EFFECTS OF DEER AND GARLIC MUSTARD ON NATIVE TREE SEEDLINGS

EFFECTS OF WHITE-TAILED DEER AND INVASIVE GARLIC MUSTARD ON NATIVE TREE SEEDLINGS IN AN URBAN FOREST

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LAY ABSTRACT

Reduced numbers of native tree saplings in urban forests have driven concerns that overabundant white-tailed deer populations and invasive plants are both suppressing the size and survival of native tree seedlings. In this study, I examined the effects of white-tailed deer and garlic mustard on transplanted seedlings of three native tree species: northern red oak, black cherry, and eastern hemlock. I found that deer browsing reduced seedling size but did not reduce survival. I found that browsing by deer is changing the species composition within McMaster Forest to favour browse tolerant tree species. Seedlings were not affected by garlic mustard removal, nor did the effects of deer depend on garlic mustard presence. These results have implications for management strategies in forests with high deer densities which should prioritize controlling the deer population in addition to invasive plants and should be tailored to conserve the most sensitive species.

ABSTRACT

An ongoing goal in forest ecology is to understand how animal populations and invasive plants affect forest communities. Reduced numbers of native tree saplings in urban forests have driven concerns that overabundant white-tailed deer (*Odocoileus virginianus*) populations and invasive plants are both suppressing the size and survival of native tree seedlings. Previous work has focused on the individual effects of either deer or invasive plants, but few studies have examined the combined effects of these two stressors. In this study, I examined the effects of white-tailed deer and garlic mustard (*Alliaria petiolata*) on transplanted seedlings of three native tree species: northern red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*). To test for their individual and combined effects on seedlings, I designed a factorial experiment where I manipulated the level of deer presence with exclosures and the level of garlic mustard presence by weeding. To measure the impacts on seedlings, I scored browse damage, tracked survival, and measured multiple size traits for each study species. I found that deer presence reduced seedling size but did not affect mortality within the short duration of the study. In addition, seedlings were not affected by garlic mustard removal, nor did the effects of deer depend on garlic mustard presence. While all species were impacted by deer, seedling browsing patterns varied among tree species. Moreover, I found that browsing by deer is changing the species composition within McMaster Forest to favour browse tolerant tree species. These results have implications for management strategies in forests with high deer densities which should prioritize controlling the deer population in addition to invasive plants and should be tailored to conserve the most sensitive species.

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INTRODUCTION

Temperate forests in North America have experienced declining plant diversity for decades (Robinson et al. 1994; Rooney and Dress 1997; Waller and Rooney 2004; Rooney et al. 2004; Rogers et al. 2008; Augspurger and Buck 2017). Land-use changes and increased nitrogen deposition have been identified as major contributors to this decline (Schulte et al. 2006; Bobbink et al. 2010) while climate change is predicted to drive large future changes in global biodiversity (Sala et al. 2000; Bellard et al. 2012). The projected climate change is also expected to exacerbate the negative effects of exotic species (Dukes et al. 2009), which continue to invade and reduce plant diversity in forests worldwide (Vilà et al. 2011). In eastern hardwood forests of the United States, the once dominant American chestnut (*Castanea dentata* (Marsh.) Borkh.) tree was effectively eliminated from forests by the introduced fungal pathogen *Cryphonectria parasitica* (Murr.) Barr. Currently, the emerald ash borer (*Agrilus planipennis* Fairmaire, 1888), an invasive beetle endemic to Asia, is causing population-wide deaths of ash (*Fraxinus* L. spp.) tree species in the United States and Canada. While the invasion of exotic species presents a clear threat to biodiversity, native herbivores can also pose a major chronic threat. In temperate forests, white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) are a keystone species (Waller and Alverson 1997) with populations having large and broad impacts on forest communities (Russell et al. 2001; Rooney 2001; Rooney and Waller 2003; Côté et al. 2004). In particular, white-tailed deer densities exceeding 10 deer/km^2 have been implicated as direct and indirect causes of declines in plant diversity (Harlow and Downing 1970; Rooney and Waller 2003).

In addition to white-tailed deer, temperate forests in North America are often threatened by the invasion of exotic plants. One particularly problematic invader is garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande) which regularly invades stable, mature forest interiors aided by its ability to grow across a wide range of abiotic resources. This generalist life strategy means garlic mustard invasion threatens many plant communities, from northern Carolinian forests in Ontario, Canada, to southern hardwood forests of Tennessee, USA, and pacific northwest plant communities in Alaska, British Columbia, and Oregon (Cavers et al. 1979; Welk et al. 2002; Heutte et al. 2003). Garlic mustard invasion drives declines in plant diversity and suppresses the growth of native tree seedlings (Stinson et al. 2006; Stinson et al. 2007). The suppression of tree seedlings can have profound effects on forests as native trees are essentially keystone species that support native biodiversity within forest communities.

Deer and garlic mustard both have profound individual effects on native plants and because they often inhabit forests concurrently, there are potential combined effects which are poorly understood. Combined effects of deer and garlic mustard are potentially non-additive and may suppress the recruitment of native forest trees.

Effects of high white-tailed deer densities in forest communities

White-tailed deer have dramatically increased in abundance since European settlement in the 1700s, and now reach densities 2 to 10 times higher than pre-European settlement deer density estimates of 3.1 to 4.3 deer/km^2 (Alverson et al. 1988; McCabe and McCabe 1997; Diefenbach et al. 1997; Russell et al. 2001). Following European settlement, bounty hunting drove the reduction and extirpation of predators like the grey wolf (*Canis lupus* Linnaeus, 1758) which relieved deer of mortality pressure. Agricultural crops provided abundant food sources for deer. Logging created younger aged forests that provided more food for deer than non-logged old-growth forests and increased the amount of edge habitat, the preferred habitat of deer, due to forest fragmentation (Alverson et al. 1988). Later, legislation was implemented to protect deer from exploitative market hunting. The combination of these factors has allowed deer populations to grow rapidly and increase their geographic range across Canada and the United States (Gill 1990).

Currently, high deer densities continue to impact forests and their inhabitants both directly and indirectly (Rooney 2001; Rooney and Waller 2003; Côté et al. 2004).

Deer primarily feed on woody plants, forbs, and grasses (Atwood 1941; Smith 1991), so plants in these groups are susceptible to the direct effects of white-tailed deer browsing. Browsing is a kind of herbivory characterized by the consumption of soft shoots, leaves, and fruits of plants by herbivores. Tree seedlings are often browsed at their terminal meristem causing an immediate reduction in aboveground biomass and height. The response to this tissue loss is dependent on the species' tolerance to browsing (Augustine and McNaughton 1998). Browse tolerance is determined by the ability of a species to regrow tissue or change morphologically to maintain fitness. In many browse tolerant species, the loss of the terminal meristem often induces compensatory growth in the form of many lateral stems and as such, stem densities are often greater for browsed tree seedlings than non-browsed seedlings (Marshall et al. 1955; Switzenberg et al. 1955; Tierson et al. 1966; Jacobs 1969; Throop and Fay 1999). Intolerant species, such as slow-growing conifers, cannot quickly regrow lost tissue so they remain stunted and can eventually die due to the cumulative effects of repeated browsing. Exclosure studies that measure elements of plant fitness demonstrate that deer browsing reduces plant heights (Ross et al. 1970; Anderson 1994; Alverson and Waller 1997; Stange and Shea 1998), tree seedling survival (Jacobs 1969; Stange and Shea 1998), and reproduction of herbaceous plants (Augustine and Frelich 1998; Augustine et al. 1998).

The reduced growth and survival of tree seedlings under high deer densities can affect the ability of a tree species' population to replace and maintain itself. High deer densities can create unsustainable population structures by intensely browsing the smallest size classes (Frelich and Lorimer 1985). As mid-size classes are not replaced, a species can eventually be eliminated from a stand. Numerous exclosure experiments have similarly demonstrated that for many species, the seedling and sapling size classes are underrepresented in high deer density areas in various forest types (Stoeckler et al. 1957; Harlow and Downing 1970; Anderson and Loucks 1979; Marquis 1981; Frelich and Lorimer 1985; Alverson et al. 1988; Trumbull et al. 1989; Healy 1997). This underrepresentation reflects increased mortality among size-classes susceptible to deer herbivory and is evidence that deer can suppress the local regeneration of certain tree species. The magnitude of regeneration suppression depends on the deer density and subsequently the browsing intensity. In mixed coniferous-deciduous forests, as browsing intensity increases, the density of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and red oak (*Quercus rubra* L.) seedlings decreases (Waller et al. 1996; Rooney and Waller 2003). In contrast, deer browsing of herbaceous plants can increase the proportion of individuals in small size classes by more frequently browsing larger plants (Augustine and Frelich 1998; Augustine et al. 1998).

Deer are selective when browsing vegetation and find some tree species more palatable than others (Hill 1946; Healy 1971; Telfer 1972). Plant species that are avoided by browsing deer are considered unpalatable as they use allelochemicals to defend from herbivory (Augustine and McNaughton 1998). Under high deer densities, this selectivity can alter the trajectory of succession to favour browse tolerant or unpalatable species. In some forests, selective deer browsing has caused differences in community composition between the overstory and understory, such that the understory exhibits a higher proportion of browse tolerant tree seedlings and unpalatable species than the overstory (Long et al. 2007). Over time, preferred or browse intolerant tree species may be eliminated from the overstory community as they die and are not recruited into the canopy. Alternatively, palatable species can persist if they are also browse tolerant (Tilghman 1989). As deer browse preferred herb species, the understory community composition changes to favour unpalatable grasses, ferns, and sedges (Rooney and Waller 2003). The deer-mediated increase in relative abundance of ferns further limits establishment of tree seedlings as seedling growth and survival are reduced in areas with abundant ferns (Horsley and Marquis 1983). Fern cover differentially suppresses natural recruitment of tree seedlings by altering microenvironmental variables like soil exposure and light levels (George and Bazzaz 1999). The shift in community composition is often accompanied by decreased species diversity and species richness of both tree seedlings and herbaceous plants (Tilghman 1989; Healy 1997; Rooney and Waller 2003).

High deer densities indirectly affect other native herbivores by limiting their food sources. Because plant diversity is frequently positively correlated with insect species diversity, a reduction in plant diversity is expected to cause a decrease in insect diversity (Murdoch et al. 1972; Haddad et al. 2001). The insect species most vulnerable to elimination are specialist pollinators and monophagous herbivores, as they require specific plant species for food and cannot simply switch to feeding on another plant species (Blakley and Dingle 1978). Insect species diversity and richness could also decline as the relative abundance of ferns and grasses increases (Stewart 2001). As intensive browsing reduces understory vegetative cover in some forests, the light level and temperature increases and soil moisture decreases. This change in microclimate decreases gastropod density as they are sensitive to changes in moisture (Suominen 1999). The loss of vegetative cover may also cause populations of small mammals to decline as avian predation increases, while species that use bare ground habitat may benefit (Flowerdrew and Ellwood 2001; Stewart 2001). Additionally, shrub-nesting and migrant birds are negatively affected by reduced vertical complexity within forests (deCalesta 1994; McShea and Rappole 2000). White-tailed deer disturb soil and disperse exotic seeds which both contribute to the spread of invasive plant species (Nuzzo 1999, Myers et al. 2004, Bartuszevige and Endress 2008).

Effects of invasive garlic mustard in forest communities

The invasive plant garlic mustard is rapidly expanding its range westward across North America and has already established populations in 36 states and five provinces in the United States and Canada respectively (USDA NRCS 2018a). Native to western Eurasia, garlic mustard was introduced by early colonists in the mid-1800s and was found naturalized on Long Island, New York in 1868. Currently, it is encroaching through forest understories aided by its phenotypic plasticity to heterogeneous light levels, as garlic mustard produces both sun and shade leaves which differ in rates of photosynthesis and chlorophyll concentration (Myers et al. 2005).

Garlic mustard has a biennial life cycle, with seedlings emerging in the spring, then forming overwintering rosettes in the fall, which then bolt in the spring of their second year and finally reproduce before dying in summer. While native plants are still dormant in early spring, bolting garlic mustard plants maximize their photosynthetic rate (Myers and Anderson 2003). This early phenology may allow garlic mustard to acquire soil and light resources before native plants, giving it a competitive advantage. Once bolted, the plant produces many flowers that are both adapted for generalist pollinators and capable of self-pollination. This flexibility ensures pollination and reproduction within a population. Garlic mustard reproduces via seeds which are produced in numerous siliques. An individual plant can produce 350 – 7900 seeds, which can be dispersed by humans, birds, small mammals, and white tailed-deer, but most often fall to the ground near the reproducing plant (Baskin and Baskin 1992). As a population, seed production can reach as high as 107, 000 seeds per m^2 (Cavers et al. 1979). Additionally, the seeds produced can remain viable in the soil seed bank for 10 years if they do not germinate in the first year. This high reproductive output coupled with a substantial seedbank allows garlic mustard populations to spread rapidly and persist over time.

The success of garlic mustard can be partly attributed to its release from herbivore predation. In its native range in Europe, garlic mustard is consumed by at least 69 insect species, none of which inhabit North America (Szentesi 1991). In addition to the absence of natural enemies, native herbivores like white-tailed deer avoid consuming garlic mustard, making herbivory of negligible impact to garlic mustard. Garlic mustard is unpalatable to white-tailed deer due to allelochemicals produced by the plant which deter herbivory. These compounds include glycosides, flavonoids, and glucosinolates (Daxenbichler et al. 1991, Haribal and Renwick 2001, Cipollini 2002). Garlic mustard also produces allelochemicals allyl isothiocyanate and benzyl isothiocyanate which are toxic to mycorrhizal fungi (Vaughn and Berhow 1999, Mayton et al. 1996). Allelochemical production is a novel weapon only in garlic mustard's invaded range as these allelochemicals do not affect mycorrhizal fungi native to Eurasia (Callaway et al. 2008). These traits collectively have contributed to the success of garlic mustard as an invader.

The continuing invasion of garlic mustard has profound effects on North American forests. Forest plant diversity has been shown to decline as abundance of garlic mustard increases, with tree seedlings most negatively affected among plant functional groups (Stinson et al. 2007). This reduction in plant diversity is expected to also reduce insect diversity (Murdoch et al. 1972, Haddad et al. 2001). Garlic mustard suppresses the growth of tree seedlings by disrupting the underground relationship between seedlings and arbuscular mycorrhizal fungi. These fungi normally help acquire nutrients from the soil for the seedling as part of a mutualistic relationship, but garlic mustard inhibits the colonization of these fungi on plants with anti-fungal allelochemicals (Stinson et al. 2006). Garlic mustard can impact forest community composition by suppressing plants which are highly dependent on arbuscular mycorrhizal fungi for obtaining nutrients, like tree seedlings, while favouring the survival of plants that are less dependent on arbuscular mycorrhizal fungi (Stinson et al. 2006).

Combined effects of white-tailed deer and garlic mustard

Garlic mustard has invaded much of the white-tailed deer range and so they often coexist within forests. Though there have been many studies on the effects of garlic mustard and deer individually (Rodgers et al. 2008; Habeck and Schultz 2015), relatively few studies have sought to determine whether the effects of one species depend on the presence of the other. Studies have either focused on their effects on herbaceous plants (Kalisz et al. 2014; Christopher et al. 2014; Dávalos et al. 2015) or have investigated invasive plants other than garlic mustard, like Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus) (Aronson and Handel 2011; Christopher et al. 2014; Johnson et al. 2015). Kalisz et al. (2014) found that overabundant deer populations facilitate the invasion success and population growth rate of garlic mustard, while garlic mustard exhibits a negative population growth rate in areas where deer are excluded. Conversely, the native herbaceous plant *Trillium grandiflorum* ((Michx.) Salisb.) experiences positive population growth where deer are excluded and negative population growth where deer regularly browse the plant. These results suggest that as deer browse native plants and avoid browsing garlic mustard, they may reduce the ability of native plant communities to compete with and resist invasion by exotic plants (Levins and Culver 1971; Augustine and

McNaughton 1998; Wardle et al. 2001; Vázquez 2002; Côté et al. 2004; Agrawal et al. 2007; Knight et al. 2009). Aronson and Handel (2011) found that the individual effects of deer exclusion and Japanese stiltgrass removal both increased the survival and height growth of tree seedlings, though the effects did not interact. However, Johnson et al (2015) observed a significant interaction between deer exclusion and Japanese stiltgrass removal where tree seedlings had greater above-ground biomass in plots with the invader removed and had the greatest biomass in plots with the invader removed and deer excluded. Because these studies examined two different suites of tree species, their differing results demonstrate how interactive effects may or may not be observed depending on the response species. Waller and Maas (2013) implemented a 2 × 2 experimental design where plots either allowed or excluded deer and either allowed or removed garlic mustard. They found that garlic mustard inhibited the growth of three native plants significantly more where deer were excluded as opposed to where deer access was allowed, suggesting that garlic mustard's competitive effects are magnified in areas where deer do not suppress native plant growth. Additionally, they found that garlic mustard enhanced growth in one species and suggested that garlic mustard could have visually or olfactorily hidden the plant from browsing deer. The researchers also found that the effects of removing either or both deer and garlic mustard were highly variable among native species and their traits.

Individual effects of deer herbivory and garlic mustard invasion are well documented, yet their combined effects are poorly understood, and non-additive effects are still unclear as they have only been observed in a single study (Waller and Maas 2013). The study reported that combined effects are highly variable among plant functional groups (Waller and Maas 2013). The few studies that have examined the combined effects of deer and garlic mustard have focused on their effects on herbaceous plants (Kalisz et al. 2014; Christopher et al. 2014; Dávalos et al. 2015), but no other studies have investigated how tree species with various levels of palatability and browse tolerance respond differently to deer and garlic mustard. Studying the combined effects of deer and garlic mustard on northern red oak, black cherry (*Prunus serotina* Ehrh.), and eastern hemlock is important because these are dominant species of northern Carolinian forests and they differ in their specific ecology.

Outline of this study

In this study I examine the individual and combined effects of white-tailed deer and garlic mustard on seedlings of three native tree species: northern red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*). These species were selected to represent a range of browse preference and plant tolerance. Seedlings were transplanted within a 2 × 2 factorial design where experimental plots differed in white-tailed deer and garlic mustard presence. I asked 1) To what extent are deer and garlic mustard suppressing the size of native tree seedlings? 2) How are red oak, black cherry, and eastern hemlock affected differently by deer and garlic mustard? 3) Do deer and garlic mustard interact synergistically to suppress size?

METHODS AND MATERIALS

Study site

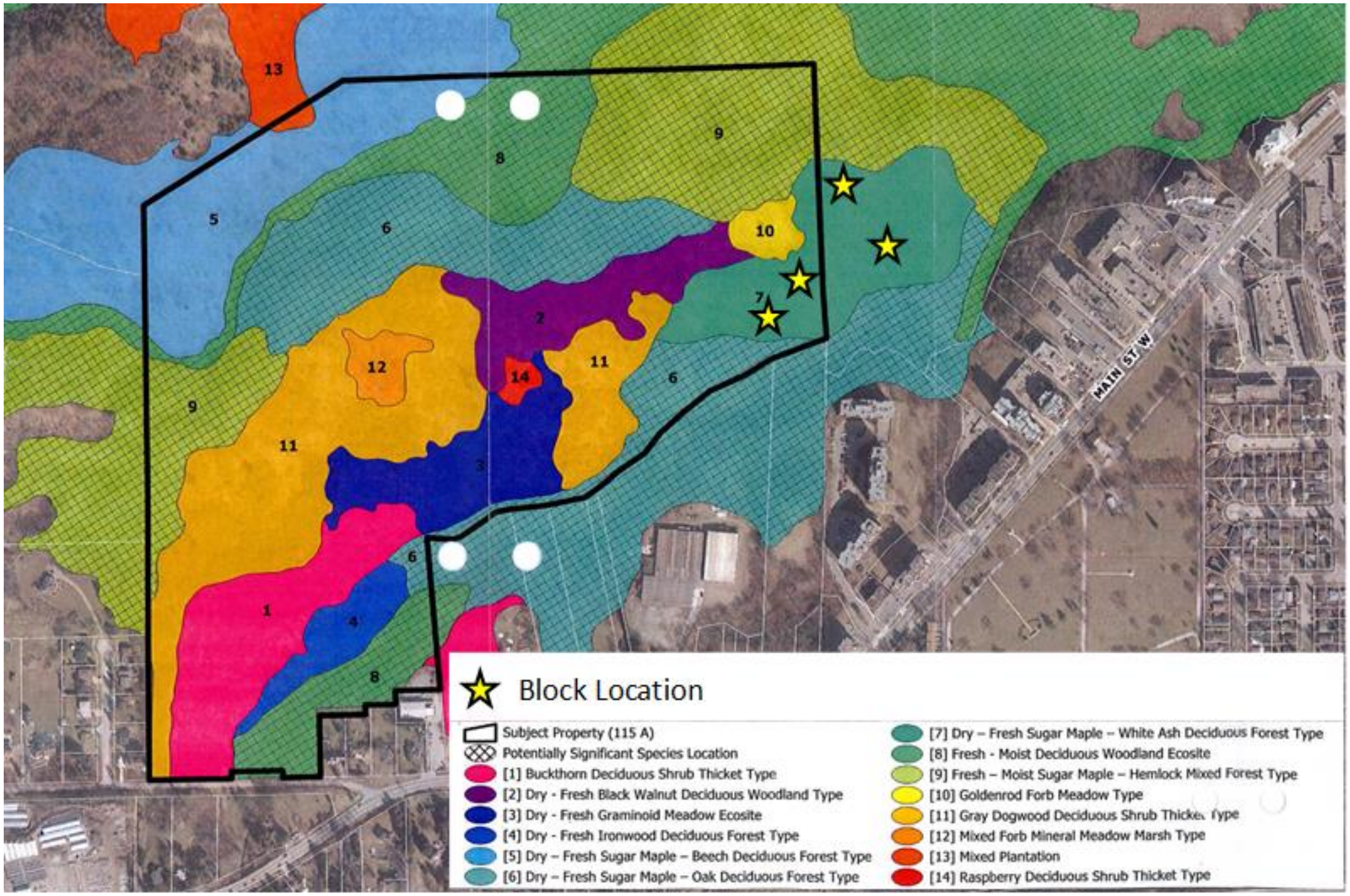
My study was conducted in McMaster Forest, a 48-hectare natural area located in Ancaster, Ontario, Canada (43°15'07.0"N, 79°56'50.0"W). The mean January temperature of the area is -4.7°C and the mean July temperature is 22.0°C. The mean annual precipitation is 897.1 mm. McMaster Forest is bordered by densely populated urban neighborhoods as well as protected natural areas Dundas Valley Conservation Area, Tiffany Falls Conservation Area, and Cootes Paradise Marsh. Much of the land was previously used as an agricultural farm until 1964 when the property was purchased by McMaster University and left to regenerate naturally (van de Hoef 2013). The land now comprises a mosaic of habitat types. Although deer densities have not been assessed within McMaster Forest, the adjacent Dundas Valley and Tiffany Falls Conservation Areas support densities of 30 deer/km^2 and 36 deer/km^2 respectively as hunting is not permitted within city limits. These densities well exceed the land's carrying capacity of 10 deer/km^2 as defined by the Ontario Ministry of Natural Resources (HCA 2013), and a similarly high density is expected for McMaster Forest which is situated between the two conservation areas. Garlic mustard is abundant within McMaster Forest and anecdotal evidence suggests the local population is growing and spreading.

The study site within McMaster Forest is located in a sugar maple – white ash deciduous forest type with dry – fresh soil and relatively flat topography as classified by the Hamilton Conservation Authority (HCA 2012, Figure 1). The dominant tree species at the study site are sugar maple, American beech, white ash, and eastern hemlock and the understory is dominated by garlic mustard. The study site is open to the public and accessible by a hiking trail, but many signs encourage users to stay on the trail and all study plots were positioned at a minimum of 25 m from the trail to prevent human disturbance. Plots were selected to encompass an abundance of garlic mustard, which ranged from 22% to 78% cover among subplots.

Study species

I chose three native tree species that represent a range of palatability and browse tolerance. Northern red oak is highly preferred by deer (Telfer 1972; Wakeland and Swihart 2009) and is moderately browse tolerant though regeneration is often limited where deer densities are high (Strole and Anderson 1992; Healy 1997; Rooney and Waller 2003). Black cherry is moderately preferred (Healy 1971; Strole and Anderson 1992; Wakeland and Swihart 2009) and is browse tolerant as seedlings can survive under intense browsing pressure (Marquis 1983; Tilghman 1989). Eastern hemlock is avoided by deer in summer but is highly preferred in winter when leaves of deciduous trees are not available (Peterson 1955; Dahlberg and Guettinger 1956; Beals et al. 1960; Moore and Johnson 1967). Eastern hemlock seedlings are browse intolerant as they are slow-growing and are unable to quickly replace lost tissue following browse damage (Curtis 1959; Anderson and Loucks 1979). High deer densities have

Figure 1. An aerial photograph of McMaster Forest overlaid with ecological land classifications (HCA 2012). The McMaster University property boundary is marked by a black line. The locations of the 4 blocks are marked by yellow stars.



caused eastern hemlock regeneration failure at a regional scale (Anderson and Loucks 1979, Frelich and Lorimer 1985, Rooney et al. 2000). In McMaster Forest, eastern hemlock exhibits a unimodal diameter distribution, where seedlings and saplings <6cm in diameter at breast height (DBH) are nearly absent (Munoz 2016). This distribution is typical of a declining population because there is an inadequate number of saplings to eventually replace the mid-sized trees.

Treatments and experimental design

To assess the individual and combined effects of white-tailed deer herbivory and the presence of garlic mustard on the growth and survival of native tree seedlings, I designed a factorial experiment with two **factors**: **deer presence** had two *levels*, *fenced* with deer excluded by a 2.4 m high fence, or *open* with no fence present; and **garlic mustard** had two levels, with the extant garlic mustard population either *present* or *removed* by hand weeding. There were four blocks, corresponding to different sites in the forest, each with the four treatment combinations: deer are excluded and garlic mustard is present, deer are allowed and garlic mustard is removed, deer are excluded and garlic mustard is removed, and a control treatment where deer are allowed and garlic mustard is present.

At each of four sites within the forest, two 14 × 14 m plots were established. Plots were paired within their respective areas so that plot pairs are considered blocks and that each treatment is equally represented in each block. One plot from each block was randomly selected to have a fence built around the perimeter to exclude deer from browsing. In each plot, half of the area, called a subplot, was randomly selected to have garlic mustard removed (Figure 2), while in the other subplot garlic mustard was left undisturbed. Each subplot was set up as a grid with walking paths defined by rope to minimize disturbance to the subplot when planting and measuring. To create a randomized complete block design, seedlings were randomly assigned a cell within the grid and were planted in a staggered array (Figure 3). This design provided 48 replicate seedlings of each species for each treatment across all four blocks. The experiment included 2 deer treatments × 2 garlic mustard treatments × 4 blocks × 3 species × 12 seedlings per species for a total of 576 tree seedlings monitored throughout the experiment.

Fence Construction, weeding, and seedling information

In May and June 2017, four fences were constructed using chain link fastened to steel posts. The steel posts were 3.6 m tall and were driven 1.2 m deep into the ground using a post pounder from a ladder. Studded T-posts were used as line posts and round posts were used as corner posts so that the chain link could be properly fastened using standard chain link tension bands and tension bars. Chain link rolls were stretched from corner to corner using a fence stretcher bar and winch. The chain link was then fastened to each corner post while still under tension from the winch and was fastened to line posts using metal fence ties. Rolls of 1.2 × 15.2 m chain link were installed one at a time, completing the bottom half of the fence first before installing the upper half of the fence from a ladder, making the fence total 2.4 m high. These two halves of chain

Figure 2. A diagram showing the experimental design and plot layout. Each of 4 blocks contain a fenced plot and an open plot. Each plot contains 2 subplots where garlic mustard is either *present* (light grey) or *removed* (white).

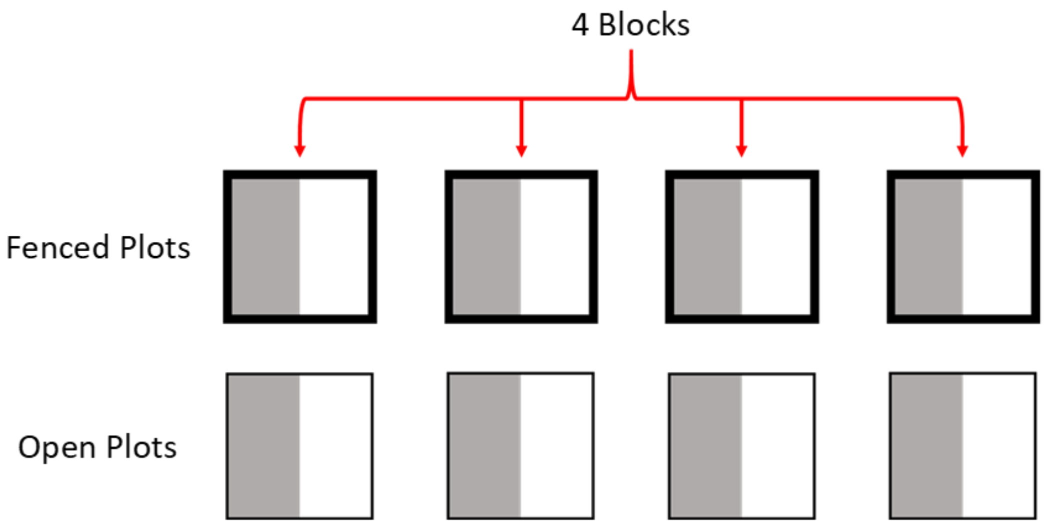
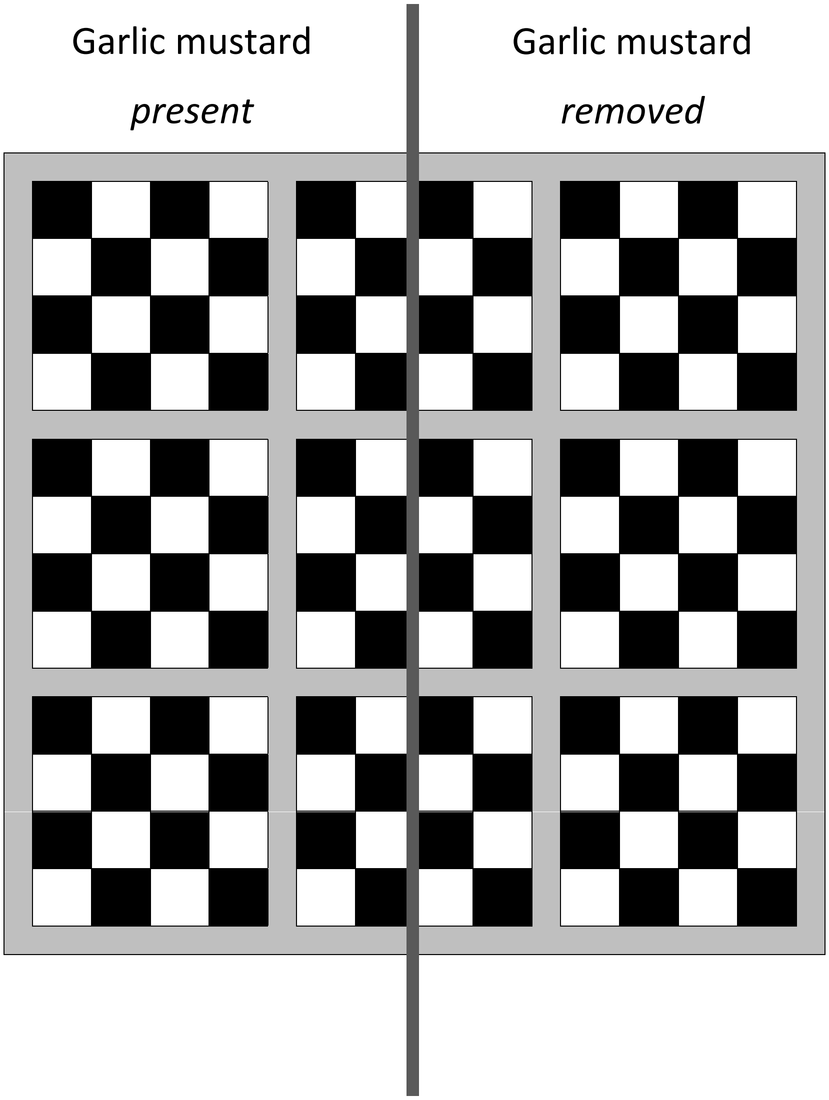


Figure 3. A diagram of a 14 m^2 plot showing 1 m^2 planting cells where seedlings were planted (white squares), 1 m^2 cells where seedlings were not planted (black squares), 0.5 m wide walking paths (light grey), and a line dividing the two garlic mustard treatment subplots (dark grey). In each subplot, 12 seedlings of each study species were randomly assigned and planted within a planting cell.



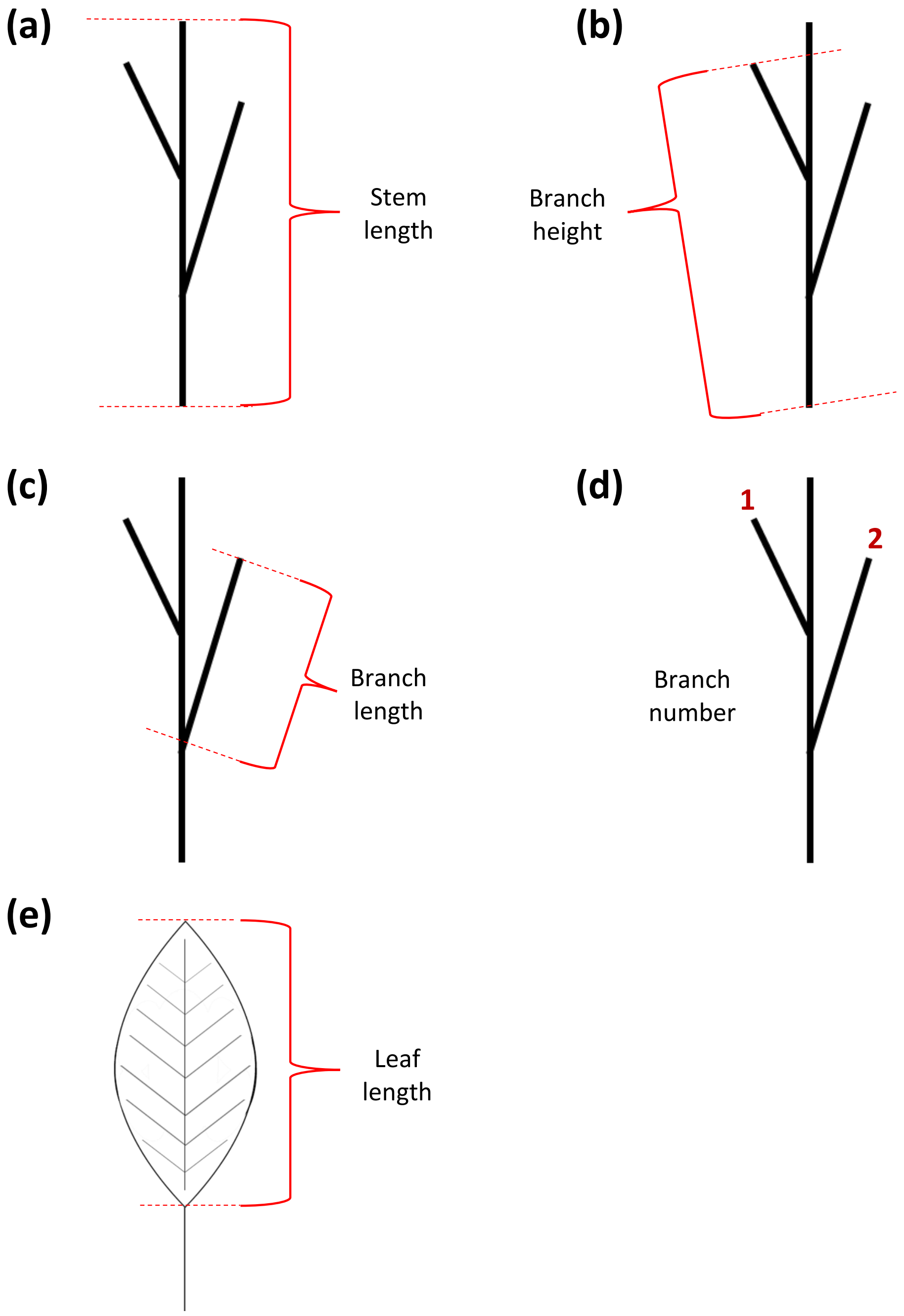
link were bound together with metal wire twist ties. Eight small holes were cut along the bottom perimeter of each fence to allow access to small mammals like the eastern cottontail (*Sylvilagus floridanus* (J. A. Allen, 1890)) and eastern grey squirrel (*Sciurus carolinensis* Gmelin, 1788). Once fence construction was complete, garlic mustard plants, both bolted and rosettes, were removed in June 2017 and again in May 2018. Plants were pulled from the base to remove the roots and were disposed of in a pile then burned.

Seedlings of northern red oak, black cherry, and eastern hemlock were obtained from St. Williams Nursery (St. Williams, ON). Red oak seedlings were two-year-old bare-root transplants that were 30-80 cm in height. Black cherry seedlings were one-year-old bare-root transplants and were 15-50 cm in height. Eastern hemlock seedlings were one-year-old plugs that contained minimal potting soil and were 10-25 cm in height. Seedlings were stored in cold storage, so no buds were open prior to planting in June 2017. During and following the planting of the seedlings, each seedling was watered twice a day for 2 weeks.

Response and environmental measurements

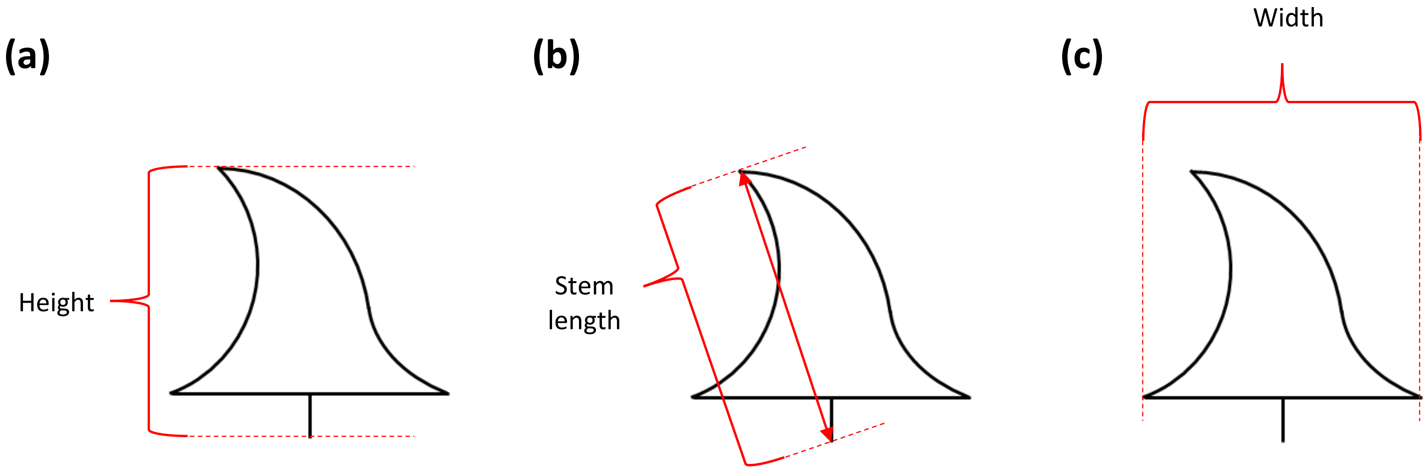
For all species, deer browse was scored as either *absent* or *present* if any part of the seedling was browsed. Survival was scored as either *alive* or *dead* if the individual had no visible living tissue, or no needles in the case of eastern hemlock seedlings. For both red oak and black cherry seedlings, size trait measurements were taken for stem length, branch height, length of the longest branch, length of the longest leaf, and the number of branches (Figure 4).

Figure 4. Size trait measures for red oak and black cherry seedlings: (a) stem length, (b) branch height, (c) branch length, (d) branch number, and (e) leaf length.



Stem length was measured as the straight distance from where the stem meets the ground to the tip of the main stem. Branch height was measured as the straight distance from where the stem meets the ground to the tip of the highest branch. The length of the longest primary branch was measured from where the branch joins the main stem to the tip of the branch. The length of longest leaf was measured from the base of the leaf blade to the tip of the point, along the surface of the midrib. Petioles were not included in this measurement. Leaves that have been subject to herbivory were measured from the base of the leaf blade to the end of the midrib. The number of branches was counted for each seedling, but first counts were taken incorrectly and so the number of branches was excluded from analyses. In addition, a measure called “highest point” was calculated as the larger value of either stem length or branch height. This measurement was calculated to control for confusing main stems for branches and vice versa on “Y“ shaped seedlings where the main stem is ambiguous. Main stems of red oak seedlings were often ambiguous and could not be distinguished from branches, and for many seedlings the identified main stem or branch remained dormant and did not grow while other size traits of the seedling did. For this reason, the stem length and branch height measures of red oak seedlings were not analyzed, and the highest point measure was used to capture the actual growth of the seedling. For eastern hemlock seedlings, size trait measurements were taken for stem length, height, and width (Figure 5). Height was measured as the absolute vertical height of the seedling aboveground and width was measured as the

Figure 5. Size trait measures for eastern hemlock seedlings: (a) height, (b) stem length, (c) width. For eastern hemlock seedlings, the tip of the apical meristem curves at the top.



widest width of the seedling. Stem length was the most biologically relevant way of measuring the size of eastern hemlock seedlings. Because the tip of the main stem curves at the top of an eastern hemlock seedling, the stem length measurement is closer than the vertical height measurement in estimating the actual length of the stem. All size traits were measured in mid-July 2017 and again in late September 2017, with eastern hemlock seedlings measured again in mid-April 2018. A haphazard sample of 20 red oak and 20 black cherry seedlings were remeasured in April 2018, and a direct in-field comparison to September measures showed that their size measures were unchanged. The size measures of the haphazard sample were not recorded, and remeasuring red oak and black cherry seedlings was delayed until September 2018 after another growing season. For red oak and black cherry seedlings, results reflect a change over a 2.5-month period while results from analyses of eastern hemlock seedlings reflect changes over a 2.5-month period and a 9-month period.

In June 2017, single observer estimated the initial percent cover of garlic mustard within each 4 × 4 m section of each treatment subplot prior to planting the seedlings and removing garlic mustard. The estimates included both adult plants and first year rosettes of garlic mustard. The June percent cover of garlic mustard was included as a covariate in all analyses to control for differences in initial cover between treatment subplots.

In August 2017, eight eastern hemlock seedlings were dug up by a human vandal and were replanted outside of their experimental plot. Two of the eastern hemlock seedlings were never recovered and were excluded from all analyses. Six of the removed eastern hemlock seedlings were recovered and replanted within their experimental plot but were nonetheless excluded from size trait analyses. Additionally, one eastern hemlock seedling that was pulled out of the ground by deer and six seedlings that died before September were excluded from size trait analyses. One eastern hemlock seedling died in an open plot before September but was never browsed and was excluded from browse analyses. Two red oak seedlings were accidentally damaged during measuring and were excluded from size trait analyses. Two black cherry seedlings were excluded from the branch length analysis because they did not have any branches.

One eastern hemlock seedling was browsed and reduced by 10 cm before September and was excluded as an outlier. One red oak seedling was excluded as an outlier because it grew 24.1 cm in height, much more than any other seedling.

Five eastern hemlock seedlings were pulled out of the ground by deer between September and April, potentially because the plugs were easy to pull out as they had not set many roots outside of the plug. These seedlings were excluded from April size trait analyses. A deer breached one exclosure in March 2018 and damaged seven eastern hemlock seedlings which were subsequently excluded from April size trait analyses as well.

Seedlings were also excluded if they exhibited a biologically implausible response, indicating incorrect measurements or mistakes when recording data.

One eastern hemlock seedling from the September analysis of stem length and one seedling from the September analysis of width were excluded on these grounds. Another eastern hemlock seedling was excluded from both September and April width analyses as the initial July width measurement was suspected as incorrect. Three red oak seedlings were excluded from the branch length analysis as the measurements were incorrect. Analysis with and without these individuals (not shown) demonstrated that excluding these seedlings did not affect the results.

On two separate occasions, exclosures were damaged by fallen trees during a windstorm. The fences were repaired within 24 hours and no evidence of deer browse within the exclosures was observed.

Data analysis

All analyses were performed using R (v3.4.3, The R Foundation for Statistical Computing). Each species was analyzed separately. Using the “Anova” function in the R package “car” (Fox and Weisberg 2011), a type III ANOVA was performed on the June percent cover of garlic mustard to test for differences in cover between blocks and treatment levels and all interactions. To examine the individual and combined effects of deer and garlic mustard, a logistic regression was performed on survival and an analysis of covariance was used to compare differences in size measures of seedlings across treatments. Additionally, to assess the impact of garlic mustard on deer browsing, a logistic regression was performed on the deer browse score of seedlings in open plots. To control for differences in starting size, the initial July 2017 measurements and the initial June percent cover of garlic mustard were used as covariates in all analyses. Residuals of all the size measures were normally distributed with homoscedastic variance, so no transformations were performed on the data.

Linear mixed-effects models were constructed using the “lme” function in the R package “nlme” (Pinheiro et al. 2017). A linear mixed model ANCOVA was performed on each size trait, using subplot nested within block as a random factor to control for unmeasured environmental differences between areas. The ANCOVA included deer presence and garlic mustard presence as main effects, and deer × garlic mustard as an interaction to determine if the effects of one species depends on the other. The ANCOVA used the restricted maximum likelihood method of estimation. The logistic regression and ANCOVA results were calculated using Wald’s chi squared test through the “summary” function in R (R Core Team 2017). For logistic regression models, goodness-of-fit was calculated as the McFadden pseudo-R^2 using the “pR2” function in the R package “pscl” (Zeileis et al. 2008). Goodness-of-fit was calculated for mixed-effects models using the “r.squaredGLMM” function in the R package “MuMIn” (Barton 2018) and was reported as the marginal R^2 which is the proportion of variance explained by the fixed effects only (Nakagawa and Shielzeth 2013). The absolute growth increment of a seedling was calculated as the final size minus initial size.

For both the stem length and width of eastern hemlock seedlings, the plots of standardized residuals showed a slightly curved trend. To investigate if a significant curve was present, quadratic terms were added to each linear model, but these terms were not significant and were therefor not included in the model.

RESULTS

Garlic mustard

The initial percent cover of garlic mustard was not significantly different between removed and present garlic mustard treatments (43.85% vs 43.92%, $F_{1,128} = 0.66$, $p = 0.42$), between fenced and open plots (37.1% vs 50.7%, $F_{1,128} = 0.25$, $p = 0.62$), or between blocks (from 24.9% in Block 2 to 63.3% in Block 4, $F_{1,128} = 2.18$, $p = 0.09$). No interaction effects were significant ($p > 0.05$).

Eastern hemlock

Deer browse from July to September and July to April was not affected by garlic mustard, June garlic mustard cover, or the July stem length measure (Table 1). In open plots, 4.3% of eastern hemlock seedlings were browsed as of September 2017 while 97.8% of hemlock seedlings were browsed by April 2018 (Table 2). No seedlings in fenced plots were browsed.

Eastern hemlock survival from July to September and from September to April was not affected by experimental treatments, June garlic mustard cover, or the July stem length measure (Table 3). From June 2017 to September 2017, 96.8% of eastern hemlock seedlings survived (Table 4). Of the six eastern hemlock seedlings that died, none were browsed by deer. From September 2017 to April 2018, 97.8% of eastern hemlock seedlings survived. Four eastern hemlock seedlings were browsed and died between September 2017 to April 2018.

Table 1. Logistic regression of deer browse for eastern hemlock seedlings in open plots from July to September (2.5 months) and from July to April 2018 after winter (9 months). July – September n = 93, df of error = 86, R^2 = 0.13; July – April n = 93, df of error = 86, R^2 = 0.57.

		July – September		July – April	
Source	df	X^2	*P*	X^2	*P*
GM	1	0.6429	0.4227	0.0000	0.9974
June % cover GM	1	0.1507	0.6978	1.3334	0.2482
July stem length	1	0.2028	0.6525	1.1844	0.2765
Block	3	0.2080	0.9763	0.0000	1.0000

Table 2. Percentage of tree seedlings browsed in fenced and open plots from July to September and from July to April. Eastern hemlock n = 93; black cherry n = 96; red oak n = 96.

	Fenced plots	Open plots	
Species	July – April	July – September	July – April
Eastern hemlock	0%	4.3%	97.8%
Black cherry	0%	84.4%	-
Red oak	0%	100%	-

Table 3. Logistic regression of survival for eastern hemlock seedlings from July to September (2.5 months) and from September to April (7 months). July – September n = 190, df of error = 181, $R^2 = 0.26$; September – April n = 184, df of error = 175, $R^2 = 0.38$.

		July – September		September – April	
Source	df	X^2	*P*	X^2	*P*
Deer	1	0.8649	0.3524	0.0000	0.9969
GM	1	0.2196	0.6393	0.1016	0.7499
Deer × GM	1	0.0000	0.9964	0.0000	1.0000
June % cover GM	1	0.0456	0.8309	1.7418	0.1896
July stem length	1	0.0014	0.9700	0.2407	0.6237
Block	3	0.5719	0.9028	0.4639	0.9267

Table 4. Percentage of tree seedlings surviving from July to September and from September to April. Eastern hemlock: July – September n = 190, September – April n = 184; black cherry n = 192; red oak n = 192.

Species	July – September	September – April
Eastern hemlock	96.8%	97.8%
Black cherry	100%	
Red oak	100%	

Size traits of eastern hemlock seedlings in September, corrected for July measures, were not affected by deer presence, garlic mustard, or deer × garlic mustard interactions (Table 5, Figure 6). The September stem length increased with increasing June garlic mustard cover, though this effect did not depend on whether garlic mustard was present or removed (Table 5).

Size traits of eastern hemlock seedlings in April, corrected for July measures, were not affected by garlic mustard, June garlic mustard cover, or deer × garlic mustard interactions (Table 6). The comparison between fenced and open plots demonstrated that deer greatly reduced the stem length, vertical height, and width of eastern hemlock seedlings (Table 7, Figure 6). All size traits were reduced by at least 39% in open plots (Table 7).

Black cherry

Deer browse was not affected by garlic mustard, June garlic mustard cover, or the July stem length measure (Table 8). In open plots, 84.4% of black cherry seedlings were browsed as of September (Table 2). All black cherry seedlings survived from June to September (Table 4).

Size traits of black cherry seedlings in September, corrected for July measures, were not affected by garlic mustard, June garlic mustard cover, or deer × garlic mustard interactions (Table 9). Deer presence reduced the final size measure of all black cherry size traits (Table 7, Figure 7). All black cherry size traits were greater in fenced plots than in open plots (Table 7).

Table 5. Analyses of covariance for September size measures of eastern hemlock seedlings. Covariates are the June % cover of garlic mustard and the corresponding July size trait measure, e.g. July stem length is the covariate for September stem length. Bolded values indicate significance ($p < 0.05$). Stem length n = 175, df of error = 156, $R^2 = 0.80$; height n = 176, df of error = 158, $R^2 = 0.61$; width n = 175, df of error = 157, $R^2 = 0.63$.

		Stem length		Height		Width	
Source	Df	X^2	*P*	X^2	*P*	X^2	*P*
Deer	1	1.83	0.2090	0.84	0.3839	1.93	0.1977
GM	1	2.04	0.1872	0.11	0.7494	0.00008	0.9929
Deer × GM	1	1.32	0.2795	0.55	0.4754	1.06	0.3296
June % cover GM	1	10.17	**0.0017**	3.67	0.0572	0.92	0.3399
July measure	1	635.72	**<0.0001**	273.47	**<0.0001**	297.87	**<0.0001**
June % cover GM × GM	1	1.76	0.1862	-	-	-	-

Figure 6. Effects of deer presence on eastern hemlock size traits over time. Bars show the mean ± 1 SE. All size traits of eastern hemlock seedlings in open plots were reduced by deer between September and April (Table 7).

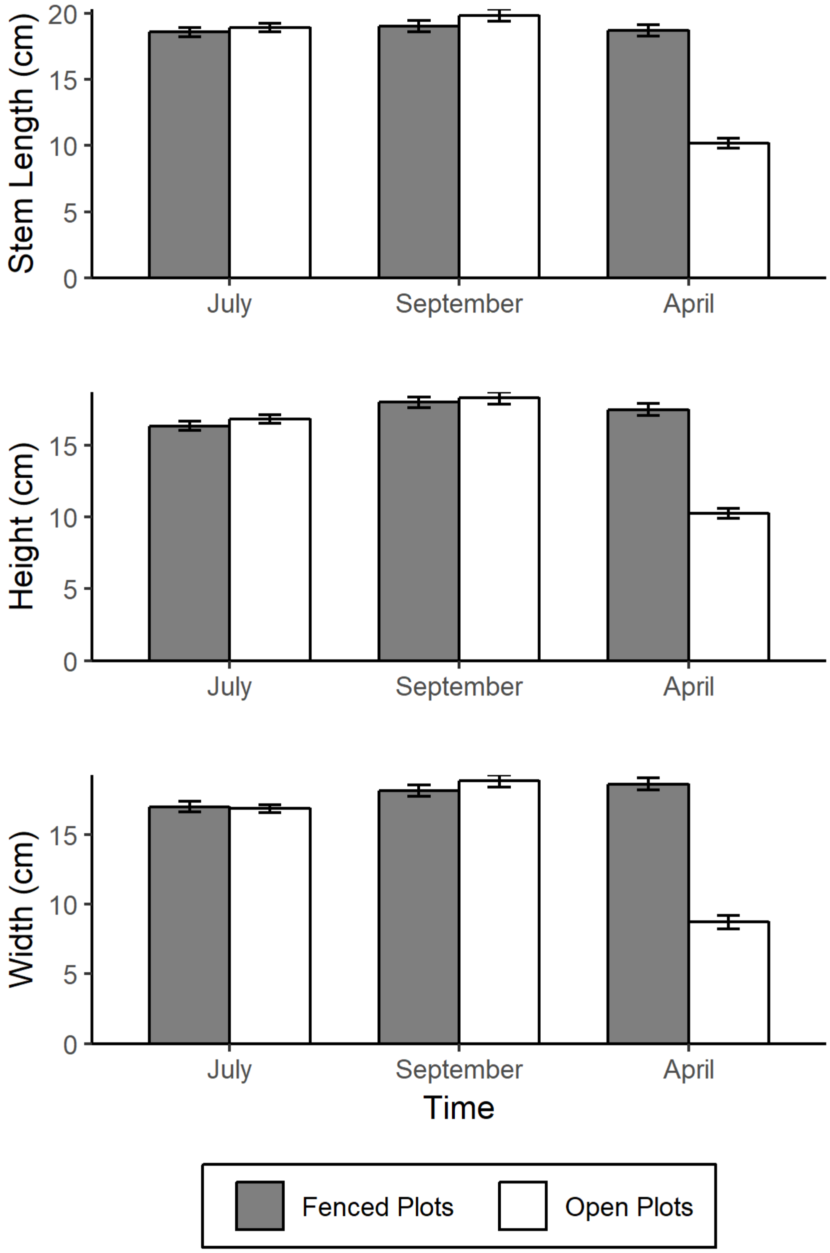


Table 6. Analyses of covariance for April size measures of eastern hemlock seedlings. Covariates are the June % cover of garlic mustard and the corresponding July size trait measure, e.g. July stem length is the covariate for April stem length. Bolded values indicate significance ($p < 0.05$). Stem length n = 165, df of error = 147, $R^2 = 0.72$; height n = 165, df of error = 147, $R^2 = 0.66$; width n = 164, df of error = 146, $R^2 = 0.69$.

		Stem length		Height		Width	
Source	Df	X^2	*P*	X^2	*P*	X^2	*P*
Deer	1	316.54	**<0.0001**	211.47	**<0.0001**	167.09	**<0.0001**
GM	1	0.21	0.6547	0.08	0.7813	0.17	0.6925
Deer × GM	1	0.45	0.5214	0.14	0.7124	1.58	0.2408
June % cover GM	1	0.00	0.9972	0.00001	0.9979	1.57	0.2129
July measure	1	86.53	**<0.0001**	72.49	**<0.0001**	52.93	**<0.0001**

Table 7. The average size in July, September, and April, and average absolute growth increment between measurement times expressed in cm and % change of size for the deer presence treatments. NS indicates no significant difference (p > 0.05). Average size trait measures are shown as the mean ± SE in cm. Difference values are calculated as mean(final height) - mean(initial height). Note: A haphazard sample of red oak and black cherry seedlings were measured in April 2018. As their April size measures were unchanged from the September measures, the measures were not recorded.

		July Measure		September Measure		April Measure		Difference	
Species	Size Trait	Fenced	Open	Fenced	Open	Fenced	Open	Fenced	Open
Eastern hemlock	Stem length	18.6 ± 0.3	18.9 ± 0.3	19.0 ± 0.4	19.8 ± 0.5	-	-	0.4 cm (2.2%)	0.9 cm (4.8%)
	Height	16.3 ± 0.3	16.8 ± 0.3	18.0 ± 0.4	18.3 ± 0.4	-	-	1.7 cm (10.4%)	1.5 cm (8.9%)
	Width	17.0 ± 0.4	16.9 ± 0.3	18.2 ± 0.4	18.8 ± 0.4	-	-	1.2 cm (7.1%)	1.9 cm (11.2%)
	Stem length	18.6 ± 0.3	18.9 ± 0.3	-	-	18.7 ± 0.4	10.2 ± 0.4	0.1 cm (0.5%)	-8.7 cm (-46.0%)
	Height	16.3 ± 0.3	16.8 ± 0.3	-	-	17.5 ± 0.4	10.3 ± 0.3	1.2 cm (7.4%)	-6.5 cm (-38.7%)
	Width	17.0 ± 0.4	16.9 ± 0.3	-	-	18.6 ± 0.4	8.7 ± 0.5	1.6 cm (9.4%)	-8.2 cm (-48.5%)
	Stem length	-	-	19.0 ± 0.4	19.8 ± 0.5	18.7 ± 0.4	10.2 ± 0.4	-0.3 cm (-1.6%)	-9.6 cm -48.5%)
	Height	-	-	18.0 ± 0.4	18.3 ± 0.4	17.5 ± 0.4	10.3 ± 0.3	-0.5 cm (-2.8%)	-8.0 cm (-43.7%)
	Width	-	-	18.2 ± 0.4	18.8 ± 0.4	18.6 ± 0.4	8.7 ± 0.5	0.4 cm (2.2%)	-10.1 cm (-53.7%)

(continued on next page)

Table 7. (Continued).

		July Measure		September Measure		April Measure		Difference	
Species	Size Trait	Fenced	Open	Fenced	Open	Fenced	Open	Fenced	Open
Black cherry	Highest point	32.6 ± 0.7	31.9 ± 0.7	35.2 ± 0.8	31.4 ± 0.7	-	-	2.6 cm (8.0%)	-0.5 cm (-1.6%)
	Stem length	31.4 ± 0.7	30.7 ± 0.7	32.9 ± 0.8	30.2 ± 0.8	-	-	1.5 cm (4.8%)	-0.5 cm (-1.6%)
	Branch height	28.7 ± 0.7	27.7± 0.7	30.4 ± 0.8	27.4 ± 0.7	-	-	1.7 cm (5.9%)	-0.3 cm (-1.1%)
	Branch length	12.8 ± 0.6	12.4 ± 0.6	15.4 ± 0.7	13.1 ± 0.6	-	-	2.6 cm (20.3%)	0.7 cm (5.6%)
	Longest leaf length	8.3 ± 0.1	8.2 ± 0.1	10.6 ± 0.3	7.3 ± 0.2	-	-	2.3 cm (27.7%)	-0.9 cm (-11.0%)
Red oak	Highest point	57.2 ± 1.1	57.6 ± 1.0	57.3 ± 1.1	57.2 ± 1.1	-	-	0.1 cm (0.2%) NS	-0.4 cm (-0.7%) NS
	Branch length	19.1 ± 0.7	19.1 ± 0.6	20.2 ± 0.7	19.2 ± 0.6	-	-	1.1 cm (5.8%)	0.1 cm (0.5%)
	Longest leaf length	13.1 ± 0.4	12.7 ± 0.4	14.6 ± 0.3	9.4 ± 0.4	-	-	1.5 cm (11.5%)	-3.3 cm (-26.0%)

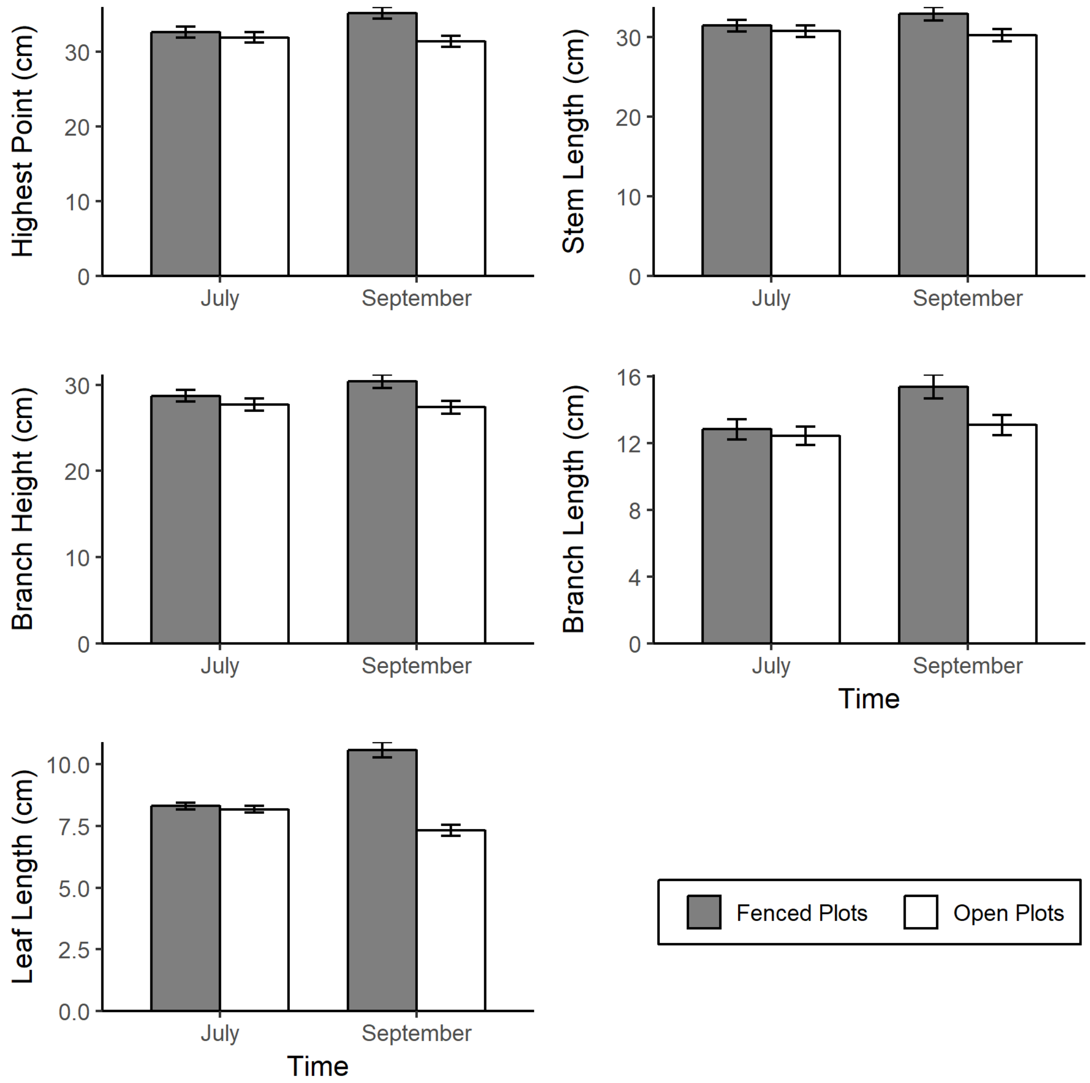
Table 8. Logistic regression of deer browse for black cherry seedlings in open plots from July to September. Black cherry n = 96, df of error = 89, R^2 = 0.09.

		July – September	
Source	df	X^2	*P*
GM	1	0.0972	0.7553
June % cover GM	1	0.1407	0.7076
July stem length	1	0.2544	0.6140
Block	3	3.9314	0.2690

Table 9. Analyses of covariance for September size measures of black cherry seedlings. Covariates are the June % cover of garlic mustard and the corresponding July size trait measure, e.g. July stem length is the covariate for September stem length. Bolded values indicate significance ($p < 0.05$). Highest point n = 192, df of error = 174, $R^2 = 0.69$; stem length n = 192, df of error = 174, $R^2 = 0.74$; branch height n = 192, df of error = 172, $R^2 = 0.74$; branch length n = 190, df of error = 172, $R^2 = 0.67$; longest leaf length n = 192, df of error = 174, $R^2 = 0.77$.

Source		Highest point		Stem length		Branch height		Branch length		Longest leaf length	
	Df	X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*
Deer	1	9.18	**0.0143**	6.51	**0.0312**	10.66	**0.0098**	10.8	**0.0094**	17.69	**0.0023**
GM	1	0.05	0.8321	0.60	0.4597	0.73	0.4145	0.42	0.534	0.61	0.4558
Deer × GM	1	0.35	0.5704	0.11	0.7432	0.48	0.5039	0.45	0.5174	0.50	0.4971
June % cover GM	1	0.90	0.3453	0.04	0.8437	0.16	0.6899	0.13	0.7181	0.85	0.3578
July measure	1	428.82	**<0.0001**	536.64	**<0.0001**	531.12	**<0.0001**	368.90	**<0.0001**	11.03	**<0.005**

Figure 7. Effects of deer presence on black cherry size traits over time. Bars show the mean ± 1 SE. All September size trait measures of black cherry seedlings were larger in fenced plots than in open plots (Table 7).



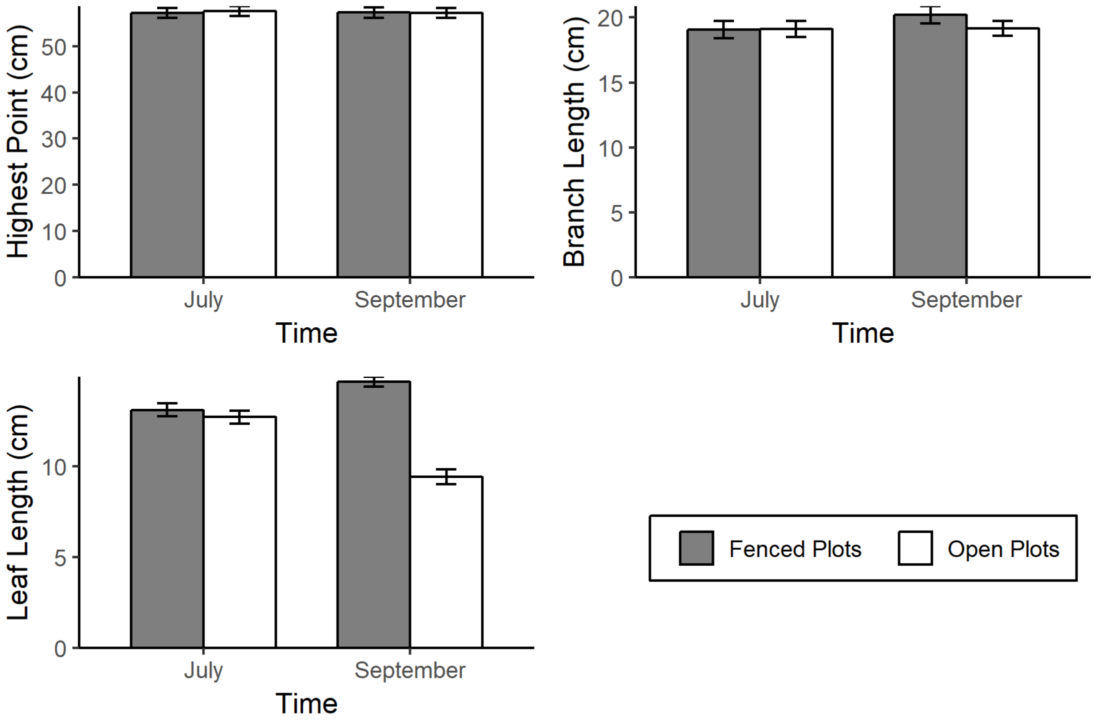
Red oak

All red oak seedlings in open plots were browsed, and all seedlings survived from June to September (Table 2, Table 4). Red oak seedlings in September, corrected for July measures, were not affected by garlic mustard, June garlic mustard cover, or deer × garlic mustard interactions (Table 10). Deer presence reduced the final size measure of branch length and longest leaf length, but not the highest point (Table 7, Figure 8).

Table 10. Analyses of covariance for September size measures of red oak seedlings. Covariates are the June % cover of garlic mustard and the corresponding July size trait measure, e.g. July stem length is the covariate for September stem length. Bolded values indicate significance ($p < 0.05$). Highest point n = 189, df of error = 171, $R^2 = 0.97$; branch length n = 187, df of error = 169, $R^2 = 0.85$; longest leaf length n = 190, df of error = 172, $R^2 = 0.45$.

		Highest point		Branch length		Longest leaf length	
Source	Df	X^2	*P*	X^2	*P*	X^2	*P*
Deer	1	3.48	0.0951	10.1	**0.0112**	27.32	**0.0005**
GM	1	1.05	0.3332	1.74	0.2196	0.18	0.6792
Deer × GM	1	0.23	0.6456	2.73	0.1329	0.01	0.9211
June % cover	1	0.56	0.4573	0.19	0.6623	0.79	0.3739
July measure	1	5856.63	**<0.0001**	1026.89	**<0.0001**	32.67	**<0.0001**

Figure 8. Effects of deer presence on red oak size traits over time. Bars show the mean ± 1 SE. September measures of branch length and longest leaf length were larger in fenced plots than in open plots (Table7). Deer presence did not affect the September highest point measure of red oak seedlings (Table 10).



DISCUSSION

In this study, I examined how native trees are affected by two major stressors of temperate North American forests. By manipulating the presence of white-tailed deer and garlic mustard, I examined their individual and combined effects on transplanted seedlings of three native tree species to determine if these stressors are suppressing size and limiting recruitment of these species in McMaster Forest. Deer browsing rates were high outside of the exclosures (84.4% to 97.8%). Deer presence reduced seedling size but did not affect mortality within the short duration of the study, consistent with what previous studies have found (Marquis 1981; Alverson and Waller 1997; Waller and Maas 2013). Surprisingly seedlings were not affected by garlic mustard removal, nor did the effects of deer depend on garlic mustard presence. While all species were impacted by deer, seedling browsing patterns varied among tree species.

Effects of garlic mustard on seedlings

In contrast to other studies, this study found no main effects of garlic mustard nor any significant interaction with deer presence. In one study (Stinson et al. 2006), soil with a history of garlic mustard reduced mycorrhizal colonization and the growth increment of tree seedlings after four months, which demonstrates that mycorrhizal colonization remains impaired in soil even after garlic mustard is removed and indicates that the negative effects of garlic mustard accumulate over time. Given that both levels of garlic mustard presence in my study have a history of garlic mustard, it is reasonable to expect that seedlings in both treatment levels experienced similarly reduced mycorrhizal colonization and growth which could explain why no main effects of garlic mustard were observed. Additionally, garlic mustard effects on eastern hemlock seedlings may have been delayed if the potting soil buffered the seedlings from garlic mustard allelochemicals. Though one other exclosure study found that garlic mustard effects were magnified in the presence of deer (Waller and Maas 2013), no interaction effects were significant in this study. Interestingly, the September stem length of eastern hemlock seedlings increased with initial June garlic mustard cover. However, this effect was independent of whether garlic mustard remained present or was removed, consistent with the possibility (potentially indicating) that the microenvironmental variation in the abiotic conditions of the site affected garlic mustard cover and eastern hemlock size similarly. Overall, garlic mustard removal did not affect seedlings in the duration of this study but may affect seedlings over time.

Effects of deer presence on seedlings

Exclosures successfully protected seedlings while deer browsed seedlings in open plots. I measured the effect of deer browsing in three different ways: 1) observable browse damage, 2) whether size differed between seedlings in fenced and open plots, and 3) if survival differed between seedlings in fenced and open plots. Though deer browsed all species in open plots, there was variation in when they were browsed. In addition, seedlings in fenced plots were larger than seedlings in open plots for 10 of 11 size traits measured across the three study species, though deer affected species and size traits in different ways. As the fenced exclosures allowed entry by small herbivores but excluded deer, the results of this study demonstrate that deer, and not other herbivores, are browsing seedlings and reducing their size in McMaster Forest.

Deer intensely browsed eastern hemlock seedlings and greatly reduced size traits, confirming that deer are suppressing seedling size in McMaster Forest. Eastern hemlock seedlings were largely avoided over the summer (4.3% browsed) but were severely browsed over the winter (97.8% browsed). This is consistent with reports that in summer deer do not browse eastern hemlock when preferred hardwood species are available (Moore and Johnson 1967; Augustine and McNaughton 1988), while in winter, when hardwood tree species are dormant and browse becomes scarce, eastern hemlock becomes a staple food for deer (Peterson 1955; Dahlberg and Guettinger 1956; Beals et al. 1960). In this study, similar to a previous study (Alverson and Waller 1997), eastern hemlock seedlings were larger when protected from deer. Compared to July measures, the April size traits of seedlings in fenced plots increased very little (width 9.4%, 1.6 cm increase, $p < 0.0001$) or not at all (stem length 0.1%, 0.5 cm, $p = 0.45$) reflecting the slow growth rate of eastern hemlock seedlings (USDA NRCS 2018b). Conversely, from September to April deer browsing greatly reduced the stem length (-48.5%, -9.6 cm, $p < 0.0001$) and width (-53.7%, -10.1 cm, $p < 0.0001$) of seedlings in open plots, consistent with reports that hemlock seedlings are very sensitive to deer browsing (Anderson and Loucks 1979;

Frelich and Lorimer 1985; Alverson et al. 1988). In open plots, deer often browsed eastern hemlock seedlings down to the leaf litter, leaving a single stem with few or no branches. Some browsed seedlings retained their width because their lateral branches were hidden under leaf litter or vegetative cover. Overall, eastern hemlock seedlings were severely reduced in size following winter browsing by deer but were not affected by deer in summer when red oak and black cherry seedlings were available for browse.

Deer browsing suppressed black cherry size, though browse patterns differed from other study species and affected size traits differently. In contrast to eastern hemlock, 84.4% of black cherry seedlings were browsed by deer from July to September, consistent with white tailed deer's moderate preference for black cherry (Healy 1971; Strole and Anderson 1992; Wakeland and Swihart 2009). Deer often browsed terminal black cherry leaves and the tips of main stems and branches (Jordan Barker pers. observ.). After 2.5 months, seedlings in fenced plots were larger than seedlings in open plots for every size trait. In fenced plots, the highest point of black cherry seedlings increased from July to September (8.0%, 2.6 cm, $p < 0.0001$) while red oak did seedlings did not grow taller (0.2%, 0.1 cm, $p = 0.52$), reflecting the rapid growth rate of black cherry (USDA NRCS 2018c). However, the highest point of black cherry seedlings in open plots did not increase from July to September (-1.6%, -0.5 cm, $p = 0.23$), indicating that deer might have suppressed seedling size by browsing new growth. Interestingly, branch length increased in open plots from July to

September (5.6%, 0.7 cm, $p < 0.05$) while other size traits were reduced (-1.1% to -11.0%). Branch length of black cherry seedlings could have increased in open plots if branches were browsed less than other parts of the seedling. Black cherry branches were usually situated lower on the seedling and may have been hidden from deer in other vegetation. As deer typically consumed the tallest parts of a seedling (pers. observ.), I would expect browsing to cause a greater reduction in the highest point and stem length than branch length of black cherry seedlings. Additionally, some seedlings had visible evidence of a branch becoming the new leader once the main apical meristem was browsed (pers. observ.). This release from apical dominance and promotion of lateral growth reflects the high browse tolerance of black cherry (Marquis 1983; Tilghman 1989). Of all black cherry size traits, the longest leaf length experienced the greatest size increase in fenced plots (27.7%, 2.3 cm, $p < 0.0001$) and the greatest reduction in open plots (-11.0%, -0.9 cm, $p < 0.01$) from July to September. This is in accordance with reports that deer prefer to browse hardwood leaves when they are available in the summer (Crawford 1982; Smith 1991). Despite high browse tolerance, black cherry seedings were negatively affected by deer browsing in ways consistent with browsing patterns on hardwood tree species.

Like black cherry, red oak seedlings were heavily browsed by deer and browse effects varied among size traits. From July to September, deer browsed 100% of red oak seedlings, consistent with deer’s high preference for red oak (Telfer 1972; Wakeland and Swihart 2009). Similar to observed browsing patterns on black cherry seedlings, deer intensely browsed leaves (pers. observ.) and greatly reduced the longest leaf length of red oak seedlings in open plots from July to September (-26.0%, 3.3 cm, $p < 0.0001$). However, because deer rarely browsed the main stems or branches of red oak seedlings, deer presence did not affect the highest point of red oak. As defoliation reduces growth in red oak seedlings (McGraw et al. 1990), over time the highest point of red oak should be greater in fenced plots than in open plots as other studies that measured red oak height have observed (Stange and Shea 1998; Waller and Maas 2013). Similarly, compared to July measures the September branch length of seedlings slightly increased in fenced plots (5.8%, 1.1 cm, $p < 0.0001$), but remained unchanged in open plots (0.5%, 0.1 cm, $p = 0.88$). From July to September, the increase in branch length in fenced plots was minimal compared to black cherry and reflects the moderate growth rate of red oak (USDA NRCS 2018d). Overall, deer selectively browsed study species according to their seasonal preferences and study species were affected by herbivory in accordance with their sensitivity to browse damage.

Effects on survival

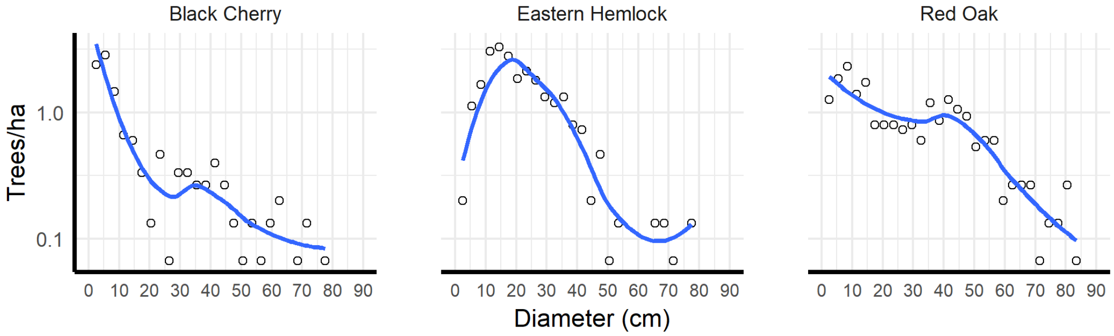
Although deer reduced seedling size, damage from browsing did not reduce survival of any of the study species. Survival was similarly unaffected by deer browsing damage in other studies of red oak (Waller and Maas 2013; Johnson et al. 2015), black cherry (Horsley and Marquis 1983), and eastern hemlock seedling survival (Alverson and Waller 1997). In the present study, all three species had very high survival, with only 10 eastern hemlock seedlings that died throughout the experiment. From July to September, six eastern hemlock seedlings died though none were browsed by deer, and four eastern hemlock seedlings died between September and April directly due to deer browse damage. I predict that mortality will increase over time as the negative effects of garlic mustard and deer browsing accumulate. Over time, eastern hemlock should experience the highest mortality of these three species as eastern hemlock seedlings are much less tolerant to browse damage (Curtis 1959; Anderson and Loucks 1979) and typically die after one or two incidents of browsing (Frelich and Lorimer 1985).

Implications

The suppression of native tree seedling size by deer has broad impacts on the forest community. As deer suppress the size and growth of tree seedlings, they limit the recruitment of tree seedlings into larger size classes and eventually the forest canopy. In extreme cases, where deer densities are very high, sustained intensive browsing can cause complete regeneration failure, where no seedlings grow tall enough to escape size suppression by deer. Limited regeneration of a species is detected when there are fewer individuals in small size classes than would be expected based on the number of mature trees. In forests with high deer densities, eastern hemlock trees often exhibit a unimodal diameter distribution (Anderson and Loucks 1979; Frelich and Lorimer 1985) which describes populations with a greater abundance of individuals in mid-size classes than in small and large size classes. This underrepresentation of seedling and sapling size classes of eastern hemlock has been observed in many hemlock-northern hardwood forests across the Laurentian Great Lakes region, where deer are recognized as a significant factor in limiting eastern hemlock seedling and sapling abundance (Anderson and Loucks 1979; Frelich and Lorimer 1985; Alverson et al. 1988; Waller et al. 1996; Rooney et al. 2000). Similarly, red oak saplings have also been shown to be underrepresented outside of deer exclosures (Healy 1997) and red oak seedling density decreases with increasing browsing intensity, indicating that deer greatly limit red oak regeneration (Rooney and Waller 2003). In contrast, as a browse tolerant species black cherry can regenerate and increase dominance in high deer density areas (Tilghman 1989), but recruitment of saplings into taller size classes can also be limited by deer (Marquis 1981).

The results of this study implicate intensive deer browsing as a cause of the observed underrepresentation of eastern hemlock and red oak seedlings in McMaster forest (Figure 9) and suggest that deer are limiting the recruitment and regeneration of both species. Eastern hemlock displays a unimodal diameter distribution characteristic of a declining population with very few trees in the smallest size classes. Red oak shows a moderately balanced diameter distribution as trees are only slightly more abundant in small size classes than in mid-size classes. Black cherry exhibits a balanced diameter distribution with an abundance of trees in small size classes. If the current deer density of McMaster

Figure 9. Diameter distributions for three native tree species in McMaster Forest: (a) black cherry, (b) eastern hemlock, and (c) red oak. Diameter distributions were produced with data from a forest census study of >20 000 trees in McMaster Forest (Muñoz 2016). Diameter classes cover a range of 3 cm beginning at 1 cm.



Forest remains high, we can expect the local eastern hemlock and perhaps red oak populations to decline and eventually be eliminated from the stand.

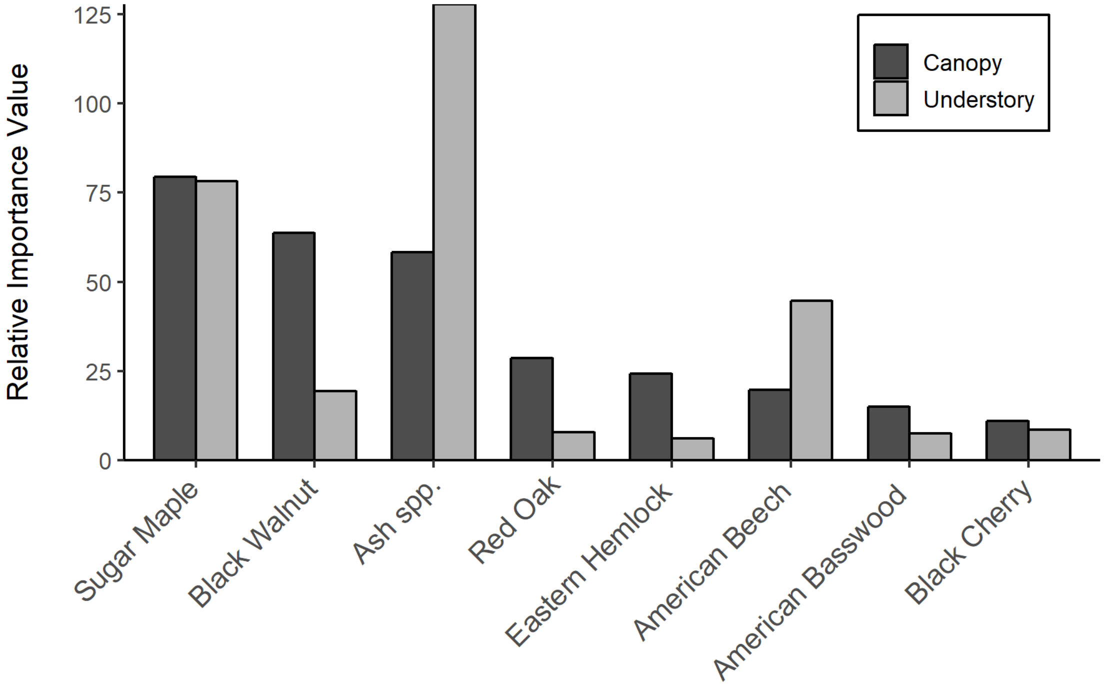
As regeneration of preferred browse species is suppressed due to high deer densities and intensive browsing, the trajectory of succession shifts to favour unpalatable or browse tolerant species. This effect has been demonstrated by exclosure and enclosure studies that compare species composition between plots differing in deer density (Anderson and Loucks 1979; Alverson and Waller 1997; Tilghman 1989; Horsley et al. 2003) and compare the species composition of the understory and overstory (Long et al. 2007). This effect is predicted to drive a compositional change in mixed conifer-hardwood forest canopies to canopies dominated by less palatable, browse tolerant hardwood species such as American beech (Peterson and Pickett 1995), paper birch (Ross et al. 1970), and sugar maple (Anderson and Loucks 1979; Frelich and Lorimer 1985, Alverson and Waller 1997). Additionally, northern hardwood forests are predicted to be converted to canopies dominated by American beech and black cherry (Tilghman 1989; Horsley et al. 2003; Long et al. 2007) while the relative importance of preferred, less tolerant species such as red oak, sugar maple, and white ash declines.

Given that deer are suppressing the size and likely limiting the recruitment of eastern hemlock and red oak in McMaster Forest, it is expected that these species would be underrepresented in the understory while American beech and black cherry would be overrepresented. Indeed, the relative importance of both eastern hemlock and red oak is much lower in the understory than in the canopy of McMaster Forest (Figure 10; J. Barker, unpublished data). In contrast, the relative importance of browse tolerant American beech is much greater in the understory than in the canopy, while black cherry exhibits similar levels of relative importance in both the understory and canopy. This evidence supports the hypothesis that selective browsing by deer is driving a compositional shift to favour browse tolerant species in McMaster Forest.

Although these results demonstrate that intensive browsing by deer is changing the tree species composition in McMaster Forest, exactly how this change will affect other native herbivores is still unknown. The deer-mediated shift in community composition often decreases species diversity of both tree seedlings (Harlow and Downing 1970; Tilghman 1989) and herbaceous plants (Rooney and Waller 2003), and this is likely to cause a decline in insect diversity by limiting insect food sources (Murdoch et al. 1972, Haddad et al. 2001). Additionally, small mammals and shrub-nesting birds may be negatively affected by reduced habitat availability as intensive browsing reduces understory vegetative cover and vertical complexity, (deCalesta 1994; McShea and Rappole 2000; Flowerdrew and Ellwood 2001; Stewart 2001)

This study was limited in the geographic extent of the study, as all experimental plots were located in one Carolinian forest stand in southern Ontario. Although this study was contained to one forest type, the results are consistent with studies across the Great Lakes region (Marquis 1981; Alverson

Figure 10. Relative importance values of canopy class tree species in McMaster Forest. Trees <10 cm DBH are classified as “understory” and trees ≥ 10 cm DBH are classified as “canopy” (J. Barker, unpublished data). Importance values were calculated as the sum of the relative density, relative frequency, and relative dominance as measured by basal area.



and Waller 1997; Stange and Shea 1998; Rooney et al. 2000; Long et al. 2007). In addition, no environmental variables (e.g. light, moisture, soil type, etc.) were measured in experimental plots, meaning that any potential effects of these variables were not examined, though environmental differences between treatment plots were controlled for by using subplot nested within plot as a random effect variable in all analyses.

These results have implications for management strategies in forests with high deer densities. Because of the extensive damage to seedlings as a result of intensive deer browsing, I recommend that managers seeking to conserve and restore biodiversity in Carolinian forests where deer are overabundant reduce and maintain the deer density at ≤7 deer/km^2 (Tilghman 1989; Tanentzap et al. 2011). Although reducing the deer density will immediately alleviate some size suppression of tree seedlings, it may take decades of protection from deer browsing to increase recruitment into larger size classes, e.g. >27 years for hemlock (Anderson and Katz 1993) and >10 years for hardwood species (Tanentzap et al. 2011). Furthermore, reducing the deer density alone may not allow a forest to recover if past deer browsing has depleted the local seed sources of preferred species (Coomes et al 2003; Long et al. 2007) or if the understory is dominated by an invasive plant (de la Cretaz and Kelty 2002; Coomes et al. 2003; Knight et al. 2009). I therefore recommend that managers increase the local seed sources of native trees and actively reduce populations of invasive plants, in addition to reducing the deer density, to promote the successful regeneration of native trees. However, in forests where deer and garlic mustard are both abundant, managers should prioritize controlling the deer population over controlling the spread of garlic mustard as reducing the deer density can facilitate the decline of garlic mustard populations (Kalisz et al. 2014). As forests are increasingly threatened by exotic plants and overabundant deer, future studies should seek to fill gaps in the growing literature by examining a broad range of forest types, deer densities, and invaders. Studies should employ repeated measurements of seedlings over long-term durations to determine how different life-stages are affected. Researchers should also consider indirect effects on other forest animals.

Conclusion

This study provides evidence for the hypothesis that deer are suppressing the size and recruitment of palatable native tree seedlings in McMaster Forest. I demonstrated that browsing deer reduce the size of palatable tree species and greatly reduce the size of species intolerant to browsing. Moreover, I show that the effects of garlic mustard removal may not be detectable in short-term studies. As forests are continually threatened by elevated deer densities, exotic invaders, and urban sprawl, it is increasingly important to support effective management techniques to conserve native vegetation and secure healthy forests for future generations. Management strategies should prioritize controlling the deer population in addition to invasive plants and should be tailored to conserve the most sensitive species.

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