck and Peckarsky 1998), estimate the contribution of each vital rate to the change in the population growth rate through life table response experiments (LTREs; e.g., Caswell 1989, 2001, Miriti et al. 2001, Garcia and Ehrlen 2002), and simulate how changes in the effects of the interactor will influence population growth parameters (e.g., Doak 1992, Parker 1997).

Herbivores can influence several vital rates of plants, including growth, survivorship, and fecundity (reviewed in Huntly 1991, Stowe et al. 2000). While only a few studies have examined the effect of herbivory on the entire life cycle of focal plant populations, and the consequent population growth rate, all have found that the effects of herbivory on fitness components of individuals scaled up to influence the plant population growth rate (Bastrenta et al. 1995, Ehrlen 1995, Rooney and Gross 2003). Pollinators positively influence fe-

Manuscript received 12 February 2003; revised 27 June 2003; accepted 17 July 2003. Corresponding Editor: D. P. C. Peters.

<sup>1</sup> Present address: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California, USA. E-mail: tknight@biology2.wustl.edu



PLATE 1. A reproductive *Trillium grandiflorum*. Photo credit: Jonathan Chase.

cundity. While hundreds of studies have estimated the degree of pollen limitation with supplemental pollination experiments (Burd 1994), to date only a few studies have examined the effects of pollen limitation on plant population growth rate (Bierzuchudek 1982, Ehrlen and Eriksson 1995, Parker 1997, Garcia and Ehrlen 2002), and most of those found that increased pollination success did not increase population growth rate. A more complete investigation on the effects of both herbivores and pollinators would allow the comparison of biotic interactions with qualitatively different effects, both in terms of the vital rates affected, as well as whether they have negative or positive effects on those vital rates.

In this study, I used a demographic matrix model to quantify the population growth rate of a population of the perennial herb, *Trillium grandiflorum*. This plant was chosen because it currently experiences high levels of herbivory by white-tailed deer (*Odocoileus virginianus* Zimmerman), a native herbivore whose increase in abundance over the past few decades has been a topic of conservation concern for many understory plants (Alverson et al. 1988, McShea et al. 1997, Augustine and Frelich 1998, Russell et al. 2001). In addition, *T. grandiflorum* is self-incompatible and relies on visitation by insect pollinators. Reproduction in *T. grandiflorum* has been shown to be limited by pollen

receipt (Kalisz et al. 1999, Wright and Barrett 1999, Irwin 2000, Knight 2003c). In concurrent studies in the study population, I found that plants were consumed by deer at high frequencies (Knight 2003a) and were pollen limited (Knight 2003c).

The goal of this study was to simulate how removing herbivory and pollen limitation would alter the population growth rate, stable stage distribution, and elasticities of this population. I created and compared four matrices for this population: (1) an ambient matrix, (2) a no herbivory matrix (all plants eaten by deer were excluded), (3) a no pollen limitation matrix (fecundity of plants in supplemental pollination treatments used), and (4) a no herbivory and no pollen limitation matrix. Finally, because herbivory affected several vital rates, I used an LTRE to determine the relative contribution of each to the variation in population growth rate,  $\lambda$ , among the ambient and no herbivory matrices.

## METHODS

### *Study system*

*Trillium grandiflorum* (see Plate 1) occurs in the understory of deciduous forests throughout eastern North America (Case and Case 1997). In northwest Pennsylvania, plants emerge in early spring (late April), bloom for two to three weeks, and senesce in mid summer (late July). Populations consist of six easily distinguished life stages: germinant (germinated seed with roots), seedling (a single cotyledon), one leaf (a stem and one true leaf), three leaf (a stem and a whorl of three leaves), dormant (no aboveground structures), and reproductive (a stem, three leaves, and a single flower).

*Trillium grandiflorum* is a preferred food of white-tailed deer. White-tailed deer have increased dramatically throughout eastern North America over the past 50+ years as a result of a variety of anthropogenic factors, including the additional food provided by modern agricultural practices and the eradication of large carnivores (McCabe and McCabe 1997). *Trillium grandiflorum* is primarily pollinated by bumblebees (*Bombus* spp.; Wright and Barrett 1999, Irwin 2000, 2001). While the mating system of *T. grandiflorum* varies across its range from self-compatible to self-incompatible (Broyles et al. 1997, Kalisz et al. 1999, Irwin 2000, 2001, Sage et al. 2001), at my study site, *T. grandiflorum* is self-incompatible, and therefore plants cannot produce seeds without receiving outcrossed pollen (Knight 2003b).

The population used for this study occurred in Tryon Webber Woods (80°21' W, 41°36' N), an old-growth beech and maple forest located in Crawford County, Pennsylvania, owned by the Western Pennsylvania Conservancy, and stewarded by the Pymatuning Laboratory of Ecology (University of Pittsburgh). In other studies on herbivory and pollen limitation in *T. grandiflorum*, I considered 12 populations that occurred

within a 50-km radius in similar forest types (for more details see Knight 2003a, b, c). The population considered in this study was the only one to have both high levels of deer herbivory (Knight 2003a) and consistent pollen limitation (Knight 2003c). Thus, it was the only population where the opportunity to look at the population-level influence of two biotic interactions existed. At the time of the study, there were <200 reproductive individuals in this population even though the area of the population encompassed >1000 m<sup>2</sup>.

#### Demography

To estimate the stage-specific vital rates of this population necessary for the construction of a matrix model, I set up plots to monitor vegetative plants and seed baskets to monitor seeds. In April 1999, I established 27 1-m<sup>2</sup> plots selected randomly throughout the range of the population. All plants within these plots were permanently tagged, classified by stage (seedling, one-leaf, three-leaf, and reproductive), and measured (leaf length). These plants were censused again in April of 2000 and 2001, when the plants first emerged, and before any herbivory occurred. New seedlings that appeared in these plots were tagged. In total, 482 individuals were followed within these plots. The fecundity of all reproductive plants in the plots was determined in 1999 and 2000. Plants that were eaten by deer or that failed to set fruit were scored as having had zero fecundity. For all reproductive plants that were not eaten by deer, I counted the number of seeds within each developed fruit in early July, just before the fruits would naturally drop from the plants.

In 1999, I estimated seed germination rate by placing sieved soil from the site and 30 seeds (from a bulk collection made from mature fruits on plants outside the plots) into each of ten 25-cm<sup>3</sup> seed baskets (1-mm mesh). These seed baskets were imbedded in the soil next to the demographic plots. Because *T. grandiflorum* germinants produce roots but no aboveground structures in their first growing season, five of these seed baskets were collected and sieved in May 2000 to estimate the germination rate of seeds. The remaining five seed baskets were examined in 2001 to estimate the proportion of seeds that survived and emerged into the seedling stage.

#### Frequency of herbivory

The frequency of herbivory on each stage was determined by observing plants in the demography plots in 1999 and 2000. I monitored these tagged plants every two days in April and May, which was when most of the herbivory occurred, and every other week in June and July. Deer herbivory is easily identified by a straight cut on the remaining stem.

#### Pollen supplementation experiments

Pollen limitation is often determined by pollen supplementation experiments (>250 studies; see Burd

1994), which consist of two treatments, supplement and control. Plants in the supplement treatment have a saturating amount of pollen applied to their stigmas. If pollen doesn't limit the seed production, then the number of seeds would not differ among plants in the supplement and control pollination treatments. Alternatively, if pollen limits seed production, then plants given supplemental pollen will mature more seeds than control plants. Burd (1994) surveyed pollen supplementation studies of 258 species and found significant pollen limitation at some times or in some sites in 62% of these. Plants that are self-incompatible, such as *T. grandiflorum*, had a higher incidence of pollen limitation than self-compatible plants (Burd 1994).

To quantify the extent to which pollen limits the seed production of plants in this population, I performed a pollen supplementation experiment in 1999 and 2000. In each year, I selected 40 pairs of reproductive plants that were similar in size and in close proximity to each other (to minimize variation in plant resource and microsite conditions). Different plants were used in each year. One plant of a pair was randomly assigned to either supplement or control pollination treatment. I applied pollen to the stigmas of flowers in the supplement treatment with a fine paintbrush once during the peak flowering time. The pollen was collected from 30 plants in a different population. These plants were also left open to natural pollination. Previous experiments have shown that there is no effect of pollen source on seed set (Knight 2003b). Plants in the control treatments were not manipulated. In early July, I determined whether each flower had set fruit, and counted the number of seeds in each fruit.

One of the advantages of this species is that each reproductive plant produces only one flower and matures at most only one fruit. This makes it easy to apply the pollen supplementation treatment to the entire plant, and judge if the reproductive success of plants is limited by pollen receipt. Pollen supplementation experiments may wrongly conclude pollen limitation when the treatments are applied at the flower level, and resource reallocation among flowers on a plant occurs (Zimmerman and Pyke 1988).

In both years, >40% of plants in the pollen supplementation experiment were consumed by white-tailed deer and were excluded from statistical analyses on pollen limitation. This reduced the sample sizes in 1999 to 16 plants in the supplement and 19 plants in the control treatment, and in 2000 to 24 plants in the supplement and 27 plants in the control treatment. However, in both years, the remaining supplement and control plants did not differ in size (estimated as leaf length; ANOVA in 1999,  $F_{1,35} = 0.92$ ,  $P = 0.35$ ; in 2000,  $F_{1,51} = 1.194$ ,  $P = 0.28$ ), suggesting that although the pairings based on size were lost, on average there was no size difference between plants in the treatments. The effects of pollination treatment, year, and treatment

× year interaction on the number of seeds per plant were analyzed using ANOVA.

An increase in the number of seeds due to pollen supplementation may come at a cost to the plant. Such costs include: (1) regression to a nonreproductive stage, (2) less growth, (3) fewer seeds produced in future years, and (4) smaller seed size or mass. These costs are particularly relevant because they may counteract the demographic benefits of increased seed production. I asked whether or not *T. grandiflorum* with higher reproductive success are more likely to regress in stage or size. To test for this, I first dissected all of the fruits from plants in the 1999 pollen supplementation experiment ( $N = 35$ ), counted the number of seeds and unfertilized ovules, and determined seed set (the proportion of ovules that had matured into seeds). In April 2000, I returned to these plants ( $N = 31$  plants) and classified them by stage. I used logistic regression to determine if seed set in 1999 predicted whether plants regressed back to a nonreproductive stage in 2000. The model for the logistic regression was

$$y = \ln[P/(1 - P)] = a + bx + e$$

where  $y$  is the stage in 2000 (0 if not reproductive, 1 if reproductive),  $P$  is the probability of being reproductive in 2000,  $x$  is seed set,  $e$  is the error, and  $a$  and  $b$  are constants. In both years, I measured the size (estimated as leaf length) of the plants in late April, and calculated the relative growth rate (RGR) as follows:

$$\text{RGR} = \log_e(\text{leaf length in 2000}) - \log_e(\text{leaf length in 1999}).$$

I used linear regression to determine if seed set in 1999 predicted RGR. I only included the RGR of plants that remained reproductive in 2000 in this analyses ( $N = 23$ ), and therefore changes in RGR are independent from changes in stage. I did not look for any other costs of increased seed production (i.e., lower seed size or mass), although these may occur. All statistical analyses were done using SYSTAT (1999).

#### DEMOGRAPHIC MATRIX MODEL CONSTRUCTION

The matrix model was

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$$

where the vector  $\mathbf{N}_t$  gives the number of individuals in each stage class at time  $t$ ,  $\mathbf{N}_{t+1}$  is the vector for the population size in the next year. The rates of survival, growth, and/or fecundity measured for each stage class from one year to the next (i.e., the vital rates) make up the elements ( $a_{ij}$ ) in a demographic matrix,  $\mathbf{A}$  (Caswell 2001). I constructed a six-stage demographic matrix ( $\mathbf{A}$ ) with 13 matrix elements ( $a_{ij}$ ) for this population of *T. grandiflorum*. The stages included: germinant (Germ), seedling (SL), one leaf (1L), small three leaf (S3L), large three leaf (L3L), and reproductive (Rep). The transition from reproductive to germinant (here-

after fecundity) is the product of seed production (no. seeds per plant) and germination rate, since both occur within a one-year time interval.

Small three-leaf plants never advanced to the reproductive stage and had some probability of regressing to the one-leaf stage, whereas three-leaf plants larger in size had some probability of advancing to the reproductive stage but never regressed to the one-leaf stage. For this reason, I divided the three-leaf stage into two stages for the model; small three-leaf (leaf length <5cm) and large three-leaf (leaf length >5cm). Both three-leaf and reproductive plants can actually become dormant, remaining below ground for one or more growing seasons (Hanzawa and Kalisz 1993). However, in this demographic model, dormant individuals were classified as large three-leaf plants for two reasons. First, the demographic fate of dormant plants was very similar to that of large three-leaf plants. Plants in both stages have no fecundity, no observed mortality, and can transition into a small three-leaf, a large three-leaf, or a reproductive stage. Second, because plants in this population rarely transition into dormancy (<5% of reproductive and large three-leaf plants), a model which combines these large three-leaf and dormant individuals into one stage will likely have less error associated with it than a more complex model with rarely observed transitions.

Several population-level parameters can be projected from  $\mathbf{A}$ . The population growth rate,  $\lambda$ , is the dominant eigenvalue of  $\mathbf{A}$ . When  $\lambda$  is <1, the population declines, and when  $\lambda$  is >1, the population grows exponentially. The reproductive value ( $\mathbf{v}$ ) and relative frequency of each stage class at stable stage distribution ( $\mathbf{w}$ ) are the left and right eigenvectors of  $\mathbf{A}$ , respectively (Caswell 2001). The reproductive value ( $\mathbf{v}$ ) gives the present value of the future offspring produced by individuals in each stage class (Caswell 2001). Typical reproductive values of perennial plants are low at birth and increase to a peak near the reproductive stages. The low value at birth reflects the high probability that individuals in the youngest stage classes will die before reproducing and the long delay before reaching a reproductive stage (Caswell 2001). The stable stage distribution,  $\mathbf{w}$ , is the proportional representation of each stage. Regardless of the initial proportion of individuals in each stage, the population will eventually reach stable stage distribution and the proportion of individuals in each stage class will remain constant (Caswell 2001). Perturbation analyses of  $\mathbf{A}$ , such as sensitivities ( $s_{ij}$ ),

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{\mathbf{v}_i \mathbf{w}_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

and elasticities ( $e_{ij}$ ),

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

calculate the absolute and proportional effects of small

changes in each matrix element on the population growth rate (de Kroon et al. 1986, Caswell 2001). These prospective analyses are used to determine the effect that small changes in a matrix element would have on  $\lambda$ .

In order to quantify how removing herbivory and pollen limitation would alter the population dynamics, I created four demographic matrices for this single population: ambient, no herbivory, no pollen limitation, and no herbivory and no pollen limitation. All plants that were part of the demographic censuses in plots and seed baskets were included in the ambient matrix.

In the “no herbivory” matrix, I excluded all plants that were consumed by deer from the matrix. This simulates the effect that removing herbivory would have on the population. When a plant was eaten in 1999 but not 2000, then the 1999–2000 data for the plant was deleted, but the 2000–2001 data was left in the data set, and vice versa for plants eaten in 2000 but not 1999.

There are several potential biases with the “no herbivory” matrix method relative to the actual removal of herbivores. First, while this method does take into account deer preference for individuals in different stage classes, it does not take into account deer preference within a stage class. For example, if deer consume only the largest reproductive plants, the demographic effects of herbivory would be underestimated. However, I suggest that deer choice of individuals within a stage is not likely to bias the predictions of the “no herbivory” matrix. In another study in this and other *T. grandiflorum* populations (Knight 2003a), I found congruence in the demographic response of plants that were naturally eaten by deer (i.e., where deer were able to choose plants), and that were experimentally clipped (i.e., where “herbivory” was randomly imposed).

Second, this method only takes into account the direct effects of herbivory (i.e., deer consumption of plants). However, deer may indirectly affect the demography of this population. For example, deer trampling and soil compaction could negatively affect seed germination rates and seedling survival. If so, the actual removal of deer would demographically benefit *T. grandiflorum* more than the “no herbivory” matrix would suggest. However, it is also possible that deer have indirect negative effects on *T. grandiflorum*. For example, many other species of understory herbs may increase in abundance if deer were removed, and compete with *T. grandiflorum* for light and nutrients. Because quantifying these indirect effects and incorporating them into the demographic matrix model were beyond the scope of this study, this study is focused solely on the direct effects of deer herbivory on *T. grandiflorum*. It is likely that these direct effects will be of greater demographic importance than indirect effects.

Third, reproductive plants in this population may currently be smaller in size, on average, than they would be if deer were actually removed. Indeed, the mean leaf length of plants in *T. grandiflorum* populations with lower levels of herbivory is 1.5 cm larger than those of this population (and another population with high levels of herbivory; Knight 2003a). This may occur because past herbivore attacks cause plants to have fewer stored resources. Larger plants produce more ovules and are more likely to remain in the reproductive stage from one year to the next (Knight 2003a). Therefore, the “no herbivory” matrix likely underestimates the demographic benefits of removing deer. One way to estimate how the removal of deer might change the average size of the reproductive plants, and their vital rates, would be to use the vital rates of populations that currently experience low levels of herbivory. I examined how changing the vital rates of reproductive plants in the “no herbivory” matrix to the values of populations with less herbivory alters the projections of the “no herbivory” matrix. However, these results should be interpreted with caution, since many other things may vary across these populations besides herbivory that influence vital rates.

To simulate how removing pollen limitation would affect the population, I created a “no pollen limitation” matrix. In this matrix, the number of seeds produced by reproductive plants was augmented by a constant value, which was the difference in the number of seeds between plants in the supplement and control pollination treatment (i.e., the effect size). Since plants consumed by white-tailed deer did not make any seeds, the number of seeds produced by these plants was not augmented.

To simulate how removing pollen limitation and herbivory would affect the population dynamics, I created a “no pollen limitation and no herbivory” matrix. In this matrix, I excluded all plants that were consumed by deer and increased the number of seeds produced by reproductive plants by a constant (the difference in the number of seeds between plants in the supplement and control pollination treatments).

#### Confidence intervals

The matrix elements ( $a_{ij}$ ) and projections ( $\lambda$ ,  $\mathbf{w}$ ,  $\mathbf{v}$ ,  $s_{ij}$ ,  $e_{ij}$ ), are based on demographic data that is collected with some degree of sampling error. To obtain 95% confidence intervals around these, when their underlying distribution was unknown, I used bootstrap resampling (McPeck and Kalisz 1993, Caswell 2001). The original demographic data set for this population included information on the fate of every individual in the plots and seed baskets, including its stage in 1999, 2000, and 2001, whether or not it was eaten by deer in each year, and its fertility. A bootstrap data set was created by sampling individuals with replacement from the original demographic data set. The sample size of the bootstrap data set was identical to the original data

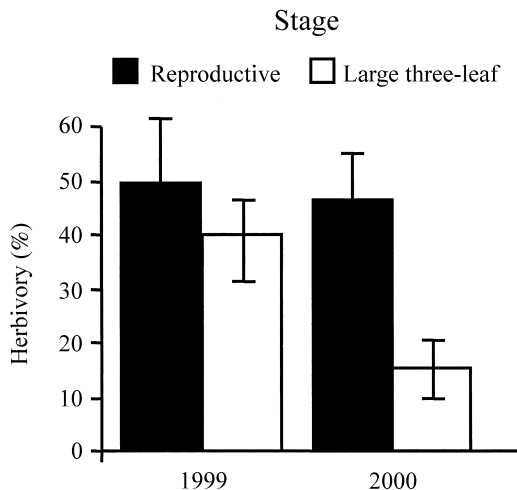


FIG. 1. The mean percentage (and 95% confidence intervals, calculated from 1000 bootstrap matrices) of reproductive and large three-leaf *Trillium grandiflorum* consumed by deer ([no. plants consumed in stage *i*/no. plants in stage *i*] × 100) in 1999 and 2000.

set. The original demographic data set contained 782 individuals (482 in plots and 300 in seed baskets). The process of creating a bootstrap data set was repeated 1000 times, to create 1000 bootstrap data sets. The population growth rate, stable stage distribution, reproductive values, sensitivities, and elasticities were calculated on each of the 1000 bootstrap matrices using MATLAB (2000). Thus, for each matrix projection of interest, I could obtain 95% confidence intervals around the median value.

This bootstrapping procedure was repeated for the “no pollen limitation,” “no herbivory,” and “no pollen limitation and no herbivory” matrices. The original data set was modified to simulate the removal of pollen limitation, deer, or both before 1000 bootstrap data sets were created. The median matrix projections (and 95% confidence intervals) were calculated from these 1000 bootstrap data sets.

*Life table response experiment*

Because herbivory occurs on both reproductive and large three-leaf plants, herbivory can potentially affect six vital rates. I used a life table response experiment (LTRE) to determine the contribution of each vital rate to the difference in  $\lambda$  between the “ambient” matrix (**A**) and the “no herbivory” matrix (**NH**). The contribution of a vital rate (i.e., matrix element,  $a_{ij}$ ) depends on both the magnitude of differences in that vital rate between **A** and **NH**, and the sensitivity of  $\lambda$  to changes in that vital rate ( $s_{ij} = \delta\lambda/\delta a_{ij}$ ):

$$\lambda^{NH} - \lambda^A \approx \sum_{ij} (a_{ij}^{NH} - a_{ij}^A) s_{ij}.$$

An average matrix, which had vital rates that were midway between the values for **A** and **NH** was created.

The sensitivities used in the LTRE were from this average matrix (Caswell 2001).

RESULTS

*Frequency of herbivory*

Herbivory was stage specific. Plants in both reproductive and large three-leaf stages experienced some herbivory in both 1999 and 2000 (Fig. 1), while plants in seedling, one-leaf, and small three-leaf stages were never consumed.

*Pollen supplementation experiments*

Plants in this population were pollen limited in both years. Plants in the supplemental pollination treatment produced, on average, five more seeds than control plants (Fig. 2). There was no main effect of year, or treatment × year interaction in the number of seeds produced (Fig. 2). I found no evidence that plants with higher seed set in 1999 had an increased probability of regressing to a nonreproductive stage in 2000 (Logistic regression:  $N = 31$ , odds ratio = 6.88,  $P = 0.28$ ). I also found no relationship between seed set in 1999 and relative growth rate of reproductive plants (Linear regression:  $N = 23$ ,  $r^2 = 0$ ,  $P = 0.52$ ).

*Demography*

Plants in younger stages had a non-zero probability of death across years. Only 31% of the individuals in the seedling stage survived and became one-leaf plants in the next growing season (the other 69% died). In contrast, no mortality was observed for plants in the large three-leaf and reproductive stages during the three years of this study (Fig. 3a). Even though plants in the

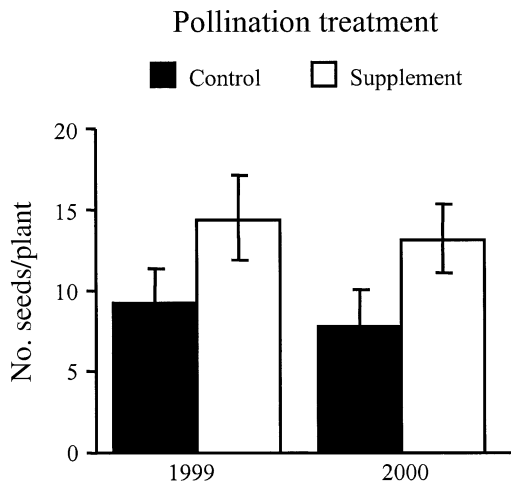
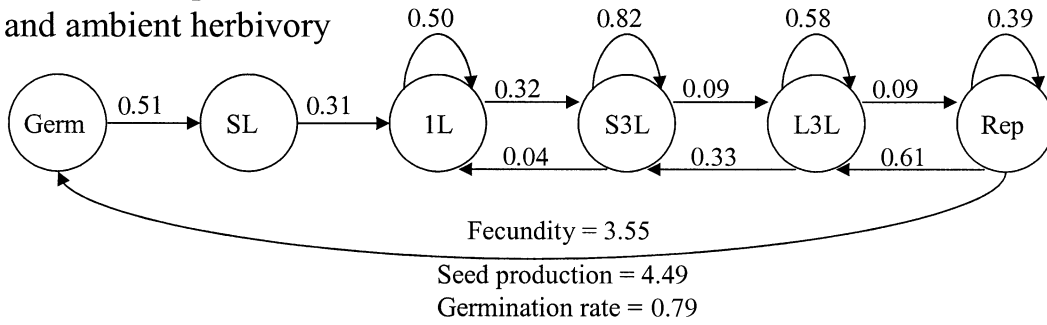
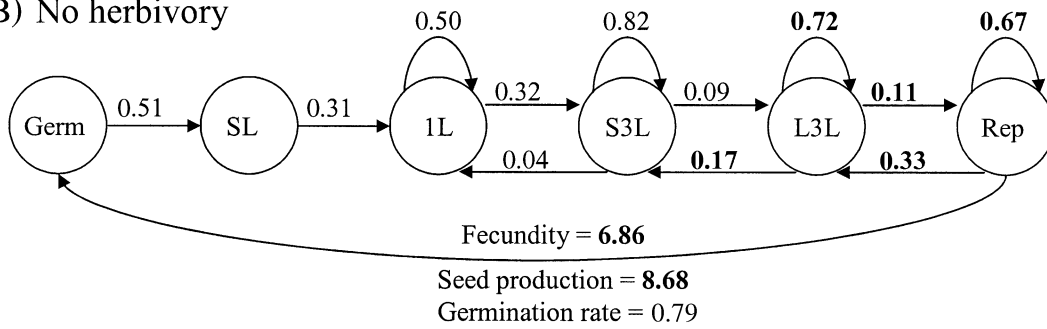


FIG. 2. Mean ( $\pm 1$  SE) number of seeds per plant in *Trillium grandiflorum* in each pollination treatment (supplement, control) and year (1999, 2000). A one-way ANOVA showed a significant effect of pollination treatment ( $F_{1,86} = 7.59$ ,  $P = 0.01$ ), but not of year ( $F_{1,86} = 0.47$ ,  $P = 0.50$ ) or of treatment × year interaction ( $F_{1,86} = 0.03$ ,  $P = 0.87$ ).

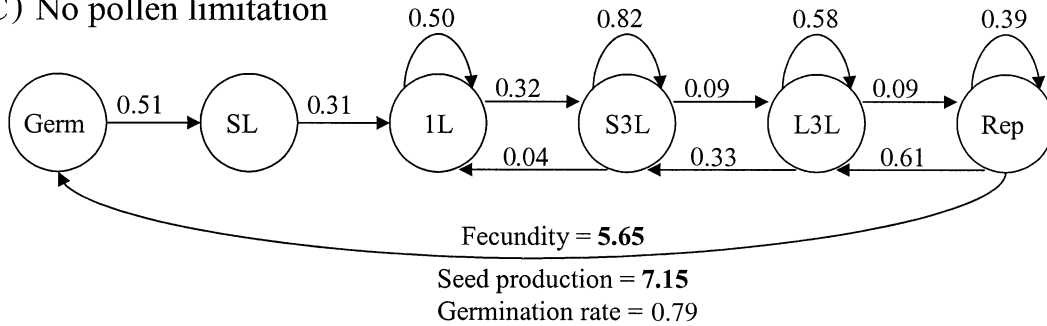
A) Ambient pollen limitation and ambient herbivory



B) No herbivory



C) No pollen limitation



D) No pollen limitation and no herbivory

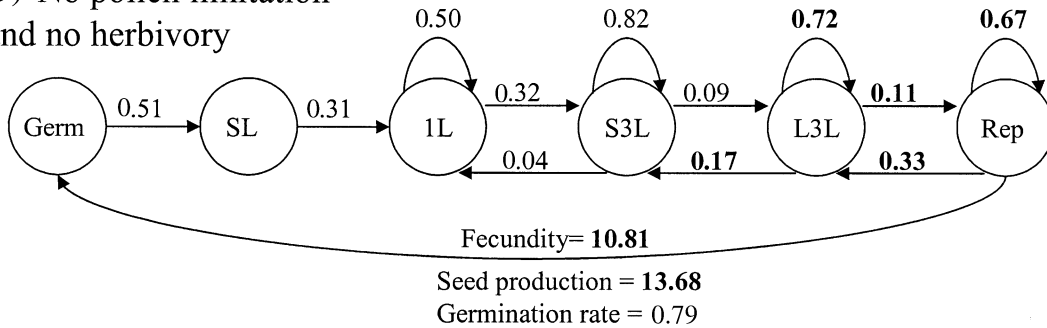


FIG. 3. Life cycle transitions of *Trillium grandiflorum* under four conditions (A–D) varying in pollen limitation and herbivory. Circles represent six demographic stages: germinant (Germ), Seedling (SL), one-leaf (1L), small three-leaf (S3L), large three-leaf (L3L), and reproductive (Rep). Numbers on the arrows represent the mean probability that plants transition to different stages from one year to the next. When all arrows leaving a stage sum to 1.0, the probability of mortality of individuals in that stage from one year to the next is zero. Boldface type indicates transitions that are changed relative to the ambient (A) life cycle graph.

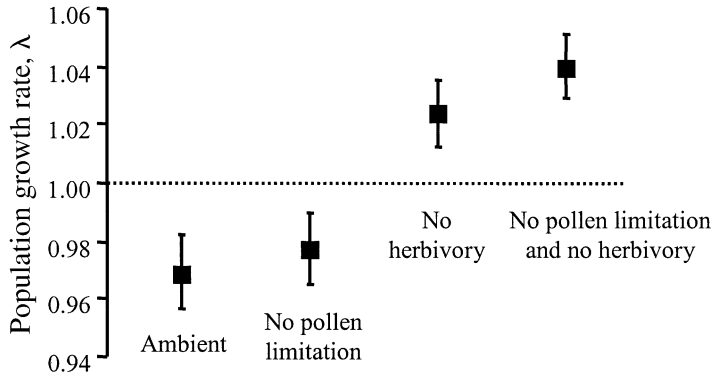


FIG. 4. The population growth rate (and 95% confidence intervals, from 1000 bootstrap samples) of a single population of *Trillium grandiflorum* under four conditions varying in pollen limitation and herbivory. When  $\lambda = 1$ , the population is neither growing nor declining. When  $\lambda > 1$ , the population is growing. When  $\lambda < 1$ , the population is declining.

reproductive stage did not have any mortality, 61% regressed to the large three-leaf stage. Similarly, 33% of the plants in the large three-leaf stage regressed to the small three-leaf stage, while only 9% advanced to the reproductive stage (Fig. 3a).

Several transitions in the life cycle were altered when plants eaten by deer were excluded from the data set (Fig. 3b). The probability of reproductive plants regressing to the large three-leaf stage decreased from 61% to 33%, and the probability of large three-leaf

plants regressing to the small three-leaf stage decreased from 33% to 17%. Similarly, the probability of reproductive plants remaining reproductive increased from 39% to 67%, and the probability of large three-leaf plants remaining in the large three-leaf stage increased from 58% to 72%. Fecundity (seed production  $\times$  germination rate) increased from 4.49 to 8.68 (Fig. 3b).

Plants in the supplemental pollination treatment produced five more seeds than control plants and there was no apparent demographic cost to this increase. Therefore, removing the effects of pollen limitation

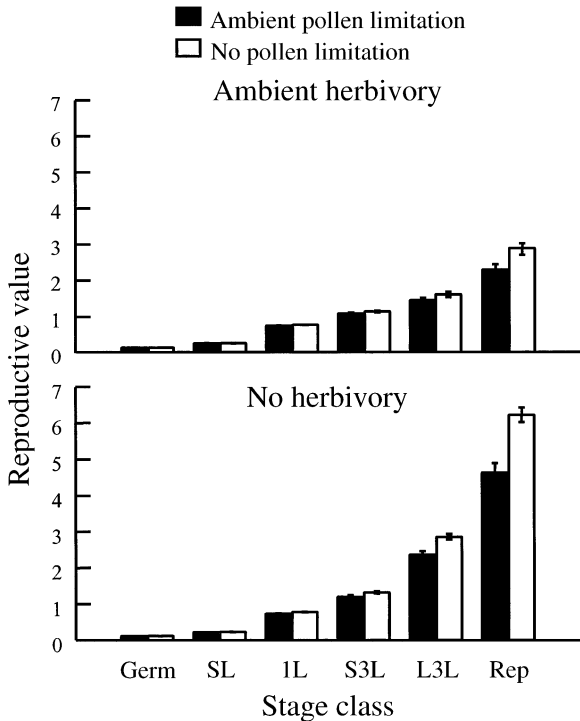


FIG. 5. The reproductive value (and 95% confidence intervals) of each stage class in the *Trillium grandiflorum* population, shown for ambient herbivory with and without pollen limitation (top panel) and for no herbivory with and without pollen limitation (bottom panel). The reproductive value, the left eigenvector of the demographic matrix, gives the present value of the future offspring produced by individuals in each stage class.

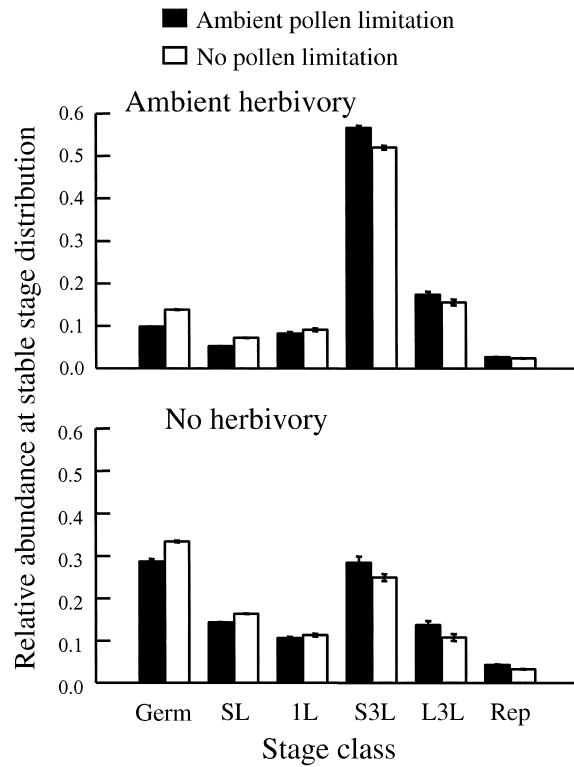


FIG. 6. The proportion of plants (and 95% confidence intervals) in each stage at stable stage distribution in the *Trillium grandiflorum* population, shown for ambient herbivory with and without pollen limitation (top panel) and for no herbivory with and without pollen limitation (bottom panel).

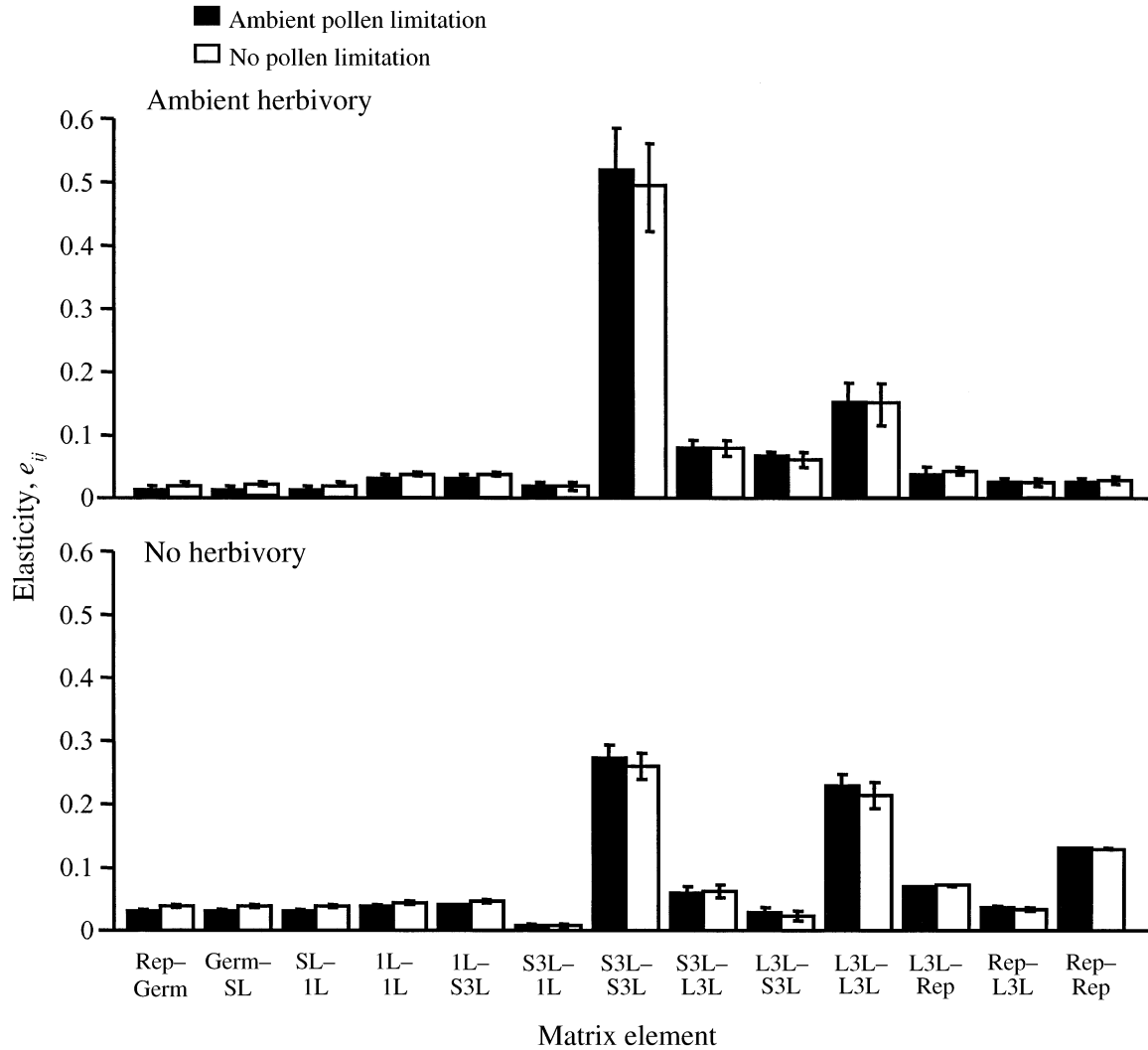


FIG. 7. Elasticity analysis of each of the matrix elements of the *Trillium grandiflorum* population, shown for ambient herbivory with and without pollen limitation (top panel) and for no herbivory with and without pollen limitation (bottom panel). Elasticities indicate the proportional effects of small changes in matrix elements on the population growth rate.

required adding five seeds to the reproductive output of all reproductive plants not eaten by deer (reproductive plants eaten by deer had zero fecundity). The seed production without pollen limitation was 7.15 seeds per plant (Fig. 3c). When both pollen limitation and herbivory were excluded, the seed production increased to 13.68 seeds per plant (Fig. 3d).

*Demographic analyses*

In the long term, the size of this population was estimated to be declining by 3% per year ( $\lambda = 0.97$ ) under ambient conditions (Fig. 4). Overall, eliminating pollen limitation had negligible effects on population growth rate, whereas eliminating herbivory had dramatic effects, shifting the population growth rate from declining to growing (Fig. 4).

The reproductive values of plants in this population are typical for a perennial plant; large three-leaf and reproductive stages have the highest values (Fig. 5). This reflects the low probability that plants in younger stage classes will survive to maturity. Elimination of herbivory resulted in an increase in the reproductive values of large three-leaf and reproductive plants (Fig. 5). The removal of pollen limitation also increased the reproductive values of large three-leaf and reproductive plants, particularly when herbivory was also removed (Fig. 5).

Removal of herbivory caused a dramatic shift in the stable stage distribution (Fig. 6); most noticeably, a decrease in the proportion of plants in the small three-leaf stage and an increase in new recruits (germinants). Removing pollen limitation caused a small increase in

TABLE 1. Life table response experiment (LTRE) of *Trillium grandiflorum*.

Life cycle transitions	$a_{ij}^{\text{NH}} - a_{ij}^{\text{A}}$	$s_{ij}$	Contribution
Rep to Germ	3.31	0.0043	0.014
Rep to L3L	-0.28	0.063	-0.018
Rep to Rep	0.28	0.11	0.031
L3L to S3L	-0.16	0.18	-0.029
L3L to L3L	0.14	0.29	0.041
L3L to Rep	0.02	0.52	0.010

*Notes:* This analysis decomposed the variation in population growth rate between a matrix that considered all plants ( $\mathbf{A}$  = ambient) and a matrix that considered only plants not consumed by deer ( $\mathbf{NH}$  = no herbivory) using the formula:  $\lambda^{\text{NH}} \equiv \lambda^{\text{A}} + \sum_{ij}(a_{ij}^{\text{NH}} - a_{ij}^{\text{A}})s_{ij}$ . For each vital rate,  $a_{ij}$ ,  $(a_{ij}^{\text{NH}} - a_{ij}^{\text{A}})s_{ij}$  gives its contribution. The differences in the vital rate between  $\mathbf{A}$  and  $\mathbf{NH}$  (column 2), and the sensitivity of the population growth rate to changes in that matrix entry (column 3), both determine the contribution of this vital rate (column 4) to the overall difference in the projected population growth rate. Abbreviations for plant stages in column 1: Rep = reproductive; Germ = germinant; L3L = large three-leaf; S3L = small three-leaf.

the proportion of new recruits, but otherwise had little effect on the stable stage distribution (Fig. 6).

Elasticity analyses of the “ambient” matrix revealed that small changes in the proportion of small three-leaf plants remaining in the small three-leaf stage have the largest effect on the population growth rate (Fig. 7 [top panel]). When herbivory was removed, the elasticity of small three-leaf plants remaining in the small three-leaf stage declined, and the elasticities of large three-leaf plants remaining in the large three-leaf stage as well as reproductive plants remaining reproductive increased (Fig. 7b [bottom panel]). Removing pollen limitation had no effect on elasticities (Fig. 7).

The actual deer removal may be more beneficial to this population than predicted by the “no herbivory” matrix model because the mean size of the reproductive plants will likely increase. In two populations with low levels of deer herbivory, the mean size of the reproductive plants is higher (1.5 cm greater leaf length) than in the study population (Knight 2003a). Further, in these populations with low herbivory, 72% of the reproductive plants not eaten by deer remained in the reproductive stage from one year to the next. This is higher than the 67% of the reproductive plants in the “no herbivory” matrix. The discrepancy may be due to the larger plant size in the natural populations with low levels of herbivory. Larger plants produce more ovules (Knight 2003a), but not necessarily more seeds (*unpublished analyses*). If the population considered in this study actually had deer removed, the size of the plants may increase, and the reproductive plants may have a 72% chance of remaining in the reproductive stage, rather than a 67% chance. This would change the population growth rate from  $\lambda = 1.018$ , as projected by the “no herbivory” matrix, to  $\lambda = 1.023$ . This is a relatively minor difference. However, these results

should be interpreted with caution, since there may be differences across these populations other than the level of herbivory that may cause differences in the size and vital rates of the reproductive plants.

#### *Life table response experiment of herbivory*

Of the 13 vital rates, six were affected by herbivory (Table 1). The LTRE analysis showed that these vital rates contributed unequally to the difference in the projected population growth rate between “ambient” and “no herbivory” matrices (Table 1). The reproductive to reproductive and the large three-leaf to large three-leaf transitions had the largest contribution. Both of these vital rates were greatly changed between “ambient” and “no herbivory” matrices, and the population growth rate was highly sensitive to changes in these vital rates (Table 1). Fecundity (i.e., reproductive to germinant) had a low contribution, despite large differences in this vital rate between “ambient” and “no herbivory” matrices, because the population growth rate was relatively insensitive to changes in it (Table 1). Regression of large three-leaf plants had a low contribution, despite the fact that the population growth rate was most sensitive to changes in this vital rate, because there was little change in this vital rate between “ambient” and “no herbivory” matrices (Table 1).

## DISCUSSION

### *Effects of herbivory*

Results from these demographic analyses suggest that white-tailed deer (*Odocoileus virginianus*) herbivory has a very large effect on the population growth rate of *Trillium grandiflorum*. At the ambient level of herbivory, the study population is expected to decrease by 3% each year ( $\lambda = 0.97$ ); whereas when I simulated a complete removal of deer herbivory, the population would increase by 2% each year ( $\lambda = 1.02$ ; Fig. 4).

The current level of deer herbivory in this population is probably unlike any in the evolutionary past of *T. grandiflorum*, which likely explains why this population is projected to be declining towards extinction today. The historic levels of deer herbivory and demographic vital rates are not known for this particular population. However, this population can be compared to other current-day populations that are experiencing considerably less herbivory. There is a negative correlation across 12 populations of *T. grandiflorum* between the population growth rate and the proportion of plants eaten by deer (Knight 2003b). This suggests that deer herbivory is the agent responsible for variation in the persistence of these populations. The population considered here had the second highest level of herbivory of these 12 populations.

While the demographic matrices with and without herbivory differed in six matrix elements, the life table response experiment (LTRE) suggests that the variation in the population growth rate is primarily due to chang-

es in the proportion of reproductive plants remaining reproductive and the proportion of large three-leaf plants remaining large three-leaf plants from one year to the next (Table 1). This result is similar to that of the only other study (on the perennial plant *Lathyrus verna*; Ehrlén 1995) to use LTREs to quantify the effect of natural herbivory on plant population growth rates. Ehrlén (1995) found that herbivory by mollusks and mammals affected several matrix entries, but that changes in the growth of individuals in the largest size class had the greatest contribution to changes in the population growth rate between eaten and uneaten plants. Both *T. grandiflorum* and *L. verna* are long-lived perennials that experience low rates of mortality once they reach the reproductive stage. Thus, factors such as herbivory that alter the survival of plants in the reproductive stage, or the probability of remaining in the reproductive stage from one year to the next, should have a large effect on the population growth rate (Silvertown et al. 1993, Crone 2001).

This study also suggests that removing (or reducing) white-tailed deer from this population would shift both the reproductive values and the stable stage distribution. The reproductive values for large three-leaf and reproductive plants are much lower in the presence of herbivory (Fig. 5). This likely results from both the loss of offspring to deer eating flowers and fruits, and from plants spending more of their lives in nonreproductive stage classes (because herbivory causes reproductive plants to regress in stage).

In the presence of herbivory, more of the population is made up of small three-leaf plants at stable stage distribution (Fig. 6). This likely reflects the high rates of regression of reproductive and large three-leaf plants. In the absence of herbivory, the relative abundances of small three-leaf plants markedly declines, and proportionally more new recruits (germinants) are present at stable stage distribution.

In a concurrent study, I examined the population growth rates of several nearby *T. grandiflorum* populations that experience little or no deer herbivory (Knight 2003b). In those populations, new recruits (germinants) were the most abundant stage at stable stage distribution. Thus, the stable stage distribution predicted from the simulated "no herbivory" matrix of the population in the current study is similar to the stable stage distribution observed in these nearby populations with much lower levels of deer herbivory. This suggests that if released from herbivory, the study population would recover from past damage and begin to resemble more intact populations.

Elasticities from the ambient matrix show that the population growth rate is most sensitive to changes in the proportion of small three-leaf plants that remain in the small three-leaf stage, and relatively insensitive to changes in all other matrix elements. In contrast, elasticities from the simulated "no herbivory" matrix show that the population is sensitive to transitions of small

three-leaf, large three-leaf, and reproductive plants (Fig. 7). In the ambient matrix, the elasticity of the proportion of small three-leaf plants that remain in the small three-leaf stage is high due to the high proportion of small three-leaf plants at stable stage distribution, and the relatively high reproductive values of these small three-leaf individuals. After many years of release from herbivory, the population growth rate would be expected to become more sensitive to changes in the transitions of large three-leaf and reproductive plants. This is because the reproductive value of plants in these stages is greatly increased (almost doubled) when herbivory is absent.

Elasticities are often used by managers to pinpoint the vital rates that the population is most sensitive to, and then direct management efforts to increasing the value of those matrix elements. However, because elasticities are local estimates, they are meant to simulate how small changes in a vital rate would affect the population growth rate, and may be misleading to managers striving to make large changes in the growth rate of a declining population (Mills et al. 1999, de Kroon et al. 2000, Bessinger 2002, Morris and Doak 2002). In this population of *T. grandiflorum*, increasing the proportion of small three-leaf plants remaining in the small three-leaf stage would initially have the largest effect on the population growth rate. However, other vital rates, such as the stage transitions of large three-leaf and reproductive plants, will play a much larger role in shifting this from a declining to a growing population. It has been suggested that elasticities of declining populations should be interpreted with the factors responsible for the decline (Mills et al. 1999, Bessinger 2002, de Kroon et al. 2000, Morris and Doak 2002). This is definitely the case for *T. grandiflorum*, since the factor responsible for the population decline, herbivory, also causes shifts in the elasticities.

There is much more biological detail that can be gained from an actual deer removal experiment. First, this would exclude both the direct (consumption) and indirect (e.g., soil compaction) effects of deer, whereas the "no herbivory" matrix presented in this study only removes the direct effects. Second, if deer were actually removed, other understory plant species would respond. Interactions with these species may affect the demography of *T. grandiflorum* in a variety of ways. For example, competition for resources or pollinators could negatively affect the demographic rates of *T. grandiflorum*. Finally, increases in the average size of plants in the reproductive stage may be observed.

#### *Effects of pollinators*

Plants in this population were consistently pollen limited. That is, plants in the pollen supplementation treatment matured significantly more seeds in both 1999 and 2000. In another study (Knight 2003c), I suggest that the consistent pollen limitation in this population may result from the low density of reproductive

plants. Indeed, in 12 population of *T. grandiflorum* studied, there was a negative relationship between the degree of pollen limitation (difference in reproductive success between supplement and control plants) and floral density. Further, the population that is the focus of this study had the lowest floral density and highest pollen limitation (Knight 2003c). While the exact mechanism of how density causes pollen limitation is unknown, there are several possibilities. Because *T. grandiflorum* has a generalist pollinator (bumblebees), this pollinator may switch to another resource when the floral density of *T. grandiflorum* gets low. Alternatively, the pollinator visitation rate may remain constant, but the amount of conspecific pollen delivered may decline. Finally, the number of self-incompatibility alleles in the population may be lower in this population, which has fewer reproductive individuals.

Although pollen limitation decreased the number of seeds per plant by 30%, eliminating pollen limitation had negligible effects on the growth rate of this population (Fig. 4). This result is not surprising, since the demographic analysis show that  $\lambda$  was relatively insensitive to changes in annual fecundity. As such, although pollination may be very important for this population in terms of gene flow and individual fitness, elimination of the problems associated with pollen limitation has only minor benefits on population-level parameters. The elimination of pollen limitation would increase the reproductive values of large three-leaf and reproductive plants, and increase the proportion of new recruits at stable stage distribution (Figs. 5, 6). However, these increases are minor relative to the benefits of removing herbivores.

Few studies have explicitly linked pollination limitation to population trajectories (Bierzychudek 1982, Ehrlén and Eriksson 1995, Parker 1997, Garcia and Ehrlén 2002). Ehrlén and Eriksson (1995) found that supplemental pollen on *Lathyrus verna* flowers increased their seed production 3.1-fold, but then the plants regressed in size and made fewer flowers in the next year relative to control plants. As a result, the overall effect of the supplemental pollen on  $\lambda$  was negligible. In contrast, Parker (1997) found that pollen supplementation did significantly increase  $\lambda$  in the invasive shrub, *Cytisus scoparius*. Her results can be attributed to (1) the large magnitude of pollen limitation in this invasive species that is without its native pollinators, and (2) the high elasticity of fecundity, which is characteristic of rapidly growing populations.

#### Implications for management

As human impacts increasingly alter the abundance of herbivores and pollinators, understanding the relative roles of these different types of interactions will allow for more informed conservation, management, and restoration of rare and declining plant populations. In perennial plants, estimating the population-level effects of herbivory and pollen limitation requires an

approach that explicitly takes stage (or age, size) structure into account (McGraw and Caswell 1996, Crone 2001). Because I found that herbivory, and not pollen limitation threatened the persistence of this *T. grandiflorum* population, I will focus on implications this study has for deer management in the remainder of this section.

Deer management is a contentious issue between those who want to prevent overbrowsing of understory plants and those who consider hunting to be cruel (Russell et al. 2001). Understanding how deer affect the viability of plant populations provides valuable information to individuals who must make management decisions about deer populations. This is one of the few studies that have linked the level of deer browse with the persistence of plant populations (see also Rooney and Gross 2003).

While this *T. grandiflorum* population is significantly declining in size by 3% every year, this decline would be difficult to notice. However, a loss of 3% per year is actually quite rapid for this species, when its long generation time is considered. In a Michigan population of *T. grandiflorum*, Hanzawa and Kalisz (1993) found that the minimum age of reproduction was 17 years. Thus, if there were 10 000 individuals in my study population (there are likely less than that), the population would likely go extinct within 200 years or in <12 generations.

In contrast, a decline in the proportion of reproductive plants present in the population should be noticeable immediately after deer herbivory begins. Indeed, two other studies have observed that populations with high levels of herbivory have fewer reproductive plants relative to nonreproductive plants (Anderson 1994, Augustine and Frelich 1998).

Land managers are interested in finding herbaceous perennials that serve as indicator species for deer abundance for several reasons. First, when deer abundance is high, the level of browse on herbaceous plants may more accurately indicate the abundance of deer than other types of counts. Second, quantifying the level of browse is usually less expensive than other methods. Third, land managers interested in conserving the biodiversity of the understory community may find the level of browse more informative than measures of deer abundance, particularly if the level of browse indicates whether or not the plant population is expected to persist (Anderson 1994, Balgooyen and Waller 1995, Webster and Parker 2000, Fletcher et al. 2001, Morellet et al. 2001, Webster et al. 2001).

Based on the results of this study, I suggest several reasons why *T. grandiflorum* may serve as a good indicator of the effects of white-tailed deer on the persistence of plants in the understory. First, this is a widespread species found in many forest understory communities throughout eastern North America. Second, this species is very long lived, and therefore it takes a long time for all of the individuals in a declining pop-

ulation to disappear. Third, changes in the proportion of plants in nonreproductive stages are obvious and immediate in this species, and likely indicate population persistence. Finally, because this is a preferred species by white-tailed deer, levels of herbivory that allow persistence of this species should also be favorable to other species. A study put forth in this journal by Anderson (1994) also suggested that *Trillium* species might serve as good indicators for understory community health in the presence of deer.

Enclosures are expensive and difficult to build. For this reason, many of these studies suffer from low replication, and may lack statistical power (Russell et al. 2001). In addition, determining population-level effects of the enclosure treatment requires the observation of at least one and preferably more than one plant generation. For long-lived perennial herbs and trees, this could take decades. While much biology that can be learned from deer enclosures is not captured in the "no herbivory" matrix method used in this study, I suggest that the demographic matrix modeling approach does capture many of the direct effects of herbivory and can be an alternative method to deer enclosure. However, the most useful information may come from the marriage of the two methods; demographic matrix models constructed in enclosure and control plots.

#### ACKNOWLEDGMENTS

I thank T.-L. Ashman, M. Barfield, J. Chase, R. Holt, S. Kalisz, R. Relyea, J. Steets, and S. Tonsor for discussions and comments; J. Chase, J. Dunn, and J. Kauffman for help in the field; H. Caswell and C. Horvitz for help with the demographic analyses; and D. Peters and two anonymous reviewers for their useful suggestions. This research was supported by the NSF (DEB-0105000), McKinley, and Darbarker research funds, Botany in Action (Phipps Conservatory and Botanical Garden), and the University of Florida Foundation. This is Pymatuning Laboratory of Ecology Publication 143.

#### LITERATURE CITED

- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* **2**:348–358.
- Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* **4**:104–109.
- Augustine, D. L., 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.
- Balگوoyen, C. P., and D. M. Waller. 1995. The use of *Clin-tonia borealis* and other indications to gauge impacts of white-tailed deer on plant communities in Northern Wisconsin, USA. *Natural Areas Journal* **15**:308–318.
- Bastrenta, B., J. Lebreton, and J. D. Thompson. 1995. Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. *Journal of Ecology* **83**:603–611.
- Beissinger, S. R. 2002. Population viability analysis: past, present, future. Pages 5–17 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Bierzchudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* **52**:335–351.
- Broyles, S. B., S. L. Sherman-Broyles, and P. Rogati. 1997. Evidence of outcrossing in *Trillium erectum* and *Trillium grandiflorum* (Liliaceae). *Journal of Heredity* **88**:325–329.
- Burd, M. 1994. Bateman's principal and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* **60**:83–139.
- Calvo, R. N., and C. C. Horvitz. 1990. Pollinator limitation, cost of reproduction, and fitness in plants: a transition-matrix demographic approach. *American Naturalist* **136**:499–516.
- Case, F. W., Jr., and R. B. Case. 1997. *Trilliums*. Timber Press, Portland, Oregon, USA.
- Caswell, H. 1989. The analysis of life table response experiments. I. Decomposition of treatment effects on population growth rate. *Ecological Modeling* **46**:221–237.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Crone, E. E. 2001. Is survivorship a better fitness surrogate than fecundity? *Evolution* **55**:2611–2614.
- de Kroon, H., A. Plaisier, J. M. van Groenendael, and H. Caswell. 1986. Elasticities: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427–1431.
- de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**:607–618.
- Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* **73**:2086–2099.
- Ehrlen, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. *Journal of Ecology* **83**:297–308.
- Ehrlen, J., and O. Eriksson. 1995. Pollen limitation and population growth in a herbaceous perennial legume. *Ecology* **76**:652–656.
- Fletcher, J. D., W. J. McShea, L. A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Natural Areas Journal* **21**(2):172–176.
- Garcia, M. B., and J. Ehrlen. 2002. Reproductive effort and herbivory timing in a perennial herb: fitness components at the individual and population levels. *American Journal of Botany* **89**:1295–1302.
- Hanzawa, F. M., and S. Kalisz. 1993. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* **80**:405–410.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477–503.
- Irwin, R. E. 2000. Morphological variation and female reproductive success in two sympatric *Trillium* species: evidence for phenotypic selection in *Trillium erectum* and *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* **87**:205–214.
- Irwin, R. E. 2001. Field and allozyme studies investigating optimal mating success in two sympatric spring-ephemeral plants, *Trillium erectum* and *T. grandiflorum*. *Heredity* **87**:178–189.
- Kalisz, S., F. M. Hanzawa, S. J. Tonsor, D. A. Thiede, and S. Voigt. 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* **80**:2620–2634.
- Knight, T. M. 2003a. Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* **90**:1207–1214.

- Knight, T. M. 2003b. The effects of herbivory and pollen limitation on the population dynamics of *Trillium grandiflorum*. Dissertation. University of Pittsburgh, Pennsylvania, USA.
- Knight, T. M. 2003c. Floral density, pollen limitation and reproductive success in *Trillium grandiflorum*. *Oecologia* **137**:557–563.
- MATLAB. 2000. MATLAB. Version 6.0. MathWorks, Natick, Massachusetts, USA.
- McCabe, R. E., and T. R. McCabe. 1997. Recounting white-tails 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 H. Caswell. 1996. Estimation of individual fitness from life-history data. *American Naturalist* **147**:47–64.
- McPeck, M. A., and S. Kalisz. 1993. Population sampling and bootstrapping in complex designs: demographic analysis. Pages 232–252 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- McPeck, M. A., and B. L. Peckarsky. 1998. Life histories and the strength of species interactions: combining mortality, growth, and fecundity effects. *Ecology* **79**:867–879.
- McShea, W. J., H. B. Underwood, and J. H. Rappole, editors. 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* **13**:815–829.
- Miriti, M. N., J. Wright, and H. F. Howe. 2001. The effects of neighbors on the demography of a dominant desert shrub (*Ambrosia dumosa*). *Ecological Monographs* **71**:491–501.
- Morellet, N., S. Champely, J. M. Gaillard, P. Ballon, and Y. Boscardin. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. *Wildlife Society Bulletin* **29**:1243–1252.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.
- Parker, I. M. 1997. Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology* **78**:1457–1470.
- Rooney, T. P., and K. Gross. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecology* **168**:267–277.
- 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.
- Sage, T. L., S. R. Griffin, V. Pontieri, P. Drobac, W. W. Cole, and S. C. H. Barrett. 2001. Stigmatic self-incompatibility and mating patterns in *Trillium grandiflorum* and *Trillium erectum*. *Annals of Botany* **88**:829–841.
- Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative demography: relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81**:465–476.
- Stowe, K. A., R. J. Marquis, C. J. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics* **31**:565–595.
- SYSTAT. 1999. SYSTAT. Version 9. SPSS, Chicago, Illinois, USA.
- Webster, C. R., M. A. Jenkins, and G. R. Parker. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana, USA. *Natural Areas Journal* **21**:149–158.
- Webster, C. R., and G. R. Parker. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) CB Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* (Ell.) as potential indicators of white-tailed deer overabundance. *Natural Areas Journal* **20**:176–188.
- Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Sciences* **7**:270–277.
- Wright, S. I., and S. C. H. Barrett. 1999. Size-dependent gender modification in a hermaphroditic perennial herb. *Proceedings of the Royal Society of London Series B* **266**:225–232.
- Zimmerman, M., and G. H. Pyke. 1988. Reproduction in *Polemonium*: assessing factors limiting seed set. *American Naturalist* **131**:723–738.