



# Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory

Tiffany M. Knight<sup>a,\*</sup>, Hal Caswell<sup>b</sup>, Susan Kalisz<sup>a</sup>

<sup>a</sup> Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, United States

<sup>b</sup> Biology Department MS\_34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, United States

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## ABSTRACT

Overabundant white-tailed deer (*Odocoileus virginianus*) are a significant management problem in North America that exerts unprecedented herbivory pressure on native understory forest communities. Conserving understory plant populations requires quantifying a sustainable level of deer herbivory. To date, most population projection models consider only deer presence and absence. To estimate population growth rate along a gradient of herbivory, we focused on *Trillium grandiflorum* because it is a common understory species and a bellwether of deer effects and forest decline. We used matrix population models, and employed both prospective and retrospective analyses using a regression life table response experiment (LTRE).

Deer affect size, stage and population dynamics of *T. grandiflorum*. Because deer target flowering and large non-flowering stages of *T. grandiflorum*, these individuals do not produce seed in the year they are browsed and are more likely to regress in stage and size in the following growing season relative to non-browsed plants. Importantly, sustained high browse levels result in populations dominated by small, non-flowering individuals. Our LTRE revealed a significant negative and decelerating relationship between herbivory and  $\lambda$ . This non-linearity occurs at the highest herbivory levels because highly browsed populations become dominated by stages that deer do not consume and are thus buffered from rapid decline. However, population extinction is expected when herbivory is greater than the pivotal value of  $\sim 15\%$ . Our study demonstrates that levels of deer herbivory commonly experienced by forest understory perennials are sufficient to cause the loss of *T. grandiflorum* and likely other co-occurring palatable species.

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## 1. Introduction

Increases in the density of white-tailed deer (*Odocoileus virginianus*), and the resulting increase in herbivory of forest understory plants, is a striking example of human-mediated change in a biotic interaction (McCabe and McCabe, 1997; Russell et al., 2001; Côté et al., 2004). Habitat fragmentation, the eradication of large carnivores, and the increase in food resources from modern agricultural practices, among other factors, have resulted in dense populations of white-tailed deer (henceforth deer) throughout eastern North America (McCabe and McCabe, 1997). Because deer are generalist herbivores, most palatable forest understory species are currently experiencing unprece-

dent herbivore pressure (McCabe and McCabe, 1997; Russell et al., 2001; Côté et al., 2004). Worldwide, deer and other large ungulate browsers threaten forest and agricultural ecosystems because their dense populations can inhibit forest plants' regeneration and reduce crop yield (Tilghman, 1989; Inouye et al., 1994; Waller and Alverson, 1997; Persson et al., 2000; Rooney, 2001; Russell et al., 2001; Augustine and DeCalesta, 2003; Horsley et al., 2003; Côté et al., 2004).

Deer densities in North America are currently 2–4-fold above historical records (McCabe and McCabe, 1997). High local deer densities have been shown to reduce overall plant biomass, shift community composition from more to less palatable plant species, and dramatically reduce overall plant biodiversity (Russell et al., 2001; Rooney and Waller, 2003; Côté et al., 2004; Wiegmann and Waller, 2006; Royo and Carson, 2006). Deer-mediated decline of many previously abundant herbaceous understory species has created conservation concern (e.g., Miller et al., 1992; Anderson, 1994; Balgooyen and Waller, 1995; Augustine and Frelich, 1998; Augustine et al., 1998; Anderson et al., 2001; Rooney and Gross,

\* Corresponding author. Current address: Department of Biology, Washington University in St. Louis, Box 1137, St. Louis, MO 63130, United States. Tel.: +1 314 935 8282.

E-mail address: [tknight@wustl.edu](mailto:tknight@wustl.edu) (T.M. Knight).

2003; Rooney and Waller, 2003; Côté et al., 2004). This concern is supported by the results of demographic matrix model analyses that demonstrate that high levels of deer herbivory can lead to increased extinction risk of plants (Rooney and Gross, 2003; Knight, 2004; McGraw and Furedi, 2005).

Most native forest species that are palatable to deer have long generation times and experience stage-specific browsing. For example, many trees are vulnerable to deer herbivory as seedlings, but reach size refugia as saplings (Russell et al., 2001). In contrast, herbaceous understory plants often experience greater herbivory at larger, reproductive stages (Augustine and Frelich, 1998; Rooney and Gross, 2003; Knight, 2003, 2004; McGraw and Furedi, 2005; Jenkins et al., 2007). In order to quantify the effects of such stage-specific herbivory on plant population dynamics, a stage-structured population model is required.

Typically, effects of deer herbivory on understory plants have been examined experimentally using fenced enclosure and control plots (e.g., Alverson et al., 1988; Augustine and Frelich, 1998; Augustine et al., 1998; Anderson et al., 2001; Townsend and Meyer, 2002). These studies show large positive effects of deer exclusion on the growth, survival and reproduction of plants. However, because these experiments typically are conducted in a single site by erecting exclusion and control plots, they cannot provide information regarding plant responses across a natural gradient of herbivory. Likewise, separate matrices can be constructed for all plants in a population (browsed and not browsed) vs. only those plants that are not browsed. Comparison of the population dynamics and persistence derived from the two matrices provides insight into the direct and indirect effect of deer (all plants) vs. only the indirect effects (Knight, 2004). Both of these approaches examine the effects of complete deer removal on the plant population dynamics. Unfortunately, the complete cessation of deer herbivory in natural areas is not a reasonable or desirable management option (Girard et al., 1993). However, determining the critical level of herbivory that allows population persistence would provide useful information for managers. In this study, we collected field data in 12 natural populations of the long-lived herb *Trillium grandiflorum* and analyzed it using demographic matrix population model projection analyses. These populations experience a gradient of deer herbivory, which permits us to determine the relationship between per capita herbivory rates on *T. grandiflorum* and plant demography.

Specifically, we ask: (1) What are the relationships between deer herbivory and *T. grandiflorum* vital rates, population growth rate ( $\lambda$ ), stage structure, reproductive value, and elasticities? (2) How do each of the vital rates contribute to the effect of herbivory on  $\lambda$ ? To answer these questions we develop a set of matrix population models that express the vital rates as functions of herbivory. We use a life table response experiment (LTRE) analysis to decompose observed variation in  $\lambda$  into contributions of variation in each of the vital rates. Because the level of herbivory is a continuous variable, we employed a regression design LTRE (Caswell, 1996, 2001); this is the first application of the LTRE regression method to a wild population (see Caswell, 1996 for a laboratory study).

## 2. Methods

### 2.1. Study species and sites

*T. grandiflorum* white trillium (Melanthiaceae; Zomlefer et al., 2001) is a preferred food of deer (Anderson, 1994; Augustine and Frelich, 1998) and is an excellent indicator species for determining sustainable deer browse level in forests (Anderson, 1994; Augustine and DeCalesta, 2003; Knight, 2004). Despite the fact

that many *T. grandiflorum* populations are suspected to be declining in size, this species remains a ubiquitous component of deciduous forests understories throughout eastern North America (Case and Case, 1997). Two prior studies applied a demographic matrix approach to *T. grandiflorum*, and both showed that deer herbivory is a critical factor that determines population persistence (Rooney and Gross, 2003; Knight, 2004). Thus, the deer impact threshold that allows for the persistence of *T. grandiflorum* populations should also support the persistence of other, less preferred herbaceous species in the same community.

In our northwestern Pennsylvania populations, *T. grandiflorum* emerges in early spring, before the forest canopy leafs out, and above-ground parts die back in mid-summer. Reproductive plants bloom for 2–3 weeks (late April to mid-May). This species is a non-clonal perennial, with distinct lifecycle stages (described below) that are easily distinguishable in the field (Kalisz et al., 2001; Knight, 2003, 2004). Deer primarily consume reproductive or large 3-leaf stage *T. grandiflorum*, typically removing all leaf and flower tissue (Knight, 2003). Complete defoliation does not usually cause mortality, but plants are unable to re-sprout until the following growing season (Augustine and Frelich, 1998; Knight, 2003; Rooney and Gross, 2003). Flowering plants that are eaten by deer lose all reproductive success for the current growing season and are more likely to regress back to a non-reproductive stage in the following growing season (Knight, 2003, 2004).

We collected data from 12 populations of *T. grandiflorum* representing a range of habitat sizes and aspects typical of northwestern Pennsylvania, USA. The sites vary in a variety of factors besides the intensity of herbivory, however, all 12 sites are in deciduous forests with an overstory dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and red oak (*Quercus rubra*). Our study populations were separated by 4–55 km (Knight, 2003).

### 2.2. Projection matrix estimates

#### 2.2.1. Transitions of plants after emergence

In each population, we set up between 5 and 27 1-m<sup>2</sup> plots, located along a single transect. The number of plots and the distance between plots (between 10 and 50 m) depended on the density and extent of the *T. grandiflorum* population in a site (see Knight, 2004 for site descriptions). The TW population was an exception; 9 transects were necessary due to the high dispersion of the plants at that site. In April 1999, we tagged and classified all *T. grandiflorum* plants within each plot by stage: seedling (a single cotyledon), 1-leaf (plants with one true leaf), 3-leaf (vegetative plant with a whorl of three leaves) and reproductive (plant with whorl of three leaves and a single flower). In addition, we tagged plants in rare stages in extra plots, until either a sample size of 40 individuals was reached for each stage, or until all plants of a stage in that population were tagged. In 1999–2002, we censused all plots to document the stage and size (estimated by leaf length) of each tagged plant, and to tag new seedlings. The structure of these *T. grandiflorum* populations is categorized by six stage-size classes (detailed below). Censuses were carried out in late April, when the plants first emerged, and before deer consumed any plants. In total, we monitored 2993 plants across all 12 populations.

After the first census, all tagged plants were checked for deer herbivory at least every other week and more frequently early in the season. Deer browsed *T. grandiflorum* can be distinguished from that of other herbivores because deer lack top front teeth so they tear vegetation, often at a horizontal angle. Rodents and lagomorphs create sharp cuts on the stem, typically at a 45 degree angle. Herbivory by species other than deer accounted for less than 1% of the observed consumption of *T. grandiflorum*.

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