



Deer density effects on vegetation in aspen forest understories over site productivity and stand age gradients

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ABSTRACT

Studies examining the interacting effects of ungulate herbivore pressure and site productivity on vegetation are mostly on grassland–grazing systems and have shown conflicting patterns. Here we examine the effects of deer density (>30 years differences in density between two landowners), site productivity (site index, SI) and stand age on subcanopy vegetation characteristics in 60 closed canopy, clear-cut origin *Populus tremuloides* dominated stands, Michigan, USA. Stand age effects were included because age varied among stands and can affect subcanopy vegetation patterns. Compared with fewer deer, stands with more deer had greater total forest floor vegetation mass, and its major components bracken fern (*Pteridium aquilinum*), sedge (mostly *Carex pensylvanica*) and trees/shrubs <0.25 m tall, but lower forb mass and lower forest floor vegetation species richness and diversity. Deer density and SI had strong interacting effects on total forest floor mass, forb mass, and species richness. Forb mass increased with SI, but only in stands with fewer deer, whilst total vegetation mass was greater in stands with more deer at lower SI and declined with SI more sharply than for stands with fewer deer. Species richness increased with SI but more so at lower than higher deer density. Deer density and age had interacting effects on mass of trees/shrubs <0.25 m tall and sedge. Compared with fewer deer, stands with more deer had greater sedge and tree/shrub mass, and sedge mass decreased and tree/shrub mass increased more sharply with age. In lower deer stands there was a dense subcanopy tree and shrub strata within and beyond the reach of deer 0.9–10 m tall whereas in higher deer stands this vegetation layer was nearly absent. We conclude that higher deer browse pressure in early successional *Populus* stands (1) strongly limits the recruitment of woody stems to larger (>0.9 m tall) size classes, which could affect long-term successional trajectories, and (2) diminishes forb density and species richness, especially at higher site productivity, but increases total forest floor vegetation mass (mostly bracken fern and sedge), especially at lower site productivity. Given associations of bracken fern and sedge with poorer and/or more open sites and assuming high palatability of forbs, this pattern may result from the combination of selective herbivory and higher light availability caused by limited recruitment of trees and shrubs to taller strata.

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1. Introduction

Ungulate browsing is a key driver of vegetation dynamics in ecosystems worldwide (Pastor and Naiman, 1992; Russell et al., 2001; Cote et al., 2004; Danell et al., 2006). In the temperate forested ecosystems of Eastern North America, white tailed deer (*Odocoileus virginianus*, hereafter called deer) are often the dominant ungulate herbivore. Since the mid-20th century, land use practices and wildlife management policies have resulted in deer populations that may be historically unprecedented in size (McCabe and McCabe, 1997). The browsing pressure from these

high deer populations are having a multitude of ecological and economic effects on forest ecosystems including: reduced growth and survival of browsed plants (Russell et al., 2001); reduction or local extirpation of highly browse sensitive species (Balgooyen and Waller, 1995; Parks et al., 1998; Rooney and Waller, 2003); decreased density of reproductive structures on browsed plants (Anderson, 1994; Tremblay et al., 2006); composition changes and decreased diversity of tree regeneration (Frelich and Lorimer, 1985; Horsley et al., 2003; Tremblay et al., 2006); and increases in non-preferred browse species (Horsley et al., 2003).

Studies to date have contributed strongly to our understanding of deer effects on vegetation, but generalizing results beyond particular study sites and treatments is a challenge and for at least two reasons. First, most studies have typically contrasted areas without deer (e.g. exclosures, uncolonized islands) and areas of high deer density (but see Tilgham, 1989; Horsley et al., 2003; Tremblay et al., 2006). However, vegetation responses are contin-

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uous, and not necessarily linear functions of deer browse pressure (Tremblay et al., 2006), and quantifying vegetation dynamics without deer, while useful to our basic understanding of deer effects, does little to inform management as “no deer” is an unlikely scenario. Second, studies have often been done at scales that are too small to explicitly consider variation in plant communities beyond harvest treatment effects (but see Alverson and Waller, 1997; Rooney, 2000; Takada et al., 2001; Didier and Porter, 2003), but plant communities vary spatially and their responses to a given browse pressure likely varies within and among plant communities (Weisberg et al., 2005; Wisdom et al., 2006; Matonis et al., submitted for publication). Several species and community characteristics may affect plant community responses to deer browse pressure, including: differences in evolutionary browse histories (Milchunas and Lauenroth, 1993); browse availability/density (Augustine et al., 1998); species composition, herbivore preference and browse response hierarchies (Tripler et al., 2005; Krueger et al., 2009), and; site productivity.

In a synthesis of 97 existing studies, Milchunas and Lauenroth (1993) reported greater grazing effects on plant community characteristics on higher than lower productivity sites. They suggested this pattern is consistent with low soil resources and frequent fires favoring greater allocation to roots and thus a lesser impact of a given amount of aboveground tissue removed on plant fitness. However, some subsequent studies have reported the opposite; greater negative herbivore impacts at lower than higher productivity (e.g. Bakker et al., 2006; Proulx and Mazumder, 1998). Moreover, regardless of the direction of response, results can be reconciled by opposing models of resource effects on plant tolerance to herbivory (Wise and Abrahamson, 2007). Whilst the recent development of models designed to reconcile apparently conflicting patterns (Wise and Abrahamson, 2007) and empirical tests of these models (e.g. Banta et al., 2010) represent significant contributions, generality regarding herbivore impacts at high vs. low resources is lacking.

Most studies on the interactive effects of site productivity and herbivores on plant communities have focused on grassland/grazing systems. Forests may react differently as they are characterized by strong competition for light. Limited light availability may exacerbate plant community responses to herbivory. This may occur because the impact of a given amount of tissue removal to a tree sapling's abilities to outgrow the reach of deer and attain canopy status, or of herb layer species ability to survive, is greater in low light than in high light (Baraza et al., 2010). The consequences of this are that in forest understories browse preferences can be more important than physiologically based difference in low-light performance (i.e. shade tolerance) in structuring competitive hierarchies among forest herbs and regenerating tree seedlings (Tripler et al., 2005; Krueger et al., 2009). It follows then that herbivore pressure could alter the rate and direction of forest succession.

Unlike grassland–grazing systems, soil resource effects on ungulate herbivore–plant community relations is lacking for forests. Like many grazed systems, forest vegetation from poorer sites may be more tolerant of ungulate herbivory due to adaptive syndromes favoring root allocation/sprouting capacity (Milchunas and Lauenroth, 1993). Consistent with this notion, plants from richer sites may be more sensitive to herbivory because, competition for light may intensify on richer sites favoring allocation to light-carbon harvesting and growth (Schreeg et al., 2005) and aboveground herbivory removes these tissues. However, due to the strong vertical stratification of vegetation and light competition in forests, predictions about community responses may not be so simple. For example, ungulate browse on superior understory competitors for light (i.e. subcanopy tree seedlings, saplings and shrubs) could alleviate competitive pressure on forest floor herbs and low shrubs and potentially increase their representation.

In this study we examine interactions between site productivity and management-related long-term differences in deer density on vegetation characteristics in the light limited understories of clear-cut origin, closed canopy aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.) dominated stands over a landscape where stand age and soil resource availability vary. Although our focus is on the interacting effects of deer and site productivity on vegetation, we also account for the impacts of aspen stand age on sub-canopy vegetation characteristics as stand age varied among our sites and could impact understory vegetation characteristics (Oliver and Larson, 1996).

Consistent with studies of deer effects on vegetation from similar systems (reviewed by Russell et al., 2001; Cote et al., 2004) we predict higher deer density will alter the composition and structure, and decrease the density, species richness and diversity of sub-canopy vegetation. Consistent with existing models of resource effects on herbivore–plant community relations (e.g. Milchunas and Lauenroth, 1993; Wise and Abrahamson, 2007), we predict that deer impacts on vegetation will be greater at higher site productivity. Furthermore we predict deer impacts on vegetation will increase with stand age given the potential accumulative nature of browse impacts and vegetation establishment in forest understories.

To examine these predictions we used 60 closed-canopy aspen stands dispersed within adjacent state-owned and hunt-club owned landscapes that have differed in deer density for more than 30 years. We used tree height–age relationships (i.e. site index) for co-dominant aspen trees as a proxy for site productivity which is likely driven largely by variation in soil water and nitrogen availability in the study region (Reich et al., 1997; Gerlach and Walters, submitted for publication). Mono-dominant aspen stands were used because, (1) aspen develops relatively uniform, closed canopy stands, and is generally able to vertically outgrow susceptibility to deer herbivory even in areas with high deer density (J. Randall, personal observation). Closed canopies result in relatively low and uniform light availability within and among study sites, and (2) aspen is broadly distributed over site moisture–nutrient gradients and is an early successional species that, barring harvest, is ultimately replaced by later successional species that establish as advanced regeneration in the aspen understory. Thus deer effects on the composition and density of forest tree regeneration in the understory could have large long-term effects on successional trajectories. In addition to site productivity and deer density, we quantified the effects of aspen stand age because understory vegetation characteristics can vary with stand age independent of deer browse pressure and resource availability (Sakai et al., 1985), and the ages of the potential pool of study stands in our study region necessitated sampling stands of different ages to achieve an adequate sample size.

2. Methods

2.1. Study area

Our study sites were on a 7317 ha private hunting club property (Mid Forest Lodge, MFL), and nearby (>1.6 km and <10 km) State of Michigan (State) lands in Roscommon, Gladwin, and Clare counties MI, USA. The study region's long-term climate averages include: annual precipitation, 730 mm; growing season (May–August) precipitation, 300 mm; annual snow fall, 192 cm; growing season length (days where the minimum temp is >0 °C), 126 days; and July mean temperature, 21 °C (NOAA National Virtual Data Systems). The region contains level to moderately undulating hills (0–18% slopes) with post-glacial geological features dominated by ice contact ridges and sandy outwash plains. Soils in the region

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