



## A demographic study of deer browsing impacts on *Trillium grandiflorum*

Thomas P. Rooney<sup>1,\*</sup> and Kevin Gross<sup>2</sup>

<sup>1</sup>Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA;

<sup>2</sup>Department of Zoology, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA;

\*Author for correspondence (e-mail: kgross@students.wisc.edu)

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### Abstract

When white-tailed deer populations reach high densities, they have negative and often dramatic effects on forest herb populations. However, it is not clear how deer affect the demographic processes of plant populations. We examined how the structure and dynamics of *Trillium grandiflorum* (Michx.) Salisb. populations are affected by deer browsing in the Upper Great Lakes region by sampling populations from nine study sites in a forested landscape in 1998 and 1999. We constructed a stage-based matrix population model for the regional population. Our model indicated that the long-term growth rate of the population to be  $-3.56\%$  per year ( $\lambda = 0.965$ ). Mortality rates were highest for seeds ( $97.5\%$ ) followed by seedlings ( $29.1\%$ ), and lower for all remaining stage classes ( $4.9$  to  $8.5\%$ ). The observed stage distribution significantly differed from the stable stage distribution, and the damping ratio ( $\rho = 1.103$ ) indicated the population would not reach its stable stage distribution anytime soon. In the absence of deer browsing, the long-term growth rate would improve to between  $-3.46\%$  and  $-1.61\%$  per year. A moderate drought during the study could account for the negative population growth rate, but deer browsing accelerates the rate of decline. Population growth is most sensitive to the proportion of plants remaining in the nonflowering stage, and deer browsing reduces this proportion. Browsing damage was relatively low in this study ( $5.4\%$  of stems in 1998,  $11.5\%$  in 1999) compared to another study of browsing impacts on *T. grandiflorum*, indicating deer could have far more severe demographic consequences in populations subject to higher levels of browsing.

### Introduction

White-tailed deer populations exist at high densities throughout the eastern United States, and have numerous impacts on forest ecosystems (Waller and Altverson 1997). Historical comparisons show forest understory communities subjected to high deer densities for decades have lost forest species diversity, suggesting a link between deer browsing and population extinction (Rooney and Dress 1997; Rooney 2001). The nature of this link is not clear. Population declines could be a consequence of browsing-induced mortality, but evidence is lacking. Alternatively, deer browsing might alter the outcome of interspecific plant competition by favoring browsing-tolerant species over browsing-intolerant species (Rooney 2001). Finally, deer might affect population vital rates other

than survival, such as the proportion of individuals that reproduce, the fertility of reproductive individuals, or the rate at which individuals move through the life cycle. Indeed, previous work indicates browsed forest herbs tend to be smaller and/or less likely to flower the season following defoliation (Edwards 1985; Rockwood and Lobstein 1994; Whigham 1990; Primack et al. 1994; Balgooyen and Waller 1995; Shelton and Inouye 1995; Rooney 1997; Augustine et al. 1998; Fletcher et al. 2001; Rooney and Waller 2001; Webster et al. 2001). Here, we use a matrix model-based approach to examine the link between deer browsing and population vital rates of *Trillium grandiflorum* (Michx.) Salisb.

*Trillium grandiflorum* is a perennial forest herb found throughout mesic deciduous and mixed coniferous forests in the eastern United States. This spe-

cies is vulnerable to deer browsing, as deer preferentially browse *T. grandiflorum* over other species (Anderson 1994). Defoliation experiments demonstrate that simulated browsing reduces the relative growth rate of individual plants (Rooney and Waller 2001). Browsing over several seasons reduces the proportion of flowering plants in a population and skews population size structure towards smaller plants (Anderson 1994; Augustine and Frelich 1998).

One conventional methodology for summarizing demographic data is the matrix population model (Leslie 1945; Lefkovich 1965; Caswell 1989). The model combines age-, size-, or stage-specific rates of survival, growth, and reproduction into a series of linear equations. Because matrix population models incorporate information about stage-specific vital rates, projections of future population dynamics are more accurate than predictions from unstructured models, at least in the short-term (Caswell and Werner 1978; Menges 1986). More importantly, matrix models can be analyzed using perturbation analysis—a class of analytical techniques including sensitivity and elasticity analysis—to determine which life cycle stage transitions most strongly influence population growth rates (Caswell (1978, 2000)). Perturbation analysis has been used to identify effective management strategies for rare plant recovery (Dixon et al. 1997; Gross et al. 1998) and exotic species control (Shea and Kelly 1998; McEvoy and Coombs 1999).

In this study, we investigate the population structure and dynamics of a regional *T. grandiflorum* population, and the effects of deer browsing on this population using a demographic matrix model. Our model allows us to assess browsing in two ways. First we determine the overall effect of browsing on *T. grandiflorum* populations by studying the population growth rate. Second, we use perturbation analysis to identify the transition rates which are most important in determining *T. grandiflorum* population growth, and investigate how variability in these vital rates is correlated with deer browsing pressure.

## Methods and materials

### *Species biology*

*Trillium grandiflorum* occupies nutrient-rich, mesic forests throughout the eastern North America (Case and Case 1997). The plant consists of a single stem

that arises from a tuber-like rhizome. Reproductive plants bear a single, showy flower subtended by a whorl of three leaves, and are often 15–45 cm tall (Hanzawa and Kalisz 1993; Anderson 1994). Plants are long-lived; individuals typically require > 15 years to become reproductive, and may live > 30 years (Hanzawa and Kalisz 1993).

In the Upper Great Lakes Region, dormancy terminates in the spring and shoots appear above-ground in late April or early May. Floral buds are present at this time, so plants can be immediately classified as reproductive or nonreproductive. Flower buds open in mid-May, and anther dehiscence occurs a few days later. Flowers are insect-pollinated. Fertilized ovules mature in a fleshy capsule, which ruptures in mid- to late- July. Seeds fall from the parent plant in mid summer and either remain beneath the parent plant, or are dispersed by animal vectors. Most of the seeds are dispersed by ants (Kalisz et al. 1999), although infrequent long-distance seed dispersal can be facilitated by vespid wasps (Jules 1996). Leaves completely senesce by August, and the plant enters dormancy until the next spring.

Seeds exhibit “double dormancy,” meaning that two winters and a summer are required to complete germination (Baskin and Baskin 1998). The radicle emerges the first year, and the long, narrow cotyledon appears above-ground the second year. *Trillium grandiflorum* does not maintain a seed bank (Hanzawa and Kalisz 1993; Kalisz et al. 1999). For the next few years, *T. grandiflorum* individuals have a single cordate leaf. Older, larger plants have three leaves (Kawano et al. 1986; Case and Case 1997). Some plants can remain dormant for the entire growing season (Gilbert and Lee (1980); S. Kalisz, personal communication).

### *Study plots*

This study was conducted in northern hardwood forests of northern Wisconsin (Ashland, Forest, and Price Co.) and western upper Michigan (Gogebic Co., adjacent to Vilas Co. in Wisconsin). The distance between sites ranged from approximately 10–150 km, and the extent of the sampling region was approximately 7200 km<sup>2</sup>. High densities of white-tailed deer and their effects on vegetation are pervasive throughout this region (Alverson et al. 1988; Waller and Alverson 1997). In 1997, we established three replicate 9 × 9 m plots, each 50–100 m apart, at random locations in each of nine *Acer saccharum*-dominated

Table 1. The relative basal area of each tree species at each of 9 sites, from Rooney (2000). Each numerical value indicates a percentage. Abbreviations are as follows: Ab, *Abies balsamea*, Ar, *Acer rubrum*, As, *Acer saccharum*, Ba, *Betula allaghaniensis*, Bp, *Betula papyrifera*, Ov, *Ostrya virginiana*, Pg, *Picea glauca*, Pt, *Populus tremuloides*, Ps, *Prunus serotina*, To, *Thuja occidentalis*, Ta, *Tilia americana*, Tc, *Tsuga canadensis*, Ur, *Ulmus rubra*.

Site	Ab	Ar	As	Ba	Bp	Ov	Pg	Pt	Ps	To	Ta	Tc	Ur
1	0	0	100	0	0	0	0	0	0	0	0	0	0
2	1	0	72	6	0	14	0	0	0	0	6	0	0
3	2	0	90	0	2	1	0	0	1	0	4	1	0
4	0	0	86	3	0	7	0	0	0	0	3	0	0
5	6	3	72	5	0	0	0	0	9	5	0	0	0
6	0	1	75	2	0	1	2	0	7	2	2	8	1
7	0	0	90	0	2	0	0	0	0	0	0	8	0
8	10	0	55	17	6	2	0	4	0	0	6	0	0
9	0	4	62	0	3	0	0	0	20	0	10	0	0

northern hardwood forest sites containing *T. grandiflorum*. The relative basal areas of all trees > 5 cm DBH in 0.04 ha plots encompassing the study plots is given in Table 1 (Rooney 2000). Canopy closure ranged from 73 to 91% (mean = 83%), and soil C/N ratios ranged from 18.4 to 27.1 (Rooney 2000).

#### Matrix model construction

We used a generalized form of the stage-structured matrix population model to analyze demographic patterns (Lefkovich 1965; Caswell 1989). The model takes the form:

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

where  $\mathbf{n}$  is a column vector whose elements  $n_i(t)$  are the number of individuals that belong to the  $i$ -th stage at time  $t$ , and  $n_i(t+1)$  is the number of individuals at time  $t+1$ . In this study, we use a time step of 1 year. Summing all of the values in the  $\mathbf{n}$  column gives the number of plants and seeds present at a site. The projection matrix  $\mathbf{A}$  is the nonnegative square matrix whose elements  $a_{ij}$  represent the transition probabilities or the fertility coefficients that provide the contributions from individuals in the  $j$ -th stage to the  $i$ -th stage over the time projection interval. In biological terms, the  $\mathbf{A}$  matrix is a matrix of vital rates.

Plants were classified into 7 stages (Figure 1, Table 2). Six of these stages are based on distinct differences associated with life cycle stages. A seventh stage, Browsed, is also included even though it is not

a life cycle stage *per se*. We included a Browsed stage for two reasons. First, plants were browsed almost as soon as they emerged in the spring, making a life cycle-based classification impossible in those numerous cases when deer visit the plants before demographers. Second, we expect plants in the Browsed state to exhibit different transition probabilities than any category of unbrowsed plants. Thus, a matrix model that includes a Browsed stage provides a more accurate description of *T. grandiflorum* demography than a matrix that does not. Because our approach combines life cycle and ecologically-meaningful states, it represents a more general approach to evaluate transition among "states" than the more specific and better known matrix population model.

#### Population sampling

In 1998, all *T. grandiflorum* plants occurring in study plots were mapped and given a unique ID number. Each 9 × 9 m study plot was divided into 324 quadrats, each 0.25 m<sup>2</sup>. When multiple plants classified as Nonflowering, Flowering and/or Browsed occupied a quadrat, plants were mapped to the nearest cm on an X-Y coordinate. When multiple Juvenile and/or Seedlings plants occupied a quadrat, they always formed a dense aggregation. Juvenile and Seedling plants in the aggregation were counted. The location of Seedlings was mapped on an X-Y coordinate to aid in relocation. We estimated 18.7 seeds were produced per flowering plant in 1998. This value was the average ( $n = 7$  observations) of observed seed set in 5 populations Vermont in 1998 (Irwin 2000) and one population in western Pennsylvania surveyed in 1981 and 1982 (Kawano et al. 1986).

Because most seeds are dispersed < 10 cm from the parent plant (Kalisz et al. 1999), we assumed these seeds stayed in the plot. In 1999, we revisited study plots to revisit plants and determine putative life cycle stage transition probabilities. We re-located each plant and classified its life cycle stage. This procedure yielded frequency data, and was used to estimate the  $\mathbf{A}$  matrix. Plants present in 1999 but absent in 1998 were classified as Dormant in 1998. Likewise, Non-Flowering, Flowering, and Browsed plants identified in 1998 but absent in 1999 were classified as Dormant. Plants which were Juveniles in 1998 but absent in 1999 were presumed dead. Seedlings present in 1999 were ignored (see below).

Identifying seedlings and distinguishing between death and dormancy for larger plants presented

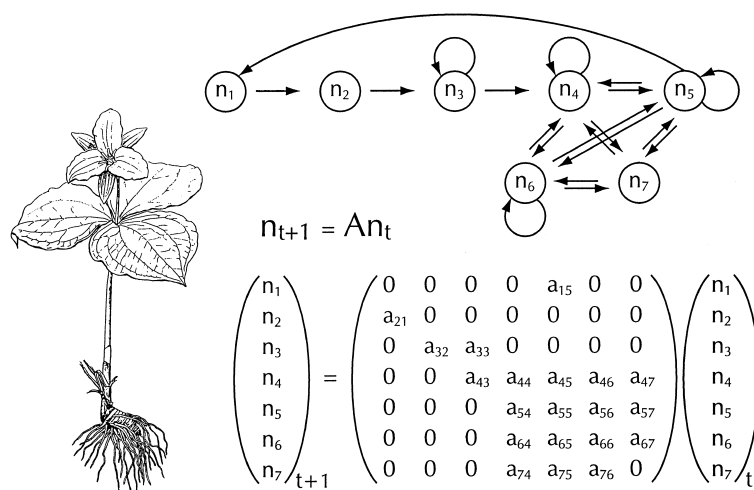


Figure 1. Life cycle graph for the 7 stage life history of *Trillium grandiflorum* and the accompanying matrix population model. Table 2 provides the names of each stage  $n_i$ . Elements in the  $A$  matrix correspond to the transition probabilities of individuals at one stage passing into another stage, or the fecundity of a stage. For example  $a_{43}$  indicates the probability of an individual in stage  $n_3$  at time  $t$  moving to stage  $n_4$  at time  $t+1$ .

Table 2. Life cycle stages of *Trillium grandiflorum* used to describe population dynamics. Leaf area estimates taken from Kawano et al. (1986).

Node	Life cycle stage	Description
1.	Seed	Ungerminated seeds and germinated seeds with a radicle but no cotyledon
2.	Seedling	Cotyledon present
3.	Juvenile	Plant has single cordate leaf, leaf area $< 10 \text{ cm}^2$
4.	Nonflowering	Plant has 3 rhomboid leaves, leaf area $> 10 \text{ cm}^2$
5.	Flowering	Plant has 3 leaves and a single flower, leaf area $> 50 \text{ cm}^2$
6.	Browsed	A nonflowering or flowering plant consumed by deer
7.	Dormant	Plant remains below-ground during growing season

unique challenges. Because of double dormancy, seedlings present above-ground in 1999 must have germinated from seeds produced in 1997 and not 1998. To determine the number of individuals that germinated from seeds in 1998, we conducted a Seedling survey in 2000 and tallied the number of Seedlings present. In order to assess the transition probability between 1998 Seeds and 1999 Seedlings, we had to make a simplifying assumption: all seeds that completed the first germination in 1999 survived the second germination in 2000. In reality, the seed to seedling transition is a multiplicative composite of two transitions, the seed to the first germination transition, and the first to second germination transition. The creation of such composite transitions is mathematically permissible, and is known as a z-transform of a life cycle graph (Caswell 1989). In 2000 we visited all plants that were classified as Dormant in 1999. If plants were still absent in 2000, we reclassified

them as dead. Plants present in 1998 and 2000 retained their Dormant classification for 1999. Thus, by the construction of our matrix, the mortality of Dormant plants is subsumed into the mortality of Nonflowering, Flowering, and Browsed plants.

#### Data analysis

We did not build matrix population models for each of our nine study sites, because the data collected at 7 of 9 sites were not complete enough to provide sensible estimates for all the vital rates in the  $A$  matrix. Specifically, at five sites, either no Seedlings were found in 2000, or no 1998 Juveniles grew to Nonflowering plants in 1999. At these sites, the estimate of the Seed  $\rightarrow$  Seedling or Juvenile  $\rightarrow$  Nonflowering transition probabilities was zero, though these rare event transitions did occur outside of the study plots. At two other sites, no Browsed plants

were found in 1998, making it impossible to estimate transitions from the Browsed stage to other stages. For these seven sites, either the solution to the projection equation was nonsensical, or we could not estimate  $\mathbf{A}$  completely. These 7 populations were not pathological or “doomed cases”—we were simply unable to estimate a sensible  $\mathbf{A}$  matrix because of sampling variability.

Therefore, we took a more conservative approach and created a summary matrix by pooling data from all nine sites into a single projection matrix. In the rest of the paper, we refer to the population described by the summary matrix as the “regional population.” Pooling data provides a summary of overall population structure and dynamics in the study region (Horvitz and Schemske 1995). Our analysis consists of two parts: (1) an analysis of the summary matrix, and (2) an examination of differences in a subset of life cycle transition values in relation to deer browsing.

#### *Analysis of summary matrix*

We used MATLAB to calculate the eigenvectors and eigenvalues for the summary matrix. The dominant eigenvalue corresponds to the finite rate of increase ( $\lambda$ ), which is related to the intrinsic rate of increase ( $r$ ) by the equation  $\lambda = e^r$ , and describes the eventual growth rate of the population. The intrinsic rate of increase is not a forecast, but is analogous to a speedometer in an automobile. A reading of 100 km per hour does not provide a forecast of how far you will travel in one hour, but it provides information about how fast you are travelling at a point in time (Keyfitz (1972), cited in Caswell (1989)). The dominant right eigenvector of the matrix corresponds to the stable stage distribution of the population—proportion of individuals in each stage class once the population growth rate converges on  $\lambda$  (Caswell 1989). We compared the stable stage distribution to the observed stage distribution using a chi-square test, and determined the rate of convergence to the stable stage structure by calculating the dampening ratio,  $\rho$ . The dampening ratio (the magnitude of the dominant eigenvalue divided by the magnitude of the second largest eigenvalue) measures the speed at which the population approaches its stable stage distribution (Caswell 1989). Values for  $\rho$  range from 1 to infinity, with large values indicating rapid convergence on the stable stage structure, and values close to 1 indicating a slow convergence. The left eigenvector represents the stage-specific reproductive values—the average

potential contribution of an individual in that class to future population growth.

From the stable stage distribution and the stage-specific reproductive values, we were able to calculate the sensitivity and elasticity values of each element ( $a_{ij}$ ) in the summary  $\mathbf{A}$  matrix. Sensitivity analysis measures the impact of each element of the  $\mathbf{A}$  matrix on  $\lambda$ , relative to the changes of the same magnitude of other elements of the  $\mathbf{A}$  matrix (Caswell 1978). In other words, sensitivity analysis measures how rapidly  $\lambda$  changes for a small change in each element of  $\mathbf{A}$ . It is difficult to compare the sensitivities of different matrix elements because a “small change” in a large matrix element (e.g. fecundities) has a different biological meaning than a “small change” in a small matrix element (e.g. rare transitions). Therefore, we also present an elasticity analysis, which measures how  $\lambda$  changes with a small proportional change in each matrix element (De Kroon et al. 1986). Elasticity values for each matrix element range from 0 to 1 and sum to 1, and thus provide a measure of the relative importance of each stage-specific transition or fecundity.

#### *Effects of browsing on demography*

Deer browsing potentially influences the dynamics of populations by changing the vital rates that govern the dynamics. To better understand the role of browsing in the demography of *T. grandiflorum*, we took two approaches. Our first approach is a modeling exercise, in which we re-classify plants that were Browsed in 1999 as either Flowering or Non-Flowering plants. Doing so helps us understand how the *T. grandiflorum* population would behave if deer browsing was eliminated. The second approach examines correlations between browsing and the transition probabilities of *T. grandiflorum* plants that were not browsed. We restrict our attention to the transition rates that were most important for *T. grandiflorum* demography, as determined by sensitivity and elasticity analysis.

Deer consume plants in the Nonflowering and Flowering stages. Once a plant is browsed, it is impossible to ascertain which stage class the plant occupied, although deer appear to prefer plants in the Flowering stage over the Nonflowering stage (Augustine and Frelich 1998). Because Flowering and Nonflowering plants have different mortality rates and reproductive values, deer could have a greater or lesser impact on population dynamics depending on which plants are consumed. To determine the extent of this impact, we developed a simple retrospective model.

Table 3. Summary population projection matrix (**A**) for the time periods  $t = 1998$  and  $t+1 = 1999$ . Values indicate the proportion of individuals from a stage at time  $t$  that become individuals in a stage at time  $t+1$ . The abundance of individuals in each size class in 1998 was: Seed (3029), Seedling (55), Juvenile (493), Nonflowering (1020), Flowering (162), Browsed (52), Dormant (222).

Stage at time $t+1$	Stage at time $t$						
	Seed	Seedling	Juvenile	Nonflowering	Flowering	Browsed	Dormant
Seed	0.000	0.000	0.000	0.000	18.700	0.000	0.000
Seedling	0.025	0.000	0.000	0.000	0.000	0.000	0.000
Juvenile	0.000	0.709	0.894	0.000	0.000	0.000	0.000
Nonflowering	0.000	0.000	0.035	0.730	0.216	0.458	0.928
Flowering	0.000	0.000	0.000	0.047	0.463	0.068	0.027
Browsed	0.000	0.000	0.000	0.070	0.154	0.220	0.045
Dormant	0.000	0.000	0.000	0.100	0.117	0.170	0.000

We eliminated the Browsed stage, and reclassified all browsed plants as either Flowering or Nonflowering. Specifically, we did seven such reclassifications, in which 100%, 90%, 75%, 60%, 50%, 25%, and 0% were classified as Flowering, and the remaining proportion as Nonflowering. For each reclassification, we re-calculated the **A** matrix and solved the population projection equation to obtain  $\lambda$ . The results from this analysis provide rates of population growth in the absence of deer browsing. We refer to this approach throughout the rest of the paper as the reclassification analysis.

Our second approach examined the effects of browsing on the demographically-important transitions of those plants that were not browsed. Since transition elements with the highest sensitivity and elasticity values have the largest impact on the finite rate of increase, we only examined stage transitions that had high sensitivities and elasticities. For each of our nine sites, we calculated deer browsing pressure by tallying consumed *T. grandiflorum* plants. We calculated the ratio of Browsed/(Browsed + Nonflowering + Flowering) for 1998 and 1999. We tested for a correlation between the proportion of plants browsed in 1998 and 1999, and calculated the mean value for the proportion of browsed plants from the two seasons. In order to avoid a spurious correlation between our measure of deer browsing pressure and the observed transition rates, we re-calculated transition rates as the fraction of plants making each transition among those plants that were not browsed in 1999. (We did not investigate the transitions of plants that were Browsed in 1998.) We arcsine square root-transformed all transition rates prior to analysis to stabilize the variance. We examined the Pearson correlation between the transitions of interest and browsing

pressure. The transitions of interest included the three transitions with the highest sensitivity values and the three with the highest elasticity values. Because there was some overlap between the transitions analysis, four correlation tests were performed. Because we performed multiple tests, we used Holm's correction to reduce the probability of committing a Type I error (Holm 1979). Holm's correction is conceptually similar to the Bonferroni correction, but is not as conservative.

When a transition rate increases or decreases, the rest of the transition rates from the same stage must also change in the opposite direction. Consequently, when we found a significant correlation, we conducted a "fate analysis" that examined the relationships between deer browsing and the rest of the transitions from that stage. By doing so, we hoped to gain a more complete understanding of how browsing was correlated with the fates of individuals in a particular stage. The correlations in the fate analyses were not subjected to a correction for multiple tests.

## Results

### *Analysis of summary matrix*

The summary projection matrix for the regional population is given in Table 3. The average mortality rate was highest for Seeds (97.5%), followed by Seedlings (29.1%). Mortality rates were 7.1% for Juveniles, 5.3% for Nonflowering, 4.9% for Flowering, and 8.5% for Browsed. The mortality rate for Dormant plants was not assessed.

The solution to the population projection equation indicated that the regional *Trillium grandiflorum* pop-

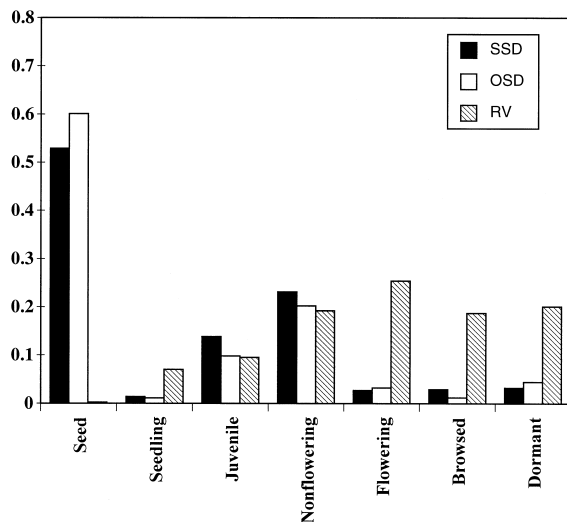


Figure 2. The stable stage distribution (black bars), observed stage distribution (open bars), and stage-specific reproductive values (hashed bars) for each of the 7 life cycle stage classes in the summary matrix analysis.

ulation was in decline. For the summary matrix,  $\lambda = 0.965$ , indicating if demographic rates remain unchanged, the population will decline by 3.56% per year in the long run. This is not a long-term forecast, however, as demographic rates do change from year to year. The projected stable age structure that corresponds with this  $\lambda$  is given in Figure 2. The Seed stage makes up the largest proportion of individuals in the stable stage distribution (60.1%), followed by the Nonflowering stage (20.2%). The stable stage distribution differed significantly from the observed stage distribution ( $df = 6$ ;  $\chi^2 = 110.98$ ;  $P < 0.0001$ ; Figure 2). The dampening ratio was 1.103, indicating that the population was converging on the stable stage distribution very slowly. Stage-specific reproductive values were lowest for Seeds and increased with the life cycle stage of individuals. Flowering individuals had the greatest reproductive value of any stage. Individuals classified as Dormant or Browsed had similar reproductive values to Nonflowering individuals (Figure 2).

Matrix sensitivities and elasticities are given in Table 4. The summary matrix was most sensitive to transitions from the Nonflowering stage to the Flowering stage. Thus, a small change in this transition would have a larger impact on  $\lambda$  than would an equally small change in any other transition probability or fecundity. The summary matrix was also quite sensitive to transitions from the Nonflowering  $\rightarrow$

Dormant stage, and from the Nonflowering  $\rightarrow$  Nonflowering stage. Elasticity values reveal that the Nonflowering  $\rightarrow$  Nonflowering transition makes the greatest proportional contribution to  $\lambda$  (43.0%), followed by the Juvenile  $\rightarrow$  Juvenile transition (15.4%) and the Dormant  $\rightarrow$  Nonflowering transition (7.7%). In other words, small changes in these demographic transitions will have more influence on  $\lambda$  than equally small changes in other demographic transitions. All other stage transitions combined proportionally contribute the remaining 34.2% to  $\lambda$ .

#### Deer browsing and demography

Our reclassification analysis revealed that deer browsing had a direct effect on *T. grandiflorum* demography. When all Browsed plants were reclassified as Nonflowering,  $\lambda = 0.966$ , which was very similar to the summary matrix ( $\lambda = 0.965$ ). Because the reproductive values for Nonflowering plants (0.192) and Browsed plants (0.187) are nearly identical, this result is not surprising. Had deer browsing not occurred, and all of the browsed plants were in the Nonflowering stage class, the population would decline at the rate of  $-3.46\%$  per year in the long run. However, if all browsed plants were reclassified as Flowering,  $\lambda = 0.984$ , and the population declines at the rate of  $-1.61\%$  per year in the long run. If deer preferentially consume Nonflowering plants, their overall impact on  $\lambda$  is negligible, but if they preferentially consume Flowering plants, the rate of decline more than doubles from  $-1.61\%$  to  $-3.56\%$ . The “true” effect of browsing observed in this study lies somewhere within this range.

Our analysis of deer impacts on vital rates provided further insight into how deer affect *T. grandiflorum* populations. The proportion of *T. grandiflorum* stems browsed by deer varied across sites from 0.0% to 24.4% in 1998 ( $n = 9$ ; mean = 5.4%), and 0.0% to 30.3% in 1999 ( $n = 9$ ; mean = 11.5%). Likewise, the average proportion of plants browsed in a population over the two years ranged from 0.0% to 27.4% ( $n = 9$ ; mean = 8.4%). Within sites, the proportion of stems browsed was positively correlated between 1998 and 1999 (Pearson  $r = 0.816$ ;  $df = 7$ ;  $P = 0.007$ ), so browsing damage on *T. grandiflorum* in one year is predictive of browsing damage in the following year.

Sensitivity and elasticity analysis revealed that the most important transitions were the Nonflowering  $\rightarrow$  Flowering, Dormant  $\rightarrow$  Nonflowering, Nonflowering  $\rightarrow$  Nonflowering, and Juvenile  $\rightarrow$  Juvenile (Ta-

Table 4. Sensitivity and elasticity matrices corresponding to the summary matrix. The 3 highest sensitivity and elasticity values appear in bold.

Stage at time t+1	Stage at time t						
	Seed	Seedling	Juvenile	Nonflowering	Flowering	Browsed	Dormant
Sensitivity							
Seed	–	–	–	–	0.001	–	–
Seedling	0.471	–	–	–	–	–	–
Juvenile	–	0.017	0.166	–	–	–	–
Nonflowering	–	–	0.338	<b>0.568</b>	0.067	0.072	0.080
Flowering	–	–	–	<b>0.749</b>	0.089	0.095	0.105
Browsed	–	–	–	0.552	0.065	0.070	0.078
Dormant	–	–	–	<b>0.593</b>	0.070	0.075	–
Elasticity							
Seed	–	–	–	–	0.012	–	–
Seedling	0.012	–	–	–	–	–	–
Juvenile	–	0.012	<b>0.154</b>	–	–	–	–
Nonflowering	–	–	0.012	<b>0.430</b>	0.015	0.034	<b>0.077</b>
Flowering	–	–	–	0.037	0.043	0.007	0.003
Browsed	–	–	–	0.040	0.011	0.016	0.004
Dormant	–	–	–	0.062	0.009	0.013	–

ble 4). Browsing diminished the proportion of unbrowsed individuals persisting in the Nonflowering stage ( $df = 7$ ;  $r = -0.810$ ;  $P < 0.05$ ), the transition with the highest elasticity value. Fate analysis further revealed more Nonflowering plants entered dormancy as browsing pressure increased, which accounted for the decrease in the proportion remaining in the Nonflowering stage ( $df = 7$ ;  $r = 0.698$ ;  $P < 0.05$ ). Browsing pressure was not significantly correlated with any other transition.

## Discussion

Previous research on *T. grandiflorum* populations revealed deer browsing reduced the proportion of flowering plants in populations and skewed size structure toward smaller plants (Anderson 1994; Augustine and Frelich 1998). Our matrix model showed that the regional population would decline in the short term without browsing, although the decline would not be as rapid. Deer browsing has a pronounced negative effect on the most important vital rate for population growth: the Nonflowering  $\rightarrow$  Nonflowering transition. Our model indicates deer browsing negatively impacts *T. grandiflorum* demography.

## Analysis of the summary matrix

Our projection analysis of the regional population revealed the regional population should decline over time. This would happen if the regional population attained a stable stage distribution, transition rates contain no sampling errors, and the vital rates remained constant over time (Caswell 1989; Bierzychudek 1999). In reality, our regional population has not yet attained this stable stage distribution, nor is it likely to given its low dampening ratio (see Bierzychudek (1999)). Although our estimates of transition rates were based on a relatively large number of observations, they still contain some sampling error. Finally, vital rates do change over time. A moderate drought in 1998 caused individual plants to decline in size between 1998 and 1999, and may have reduced the number of plants making the Nonflowering  $\rightarrow$  Flowering transition (Rooney and Waller 2001). Caswell (1989) emphasizes that projection analysis is best regarded as a thought experiment. It tells us what would happen if current conditions were maintained, but not what will happen—it does not provide a forecast. The utility of projection analysis is that it provides a “snapshot in time” of the population trajectory.

The vital rates we observed were very typical of other forest herbs in that mortality rates were high for

early life cycle stages (Seed and Seedling), and low for later life cycle stages (Bierzuchudek 1982). The reported vital rates appear representative of what other researchers have observed with *T. grandiflorum*. Seed mortality rates were somewhat higher in this study (97.5%) than observed in Michigan (86 – 88%) by Kalisz et al. (1999) or inferred by Kawano et al. (1986) in Pennsylvania (~90%). Our observed stage distribution was similar to the distribution studied by Kawano et al. (1986), although we observed a smaller proportion of Seedlings and a larger proportion of Nonflowering plants in this study.

Silvertown et al. (1993) reported that most iteroparous (polycarpic) forest herbs had relatively low elasticity values related to fecundity. *Trillium grandiflorum* is no exception; elasticities affecting fecundity elements (i.e. seed production and seedling recruitment) summed to 0.024. Silvertown et al. (1993) also noted that forest herbs show a large range of values for survival elements (i.e. stasis and retrogression transitions). Here, *T. grandiflorum* weighs in at the high end of the scale, with survival elements summing to 0.831.

#### *Deer browsing and demography*

Our reclassification analysis demonstrated that deer browsing has a direct effect on *T. grandiflorum* demography. With browsing, the regional population was declining by 3.56% per year in the long run. When we reclassified Browsed plants as Flowering or Nonflowering to simulate the effects of no browsing, the regional population would have declined by 1.61% to 3.46% per year in the long run. If deer consume mostly flowering plants, the decline would be more severe than if they consumed mostly nonflowering plants. Deer prefer flowering plants over nonflowering ones (Augustine and Frelich 1998), making it likely that the rate of population decline would be closer to 1.61% per year than 3.46% per year if browsing was completely eliminated. This result provides empirical evidence that deer browsing can adversely affect rates of population by reducing the proportion of flowering plants in the population.

The proportion of individual Nonflowering + Flowering *T. grandiflorum* plants consumed by deer was lower in this study (5.4% in 1998 and 11.5% in 1999) than Augustine and Frelich (1998) reported in the maple-basswood region of southern Minnesota (19.8% and 25.6%). Had we observed such high pro-

portions of browsed plants, we would expect rates of population decline to be faster than -3.56% per year.

Because population vital rates vary in both space and time (Horvitz and Schemske 1995), it was instructive to examine how browsing affect this variation. We found that the proportion of Nonflowering plants persisting in that stage decreased as browsing damage increased. (Recall that we factored out Browsed plants in our calculation of this transition to prevent a spurious correlation between the two variables.) Browsing damage at a site was positively correlated between years. Fate analysis revealed that as browsing increased at a site, there was a corresponding increase in the number of individuals making the Nonflowering → Dormant transition that detracted from the number of individuals making the Nonflowering → Nonflowering transition. Because browsing affected the stage transition with the highest elasticity value, it is reasonable to infer that deer browsing on Nonflowering plants accounts for the magnitude of  $\lambda$  for the regional population. This is an important finding, because it indicates deer browsing does not only affect plant populations by affecting the vital rates of Flowering individuals, but by affecting the fates of Nonflowering individuals as well.

To summarize, we found two pathways whereby deer browsing could affect the population. First, the selective browsing of plants with the greatest reproductive value (Flowering plants in this study) accelerates the rate of population decline. We expected this to occur. Second, deer browsing had a significant negative correlation with the vital rate with the highest measured elasticity (the Nonflowering → Nonflowering transition). This result was unexpected. It illustrates that the mechanisms by which deer browsing affects plant populations are not always obvious.

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