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The influence of white-tailed deer on plant communities in West Virginia and stakeholder attitudes toward deer management with respect to plant conservation

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THE INFLUENCE OF WHITE-TAILED DEER ON PLANT
COMMUNITIES IN WEST VIRGINIA AND STAKEHOLDER
ATTITUDES TOWARD DEER MANAGEMENT WITH RESPECT
TO PLANT CONSERVATION

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Abstract

The influence of white-tailed deer on plant communities in West Virginia and stakeholder attitudes toward deer management with respect to plant conservation

Kelley L. Flaherty

White-tailed deer (*Odocoileus virginianus*) may impact plant species by reducing individual survival or reduce reproductive potential by feeding on flowering parts or seeds. Herbivory may benefit plant populations by increasing dispersal of seeds. The combination of these factors may influence the composition of native plant communities. Plants adapted to browsing herbivores of the deciduous forests of the eastern United States may be depleted under heavy browsing pressure. The recovery of deer populations from near extirpation was seen as a wildlife management success story. However, the maintenance of abnormally high deer density levels over many years may have taken a toll on plant communities. Some biologists now question whether or not white-tailed deer could be considered overabundant in some parts of their range. An overabundant population of white-tailed deer may affect ecosystem function by changing the abundance and distribution of preferred browse plants. Much of the research concerning the effects of deer on plant communities has focused on their role as browsers and the potential for overbrowsing of upland plant species. Fewer studies of deer diet have been directed solely toward rare or endangered herbaceous or woody plants. Populations of rare species often have a metapopulation distribution. That is, they exist in a series of local populations, due either to natural distribution or to the effects of human disturbance that are linked by dispersal. Many rare or declining species exist in non-equilibrium metapopulations in which the rate of colonization is not sufficient to counter rates of local extinction. Dispersal of plants is tied directly to reproduction and some plant species may rely on herbivores as seed dispersers to aid seed dispersal into new patches. The purpose of this study is to evaluate the influences of white-tailed deer browse on plant populations in West Virginia. The study was organized into three general sections: 1) the influence of white-tailed deer browse and seed dispersal on rare plant species and communities in Canaan Valley, West Virginia, 2) the impact of white-tailed deer density on forest understory recruitment in upland forests throughout West Virginia, and 3) public attitudes toward rare plant conservation and white-tailed deer management.

I located eight populations of the rare, wetland herb *Polemonium vanbruntiae* Britt. in May 2005 and an additional two populations in 2006. I monitored these populations from the first week of May through September from 2005 through 2007. I established 10 semi-permanent sampling quadrats within each population and identified individual ramets that were; seedlings, non-flowering vegetative ramets, and flowering ramets. I monitored flowering stems within the population every three weeks from early June until late September to determine the number of seeds produced per stem as well as the number of stems lost to white-tailed deer herbivory. I analyzed 13 *a priori* models, created using morphometric characteristics, using linear regression along with information theoretic methods to rank these characteristics as predictors of seed production. I used the best performing model to estimate the percentage of seeds lost due to white-tailed deer florivory. Lastly, I compared the percentages of stems browsed and the percentages of seeds browsed in Canaan Valley NWR to those in Canaan Valley State Park with a two-factor analysis of variance. I used stage-structured matrix modeling to predict the population growth rate and estimate extinction rates for each population monitored. I compared the rates of population increase (λ) with and without white-tailed deer florivory using a paired *t-test*. Extinction probabilities were calculated with and without

the effects of deer florivory for each population. I monitored 789 flowering ramets over three years. Seed loss due to consumption of flowering stems ranged between 0 and 99% within individual populations and stem loss ranged between 0 and 97%. I found a significant difference in percent stems browsed between the Canaan Valley State Park populations ($\bar{x} = 57 \pm 19\%$) and the Canaan Valley NWR populations ($\bar{x} = 40 \pm 18\%$). There was a significant difference in percent predicted seed loss between the Canaan Valley State Park ($\bar{x} = 64 \pm 6\%$) populations and the Canaan Valley NWR populations ($\bar{x} = 36 \pm 5\%$). The estimated population growth rate ranged from 1.09 to 1.24 ($\bar{x} = 1.17 \pm 0.11$) without deer florivory and was 0.99 to 1.20 ($\bar{x} = 1.08 \pm 0.13$) with deer florivory. In only one population, λ was reduced to less than 1, indicating a population decline.

At the wetland community level, I sampled *Solidago* spp.-*Rubus hispidus* dominated wet meadow communities and regenerating *Populus* spp. dominated communities in Canaan Valley, WV. Within each community, I randomly established three types of treatment plots (early, late, and continuously protected) and located a paired control plot 4 m from each treatment plot. Treatment plots were 1 m² and surrounded by fenced 2 m x 2 m exclosures. I recorded all plant species within each plot along with Daubenmire cover-class ratings for all species. I used Blocked Multiple Response Permutation Procedures (MRBP) in PC-Ord to compare vegetation communities in treatment with control plots and compared species richness within plots after two years protection from browse using a repeated-measure, two-way analysis of variance. I also examined the changes in woody, forb and graminoid metacommunities as well as the differences between wetland indicator status categories. I recorded 75 species in plots in *Solidago* spp.-*Rubus hispidus* communities and 99 species within plots in *Populus* spp. regeneration communities. There were no significant differences in species richness found between fenced and control plots in either community. In *Solidago* spp.-*Rubus hispidus* communities I found that community composition differed significantly between treatment and control plots in the early plots when data were gathered in the spring and in the late plots when data were gathered in the fall. When plots were protected year-round, a significant change in community composition was only apparent on data gathered in the spring. In *Solidago* spp.-*Rubus hispidus* communities, woody species cover class increased more in the continuously protected plots than in both the early and late plots when data were gathered in the fall. There were significant changes detected in the forb species cover classes between control and fenced plots when measured in the fall. I measured an increase in cover class of forbs in plots that were fenced early in the year and a decrease in forb cover class of associated control plots. In *Populus* spp. communities, differences between control and treatment plots in community composition were only apparent in data gathered in the spring for plots protected in the late plots and year-round. In *Populus* spp. communities, forb communities measured in the fall differed between fenced and control plots. Though the forb cover class increased for both fenced and control plots under all fencing regimes, the change in forb communities was greater for fenced plots protected early, late and continuously than in the paired control plots. I also found a difference in the change in woody species cover class between control and fenced plots when measured in the spring but not in the fall. There was no significant difference in the changes between wetland indicator status categories for either community.

I also analyzed a dataset collected from twenty sites that were selected from upland forests throughout West Virginia by West Virginia Division of Natural Resources (WVDNR) biologists. Vegetation-monitoring sites were constructed between 1984 and 1990 using two strands of 1.22 m tall woven wire fencing to create a 100 m² treatment plot. Within each treatment plot and paired control plot, nine 1 m by 1 m subplots were nested within nine 2 m by 2 m subplots. Plots were monitored by WVDNR personnel in 3-year intervals between June and September by counting and identifying all stems in the ground cover and understory vegetation within subplots. I pooled data based on the number of years following plot establishment and used a 2-way repeated measures

analysis of variance to compare the number of stems, species richness, and the Shannon diversity values between control plots and treatment plots over time. I used blocked Multiple Response Permutation Procedures (MRBP) to determine if differences existed between fenced and control plots at 3-year intervals after fence construction. Finally, I calculated an index representing the difference between control plots and treatment plots for each species using those species with the greatest differences in a seedling-sapling ratio index and used linear regression to evaluate the relation between the seedling-sapling ratio for control plots and the total deer density at the site from 1993 – 2007 as measured by West Virginia Division of Natural Resources harvest data. I recorded 197 species present in the ground cover; and 79 species present in the understory over the study period. After 21 years, I found no significant difference between treatment groups in predicting stem abundance, species richness or Shannon diversity values in the ground cover however, treatment had an effect on the stem abundance and Shannon diversity values at the understory level. Understory species richness also differed between control and treatment plots in years 6, 9, 15, 18, and 21. At the ground cover level, I found no significant difference in community composition occurred 21 years after plot initiation, but significant differences occurred in understory community composition between treatment plots and control plots 6, 15, 18, and 21 years after plot establishment. I found no relation between the seedling-sapling ratio and deer density.

I collected fresh white-tailed deer fecal pellet groups bi-monthly from May to December 2005 and 2006 in wetland habitats along 300 m randomly placed transects through both herbaceous, shrub and forested wetlands within the Canaan Valley NWR and Canaan Valley State Park. Following a three month period of cold stratification the seeds were spread on top of a layer of potting mix within 10 cm diameter planting pots and kept moist. I determined the wetland indicator status of all plants germinated from pellet piles. I also classified each species as graminoid, forb or woody species. I used a chi-square test to compare the proportion of species germinated and frequency of occurrence each year that were either upland (UPL) or facultative upland (FACU) with those that were either facultative wetland (FACW) or obligate wetland (OBL) species. I repeated these tests for the proportion and frequency of germination of plants that were graminoid, forbs or woody. I collected 55 pellet piles in 2005 and 160 pellet piles in 2006. Of those collected in 2005, 45% of the pellet piles planted germinated at least one species resulting in a total of 14 species. Of those collected in 2006, 38% of the pellet piles germinated at least one species resulting in a total of 32 species. There was no significant difference between the proportion of species germinated in either 2005 or 2006 that have a FACW or OBL wetland indicator status and those that had a FACU status. In 2005, the proportion of individual stems that were FACU not significantly different than those that were FACW and OBL stems combined. However, the proportion of individual stems that were FACU (59%) was significantly more than the combined proportion of FACW (7%) and OBL (9%) stems counted. In 2005 and 2006, the proportion of germinated species that were graminoids, forbs and woody species did not significantly differ. The frequency and proportion of stems germinated of both graminoids and forbs were significantly higher than for woody species in 2005. In 2006, the frequency of pellet piles germinating graminoid species was significantly higher than the frequency of woody species, but was not higher than the frequency of forbs. The proportion of individual stems that were forbs and graminoids were significantly greater than the proportion of woody stems.

I surveyed residents of Canaan Valley as well as residents of the surrounding areas in Tucker County, WV, nonresident who owned land in Canaan Valley as well as those who only visit Canaan Valley to assess attitudes toward rare plant conservation and the status and management of white-tailed deer in Canaan Valley. I sampled residents and nonresident landowners in 2005 by mail surveys and visitors to Canaan Valley by providing survey forms to the visitors' centers at Canaan Valley NWR and Canaan Valley State Park. Opinion questions were subjected to Principal Components Analysis (PCA) to identify underlying constructs. I modeled three principal component

scores as a function of socio-demographic factors determined from the questionnaire and their two-way interaction using a multi-factor analysis of variance (ANOVA). Additionally, I examined the principal components using a Potential for Conflict Index (PCI) that numerically described the amount of disparity between respondents in a particular group. I received a response rate of 35% for mailed surveys and received 46 visitors' responses. The three retained principal components accounted for 60% of the variation in the data. I found that people who had experienced crop or landscape damage had significantly larger mean principal component (PC) 1 scores than those who did not corresponding with a lower tolerance of deer. Those that had experienced crop or landscape damage were more likely to describe Canaan Valley white-tailed deer populations as being overabundant. Tucker County residents had higher PC 2 scores on average than nonresident landowners indicating lower valuation of plants and plant communities. While for the most part stakeholder groups agreed that they enjoyed seeing wild plants, Tucker County residents appeared less likely to agree that deer could harm plant communities and that plants should be protected from deer. Hunters had significantly higher PC 3 scores on average than nonhunters that corresponded to a greater support for management actions for white-tailed deer.

My study suggests that white-tailed deer may consume almost 100% of the sexually reproductive ramets within some *P. vanbruntiae* populations in a given year. As *P. vanbruntiae* can reproduce clonally, high levels of seed loss such as those exhibited here may not immediately affect population persistence. However, a reduction in dispersal may reduce genetic diversity and the formation of new populations. At the community level, elevated deer densities present in the post-logging era impact the herbaceous community by selectively browsing forb species, especially in the spring. On a state-wide scale, the density of white-tailed deer impacting the control plots at many of these sites has been at or exceeded the capacity of the upland forest to regenerate the current community. At some sites, few, overstory species are currently reaching the understory growth level thus the future of the forest cover at these sites is uncertain. However, the potential still exists to regenerate the current forest community at many sites. However, if browse pressure persists as the seed sources decline, the potential for recovery of the current ecosystem will likewise decline. A difference in proportion of stems from upland species that germinated from fecal samples in 2006 suggests that upland plants may be more adapted to dispersal by white-tailed deer, though this difference in frequency might be attributed to the success of a few FACU plants. As dispersers, white-tailed deer could play a role in maintaining or enhancing metapopulations of wetland plants patchily distributed in an upland matrix; however, deer may also confound wetland restoration by dispersing seeds of some exotic, invasive species. Dispersal of graminoid species by deer may help to maintain or expand herbaceous openings at both wetland and upland sites by dispersing the seeds of graminoid species as well as reducing the capacity for woody species regeneration. Although many of the views of residents and nonresidents were similar, Tucker County residents were less likely to favor rare plant conservation. Many of the visitors and nonresidents come to Canaan Valley specifically because of its unique characteristics and appear to place more value on these unique plants. Recognition of differences in attitudes between stakeholder groups could be helpful in designing educational programs for users of natural areas. In this case, education and emphasis on the importance of rare plant diversity in Canaan Valley may bring more local support for their conservation.

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I dedicate this manuscript to the memory of Mr. William Grafton. His infectious good humor in the face of the rain and black flies made field work in Canaan Valley much more enjoyable. Mr. Grafton has motivated me to develop both as a naturalist and a teacher and I can only hope to inspire my students in the future as he has.

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CHAPTER I

WHITE-TAILED DEER HERBIVORY AND RARE PLANTS: INTRODUCTION AND LITERATURE REVIEW

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INTRODUCTION AND JUSTIFICATION

As the wildlife management discipline moves away from a focus on game production and toward a more holistic ecological approach, the role of white-tailed deer (*Odocoileus virginianus* Zimm.) as a keystone herbivore comes more into question (Waller and Alverson 1997). Along with many other native herbivores, white-tailed deer were nearly extirpated due to over-hunting in the 19th and early 20th century. Recognizing the potential loss of this game species, stocking efforts and strict game laws, including prohibiting the killing of does, were implemented in many states to control unrestricted hunting. Numbers of deer remained low throughout the early 1900s (McCabe and McCabe 1984). Eastern hardwood and coniferous forests were intensively logged at the same time which created an abundance of early successional growth benefiting existing deer populations by providing ideal food sources and cover. At the same time, a lack of natural predators due to hunting and trapping reduced mortality. The recovery of deer populations from near extirpation was seen as a wildlife management success story (Waller and Alverson 1997).

In 2006, big game hunters spent more than \$11.8 billion (2006 data; US Department of the Interior 2006) on hunting licenses as well as related travel and equipment. Higher deer densities were a boon for rural communities that depended on natural resource tourism (i.e., hunting, fishing, and wildlife viewing) as a major annual source of income. Likewise, hunters as

well as other recreational tourists enjoyed the benefits of higher deer densities. Deer feed preferentially on some exotic species (Sheldon and Causey 1974) and therefore high herbivore densities may reduce the abundance or prevent the invasion of some invasive plant species (Maron and Vila 2001). For these reasons, there are many advocates for the maintenance of high deer densities (Diefenbach et al. 1997). However, the maintenance of abnormally high deer density levels over many years may have taken a toll on the habitat on which the population depends (Tilghman 1989, deCalesta and Stout 1997). Some biologists now question whether or not white-tailed deer could be considered overabundant in some parts of their range (McShea and Rappole 1997b, Stromayer and Warren 1997). Overabundance of a wildlife population has been defined as fitting into one of four categories: when an animal threatens human life and livelihood, when animals depress the densities of favored species (e.g. crops or timber), when animals are too numerous for their own good, and when their numbers cause ecosystem dysfunction (Caughley 1981).

Many plant species are distributed in metapopulations, defined as a set of local populations characterized by local extinctions in which dispersal and colonization play an important role in the maintenance of the metapopulation as a whole (Hanski 1991). This patchy distribution may be a natural characteristic of the species or brought on by human induced environmental changes and fragmentation and is particularly evident by the numerous rare or declining plant species (Craighead and Vyse 1996).

The rates of local extinctions and colonizations are central to metapopulation theory and the resulting models (Hanski 1991). Large herbivores may impact plant metapopulation dynamics through several routes. At the microhabitat level, feeding on plant parts may alter the growth rate and ultimately the survival of individuals (Anderson and Loucks 1979, Whitney

1984, Alverson and Waller 1997, Stromayer and Warren 1997). Feeding on flowering parts of accessible herbaceous species reduces or eliminates the chances of fertilization for the individual and potential for fertilization of other individuals in the population (Loeffler and Wegner 2000). Large herbivores also may be considered seed dispersers or seed predators of certain species (Cambell and Gibson 2001, Vellend et al. 2003, Furedi and McGraw 2004, Myers et al. 2004). Many plant species have evolved to use fruit to attract herbivores to consume and disperse seeds (Drezner et al. 2001). Plant species with smaller seeds may use the plant's foliage to attract herbivores that consume and disperse smaller seeds along with plant parts or carry seeds externally (Janzen 1984). In this aspect, herbivores can benefit plant populations by distributing seeds, along with fertilization in the form of fecal matter, into new areas and thus increasing the colonization rate. However, as not all seed types have evolved to pass through the digestive tract of all herbivorous species, seeds may fall prey to herbivores that consume and digest them (Furedi and McGraw 2004). In this aspect, seed predators inadvertently work to reduce the potential for colonization within a metapopulation.

On a community scale, the combination of these factors may influence the composition of plant communities that in turn affect other organisms dependent on these communities (deCalesta 1994, Flowerdew and Elwood 2001). While some ecosystems such as prairies and savannahs are dependent on large population of migrating grazers, plants adapted to browsing herbivores of the deciduous forests of the eastern United States may be depleted under heavy browsing pressure (Waller and Alverson 1997). The selection of preferred plant species for consumption by an overabundant population of herbivores may result in the loss of that component of the plant community as well as a loss of plant community diversity.

These factors may be even more important in rare plant communities. In the 200 years between 1780 and 1980, it is estimated that the amount of land occupied by wetlands across the contiguous United States has declined by 53% due, in part to drainage for agricultural use and land development (Dahl 1990). Many of the plants found in wetland habitats are considered obligate (OBL), meaning they are adapted to saturated or flooded soils and are found in wetland conditions > 99% of the time (Tiner 2000). Additionally, facultative (FAC) and facultative wetland (FACW) plants occur in wetlands 34 – 66 and 66 – 99% of the time (Tiner 2000). Many obligate wetland and facultative wetland plant species have become extinct, threatened, or rare or have decreased ranges due to loss of suitable wetland habitat (Tiner 2000). As a whole, West Virginia has the lowest percentage of land area in wetlands of any state, in part, because of the topography (Tiner 2000), thus making existing wetland habitat extremely valuable. Moreover, the state, boasts some of the few high elevation wetlands in the east.

Recently, there has been an increased interest in restoring wetlands across the United States to prevent the loss of wetland-dependent species and restore more economically tangible wetland functions such as flood control and water purification (Tiner 2000). Likewise, there has been an increasing interest in native plant conservation including those characteristic of wetlands. While there has been extensive research on the relations of white-tailed deer to upland plant communities (Alverson and Waller 1997, deCalesta and Stout 1997, Stromayer and Warren 1997, Rooney and Waller 2003), few have examined wetland plants. Two studies focused on the influence of white-tailed deer herbivory in a coastal marsh (Geddes and Mopper 2006, Tobler et al. 2006) and a mangrove wetland (Barrett et al. 2006). Few published studies have examined the relation of deer to freshwater wetland plant species (Loeffler and Wegner 2000, Gregg 2004, Kery and Gregg 2004).

LITERATURE REVIEW

The Role of Metapopulation Theory in Conservation Biology

Metapopulation theory describes a population of species or communities that exists as a set of smaller populations that are connected by dispersal or colonization (Hastings 1991, Alexander et al. 2012). The rates of local population extinction and colonization are central to metapopulation dynamics models such as that given by Levins (1969) which describes the metapopulation in terms of local populations;

$$dp/dt = mp(1-p) - ep$$

in which $p(t)$ is the proportion of available patches that are occupied at time t , e is the rate of local extinction and m is the rate of colonization rate of empty patches (Hanski 1991). The concept of metapopulation dynamics is similar to the theory of island biogeography (Alexander et al. 2012, May et al. 2013); however, in island biogeography theory the source of colonists is a mainland population with little chance of extinction. In a metapopulation, the source of colonists is the existing set of local populations each with a finite lifetime and a given chance of going extinct (Hanski and Gilpin 1991, May et al. 2013).

Populations of rare species often have a metapopulation distribution. That is, they exist in a series of local populations due either to natural distribution or to the effects of human disturbance (Hansson 1991). Hanski (1991) described three types of rare species with respect to metapopulation distribution; species with a large local abundance (N) and a small proportion of occupied patches (p) are known as urban species, species with a large p but small N are termed rural species, and species with both small N and p are satellite species. If, the rates of colonization and local extinction are in balance the metapopulation as a whole will not go extinct. However, many rare or declining species exist in nonequilibrium metapopulations in

which the rate of colonization is nonexistent or is not sufficient to counter rates of local extinction (Harrison 1991, Noël et al. 2013). Anthropogenic influences on species such as habitat fragmentation or changes in the environment may not only decrease the rate of colonization but may increase the rate of local population extinction thus driving the entire metapopulation toward extinction (Heinken and Weber 2013, Noël et al. 2013).

The fields of conservation and restoration biology are particularly interested in the effects of human influences on metapopulation of rare species (Primack and Miao 1992). Human induced environmental and habitat changes have contributed to the rarity and current decline of many species. The rates of local population extinction may not be important for species that are colonizing new patches, but these rates may be more critical for rare species (Harrison 1991, Marini et al. 2012). If all local populations of a patchily distributed metapopulation become extinct at the same time then the entire metapopulation and thus species becomes extinct (Hanski 1991). Understanding what contributes to the decline of local populations contributes to efforts in conserving and restoring local populations which, in turn, contributes to the conservation of the species as a whole. Some species naturally occur in a patchy distribution; however, some species that occur in naturally continuous populations have been converted to a metapopulation because a change in some environmental factor fragmented some aspect of the species' habitat (Craighead and Vyse 1996, May et al. 2013). An overabundant population of white-tailed deer may, as a human induced factor of a changing environment, have the ability to change the abundance and distribution of preferred browse plants (deCalesta and Stout 1997, Martin et al. 2011, Tanentzap et al. 2011).

Plant populations differ from animals in that they are sessile and individuals cannot actively disperse from patch to patch (Husband and Barrett 1996). Instead, dispersal is tied

directly to reproduction and is often more random in nature than dispersal of animal populations (Hansson 1991; Marini et al. 2012). Plants use a variety of vectors as both pollen and seed transports (Drezner et al. 2001). Some plants do not disperse seeds or use a ballistic dispersal mechanism to distribute seeds within their immediate surroundings (Loeffler and Wegner 2000, Drezner et al. 2001). While this may guarantee that seeds fall into a patch that would favor growth and may increase the local population, there is little or no colonization to external patches. Many plants rely on wind or water to disperse pollen and seeds that may allow them to colonize patches at great distances, but in patchy environments, wind dispersal does not ensure pollen or seeds reach patches with favorable growing conditions (Drezner et al. 2001). Plants that rely on herbivores as seed dispersers may ensure seedling establishment in other suitable patches by using fruit or foliage as an attractant to occupied patches (Janzen 1984). The evolution of fruit is believed to have occurred as a means to attract herbivores and frugivores to consume both fruit and seed to be deposited after digestion, ideally in nutrient rich fecal material (Willson and Whelan 1990). Additionally, Janzen (1984) hypothesized that in many plants that do not bear fruit the vegetation acts as an attractant to herbivores who then consume seeds with vegetative matter. However, the colonization of unoccupied patches may still be random as plants cannot attract the herbivores to suitable patches that they do not occupy. Conversely, some herbivores may consume seeds that are not adapted to pass through the digestive tract thus reducing the potential for both increasing the local population or colonization of new patches (Furedi and McGraw 2004, Alexander et al. 2012). Potential for long distance dispersal differs with the species and capacity for movement of the disperser (Willson 1993, Jaroszewicz and Piroznikow 2011). Finally, in a situation where flowering plants are consumed before the production of seeds, overall plant reproduction is decreased by the loss of seed production.

Drezner et al. (2001) discussed the method of seed dispersal of riparian plants and argued that obligate wetland plants are more often dispersed by water or wind while upland plants are more often dispersed by animals. This study, however, looked at few obligate wetland plants ($n = 3$) and many upland plants. Additionally, the traditional method of determining dispersal mechanism is to classify a plant based on seed characteristics. However, many seeds do not have characteristic signs for a particular dispersal method, some species may have more than one dispersal method (Drezner et al. 2001, Panter and Dolman 2012), and though a seed may be physically adapted for one type of dispersal, it is not known whether or not, that seed could still germinate if consumed by an herbivore.

Overpopulation and Vegetation Communities

Behind studies on deer foods and habits, the effect of white-tailed deer on their habitat is one of the most studied and controversial topics in the fields of wildlife management, forestry, and ecology (Warren 1997). Many studies have been driven by economical factors such as loss of crops or regeneration of preferred timber species. This, in fact, is a major concern of the forestry profession. As early as 1947, Aldo Leopold, known as the father of wildlife management, recognized the impact that overabundant populations of white-tailed deer may have on vegetation (Leopold et al. 1947). In compilation of information from across the United States, Leopold et al. (1947) showed that deer “irruptions” were occurring and having a detrimental effect on local vegetation as well as the deer populations themselves. In Pennsylvania, Hough (1965) found that high densities of deer changed the occurrence of certain plant species in permanent forested plots. Through a 20-year photographic record, he observed a loss of preferred species first, followed by a reduction in less desirable plant species. Species-specific studies found deer had detrimental effects on hemlock (*Tsuga canadensis*) (Anderson

and Loucks 1979, Whitney 1984, Alverson and Waller 1997, Stromayer and Warren 1997), white cedar (*Thuja occidentalis*), yellow birch (*Betula lutea*)(Stromayer and Warren 1997), and various oak species (*Quercus* spp.)(Healy 1997, Rooney and Waller 2003, Griscom et al. 2011, Long et al. 2012). A simulated browse study in individual young red (*Pinus resinosa*) and white pine (*Pinus strobus*) trees showed that repeated severe browsing has a detrimental effect on height of trees and survival (Marshall et al. 1955). Similarly, Saunders and Puettmann (1999) found that heavy artificial browsing reduced both height and diameter growth of white pine seedlings.

Exclosure studies examining community level changes suggest that high levels of deer browse tend to decrease stem density and species richness (Goetsch et al. 2011, Levine et al. 2012, McGarvey et al. 2013) affecting the community composition at the sapling stage that may translate into the overstory when chronic high densities persist (Nuttle et al. 2011, Tanentzap et al. 2011, Holm et al. 2013). Similar results were found concerning species composition and stem density on fixed deer density plots within enclosures (Tilghman 1989, deCalesta and Stout 1997, DiTommaso et al. 2014). Natural refugia from deer browse can provide clues as to the effects of deer densities on forest communities. Community composition differs within the same location on the forest floor and on top of boulders (Carson et al. 2005, Comisky et al. 2005). Root wads from trees that had blown down may also act as refugia for a variety of species (Krueger and Peterson 2006, Chollet et al. 2013).

While much of the research on the effects of white-tailed deer on vegetative communities has thus far been concentrated on economically important forest species, deer also have been shown to have negative impacts on herbaceous communities (Royo et al. 2010, Urbanek et al. 2012, Bugalho et al. 2013). Augustine and Frelich (1998) found that trillium species (*Trillium*

spp.), which are locally rare in some areas of their range, can be used as an index of deer browsing intensity. Glade spurge (*Euphorbia purpurea*), a globally rare plant is affected by consumption of leaves as well as limited in reproduction by browsing of flowering parts by white-tailed deer (Loeffler and Wegner 2000). Deer may reduce or extirpate local populations of American ginseng (*Panax quinquefolius*) in West Virginia (McGraw and Furedi 2005), Turk's cap lily in Virginia (*Lilium supurbum*; Fletcher et al. 2001) and sundial lupine (*Lupinus perennis*; Frye 2012). Additionally, deer herbivory has been cited as a detriment to tallgrass prairie forbs (Anderson et al. 2001), riparian willow species (Brookshire et al. 2002), cultivated native wildflower species (DeGroote et al. 2011), and additional riparian (Opperman and Merenlender 2000) and savanna (Urbanek et al. 2012) plant community restoration efforts. Peek and Stahl (1997) described an instance in which a large population of deer extirpated 150 vascular plant species from a city park in Ohio.

More recently, ecologists have suggested the indirect detrimental effects of too many deer. A change in vegetation can affect animal communities which use the same habitat. A change in understory species composition or a reduction in the density of the understory may affect nesting songbirds (deCalesta 1994, McShea et al. 1995, McShea and Rappole 1997a, Martin et al. 2011, Chollet and Martin 2013). Deer herbivory may either negatively affect small mammal populations through loss of ground cover species or positively affect populations by indirectly increasing fern cover (Flowerdew and Elwood 2001, Byman 2011, Bush et al. 2012). Deer also may influence invertebrate species by selectively browsing host plant species (Frye 2012) or reducing the abundance of flowers available to pollinators.

Despite the extensive amount of literature on white-tailed deer browse and the variety of species studied, there are comparatively few studies that focus on freshwater wetland species in

particular (Loeffler and Wegner 2000, Kery and Gregg 2004). Barrett et al. (2006) examined the influence of deer herbivory on mangrove wetland communities, Cogger et al. (2014) examined deer herbivory in bottomland hardwoods, and Urbanek et al. (2012) included two wetland sites in a study involving the influence of deer on restored communities. Given the historic decline, wetlands may harbor a disproportionate number of threatened and endangered plant species. It is important to consider the role of white-tailed deer herbivory in determining the distribution and abundance of these species as well as the structure of wetland communities.

Alternate Stable States

White-tailed deer have the potential to exert a long-term influence on forest communities through alternative means. Selective browsing resulting in a lack of a vegetative understory can promote the growth of unpalatable ground cover species such as hay-scented fern (*Dennstaedtia punctilobula*) (de la Cretaz and Kelty 2002, Tanentzap et al. 2011, Nuttle et al. 2014). Heavy growth of unpalatable ground cover plants can prevent the growth of tree species by reducing the amount of sunlight available on the forest floor (de la Cretaz and Kelty 2002, Royo and Carson 2006) and may exert a bottom-up control on vegetation persisting even after herbivore reductions (Royo et al. 2010, Nuttle et al. 2011). While a reduction in understory richness and diversity may negatively affect small mammal density (Bush et al. 2012, Byman et al. 2013), ground cover growth can also provide shelter for small mammals that consume seeds from overstory tree species thus preventing reproduction of the existing overstory community (Royo and Carson 2006). Thus, white-tailed deer may have the ability to influence the creation of alternate stable states in an ecosystem (Augustine et al. 1998) that is a community that exists in a different state than would be predicted by ecological succession and remains stable without a disturbance event

(Stromayer and Warren 1997) particularly when combined with a loss of canopy species through disturbance (Holm et al. 2013, Nuttle et al. 2013).

The Role of White-tailed Deer in Seed Dispersal

Much of the research concerning the effects of deer on plant communities have focused on their role as browsers and the potential for overbrowsing of plants (Stromayer and Warren 1997, Royo et al. 2010, Kribel et al. 2011, Tanentzap et al. 2011, Nuttle et al. 2013). However, several studies have looked at the role of white-tailed deer as both seed predators and seed dispersers (Cambell and Gibson 2001, Vellend et al. 2003, Myers et al. 2004, Levine et al. 2012). Due to their large homerange size (Janzen 1984) and the potential to retain material in the digestive tract for three or more days (Mautz and Petrides 1971), white-tailed deer have the potential to carry seeds great distances. Vellend et al. (2003) suggested that this would result in 95% of germinable seeds being deposited more than 100 m from the parent plant and 30% deposited more than one kilometer from the parent plant. This may have a considerable effect on metapopulation initiation, growth, and gene flow of irregularly distributed and rare plant species (Myers et al. 2004). Additionally, the ability of a plant to disperse long distances can affect the genetic structure of a metapopulation by increasing homogeneity between subpopulations (Hedrick 1996, Alexander et al. 2012).

Myers et al. (2004) found that 72 species of forest and old field plants germinated from fecal pellet samples with a mean of 38 germinations per pellet group. The germinated seeds ranged from forbs to tree species and while some were seeds distributed through fruiting mechanisms, most were not. However, Cambell and Gibson (2001) found only two species germinated from 22 pellet group samples. Williams et al. (2008) found that deer dispersed 40 different exotic species and suggested that, in addition to reducing reproduction of native plants,

dispersal of exotics could help to reduce native plant populations. While deer may play an important part in the dispersal of seed for many plants, they also may play a role in the spread of exotic species (Cambell and Gibson 2001, Vellend 2002, Robertson 2012, Castellano and Gorchev 2013, Kalisz et al. 2014). Additionally, for some plant species including American ginseng (Furedi and McGraw 2004), white-tailed deer are demonstrated seed predators or consumers, that is, all seeds consumed in the act of herbivory are digested or are non-viable once passed through the digestive system thus reducing the realized reproductive output of these plants.

Bog Jacob's-Ladder (*Polemonium vanbruntiae* Britt.)

Bog Jacob's-ladder (Figure 1) is a perennial that ranges from Quebec south to West Virginia and from Maine east to West Virginia (Bermingham and Brody 2011). It is found in habitats varying from shrub swamps and forested wetlands to moist roadsides occurring mostly at elevations above 305 m (Maine Department of Conservation 2004) and is considered a facultative wetland (FACW) plant species (USDA 2012). It is ranked as a G3/G4 (rare or uncommon/common) globally and an S2 (very rare and imperiled) in the state of West Virginia (WV DNR 2012). This plant has been propagated successfully ex situ but is rare in natural populations. Bog Jacob's-ladder may reproduce sexually or asexually (Committee on the Status of Endangered Wildlife in Canada 2002).

Current threats to bog Jacob's-ladder populations in the northern part of its range include agriculture, forestry, and wetland drainage or development (Deller 2002). In Canaan Valley, past threats have included logging, agriculture, and potential activity of all-terrain vehicles. Many of the populations in Canaan Valley are now protected by the location of state and government owned land. Current threats to these populations my include flooding caused by

beaver (*Castor canadensis*) activity in the valley (Figure 2). There is anecdotal evidence of white-tailed deer browsing on this species but it is not currently considered a management concern in Canadian populations. However, the deer densities at these locations may not be as high as Canaan Valley populations (Michael 1992).

Public Attitudes Toward White-tailed deer Management

In the 1940s, Leopold et al. (1947) found that it was difficult to convince hunters and the general public, who experienced first hand the shortage of deer as a result of over-hunting, that an overabundance of deer could exist at all much less be a detriment to their habitat. Today, it is still difficult to convince hunters, who have experienced the low abundance of deer in earlier decades of the 1900s, that overabundance is a problem and, in the case of reduced deer herds, that the problem exists at all (Diefenbach et al. 1997). Since the early 1900s, a greater proportion of the nation's general public is disconnected with wildlife and its habitat. Though the urban sprawl phenomenon brought many more people out of the cities and created suburban centers out of formally rural land, the suburbanites have not embraced the hunting heritage of rural America. Instead, white-tailed deer have taken on roles which range from lawn ornament, to garden pest, to road hazard. As hunting has decreased as a pastime (Diefenbach and Shea 2011), more people have embraced animal welfare or animal rights perspectives which do not condone the use of hunting as a management tool for deer populations (Rutberg 1997).

As wildlife is considered a public resource, its management often involves input from the public sector (Green et al. 1997, McShea and Rappole 1997b, Shafer-Nolan 1997). Thus, state and local agencies charged with managing deer herds need to balance the attitudes of hunters, antihunters, and nonhunters with public safety and sound biology (Urbanek et al. 2013).

Justification

There has been increasing interest in exploring the effects of deer in an ecological context. As early as the 1940s, wildlife biologists as well as foresters began noticing the effect of abnormally high populations of deer on the regeneration of timber species (Leopold et al. 1947). Since then, most of these efforts have been directed at forested upland habitats, specifically at the reproduction of economically important species (Healy 1997, Rooney and Waller 2003). Fewer studies of deer diet have been directed solely toward rare or endangered herbaceous or woody plants (Miller et al. 1992, Russel et al. 2001).

To date, there has been comparatively little research on the effects of white-tailed deer browsing on herbaceous wetland plants primarily because wetlands have not been a focus of white-tailed deer study in general (Russel et al. 2001). Many plant species found in the wetlands of West Virginia may be considered rare or endangered because of the relative rarity of this habitat in the state. In the high elevation wetlands of West Virginia, this situation is even more evident as many of the plants are typical of northern climates and may be locally rare in the state (Fortney 1993, WV DNR 2012). White-tailed deer densities in the Canaan Valley today are drastically different from historical estimates of deer population densities primarily as a result of human intervention in the species' environment (i.e., fragmentation, vegetation alteration and reduction of the predator community). The potential for over-browsing by white-tailed deer could be considered as another human mediated environmental change (Primack and Miao 1992, Stromayer and Warren 1997). It is important to understand how these changes may affect metapopulation extinction and colonization rates of rare plants to inform conservation decisions for these species (Primack and Miao 1992, Alexander et al. 2012).

Canaan Valley provides an ideal area to research these effects because of the protected

status of much of the land, the economic draw of the wetlands, the high density of white-tailed deer in areas restricted to hunting, and the rarity of many of the plant species in the valley. Michael (1992) suggested that a difference in white-tailed deer abundance existed between several existing balsam fir stands within Canaan Valley. Deer abundance in Canaan Valley may be different from West Virginia Division of Natural Resource estimates for the entire county because of differences in vegetation, human development, and hunting restriction on both the National Wildlife Refuge (permit) and Canaan Valley State Park (prohibited). It is important to determine the relative abundance of deer in Canaan Valley as a whole and whether or not abundance differs by area to determine the relation to vegetation characteristics and make future management recommendations regarding deer numbers.

Objectives

White-tailed deer have had demonstrated browsing effects on numerous plant species. While research on browse effects on wetland plants is limited, there is evidence that white-tailed deer affect many other herbaceous species through herbivory. Deer have been implicated in the decline of many rare species. However, many other plants benefit from the consumption and dispersal of seeds by deer. The purpose of this study is to evaluate the influences of white-tailed deer herbivory, florivory, and seed consumption on plant populations in West Virginia. The study is organized into three general sections: 1) the influence of white-tailed deer browsing and seed dispersal on rare plant species and communities in Canaan Valley, West Virginia, 2) the influence of white-tailed deer density on forest understory recruitment in upland forests throughout West Virginia, and 3) public attitudes toward rare plant conservation and white-tailed deer management.

The specific objectives of the first portion of the study are to:

1. Quantify the rates of browsing on *Polemonium vanbruntiae* in Canaan Valley, WV;
2. Estimate demographics of local populations within metapopulations with respect to local population extinction rates and evaluate the rates of growth or decline for local population with respect to the effects of white-tailed deer browsing;
3. Estimate the seed loss of these species due to white-tailed deer herbivory;
4. Conduct feeding trials of seeds from wetland plant species of interest on captive deer to determine the percentage of seeds that pass through the digestive tract and that are germinable after digestion;
5. Collect natural fecal pellet piles from in and around Canaan Valley wetlands to determine the species of germinable seeds they contain as well as what percentage come from wetland plants; and
6. Evaluate the effects of white-tailed deer browsing on community composition in aspen (*Populus tremuloides*) regeneration cuts and *Solidago* spp.-*Rubus hispidus* dominated wet meadow communities.

I anticipate that rates of browsing on *P. vanbruntiae* populations will increase with increasing relative deer densities. I predict that, due to the conspicuous nature of *P. vanbruntiae* flowers within their environment, white-tailed deer may selectively browse the largest flowers disproportionately affecting seed production and dispersal potential. I predict that white-tailed deer will take advantage of regenerating aspen as winter browse. I hypothesize that many wetland plants, in particular, those considered rare, are not adapted to long distance seed dispersal by herbivores associated with upland habitats such as the white-tailed deer and are thus consumed rather than carried by deer.

In reference to these predictions, the following null hypotheses will be tested:

1. Rates of browse for *P. vanbruntiae* populations will not vary with respect to density of white-tailed deer;
2. Estimated seed production will not differ between browsed and unbrowsed ramets within a population;
3. A greater proportion of germinable seeds collected from natural fecal pellet piles will be from upland plant species as opposed to obligate wetland plant species; and
4. There will be no difference between control (unfenced) and exclosure plots in *Populus tremuloides* regeneration cuts and *Solidago* spp.-*Rubus hispidus* dominated wet meadow communities.

The specific objectives of the second portion of the study are to:

1. Determine which species of ground cover (< 50 cm) and understory (> 50 cm but < 2.54 cm DBH) are most susceptible to deer browsing at different densities; and
2. Evaluate a relationship between deer density and the recruitment of species into the understory of upland forests in West Virginia.

I anticipate that highly palatable browse species would show a difference in abundance between control plots and fenced plots even at low deer densities thus there will be a difference in the understory of unfenced plots as a result of white-tailed deer browse. At high deer densities, only species that are not preferred by white-tailed deer will appear in the understory community. At all densities, abundance of species in the ground cover layer may not be affected by white-tailed deer browse (Sweetapple and Nugent 2004). I predict that, as deer density increases, the number of palatable species that are present in the understory will decline due to increased browsing pressure.

In reference to these predictions, the following null hypotheses will be tested:

1. There will be no difference in abundance of species between the control and fenced plots;
2. There will be no difference in the magnitude of difference between control and fenced plots between species at different deer densities, and
3. There is no relation between the species richness of preferred species in the understory and deer density.

The specific objective of the third portion of the study is to:

1. Compare the attitudes of residents and nonresidents of Canaan Valley and Tucker County, WV toward rare plant conservation and white-tailed deer management.

Many of the visitors to Canaan Valley may have a different demographic makeup in terms of age, education, and recreational goals than residents. I anticipate that nonresidents would be more likely to favor the conservation of rare plants but less likely to advocate lethal means for control of white-tailed deer numbers.

In reference to this prediction, the following null hypothesis will be tested;

1. There will be no difference between attitudes of residents and nonresidents of Canaan Valley with respect to rare plant conservation and white-tailed deer management.

Study Area

Canaan Valley

The Canaan Valley, located in Tucker County, West Virginia (Figure 3), is the highest elevation valley east of the Rocky Mountains (Fortney 1975). As such, the climate and accordingly, the vegetation, of the valley is more similar to northern boreal forests than to the deciduous forests of surrounding West Virginia. Once home to large stands of red spruce (*Picea*

rubens), intense logging followed by fires drastically changed the soils and vegetation of the valley to their present condition (Fortney 1975). The valley floor averages 975 m above sea level. This coupled with surrounding mountains which rise 150–240 m above the valley create a relatively cool, moist climate and a short growing season. The average annual precipitation is 141 cm (National Climate Data Center 2014). In addition, high-elevation valleys in the Appalachian region often function as frost pockets that trap and hold cooler air (Byers et al. 2007). The average growing season is approximately 90 days (Griscom et al. 2011). These characteristics set Canaan Valley apart from lower elevation wetland and upland areas in the surrounding counties.

The Canaan Valley, West Virginia encompasses about 176 km² (17,600 ha) of land. Approximately 20% of the land area is made up of various wetland community types and another 23% is northern hardwood forest (Figure 4). Of all the high-elevation wetlands in West Virginia, Canaan Valley is home to the largest contiguous wetland areas (3,000 ha, Byers et al. 2007). Fortney (1975) described 27 distinct wetland community types ranging from quaking aspen (*Populus tremuloides*) stands to sphagnum (*Sphagnum* spp.) and polytrichum (*Polytrichum* spp.) bogs. Agriculture, rural development, and recreational land make up another portion of the valley (Michael 1992). The Canaan Valley is home to Canaan Valley State Park and the Canaan Valley National Wildlife Refuge as well as land owned by the West Virginia Division of Natural Resources. Deer hunting is allowed by permit within the National Wildlife Refuge lands and is conducted on private holdings throughout Canaan Valley. However, hunting has been prohibited in sections of the southern end of the Valley (i.e., Canaan Valley Resort State Park) since 1971 (Michael 2002). Sampling was conducted on a combination of these public access properties in the valley.

The impact of white-tailed deer on plant populations has previously been studied on balsam fir (*Abies balsamea*) and showy lady's slipper (*Cypripedium reginae*) (Gregg 2004, Kery and Gregg 2004) in the Canaan Valley. Study of balsam fir communities in Canaan Valley, WV indicated that higher deer densities reduced balsam fir reproduction (Michael 1992; Cherefko et al. 2009). The status of balsam fir as a preferred browse species is unclear. Michael (1992) considered balsam fir to be a preferred browse species. However, Stromayer and Warren (1997) suggested the opposite. This discrepancy may be due to geographic variation in abundance and additional browse species availability. Leopold et al. (1947) noted that, in Wisconsin, evidence of heavy browse on balsam fir was a precursor to fawn starvation in winter suggesting that it was one of the last plants to be browsed heavily by an overabundant population. Cherefko et al. (2009) found that deer browse in Canaan Valley had an impact on young balsam fir trees. Though significant negative impacts of white-tailed deer browse on balsam fir have not been extensively reported elsewhere, Canaan Valley may have the highest densities (32 deer/km²) of deer within balsam fir range (Michael 1992).

West Virginia Deer Exclosure Sites

Upland forest sites were randomly selected by the West Virginia Division of Natural Resources for the location of fenced deer exclosures. Nineteen sites were located in 14 counties throughout the state (Figure 3). Most sites were located in oak-hickory stands, however, several were located in mixed or northern hardwood stands. Sites were grouped into areas of low deer density (buck kill of < 2 per square mile or < 5.18 per square km), moderate deer density (2–5 bucks killed per square mile or 5.19–12.95 per square km) and high deer density (> 5 bucks killed per square mile or > 12.96 per square km) according to annual harvest data.

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Figure 1. Flowering stem of bog Jacob's-ladder (*Polemonium vanbruntiae*) in Canaan Valley, West Virginia, USA. Photo by Stephen M. Young. Accessed U.S. Forest Service Website

Figure 2. Bog Jacob's-ladder (*Polemonium vanbruntiae*) populations are often associated with alder communities and beaver ponds in Canaan Valley, West Virginia, USA.

Figure 3. Study areas located throughout West Virginia, USA. Red stars indicate West Virginia Division of Natural Resource white-tailed deer exclosure study sites located throughout the state. Canaan Valley located in Tucker County, WV, is shown in black.

Figure 4. Land cover types in Canaan Valley, West Virginia. Study sites were concentrated in the wetland forest, wetland shrub, and wetland herbaceous and moss cover types.

CHAPTER II

White-tailed Deer Florivory Influences the Population Demography of *Polemonium vanbruntiae* in Canaan Valley, West Virginia, USA

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ABSTRACT: White-tailed deer (*Odocoileus virginianus* Zimm.) may influence the reproduction and dispersal of plant species through herbivory of flowering stems. Whether or not seeds are adapted for dispersal by white-tailed deer (*Odocoileus virginianus* Zimm.), the consumption of flowers before seed formation reduces seed production and the genetic contribution of that individual through pollen dispersal. We examined the effects of white-tailed deer herbivory on the seed production of Bog Jacob's-ladder (*Polemonium vanbruntiae* Britt.), a facultative wetland plant considered rare throughout its range. Seed loss to herbivory was modelled using the basal stem width and number of flowers as predictors. We monitored life-stage transitions in ten local populations in Canaan Valley, West Virginia from 2005–2007 and modelled the population growth rate and estimated extinction rates for each population accounting for the loss of seeds due to white-tailed deer florivory. Seed loss due to consumption of flowering stems ranged between 0 and 96% within individual populations ($\bar{x} = 52 \pm 4.5\%$). A significant

difference in seed production occurred between browsed ($\bar{x} = 0.6 \pm 0.18$) and unbrowsed ($\bar{x} = 24 \pm 1.43$) plants. Predicted seed loss was significantly higher in the Canaan Valley State Park ($\bar{x} = 57 \pm 19\%$) than in the Canaan Valley National Wildlife Refuge ($\bar{x} = 40 \pm 18\%$) populations. The observed levels of white-tailed deer florivory have the potential to significantly reduce population growth rates ($p < 0.0001$); however, we found consumption of flowers alone by white-tailed deer is not enough to cause a decline in *P. vanbruntiae* populations. A high rate of seed production coupled with the perennial and clonal nature of this species make it less susceptible to declines due to seed loss. Although white-tailed deer florivory may not increase local population extinction rates, loss of seed production may result in a loss of the potential for colonization of new patches.

INTRODUCTION

By virtue of their rarity and dependence on specialized habitats, many threatened and endangered species exhibit a metapopulation distribution (Hansson, 1991; Alexander et al., 2012). The balance between the rates of colonization and local population extinction is critical to the maintenance of a metapopulation. In many rare or declining species, the rate of colonization (local population establishment) is not sufficient to counter the rate of local population extinction (Harrison, 1991). Thus, it is necessary to understand the factors that contribute to the decline of local populations as well as to understand the role of dispersal and colonization to conserve the metapopulation as a whole.

In terms of metapopulation survival, plant populations differ from animals in that individuals cannot disperse. Instead, dispersal is tied directly to reproduction and is often more random in nature than the dispersal of animal populations (Hansson, 1991; Alexander et al., 2012). Plant species have evolved to use a variety of seed dispersal mechanisms (Drezner et al.,

2001). Each method has implications for metapopulation persistence in fragmented habitat. Seed dispersal by herbivores may be an adaptation to ensure both long-distance dispersal and colonization of suitable patches by using fruit or foliage as an attractant to occupied patches (Janzen, 1984; Alexander et al., 2012). In this way, white-tailed deer (*Odocoileus virginianus*) could increase metapopulation persistence through increased dispersal and colonization. Conversely, when seeds that are not adapted for endozoochory are consumed, reproduction within the local population is reduced along with the potential for dispersal and colonization of new patches.

Although browsing on plant parts can alter the growth rate and ultimately the survival of individual plants (Alverson and Waller, 1997; Stromayer and Warren, 1997; Byman, 2011; Griscom et al., 2011; Masse and Cote, 2012), feeding on flowering parts of accessible herbaceous species reduces or eliminates the chances of fertilization for the individual and potential for fertilization of other individuals in the population (Loeffler and Wegner, 2000; Alexander et al., 2012; Frye, 2012). Conversely, by distributing seeds, along with fertilization in the form of fecal matter, into new areas and thus increasing the colonization rate, herbivores may benefit plant populations for which they are seed dispersers. However, loss of seeds to herbivores that consume and digest them can reduce the potential for both increasing the local population and colonization of new patches within a metapopulation (McGraw and Furedi, 2005; Levine et al., 2012).

The Role of White-tailed Deer in Seed Dispersal

The influence of white-tailed deer browsing on the survival of plant species has been well studied. However, the vast majority of available literature has focused on the effects of browsing on the survival of upland plant species and in particular commercially important timber

and agricultural species (Russel et al., 2001). Less well studied is the impact of white-tailed deer herbivory on herbaceous species and plant reproduction (Urbanek et al., 2012). Few studies have been conducted on the impact of white-tailed deer on wetland herbaceous plant species (Loeffler and Wegner, 2000; Kery and Gregg, 2004) primarily because wetlands have not been a focus of white-tailed deer studies in general (Russel et al., 2001). As many of the studies of white-tailed deer browse have previously been driven by economic factors, few have been directed solely toward rare or endangered herbaceous or woody plants (Miller et al., 1992). To date, there has been little research on the effects of white-tailed deer browsing on herbaceous wetland plants (Geddes and Mopper, 2006; Tobler et al., 2006) and even less focus on freshwater wetland plant species (Loeffler and Wegner, 2000; Bermingham, 2010).

Recently, however, the role of white-tailed deer as both seed predators and seed dispersers has been more closely examined (Campbell and Gibson, 2001; Vellend et al., 2003; Furedi and McGraw, 2004; Myers et al., 2004). White-tailed deer have a relatively large home-range (Janzen, 1984) and the potential to retain material in the digestive tract for three or more days (Mautz and Petrides, 1971). Thus, they have the potential to carry seeds distances of up to 10 km (Gill and Beardall, 2001). Vellend et al. (2003) suggested that this would result in 95% of germinable seeds being deposited more than 100 m from the parent plant and 30% deposited more than 1 km from the parent plant. Dispersal by herbivores could greatly expand the potential dispersal distance of plants and could have a considerable effect on metapopulation initiation, growth, and gene flow of irregularly distributed and rare plant species (Myers et al., 2004). However, long distance dispersal by herbivores may move some wetland seeds into upland conditions where they may be less likely to germinate. Increased dispersal distance may also benefit exotic, invasive plant species that could be detrimental to native plant populations

(Maron and Vila, 2001; Vellend, 2002; Williams and Ward, 2006). Although deer may play an important part in the dispersal of seed for many plants, for some plant species including American ginseng (*Panax quinquefolius* L.; Furedi and McGraw, 2004), white-tailed deer are demonstrated seed predators or consumers, that is, all seeds consumed in the act of herbivory are digested or are non-viable once passed through the digestive system thus reducing the realized reproductive output of these plants.

Whether or not seeds are adapted for dispersal by white-tailed deer, the consumption of flowers before seed formation reduces seed production and the genetic contribution of that individual through pollen dispersal. White-tailed deer florivory has the potential to reduce population viability of rare plant species through reduced seed production as well as the survival of browsed individuals (Loeffler and Wegner, 2000; Tobler et al., 2006; Frye, 2012). The extent of this effect may vary based on the contributions of reproductive individuals to the population.

Polemonium vanbruntiae

Polemonium vanbruntiae is a perennial wetland plant that ranges from Quebec south to West Virginia and from Maine west to West Virginia (Britton and Brown, 1913; Sabourin, 2002). It is found in areas varying from shrub swamps and forested wetlands to moist roadsides occurring mostly at elevations above 305 m (Hill et al., 2008; Bermingham and Brody, 2011). It is ranked as G3 (rare or uncommon) globally (Bermingham, 2010) and S2 in the state of West Virginia (WV DNR, 2012). This plant has been propagated successfully *ex situ* but is rare in natural populations. *Polemonium vanbruntiae* may reproduce sexually or asexually (Sabourin, 2002).

Polemonium vanbruntiae ramets can be detected above the soil beginning in late April to early May. Flowering ramets can be distinguished from vegetative ramets by alternate, pinnately

compound leaves along a main stalk (Figure 1). Vegetative ramets generally originate as single, pinnately compound leaves from a common origin. Buds are produced in early June with ramets producing flowers from late June to mid-July. Seed production can be measured by mid-August. In mid-September, the seed head and portions of the stem begin to dry and the fruit opens (Figure 2). The dispersal mode of *Polemonium vanbruntiae* seed is thought to be primarily passive. However, seed heads may also be moved by spring flooding or wind dispersal of seed heads over the winter snow crust (Sabourin, 2002; Hill et al., 2008). Winter seed dispersal can allow seed to travel hundreds of meters. Deer herbivory of flowering stems could have the potential to reduce winter dispersal in populations.

Current threats to *P. vanbruntiae* populations in the northern part of its range include agriculture, forestry, and wetland drainage or development (Deller, 2002). In Canaan Valley, West Virginia past threats have included logging, agriculture, and potential activity of all-terrain vehicles. Many, but not all of the populations in Canaan Valley are now protected by the location of state and government owned land. Current threats to these populations may include flooding caused by beaver (*Castor canadensis*) activity in the valley (Anderson and Bonner, 2014). There is evidence of white-tailed deer browsing on this species but it is not currently considered a management concern in northern populations (Bermingham, 2010). However, the deer densities at these locations may not be as high as Canaan Valley populations (Sabourin, 2002; 2.8–3.8 deer/ha, Cherefko et al., 2009).

Throughout much of the range of *Polemonium vanbruntiae* Britt., white-tailed deer densities are considered to be higher than during pre-colonial times and high deer densities have been blamed for the decline of many flowering species (deCalesta and Stout, 1997; Royo et al., 2010). Previous studies have detected correlations between deer density and some wildflower

species (Augustine and Frelich, 1998; Loeffler and Wegner, 2000; Royo et al., 2010; Urbanek et al., 2012). It is unclear how the maintenance of high deer densities affects conservation efforts for this species. There is anecdotal evidence of heavy white-tailed deer browsing on this species in West Virginia (Elizabeth Byers, West Virginia Division of Natural Resources, Personal Communication). However, it is not known whether the annual loss of reproduction translates into long-term declines in population viability in a perennial, clonal species.

The objective of this study was to determine if browsing by white-tailed deer has the potential to affect the viability of localized populations of *Polemonium vanbruntiae* by reducing seed production. We test the null hypothesis that natural rates of deer florivory have no effect on the rate of population growth (λ) within local *Polemonium vanbruntiae* populations.

METHODS

Study Area

Canaan Valley, located in Tucker County, West Virginia, is the largest high-elevation valley east of the Rocky Mountains (Fortney, 1975). The valley floor averages 943 m above sea level. The mountains that surround Canaan Valley rise 150–240 m above the valley and help to create a relatively cool, moist climate and a short growing season. Canaan Valley functions as a frost pocket that traps and holds cooler air (Byers et al., 2007). The average annual precipitation is 141 cm (National Climate Data Center, 2014). The average freeze period is approximately 90 days (Griscom et al., 2011). These characteristics make the climate and accordingly, the vegetation, of Canaan Valley more similar to boreal forests of the northeastern United States and Canada than to the deciduous forests of surrounding West Virginia and make Canaan Valley a unique wetland habitat in West Virginia (Fortney, 1993).

Canaan Valley, West Virginia encompasses about 176 km² (17,600 ha) of land.

Approximately 20% of this land area is made up of various wetland community types. Canaan Valley is home to the largest contiguous high-elevation wetland area in West Virginia (3,000 ha, Byers et al., 2007). Canaan Valley is home to Canaan Valley Resort State Park and the Canaan Valley National Wildlife Refuge as well as the Little Canaan Wildlife Management Area (WMA). Deer hunting is allowed within the National Wildlife Refuge lands (by permit), at Little Canaan WMA, and is conducted on private holdings throughout Canaan Valley. However, hunting has been prohibited in sections of the southern end of the Valley (i.e., Canaan Valley Resort State Park) since 1971 (Michael, 2002). Sampling was conducted in Canaan Valley Resort State Park, Canaan Valley Wildlife Refuge, and Little Canaan WMA.

The impact of white-tailed deer on plant populations in Canaan Valley has previously been studied on balsam fir (*Abies balsamea*, Michael, 1992), showy lady's slipper (*Cypripedium reginae*, Gregg, 2004; Kery and Gregg, 2004), and red spruce (*Picea rubens*)(Griscom et al., 2011). Higher deer densities reduced balsam fir reproduction (Michael, 1992) and young balsam fir trees (Cherefko et al., 2009).

Flowering Ramet Monitoring

We located eight populations of *P. vanbruntiae* in May 2005 and an additional two populations in 2006 (Figure 3). Populations were located by historical data and active searching. We monitored these populations from the first week of May through September from 2005 through 2007. The perimeter of all populations was delineated using a Trimble hand-held Geographic Positioning System (GPS) unit. In small populations (< 50 flowering individuals), all flowering ramets were marked at the base of the stem with a uniquely numbered aluminum tag for future identification. Tags were concealed in the vegetation at the base of the plant. Where possible a small piece of colored tape was attached to overhanging vegetation 0.5 m

above the stem to permit future identification of individual plants. Alternately, a colored flag was placed 1 m from the marked stem. In larger populations (> 50 flowering individuals), >25 flowering ramets were randomly selected by marking every 10th individual along a transect through the length of the population. Transects were used to prevent excessive trampling of unmonitored ramets.

We visited each plant every three weeks to monitor flower production and browse pressure. We recorded the height (cm) of each flowering stem, the width (mm) of the stem at its base, and the number of leaflets present on the main flowering stem of the plant (Figure 1). Additionally, we recorded the number of flowers present during the monitoring event that fell during the second week of June in all years. We determined the number of seeds that were produced on unbrowsed stems during subsequent visits produced by feeling each bud to determine if a seed capsule had formed. The number of browsed stems was recorded for each three week period.

We established 10 semi-permanent sampling quadrats within each population. Within each sampling quadrat, we identified individual ramets that were; seedlings (≤ 3 leaves), non-flowering vegetative ramets, and flowering ramets. We counted the number of ramets in each stage within a sample plot. We averaged the number within each category over all plots within the population and multiplied the average by the area of the population calculated in ArcGIS to determine the total number in each category for the population each year. Population structure was observed once per year between 15 June and 30 June during 2005–2007. We monitored flowering stems within the population every three weeks from early June until late September to determine the number of seeds produced per stem as well as the number of stems lost to white-tailed deer herbivory.

Seed Feeding Trials

We conducted feeding trials of seeds to captive white-tailed deer to evaluate whether deer could act as dispersers or predators of seeds. Due to the global rarity of the species, we used commercially available seeds of *Polemonium reptans*, the only other species of the *Polemonium* genus found naturally in West Virginia. We used 10 captive deer that were housed at the West Virginia Wildlife Center located in French Creek, WV.

Feeding trials were initiated on 25 July 2008 and continued for a period of three weeks. We mixed approximately 1300 *Polemonium* seeds per day with the normal feed of corn and grain. One day after the initiation of the feeding trials, we began collecting fecal pellets from the deer enclosure. Pellets were collected every other day for a period of 21 days. After collection fecal pellets were washed through a 500 μm sieve. All residual material collected was examined for the presence of *Polemonium* seeds.

Statistical Analysis

We measured four external morphometric characteristics (number of leaflets per stem [stem], height [height], basal width of the stem [width], the number of flowers present [flowers]) of flowering ramets found in ten populations throughout Canaan Valley, West Virginia during the 2005–2007 growing seasons. We created 13 a priori models using these variables as predictors of seed production (Table 1). We used linear regression along with information theoretic methods (Burnham and Anderson, 1998) to rank these variables as predictors of seed production. We selected the height of a flowering stem as an indicator because height has been used as a predictor of moist soil plant seed production (Anderson, 2006) and may be an indicator of deer browsing intensity (Anderson, 1994). We also selected the basal stem width as a potential indicator of flowering stem height that would remain constant even if flowering stems

were browsed (Loeffler and Wegner, 2000). We examined all variables for multicollinearity using the variance inflation factors ($\text{vif} \leq 5$) and condition number ($\kappa < 30$). From these variables, all possible models were fit using linear regression on data from unbrowsed stems. We did not examine interactions between the variables. We ranked the models using Akaike's information criterion corrected for small sample size (Burnham and Anderson, 1998).

We calculated the number of seeds produced on unbrowsed stems in each population. We used the morphometric characteristics found in the model with the best predictive power to estimate the number of seeds that would have been produced from browsed stems. We used these numbers to estimate the percentage of seeds lost due to herbivory as a percentage of all seeds that would have been produced from browsed plants. To estimate the predictive power of the model over time, we used linear regression to determine the relation between the number of seeds our 2005–2006 model predicted would have been produced from unbrowsed stems in 2007 to the number that were actually produced.

We compared the number of seeds produced on unbrowsed stems to the number of seeds actually produced by browsed stems as well as the number of seeds we estimated the browsed stems would potentially produce using analysis of variance on rank transformed values to determine if there was a selection pressure toward larger and potentially more productive ramets. We also compared the values of the predictive characteristics used in the model between browsed and unbrowsed stems. We arcsine square root transformed the percentages of stems browsed and the percentages of seed loss due to deer herbivory and compared these values using Pearson Product Moment Correlation. We also fit a regression equation through the origin and tested whether the slope of this line was equal to one. A significant difference from one would suggest that the seed model either over or under-estimated potential seed production.

Lastly, we compared the percentages of stems browsed and the percentages of seeds browsed in sites on the Canaan Valley National Wildlife Refuge to sites in Canaan Valley State Park by arcsine square root transforming percentage values and comparing refuge and state park sites across years with a two-factor analysis of variance. All analysis was done in Program R (R Development Core Team., 2008).

We used an α level of 0.1 for all analyses to reduce type II error because *Polemonium vanbruntiae* is considered very rare or imperiled in West Virginia (National Research Council Committee on Scientific Issues in the Endangered Species Act, 1995).

Population modeling

We determined the status of individually marked stems during the spring following their initial marking. Those stems that did not germinate the following spring but were present the year after were considered to be dormant during the previous year. As we could not determine if a plant was dormant until two years following, the transition rate from dormancy to vegetative ramets was considered for plants from the 2005 growing season and was pooled over all populations. Fecundity rates of flowering ramets were determined by counting the number of seed capsules produced on unbrowsed stems during seed production. Each seed capsule present on a ramet represented the number of possible seeds. We multiplied seed capsule production by an average of 10 seeds per capsule (Hill et al., 2008). We used a seed germination value of 23.75% from *Polemonium vanbruntiae* seed germination trials in Vermont (Hill et al., 2008) as the rate for all of our populations.

We used stage-structured matrix modeling to predict the population growth rate and estimate extinction rates for each population monitored. We created a stage-structured transition matrix (Table 2) to represent these three visible stages as well as seeds and a dormant stage

(Figure 4). Each populated cell in a transition matrix represented the probability of transition from stage a_i to stage a_j . Stage transition probabilities were estimated by monitoring individual ramets within semi-permanent study plots.

We used the *Popbio* (Stubben and Milligan, 2007) package for Program R to calculate the rate of population increase (λ) and the 95% confidence intervals for this statistic for each of the populations monitored in Canaan Valley based on our stage-transition matrix (Appendix 2). The *Popbio* package was created to run MATLAB code for matrix analysis (Morris and Doak, 2002). We calculated these statistics twice, with and without deer florivory, for each population. We constructed matrices without the effects of deer florivory by using the average number of seeds per flowering ramet as the measure of fecundity (stage transition a_{14} , Table 3). Next, we compared these to matrices that included the effects of deer florivory. We reduced the fecundity by dividing the seed production in each population by the total number of flowering ramets (browsed and unbrowsed) monitored in each population. We compared the rates of population increase (λ) with and without white-tailed deer florivory using a paired *t-test*.

We calculated the sensitivity and elasticity of the mean matrix of all populations without florivory using the Poptools extension to Microsoft Excel (Hood, 2008). The sensitivity of a transition matrix represents the absolute change in λ given a small change in each stage transition probability. As fecundity rates are typically higher than survival rates that are restricted from 0 to 1, the elasticity of a matrix is the relative contribution of each stage transition to changes in λ .

We calculated a cumulative distribution function from the transition matrices using the *stoch.quasi.ext* function within the *Popbio* program (Appendix 3) and used the cumulative proportion of extinction after 50 years as the probability of extinction for each population. We used the densities from the final population estimates in 2007 as the input vector for N_t . We

removed the seeds, seedlings and dormant individuals from the quasi-extinction threshold because of difficulty in counting these individuals (Morris and Doak, 2002). Extinction probabilities were calculated with and without the effects of deer florivory for each population.

RESULTS

We monitored 276 flowing ramets in 2005, 263 in 2006, and 250 in 2007 (Table 4). Our best performing model included the basal stem width and number of flowers as predictors of seed production ($\text{Seeds} = -14.2577 + 8.06308[\text{width}] + 0.48648[\text{flowers}]$, $R^2 = 0.50$, Table 2). We found that our model explained approximately 53% of the variance observed in 2007 seed production across populations (Figure 5). We found no difference between the stem width and flower number on unbrowsed plants (width $\bar{x} = 3.8 \pm 0.08$ mm, flower number $\bar{x} = 11 \pm 3.0$) and those of browsed plants (stem width $\bar{x} = 3.49 \pm 0.06$ mm, flower number $\bar{x} = 9.0 \pm 2.0$, $P > 0.05$). We found a significant difference between the mean number of seeds produced by unbrowsed plants ($\bar{x} = 24 \pm 1.43$) and those actually produced on browsed plants ($\bar{x} = 0.6 \pm 0.18$) in 2007 ($F_{1,234} = 1.43$, $P < 0.001$). We found a significant difference in potential mean seed production of browsed plants as predicted by the model above and actual production of unbrowsed plants ($F_{1,234} = 1.23$, $P < 0.001$) in 2007. However, there was a significant interaction between browse variable and the population ID ($F_{1,234} = 3.66$, $P < 0.001$) suggesting that this difference does not exist for all populations (Figure 6). We also found a significant difference between the potential mean seed production of both browsed ($\bar{x} = 15 \pm 0.56$) and unbrowsed ramets ($\bar{x} = 18 \pm 0.78$, $F_{1,234} = 12.91$, $P < 0.001$) in 2007. Seed loss due to consumption of flowering stems ranged between 0 and 96% within individual populations ($\bar{x} = 52 \pm 4.5\%$, Figure 7).

Overall stem loss ranged between 26 and 97% ($\bar{x} = 50 \pm 3.5\%$, Figure 8). We found a significant difference in percent stems browsed between the Canaan Valley State Park

populations ($\bar{x} = 57 \pm 19\%$) and the Canaan Valley NWR populations ($\bar{x} = 40 \pm 18\%$, $F_{1,16} = 3.27$, $P = 0.085$), but there was no difference between years ($F_{1,16} = 0.5349$, $P = 0.59$) and no significance to the interaction between these terms ($F_{1,16} = 1.04$, $P = 0.37$). There was a significant difference in potential loss of seed production to deer browse as predicted by the model above between the Canaan Valley State Park ($\bar{x} = 64 \pm 6\%$) populations and the Canaan Valley NWR populations ($\bar{x} = 36 \pm 5\%$, $F_{1,16} = 11.8$, $P < 0.003$), but there was no difference between years ($F_{1,16} = 0.25$, $P = 0.621$) and no significance to the interaction between these terms ($F_{1,16} = 0.049$, $P = 0.827$). The percentages of stems browsed and seed loss within populations was highly-correlated ($r = 0.81$, $SE = 0.001$, $t_{25} = 6.92$, $P < 0.0001$). We found that the slope of regression equations through the origin was significantly different than one in 2006 (slope = 0.73 ± 0.011 , $t_8 = 2.432$, $P = 0.038$), but not in 2005 (slope = 0.618 ± 0.262 , $t_6 = 1.458$, $P = 0.188$) or 2007 (slope = 0.63 ± 0.21 , $t_7 = 1.75$, $P = 0.119$)(Figure 9).

White-tailed deer in Canaan Valley tended to browse flowering ramets of *Polemonium vanbruntiae* early in the growing season, before seeds were produced and sometimes before flower emergence. We rarely found evidence of browse on vegetation that was not associated with flowering ramets. The estimated population growth rate ranged from 1.09 to 1.24 ($\bar{x} = 1.17$, $SE = 0.11$) without deer florivory. This translates to an annual rate of increase of 9% to 24% without florivory. With deer florivory, the estimated growth rate ranged from 0.99 to 1.20 ($\bar{x} = 1.08$, $SE = 0.13$). This represents an annual change in population ranging from a 1% decrease to a 20% increase across populations. In all populations, reduction of seed production through the consumption of flowers by deer reduced estimates of the population growth rate (Figure 10). The reduction of λ was considered statistically significant ($p < 0.0001$); however, in

only one population (State Park Population A), was λ reduced to less than 1 indicating a population decline.

Sensitivity analysis of the mean matrix (Table 3) without florivory suggested that the population growth rate was most sensitive to changes in seed germination rates and the transition from vegetative ramets to flowering ramets (Table 5). However, when we examined the elasticities for the same matrix, we found that seed production was proportionally as important as other stage transitions (Table 6).

Given the current population size, white-tailed deer florivory did not tend to increase the probability of local population extinction within the next 50 years. Only one population (A-Frame 1) that currently consists of only a few flowering ramets was in danger of extinction within the next 50 years given current rates of florivory. However, the probability of extinction in this population was only 1.2% after 50 years.

All deer pellet piles collected, were evaluated for the presence of undigested *Polemonium reptans* seeds. No seeds were detected in any pellet pile samples.

DISCUSSION

We found that actual mean seed production of browsed stems was significantly less than production of unbrowsed stems. In order to calculate the potential production from browsed ramets, we used a model that included both stem width and the number of flowers as predictive characteristics of seed production. Annual browse pressure, as measured by the percent of browsed stems within populations was moderate (26%) to extremely high (97%) in some populations. As monitored stems were marked in late May and ramets that were browsed prior to this visit may not have been visible, actual browse pressure may be even higher. Seed consumption by deer represents a potentially significant loss of sexual reproduction within the

population and may lead to a loss of genetic diversity and colonization potential. Furedi and McGraw (2004) found that more than 50% of fruit-bearing ginseng plants were browsed completely by deer in most populations and in some as much as 100% of fruit-bearing plants were browsed. These authors also observed that ginseng plants were often browsed prior to fruit production. This was the case for the majority of the browsed *P. vanbruntiae* in this study. Comparatively, white-tailed deer consumed only 28% of the terminal stems in populations of Turk's cap lily (*Lilium superbum*, Fletcher et al., 2001). Protected clusters of sundial lupine (*Lupinus perennis*) had a greater number of inflorescences and seed pods than those exposed to deer browsing (Frye, 2012). Selection of flowers may be a result of nutritional differences between flowers and leaves or from the seasonally conspicuous nature of the flowers.

The similarity in predictive characteristics of browsed and unbrowsed ramets suggests that white-tailed deer randomly select *P. vanbruntiae* flowers rather than select larger, more productive ramets. However, we found that the slope of a line examining the relation between percent of stems browsed and the percent of seeds browsed was significantly different from one in 2006. Had there been a direct relation between the numbers of stems browsed and the number of seeds browsed, we would have expected this line to approximate a 1:1 relation. Additionally, we found a significant difference between the average numbers of seeds produced from unbrowsed plants and the number we estimated would have been produced from browsed stems for some populations. These two comparisons point to the fact that differences between expected and actual production may have arisen from model error rather than from browse selection.

The impacts of deer browse on flowering stems may be more severe in small population

than larger ones (Loeffler and Wegner, 2000, Diamond and Boyd, 2004; Bermingham and Brody, 2011). In our study, however, we found that high browse rates were more a factor of location of the population. We found both percent stems browsed and percent predicted seed loss were higher in the state park than the wildlife refuge populations. Hunting was prohibited within the state park boundaries, but is permitted within the national wildlife refuge. The monitored populations in the state park are localized around high-traffic areas of the park whereas the populations on the national wildlife refuge are distributed throughout the length of the valley including the more remote portions of the northern end of Canaan Valley. Deer are often seen around the main road through the wetland portions of the state park and surrounding the resort hotel. They have been a tourist attraction to the park and might be attracted to vehicles and visitors that provide food (though feeding is prohibited in the park and refuge) and more accustomed to human presence. Localization of deer around specific populations (i.e. Abes Run B, State Park Parking lot, State Park A and State Park B, Figure 3) may lead to increased time within *P. vanbruntiae* populations and increased browsing rates. Additionally, the close proximity of these populations might increase the probability of a few deer encountering multiple populations whereas some populations on the wildlife refuge (i.e. A-Frame A and B) consisted of only a few flowering stems and no known populations within close proximity.

We found that rates of seed loss in *Polemonium vanbruntiae* due to deer florivory was generally not sufficient to cause population declines where populations were in relatively large numbers. Populations with fewer flowering stems (A-frame A, State Park Populations A and B) may be at risk for declines due to deer browse given a $\lambda < 1$ or confidence intervals on $\lambda < 1$. However, population projections show that even with deer florivory, these populations were not at risk of extinction within the next 50 years.

Our estimation of seed production as a measure of the fecundity of flowering ramets includes individuals that may be dispersing outside the localized population. As *Polemonium vanbruntiae* is potentially dispersed outside the local population by wind and water, the rate of emigration depends on annual variation in winter snowfall and flooding and is likely highly variable. Previous work has suggested that seed heads may travel up to 200 m from the parent plant over frozen snow (Sabourin, 2002). However, it is unclear how often such long distance travel takes place. Additionally, populations may be linked by dispersal through waterways. Dispersing individuals may be critical for metapopulation persistence, they should be considered as emigrants from a population rather than a factor in local population viability analysis. Measurement of the potential for seed loss through other means as well as the potential for dispersal is needed to examine mechanisms for connectivity between existing populations and the formation of additional populations.

We selected a quasi-extinction threshold of eight individuals (not including seeds, seedlings or dormant individuals) hopefully allowing for at least two flowering ramets and additional vegetative ramets. While the presence of one individual ramet can lead to the production of clones as well as to the production of seeds through selfing (Hill et al., 2008; Bermingham and Brody, 2011), it is not known what the long-term effects of inbreeding may be on a local population.

We found that the transition state that contribute to stasis such as the transition from vegetative to flowering ramets and maintenance of vegetative ramets contributed most to local population persistence (Table 5). This may be typical for perennial species (Furedi, 2004). Thus, maintenance of vegetative ramets may increase the chance of local population persistence. Besides the contribution to population persistence and growth, a population may persist as

vegetative ramets and may be less likely to attract white-tailed deer through flowering.

Herbivory may also result in increased vegetative growth of browsed ramets.

Our analysis indicates that deer herbivory of flowering ramets may not, by itself, cause a decline in local populations. However, deer florivory seemed to have a larger effect on λ in smaller populations. It is not known whether historic browse has reduced these populations to their current level or if other factors limit their size. Many of the smaller population existed as clumped ramets associated with alder (*Alnus* spp.) root clumps, whereas larger populations were more uniform. This variation is also found in other parts of the range (Hill et al., 2008). Clumped populations may be a result of periodic flooding and hydrology may be an abiotic limiting factor.

While loss of seed production may not increase population extinction rates, seed loss reduces the availability of seeds for both sexual reproduction and emigration. The persistence of the metapopulation as a whole relies on both local population persistence and the colonization of new patches. A reduction in seed production may make less seeds available for dispersal to unoccupied patches. Nonetheless, deer appear to have little impact on the long-term persistence of *Polemonium vanbruntiae* populations in West Virginia.

White-tailed Deer Seed Feeding Trial

We recognize that white-tailed deer have the potential to disperse seeds of browsed plants when consumed, increasing the effective potential for dispersal in many plants. However, our seed feeding trials of *Polemonium reptans* seeds to captive white-tailed deer indicate that white-tailed deer, when they consume *Polemonium* seeds, are seed predators rather than dispersers and would not contribute to movement of seeds between or contribute to the establishment of new localized populations of *P. vanbruntiae* in Canaan Valley. Thus consumption of flowering

ramets can reduce the potential for local population growth, reduce the chance of establishing new populations, and reduce gene flow between populations. While we did not conduct trials with *P. vanbruntiae* seeds, we believe that our results would apply to the dispersal of that species.

MANAGEMENT IMPLICATIONS

Our study suggests that white-tailed deer may consume almost 100% of the sexually reproductive ramets within *P. vanbruntiae* populations in a given year. In some cases, small populations in Canaan Valley produced only two flowering ramets in a year (A-Frame 2007, Table 1). A difference in browse rates exists between the Canaan Valley Resort State Park and Canaan Valley NWR populations that could be attributed to a difference in deer densities and management practices between the two public areas.

As *P. vanbruntiae* can reproduce clonally, high levels of seed loss such as those exhibited here may not have an immediate effect on population persistence. However, a loss of flower and seed production can reduce dispersal into new populations and will reduce genetic variation in a population due to a reduction in sexual reproduction. Although, many populations of *P. vanbruntiae* in Canaan Valley are large enough that browse rates recorded in this study will not threaten population viability, some historically recorded populations were not present during this study. If smaller populations are threatened by seed loss and dispersal is limited from larger populations, isolated populations are at risk of localized extirpation. A reduction in the number of localized populations threatens the metapopulation as a whole.

The alteration of deer densities in Canaan Valley to reduce browsing may not immediately benefit *P. vanbruntiae* populations and may be impractical for this sole purpose. The protection of flowering stems in smaller populations from browsing through fencing may be

a reasonable short-term alternative. However, previous fencing efforts to protect *Cypripedium reginae* in Canaan Valley Resort State Park have been inadequate. To be effective, fencing should be tall enough to prevent deer browsing and must be maintained. Alternately, a method of protecting flowering stems individually until seed formation could be conceived.

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Table 1. Akaike's Information Criterion values for 13 models predicting the seed production of *Polemonium vanbruntiae* 2005 and 2006.

Model	Terms	AIC	K ^a	Δ_i^b	w_i^c	R ²
1	Stems ^d	1535.58	2	116.37	0.00	0.07
2	Width ^e	1442.91	2	23.70	0.00	0.42
3	Population ^f	1627.76	11	208.55	0.00	0.13
4	Flowers ^g	1484.92	2	65.71	0.00	0.28
5	Height ^h	1505.29	2	86.08	0.00	0.20
6	Year	1547.22	3	128.01	0.00	0.02
7	Year + Population	1658.06	13	238.85	0.00	0.15
8	Stems + Width + Height + Flowers + Population + Year	1655.14	17	235.93	0.00	0.53
9	Stems + Width + Height + Flowers	1432.03	5	12.82	0.00	0.51
10	Width + Height	1444.51	3	25.30	0.00	0.43
11	Height + Flowers	1466.54	3	47.33	0.00	0.36
12	Width + Flowers	1419.21	3	0.00	0.94	0.50
13	Width + Height + Flowers	1425.03	4	5.82	0.05	0.51

a. K is the number of estimable parameters in the model

b. Δ_i is $|AIC_{\text{lowest}} - AIC_{ij}|$ for the *i*th model in comparison

c. w_i is the Akaike weight of the model

d. Stems refers to the number of leaflets associated with the main stem

e. Width is the width of the stem at its base

f. Population refers to individual populations of *Polemonium vanbruntiae*

g. Flowers refers to the number of flowers present during one sampling period

h. Height is the height of the flowering stem

Table 2. Transition matrix model (A) for *Polemonium vanbruntiae*. Each matrix element (a_{ij}) represents the probability that each individual in stage i will be derived from an individual at stage j in one time interval.

	Seeds	Seedlings	Vegetative Ramets	Flowering Ramets	Dormancy
Seeds	0	0	0	a_{14}	0
Seedlings	a_{21}	0	0	0	0
Vegetative Ramets	0	a_{32}	a_{33}	0	a_{53}
Flowering Ramets	0	0	a_{43}	a_{44}	0
Dormancy	0	0	0	a_{54}	0

Table 3. Mean matrix of transition probabilities for 10 *Polemonium vanbruntiae* populations without white-tailed florivory in Canaan Valley, West Virginia, 2005–2007.

	Seeds	Seedlings	Vegetative Ramets	Flowering Ramets	Dormancy
Seeds	0	0	0	134	0
Seedlings	0.2375	0	0	0	0
Vegetative Ramets	0	0.058	0.64	0.86	0.05
Flowering Ramets	0	0	0.3251	0.015	0
Dormancy	0	0	0.01	0.02	0

Table 4. Percent of *Polemonium vanbruntiae* flowering stems browsed in years 2005–2007. Populations 1–5 are located in Canaan Valley State Park. Populations 6–10 are located in Canaan Valley National Wildlife Refuge.

Population ID	2005			2006			2007		
	# Monitored	# Browsed	% Browsed	# Monitored	# Browsed	% Browsed	# Monitored	# Browsed	% Browsed
1 State Park Pop A	13 _a	9	69	19 _a	13	68	29 _a	28	97
2 State Park Pop B	13 _a	4	31	20 _a	12	60	31 _a	15	48
3 State Park Parking Lot	50 _b	32	64	39 _b	27	69	45 _b	19	42
4 Abes Run A	50 _b	13	26	50 _b	21	42	50 _b	22	44
5 Abes Run B	-	-	-	14 _a	9	64	35 _b	25	71
6 A- Frame A	14 _a	7	50	5 _a	3	60	2 _a	1	50
7 A-Frame B	-	-	-	4 _a	0	0	18 _b	14	78
8 Cortland Pop A	35 _b	11	31	36 _b	12	33	40 _b	11	28
9 Cortland Pop B	26 _b	11	42	25 _b	11	44	-	-	-
10 Camp 70	75 _b	26	35	51 _b	18	35	50 _b	17	34
Total	276	113	$\bar{x} = 43.5$	263	126	$\bar{x} = 47.5$	250	130	$\bar{x} = 54.6$

a represents populations with all flowering individuals monitored.

b represents populations where random samples of flowering individuals were monitored.

Table 5. Sensitivity analysis of the mean transition matrix model for *Polemonium vanbruntiae* populations without white-tailed florivory in Canaan Valley, West Virginia, 2005–2007.

	Seeds	Seedlings	Vegetative Ramets	Flowering Ramets	Dormancy
Seeds	0	0	0	0.002	0
Seedlings	1.545	0	0	0	0
Vegetative Ramets	0	0.633	0.362	0.058	0.003
Flowering Ramets	0	0	1.449	0.232	0
Dormancy	0	0	0.01	0.002	0

Table 6. Elasticity analysis of the mean transition matrix model for *Polemonium vanbruntiae* populations without white-tailed florivory in Canaan Valley, West Virginia, 2005–2007.

	Seeds	Seedlings	Vegetative Ramets	Flowering Ramets	Dormancy
Seeds	0	0	0	0.203	0
Seedlings	0.203	0	0	0	0
Vegetative Ramets	0	0.203	0.132	0.028	0
Flowering Ramets	0	0	0.23	0.002	0
Dormancy	0	0	0	0	0

Figure 1. A single flowering ramet of *Polemonium vanbruntiae*. Arrows depict the location of measurements for model formation. Image Source Britton and Brown. 1913. Accessed: USDA Plants Database.

Figure 2. The flowering stem and seed head of *Polemonium vanbruntiae* dries in late fall.

Figure 3. Locations of *Polemonium vanbruntiae* populations in Canaan Valley, West Virginia monitored from 2005 – 2007.

Figure 4. Direction of transition probabilities from the transition matrix for *Polemonium vanbruntiae* where class 1 represents seeds, class 2 represents seedlings, class 3 represents vegetative ramets, class 4 represents flowering ramets, and class 5 represents dormant individuals.

Figure 5. Scatter plot of the estimated seed production for unbrowsed plants in 2007 based on the best fitting model from 2005 and 2006 data compared to the seeds that were actually produced.

Figure 6. The potential mean seed production of browsed plants and actual production of unbrowsed plants in monitored populations of *Polemonium vanbruntiae* in Canaan Valley, WV in 2007

Figure 7. The estimated percent of *Polemonium vanbruntiae* seeds consumed by white-tailed deer in 10 populations in Canaan Valley, West Virginia in 2005–2007.

Figure 8. The estimated percent of *Polemonium vanbruntiae* stems consumed by white-tailed deer in 10 population in Canaan Valley, West Virginia in 2005–2007.

Figure 9. Comparison of the percentage of *Polemonium vanbruntiae* stems browsed to the estimated percent of seeds consumed by white-tailed deer in Canaan Valley, West Virginia in 2005–2007.

Figure 10. Predicted population increase rates (λ) for all *Polemonium vanbruntiae* populations with and without white-tailed deer florivory. Standard error bars represent the 95% error estimates of λ calculated in the *Popbio* package of Program R.

CHAPTER III

The influence of white-tailed deer herbivory on herbaceous wetland plant communities in Canaan Valley, West Virginia (USA)

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Abstract White-tailed deer (*Odocoileus virginianus* Zimm.) may have the potential to alter plant community composition and successional trajectory by browsing differentially on forb, graminoid, and woody species metacommunities. The objective of this study was to determine if the elimination of deer browsing resulted in a change in wetland plant community composition and structure. We established 66 deer exclosure plots in two wetland vegetation communities in Canaan Valley, West Virginia, USA. Plots were 1 m² and surrounded by 2 m x 2 m exclosures including a 0.5 m buffer between the plot and the fence. Plots were established in April 2005 and monitoring was conducted in late-June and late October from 2005 – 2007. We evaluated the differences in community composition between control and treatment plots using Blocked Multiple Response Permutation Procedures (MRBP) in program PC-Ord. We also examined the changes in woody, forb and graminoid metacommunities as well as the differences between wetland indicator status categories. We found composition differed between control and treatment plots in *Solidago* spp.-*Rubus hispidus* communities in late-protected plots when data were gathered in the fall and early-protected plots when data were gathered in the spring. We found that forb cover increased in treatment plots in *Solidago* spp.-*Rubus hispidus* communities. Composition differed in *Populus* spp. communities in late-protected and continuously-protected plots. There was no significant increase in cover by any one wetland indicator status category after two years of protection. Timing of browse plays a significant role in the effect that white-tailed deer have on wetland plant communities. Increased forb cover in treatment plots suggests that historical deer densities have depressed forb species through selective browsing. Whereas exclosure studies typically represent a scenario without deer, our results suggest that reducing browsing pressure can increase forb and woody species cover where previously depleted.

Keywords herbaceous · herbivory · wetland · white-tailed deer

Introduction

The effect of white-tailed deer (*Odocoileus virginianus*) on their habitat is one of the most studied and controversial topics in the fields of wildlife management, forestry, and ecology. However, the focus of these studies have been on upland species as opposed to wetland species. In the past, economic factors such as loss of crops or regeneration of preferred timber species have provided the impetus for many studies. Species-specific studies found deer had detrimental effects on hemlock (*Tsuga canadensis*)(Anderson and Loucks 1979; Whitney 1984; Alverson and Waller 1997; Stromayer and Warren 1997), white cedar (*Thuja occidentalis*)(White 2012), yellow birch (*Betula lutea*)(Stromayer and Warren 1997), balsam fir (*Abies balsamea*)(Tremblay et al. 2007), and various oak species (*Quercus* spp.)(Healy 1997).

More recently there has been an increased interest in the effect of high densities of white-tailed deer on individual threatened and endangered understory species (Miller et al. 1992; Gregg 2004). Glade spurge (*Euphorbia purpurea*), a globally rare plant is affected by consumption of leaves as well as limited in reproduction by browsing of flowering parts by white-tailed deer (Loeffler and Wegner 2000). Deer may reduce or extirpate local populations of American ginseng (*Panax quinquefolius*) in West Virginia (McGraw and Furedi 2005) and Turk's cap lily (*Lilium supurbum*) in Virginia (Fletcher et al. 2001).

There has also been an increased focus on species richness and diversity of understory and herbaceous plant communities. Myriad studies cite white-tailed deer herbivory as an important contributing factor to the decline in species richness of forest understory forb species (Leege et al. 2010; Pellerin et al. 2010; DeGroote et al. 2011; Duguay and Farfaras 2011; Randall and Walters 2011) and the decline in sapling recruitment of preferred woody browse (Augustine and McNaughton 1998; Levine et al. 2012). Deer herbivory has been cited as a

detriment to tallgrass prairie forbs (Anderson et al. 2001) and riparian willow species (Brookshire et al. 2002). Peek and Stahl (1997) cited an instance in which a large population of deer extirpated 150 vascular plant species from one city park in Ohio. While the majority of studies on this topic cite negative impacts to woody and forb species (Goetsch et al. 2011), several recognize an increase in graminoid species (Merrill et al. 2003; Rooney 2009; Thiemann et al. 2009; Randall and Walters 2011), less palatable woody species (Koda and Fujita 2011), and exotic species (Knight et al. 2009; Duguay and Farfaras 2011; Lefcort and Pettoello 2012) that often accompany the decline in preferred browse species.

The ability of white-tailed deer to affect plant communities may have long-term implications for trajectory of plant community restoration after disturbance (Opperman and Merenlender 2000; Rooney 2009; Holmes and Webster 2011; Tanzentap et al. 2012). Many of the ecosystems in the eastern United States have been disturbed either through timber harvest or conversion to agricultural land. The ability of a forest community to undergo a predictable secondary successional path following disturbance such as timber harvest or historical cultivation depends primarily on the ability of forest species to reach the canopy (Tanzentap et al. 2011; White 2012). Browsing by white-tailed deer prevents this by reducing the recruitment of those species into the sapling layer directly through browse (Pellerin et al. 2010) and indirectly by increasing the prevalence of less palatable graminoid and fern species that shade woody species seedlings (Augustine and McNaughton 1998; Jensen et al. 2011; Randall and Walters 2011). Numerous studies have demonstrated a loss of preferred browse species and an increase in non-preferred browse species in the sapling layer (Holmes et al. 2008). The loss of preferred browse species has included mast producing species that provide important seasonal food sources for white-tailed deer throughout much of their range (Clements et al. 2011). Thus

altering the existing sapling community composition has repercussions far into the future. Some have even suggested that the loss of species today could lead to an alternate stable state or a community that exists in a different state than would be predicted by ecological succession and remains stable without a disturbance event (Stromayer and Warren 1997; Beschta and Ripple 2009).

Seasonal variation in browse pressure may affect the way that different types of plants respond to herbivory (Stewart et al. 2008; DeGroote et al. 2011; Jensen et al. 2011). As the primary winter food source, populations of woody plant species may be significantly reduced through winter browse pressure. Browsing during the early spring appropriates nutrients and energy seedlings and saplings would have allocated to leaf, shoot, or root production (Stewart et al. 2008; Clements et al. 2011). Repeated browsing can prevent individuals from growing out of the range of white-tailed deer browse. Deer browse on forbs is generally associated with the new growth of early spring; however, deer may also browse on senescent forms during winter months when plant tissues may be higher in crude protein and lower in tannins than woody browse species available at the same time (Windels and Jordan 2008). Browsing in spring may prevent forbs from producing flowers which reduces reproductive output.

The effect of timing on browsing of metacommunities (i.e., forbs, woody species, and graminoids) in the same environment has seldom been studied. Additionally, most studies that have measured the impact of deer browse on plant communities have focused on forest and grassland communities. Fewer studies have included wetland ecosystems (Cipollini and Cipollini 2011). We examined the effects of a high-density (2.8-3.8 deer/ha, Cherefko et al. 2009) white-tailed deer population on plant community metrics in a high-elevation wetland ecosystem by comparing communities in both unfenced (control) and fenced (treatment) plots.

We focused on the effect of timing on browse susceptibility of forb, woody, and graminoid species, by varying the exposure of treatment plots to browse throughout the year.

Our objectives were to determine if a reduction in deer browsing affected the plant species richness, plant community composition, prevalence of wetland species, and cover of forb, graminoid, and woody species in *Solidago* spp.-*Rubus hispidus* wet meadow communities and *Populus* spp. regeneration communities. We tested the null hypotheses that there will be no overall change in plant species richness, plant community composition, and cover of forb, graminoid, and woody species in plots protected continuously over the two years of the study period when compared to paired control plots that are not continuously protected from deer browse. We also tested the null hypotheses that there would be no difference in the average change in cover between different wetland plant indicator classes after two years of protection from deer browse.

Methods

Site Description

Canaan Valley is a high-elevation wetland complex, located in Tucker County, West Virginia, USA. The valley floor averages 975 m above sea level. This coupled with surrounding mountains which rise 150–240 m above the valley create a relatively cool, moist climate and a short growing season. As such, the climate and accordingly, the vegetation, of the valley are more similar to northern boreal forests than to the deciduous forests of surrounding West Virginia. Once home to large stands of red spruce (*Picea rubens*), intense logging followed by fires drastically changed the soils and vegetation of the valley to their present condition (Fortney 1975). The average annual precipitation is 137 cm and annual snowfall is 305 cm (Stephenson 1993). The average growing season is approximately 90 days (Beverage 1967). These

characteristics set this area apart from drier and warmer, low-elevation wetland and upland areas in the surrounding counties.

Canaan Valley encompasses about 176 km² (17,600 ha) of land. Approximately 20% of the land area is made up of various wetland community types and another 23% is northern hardwood forest (Fig. 1). Fortney (1975) described 27 distinct wetland community types ranging from quaking aspen (*Populus tremuloides*) groves to sphagnum (*Sphagnum* spp.) and polytrichum (*Polytrichum* spp.) bogs.

Canaan Valley is home to Canaan Valley State Park and the Canaan Valley National Wildlife Refuge (NWR) as well as land managed by the West Virginia Division of Natural Resources for hunting. Deer hunting is allowed by permit within the National Wildlife Refuge lands and is conducted on private holdings throughout Canaan Valley. However, hunting has been prohibited in sections of the southern end of the Valley (i.e., Canaan Valley Resort State Park) for at least 20 years (Michael 1992).

Plant Community Analysis

We selected two types of wetland plant communities from those present in Canaan Valley. *Solidago* spp.-*Rubus hispidus* dominated communities and regenerating *Populus* spp. dominated communities were selected from the wet meadow communities found in Canaan Valley identified by Canaan Valley NWR staff. We chose *Solidago* spp.-*Rubus hispidus* dominated communities because these wet-meadow communities are rare within the state and may have an increased likelihood of rare species within these communities (e.g. *Euphorbia purpurea* and *Luzula bulbosa*, Fortney 1975). These communities were dominated by *S. uliginosa* and *S. rugosa* as well as *R. hispidus*. Additionally, the initiation of our monitoring coincided with *Populus* spp. regeneration cuts conducted on the Canaan Valley National Wildlife

Refuge. These communities were dominated by *P. tremuloides*. We chose to monitor the effect of herbivory on those communities during regeneration. Within the valley, we randomly selected 10 *Solidago* spp.-*Rubus hispidus* communities previously identified by refuge staff (Fig. 1). Within each community we randomly established three treatment plots and located a paired control plot 4 m from each treatment plot (Fig. 2). One of the treatment plots was enclosed year-round for three years from 2005–2007 (continuous plots). Another plot was enclosed from late April through mid-July of each year (early plots). The third treatment plot was enclosed from mid-July through mid-October of each year (late plots).

We also selected four recently-cut *Populus* spp. communities (Fig. 1). In each of these, we randomly located three blocks of three pairs of control and treatment plots as described above. At each site, three of the treatment plots were enclosed year-round for three years (continuous plots). Three plots were enclosed from late April through mid-October (early plots). The final three treatment plots were enclosed from mid-October through late April (late plots).

Treatment plots were 1 m² and surrounded by fenced 2 m x 2 m exclosures such that a 0.5 m buffer occurred between the plot and fence. We constructed deer exclosures from 12 ga. woven wire fencing. Plots were established in April 2005 and monitored in late-June and late October from 2005 – 2007. We recorded all plant species within the plot and recorded a Daubenmire cover-class rating for all species such that; species with < 5% plot coverage received a score of 1, species with > 5% – 25 % plot coverage received a score of 2, species with > 25% – 50% plot coverage received a score of 3, species with > 50% – 75% plot coverage received a score of 4, species with > 75% – 95% plot coverage received a score of 5, species with > 95% plot coverage received a score of 6 (Daubenmire 1959). We used cover class scores

to improve normality and homogeneity of variances between *a priori* groups. Use of cover class scores also reduces bias against species with low abundance (McCune et al. 2002).

Data Analyses

We were interested in comparing the change in plant community composition after eliminating deer browsing pressure both seasonally and year-round. Therefore, we created species-by-site matrices for each of our sampled communities. We adjusted our response variable to reflect a change in species composition from the original community. For example, if the species cover was initially recorded as a 4 and was later recorded as a 3 over two years of monitoring, the response matrix would reflect this as a -1 indicating a decline in the frequency of that species within the plot. We compared the change in frequency between control (unfenced) and treatment (fenced) plots for our three groups; early, late, and year-round. We analyzed the results for the *Solidago* spp.-*Rubus hispidus* and *Populus* spp. communities separately.

We used Blocked Multiple Response Permutation Procedure (MRBP) in PC-Ord (McCune and Mefford 1999) to compare vegetation communities in treatment vs. control plots. Multiple Response Permutation Procedure (MRPP) is a non-parametric technique for analyzing multivariate data and requires the *a priori* selection of test groups. Blocking the MRPP allows for the analysis of randomized block designs or paired plot data (McCune et al. 2002).

Communities were analyzed using the Euclidean distance measure. This procedure describes the homogeneity within a group using the A-statistic. An observed A statistic of one indicates identical communities within plots in a group. The separation between the control and treatment groups is described with a T-statistic. The resulting P-value describes the likelihood for finding the observed separation between random groups given the data. All species cover data are presented as raw cover class data unless otherwise specified.

We also compared species richness within plots after two years protection from browse. A Shapiro-Wilk normality test indicated that data were not normal in either *Solidago* spp.-*Rubus hispidus* or *Populus* spp. regeneration communities ($p < 0.05$). Thus a repeated-measures, two-way analysis of variance was performed on rank-transformed species richness data to compare richness between fenced and control plots and between early, late, and continuously protected plots. We identified the wetland indicator class for each species that exhibited a change in average cover class rating between 2005 and 2007. These groups include facultative wetland (FACW; plants with 67 – 99% frequency of occurrence in wetlands), obligate wetland (OBL; plants with > 99% frequency of occurrence in wetlands), Facultative (FAC; plants with equal chance of occurring in wetland or uplands), facultative upland (FACU; plants with 67 – 99% frequency of occurrence in non-wetlands), and upland (UPL; plants with > 99% frequency of occurrence in non-wetlands; Lichvar et al. 2014). We compared the mean change in species cover from 2005 and 2007 in fenced plots between wetland plant indicator classes using a Kruskal-Wallis rank sum test.

Results

Species Richness

We recorded 75 species in plots in *Solidago* spp.-*Rubus hispidus* communities (Appendix 4) and 99 species within plots in *Populus* spp. regeneration communities (Appendix 5). *Solidago* spp.-*Rubus hispidus* community species richness within square-meter plots ranged from 6.4 ± 0.37 species/m² in control plots associated with late-protected plots when measured in the spring to 7.5 ± 0.50 species/m² recorded in control plots associated with early-protected plots when measured in the fall (Fig. 3). There were no significant differences found between fenced and control plots in *Solidago* spp.-*Rubus hispidus* communities for any treatment measured in both

spring and fall ($p > 0.05$, Fig. 3). *Populus* spp. regeneration community species richness within square-meter plots ranged from 8.4 ± 0.80 species/m² in control plots associated with continuously protected plots to 10.6 ± 0.56 species/m² recorded in fenced plots protected continuously (Fig. 4). There were no significant differences found between fenced and control plots in *Populus* spp. regeneration communities for any treatment measured in both spring and fall ($p > 0.05$, Fig. 4).

Solidago spp.-*Rubus hispidus* Community Analysis

We found significant differences in the change in community composition for some, but not all of our treatment regimes. In *Solidago* spp.-*Rubus hispidus* communities we found that community composition differed significantly between treatment and control plots for those protected in the early plots when data were gathered in the spring ($T = -3.474$, $p < 0.01$) and in the late plots when data were gathered in the fall ($T = -5.547$, $p < 0.01$) (Table 1). When plots were protected year-round, a significant change in community composition was only apparent on data gathered in the spring ($T = -2.386$, $p < 0.05$) (Table 1).

For treatment regimes in *Solidago* spp.-*Rubus hispidus* communities that showed a significant difference in community composition between treatment and control plots, we determined which species exhibited the greatest average change in fenced plots. The grasses; *Agrostis gigantea* Roth, *Danthonia compressa* Aust., and *Festuca trachyphylla* (Hack.) declined in fenced plots from 2005 under more than one treatment regime or monitoring period (Table 2). The forbs; *Doellingeria umbellata* (P. Mill.) Nees var. *umbellata*, *Rubus hispidus* L., *Solidago rugosa* Mill., and *Solidago uliginosa* Nutt. increased in fenced plots from 2005 under more than one treatment regime or monitoring period (Table 2).

In *Solidago* spp.-*Rubus hispidus* communities, there was a significant difference in the change in woody species cover class between fencing periods when data were gathered in the spring ($F_{2,52} = 4.62$, $p < 0.05$; Fig. 5). There was an increase in woody species cover class ($\bar{x} = 0.029 \pm 0.020$) for plots protected early in the year and a decrease for plots protected later ($\bar{x} = -0.064 \pm 0.020$). There was no change in cover class for continuously protected plots or a difference between control and fenced plots for woody species. A significant difference in cover class also was detected for woody species between early, late, and continuously protected plots when data were gathered in the fall ($F_{2,52} = 3.33$, $p < 0.044$; Fig. 6). Woody species cover class increased more in the continuously protected plots ($\bar{x} = 0.021 \pm 0.01$) in both the early ($\bar{x} = 0.007 \pm 0.022$) and late ($\bar{x} = 0.007 \pm 0.013$) plots. There was no significant difference in cover class between control and fenced plots when measured in the fall ($F_{1,52} = 0.31$, $p > 0.50$; Fig. 6). There were no significant interactions between fencing period and treatment in either season for woody species.

There were significant changes detected in the forb species cover classes between control and fenced plots when measured in the fall ($F_{1,52} = 4.12$, $p < 0.048$; Fig. 6). We measured an increase in cover class of forbs in plots that were fenced early in the year ($\bar{x} = 0.022 \pm 0.031$) and a decrease in forb cover class of associated control plots ($\bar{x} = -0.00013 \pm 0.025$). We measured a decrease in forb cover class in both fenced plots protected late in the year ($\bar{x} = -0.0037 \pm 0.017$) and the associated control plots ($\bar{x} = -0.0022 \pm 0.035$). There was an increase in forb cover class in both fenced plots protected continuously ($\bar{x} = -0.0074 \pm 0.019$) and the associated control plots ($\bar{x} = -0.00086 \pm 0.018$). There were no significant interactions between fencing period and treatment for forb species. No differences in graminoid species cover class were detected for fencing period or treatment in either season. There were no significant

interactions ($p > 0.05$) between the the fencing period and the fencing treatment in *Solidago* spp.-
Rubus hispidus communities. There were no significant difference in mean change based on
wetland indicator class for data collected from plots protected late in the year when data were
collected in the fall ($\chi^2_5 = 5.73$, $p = 0.3332$), from plots protected early in the year when data
were gathered in the spring ($\chi^2_5 = 8.98$, $p = 0.1098$), and from continuously protected plots when
data were gathered in the spring ($\chi^2_5 = 2.51$, $p = 0.7753$, Table 4).

Populus spp. Community Analysis

In *Populus* spp. communities, differences between control and treatment plots in
community composition were only apparent in data gathered in the spring for the late plots ($T = -$
 2.101 , $p < 0.05$) and year-round plots ($T = -2.077$, $p < 0.05$)(Table 1). *Carex debilis* Michx. and
Pteridium aquilinum (L.) Kuhn. declined in fenced plots from 2005 under more than one
treatment regime or monitoring period (Table 3). *Danthonia compressa* Aust. and *Rubus*
hispidus L. increased in fenced plots from 2005 under more than one treatment regime or
monitoring period (Table 3).

In *Populus* spp. communities, there was a significant difference between fencing periods
in the change in forb species cover class ($F_{2,64} = 4.12$, $p < 0.048$; Fig. 7) when data were gathered
in the spring. Forb species cover class increased in both fenced plots ($\bar{x} = 0.044 \pm 0.026$)
protected early in the year and their associated control plots ($\bar{x} = 0.035 \pm 0.004$). Forb species
cover class decreased in both fenced plots ($\bar{x} = -0.042 \pm 0.017$) protected late in the year and
their associated control plots ($\bar{x} = -0.01 \pm 0.029$). Forb communities measured in the fall
differed between fenced and control plots ($F_{1,64} = 15.69$, $p < 0.001$; Fig. 8). Though the forb cover
class increased for both fenced and control plots under all fencing regimes, the change in forb
communities was greater for fenced plots protected early ($\bar{x} = 0.076 \pm 0.018$), late ($\bar{x} = 0.046 \pm$

0.015), and continuously ($\bar{x} = 0.076 \pm 0.016$) than in the control plots paired with early ($\bar{x} = 0.026 \pm 0.015$), late ($\bar{x} = 0.03 \pm 0.015$), and continuous ($\bar{x} = 0.046 \pm 0.030$) treatments. In *Populus* spp. communities, we also found a difference in the change in woody species cover class between control and fenced plots when measured in the spring ($F_{1,64} = 13.23$, $p < 0.001$; Figure 8) but not in the fall ($F_{1,64} = 0.36$, $p > 0.50$). Woody species cover class decreased in both fenced plots that were protected early ($\bar{x} = -0.021 \pm 0.014$) and late ($\bar{x} = -0.031 \pm 0.016$). However, woody species increased in control plots associated with fenced plots protected early ($\bar{x} = 0.024 \pm 0.014$). Woody species cover class increased in both fenced plots that are protected continuously ($\bar{x} = 0.020 \pm 0.031$) and the associated control ($\bar{x} = 0.025 \pm 0.005$) plots. There were no significant interactions ($p > 0.05$) between the the fencing period and the fencing treatment in *Populus* spp. communities. There was no significant difference in mean change based on wetland indicator class for data collected from plots protected late in the year when data was collected in the spring ($\chi^2_5 = 2.01$, $p = 0.8475$), and from plots protected continuously when data were gathered in the spring ($\chi^2_5 = 3.55$, $p = 0.6157$, Table 4).

Discussion

We tested the null that overall species richness would not change with protection from browsing. We found that this was the case for both *Solidago* spp.-*Rubus hispidus* communities and regenerating *Populus* spp. stands. Other studies (Stromayer and Warren 1997; Holmes et al. 2008; Jensen et al. 2011; Levine et al. 2012) have found similar results when measuring species richness and have attributed the absence of change to a balance between an increasing number of graminoid species and a decreasing number of forb and woody species. We did not expect a decrease in species richness in unfenced areas because of a history of high deer densities in the study area. Rather, we expected to see an increase in woody and forb

species and a resulting decline in graminoid species after establishing exclosures. We did not find a significant difference in the change in graminoid species cover between fenced and control plots suggesting that we cannot attribute an overall similarity in species richness to a balance between increasing forb and woody species and declining graminoid species. However, we did observe a decline in graminoid species cover in most plots (Figs. 5 – 8). The fact that this is not reflected in species richness may be because a single individual recorded in a plot would increase species richness but would likely not impact the percent cover of that species as was the case with many woody seedlings identified by a single individual in the plot such as the lone red maple (*Acer rubrum*) seedling recorded in the *Solidago* spp.-*Rubus hispidus* communities.

We found that there were changes in community composition in both *Solidago* spp.-*Rubus hispidus* and regenerating *Populus* spp. communities but not under all treatment regimes. We also found that overall community composition was different between plots protected both continuously and in the spring when we gathered the data in the spring but only in late plots for data gathered in the fall. In *Populus* spp. stands, we found that there was a difference in communities in late protected plots and continuously protected plots when data were gathered in the spring. As we planned these exclosures specifically around *Populus* spp., we might be tempted to attribute these differences specifically to woody species. We did not see a difference in plots protected in the spring. When we focused specifically on woody species, we found that there was a decrease in woody species in these plots and, in fact, the woody species increased in the associated control plots. We did find that woody species increased in plots protected continuously. However, they also increased in the associated control plots. Randall and Walters (2011) found that, in clear-cut *Populus* spp. stands, high levels of deer browse would likely reduce the growth of other woody species. Loss of woody species at the seedling and sapling

stages as a result of deer browse has the potential to affect the over-story community trajectory for years to come.

The changes in forb cover in *Populus* spp. communities were not straightforward and interpretations differed based on when data were collected. When collected in the spring, increases (for spring protected plots) and decreases (for late protected plots) were similar for the treatment and control plots. An increase in forb species in plots protected in the spring would support the idea that forbs are especially susceptible to white-tailed deer browse when new growth appears in the spring. However, a similar response in the control plots was not expected. Likewise, an average decline in forb species was not expected in late plots as the spring browse pressure should not have differed from pre-fencing conditions. Several authors have attributed similar results to “fenceline effects” that result from control plots located next to exclosures. These “fenceline effects” also might bias the results toward the extreme because of higher rates of deer herbivory immediately surrounding the exclosures (Russell et al. 2001, Comisky et al. 2005). The *Populus* spp. regeneration cuts themselves may have attracted deer from the surrounding herbaceous wetland areas (Barrett and Stiling 2006). However, it is more likely that similarity between treatment and control plots resulted from the effects of canopy removal on these communities. These changes may have masked any potential impacts resulting from elimination of browse. Likewise, the increased availability of *Populus* spp. to deer may have reduced browse pressure on other species.

Although we considered more than the frequency of *Populus* spp. when measuring the woody species in *Populus* spp. dominated communities, they were the most abundant woody species within these plots. The growth rate of *Populus* spp. saplings following harvest may have impacted our results. The fencing used for exclosures was only 99 cm tall. Regenerating

Populus spp. saplings grew higher than the exclosures within their first year of growth whereas other seedlings and saplings would have been better protected by the fence. Although the saplings were not completely protected from browse, they may have been less susceptible to browse than those growing in unfenced control plots.

In *Solidago* spp.-*Rubus hispidus* communities, our data agree with the null hypothesis of no change in species richness in treatment plots when compared to control plots. When we gathered data in the fall, plots that were continuously protected increased in woody species more so than other treatment plots. We might expect to see an increase in woody species in these plots; however, we would also expect to see a difference from the associated control plots. Also, we saw a greater increase in woody species in control plots associated with other fencing treatments. These results might be explained by the low frequency of woody species initially found in this community. Low woody species frequency may be a result of historical alterations to the vegetation and soils of the area or might be a result of long-term exposure to high-deer densities (Beschta and Ripple 2009; Chaideftou et al. 2011).

Forb species composition in *Solidago* spp.-*Rubus hispidus* communities increased in spring-protected plots and continuously-protected plots. We also saw a simultaneous decrease in graminoid species in the same plots; however, this difference was not considered statistically significant. Studies have found that high-density white-tailed deer populations tend to reduce forb cover and increase the less-preferred graminoid species (Thiemann et al. 2009; Goetsch et al. 2011; Urbanek et al. 2012a; Urbanek et al. 2012b). These results suggest that the trend can be reversed with protection from deer browse. Additionally, the lack of change in late protected plots suggests that timing of browse does make a difference in forb species composition. Merrill

et al. (2003) determined that a reduction in graminoid cover resulted from an increase in woody shrub cover.

Our results suggest that protection from deer browse does not favor either wetland or upland plants. We found that there was not a significant difference in the average change between wetland plant indicator status categories though individual species may have increased or decreased. Thus, a reduction in deer density would not likely shift community composition away from wetland species. Conversely, while high deer densities may negatively impact individual species, they do not tend to reduce overall wetland plant cover.

White-tailed deer exclosure studies used to measure the impacts of deer herbivory on plant populations have been criticized for a variety of reasons. Nonrandom location of study plots in areas of high deer density may bias the results toward greater impacts of herbivory (Russell et al. 2001). Many exclosure studies are criticized for small sample size (Russell et al. 2001) resulting from the difficulty and expense of building and maintaining large exclosures (Kirschbaum and Anacker 2005). Lastly, exclosure studies generally provide results from two extremes; no deer or high deer densities. Neither of these scenarios are a natural management goal for white-tailed deer populations (Russell et al. 2001). Studies of deer enclosures, while much more expensive and difficult to maintain, may provide insight in effects at multiple deer densities (deCalesta 1994).

Our study of deer exclusion plots in Canaan Valley attempted to remedy some of these problems through study design. We used smaller exclosures that were easier and less expensive to build and transport into wetland areas. This allowed us to increase the sample size beyond some limited exclosure studies of the past. However, the small exclosure size may not have been sufficient in *Populus* spp. regeneration cuts as the fence was not tall enough to completely

protect the fast growing *Populus* spp. saplings (Westell 1954). Although deer were not able to affect herbaceous cover within these exclosures, impacts to *Populus* spp. growth may have influenced microhabitat characteristics that affect understory growth. More fenced plots also allowed us to investigate the effects of timing on herbivory. Periodic removal of exclosures helped us to address the failure of exclosure studies to simulate management regimes that include some deer herbivory.

Rooney and Waller (2003) increased exclosure sample size to survey rare forest herbaceous species. We also had a relatively large sample size compared to other exclosure studies; however, we randomly located plots within our study sites. Although this prevented bias in selecting areas of high or low deer herbivory and allowed us to examine the community composition as a whole, we were not able to examine the effect of herbivory on specific rare plant species.

Several authors have used natural refugia such as boulders or island isolation to study the impact of deer on plant communities without the effects of artificial exclosures (Balgooyen and Waller 1995; Rooney 1997; Comisky et al. 2005). This type of study was not possible in the *Solidago* spp.-*Rubus hispidus* of Canaan Valley because of the open nature of such herbaceous wet-meadow communities. Future study of the regeneration of woody plant communities such as the *Populus* spp. cuts examined here could benefit from a cutting plan designed to create “exclosure” that mimic natural phenomena.

An extended study period may allow for additional change in community composition and differentiation. Other studies have found higher species richness within exclosures > 4 years after initiation (Holmes et al. 2008; Pellerin et al. 2010; Duguay and Farfaras 2011; Holmes and Webster 2011; Urbanek et al. 2012b). However, Rutherford and Schmitz (2010) found that deer

may not impact richness and abundance of plant species, in part, because historical deer densities may have limited the number of palatable species. Anecdotal observation of control and treatment plots in 2008, suggest a difference in species cover between treatment plots and surrounding vegetation community that may not be measurable with percent cover estimates. Though stem count methods are tedious and often prohibitive in herbaceous community studies, percent cover estimates may be too subjective to detect differences in species cover and community composition over short time periods. Other methods of quantification should be examined for future studies.

Conclusion

Historically, the red spruce climax community that covered Canaan Valley likely supported lower white-tailed deer densities than are present today. The herbaceous wet-meadow communities in Canaan Valley today increase the availability of forage during the spring and summer and may increase the carrying capacity from historical densities. However, our study suggests, that the elevated deer densities present in the post-logging era impact the herbaceous community by selectively browsing forb species, especially in the spring. Suppression of woody species through selective browsing may play a role in suppressing succession to the historical spruce communities.

Our study indicates that timing of herbivory may be a factor in the impact of white-tailed deer browse on some species. However, protecting wetland communities seasonally should not be considered a time or cost effective measure to increase the frequency of wetland species. On a small scale, these exclosures were not difficult to move periodically; however, there is likely no incentive to employ seasonal exclosures in place of continuous protection (Merrill et al. 2003; Clements et al. 2011; DeGroote et al. 2011). Seasonal protection may be more effective on

individual plants representing threatened or endangered species where yearlong protection may not be appropriate. Our study did not examine the seed bank present at each site. It is unlikely that increased frequency of certain species is a result of seed input from outside sources but rather the reduction of browse in species already present on site. Levine et al. (2012) found that deer did not alter seed banks but did alter sapling richness. Our results suggest that extended reduction of deer browse through protection of plant communities may alter the trajectory of these communities toward a community with more woody cover.

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Table 1. Blocked Multiple Response Permutation Procedure (MRBP) tests of plant community composition differences between fenced and unfenced plots in Canaan Valley, WV from 2005 – 2007 grouped by period of protection and time of data collection. The T-statistic (T) describes the difference between selected groups. The p-value (p) describes the likelihood of reaching the observed T-statistic. The A-statistic (A) describes within group homogeneity compared to what is expected by chance. Bold text indicates significant differences ($P < 0.05$).

	Monitoring Period	Early			Late			Continuous		
		T	P	A	T	P	A	T	P	A
<i>Solidago</i> spp.- <i>Rubus hispidus</i>	Fall	-1.635	0.066	0.027	-4.547	0.002	0.010	-0.863	0.181	0.019
<i>Solidago</i> spp.- <i>Rubus hispidus</i>	Spring	-3.474	0.004	0.071	-0.192	0.400	0.003	-2.386	0.026	0.055
<i>Populus</i> spp.	Fall	-0.516	0.258	0.027	0.490	0.673	-0.026	-1.282	0.107	0.064
<i>Populus</i> spp.	Spring	-1.340	0.087	0.076	-2.1013	0.038	0.116	-2.0775	0.039	0.073

Table 2. Species displaying the largest changes within fenced plots in *Solidago* spp. - *Rubus hispidus* communities in Canaan Valley, WV. Mean values represent the difference in percent cover based on the midpoint of cover class categories between 2005 and 2007. A positive value indicates higher percent coverage in 2007. Negative values indicate lower percent coverage in 2007 than 2005. Blank values indicate no change recorded for that monitoring period. Wetland Indicator Status was recorded from the 2014 Army Corps of Engineers National Wetland Plant List.

	Wetland Indicator Status	Fall Late		Spring Early		Spring Continuous	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	FACU			1.50	1.42	-1.50	-1.50
<i>Agrostis gigantea</i> Roth	FACW	-0.25	0.24	-0.25	0.24	-0.50	-0.50
<i>Amelanchier</i> spp.	FACU-FACW	1.25	1.19	-1.50	2.43		
<i>Anthoxanthum odoratum</i> L.	FACU	0.25	0.24			-2.00	-2.00
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	FAC	2.25	1.64	-5.75	3.50	-0.50	-0.50
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	FACW					4.00	4.00
<i>Crataegus</i> spp.	Kn.			-1.50	1.42		
<i>Danthonia compressa</i> Aust.	FACU	-7.00	3.39	-2.75	7.73	-6.75	-6.75
<i>Doellingeria umbellata</i> (P. Mill.) Nees var. <i>umbellata</i>	FACW	2.25	2.13			5.50	5.50
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	FAC	-2.50	3.87	4.25	2.24	1.25	1.25
<i>Festuca trachyphylla</i> (Hack.) Krajina	UPL	-4.75	4.51	-1.50	1.42	-3.75	-3.75
<i>Holcus lanatus</i> L.	FAC	1.25	1.19			-0.25	-0.25
<i>Populus tremuloides</i> Michx.	FAC	-0.25	1.95	3.75	3.56	-1.25	-1.25
<i>Potentilla canadensis</i> L.	Kn.	-1.50	1.23				
<i>Potentilla simplex</i> Michx.	FACU			-3.00	7.38	1.50	1.50
<i>Pteridium aquilinum</i> (L.) Kuhn	FACU	-4.50	2.85	7.00	7.86	12.25	12.25
<i>Rubus hispidus</i> L.	FACW	6.25	4.50	24.75	6.52	16.25	16.25
<i>Solidago rugosa</i> Mill.	FAC	3.00	4.57	14.25	6.08	7.75	7.75
<i>Solidago uliginosa</i> Nutt.	OBL	1.25	3.40	2.75	4.02	15.00	15.00
<i>Spiraea alba</i> Du Roi	FACW	2.75	1.75	-1.75	1.46	3.75	3.75
<i>Vaccinium angustifolium</i> Ait.	FACU			3.75	3.56	-0.25	-0.25
<i>Vaccinium myrtilloides</i> Michx.	FACW			1.75	2.55		
<i>Vaccinium pallidum</i> Ait.	Kn.					-3.75	-3.75
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> (L.) Torr. & Gray	OBL	-1.50	1.42	1.50	1.42		
<i>Viburnum recognitum</i>	FAC					1.50	1.50

Table 3. Species displaying the largest changes within fenced plots in *Populus* spp. communities in Canaan Valley, WV. Mean values represent the difference in percent cover between 2005 and 2007. A positive value indicates higher percent coverage in 2005. Negative values indicate lower percent coverage in 2007 than 2005. Blank values indicate no change recorded for that monitoring period.

	Wetland Indicator Status	Spring Continuous		Spring Late	
		$\bar{x}$	SE	$\bar{x}$	SE
<i>Anthoxanthum odoratum</i> L.	FACU	-2.83	1.62	1.17	2.18
<i>Apocynum cannabinum</i> L.	FACU	1.25	1.20		
<i>Doellingeria umbellata</i> (P. Mill.) Nees	FACW	-4.42	4.36	2.63	1.62
<i>Carex brunnescens</i> (Pers.) Poir.	FACW	0.83	0.34		
<i>Carex bushii</i> Mack.	FACW	0.42	0.27		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	FAC	-1.71	1.43	-0.25	0.13
<i>Carex folliculata</i> L.	OBL	-1.04	1.00		
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	FACW	0.42	0.27		
<i>Carex virescens</i> Muhl ex. Willd.	Kn.	-3.29	2.98		
<i>Crataegeus</i> spp.	Kn.			0.13	0.23
<i>Danthonia compressa</i> Aust.	FACU	1.58	1.20	0.42	0.28
<i>Dichanthelium clandestinum</i> (L.) Gould	FAC			1.42	1.16
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	FAC			0.13	0.23
<i>Glyceria striata</i> (Lam.) Hitchc.	OBL	-1.33	1.19		
<i>Hypericum punctatum</i> Lam.	FAC	-2.50	1.61		
<i>Juncus effusus</i> L.	FACW	0.33	0.29		
<i>Poa trivialis</i> L.	FACW			0.13	0.23
<i>Polygonum sagittatum</i> L.	OBL			0.13	0.23
<i>Populus tremuloides</i> Michx.	FAC	20.17	4.03	-3.63	5.27
<i>Potentilla simplex</i> Michx.	FACU	3.75	1.78	-0.92	1.08
<i>Prunus serotina</i> Ehrh..	FACU			-0.08	0.08
<i>Pteridium aquilinum</i> (L.) Kuhn	FACU	-2.08	1.99	-1.04	1.29
<i>Ranunculus acris</i> L. var. <i>acris</i>	FAC			1.08	1.18
<i>Rubus hispidus</i> L.	FACW	9.58	4.12	3.25	3.03
<i>Solidago rugosa</i> Mill.	FAC	8.50	5.47	-4.88	4.60
<i>Solidago uliginosa</i> Nutt.	OBL	-5.04	3.23	0.13	0.23
<i>Spiraea alba</i> Du Roi	FACW			0.21	0.21

Table 4. Number of species within each wetland plant indicator status category showing a change (increase or decrease) in average cover class category after two years (2005 –2007) of fencing treatment in *Populus* spp. and *Solidago* spp.-*Rubus hispidus* dominated communities in Canaan Valley, WV. Early and late plots were protected for a portion of the year while continuous plots were protected year-round.

	<i>Populus</i> spp.				<i>Solidago</i> spp. - <i>Rubus hispidus</i>					
	Continuous		Late		Continuous		Late		Early	
	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease
OBL	3	7	3	2	1	0	1	2	2	0
FACW	7	6	3	0	3	3	3	1	6	0
FAC	4	4	3	3	4	4	5	2	4	2
FACU	7	4	4	3	3	4	2	4	3	6
UPL	0	0	0	0	0	1	0	1	0	1

Fig. 1. Map of Canaan Valley, WV with locations of *Populus* spp. exclosures (red) and *Solidago* spp.-*Rubus hispidus* exclosures (blue) that were in place from 2005–2007.

Fig. 2. Plot location within each study site indicating the sizes of exclosures and relative spacing of control plots. Spacing between exclosures is not to scale. Exclosures were constructed in 2005 and removed in 2007.

Fig. 3. Average plant species richness in control and fenced plots within *Solidago* spp.-*Rubus hispidus* communities in Canaan Valley, WV, from 2005–2007.

Fig. 4. Average plant species richness in control and fenced plots within *Populus* spp. regeneration communities in Canaan Valley, WV, from 2005–2007.

Fig. 5. Average change in cover for forbs, graminoids, and woody species that are protected early, late and continuously in *Solidago* spp.-*Rubus hispidus* communities in Canaan Valley, WV, when data were collected in the spring of 2005 through 2007.

Fig. 6. Average change in cover for forbs, graminoids, and woody species that are protected early, late and continuously in *Solidago* spp.-*Rubus hispidus* communities in Canaan Valley, WV, when data were collected in the fall 2005 through 2007.

Fig. 7. Average change in cover for forbs, graminoids and woody species that are protected early, late and continuously in *Populus* spp. regeneration communities in Canaan Valley, WV, when data were collected in the spring of 2005 through 2007.

Fig. 8. Average change in cover for forbs, graminoids and woody species that are protected early, late and continuously in *Populus* spp. regeneration communities in Canaan Valley, WV when data were collected in the fall of 2005 through 2007.

CHAPTER IV

The Influence of White-tailed Deer on the Structure and Composition of Eastern Deciduous Forest Understory

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Abstract

Browsing by white-tailed deer (*Odocoileus virginianus* Zimm.) can lead to long-term changes in forest community composition by inhibiting regeneration and changing the forest habitat for understory-dependent wildlife species. We analyzed a 21 – year vegetation data set collected by the West Virginia Division of Natural Resources on randomly selected forest community sites throughout West Virginia from 1984 to 2007. Each site consisted of paired 100 m² plots; an unfenced control plot and a treatment plot bounded by a 2.44 m woven wire fence. We used blocked Multiple Response Permutation Procedures to determine if differences in community composition existed between fenced and control plots at 3-year intervals after fence construction. Finally, we tested whether the frequency of saplings in control plots could predict deer abundance using a seedling/sapling ratio of “preferred species.” We observed significant differences in understory community composition between treatment and control plots 6 years ($P = 0.024$) after plot establishment and continued through the 21 years ($P = 0.006$) analyzed. We found no difference in ground cover community composition throughout the 21 years of data collection. Diversity values were greater in fenced than in control plots ($P < 0.001$), suggesting that changes in understory communities were not driven by the success of a single species. Species richness in the understory declined in control plots (from 5.13 ± 2.11 to 4.00 ± 2.38) and

increased in treatment plots (from 5.67 ± 1.54 to 8.92 ± 1.60) throughout the course of the study. Understory stem density also increased in treatment plots (from 5.25 ± 1.83 to 11.59 ± 8.56 stems/m²) after 9 years, but similar increases were not measured in control plots. The seedling-sapling ratio of preferred species was not a significant predictor of deer density ($P < 0.05$). These results suggest that forest understories may begin to recover from chronic over-browsing within 6 years after herd elimination from a stand, provided the seed bank and seed rain from mature trees are unaffected. However, our results indicate that after 21 years, the seed bank may be affected to the degree that the ground cover community is affected. As our study sites reflect conditions throughout West Virginia, this may be the reality for many of the state's forests.

Keywords: *Odocoileus virginianus*, deciduous forest, MRBP, community, density, West Virginia, sapling ratio, preferred species

1. Introduction

The recovery of white-tailed deer (*Odocoileus virginianus*) populations in the eastern United States from near extirpation has been considered one of the greatest natural resource conservation success stories of the 20th century (Waller and Alverson, 1997). Historic estimates of deer densities from the time of European colonization of the Americas have ranged from 3 – 6 deer/km². Chronic overhunting led to declines in densities to the point of localized extirpation in some areas (Warren, 2011). To prevent the loss of this species, game laws were enacted as early as 1646 (McCabe and McCabe, 1984) to reduce harvest of males and, in some cases, eliminate harvest of females (Rooney and Waller, 2003). Harvest restrictions coincided with an increase in early successional growth of eastern deciduous and coniferous forests following widespread intensive timber harvest for industry (McShea, 2012). Thus, the carrying capacity of much of the east was increased over that of the old-growth forest habitat. Finally, populations of natural predators were reduced or eliminated through hunting and trapping, reducing natural mortality of white-tailed deer populations (Cote et al., 2004; Abrams and Johnson, 2012; Potvin et al., 2003). As a result, white-tailed deer populations have reached and exceeded historical densities throughout much of their range (Abrams and Johnson, 2012; Knight et al., 2009; Rooney, 2001; Webster et al., 2005). Many biologists now question whether or not white-tailed deer could be considered overabundant in some parts of their range (Nuttall et al., 2013; Stromayer and Warren, 1997).

Overabundance of a wildlife population has been defined as fitting into one of four categories: 1) when an animal threatens human life and livelihood, 2) when animals depress the densities of favored species, 3) when animals are too numerous for their own good, and 4) when their numbers cause ecosystem dysfunction (Caughley 1981). Extensive browsing by white-tailed deer may fit into each of these categories by reducing regeneration of desirable timber species, altering plant and animal community composition, reducing the carrying capacity of their environment by reducing palatable browse species and preventing regeneration of mast species, and potentially affecting decomposition rates by altering the forest floor microclimate.

Early research on the interaction of white-tailed deer and plant species was concentrated on economically important agricultural and timber species. Many studies have focused on just one species. White-tailed deer can have detrimental effects on the growth of eastern hemlock (*Tsuga canadensis*)(Alverson and Waller, 1997; Anderson and Loucks, 1979; Krueger and Peterson, 2006; Stromayer and Warren, 1997; Whitney, 1984), white cedar (*Thuja occidentalis*), yellow birch (*Betula lutea*)(Stromayer and Warren, 1997), white pine (*Pinus strobus*) (Marshall et al., 1955; Saunders and Puettmann, 1999), and various oak species (*Quercus* spp.)(Healy, 1997; Rooney and Waller, 2003). Fewer studies have examined multiple species at the community level (Russel et al., 2001). Hough (1965) recorded a loss of preferred species and decline of less preferred species through a 20-year photographic record. Similar results were found concerning species composition and stem density on fixed deer density plots within exclosures (deCalesta and Stout, 1997; Tilghman, 1989). Several studies using natural refugia rather than man-made exclosures also found differences in plant communities that were protected from white-tailed deer browsing such as higher stem abundance than exposed plots and altered community composition with fewer palatable plants present in exposed plots (Carson et al., 2005; Comisky et al., 2005; DiTommaso et al., 2014; Krueger and Peterson, 2006). At the community level, Peek and Stahl (1997) found that white-tailed deer had extirpated 150 vascular plant species from one city park in Ohio.

More recently, additional studies have indicated that intensive white-tailed deer browsing may impact herbaceous forest species (Augustine and Frelich, 1998; Russel et al., 2001), endangered plant species (Loeffler and Wegner, 2000), and animal communities (Martin et al., 2011; McShea and Rappole, 1997; Miller et al., 1992). Deer herbivory has been cited as a detriment to tall grass prairie forbs (Anderson et al., 2001), riparian willow species (Brookshire

et al., 2002), and additional riparian vegetation restoration efforts (Opperman and Merenlander, 2000). White-tailed deer can reduce and potentially extirpate local populations of American ginseng (*Panax quinquefolius*)(Furedi and McGraw, 2004), Turk's cap lily (*Lilium superbum*)(Fletcher et al., 2001), and showy lady slipper (*Cypripedium reginae*)(Gregg, 2004).

Historically, large populations of herbivores such as the American bison (*Bison bison*) were responsible for maintaining ecosystems such as tall grass prairies through seasonally heavy grazing. Species of the eastern deciduous forest that are adapted to year-long browsing by lower densities of herbivores could be depleted when browsing pressure increases (Waller and Alverson, 1997; Warren, 1997). The selection of certain plants for nutrient content or palatability can result in the loss of individual plant species and a decrease in community diversity (Dostaler et al., 2011; Moseley et al., 2011). The loss of plant community components can affect organisms that rely on those communities (deCalesta, 1994; Flowerdew and Elwood, 2001; Martin et al., 2011) and a reduction of other ecosystem services.

Through excessive browsing, white-tailed deer populations have the potential to exert long-term influence on forest communities (Heckel et al., 2010; Tremblay et al. 2006). A reduction in understory plant density may encourage the growth of ground cover species such as hay-scented fern (*Dennstaedtia punctilobula*)(de la Cretaz and Kelty, 2002; Powers and Nagel, 2009). Heavy growth of unpalatable ground cover plants can prevent the growth of tree species by reducing the amount of sunlight available on the forest floor and through allelopathy (de la Cretaz and Kelty, 2002; Royo and Carson, 2006). Ground cover growth also can provide shelter for small mammals which consume seeds from overstory tree species, thus preventing reproduction of the existing overstory community (Royo and Carson, 2006). Thus, white-tailed deer may have the ability to influence the creation of alternate stable states in an ecosystem (Augustine et al., 1998). An alternate stable state is a community that exists in a different state than would be predicted by ecological succession and remains stable without a disturbance event (Stromayer and Warren, 1997). A lack of recruitment of currently dominant overstory species may result in the loss of these species from the community once the seed production is reduced as mature overstory trees are lost. Likewise, future herbaceous plant communities may be changed in composition under high browse pressure once the seed bank is depleted.

This study was designed to evaluate the effects of white-tailed deer exclusion on the ground cover (< 0.5 m) and understory (> 0.5 m and < 2.54 cm diameter at breast height [DBH])

forest layers. The specific objectives of our study are to evaluate the effect of white-tailed deer browse on stem density, species diversity, and composition in the understory and ground cover forest levels using fenced areas (treatment plots) and associated unfenced control plots and to determine if the recruitment of preferred species into the understory can act as a predictor of white-tailed deer density.

2. Methods

2.1 Study area

Twenty sites were selected from public lands throughout West Virginia (Fig. 1). These lands included West Virginia Division of Natural Resources (WVDNR) wildlife management areas (WMAs) and sites on national forest land located in the state. The majority of the sites were located in oak (*Quercus* spp.)–hickory (*Carya* spp.) dominated stands that were in the pole to mixed pole-saw timber stage when the study began. Sites were established to include low, medium, and high deer density based on the buck harvest per square kilometer as reported to the WVDNR during annual hunting seasons. Low density sites had < 0.77 bucks/km² harvested, medium had $0.78 - 1.9$ bucks/km² harvested, and high density areas had > 1.93 bucks/km² harvested when the sites were selected between 1984 and 1990. All sites were open to public hunting according to annually established regulations. Exclosure sites were selected so that they were distributed by elevation, slope, and aspect in all regions of the state. Specific sites were selected by district biologists or area managers based on cover types typical of the area as well as accessibility by road. While most exclosures were constructed in oak-hickory stands ($n = 9$), exclosures were also established in a clearcut ($n = 1$), early successional cover ($n = 2$), in northern hardwoods (conifers and hardwoods makeup the canopy cover with conifers contributing $< 25\%$, $n = 3$), and in mixed hardwoods (conifers and hardwoods makeup the canopy cover with conifers contributing $> 25\%$ (Fike, 1999, $n = 5$). Of those constructed in forested cover types, the majority were located in stands that were in pole or saw-timber stages, averaging 12.7 cm DBH (Allen, 1990).

2.2 Vegetation Monitoring

Vegetation-monitoring sites were constructed throughout the state between 1984 and 1990 (Table 1). At each site, a 100 m² (10 m by 10 m square) treatment plot was constructed using two strands of 1.22 m tall woven wire fencing for a total fence height of 2.44 m. Control plots were established immediately adjacent to the treatment plot on a similar aspect and slope.

Within each treatment and control plot, nine 1 m by 1 m subplots were nested within nine 2 m by 2 m subplots (Fig. 2).

Plots were monitored in 3-year intervals between June and September by counting all stems within subplots and identifying each to species. Stems were grouped in two vegetation categories; ground cover included herbaceous stems and woody stems that were < 0.5 m tall and that fell within 1 m² subplots. Understory vegetation was defined as all stems that grew within 4 m² subplots that were > 0.5 m tall and < 2.54 cm DBH.

2.3 Data Analysis

We pooled data based on the number of years following plot establishment. For example, we treated data collected in 1987 for plots established in 1984 and data collected in 1989 for plots established 1986 as three years post-establishment. We summarized stem counts for each control plot and treatment plot by averaging the number of stems in each subplot for each species. We calculated the species richness and Shannon diversity values for each control plot and treatment plot as a whole. We used a 2-way repeated measures analysis of variance to compare the number of stems, the number of species, and the Shannon diversity values between control plots and treatment plots over time. We considered differences to be significant at the $\alpha = 0.05$ level.

We used blocked Multiple Response Permutation Procedures (MRBP) in program PC-Ord (McCune and Mefford 1999) to determine if differences in community composition existed between fenced and control plots at 3-year intervals after fence construction. A multiple-response permutation procedure test is a non-parametric multivariate test of differences between *a priori* groups (treatment and control plots). PC-Ord calculates a T-statistic that describes the difference between selected groups; a P-value that describes the likelihood of reaching the observed T-statistic; and an A-statistic that describes within group homogeneity compared to what is expected by chance. When $A = 1$ the plots are completely identical and when $A = 0$ the communities are equal to what is expected by chance. We excluded all species that only occurred in one plot during each monitoring period. We chose to use Euclidean distance measures as other measures were not available with the blocked design in PC-Ord (McCune and Mefford 1999). We repeated this process for 2 subsets of the overall data to control for the influence of variation in initial communities. We selected those sites created in oak-hickory dominated stands and those created within the Northern Ridge and Valley ecoregion of West

Virginia (Fig. 1). In addition, we examined the data for natural groupings using cluster analysis in PC-Ord. We used the Sorensen distance measure and flexible beta ($\beta = -0.25$) as the linkage method to reduce chaining in group selection.

We used Indicator Species Analysis (ISA; (Dufrene and Legendre, 1997) in program PC-Ord (McCune and Mefford 1999) to determine if individual species were characteristic of protected plots or open plots for each year that we found significant differences in community composition using MRBP. The ISA combines the relative abundance and relative frequency of each species used in the MRBP analysis to provide a final indicator value (IV) for each species. We used a Monte Carlo randomization analysis using 1,000 runs to determine the statistical significance of each indicator value given by a *P*-value. In addition to ISA, we estimated the influence of each species on overall community differences by calculating an index representing the difference between control plots and treatment plots during years when a significant community difference was detected using MRBP. The index was calculated by multiplying the mean difference between treatment plots and control plots by the frequency of sites on which a difference occurred. Each species was ranked so that the highest values indicated species with greater abundance inside fenced areas and the lowest (most negative) values indicated species with greater abundance outside the fenced areas.

Finally, we created an index using the seedling-sapling ratio index following Sweetapple and Nugent (2004). This ratio was calculated by the following equation:

$$\frac{\text{sapling} - \text{seedling}}{\text{sapling} + \text{seedling}}$$

for all species. From those species found at the understory level, we selected a subset that were consistently (i.e. they only displayed positive values for the index described above) more abundant in treatment plots than control. We used linear regression to evaluate the relation between the seedling-sapling ratio for control plots and the total deer density at the site from 1993 – 2007 as measured by WVDNR harvest data. We removed all sites in which the seedling-sapling ratio was one for all time periods (e.g. Cheat Mountain, Daniel's Run, Dice Run).

3. Results

3.1 Ground cover level

We recorded 197 species present in the ground cover over the study period (Appendix 6). Immediately after plot initiation, the mean stem abundance in control plots was 31.5 ± 8.63

stems/m² whereas the stem abundance in treatment (fenced) plots was 35.5 ± 12.71 stems/m² (Fig. 3). After 21 years, the stem abundance in the treatment plot decreased slightly to 32.14 ± 15.5 stems/m² and the stem abundance in the control plots increased to 37.67 ± 15.5 stems/m². We found no significant difference based on time ($F_{1,19} = 0.09$, $P = 0.77$) or treatment ($F_{1,19} = 0.13$, $P = 0.17$) in predicting stem abundance. There was no significant interaction between treatment and time ($F_{1,19} = 0.39$, $P = 0.53$). Immediately, after plot initiation, the average species richness of control plots was 15.0 ± 2.84 ; in treatment plots the average was 15.47 ± 2.60 . After 18 years, the average species richness in control plots increased to 18.69 ± 4.87 and increased in treatment plots to 18.46 ± 4.14 (Fig. 4). The species richness decreased by year 21 to 15.5 ± 5.23 in control plots and 15.5 ± 4.60 in treatment plots. We found no significant differences based on time ($F_{1,19} = 0.57$, $P = 0.44$) or treatment ($F_{1,19} = 0.21$, $P = 0.65$) in predicting species richness. There was no significant interaction between treatment and time ($F_{1,19} = 0.039$, $P = 0.84$). Average Shannon diversity values for the ground cover were similar between control plots and treatment plots throughout the study. In year 21, the diversity of treatment plots was higher (1.61 ± 0.17) than control plots (1.27 ± 0.26). However, we found no significant differences based on time ($F_{1,19} = 0.01$, $P = 0.92$) or treatment ($F_{1,19} = 0.89$, $P = 0.36$) in predicting Shannon diversity values (Fig. 5). There was no significant interaction between treatment and time ($F_{1,19} = 1.59$, $P = 0.22$).

3.2 Understory level

We recorded 79 species present in the understory over the study period (Appendix 7). Immediately after plot initiation, the mean stem abundance in control plots was 4.94 ± 3.72 stems/m², whereas the stem abundance in treatment plots was 5.25 ± 5.10 stems/m² (Fig. 6). The stem abundance in treatment plots increased to 11.59 ± 8.56 stems/m² by year 9. After 21 years, the stem abundance in the treatment plot decreased to 5.25 ± 1.83 stems/m² and the stem abundance in the control plots was 2.45 ± 1.23 stems/m². We found that treatment ($F_{1,19} = 12.22$, $P < 0.001$) had an effect on the stem abundance, but time did not ($F_{1,19} = 0.78$, $P = 0.37$, Fig. 6). There was no significant interaction between treatment and time ($F_{1,19} = 0.14$, $P = 0.71$). After plot initiation, the average species richness of control plots was 5.13 ± 2.11 and in treatment plots, the average was 5.67 ± 1.54 . After 21 years, the average species richness in control plots decreased to 4.00 ± 2.38 and increased in treatment plots to 8.92 ± 1.60 (Fig. 7). We found that treatment ($F_{1,19} = 78.77$, $P < 0.001$) had a significant effect on the species richness, but time did

not ($F_{1,19} = 1.32$, $P = 0.37$, Fig. 7). There was a significant interaction between time and treatment factors ($F_{1,19} = 9.55$, $P < 0.01$). Using Tukey's HSD for post hoc analysis, we found that species richness did not differ between control and treatment plots in year 1 ($P = 1.00$), and year 3 ($P = 0.89$); species richness was significantly different in subsequent years ($P < 0.05$) with the exception of year 12 ($P = 0.15$). Average Shannon diversity values for the understory were higher for treatment plots than control plots throughout the study. Average diversity values were highest (1.70 ± 0.12) in treatment plots in year 18. In the same year, the average diversity values in control plots had reached their lowest value (0.74 ± 0.14 , Fig. 8). We found a significant difference based on treatment ($F_{1,19} = 40.82$, $P < 0.001$), but not time ($F_{1,19} = 0.49$, $P = 0.49$) in predicting Shannon diversity values (Fig. 8). There was no significant interaction between treatment and time ($F_{1,19} = 2.38$, $P = 0.14$).

3.3 Community Analysis

We found no difference in understory community composition during the initial observation ($T = 1.10$, $P = 0.87$) and 3 years ($T = -1.68$, $P = 0.057$) following initiation for each site. Significant differences between treatment plots and control plots were observed 6 years ($T = -4.34$, $P = 0.001$) after plot establishment and during 9 ($T = -4.16$, $P = 0.002$), 15 ($T = -4.49$, $P = 0.002$), 18 ($T = -4.63$, $P < 0.001$), and 21 ($T = -4.20$, $P = 0.001$) years after plot establishment. In the oak-hickory subset, we found significant differences between treatment and control plots at the understory level 6 years ($T = -1.67$, $P < 0.05$) and 9 years ($T = -2.66$, $P < 0.01$) after plot establishment, but not in subsequent years (Table 3). At the ground cover level, we found a significant difference occurred 21 years after plot initiation ($T = -0.20$, $P = 0.03$, Table 3). In the Northern Ridge and Valley ecoregion subset, we observed significant differences between treatment plots and control plots at the understory level 6 years ($T = -2.60$, $P = 0.01$), 15 years ($T = -2.33$, $P = 0.02$), and 18 years ($T = -1.98$, $P = 0.02$, Table 4) after plot establishment. At the ground cover level, we observed significant differences between treatment and control plots at the understory level 12 years ($T = -2.17$, $P = 0.02$), 15 years ($T = -2.66$, $P < 0.01$), and 21 years ($T = -2.23$, $P = 0.03$, Table 4) after plot establishment. The subset of plots analyzed using hierarchical cluster analysis included the Bluestone, Centrailia, Hughes River, Jug, R.D. Bailey, and Stoney River sites (Figure 1). At the understory level, we found a significant difference between control and treatment plots in this subset after 9 years ($T = -1.96$, $P < 0.02$) and 18 years ($T = -2.19$, $P = 0.035$, Table 5).

We found that black gum (*Nyssa sylvatica*) was an indicator of treatment plots 6 years after initiation ($P = 0.041$). Both greenbrier (*Smilax* spp.) and sugar maple (*Acer saccharum*) were indicators of treatment plots 12 years ($P = 0.028$ and $P = 0.029$, respectively) and 15 years ($P = 0.033$ and $P = 0.030$, respectively) after initiation. Red maple (*A. rubrum*) was an indicator of treatment plots 21 years after initiation ($P = 0.007$). We found that *Rubus* spp. were the only species found to indicate treatment plots within the oak–hickory, Northern Ridge and Valley, and clustered subsets of data analyzed.

Species that consistently showed higher abundance in treatment plots were bellwort (*Uvularia* spp.) and Virginia creeper (*Parthenocissus quinquefolia*) at the ground cover level (Table 6) and *Rubus* spp. and greenbrier at the understory level (Table 7). Species that consistently showed higher abundance in control plots were blueberry (*Vaccinium* spp.) and red maple at the ground cover level (Table 6) and beech (*Fagus grandifolia*) and pawpaw (*Asimina triloba*) at the understory level (Table 7).

We examined the potential for the seedling-sapling ratio to act as a predictor of density (Table 8) at all sites combined. We found no relation between the seedling-sapling ratio and deer density ($R^2 = 0.02$, $P = 0.17$, Fig. 9).

4. Discussion

Our results indicate that white-tailed deer populations do have the potential to impact understory vegetative communities in eastern deciduous forests. We found that the community composition of forest communities relieved of white-tailed deer browse changed after 6 years at the understory level. However, at the ground cover level, no difference was observed over the 21 years of the study. Lack of seedling recruitment into the understory level is a common finding among deer exclosure or variable density studies (DiTommaso et al., 2014; Fujiki et al., 2010; Powers and Nagle, 2009; Rooney, 2009; Tanentzap et al., 2009). In a similar, 16-year study Rooney (2009) found that the species composition of exclosure plots differed significantly from control plots, but the richness and diversity of the plots did not change. This suggests that a shift toward a community based on less palatable species may be underway. He also found that his control plots grew more similar in species composition throughout the study suggesting that high densities of white-tailed deer can tend to homogenize the forest community on a regional scale.

A common criticism of deer exclosure studies is that they exclude deer entirely from treatment plots. Rather than simulate precolonial conditions, exclosures simulate the undesirable extreme scenario of no white-tailed deer (or other large herbivores) within the community. The control plots within this study represent plots exposed to a wide range of local deer densities (Table 8) at different sites throughout the state. Though this study was initially designed to monitor plots at low, intermediate, and high deer densities, these densities did not remain static from year to year making it difficult to assign sites to *apriori* groups for the duration of the study. However, we believe the length of our study allows a better representation of the impact of deer populations over time, as plant communities may be influenced not only by the current deer density, but by the legacy of past higher or lower densities (Royo et al., 2010).

Indicator species analysis seeks to find species that are present in a large proportion of one treatment group and found rarely in another (McCune and Grace, 2002). Though the MRBP indicated that there was a difference between control and treatment plots, few significant indicator species were identified that increased in all plots with the relief from browse pressure. This may reflect the large range of initial forest communities in which the monitoring plots were established. In addition to indicator species analysis, we quantified which species were found more often in treatment plots and which were more abundant in control plots. The species that were more prevalent in treatment plots such as *Rubus* spp. and greenbrier (*Smilax* spp.) have been cited by others as species “preferred” by deer (Comisky et al., 2005; Dostaler et al., 2011; Healy, 1997). Likewise, species like American beech (*Fagus grandifolia*) and blueberry (*Vaccinium* spp.) are typically considered not preferred by deer (Carson et al., 2005; Kribel et al., 2011; Webster et al., 2005) and were more abundant in control plots in our study. Our results support the idea that deer impact species composition without necessarily impacting the amount of cover.

Several studies predicted that, with continued exposure to high deer densities, the increasing grass and fern cover may have secondary effects on species composition; reducing the cover of even “non-preferred” species (de la Cretaz and Kelty, 2002; Royo and Carson, 2006). We found that several taxa, including New York fern (*Thelypteris noveboracensis*), hay-scented fern (*Dennstaedtia punctilobula*), and *Carex* spp. declined in fenced plots over time and tended to increase in control plots over time (Appendix 6). However, the mean values for each of these varied through time.

Alteration of the vegetative communities can have more far-reaching impacts on the ecosystem as a whole (Kishimoto et al., 2010). The treatment plots in this experiment shed light on the process of ecosystem recovery after the exclusion of a chronic disturbance in the form of high white-tailed deer densities. Although removal of deer from the plots resulted in an increase in understory level vegetation, this may not be considered true ecological restoration to a pre-disturbance state, because white-tailed deer existed naturally in these ecosystems though seemingly at lower densities. Though our results indicate plant species richness and abundance increase after the removal of deer, it is difficult to determine what species may have been lost prior to the initiation of the experiment and therefore, do not have the potential to return without an influx from an outside source population. Tanentzap et al. (2009) found that ecosystem recovery may not be complete 38–46 years after deer density reduction methods are implemented. This suggests that extended exposure to high-densities of white-tailed deer may exceed the capacity of certain species to recover. Thus, these extended disturbances may lead to a permanent change in community composition.

Our results indicate that there were no measurable changes in ground cover community composition after 21 years. This suggests that there are still seed sources for species from the seed bank, from the overstory species still present, or from dispersal from surrounding areas. However, the fact that there were significant differences in both stem abundance and species richness in the understory layer after a period of years suggests that, under the influence of existing deer densities, many of the tree species included in this analysis will not reach the overstory to continue to produce seeds for the ground cover layer. When the current overstory is lost, either naturally or through harvest, these species may be eliminated from the ecosystem. The true cost to the ecosystem of extended exposure of the vegetation community to high deer densities remains to be seen, because no study has continued for the extended time that it would take for many species to become reproductive and reach the overstory.

While these effects have not been empirically measured, several studies have modeled the long-term effects of data similar to what we have collected. Akashi (2009) found that when food was the only factor limiting the growth of deer populations, the forest vegetation could not remain in a stable state. However, management of the modeled deer population allowed for continued forest regeneration. As the carrying capacity and thus vegetation-herbivore balance is constantly variable, there may not be a simple threshold density at which to maintain a stable

state (Akashi, 2009). Rather, the response of vegetation parameters to current densities must be monitored. The alteration of the vegetative community has far reaching impact throughout an ecosystem. The loss of understory diversity and density may negatively impact the understory songbird community (deCalesta, 1994, McShea et al., 1995). Changes to the vegetation community may also increase (Royo and Carson, 2006) or decrease (Flowerdew and Elwood, 2001) the density of small mammals that inhabit forest floor communities.

We did not find that the abundance of preferred browse at the understory level was a significant predictor of deer density. This may be a reflection of those species used to calculate the seedling-sapling ratios; we used all of those species found at higher abundance in treatment plots during the years that community composition was significantly different in the sapling layer. We also examined multiple subsets of these species by reducing the number of species considered and found no relation to deer density indices. Additionally, the removal of a potential outlier did not improve the fit of stem ratio as a predictor of deer density ($R^2 < 0.01$, $P = 0.52$, Fig. 9). We believe that the deer density estimates used may not have been ideal for assessing site-specific density. The estimates used in this analysis were based on hunter harvest at the management area level. We believe large-scale estimates may not necessarily reflect what occurs at the control plot within the management area, affecting the ability to relate the presence of preferred species in the sapling layer to density. However, Bennett and Coulson (2012) tested the seedling/sapling ratio method using site-level browse counts and fecal pellet indices and also failed to relate the sapling ratio to deer browsing impacts. The aforementioned study included both native and introduced herbivores whereas Sweetapple and Nugent (2004) included only introduced herbivores. Our results suggest that more study is necessary before the seedling ratio method is used as an index of deer abundance in North America.

5. Conclusions

Our results indicate the density of white-tailed deer impacting the control plots and our sites has reached or exceeded the capacity of the forest to regenerate the current community. The response of vegetation to different densities was visibly apparent though not measured through this study. At some of our sites, an alternate complement of overstory tree species may replace the dominant vegetation. At some sites, few if any overstory species are currently reaching the understory growth level thus the future of the forest cover at these sites is uncertain. It is important to determine; a) the economic and intrinsic importance of the current complement

of overstory species, b) the extent to which changes to the vegetative community will affect the local fauna, and c) the extent to which changes to the vegetative community will affect the local deer population. We believe that the seed sources still remain to produce the current complement of species. However, the impacts to the abundance of stems and species in the understory level have been chronic. We saw a significant change in this level 6 years after removal of browse pressure. Thus, the potential still exists to regenerate the current forest state. However, if browse pressure persists as the seed source declines, the potential for recovery of the current ecosystem even after removal of browse pressure is uncertain.

Though a difference in community composition occurred after 6 years at the understory level, there was no difference between control plots and treatment plots statewide at the ground cover level until year 21. Whether those seedlings were a result of the seed bank, seed rain from the existing overstory or dispersal is unclear. Continued monitoring of existing study sites could determine if the difference in ground cover composition remains after year 21. Few studies have examined forest regeneration with respect to deer over extended time periods (Rooney and Dress, 1997; Tanentzap et al., 2009). Extended monitoring could determine the fate of the ground cover layer in treatment plots after the loss of the existing overstory and potential loss of seed rain contributing to the ground cover composition. However, monitoring at the current frequency may be unnecessary to achieve that goal.

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Table 1. West Virginia Division of Natural Resources monitoring sites and monitoring dates, 1984 – 2007.

Plot Location	WV Ecoregion	1984	1986	1987	1989	1990	1992	1993	1995	1996	1999	2001	2002	2004	2005	2006	2007
Beaverdam	Allegheny Mountains	X		X		X		X		X	X		X			X	
Bluestone	N. Ridge and Valley		X		X		X		X			X		X			X
Centrallia	Allegheny Mountains	X		X		X		X		X	X		X		X		
Cheat Mountain	Allegheny Mountains	X		X		X		X		X	X		X			X	
Coopers Rock	Allegheny Mountains		X		X		X		X			X		X			X
Daniels Run	Allegheny Mountains					X		X		X	X		X		X		
Dice Run	N. Ridge and Valley		X		X		X		X			X		X			X
Holly River	Allegheny Mountains	X		X		X		X		X	X		X		X		
Hughes River	Southern Unglaciaded	X		X		X		X		X			X		X		
Jug	Southern Unglaciaded	X		X		X		X		X			X		X		
Lewis Wetzel	Southern Unglaciaded	X		X		X		X		X	X		X		X		
Little River	N. Ridge and Valley	X		X		X		X		X	X		X		X		
Nathaniel Mountain	N. Ridge and Valley	X		X		X		X		X			X		X		
Neola	N. Ridge and Valley		X		X		X		X			X		X			X
Potts Creek	Ridge and Valley		X		X		X		X			X		X			X
	N. Cumberland																
R.D. Bailey	Mountain	X		X		X		X		X			X		X		
Sleepy Creek	N. Ridge and Valley	X		X		X		X		X			X		X		
Stonecoal	Southern Unglaciaded	X		X		X		X		X	X		X			X	
Stoney Run	N. Ridge and Valley	X		X		X		X		X	X		X		X		
Trout Run	N. Ridge and Valley	X		X		X		X		X	X		X		X		

Table 2. Multiple Response Blocked Permutation values calculated every three years after plot initiation on West Virginia Division of Natural Resources deer-browse exclosure sites, 1984 – 2007. The T-statistic describes the difference between selected groups. The A-statistic describes within group homogeneity compared to what is expected by chance. The P-value describes the likelihood of reaching the observed T-statistic.

Year	Ground Cover			Understory		
	T	A	P	T	A	P
Initial	1.498	-0.007	0.945	1.100	-0.011	0.8700
3	-0.338	-0.002	0.338	-1.680	0.021	0.0570
6	0.199	-0.001	0.562	-4.342	0.039	0.001
9	-0.648	0.005	0.224	-4.158	0.066	0.002
12	-0.397	0.002	0.327	-1.476	0.034	0.080
15	-0.500	0.004	0.287	-4.486	0.115	0.002
18	-1.151	0.013	0.128	-4.626	0.059	0.000
21	-0.766	0.011	0.214	-4.202	0.061	0.001

Table 3. Multiple Response Blocked Permutation values calculated every three years after plot initiation on West Virginia Division of Natural Resources deer-browse exclosure sites located in Oak-Hickory (*Quercus* spp. - *Carya* spp.) dominated stands, 1984 – 2007. The T-statistic describes the difference between selected groups. The A-statistic describes within group homogeneity compared to what is expected by chance. The P-value describes the likelihood of reaching the observed T-statistic.

Year	Ground Cover			Understory		
	T	A	P	T	A	P
Initial	-0.419	0.006	0.316	-0.148	0.002	0.406
3	-1.101	0.041	0.136	1.093	-0.040	0.880
6	-0.804	0.004	0.206	-1.667	0.022	0.048
9	-0.630	0.007	0.253	-2.662	0.006	0.008
12	-1.524	0.024	0.069	0.159	-0.001	0.572
15	-0.302	< 0.001	0.449	-1.057	0.018	0.146
18	0.970	-0.028	0.852	-1.691	0.011	0.058
21	-0.201	0.034	0.030	-1.526	0.019	0.076

Table 4. Multiple Response Blocked Permutation values calculated every three years after plot initiation on West Virginia Division of Natural Resources deer-browse exclosure sites located in the Northern Ridge and Valley Ecoregion, 1984 – 2007. The T-statistic describes the difference between selected groups. The A-statistic describes within group homogeneity compared to what is expected by chance. The P-value describes the likelihood of reaching the observed T-statistic.

Year	Ground Cover			Understory		
	T	A	P	T	A	P
Initial	-1.580	0.019	0.124	-0.545	< 0.001	0.432
3	-0.487	0.002	0.310	1.220	-0.010	0.890
6	-0.950	0.006	0.171	-2.603	0.009	0.011
9	-1.220	0.015	0.111	-0.734	0.011	0.233
12	-2.170	0.010	0.020	-0.332	< 0.001	0.486
15	-2.017	0.021	0.031	-2.330	0.010	0.019
18	0.979	-0.019	0.836	-1.975	0.005	0.023
21	-2.230	0.053	0.026	0.339	-0.003	0.615

Table 5. Multiple Response Blocked Permutation values calculated every three years after plot initiation on a subset of West Virginia Division of Natural Resources deer-browse exclosure sites selected through hierarchical clustering, 1984 – 2007. The T-statistic describes the difference between selected groups. The A-statistic describes within group homogeneity compared to what is expected by chance. The P-value describes the likelihood of reaching the observed T-statistic.

Year	Ground Cover			Understory		
	T	A	P	T	A	P
Initial	0.902	-0.008	0.816	0.843	-0.042	0.795
3	1.320	-0.034	0.911	-1.143	0.048	0.086
6	-0.984	0.002	0.452	-1.396	0.011	0.073
9	-1.146	0.026	0.128	-1.957	0.027	0.015
12	0.725	-0.007	0.764	-1.000	0.030	0.159
15	-0.563	0.025	0.282	-1.000	0.053	0.159
18	-0.858	0.024	0.196	-2.190	0.053	0.034
21	1.000	<0.001	0.841	-0.209	0.005	0.421

Table 6. Index values for species showing the greatest difference in ground cover stem abundance in years 12, 15, and 21 on West Virginia Division of Natural Resources deer-browse exclosure sites. The index was calculated by multiplying the average difference between treatment and control plots by the number of sites at which a difference occurred. Positive values indicate higher abundance on treatment plots. Negative values indicate higher abundance on control plots. Blank cells indicate an index value of 0 for that year.

Species	Year		
	12	15	21
Bedstraw (<i>Galium</i> spp.)	-1.67		
Bellwort (<i>Uvularia</i> spp.)	5.81	3.86	0.98
Blueberry (<i>Vaccinium</i> spp.)	-2.06	-10.61	-9.70
Buckberry (<i>Gaylussacia ursina</i> (M.A. Curtis) Torr)		-1.15	-3.63
Buttercup (<i>Ranunculus</i> spp.)		-1.05	
Canada Mayflower (<i>Maianthemum canadense</i> Desf.)			0.93
Cherry (<i>Prunus</i> spp.)	11.55	-15.89	
Christmas Fern (<i>Polystichum acrostichoides</i> (Michx.) Schott)		-3.12	
Cinquefoil (<i>Potentilla</i> spp.)	1.50		-5.44
Desmodium (<i>Desmodium</i> spp.)	-0.89		-4.59
Dewberry (<i>Rubus</i> spp. L.H.Bailey)		1.54	
Geranium (<i>Geranium</i> spp. L.)	1.40		
Goldenrod (<i>Solidago</i> spp.)			2.59
Ironwood (<i>Ostrya virginiana</i> (Mill.) K. Koch)		-0.95	
Jack in the Pulpit (<i>Arisaema triphyllum</i> (L.))			
Multiflora Rose (<i>Rosa multiflora</i> Thunb.)			1.44
New York Fern (<i>Thelypteris noveboracensis</i> (L.) Nieuwl.)		2.19	-20.11
Panicum (<i>Panicum</i> spp.)	-3.39	-6.79	-1.76
Poison Ivy (<i>Toxicodendron radicans</i> (L.) Kuntze)	2.49	1.52	
Red Maple (<i>Acer rubrum</i> L.)	-39.60	-24.44	-20.57
Red Oak (<i>Quercus rubra</i> L.)	-1.39		
Rubus (<i>Rubus</i> spp.)	9.17	4.06	
Sassafras (<i>Sassafras albidum</i> (Nutt.) Nees)	-1.67		
Sedge (<i>Carex</i> spp.)			-1.99
Serviceberry (<i>Amelanchier arborea</i> Michx.)			-1.62
Sheep Sorrel (<i>Rumex acetosella</i> L.)		-1.51	
Sugar Maple (<i>Acer saccharum</i> Marshall)	2.78		1.52
Teaberry (<i>Gaultheria procumbens</i> L.)	3.27	3.83	14.39
Violet (<i>Viola</i> spp. L.)	-50.73	-9.78	12.22
Virginia Creeper (<i>Parthenocissus quinquefolia</i> (L.) Planch.)	4.86	3.17	2.39
White Oak (<i>Quercus alba</i> L.)	-3.56		
White Snakeroot (<i>Ageratina altissima</i> (L.) King & H. Rob.)	-4.58	2.33	-1.31
Wood Fern (<i>Dryopteris</i> spp.)			5.19

Table 7. Index values for species showing the greatest difference in understory stem abundance in years 6, 9, 15, 18, and 21 on West Virginia Division of Natural Resources deer-browse exclosure sites. The index was calculated by multiplying the average difference between treatment and control plots by the number of sites at which a difference occurred. Positive values indicate higher abundance on treatment plots. Negative values indicate higher abundance on control plots. Blank cells indicate an index value of 0 for that year.

Species	Year				
	6	9	15	18	21
Beech (<i>Fagus grandifolia</i> Ehrh.)		-0.37	-0.77	-0.35	-0.76
Black Gum (<i>Nyssa sylvatica</i> Marshall)			0.53		
Black Locust (<i>Robinia pseudoacacia</i> L.)					-0.02
Black Oak (<i>Quercus velutina</i> Lam.)			-0.06	-0.14	-0.17
Blueberry (<i>Vaccinium</i> spp.)		-0.08			
Buckberry (<i>Gaylussacia ursina</i> Torr)	-0.01	-0.38	-0.40	-0.53	-0.05
Buckeye (<i>Aesculus glabra</i> Willd.)	-0.01	-0.01			
Cherry (<i>Prunus</i> spp.)		1.20			0.55
Crabapple (<i>Malus</i> spp.)	-0.01				
Dogwood (<i>Cornus florida</i> L.)	1.16	0.77			
Euonymus (<i>Euonymus bungeanus</i> Maxim.)		-0.01		-0.01	
Greenbrier (<i>Smilax</i> spp.)	1.40	2.06	6.10	7.64	6.28
Hazelnut (<i>Corylus americana</i> Walter)	0.55	1.86	1.64	2.04	
Huckleberry (<i>Gaylussacia</i> spp. Kunth)	-0.47		-0.02		
Ironwood (<i>Ostrya virginiana</i> (Mill.) K. Koch)	0.70			1.43	0.64
Japanese Honeysuckle (<i>Lonicera japonica</i> Thunb.)	0.47		0.55	1.66	
Maple Leaf Viburnum (<i>Viburnum acerifolium</i> L.)	-0.01				
Mountain Laurel (<i>Kalmia latifolia</i> L.)		0.76		1.09	-0.73
Mountain Maple (<i>Acer spicatum</i> Lam.)		-0.01			
Multiflora Rose (<i>Rosa multiflora</i> Thunb.)					0.79
PawPaw (<i>Asimina triloba</i> (L.) Dunal)	-0.07	-0.37	-0.09	-0.34	-0.18
Red Cedar (<i>Juniperus virginiana</i> L.)				-0.01	
Red Maple (<i>Acer rubrum</i> L.)	1.33	2.40	2.00	3.34	3.64
Red Oak (<i>Quercus rubra</i> L.)					0.57
Red Spruce (<i>Picea rubens</i> Sarg.)		-0.01			
Redbud (<i>Cercis canadensis</i> L.)			-0.01		
Rubus (<i>Rubus</i> spp.)	12.97	21.54	4.68	3.31	2.14
Sassafras (<i>Sassafras albidum</i> (Nutt.) Nees)	0.67	0.70	0.59		
Serviceberry (<i>Amelanchier arborea</i> Michx.)		0.62	0.62	3.12	0.55
Spice Bush (<i>Lindera benzoin</i> (L.) Blume)					-0.13
Striped Maple (<i>Acer pensylvanicum</i> L.)			-0.06		
Sugar Maple (<i>Acer saccharum</i> Marshall)			3.25	1.55	1.33

Table 7. Continued

Species	Year				
	6	9	15	18	21
Sumac (<i>Rhus</i> spp.)	5.12				
Tatarian Honeysuckle (<i>Lonicera tatarica</i> L.)				-0.01	-0.02
Virginia Pine (<i>Pinus virginiana</i> Mill.)		-0.01	-0.01		
White Oak (<i>Quercus alba</i> L.)	-0.02		-0.09	-0.06	-0.05
White Pine (<i>Pinus strobus</i> L.)	-0.16	-0.04	-0.18	-0.19	-0.14

Table 8. Deer harvest per square kilometer at West Virginia Division of Natural Resources management areas corresponding to monitoring sites, 1993 – 2007.

Plot Location	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
1. Beaverdam	3.89	3.72	5.48	2.97	3.69	3.93	4.33	3.55	2.38	3.27	1.06	0.70	0.56	0.76	0.68
2. Bluestone	4.78	4.76	3.32	5.72	5.61	4.89	3.96	4.99	6.44	7.10	2.32	2.33	3.03	2.60	3.82
3. Centrailia	2.79	2.24	4.05	3.51	5.20	3.00	3.65	2.91	3.55	3.37	1.50	1.17	0.87	1.06	1.86
4. Cheat Mountain	4.41	3.55	4.83	2.61	3.45	2.53	3.55	3.16	1.46	1.74	0.73	0.58	0.50	0.59	0.46
5. Coopers Rock	4.45	4.59	6.74	9.19	7.99	5.21	4.41	5.54	4.39	4.74	4.20	3.21	3.63	1.17	1.52
6. Daniels Run	5.95	4.65	6.28	4.65	2.53	3.10	2.20	2.61	1.71	2.04	1.39	1.55	2.20	3.02	2.12
7. Dice Run	3.28	2.01	3.57	2.64	3.20	2.65	2.59	2.77	2.17	1.21	0.84	0.72	0.89	1.05	0.51
8. Holly River	2.79	2.24	4.05	3.51	5.20	3.00	3.65	2.91	3.55	3.37	1.50	1.17	0.87	1.06	1.86
9. Hughes River	6.40	6.37	7.14	7.21	10.37	6.22	4.67	6.79	7.16	7.04	3.78	3.90	3.88	2.57	1.19
10. The Jug	7.11	8.41	12.06	11.10	15.52	6.59	8.33	8.15	7.63	6.50	5.03	5.55	4.77	3.21	2.60
11. Lewis Wetzel	1.96	1.96	3.36	4.51	6.20	3.49	4.23	5.65	4.60	6.45	5.67	4.05	2.89	1.89	2.42
12. Little River	3.03	2.12	3.75	3.38	3.15	2.30	3.07	3.47	2.06	2.14	0.44	0.62	0.64	0.82	0.73
13. Nathaniel Mountain	1.97	1.99	2.87	2.82	4.33	1.94	1.67	2.15	2.24	1.85	1.11	1.02	1.04	1.20	1.46
14. Neola	1.71	1.41	1.60	1.74	1.81	1.15	1.57	1.66	1.29	1.22	0.72	0.59	0.49	0.58	0.43
15. Potts Creek	4.20	3.89	4.73	4.20	6.63	5.40	4.59	4.79	4.07	2.45	1.44	0.97	0.88	1.64	1.08
16. R.D. Bailey	0.60	0.40	0.47	0.46	0.47	0.44	0.51	0.49	0.53	0.70	1.34	0.60	0.77	1.30	1.90
17. Sleepy Creek	5.09	4.90	6.00	6.02	5.56	3.90	4.34	4.48	4.47	4.56	3.07	2.01	2.21	3.17	3.01
18. Stonecoal	7.78	5.05	7.78	6.79	6.29	3.64	6.95	5.30	4.22	3.97	2.57	2.90	3.06	4.05	3.23
19. Stoney Run	3.28	2.01	3.57	2.64	3.20	2.65	2.59	2.77	2.17	1.21	0.84	0.72	0.89	1.05	0.51
20. Trout Run	2.92	3.13	4.09	4.41	5.43	3.71	5.29	4.81	3.36	3.01	2.31	1.92	2.02	1.83	1.66

Figure 1. Locations of West Virginia Division of Natural Resources deer-browse exclosure sites, 1984 – 2007.

1. Beaverdam	5. Coopers Rock	9. Hughes River	13. Nathaniel Mt.	17. Sleepy Creek
2. Bluestone	6. Daniels Run	10. The Jug	14. Neola	18. Stonecoal
3. Centrailia	7. Dice Run	11. Lewis Wetzel	15. Potts Creek	19. Stoney Run
4. Cheat Mt.	8. Holly River	12. Little River	16. R.D. Bailey	20. Trout Run

Figure 2. Design of control and treatment plots. Ten meter squares indicate the location of fence and boundary of control plots. Two meter squares indicate the plots measuring understory cover. One meter square indicates the plots measuring ground cover.

Figure 3. The average stem abundance at ground cover level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 4. The average species richness at ground cover level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 5. Average Shannon diversity index at the ground cover level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 6. The average stem density at understory level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 7. The average species richness at understory level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 8. Average Shannon diversity index at the understory level in West Virginia Division of Natural Resources control and exclosure plots, 1984 – 2007.

Figure 9. Hierarchical cluster analysis of West Virginia Division of Natural Resources groundcover exclusion plots, 1984 – 2007.

Figure 10. The relation between seedling/sapling ratio of preferred browse species and total white-tailed deer harvest at West Virginia Division of Natural Resource exclosure sites, 1993 – 2005.

CHAPTER V

WETLAND SEED DISPERSAL BY WHITE-TAILED DEER IN CANAAN VALLEY, WV

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ABSTRACT: Endozoochory, the consumption and dispersal of seeds by animals, plays an important role in the propagation and dispersal of many plant species. White-tailed deer (*Odocoileus virginianus* Zimm.) have been cited as potential long-distance dispersers of both native and exotic plant species in North America. The potential for dispersal of wetland plants by deer has not been examined. We collected naturally-deposited white-tailed deer fecal pellet piles from wetlands in Canaan Valley, WV in the summer and fall of 2005 and 2006. We cold-stratified all pellet piles and germinated seedlings over a layer of sterile potting mix. We determined the percentage of germinated seedlings with a facultative wetland (FACW; plants with 67 – 99% frequency of occurrence in wetlands) or obligate wetland (OBL; plants with > 99% frequency of occurrence in wetlands) plant indicator status in the northeastern United States and compared the frequency of occurrence to those of germinated plants with facultative upland (FACU; plants with 67 – 99% frequency of occurrence in non-wetlands) indicator status. We identified 38 unique species germinating from pellet piles over the two year period. Of these 38 species, 38% had a FACU status, 18% were FACW, and 21% were OBL. Additionally, 42% were graminoid species; forbs and woody species accounted for 29% each. Seed dispersal by large herbivores is often not considered for wetland plants; however, these data suggest that

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passage by herbivores may be as viable for wetland adapted plants as for upland plants.

Additionally, as these herbivores tend to have larger home ranges than some other wetland-adapted mammals, they could be a valuable means of seed transport between isolated wetland patches and could function in maintaining metapopulations of wetland species.

INTRODUCTION

Plant populations differ from animals in that they are sessile and individuals cannot actively disperse from patch to patch. Instead, dispersal is tied directly to reproduction and is often more random in nature than dispersal of animal populations (Hansson 1991). Plants use a variety of vectors as both pollen and seed transports (Drezner et al. 2001). Many plants rely on wind or water to disperse pollen and seeds. That may allow them to colonize patches at great distances but in patchy environments, wind dispersal does not ensure pollen or seeds reach patches with favorable growing conditions (Drezner et al. 2001). Plants that rely on herbivores as seed dispersers may ensure seedling establishment in other suitable patches by using fruit or foliage as an attractant to occupied patches (Janzen 1984; Willson 1993; Witmer 2001; Williams et al. 2008; Iravani et al. 2011). Up to 60% of the plants in temperate forests may be adapted for endozoochory (Grünwald et al. 2010; Thorsen et al. 2011); however, the type of disperser may affect the distance and time it takes for plant species to disperse via endozoochory (Tanentzap et al. 2012).

The evolution of fruit is believed to have occurred as a means to attract herbivores and frugivores to consume both fruit and seed to be deposited after digestion, ideally in nutrient rich fecal material (Willson and Whelan 1990; Beck and Vander Wall 2010). Additionally, Janzen (1984) hypothesized that in many plants that do not bear fruit, the vegetation acts as an attractant to herbivores who then consume seeds with vegetative matter. However, the colonization of unoccupied patches may still be random as plants cannot attract the herbivores to suitable patches which they do not occupy. Conversely, some herbivores may consume seeds that are not adapted to pass through the digestive tract thus reducing the potential for both increasing the local population or colonization of new patches (Furedi and McGraw 2004).

Drezner et al. (2001) discussed the method of seed dispersal of riparian plants and argued that obligate wetland plants are more often dispersed by water or wind while upland plants are more often dispersed by animals. This study evaluated few obligate wetland plants ($n = 3$) and many upland plants. Additionally, the traditional method of determining dispersal mechanism is to classify plants based on seed characteristics. However, many seeds do not have characteristic signs for a particular dispersal method, some species may have more than one dispersal method (Drezner et al. 2001) and, though a seed may be physically adapted for one type of dispersal, it is not known whether or not that seed could still germinate if consumed by an herbivore.

The Role of White-tailed Deer in Seed Dispersal

Much of the research concerning the effects of deer on plant communities have focused on their role as browsers and the potential for overbrowsing of plants (Alverson and Waller 1997; Stromayer and Warren 1997; Royo et al. 2010). However, several studies have looked at the role of white-tailed deer as both seed predators and seed dispersers (Cambell and Gibson 2001; Vellend et al. 2003; Furedi and McGraw 2004; Myers et al. 2004; Bartuszevige and Endress 2008). Due to their large home-range size (e.g. 66 – 235 ha in WV, Campbell et al. 2004) and the potential to retain material in the digestive tract for three or more days (Mautz and Petrides 1971; Moussie et al. 2005), white-tailed deer have the potential to carry seeds great distances (Janzen 1984). Vellend et al. (2003) suggested that this would result in 95% of germinable seeds being deposited more than 100 m from the parent plant and 30% deposited more than 1 km from the parent plant. This may have a considerable effect on metapopulation initiation, growth, and gene flow of irregularly distributed and rare plant species (Myers et al. 2004).

Myers et al. (2004) found that 72 species of forest and old-field plants germinated from fecal pellet samples with a mean of 38 germinations per pellet group. The germinated seeds ranged from forbs to tree species and while some were seeds distributed through fruiting mechanisms, most were not. However, Cambell and Gibson (2001) found only 2 species germinated from 22 pellet group samples.

Although deer may play an important part in the dispersal of seed for many plants, they may also play a role in the spread of exotic species (Cambell and Gibson 2001; Bartuszevige and Endress 2008; Williams et al. 2008). Additionally, for some plant species, including American ginseng (*Panax cinquefolius*) (Furedi and McGraw 2004), white-tailed deer are demonstrated seed predators or consumers, that is, all seeds consumed in the act of herbivory are digested or are non-viable once passed through the digestive system, thus reducing the realized reproductive output of these plants.

Obligate or facultative wetland plants are most likely adapted for dispersal within a small area by wind, water, or animals that frequent various wetland habitats (i.e., waterfowl) to ensure that seeds are deposited in favorable growing conditions. As a result, long-distance colonization rates for wetland plant metapopulations, especially in fragmented wetland habitats, may be low. We believe many wetland plants are not adapted to long distance seed dispersal by large ungulate herbivores such as white-tailed deer and are thus consumed rather than carried by deer. We tested the null hypothesis that there would be no difference in the proportion of wetland and upland plants that are able to germinate after being consumed by white-tailed deer by collecting natural fecal pellet piles from in and around the Canaan Valley, WV, high-elevation wetland complex to determine the species of germinable seeds they contain as well as what percentage come from obligate and facultative wetland plant species.

METHODS

Study Area

Canaan Valley, located in Tucker County, West Virginia, is the highest elevation valley east of the Rocky Mountains (Fortney 1975). As such, the climate and accordingly, the vegetation, of the valley are more similar to northern boreal forests than to the deciduous forests of surrounding West Virginia. Once home to large stands of red spruce (*Picea rubens*), intense logging followed by fires drastically changed the soils and vegetation of the valley to their present condition (Fortney 1975). The valley floor averages 975 m above sea level. This, coupled with surrounding mountains which rise 150 – 240 m above the valley, creates a relatively cool, moist climate and a short growing season. The average annual precipitation is 137 cm and annual snowfall is 305 cm (Fortney 1993). The average growing season is approximately 90 days (Beverage 1967). Both of these characteristics set this area apart from low elevation wetland and upland areas in the surrounding counties.

Canaan Valley encompasses about 176 km² (17,600 ha) of land. Approximately 20% of the land area is made up of various wetland community types and another 23% is northern hardwood forest (Figure 1). Of all the high-elevation wetlands in West Virginia, Canaan Valley is home to the largest contiguous wetland complex (3,000 ha, Byers et al. 2007). Fortney (1975) described 27 distinct wetland community types ranging from quaking aspen (*Populus tremuloides*) groves to sphagnum (*Sphagnum* spp.) and polytrichum (*Polytrichum* spp.) bogs. Agriculture, rural development, and recreational land make up the remaining portion of the valley (Michael 1992). Of the 583 plant species recorded in Canaan Valley, 229 (39%) are forbs, 130 (22%) are graminoids, and 89 (15%) are woody species (trees and shrubs)(Fortney 1975).

Canaan Valley is home to Canaan Valley State Park (2,433 ha) and the Canaan Valley National Wildlife Refuge (6,729 ha) and, at the time of this study, land owned by the Canaan Valley Institute (1,298 ha), a nonprofit organization. Sampling took place on a combination of these three public access properties in the valley.

Field Methods

We collected fresh white-tailed deer fecal pellet groups bi-monthly from May to December 2005 and 2006 in wetland habitats. In 2005, we collected pellet piles from along three 300 m randomly placed transects through both herbaceous, shrub, and forested wetlands within the Canaan Valley National Wildlife Refuge and Canaan Valley State Park. In 2006, six additional transects were added for a total of nine transects at sampling locations within the refuge and state park (Figure 1). We collected piles by walking along transects and selecting fresh pellet piles from those within view. We chose piles that were visibly moist and dark in color. All visible pellets were removed from surrounding vegetation and placed in plastic bags. We did not observe any obvious fallen seeds on pellet piles. We attempted to collect pellets without including surrounding debris, including seeds that may have come from the surrounding vegetation rather than through endozoochory. However, we did not search pellets extensively for these seeds.

Individual pellets were broken by rinsing gently through a 0.5 mm sieve. The resulting seeds and residual matter were stored in petri dishes at 4° C for a period of three months to simulate over-wintering (Myers et al. 2004). Following a three month period of cold stratification, the seeds were spread on top of a layer of potting mix in 10 cm diameter planting pots and kept moist. Piles were then planted in mid-March in individual pots containing sterile growing medium and were subsequently housed in a greenhouse and watered when needed. The

trays were kept in greenhouse conditions until germination and identification of species germinated was possible. The number of each plant species that germinated from each pellet group was recorded.

Statistical analysis

We determined the wetland indicator status of all plants germinated from pellet piles. For the purposes of our analysis, we pooled the species that had OBL (plants with > 99% frequency of occurrence in wetlands) or FACW (plants with 67 – 99% frequency of occurrence in wetlands; Lichvar et al. 2014) status as these plants are most likely to be adapted for growth and dispersal in wetlands. We used wetland indicator status values for Eastern Mountains and Piedmont region as listed in the U.S. Army Corps of Engineers National Wetland Plant List (Lichvar et al. 2014). We excluded species that were considered facultative (FAC; plants that are equally likely to be found in uplands and wetlands), species with an unknown status, and species that were only identified to the genus level. We also classified each species as graminoid, forb, or woody species (including trees and shrubs). We used a chi-square test to compare the proportion of species germinated each year that were either UPL (plants with < 1% frequency of occurrence in wetlands) or FACU (plants with 1 – 33% frequency of occurrence in wetlands) with those that were either FACW or OBL. We considered differences at the $P < 0.05$ level to be significant. We defined the frequency of occurrence as the number of times each species occurred out of the number of total *germinated* pellet piles. We also compared the frequency of germination events each year that were either UPL or FACU with those that were either FACW or OBL. We repeated these tests for the proportion and frequency of germination of plants that were graminoid, forbs, or woody.

RESULTS

We collected 55 pellet piles in 2005 and 160 pellet piles in 2006. Of those collected in 2005, 45% of the pellet piles planted germinated at least one species resulting in a total of 14 species (Table 1). Of those collected in 2006, 38% of the pellet piles germinated at least one species resulting in a total of 32 species (Table 2). A total of 38 unique species were identified over a period of two years (two additional seedlings were identified to the genus level). In 2005, there was no significant difference between the proportion of species germinated that have a FACW ($n = 3$) or OBL ($n = 5$) wetland indicator status (57%) and those that had a FACU ($n = 5$, 35%) status ($\chi^2 = 5.29$, $P > 0.07$, $n = 14$) (Table 1). There was also no difference in the frequency of FACW ($n = 6$) and OBL ($n = 8$) (52%) plants versus FACU plants ($n = 12$, 44%) ($\chi^2 = 0.154$, $P = 0.695$, $n = 27$). In 2005, both graminoids ($n = 6$) and forbs ($n = 6$) made up 43% of the species that germinated from pellet piles. This was more than the proportion of woody species ($n = 2$, 14%) that germinated; however, the difference was not considered significant ($\chi^2 = 2.29$, $P < 0.31$, $n = 14$). The frequency of both graminoids ($n = 12$) and forbs ($n = 12$) (44% for both) was significantly higher than for woody species (11%, $\chi^2 = 6.00$, $n = 3$, $P = 0.049$, $n = 27$). In 2005, the proportion of individual stems that were FACU (53%) was more than the combined proportion of FACW (13%) and OBL (32%) stems counted (Figure 2); however, this difference was not significant ($\chi^2 = 0.373$, $P = 0.541$, $n = 68$). The proportion of individual stems that were forbs (48%) and graminoids (45%) were significantly greater than the proportion of woody stems (6%, $\chi^2 = 23.14$, $P < 0.001$, $n = 68$), but the proportion of graminoids and forbs did not significantly differ ($\chi^2 = 0.06$, $P = 0.80$, $n = 68$) (Figure 3).

In 2006, 31% ($n = 10$) of species germinated had a FACU status and 3% ($n=1$) had UPL status while 16% had FACW ($n = 5$) and 25% had OBL ($n = 8$) wetland indicator status. There

was no significant difference between the proportion with either UPL or FACU and the proportion with either FACW or OBL status ($\chi^2 = 0.36$, $P = 0.55$, $n = 32$). In 2006, there was no significant difference between the frequency of species with either UPL (1%, $n = 1$) or FACU (45%, $n = 31$) and those with either FACW (13%, $n = 9$) or OBL (19%, $n = 13$) status ($\chi^2 = 2.28$, $P < 0.13$, $n = 69$). In 2006, 44% of the species germinated were graminoid ($n = 14$), 22% were forbs ($n = 7$), and 34% were tree or shrub species ($n = 11$). There were no significant differences between the proportion of species that germinated that were classified as graminoids, forbs, or woody species ($\chi^2 = 2.31$, $P = 0.31$, $n = 32$). The frequency of pellet piles germinating graminoid species (46%, $n = 32$) in 2006 was significantly higher than the frequency of woody (20%, $n = 14$) species ($\chi^2 = 7.04$, $P < 0.008$, $n = 69$), but was not higher than the frequency of forbs (33%, $\chi^2 = 1.43$, $P > 0.22$, $n = 69$). In 2006, the proportion of individual stems that were either UPL (2%) or FACU (57%) was significantly more than the combined proportion of FACW (7%) and OBL (14%) stems counted ($\chi^2 = 29.12$, $P < 0.0001$, $n = 169$) (Figure 2). The proportion of individual stems that were forbs (39%) and graminoids (49%) were significantly greater than the proportion of woody stems (12%, $\chi^2 = 35.51$, $P < 0.001$, $n = 169$) but the proportion of graminoids and forbs did not significantly differ ($\chi^2 = 1.73$, $P = 0.19$, $n = 169$) (Figure 3). In 2005, only one annual species (7%) germinated and, in 2006, only two annual species (6%) germinated.

DISCUSSION

We observed no difference in the frequency of wetland and upland plants germinating in pellet piles collected in 2005. In 2006, however, we observed a significantly higher abundance of upland germinations though there was no difference in the proportion of species attributed to each group. We attribute the inability to detect a difference in 2005 to the smaller sample size.

While a difference in frequency of 2006 plants seems to agree with the hypothesis that upland plants may be more adapted to dispersal by white-tailed deer, there was no difference in the proportion of wetland and upland species. The difference in frequency could be attributed to the success of several FACU plants (Table 2), such as *Oxalis dilleni*, which occurred in 11 pellet piles collected that year.

Although we did observe the presence of FACW and OBL wetland species germinating in pellet piles, these observations may underestimate the actual presence of germinable wetland species in pellet piles. All pellet piles were grown in moistened but not saturated soil. Alternate conditions may be required to germinate all wetland species present in a sample. Saturated conditions would be present for at least some of the pellet piles deposited naturally by white-tailed deer. By definition, FACU plants may occur in wetlands between 1 and 33% of the time. Likewise, FACW plants may occur in uplands between 1 and 33% of the time (Lichvar et al. 2014). Therefore, the distinction between plants adapted for uplands and those adapted for wetlands is not necessarily clear-cut and may confound the findings of this study. Drezner et al. (2001) discussed the characteristics of seeds that support wind, water, and animal dispersal. However, they noted that many seeds do not have characteristics that fit neatly into one of these categories. Many of the small graminoid wetland seeds (e.g. *Juncus effusus* and *Glyceria canadensis*) germinated in this study may fall into that category.

Our study shows that some wetland plants can be successfully dispersed by white-tailed deer. As they have relatively large home ranges compared to other mammal species (Willson 1993), deer have the potential to disperse seeds of wetland species between isolated wetland patches. As dispersers, white-tailed deer could play a role in maintaining or enhancing metapopulations of wetland plants patchily distributed in an upland matrix (Vellend et al. 2003).

However, white-tailed deer may also confound wetland restoration by successfully dispersing seeds of some exotic species (Vellend 2002; Myers et al. 2004; Bartuszevige and Endress 2008). We found seven exotic species germinated in our pellet piles (Tables 1 and 2).

A high proportion of germinated species were graminoids. In both years, there was no significant difference between proportions of species that were graminoids, forbs, or woody species. We found no difference in the frequency of species in pellet piles in 2005. Again, we believe this was due to the low sample size. In 2006, we found that there was significantly more graminoids than woody species. Endozoochory by large mammals is often associated with the coevolution of fleshy fruits (Willson 1993; Beck and Vander Wall 2010). However, Janzen (1984) suggested that the foliage of forbs and grasses may attract herbivores to disperse small seeds. While fleshy fruit may attract seed dispersers, the mastication process may destroy larger seeds. Small, rounded, hard seeds may support passage through the digestive tract of ungulates better than larger seeds (Moussie et al. 2005; Iravani et al. 2011). Our results support this “foliage as fruit” hypothesis (Janzen 1984) and suggest that graminoids may be better adapted to dispersal by herbivores even though they are not traditionally classified as animal-dispersed seeds.

Successful propagation and dispersal of graminoid species by deer may help to maintain or expand herbaceous openings at both wetland and upland sites. Large areas of Canaan Valley consist of wet meadow habitat. White-tailed deer may help to maintain these meadows, not only by reducing the growth of woody species through browse, but also by dispersing the seeds of graminoid species (Bartuszevige and Endress 2008; Iravani et al. 2011). Many studies have examined the influence of white-tailed deer on upland forest habitat. They are thought to affect the regeneration of forest species through the over-browsing of seedlings (Rooney 2009;

Griscom et al. 2011; Tanentzap et al. 2012). Over-browsing by deer can have secondary effects by increasing the growth of unpalatable ferns that shade seedlings, which in turn, harbor small mammals that may act as seed predators (de la Cretaz and Kelt 2002; Royo et al. 2010; Griscom et al. 2011). As dispersers of graminoid species, deer also may reduce the capacity for woody species regeneration by increasing the prevalence of grass species on the forest floor. Many studies on the effects of white-tailed deer density on vegetation have been conducted with the use of deer exclosures which effectively reduce the deer density to zero (Rooney 2009; Tanentzap et al. 2012). These studies have been criticized because eliminating native deer from an ecosystem is not a viable or desirable option. These studies may also be criticized because they eliminate both the positive and negative potential for seed germination from pellet piles.

A key question raised by the results of this study are to what degree these data are representative of the species present in the Canaan Valley ecosystem that are germinable when passed through the digestive system of white-tailed deer and what percentage of the total seeds consumed remain intact for each species. Of those species recorded in Canaan Valley, 20% are obligate wetland species (OBL), 18% are facultative wetland species (FACW), 15% are facultative species (FAC), 24% are facultative upland species (FACU), and only 3% are upland species (UPL). We believe the abundance and frequency of seeds in pellet piles is likely not a good indicator of the proportions of these plants in the diet of white-tailed deer and should not be used as an indicator of such. Additionally, of those plants eaten, some may not have germinated under the conditions provided. We recorded the presence of species at our study sites that have been reported by others as having germinated from deer pellet piles but did not occur in our samples (e.g. *Achillea millefolium* and *Festuca ovina*; Myers et al. 2004; Iravani et al. 2011). A higher sample size may lead to additional species that were not present in our samples as well as

the opportunity to apply different treatments that could promote the germinations of different species. All studies that we are aware of concerning the germination of plant species from pellet piles have been conducted under highly controlled conditions. It remains to be seen, however, if these results translate to pellet piles that germinate under more natural conditions.

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Table 1. Species germinated from 55 white-tailed deer pellet piles collected in 2005 from 3 locations in Canaan Valley, West Virginia.

Latin Name	Common Name	Form ^a	Life ^b	Frequency	Abundance	Indicator Status
<i>Carex crinita</i> (L.)	fringed sedge	G	P	3	10	OBL
<i>Danthonia compressa</i> (Austin)	flattened oatgrass	G	P	2	12	FACU
<i>Glyceria canadensis</i> (Michx.)	rattlesnake mannagrass	G	P	1	1	OBL
<i>Juncus canadensis</i> (J. Gay ex Laharpe)	Canadian rush	G	P	1	2	OBL
<i>Juncus effusus</i> (L.)	common rush	G	P	4	5	FACW
<i>Lobelia inflata</i> (L.)	Indian-tobacco	F	A	2	2	FACU
<i>Lycopus uniflorus</i> (Michx.)	northern bugleweed	F	P	1	1	OBL
<i>Mimulus ringens</i> (L.)	Allegheny monkey flower	F	P	1	9	OBL
<i>Muhlenbergia schreberi</i> (Scribn)	nimblewill	G	P	1	1	FAC
<i>Oxalis dillenii</i> (Jacq.)	wood sorrel	F	P	6	18	FACU
<i>Plantago rugelii</i> (Decne.)	blackseed plantain	F	P	2	1	FACU
<i>Spiraea alba</i> (Du Roi)	meadowsweet	W	P	1	1	FACW
<i>Spiraea tomentosa</i> (L.)	steeplebush	W	P	2	3	FACW
<i>Veronica officinalis</i> (L.)*	common speedwell	F	P	1	2	FACU

a. Forms are designated by G = graminoid, F = forb, and W = woody species.

b. Life forms are designated by A = annual and P = perennial.

An [*] indicates plants are exotic to the U.S.

Table 2. Species germinated from 160 white-tailed deer pellet piles collected in 2006 from 9 locations in Canaan Valley, WV.

Latin Name	Common Name	Form ^a	Life ^b	Frequency	Abundance	Indicator Status
<i>Agrostis perennans</i> (Walter)	upland bentgrass	G	P	2	13	FACU
<i>Anthoxanthum odoratum</i> (L.)*	sweet vernal grass	G	P	3	4	FACU
<i>Apocynum cannabinum</i> (L.)	Indian hemp	F	P	1	2	FACU
<i>Carex crinita</i> (L.)	fringed sedge	G	P	3	8	OBL
<i>Carex debilis</i> (Michx.)	white-edge sedge	G	P	4	7	FAC
<i>Carex folliculata</i> (L.)	northern long sedge	G	P	2	4	OBL
<i>Carex leptalea</i> (Wahlenb.)	bristly-stalked sedge	G	P	1	1	OBL
<i>Crataegus</i> spp.	hawthorne	W	P	1	1	FAC
<i>Danthonia compressa</i> (Austin)	flattened oatgrass	G	P	4	17	FACU
<i>Dichanthelium clandestinum</i> (L.)	deertongue grass	G	P	3	12	FAC
<i>Eleagnus umbellata</i> (Thunb)*	autumn olive	W	P	1	2	Kn.
<i>Festuca subverticillata</i> (Pers.)	nodding fescue	G	P	1	1	FACU
<i>Glyceria canadensis</i> (Michx.)	rattlesnake manna grass	G	P	1	1	OBL
<i>Glyceria striata</i> (Lam.)	fowl manna grass	G	P	1	1	OBL
<i>Holcus lanatus</i> (L.)*	velvet Grass	G	P	2	3	FAC
<i>Hypericum densiflorum</i> (Pursh.)	glade St. John's-wort	W	P	1	2	FACW
<i>Juncus canadensis</i> (J. Gay ex Laharpe)	Canadian rush	G	P	4	7	OBL
<i>Lobelia inflata</i> (L.)	Indian-tobacco	F	A	1	1	FACU
<i>Oxalis dillenii</i> (Jacq.)	wood sorrel	F	P	11	34	FACU
<i>Poa</i> spp.	bluegrass spp.	G	P	1	3	FACW - FACU
<i>Persicaria pensylvanicum</i> (L.)	pinkweed	F	A	3	4	FACW
<i>Prunus serotina</i> (Ehrh.)	black cherry	W	P	1	1	FACU
<i>Ranunculus acris</i> (L.)	tall buttercup	F	P	1	2	FAC
<i>Rosa multiflora</i> (Thunb.)*	multiflora rose	W	P	2	3	FACU
<i>Rumex acetosella</i> (L.)*	sheep sorrel	F	P	1	3	UPL

a. Forms are designated by G = graminoid, F = forb, and W = woody species.

b. Life forms are designated by A = annual, and P = perennial.

An [*] indicates plants are exotic to the U.S.

Table 2. Continued

Latin Name	Common Name	Form ^a	Life ^b	Frequency	Abundance	Wetland Indicator Status
<i>Spiraea alba</i> (Du Roi)	meadowsweet	W	P	2	4	FACW
<i>Spiraea tomentosa</i> (L.)	steeplebush	W	P	1	1	FACW
<i>Trifolium repens</i> (L.)*	white clover	F	P	5	20	FACU
<i>Vaccinium myrtilloides</i> (Michx.)	velvetleaf blueberry	W	P	2	3	FACW
<i>Viburnum nudum</i> (L.)	wild raisin	W	P	1	1	OBL
<i>Viburnum recognitum</i> (Fernald)	smooth arrowwood	W	P	1	1	FAC
<i>Viola sagittata</i> (Aiton)	arrowleaf violet	W	P	1	2	FAC

a. Forms are designated by G = graminoid, F = forb, and W = woody species.

b. Life forms are designated by A = annual and P = perennial.

An [*] indicates plants are exotic to the U.S.

Figure 1. Pellet pile survey locations from 2005–2006 in Canaan Valley, West Virginia. Inset picture shows the location of Canaan Valley in West Virginia.

Figure 2. The frequency (number of pellet piles) and abundance (number of individual seedlings) of germinated seedlings from pellet groups collected in 2005–2006 in Canaan Valley, WV, displayed as the proportion from each wetland status group. These groups include facultative wetland (FACW; plants with 67 – 99% frequency of occurrence in wetlands), obligate wetland (OBL; plants with > 99% frequency of occurrence in wetlands), facultative upland (FACU; plants with 67 – 99% frequency of occurrence in non-wetlands), and upland (UPL; plants with > 99% frequency of occurrence in non-wetlands).

Figure 3. The frequency (number of pellet piles) and abundance (number of individual seedlings) of germinated seedlings from pellet groups collected in 2005–2006 in Canaan Valley, WV, displayed as the proportion from each growth form.

CHAPTER VI

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RH: Flaherty et al. · Stakeholders and Deer Management

Comparing Stakeholder Attitudes toward White-tailed Deer Management in Canaan Valley, West Virginia

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Canaan Valley, West Virginia provides habitat for many plants considered rare in West Virginia. The local white-tailed deer (Odocoileus virginianus Zimm.) are a popular attraction for visitors as well as resident and nonresident hunters. However, there are concerns over the impact of white-tailed deer herbivory on rare plant communities in the wetlands. The purpose of this study was to evaluate the stakeholder attitudes regarding white-tailed deer management and rare plant conservation. We mailed surveys to property owners in Canaan Valley and Tucker County, WV and provided surveys to visitors at Canaan Valley State Park and National Wildlife Refuge. Incurred crop damage affected attitudes toward deer abundance while residency status affected attitudes toward the presence of deer and rare plant conservation. We found differences between hunters and the nonhunting public attitudes toward white-tailed deer management. Results of this survey may help managers to direct management and education goals toward actual rather than perceived stakeholder attitudes.

Key Words: white-tailed deer, stakeholder, nonresident, visitor, plant conservation.

Introduction

Wildlife species are held in public trust; that is, they belong to the people. Many species are managed by state and federal agencies which must take into account the health of the wildlife population, the impact on other plant and animal species, habitat quality, and the wishes of the public for the wildlife population. Public sentiment over the management of white-tailed deer (*Odocoileus virginianus*) herds in the eastern United States has changed with deer abundance, levels of human-wildlife conflict, increasing rural development, and an increasing interest in nongame wildlife and noncommercial plant species (Holsman & Peyton, 2003). Public opinions toward white-tailed deer management may vary with the extent of negative experience (Messmer, Cornicelli, Decker, & Hewitt, 1997; Loker, Decker, & Schwager, 1999; West & Parkhurst, 2002), profession (West & Parkhurst, 2002), and participation in outdoor recreation such as hunting (Brooks, Warren, Nelms, & Tarrant, 1999; Holsman & Peyton, 2003). Wildlife is considered a public resource, so its management often involves input from the public sector (McShea & Rappole, 1997; Shafer-Nolan, 1997). Thus state and local agencies charged with managing deer herds need to balance the attitudes of hunters, antihunters, and nonhunters with public safety and sound biology.

In the 1940s, Leopold, Sowls, and Spencer (1947) found that it was difficult to convince hunters and the general public, who experienced firsthand the shortage of deer as a result of overhunting, that an overabundance of deer could exist at all, much less be a detriment to their habitat. Today, it is still difficult to convince stakeholders, defined here as those who have an interest in the management of white-tailed deer and rare plant conservation, who have experienced the lack of abundance of deer in earlier decades that a problem exists at all (Diefenbach, Palmer, & Shope, 1997). Since the early 1900s, a greater proportion of the nation's

general public is disconnected with wildlife and its habitat. Though the urban sprawl phenomenon brought many more people out of the cities and created suburban centers out of formerly rural land, the suburbanites have not embraced the hunting heritage of rural America (Warren, 1997). In the eyes of many, white-tailed deer have become garden pests and road hazards (Warren, 1997). As hunting has decreased as a pastime, more people have embraced animal-welfare or animal-rights perspectives that do not condone the use of hunting as a management tool for deer populations (Rutberg, 1997).

Overabundance of a wildlife population has been defined as fitting into 1 of 4 categories: when an animal threatens human life or livelihood, when animals depress the densities of favored species, when animals are too numerous for their own good, and when their numbers cause ecosystem dysfunction (Caughley 1981). Several studies have shown that threats to human life or livelihood may affect the attitudes of stakeholders toward populations of white-tailed deer. Deer-vehicle collisions (Loker et al., 1999; West & Parkhurst, 2002), increased rates of lyme disease (West & Parkhurst, 2002), and damage to crops and home landscaping (Stout, Knuth, & Curtis, 1997) can lead citizens to view high-density deer populations in a negative light and seek methods of population reduction. Stakeholders were less likely to look negatively on high deer abundance in light of ecosystem dysfunction and depression of nongame wildlife species (Diefenbach et al., 1997; Holsman & Peyton, 2003).

Canaan Valley, West Virginia (Tucker County) is home to Canaan Valley State Park and the Canaan Valley National Wildlife Refuge. Deer densities in Canaan Valley may be as high as 30 deer/km² in the southern end of the valley (Appendix 1). Deer hunting is allowed by permit within the National Wildlife Refuge lands and is conducted on private holdings throughout Canaan Valley. However, hunting has been prohibited in sections of the southern end of the

valley (i.e., Canaan Valley Resort State Park) for at least 30 years prior to this study (Michael, 1992). Recently, the West Virginia legislature has permitted the use of hunting in state parks at the discretion of the West Virginia Division of Natural Resources. Canaan Valley State Park has been considered as a potential location for an organized hunt.

The formation of these public lands has centered on the protection of the unique wetland areas found in Canaan Valley. These provide habitat for over 580 plant species including 80 wetland plants and 34 wetland plant communities that are considered rare or endangered within the state (Fortney, 1975; Michael, 1992; West Virginia Division of Natural Resources, 2012). The wetlands of Canaan Valley support nannyberry (*Viburnum lentago*), considered rare and imperiled in West Virginia (ranked S2), woodland horsetail (*Equisetum sylvaticum*), considered rare and critically imperiled (ranked S1) and bog Jacob's-ladder (*Polemonium vanbruntiae*) (ranked S2) (Rentch & Anderson, 2008; West Virginia Division of Natural Resources, 2012).

Our objectives were to: a) determine whether the attitudes of residents of Canaan Valley and Tucker County differed from the attitudes of nonresident landowners and visitors with respect to white-tailed deer management and plant conservation; b) determine whether the attitudes of hunters differed from the attitudes of nonhunters with respect to white-tailed deer management and plant conservation, and c) determine how negative experiences with white-tailed deer may influence their attitudes toward management decisions. We hypothesized that the nonresident landowners and visitors to Canaan Valley may have a more urban or suburban background and thus might be less likely to participate in hunting or approve of lethal control methods, and more likely to view white-tailed deer management in an ecosystem context and thus favor the conservation of rare plant species. We hypothesized that hunters were more likely to consider a reduction in deer abundance as an unacceptable "cost" of rare plant conservation

and were therefore more likely to respond unfavorably toward rare plant conservation. Lastly, we hypothesized that respondents who had experienced negative interactions with deer were more likely to view local deer populations as overabundant and accept measures of deer management.

Study Area

The Canaan Valley, located in Tucker County, West Virginia, is the largest high-elevation valley east of the Rocky Mountains (Fortney, 1975). It is 21 km long and ranges in width from 4.8 - 8.0 km. The valley encompasses about 176 km² (17,600 ha) of land. The average valley floor elevation is 980 m above sea level and the mountains surrounding the valley rise another 300 m in elevation. The high elevation and topography of Canaan Valley results in a climate more similar to northern boreal forests than to the deciduous forests of surrounding areas in West Virginia. Canaan Valley is home to sub-arctic bogs and stands of conifers such as balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*).

About 20% of the land area is made up of various wetland community types and another 23% is northern hardwood forest. Of all the high-elevation wetlands in West Virginia, Canaan Valley is home to the largest contiguous wetland areas (3,000 ha, Byers, Vanderhorst & Streets, 2007). Agriculture, rural development, and recreational land make up the remaining land area (Michael, 1992).

Methods

Selecting Stakeholder Groups

We chose 4 stakeholder groups that had the potential to influence wild plant conservation and white-tailed deer management in Canaan Valley and the surrounding areas. We surveyed residents of Canaan Valley as well as residents of the surrounding areas in Tucker County, WV,

who might work or travel through Canaan Valley frequently. Additionally, we sampled nonresidents who owned land in Canaan Valley as well as those who only visit Canaan Valley. We sampled residents and nonresident landowners in 2005 by mail surveys that were sent to addresses selected by systematic random sampling from Tucker County tax records. We mailed the surveys with an included self-addressed, stamped envelope for the return of responses. To assess the attitudes of visitors to Canaan Valley, we supplied survey forms to the visitors' centers at Canaan Valley National Wildlife Refuge and Canaan Valley State Park. Surveys also were distributed to Canaan Valley State Park Ski Lodge and several local businesses; however, no surveys were successfully retrieved from locations outside the state park and national wildlife refuge.

Questionnaire Design

We created a survey that consisted of 25 questions (Appendix 8). Respondents were asked demographic questions including their age, sex, education level, and residency status. The respondents' views toward rare plant conservation and the status and management of white-tailed deer in Canaan Valley were assessed with 16 opinion questions. Responses to opinion questions were rated on the Likert scale with 6 categories: strongly disagree (-2), disagree (-1), neutral (0), agree (+1), strongly agree (+2), and no opinion. The participants' attitude toward hunting as a management tool as well as their participation in hunting activities was addressed with 3 questions. Two other questions addressed personal experience with a deer-vehicle collision and property damage (e.g., crops).

Statistical Analysis

We used only the data from respondents that had fully completed surveys. No Opinion responses were pooled with the Neutral responses. The 16 opinion questions were subjected to

Principal Components Analysis (PCA) to minimize redundancy among the questions and to identify underlying constructs. We standardized and rotated our principal components using the varimax rotation method. We selected three principal components from the correlation matrix based on a scree plot, so that any component left in the analysis explained >10% of the total variance in the data set, magnitude of the eigenvalues, and interpretability (Hatcher, 1994). We considered the loadings to be “large” for a question if it was > 0.5 .

We modeled the principal component scores as a function of 4 sociodemographic factors determined from the questionnaire (Residency Status, hunting participation from Question 19, deer-vehicle collisions from Question 7, and deer landscape-crop damage from Question 8) and their two-way interaction using a multi-factor analysis of variance (ANOVA) in program R (R Development Core Team, 2008). We maintained the 0.05 experimentwise α level using a Bonferroni correction; that is, the α level was set to 0.005 for individual tests. Post-hoc multiple comparisons were made using a Bonferroni procedure to compare least squares means between factor levels. Residual diagnostics were run to assess validity of the model assumptions. Additionally, we examined the principal components using a Potential for Conflict Index (PCI)(Vaske, Needham, Newman, Manfredi, & Petchenik, 2006). The PCI numerically described the amount of disparity between respondents in a particular group by giving more weight to extreme responses and no weight to neutral responses. Thus, the higher the PCI value, the greater the range of responses within a group.

Results

We received 174 responses from a total of 500 mailed surveys for a response rate of 35% (Table 1). Additionally, we received 46 visitors’ responses. From the 220 total responses, we removed 26 from analysis because of incomplete responses. The three retained principal

components are summarized in Table 2. Together these components accounted for 60% of the variation in the data. Interpretation of the loadings on each principal component suggested that each component could be attributed to a distinct construct as measured by several original questions. Principal component 1 (PC1) dealt mainly with attitudes toward seeing deer and overabundance in Canaan Valley and West Virginia (Questions 1–4, and 10, Appendix 8). Component 1 also included an opinion on using professional sharpshooters to reduce deer numbers (Question 21, Appendix 8). Principal component 2 (PC2) focused on attitudes toward plant conservation and the relation to deer abundance (Questions 6, and 13–15, Appendix 8). Principal component 3 (PC3) focused on management of white-tailed deer (Questions 9, 11, 12, and 17, Appendix 8).

When we modeled the scores for PC1 with respect to the 4 factors (residency status, hunting participation, deer-vehicle collisions and deer landscape/crop damage) we found only the *F* test for the deer landscape/crop damage was significant ($F_{1,163} = 12.87, p < 0.001$). We found that people who had experienced crop or landscape damage had significantly larger mean principal component 1 scores ($\bar{x} = 0.299, SE = 0.118$) than those who did not ($\bar{x} = -0.359, SE = 0.170$). Larger PC1 scores correspond with a lower tolerance of deer. Of the questions that were a part of PC1, the 2 groups tended to differ in opinion the most on the subject of overabundance in Canaan Valley and West Virginia with those that had experienced crop or landscape damage being more likely to describe these populations as being overabundant. There was a substantial amount of conflict among those that had experienced crop or landscape damage with respect to views on professional sharpshooting as a deer population management tool (PCI = 0.54; Figure 2).

Results from modeling PC2 as a function of the 4 sociodemographic factors showed only a significant F test for the residency factor ($F_{3,163} = 4.91, p < 0.003$). Tucker County residents ($\bar{x} = 0.578, SE = 0.145$) had higher P2 scores on average than nonresident landowners ($\bar{x} = -0.172, SE = 0.153$) ($t = -3.55, p < 0.001$; Figure 3). Larger PC2 scores indicated lower valuation of plants and plant communities. Tucker County residents also tended to value plants less than Canaan Valley visitors ($\bar{x} = -0.163, SE = 0.269$); however, this difference ($t_{163} = 2.46, p = 0.015$) was not considered significant due to the conservative nature of the Bonferroni correction. While for the most part stakeholder groups agreed that they enjoyed seeing wild plants, Tucker County residents appeared less likely to agree that deer could harm plant communities and that plants should be protected from deer (Table 3). PCI scores were higher for Tucker County residents on these topics indicating moderate conflict within that group.

Due to a violation of the assumption of normal errors under ANOVA, the Box-Cox procedure was used to select a normalizing power transformation for the PC3 scores (Box & Cox 1964). Hunters ($\bar{x} = 0.414, SE = 0.037$) had significantly higher PC3 scores on average than nonhunters ($\bar{x} = -0.308, SE = 0.049$) ($F_{1,163} = 14.80, p < 0.001$; Figure 4) where least squares means estimates were back-transformed to the original scale and the standard errors in the original scale were approximated via the Delta method. Larger PC3 scores corresponded to a greater support for management actions for white-tailed deer. Of the questions contributing to PC3, nonhunters were more likely than hunters to disagree that deer densities should be managed to increase hunter harvest (Figure 5) and there was moderate conflict within the nonhunting group (PCI = 0.32).

Discussion

Overall, we found that those respondents who had experienced damage to landscaping or crops

were less likely to exhibit tolerance of high deer densities and support an increase in the deer herd. Lischka, Riley, and Rudolph (2007) found a positive association between hunting participation and attitudes toward deer abundance and a negative association between farming and deer abundance. People are generally willing to accept deer until they reach some threshold of deer-human conflict (Stout et al., 1997), after which they are more likely to be open to lethal control methods (Messmer et al., 1997).

We did not find a difference between permanent residents, nonresident, and visitor stakeholder opinions regarding white-tailed deer abundance as measured by PC1 ($F_{3,163} = 2.17$, $p < 0.093$). Many of the nonresident landowners and visitors surveyed came from urban or suburban centers such as Baltimore, MD, and Washington, D.C. These respondents may be more acquainted with issues of deer overabundance in suburban parks and refuges (Raik, Siemer, & Decker, 2005). However, this did not lead them to view the Canaan Valley deer herd as overabundant. The lack of an urban-rural divide might be due to the values of stakeholders who choose to recreate in rural areas. Clendenning, Field, and Kapp (2005) found that many exurbanites seek a return to rural roots and therefore might have values that align more closely with residents.

There were lower percentages of hunters for the visitors and nonresident landowner groups. Holsman and Peyton (2003) found hunters tended to believe that there were fewer deer present in an ecosystem than other groups surveyed. We did not find an association between participation in hunting and attitudes toward deer abundance as measured by PC1 ($F_{1,163} = 3.59$, $p < 0.060$) nor did we find sufficient evidence of interaction between hunting participation and residency ($F_{3,163} = 2.67$, $p < 0.049$).

Visitors and nonresident landowners were less likely than residents to have been involved in a deer-vehicle collision (Question 7; Table 1). There did not appear to be a desire for fewer deer among those who had recently been involved in a collision. There was no difference with respect to PC1 between those who had been involved in a collision and those who had not ($F_{3,163} = 0.25, p < 0.861$) nor did we find sufficient evidence of interaction between car collision involvement and residency ($F_{9,163} = 0.86, p < 0.566$). Loker et al. (1999) found that negative experiences with wildlife species did not necessarily result in a feeling of concern over that species.

Views toward professional sharpshooting as a means of reducing deer populations were negative overall (Question 21; Table 1). The mean response of stakeholders that had experienced crop or landscape damage was circumneutral; however, the PCI score for this group was 0.54 indicating strong disagreement within the group (Figure 2). Messmer et al. (1997) found that the general public had a low opinion of sharpshooting compared to other methods of herd reduction. Stout et al. (1999) also found low public support for sharpshooting as a management technique among suburban residents. However, they found that the level of acceptance did not change with increases in deer densities. We also found that many respondents were unsure of the practice of herd reduction by this method and some mentioned that they would be likely to agree contingent upon the use of the deer afterward. Many of those opposed voiced a preference for a controlled public or permit hunt for West Virginia license holders.

Regarding PC2, Tucker County residents were less likely than nonresident landowners and visitors to Canaan Valley to value rare and endangered plants, especially if it meant a need to protect those plants from the local white-tailed deer herd. Clendenning et al. (2005) found that

there were differences between urbanites and rural residents on some aspects of wildlife management and that seasonal homeowners hold attitudes that support the preservation of the natural amenities around their homes.

Holsman and Peyton (2003) found that stakeholders expressed value for ecosystem management goals in the absence of costs and that deer hunters were unwilling to accept reductions in the deer herd to protect stands of white cedar (*Thuja occidentalis*). Similarly, others have found that participation in hunting was related to low support for biodiversity and other broad ecological management objectives (Holsman, 2000). We did not find sufficient evidence of an association between hunting participation and valuation of rare plant species as measured by PC2 ($F_{1,163} = 4.13, p < 0.044$) nor did we find sufficient evidence of interaction between hunting participation and residency ($F_{3,163} = 0.39, p < 0.759$). We believe that hunters may not have interpreted questions 6, 13, 14, and 15 as support for a reduction in the deer herd and therefore were more likely to value rare plant conservation since no “cost” was involved.

While hunters were more likely than nonhunters to support management actions for white-tailed deer as measured by PC3, the vast majority of respondents from all groups accepted hunting as a tool to manage white-tailed deer populations (Questions 9, 12, and 17; Table 1) with the exception of management for the purpose of increasing hunter harvest (Question 11; Table 1). This suggests that the stereotype of the suburbanite “antihunter” might be unfounded in Canaan Valley and might be the result of a vocal minority (Curtis & Hauber, 1997; West & Parkhurst, 2002). Some of the comments received as a part of the survey seemed to reflect this view. Loker et al. (1999) found that suburban residents were generally open to wildlife management, even lethal control options, and believed that managers should use caution in stereotyping the attitudes of suburban residents. The large degree of acceptance seen here might

be due to the backgrounds of respondents who choose to visit or buy land in Canaan Valley (Clendenning et al., 2005). High deer abundance once made Canaan Valley a popular hunting area within West Virginia. Many visitors and nonresident landowners might actually be coming to the area to hunt and therefore these results might not be applicable to other areas.

We caution the reader that the results given here are exploratory in nature, and are not meant to be construed as confirmatory. The reason is because of the presence of possible sources of selection bias; namely, bias due to undercoverage, nonresponse, and voluntary response sampling. The presence of nonresponse does not ensure that a bias exists. Further follow-up would be necessary to assess the effect of nonresponse bias, if it exists, and to statistically account for it. Nevertheless, our conclusions are at least suggestive and could certainly help Canaan Valley management organizations design more rigorous probability sampling designs that could be analyzed with the same formal approach we have developed here.

It is important to understand public perceptions to successfully execute management plans in the public domain (Swihart & DeNicola, 1997). Contrary to perceptions, the majority of the visitors and nonresident landowners in Canaan Valley thought that there were too many deer in Canaan Valley State Park and National Wildlife Refuge (Question 4; Table 1). These stakeholder groups also indicated that it was important to conserve rare and endangered plant species even at the expense of white-tailed deer herds (Question 15; Table 1). Management organizations in Canaan Valley including the West Virginia Division of Natural Resources and the United States Fish and Wildlife Service should use the information gathered in this study along with biological data to inform management decisions on the white-tailed deer herd in Canaan Valley.

Management Implications

Although many of the views of residents and nonresidents were similar, Tucker County residents were less likely to favor rare plant conservation. Many of the visitors and nonresidents come to Canaan Valley specifically because of its unique characteristics and appear to place more value on these unique plants. Recognition of differences in attitudes between stakeholder groups could be helpful in designing educational programs for users of natural areas (Brooks et al., 1999). In this case, education and emphasis on the importance of rare plant diversity in Canaan Valley may bring more local support for their conservation.

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Table 1.

Mean likert scores for 4 stakeholder groups regarding white-tailed deer in Canaan Valley, West Virginia, 2005.

	Canaan Valley Residents		Nonresidents		Tucker County Residents		Visitors	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1 I enjoy seeing white-tailed deer around/near my home.	1.0	0.2	1.6	0.1	1.3	0.1	1.3	0.2
2 I enjoy seeing white-tailed deer when I visit state or national parks, forests or wildlife refuges.	1.4	0.1	1.6	0.1	1.6	0.1	1.4	0.2
3 I believe deer are overabundant in the state of West Virginia.	0.5	0.4	1.4	0.2	0.2	0.3	1.1	0.2
4 I believe deer are overabundant in Canaan Valley National Wildlife Refuge and/or Canaan Valley Resort State Park.	0.8	0.4	1.2	0.2	0.7	0.2	1.5	0.2
5 I place value on wild plants and trees as sources of food and timber.	1.5	0.2	1.5	0.1	1.6	0.1	1.5	0.1
6 I enjoy seeing wild plants, flowers, and trees.	1.5	0.1	1.5	0.1	1.4	0.1	1.7	0.1
7 I, or a member of my immediate family, have been involved in a deer/vehicle collision.	1.4	0.2	1.0	0.1	1.8	0.1	0.8	0.1
8 I, or a member of my immediate family, have incurred damage to landscaping, crops or other property (excluding vehicles) from deer.	0.4	0.2	0.2	0.1	0.3	0.1	0.1	0.1
9 I believe it is ethical to manage wild populations of white-tailed deer.	1.3	0.3	1.4	0.1	1.4	0.2	1.6	0.1
10 I believe white-tailed deer numbers should be increased in West Virginia.	1.6	0.4	1.5	0.2	0.8	0.3	1.9	0.2
11 I believe white-tailed deer numbers should be managed to increase hunter harvest.	1.1	0.4	0.8	0.2	1.2	0.2	1.0	0.3
12 I believe white-tailed deer numbers should be managed in balance with their environment.	1.0	0.3	1.3	0.1	1.3	0.2	1.7	0.1
13 I believe white-tailed deer may have a detrimental effect on some plant communities.	2.0	0.2	1.5	0.1	1.0	0.2	1.5	0.2
14 I believe rare or endangered plant species should be protected.	1.6	0.2	1.6	0.1	1.1	0.2	1.7	0.1
15 I believe rare or endangered plant species should be protected from white-tailed deer browsing if it reduces the abundance of those plants.	1.7	0.3	1.5	0.1	0.9	0.2	1.6	0.2
16 I would not have a problem seeing fenced areas to protect plants when I visit state or national parks, forests or wildlife refuges.	0.7	0.3	0.8	0.2	0.9	0.2	1.1	0.2
17 I believe hunting is an acceptable tool for managing deer populations.	1.4	0.2	1.2	0.1	1.5	0.1	1.8	0.1
18 I have participated in legal hunting activities within my lifetime.	0.2	0.2	0.0	0.1	0.6	0.1	0.2	0.1
19 I have participated in legal hunting activities within the past year.	-0.5	0.2	-0.6	0.1	0.2	0.1	-0.1	0.1
20 Another member of my household participates in legal hunting activities.	-0.5	0.2	-0.4	0.1	0.5	0.1	-0.1	0.2
21 I believe professional sharp-shooting is an acceptable tool for managing deer populations.	1.1	0.5	0.5	0.2	-0.4	0.3	1.0	0.3
Number of Responses returned	20		72		53		46	

Table 2.

Principal components and constructs derived from survey dataset groups regarding white-tailed deer in Canaan Valley, West Virginia, 2005.

Component	Eigenvalue	Proportion	Cumulative Proportion	Construct
PC 1	5.4946	0.3434	0.3434	Deer abundance/tolerance
PC 2	2.1058	0.1316	0.4750	Rare plant conservation
PC 3	1.9480	0.1218	0.5968	Deer management

Table 3.

Mean and Potential for Conflict Index (PCI) values for four questions contributing to Principal Component 2 by resident group. Mean values of -2 correspond to strongly disagree and 2 corresponds to strongly agree. Higher PCI values indicate higher potential for conflict among group members.

	Question 6 ^a		Question 13 ^b		Question 14 ^c		Question 15 ^d	
	Mean	PCI	Mean	PCI	Mean	PCI	Mean	PCI
Canaan Valley Residents	1.30	0.00	0.90	0.00	0.85	0.05	0.35	0.15
Nonresident Landowners	1.47	0.00	0.92	0.11	0.96	0.03	0.77	0.08
Tucker County Residents	1.22	0.02	0.26	0.33	0.24	0.30	0.02	0.33
Visitors	1.62	0.00	0.98	0.11	1.13	0.06	0.81	0.20

^aQuestion 6: I enjoy seeing wild plants, flowers, and trees.

^bQuestion 13: I believe white-tailed deer may have a detrimental effect on some plant communities.

^cQuestion 14: I believe rare or endangered plant species should be protected.

^dQuestion 15: I believe rare or endangered plant species should be protected from white-tailed deer browsing if it reduces the abundance of those plants.

Figure 1. Scatter plot matrix for all three Principal Component Scores for respondents that had (Yes) and had not (No) experienced damage to crops or landscaping attributable to white-tailed deer, 2005.

Figure 2. Potential for Conflict Indices (PCI) for the six questions contributing to Principal Component One by respondents that had and had not experienced damage to crops or landscaping.

Circles are centered on the mean response for each group where -2.0 corresponds to strongly disagree and 2.0 corresponds to strongly agree. Larger circles indicate higher potential for conflict within group members. PCI values are given next to the corresponding point. The questions are the following;

1. Question 1: I enjoy seeing white-tailed deer around/near my home.
2. Question 2: I enjoy seeing white-tailed deer when I visit state or national parks, forests or wildlife refuges.
3. Question 3: I believe deer are overabundant in the state of West Virginia.
4. Question 4: I believe deer are overabundant in Canaan Valley National Wildlife refuge and/or Canaan Valley Resort State Park.
5. Question 10: I believe white-tailed deer numbers should be increased in West Virginia (reversed scale).
6. Question 21: I believe professional sharpshooting is an acceptable tool for managing deer populations.

Figure 3. Scatter plot matrix for all three Principal Component Scores for respondents that were Canaan Valley residents (CV), nonresident landowners (NR), Tucker County residents (TC), and visitors to Canaan Valley (V), 2005.

Figure 4. Scatter plot matrix for all three Principal Component Scores for respondents that had (Yes) and had not (No) participated in hunting of any species within the past year, 2005.

Figure 5. Potential for Conflict Indices (PCI) for the four questions contributing to Principal Component Three by hunters and nonhunters. Circles are centered on the mean response for each group where -2.0 corresponds to strongly disagree and 2.0 corresponds to strongly agree. Larger circles indicate higher potential for conflict among group members. PCI values are given next to the corresponding point. The questions are the following;

1. Question 9: I believe it is ethical to manage populations of white-tailed deer.
2. Question 11: I believe white-tailed deer numbers should be managed to increase hunter harvest.
3. Question 12: I believe white-tailed deer numbers should be managed in balance with their environment.
4. Question 17: I believe hunting is an acceptable tool for managing deer populations

CHAPTER VII

MANAGEMENT IMPLICATIONS FOR WHITE-TAILED DEER HERBIVORY: COMMUNITY INFLUENCE AND STAKEHOLDER RESPONSE

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Much of the research concerning the effects of deer on plant communities have focused on their role as browsers and the potential for over-browsing of upland plant species (Whitney 1984; Alverson and Waller 1997; Stromayer and Warren 1997). Fewer studies of deer diet have been directed solely toward rare or endangered herbaceous or woody plants (Miller et al. 1992; Urbanek et al. 2012). While research on browse effects on wetland plants is limited, there is evidence that they affect many other herbaceous species through herbivory. Deer have been implicated in the decline of many rare species. The purpose of this study is to evaluate the influences of white-tailed deer browse on plant populations in West Virginia. The study was organized into three general sections: 1) the influence of white-tailed deer browse and seed dispersal on rare wetland plant species and communities in Canaan Valley, West Virginia, 2) the impact of white-tailed deer density on forest understory recruitment in upland forests throughout West Virginia, and 3) public attitudes toward rare plant conservation and white-tailed deer management.

Study Area

Canaan Valley, in Tucker County, West Virginia, is the largest high-elevation valley east of the Rocky Mountains (Fortney 1975) and is characterized by a relatively cool, moist climate and a short growing season that make the climate and accordingly, the vegetation, of this area more similar to boreal forests of the northeastern United States and Canada than to the deciduous forests of surrounding West Virginia. Canaan Valley is home to the largest contiguous high-elevation wetland area in West Virginia (3,000 ha, Byers et al. 2007) making up about 20% of the valley floor. Areas

of Canaan Valley have been set aside as Canaan Valley State Park and Canaan Valley National Wildlife Refuge (NWR).

The Influence of White-tailed Deer Florivory on Polemonium vanbruntiae

We monitored flowering stems in ten populations of bog Jacob's ladder (*Polemonium vanbruntiae*) from May 2005 to 2006 to determine the proportion of seeds and stems lost to white-tailed deer florivory. We compared the proportion of stems and seeds lost to browse in sites on the Canaan Valley NWR to sites in Canaan Valley State Park. We used stage-structured matrix modeling to compare the rates of population increase (λ) with and without white-tailed deer florivory.

Loss of seeds to white-tailed deer florivory ranged between 0 and 99% within individual populations and stem loss ranged between 0 and 97%. We found a significant difference in percent stems browsed between the Canaan Valley State Park populations ($\bar{x} = 57 \pm 19\%$) and the Canaan Valley NWR populations ($\bar{x} = 40 \pm 18\%$, $F_{1,16} = 3.27$, $p = 0.085$). Deer florivory reduced the average growth rate from 1.17 (SE = 0.11) to 1.08 (SE = 0.13). In only one population, λ was reduced to less than 1, indicating a population decline.

Our study suggests that white-tailed deer may consume almost 100% of the sexually reproductive ramets within *P. vanbruntiae* populations in a given year. As *P. vanbruntiae* can reproduce clonally, high levels of seed loss such as those exhibited here may not have an immediate effect on population persistence. However, a loss of flower and seed production can reduce dispersal into new populations and will reduce genetic variation in a population due to a reduction in sexual reproduction.

- The alteration of deer densities in Canaan Valley to reduce browsing may not immediately benefit *P. vanbruntiae* populations and may be impractical for this sole purpose.
- We believe that short term (May – July) fencing of smaller populations or individuals stems

would significantly reduce the loss of seed production as flowering ramets were most susceptible immediately prior to and during flowering. The protection of flowering ramets would allow for gene flow through pollination as well the formation of seeds for dispersal.

- Translocation of seeds or individuals from existing populations to suitable, but currently unoccupied patches within Canaan Valley may reduce the chance of localized extirpation through the loss of existing subpopulations.

The Influence of White-tailed Deer Herbivory on Wetland Communities

We monitored two types of wetland plant communities from those present in Canaan Valley; *Solidago* spp.-*Rubus hispidus*. dominated wet meadow communities and regenerating aspen (*Populus* spp.) dominated communities from 2005–2007. Within each community, we compared the change in species composition in early, late, and continuously fenced treatment plots with control plots using Blocked Multiple Response Permutation Procedures (MRBP) in PC-Ord (McCune and Mefford 1999). We also compared species richness within plots after two years protection from browse. We also examined the changes in woody, forb and graminoid metacommunities as well as the differences between wetland indicator status categories.

There were no significant differences in species richness found between fenced and control plots in either community for any treatment measured in both spring and fall ($p > 0.05$). In both *Solidago* spp.-*Rubus hispidus*. and *Populus* spp. communities we found that differences in community composition between treatment and control plots depended on both the treatment period and the season of data collection. In both communities, increases in woody species cover were apparent in fenced plots under some, but not all, treatment regimes. Changes in forb cover occurred in both communities but were only apparent when measured in the fall. No differences in graminoid species cover class were detected for fencing period or treatment in either season. There was no

significant difference in the changes between wetland indicator status categories for either community.

Our study suggests that the elevated deer densities present in the post-logging era impact the herbaceous community by selectively browsing forb species, especially in the spring. Suppression of woody species through selective browsing may play a role in suppressing succession to the historical spruce communities. The timing of herbivory may be a factor in determining the influence of white-tailed deer browse on some species.

- We believe that continuous protection of herbaceous wetland communities on a large scale for the protection of individual threatened and endangered species or the regeneration of historical communities is not feasible in Canaan Valley.
- Small-scale protection of individuals or small populations may increase the survival of woody or forb species.
- However, continuous protection may not be appropriate everywhere in Canaan Valley. Seasonal protection may be more effective on individual plants representing threatened or endangered species where year-long protection may not be appropriate.

Protection of forb species should occur in the spring and woody species in the fall and winter.

The Influence of White-tailed Deer Herbivory on Upland Communities

We analyzed a dataset collected from twenty, paired treatment (fenced) and control sites from upland forests throughout West Virginia between 1984 and 1990. We counted the number of stems for each species in the ground cover and understory vegetation subplots. We compared the number of stems, species richness, and the Shannon diversity values between control plots and treatment every three years following plot establishment. We used MRBP to determine if differences existed in the groundcover and understory communities between fenced and control plots. Finally, we

evaluated the relation between the seedling-sapling ratio (Sweetapple and Nugent 2004) in control plots and the total deer density at the site from 1993 – 2007.

In upland communities, we recorded 197 species present in the ground cover over the study period. After 21 years, we found no significant difference in stem abundance, species richness, or Shannon diversity values in the ground cover. At the ground cover level, we found a significant difference in community composition occurred 21 years after plot initiation ($t = -0.20$, $p = 0.03$). We recorded 79 species present in the understory over the study period. We found that treatment had an effect on the stem abundance ($F_{1,19} = 12.22$, $p < 0.001$) and Shannon diversity values ($F_{1,19} = 40.82$, $p < 0.001$). There was a significant difference in both species richness and understory community composition 6 years after plot establishment and in most years thereafter ($p > 0.05$). We found no relation between the seedling-sapling ratio and deer density ($R^2 = 0.02$, $p = 0.17$).

Our results indicate the density of white-tailed deer impacting the control plots at our sites has met or exceeded the capacity of the upland forest to regenerate the current community. The potential still exists to regenerate the current forest state. However, if browse pressure persists as the seed sources decline; the potential for recovery of the current ecosystem will likewise decline (Levine et al. 2012).

- At many locations throughout the state, deer densities must be reduced in order for regeneration of the current complement of overstory species to regenerate.
- Alternately, larger scale ($> 10 \text{ m} \times 10 \text{ m}$) protection of the groundcover and understory communities may allow for localized regeneration of the understory providing for a future seed source.
- Our results suggest that it takes only 6 years of protection to allow species to enter the understory. However, longer protection is necessary to allow those individuals to escape deer browse.
- As differences in groundcover vegetation were found in the 21st year post construction, the

ability of the community to regenerate on its own may already be diminished. At some sites, a decrease in deer density may not be enough for regeneration. Fencing in conjunction with seeding or transplants may be necessary to restore desirable species.

- At some sites, graminoid and fern cover may also present an obstacle for regeneration.
- We recommend using caution in the application of the seedling-sapling ratio method, or any other vegetation-based deer density index without first testing its applicability to local flora.

White-tailed Deer Seed Dispersal through Endozoochory

We collected fresh white-tailed deer fecal pellet groups bi-monthly from May to December in wetland habitats within the Canaan Valley National Wildlife Refuge and Canaan Valley State Park. Following a three month period of cold stratification the seeds were spread on top of a layer of potting mix within 10 cm diameter planting pots and kept moist. We determined the wetland indicator status (Lichvar et al. 2014) and classified each species as graminoid, forb, or woody species. We compared the proportion of species germinated and frequency of occurrence. We repeated these tests for the proportion and frequency of germination of plants that were graminoid, forbs, or woody. We identified 14 species in 2005 and 32 species in 2006. We did not find a significant difference in the proportion of species by wetland indicator status or growth habit. The proportion of stems germinated of both graminoids and forbs were significantly higher than for woody species in both years ($p < 0.05$). The proportion of upland stems (UPL and FACU) germinating was significantly more than proportion of wetland stems (FACW and OBL) in 2006, but not in 2005.

A difference in frequency of upland species that germinated from fecal samples in 2006 seems to agree with the hypothesis that upland plants may be more adapted to dispersal by white-tailed deer, though this difference in frequency might be attributed to the success of a few FACU plants. We observed the presence of FACW and OBL wetland species germinating in pellet piles; however, these observations may underestimate the actual presence of germinable wetland species in

pellet piles as we did not provide our samples with wetland conditions for germination. As dispersers, white-tailed deer could play a role in maintaining or enhancing metapopulations of wetland plants patchily distributed in an upland matrix (Vellend et al. 2003).

- White-tailed deer do act as dispersers of exotic plants in Canaan Valley. However, it is unclear if exotic plants are consumed and dispersed disproportionately or if dispersal significantly increases the colonization rate of these species into new areas.
- While dispersal by herbivores is often linked to the production of fleshy fruit, the prevalence of graminoids and small forbs in our sample lends support to the “foliage as fruit” hypothesis (Janzen 1984).
- These results coupled with those of the exclosure studies suggest that white-tailed deer may contribute to increases in graminoid cover through seed dispersal as well as through selective browsing and deer exclusion may serve to change groundcover communities by altering both means.

Stakeholder Views of White-tailed Deer Management and Plant Conservation

We surveyed stakeholders including residents of Canaan Valley, residents of Tucker County, West Virginia, nonresident landowners and visitors to Canaan Valley using 25 questions designed to assess views toward rare plant conservation and the status and management of white-tailed deer in Canaan Valley. Responses were subjected to Principal Components Analysis (PCA) to identify underlying constructs and we modeled these as a function of socio-demographic factors. Additionally, we examined the principal components using a Potential for Conflict Index (PCI) (Vaske et al. 2006) that numerically described the amount of disparity between respondents in a particular group.

We found that people who had experienced crop or landscape damage tended to have a lower tolerance of deer. Those that had experienced crop or landscape damage were more likely to describe Canaan Valley white-tailed deer populations as being overabundant. Tucker County

residents tended to value plants and plant communities less than nonresident landowners ($t = -3.55$, $p < 0.001$). Although, for the most part, stakeholder groups agreed that they enjoyed seeing wild plants, Tucker County residents appeared less likely to agree that deer could harm plant communities and that plants should be protected from deer. Hunters, in general, showed greater support for management actions for white-tailed deer than nonhunters ($F_{1,163} = 14.80$, $p < 0.001$).

Many of the visitors and nonresidents come to Canaan Valley specifically because of its unique characteristics and appear to place more value on these unique plants. Recognition of differences in attitudes between stakeholder groups could be helpful in designing educational programs for users of natural areas (Brooks et al. 1999). In this case, education and emphasis on the importance of rare plant diversity in Canaan Valley may bring more local support for their conservation.

- Local rural residents were less likely to favor rare plant conservation. This suggests the need for building awareness of the unique nature of Canaan Valley vegetation among local residents.
- Many of the Tucker County residents may be less likely to frequent Canaan Valley State Park and National Wildlife Refuge. Thus, educational efforts should not be limited to these two venues to reach the local community.

CONCLUSION

The plant communities of Canaan Valley today are much different than those that existed in precolonial times. Humans have altered plant communities from a thick overstory dominated by conifers to open herbaceous and shrub-dominated wetlands. It may be unlikely that species such as the *P. vanbruntiae* that rely on mid-successional, wetland habitat were as prevalent at that time as they are today. Therefore, white-tailed deer florivory at current levels is not likely to reduce the Canaan Valley *P. vanbruntiae* populations below historical levels. However, the loss of colonization potential, when combined with other anthropogenic threats to individual subpopulations persistence,

may have the potential to lead to extirpation. As *P. vanbruntiae* is rare throughout much of its range, localized extinction of the Canaan Valley population, one of the southernmost populations, may represent a significant loss of diversity in this species. Herbaceous wetland plant communities on the valley floor also represent a significantly different condition than was present in the past. While many of the native species were likely present, they may have been less abundant under thick conifer cover. Thus, increased deer densities in Canaan Valley are not driving native plant densities below historic levels. However, increases in woody plant cover in fenced plots suggest the possibility that high densities of white-tailed deer may prevent the succession of overstory species once prevalent in the valley.

The surrounding upland forests of West Virginia are also likely different from historical communities. Extirpation of dominant species such as the American chestnut (*Castanea dentata*) as well as harvest practices has changed overstory species composition. At many sites, however, the current complement of overstory species is not being regenerated and, if current deer densities are maintained, may be replaced with species that are less valuable for both timber and wildlife. The native herbaceous ground cover at our upland sites may represent the historical community. However, at high deer density sites species composition has shifted toward graminoid species potentially further reducing the survival of tree seedlings. White-tailed deer, at high densities, do have the potential to negatively affect both woody and herbaceous forest and wetland communities.

FUTURE RESEARCH NEEDS

The findings of our study indicate the following needs for future research at both the state and national level:

- Estimation of the natural rate of colonization of new patches for *P. vanbruntiae* as well as other native threatened and endangered species to determine the actual effect florivory may have on species' dispersal.

- Examine the role of other landscape factors such as topography and anthropogenic influences in limiting the dispersal of *P. vanbruntiae*.
- Germination of fecal pellet samples under alternate regimes to increase the potential of wetland seed germination.
- Comparison of the actual seed bank potential at WV DNR exclosure sites through *ex situ* germination studies to determine the relative importance of seed bank, seed rain or seed dispersal in maintaining ground cover diversity.
- Examine the influence of an abundant sapling community on the microclimate and nutrient cycling within WV DNR exclosures and the subsequent influence of those variables on seedling growth.
- Separation of farmers and hunters in determining attitudes toward deer management and plant conservation.

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Appendix 1. Deer density estimates from spotlight sampling conducted in Canaan Valley, WV in 2005 – 2006. Estimates were calculated using the distance sampling program Distance version 6.2 release 1. Strip width refers to the effective strip width of the detection function for each sampling event. The upper and lower confidence limit for deer density was calculated in Distance.

Sampling Date			Deer/ha	Lower CL (Deer/km ²)	Deer/km ²	Upper CL (Deer/km ²)	Deer/mi ²	Strip Width (m)
May	31	2005	0.332	25.8	33.2	42.9	86.0	43.70
June	10	2005	0.166	N/A	16.6	N/A	43.0	N/A
July	12	2005	0.304	21.6	30.4	42.7	78.7	82.78
July	26	2005	0.321	25.1	32.1	40.5	83.1	77.19
August	23	2005	0.244	17.3	24.4	34.4	61.2	132.18
December	15	2005	0.183	12.4	18.3	26.4	47.4	85.91
March	24	2006	0.257	16.7	25.7	39.3	66.6	82.17
May	10	2006	0.302	21.3	30.2	42.7	78.2	95.97
May	24	2006	0.153	11.1	15.3	21.2	39.6	151.28
June	15	2006	0.285	20.6	28.5	39.4	73.8	64.00
July	26	2006	0.092	6.9	9.2	12.3	23.8	78.12
December	19	2006	0.249	16.0	24.9	38.7	64.5	85.91
Average			0.241		24.1		62.33	93.55

Appendix 2. R Code for the calculation of population growth rates and confidence intervals with the popbio package.

```
> library(popbio)

> A <- matrix(c(0,.2375,0,0,0,0,0,.041,0,0,0,0,.88,.101,.01,175.4,0,.89,.02,.02,0,0,.03,0,0),
nrow=5)

> B <- matrix(c(0,.2375,0,0,0,0,0,.056,0,0,0,0,.89,.98,.01,123.9,0,.89,.02,.02,0,0,.03,0,0),
nrow=5)

> C <- matrix(c(0,.2375,0,0,0,0,0,.048,0,0,0,0,.86,.12,.01,280,0,.85,.02,.02,0,0,.03,0,0), nrow=5)

> MatrixList <- list(A,B,C)

> rate <- stoch.growth.rate(MatrixList, prob=NULL, maxt = 50)
[1] Calculating stochastic growth at time 1

> exp(rate$sim)
[1] 1.120016

> exp(rate$sim.CI)
[1] 1.024679 1.224224
```

Appendix 3. R Code for the calculation of probability of reaching quasi-extinction thresholds with the popbio package.

```
> library(popbio)

> A <- matrix(c(0,.2375,0,0,0,0,0,.041,0,0,0,0,.88,.101,.01,175.4,0,.89,.02,.02,0,0,.03,0,0),
nrow=5)

> B <- matrix(c(0,.2375,0,0,0,0,0,.056,0,0,0,0,.89,.98,.01,123.9,0,.89,.02,.02,0,0,.03,0,0),
nrow=5)

> C <- matrix(c(0,.2375,0,0,0,0,0,.048,0,0,0,0,.86,.12,.01,280,0,.85,.02,.02,0,0,.03,0,0), nrow=5)

> MatrixList <- list(A,B,C)

> n<-c(4264, 30,16,25,5)

## exclude seeds, seedlings and dormant individuals using sumweight

x<-stoch.quasi.ext(MatrixList, n, Nx=8, nreps=500, sumweight=c(0,0,1,1,0)

matplot(x, xlab="Years", ylab="Quasi-extinction probability",
```

Appendix 4. Mean and standard deviation of percent cover of species sampled in *Solidago* spp.-*Rubus hispidus* communities in Canaan Valley, WV from 2005 – 2007. Blank values indicate the species was not recorded in the treatment group.

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Achillea millefolium</i> L. var. occidentalis DC	Spring 2005						1.750 4.721
<i>Agrostis gigantea</i> Roth	Spring 2005					0.500 1.549	1.750 4.721
<i>Amelanchier</i> spp.	Spring 2005	0.250 0.796		0.250 0.796			
<i>Anthoxanthum odoratum</i> L.	Spring 2005	3.500 6.146	2.000 4.684	0.500 1.549	0.500 1.549	0.750 4.632	0.500 4.684
<i>Apocynum cannabinum</i> L.	Spring 2005	0.250 0.796	0.250 0.796	0.250 0.796	0.500 1.549		
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2005		0.500 1.549	0.250 0.796	0.250 0.796	0.250 0.796	0.250 0.796
<i>Carex bushii</i> Mack.	Spring 2005						
<i>Carex debilis</i> Michx. var. rudgei L. Bailey	Spring 2005	7.250 12.216	5.750 12.792	4.750 7.569	6.750 12.475	1.750 4.721	1.750 4.721
<i>Carex folliculata</i> L.	Spring 2005		0.250 0.796	0.250 0.796			
<i>Carex hirsutella</i> Mack.	Spring 2005			0.250 0.796			0.250 0.796
<i>Carex scoparia</i> Schkuhr ex Willd. var. scoparia	Spring 2005			0.250 0.796			
<i>Carex virescens</i> L.	Spring 2005			0.250 0.796	1.500 4.743		

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Cratagus</i> spp.	Spring 2005		1.500 4.743	0.750 1.276			
<i>Danthonia compressa</i> Aust.	Spring 2005	9.250 11.429	21.250 23.422	14.750 21.545	18.500 25.139	23.750 19.497	19.250 22.732
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2005		0.250 0.796		0.250 0.796		
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Spring 2005	4.500 12.475	6.750 12.475	3.250 6.242	1.500 12.273	0.750 19.536	2.250 11.972
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Spring 2005	1.750 4.721	3.250 6.242	2.000 4.684	2.250 4.632	0.250 0.796	0.250 4.721
<i>Festuca trachyphylla</i> (Hack.) Krajina	Spring 2005	1.500 4.743	3.750 11.859	1.500 4.743	6.250 19.764	3.750 11.859	0.250 0.796
<i>Glyceria striata</i> (Lam.) Hitchc.	Spring 2005			0.500 1.549			
<i>Hieracium floribundum</i> Wimm. & Grab.	Spring 2005		0.250 0.796			0.250 0.796	0.250 0.796
<i>Holcus lanatus</i> L.	Spring 2005				0.250 0.796	0.250 0.796	0.250 0.796
<i>Houstonia caerulea</i> L.	Spring 2005	0.250 0.796			0.250 0.796		1.500 4.743
<i>Hypericum punctatum</i> Lam.	Spring 2005						
<i>Juncus effusus</i> L.	Spring 2005		0.500 1.549	0.500 1.549	0.750 1.276	0.250 0.796	0.750 1.276

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Luzula bulbosa</i> (Alph. Wood)	Spring 2005						0.500 1.549
<i>Lycopodium</i> spp.	Spring 2005	0.250 0.796				0.500 1.549	2.000 4.684
<i>Photinia melanocarpa</i> Michx.	Spring 2005				0.250 0.796	0.250 0.796	
<i>Poa trivialis</i> L.	Spring 2005			0.250 0.796			0.250 0.796
<i>Populus tremuloides</i> Michx.	Spring 2005		0.500 1.549	2.000 4.684		1.500 4.743	0.250 0.796
<i>Potentilla simplex</i> Michx.	Spring 2005	2.500 19.497	1.000 4.564	1.500 1.300	2.750 5.780	1.000 11.574	2.500 5.917
<i>Prunus serotina</i> Ehrh.	Spring 2005						
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2005	4.750 11.574	5.750 12.792	1.250 1.318	3.500 6.146	1.000 1.300	3.750 6.387
<i>Ranunculus acris</i> L. var. <i>acris</i>	Spring 2005						0.250 0.796
<i>Ribes</i> spp.	Spring 2005	0.250 0.796					
<i>Rubus hispidus</i> L.	Spring 2005	26.250 19.230	32.250 21.776	22.000 13.323	21.000 11.619	21.250 18.257	16.500 11.292
<i>Rumex acetosella</i> L.	Spring 2005		0.750 1.276				

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Solidago rugosa</i> Mill.	Spring 2005	1.000 15.138	7.750 7.458	8.250 15.296	9.250 11.789	1.000 2.792	12.750 2.448
<i>Solidago uliginosa</i> Nutt.	Spring 2005	9.250 7.458	12.000 6.325	15.250 13.486	6.500 11.738	14.500 9.916	13.750 14.252
<i>Spiraea alba</i> Du Roi	Spring 2005	2.000 4.684	0.250 4.721	0.500 11.729	3.250 6.242		
<i>Vaccinium angustifolium</i> Ait.	Spring 2005		0.250 0.796			0.250 0.796	5.250 12.273
<i>Vaccinium myrtilloides</i> Michx.	Spring 2005	1.500 4.743	2.000 4.684	0.500 1.549	1.500 4.743	4.500 7.246	4.750 7.115
<i>Vaccinium pallidum</i> Ait.	Spring 2005			1.500 4.743	0.250 0.796	3.750 11.859	
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Spring 2005			0.250 11.797			0.250 0.796
<i>Viburnum recognitum</i>	Spring 2005			1.500 4.743			0.250 0.796
<i>Acer rubrum</i> L.	Fall 2005				0.250 0.796		
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2005		1.500 4.743	0.250 0.796		4.743	0.250 0.796
<i>Agrostis gigantea</i> Roth	Fall 2005	2.000 4.684	0.750 1.276	0.500 1.549	0.500 1.549	1.750 6.242	0.250 11.797
<i>Agrostis perennans</i> (Walt) Tuckerman	Fall 2005		0.250 0.796				

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Amelanchier</i> spp.	Fall 2005	0.250 0.796	0.250 0.796	0.250 0.796		0.250 0.796	
<i>Anthoxanthum odoratum</i> L.	Fall 2005	0.250 4.721	0.250 0.796	0.750 1.276	1.750 4.721		
<i>Carex blanda</i> Dewey	Fall 2005				0.250 0.796		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2005	0.500 1.549	0.750 1.276	0.750 4.632	0.750 1.276	0.750 1.276	2.500 4.564
<i>Carex folliculata</i> L.	Fall 2005	0.250 0.796		0.250 0.796	0.250 0.796		0.250 0.796
<i>Carex vulpinoidea</i> Michx.	Fall 2005		0.250 0.796				
<i>Danthonia compressa</i> Aust.	Fall 2005	24.500 2.325	21.000 17.498	28.000 23.553	18.750 19.864	29.250 21.828	25.250 2.156
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2005	1.500 4.743			0.250 0.796	0.250 0.796	
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Fall 2005	9.000 25.261	7.250 15.147	7.500 7.957	1.500 17.129	4.750 19.373	9.500 21.116
<i>Equisitum</i> spp.	Fall 2005				3.750 11.859		0.250 0.796
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Fall 2005	1.500 4.743	7.000 19.536	4.250 15.581	2.000 4.684	1.500 6.325	1.500 12.273
<i>Festuca trachyphylla</i> (Hack.) Krajina	Fall 2005	6.250 19.764	1.500 4.743				

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Fragaria virginiana</i> Duchesne	Fall 2005	0.250 0.796					
<i>Hieracium praealtum</i> Vill. ex Gochnat	Fall 2005		0.500 1.549				0.250 0.796
<i>Holcus lanatus</i> L.	Fall 2005		0.250 0.796	0.250 0.796	0.250 0.796		0.250 0.796
<i>Hypericum punctatum</i> Lam.	Fall 2005						0.250 0.796
<i>Juncus effusus</i> L.	Fall 2005	0.250 0.796		0.500 1.549	0.250 0.796		0.250 0.796
<i>Luzula bulbosa</i> (Alph. Wood)	Fall 2005					0.250 0.796	
<i>Lycopus virginicus</i> L.	Fall 2005		0.250 0.796				
<i>Lycopodium</i> spp.	Fall 2005	0.250 0.796	1.500 4.743			0.250 0.796	0.250 0.796
<i>Phleum pratense</i> L.	Fall 2005					0.250 0.796	
<i>Poa pratensis</i> L. ssp. pratensis	Fall 2005	0.250 0.796	0.250 0.796		0.250 0.796	0.250 0.796	0.250 0.796
<i>Poa trivialis</i> L.	Fall 2005		0.250 0.796				
<i>Populus tremuloides</i> Michx.	Fall 2005	2.000 4.684	0.250 0.796	1.750 4.721			

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Potentilla canadensis</i> L.	Fall 2005	1.000 1.300	0.750 1.276	1.000 4.564	0.750 4.632	0.500 4.684	1.750 6.242
<i>Potentilla simplex</i> Michx.	Fall 2005		0.500 1.549		0.250 0.796		0.250 0.796
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2005	7.500 12.761	4.750 7.115	9.250 15.592	8.500 12.315	11.750 17.798	6.750 12.475
<i>Ranunculus acris</i> L. var. <i>acris</i>	Fall 2005		0.250 0.796				
<i>Rubus hispidus</i> L.	Fall 2005	2.250 27.693	19.500 25.452	13.000 2.642	24.000 27.354	34.000 2.513	21.000 23.364
<i>Rumex acetosella</i> L.	Fall 2005	0.500 1.549	0.250 0.796				
<i>Scirpus</i> spp.	Fall 2005			0.250 0.796			
<i>Solidago caesia</i> L.	Fall 2005			0.250 0.796			
<i>Solidago rugosa</i> Mill.	Fall 2005	13.500 2.956	12.750 18.297	11.250 18.836	14.000 19.129	6.000 12.273	9.750 14.491
<i>Solidago uliginosa</i> Nutt.	Fall 2005	11.750 11.368	9.000 11.972	1.000 12.761	5.250 6.816	15.750 8.979	13.000 12.368
<i>Spiraea alba</i> Du Roi	Fall 2005	1.750 4.721	0.250 4.721	0.250 0.796	1.750 4.721		0.250 0.796
<i>Symphytotrichum lateriflorum</i> L.	Fall 2005	0.250 0.796					

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Taraxacum officinale</i> F.H. Wigg.	Fall 2005		0.250 0.796				
<i>Vaccinium angustifolium</i> Ait.	Fall 2005	1.549 0.500	1.549 0.500	0.796 0.250	0.796 0.250	1.549 0.500	6.242 3.250
<i>Vaccinium myrtilloides</i> Michx.	Fall 2005	4.743 1.500	0.796 0.250	0.796 0.250		4.743 1.500	0.796 0.250
<i>Vaccinium pallidum</i> Ait.	Fall 2005	1.549 0.500			4.743		1.276 0.750
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Fall 2005			1.500 4.743	1.500		
<i>Viburnum recognitum</i>	Fall 2005			1.500 4.743	0.250 0.796		0.250 0.796
<i>Violet</i> spp.	Fall 2005	0.250 0.796					
<i>Acer rubrum</i> L.	Spring 2006				0.250 0.796		
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Spring 2006	0.250 0.796	0.500 1.549	0.250 0.796			0.250 0.796
<i>Agrostis gigantea</i> Roth	Spring 2006	0.250 0.796		0.250 0.796			
<i>Anthoxanthum odoratum</i> L.	Spring 2006	2.000 4.684	1.000 1.300	0.750 1.276	0.500 1.549	0.250 0.796	0.750 1.276
<i>Apocynum cannabinum</i> L.	Spring 2006			0.250 0.796	0.250 0.796		

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2006					0.250 0.796	
<i>Carex bushii</i> Mack.	Spring 2006	0.250 0.796			0.250 0.796		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Spring 2006	2.250 6.387	2.250 6.387	2.000 19.488	2.000 6.146	1.000 1.300	5.250 15.732
<i>Carex folliculata</i> L.	Spring 2006						0.250 0.796
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Spring 2006		0.250 0.796	1.500 4.743	1.500 4.743	1.750 4.721	1.500 4.743
<i>Crataegus</i> spp.	Spring 2006					1.500 4.743	0.250 0.796
<i>Danthonia compressa</i> Aust.	Spring 2006	14.750 16.264	22.750 28.426	23.250 26.426	1.750 16.967	15.000 16.457	16.000 24.574
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2006					0.250 0.796	
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Spring 2006	6.000 11.972	4.000 5.917	5.250 6.816	14.750 16.685	7.500 12.761	7.750 18.492
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Spring 2006	2.250 4.632	1.000 1.300	0.750 1.276	0.500 1.549	0.250 0.796	0.500 1.549
<i>Hieracium praealtum</i> Vill. ex Gochnat	Spring 2006	0.250 0.796	0.250 0.796				0.250 0.796
<i>Holcus lanatus</i> L.	Spring 2006	0.250 0.796		0.250 0.796			

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Hypericum densiflorum</i> Pursh	Spring 2006				0.250 0.796		
<i>Hypericum ellipticum</i>	Spring 2006		0.250 0.796				
<i>Juncus effusus</i> L.	Spring 2006		0.250 0.796				
<i>Poa trivialis</i> L.	Spring 2006	0.250 0.796					
<i>Populus tremuloides</i> Michx.	Spring 2006	0.250 0.796		1.500 4.743	1.500 4.743	0.250 0.796	0.250 0.796
<i>Potentilla simplex</i> Michx.	Spring 2006	2.000 12.792	0.250 11.797	0.750 11.655	0.750 4.632	2.500 4.564	1.250 4.480
<i>Prunus serotina</i> Ehrh.	Spring 2006		0.250 0.796				
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2006	1.500 21.663	6.000 11.972	12.000 21.370	8.250 19.616	1.500 11.655	9.500 15.447
<i>Rubus hispidus</i> L.	Spring 2006	1.500 15.299	22.500 22.244	26.250 2.917	17.500 18.673	27.000 21.348	23.750 17.874
<i>Rumex acetosella</i> L.	Spring 2006		0.250 0.796		0.250 0.796		0.250 0.796
<i>Solidago rugosa</i> Mill.	Spring 2006	12.000 22.593	5.000 6.972	11.750 21.116	14.000 17.418	8.000 2.448	4.000 19.237
<i>Solidago uliginosa</i> Nutt.	Spring 2006	1.750 15.323	13.500 17.127	14.750 2.597	6.250 11.929	19.000 13.944	13.750 14.252

Appendix 4 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Spiraea alba</i> Du Roi	Spring 2006	0.250 0.796	4.743	0.250 0.796	3.250 6.242	1.500 6.325	1.500 6.325
<i>Vaccinium angustifolium</i> Ait.	Spring 2006	3.750 11.859	3.750 11.859				
<i>Vaccinium myrtilloides</i> Michx.	Spring 2006	2.000 4.684	3.000 6.325	3.000 6.325		3.250 6.242	3.250 6.242
<i>Vaccinium pallidum</i> Ait.	Spring 2006						
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Spring 2006	1.500 4.743	0.250 0.796	4.000 11.797	1.500 4.743		0.250 0.796
<i>Viburnum recognitum</i>	Spring 2006			0.250 0.796		0.250 0.796	0.250 0.796
<i>Acer rubrum</i> L.	Fall 2006				0.250 0.796		
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2006		1.500 4.743	0.250 0.796		4.743	4.743
<i>Agrostis gigantea</i> Roth	Fall 2006	1.500 4.743	1.500 4.743	0.250 0.796	1.500 4.743	0.500 1.549	0.500 1.549
<i>Amelanchier</i> spp.	Fall 2006	1.500 4.743	0.250 0.796	0.250 0.796		0.250 0.796	
<i>Anthoxanthum odoratum</i> L.	Fall 2006	0.250 4.721	0.250 0.796	1.000 1.300	1.750 4.721	11.859	4.743
<i>Carex blanda</i> Dewey	Fall 2006				0.250 0.796		

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2006	0.500 1.549	1.750 6.242	1.750 6.242	0.750 1.276	2.000 4.684	3.750 6.387
<i>Carex folliculata</i> L.	Fall 2006	0.250 0.796		0.250 0.796	0.250 0.796	0.250 0.796	
<i>Carex vulpinoidea</i> Michx.	Fall 2006		0.250 0.796				
<i>Danthonia compressa</i> Aust.	Fall 2006	34.250 17.442	23.500 18.646	25.750 23.733	18.000 14.521	29.250 18.184	21.500 17.895
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2006		1.500 4.743		0.250 0.796	0.250 0.796	
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Fall 2006	15.250 13.944	6.250 11.859	7.500 7.957	4.750 12.315	8.250 15.831	5.750 15.447
<i>Equisitum</i> spp.	Fall 2006				1.500 4.743		0.250 0.796
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Fall 2006	1.500 4.743	5.250 12.273	6.750 19.616	1.750 4.721	11.859	4.743
<i>Festuca trachyphylla</i> (Hack.) Krajina	Fall 2006	3.750 11.859	1.500 4.743	6.250 19.764		1.581	1.581
<i>Hieracium praealtum</i> Vill. ex Gochnat	Fall 2006		0.500 1.549				0.250 0.796
<i>Holcus lanatus</i> L.	Fall 2006		4.743	0.250 0.796	0.250 0.796		0.250 0.796
<i>Juncus effusus</i> L.	Fall 2006	0.250 0.796		0.750 1.276	0.250 0.796		0.250 0.796

Appendix 4 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Luzula bulbosa</i> (Alph. Wood)	Fall 2006					0.250 0.796	
<i>Lycopodium</i> spp.	Fall 2006	0.250 0.796	1.500 4.743			0.250 0.796	0.250 0.796
<i>Poa pratensis</i> L. ssp. pratensis	Fall 2006	0.250 0.796	1.500 4.743		0.250 0.796	0.250 0.796	0.250 0.796
<i>Poa trivialis</i> L.	Fall 2006		0.250 0.796				
<i>Populus tremuloides</i> Michx.	Fall 2006	0.250 0.796		1.500 4.743			
<i>Potentilla canadensis</i> L.	Fall 2006	3.500 6.146	0.750 1.276	0.500 4.684	2.000 6.146	0.250 4.721	1.500 6.325
<i>Potentilla simplex</i> Michx.	Fall 2006	0.250 0.796		0.250 0.796	0.500 1.549	1.500 4.743	1.750 4.721
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2006	13.500 2.956	3.500 6.146	7.000 12.350	5.000 6.972	1.750 15.323	4.500 7.246
<i>Ranunculus acris</i> L. var. acris	Fall 2006		0.250 0.796				
<i>Rubus hispidus</i> L.	Fall 2006	3.000 22.158	24.500 22.927	27.750 23.813	23.000 24.839	36.500 21.596	24.250 22.852
<i>Rumex acetosella</i> L.	Fall 2006	0.250 0.796	0.250 0.796		1.500 4.743		0.250 0.796
<i>Solidago rugosa</i> Mill.	Fall 2006	12.000 21.370	5.250 15.555	11.000 2.597	7.500 11.972	8.250 15.831	8.500 14.881

Appendix 4 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Solidago uliginosa</i> Nutt.	Fall 2006	24.500	1.250	12.250	5.500	16.500	12.000
		21.423	11.872	14.881	6.646	12.772	11.156
<i>Spiraea alba</i> Du Roi	Fall 2006	1.750	0.250	3.000	0.250		0.500
		4.721	4.721	6.325	0.796		1.549
<i>Vaccinium myrtilloides</i> Michx.	Fall 2006	3.000	1.750	0.250	0.250	1.750	2.000
		6.325	4.721	0.796	0.796	4.721	4.684
<i>Vaccinium pallidum</i> Ait.	Fall 2006	1.500	0.250	0.250		1.500	1.500
		4.743	0.796	0.796		4.743	4.743
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Fall 2006	0.250	0.250				0.500
		0.796	0.796				1.549
<i>Viburnum recognitum</i>	Fall 2006			1.500	0.250		1.500
				4.743	0.796		4.743
<i>Acer rubrum</i> L.	Spring 2007				0.250		
					0.796		
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Spring 2007		0.500	0.250			0.250
		4.743	1.549	0.796			0.796
<i>Agrostis gigantea</i> Roth	Spring 2007	0.250		0.250			
		0.796		0.796			
<i>Anthoxanthum odoratum</i> L.	Spring 2007	2.000	2.250	0.500	0.500	0.250	0.500
		4.684	4.632	1.549	1.549	0.796	4.684
<i>Apocynum cannabinum</i> L.	Spring 2007			0.250			
				0.796			
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2007					0.250	
						0.796	

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Carex bushii</i> Mack.	Spring 2007	0.250 0.796			0.250 0.796		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Spring 2007	1.500 1.300	7.500 7.746	2.250 12.761	4.750 12.315	1.250 1.318	3.000 7.246
<i>Carex folliculata</i> L.	Spring 2007						0.250 0.796
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Spring 2007		0.250 0.796	0.250 0.796	1.500 4.743	4.000 11.797	1.500 4.743
<i>Crataegus</i> spp.	Spring 2007					0.250 0.796	0.250 0.796
<i>Danthonia compressa</i> Aust.	Spring 2007	17.500 21.487	26.500 27.473	19.750 27.543	5.000 12.148	17.000 18.174	23.500 24.866
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2007					0.250 0.796	
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Spring 2007	8.500 12.315	2.750 4.480	9.500 15.447	6.750 7.173	12.500 14.672	8.000 11.773
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Spring 2007	4.500 7.746	1.000 1.300	2.000 4.684	1.750 4.721	1.500 4.743	0.500 1.549
<i>Hieracium praealtum</i> Vill. ex Gochnat	Spring 2007	0.250 0.796					
<i>Holcus lanatus</i> L.	Spring 2007	0.250 0.796			0.250 0.796		
<i>Hypericum densiflorum</i> Pursh	Spring 2007				0.250 0.796		

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Hypericum ellipticum</i>	Spring 2007		0.250 0.796				
<i>Juncus effusus</i> L.	Spring 2007		0.250 0.796				
<i>Poa trivialis</i> L.	Spring 2007	0.250 0.796					
<i>Populus tremuloides</i> Michx.	Spring 2007	3.750 11.859		1.500 4.743		0.250 0.796	
<i>Potentilla simplex</i> Michx.	Spring 2007	2.000 12.792	0.250 11.797	2.000 12.792	0.500 4.684	4.750 7.569	1.500 1.300
<i>Prunus serotina</i> Ehrh.	Spring 2007		0.250 0.796				
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2007	11.750 21.574	3.750 6.387	9.500 15.447	7.000 19.536	13.250 1.699	7.250 12.216
<i>Rubus hispidus</i> L.	Spring 2007	27.750 26.797	2.000 19.497	29.750 21.293	21.750 22.264	32.750 21.183	19.000 13.944
<i>Rumex acetosella</i> L.	Spring 2007		0.250 0.796		0.250 0.796		0.250 0.796
<i>Solidago rugosa</i> Mill.	Spring 2007	16.750 21.345	5.000 6.972	11.750 22.478	1.500 14.376	13.750 18.937	4.000 11.929
<i>Solidago uliginosa</i> Nutt.	Spring 2007	12.000 15.831	9.000 11.972	13.250 16.685	6.250 11.929	25.750 17.981	9.250 7.458
<i>Spiraea alba</i> Du Roi	Spring 2007	0.250 0.796		1.500 4.743	1.750 4.721	3.750 11.859	1.500 4.743

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Vaccinium angustifolium</i> Ait.	Spring 2007	3.750 11.859	3.750 11.859				
<i>Vaccinium myrtilloides</i> Michx.	Spring 2007	3.250 6.242	1.750 4.721	3.000 6.325		4.500 7.246	0.750 1.276
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Spring 2007	1.500 4.743	0.250 0.796	5.250 12.273	0.250 0.796		0.250 0.796
<i>Viburnum recognitum</i>	Spring 2007			0.250 0.796		1.500 4.743	4.743
<i>Acer rubrum</i> L.	Fall 2007				0.250 0.796		
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2007		1.500 4.743	0.250 0.796			0.250 0.796
<i>Agrostis gigantea</i> Roth	Fall 2007	1.500 4.743	1.500 4.743	0.250 0.796	1.500 4.743	0.500 1.549	1.500 6.325
<i>Amelanchier</i> spp.	Fall 2007	1.500 4.743	0.250 0.796	1.500 4.743		0.250 0.796	
<i>Anthoxanthum odoratum</i> L.	Fall 2007	0.500 1.549	0.250 0.796	1.000 1.300	1.750 4.721		4.743 4.743
<i>Carex blanda</i> Dewey	Fall 2007			0.250 0.796			
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2007	0.500 1.549	2.000 6.146	3.000 7.246	0.750 1.276	2.000 4.684	5.000 6.972
<i>Carex folliculata</i> L.	Fall 2007	0.250 0.796		0.250 0.796	0.250 0.796	0.250 0.796	

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Carex vulpinoidea</i> Michx.	Fall 2007		1.500 4.743				
<i>Danthonia compressa</i> Aust.	Fall 2007	27.250 16.299	22.250 2.325	21.000 2.412	16.750 1.869	23.750 17.874	22.500 19.230
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2007		3.750 11.859		0.250 0.796	0.250 0.796	
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Fall 2007	12.750 15.599	4.000 5.917	6.000 12.273	6.250 7.569	1.500 17.129	4.750 12.315
<i>Equisitum</i> spp.	Fall 2007				1.500 4.743		0.500 1.549
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Fall 2007		3.000 6.325	4.000 12.179	1.750 4.721	4.000 11.859	
<i>Festuca trachyphylla</i> (Hack.) Krajina	Fall 2007	3.750 11.859	1.500 4.743	3.750 11.859		6.250 19.764	1.581
<i>Hieracium praealtum</i> Vill. ex Gochnat	Fall 2007		0.500 1.549				0.250 0.796
<i>Holcus lanatus</i> L.	Fall 2007			4.000 4.743	0.250 0.796		0.250 0.796
<i>Juncus effusus</i> L.	Fall 2007	0.250 0.796		0.750 1.276	0.250 0.796		0.250 0.796
<i>Luzula bulbosa</i> (Alph. Wood)	Fall 2007					0.250 0.796	
<i>Lycopodium</i> spp.	Fall 2007	0.250 0.796	1.500 4.743			0.250 0.796	0.250 0.796

Appendix 4 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Poa pratensis</i> L. ssp. <i>pratensis</i>	Fall 2007	0.250 0.796	1.500 4.743		0.250 0.796	0.250 0.796	0.250 0.796
<i>Poa trivialis</i> L.	Fall 2007		0.250 0.796				
<i>Populus tremuloides</i> Michx.	Fall 2007	4.743		1.500 4.743			
<i>Potentilla canadensis</i> L.	Fall 2007	3.250 7.115	0.750 1.276	1.000 1.300	2.250 6.387	3.000 7.246	1.750 6.242
<i>Potentilla simplex</i> Michx.	Fall 2007	0.250 0.796			0.250 0.796		0.250 0.796
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2007	12.250 14.881	3.500 6.146	4.750 7.115	5.000 6.972	13.000 17.512	5.500 12.179
<i>Ranunculus acris</i> L. var. <i>acris</i>	Fall 2007		0.250 0.796				
<i>Rubus hispidus</i> L.	Fall 2007	3.000 19.223	27.250 16.299	25.250 23.813	28.000 22.758	29.250 22.794	17.000 19.832
<i>Rumex acetosella</i> L.	Fall 2007	0.250 0.796	0.250 0.796		1.500 4.743		0.250 0.796
<i>Solidago rugosa</i> Mill.	Fall 2007	9.000 17.129	4.500 5.627	12.000 16.375	5.250 7.173	6.000 12.273	7.250 12.148
<i>Solidago uliginosa</i> Nutt.	Fall 2007	25.750 19.932	1.250 11.872	9.750 11.859	4.500 5.627	17.500 14.965	7.250 6.713

Appendix 4 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$	Control $\bar{x}$	Fenced $\bar{x}$	Control $\bar{x}$	Fenced $\bar{x}$	Control $\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Spiraea alba</i> Du Roi	Fall 2007	1.500	0.250	3.000	1.500		0.500
		6.325	4.721	6.325	4.743		1.549
<i>Vaccinium myrtilloides</i> Michx.	Fall 2007	3.000	1.750	0.250	0.250	1.750	0.750
		6.325	4.721	0.796	0.796	4.721	1.276
<i>Vaccinium pallidum</i> Ait.	Fall 2007	1.500	0.250	0.250		1.500	0.250
		4.743	0.796	0.796		4.743	0.796
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Fall 2007	0.250	0.250			1.500	0.250
		0.796	0.796			4.743	0.796
<i>Viburnum recognitum</i>	Fall 2007			1.500	0.250		1.500
				4.743	0.796		4.743

Appendix 5. Mean and standard deviation of percent cover for species sampled in *Populus* spp. communities in Canaan Valley, WV from 2005 – 2007. Blank values indicate the species was not recorded in the treatment group.

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Acer rubrum</i> L.	Spring 2005		0.250 0.722				
<i>Achillea millefolium</i> L. var. occidentalis DC	Spring 2005	0.250 0.722		0.250 0.722			0.250 0.722
<i>Agrostis gigantea</i> Roth	Spring 2005	0.750 1.137	0.750 1.137	0.250 0.722	1.000 1.239	0.250 0.722	
<i>Amelanchier</i> spp.	Spring 2005			0.250 0.722			
<i>Anthoxanthum odoratum</i> L.	Spring 2005	13.250 13.676	8.500 7.173	8.750 6.864	12.500 19.433	7.000 1.128	6.500 5.823
<i>Asclepias incarnata</i> L.	Spring 2005		0.250 0.722			0.250 0.722	0.250 0.722
<i>Brachyelytrum erectum</i> Schreb.	Spring 2005		0.250 0.722				1.500 4.331
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	Spring 2005			1.500 4.331	6.250 18.422	4.000 1.784	3.000 5.839
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2005	1.500 4.331					
<i>Carex bushii</i> Mack.	Spring 2005	0.250 0.722			0.250 0.722		0.250 0.722
<i>Carex crinita</i> var. crinita	Spring 2005		1.500 4.331	1.500 4.331	0.250 0.722		
<i>Carex debilis</i> Michx. var. rudgei L. Bailey	Spring 2005	2.750 4.191	3.000 4.129	4.250 6.258	1.000 1.239	2.250 1.196	1.750 4.325

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Carex folliculata</i> L.	Spring 2005			0.250	0.500	1.500	0.500
				0.722	0.973	0.577	0.973
<i>Carex grascilescens</i> Steud.	Spring 2005						0.250
							0.722
<i>Carex hirsutella</i> Mack.	Spring 2005			0.250			
				0.722			
<i>Carex scoparia</i> Schkuhr ex Willd. var. scoparia	Spring 2005	3.250	0.750	2.000	3.250		0.250
		5.786	1.137	4.382	5.786		0.722
<i>Carex stipata</i> Muhl.	Spring 2005		0.250	1.500		1.500	0.250
			0.722	4.331		0.577	0.722
<i>Carex tribuloides</i> Wahl.	Spring 2005				0.250		
					0.722		
<i>Carex virescens</i> Muhl. ex Willd.	Spring 2005			1.750	0.250	4.250	
				4.325	0.722	1.737	
<i>Carex vulpinoidea</i> Michx.	Spring 2005					0.250	
						0.722	
<i>Crataegus</i> spp.	Spring 2005		0.750	0.250	0.250	1.500	0.500
			1.137	0.722	0.722	0.577	0.973
<i>Danthonia compressa</i> Aust.	Spring 2005	0.500	0.250	0.250	4.500	0.250	0.250
		0.973	0.722	0.722	6.785	0.722	11.223
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2005	7.000	2.500	5.750	15.500	8.250	19.500
		11.498	4.242	11.447	2.817	1.750	21.729
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Spring 2005	8.250	8.000	12.000	11.500	9.750	6.500
		7.240	17.623	13.147	17.624	17.627	7.138

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Equisitum</i> spp.	Spring 2005			0.250	0.250		0.250
				0.722	0.722		0.722
<i>Euthamia graminifolia</i> L. Nutt.	Spring 2005	2.250	3.750	8.250	5.750	8.250	4.000
		4.286	5.653	7.240	6.258	1.967	6.381
<i>Galium tinctorium</i> (L.) Scop.	Spring 2005			0.250			0.250
				0.722			0.722
<i>Glyceria striata</i> (Lam.) Hitchc.	Spring 2005	0.250	0.500	0.250		1.750	
		0.722	0.973	0.722		0.882	
<i>Hieracium praealtum</i> Vill. ex Gochnat	Spring 2005		0.250	0.250		0.250	
			0.722	0.722		0.722	
<i>Holcus lanatus</i> L.	Spring 2005			0.250	0.250		
				0.722	0.722		
<i>Hypericum androsaemum</i> L.	Spring 2005			3.750	4.000	3.000	
				1.825	1.784	0.778	
<i>Hypericum densiflorum</i> Pursh	Spring 2005	0.250					0.250
		0.722					0.722
<i>Juncus effusus</i> L.	Spring 2005	0.500	0.250	0.250	0.750	0.250	1.750
		0.973	0.722	0.722	1.137	0.722	4.325
<i>Luzula bulbosa</i> (Alph. Wood)	Spring 2005	0.250		0.250			0.250
		0.722		0.722			0.722
<i>Lysimachia</i> spp.	Spring 2005		0.250	0.250			
			0.722	0.722			
<i>Mimulus ringens</i> var. <i>ringens</i>	Spring 2005		0.250	0.250			
			0.722	0.722			

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Packera aurea</i> (L.) A.&D. Löve	Spring 2005	0.250 0.722					
<i>Poa trivialis</i> L.	Spring 2005		0.250 0.722			0.250 0.722	
<i>Polygonum sagittatum</i> L.	Spring 2005		0.250 0.722				
<i>Populus tremuloides</i> Michx.	Spring 2005	2.500 4.242	9.000 17.858	1.250 1.287	2.000 4.382	3.750 1.196	4.250 6.258
<i>Potentilla simplex</i> Michx.	Spring 2005	5.750 6.258	5.500 6.381	4.000 5.573	1.250 1.287	1.250 1.270	2.000 4.382
<i>Prunus serotina</i> Ehrh.	Spring 2005		0.250 0.722			0.250 0.722	
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2005	5.500 11.223	1.750 14.478	1.750 4.325	3.250 5.786	6.250 18.422	3.250 5.786
<i>Ranunculus acris</i> L. var. <i>acris</i>	Spring 2005	0.750 1.137	2.250 4.286	2.000 4.382	3.000 5.839	2.250 1.177	2.000 4.382
<i>Rubus hispidus</i> L.	Spring 2005	19.500 17.123	15.500 12.673	24.750 13.694	19.000 14.934	18.000 13.995	24.500 16.667
<i>Scirpus</i> spp.	Spring 2005	0.250 0.722	0.500 0.973	1.500 4.331			
<i>Sisyrinchium angustifolium</i> P. Mill.	Spring 2005		0.250 0.722	0.250 0.722			

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Solidago rugosa</i> Mill.	Spring 2005	22.500	2.250	7.000	1.000	9.750	11.250
		24.242	21.798	7.577	6.728	14.193	11.288
<i>Solidago uliginosa</i> Nutt.	Spring 2005	3.000	2.750	4.250	3.250	7.500	1.750
		5.839	4.191	5.483	5.786	1.587	4.325
<i>Spiraea alba</i> Du Roi	Spring 2005		1.500	2.000	1.750	1.750	4.750
			4.331	4.382	4.325	0.882	11.626
<i>Stellaria</i> spp.	Spring 2005				0.250		
					0.722		
<i>Trifolium repens</i> L.	Spring 2005	0.250			0.250		
		0.722			0.722		
<i>Vaccinium myrtilloides</i> Michx.	Spring 2005		0.250	1.500	1.750	0.250	
			0.722	4.331	4.325	0.722	
<i>Vaccinium pallidum</i> Ait.	Spring 2005		1.500	1.500			
			4.331	4.331			
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> Torr. & Gray	Spring 2005	0.250	1.750	0.250	0.250	1.750	0.250
		0.722	4.325	0.722	0.722	0.882	0.722
<i>Viburnum recognitum</i> Fernald	Spring 2005					0.500	
						0.973	
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2005	0.500					
		0.973					
<i>Ageratina altissima</i> (L.) King & H. Rob.	Fall 2005	6.250	8.750	2.500	8.750	17.000	1.000
		7.266	11.454	16.196	11.539	12.673	11.423
<i>Agrostis gigantea</i> Roth	Fall 2005	2.500	0.500	3.500	0.500	2.500	1.750
		0.722	0.722		4.325		0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Agrostis perennans</i> (Walt) Tuckerman	Fall 2005	1.000 1.239	0.250 0.722	0.250 0.722	1.750 4.325	1.500 1.356	1.750 4.325
<i>Agrostis hyemalis</i> (Walt.) B.S.P.	Fall 2005				0.250 0.722		0.250 0.722
<i>Amelanchier</i> spp.	Fall 2005			0.250 0.722			
<i>Anthoxanthum odoratum</i> L.	Fall 2005	1.250 11.454	6.750 7.458	4.000 5.573	4.000 5.573	2.250 17.959	3.500 5.725
<i>Apocynum cannabinum</i> L.	Fall 2005					0.250	0.250
<i>Bromus kalmii</i> Gray	Fall 2005	0.250 0.722			0.250 0.722		0.250 0.722
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	Fall 2005	0.250 0.722	6.250 18.422	1.500 4.331	6.250 18.422	6.250 18.422	6.250 18.422
<i>Carex bushii</i> Mack.	Fall 2005				0.250 0.722		
<i>Carex crinita</i> var. <i>crinita</i>	Fall 2005			1.500 4.331	0.250 0.722		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2005	0.500 0.973	0.250 0.722	0.500 0.973	0.250 0.722		0.750 1.137
<i>Carex folliculata</i> L.	Fall 2005			0.250 0.722	0.250 0.722	1.500 4.331	0.250 0.722
<i>Carex hirsutella</i> Mack.	Fall 2005	0.250 0.722			0.250 0.722		

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Carex leptalea</i> Wahl. ssp. leptalea	Fall 2005	0.250 0.722		0.250 0.722		1.500 4.331	0.250 0.722
<i>Carex lurida</i> Wahl.	Fall 2005		0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722
<i>Carex scoparia</i> Schkuhr ex Willd. var. scoparia	Fall 2005	4.000 1.784	0.500 0.973	0.250 0.722	1.750 4.325	1.750 4.325	
<i>Carex stipata</i> Muhl.	Fall 2005		1.500 4.331				
<i>Carex swanii</i> Fern. (Mack.)	Fall 2005			0.250 0.722	0.250 0.722		
<i>Carex vulpinoidea</i> Michx.	Fall 2005	1.500 4.331	3.750 1.825	1.750 4.325	0.250 0.722	0.500 0.973	0.250 0.722
<i>Crataegus</i> spp.	Fall 2005		0.500 0.973	0.500 0.973			0.750 1.137
<i>Danthonia compressa</i> Aust.	Fall 2005	6.750 11.586	1.750 14.478	12.750 17.746	8.500 11.432	3.750 6.495	9.250 19.896
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2005	4.500 1.687	5.250 6.495	3.500 5.725	5.500 11.129	13.500 24.575	12.000 13.837
<i>Doellingeria umbellata</i> (P. Mill.) Nees	Fall 2005	8.750 11.454	16.750 21.491	12.500 13.790	12.000 14.122	17.250 26.317	5.000 17.937
<i>Equisitum</i> spp.	Fall 2005	0.250 0.722	1.750 4.325				0.250 0.722
<i>Euthamia graminifolia</i> L. Nutt.	Fall 2005			0.250 0.722			

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Glyceria striata</i> (Lam.) Hitchc.	Fall 2005		0.250 0.722				0.250 0.722
<i>Hamamelis virginiana</i> L.	Fall 2005	0.250 0.722	0.250 0.722	1.750 4.325		0.250 0.722	
<i>Hieracium aurantiacum</i> L.	Fall 2005		0.250 0.722				
<i>Hieracium floribundum</i> Wimm. & Grab.	Fall 2005	0.250 0.722					
<i>Hypericum densiflorum</i> Pursh	Fall 2005	1.500 4.331		6.250 18.422	3.750 1.825	1.500 4.331	
<i>Lycopus virginicus</i> L.	Fall 2005	0.500 0.973	1.500 4.331	0.250 0.722		0.250 0.722	1.500 4.331
<i>Luzula bulbosa</i> (Alph. Wood)	Fall 2005	0.250 0.722					
<i>Mimulus ringens</i> var. <i>ringens</i>	Fall 2005					0.250 0.722	0.250 0.722
<i>Oclemena acuminata</i> (Michx.) Greene	Fall 2005				1.500 4.331		
<i>Panicum</i> spp.	Fall 2005		0.500 0.973		0.250 0.722		0.250 0.722
<i>Polygonum sagittatum</i> L.	Fall 2005			0.500 0.973			
<i>Populus tremuloides</i> Michx.	Fall 2005	0.250 0.722			0.250 0.722		

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Potentilla canadensis</i> L.	Fall 2005	3.250 27.283	15.750 15.489	11.500 14.952	17.750 2.379	2.250 15.379	8.000 13.958
<i>Potentilla simplex</i> Michx.	Fall 2005	5.750 11.153	3.500 5.725	0.750 1.137	0.750 1.137	2.000 4.382	2.500 4.242
<i>Prunus serotina</i> Ehrh.	Fall 2005	2.000 4.382		0.750 1.137	0.500 0.973	0.500 4.382	0.250 0.722
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2005					0.250 0.722	
<i>Ranunculus acris</i> L. var. <i>acris</i>	Fall 2005	6.750 11.586	9.250 14.478	3.500 5.725	3.750 5.653	3.750 1.825	
<i>Ribes</i> spp.	Fall 2005	2.000 4.382	1.000 1.239	2.000 4.382	0.500 0.973	0.250 0.722	2.500 4.242
<i>Rubus hispidus</i> L.	Fall 2005	19.250 16.938	28.250 22.118	23.000 16.833	27.500 18.354	26.750 16.667	32.500 15.134
<i>Packera aurea</i> (L.) A.&D. Löve	Fall 2005	0.250 0.720					0.250 0.720
<i>Solidago rugosa</i> Mill.	Fall 2005	6.750 6.265	18.000 17.854	15.250 13.533	16.750 12.673	12.500 13.790	14.500 17.336
<i>Solidago uliginosa</i> Nutt.	Fall 2005	8.500 11.626	5.000 6.646	6.250 7.266	4.500 6.785	9.250 14.556	3.250 5.786
<i>Spiraea alba</i> Du Roi	Fall 2005	0.250 0.722	1.750 4.325	2.250 4.286	2.000 4.382	0.500 0.973	2.750 4.191
<i>Symphytotrichum lateriflorum</i> (L.)	Fall 2005						0.250 0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Symphyotrichum puniceum</i> L. Nesom	Fall 2005	1.750 4.325	0.250 0.722	0.500 0.973	0.250 0.722	1.500 4.331	
<i>Vaccinium pallidum</i> Ait.	Fall 2005		0.500 0.973	0.250 0.722	0.500 0.973		
<i>Viburnum nudum</i> L. var. <i>cassinoides</i>	Fall 2005	2.000 4.382	0.750 1.137		0.250 0.722	1.750 4.325	0.250 0.722
<i>Viburnum recognitum</i> Fernald	Fall 2005			0.500 0.973	0.250 0.722	0.250 0.722	
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Spring 2006	0.250 0.722			0.250 0.722	0.250 0.722	0.250 0.722
<i>Ageratina altissima</i> (L.) King & H. Rob. var. <i>altissima</i>	Spring 2006	0.250 0.722					
<i>Agrostis gigantea</i> Roth	Spring 2006	0.250 0.722	0.500 0.973	0.500 0.973	0.500 0.973	0.250 0.722	0.750 1.137
<i>Anthoxanthum odoratum</i> L.	Spring 2006	3.750 3.862	11.000 17.559	5.750 6.258	5.750 1.365	5.750 6.258	3.250 4.534
<i>Apocynum cannabinum</i> L.	Spring 2006	1.500 4.331			1.500 4.331		0.250 0.722
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2006	0.500 0.973	0.250 0.722	0.750 1.137	0.750 1.137		0.500 0.973
<i>Carex bushii</i> Mack.	Spring 2006	0.750 1.137	1.000 1.239	0.250 0.722	0.250 0.722	0.750 1.137	1.000 1.138
<i>Carex crinita</i> var. <i>crinita</i>	Spring 2006			0.500 0.973			0.250 0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Spring 2006	5.250	4.750	0.750	4.000	3.000	2.000
		6.495	6.696	1.137	5.573	4.129	4.382
<i>Carex folliculata</i> L.	Spring 2006	0.500	0.250	0.250	0.250		
		0.973	0.722	0.722	0.722		
<i>Carex grascilescens</i> Steud.	Spring 2006		0.250		0.500		0.250
			0.722		0.973		0.722
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Spring 2006	0.500		0.500	0.500	0.500	0.500
		0.973		0.973	0.973	0.973	0.973
<i>Carex stipata</i> Muhl.	Spring 2006				0.250	0.250	0.250
					0.722	0.722	0.722
<i>Carex striata</i> Michx.	Spring 2006	0.250					
		0.722					
<i>Carex vulpinoidea</i> Michx.	Spring 2006	0.250	1.750	0.250		3.750	0.250
		0.722	18.136	0.722		1.825	0.722
<i>Crataegus</i> spp.	Spring 2006		0.500	0.750	0.250		0.500
			0.973	1.137	0.722		0.973
<i>Danthonia compressa</i> Aust.	Spring 2006	1.500	11.000	5.000	8.750	6.000	8.750
		2.142	18.383	1.578	11.539	11.782	11.539
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2006	5.250	5.500	9.750	7.250	5.000	3.750
		11.586	11.498	18.317	11.447	6.646	5.653
<i>Doellingeria umbellata</i> (P. Mill.) Nees var. <i>umbellata</i>	Spring 2006	4.500	7.000	8.250	8.750	6.500	14.000
		1.982	24.324	7.240	6.785	19.573	19.433
<i>Equisitum</i> spp.	Spring 2006		0.250		0.250		0.250
			0.722		0.722		0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Euthamia graminifolia</i> L. Nutt. var. graminifolia	Spring 2006	3.000 4.129	1.500 1.356	4.750 5.272	4.000 5.573	2.500 4.242	2.500 4.242
<i>Fragaria virginiana</i> Duchesne	Spring 2006		0.250 0.722	0.250 0.722		0.250 0.722	0.250 0.433
<i>Galium tinctorium</i> (L.) Scop.	Spring 2006	0.250 0.722					
<i>Glyceria striata</i> (Lam.) Hitchc.	Spring 2006	0.250 0.722		0.250 0.722			
<i>Hieracium aurantiacum</i> L.	Spring 2006		0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722	
<i>Hieracium praealtum</i> Vill. ex Gochnat	Spring 2006					0.250 0.722	
<i>Holcus lanatus</i> L.	Spring 2006	0.250 0.722					
<i>Houstonia caerulea</i> L.	Spring 2006		0.250 0.722				
<i>Hypericum densiflorum</i> Pursh	Spring 2006	0.250 0.722	1.500 4.331	1.500 4.331		0.250 0.722	
<i>Hypericum ellipticum</i> Hook.	Spring 2006						0.250 0.722
<i>Juncus effusus</i> L.	Spring 2006	0.250 0.722	0.250 0.722	0.500 0.973	0.250 0.722	0.250 0.722	0.500 0.973
<i>Luzula bulbosa</i> (Alph. Wood)	Spring 2006	0.250 0.722	0.250 0.722	0.250 0.722			0.250 0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Lysmachia</i> spp.	Spring 2006	0.500 0.973	0.250 0.722	0.250 0.722	1.750 4.325	0.500 0.973	0.250 0.722
<i>Poa trivialis</i> L.	Spring 2006	0.250 0.722		0.250 0.722	0.250 0.722		0.250 0.722
<i>Polygonum sagittatum</i> L.	Spring 2006			0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722
<i>Populus tremuloides</i> Michx.	Spring 2006	5.750 6.437	12.000 13.817	11.000 18.498	8.750 1.744	11.000 13.248	24.750 19.365
<i>Potentilla simplex</i> Michx.	Spring 2006	3.000 4.129	4.000 6.381	2.000 4.382	3.250 4.534	6.500 11.953	5.750 11.175
<i>Prunus serotina</i> Ehrh.	Spring 2006				0.250 0.722		
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2006		0.500 0.973	4.000 1.784	2.000 4.382	1.500 4.331	4.750 6.696
<i>Ranunculus acris</i> L. var. <i>acris</i>	Spring 2006	0.500 0.973	0.500 0.973	1.750 4.325	0.250 0.722	0.250 0.722	0.500 0.973
<i>Rubus hispidus</i> L.	Spring 2006	14.500 14.673	19.000 21.858	15.000 22.899	18.750 2.173	24.750 13.694	1.000 19.819
<i>Scirpus</i> spp.	Spring 2006	0.250 0.722					
<i>Solidago rugosa</i> Mill.	Spring 2006	3.750 17.832	7.000 6.853	16.750 18.813	7.000 1.862	5.500 6.853	14.000 17.216
<i>Solidago uliginosa</i> Nutt.	Spring 2006	1.000 11.596	2.500 4.242	6.000 11.782	1.500 4.331	9.500 14.453	2.250 5.653

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Spiraea alba</i> Du Roi	Spring 2006	5.250 11.288	0.250 0.722	5.750 11.153	1.250 1.287		3.500 5.738
<i>Symphyotrichum praealtum</i>	Spring 2006			0.250 0.722	0.500 0.973		
<i>Sisyrinchium angustifolium</i> P. Mill.	Spring 2006						0.250 0.722
<i>Vaccinium myrtilloides</i> Michx.	Spring 2006	0.250 0.722	0.500 0.973		0.250 0.722	0.250 0.722	0.500 0.973
<i>Vaccinium pallidum</i> Ait.	Spring 2006						
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> Torr. & Gray	Spring 2006	0.250 0.722	0.250 0.722	0.250 0.722		0.500 0.973	0.750 1.137
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2006	0.500 0.973					
<i>Ageratina altissima</i> (L.) King & H. Rob. var. <i>altissima</i>	Fall 2006	14.250	7.500 0.722	22.750	6.500	21.500	5.500 0.722
<i>Agrostis gigantea</i> Roth	Fall 2006	1.250 0.722	0.750 4.331	1.000	2.000 0.722	1.000	1.750 4.331
<i>Agrostis perennans</i> (Walt) Tuckerman	Fall 2006	0.500 0.973			0.250 0.722	0.500 4.382	1.500 4.331
<i>Amelanchier</i> spp.	Fall 2006			0.250 0.722			
<i>Anthoxanthum odoratum</i> L.	Fall 2006	9.750 7.240	9.250 11.254	2.750 4.191	5.250 6.495	3.500 18.317	3.750 5.653

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Apocynum cannabinum</i> L.	Fall 2006					0.250 0.722	0.250 0.722
<i>Bromus kalmii</i> Gray	Fall 2006	0.250 0.722			0.250 0.722		0.250 0.722
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	Fall 2006	0.250 0.722	3.750 1.825	1.500 4.331	3.750 1.825	3.750 1.825	6.250 18.422
<i>Carex bushii</i> Mack.	Fall 2006				0.250 0.722		
<i>Carex crinita</i> var. <i>crinita</i>	Fall 2006			1.500 4.331	0.250 0.722		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2006	0.500 0.973	4.331	0.750 1.137	0.250 0.722	0.250 0.722	0.500 0.973
<i>Carex folliculata</i> L.	Fall 2006				0.250 0.722	3.000 5.839	0.250 0.722
<i>Carex hirsutella</i> Mack.	Fall 2006	0.250 0.722			0.250 0.722		
<i>Carex leptalea</i> Wahl. ssp. <i>leptalea</i>	Fall 2006	0.250 0.722		0.250 0.722		0.250 0.722	0.250 0.722
<i>Carex lurida</i> Wahl.	Fall 2006		0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Fall 2006	0.250 0.722	1.750 4.325	0.250 0.722	1.750 4.325	2.000 4.382	0.250 0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Carex stipata</i> Muhl.	Fall 2006		1.500 4.331				
<i>Carex swanii</i> Fern. (Mack.)	Fall 2006				0.500 0.973		
<i>Carex vulpinoidea</i> Michx.	Fall 2006	1.500 4.331	1.500 4.331	0.500 0.973	1.500 4.331	0.500 0.973	1.500 4.331
<i>Crataegus</i> spp.	Fall 2006	0.250 0.722	0.250 0.722	0.250 0.722		0.500 0.973	0.500 0.973
<i>Danthonia compressa</i> Aust.	Fall 2006	4.500 6.785	12.000 14.426	12.750 13.986	15.500 21.287	6.250 14.236	11.500 2.833
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2006	4.250 5.483	3.500 5.725	5.750 11.153	13.250 19.785	17.500 2.529	11.500 1.740
<i>Doellingeria umbellata</i> (P. Mill.) Nees var. umbellata	Fall 2006	17.250 16.963	12.750 13.615	15.500 12.673	7.750 7.647	27.250 18.585	2.750 1.915
<i>Equisitum</i> spp.	Fall 2006	0.250 0.722	1.750 0.722	0.250 0.722	0.250 0.722		
<i>Euthamia graminifolia</i> L. Nutt. var. graminifolia	Fall 2006	17.965 16.450	15.636 11.382	0.250 17.383	0.250 7.138	17.613 18.933	9.150 6.381
<i>Glyceria striata</i> (Lam.) Hitchc.	Fall 2006		0.250 0.722		0.250 0.722		
<i>Hamamelis virginiana</i> L.	Fall 2006		0.250 0.722				
<i>Hieracium aurantiacum</i> L.	Fall 2006	0.250 0.722					

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Hieracium floribundum</i> Wimm. & Grab.	Fall 2006	0.250 0.722					
<i>Houstonia caerulea</i> L.	Fall 2006	0.250 0.722					
<i>Hypericum densiflorum</i> Pursh	Fall 2006	1.500 4.331		3.750 1.825	1.500 4.331	1.500 4.331	
<i>Lycopus virginicus</i> L.	Fall 2006	0.250	0.250 0.722	0.500	1.500	1.750	
<i>Luzula bulbosa</i> (Alph. Wood)	Fall 2006		0.250 0.722				
<i>Mimulus ringens</i> var. <i>ringens</i>	Fall 2006						0.250 0.722
<i>Oclemena acuminata</i> (Michx.) Greene	Fall 2006				1.500 4.331		
<i>Panicum</i> spp.	Fall 2006		0.500 0.973		0.250 0.722		0.250 0.722
<i>Polygonum sagittatum</i> L.	Fall 2006	0.250 0.722		0.250 0.722	0.250		
<i>Populus tremuloides</i> Michx.	Fall 2006	19.723	9.621	19.842	7.449	15.551	7.256
<i>Potentilla canadensis</i> L.	Fall 2006	45.250 14.135	16.250 5.653	23.750 5.483	9.500 1.287	31.750 7.572	9.500 5.573
<i>Potentilla simplex</i> Michx.	Fall 2006	12.500	3.750	4.250	1.250	6.250 0.722	4.000

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2006	5.839	5.725	1.137	1.239	0.250 1.825	
<i>Ranunculus acris</i> L. var. <i>acris</i>	Fall 2006	3.000 4.382	2.000 4.382	0.750 4.382	1.000 0.973	3.750 0.722	1.287
<i>Ribes</i> spp.	Fall 2006	2.000	2.000	2.000	0.500	0.250	1.250
<i>Rubus hispidus</i> L.	Fall 2006	17.969	14.360	2.772	18.694	16.148	6.495
<i>Rumex acetosella</i> L.	Fall 2006	31.750	15.500	32.500	21.750	35.750	18.750
<i>Solidago caesia</i> L.	Fall 2006		0.250 0.722				0.250 0.722
<i>Solidago rugosa</i> Mill.	Fall 2006	2.992	15.317	19.752	11.153	15.864	11.953
<i>Solidago uliginosa</i> Nutt.	Fall 2006	17.250 11.733	16.750 6.495	16.250 11.782	18.250 6.696	19.750 14.556	11.500 11.223
<i>Spiraea alba</i> Du Roi	Fall 2006	8.250 0.722	3.750 0.722	6.000 0.722	4.750 0.973	5.500 0.722	5.500 4.242
<i>Stellaria</i> spp.	Fall 2006	0.250	0.250	0.250	0.500	0.250	2.500
<i>Symphyotrichum lateriflorum</i> (L.)	Fall 2006						0.250 0.722
<i>Symphyotrichum puniceum</i> L. Nesom var. <i>puniceum</i>	Fall 2006	2.000 4.382	0.250 0.722	1.750 4.325	0.250 0.722	1.500 4.331	

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Vaccinium pallidum</i> Ait.	Fall 2006		0.500 0.973	0.250 0.722	0.500 0.973		
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> Torr. & Gray	Fall 2006	0.500 0.973	0.750 1.137		0.250 0.722	2.000 4.382	0.250 0.722
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Spring 2007	0.250 0.722		0.500 0.973		0.250 0.722	
<i>Ageratina altissima</i> (L.) King & H. Rob. var. <i>altissima</i>	Spring 2007					0.250 0.722	
<i>Agrostis gigantea</i> Roth	Spring 2007		1.000 1.239	0.500 0.973	0.500 0.973		2.000 4.382
<i>Amelanchier</i> spp.	Spring 2007					0.250 0.722	
<i>Anthoxanthum odoratum</i> L.	Spring 2007	3.500 3.965	5.750 6.696	9.500 13.851	7.500 6.528	3.000 4.129	6.250 5.979
<i>Apocynum cannabinum</i> L.	Spring 2007	0.250 0.722				1.500 4.331	1.500 4.331
<i>Carex brunnescens</i> (Pers.) Poir.	Spring 2007		0.250 0.722	1.000 1.239	0.250 0.722	1.000 1.239	0.250 0.722
<i>Carex bushii</i> Mack.	Spring 2007	1.250 1.287	0.500 0.973	0.500 0.973	3.250 5.786	0.500 0.973	0.250 0.722
<i>Carex crinita</i> var. <i>crinita</i>	Spring 2007	1.500 4.331	0.250 0.722	0.250 0.722		0.250 0.722	0.750 1.137
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Spring 2007	4.000 5.573	0.500 4.382	6.750 7.458	3.500 5.725	1.250 1.287	2.250 4.286

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Carex folliculata</i> L.	Spring 2007			0.250	0.750	0.250	
				0.722	1.137	0.722	
<i>Carex grascilescens</i> Steud.	Spring 2007			0.250	0.500	0.250	
				0.722	0.973	0.722	
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Spring 2007	0.500	0.500	0.500		0.500	2.250
		0.973	0.973	0.973		0.973	4.286
<i>Carex stipata</i> Muhl.	Spring 2007	0.250				0.250	0.250
		0.722				0.722	0.722
<i>Carex striata</i> Michx.	Spring 2007						0.250
							0.722
<i>Carex vulpinoidea</i> Michx.	Spring 2007		2.000	3.750	6.750		0.250
			4.382	1.825	11.586		0.722
<i>Crataegus</i> spp.	Spring 2007	0.250	0.500	0.250		0.500	1.750
		0.722	0.973	0.722		0.973	4.325
<i>Danthonia compressa</i> Aust.	Spring 2007	4.000	8.750	1.750	1.500	2.000	1.500
		5.573	11.454	14.478	14.597	4.382	11.367
<i>Dichanthelium clandestinum</i> (L.) Gould	Spring 2007	3.250	3.750	7.750	9.750	8.000	11.000
		5.786	6.495	18.168	18.317	7.412	14.355
<i>Doellingeria umbellata</i> (P. Mill.) Nees var. <i>umbellata</i>	Spring 2007	14.750	7.250	7.750	3.250	14.750	4.500
		21.822	22.347	7.647	5.272	16.457	5.384
<i>Euthamia graminifolia</i> L. Nutt. var. <i>graminifolia</i>	Spring 2007	5.000	2.750	4.000	1.750	5.250	2.750
		6.646	4.191	6.381	1.287	11.586	4.191
<i>Fragaria virginiana</i> Duchesne	Spring 2007	0.250			0.250		
		0.722			0.722		

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Galium tinctorium</i> (L.) Scop.	Spring 2007					0.250 0.722	0.250 0.722
<i>Glyceria striata</i> (Lam.) Hitchc.	Spring 2007			0.250 0.722			
<i>Hieracium aurantiacum</i> L.	Spring 2007	0.500 0.973		0.250 0.722			0.250 0.722
<i>Hieracium praealtum</i> Vill. ex Gochnat	Spring 2007		0.250 0.722				
<i>Holcus lanatus</i> L.	Spring 2007			0.250 0.722			
<i>Houstonia caerulea</i> L.	Spring 2007				0.250 0.722		
<i>Hypericum densiflorum</i> Pursh	Spring 2007	0.250 0.722	1.500 4.331	1.500 4.331		0.250 0.722	
<i>Hypericum ellipticum</i> Hook.	Spring 2007	0.250 0.722					
<i>Juncus effusus</i> L.	Spring 2007	0.250 0.722	0.250 0.722	0.250 0.722	0.250 0.722	0.500 0.973	0.500 0.973
<i>Luzula bulbosa</i> (Alph. Wood)	Spring 2007	0.250 0.722		0.250 0.722		0.250 0.722	0.250 0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Lysmachia</i> spp.	Spring 2007	0.250 0.722	0.250 0.722				0.500 0.973
<i>Packera aurea</i> (L.) A.&D. Löve	Spring 2007	0.250 0.722					
<i>Poa trivialis</i> L.	Spring 2007	0.250 0.722	0.250 0.722				1.500 4.331
<i>Polygonum sagittatum</i> L.	Spring 2007		0.500 0.973		0.250 0.722	0.250 0.722	
<i>Populus tremuloides</i> Michx.	Spring 2007	22.750 13.291	13.750 17.237	19.000 23.366	12.000 15.489	22.250 16.196	13.750 12.193
<i>Potentilla simplex</i> Michx.	Spring 2007	9.250 11.153	2.750 4.191	6.750 7.458	1.500 1.356	5.000 7.138	3.750 5.653
<i>Prunus serotina</i> Ehrh.	Spring 2007			0.250 0.722	0.250 0.722		
<i>Pteridium aquilinum</i> (L.) Kuhn	Spring 2007	1.750 4.325	3.500 5.725	3.000 5.839	0.250 0.722	3.750 1.825	2.000 4.382
<i>Ranunculus acris</i> L. var. <i>acris</i>	Spring 2007	3.500 5.725	6.750 11.586	4.750 6.696	0.750 1.137	0.750 1.137	1.000 1.239
<i>Rubus hispidus</i> L.	Spring 2007	2.500 23.618	17.750 15.625	8.750 23.557	11.750 15.126	17.250 2.431	11.500 16.765
<i>Scirpus</i> spp.	Spring 2007		0.250 0.722				
<i>Solidago rugosa</i> Mill.	Spring 2007	15.000 18.478	14.250 13.615	5.250 6.495	6.500 5.823	17.250 18.969	7.750 7.647

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Solidago uliginosa</i> Nutt.	Spring 2007	4.500	2.250	2.000	3.250	1.000	0.250
		7.385	4.286	5.725	5.786	1.239	0.722
<i>Spiraea alba</i> Du Roi	Spring 2007	1.750	0.250	5.750	1.750	0.500	3.750
		4.325	0.722	11.153	4.325	0.973	5.653
<i>Symphyotrichum praealtum</i>	Spring 2007			0.500		0.250	
				0.973		0.722	
<i>Trifolium repens</i> L.	Spring 2007	1.500			0.250	0.250	
		4.331			0.722	0.722	
<i>Vaccinium myrtilloides</i> Michx.	Spring 2007	0.500	0.500		1.750		1.500
		0.973	0.973		4.325		4.331
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> Torr. & Gray	Spring 2007	0.250	0.250	0.250	0.250	0.500	0.250
		0.722	0.722	0.722	0.722	0.973	0.722
<i>Viburnum recognitum</i> Fernald	Spring 2007	0.250				0.250	
		0.722				0.722	
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC	Fall 2007	0.000	0.250	0.000	0.000	0.000	0.000
		0.000	0.722	0.000	0.000	0.000	0.000
<i>Ageratina altissima</i> (L.) King & H. Rob.	Fall 2007	14.250	5.250	2.750	6.500	28.500	3.750
		16.450	7.458	13.461	7.138	22.262	6.495
<i>Agrostis gigantea</i> Roth	Fall 2007	1.250	2.000	0.750	0.500	2.250	1.500
		0.722	4.331	0.000	0.722	0.000	4.331
<i>Agrostis perennans</i> (Walt) Tuckerman	Fall 2007	1.000	0.500	0.000	1.500	2.750	3.000
		1.239	0.973	0.000	4.331	4.191	5.839
<i>Agrostis hyemalis</i> (Walt.) B.S.P.	Fall 2007	0.000	0.000	0.000	0.250	0.000	0.000
		0.000	0.000	0.000	0.722	0.000	0.000

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Amelanchier</i> spp.	Fall 2007			0.250			
				0.722			
<i>Anthoxanthum odoratum</i> L.	Fall 2007	9.750	9.250	6.250	5.250	6.000	6.250
		7.240	11.254	1.999	6.495	11.782	7.266
<i>Apocynum cannabinum</i> L.	Fall 2007					0.250	0.250
						0.722	0.722
<i>Brachyelytrum erectum</i> (Schreb. ex Spreng.) P. Beauv.	Fall 2007						
<i>Bromus kalmii</i> Gray	Fall 2007				0.250		0.250
					0.722		0.722
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	Fall 2007	0.250	1.500	1.500	3.750	3.750	6.250
		0.722	4.331	4.331	1.825	1.825	18.422
<i>Carex bushii</i> Mack.	Fall 2007				0.250		
					0.722		
<i>Carex crinita</i> var. <i>crinita</i>	Fall 2007			1.500	0.250		
				4.331	0.722		
<i>Carex debilis</i> Michx. var. <i>rudgei</i> L. Bailey	Fall 2007	0.500	1.500	0.750	0.250	0.500	0.250
		0.973	4.331	1.137	0.722	0.973	0.722
<i>Carex folliculata</i> L.	Fall 2007				0.250	0.500	0.250
					0.722	0.973	0.722
<i>Carex hirsutella</i> Mack.	Fall 2007	0.250	0.250		0.250		
		0.722	0.722		0.722		
<i>Carex leptalea</i> Wahl. ssp. <i>leptalea</i>	Fall 2007	0.250		0.250		0.250	0.250
		0.722		0.722		0.722	0.722

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Carex lurida</i> Wahl.	Fall 2007	0.250	0.250	0.250	0.250	0.250	0.500
		0.722	0.722	0.722	0.722	0.722	0.973
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	Fall 2007	0.250	0.500	0.250	0.500	2.000	0.250
		0.722	0.973	0.722	0.973	4.382	0.722
<i>Carex stipata</i> Muhl.	Fall 2007		1.500				
			4.331				
<i>Carex vulpinoidea</i> Michx.	Fall 2007	0.250	0.250	0.500	3.000	0.500	1.500
		0.722	0.722	0.973	5.839	0.973	4.331
<i>Crataegus</i> spp.	Fall 2007	0.250	0.250	1.500		1.750	0.500
		0.722	0.722	4.331		4.325	0.973
<i>Danthonia compressa</i> Aust.	Fall 2007	6.750	11.250	8.250	12.000	5.500	5.500
		11.586	11.586	7.240	14.426	6.381	11.223
<i>Dichanthelium clandestinum</i> (L.) Gould	Fall 2007	2.750	6.000	5.750	11.000	12.750	14.250
		4.191	7.385	11.153	18.383	13.986	17.623
<i>Doellingeria umbellata</i> (P. Mill.) Nees var. <i>umbellata</i>	Fall 2007	16.000	17.000	14.250	6.500	17.750	7.000
		16.667	12.673	14.886	7.412	14.360	6.853
<i>Glyceria striata</i> (Lam.) Hitchc.	Fall 2007		0.250				
			0.722				
<i>Hieracium aurantiacum</i> L.	Fall 2007					0.722	
						0.250	
<i>Hypericum densiflorum</i> Pursh	Fall 2007	1.500	0.250	3.750	1.500	1.500	
		4.331	0.722	1.825	4.331	4.331	

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Lycopus virginicus</i> L.	Fall 2007	0.250	1.500	0.500	1.500	1.750	1.500
		0.722	4.331	0.973	4.331	4.325	4.331
<i>Mimulus ringens</i> var. <i>ringens</i>	Fall 2007						0.250
							0.722
<i>Oclemena acuminata</i> (Michx.) Greene	Fall 2007				1.500		
					4.331		
<i>Panicum</i> spp.	Fall 2007		0.500		0.250		0.250
			0.973		0.722		0.722
<i>Polygonum sagittatum</i> L.	Fall 2007				0.250		
		0.722					
<i>Populus tremuloides</i> Michx.	Fall 2007	0.250					
		2.173	9.621	21.822	6.853	18.682	6.696
<i>Potentilla canadensis</i> L.	Fall 2007	45.500	16.250	24.750	7.000	39.000	5.750
		11.423	5.653	5.384	1.239	11.423	4.242
<i>Potentilla simplex</i> Michx.	Fall 2007	11.500	3.750	3.000	1.000	1.000	2.500
						0.722	
<i>Pteridium aquilinum</i> (L.) Kuhn	Fall 2007					0.250	
						4.325	
<i>Ranunculus acris</i> L. var. <i>acris</i>	Fall 2007	4.500	3.750	2.250	3.750	1.750	
		5.786	0.973	4.286	0.973	4.382	

Appendix 5 continued

		Early		Late		Continuous	
		Fenced	Control	Fenced	Control	Fenced	Control
		$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
		SD	SD	SD	SD	SD	SD
<i>Rubus hispidus</i> L.	Fall 2007	3.250	0.500	2.250	0.500	2.000	0.750
		17.270	12.437	23.537	11.863	18.273	9.324
<i>Rumex acetosella</i> L.	Fall 2007	32.000	15.750	36.000	17.000	32.000	15.000
		17.567	9.266	18.468	5.696	17.138	5.722
<i>Solidago rugosa</i> Mill.	Fall 2007		0.250				0.250
		2.992	14.886	21.289	1.470	22.734	13.533
<i>Solidago uliginosa</i> Nutt.	Fall 2007	17.250	16.500	2.750	13.750	22.750	1.000
		14.597	7.266	11.447	6.696	7.138	5.725
<i>Spiraea alba</i> Du Roi	Fall 2007	1.500	4.750	5.750	4.750	6.500	3.500
		0.722	4.325	4.286	4.382	5.839	4.191
<i>Stellaria</i> spp.	Fall 2007	0.250	1.750	2.250	2.000	3.000	2.750
<i>Symphyotrichum lateriflorum</i> (L.)	Fall 2007						0.250
							0.722
<i>Symphyotrichum puniceum</i> L. Nesom var. puniceum	Fall 2007	0.750	0.250	0.500	0.250	1.500	
		1.137	0.722	0.973	0.722	4.331	
<i>Vaccinium pallidum</i> Ait.	Fall 2007		0.500	0.250	0.500		
			0.973	0.722	0.973		
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> Torr. & Gray	Fall 2007	0.500	0.750		0.250	3.250	0.250
		0.973	1.137		0.722	5.786	0.722
<i>Violet</i> spp.	Fall 2007			1.750	0.250	0.250	
				4.325	0.722	0.722	

Appendix 6. Mean and standard deviation of stem densities for species observed in the ground cover in West Virginia Division of Natural Resource deer exclosure plots and corresponding control plots, 1984 – 2007.

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Agrimonia</i> spp.		0.585 0.248		0.433 0.173		0.819 0.347
<i>Acer pensylvanicum</i> L.	0.643 0.175	0.359 0.185	0.864 0.239	0.265 0.572	0.762 0.250	0.526 0.152
<i>Acer rubrum</i> L.	1.456 2.276	3.316 7.952	2.556 2.796	2.754 4.815	2.958 4.640	4.544 1.813
<i>Acer saccharum</i> Marshall	0.292 0.195	0.153 0.397	0.679 0.182	0.185 0.547	0.153 0.232	0.199 0.596
<i>Acer spicatum</i> Lam.					0.494 0.174	0.718 0.298
<i>Achillea millefolium</i> L. var. <i>puberula</i> (Rydb.) Nobs	0.468 0.198					
<i>Actaea racemosa</i> L.			0.374 0.128	0.123 0.495		
<i>Aesculus glabra</i> Willd			0.617 0.255	0.123 0.495		
<i>Ageratina altissima</i> (L.) King & H. Rob.	0.129 0.448	0.494 0.150	0.222 0.578	0.825 0.176	0.333 1.379	0.544 2.261
<i>Adiantum</i> L.		0.585 0.248		0.617 0.248		
<i>Alcalypha virginica</i> spp. L.	0.718 0.195	0.135 0.412	0.123 0.593	0.117 0.335	0.117 0.496	0.175 0.719
<i>Allium tricoccum</i> Aiton		0.117 0.496		0.617 0.248		

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Ambrosia artemisiifolia</i> L.	0.895 3.567				0.585 0.248	0.117 0.496
<i>Amianthium muscitoxicum</i> (Walter) A. Gray	0.123 0.521	0.526 0.223	0.386 1.273	0.386 0.124	0.164 0.695	0.526 0.223
<i>Amelanchier arborea</i> Michx.	0.234 0.579	0.152 0.346	0.444 1.625	0.149 0.369	0.494 0.150	0.494 0.133
<i>Anemone virginiana</i> L.					0.158 0.464	0.292 0.125
<i>Antennaria</i> spp. Gaertn.	0.257 0.618	0.494 0.174	0.988 0.472	0.556 0.223	0.333 1.179	0.292 0.871
<i>Apocynum</i> spp. L.						0.292 0.125
<i>Aralia nudicaulis</i> L.					0.585 0.248	0.585 0.248
<i>Arisaema triphyllum</i> L.	0.345 1.269	0.246 0.943	0.636 1.312	0.414 0.736	0.682 1.642	0.146 0.325
<i>Aronia melanocarpa</i> Michx.					0.117 0.496	
<i>Asarum canadense</i> L.	0.494 0.174	0.181 0.743	0.315 1.359	0.327 1.794	0.117 0.350	0.247 0.772
<i>Asimina triloba</i> (L.) Dunal	0.292 0.125	0.819 0.255	0.247 0.119	0.123 0.495	0.117 0.496	0.117 0.350
<i>Asplenium platyneuron</i> (L.) Britton, Sterns & Poggenb.	0.585 0.248	0.292 0.125	0.123 0.593		0.175 0.744	0.117 0.496

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Betula</i> spp.	0.877	0.936	0.456	0.247	0.287	0.263
	0.230	0.229	1.126	0.762	0.987	0.988
<i>Botrychium virginianum</i> (L.) Sw.						0.585
						0.248
<i>Botrychium</i> spp.		0.359		0.433	0.175	0.585
		0.125		0.137	0.542	0.248
<i>Bouteloua</i> spp. Lag.			0.111			0.585
			0.458			0.248
<i>Cardamine nuttallii</i> Greene	0.994	0.292				
	0.422	0.125				
<i>Carex</i> spp.	0.614	0.538	0.299	1.825	0.696	0.668
	1.545	1.216	0.539	1.946	1.592	1.339
<i>Carya</i> spp.	0.123	0.129	0.148	0.117	0.158	0.158
	0.228	0.243	0.272	0.286	0.258	0.253
<i>Cassia</i> spp. L.	0.234	0.135	0.433	0.617	0.585	
	0.992	0.576	0.178	0.248	0.248	
<i>Castanea dentata</i> (Marshall) Borkh.	0.175					
	0.744					
<i>Celastrus scandens</i> L.					0.585	
					0.248	
<i>Centaurea nigra</i> L.	0.585					
	0.248					
<i>Cercis canadensis</i> L.	0.292	0.117	0.617	0.123	0.146	0.819
	0.125	0.496	0.255	0.495	0.623	0.279

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Chamaecrista fasciculata</i> (Michx.) Greene	0.585 0.248	0.339 0.991	0.617 0.255	0.494 0.198	0.175 0.542	0.643 0.273
<i>Chamerion angustifolium</i> (L.) Holub		0.585 0.248				
<i>Chimaphila maculata</i> (L.) Pursh	0.585 0.248	1.175 4.987	0.617 0.255		0.117 0.496	0.585 0.248
<i>Chimaphila umbellata</i> (L.) W.P.C. Barton						
<i>Chrysanthemum</i> spp. L.	0.936 0.397		0.617 0.255	0.123 0.495	0.359 0.149	0.585 0.248
<i>Clintonia borealis</i> (Aiton) Raf.		0.117 0.496	0.617 0.255			
<i>Cornus florida</i> L.	0.515 1.951	0.251 0.664	0.414 1.394	0.235 0.525	0.333 0.787	0.152 0.273
<i>Corylus americana</i> Walter	0.359 0.185	0.585 0.223	0.617 0.255	0.247 0.999	0.175 0.744	0.585 0.248
<i>Crataegus</i> spp.	0.877 0.372	0.117 0.386	0.136 0.488	0.617 0.248	0.994 0.396	0.819 0.272
<i>Daucus carota</i> L.	0.585 0.248				0.229 0.968	
<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore			0.679 0.280	0.926 0.372		
<i>Desmodium</i> spp.	0.263 0.967	1.444 5.588	1.512 6.482	0.148 0.324	1.158 3.731	0.854 2.653

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Dioscorea villosa</i> L.	0.585 0.137	0.718 0.163	0.130 0.257	0.386 0.638	0.819 0.234	0.468 0.121
<i>Dryopteris</i> spp. L.	0.936 2.729	1.696 5.595	0.649 2.184	1.265 3.620	0.251 1.669	
<i>Elaeagnus umbellata</i> Thunb.						
<i>Elymus hystrix</i> L.	0.158 0.670	0.175 0.744				
<i>Epigaea repens</i> L.			0.185 0.764		0.175 0.744	0.117 0.496
<i>Euonymus alatus</i> (Thunb.) Siebold	0.585 0.248	0.117 0.496		0.123 0.495	0.468 0.198	
<i>Euonymus americanus</i> L.			0.747 0.354			
<i>Eutrochium purpureum</i> (L.) E.E. Lamont		0.117 0.496	0.185 0.764	0.617 0.248	0.468 0.198	0.494 0.150
<i>Eutrochium</i> spp.			0.617 0.255			
<i>Fagus grandifolia</i> Ehrh.	0.152 0.594	0.215 0.566	0.825 0.350	0.111 0.395	0.819 0.297	0.158 0.467
<i>Fraxinus americana</i> L.	0.117 0.350	0.175 0.744	0.123 0.593	0.123 0.495	0.117 0.350	0.117 0.496
<i>Galium</i> spp.	0.819 0.347	0.175 0.744	0.747 0.280		0.117 0.496	0.718 0.277

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Geranium</i> spp. L.	0.111	0.234	0.111	0.926	0.359	0.123
	0.351	0.992	0.219	0.256	0.995	0.342
<i>Gaultheria procumbens</i> L.	2.673	2.643	2.216	1.944	4.427	1.529
	1.364	6.293	6.262	7.389	13.958	4.897
<i>Gaylussacia</i> spp. Kunth						0.494
						0.174
<i>Gaylussacia ursina</i> (M.A. Curtis) Torr.	0.762	0.292	0.165	0.291	0.718	0.117
	0.323	0.125	0.563	0.955	0.298	0.496
<i>Geum</i> spp. L.		0.585				
		0.248				
<i>Gillenia trifoliata</i> (L.) Moench	0.234	0.585		0.123		
	0.992	0.248		0.495		
<i>Glycyrrhiza lepidota</i> Pursh					0.585	
					0.248	
<i>Gnaphalium obtusifolium</i> L.	0.292					
	0.125					
<i>Hamamelis virginiana</i> L.	0.234	0.117		0.617	0.494	0.585
	0.992	0.496		0.248	0.195	0.248
<i>Hedeoma pulegioides</i> L.	0.637					
	2.744					
<i>Hepatica nobilis</i> Schreb. var. obtusa (Pursh)				0.617		
Steyerm.				0.248		
<i>Hieracium fendleri</i> Sch. Bip				0.617	0.117	
				0.248	0.496	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Hieracium venosum</i> L.		0.135 0.412				0.234 0.992
<i>Houstonia canadensis</i> Willd. ex Roem. & Schult.				0.926 0.372		
<i>Hymenocallis</i> spp. Salisb.	0.494 0.174					
<i>Hypericum punctatum</i> L.	0.427 1.785				0.994 0.351	0.515 2.183
<i>Hypericum prolificum</i> L.	0.246 1.425					1.468 4.441
<i>Juniperus virginiana</i> L.					0.585 0.248	
<i>Kalmia latifolia</i> L.	0.247 0.595	0.368 1.554	0.396 0.900	0.778 2.143	0.222 0.531	0.215 0.554
<i>Lespedeza</i> spp. Michx.	0.494 0.174					0.585 0.248
<i>Lindera benzoin</i> (L.) Blume	0.292 0.125	0.679 0.174	0.386 0.869			0.359 0.149
<i>Liriodendron tulipifera</i> L.	0.585 0.248	0.585 0.747	0.617 0.248		0.292 0.195	0.819 0.129
<i>Lobelia cardinalis</i> L.	0.292 0.125					
<i>Lonicera japonica</i> Thunb.	0.345 1.464	0.117 0.496	0.165 0.563	0.148 0.595	0.936 0.397	1.287 5.458

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Lonicera tatarica</i> L.						
<i>Lycopodium dendroideum</i> Michx.			0.825		0.468	
			0.339		0.198	
<i>Lyonia ligustrina</i> (L.) DC.					0.877	0.494
					0.324	0.174
<i>Lysmachia quadrifolia</i> L.	0.240	0.556	0.148	0.389	0.135	0.298
	0.843	1.656	0.378	1.186	0.350	1.163
<i>Maianthemum canadense</i> Desf.	0.585	0.359	0.617	0.123	0.170	0.146
	0.248	0.123	0.255	0.446	0.669	0.430
<i>Malus</i> spp.	0.585					
	0.248					
<i>Magnolia acuminata</i> L.	0.643	0.175		0.185	0.585	
	0.173	0.452		0.743	0.248	
<i>Maianthemum racemosum</i> (L.) Link	0.292				0.585	
	0.871				0.248	
<i>Medeola virginiana</i> L.	0.175	0.359	0.617	0.386	0.994	0.234
	0.744	0.149	0.255	0.869	0.373	0.771
<i>Menziesia pilosa</i> (Michx. ex Lam.)	0.762	0.877	0.117	0.386	0.494	
Juss. ex Pers	0.323	0.324	0.484	0.124	0.150	
<i>Monotropa uniflora</i> L.					0.585	
					0.248	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Nyssa sylvatica</i> Marshall	0.468 0.113	0.468 0.159	0.247 0.796		0.468 0.113	0.585 0.248
<i>Oenothera</i> spp. L.	0.468 0.198					
<i>Onoclea sensibilis</i> L.	0.585 0.248	0.718 0.298				
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.585 0.163	0.153 0.396	0.433 0.918	0.179 0.642	0.877 0.256	0.240 0.559
<i>Oxalis</i> spp.	0.740 2.973	0.164 0.558	0.123 0.349	0.123 0.495	0.374 1.234	0.287 0.765
<i>Oxydendrum arboreum</i> (L.) DC.	0.175 0.744	0.292 0.766	0.123 0.593			
<i>Panicum</i> spp.	0.754 2.594	0.117 0.325	0.272 0.562	0.444 0.783	0.953 1.926	1.234 3.242
<i>Packera aurea</i> (L.) Á. Löve & D. Löve	1.422 6.292	0.359 1.463		0.123 0.495	0.216 0.819	0.111 0.471
<i>Paronychia</i> spp. L.					0.585 0.248	
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0.164 0.545	0.175 0.569	0.185 0.539	0.198 0.573	0.215 0.663	0.216 0.574
<i>Phlox</i> spp. L.		0.399 1.315				

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Phytolacca americana</i> L.						0.359
						0.149
<i>Pilea pumila</i> (L.) A. Gray		0.292				0.762
		0.125				0.323
<i>Pinus strobus</i> L.		0.643	0.617	0.617	0.359	0.468
		0.166	0.255	0.248	0.149	0.175
<i>Pinus virginiana</i> Mill.	0.175	0.349			0.585	
	0.542	1.264			0.248	
<i>Podophyllum peltatum</i> L.	0.181	0.819	0.247	0.185	0.494	0.175
	0.769	0.279	0.119	0.547	0.133	0.744
<i>Polygala paucifolia</i> Willd.	0.117					0.117
	0.496					0.496
<i>Polygonum</i> spp. L.		0.585	0.374	0.185		0.292
		0.248	0.111	0.547		0.125
<i>Polygonum convolvulus</i> L.	0.234	0.175			0.117	0.359
	0.682	0.744			0.350	0.185
<i>Polygonum hydropiper</i> L.			0.617		0.585	0.468
			0.255		0.248	0.198
<i>Polygonatum</i> spp. Mill.			0.374		0.234	
			0.148		0.771	
<i>Polystichum acrostichoides</i> (Michx.) Schott	0.585	0.111	0.299	0.123	0.117	
	0.223	0.332	0.839	0.495	0.445	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Potentilla</i> spp.	1.740 5.168	0.453 1.172	0.556 1.369	0.525 1.497	1.550 3.156	0.813 1.882
<i>Prenanthes alba</i> L.	0.117 0.350	0.877 0.372	0.185 0.556		0.175 0.542	
<i>Prunella vulgaris</i> L.	0.216 0.918	0.263 1.116				
<i>Prunus</i> spp.	3.368 8.767	2.374 5.743	2.864 8.176	3.123 5.666	7.368 2.590	1.762 2.636
<i>Prunus pensylvanica</i> L.			0.185 0.764			0.585 0.248
<i>Pyrularia pubera</i> Michx.					0.359 0.149	
<i>Pycnanthemum virginianum</i> L.	0.152 0.493		0.123 0.593	0.617 0.248	0.386 1.439	0.585 0.248
<i>Quercus alba</i> L.	0.117 0.496	0.292 0.195	0.433 0.753	0.679 0.145	0.292 0.195	0.819 0.266
<i>Quercus berberidifolia</i> Liebm.		0.234 0.992	0.617 0.255	0.165 0.645	0.359 0.149	0.936 0.293
<i>Quercus coccinea</i> Münchh.	0.585 0.248	0.494 0.174				
<i>Quercus prinus</i> L.	0.152 0.346	0.117 0.254	0.148 0.387	0.988 0.239	0.135 0.344	0.936 0.196

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Quercus rubra</i> L.	0.123	0.135	0.185	0.519	0.762	0.287
	0.260	0.350	0.370	1.526	0.132	0.454
<i>Quercus velutina</i> Lam	0.175	0.585	0.617	0.123	0.585	
	0.744	0.248	0.255	0.340	0.248	
<i>Rhododendron</i> spp.	0.270	0.529	0.299	0.519	0.216	0.345
	0.953	2.177	0.839	1.954	0.793	1.339
<i>Rhus</i> spp.	0.117	0.175	0.123			0.585
	0.350	0.542	0.593			0.248
<i>Robinia pseudoacacia</i> L	0.117			0.617	0.234	0.585
	0.350			0.248	0.771	0.248
<i>Rosa multiflora</i> Thunb.	0.994	0.359	0.130	0.494	0.468	0.275
	0.322	0.185	0.460	0.899	0.154	0.842
<i>Rubus</i> spp. L.H.Bailey (Dewberry)	0.529	0.485	2.377	0.994	1.359	0.964
	2.134	2.593	9.799	3.988	4.392	2.897
<i>Rubus</i> spp.	1.386	1.298	6.543	2.975	1.947	1.193
	3.924	2.692	18.438	8.421	4.434	3.138
<i>Rudbeckia hirta</i> L.				0.617		
				0.248		
<i>Rumex acetosella</i> L.	0.117	0.936				0.953
	0.496	0.397				3.672
<i>Smilax herbacea</i> L.	0.585		0.123		0.494	
	0.248		0.593		0.174	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Sambucus</i> spp.	0.585					
	0.248					
<i>Sassafras albidum</i> (Nutt.) Nees	0.468	0.229	0.374	0.191	0.374	0.585
	1.124	0.636	0.845	0.496	1.282	1.769
<i>Sanguinaria canadensis</i> L.	0.585	0.117	0.247	0.617	0.718	0.175
	0.248	0.496	0.796	0.223	0.253	0.542
<i>Smilax</i> spp.	0.386	0.444	0.481	0.315	0.588	0.399
	0.629	0.529	0.584	0.594	0.598	0.414
<i>Solanum americanum</i> Mill.	0.153	0.363		0.198		
	0.421	1.512		0.767		
<i>Solidago</i> spp.	0.392	0.485	0.364	0.265	0.525	0.498
	1.757	1.165	0.749	0.911	1.174	1.229
<i>Sedum</i> spp.	0.175	0.585	0.123	0.556		
	0.744	0.248	0.593	0.223		
<i>Stellaria media</i> L.	0.322	0.600	0.494	0.679	0.585	0.585
	1.365	2.482	0.236	0.187	0.248	0.185
<i>Streptopus lanceolatus</i> (Aiton) Reveal	0.234		0.327	0.679	0.718	0.357
	0.992		1.699	0.226	0.136	1.276
<i>Symphotrichium</i> spp.	0.117	0.216	0.374	0.593	0.275	0.737
	0.232	0.697	1.168	1.844	0.497	1.737
<i>Taraxacum officinale</i> F.H. Wigg.					0.585	
					0.248	
<i>Thalictrum</i> spp. L.	0.359	0.585			0.585	
	0.149	0.248			0.248	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	4.854	1.942	2.933	1.519	4.556	3.872
	11.753	4.437	6.773	2.696	8.862	11.647
<i>Toxicodendron radicans</i> (L.) Kuntze	0.994	0.234	0.154	0.185	0.819	0.359
	0.299	0.453	0.344	0.434	0.249	0.123
<i>Trifolium</i> spp.	0.357				0.164	0.819
	1.513				0.695	0.347
<i>Triodanis perfoliata</i> (L.) Nieuwl.		0.117	0.617	0.374		0.234
		0.496	0.255	0.149		0.992
<i>Tsuga canadensis</i> L.				0.617		
				0.248		
<i>Ulmus</i> spp.		0.117	0.679	0.617	0.585	0.117
		0.496	0.280	0.248	0.248	0.496
<i>Trillium</i> spp.	0.234	0.819		0.617		
	0.992	0.347		0.248		
<i>Urtica gracilis</i> Ait.	0.153	0.146	0.123	0.617		
	0.421	0.623	0.349	0.248		
<i>Uvularia</i> spp.	0.111	0.994	0.426	0.117	0.386	0.494
	0.324	0.293	1.391	0.283	1.122	0.898
<i>Vaccinium</i> spp.	2.359	2.444	3.519	2.864	1.345	1.251
	3.763	4.469	7.659	7.451	2.987	31.616
<i>Veronica</i> spp.		0.585		0.617	0.359	
		0.248		0.248	0.149	
<i>Viburnum prunifolium</i> L.	0.585	0.585			0.494	
	0.248	0.248			0.174	

Appendix 6 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Viburnum acerifolium</i> L.	0.175 0.744	0.339 1.388	0.358 1.476	0.374 0.149	0.359 0.149	0.193 0.819
<i>Viburnum lantanoides</i> Michx.	0.292 0.125	0.215 0.893	0.111 0.458	0.173 0.694	0.762 0.323	
<i>Viburnum</i> spp.	0.585 0.178	0.468 0.198	0.679 0.232	0.864 0.347	0.494 0.195	0.994 0.335
<i>Verbesina alternifolia</i> (L.) Britton ex Kearney		0.117 0.496				0.585 0.248
<i>Viola</i> spp. L.	1.725 3.554	0.825 1.495	1.259 2.577	1.562 2.445	2.684 7.344	1.912 4.642
<i>Vitis</i> spp.	0.585 0.248	0.292 0.871			0.718 0.298	0.181 0.537
<i>Zanthoxylum clava-herculis</i> L.						0.117 0.496
<i>Vicia caroliniana</i> Walter	0.585 0.248	0.175 0.744		0.123 0.495	0.234 0.771	0.111 0.446

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Acer pensylvanicum</i> L.	0.988 0.219	0.556 0.145	0.111 0.253	0.156 0.412	0.119 0.347	0.214 0.612
<i>Acer saccharum</i> Marshall	2.747 6.660	1.374 3.244	0.617 2.386	0.339 0.752	0.595 1.826	0.239 0.458
<i>Acer spicatum</i> Lam.		0.433 0.178				
<i>Ageratina altissima</i> (L.) King & H. Rob.	0.165 0.380	0.956 2.715	0.561 1.853	1.133 2.793	1.635 2.397	0.675 2.717
<i>Agrimonia</i> spp.		0.617 0.255				
<i>Aesculus glabra</i> Willd	0.123 0.593				0.794 0.286	
<i>Actaea racemosa</i> L.	0.617 0.255				0.239 0.620	
<i>Alcalypha virginica</i> spp. L.	0.494 0.236	0.185 0.764	0.389 0.170	0.222 0.567	0.794 0.286	0.159 0.572
<i>Amianthium muscitoxicum</i> (Walter) A. Gray	0.191 0.789	0.747 0.354	0.128 0.557	0.944 0.412	0.175 0.630	
<i>Antennaria</i> spp. Gaertn.	0.315 1.220	0.254 1.169	0.561 2.425	0.256 0.846	0.111 0.462	0.239 0.858
<i>Ambrosia artemisiifolia</i> L.		0.386 0.127	0.556 0.242	0.556 0.242		

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Acer rubrum</i> L.	2.389 3.143	5.457 1.944	1.356 1.837	3.556 8.280	1.895 2.377	3.556 4.775
<i>Amelanchier arborea</i> Michx.	0.556 0.158	0.617 0.145	0.556 0.173	0.722 0.226	0.397 0.798	0.714 0.116
<i>Anemone virginiana</i> L.			0.944 0.288	0.778 0.339	0.397 0.144	
<i>Apocynum</i> spp. L.		0.185 0.764	0.556 0.242			
<i>Aralia nudicaulis</i> L.	0.123 0.593		0.167 0.530			
<i>Aronia melanocarpa</i> Michx.	0.617 0.255		0.222 0.969		0.794 0.286	
<i>Arisaema triphyllum</i> L.	0.562 1.241	0.799 1.862	0.444 1.294	0.550 1.168	0.763 1.839	0.316 0.554
<i>Asarum canadense</i> spp. L.	0.864 0.367	0.278 0.995	0.167 0.530	0.144 0.439	0.952 0.343	
<i>Asimina triloba</i> (L.) Dunal	0.617 0.255	0.123 0.349	0.222 0.969	0.500 0.174	0.794 0.286	0.159 0.572
<i>Asplenium platyneuron</i> (L.) Britton, Sterns & Poggenb.	0.185 0.556	0.123 0.593	0.111 0.333	0.556 0.242		
<i>Betula</i> spp.	0.864 0.244	0.222 0.499	0.667 0.170	0.556 0.134	0.556 0.138	0.159 0.389
<i>Botrychium virginianum</i> (L.) Sw.		0.926 0.332	0.556 0.242	0.444 0.138		0.873 0.285

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Cardamine nuttallii</i> Greene					0.794 0.286	
<i>Carex</i> spp.	1.165 2.966	1.396 2.324	0.217 0.442	0.317 0.956	0.167 0.422	0.232 0.374
<i>Carya</i> spp.	0.864 0.164	0.179 0.252	0.944 0.244	0.100 0.175	0.111 0.232	0.714 0.132
<i>Cassia</i> spp. L.		0.123 0.593				
<i>Celastrus scandens</i> L.	0.185 0.764	0.123 0.593	0.444 0.194	0.111 0.484	0.397 0.144	
<i>Cercis canadensis</i> L.	0.679 0.280	0.679 0.153	0.667 0.266	0.667 0.163	0.952 0.343	0.397 0.144
<i>Chamaecrista fasciculata</i> (Michx.) Greene	0.185 0.556	0.259 0.742	0.167 0.530	0.156 0.255	0.317 0.114	0.317 0.884
<i>Chimaphila maculata</i> (L.) Pursh	0.617 0.255		0.111 0.333		0.794 0.286	0.317 0.778
<i>Chimaphila umbellata</i> (L.) W.P.C. Barton	0.617 0.255	0.617 0.255		0.556 0.242		
<i>Chrysanthemum</i> spp. L.		0.617 0.255				
<i>Cicuta maculata</i> L.				0.556 0.242		

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Clintonia borealis</i> (Aiton) Raf.			0.111			
			0.484			
<i>Cornus florida</i> L.	0.154	0.173	0.944	0.194	0.239	0.556
	0.275	0.419	0.293	0.377	0.858	0.172
<i>Corylus americana</i> Walter	0.988	0.386	0.944	0.167	0.127	
	0.335	0.127	0.324	0.726	0.458	
<i>Crataegus</i> spp.	0.247	0.130	0.144	0.889	0.952	0.132
	0.462	0.319	0.588	0.363	0.314	0.372
<i>Danthonia spicata</i> (L.) Beauv.						0.232
						0.830
<i>Desmodium</i> spp.	1.475	0.846	0.617	0.744	0.476	0.476
	3.827	2.933	1.417	2.756	0.144	0.144
<i>Dioscorea villosa</i> L.	0.433	0.386	0.944	0.222	0.143	0.556
	0.112	0.135	0.254	0.754	0.345	0.172
<i>Dryopteris</i> spp. L.	0.685	1.123	0.356	0.261	1.794	1.294
	2.281	3.419	0.834	0.761	3.429	4.247
<i>Elaeagnus umbellata</i> Thunb.						0.159
						0.572
<i>Epigaea repens</i> L.	0.864	0.747	0.111	0.111	0.794	
	0.356	0.222	0.484	0.484	0.286	
	0.617	0.617	0.122	0.111	0.167	
<i>Euonymus alatus</i> (Thunb.) Siebold	0.255	0.255	0.533	0.484	0.693	
<i>Euonymus americanus</i> L.			0.111	0.278		
			0.484	0.122		

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Eutrochium purpureum</i> (L.) E.E. Lamont	0.433	0.185	0.222			
	0.153	0.764	0.969			
<i>Fagus grandifolia</i> Ehrh.	0.247	0.123	0.556	0.500	0.794	0.317
	0.119	0.381	0.242	0.151	0.286	0.114
<i>Fraxinus americana</i> L.	0.123	0.123	0.278	0.389	0.317	
	0.349	0.349	0.692	0.117	0.778	
<i>Galium</i> spp.	0.654	0.352	0.256	0.494	0.127	0.111
	1.526	0.714	0.393	1.131	0.275	0.320
<i>Gaultheria procumbens</i> L.	3.679	0.438	1.311	0.494	1.278	
	11.493	1.289	3.554	1.620	3.926	
<i>Gaylussacia</i> spp. Kunth	0.926		0.278	0.133	0.127	
	0.332		0.122	0.581	0.458	
<i>Gaylussacia ursina</i> (M.A. Curtis) Torr.	0.247	0.299	0.256	0.333	0.794	0.239
	0.119	0.742	0.823	0.868	0.286	0.714
<i>Geranium</i> spp. L.	0.278	0.352	0.417	0.667	0.278	
	0.483	0.789	1.477	0.170	0.834	
<i>Gillenia trifoliata</i> (L.) Moench			0.556		0.794	
			0.242		0.286	
<i>Gnaphalium obtusifolium</i> L.		0.123				
		0.593				
<i>Hamamelis virginiana</i> L.	0.494	0.988	0.556	0.111	0.476	0.135
	0.135	0.381	0.160	0.333	0.894	0.399

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Hieracium fendleri</i> Sch. Bip			0.556	0.389		0.794
			0.242	0.146		0.286
<i>Hieracium venosum</i> L.		0.117		0.833		
		0.344		0.255		
<i>Houstonia canadensis</i> Willd. ex Roem. & Schult.	0.123		0.278	0.111		
	0.593		0.122	0.484		
<i>Hypericum prolificum</i> L.	0.123	0.179				
	0.593	0.739				
<i>Hypericum punctatum</i> L.	0.154	0.327	0.722	0.311		0.397
	0.636	1.349	0.315	1.356		0.144
<i>Isotria vertucillata</i> Willd.	0.154				0.294	
	0.636				1.588	
<i>Juniperus virginiana</i> L.	0.617		0.556	0.556	0.794	
	0.255		0.242	0.242	0.286	
<i>Kalmia latifolia</i> L.	0.173	0.165	0.256	0.722	0.159	0.316
	0.430	0.466	0.587	0.293	0.293	0.749
<i>Lindera benzoin</i> (L.) Blume	0.617	0.556	0.944	0.194		0.239
	0.167	0.140	0.288	0.586		0.858
<i>Liriodendron tulipifera</i> L.	0.617	0.747	0.444	0.944	0.239	0.397
	0.255	0.192	0.147	0.273	0.620	0.679
<i>Lobelia cardinalis</i> L.	0.617	0.247				
	0.255	0.119				
<i>Lespedeza</i> spp. Michx.	0.247	0.216	0.100	0.556		
	0.119	0.898	0.436	0.242		

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Lonicera japonica</i> Thunb.	0.438 1.874	0.179 0.594	0.639 2.451	0.744 2.778		
<i>Lonicera tatarica</i> L.			0.161 0.723	0.167 0.726		
<i>Lycopodium dendroideum</i> Michx.	0.149 0.433		0.100 0.436		0.167 0.693	
<i>Lyonia ligustrina</i> (L.) DC.	0.278 1.145	0.352 1.457	0.228 0.968	0.317 1.214		
<i>Lysmachia quadrifolia</i> L.	0.179 0.413	0.325 0.842	0.611 0.159	0.389 0.178	0.794 0.286	0.159 0.389
<i>Maianthemum racemosum</i> (L.) Link	0.185 0.764		0.111 0.333		0.159 0.572	
<i>Maianthemum canadense</i> Desf.	0.165 0.662	0.167 0.466	0.667 0.266	0.444 0.157	0.794 0.286	
<i>Magnolia acuminata</i> L.		0.617 0.255	0.556 0.242	0.222 0.754		
<i>Medeola virginiana</i> L.	0.556 0.158	0.185 0.556	0.278 1.186	0.389 0.178	0.135 0.486	
<i>Menziesia pilosa</i> (Michx. ex Lam.) Juss. ex Pers	0.265 1.678		0.144 0.498		0.556 2.384	
<i>Monotropa uniflora</i> L.			0.444 0.194			
<i>Morus</i> spp.						0.794 0.286

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Nyssa sylvatica</i> Marshall	0.185	0.247	0.389	0.556	0.794	0.159
	0.415	0.593	0.178	0.242	0.978	0.389
<i>Osmorhiza</i> spp.	0.123			0.556		
	0.593			0.242		
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.259	0.386	0.500	0.650	0.825	1.627
	0.679	0.578	1.383	1.548	1.892	4.165
<i>Oxalis</i> spp.	0.130	0.142	0.122	0.156	0.239	
	0.384	0.414	0.459	0.234	0.858	
<i>Oxydendrum arboreum</i> (L.) DC.			0.556		0.794	
			0.242		0.286	
<i>Packera aurea</i> (L.) Á. Löve & D. Löve	0.185	0.386	0.256	0.311		
	0.764	0.127	1.887	1.356		
<i>Packera</i> spp.		0.123				
		0.593				
<i>Panicum</i> spp.	0.352	0.396	0.450	0.789	0.429	1.183
	0.776	0.533	1.164	1.558	1.224	1.755
<i>Paronychia</i> spp. L.						
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0.426	0.142	0.889	0.194	0.675	0.397
	1.154	0.414	2.323	0.546	1.361	0.914
<i>Phytolacca americana</i> L.				0.333		0.794
				0.145		0.286
<i>Pilea pumila</i> (L.) A. Gray				0.333		
				0.145		

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Pinus strobus</i> L.	0.386	0.130	0.222	0.611	0.317	0.119
	0.135	0.434	0.969	0.243	0.884	0.372
<i>Pinus taeda</i> L.						0.159
						0.572
<i>Pinus virginiana</i> Mill.				0.111		0.794
				0.484		0.286
<i>Podophyllum peltatum</i> L.	0.617	0.247	0.117	0.556	0.143	
	0.167	0.119	0.329	0.242	0.457	
<i>Polygonatum</i> spp. Mill.	0.494		0.222		0.714	
	0.178		0.969		0.258	
<i>Polygonum</i> spp. L.	0.185	0.123	0.222			
	0.764	0.593	0.969			
<i>Polygonum convolvulus</i> L.	0.386				0.794	
	0.127				0.286	
<i>Polygonum hydropiper</i> L.				0.111		
				0.484		
<i>Polygonum persicaria</i> L.			0.556	0.944		
			0.242	0.412		
<i>Polystichum acrostichoides</i> (Michx.) Schott	0.247		0.217	0.217	0.556	1.952
	0.796		0.919	0.765	0.144	3.949
<i>Potentilla</i> spp.	0.796	0.433	0.683	0.433	0.158	0.794
	1.335	1.389	1.368	1.182	0.324	0.286
<i>Prenanthes alba</i> L.	0.617		0.278	0.333	0.635	0.556
	0.255		0.692	1.000	0.215	0.124
<i>Prunus</i> spp.	3.956	3.457	2.433	1.150	1.786	4.556
	1.967	11.874	9.237	2.266	4.718	11.876

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Pycnanthemum virginianum</i> L.	0.247 0.796	0.247 0.119 0.994	0.111 0.484 0.556	0.111 0.333	0.159 0.572 0.794	
<i>Pyrola americana</i> Sweet		4.977	0.242		0.286	
<i>Pyrularia pubera</i> Michx.	0.185 0.764		0.611 0.266	0.410 1.690	0.119 0.429	0.794 0.286
<i>Quercus alba</i> L.	0.617 0.229	0.825 0.177	0.278 0.712	0.722 2.797	0.635 0.177	0.143 0.321
<i>Quercus berberidifolia</i> Liebm.	0.386 0.127	0.142 0.585	0.200 0.847	0.222 0.969	0.366 1.316	0.500 1.828
<i>Quercus coccinea</i> Münchh.						0.794 0.286
<i>Quercus prinus</i> L.	0.136 0.377	0.136 0.322	0.444 0.177	0.222 0.649	0.159 0.572	0.794 0.199
<i>Quercus rubra</i> L.	0.111 0.264	0.299 0.355	0.122 0.276	0.261 0.472	0.214 0.467	0.132 0.247
<i>Quercus velutina</i> Lam					0.159 0.389	0.635 0.150
<i>Ranunculus</i> spp.				0.389 1.695	0.794 0.286	0.532 1.769
<i>Rhododendron</i> spp.	0.123 0.349	0.222 0.864	0.222 0.969	0.778 0.339	0.476 0.172	0.476 0.172

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Robinia pseudoacacia</i> L.		0.494	0.556	0.333	0.239	0.794
		0.236	0.242	0.122	0.858	0.286
<i>Rosa multiflora</i> Thunb.	0.179	0.191	0.178	0.150	0.556	0.952
	0.435	0.455	0.629	0.365	0.144	0.237
<i>Rubus</i> spp. L.H.Bailey (Dewberry)	1.185		1.250	0.839	1.540	
	4.887		5.449	3.657	5.551	
<i>Rubus</i> spp.	1.912	1.833	1.122	0.256	2.468	1.889
	4.882	4.659	1.948	0.359	5.670	5.171
<i>Ruellia</i> spp. L.				0.222		
				0.969		
<i>Rumex acetosella</i> L.		0.623		0.183		0.754
		2.156		0.726		2.496
<i>Sanguinaria canadensis</i> L.	0.386	0.747	0.333			
	0.127	0.354	0.160			
<i>Sassafras albidum</i> (Nutt.) Nees	0.747	0.414	0.122	0.400	0.143	0.263
	0.354	1.496	0.296	1.126	0.318	0.744
<i>Scutellaria lateriflora</i> L.				0.778		
				0.339		
<i>Sedum</i> spp.			0.667	0.222	0.111	0.132
			0.296	0.969	0.462	0.372
<i>Smilax</i> spp.	0.291	0.396	0.544	0.556	0.926	0.944
	0.350	0.527	0.594	0.718	1.387	0.982
<i>Smilax herbacea</i> L.	0.864					
	0.367					

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Solanum americanum</i> Mill.		0.123 0.593		0.167 0.726		
<i>Solidago</i> spp.	0.358 0.824	0.148 0.399	0.278 0.846	0.200 0.528	0.873 0.193	
<i>Streptopus lanceolatus</i> (Aiton) Reveal	0.386 0.812	0.617 0.255		0.389 0.146	0.952 0.287	0.317 0.654
<i>Stellaria media</i> L.		0.617 0.255	0.556 0.242	0.278 0.919		0.635 0.229
<i>Symphotrichium</i> spp.	0.340 1.915	0.296 1.657	0.367 1.472	0.278 0.923	0.325 0.846	0.317 0.654
<i>Thalictrum</i> spp. L.				0.278 0.986		
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	4.912 14.662	1.963 3.572	1.333 2.533	2.811 8.956	4.619 11.187	4.714 12.385
<i>Toxicodendron radicans</i> (L.) Kuntze	0.198 0.358	0.617 0.140	0.328 0.526	0.167 0.397	0.397 0.830	0.143 0.312
<i>Triodanis perfoliata</i> (L.) Nieuwl.	0.123 0.593	0.185 0.764				
<i>Ulmus</i> spp.		0.617 0.255	0.333 0.122	0.222 0.567		
<i>Uvularia</i> spp.	0.791 1.688	0.386 0.812	0.567 1.334	0.389 0.882	0.675 1.689	0.317 0.778

Appendix 6 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Vaccinium</i> spp.	1.825	2.825	2.144	2.350	0.841	2.357
	3.575	4.266	4.139	5.189	1.693	7.220
<i>Verbesina alternifolia</i> (L.) Britton ex Kearney		0.185		0.222		
		0.764		0.667		
<i>Veronica</i> spp.	0.191	0.247				
	0.762	0.119				
<i>Viola</i> spp. L.	2.562	1.840	1.250	5.478	0.366	1.587
	6.556	3.129	3.693	17.170	0.449	3.326
<i>Viburnum</i> spp.	0.374	0.679	0.556	0.100	0.794	0.159
	0.148	0.280	0.173	0.386	0.286	0.572
<i>Viburnum acerifolium</i> L.	0.556	0.140		0.389	0.952	0.556
	0.230	0.560		0.170	0.343	0.238
<i>Viburnum lantanoides</i> Michx.	0.386		0.500			
	0.127		0.218			
<i>Viburnum prunifolium</i> L.	0.617	0.185	0.128	0.444		
	0.255	0.764	0.557	0.194		
<i>Vicia caroliniana</i> Walter		0.926		0.500		
		0.382		0.174		
<i>Vitis</i> spp.	0.386	0.179	0.444	0.833	0.794	0.714
	0.127	0.594	0.147	0.215	0.286	0.229

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Acer pensylvanicum</i> L.	0.119 0.347	0.214 0.612	0.256 0.888	0.179 0.454
<i>Acer rubrum</i> L.	1.895 2.377	3.556 4.775	2.154 3.152	2.838 4.584
<i>Acer saccharum</i> Marshall	0.595 1.826	0.239 0.458	1.942 2.914	0.197 0.412
<i>Ageratina altissima</i> (L.) King & H. Rob.	1.635 2.397	0.675 2.717	0.299 0.944	0.342 0.576
<i>Agrimonia</i> spp.				0.598 0.273
<i>Aesculus glabra</i> Willd	0.794 0.286		0.855 0.297	
<i>Actaea racemosa</i> L.	0.239 0.620			
<i>Alcalypha virginica</i> spp. L.	0.794 0.286	0.159 0.572	0.855 0.297	0.179 0.489
<i>Amelanchier arborea</i> Michx.	0.397 0.798	0.714 0.116	0.239 0.331	0.154 0.188
<i>Amianthium muscitoxicum</i> (Walter) A. Gray	0.175 0.630			
<i>Anemone virginiana</i> L.	0.397 0.144		0.179 0.489	0.179 0.592
<i>Antennaria</i> spp. Gaertn.	0.111 0.462	0.239 0.858	0.983 3.279	0.256 0.888

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Apocynum</i> spp. L.			0.342 0.118	
<i>Aronia melanocarpa</i> Michx.	0.794 0.286			
<i>Arisaema triphyllum</i> L.	0.763 1.839	0.316 0.554	0.256 0.640	0.179 0.391
<i>Asarum canadense</i> spp. L.	0.952 0.343			
<i>Asimina triloba</i> (L.) Dunal	0.794 0.286	0.159 0.572	0.855 0.297	
<i>Asplenium platyneuron</i> (L.) Britton, Sterns & Poggenb.			0.342 0.118	0.256 0.888
<i>Betula</i> spp.	0.556 0.138	0.159 0.389		0.126 0.355
<i>Botrychium virginianum</i> (L.) Sw.		0.873 0.285	0.111 0.355	0.179 0.569
<i>Cardamine nuttallii</i> Greene	0.794 0.286			
<i>Carex</i> spp.	0.167 0.422	0.232 0.374	0.462 1.258	0.538 0.855
<i>Carya</i> spp.	0.111 0.232	0.714 0.132	0.942 0.235	0.111 0.174
<i>Celastrus scandens</i> L.	0.397 0.144			

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Cercis canadensis</i> L.	0.952 0.343	0.397 0.144	0.111 0.355	0.427 0.126
<i>Chamerion angustifolium</i> (L.) Holub				0.393 1.362
<i>Chamaecrista fasciculata</i> (Michx.) Greene	0.317 0.114	0.317 0.884	0.145 0.533	0.265 0.886
<i>Chimaphila maculata</i> (L.) Pursh	0.794 0.286	0.317 0.778	0.769 0.192	0.513 0.128
<i>Chimaphila umbellata</i> (L.) W.P.C. Barton				0.855 0.297
<i>Cicuta maculata</i> L.				0.855 0.297
<i>Claytonia</i> spp. L.			0.855 0.297	
<i>Cornus florida</i> L.	0.239 0.858	0.556 0.172	0.239 0.526	0.154 0.336
<i>Corylus americana</i> Walter	0.127 0.458			
<i>Crataegus</i> spp.	0.952 0.314	0.132 0.372		
<i>Danthonia spicata</i> (L.) Beauv.		0.232 0.830		

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Desmodium</i> spp.	0.476 0.144	0.476 0.144	0.419 0.959	0.889 2.926
<i>Dioscorea villosa</i> L.	0.143 0.345	0.556 0.172	0.855 0.185	0.513 0.149
<i>Dryopteris</i> spp. L.	1.794 3.429	1.294 4.247	0.239 0.829	0.564 1.334
<i>Elaeagnus umbellata</i> Thunb.		0.159 0.572	0.342 0.118	
<i>Epigaea repens</i> L.	0.794 0.286		0.111 0.355	0.126 0.298
<i>Euonymus alatus</i> (Thunb.) Siebold	0.167 0.693			0.855 0.297
<i>Eutrochium purpureum</i> (L.) E.E. Lamont				0.855 0.297
<i>Fagus grandifolia</i> Ehrh.	0.794 0.286	0.317 0.114	0.179 0.592	0.256 0.640
<i>Fraxinus americana</i> L.	0.317 0.778		0.855 0.297	0.179 0.489
<i>Galium</i> spp.	0.127 0.275	0.111 0.320	0.325 1.934	0.769 0.236
<i>Gaultheria procumbens</i> L.	1.278 3.926		3.325 7.681	0.543 1.385
<i>Gaylussacia</i> spp. Kunth	0.127 0.458			
<i>Gaylussacia ursina</i> (M.A. Curtis) Torr.	0.794 0.286	0.239 0.714	0.120 0.294	0.834 1.493

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Geum</i> spp. L.			0.427	0.479
			0.148	1.628
<i>Geranium</i> spp. L.	0.278		0.179	0.942
	0.834		0.592	0.296
<i>Gillenia trifoliata</i> (L.) Moench	0.794			
	0.286			
<i>Hamamelis virginiana</i> L.	0.476	0.135	0.342	0.179
	0.894	0.399	0.913	0.489
<i>Hieracium fendleri</i> Sch. Bip		0.794		0.684
		0.286		0.269
<i>Hieracium venosum</i> L.				0.111
				0.385
<i>Hypericum punctatum</i> L.		0.397		
		0.144		
<i>Isotria verticillata</i> Willd.	0.294		0.145	0.427
	1.588		0.347	0.126
<i>Juniperus virginiana</i> L.	0.794			
	0.286			
<i>Kalmia latifolia</i> L.	0.159	0.316	0.251	0.197
	0.293	0.749	0.422	0.650

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Lindera benzoin</i> (L.) Blume		0.239	0.179	0.427
		0.858	0.592	0.148
<i>Liriodendron tulipifera</i> L.	0.239	0.397	0.513	0.162
	0.620	0.679	0.133	0.319
<i>Lonicera japonica</i> Thunb.			0.418	0.251
			1.298	0.716
<i>Lonicera tatarica</i> L.)			0.256	
			0.888	
<i>Lycopodium dendroideum</i> Michx.	0.167		0.238	
	0.693		0.799	
<i>Lyonia ligustrina</i> (L.) DC.			0.179	
			0.592	
<i>Lysmachia quadrifolia</i> L.	0.794	0.159	0.513	0.179
	0.286	0.389	0.133	0.489
<i>Maianthemum racemosum</i> (L.) Link	0.159			
	0.572			
<i>Maianthemum canadense</i> Desf.	0.794		0.128	0.342
	0.286		0.337	0.913
<i>Magnolia acuminata</i> L.			0.855	0.855
			0.297	0.297
<i>Magnolia tripetala</i>				0.855
				0.297

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Medeola virginiana</i> L.	0.135		0.126	
	0.486		0.355	
<i>Menziesia pilosa</i> (Michx. ex Lam.) Juss. ex Pers	0.556		0.359	
	2.384		1.244	
<i>Morus</i> spp.		0.794		
		0.286		
<i>Nyssa sylvatica</i> Marshall	0.794	0.159	0.513	0.256
	0.978	0.389	0.133	0.468
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.825	1.627	0.419	0.413
	1.892	4.165	1.145	0.819
<i>Oxalis</i> spp.	0.239		0.256	0.342
	0.858		0.640	0.673
<i>Oxydendrum arboreum</i> (L.) DC.	0.794		0.179	
	0.286		0.592	
<i>Packera aurea</i> (L.) Á. Löve & D. Löve			0.111	0.265
			0.385	0.918
<i>Panicum</i> spp.	0.429	1.183	0.179	0.863
	1.224	1.755	0.441	1.291
<i>Paronychia</i> spp. L.				
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0.675	0.397	0.966	0.598
	1.361	0.914	2.270	0.123
<i>Phytolacca americana</i> L.		0.794		
		0.286		
<i>Pinus strobus</i> L.	0.317	0.119	0.598	0.564
	0.884	0.372	1.737	1.346

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Pinus taeda</i> L.		0.159 0.572		
<i>Pinus virginiana</i> Mill.		0.794 0.286		
<i>Podophyllum peltatum</i> L.	0.143 0.457 0.714		0.162 0.531	0.342 0.118
<i>Polygonatum</i> spp. Mill.	0.258 0.794 0.286			
<i>Polygonum convolvulus</i> L.			0.684 0.237 0.855	0.179 0.592 0.342
<i>Polygonum hydropiper</i> L.			0.297 0.598	0.118 0.238
<i>Polystichum acrostichoides</i> (Michx.) Schott	0.556 0.144 0.158	1.952 3.949 0.794	0.273 0.889	0.738 1.427
<i>Potentilla</i> spp.	0.324 0.635 0.215	0.286 0.556 0.124	1.933 0.342 0.818	3.930 0.256 0.888
<i>Prenanthes alba</i> L.	1.786 4.718 0.159	4.556 11.876	2.598 5.593	0.786 1.441
<i>Prunus</i> spp.			0.342 0.118	
<i>Pycnanthemum virginianum</i> L.	0.572 0.794 0.286			0.179 0.592
<i>Pyrola americana</i> Sweet				

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Pyrularia pubera</i> Michx.	0.119 0.429	0.794 0.286	0.145 0.533	0.179 0.592
<i>Quercus alba</i> L.	0.635 0.177	0.143 0.321	0.256 0.485	0.251 0.414
<i>Quercus berberidifolia</i> Liebm.	0.366 1.316	0.500 1.828	0.855 0.297	0.855 0.297
<i>Quercus coccinea</i> Münchh.		0.794 0.286		0.855 0.297
<i>Quercus prinus</i> L.	0.159 0.572	0.794 0.199	0.128 0.337	0.126 0.245
<i>Quercus rubra</i> L.	0.214 0.467	0.132 0.247	0.239 0.414	0.154 0.233
<i>Quercus velutina</i> Lam	0.159 0.389	0.635 0.150	0.179 0.489	0.598 0.142
<i>Ranunculus</i> spp.	0.794 0.286	0.532 1.769		
<i>Rhododendron</i> spp.	0.476 0.172	0.476 0.172	0.427 1.354	0.513 1.413
<i>Robinia pseudoacacia</i> L	0.239 0.858	0.794 0.286		0.855 0.297
<i>Rosa multiflora</i> Thunb.	0.556 0.144	0.952 0.237	0.487 1.264	0.197 0.438
<i>Rubus</i> spp. L.H.Bailey (Dewberry)	1.540 5.551			
<i>Rubus</i> spp.	2.468 5.670	1.889 5.171	0.960 1.345	0.942 3.343

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Rumex acetosella</i> L.		0.754		0.265
		2.496		0.772
<i>Sanguinaria canadensis</i> L.			0.513	0.942
			0.178	0.326
<i>Sassafras albidum</i> (Nutt.) Nees	0.143	0.263	0.179	0.120
	0.318	0.744	0.253	0.256
<i>Sedum</i> spp.	0.111	0.132	0.120	
	0.462	0.372	0.415	
<i>Smilax</i> spp.	0.926	0.944	0.573	1.855
	1.387	0.982	0.826	1.289
<i>Solanum americanum</i> Mill.			0.684	0.942
			0.237	0.326
<i>Solidago</i> spp.	0.873		0.479	0.137
	0.193		1.438	0.269
<i>Streptopus lanceolatus</i> (Aiton) Reveal	0.952	0.317	0.684	0.179
	0.287	0.654	0.177	0.489
<i>Stellaria media</i> L.		0.635	0.513	0.248
		0.229	0.178	0.859
<i>Symphotrichum</i> spp.	0.325	0.317	0.530	0.615
	0.846	0.654	0.817	2.457
<i>Thalictrum</i> spp. L.			0.855	0.427
			0.297	0.148
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	4.619	4.714	3.479	6.479
	11.187	12.385	7.940	17.864
<i>Toxicodendron radicans</i> (L.) Kuntze	0.397	0.143	0.641	0.598
	0.830	0.312	0.987	0.128

Appendix 6 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Uvularia</i> spp.	0.675 1.689	0.317 0.778	0.385 1.237	0.855 0.297
<i>Vaccinium</i> spp.	0.841 1.693	2.357 7.220	3.735 8.454	2.794 4.393
<i>Verbesina alternifolia</i> (L.) Britton ex Kearney				0.855 0.297
<i>Veronica</i> spp.			0.855 0.297	
<i>Viola</i> spp. L.	0.366 0.449	1.587 3.326	0.615 1.438	2.769 7.863
<i>Viburnum</i> spp.	0.794 0.286	0.159 0.572	0.154 0.363	0.120 0.415
<i>Viburnum acerifolium</i> L.	0.952 0.343	0.556 0.238		
<i>Viburnum lantanoides</i> Michx.			0.128 0.444	
<i>Viburnum prunifolium</i> L.			0.256 0.888	
<i>Vicia caroliniana</i> Walter				0.137 0.474
<i>Vitis</i> spp.	0.794 0.286	0.714 0.229	0.942 0.217	0.128 0.265

Appendix 7. Mean and standard deviation of stem densities for species observed in the understory of West Virginia Division of Natural Resource deer exclosure plots and corresponding control plots, 1984 – 2007.

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Acer pensylvanicum</i> L.	0.155	0.189	0.725	0.885	0.178	0.440
	0.297	0.592	0.236	0.239	0.417	0.182
<i>Acer saccharum</i> Marshall	0.440	0.665	0.330	0.165	0.775	0.220
	0.880	0.174	0.859	0.719	0.199	0.660
<i>Acer spicatum</i> Lam.			0.165			
			0.719			
<i>Actaea racemosa</i> L.			1.255			
			5.255			
<i>Aesculus glabra</i> Willd				0.555		0.550
				0.218		0.240
<i>Amelanchier arborea</i> Michx.	0.275	0.945	0.885	0.110	0.275	0.110
	0.590	0.363	0.288	0.479	0.590	0.330
<i>Aronia melanocarpa</i> Michx.					0.335	
					0.146	
<i>Betula</i> spp.	0.665	0.110	0.155	0.615	0.440	0.165
	0.134	0.330	0.245	0.168	0.946	0.393
<i>Carya</i> spp.	0.665		0.110	0.110	0.220	0.220
	0.177		0.330	0.479	0.747	0.959
<i>Castanea dentata</i> (Marshall)	0.165	0.347		0.110	0.110	0.110
Borkh.	0.719	0.113		0.479	0.330	0.479
<i>Celastrus scandens</i> L.					0.390	
					0.170	
<i>Cercis canadensis</i> L	0.445	0.500	0.445	0.665	0.775	0.720
	0.151	0.174	0.129	0.226	0.267	0.268

Appendix 7 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Cornus florida</i> L.	0.178 0.346	0.227 0.568	0.150 0.159	0.775 0.161	0.289 0.649	0.144 0.296
<i>Corylus americana</i> Walter	0.720 0.193	0.195 0.775	0.189 0.571	0.161 0.718	0.300 1.283	0.117 0.578
<i>Crataegus</i> spp.	0.165 0.525	0.550 0.240	0.155 0.435		0.720 0.244	0.110 0.330
<i>Euonymus bungeanus</i> Maxim.					0.110 0.479	
<i>Fagus grandifolia</i> Ehrh.	0.166 0.462	0.139 0.339	0.940 0.272	0.495 0.123	0.194 0.648	0.178 0.523
<i>Fraxinus americana</i> L.	0.220 0.569	0.445 0.147	0.220 0.569	0.390 0.147	0.330 0.743	0.165 0.719
<i>Gaylussacia</i> spp. Kunth			0.335 0.146	0.165 0.719	0.100 0.436	0.256 0.860
<i>Gaylussacia ursina</i> Torr	0.467 1.763	0.300 1.258	0.534 1.770	0.217 0.539	0.665 0.290	0.725 0.218
<i>Hamamelis virginiana</i> L.	0.445 0.151	0.110 0.479	0.725 0.224		0.500 0.139	0.550 0.240
<i>Kalmia latifolia</i> L.	0.317 0.744	0.328 0.939	0.233 0.524	0.183 0.529	0.272 0.628	0.239 0.734
<i>Liriodendron tulipifera</i> L.	0.835 0.340	0.550 0.240	0.165 0.525		0.165 0.525	0.550 0.240
<i>Lindera benzoin</i> (L.) Blume	0.117 0.460	0.500 0.218	0.211 0.870	0.500 0.194	0.200 0.872	0.111 0.317
<i>Lonicera japonica</i> Thunb	0.161 0.718	0.161 0.718	0.500 2.179		0.667 2.953	0.200 0.872

Appendix 7 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Lyonia ligustrina</i> (L.) DC.					0.250 1.897	
<i>Magnolia acuminata</i> L.	0.110 0.330	0.200 0.823			0.220 0.569	
<i>Malus</i> spp.	0.550 0.240		0.165 0.719			0.550 0.240
<i>Menziesia pilosa</i> (Michx. ex Lam.) Juss. ex Pers		0.110 0.479				
<i>Morus</i> spp.			0.550 0.240		0.550 0.240	
<i>Nyssa sylvatica</i> Marshall	0.330 0.859	0.110 0.479	0.275 0.768	0.110 0.330	0.825 0.134	0.550 0.240
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.330 0.990	0.385 0.871	0.385 0.159	0.720 0.290	0.133 0.285	0.335 0.123
<i>Oxydendrum arboreum</i> (L.) DC.	0.500 0.148	0.550 0.240	0.110 0.479	0.550 0.240	0.110 0.330	
<i>Pinus strobus</i> L.	0.335 0.146	0.665 0.290	0.220 0.959	0.256 0.859	0.940 0.318	0.133 0.531
<i>Pinus taeda</i> L.			0.110 0.479			
<i>Pinus virginiana</i> Mill.	0.390 0.170		0.165 0.719		0.550 0.240	0.550 0.240
<i>Prunus</i> spp.	1.500 4.514	1.820 4.616	0.275 0.976	1.517 6.586	0.455 1.448	0.372 1.622

Appendix 7 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Prunus pensylvanica</i> L.			0.172		0.945	
			0.750		0.412	
<i>Pyrularia pubera</i> Michx.			0.280		0.780	
			0.122		0.340	
<i>Quercus alba</i> L.	0.228	0.220	0.500	0.335	0.220	0.275
	0.917	0.747	0.125	0.146	0.569	0.976
<i>Quercus berberidifolia</i> Liebm.	0.695	0.495	0.428	0.461	0.355	0.184
	3.273	2.155	1.866	1.984	1.366	0.775
<i>Quercus coccinea</i> Münchh.						
<i>Quercus prinus</i> L.		0.550	0.550		0.220	0.110
		0.240	0.240		0.747	0.330
<i>Quercus rubra</i> L.	0.165	0.500	0.440	0.280	0.550	0.445
	0.525	0.194	0.182	0.122	0.953	0.125
<i>Quercus velutina</i> Lam.	0.550		0.165		0.330	
	0.240		0.525		0.786	
<i>Rhododendron</i> spp.	0.165		0.275		0.670	
	0.719		0.976		0.185	
<i>Robinia pseudoacacia</i> L.	0.550	0.550	0.550		0.220	0.550
	0.240	0.240	0.240		0.747	0.240
<i>Rosa multiflora</i> Thunb.	0.550		0.110		0.610	0.110
	0.240		0.330		0.197	0.330

Appendix 7 Continued

	Year 1		Year 3		Year 6	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Rubus</i> spp.	0.495	0.220	0.945	0.111	2.588	0.967
	0.885	0.660	3.598	0.484	8.228	4.163
<i>Sambucus</i> spp.			0.550			
			0.240			
<i>Sassafras albidum</i> (Nutt.) Nees	0.610	0.720	0.665	0.445	0.172	0.610
	0.242	0.265	0.266	0.174	0.551	0.218
<i>Smilax</i> spp.	0.184	0.660	0.215	0.660	0.339	0.184
	0.591	0.127	0.417	0.127	0.757	0.418
<i>Symphoricarpos orbiculatus</i> Moench					0.550	
					0.240	
<i>Ulmus</i> spp.					0.220	
					0.747	
<i>Vaccinium</i> spp.	0.489	0.339	0.139	0.110	0.400	0.228
	1.769	1.151	0.659	0.479	1.744	0.994
<i>Viburnum acerifolium</i> L.	0.220	0.720		0.220	0.550	0.110
	0.959	0.314		0.959	0.240	0.479
<i>Viburnum lantanoides</i> Michx.	0.445	0.178	0.280	0.110	0.780	
	0.194	0.776	0.122	0.479	0.340	
<i>Viburnum prunifolium</i> L.	0.445	0.335			0.610	0.335
	0.194	0.146			0.266	0.146
<i>Vitis</i> spp.	0.110	0.385	0.220	0.550	0.385	0.165
	0.330	0.159	0.747	0.240	0.164	0.525

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Acer pensylvanicum</i> L.	0.115	0.330	0.148	0.220	0.660	0.813
	0.297	0.786	0.422	0.440	0.126	0.248
<i>Acer rubrum</i> L.	0.339	0.139	0.467	0.185	0.319	0.118
	0.400	0.265	0.453	0.344	0.383	0.299
<i>Acer saccharum</i> Marshall	0.139	0.110	0.893	0.733	0.333	0.733
	0.413	0.330	0.289	0.274	0.350	0.274
<i>Acer spicatum</i> Lam.		0.550				
		0.240				
<i>Actaea racemosa</i> L.					0.733	
					0.274	
<i>Aesculus glabra</i> Willd		0.550				
		0.240				
<i>Albizia julibrissin</i> Durazz.	0.550					
	0.240					
<i>Amelanchier arborea</i> Michx.	0.885	0.110	0.593		0.133	0.147
	0.156	0.479	0.195		0.197	0.549
<i>Aronia melanocarpa</i> Michx.	0.390				0.733	
	0.170				0.274	
<i>Asimina triloba</i> (L.) Dunal	0.100	0.284		0.178	0.178	0.267
	0.436	0.914		0.666	0.666	0.998
<i>Betula</i> spp.	0.660	0.550	0.887	0.733	0.813	0.147
	0.146	0.240	0.182	0.274	0.174	0.374

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Carya</i> spp.	0.885	0.220	0.125	0.513	0.880	0.367
	0.265	0.747	0.326	0.113	0.151	0.111
<i>Castanea dentata</i> (Marshall) Borkh.	0.110	0.550	0.733		0.733	
	0.330	0.240	0.274		0.274	
<i>Celastrus scandens</i> L.	0.165				0.373	
	0.719				0.140	
<i>Cercis canadensis</i> L	0.500	0.390	0.164	0.373		0.147
	0.139	0.129	0.423	0.140		0.549
<i>Cornus florida</i> L.	0.189	0.650	0.133	0.367	0.133	0.147
	0.385	0.951	0.216	0.111	0.212	0.374
<i>Corylus americana</i> Walter	0.500	0.335			0.830	0.733
	2.311	0.146			2.931	0.274
<i>Crataegus</i> spp.	0.610	0.550	0.520		0.593	0.147
	0.174	0.240	0.167		0.195	0.549
<i>Euonymus bungeanus</i> Maxim.		0.550	0.733		0.147	
		0.240	0.274		0.549	
<i>Fagus grandifolia</i> Ehrh.	0.178	0.239	0.214	0.333	0.178	0.333
	0.559	0.736	0.494	0.763	0.422	0.777
<i>Fraxinus americana</i> L.	0.610	0.110	0.147	0.733	0.740	0.733
	0.130	0.479	0.549	0.274	0.156	0.274
<i>Gaylussacia</i> spp. Kunth	0.280			0.667		0.220
	0.122			0.249		0.823

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Gaylussacia ursina</i> Torr	0.156	0.284	0.293	0.520	0.237	0.437
	0.629	0.941	0.198	0.146	0.625	1.292
<i>Hamamelis virginiana</i> L.	0.220	0.110	0.513		0.667	0.147
	0.959	0.479	0.120		0.198	0.549
<i>Kalmia latifolia</i> L.	0.316	0.161	0.252	0.185	0.473	0.385
	0.717	0.486	0.650	0.693	1.135	1.229
<i>Lindera benzoin</i> (L.) Blume	0.183	0.835	0.293	0.520	0.259	0.133
	0.749	0.225	0.748	0.167	0.941	0.358
<i>Liriodendron tulipifera</i> L.	0.275		0.293		0.147	
	0.685		0.849		0.549	
<i>Lonicera japonica</i> Thunb	0.378	0.289			0.578	0.293
	1.648	1.260			2.163	0.198
<i>Lonicera tatarica</i> L	0.165	0.165	0.813	0.520		
	0.719	0.719	0.343	0.195		
<i>Lyonia ligustrina</i> (L.) DC.	0.156	0.110	0.520	0.593	0.667	
	0.678	0.479	0.146	0.223	0.249	
<i>Magnolia acuminata</i> L.	0.220	0.550	0.293	0.733	0.367	0.733
	0.440	0.240	0.486	0.274	0.656	0.274
<i>Morus</i> spp.	0.110		0.733		0.733	
	0.479		0.274		0.274	
<i>Nyssa sylvatica</i> Marshall	0.830		0.367		0.133	
	0.168		0.111		0.245	
<i>Ostrya virginiana</i> (Mill.) K.	0.385	0.220	0.440	0.147	0.156	0.887
Koch	0.159	0.747	0.112	0.549	0.417	0.195

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Oxydendrum arboreum</i> (L.) DC.	0.335 0.146		0.440 0.112		0.593 0.157	0.147 0.549
<i>Parthenocissus quinquefolia</i> (L.) Planch.					0.147 0.549	
<i>Picea rubens</i> Sarg.		0.550 0.240	0.733 0.274		0.733 0.274	
<i>Pinus strobus</i> L.	0.128 0.356	0.139 0.581	0.133 0.349	0.170 0.673	0.148 0.324	0.193 0.729
<i>Pinus virginiana</i> Mill.		0.550 0.240		0.733 0.274	0.147 0.549	0.220 0.596
<i>Prunus</i> spp.	0.355 1.142	0.184 0.775	0.520 0.167	0.733 0.274	0.126 0.274	0.293 0.638
<i>Pyrularia pubera</i> Michx.	0.155 0.460		0.185 0.693	0.733 0.274	0.193 0.729	
<i>Quercus alba</i> L.	0.440 0.946	0.275 0.768	0.513 0.973	0.367 0.111	0.293 0.638	0.513 0.132
<i>Quercus berberidifolia</i> Liebm.	0.289 1.260	0.835 0.364	0.373 0.140		0.422 1.579	0.111 0.417
<i>Quercus prinus</i> L.	0.280 0.122	0.110 0.479	0.367 0.111	0.147 0.549	0.733 0.274	
<i>Quercus rubra</i> L.	0.940 0.256	0.280 0.122	0.155 0.390	0.293 0.198	0.440 0.967	
<i>Quercus velutina</i> Lam.			0.147 0.374		0.147 0.374	0.447 0.167

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD	$\bar{x}$ SD
<i>Robinia pseudoacacia</i> L.			0.733 0.274			
<i>Rhododendron</i> spp.	0.220 0.959	0.220 0.959	0.447 0.144		0.593 0.172	
<i>Rhus</i> spp.	0.275 0.843		0.447 0.144			
<i>Rosa multiflora</i> Thunb.	0.440 0.182	0.110 0.330	0.197 0.429	0.667 0.249	0.147 0.549	
<i>Rubus</i> spp.	4.350 11.944	1.272 5.494	3.943 7.291	1.933 7.234	1.185 3.896	2.740 7.762
<i>Sambucus</i> spp.					0.733 0.274	
<i>Sassafras albidum</i> (Nutt.) Nees	0.150 0.185	0.550 0.240	0.813 0.160		0.148 0.324	
<i>Smilax</i> spp.	0.389 0.769	0.183 0.468	0.489 1.119	0.200 0.417	0.933 1.413	0.147 0.312
<i>Toxicodendron radicans</i> (L.) Kuntze	0.550 0.240					
<i>Ulmus</i> spp.	0.550 0.240				0.293 0.198	
<i>Vaccinium</i> spp.	0.200 0.626	0.228 0.691	0.126 0.471	0.667 0.222	0.170 0.395	0.133 0.386
<i>Viburnum</i> spp.	0.110 0.479		0.593 0.195		0.813 0.252	

Appendix 7 Continued

	Year 9		Year 12		Year 15	
	Fenced	Control	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD	SD	SD
<i>Viburnum acerifolium</i> L.	0.165		0.293		0.147	
	0.719		0.198		0.549	
<i>Viburnum lantanoides</i> Michx.	0.390		0.667		0.447	
	0.170		0.249		0.167	
<i>Viburnum prunifolium</i> L.	0.100	0.555			0.178	0.667
	0.436	0.242			0.666	0.249
<i>Vitis</i> spp.	0.165	0.110	0.733	0.733	0.367	0.147
	0.393	0.330	0.274	0.274	0.868	0.374

Appendix 7 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Acer pensylvanicum</i> L.	0.115	0.700	0.950	0.786
	0.267	0.272	0.285	0.283
<i>Acer rubrum</i> L.	0.489	0.153	0.459	0.950
	0.618	0.221	0.687	0.187
<i>Acer saccharum</i> Marshall	0.233	0.116	0.246	0.236
	0.496	0.338	0.450	0.614
<i>Actaea racemosa</i> L.	0.579			
	0.246			
<i>Amelanchier arborea</i> Michx.	0.456	0.116	0.117	
	1.556	0.491	0.231	
<i>Aronia melanocarpa</i> Michx.	0.116			
	0.491			
<i>Asimina triloba</i> (L.) Dunal	0.234	0.437	0.157	0.197
	0.966	1.236	0.567	0.688
<i>Berberis</i> spp.			0.236	
			0.850	
<i>Betula</i> spp.	0.637		0.393	
	0.125		0.892	
<i>Carya</i> spp.	0.123	0.700	0.157	0.793
	0.257	0.158	0.271	0.155
<i>Castanea dentata</i> (Marshall)	0.116		0.557	
Borkh.	0.338		0.173	
<i>Celastrus scandens</i> L.	0.116			
	0.491			

Appendix 7 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Cercis canadensis</i> L.	0.140	0.579	0.166	0.636
	0.500	0.246	0.516	0.229
<i>Cornus florida</i> L.	0.874	0.579	0.714	
	0.163	0.246	0.162	
<i>Corylus americana</i> Walter	0.678		0.314	
	2.649		0.113	
<i>Crataegus</i> spp.	0.647		0.557	
	0.190		0.289	
<i>Euonymus bungeanus</i> Maxim.		0.116		0.786
		0.491		0.283
<i>Fagus grandifolia</i> Ehrh.	0.140	0.198	0.127	0.254
	0.400	0.499	0.235	0.517
<i>Fraxinus americana</i> L.	0.522	0.116	0.393	0.786
	0.192	0.491	0.671	0.283
<i>Gaylussacia</i> spp. Kunth	0.758			
	0.322			
<i>Gaylussacia ursina</i> Torr	0.128	0.234	0.167	0.182
	0.374	0.480	0.470	0.414
<i>Hamamelis virginiana</i> L.	0.584	0.174	0.793	
	0.225	0.737	0.257	
<i>Juniperus virginiana</i> L.		0.579		
		0.246		
<i>Kalmia latifolia</i> L.	0.497	0.316	0.126	0.393
	1.377	1.216	0.340	1.115

Appendix 7 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Lindera benzoin</i> (L.) Blume	0.228	0.169	0.393	0.129
	0.818	0.525	0.984	0.379
<i>Liriodendron tulipifera</i> L.	0.116		0.236	0.786
	0.491		0.850	0.283
<i>Lonicera japonica</i> Thunb.	0.889	0.584	0.314	0.786
	3.720	0.248	0.113	0.283
<i>Lonicera tatarica</i> L	0.295	0.353	0.479	0.636
	0.125	0.150	0.173	0.229
<i>Lyonia ligustrina</i> (L.) DC.	0.463		0.314	
	0.135		0.875	
<i>Magnolia acuminata</i> L.	0.174		0.236	
	0.412		0.451	
<i>Morus</i> spp.	0.579		0.786	
	0.246		0.283	
<i>Nyssa sylvatica</i> Marshall	0.584		0.236	
	0.155		0.614	
<i>Ostrya virginiana</i> (Mill.) K.	0.222	0.174	0.175	0.157
Koch	0.495	0.537	0.423	0.385
<i>Oxydendrum arboreum</i> (L.)	0.174	0.116	0.236	0.157
DC.	0.737	0.491	0.850	0.567
<i>Picea rubens</i> Sarg.	0.579			
	0.246			
<i>Pinus strobus</i> L.	0.116	0.164	0.117	0.254
	0.380	0.669	0.343	0.855

Appendix 7 Continued

	Year 18		Year 21	
	Fenced	Control	Fenced	Control
	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$
	SD	SD	SD	SD
<i>Pinus virginiana</i> Mill.	0.174	0.174	0.786	
	0.737	0.537	0.283	
<i>Prunus</i> spp.	0.134	0.116	0.118	0.786
	0.262	0.338	0.163	0.283
<i>Pyrularia pubera</i> Michx.	0.158		0.214	0.786
	0.670		0.773	0.283
<i>Quercus alba</i> L.	0.522	0.642	0.550	0.714
	0.192	0.219	0.123	0.229
<i>Quercus berberidifolia</i> Liebm.	0.252	0.174	0.714	
	0.861	0.737	0.258	
<i>Quercus prinus</i> L.	0.415	0.289	0.714	0.479
	0.153	0.999	0.229	0.173
<i>Quercus rubra</i> L.	0.140		0.190	
	0.446		0.568	
<i>Quercus velutina</i> Lam.	0.453	0.758	0.471	0.129
	0.889	0.297	0.994	0.342
<i>Rhododendron</i> spp.	0.758		0.117	
	0.274		0.295	
<i>Rhus</i> spp.	0.116			
	0.491			
<i>Robinia pseudoacacia</i> L.	0.174		0.786	0.236
	0.537		0.283	0.850
<i>Rosa multiflora</i> Thunb.	0.187	0.300	0.294	0.950
	0.549	0.127	0.765	0.285

Appendix 7 Continued

	Year 18		Year 21	
	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD	Fenced $\bar{x}$ SD	Control $\bar{x}$ SD
<i>Rubus</i> spp.	0.917 2.361	0.444 1.885	0.460 1.460	0.314 0.113
<i>Sambucus</i> spp.	0.579 0.246			
<i>Sassafras albidum</i> (Nutt.) Nees	0.816 0.232	0.174 0.737	0.557 0.158	0.157 0.567
<i>Smilax</i> spp.	0.795 1.537	0.158 0.367	0.864 1.562	0.166 0.338
<i>Ulmus</i> spp.	0.295 0.125			
<i>Vaccinium</i> spp.	0.932 0.284	0.758 0.248	0.714 0.245	0.157 0.385
<i>Viburnum</i> spp.	0.995 0.352		0.159 0.488	
<i>Viburnum acerifolium</i> L.	0.116 0.491		0.236 0.850	
<i>Viburnum lantanoides</i> Michx.	0.295 0.125		0.479 0.173	
<i>Viburnum prunifolium</i> L.	0.128 0.495	0.353 0.150	0.157 0.385	
<i>Vitis</i> spp.	0.463 0.897	0.579 0.246	0.236 0.451	0.786 0.283

Appendix 8. Survey Instrument administered by mail to stakeholder groups in Canaan Valley and Tucker County, WV. Survey instrument was provided to visitors at Canaan Valley State Park and National Wildlife Refuge.

Canaan Valley White-tailed Deer Survey

Date _____

This survey was developed in cooperation with West Virginia University, Canaan Valley National Wildlife Refuge and Canaan Valley Resort State Park to gather public opinion regarding the local deer herd and the importance of rare plant species found in Canaan Valley. Please take a few moments to answer the following 25 questions. Your answers will remain completely confidential. If you have already filled out this survey in another location, please indicate so below and return the uncompleted form in the provided envelope

I have previously completed this survey ☐

Please fill in all boxes that apply to you

Residential Status: I am a:

☐ Visitor to Canaan Valley	☐ Resident of Canaan Valley (# years____)
☐ Resident of Tucker County (# years____)	☐ Own or rent 2 nd home in Canaan Valley

Age: My age (years) is:

- ☐ 18-25 ☐ 26-45 ☐ 46-60 ☐ More than 60

Education Level: What is the highest level of education you have completed?

☐ Below High School	☐ High school	☐ Some Undergraduate college
☐ Undergraduate college	☐ Graduate College	

Gender:

- ☐ Male ☐ Female

Please circle the response that most closely fits your opinion.

1. I enjoy seeing white-tailed deer around/near my home.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

2. I enjoy seeing white-tailed deer when I visit state or national parks, forests or wildlife refuges.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

3. I believe deer are overabundant in the state of West Virginia.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

4. I believe deer are overabundant in Canaan Valley National Wildlife Refuge and/or Canaan Valley Resort State Park.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

5. I place value on wild plants and trees as sources of food and timber.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

6. I enjoy seeing wild plants, flowers, and trees.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

7. I, or a member of my immediate family, have been involved in a deer/vehicle collision.

Never In the past year In the past 5 years More than 5 years ago

8. I, or a member of my immediate family, have incurred damage to landscaping, crops or other property (excluding vehicles) from deer.

Yes No

9. I believe it is ethical to manage wild populations of white-tailed deer.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

10. I believe white-tailed deer numbers should be increased in West Virginia.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

11. I believe white-tailed deer numbers should be managed to increase hunter harvest.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

12. I believe white-tailed deer numbers should be managed in balance with their environment.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

13. I believe white-tailed deer may have a detrimental effect on some plant communities.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

14. I believe rare or endangered plant species should be protected.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

15. I believe rare or endangered plant species should be protected from white-tailed deer browsing if it reduces the abundance of those plants.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

16. I would not have a problem seeing fenced areas to protect plants when I visit state or national parks, forests or wildlife refuges.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

17. I believe hunting is an acceptable tool for managing deer populations.

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

18. I have participated in legal hunting activities within my lifetime.

Yes No

19. I have participated in legal hunting activities within the past year.

Yes No

20. Another member of my household participates in legal hunting activities.

Yes No

21. I believe professional sharp-shooting is an acceptable tool for managing deer populations. (This statement refers to people who are hired to kill a large number of deer in order to reduce herd numbers).

Strongly Agree Agree Neutral Disagree Strongly Disagree No Opinion

Optional- Please provide your zip code only so that we may determine where our respondents are from. (This answer is completely optional)

Additional Comments

Thank you for taking the time to participate in this survey. Your cooperation is greatly appreciated.