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Department of Horticultural Science
University of Minnesota, St.Paul, MN

The effects of *Odocoileus virginianus* (white-tailed deer) herbivory on the restoration of deciduous forests in eastern North America

Sean Jergens

Introduction

Odocoileus virginianus (white-tailed deer) is a common mammal in eastern North America. White-tailed deer inhabit rural and suburban areas east of the Rocky Mountains (Figure 1), and are important economically and culturally as game animals for millions of hunters throughout their range. Yet the population of white-tailed deer in many locales has not always been as high as it is today. Populations crashed in the early 20th Century, largely due to over-hunting and habitat loss. Early conservation practices such as hunting regulations and land management were established (Stout 1999). Many states cancelled annual deer hunting seasons throughout the 1920's and 1930's because of too few deer, a fact that is difficult for many of the current hunting generation to imagine (Rue 1999, Anderson 2003). As recently as 1971, Minnesota cancelled its deer-hunting season because of a low population. Today, the Minnesota deer herd is estimated to be 1.1 million animals (Anderson 2003).

Deciduous forests once covered much of the eastern continent (Figure 2). The logged and cleared forests of the early 20th century provided huge areas of ideal deer feeding habitat and populations recovered quickly. Population recovery in the 20th century is one of the most successful stories in conservation history. However, management of white-tailed deer has been so successful that populations throughout North America are now at or near their carrying capacities (Tilghman 1989), exceeding targeted densities by up to 200% (Alverson et al. 1988, Stout 1999).

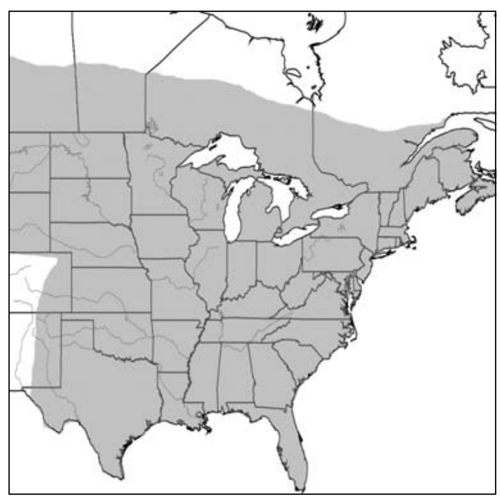

Figure 1. Approximate range of white-tailed deer in eastern North America. GIS Data from ESRI 1998. Adapted from Rue (2000).

While hunters are pleased (Anderson 2003), the rapid expansion of the deer population concerns ecologists because intense deer herbivory adversely influences forests and other resources (Hough 1965, Anderson 1994, Anderson 2003). There is high pressure from hunters to keep the deer populations at higher than historic levels. Therefore, state wildlife management officials are unlikely to decrease the deer population to levels that would reduce the damaging effects of deer in many areas (Anderson 2003). Ecologists cannot overlook the effects of white-tailed deer on regeneration and restoration of deciduous forests. Current forest conservation plans in eastern North America call for protection of remnants of existing old-growth mature forest, restoration of corridors between patches of forest, and restoration of characteristic forest species (Augustine and

Frelich 1997). Studies of the effects of white-tailed deer herbivory on forest regeneration suggest that it is necessary for restorationists to plan for and manage deer herbivory to ensure diverse and successful forest growth.

Deer and the Deciduous Forest Ecosystem

The temperate deciduous forests of North America are typically dominated by deciduous tree species such as *Acer spp., Betula spp.*, *Fraxinus spp*., *Quercus spp.*, and *Tilia americana*. Locally important species include coniferous trees (*Tsuga canadensis, Pinus strobus, and Thuja occidentalis*) as well as a diverse deciduous sub-canopy and ground layer herbaceous plants (Tester 1995, McLachlan and Bazely 2001). Human-caused habitat loss and fragmentation has reduced the richness and diversity of native species in the forests of eastern North America. Logging and clearing have disturbed natural systems. However, the amount of deciduous forest in North America has increased over the past few decades, largely due to abandonment of marginal agricultural land, but increasingly because of restoration and preservation (McLachlan and Bazely 2001).

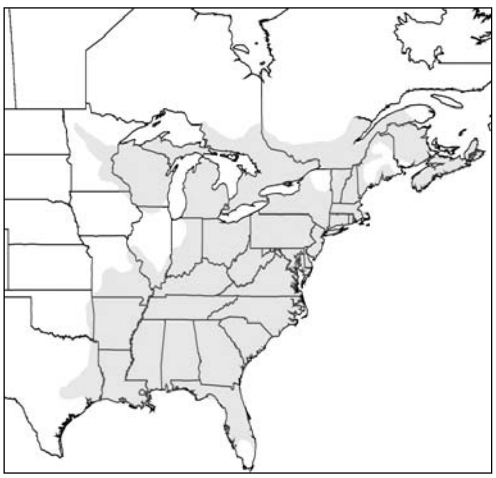

Figure 2. Approximate historic location of deciduous forests in eastern North America. GIS Data from ESRI 1998. Adapted from

Studies in Wisconsin, Pennsylvania, and Ontario show that populations of white-tailed deer were historically lower than current levels in the heavily forested landscapes that existed before settlement by Europeans in the 18th and 19th centuries (Alverson et al. 1988, Tilghman 1989, McLachlan and Bazely 2001). Ideal feeding habitat is comprised of grassy opening and forest edges typical of highly fragmented systems. Forest clearing and agricultural land use increased the amount of habitat and food for white-tailed deer, causing their numbers to rise sharply. Resource managers encouraged the creation of grassy, open clearings in mature forests to promote deer numbers for the benefit of hunters on public lands, including the national forests in eastern North America (Waller and Alverson 1997). White-tailed deer consume woody browse such as seedlings, twigs and buds (Frelich and Lorimer 1985), mast such as acorns (Rue 2000), and graze on herbaceous plants (Augustine and Frelich 1998). The current relationship between white-tailed deer and the deciduous forests is very different than the natural system that evolved over thousands of years because of the near removal of deer's natural predators, habitat and landscape change, and hunting by humans.

Effects on Trees and Shrubs

White-tailed deer can have a significant effect on the composition and abundance of woody forest species (Waller and Alverson 1997). Some species are more browse-sensitive than others are because of unique growth characteristics, reproductive strategy, or palatability. Deer are able to influence the species diversity by consuming browsing-sensitive species, which favors the recruitment of seedling species that are not palatable or are browsing tolerant. The results can be a slow conversion of a diverse forest to a stand of less palatable species that have competitive advantage, such as *Fagus grandifolia* (American beech) (Waller and Alverson 1997). A total elimination of woody understory results in a "fern parkland" forest groundcover of grasses, sedges and ferns. Even more troubling is the fact that ferns can inhibit the subsequent germination of woody species, further inhibiting tree and shrub growth (Waller and Alverson 1997). A study in the mixed hardwood forests of Massachusetts suggested that the fern dominated understoy caused by intense deer herbivory produced "differential interference among species with seedling development after reduction of deer browse (De la Cretaz and Kelty 2002)". Species such as oak

(*Quercus*) and ash, (*Fraxinus*) with delayed leaf development, were the most affected. In suburban areas, the shift in forest understory is compounded by invasion of exotic woody and herbaceous plants and direct human impact (Waller and Alverson 1997) Deer herbivory can affect the viability and success of plant reproduction as well. One study of an Ohio woodland showed that deer browse was the single most important factor in determining the mortality and longevity of seedlings, ahead of environmental gradients or climatic factors (Boerner and Brinkman 1996).

Much of the data concerning deer browse and woody vegetation was measured using exclosure systems or islands where deer densities vary (Beals et al. 1960, Tilghman 1989, Operman and Merenlender 2000). Tilghman (1989) found that after five years of study, the density, species composition, and rates of regeneration were very different within deer exclosure areas in Pennsylvania compared to the surrounding deer-inhabited forests. One of the most obvious differences was that the height of woody stems within the exclosures was up to 100% taller than those outside the exclosures. Tilghman studied the effects of density on deer herbivory by controlling the density of deer within different fenced forest enclosures. At the highest deer density, the deer had the highest mortality rate, seedling height was the smallest, and the cover of invasive ferns was the greatest. Not surprisingly, at the highest densities both the deer and forests were unhealthy.

Effects on Herbaceous Plants

Despite the recent overall increases in deciduous forest cover, studies suggest that understory plant communities take much longer to recover than overstory species (McLachlan and Bazely 2001). For example, an undisturbed mature forest has higher species diversity than adjacent second growth stands (McLachlan and Bazely 2001). The effect of white-tailed deer herbivory on forest herbaceous flora has not been studied closely, likely because herbaceous plants lack economic value to the timber industry (Anderson 1994, Augustine and Frelich 1997, Waller and Alverson 1997). Most of the species diversity within a deciduous forest, however, is in the herbaceous community. For example, a typical deciduous forest species list for the Minneapolis-St. Paul, Minnesota area published by Great River Greening (2003) lists 29 woody species and 85 herbaceous species. As with woody plants, deer can have significant impacts on the composition, richness, and diversity of the native groundlayer flora. Deer may destroy herbaceous communities without a trace, leaving no evidence of their former presence in a plant community (Waller and Alverson 1997). Important genetic and functional characteristics of the herbaceous plant species can be lost. Deer will selectively graze on palatable species of understory forbs, eliminating selected species from forest patches (Anderson 1994, Augustine and Frelich 1997). While tree species may eventually grow out of the reach of deer, herbaceous plant species cannot (Stout 2002). Augustine and Frelich (1997) suggest that because of the changes to landscape structure and increases in deer abundance, deer grazing can result in local extinction of grazing-sensitive forbs. The increased recovery time required for herbaceous plants is due to changes associated with fragmentation, increased herbivory, invasion by exotic species, intense human use of the surrounding landscape, and alteration of the physical condition of the forest (McLachlan and Bazely 2001). However, Anderson (1994) showed that deer removal tended to stabilize the effects of herbivory on forest understory.

The presence of a diverse herbaceous understory is an indication of a high quality forest ecosystem. The herbaceous ground layer is the most sensitive plant community to disturbance by herbivory (Figure 3) because many species within the herbaceous understory have limited dispersal ranges (McLachlan and Bazely 2001). Augustine et al. (1998) suggest that herbivore impacts to native plant species will be most detrimental when species are rare, and that small changes in herbivore density when they are very abundant can cause sudden and dramatic crash of a plant species population. Rare native forbs, which often have limited or complex dispersal regimes, are especially threatened if they are palatable to deer (Augustine et al. 1998). Rare lilies and native orchids such as *Lilium superbum, Liparis loeselii, Platanthera integrilabia,* and *Cypripedium spp.* are vulnerable to deer herbivory and potential extirpation (Waller and Alverson 1997, McLachlan and Bazely 2001).

Figure 3. A diverse herbaceous ground layer that includes *Asarum canadense, Cypripedium calceolus*, *Hydrophyllum virginianum*, and *Sanguinaria canadensis* is highly sensitive to intense herbivory.
Photo Jergens 2002

Several studies of large-flowered trillium (*Trillium grandiflorum*), a grazing-sensitive forb, demonstrate that size structure, plant distribution, and leaf length were significantly affected by deer herbivory (Anderson 1994, Augustine and Frelich 1997). The cumulative effects over several growing seasons can lead to the local extirpation of this species. Tilghman (1989) indicated that populations of ferns (*Dennstaedtia punctilobula* and *Thelypteris noveboracensis*) increased and forbs decreased with higher deer densities in forest clear cuts. While the impacts of deer on woody plants tend to be reversible over a short time span (Tilghman 1989), it seems that the impacts to herbaceous plant diversity can persist for 30 years or more after deer are removed (Waller and Alverson 1997).

Ecosystem Effects

White-tailed deer herbivory affects more than just the plant species on which they feed, affecting the entire ecosystem at different trophic levels. Waller and Alverson (1997) consider them to be a "keystone herbivore" because their effects can be measured throughout other trophic levels in the deciduous forest. If deer herbivory affects the composition of trees, shrubs, and forbs, the other species in the ecosystem that depend on those plant communities will be affected. For example, canopy-nesting bird abundance declined 37% and species diversity declined 27% in areas with high deer density (DeCalesta 1994). Deer consumed an entire population of lupine (*Lupine perennis*) over a short period in New York, which led to the eradication of a deme of endangered Karner blue butterflies (*Lycaeides melissa*) from a reserve (Schweitzer 1999). Deer herbivory and resulting changes in species composition and dynamics may have profound influence on pollinators and other herbivores in forest ecosystems (Anderson 1994).

Restoration Techniques and Recommendations

A review of the restoration literature turns up little about the effects of white-tailed deer in the restoration of deciduous forests. It is well established that high population densities of white-tailed deer may have negative ecological consequences in the deciduous forests of eastern North America. Most of the studies that have been done have measured the effects of deer in established mature forests or second growth forests following clearing from logging. The goals of silviculturalist or foresters may be different from the goals of an ecological restorationist. A forester's main objective might be maximizing production of board feet for economic gain. Other natural resource managers might only be concerned with structural forest recovery for purposes of recreation or game habitat. Ecological restoration is different because its objective is the "complete structural and functional return to pre-disturbance states" of an ecosystem (Galatowitsch 2003). This includes the full array of species richness, diversity, and plant-animal functional interaction. Restoration also differs in that it often includes re-introduction or encouragement of re-colonization of many species, rather than a "hands-off" forest regeneration or planting of only targeted forest product species (Stout 2002). However, data from other disciplines are applicable to restoration and provide valuable insight into the effects of white-tailed deer herbivory and plant community response. The techniques employed by the range of forest management disciplines in the field can be used by restorationists to promote the unique goals of ecological restoration of deciduous forests. Full and complex forest communities include white-tailed deer, so the dilemma for managers is to manage white-tailed deer in a way that promotes diverse forest systems. Many opportunities exist for restoration of forests in eastern North America. The discussion will include the following techniques: control of deer density, deer exclosure systems, encouragement of re-colonization, and plant protection methods.

The interaction between white-tailed deer and forest plants is complex and dynamic. As with other animal-plant interactions, white-tailed deer herbivory has the potential to cause an "alternate stable state" within the forest system, which can significantly influence management and restoration decisions for a site (Hobbs and Norton 1996, Augustine et al. 1998, Cretaz and Kelty 2002). The alternate stable state hypothesis posits that removal of the causal factor in a degraded ecosystem will not cause the system to return to its original stable composition and function (Cretaz and Kelty 2002). The original stable state is an intact deciduous forest that includes both deer and a diverse plant community. After disturbance (extinction of natural predators, habitat and landscape change), white-tailed deer numbers rise and plant diversity decreases. In this case, the implication is that reduction of deer herbivory alone is not enough of an action to allow degraded deciduous forest to regenerate its original ecological function and species diversity. For example, areas of the Quabbin Reservation forest that became dominated by hay-scented fern (*Dennstaedtia punctilobula*) after intense deer herbivory did not show signs of increased seedling growth even after deer populations were reduced from 23 deer per km² to < 3 deer per km² (Cretaz and Kelty 2002). It is possible that herbivory alone is not the sole reason that a system would reach a new stable plant-herbivore equalibria. Augustine et al. (1998) indicate that deer do not change the system by pushing plant density to a certain breakpoint, but rather the plant population reaches a new equalibria after some other "perturbing factor causes plant density to reach the breakpoint." At Quabbin Reservation, this perturbing factor is the resilient population of hay-scented fern, which prevents seedlings from growing even in the absence of herbivory; thus, restoration planners must consider the resiliency of a degraded forest during the initial stages of restoration planning.

Deer density has a significant impact on the successful regeneration of deciduous forests (Tilghman 1989). Increased deer densities affect the plant communities in two ways: by increasing the intensity of browsing and increasing the length of time that browsing occurs (Beals et al. 1960). Natural resource managers, hunters, and ecologists differ in their opinions of ideal white-tailed deer densities in eastern North America. Targeted deer densities cannot be generalized for an entire region, since specific local factors will affect the impact that deer have on woody and herbaceous communities (Waller and Alverson 1997). In Wisconsin, the USDA Forest Service has set management goal deer densities at 9.3 deer per km², while historic densities were probably 2-4 deer per km² and current density is about 5-12 deer per km² in national forest units (Alverson et al. 1988). Alverson et al. (1988) critique the management policy, saying that, "plans to maintain dense populations of deer (8-9.3/ km²) by state and federal land stewards work directly against the preservation of these components of natural diversity." Some areas of Pennsylvania and New Jersey have much higher densities, as high as 60 deer per km² in what ecologists call "catastrophic" densities (DeVito 2002, Stout 2002). Researchers agree that deer populations should be actively managed to limit deer densities (Tilghman 1989, Augustine and Frelich 1997, Waller and Alverson 1997, DeVito 2002). Clearly, restorationists must consider the local current and long-term densities of deer during the planning stage of any forest restoration.

Several innovative techniques for control of white-tailed deer population density have been proposed. Liberalized hunting regulations, such as increasing the harvest of antler-less (female) deer is one of the typical techniques that are tried in many areas (Alverson et al. 1988). Waller and Alverson (1997) propose that a portion of revenues from hunting licenses be used to monitor the specific impacts of deer herbivory. DeVito (2002) states that the deer population in New Jersey must be reduced to 10 deer per km² to give the decimated forests any chance of recovery. Some interesting ideas in New Jersey are to give hunters an income tax credit for every female deer that they harvest, require landowners receiving woodland assessments to implement deer removal, economic incentives for local units of government implementing deer control, and legalizing the sale of venison under certain conditions (DeVito 2002). Restoration ecologists should consider how deer density will affect forests and how they can work with policy makers, land managers, and local government officials to achieve restoration goals.

One of the most frequently studied methods to control effects of deer herbivory is the use of fenced exclosure systems (Tilghman 1989, Anderson and Katz 1993, Operman and Merenlender 2000). This technique becomes less effective with large project sites because it is more difficult to ensure that deer have not entered the area. It is a very good technique for small areas, and is often used in plant conservancy areas such as the Eloise Butler Wildflower Sanctuary in Minneapolis, Minnesota. In areas that are aggressively browsed by deer, it is not expected that forests will automatically recover after the erection of an exclosure. Forests subjected to intense continuous browsing took up to 70 years to recover woody species after release from browsing in Wisconsin (Anderson and Katz 1993). Herbaceous species are even less likely to recover from re-colonization alone.

The most direct method to re-establishing plant species is by installing live plants or sowing seed. The composition, density, and type of planting can vary greatly and should be considered as part of the larger restoration plan. Another strategy is re-colonization, which can be encouraged and enhanced in a restoration site in several ways. Forest restorations should be targeted in areas with nearby intact forest systems to increase chances of re-colonization from adjacent seed sources (McLachlan and Bazely 2001). Since deer prefer edges and open areas within forests, restorations that increase the patch size of a forest and increase patch core area should be implemented as a way to decrease the effects of deer herbivory. Restoration ecologists should implement plans for re-introduction of forbs and woody species within deer exclosures as a supplement to re-colonization to restore biodiversity on sites where much of the native flora is destroyed. A combination of several techniques can maximize the chances of restoration success.

Plant protection schemes could have been used in this example for greater protection of seedlings. Foresters have used plant protection schemes for some time (Johnson 1997). The most common technique is the use of tree shelters, which are plastic structures developed to protect seedlings from browsing. The seedling grows within a tube until it is tall enough to be out of browse range. However, tree shelters are not useful in every case because they are species and site specific, may cause wind abrasion damage to seedlings, may not photo-degrade, and may not provide sufficient protection where deer browse intensity is highest (Johnson 1997). Tree guards are a similar product that is made of mesh; therefore, they do not affect the microclimate of the seedling. There is a range of products and materials that restorationists should consider. Seedling protection is effective in conjunction with herbicide treatments, weed control, and mowing to maximize survivorship of tree species (Sweeney et al. 2002). This technique is most appropriate in smaller projects where individual plants are monitored. Johnson

(1997) recommends that before implementation of a tree shelter scheme into a restoration plan, that species, site microclimate and nutrition, and the "spatial scale" of the project should be considered.

Conclusion

The forest management disciplines can contribute valuable insight and helpful advice for restoration of the deciduous forests of eastern North America. A complete deciduous forest restoration that restores function and species diversity includes strategies for regrowth of herbaceous and woody species, as well as their protection from herbivores, especially white-tailed deer.

Managers should consider how deer density can be controlled through habitat manipulation to reduce herbivory pressure and regeneration damage, rather than through game harvest alone. This is an opportunity for wildlife managers and restoration ecologists to work together to accomplish their objectives under one long-term plan. For example, one strategy might be to promote restoration of deciduous forest clear-cuts to reduce forest fragmentation. Large patches of forest promote re-colonization of plant species from adjacent populations and reduce the carrying capacity for white-tailed deer because of the reduction of preferred feeding habitat.

Many state hunting seasons are structured around small management areas. For example, Minnesota is broken up into 143 deer management units, which recognize that deer populations and habitat can vary greatly over large areas. This is an opportunity for restoration scientists to concentrate their efforts within these management units, and work closely with wildlife managers to keep deer densities at target levels that benefit local or regional forest restoration plans. Wildlife managers can use forest restoration as a tool for controlling populations.

Any restoration plan must consider the unique the ecological characteristics of a system, including plant-animal interaction and the resiliency of the degraded state. Creative scientists, land managers, and natural resource professionals can use creative methods to control deer population and restore ecological function and biodiversity to the deciduous forests of eastern North America.

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