FACILITATION OF PLANT-PLANT INTERFERENCE BY HERBIVORY IN THE ALLEGHENY HARDWOOD FOREST, PENNSYLVANIA, USA: A VEGETATION MANAGEMENT PROBLEM

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SUMMARY

Advance seedlings are the primary source of regeneration in Prunus-Acer Allegheny hardwood stands in Pennsylvania, USA. Most stands lack adequate numbers of advance seedlings. Research conducted in the 1960s and 1970s showed that this was due to herbivory by white-tailed deer *(Odocoileus virginianus virginianus* (Boddart)) and plant-plant interference from ferns, gasses and sedges, and shade-tolerant hardwoods. Effects of deer density and forest cutting on vegetation development were evaluated on four 65-ha sites for 10 years in a large enclosure where deer were maintained at 0, 4, 8, 15, and 25 animals/km². At each site 10% of the-area was clearcut, 30% was thinned, and 60% remained uncut.

Deer density affected advance regeneration abundance, height, and species composition-through direct removal of seedlings and facilitation of plant-piant interference between the ferns, grasses and sedges, shade-tolerant hardwoods and seedlings of commercially desirable Allegheny hardwood species. Vegetation observed in uncut, thinned, and clearcut stands is the result of an interaction between herbivory and plant species response to light.

INTRODUCTION

Abundant advance regeneration before the Final overstory removal cut is required for successful establishment of new Prunus-*Acer* Allegheny hardwood stands in Pennsylvania, USA. Most stands lack adequate numbers of advance seedlings for regeneration. When desirable seedlings are present, they nearly always are black cherry *(Prunus serotina* Ehrh.)(1). Pennsylvania's forests have experienced high deer densities (up to 26 deer/km²) for the last 70 years (2). Changes in relative abundance, height, and species composition of vegetation in the forest understory have been observed during this period. In the 1960s, exclosure studies showed that herbivory by deer was a strong contributor to lack of advance regeneration establishment, though the deer density associated with failure of seedling establishment was not Dense understories of ferns *(Dennstaedria punctilobula (Michx.*) Moore, *Thelypteris noveboracensis L.),* grasses and sedges, and shade-tole hardwoods (American beech Fagus *grandifolia*

Ehrh., striped maple *Aces* L.) also interfere with advance regeneration establishment, though the conditions under which these understories developed were not well understood (3). In 1979, a study was initiated to determine the effects of deer density and forest cutting on forest vegetation development.

METHODS AND MATERIALS

The effects of deer density and forest cutting were evaluated on four 65-ha sites for 10 years in a large enclosure where deer were maintained at 4, 8, 15, and 25 animals/km² in 13 or 26-ha fenced areas. The effect of 0 deer/km² was measured on all exclosures inside each enclosure.. At each site, 10% of the area was clearcut, 30% was thinned, and 60% remained uncut. This established a forage level using timber harvests that were typical of those made in a 100-year rotation. Abundance and height of woody and herbaceous vegetation was recorded by species on a series of 0.0004-ha permanent sample plots just before and 1, 3, 5, and 10 growing seasons after cutting.

RESULTS AND DISCUSSION

Deer density affected abundance, height, and species composition of commercially desirable Allegheny hardwood species through both direct removal of seedlings and facilitation of plant-plant interference by ferns, grasses and sedges, and shade-tolerant hardwoods in all cutting treatments.

In uncut stands, both species richness and abundance of seedlings were lower at higher deer densities. At 25 deer/km², black cherry (low palatability, shade-intolerant), beech and striped maple (both browse-resistant, shade-tolerant) were the most abundant species. Ground cover of fern (unpalatable, intermediate shade-tolerant) was higher and that of *Rubus (Rubus allegheniensis* Porter, *Rubus occidentals* L.) (very palatable, intermediate shade-tolerant) was lower at 15 and 25 deer/km². Thus, herbivory by deer was responsible not only for the lack of diversity among small advance seedlings of desirable hardwoods, but also for increase in abundance of less palatable, browse-resistant, or shade-tolerant herbaceous and woody understory plants that interfere with establishment of advance seedlings.

In thinned stands, there was a strong relationship developed over, time between the abundance of Rub-us and the abundance or ferns. At higher deer densities, the abundance of *Rubus s-pp.* was lower and the abundance of ferns was higher. Ferns had a strong effect on abundance of black cherry and other commercially desirable hardwoods through interference with the availability of light (4). As fern cover increased, establishment of commercially desirable hardwood species decreased. Deer density also determined which tree species dominated thinned stands. Where shade-tolerant striped maple was present, thinning favored its dominance dyer less shade-tolerant species. In the absence of striped maple, deer density determined whether birches *(Benda alleghaniensis* Betula *lenia* L.) (intermediate palatability, intermediate shade-tolerant) (0-15 deer/km²) or black cherry (25 deer/km²) became the dominant

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In clearcuts, deer density determined species composition. At 25 deer/km², 15 to 37% of the area in individual clearcuts failed to develop tee species. Instead, these areas were dominated by ferns, and grasses and sedges Clow palatability, intermediate shade-tolerance). When tree seedlings were present, deer density determined the species. At 0, 4, and. 8 deer/km² pin cherry (Prunas *pensylvanica* L.) (very palatable, very shade-intolerant) became the tallest spccses shortly after cutting. Where large numbers of pin cherry were present, other shade-intolerant and intermediate shade-tolerant species died by age 10. Since Allegheny hardwood stands generally lack desirable shade-tolerant species such as sugar maple (Acer *saccharum* Marsh.) (palatable) and eastern hemlock *(Tsuga canadensis* L.) (very palatable) in the understory, loss of the less shade-tolerant species has serious implications for sustainability of the present overstory species composition. More diverse stands resulted where smaller numbers of pin cherry were present at the lower deer densities. At 15 and 25 deer/ 2, near monocultures of black cherry became established.

CONCLUSIONS

This study showed that deer density is a primary factor controlling the species composition of the next Allegheny hardwood forest in Pennsylvania, USA. This control is achieved directly by selective species removals and indirectly by facilitation of plants that interfere with desirable hardwood seedling establishment. The vegetation observed in the forest is not the result of herbivory alone, but the interaction of deer density and plant species response to light. Long-term herbivory in uncut stands has resulted in establishment of less palatable, browse-resistant or shade-tolerant Species. When stands are thinned, the shade-tolerant (striped maple, beech) and intermediate shade-tolerant (ferns, grasses and sedges, birches) species respond to the increased availability of light. Shade-intolerant species such as black cherry remain limited by light and die over time as shade from more tolerant species increases. Where interfering plants are not naturally abundant or have been removed with herbicide, black cherry usually is the only desirable species present. Thus, it is not surprising that near monocultures of black cherry are created by final overstory removal cuts. In stands with large numbers of pin cherry, lack of species that are desirable, palatable, and shade-tolerant (sugar maple, eastern hemlock) threatens sustainabiiity of forest cover because pin cherry *is* a short-lived species. Understanding how deer, site and environmental resources, and plant species interact to determine the development of vegetation is an important step in learning how to regulate the impact of deer.

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