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Impacts of Deer and Honeysuckle on the Endangered Trillium Reliquum and Its Associated Plant Community

Jacob Seth Thompson

IMPACTS OF DEER AND HONEYSUCKLE ON THE ENDANGERED *TRILLIUM RELIQUUM* AND ITS ASSOCIATED PLANT COMMUNITY

by

JACOB S. THOMPSON

(Under the Direction of Lissa M. Leege)

ABSTRACT

The effects of herbivores and invasive plants on native plants are well known, but few studies have addressed their impacts on rare plants. Threatened or endangered plant species may be more susceptible to negative effects of biotic factors due to their already low distributions. My study quantifies the interactions between deer, an invasive plant, a rare herb and its associated plant community to assist in the conservation of native plants. *Trillium reliquum* is an endangered spring ephemeral herb that is native to three states in the southeast. It is threatened by the encroachment of Japanese honeysuckle (*Lonicera japonica*) and white-tailed deer (*Odocoileus virginianus*) herbivory. I selected five sites in Georgia to examine the impacts of deer and honeysuckle on *T. reliquum* across its Georgia range. Four treatment combinations were established within each population, including: 1) deer excluded, honeysuckle present 2) deer excluded, honeysuckle removed 3) deer accessible, honeysuckle present 4) deer accessible, honeysuckle removed. I measured deer and honeysuckle impacts on *T. reliquum* and plant community structure in 2005 and 2006. *Trillium reliquum* was found in both species rich and species poor habitats. Deer and honeysuckle did not negatively impact species richness. Levels of deer browse intensity varied across sites and honeysuckle was the most frequent vine at most sites. White-tailed deer decreased fruit production and increased dormancy in *T.*

reliquum. Honeysuckle was associated with small but stable trillium populations. Empirical data and matrix models demonstrated that removal of honeysuckle results in significant population increases. This suggests that honeysuckle suppresses *T. reliquum* emergence. Conservation efforts for *T. reliquum* should focus on long-term deer population management and the control of invaders. Also, the conservation of subadult and reproductive individuals is important to *T. reliquum* population growth.

KEYWORDS: *Trillium reliquum*, White-tailed deer, Spring ephemeral, *Lonicera japonica*, Invasive, Matrix model, Herbivory, Population dynamics, Dormancy, Fruiting success, Plant community

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

Literature Review

Objectives

Spring ephemerals are a rich component of biodiversity in the understory of deciduous forests. Because ephemeral plants emerge early in the spring and photosynthesize for an abbreviated growing season, these species may be increasingly threatened by competition with evergreen invasive plants as well as herbivores that consume individuals before they are able to store nutrients. *Trillium reliquum* Freeman (relict trillium) is a federally endangered, ephemeral herb whose populations are restricted to locations near the Fall Line that separates the Coastal Plain and Piedmont Plateau of Alabama, Georgia, and South Carolina (US Fish and Wildlife Service 1988, 1990, Patrick et al. 1995). *Trillium reliquum* is an important constituent of spring ephemeral communities in the mesic deciduous forests where it occurs. Although the major threat to the species is loss or alteration of habitat due to human activities (US Fish and Wildlife Service 1990), *T. reliquum* is also threatened by encroachment of two invasive vines, *Lonicera japonica* and *Pueraria montana* (Patrick et al. 1995, Heckel 2004), and white-tailed deer (*Odocoileus virginianus*) herbivory (Heckel and Leege 2007).

Non-native invasive plants (Mooney and Drake 1986, Equihua and Usher 1993, Mooney and Cleland 2001) and herbivores (reviewed in Huntly 1991, Stowe et al. 2000) are both known to have various effects on plant fitness. Though their effects on plants have been studied intensively, few studies have assessed their importance from the viewpoint of an endangered plant species and its community. My study examines the interactions between an invasive vine, an herbivore, and a rare herb and its associated community. The purpose of this study is to determine how deer and honeysuckle impact the population dynamics of *T. reliquum* and its associated plant community and to assist in the conservation and management of a rare herb.

Biodiversity and plant rarity

At a worldwide level, species extinctions due to global changes are decreasing total biodiversity (Diamond 1989). Nearly 26,000 species are currently threatened with extinction worldwide (Smith et al. 1993). Many types of global changes may be responsible for species extinctions, although human-induced extinctions are the most extensive. Wilson (1992) suggests that four major categories of human activity are responsible for decreases in biodiversity including overexploitation, the introduction of exotic species, habitat destruction, and the spread of disease by alien species. All of these factors may contribute to the endangerment and eventual extinction of native species.

Rare and endangered species are an important component of the biodiversity on earth. They are also often a necessary precursor to extinction, and to explain extinction, the causes of rarity are often examined. Rabinowitz (1986) classified forms of rarity based on geographic range, habitat specificity, and local population size; Fiedler and Ahouse (1992) added temporal persistence of the taxon as a condition for assessing rarity. Based on Rabinowitz's work, rarity describes three conditions: 1) taxa whose distribution is broad but population sizes are never large, 2) those whose distribution is clumped or narrow but with large populations, and 3) those with clumped distributions and low individual abundance. Because managers are often faced with the decision of how to protect a rare species, it is important to understand which class of rarity the species represents.

Identifying the causes of rarity is also a crucial step in the conservation and restoration of rare species (Schemske et al. 1994). The nature of the factors contributing to the rarity of a plant species can range from intrinsic characteristics such as low fecundity, lack of genetic variability and limited dispersal abilities, to extrinsic factors such as habitat destruction, competition, predation, and lack of pollinators (Pantone et al. 1995, Miller and Duncan 2003). Extrinsic factors are often found to be more important than intrinsic ones in limiting populations of rare plants (Pavlik et al 1993, Pantone et al 1995). Competition with invasive species (Huenneke and Thomson 1995, Walck et al. 1999, Matsumoto et al. 2000, Thomson 2005a) and damage by herbivores (Bevill et al. 1999, Pfab and Witkowski 1999, Fletcher et al. 2001, Maschinski 2001) are two extrinsic factors that negatively impact rare plant populations.

Non-native plant invasions

A non-native plant invasion occurs when a species expands into a new range and is accompanied by adverse economic, ecological, or aesthetic effects (Mack 1996). Second to habitat destruction, the introduction of invasive species is the most significant factor in the decline of native species (Wilcove et al. 1998). The global spread of non-indigenous species has resulted in biotic homogenization, or the replacement of unique native species with already widespread species (McKinney and Lockwood 1999).

Invasive plants affect native plant species by impacting ecosystem processes and altering community structure (reviewed in Levine et al. 2003), as well as by affecting population dynamics and life history strategies of native plants. Invasive plants may affect ecosystems by altering geomorphological processes (Heyligers 1985), hydrological cycling (Dyer and Rice 1999, Gerlach 2000, Zavaleta 2000), nutrient cycling (Vitousek et al. 1987, Vitousek and Walker 1989), and disturbance regimes (reviewed in D'Antonio and Vitousek 1992 and Mack and D'Antonio 1998). Native plant communities may lose diversity and richness resulting from the introduction of a new plant species and subsequent changes in vertical structure (Alverez and Cushman 2002). The invasion of exotic species may also impact plant populations by competing for resources and decreasing recruitment (Walker and Vitousek 1991, Equihua and Usher 1993). Ultimately, invasive plants may outcompete natives, particularly those that are threatened or rare (Huenneke and Thomson 1995, Walck et al. 1999, Thomson 2005a; 2005b). Wilcove et al. (1998) examined several sources, including the Federal Register, TNC databases, and interviews with specialists and found that almost half of the 723 plant species that are threatened or endangered in the United States are declining due to the impacts of invasive species.

Invasive plants often have characteristics associated with high growth and reproduction, therefore increasing their competitive ability (Baker 1974). *Lonicera japonica*, Japanese honeysuckle (henceforth honeysuckle) demonstrates many of these characteristics and has become a dominant invader throughout much of its invaded range. Honeysuckle is a perennial, climbing or trailing woody vine, native to East Asia that was introduced into the United States in the late 19^{th} century (Allison 2003, Shierenbeck 2004). It is an invasive species that damages natural plant communities by outcompeting native vegetation for light (Thomas 1980, Bruner 1967) and below-ground resources (Dillenburg et al. 1993a, 1993b, Whigham 1984), and by changing stand structure (Sasek and Strain 1990, 1991). Honeysuckle grows rapidly often forming mats up to 1.5 m deep with 100% cover that can exclude herbs (Oosting 1956, Hardt 1986). Its most obvious threat to native species is shading caused by extensive growth. There are no identified pests or diseases that cause serious harm to this invader (Gilman 1999). Even with heavy grazing from wildlife, it remains the dominant groundcover in many forest communities (Oosting 1942, Leatherman 1955).

Impacts of herbivory

The impacts of herbivory on plants ranges from insignificant to disastrous depending on the intensity (Hickman and Hartnett 2002), part of the plant removed (Ehrlen 1995), time of attack during the growing season (Marquis 1992, Garcia and Ehrlen 2002, Knight 2003) and the plant's history of herbivory (Crawley 1983). Plant life history strategies play an important role in determining the effects of herbivory. Herbivores that feed on reproductive parts may be extremely damaging to annuals or biennials but have little effect on a perennial (Lesica 1995). Herbivores that remove non-reproductive parts of perennials are not likely to kill the plant due to carbohydrate reserves in below-ground, perenniating organs. However, repeated defoliation can deplete carbohydrate reserves in rhizomes (Lubbers and Lechowicz 1989). These depletions can decrease the plant's ability to re-grow leaves or produce reproductive parts (Lubbers and Lechowicz 1989, Anderson 1994). Reduced plant growth resulting from decreased photosynthetic area can also increase mortality (Crawley 1983, Ehrlen 1995). Increased mortality rates may have devastating effects on plant populations particularly those that are already threatened or endangered.

White-tailed deer (*Odocoileus virginianus*) have become an important herbivore in forest ecosystems in the eastern United States as their population densities continue to increase (Alverson et al. 1988, McShea et al. 1997, Augustine and Frelich 1998, Russell et al. 2001). Habitat fragmentation has increased the amount of edge within forest communities and along with decreased hunting pressure, resulted in abundant populations of deer (Alverson et al. 1988, McShea et al. 1997). These increases in edge provide deer with greater access to vulnerable plant species (Augustine and Frelich 1998). Although many studies have documented the impacts of winter browsing by white-tailed deer on woody species (Strole and Anderson 1992, Anderson and Katz 1993), few studies have assessed their effects during the growing season on herbaceous plant communities (but see Rooney and Dress 1997, Webster et al. 2005).

White-tailed deer may have numerous deleterious impacts on forest ecosystems, including adverse effects on the fitness of forest herbs (Waller and Alverson 1997, Augustine and Frelich 1998, Knight 2003, 2004). Forest understory communities that are subjected to high levels of deer browsing for long periods of time have been shown to lose species diversity (Rooney and Dress 1997, Rooney 2001, Rooney and Waller 2003, Webster et al. 2005), suggesting that species extinctions may be associated with deer browsing. Deer may also affect plant population dynamics by reducing the proportion of reproductive plants in a population (Anderson 1994, Augustine and Frelich 1998, Knight 2003) and slowing the rates of plant life cycle changes (Rooney and Gross 2003, Knight 2004).

Spring ephemerals

Spring ephemeral communities are composed of a diverse group of flora and provide significant biodiversity in southeastern deciduous forests. Spring ephemerals are perennial herbs that emerge each spring from an underground storage organ and take advantage of the short photosynthetic period before canopy closure (Routhier and Lapointe 2002), which may make them more vulnerable to biotic threats. White-tailed deer often change their diet from primarily woody species to as much as half herbs when they become available in spring (Chamrad and Box 1968, Skinner and Telfer 1974, Korschgen et al. 1980). Loss of reproductive parts and photosynthetic tissue in early spring may affect the fitness of these herbs. McGraw and Furedi (2005) found that populations of a widespread but sparse ephemeral herb, American ginseng (*Panax quinquefolius*), are threatened with extirpation in the coming century due to white-tailed deer herbivory. Many invasive plants such as *L. japonica*, are evergreen or semi-evergreen in warmer portions of their range and can take advantage of the open canopy in early spring (Shierenbeck 2004). Competition for light resources in this crucial photosynthetic period decreases the ability of spring ephemerals to store carbohydrates.

Trillium reliquum, a rare herb

Trillium reliquum Freeman (relict trillium) is a federally endangered, ephemeral herb that occurs in undisturbed moist hardwood forests near the Fall Line separating the Coastal Plain and Piedmont Plateau of Alabama, Georgia, and South Carolina (Federal Register 1988, US Fish and Wildlife Service 1990, Patrick et al. 1995). The species is known from only 21 populations and was placed on the Federal endangered species list in 1988 (U.S. Fish and Wildlife Service 1988). Like most perennial herbs, *T. reliquum* is a long-lived species with low growth and reproductive rates, and competes poorly with invasive species. *Trillium reliquum* is threatened by the encroachment of invasive honeysuckle (US Fish and Wildlife Service 1990, Patrick et al. 1995). Heckel (2004) found that honeysuckle is directly associated with reduced population sizes in *T. reliquum* and with a regression of reproductive and subadult individuals to earlier lifestages. A decrease in the number of reproductive individuals may be deleterious to the long term persistence of *T. reliquum*. Honeysuckle is considered preferred browse to white-tailed deer (Ripley and McClure 1963), and may indirectly impact *T. reliquum* by increasing herbivory.

Evidence of white-tailed deer browsing on *T. reliquum* has been reported (Heckel and Leege 2007), and could be detrimental to the already globally small populations of this endangered species. Studies with *Trillium grandiflorum*, the most abundant member of the genus, have indicated negative impacts of white-tailed deer herbivory on population dynamics (Rooney and Gross 2003, Knight 2003, 2004), which might suggest similar impacts on *T. reliquum*. A direct effect on populations occurs because white-tailed deer often consume both vegetative and reproductive parts of the *Trillium* plant, eliminating reproductive success for that season. Knight (2003, 2004) showed a regression of reproductive plants to non-reproductive stages and a decrease in size of the reproductive plants that survive when consumed by white-tailed deer. Decreases in size of reproductive plants may indirectly impact reproduction by reducing the number of ovules produced, therefore reducing potential for seed production in the plant (Knight 2004).

Demographic models

Extrinsic factors such as deer herbivory and encroachment by invasive plants are both known to affect the fitness of rare plants, therefore it is important to examine rare plant population dynamics to determine whether or not the species is declining, stable or growing (Caswell 2001). Stage structured transition matrix models can be used to summarize how the interactions of survival, growth, and reproduction at different stages impact population growth (Caswell 2001). Because matrix projections assume density-independent growth and constant conditions, they may not accurately predict long-term population growth, but are useful in summarizing short-term population dynamics (Lesica 1995, Caswell 2001). Determining the population dynamics of a rare species is crucial to the planning of management approaches that will assist in conservation (Schemske et al. 1994, Caswell 2001).

There are no previous studies examining the combined impacts of white-tailed deer and an invasive plant on a threatened or endangered plant species and its associated community. The objectives of this project are: 1) to examine the plant community characteristics of deciduous forests containing the endangered *T. reliquum* and the impacts of white-tailed deer herbivory and a non-native, invasive vine, *Lonicera japonica* on plant community structure, 2) to quantify the effects of both deer-browsing and *Lonicera japonica* on the population dynamics of the endangered spring ephemeral, *Trillium reliquum*, and based on the results of this study, and 3) to provide management recommendations for the federally endangered *Trillium reliquum* and its associated plant community.

CHAPTER II

Characteristics of Plant Communities Associated with the Endangered *Trillium reliquum* and Their Response to White-tailed Deer (*Odocoileus virginianus*) and Invasive *Lonicera japonica*

The deciduous forest is one of the major vegetation types in the eastern United States and contains a diverse assemblage of herbaceous and woody plant species. Woodland herbs account for most of the vascular plant species diversity in deciduous forests of North America (Ramsey et al. 1993, McCarthy and Bailey 1996, McCarthy 2003). Many of these herbs have become threatened or endangered due to land use changes or biotic factors, such as the introduction of invasive species and increasing wildlife (e.g., white-tailed deer) herbivory (reviewed in Whigham 2004). These biotic factors may also influence the recruitment of woody seedlings (Alverson et al. 1988, Dillenburg et al. 1993a, 1993b), thus, altering community structure. The documentation and protection of these herb layer communities is essential to conserving diversity in eastern deciduous forests.

The invasive vine, *Lonicera japonica* (Japanese honeysuckle), is a frequent and successful competitor in many deciduous forest understories (reviewed in Shierenbeck 2004). Because it persists year-round, honeysuckle may undergo continuous growth, giving it a competitive advantage over other species (Slezak 1976). Honeysuckle alters community structure by decreasing recruitment of seedlings and inhibiting reproductive success of reproductive individuals (Friedland and Smith 1982, Nyboer 1990). Dillenburg et al. (1993a, 1993b) found that honeysuckle decreases leaf photosynthetic capability, biomass allocation, and nitrogen-use efficiency of sweetgum (*Liquidambar styraciflua*) saplings through root competition.

White-tailed deer herbivory can significantly modify the structure of forest communities. By consuming preferred plant species, deer may cause shifts in species composition (reviewed in Rooney and Waller 2003). Forest understory communities that are subjected to high levels of deer browsing for long periods of time have been shown to lose species diversity (Rooney and Dress 1997, Rooney 2001, Rooney and Waller 2003, Webster et al. 2005). Often, recovery from long periods of deer herbivory may not occur in browse sensitive species (Anderson 1994).

Trillium reliquum Freeman (relict trillium) is a federally endangered spring ephemeral herb that occurs in three states in the southeastern United States. This species is threatened by invasive Japanese honeysuckle and white-tailed deer herbivory (Patrick et al. 1995, Heckel 2004, Heckel and Leege 2007). *Trillium reliquum* is often found with a rich group of perennial herbs in the understory of mesic deciduous forests. No study has formally examined the associated flora of *T. reliquum* or fully quantified species richness in the deciduous forest communities across its range.

Both honeysuckle and white-tailed deer have the potential to alter plant community structure within *T. reliquum* habitat. While many studies have documented the invasive qualities of honeysuckle (reviewed in Schierenbeck 2004), few studies have addressed its impacts on plant communities, particularly on forest herb diversity and richness (Heckel 2004). Numerous studies have documented the effects of white-tailed deer browsing on both woody species and forest herbs (reviewed in Rooney and Waller 2003). Many of these studies have been performed in the Northeastern U.S. and are often local. Few studies have examined the impacts of deer on deciduous forest communities of the southeast and across a broad geographic scale. The objectives of this study were

1) to describe the plant community associated with *T. reliquum* across its range in Georgia, 2) to determine the frequency of honeysuckle and the intensity of deer browse in these plant communities, and 3) to examine the effects of white-tailed deer herbivory and *L. japonica* on plant communities associated with *T. reliquum*. By excluding deer and removing honeysuckle, I tested the hypothesis that herbivores and invasive plants have negative effects on plant communities.

Methods

Study sites

I selected five sites in Georgia for sampling based on *Trillium reliquum* population size, evidence of deer browsing, and the presence of *Lonicera japonica* (Figure 2.1). I chose sites along the Fall Line separating the Coastal Plain and the Piedmont Plateau where *Trillium reliquum* populations are located. I established study plots at 1) Montezuma Bluffs Natural Area in Macon County (N32˚20'W84˚1'), 2) a site owned by Dan Bullard IV near Colarparchee Creek in Bibb County (N32˚53'W83˚47'), 3) a site owned by Mead-Westvaco near Mulberry Creek in Harris County (N32˚40'W85˚1'), 4) a site owned by Tommy Hutcherson near Mulberry Creek in Harris County (N32˚42'W84˚55'), and 5) a site owned by John Spears at Fort Gaines in Clay County (N31˚35'W85˚2'). Each of these sites exhibited conditions favorable to colonization by *T. reliquum* and were located close to a creek or river system. Two of the sites, Montezuma Bluffs and Fort Gaines, exhibit geologic traits associated with the Coastal Plain including sandy soils as well as boulders and ledges of limestone. The other three sites have characteristics associated with the Piedmont region including deep, loamy soils in ravines or alluvial terraces.

Experimental design

To determine the effects of white-tailed deer herbivory and encroachment by *Lonicera japonica* on plant communities containing *Trillium reliquum*, I established four treatment combinations at each site in Spring 2005: 1) deer-excluded, honeysuckle-present 2) deer-excluded, honeysuckle-removed 3) deer-accessible, honeysuckle-present (control) and 4) deer-accessible, honeysuckle-removed (Figure 2.2). I also used these treatment combinations in a companion study to determine the impacts of deer and honeysuckle on the population dynamics of *T. reliquum* (Chapter 3). I placed treatments in high densities of both *T. reliquum* and *L. japonica* and where there was evidence of white-tailed deer herbivory. Deer excluded treatments were established by installing metal chain-link fence exclosures with the dimensions 10m x 25m x 2.5m tall. Exclosures were installed at the Mead-Westvaco, Hutcherson, and Montezuma Bluffs Natural Area sites on March 9 and 10, at Fort Gaines on March 15, and at Bibb County on March 29, 2005.

I randomly selected one half of each exclosure for treatment with Roundup™ Weed and Grass Killer (12.5% glyphosate) to remove honeysuckle. Before applying herbicide, I placed 0.47L plastic cups over individual trillium plants to ensure protection from the herbicide. From April 23 to April 25, 2005, I used a 9.5L compression sprayer to spot apply the herbicide. I applied herbicide to all honeysuckle within the treatment area. I established an adjacent unfenced 10m x 25m area at least 5m from the long edge of the exclosure to serve as a deer accessible plot. I treated one half of the unfenced area with herbicide as described earlier to remove honeysuckle.

Because ants can disperse trillium seeds as far as 3.3m (maximum) and 0.6m on average (Ohara and Higashi 1987), a buffer of at least 5m was established between treatments to discourage seed transfer. Herbicide was not applied to the buffer area. Based on other studies with *Trillium grandiflorum* (Heckel pers. comm.), edge effects were prevented by honoring a 0.25m buffer along the edge of each treatment area. Honeysuckle and other vines were periodically pruned from exclosure fencing to prevent encroachment into honeysuckle removal areas and shading of herb layer.

Plant community measurements

In late Spring 2006, plant community measurements were taken at each site to determine *T. reliquum* habitat characteristics across its range, as well as the impacts of white-tailed deer herbivory and honeysuckle on herb layer richness. Measurements were taken at Montezuma Bluffs on May 28, 2006, at Fort Gaines on May 29, 2006, at Mead-Westvaco on June 3, 2006, at Hutcherson on June 4, 2006, and at Bibb County on June 5, 2006.

Tree Layer: For each full treatment at each site, I recorded tree species identity at least to genus and diameter at breast height (DBH) for each tree (≥ 1cm DBH). I also mapped each tree. I determined stand density for each treatment.

Shrub Layer: I assessed species composition and density of shrubs (≤ 1cm DBH, ≥ 30cm tall) for each treatment at each site. I sampled each full treatment at all sites excluding Mead-Westvaco and the deer excluded/honeysuckle present treatment at the Hutcherson site, where I subsampled four randomly chosen 2m x 2m plots (representing 16% of the treatment) due to high shrub densities.

Herb Layer: At three of the sites (Bibb County, Hutcherson, and Mead-Westvaco), I randomly selected 25 1m x 1m plots in each treatment to sample herb layer vegetation (< 30cm tall), while at two of the sites (Montezuma Bluffs and Fort Gaines) and the deer excluded/honeysuckle present treatment at Hutcherson, I sampled vegetation in full treatments (80-100m^2). Because exclosures were not exactly 10m wide at Montezuma Bluffs, Fort Gaines, and Hutcherson, full treatment sampling was reduced to 80m^2 in exclosures at these sites. I used these permanent plots for this study and to determine the impacts of deer herbivory and invasive honeysuckle on the population dynamics of *T. reliquum* (Chapter 3). I identified and counted the number of all vascular plant species present (species richness) and determined the abundance (# of stems) of each forb or woody species in each plot. In Spring 2005 and 2006, percent cover of honeysuckle was determined for each plot in honeysuckle removal treatments to make sure honeysuckle removal treatment was effective. In Spring 2005 and 2006, percent cover of all species and percent cover of honeysuckle was determined at Bibb County to determine if honeysuckle removal had an effect on percent cover. I identified plant specimens in the field and in the lab using field guides (Taylor 1998, Porcher and Rayner 2001) and taxonomic keys (Radford et al. 1968).

To determine the most important species at each site, I calculated importance values of all forb and woody species in deer accessible/honeysuckle present (control) treatments. I calculated modified importance values (IV) of herb layer forbs and woody species by summing the relative abundance and the relative frequency:

$$\text{Relative abundance of species i} = \frac{\text{Absolute abundance of species i}}{\sum \text{Absolute abundance of all species}}$$

and

$$\text{Relative frequency of species i} = \frac{\text{Absolute frequency of species i}}{\sum \text{Absolute frequency of all species}}$$

Importance values are usually calculated by summing the relative frequency, relative abundance, and relative cover (Curtis and McIntosh 1951). Because percent cover was not determined for each species, I summed two relative values, abundance and frequency, as described in Ayyad and Dix (1964). I then determined the ten species with the highest IV at each site. Because this study was conducted in late May/early June, many important spring ephemerals including *T. reliquum* could not be included in this analysis. This calculation did not account for vine species, in which separate individuals were difficult to distinguish. Most sites had five to six vine species in the understory. Therefore, the five most frequent vines in control treatments were used to determine relative frequency of each vine species. Vines were then ranked from highest to lowest relative frequency to determine the most frequent vine at each site. Because it often takes long periods of time for plant community composition to change, importance values of forbs and woody species and relative frequency of vines were only used to examine the associated flora across the range of *T. reliquum* and not compared among treatments.

To examine white-tailed deer browse intensity, I established four 20m transects at least 5m away from treatments and in four cardinal directions at each site on April 24 and 25, 2006. I counted all stems in the herb layer that touched the transect line and indicated if they were browsed by deer, and divided the number of plants browsed by the total number of plants to determine browse intensity. Because the data were not normally distributed, I log transformed them to normality. To test whether deer browse intensity varied across sites, I used a one-way ANOVA with each of the four transects as a replicate and site as an effect. In Spring 2005, honeysuckle cover was determined for each treatment at each site. To determine honeysuckle removal effects, I compared pre- and post-herbicide treatment honeysuckle cover at all sites, and total understory cover and cover of all species excluding honeysuckle at one site (Bibb County). Bibb County was used because it was the only site in which full community measurements were taken pre- and post-herbicide treatment.

I determined total herb layer species richness for each treatment at three sites: Bibb County, Hutcherson, and Mead-Westvaco. Two of the sites (Montezuma Bluffs and Fort Gaines), as well as the deer excluded/honeysuckle present treatment at Hutcherson were not used in this analysis because sampling areas were different. When determining total herb layer richness in honeysuckle-present treatments, honeysuckle was not included. To determine if treatment had an effect on total richness, I used a two-way ANOVA with site as a block and deer, honeysuckle, and deer x honeysuckle interaction as effects. I used JMP IN 6.0 (SAS, Cary, NC, 2005) for all statistical analyses.

In Spring 2006, I examined the flowering and fruiting success as well as the effects of white-tailed deer on several perennial herbs associated with *T. reliquum*. These species included: *Trillium cuneatum*, *Trillium maculatum*, *Hexastylis arifolia*, *Cynoglossum virginianum*, *Sanguinaria canadensis*, *Cardamine angustata*, and *Viola* species. I conducted this study in deer accessible treatments at three of the five study sites:. Bibb County, Montezuma Bluffs, and Fort Gaines. All perennial herbs were censused within permanent plots also used for herb layer vegetation sampling and *T. reliquum* censuses. I made an initial census in late March to examine density, reproductive status (flowering or non-flowering), and early season deer herbivory. During this first census, each individual plant was marked with a paper tag and mapped. I conducted a final census in late April/early May to examine fruiting success, fruit to flower ratios, and late season deer herbivory. Because these perennial herbs were not as abundant in exclosures, I could not make comparisons between deer accessible and deer excluded treatments. Because *Viola* flowered in early March, reproductive data may be incomplete and should be interpreted with caution. Most species were not available across multiple sites, therefore, replication was minimal and deer preference for perennial herb species should be interpreted with caution.

Results

Trillium reliquum habitat

All sites included an upper forest canopy composed mainly of hardwoods such as *Fagus americana*, *Liriodendron tulipifera*, *Carya* and *Quercus* species. The subcanopy layer was composed mainly of *Ostrya virginiana*, *Cornus florida*, *Cercis canadensis*, *Halesia carolina*, *Morus rubra*, and *Acer barbatum*. Stand density ranged from $0.06/m^2$ to $0.45/m^2$ with a mean of $0.19 \pm 0.02/m^2$. The shrub layer was often composed of tree saplings and shrub density ranged from $0.10/m^2$ to $3.75m^2$ with a mean of $0.93 \pm 0.25/\ m^2$. Total herb layer richness was variable across sites and ranged from 2.1 (Fort Gaines) to 11.4 species/m^2 (Mead-Westvaco) with a mean of 6.8 ± 1.5 species/m^2.

Importance values revealed that many herbaceous understory species such as *Geranium maculatum*, *Hexastylis arifolia*, and *Viola* are common across the geographic range of *T. reliquum* (Table 2.1). Important understory woody species across the range of *T. reliquum* included *Euonymus americana*, *Ostrya virginiana*, and *Acer* species (Table 2.1). Woody species were more important at Montezuma Bluffs and Mead-Westvaco, while herbs were more dominant at the other sites. Invasive *Ligustrum sinense* (Chinese privet) was found at three sites and was an important species at two sites. Honeysuckle was the most frequent vine at Montezuma Bluffs, Hutcherson, and Fort Gaines and in the top three at the two other sites (Table 2.2). Other frequent vines included *Parthenocissus quinquefolia* and *Toxicodendron radicans* (Table 2.2).

Impacts of deer and honeysuckle

Deer browse intensity differed significantly across sites ranging from 4.16±0.56% to 32.6±7.6% (Figure 2.3). Percent cover of honeysuckle was variable across sites and ranged from 17.2±1.6% at Fort Gaines to 41.6±2.5% at Bibb County (Figure 2.4). At Bibb County, total percent cover and percent honeysuckle cover decreased after honeysuckle removal, however percent cover of all other species excluding honeysuckle was not affected (Figure 2.5). Total cover decreased by nearly three-fourths (paired t-test, $t=-12.846$, $P=<0.0001$, $df=49$). Across all sites honeysuckle decreased by nearly 100% (paired t-test, $t=-21.479$, $P=<0.0001$, $df=253$). These results show that honeysuckle removal treatment was effective and did not impact cover of other species. Total species richness was significantly lower in honeysuckle removal treatments in three sites (Table 2.3, Figure 2.6), suggesting that honeysuckle removal methods may have impacted some plant species.

Deer herbivory on spring perennials

White-tailed deer herbivory on perennials was variable across sites and species, ranging from 0 to 43% (Table 2.4). Montezuma Bluffs had little to no deer herbivory on all herbs except *Trillium maculatum*, while at Fort Gaines and Bibb County, most herbs experienced some level of herbivory. *Cynoglossum virginianum* and *Cardamine angustata* were the only herbaceous species that showed no signs of deer herbivory in sites where they were found. Several spring ephemeral species, *Trillium cuneatum, Trillium maculatum* and *Sanguinaria canadensis* experienced high levels of herbivory, ranging from 20 to 40 percent. Trillium species (*T. cuneatum* and *T. maculatum*) sustained high levels of herbivory, had few reproductive individuals, and low fruiting.

Discussion

Trillium reliquum was found in habitat typically associated with deciduous bluff, slope, and ravine forests. Some of these sites contained a rich community of perennial herbs including *Trillium* (*cuneatum, maculatum,* and *reliquum*), *Sanguinaria canadensis*, *Podophyllum peltatum*, *Geranium maculatum*, *Arisaema triphyllum*, *Hexastylis arifolia*, and *Viola* species. Vines and woody species were also major constituents of each understory community. Honeysuckle was the predominant invasive species found at each site, while invasive *Ligustrum sinense* (Chinese privet) was found at a few sites (Hutcherson, Bibb County, Montezuma Bluffs) and *Elaeagnus umbellata* was a dominant invasive shrub species at Bibb County and was also found at Fort Gaines. These observations demonstrate that multiple non-native plants are invading the rich deciduous forests of Georgia and warrant ecological studies detailing their impacts on native plant communities.

While experimental removal of honeysuckle did not elicit an increase in richness, honeysuckle was often the most frequent vine species, providing a mean 20 to 40% cover in each treatment. Heckel (2004) compared species richness in a habitat with no invasive vines versus a habitat containing honeysuckle and detected no significant differences. Other studies have described the competitive abilities and losses in diversity associated with the presence of honeysuckle (Davidson and Forman 1982, Bell et al. 1988). Exclusion from deer also had little effect on species richness. Most exclosure studies are long term. It may take an extended period of time to detect differences in species composition and richness between communities inside and outside a deer exclosure, depending on species dispersal (Matlack 1994).

Trillium reliquum was found in both species rich and species poor habitats. Interestingly, the site with the highest richness (11.4 species/ m^2), Mead-Westvaco, had the lowest deer browse intensity (4% browsed), whereas the site with the lowest richness (2.1 species/ m^2), Fort Gaines, had the highest deer browse intensity (33% browsed). Also, many woody species, which have often been considered preferred deer browse, were less important at sites with high deer browse intensity, whereas herbaceous species were more abundant at sites with low deer herbivory. While it is difficult to assess whether deer are fully responsible for this variation in richness due to the numerous abiotic and biotic factors that may be involved, many studies have documented the significance of white-tailed deer as consumers and changes in plant composition as a result of deer herbivory (Rooney and Dress 1997, Webster et al. 2005). It will be important for future research to elucidate the causes responsible for these richness gradients in southeastern deciduous forests.

All perennial herbs excluding *Cynoglossum virginianum* and *Cardamine angustata*, experienced some level of deer herbivory. *Trillium*(s) *cuneatum*, *maculatum*, and *reliquum* were preferred by deer and had low fruiting success. Early spring flowering species, including trilliums, may be more susceptible to intense deer herbivory, due to the brief growing season needed to complete their life cycles before overstory leaf out (Augustine and Jordan 1998). Most studies of deer herbivory have addressed the impacts of deer on woody browse (Strole and Anderson 1992, Anderson and Katz 1993). As mentioned earlier, replication across sites was minimal and deer preference on perennial herb species should be interpreted with caution. The results of this study merely add support to other studies that have documented the importance of herbaceous species to deer diet in early spring (Chamrad and Box 1968, Skinner and Telfer 1974, Korschgen et al. 1980).

The results of this study found that *T. reliquum* may be found in species rich and species poor habitats and that white-tailed deer herbivory and honeysuckle are frequent across its Georgia range. The Georgia Department of Natural Resources (2003) has detected significant increases in deer within the last 20 years, with populations nearly doubling in size. This study found that deer disturb multiple spring perennials across the Georgia range of *T. reliquum* and that deer may be impacting forest structure. Honeysuckle is often a major constituent in many forest understories (reviewed in Shierenbeck 2004). Long term studies are necessary to determine the interactions of these two biotic variables with plant communities in the southeast.

Table 2.1. Relative frequency, relative abundance, and importance value (IV) of the ten most important forb and woody species in the control treatment at each site. Habits: W=Woody and F=Forb.

Site	Species	Habit	Rel. Freq.	Rel. Abun.	IV
Montezuma Bluffs	*Euonymus americana*	W	0.098	0.470	0.568
	Quercus sp.	W	0.196	0.128	0.324
	Carya sp.	W	0.156	0.102	0.259
	Ostrya virginiana	W	0.156	0.068	0.225
	Hexastylis virginiana	F	0.058	0.085	0.144
	Acer barbatum	W	0.078	0.042	0.121
	Trillium reliquum	F	0.078	0.034	0.112
	Prunus serotina	W	0.078	0.034	0.112
	Tradescantia sp.	F	0.058	0.034	0.093
	Viola sp.	F	0.039	0.017	0.056
Bibb County	*Hexastylis arifolia*	F	0.206	0.459	0.666
	Carya sp.	W	0.218	0.255	0.470
	Ostrya virginiana	W	0.149	0.126	0.275
	Mitchella repens	F	0.155	0.071	0.226
	Sanguinaria canadensis	F	0.045	0.045	0.091
	Cynoglossum virginianum	F	0.057	0.025	0.082
	Quercus sp.	W	0.057	0.025	0.082
	Ligustrum sinense	W	0.045	0.020	0.066
	Morus rubra	W	0.034	0.015	0.049
	Cercis Canadensis	W	0.034	0.015	0.049
Mead-Westvaco	*Geranium maculatum*	F	0.114	0.198	0.313
	Acer barbatum	W	0.145	0.158	0.304
	Ostrya virginiana	W	0.135	0.115	0.251
	Euonymus americana	W	0.114	0.102	0.217
	Arisaema triphyllum	F	0.104	0.076	0.180
	Trillium reliquum	F	0.104	0.052	0.157
	Halesia carolina	W	0.031	0.105	0.137
	Viola sp.	F	0.062	0.062	0.125
	Unknown Aster	F	0.041	0.046	0.088
	Polygonatum biflorum	F	0.052	0.033	0.085
Hutcherson	*Podophyllum peltatum*	F	0.152	0.278	0.431
	Geranium maculatum	F	0.067	0.155	0.223
	Acer barbatum	W	0.152	0.065	0.218
	Carya sp.	W	0.135	0.081	0.217
	Duchesnia indica	F	0.135	0.065	0.201
	Viola sp.	F	0.101	0.090	0.191
	Euonymus americana	W	0.033	0.139	0.173
	Ligustrum sinense	W	0.084	0.049	0.133
	Prunus serotina	W	0.067	0.040	0.108
	Cercis Canadensis	W	0.067	0.032	0.100
Fort Gaines	*Euonymus americana*	W	0.200	0.560	0.760
	Mitchella repens	F	0.210	0.061	0.420
	Viola sp.	F	0.190	0.165	0.355
	Geranium maculatum	F	0.070	0.041	0.111
	Cynoglossum virginianum	F	0.060	0.026	0.086
	Hexastylis arifolia	F	0.040	0.044	0.084
	Carya sp.	W	0.060	0.020	0.080
	Acer barbatum	W	0.050	0.017	0.067
	Callicarpa americana	W	0.030	0.020	0.050
	Halesia Carolina	W	0.010	0.008	0.028

Table 2.2. Relative frequency of the five most frequent vines in control treatments at each site.

Site	Species	Relative Frequency
Montezuma Bluffs	*Lonicera japonica*	0.285
	Toxicodendron radicans	0.232
	Parthenocissus quinquefolia	0.214
	Bignonia capreolata	0.160
	Vitis rotundifolia	0.107
Bibb County	*Parthenocissus quinquefolia*	0.280
	Toxicodendron radicans	0.235
	Lonicera japonica	0.224
	Smilax sp.	0.168
	Vitis rotundifolia	0.089
Mead-Westvaco	*Parthenocissus quinquefolia*	0.315
	Lonicera japonica	0.298
	Toxicodendron radicans	0.175
	Smilax sp.	0.122
	Vitis rotundifolia	0.087
Hutcherson	*Lonicera japonica*	0.285
	Toxicodendron radicans	0.214
	Parthenocissus quinquefolia	0.200
	Bignonia capreolata	0.171
	Vitis rotundifolia	0.128
Fort Gaines	*Lonicera japonica*	0.340
	Smilax sp.	0.300
	Toxicodendron radicans	0.160
	Parthenocissus quinquefolia	0.140
	Bignonia capreolata	0.060

Table 2.3. Results from 2-way ANOVA of deer and honeysuckle effects on total species richness.

Variable	Source	df	F	P-value
Total Species Richness	Block (site)	2		
	Deer	1	0.42	0.54
	Honeysuckle	1	10.70	**0.02**
	Deer x Honeysuckle	1	0.27	0.29
	Error	5		

Table 2.4. Spring perennial plant species in deer accessible treatments at three sites in 2006 (Treatments: A/H=Deer Accessible/Honeysuckle Present, A/R=Deer Accessible/Honeysuckle Removed). Measurements taken are: n (number of individuals censused, density (#/m^2), mean number of fruit per reproductive, percent of reproductives that fruited, fruit to flower ratio, and percent deer herbivory on all individuals.

Site	Treat-ment	Species	n	#/m^2	% rep	Mean # fruit	fr:fl	% herb
Bibb County	A/H	*Cynoglossum virginianum*	16	0.60	12.5	26.5	88.3	0
		Hexastylis arifolia	49	2.00	24.5	1.14	46.6	12.2
		Sanguinaria canadensis	12	0.50	58.3	1	100	41.6
		Trillium cuneatum	49	2.00	10.2	-	0	14.3
		Trillium reliquum	120	5.00	23.5	1	0	9.4
	A/R	*Cynoglossum virginianum*	3	0.20	0	-	-	0
		Hexastylis arifolia	23	1.20	17.4	-	0	26.1
		Sanguinaria canadensis	28	1.50	35.7	1	20	42.9
		Trillium cuneatum	53	2.80	1.8	-	0	5.6
		Trillium reliquum	158	8.31	19.8	1	6.4	3.3
Monte-zuma Bluffs	A/H	*Cardamine angustata*	49	0.50	10.2	2	7.8	0
		Hexastylis arifolia	25	0.25	0	-	-	0
		Trillium maculatum	24	0.24	12.5	-	-	20.8
		Trillium reliquum	57	0.57	28.5	1	6.2	7.7
		Viola sp.	9	0.09	0	-	-	11.1
	A/R	*Cardamine angustata*	282	2.82	42.6	8.24	72.3	0
		Hexastylis arifolia	4	0.04	50	-	-	0
		Trillium maculatum	47	0.47	51.4	1	7.1	19.1
		Trillium reliquum	187	1.87	24.6	1	32.5	6.7
		Viola sp.	17	0.17	0	-	-	0
Fort Gaines	A/H	*Cynoglossum virginianum*	47	0.47	2.1	18	76.4	0
		Hexastylis arifolia	42	0.48	0	-	-	2.4
		Trillium reliquum	92	0.92	2.3	-	-	16.3
		Viola sp.	144	1.44	2.8	1	100	20.3
	A/R	*Cynoglossum virginianum*	22	0.22	18.2	12.7	79.6	0
		Hexastylis arifolia	208	2.08	0	-	-	0
		Trillium reliquum	173	1.73	0.6	-	-	14.5
		Viola sp.	66	0.66	10.6	1.1	88.8	9.1

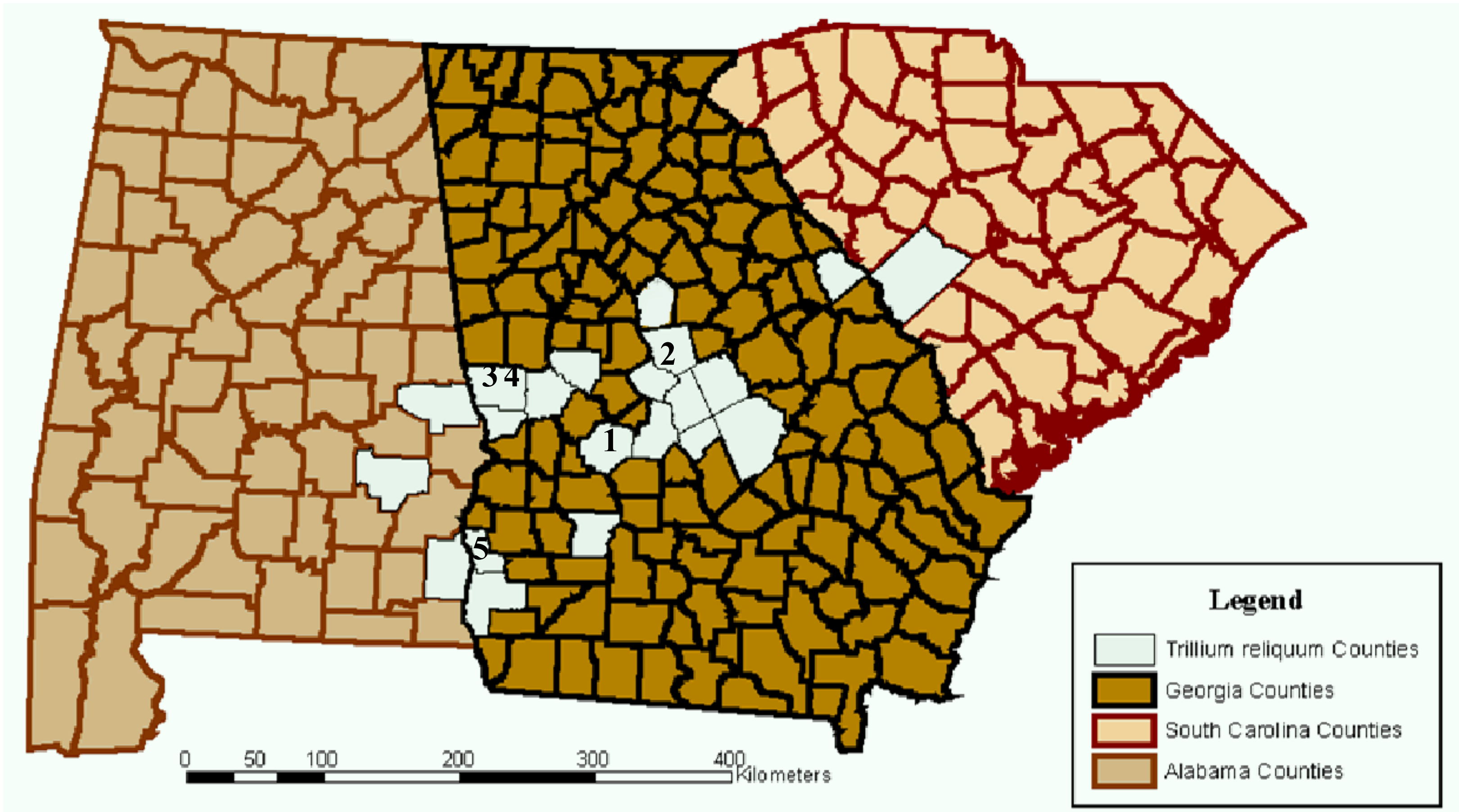

Figure 2.1. Distribution of *Trillium reliquum*. Study sites are identified with numbers: 1) Montezuma Bluffs Natural Area, 2) Bibb County site, 3) Mead-Westvaco property, 4) Hutcherson property, 5) Fort Gaines site

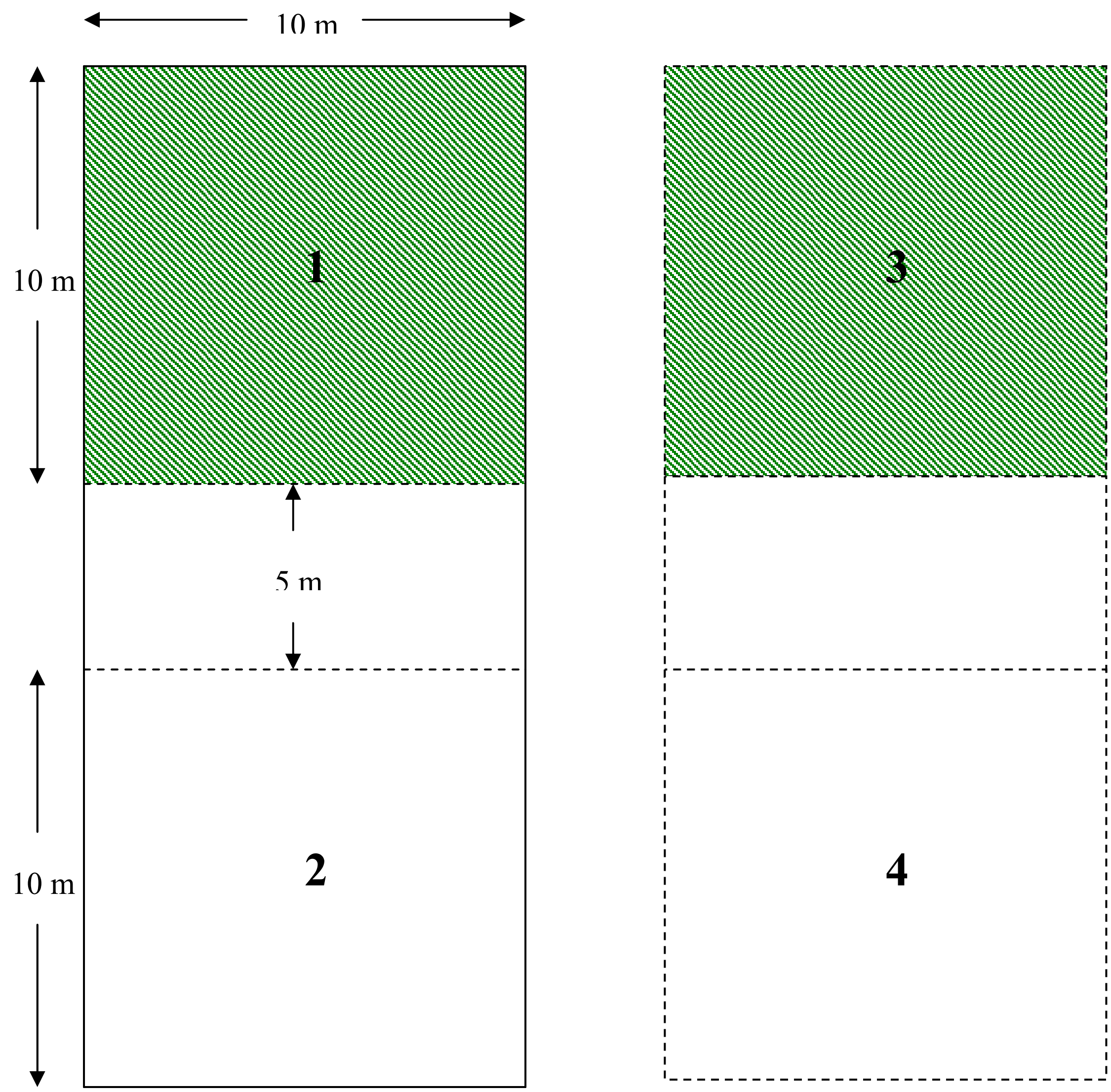

Figure 2.2. Four treatment combinations established at each site in Spring 2005: 1) deer excluded, honeysuckle present 2) deer excluded, honeysuckle removed 3) deer accessible, honeysuckle present (control) 4) deer accessible, honeysuckle removed. The five meter space between treatments is a buffer zone. Solid lines represent fencing, while dashed lines represent open space. Shaded areas represent honeysuckle present treatments, whereas open areas (excluding buffer) represent honeysuckle removal treatments.

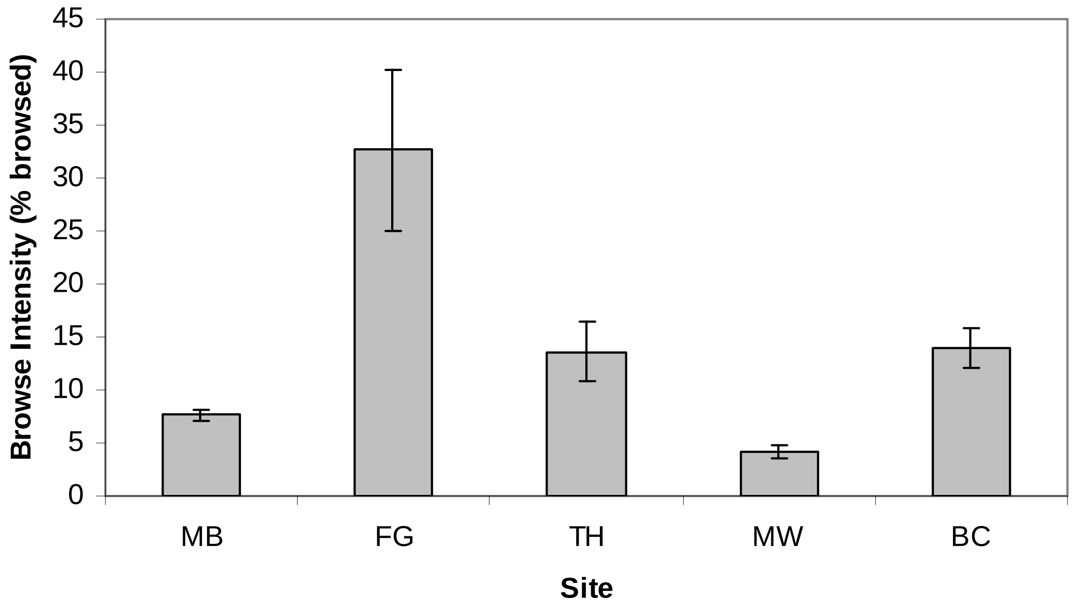

Figure 2.3. Deer browse intensity (±1 SE) in 2006 at five sites; (MB=Montezuma Bluffs Natural Area, FG=Fort Gaines, TH=Hutcherson, MW=Mead-Westvaco, BC=Bibb County). Mean deer browse intensity was determined at each site by averaging the percent of deer herbivory on all stems on four 20m transects. Sites were significantly different (one-way ANOVA, $F_{4,15}$ =16.59, P=<0.0001).

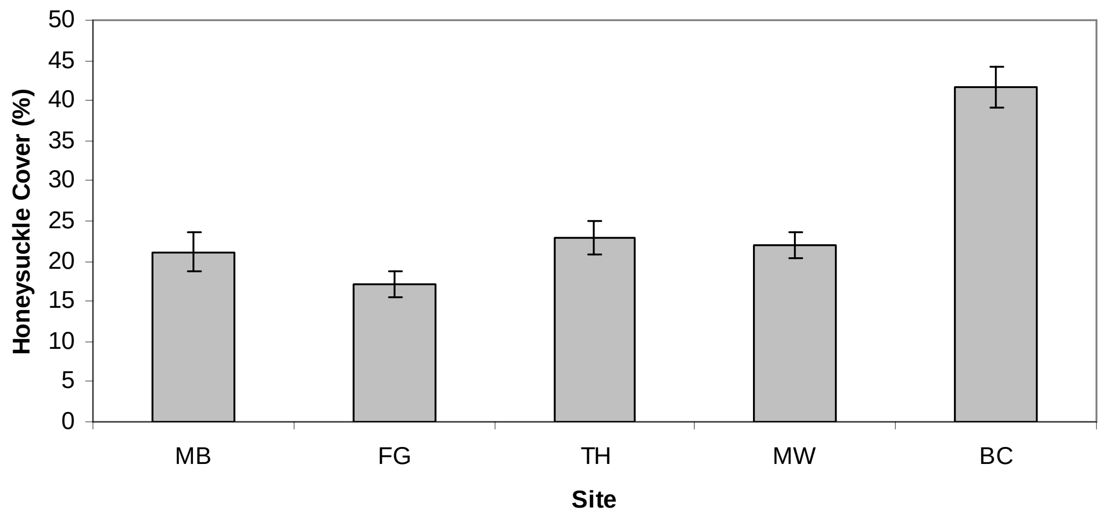

Figure 2.4. Percent honeysuckle (± 1SE) in all treatments at five sites in 2005; (MB=Montezuma Bluffs Natural Area, FG=Fort Gaines, TH=Hutcherson, MW=Mead-Westvaco, BC=Bibb County).

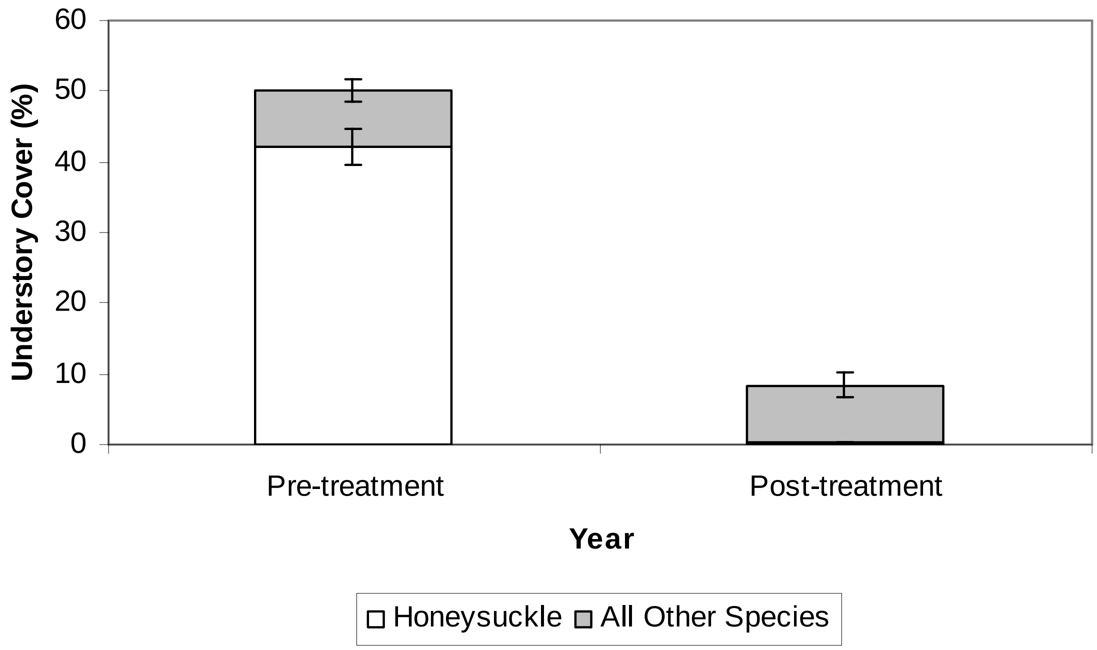

Figure 2.5. Mean understory cover (±1 SE) at Bibb County before (2005) and after (2006) herbicide treatment to remove honeysuckle.

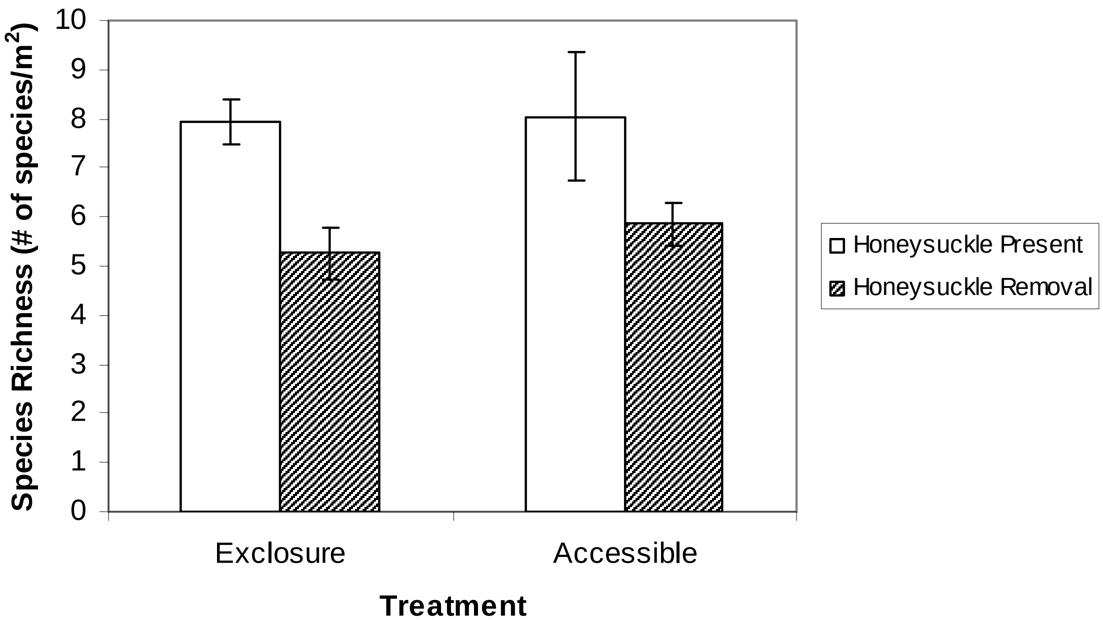

Figure 2.6. Total species richness (±1 SE) in four treatment combinations at three sites in 2006.

CHAPTER III

Impacts of White-tailed Deer (*Odocoileus virginianus*) and Invasive *Lonicera japonica* on the Population Dynamics of *Trillium reliquum*

Two significant limiting factors associated with decreased fitness in native plant populations are interactions with non-native invasive plants (Equihua and Usher 1993, Miller and Gorchov 2004) and herbivores (Edwards 1985, Doak 1992, Bastrenta et al. 1995, Lesica 1995, Garcia and Ehrlen 2002, Warner and Cushman 2002). These biotic variables may impose different constraints on the population dynamics of a native plant. Invasive plants often impact native plant populations through competition for and/or disruption of above and below ground resources, therefore, inhibiting population growth (Thomson 2005b, Williams and Crone 2006) and decreasing recruitment (Walker and Vitousek 1991, Equihua and Usher 1993, Walck et al. 1999, Thomson 2005b). Herbivores remove photosynthetic tissue and reproductive structures, thus, slowing transitions from smaller to larger lifestages (Rooney and Gross 2003, Knight 2003; 2004), reducing the proportion of reproductive individuals in the population (Anderson 1994, Augustine and Frelich 1998, Knight 2003, 2004), and impacting survivorship (Rausher and Feeny 1980, Crawley 1983, Ehrlen 1995). A combination of these negative biotic factors could be detrimental to native plant populations. Rare plant species in particular may be more susceptible to biotic threats due to human activities, such as habitat fragmentation and land use changes that may encourage new competitors and predators (Schemske et al. 1994, Oostermeijer 2003).

When teasing apart the effects of multiple threats to a rare plant, it is important to examine how different components of population dynamics are being affected by different impacts. Determining how vital rates are influenced by specific threats is necessary for the conservation of rare species (Schemske et al. 1994). By tracking the responses of populations to these impacts, as well as management or removal of these threats, conservation strategies that are best suited for a species can be determined and implemented.

Demographic models have become a vital method for determining how different impacts and management techniques affect population dynamics of rare plant species (Caswell 2001, Brigham and Thomson 2003). The projection matrix model is a versatile demographic tool that can be used to assess changes in population growth and persistence using λ (finite rate of increase; Caswell 2001). Elasticity and sensitivity analyses help determine which life stages have the greatest impact on changes in population size (Caswell 2001). Another significant attribute of matrix models is the ability to project future population sizes based on transitions within the matrix and current population sizes. To gain a better understanding of the status of a rare plant, it is imperative to incorporate demographic models in future conservation and management plans (Schemske et al. 1994, Menges 2000, Caswell 2001, Brigham and Thomson 2003).

Trillium reliquum is an endangered spring ephemeral herb that is native to Alabama, Georgia, and South Carolina. It is threatened by loss and alteration of habitat and encroachment of invasive vines, Japanese honeysuckle (*Lonicera japonica*) and kudzu (*Pueraria montana*) (US Fish and Wildlife Service 1990, Patrick et al. 1995, Heckel 2004). It may also be threatened by white-tailed deer (*Odocoileus virginianus*) herbivory (Heckel and Leege 2007). Honeysuckle is a well-studied invasive vine that has become naturalized in many deciduous forest ecosystems in the southeastern United

States. Since its introduction in the 19^{th} century, honeysuckle has become a dominant ground cover species ranging from 6% cover in young stands to 100% cover in mid-successional forests (Oosting 1942). White-tailed deer have become an important herbivore in the southeast due to significant population increases (McShea et al. 1997, Augustine and Frelich 1998, Russell et al. 2001). Increased presence of a non-native invader and herbivore may be detrimental to a spring ephemeral herb that is already threatened by habitat loss. This study examines the impacts of honeysuckle and white-tailed deer herbivory on the population dynamics of *T. reliquum*.

Few studies have addressed the impacts of invasive plants (Wester 1994, Huenneke and Thomson 1995, Walck et al. 1999, Thomson 2005a; 2005b) or white-tailed deer herbivory (Miller et al. 1992, Fletcher et al. 2001, McGraw and Furedi 2005) on rare plants. Furthermore, previous studies have not examined the combined effects of an herbivore and an invasive plant on a rare plant. The purpose of my research was to identify how two biotic threats, white-tailed deer and honeysuckle, are impacting an endangered herb, *Trillium reliquum*, and to provide management recommendations for the conservation of the species. The questions I addressed with this study were: 1) What is the status of *T. reliquum* across its range in Georgia? 2) What are the effects of white-tailed deer and honeysuckle on establishment, survival, and reproduction of *T. reliquum*? 3) How do white-tailed deer and honeysuckle impact *T. reliquum* population size and growth rate? 4) Do different life stages of *T. reliquum* differ in their impact on population growth, and if so, which life stages are most sensitive to these biotic threats? By excluding deer and removing honeysuckle, I tested the hypothesis that herbivores and invasive plants, when in abundance, negatively impact the population dynamics of a rare plant.

Methods

Study sites

I selected five sites for sampling based on *T. reliquum* population size, evidence of deer browsing, and the presence of honeysuckle. I chose sites along the Fall Line that separates the Coastal Plain and the Piedmont Plateau where *T. reliquum* populations are located. Study plots were established across the geographic range of *T. reliquum* in Georgia (see Chapter 2 for description of sites).

Study system

Trillium reliquum Freeman (relict trillium) is a perennial herb found primarily in relatively undisturbed mesic hardwood forests and is restricted to 21 populations separating the Fall Line of the Coastal Plain and Piedmont regions of Alabama (four populations), Georgia (14 populations), and South Carolina (three populations) (US Fish and Wildlife Service 1990, Figure 2.1). There is little gene flow between populations and the species rarity and population isolation associated with *T. reliquum* are thought to be of ancient origins and not due to anthropogenic fragmentation (Gonzales and Hamrick 2005).

Trillium reliquum produces a single, sessile, purplish flower in the center of a whorl of three strongly mottled leaves (Patrick et al. 1995). *T. reliquum* flowers from March to April, produces fruit in June, and as with other members of the genus, individuals persist underground during the rest of the year as a rhizome (Freeman 1975, Patrick et al. 1995). Individuals undergo distinct life stages including seedling, juvenile (one-leaf), subadult (three leaf), and reproductive stages (Figure 3.1), and may also exist in a dormant stage with no above-ground shoots during the spring growing season (Heckel and Leege 2007). Although little is known about specific pollinator species, *Calliphoridae* flies and beetles are both known to pollinate *T. reliquum* (Hamrick et al. 2006). Seeds are typically dispersed short distances by ants due to their oil-rich eliaosomes, although deer (as for other species of the genus) may disperse seeds over longer distances (Vellend et al. 2003).

Trillium reliquum demography

To assess the effects of white-tailed deer herbivory and encroachment by *Lonicera japonica* on the population dynamics of *Trillium reliquum*, I established four treatment combinations at each site in Spring 2005: 1) deer excluded, honeysuckle present 2) deer excluded, honeysuckle removed 3) deer accessible, honeysuckle present (control) and 4) deer accessible, honeysuckle removed (see Chapter 2 for experimental design).

I completed an initial census from March 9 to April 11, 2005 after *T. reliquum* emergence. Depending on population density of *T. reliquum*, either 1m x 1m quadrats were chosen randomly for censusing until 100 or more individuals were marked or a complete census using 2m x 2m quadrats was completed (Table 3.1). All corners of quadrats sampled were marked with wire flags to aid in future plot identification. *Trillium reliquum* individuals within each plot were permanently marked using uniquely numbered aluminum tags affixed into the ground with 9 cm nails, and the location of each individual was mapped. Tags were placed at least 3-4 cm away from plants so as not to inhibit emergence and growth in the next season. Individual seedlings were marked with aluminum tags and mapped, while large clusters were only mapped. Life stage (seedling, juvenile, sub-adult, and reproductive) was noted for each individual. Trilliums browsed by deer early in the season were marked and mapped as well, but because deer eat the entire vegetative portion of the plant, life stages were impossible to determine. To determine plant size, I measured length and width of a representative leaf for each individual plant except those in the seedling stage.

A second census was taken in mid-June 2005 at fruiting to determine survivorship of fruiting individuals, fruit diameter, and seed production. In each treatment, diameter of individual fruits was measured using digital calipers to determine fruit size (as in Heckel 2004). At each site, fifteen fruits were collected from plants outside of treatments (excluding Fort Gaines because of insufficient fruit numbers) and fruit diameter and number of seeds per fruit was evaluated to determine if fruit diameter was a sufficient measure of *T. reliquum* seed production. The relationship between diameter of fruit and number of seeds produced per fruit was examined using linear regression.

Three censuses of *T. reliquum* populations were made in Spring 2006. I conducted a census at *T. reliquum* emergence from March 10 to March 17, 2006 to evaluate over-winter survival, determine life stage transitions of each individual, and to mark and map new individuals. I made a second census from April 2 to April 14, 2006 to examine the effects of deer browsing on *T. reliquum*. Deer browse on *T. reliquum* individuals was evident if the entire vegetative portion of the plant was eaten leaving only a stem. A final census was made from June 17 to 18, 2006 at fruiting to determine *T. reliquum* fruiting success and to measure fruit diameter.

Deer herbivory on Trillium reliquum and its associated plant community

To determine white-tailed deer browse intensity, I established four 20m transects at least 5m away from treatments at each site on April 24 and 25, 2006. I counted all plants and all plants browsed by deer that touched the transect line, and divided the number of plants browsed by the total number of plants to determine browse intensity. Deer browse on plants was distinguished from insect and rodent herbivory if stems and/or entire leaves appeared chewed off. To determine if deer were selecting trillium over all other plant species, I calculated mean browse intensity for each site and compared it to the proportion of *T. reliquum* browsed by deer in the deer accessible/honeysuckle present (control) treatments using linear regression. I also used linear regression to examine the relationship between *T. reliquum* population density and browse rates on *T. reliquum*. I used a one-way ANOVA with site as a block to determine if there were differences in proportions of trillium browsed between the deer accessible/honeysuckle present and the deer accessible/honeysuckle removed treatments.

Impacts of deer and honeysuckle on Trillium reliquum population dynamics

I used data from the 2005 and 2006 censuses to determine the effects of each treatment on: *T. reliquum* density (# individuals/m^2), λ (lambda), and to project population size over time. I used the spring 2006 data to examine white-tailed deer herbivory rates on *T. reliquum*. I also used these data to determine treatment effects on proportions of individuals in 2005 that went dormant in 2006, proportions of reproductives that fruited in 2006, and 2006 fruit size. To calculate *T. reliquum* density, I divided the total number of individuals in each treatment by the total area sampled (20m^2 to 100m^2 sampled in each treatment). I used a two-way ANCOVA with deer and honeysuckle as effects and 2005 density as a covariate to determine if treatment had an effect on *T. reliquum* density. I excluded the deer excluded/honeysuckle present treatment at Mead-Wesvaco from this analysis because it was an extreme outlier. To determine if treatment had an effect on the proportion of plants entering dormancy in 2006, I divided the number of plants that went dormant in 2006 by the total number of plants in each treatment at each site in 2005. The Bibb County site was excluded from this analysis because of the late installation of exclosure at that site. Because the data were not normally distributed, I log transformed the data to normality and used a two-way ANOVA with deer and honeysuckle as effects. To examine if treatment had an effect on the proportion of reproductive plants that fruited in 2006, I divided the number of fruiting reproductive plants by the total number of reproductive plants. Fort Gaines was excluded from this analysis, due to low numbers of reproductive plants in 2006. I used a two-way ANOVA with deer and honeysuckle as effects. To determine the effects of treatments on fruit diameter, I used a two-way ANOVA with deer and honeysuckle as effects. I used each site as a block for all ANOVAs.

Trillium reliquum germination study

A germination study was established in four sites on June 22 and 23, 2005 to determine if *T. reliquum* germination rates differed between treatments and sites. Seed baskets measuring approximately 0.3m x 0.3m x 0.05m tall with an opening on top were constructed out of fiberglass mesh. Soil to be placed in each basket was taken from each site and sterilized. Two seed baskets were placed in randomly selected locations in each treatment at each site. Fifteen fruits were collected at four of the five sites from plants that were at least 5 m outside of study plots. Fruits were not collected from Fort Gaines because very few reproductive plants were available. Seeds were removed from fruits on site and placed into a bag to homogenize seeds. Thirty seeds from fruits at the same sites were haphazardly chosen from the bag and placed immediately in each seed basket. Sterilized soil was used to cover the seeds. In Spring 2006, seed baskets were examined to determine germination rates in each treatment. I used a two-way ANOVA with site as a block to determine effects of deer and honeysuckle on germination rates.

Population growth rates and projection models

Transition matrices have become an important demographic tool in examining the viability of plant populations (Schemske 1994, Rooney and Gross 2003, Thomson 2004, McGraw and Furedi 2005). Because the age of perennial plants like trilliums can not be determined without causing harm or destroying the plant (Patrick 1973), transitions between stages in different years are often examined to determine the stability of a population. To account for plants that could not be used in matrix models because they were dormant in 2005 and emerged in 2006, I used two methods to calculate λ. To determine population growth rates for each treatment during 2005 to 2006, I used the formula $\lambda=N_t/N_{t+1}$ where N_t is population size at time t and N_{t+1} is population size at one time interval into the future. I used a two-way ANOVA with site as a block to determine deer and honeysuckle effects on λ. I excluded the deer excluded/honeysuckle present treatment at Mead-Wesvaco from this analysis because it was an extreme outlier (512.5% increase).

To calculate λ for the purpose of projecting future population sizes and for elasticity and sensitivity analyses I used stage-based transition matrices. Deer excluded treatments could not be included in the matrix analysis due to a lack of forward transitions of seedlings to juveniles, therefore causing matrices to be non-functional. I could not build matrices with Fort Gaines data due to a lack of reproductives in 2005. To calculate λ and to project future population sizes. I used the model:

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

where $\mathbf{n}_t$ is the population size at time t and $\mathbf{n}_{t+1}$ is the population size one projection interval later. The projection matrix **A** is the nonnegative square matrix whose elements a_{ij} represents a vital statistic for a particular stage class within the population. Plants were classified into four stages based on distinct differences associated with each life stage. I used census data from 2005 and 2006 to determine transition probabilities based on a life cycle diagram (Figure 3.2) that summarized all possible transitions within and between stages for trilliums in each treatment (Table 3.2). I calculated transition probabilities by dividing the number of individuals that transitioned in 2006 by the total number of individuals in that life stage in 2005. Fecundity was calculated by dividing the dividing the total number of seedlings in 2006 by the total number of reproductive plants in 2005. Plants that were eaten by deer in early 2005 were not included because it was impossible to determine life stage. Due to a lack of forward transitions of seedlings at some sites, I created summary matrices by pooling data from all sites (excluding Fort Gaines) into a single matrix for each treatment. These matrices do not account for dormancy and because the seed bank for *T. reliquum* is unknown, I did not use seeds in the construction of these matrices.

I calculated the eigenvectors and eigenvalues to determine population parameters using the matrix model. The dominant eigenvalue, λ, describes the eventual growth rate of the population, the dominant right eigenvector, **w**, corresponds to the stable stage distribution of the population, and the left eigenvector, **v**, represents the stage specific reproductive values, or the potential contribution of an individual in a stage class to future population growth (Caswell 2001). When $\lambda > 1$, population size is increasing, when $\lambda < 1$, population size is decreasing, and when $\lambda = 1$, the population is stable. Using the stable stage distribution and the reproductive values, I calculated sensitivities and elasticities of the matrices. Sensitivity analysis measures the effects of changes of any element of the **A** matrix on λ and is defined by the formula:

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

Elasticities measure how λ changes with small proportional change in each matrix element and is defined by the formula:

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

Since fecundities are often greater than one, whereas other elements can never be greater than one, sensitivities represent an absolute effect on λ. Elasticity values range from 0 to 1 and sum to 1, providing a measure of the relative importance of each stage transition of fecundity. I measured sensitivities and elasticities of honeysuckle removal and honeysuckle present matrices to determine which transitions to which λ is most sensitive. I used JMP IN 6.0 (SAS, Cary, NC, 2005) for all statistical analyses and Poptools 2.6 (2005) to analyze matrix models.

Results

Pre-experimental conditions

Initial censusing in the first growing season determined variation among *T. reliquum* populations in density, stage structure, and fruit production. In Spring 2005, *T. reliquum* population density ranged from 1.9±0.9/m^2 at Fort Gaines to 5.3±1.4/m^2 at Bibb County (Table 3.1). In 2005, stage structure varied widely across populations (Table 3.3), with subadults (52.0±3.4%) being the best represented life stage. Populations at Fort Gaines were the most under-represented in seedling and reproductive life stages, whereas some treatments at Mead-Westvaco had high percentages of larger life stages. Out of 385 reproductive *T. reliquum* plants censused in the first season, 100 (26%) were successful in producing fruit.

The two biotic variables, deer and honeysuckle, also varied across *T. reliquum* populations. Percent honeysuckle cover ranged from 17.2±1.6% at Fort Gaines to 41.6±2.5% at Bibb County (see Chapter 2). Although deer browse on trillium was not tracked throughout the entire first growing season, early growing season browse ranged from 0-10%. More specifically, the initial census after emergence revealed percent trillium browsed (excluding seedlings) was 9.2% at the Hutcherson site, 4.4% at Montezuma Bluffs, 2.1% at Bibb County, 1.3% at Fort Gaines, and 0.8% at Mead-Westvaco.

Deer herbivory on Trillium reliquum

In the second year, deer herbivory on *T. reliquum* was tracked through the entire season, which revealed a range of deer browse intensity across populations. In Spring 2006, the percent of trillium browsed by deer (n=5, mean=12.6±0.03) ranged from 3.3%

(Mead-Westvaco) to 32.2% (Fort Gaines; Figure 3.3). Across all populations, 3.9±1.6% of juveniles, 8.9±4.8% of subadults, and 9.8±8.2% of reproductives were browsed by deer (Figure 3.4). In four populations (excluding Hutcherson), there was a significant negative relationship between *T. reliquum* population density and deer herbivory on *T. reliquum* (Figure 3.5). In three of the populations (Fort Gaines, Mead-Westvaco, Bibb County), there was a strongly significant negative relationship between *T. reliquum* density and deer herbivory on *T. reliquum* (Linear Regression, slope= -0.017, P=0.0003). At all populations except Hutcherson, there was a significant positive relationship between deer browse intensity on all species of plants and proportion of *T. reliquum* browsed by deer (Figure 3.6). There was no significant difference between the percent of trilliums browsed in honeysuckle present treatments (13.8±5.1%) and honeysuckle removal treatments (11.4±4.5%; one-way ANOVA, $F_{1,4}$ =2.92, P=0.16).

Impacts of deer and honeysuckle on Trillium reliquum population dynamics

After installation, there was no indication of deer herbivory on *T. reliquum* in exclosures. Cover of honeysuckle was reduced by nearly 100% in removal treatments (see Chapter 2). *Trillium reliquum* density in 2006 did not vary significantly with treatment, although it co-varied significantly with the previous years (2005) density (Table 3.1 and 3.4, Figure 3.7). Proportion of trilliums that went dormant in 2006 was significantly higher in deer accessible treatments than in deer excluded treatments (Figure 3.8), while honeysuckle effect and interaction was not significant (Table 3.5). Deer had a significant effect on fruiting between 2005 and 2006, increasing fruit production 5-7% in deer excluded treatments and decreasing fruit production 13-15% in deer accessible treatments (Figure 3.9). The proportion of fruiting trilliums was significantly lower in deer accessible treatments than in deer excluded treatments after exclosures had been established for one year (Figure 3.9), whereas honeysuckle had no significant effect and an interaction between deer and honeysuckle was not detected (Table 3.5).

There was a significant positive relationship between fruit diameter and seed number (Figure 3.10), therefore fruit diameter is a good predictor of seed production. Deer, honeysuckle, and interaction had no significant effect on fruit diameter (Table 3.5, Figure 3.10). Forty-four to fifty-seven percent of seeds germinated in seed baskets, but treatments were not significantly different (Table 3.5, Figure 3.12).

Population growth rates and projection models

Using population growth rate calculated by dividing the 2006 population size by the 2005 population size, populations in honeysuckle removal treatments increased by 40.9±12.8% (deer excluded) and 33.7± 6.8% (deer accessible) between 2005 and 2006 (Table 3.7, Figure 3.13). This is contrasted by an increase of 17.4±13.4% (deer excluded) and 14.8±6.3% (deer accessible) in the honeysuckle present treatments (Table 3.6, Figure 3.13). This calculation allowed for the inclusion of plants that were dormant in 2005 and could not be included in projection matrix models. Populations in honeysuckle removal treatments had a significantly greater increase in population growth in 2006 than populations in honeysuckle present treatments (Figure 3.13), while deer did not impact population growth and an interaction between deer and honeysuckle was not evident (Table 3.5). Although deer did not have a significant effect on population growth across all sites, it is worth noting that the site with the greatest deer pressure, Fort Gaines, displayed sizable increases in *T. reliquum* population size in exclosures (honeysuckle:

λ=1.54, honeysuckle removal: λ=1.72) compared to deer accessible treatments (honeysuckle: λ=1.08, honeysuckle removal: λ=1.10).

Projection matrix models (Table 3.7) showed that deer-accessible/honeysuckle present (control) *T. reliquum* populations were stable and that populations in deer-accessible/honeysuckle removal treatments would increase dramatically in 25 years (Figure 3.14). In the deer accessible/honeysuckle removal treatments, λ calculated from projection matrix models predicts an annual rate of increase of 10.8%. In the deer accessible/honeysuckle present treatments, the predicted annual rate of increase is 3.9%. Population size projections revealed slower growth in the honeysuckle present treatments, tripling initial population size in 25 years (Figure 3.14). The honeysuckle removal treatments had a high growth rate, tripling the initial population size in just 10 years and increasing seventeen times the initial population in 25 years (Figure 3.14).

Stable stage distributions (the stage structure at which populations will stabilize) predicted by matrices differed between honeysuckle present and honeysuckle removal treatments (Figure 3.15). In honeysuckle removal treatments, the proportion of seedlings was greatest followed by juveniles, subadults, and reproductives. In the honeysuckle present treatments, seedlings and subadults were nearly evenly proportioned, accounting for about 60% of the stable stage distribution, followed by juveniles and reproductives. The reproductive value in both the honeysuckle removal and honeysuckle present treatments show that as individuals progress to higher life-stages their contribution to population growth increases (Figure 3.16).

Matrix sensitivity analysis showed the transition probabilities of subadults to have the greatest impact on λ (Table 3.8). The transition with the greatest effect on λ is the subadult to reproductive transition, which had the highest sensitivity in both the honeysuckle removal and honeysuckle present treatments. The reproductive to reproductive transition also had a great impact. Based on elasticities, subadults and reproductives had the greatest impact on λ (Table 3.8). In both treatments, stasis of reproductives was the most important transition and stasis of subadults was the second most important transition.

Discussion

Across its Georgia distribution, *T. reliquum* exhibits a wide range of population densities and stage structures. Seedlings and reproductive individuals were often the most poorly represented life stages at each site. Only one-fourth of all reproductive plants fruited in 2005. Although there was low recruitment and fruiting across five populations, none of the populations studied were declining.

Deer herbivory on Trillium reliquum

My results show that deer browse on *T. reliquum* is highly variable across the five study populations (Figure 3.3). Although all populations experienced some level of herbivory, deer browse on trilliums ranged from minimal to nearly one-third of the population. This may be attributed to differences in deer population size in each region as well as landscape differences. The Mead-Westvaco population is located on lands that are hunted often (Donnie Wood pers. comm.), is the most remote, and experiences minimal herbivory. The Hutcherson population is located on property that has not been hunted recently (Tommy Hutcherson pers. comm.), is in close proximity to a fragmented residential area, and experiences the most herbivory. Differences in *T. reliquum* population density may also be responsible for varying levels of herbivory. At four populations, deer browse on *T. reliquum* decreased as *T. reliquum* density increased. This relationship is consistent with a study by Fletcher et. al (2001), where an endangered herb, *Lilium superbum* (Turk's cap lily), was browsed more by deer in smaller patches than in larger patches.

At four of the five populations, deer did not select trillium over other species, while at the Hutcherson population, trillium was preferentially browsed. This observation marks a contrast to *Trillium grandiflorum*, a more abundant trillium, which is preferred by deer over other species (Anderson 1994).

Impacts of deer and honeysuckle on Trillium reliquum population dynamics

Neither white-tailed deer nor honeysuckle affected *T. reliquum* density. This contradicts Heckel's (2004) findings of significant increases in *T. reliquum* density following honeysuckle removal. While surprising, this observation warrants the use of demographic modeling in conjunction with empirical studies to determine the impacts of invasive plants on rare plant species. Traditional monitoring techniques such as yearly censusing and counts are important, but may not always be adequate methods in determining the condition of plant populations.

Deer impact *T. reliquum* population dynamics by decreasing reproductive success and increasing dormancy. Deer have been found to prefer reproductive trilliums over all other life stages (Augustine and Frelich 1998). Because of the importance of the reproductive stage in determining fecundity and persistence of populations, increased deer browse on this stage may affect the stability of trillium populations. Dormancy in perennial plants is frequently a result of increased stress during the previous growing season and is often caused by harsh environmental conditions or herbivory (Tamm 1972, Kull 1995). Therefore, defoliation of plants by deer in the growing season may result in dormancy in the next season. Dormant individuals may be more susceptible to mortality than individuals with above ground shoots and may exert costs on fecundity (Hutchings 1987, Shefferson et al. 2003). Although herbivory on *T. reliquum* individuals was not tracked throughout the entire first season, dormancy in the second season was significantly higher in deer accessible treatments.

Population growth rates and projection matrix models

Empirical data and matrix models provide evidence that honeysuckle is playing a key role in determining *T. reliquum* population size. In comparison to honeysuckle treatments, population sizes in removal treatments increased dramatically after removal. Heckel (2004) demonstrated that after removal of honeysuckle at Montezuma Bluffs Natural Area, *T. reliquum* population size increased by 50%. He also suggested that with removal of honeysuckle, the carrying capacity for *T. reliquum* is raised. In my study, upon removal of honeysuckle, populations increased by an average of 33-41% (Table 3.7, Figure 3.13). This study adds further support to Heckel's findings throughout a broader range. Transition matrices predicted a population growth rate (λ) of 1.108 in removal treatments and 1.039 in honeysuckle (control) treatments. These results are consistent with other studies that have documented increased population growth of native plant populations associated with the removal of non-native plant invasives (Thomson 2005b, Williams and Crone 2006).

Summary matrix projections in honeysuckle removal treatments reveal a population growth of seventeen times the size of current populations in 25 years, while *T. reliquum* populations in honeysuckle present treatments are projected to increase by only three times their initial size. Because matrices do not take density dependence into account, this is not a realistic prediction of *T. reliquum* population growth. Rather, it is an indication of how honeysuckle is negatively impacting the species and how eradication of honeysuckle from *T. reliquum* populations may stimulate population growth.

The stable stage distributions of both the honeysuckle and honeysuckle removal treatments are somewhat evenly spread. Seedlings are the best represented stage while reproductives are least represented. This provides evidence that recruitment is important in both the honeysuckle present and honeysuckle removal treatments. The reproductive stage makes up approximately 50% of the reproductive value in both honeysuckle and honeysuckle removal treatments. As individuals move to larger life stages their contribution to the future of the population increases. Elasticities and sensitivities determined that λ is most sensitive to the transitions of subadult and reproductive stages. Biotic threats impacting these stages are most likely to affect the overall population dynamics of *T. reliquum*. Honeysuckle impacts both subadults and reproductives by increasing back-transitions. Also, fewer progressive transitions of subadults to reproductives are associated with the presence of honeysuckle.

White-tailed deer and invasive honeysuckle appear to be impacting different components of *T. reliquum* population dynamics. Deer directly affected reproduction by decreasing the number of fruit produced, therefore decreasing recruitment in the next season. Deer also increased the proportion of plants going dormant, which implies a depletion of carbohydrate reserves. Repeated depletion of nutrients may negatively affect survival and reproduction of *T. reliquum*.

In a twenty year span from 1983 to 2002, deer population estimates in the upper Coastal Plain region of Georgia increased from 12.8 to 30.2 deer per square mile and from 19.5 to 46.3 deer per square mile in the Piedmont region (Georgia Department of Natural Resources 2003). Further increases in deer populations would raise the already elevated levels of herbivore pressure on *T. reliquum* and could be detrimental to the species.

Honeysuckle has become a major constituent of forest understories where it is found. This study demonstrates that it co-occurs with *T. reliquum* in at least one-fourth of the 21 sites where populations of *T. reliquum* are found. Honeysuckle impacts trillium populations by decreasing transitions to higher life stages as well as increasing back-transitions to earlier life stages in deer accessible treatments. Removal of honeysuckle resulted in increased population sizes, which suggests that honeysuckle may reduce the carrying capacity of *T. reliquum*.

My research has determined multiple constraints on *T. reliquum* populations facilitated by an invasive plant and an herbivore. Although *T. reliquum* populations appear to be stable or growing, deer and honeysuckle were found to be important limiting factors in reproduction, survivorship, and population growth (Table 3.9). Because occurrence of deer herbivory is proportionally higher in smaller patches, populations with low densities may be at greater risk. This study also found that the conservation of subadults and reproductives may be necessary to the persistence of this rare species.

Implications for Management

My research has elucidated multiple negative effects on *T. reliquum* populations caused by deer and honeysuckle. Although none of the populations I examined in this study were currently declining, careful management of *T. reliquum* populations is necessary for the preservation of the species. Conservation efforts for *T. reliquum* should focus on:

1) White-tailed Deer Management

This research has made clear the importance of white-tailed deer as a limiting factor in the fruiting success of *T. reliquum*. After just one year of protection from deer, fruiting success increased 5-7% and was 20% higher than reproductive individuals that had been exposed to deer (Figure 3.9). Also, individuals that had been exposed to deer in one year were more likely to go dormant in the following year (Figure 3.8). These results suggest that deer are playing a negative role in the reproduction and survival of this endangered herb.

To curtail these impacts on *T. reliquum*, I suggest long-term management of deer in *T. reliquum* populations that are declining. Reducing deer browse will increase trillium reproductive success and survivorship needed to boost population growth.

2) Honeysuckle removal

This study found that honeysuckle is a common invader across the Georgia range of *T. reliquum*. Honeysuckle was often the most frequent vine in the study populations and covered 20-40% of the herbaceous layer (Table 2.2, Figure 2.4). Honeysuckle impacts *T. reliquum* by lowering its carrying capacity, thus, decreasing population growth. Here, I have demonstrated that removal of honeysuckle results in significant population increases (Figure 3.13). Therefore, careful removal of honeysuckle in populations that are most endangered (i.e. small population sizes, few reproductive plants), will stimulate population growth.

Managers should take note of populations with few subadult and reproductive individuals. Heckel (2004) suggested that to conserve populations of *T. reliquum*, focus should be placed on subadult and reproductive individuals. This study supports Heckel's suggestion in a broader context. Conservation of *T. reliquum* in habitats containing honeysuckle should focus on the stasis of subadults and reproductives and increasing transitions of subadults to the reproductive stage. Because larger life stages are important in determining population growth, it is necessary to develop management plans with these life stages in mind.

3) Private Landowner Contacts

Currently, very few *T. reliquum* populations are located on State or Federal lands or are protected by land trusts. Because many of the sites where *T. reliquum* populations occur are privately owned, it is important to develop and maintain contacts with land-owners. Making landowners more aware of the importance of rare species like *T. reliquum*, will assist in management and conservation efforts.

Table 3.1. Area sampled and density of *T. reliquum* in 2005 and 2006 at five sites in four treatment combinations. Sites: MB=Montezuma Bluffs Natural Area, FG=Fort Gaines, TH=Hutcherson, MW=Mead-Westvaco, BC=Bibb County. Treatments: E/H = deer excluded, honeysuckle present, E/R = deer excluded, honeysuckle removed, A/H = deer accessible, honeysuckle present, A/R = deer accessible, honeysuckle removed.

		2005		2006	
Site	**Treatment**	**Area (m^2)**	**Density ($\#/m^2$)**	**Area (m^2)**	**Density ($\#/m^2$)**
MB	E/H	23	6.26	23	5.61
	E/R	80	1.54	80	1.64
	A/H	100	0.54	100	0.57
	A/R	100	1.6	100	1.87
FG	E/H	80	2.3	20	3.54
	E/R	80	3.05	80	5.25
	A/H	100	0.85	100	0.92
	A/R	100	1.57	100	1.73
TH	E/H	44	2.7	44	3.09
	E/R	80	1.35	80	1.7
	A/H	50	3.02	50	4.08
	A/R	50	2.32	50	3.46
MW	E/H	24	2.33	24	11.95
	E/R	33	3.12	33	5.27
	A/H	25	6.52	25	8.32
	A/R	25	4.16	25	6.04
BC	E/H	21	5.28	21	5.95
	E/R	29	3.76	29	5.0
	A/H	24	4.92	24	5.0
	A/R	20	7.21	20	8.32

Table 3.2. Transition matrix showing possible transitions for *T. reliquum*. In column and row headings S=seedling, J=juvenile, A=subadult, R=reproductive.

Life Stage in year 2	**Life Stage in year 1**			
	S	**J**	**A**	**R**
S	-	-	-	F
J	P_{sj}	P_{jj}	P_{aj}	-
A	-	P_{ja}	P_{aa}	P_{ra}
R	-	-	P_{ar}	P_{rr}

Table 3.3. Stage structure of *T. reliquum* in 2005 and 2006. Lifestages: Seedling (S), one-leaf Juvenile (J), three-leaf subadult (A), and Reproductive (R). Sites: MB=Montezuma Bluffs Natural Area, FG=Fort Gaines, TH=Hutcherson, MW=Mead-Westvaco, BC=Bibb County. Treatments: E/H = deer excluded, honeysuckle present, E/R = deer excluded, honeysuckle removed, A/H = deer accessible, honeysuckle present, A/R = deer accessible, honeysuckle removed.

		2005 lifestages (%)				**2006 lifestages (%)**			
Site	**Treatment**	**S**	**J**	**A**	**R**	**S**	**J**	**A**	**R**
MB	E/H	24.1	5.67	51.0	19.14	9.3	8.52	47.28	37.88
	E/R	0.8	12.6	68.0	18.48	9.8	9.09	59.09	21.96
	A/H	0	13.2	69.81	16.98	3.57	1.78	66.07	28.57
	A/R	6.1	9.58	65.08	19.17	12.93	11.11	51.23	24.69
FG	E/H	1.63	64.67	33.69	0	0.69	53.49	453.1	0.69
	E/R	1.61	83.06	15.32	0	0	62.06	37.93	0
	A/H	0	45.23	54.76	0	0	36.78	60.91	2.29
	A/R	1.92	60.25	37.82	0	0.63	40.12	58.59	0.63
TH	E/H	0.84	22.03	60.16	16.94	11.45	17.55	48.85	22.13
	E/R	0.96	15.38	67.3	16.34	17.16	11.94	50.0	20.89
	A/H	12.69	14.28	60.31	12.69	30.69	8.41	44.55	16.33
	A/R	6.45	5.37	72.04	13.12	28.57	11.68	41.55	18.18
MW	E/H	23.63	30.9	30.9	14.54	51.245	12.45	29.53	6.76
	E/R	11.11	12.03	49.07	27.77	41.95	7.47	28.7	21.83
	A/H	2.63	39.47	37.5	20.39	27.75	25.35	30.62	16.26
	A/R	4.25	25.53	45.74	24.46	35.71	16.88	26.62	20.77
BC	E/H	3.3	23.14	49.58	23.96	21.13	18.69	31.7	28.45
	E/R	1.53	21.53	61.53	15.38	18.518	20.7	40.0	20.74
	A/H	2.65	15.04	62.83	19.46	5.66	18.86	51.88	23.58
	A/R	11.19	25.37	54.47	8.95	25.0	20.51	34.61	19.87
Means:		**5.87**	**27.22**	**52.35**	**14.39**	**17.59**	**20.67**	**64.64**	**17.63**

Table 3.4. Results from 2-way ANCOVA for deer, and honeysuckle effects on *T. reliquum* density.

Variable	Source	df	F	P-value
Density	Block (site)	4		
	Deer	1	0.313	0.58
	Honeysuckle	1	2.556	0.14
	Deer x Honeysuckle	1	0.394	0.54
	2005 Density	1	85.138	**<0.0001**
	Error	11		

Table 3.5. Results from 2-way ANOVA for deer and honeysuckle effects on *T. reliquum* dormancy rates, fruiting, 2005-2006 population growth (λ), fruit diameter, and germination rates.

Variable	Source	Df	F	P-value
Dormancy	Block (site)	3		
	Deer	1	13.265	**0.005**
	Honeysuckle	1	0.07	0.79
	Deer x Honeysuckle	1	1.947	0.19
	Error	9		
Fruiting (2006)	Block (site)	3		
	Deer	1	14.971	**0.003**
	Honeysuckle	1	2.392	0.15
	Deer x Honeysuckle	1	0.956	0.35
	Error	9		
Population Growth (λ)	Block (site)	4		
	Deer	1	0.594	0.45
	Honeysuckle	1	4.346	**0.06**
	Deer x Honeysuckle	1	0.0003	0.98
	Error	11		
Germination Rates (in seed baskets)	Block (site)	3		
	Deer	1	1.778	0.19
	Honeysuckle	1	3.569	0.07
	Deer x Honeysuckle	1	0.308	0.58
	Error	28		
Fruit Diameter (2006)	Block (site)	2		
	Deer	1	0.052	0.82
	Honeysuckle	1	5.724	**0.02**
	Deer x Honeysuckle	1	0.144	0.70
	Error	93		

Table 3.6. Population growth rates for treatment combinations. λ (model) is the dominant eigenvector of a transition-based stage matrix. λ (N_t/N_{t+1}) (±1 SE) was calculated with empirical data from 2005 and 2006 using the formula N_t/N_{t+1}.

	Population Growth Rate	
Treatments	**λ(model)**	**λ(N_t/N_{t+1})**
Deer excluded/honeysuckle present	-	1.174±0.134
Deer excluded/honeysuckle removal	-	1.409±0.128
Deer accessible/honeysuckle present	1.039	1.148±0.063
Deer accessible/honeysuckle removal	1.108	1.337±0.068

Table 3.7. Summary transition matrices for: A) honeysuckle present and B) honeysuckle removal treatments in deer accessible areas. In column and row headings S=seedling, J=juvenile, A=subadult, R=reproductive.

A) Honeysuckle Present

		2005			
		S	**J**	**A**	**R**
2006	**S**	0.0000	0.0000	0.0000	1.6842
	J	0.2903	0.5290	0.0663	0.0000
	A	0.0000	0.3235	0.6902	0.1710
	R	0.0000	0.0000	0.1725	0.7763

lamda = 1.039

B) Honeysuckle Removal

		2005			
		S	**J**	**A**	**R**
2006	**S**	0.0000	0.0000	0.0000	2.0921
	J	0.3414	0.5789	0.0420	0.0000
	A	0.0000	0.3157	0.6428	0.1298
	R	0.0000	0.0000	0.2731	0.7922

lamda = 1.108

Table 3.8. Sensitivities and elasticities of all transitions in deer accessible treatments (A/H=deer accessible, honeysuckle present A/R=deer accessible/honeysuckle removal). Numbers in bold are the two most important transitions having the greatest impact on λ. s=seedling, j=juvenile, a=subadult, r=reproductive

	Transition								
	s-j	**j-j**	**j-a**	**a-j**	**a-a**	**a-r**	**r-a**	**r-r**	**r-s**
Treatment	**Sensitivity**								
A/H	0.2382	0.1650	0.2602	0.2248	0.3546	**0.6316**	0.2323	**0.4138**	0.0411
A/R	0.2863	0.1987	0.3331	0.1777	0.2979	**0.4803**	0.2575	**0.4151**	0.0473
Treatment	**Elasticity**								
A/H	0.0666	0.0840	0.0810	0.0144	**0.2354**	0.1048	0.0382	**0.3090**	0.0666
A/R	0.0881	0.1038	0.0949	0.0067	**0.1728**	0.1184	0.0302	**0.2968**	0.0882

Table 3.8. Summary of the impacts of deer and honeysuckle on *T. reliquum*.

Variable	***Deer herbivory***	***Honeysuckle***
Fruiting	**Decrease**	**-**
Dormancy	**Increase**	**-**
Population Growth (λ)	**-**	**Decrease**

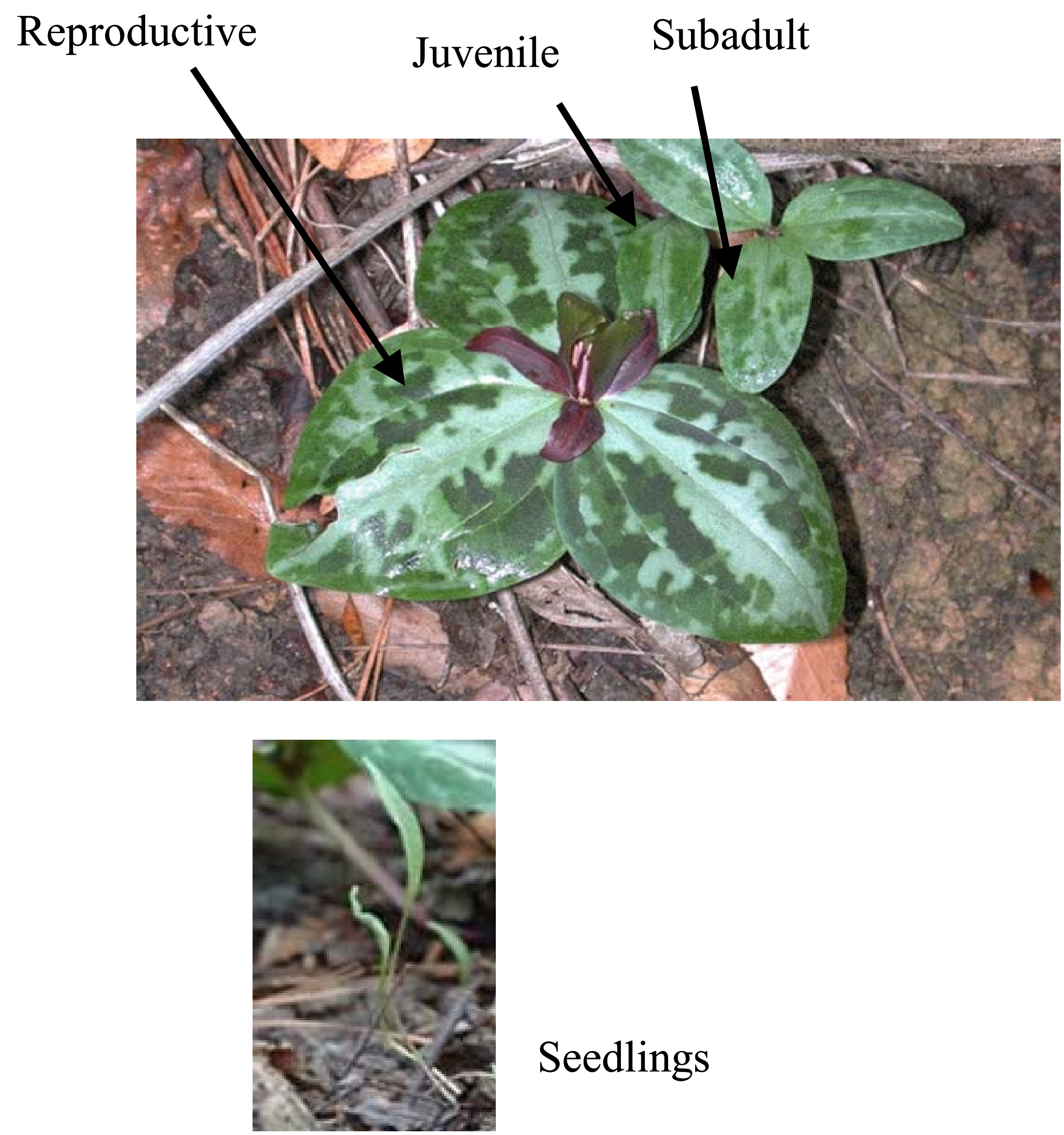

Figure 3.1. Life-stages of *Trillium reliquum*.

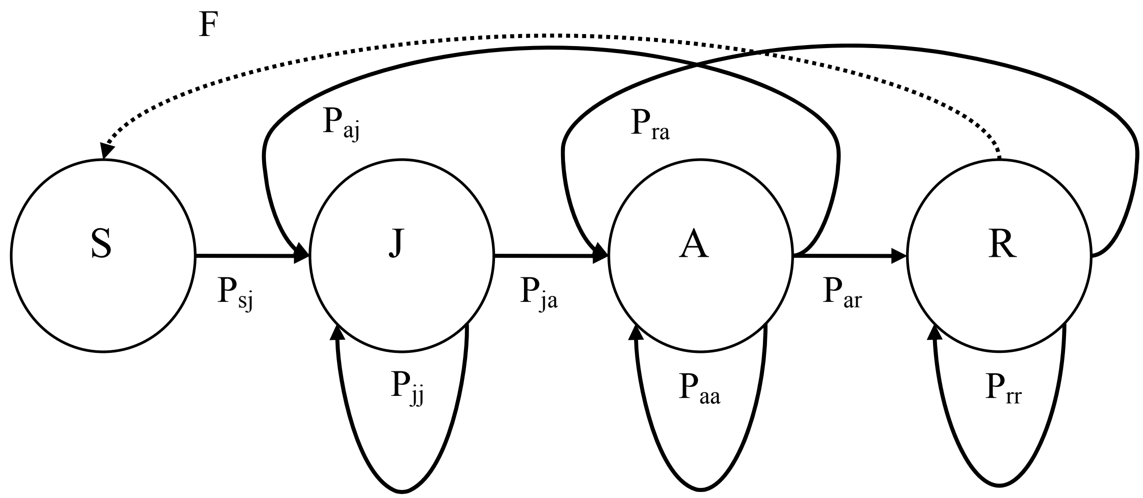

Figure 3.2. Life cycle transition of *T. reliquum*. Circles represent four demographic life stages: Seedling (S), one-leaf Juvenile (J), three-leaf subadult (A), and Reproductive (R). Values (ex. P_{aj}) below or above arrows represent the mean probability that a lifestage will transition to another lifestage from one year to the next. F represents fecundity.

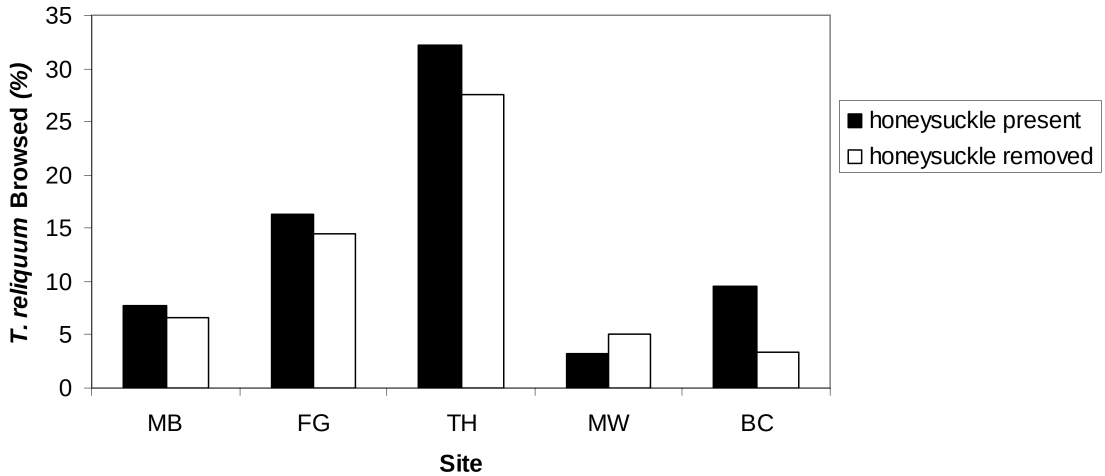

Figure 3.3. Percent of *T. reliquum* individuals browsed by deer in 2006 at five populations (excluding Seedlings); (MB=Montezuma Bluffs Natural Area, FG=Fort Gaines, TH=Hutcherson, MW=Mead-Westvaco, BC=Bibb County).

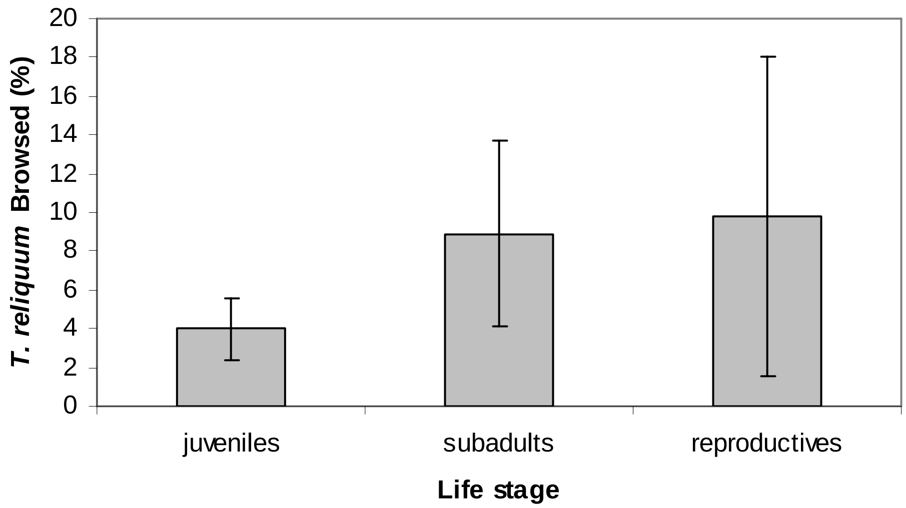

Figure 3.4. Percent of each life stage browsed by deer (±1 SE) in deer accessible treatments in 2006.

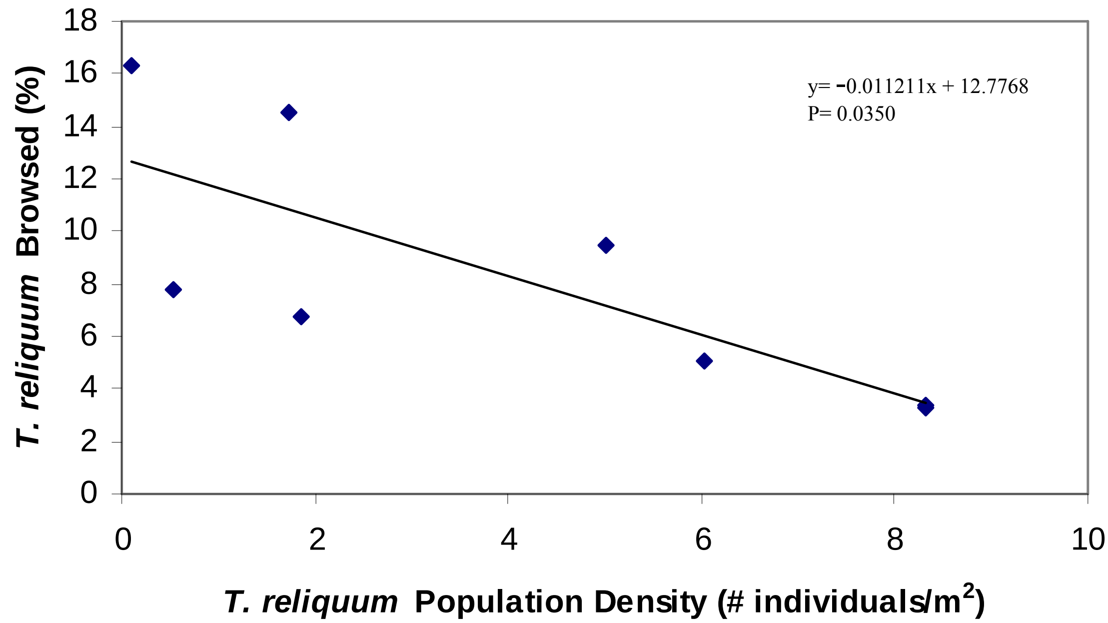

Figure 3.5. Linear regression of percent *T. reliquum* browsed versus *T. reliquum* density at four sites (excluding Hutcherson). Each point represents a deer accessible treatment in four sites.

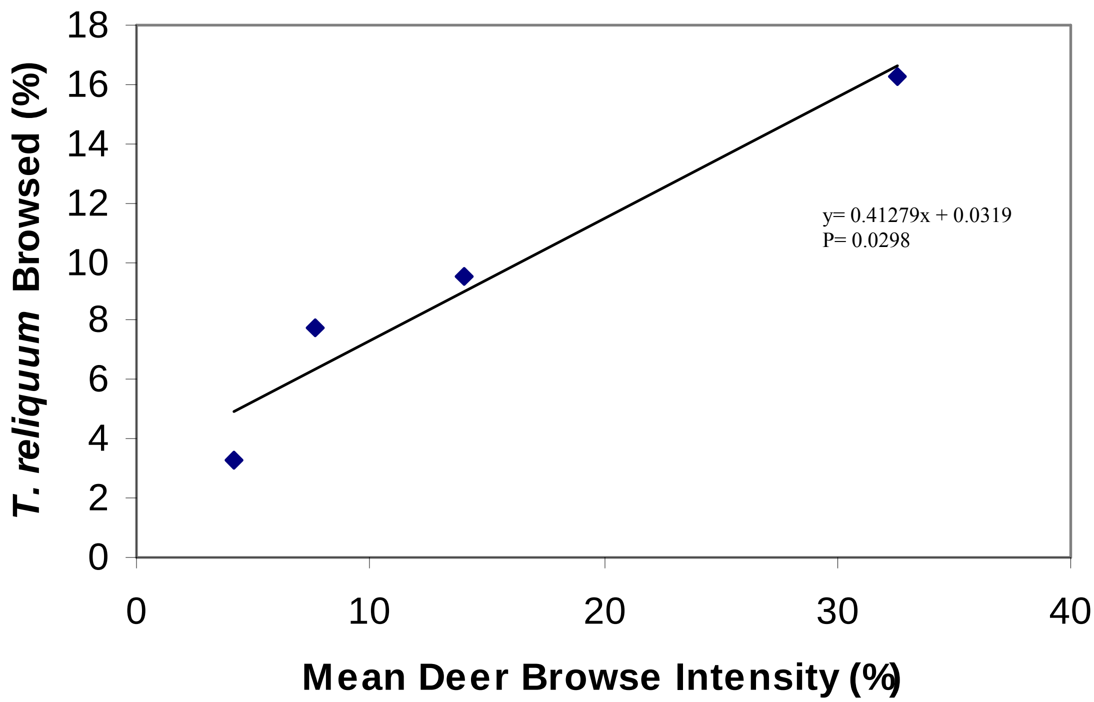

Figure 3.6. Linear regression of percent *T. reliquum* browsed versus percent deer browse intensity at four sites (excluding Hutcherson). Mean deer browse intensity was determined at each site by averaging the percent stems of all species browsed by deer on four 20m transects.

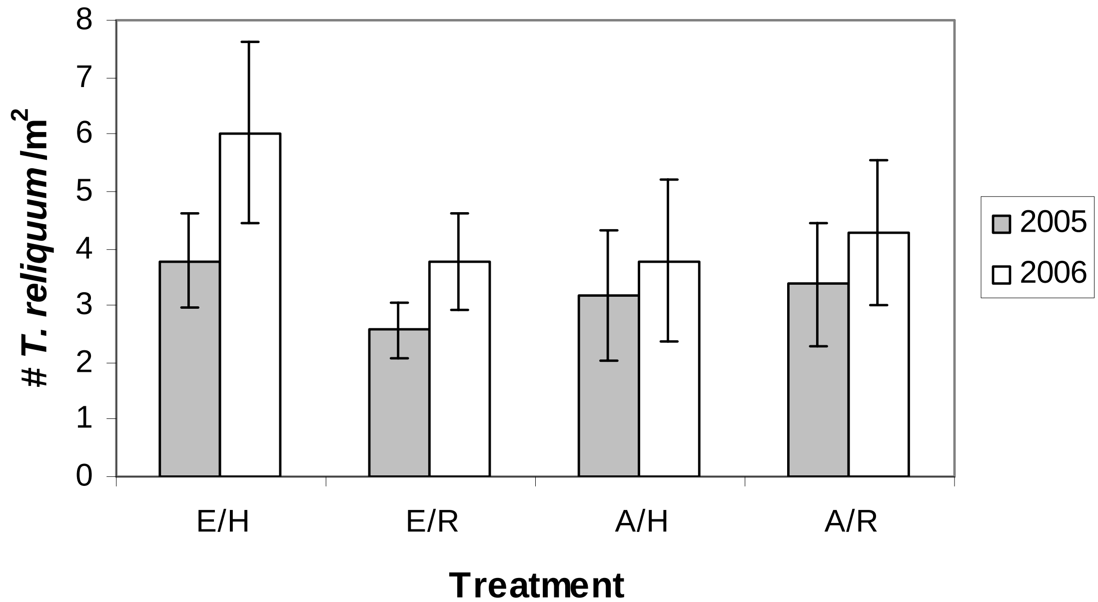

Figure 3.7. Mean density of trillium (±1 SE) in four treatment combinations in 2005 and 2006. Treatments are: E/H = deer excluded, honeysuckle present, E/R = deer excluded, honeysuckle removed, A/H = deer accessible, honeysuckle present, A/R = deer accessible, honeysuckle removed.

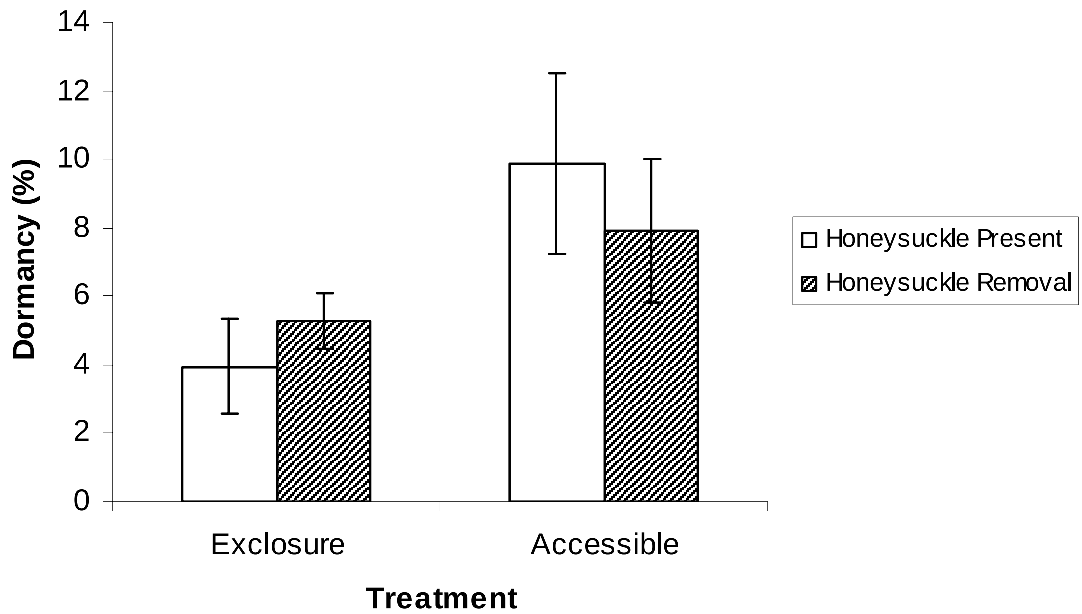

Figure 3.8. Mean percent of plants in 2005 that went dormant (±1 SE) in 2006. Deer treatments were significantly different (2-way ANOVA, $F_{1,9}$ =13.265, P=0.005).

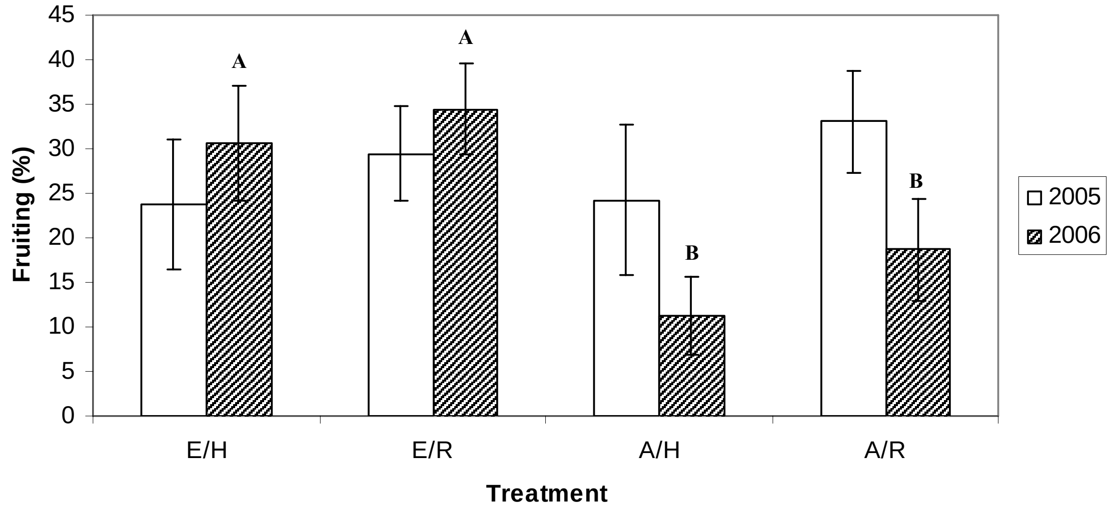

Figure 3.9. Mean percent of reproductive plants that produced fruit (±1 SE) in 2005 and 2006. Treatments are: E/H = deer excluded, honeysuckle present, E/R = deer excluded, honeysuckle removed, A/H = deer accessible, honeysuckle present, A/R = deer accessible, honeysuckle removed. Different letters above bars indicate significant differences among treatments within year (2-way ANOVA, $F_{1,9}$ =14.971, P=0.003).

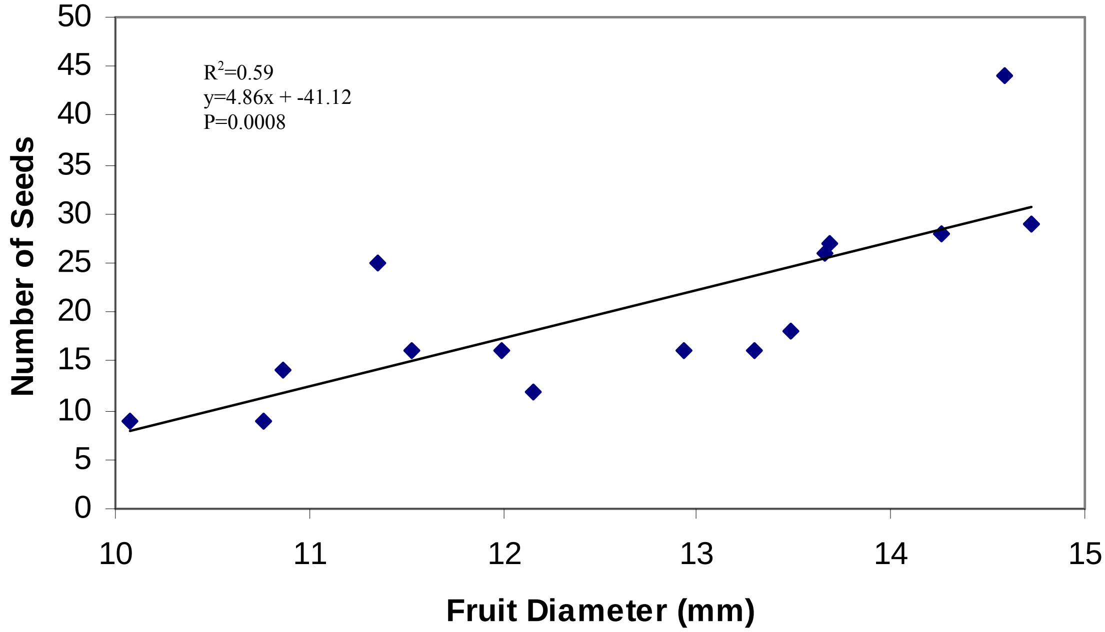

Figure 3.10. Linear regression of fruit diameter versus number of seeds at Montezuma Bluffs Natural Area.

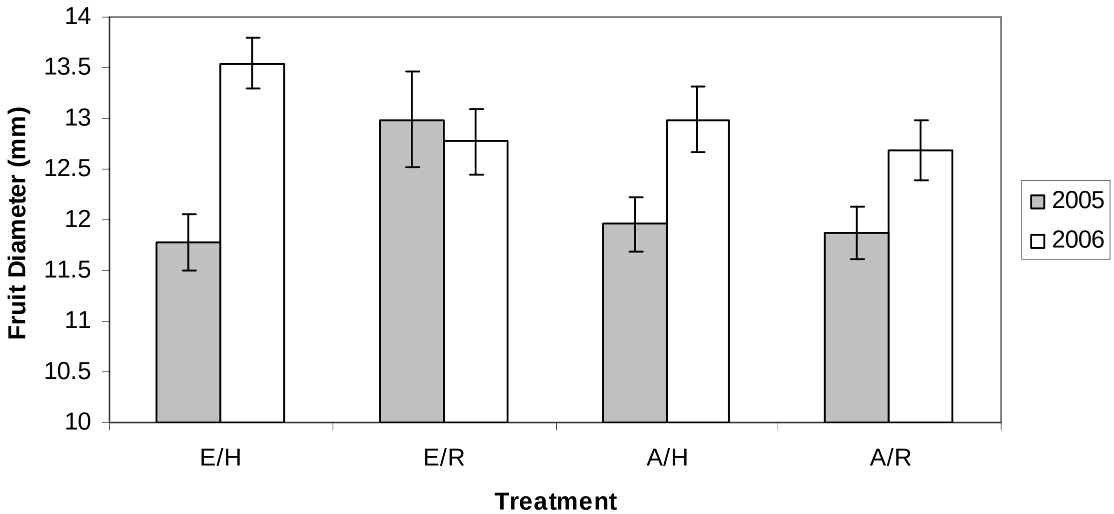

Figure 3.11. Fruit diameter (±1 SE) in 2005 and 2006. Treatments are: E/H = deer excluded, honeysuckle present, E/R = deer excluded, honeysuckle removed, A/H = deer accessible, honeysuckle present, A/R = deer accessible, honeysuckle removed.

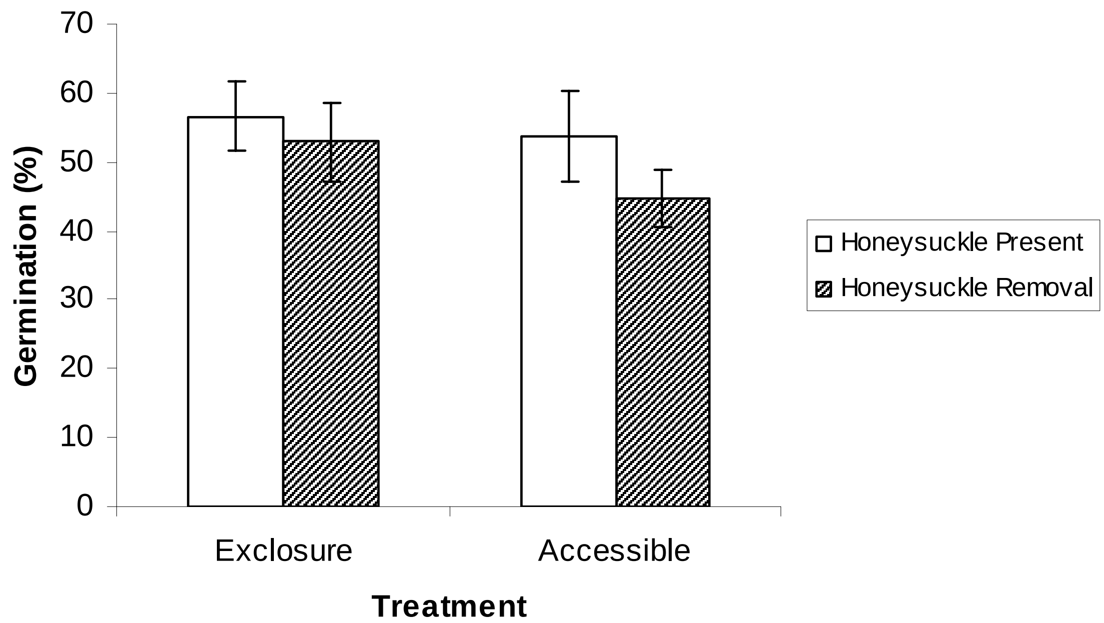

Figure 3.12. Mean percent germination (±1 SE) in seed baskets in 2006.

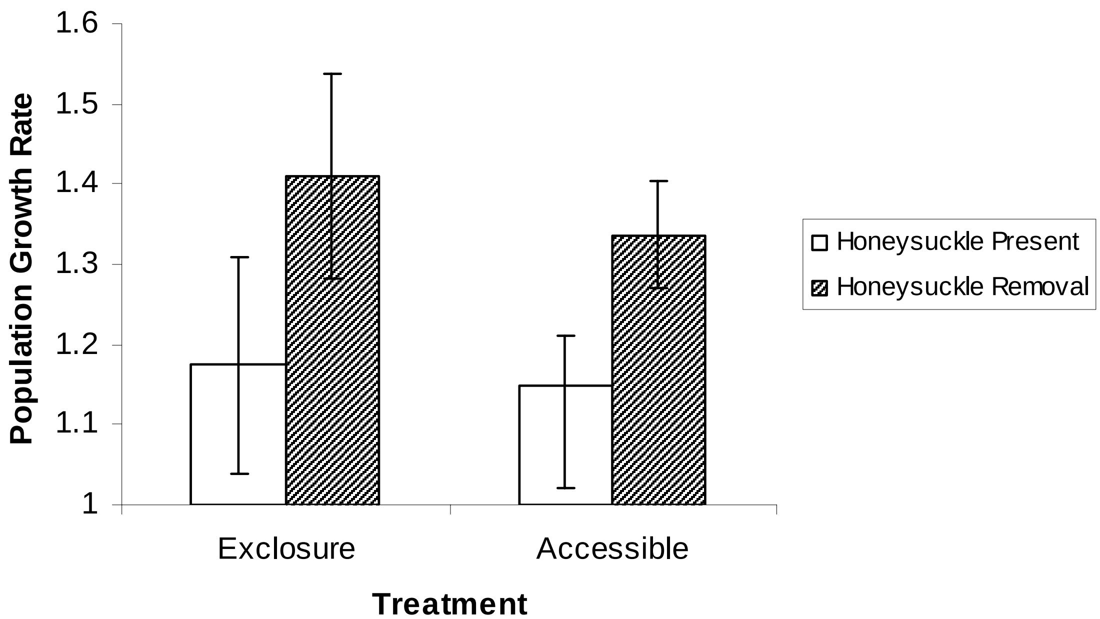

Figure 3.13. Population growth rates (±1 SE) from 2005 to 2006. There was a nearly significant difference between honeysuckle treatments (2-way ANOVA, $F_{1,11} = 4.346$, $P = 0.061$).

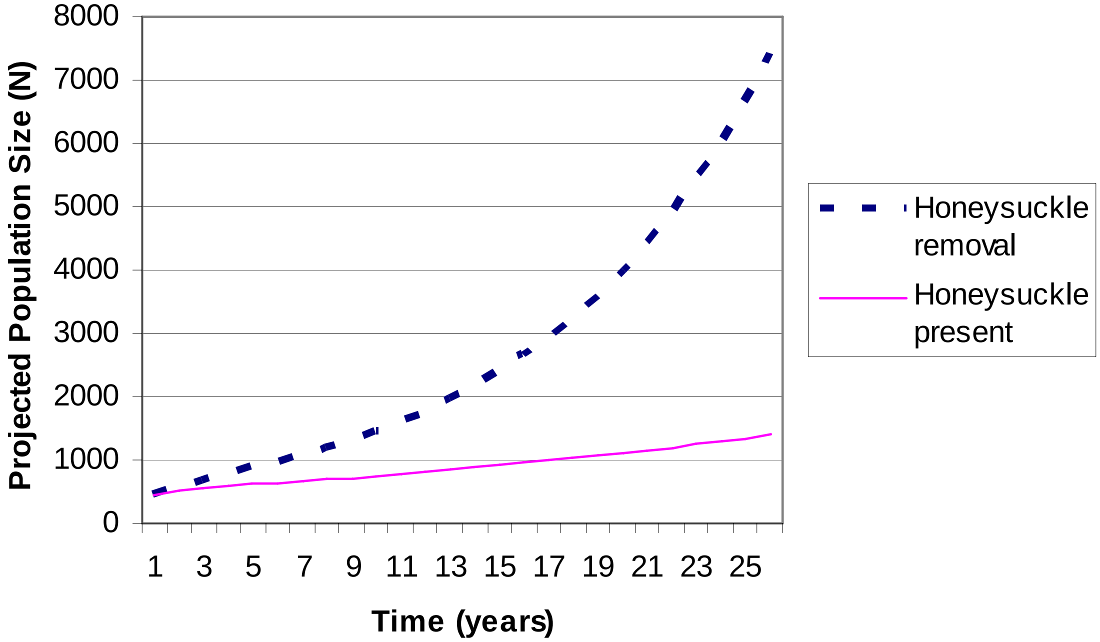

Figure 3.14. Projections of trillium population size over 25 years in honeysuckle and honeysuckle removal treatments.

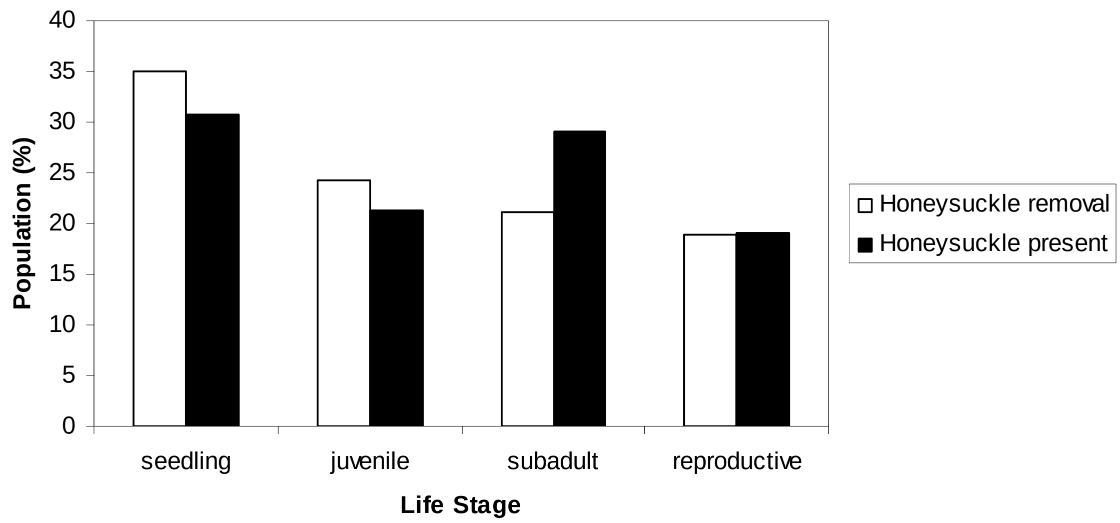

Figure 3.15. Stable stage distribution predicted by matrix models in honeysuckle and honeysuckle removal treatments.

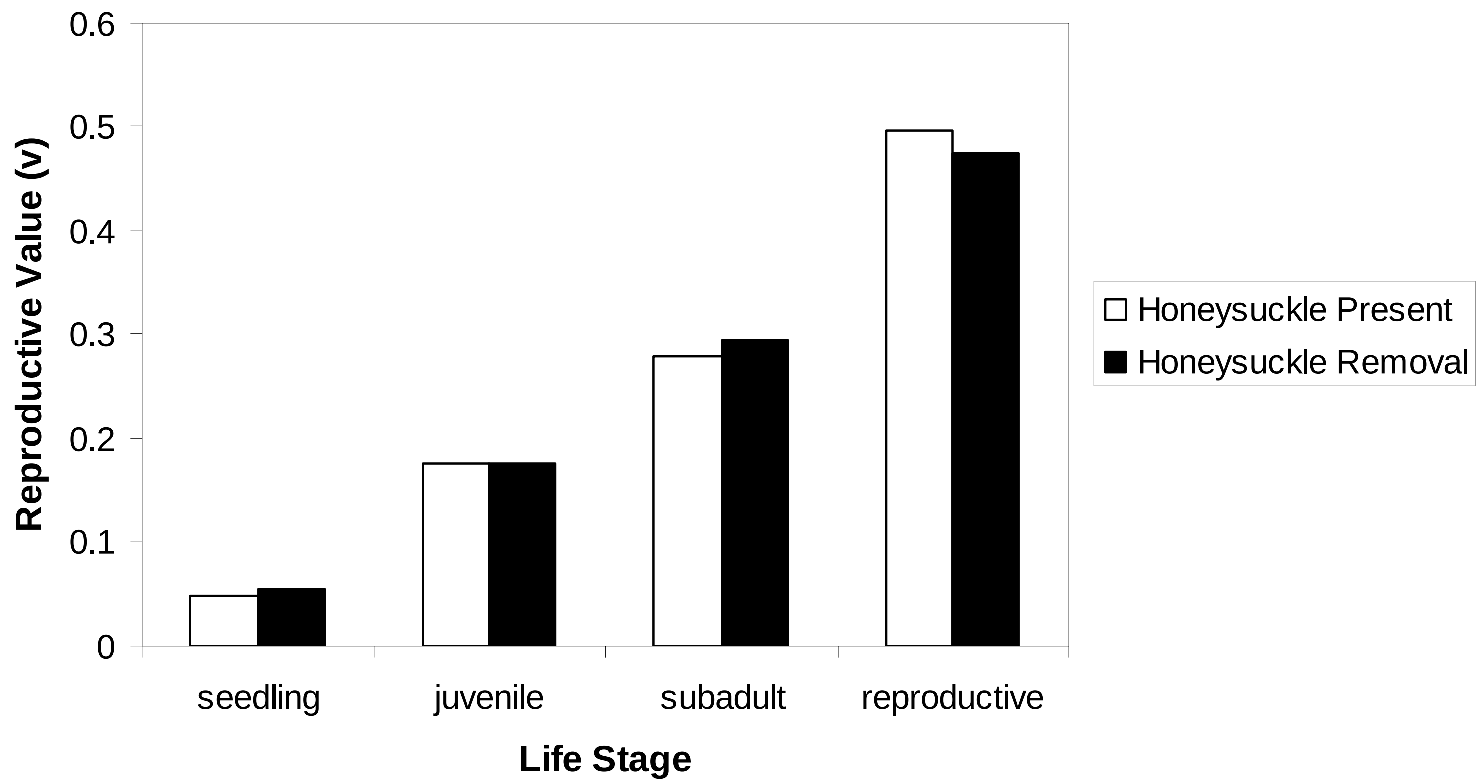

Figure 3.16. Reproductive value of *T. reliquum* life stages. The reproductive value, the left eigenvector of the transition matrix, gives the present value of the future offspring by individuals in each life stage.

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