

2006

## Population Demography and Herbivory of *Trillium Grandiflorum*

Thomas P. Rooney  
*University of Wisconsin-Madison*

Kendra C. Millam  
*University of Wisconsin-Madison*

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>



Part of the [Botany Commons](#)

---

### Recommended Citation

Rooney, Thomas P. and Millam, Kendra C. (2006) "Population Demography and Herbivory of *Trillium Grandiflorum*," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 22: Iss. 1, Article 46.  
Available at: <https://scholarship.claremont.edu/aliso/vol22/iss1/46>

POPULATION DEMOGRAPHY AND HERBIVORY OF *TRILLIUM GRANDIFLORUM*:  
IMPLICATIONS FOR *TRILLIUM* CONSERVATION

THOMAS P. ROONEY<sup>1,2</sup> AND KENDRA C. MILLAM<sup>1</sup>

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

<sup>2</sup>Corresponding author (tprooney@wisc.edu)

ABSTRACT

Numerous pedicellate and sessile *Trillium* species are endemic to eastern North America, where white-tailed deer (*Odocoileus virginianus*) populations have been growing in recent decades. Deer feed on *Trillium* plants, and because they often consume all leaves and flowers, the photosynthetic capacity of browsed plants is greatly diminished. To determine if deer can influence *Trillium* population dynamics, we review two recent studies that applied matrix population models to understand how deer browsing affects *Trillium grandiflorum*. Research conducted in the Great Lakes region indicated *Trillium* populations in which 6–12% plants were browsed declined 3.6% per year. Simulations show that with additional browsing, the rate of population decline accelerates. Similar research conducted in the Appalachian plateau region by a different researcher yielded nearly identical results. We apply insights from these matrix population models to two additional conservation problems in *Trillium*: unsustainable collecting of wild plants and forest fragmentation. Because other *Trillium* in the eastern United States are similar morphologically and ecologically, our results from *Trillium grandiflorum* might be generalized to apply to other members of the genus.

Key words: eastern United States, habitat fragmentation, harvesting, matrix population model, population demography, white-tailed deer.

INTRODUCTION

The genus *Trillium* L. (Melanthiaceae) contains at least 42 species of herbaceous perennials with an Arcto-Tertiary distribution (Chase et al. 1995; Kawano and Kato 1995; Case and Case 1997; Osaloo et al. 1999). Over half are found in eastern North America, where they occur in forest understory environments. In recent decades, white-tailed deer (*Odocoileus virginianus* Zimm.) have become more abundant throughout this region (Alverson et al. 1988; Rooney and Waller 2003). Adult deer consume 2–4% of their body weight per day, which amounts to 2–3 kg of plant material (Cypher and Cypher 1988). As foraging generalists, they consume herbaceous plants, grasses, woody plant leaves, large seeds, fruits, and twigs (Short 1975). Deer appear to disproportionately consume *Trillium* relative to other forest herbs (Anderson 1994; Augustine and Frelich 1998). Further, they often consume 100% of leaf and flower biomass, making it a good genus to examine to determine whether deer affect population persistence of forest and woodland perennial herbs.

Researchers have been using *Trillium grandiflorum* (Michx.) Salisb. as a model species for investigating deer herbivory impacts. *Trillium grandiflorum* has four desirable traits that make it ideal for this type of research. First, *T. grandiflorum* is long-lived. Using Cochran and Ellner's (1992) method, Knight (pers. comm.) found the average generation time for *T. grandiflorum* was 39.3 years. In the absence of very high mortality rates, longevity can slow the rate at which populations go extinct. Second, *T. grandiflorum* shows a clear negative response to herbivory. Following defoliation, plants do not replace lost shoots until the following season (Rooney and Waller 2001; Knight 2003). Defoliated flowering plants are less likely to flower in the sub-

sequent season than plants not defoliated, so browsing reduces current and future reproduction (Knight 2003). Non-flowering plants are still browsed by deer, although at a lower incidence than browsing on flowering plants (Augustine and Frelich 1998). Over time, individual plants protected from deer tend to be larger and more likely to flower than unprotected plants, indicating browsing is a key determinant of population structure (Anderson 1994; Augustine and Frelich 1998). Third, *T. grandiflorum* has a broad ecological amplitude and is widely distributed throughout the eastern deciduous forest region. Fourth, the species is nonclonal and has discrete life stages, making demographic analysis relatively straightforward. Thus, it is ideal for monitoring and evaluating deer impacts. Because it is morphologically and ecologically similar to other eastern North American species (Ohara 1989), the response of *T. grandiflorum* could be used to predict how these other species will respond to increasing deer browsing pressure.

Between 1999–2002, we attempted to revisit vouchered populations of all seven taxa in the *Trillium erectum* L. complex from hundreds of sites throughout eastern North America. Over half of these populations were extirpated, even though the forest remained intact. We hypothesized deer were responsible, because where populations were extirpated, we often saw evidence of high deer densities. As deer densities are likely to remain high in this region in coming decades (Rooney and Waller 2003), additional populations may be at risk. While deer browsing has a negative effect on individual plants, it is not clear if deer significantly influence population growth and thus potentially account for the extirpations of the plants of *T. erectum* that we observed. If deer have a significant impact on *Trillium* populations, then it is important to determine what levels of deer browsing affect population viability. Here, we report on some of

the insights gained from applying matrix population models to *T. grandiflorum* populations. After briefly describing how these models are constructed, we use real and simulated data to examine how *T. grandiflorum* populations respond to deer browsing. We conclude by showing how insights from demographic models can be extended to other conservation problems involving *Trillium*.

#### MATRIX POPULATION MODELS

Our ability to predict the size of the population in subsequent years depends not only on knowing how many individuals are in the population, but also on what life stage those plants are in. Demographic studies that rely on matrix population models link differences in vital rates (i.e., survival, growth, and reproduction rates) with specific stages in a plant's life cycle (Caswell 2001). In other words, the behavior of a demographic model depends not only on how many individuals are in the population, but also on the fraction of individuals in each life-cycle stage. Demographers divide life cycles into classes based on age (Leslie 1945), stage (Lefkovitch 1965), or size (Caswell 2001). Individual plants are marked and assigned to a specific class. After a period of time (often one year), those individuals are rechecked, and their stage is recorded and any reproductive activity is quantified. From these data, demographers can construct class-specific vital rates: schedules of survivorship, growth into new classes, or reproduction. A minimum of two years is required to obtain vital rate data, but many demographic studies last longer. The matrix population model combines class-specific rates of survival, growth, and reproduction into a series of linear equations. When solved, these equations give insight into the dynamics of populations over short time periods. Perturbation analysis of the models can reveal which life-cycle stage transitions most strongly influence population growth rates (Caswell 1978, 2000).

The matrix population 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 life-cycle class at time  $t$ , and  $n_i(t+1)$  is the number of individuals at time  $t+1$ . Summing all of the values in the  $\mathbf{n}$  column gives the number of individuals present at a site. The projection matrix  $\mathbf{A}$  is the nonnegative square matrix whose elements  $a_{ij}$  represent the average number of offspring produced by plants in the reproductive classes, the probability of remaining in the same class, or the probability of growth or regression to a new class, thus providing the contributions from individuals in the  $j$ -th life-cycle class to the  $i$ -th life-cycle class over the time projection interval. In biological terms, the  $\mathbf{A}$  matrix is a matrix of vital rates.

From the  $\mathbf{A}$  matrix, we can obtain the eigenvectors and eigenvalues. These values have biological meaning. The left eigenvector of the  $\mathbf{A}$  matrix, for example, represents the stage-specific reproductive values. The reproductive value of a stage class measures the average potential contribution of an individual in that class to future population growth. The dominant right eigenvector of the  $\mathbf{A}$  matrix corresponds to the stable-stage distribution of the population. The stable-stage distribution is the proportion of individuals in each

stage class once the population growth rate ceases to change (Caswell 2001). The dominant eigenvalue corresponds to the finite rate of increase,  $\lambda$ , which is the growth rate of the population once the stable-stage distribution is attained. From the left and right eigenvectors (the stage-specific reproductive values and the stable-stage distribution), two other useful properties of the population can be calculated: 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  $\lambda$  changes in response to 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 meaning biologically than a "small change" in a small matrix element (e.g., rare transitions). Elasticity analysis overcomes this problem, as it measures how  $\lambda$  changes with a small proportional change in each matrix element (deKroon et al. 1986). Elasticity values for each matrix element range from 0–1 and sum to 1 over the entire matrix. In other words, elasticity values measure the relative importance of each stage-specific transition or fecundity.

#### TRILLIUM GRANDIFLORUM DEMOGRAPHY

Several previous studies provide a comparative analysis of *Trillium* reproductive biology, population structures, and life history strategies of several species throughout the geographic range of the taxon (Kawano et al. 1986, 1992; Ohara and Kawano 1986a, b; Ohara 1989; Ohara and Utech 1986, 1988). There are remarkable similarities that link all species studied. *Trillium* life-cycle stages can be delimited based on leaf-area size classes or gross morphology. Plants in different stages experience different survival and reproductive rates. Individuals in the smallest leaf-area size classes experience highest mortality rates, while individuals in the largest size classes show high survivorship and reproductive rates.

Ohara et al. (2001) conducted a 12-year demographic study of the Japanese pedicellate *Trillium apetalon* Makino. They identified four life-cycle classes (seedling, 1-leaf, nonreproductive 3-leaf, and reproductive). The population grew at the rate of 2% per year, and elasticity analysis revealed that the most important life-cycle transitions were stasis in the reproductive stage (0.71), followed by stasis in the nonreproductive (3-leaf) stage (0.11).

Two recent studies address the impact of deer on *Trillium* demography. Rooney and Gross (2003) studied *T. grandiflorum* in the Great Lakes region of North America. They delimited six life-cycle classes based on discrete stages: seeds, seedlings, juvenile (1-leaf) plants, nonreproductive (3-leaf) plants, reproductive plants, and dormant plants. They added browsed plants as a distinct seventh class even though it is technically not a life-cycle stage. Their rationale was straightforward; the vital rates for browsed plants would probably differ from nonreproductive 3-leaf plants and reproductive plants, so they should be treated separately. Knight (2004), also using matrix population models to examine deer impacts on *T. grandiflorum* in the Appalachian

plateaus region, used an alternate scheme in delimiting life-cycle classes. She divided nonreproductive 3-leaf plants into two size classes: small and large. In addition, she did not use dormant or browsed classes. A browsed class was unnecessary because she knew the stage of individual plants prior to herbivory.

Despite the different life-cycle models used by Rooney and Gross (2003) and Knight (2004) and despite the studies being conducted in different regions, their results were remarkably similar. Deer consumed 6–12% of all plants in the Great Lakes region, and 15–50% in the Appalachian plateaus. Both populations were in decline: 3.6% per year in the Great Lakes region, and 3% per year in the Appalachian plateaus. Both studies found that flowering plants had the highest reproductive values, and that stasis in the 3-leaf nonreproductive stage had the highest elasticity value. Rooney and Gross (2003) found this transition had an elasticity value of 0.43. Knight (2004), who differentiated between small and large 3-leaf plants, found that the elasticity value for stasis in the smaller plants (ca. 0.5) was greater than that for large plants (ca. 0.1).

Both studies reported that deer reduced population growth. Rooney and Gross (2003) asked what would happen if browsed plants were not browsed. In the matrix model, they reclassified browsed plants with a fraction of reproductive and nonreproductive plants, and found that the rate of population growth increased with an increase in the number of reproductive plants. Even when 100% of the browsed plants were reclassified as nonreproductive, the population growth rate was higher than the population with browsed plants. However, even complete replacement of browsed plants by reproductive ones did not cause the population to increase; instead it declined at the rate of 1.6% per year. Rooney (2000) also used a simulation approach to examine the consequences of doubling the number of individuals browsed by deer, assuming that stage transition rates were invariant and no immigration or emigration occurred. The simulations revealed that doubling the herbivory rate observed by Rooney and Gross (2003) caused the population to decline at the rate of 4.8% per year. Knight (2004) removed browsed plants from her analysis to determine what effect browsing had on population growth. She found that without herbivory, the population would increase 2% per year.

Elasticity analysis of *T. apetalon* and *T. grandiflorum* provides insights into the life history strategy of these forest herbs. Elasticity values for fecundity-related transitions (i.e., seed production and seedling recruitment) are low, while values for survival elements (i.e., stasis and retrogression transitions) are high. A life history strategy with low elasticity values for fecundity and high elasticity values for survival is typical of other late successional forest herbs (Silvertown et al. 1993). For such species, recruitment of new individuals into the population from seed is often a rare event. Factors affecting the survival of reproductive or large nonreproductive plants are more critical determinants of long-term population persistence than shorter-term fluctuations in seed set or recruitment.

#### GENERALIZATIONS FROM DEMOGRAPHIC ANALYSIS

The demographic results from *T. apetalon* and *T. grandiflorum* can also provide insight into two additional con-

servation problems: overharvesting and forest fragmentation. Because they are so beautiful and charismatic, collectors and gardeners avidly seek *Trillium* plants. They are very slow growing in the wild, often requiring over 17 years before they become reproductive (Hanzawa and Kalisz 1993). Because of their long generation time, unregulated or illegal collecting of wild plants for gardens or nurseries can lead to overharvesting. Demographic models have been constructed for other long-lived herbs subjected to harvesting. A demographic model of the medicinal herb ginseng, *Panax quinquefolius* L. (Araliaceae), reveals that some of the adult plants could be harvested in a sustainable manner, but only in years when the population exhibited strong growth in sites where populations are large (Charron and Gagnon 1991; Nantel et al. 1996). As with *T. apetalon* and *T. grandiflorum*, elasticity values for *P. quinquefolius* were highest for survival of the largest plants in the population. In other words, removal of the largest plants in the population would influence the population growth rate more strongly than the removal of plants of any other size. If *Trillium* populations grew under ideal conditions (no herbivory or habitat loss, for example), some adult *Trillium* plants (rhizomes and shoots) could probably be harvested in a sustainable manner in good years where populations are large. Simulations of elevated mortality in the nonreproductive 3-leaf and reproductive stage classes, similar to the approach used by Nantel et al. (1996) could reveal what levels of harvest could be sustained. With deer browsing, however, it is unlikely that any level of *Trillium* harvesting would be sustainable.

Forest fragmentation and edge effects also impact some *Trillium* species. In western North America, *T. ovatum* Pursh. appears to be in decline (Jules 1998). Clearcutting and subsequent conifer planting kills >95% of all *T. ovatum* individuals. In intact forest adjacent to these clearcuts, *T. ovatum* populations showed low recruitment (Jules and Rathcke 1999). Two putative factors are examined: pollen limitation and seed predation. Individuals growing along forest edges were the most pollen-limited, perhaps because the edge was suboptimal for pollinators. This might not prevent population persistence, though, as Knight (2004) reports, chronic pollen limitation does not prevent population persistence. Densities of deer mice, *Peromyscus maniculatus* Wagner, are often higher in clearcuts than intact forest (Sullivan 1979, 1980; Tallmon et al. 2003), and appear to be more abundant along forest edges than in the forest interior (Jules and Rathcke 1999). These mice are voracious seed predators, and populations closest to the forest edge suffered the highest levels of seed predation (Jules and Rathcke 1999; Tallmon et al. 2003). In the conclusion of their paper, they noted that a matrix population model would reveal the extent to which seed predation and pollen limitation affected the viability of these *T. ovatum* populations. Given what we know about both pollen limitation and *Trillium* demography (Rooney and Gross 2003; Knight 2004), it is likely that *T. ovatum* could experience several years of elevated seed predation without reducing the probability of population persistence, given the low elasticity values for reproduction-related transitions (Ohara et al. 2001; Rooney and Gross 2003; Knight 2004). Knight (2004) examined the consequences of increasing seed production by 30%, and found that it had a negligible effect on population growth. For *T. ovatum*, the critical

question is: how many years do edge effects persist? If these edge effects persist for 5–10 years, *Trillium* populations could persist. However, lasting edge effects could undermine population viability.

Small forest fragments embedded within an agricultural landscape in eastern Hokkaido, Japan, pose several problems for *Trillium camschatcense* Ker Gawl. populations. As fragments get smaller, the fraction of the population influenced by edge effects increases (Tomimatsu and Ohara 2002, 2004). Close to forest edges, densities of seedlings, 1-leaf, and flowering plants were significantly lower than in the forest interior (Tomimatsu and Ohara 2004). In addition, as fragments get smaller, population sizes decline (Tomimatsu and Ohara 2003). Small populations suffer lower levels of genetic diversity and reduced seed production and seedling recruitment (Tomimatsu and Ohara 2002, 2003), raising questions about the long-term viability of these small populations.

In conclusion, demographic analyses reveal that deer can significantly influence *T. grandiflorum* population growth. Browsing on other nonclonal *Trillium* species with similar life history strategies and intolerance of herbivory could have similar, negative results on populations. While we do not know if the extirpations of *Trillium erectum* taxa we observed were caused by deer browsing, it is plausible that deer could have been partially or fully responsible for some of these population losses. In the absence of additional data, it seems reasonable to use these demographic findings to predict how populations of additional *Trillium* species in other regions will respond to deer browsing.

#### ACKNOWLEDGMENTS

We thank Scott Mills for bringing the *Trillium ovatum* recruitment limitation to our attention, Tiffany Knight both for sharing her research findings with us prior to publication, and commenting on an early draft of this chapter, and three anonymous reviewers for helpful comments. This research was supported by a Conservation and Research Foundation grant and an EPA STAR fellowship to TPR.

#### LITERATURE CITED

- ALVERSON, W. S., D. M. WALLER, AND S. L. SOLHEIM. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biol.* **2**: 348–358.
- ANDERSON, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Applic.* **4**: 104–109.
- AUGUSTINE, D. J., AND L. E. FRELICH. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conservation Biol.* **12**: 995–1004.
- CASE, F. W., AND R. B. CASE. 1997. *Trilliums*. Timber Press, Portland, Oregon. 285 p.
- CASWELL, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theor. Populat. Biol.* **14**: 215–230.
- . 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**: 619–627.
- . 2001. Matrix population models: construction, analysis, and interpretation, Ed. 2. Sinauer Associates, Inc., Sunderland, Massachusetts. 722 p.
- CHARRON, D., AND D. GAGNON. 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). *J. Ecol.* **79**: 431–445.
- CHASE, M. W., M. R. DUVAL, H. G. HILLIS, J. G. CONRAN, A. V. COX, L. E. EGUIARTE, J. HARTWELL, M. F. FAY, L. R. CADDICK, K. M. CAMERON, AND S. HOOT. 1995. Molecular phylogenetics of Liliaceae, pp. 109–137. In P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries, [eds.], *Monocotyledons: systematics and evolution*. The Royal Botanical Gardens, Kew, Richmond, Surrey, UK.
- COCHRAN, M. E., AND S. ELLNER. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecol. Monogr.* **62**: 345–364.
- CYPHER, B. L., AND E. A. CYPHER. 1988. Ecology and management of white-tailed deer in northeastern coastal habitats. *U.S. Fish and Wildlife Service Biological Report* **88**: 1–52.
- DE KROON, H., A. PLAISIER, J. VAN GROENENDAEL, AND H. CASWELL. 1986. Elasticity as a measure of the relative contribution of demographic parameters to population growth rate. *Ecology* **67**: 1427–1431.
- HANZAWA, F. M., AND S. KALISZ. 1993. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). *Amer. J. Bot.* **80**: 405–410.
- JULES, E. S. 1998. Habitat fragmentation and demographic change for a common plant: trillium in old-growth forest. *Ecology* **79**: 1645–1656.
- , AND B. J. RATHCKE. 1999. Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. *Conservation Biol.* **13**: 784–793.
- KAWANO, S., AND H. KATO. 1995. Evolutionary biology of *Trillium* and related genera (Trilliaceae), Vol. 2. Cladistic analysis on gross morphological characters, and phylogeny and evolution of the genus *Trillium*. *Pl. Spec. Biol.* **10**: 169–183.
- , M. OHARA, AND F. D. UTECH. 1986. Life history studies on the genus *Trillium* (Liliaceae), vol. 2. Reproductive ecology and survivorship of four eastern North American species. *Pl. Spec. Biol.* **1**: 47–58.
- , ———, AND ———. 1992. Life history studies on the genus *Trillium* (Liliaceae), Vol. 6. Life history characteristics of three western North American species and their evolutionary-ecological implications. *Pl. Spec. Biol.* **7**: 21–36.
- KNIGHT, T. M. 2003. Effects of herbivory and its timing across populations of *Trillium grandiflorum*. *Amer. J. Bot.* **90**: 1207–1214.
- . 2004. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecol. Applic.* **14**: 915–928.
- LEFKOVITCH, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* **21**: 1–18.
- LESLIE, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**: 183–212.
- NANTEL, P., D. GAGNON, AND A. NAULT. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. *Conservation Biol.* **10**: 608–621.
- OHARA, M. 1989. Life history evolution in the genus *Trillium*. *Pl. Spec. Biol.* **4**: 1–28.
- , AND S. KAWANO. 1986a. Life history studies on the genus *Trillium* (Liliaceae), Vol. 1. Reproductive biology of four Japanese species. *Pl. Spec. Biol.* **1**: 35–45.
- , AND ———. 1986b. Life history studies on the genus *Trillium* (Liliaceae), Vol. 4. Stage class structures and spatial distribution of four Japanese species. *Pl. Spec. Biol.* **1**: 147–161.
- , T. TAKADA, AND S. KAWANO. 2001. Demography and reproductive strategies of a polycarpic perennial, *Trillium apetalum* (Trilliaceae). *Pl. Spec. Biol.* **16**: 209–217.
- , AND F. H. UTECH. 1986. Life history studies on the genus *Trillium* (Liliaceae), Vol. 3. Reproductive biology of six sessile-flowered species occurring in the southeastern United States with

- special reference to vegetative reproduction. *Pl. Spec. Biol.* **1**: 135–145.
- , AND ———. 1988. Life history studies on the genus *Trillium* (Liliaceae). Vol. 5. Reproductive biology and survivorship of three declinate-flowered species. *Pl. Spec. Biol.* **3**: 35–41.
- OSALOO, S. K., F. H. UTECH, M. OHARA, AND S. KAWANO. 1999. Molecular systematics of Trilliaceae I. Phylogenetic analyses of *Trillium* using *matK* gene sequences. *J. Pl. Res.* **112**: 35–49.
- ROONEY, T. P. 2000. Influence of light, soil fertility, and deer browsing on the spatial structure, relative growth rate, and population demography of *Trillium grandiflorum*. Ph.D. dissertation, University of Wisconsin–Madison. 139 p.
- , AND K. GROSS. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Pl. Ecol.* **168**: 267–277.
- , AND D. M. WALLER. 2001. How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum*. *J. Torrey Bot. Soc.* **128**: 393–399.
- , AND ———. 2003. Direct and indirect effects of deer in forest ecosystems. *Forest Ecol. Managem.* **181**: 165–176.
- SHORT, H. L. 1975. Nutrition of southern deer in different seasons. *J. Wildlife Managem.* **39**: 321–329.
- SILVERTOWN, J., W. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* **81**: 465–476.
- SULLIVAN, T. P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. *Canadian Journal of Zoology* **57**: 1636–1648.
- . 1980. Comparative demography of *Peromyscus maniculatus* and *Microtus oregoni* populations after logging and burning of coastal forest habitats. *Canadian Journal of Zoology* **58**: 2252–2259.
- TALLMON, D. A., E. S. JULES, N. J. RADKE, AND L. S. MILLS. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. *Ecol. Applic.* **13**: 1193–1203.
- TOMIMATSU, H., AND M. OHARA. 2002. Effects of forest fragmentation on seed production of the understory herb *Trillium camschatcense*. *Conservation Biol.* **16**: 1277–1285.
- , AND ———. 2003. Genetic diversity and local population structure of fragmented populations of *Trillium camschatcense* (Trilliaceae). *Biol. Conservation* **109**: 249–258.
- , AND ———. 2004. Edge effects on recruitment of *Trillium camschatcense* in small forest fragments. *Biol. Conservation* **117**: 509–519.