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Graduate Studies

THE INTERACTIVE EFFECTS OF DEER HERBIVORY AND FLOODING ON TREE
RECRUITMENT IN FLOODPLAIN FORESTS OF THE
UPPER MISSISSIPPI RIVER SYSTEM

A Chapter Style Thesis Submitted in Partial Fulfillment of the Requirements for the
Degree of Master of Science in Biology

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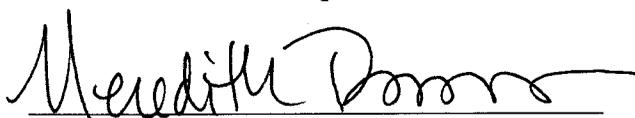
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UPPER MISSISSIPPI RIVER SYSTEM

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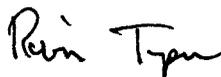
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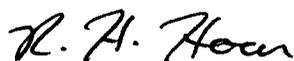


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ABSTRACT

Cogger, B.J. The interactive effects of deer herbivory and flooding on tree recruitment in floodplain forests of the Upper Mississippi River system. MS in Biology, December 2011, 80 pp. (M. Thomsen and N. De Jager)

Floodplain forests are a critical link between land and river ecosystems, moderating nutrient fluxes, providing animal habitat, and stabilizing the river corridor. In the Upper Mississippi River (UMR), floodplain tree recruitment appears to be limited by white-tailed deer browsing. The effects of landscape position and species composition on deer activity in floodplain forest restoration sites were examined, along with the ways in which deer browsing and flooding interact to affect the growth of young trees. Surveys of restoration sites in the UMR indicated that higher tree density corresponded to increased consumption levels. Degree of isolation and species composition also influenced consumption rates. An enclosure study indicated that plastic mesh fences reduced consumption by deer more than electric or chemical fences. Mesh enclosures also contained the highest percent of trees above escape height (200 cm), and trees that experienced the highest levels of consumption were a meter shorter than unbrowsed trees after two years. Tree density was affected by plot elevation; low plots with short trees had high rates of mortality and composition change, presumably as a result of longer periods of inundation. Thus, deer herbivory and flooding appear to interact to limit tree performance in floodplain forest restoration sites.

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CHAPTER I
FLOODPLAIN FORESTS
General Characteristics

Ecosystem function within river floodplains is highly dependent on the complex hydrology that mediates interactions between adjacent terrestrial and aquatic habitats (Bayley 1995, Yin and Nelson 1996, Clawson *et al.* 2001). The dynamics occurring in the aquatic-terrestrial interface regulate rates and types of materials exchanged between the two systems (Junk *et al.* 1989) as well as floodplain community composition and structure (Yin *et al.* 2009). Disturbance caused by flooding increases habitat heterogeneity, alters micro-topography, prolongs inundation, and provides a transport mechanism for propagules of vascular plants (Naimen *et al.* 1993, Richter and Richter 2000). Due to a high degree of spatial and temporal variation in flooding, these ecosystems are among the most diverse and productive in the world (Naimen *et al.* 1993, Yin and Nelson 1996).

Floodplains receive a large influx of nutrients associated with sediment deposited by flood waters (Yin and Nelson 1996). Forested riparian areas and floodplains have been found to import both suspended sediment and particulate nitrogen during flood periods (Brunet *et al.* 1994). At the same time, other nutrients found in dissolved or particulate inorganic matter as well as plant materials are often exported from the floodplain to the river (Junk *et al.* 1989, Sweeney 1993, Bayley 1995, Wallace *et al.* 1995). This aquatic-

terrestrial connectivity may explain high levels of productivity in floodplain forests; periodically flooded forested wetlands have been found to be nearly twice as productive as wetlands that are constantly inundated (Mitsch *et al.* 1991). Net above-ground biomass accrual in bottomland hardwood forests ranges from 1300 g/m²/y in Ohio (Mitsch *et al.* 1991) to 1700 g/m²/y in Louisiana (Conner and Day 1976). However, it is unclear exactly how flooding influences productivity (Migonigal *et al.* 1997). Certain flood-tolerant tree species have been found to grow faster in response to periodic flooding. On a small scale, micro-topographical variations have been found to influence tree species composition based on a tree's ability to withstand inundation (Streng *et al.* 1989).

Structure in floodplain forests is typically provided by a variety of tree species tolerant of periodic flooding. These trees serve as foundation species, providing a number of ecosystem services as well as habitat in their physical architecture (Ellison *et al.* 2005). Fast-growing tree species such as cottonwood (*Populus* spp.) provide three-dimensional structure in early-successional stages and eventually give way to slower-growing, longer lived tree species that continue to provide habitat (Twedt and Portwood 1997). Several rare avian species are dependent on tall, large-diameter trees. For example, bald eagles (*Haliaeetus leucocephalus*) prefer large trees with a horizontal limb structure near a food source for shelter and feeding purposes (Isaacs *et al.* 1993). Females of the endangered Indiana bat (*Myotis sodalis*) rely on loose tree bark in the floodplain as a shelter for roosting and rearing young. The bats prefer mature or senescent large-diameter trees as they provide thermal protection that is essential for successful gestation (Callahan *et al.* 1997).

Trees adjacent to a stream channel may be the most important factor affecting structure and function of aquatic macroinvertebrate communities in some streams. Shade moderates stream light and temperature regimes, and trees provide habitat structure in the form of roots and debris inputs. Leaves, twigs, bark and logs are all important sources of allochthonous food materials in streams (Sweeney 1993). Wallace *et al.* (1995) found that increased habitat heterogeneity resulting from log addition resulted in increased benthic macroinvertebrate diversity. As logs from dead trees entered a stream, they formed debris dams and pools and provided excellent habitat for macroinvertebrates. Furthermore, the dead trees increased water retention time, resulting in a larger standing crop of particulate organic matter (POM), a food source for many species of benthic macroinvertebrates. Not only was POM retained longer, but organisms also used the resource more efficiently in debris dam pools. Many macroinvertebrates are prey for fish that also rely on woody structure in a river for food, shelter and protection (Angermeier and Karr 1984, Yin and Nelson 1996). Fish diversity, richness and abundance have been found to be higher in streams containing woody debris in various regions (Angermeier and Karr 1984, Wright and Flecker 2004).

Trees in floodplain forests not only provide habitat structure for other organisms, they also influence nutrient influx and the channel morphology of a river. Tree root systems in forests are typically deeper and more expansive than grasses, forbs, or shrubs (Canadell *et al.* 1996). Deep roots and high transpiration rates give trees the capacity to moderate bank stability and hydrologic regimes, controlling rates of runoff and material input to the stream. A well-developed forest typically has high rates of infiltration and low runoff as forest litter slows the rate at which water and sediment reaches the channel.

Following flooding, forested riparian areas retain a large amount of the particulate and nutrient load that would be otherwise exported downstream (Brunet *et al.* 1994). In watersheds where forests are converted to agriculture, lawns or pastureland, water quality usually declines (Neary *et al.* 2009).

The loss of riparian trees has broad implications that affect humans through the diminishment of the aesthetic beauty found in a forest's diversity of life, as well as physically and economically through costs associated with pollution. Because trees retain aboveground biomass throughout the year, as opposed to non-woody vegetation, ecosystem storage of nitrogen (N) in a forested site is likely greater than in communities dominated by herbaceous species. Furthermore, high rates of microbial denitrification are often found in saturated soils (Pezeshki 2001). This suggests that where floodplain forest is lost, denitrification rates and ecosystem N storage may decline. There is widespread concern about N runoff from farm fields, resulting hypoxic water conditions and the "dead-zone" at the mouth of the Mississippi River (Ferber 2004). Thus, it is imperative to find ways to restore riparian forests where they have been lost, and thereby maximize N storage in floodplain ecosystems, as well as retain habitat structure, stream bank stability, and associated ecosystem services.

Floodplain Forests of the Upper Mississippi River

An important river-floodplain ecosystem in the Midwestern United States is found along the Upper Mississippi River (UMR). The UMR is the portion of the Mississippi River stretching from Lake Itasca, Minnesota, 800 miles south to Cairo, Illinois at its confluence with the Ohio River (Theiling 1996). The floodplain forests of the UMR are home to an array of native plant species that have adapted to periodic flooding. The forest

also provides food, shelter, breeding grounds, and nursery habitat for a multitude of animal species (De Calesta 1994, Smith 1996, Yin and Nelson 1996). At least 59 species of amphibians and reptiles rely on the UMR floodplain forests as a habitat (Smith 1996) as well as numerous species of waterfowl and other birds (Isaacs *et al.* 1993, Yin and Nelson 1996).

Within the last 200 years, floodplain forest cover in the UMR has diminished, becoming more fragmented and less diverse (Theiling 1996). The floodplain has been degraded by human activities such as damming, urbanization, agriculture, and invasive species introduction (Yin and Nelson 1996, Kellogg and Bridgham 2004). A widespread invasive species of concern in the UMR is *Phalaris arundinacea* (reed canary grass) (Miller and Zedler 2003, Romano 2010). The grass is well suited to the moist conditions found in floodplains and rapidly outcompetes native wetland vegetation (Herr-Turoff and Zedler 2007, Reinhardt Adams and Galatowitsch 2008). As trees senesce, the grass quickly takes advantage of increased light availability in canopy gaps, and forest structure erodes as trees and shrubs give way to *Phalaris* monocultures (Naimen *et al.* 1993). In riparian forests along the Willamette River, Oregon, a high cover of *Phalaris* resulted in a loss of diversity and tree density over time, yielding a much restricted canopy cover and forest structure (Fierke and Kaufmann 2005). Kellogg and Bridgham (2004) found that competition from native subdominant species had little effect on *Phalaris* cover and biomass. *Phalaris* control can be achieved by burning, herbicides and mechanical disturbance (Apfelbaum and Sams 1987, Annen *et al.* 2005, Jenkins *et al.* 2008); however, *Phalaris* densities continue to increase in the floodplain forests of the UMR valley (Pierce *et al.* 2008, Romano 2010).

Restoring floodplain forests across the greater Mississippi River Valley is becoming a priority of many land-owners and management agencies (Romano 2010) and herbicidal control of *Phalaris* in the UMR has been moderately successful in some locations. However, recent observations suggest that even after *Phalaris* is controlled, complex interactions among flooding, and consumption by overabundant herbivore populations may continue to prevent tree regeneration in many locations (Thomsen *et al. in review*). Detailed information is needed to determine the best management practices to protect seedlings against herbivory while accounting for underlying factors associated with flooding and reestablish a functional riparian forest ecosystem in a hydrologically modified large river system.

Effects of Flooding

The construction of navigational dams in the UMR has altered the natural flooding regime of the river. Floodplains upstream from a dam experience longer periods of inundation during low flow conditions than prior to dam construction (Theiling 1996). Although tree species within floodplain forests are well adapted to periodic flooding, altered hydrology may affect tree performance and influence succession (Bell 1974, Yin *et al.* 2009). Flooding has the potential to affect trees at all life stages from seed dispersal and germination (Streng *et al.* 1989) to scour and uprooting of mature trees (Yin *et al.* 2009). The effects of flooding are species-specific and tolerance to flooding varies throughout a tree's life. For example, light-seeded species (e.g. *Acer* spp.) are more easily dispersed by flooding than heavy seeded *Quercus* species (spp.), although light seeds are more prone to flood and drought related mortality (Streng *et al.* 1989). Following germination, a seedling on an intermittently flooded substrate must overcome stresses

related to variations in soil moisture and submersion (Pezeshki 2001). As soil becomes saturated, pore spaces fill with water, oxygen diffusion slows dramatically, redox potentials decrease and the remaining oxygen in a plant's rhizosphere is quickly depleted by the metabolic demands of roots and soil microbes (Parent *et al.* 2008). Microbial phytotoxic byproducts of anaerobic respiration such as sulfides accumulate in saturated soil requiring a plant to oxygenate its rhizosphere to oxidize the toxins. Further belowground oxygen demand is driven by respiratory needs in roots to metabolize stored carbohydrates. To facilitate belowground oxygen transfer a plant often begins to elaborate oxygen transferring structures such as adventitious roots, hypertrophied lenticels and aerenchyma tissue (Sena Gomes and Kozlowski 1980, Armstrong *et al.* 1991). A plant's ability to efficiently allocate resources determines initial tolerance to flooding. A floodplain tree also faces mechanical stresses including erosion of substrate, shear, and ability to withstand sweeping floods, all factors that determine individual success in a dynamic floodplain forest (Kramer *et al.* 2008, Yin *et al.* 2009). Abiotic factors associated with flooding are strong drivers of successional patterns in floodplain forest and changes to the natural flood regime may explain a compositional shift in the UMR (Yin *et al.* 2009). However, biotic factors such as competition from invasive species and/ or herbivory have also been shown to affect composition in wetland habitats (Miller and Zedler 2003). Yet little research has focused on how the effects of flooding on tree performance might depend on such biotic factors.

Effects of Deer Herbivory

The white-tailed deer (*Odocoileus virginianus*) is an herbivore of concern in the UMR and across the Midwest. Deer densities in North America are much higher than historically, likely a result of more abundant forage and decreased predation (Côté *et al.* 2004). Deer have the ability to modify rates of ecosystem processes such as nutrient cycling, and to initiate shifts to alternate stable states of community composition and dynamics (Augustine *et al.* 1998, Hobbs 1996, Liang and Seagle 2002). Increased deer densities often lead to widespread changes in forest structure as unbrowsed plant species have a competitive advantage (Horsley *et al.* 2003).

As a result of browsing impacts on plant community composition, deer have the potential to slow or dramatically alter successional patterns in a forest. Continual browsing pressure may keep trees in a perpetual sapling stage. Ross *et al.* (1970) found that over the course of 32 years, nearly four times as many sapling-size trees persisted outside a deer exclosure as compared to within. Deer browsing on preferred tree species can significantly alter the probability of tree survival. Typically, the probability of tree survival increases with growth and time (Long *et al.* 2007). However, seedling mortality is typically higher in forests with high deer densities, altering survival probability predictions. In contrast, forests released from deer herbivory often have greater seedling density, abundance, diversity and biomass (Ross *et al.* 1970, Ritchie *et al.* 1998, Horsley *et al.* 2003, Persson *et al.* 2005, Long *et al.* 2007).

High deer densities often negatively impact biodiversity, but their total exclusion from an ecosystem may not be the most practical option. Rooney and Waller (2003) found that white-tailed deer browsing suppressed seedling densities of certain deciduous

species, but the relationship between deer density and seedling success was not linear. In some cases, the highest abundance of seedlings occurred at intermediate deer densities and the lowest at low and high deer densities. Moderate levels of herbivory may induce so-called overcompensation in plant biomass, whereby plants respond to herbivory with increased growth that more than compensates for lost tissue (McNaughton 1983). For example, Strauss (1988) found that browsed saplings produced larger, longer shoots than unbrowsed counterparts. Similar findings have been reported for the response of shoot density to increased moose browsing for deciduous tree species (De Jager and Pastor 2008, De Jager *et al.* 2009, De Jager and Pastor 2010). Thus, moderate herbivory by deer could stimulate the production forage biomass of some tree species. However, rates of tree height growth often decline even when shoot density increases following herbivory (Persson *et al.* 2005, De Jager and Pastor 2010). Suppression of vertical growth may favor the herbivore by keeping edible portions of the forage within reach for longer periods of time. Browsing rates in floodplain forests may be influenced by a number of additional factors including flooding, distance to forest edge and time of year. Oftentimes, woody stems and tree material become a food source for deer during winter when other herbaceous food sources diminish (Rose and Harder 1985).

Objectives

Little is known about the foraging behavior or effects of deer browsing on plant growth and survival in highly productive and dynamic floodplain forests. Some efforts to restore floodplain forests have been hindered by high levels of deer herbivory (Thomsen *et al.* 2011), but it is unclear if this is a universal problem in the UMR, or what the ultimate consequences of this herbivory are for successional trajectories.

This study was designed to address two main questions:

- 1) What levels of deer herbivory are found in floodplain forest restorations across the UMR?
- 2) What methods best control deer herbivory in the floodplain, and what are the interactive effects of flooding and herbivory on tree performance in floodplain forests?

A regional survey of floodplain forest restorations in the UMR was conducted to address the first objective. The survey provided detailed information on tree species composition, levels of deer herbivory, and species specific deer forage preference in numerous restoration settings. The synthesis of information gathered from this study provides a better understanding of the potential importance of deer browsing on tree regeneration at a regional scale. To address the second objective, an exclosure experiment was constructed testing three different fence types in a floodplain forest restoration area. Tree performance in response to browsing and flooding across a hydrological gradient at the site was quantified over two years. The most effective exclosure fence type and interactive effects of abiotic (flooding) and biotic (browsing) factors were quantified.

CHAPTER II
WHITE-TAILED DEER HERBIVORY IN FLOODPLAIN FOREST
RESTORATIONS OF THE UPPER MISSISSIPPI RIVER SYSTEM

Introduction

White-tailed deer (*Odocoileus virginianus*) densities in North America are currently much higher than they were historically, a consequence of decreased predation and more abundant forage following increases in forest edge and agriculture (Côté *et al.* 1994). Browsing by white-tailed deer can modify rates of ecosystem processes and nutrient cycling, and initiate changes in forest structure and community composition that lead to the development of alternate stable states (Hobbs 1996, Augustine *et al.* 1998, Liang and Seagle 2002, Horsley *et al.* 2003). As a result, deer have become an herbivore of concern, especially in upland forests of the Midwest. Alverson *et al.* (1988) implicated deer herbivory in nearly eliminating the recruitment of formerly dominant species in northern Wisconsin, including Canada yew (*Taxus canadensis*), eastern hemlock (*Thuja canadensis*) and white cedar (*Thuja occidentalis*). The same authors further suggested that historical deer densities in much of Wisconsin were between 2-4 deer per km², and a return to these levels is needed to ensure survival of browse-sensitive species. Currently, Wisconsin statewide deer densities exceed this estimate with approximately 8 deer per km² overwintering in 2010 (Wisconsin Department of Natural Resources 2011).

Although much of what we know about deer populations and how they affect ecosystems comes from studies in upland settings, high levels of deer herbivory have also been documented in floodplain forests (Ruzicka *et al.* 2010, Thomsen *et al. in review*). How widespread herbivory is in floodplains and what factors influence browsing rates and preference for particular species in floodplain forests are not well known. The effects of deer in floodplain versus upland settings may differ for several reasons. First, the periodic flooding found in riparian ecosystems profoundly affects plant community composition and structure (Bayley 1995, Yin and Nelson 1996, Clawson *et al.* 2001), adding a level of complexity that does not exist in upland forests. Periodic flooding has also been suggested as a cause of the overall higher productivity of floodplain forests (Junk *et al.* 1989); high nutrient levels may allow plants to compensate for tissue lost to deer browsing better than plants found in upland areas.

Deer activity may also be influenced by periodic flooding in floodplain forests where flooding limits forage accessibility during periods of high water. However, Bowman *et al.* (1998) found that periodic flooding reduces predation on deer and increases fawn survival. Hence, some degree of flooding could attract deer by decreasing habitat quality for predators. It is also possible that deer activity is limited to sites that are highly connected to the mainland and restricted on islands, which are common in geomorphically complex floodplain landscapes.

Furthermore, tree species composition in floodplain forests is dependent on the local flooding regime and geomorphology, since flood tolerance varies among species (Hosner 1958, Sena Gomes and Kozlowski 1980, Yin *et al.* 2009). Deer herbivory may be spatially variable based on variation in tree species composition from site to site,

because deer tend to forage nonrandomly with respect to tree species (Brown and Doucet 1991).

Thus, an interacting suite of factors could influence deer activity in the Upper Mississippi River (UMR) floodplain. Patterns of herbivory are, in turn, likely to influence the success of floodplain forest restoration actions. It is estimated that up to 75% of the historical extent of the UMR floodplain forest has been lost as a result of altered land use including agriculture, urbanization, altered hydrology and invasive species (Yin and Nelson 1996, Knutson and Klass 1998). Restoring floodplain forests in the UMR is becoming a priority of many land-owners and management agencies in this “nationally significant ecosystem” (U.S. Congress 1986, Romano 2010). However, complex interactions among flooding, deer herbivory and invasive *Phalaris arundinacea* (reed canary grass) may prevent tree regeneration in many locations. *Phalaris* is well suited to the moist conditions found in floodplains and rapidly out-competes native wetland vegetation (Herr-Turoff and Zedler 2007, Reinhardt Adams and Galatowitsch 2008); this widespread invasive species is of concern to conservation land managers in the UMR (Miller and Zedler 2003, Romano 2010). It is possible that selective foraging on other species and avoidance of *Phalaris* by white-tailed deer could further increase the likelihood of invasion by the grass (Kellogg and Bridgham 2004).

To assess the role of deer herbivory in floodplain forest restorations of the UMR, we surveyed deer browsing intensity (i.e. proportional plant tissue removal) across fifteen restoration sites of similar age within the UMR floodplain. Data collected from these sites was used to determine: 1) the amount of plant tissue removal by deer in forest

restorations, 2) how flooding affects plant tissue removal, 3) whether plant tissue removal differs on islands and 4) whether deer display preferences for particular tree species.

Methods

Study Sites

Field surveys at 15 floodplain forest restoration sites within eight management areas along the UMR and its tributaries were conducted in the summers of 2010 and 2011 (Figure 1). Management areas were defined as land under the control of a single management entity. Some management areas contained multiple restoration sites; when multiple sites were surveyed within a single management area, they were separated by a minimum of 200 m. Management areas ranged from Wabasha, Minnesota in the north to New Albin, Iowa in the south, spanning approximately 120 km along the UMR. Land management agencies were contacted to locate sites similar in age (~ 3 years old) and size (greater than 0.5 ha) to a restoration site near La Crosse, WI (WKTY), where an experimental manipulation of deer browsing was being conducted (Chapter 3). We selected sites that were in areas historically considered bottomland hardwood forests (Great Lakes Ecological Assessment 2011). In all sites included in the study, *Phalaris* had either been partially controlled through herbicide applications or was naturally absent from the site. Sites were also selected to compare mainland with island settings (70-1200 m from the riverbank; Table 1). Information about site history, including year and method of *Phalaris* control, seeding and planting, are presented in Table 1.

Field Surveys

Sampling took place during late summer to early fall in 2010 within plots measuring 2.25 m² placed at 10 m intervals along three evenly spaced (~20 m) parallel

transects 50 m in length at each site. If site size or shape was not suitable for three transects, fewer transects or plots were used. A smaller 0.25 m² quadrat was centered within each plot. Measurements were taken on each tree within the 0.25 m² quadrat if tree density was greater than 12 trees/m². If density was less than 12 trees/m² within the 0.25 m² quadrat, measurements were taken in the larger 2.25 m² plot. Trees greater than 200 cm in height were not included in the survey as they are assumed to have escaped white-tailed deer browse height (Ross *et al.* 1970). At WKTY, permanent sample points not situated along transects were used because they had been previously established in a concurrent study. Plot-level averages of five subplots within each of five large (300 m²) control (unfenced) plots were used instead (Chapter 3). The Kruger, Root River, Spring 1-3, Walter, WKTY, and Zumbro 2 & 3 sites were resurveyed in late summer of 2011.

Trees were identified to species, or genus in the case of willows, oaks, ashes and hickories. To document the amount of plant tissue removed by deer, the number of stems browsed in the winter prior to sampling was counted on each tree greater than one year old that occurred within each plot. Winter browsing was distinguished by noting the season in which a bite was taken, which was identifiable by the bite location and appearance of growth from the previous year (Figure 2). Percent consumption at a site was calculated as the mean of percent consumed across all sample plots. Individual percent cover estimates of *Phalaris*, other herbaceous plants, and tree species were made visually within each plot (percent covers for the three groups together typically exceeded 100%). Cover in a site was calculated as the mean of each respective cover across all plots. The height of the three trees closest to three corners of each plot was measured to

the nearest 5 cm, and a mean of plot values was used to estimate site tree heights. Due to lower stem densities in 2011 all measurements were taken in a 1 m² plot.



Figure 1. Regional surveys were conducted summer 2010 at 15 floodplain restoration sites within eight management areas (○) along the Upper Mississippi River and its tributaries. Ten restoration sites were resurveyed in summer 2011.

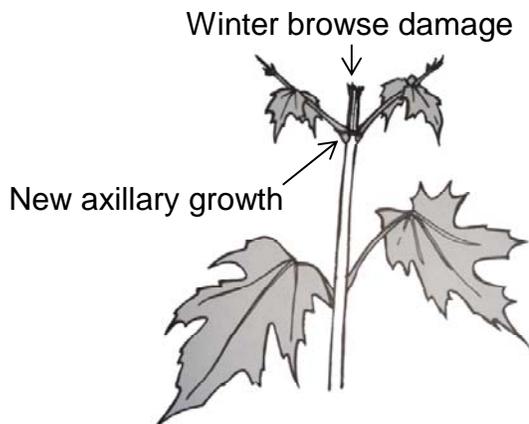


Figure 2. Diagram of winter browse evidence on a silver maple sapling. A withered, woody stem with a frayed bite indicates terminal bud removal from winter deer browsing. New growth from axillary buds directly below browsed bud indicates that browsing occurred during the winter previous to observation. Assuming that what is shown comprises all branches for a particular tree, this would be scored as one bite taken out of one available, or 100% consumption during the previous winter.

Table 1. Site locations and treatment history information of floodplain forest restoration management areas in the Upper Mississippi River system and its tributaries surveyed in summers 2010 and/or 2011.

Management area	Location	Manager	Coordinates (DD)	Area (ha)	Treatment history
Kruger 1 & 2	Trib.-FPF	MNDNR	44.336° -92.074°	12.6	Even-aged timber harvest, planted* 2008; planted 2009
Goose Island	UMR-FPF	USACE	43.719° -91.232°	6.7	Site prep, seeded, planted ~2005
New Albin	UMR-WM	USFWS	43.508° -91.279°	2.1	Herbicide 2007, 2008; seeding or natural seed input 2009
Root River	UMR-FPF	USFWS	43.769° -91.289°	2.8	Natural seed input 2009; selective herbicide and site prep, planted 2010
Spring 1	UMR-ISL	USACE	44.204° -91.837°	6.5	Island constructed, natural seed input 2006; planted 2008; herbicide 2009
Spring 2	UMR-ISL	USACE	44.194° -91.841°	2.1	Island constructed, natural seed input 2006; planted 2008; herbicide 2009
Spring 3	UMR-ISL	USACE	44.202° -91.844°	2.6	Island constructed, natural seed input 2006; planted 2008; herbicide 2009
Spring 4	UMR-ISL	USACE	44.208° -91.861°	1.7	Island constructed, natural seed input 2006; planted 2008; herbicide 2009
Spring 5	UMR-ISL	USACE	44.212° -91.866°	2.1	Island constructed, natural seed input 2006; planted 2008; herbicide 2009
Walter	UMR-FPF	USFWS	43.761° -91.278°	0.7	Herbicide 2007, 2008; seeding or natural seed input 2009
WKTY	UMR-FPF	USACE	43.740° -91.210°	4.2	Mechanical site prep 2006, herbicide 2006, 2007, 2008; seeded 2007, 2008, 2009, stake planting 2007, 2008
Zumbro 2 & 3	Trib.-FPF	MNDNR	44.312° -92.119°	13.1	Disking site prep, broadcast seeded 2008, 2009; herbicide 2009
Zumbro 4	Trib.-FPF	MNDNR	44.321° -92.125°	5.0	Mechanical site prep and broadcast seeded, herbicide 2003; planted and seeded, herbicide 2004; browse barrier 2006

UMR=Upper Mississippi River; FPF=floodplain forest; Trib.=tributary to Mississippi River; WM=wet meadow; ISL=island; MNDNR=Minnesota Department of Natural Resources, USACE=US Army Corps of Engineers, USFWS=US Fish and Wildlife Service; Planted= planting of seedlings or saplings

Analysis

We examined the relationship between flooding and plant tissue removal by deer qualitatively at WKTY because measurements of water surface elevation and seasonal consumption by white-tailed deer were being made as part of a concurrent study (see Chapter 3 for methodology). Mean 2010 tree densities in sites with and without reed canary grass were compared with a Student's t-test. The effects of mean 2010 percent cover of other herbaceous plants on tree density and percent consumed were evaluated using simple linear regression. We also compared mean percent consumption during winter 2010 with mean percent consumption during winter 2011 with a Student's t-test. To determine whether plant tissue removal differed between isolated island sites and mainland sites, we used Student's t-tests of differences in mean percent consumption between island sites and all other sites during 2010 and 2011 respectively. Proportional data were arcsine-square root transformed, and other data were transformed as necessary to improve their normality and equality of variances.

Finally, deer preferences for particular tree species were examined using an electivity index (E) (Jenkins 1979):

$$E = \ln \left[\frac{r \times (1 - p)}{p \times (1 - r)} \right] \quad \text{Eq. 1}$$

where r = proportion of a species' stems browsed relative to all stems browsed across species and p = proportion of a species' stems available relative to all stems available across species). This calculation standardizes for unequal stem abundances and indicates a difference in preference based on the assumption the browsing is equal among species. Index values less than zero indicate avoidance, whereas E values greater than zero suggest a preference for a given species. A X^2 calculation:

$$X^2 = \frac{E_i^2}{\left(\frac{1}{x_i} + \frac{1}{m - x_i}\right) + \left(\frac{1}{y_i} + \frac{1}{n - y_i}\right)} \quad \text{Eq. 2}$$

was used to compare E values among species using a χ^2 distribution with one degree of freedom. For species i , E is electivity, x = stems browsed, y = stems available $m = \Sigma$ all stems browsed, $n = \Sigma$ all stems available. Regional electivity was calculated from the sums of all browsed and available stem estimates from 2010 and 2011. Electivities for certain species that were either unbrowsed or rare were not calculable. Management area-specific electivities were calculated for Kruger, Spring, WKTY and Zumbro from the sum of all stems browsed and available in each respective management area. All data analyses were performed with JMP[®] 9.0.2 (SAS Institute Inc., Cary North Carolina) and SigmaPlot[®] 12.0 (Systat Software Inc., San Jose, California).

Results

Site Characteristics

The sites we surveyed were highly variable in plant cover, tree density and height as well as consumption (Table 2). A comparison of all sites surveyed in 2010 found that sites with *Phalaris* had significantly lower tree densities than sites without the grass ($t_{15} = -2.42$, $P < 0.029$; Figure 3). *Phalaris* cover ranged from nearly 95% at the Root River site in 2010 to 0% at several sites. On average, *Phalaris* cover across the region 2010-11 was approximately 14%. Other herbaceous plants represented the largest percent cover regionally with 57% cover on average over the sampling period, reflecting ongoing management actions aimed at suppressing *Phalaris* at these sites. Other herbaceous cover was negatively related to tree density ($R^2 = 0.26$, $F_{1,15} = 5.32$, $P < 0.036$; Figure 4). Other herbaceous cover was greater than 90% in 2010 at both Kruger sites as well as the New

Albin 2, where tree densities were near zero percent tree cover in Zumbro 2 and 3 was high in 2011 with greater than 53% cover compared to less than 1% found in several other sites, which were best characterized as herbaceous wet meadow (New Albin). Density of trees greater than one year old and less than 200 cm tall was substantially higher at the WKTY site than any other site in 2010, with four times as many trees/m² as the site with the second highest density (Root River). However, in 2011, the Root River site surpassed WKTY in density following a decline of more than 50% at WKTY and a greater than three-fold increase at Root River. Regionally, average tree density was about 4.6 trees/m².

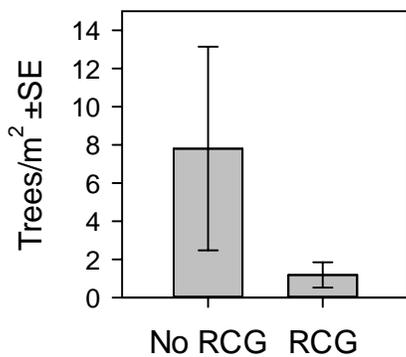


Figure 3. Sites surveyed in summer 2010 that contained *Phalaris* (RCG) had significantly lower tree densities than sites without (see text for t-test statistics).

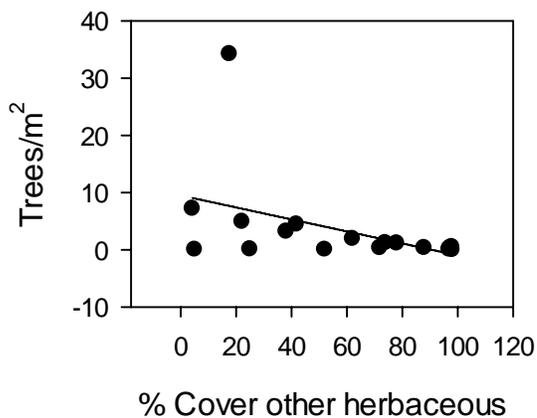


Figure 4. Other herbaceous cover in all sites surveyed summer 2010 was negatively related tree density (see text for regression statistics).

Table 2. Data from summer 2010 and 2011 surveys of UMR floodplain forest restoration sites. Names refer to management areas, numbers to the individual sites we sampled within some management areas.

Site	Year	% <i>Phalaris</i>	% Other	% Trees	Trees/m ²	Tree height	% Consumed
Goose Island	2010	48.4±12.9	52.0±13.0	3.5±3.3	0.03±0.03	98.0	0
Kruger 1	2010	0.2±0.1	97.9±1.7	0.5±0.1	0.50±0.16	40.3±11.3	13.54±8.02
	2011	4.8±4.7	80.6±7.7	0.3±0.3	0.06±0.06	55.0	66.67
Kruger 2	2010	2.7±2.3	97.3±2.3	0	0.36±0.36	11.1	0
	2011	0	86.7±8.4	7.5±7.5	0.10±0.10	375.0	0
New Albin 1	2010	2.6±0.6	96.9±0.7	0.1±0.1	0.04±0.04	-	-
New Albin 2	2010	1.5±0.5	98.0±0.7	0.3±0.1	0	-	-
New Albin 3	2010	45.8±8.2	25.0±5.9	0	0.07±0.05	75.0±20.0	80.77±11.54
Root River	2010	94.7±2.1	4.2±1.7	5.5±2.1	7.20±1.80	94.1±10.4	1.82±0.98
	2011	78.8±6.7	20.7±7.2	36.3±9.9	26.1±6.73	64.1±6.8	2.08±2.08
Spring 1	2010	0.4±0.3	87.9±5.1	3.9±2.2	0.36±0.20	43.8±12.0	0
	2011	0	89.3±4.6	8.5±5.3	3.20±1.95	85.7±11.2	0
Spring 2	2010	0.7±0.7	73.9±4.5	5.4±2.1	1.19±0.26	83.0±16.5	10.28±8.34
	2011	0	83.2±3.6	23.1±6.5	3.40±0.80	124.2±14.5	0
Spring 3	2010	0	62.0±8.5	9.8±3.4	1.87±0.44	58.9±7.2	0.77±0.77
	2011	0	74.8±5.2	6.4±4.9	2.20±0.85	69.8±12.3	0
Spring 4	2010	0	78.0±5.5	4.4±2.4	1.11±0.53	67.4±13.7	8.93±8.23
Spring 5	2010	0	71.9±7.6	1.1±0.7	0.31±0.18	108.3±53.2	4.17±4.17

Walter	2010	4.5±1.5	5.0±3.0	0.8±0.1	0.03±0.03	-	-
	2011	76.8±7.4	26.4±7.1	0.5±0.2	1.42±0.66	15.6±1.8	0
WKTY	2010	0	17.6±5.9	-	34.2±4.28	40.7±1.8	57.88±5.34
	2011	0	-	-	16.32±2.49	86.9±6.7	0.07±0.04
Zumbro 2	2010	0	22.1±6.6	14.6±3.5	4.89±1.24	21.6±2.1	47.30±6.41
	2011	0.3±0.3	40.9±9.2	60.7±7.7	5.36±1.03	74.8±8.5	7.87±3.31
Zumbro 3	2010	0	41.8±9.5	10.0±2.6	4.41±0.86	20.6±1.0	36.17±5.75
	2011	0	10.3±3.2	53.8±7.2	5.75±0.76	73.7±10.4	3.73±1.56

-= no measure

Factors Affecting Deer Browsing

Herbivory varied widely among sites, but the majority of sites we surveyed experienced some level of consumption (Table 2). Estimates of over-winter deer densities during 2010 and 2011 were similar; in survey sites located in Wisconsin densities ranged from 8-11 deer/km²(Wisconsin Department of Natural Resources 2011), and in Minnesota sites from 4-8 deer/km² (Minnesota Department of Natural Resources 2011). A large reduction in consumption occurred from winter 2010 to 2011, coincident with unusually high flood levels. At the WKTY site, where the mean site elevation was submerged 28.8% and 90.2% during the growing seasons of 2010 and 2011 (Chapter 3, Figure 5a), consumption decreased from 57% to less than 1%. Similar declines in consumption occurred regionally, with consumption declining significantly from greater than 20% on average in winter 2010 to less than 5% in winter 2011 ($t_{14}=-2.40$, $P<0.03$; Figure 5b).

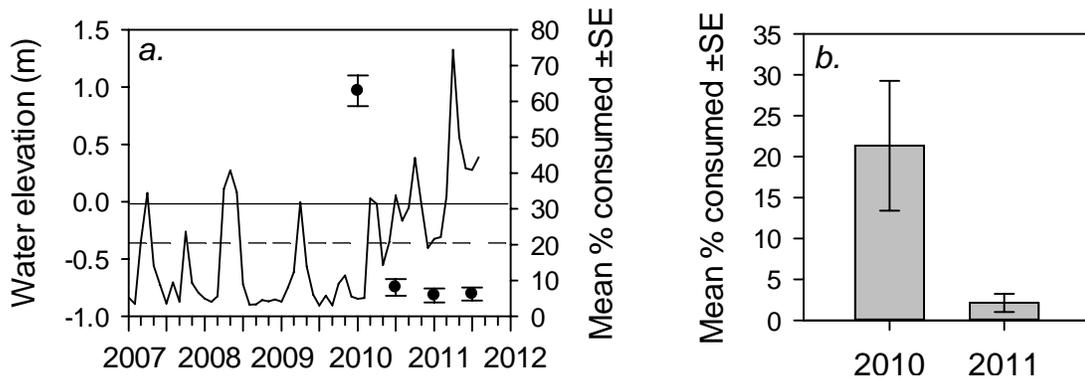


Figure 5. a) Hydrograph of Mississippi River water levels and consumption at the WKTY research site. Solid horizontal line indicates mean plot elevation (193.27 m above sea level), whereas dashed line is the lowest plot (0.24 m lower than mean elevation). See Chapter 3 for details on how elevations were estimated. b) Mean percent consumed in winters 2010 and 2011 in UMR restoration sites. Mean consumption in winter 2010 was significantly greater than winter 2011 (see text for t-test statistics).

Mean percent consumption during winter 2010 and 2011 was significantly greater at mainland sites than at island sites ($t_{17}=-2.11$, $P<0.05$; Figure 6). Percent consumption on mainland sites was on average nearly six times as great as island sites during 2010 and 2011. The highest consumption level on an island was 16% in 2010 compared to 61% on the mainland. In 2011 no consumption occurred on islands whereas the highest level found on the mainland was 8%.

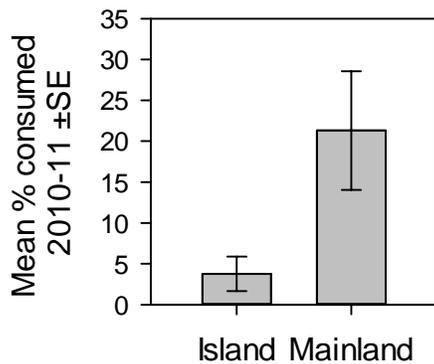


Figure 6. Mean percent consumption on island and mainland sites over winter 2010 and 2011. Percent consumption was significantly different between the two settings (see text for t-test statistics).

Consumption in winter 2010 increased with the density of trees present in a site (Table 3; Figure 7a). Low levels of consumption were never found at sites with greater than 3 trees/m². The relationships shown in Figure 4 also suggest that percent consumption plateaus at high tree densities; a consumption threshold appeared to be near 55% with increases in tree density beyond approximately four trees/m². A significant relationship between density and percent consumed was also found in 2011 (Table 3), but consumption levels were much lower than in those measured in 2010. A consumption threshold was also apparent in 2011 as sites with fewer than four trees/m² experienced very little browsing.

Table 3. Results of three-parameter sigmoidal regression analyses for the relationship between mean percent consumed and tree density at regional sites in 2010 and 2011.

Year	R ²	F	P
2010	0.84	F _{2,8} =21.62	<0.001
2011	0.74	F _{2,5} =6.98	<0.036

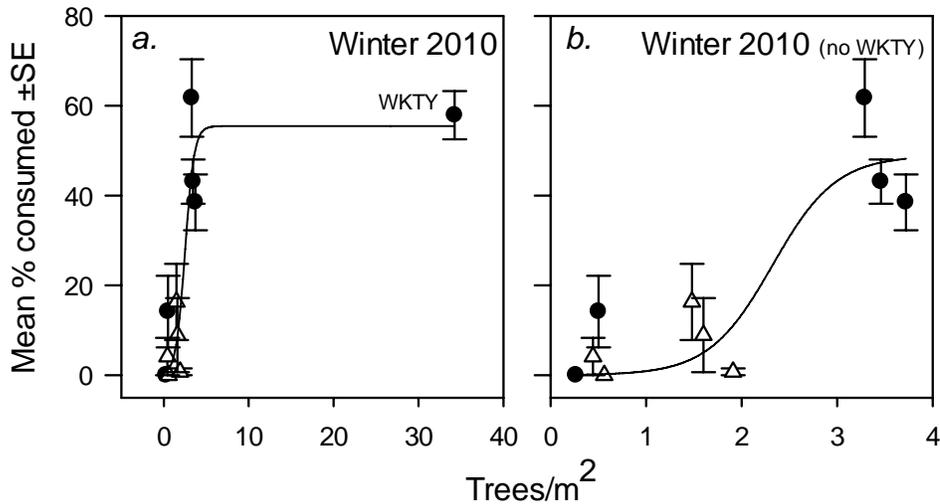


Figure 7. a) Mean winter 2010 percent consumption was significantly related to tree density (see Table 3 for regression statistics). The WKTY site had much higher tree densities than other sites in 2010. b) A comparison of island sites (Δ) and other floodplain (\bullet) sites excluding WKTY illustrating density and isolation effects on consumption.

Tree species composition varied among sites in 2010 and 2011, but in general silver maple, cottonwood, box elder, elm, and willow spp. were found most frequently (Table 4). General electivity estimated across all sites suggested that deer showed the strongest preference for silver maple while ash and elm were also slightly preferred (Table 4, Figure 8). Deer most strongly avoided oak and willow while elm and silver maple were highly preferred.

Table 4. Species frequency and electivity χ^2 statistics for all trees in observed and/or measured during summers 2010 and 2011. Frequency indicates the number of sites in which a species was found at least once.

Common name	Scientific name	Frequency	χ^2	P
American elm	<i>Ulmus americana</i>	7	398.8	<0.001
Ash spp.	<i>Fraxinus</i> spp.	6	15.52	<0.001
Black locust	<i>Robinia pseudoacacia</i>	3	-	-
Black walnut	<i>Juglans nigra</i>	3	0.87	>0.05
Box elder	<i>Acer negundo</i>	7	0	>0.05
Eastern cottonwood	<i>Populus deltoides</i>	8	7.63	<0.01
Hackberry	<i>Celtis occidentalis</i>	2	-	-
Hickory spp.	<i>Carya</i> spp.	1	0.58	>0.05
Oak spp.	<i>Quercus</i> spp.	6	6.32	<0.03
River birch	<i>Betula nigra</i>	2	-	-
Silver maple	<i>Acer saccharinum</i>	9	175.9	<0.001
Willow spp.	<i>Salix</i> spp.	7	51.53	<0.001

-= not measured or uncalculable

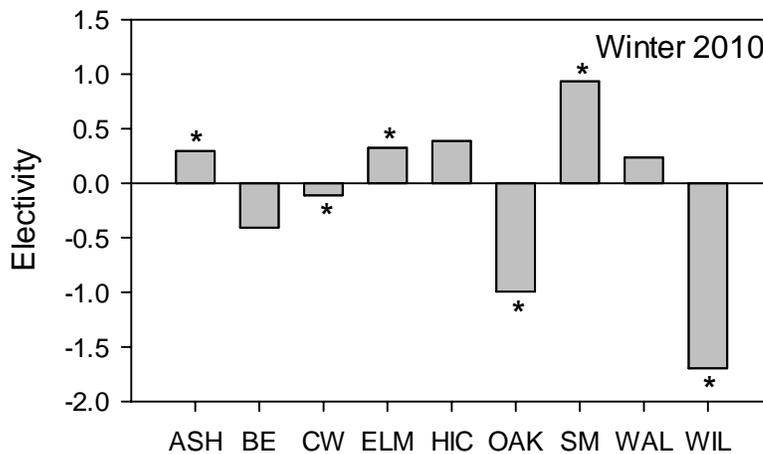


Figure 8. Electivity index based on winter 2010 browse and tree abundances. Trees evaluated included ash spp. (ASH), box elder (BE), cottonwood (CW), American elm (ELM), hickory spp. (HIC), oak spp. (OAK), silver maple (SM), black walnut (WAL) and willow spp. (WIL). Preferences for ash, elm and silver maple and avoidance of cottonwood, oak spp. and willow spp. were statistically significant, * indicates statistical significance (see Table 4 for χ^2 statistics).

Within individual management areas (Table 5), negative electivity values for winter 2010 consumption indicate that box elder, hackberry and black locust were avoided; no consumption was ever observed on either hackberry or black locust. Certain species were slightly preferred or avoided depending on the area, these included; ash

spp., cottonwood, oak and willow spp. Deer appeared to browse randomly in the Kruger and WKTY areas. Significant preference and avoidance was found for some tree species in two restoration areas; in the Spring area deer preferentially selected cottonwood while willow was highly avoided, whereas in the Zumbro area deer significantly avoided box elder and preferred American elm.

Table 5. Comparison of stems available (A), consumed (C) and electivity (E) winter 2010 by tree species in select management areas. Consumption levels that were significantly* different than proportional abundance are shown in bold.

Restoration area	Ash spp.			Box elder			Cottonwood			American elm			Hackberry			Hickory spp.		
	A	C	E	A	C	E	A	C	E	A	C	E	A	C	E	A	C	E
Kruger	11	0	<i>NB</i>	6	0	<i>NB</i>	-	-	-	13	2	0.61	-	-	-	2	1	1.76
Spring	-	-	-	-	-	-	142	13	1.22	-	-	-	-	-	-	-	-	-
WKTY	77	38	-0.17	-	-	-	2	1	-0.12	-	-	-	-	-	-	-	-	-
Zumbro	17	8	-0.20	75	23	-0.69	76	31	-0.38	327	228	0.52	7	0	<i>NB</i>	-	-	-

Restoration area	Black locust			Oak spp.			Silver maple			Black walnut			Willow spp.		
	A	C	E	A	C	E	A	C	E	A	C	E	A	C	E
Kruger	-	-	-	-	-	-	-	-	-	5	1	0.76	-	-	-
Spring	3	0	<i>NB</i>	57	2	-0.35	-	-	-	-	-	-	237	6	-1.08
WKTY	-	-	-	-	-	-	240	140	0.11	-	-	-	20	13	0.16
Zumbro	-	-	-	16	9	-0.02	66	34	-0.12	2	2	0.56	-	-	-

* χ^2 analysis (df=1, $P < 0.05$), -= no measure, *NB*= no browse observed, -= uncalculatable

Discussion

The effects of deer browsing in upland forests have been well documented (Brown and Doucet 1991, Horsley *et al.* 2003, Miller *et al.* 2009, Wakeland and Swihart 2009, Crimmins *et al.* 2010). Relatively few studies have investigated deer browsing in periodically inundated floodplain sites. In this study we have shown that browsing occurs in the floodplain forest of the UMR, that it is spatially and temporally variable, and that it is influenced by numerous site characteristics. On average, deer removed 21% of all available stems across our sites during 2010 (as high as 61%), but consumption declined to less than 5% during 2011. These estimates are comparable to consumption levels found in similarly aged upland sites. In upland forests, consumption has been found ranging from less than 5% (Miller *et al.* 2009, Crimmins *et al.* 2010) to approximately 35% in hardwood forest of the northeast (Kitteredge 1995).

We conclude that the large decrease in consumption by deer from 2010 to 2011 reflected two consecutive long-duration flood events in 2010 and 2011. The high water of 2010-11 was preceded by several years of very low water conditions on the UMR. Flooding appears to be a regional factor that limits deer browsing in floodplains during the early parts of the growing season. When flooding extends into the growing season, it may significantly reduce floodplain accessibility and shorten the duration that sites are exposed to deer.

Geomorphic context also appeared to limit herbivory in some floodplain sites. Island sites ranged between 70-1200 m from the mainland and it appeared that the cost associated with reaching these sites outweighed the benefit of forage availability. Mainland sites with densities lower than the islands were often browsed more heavily;

mainland sites with only two trees/m² more than islands experienced twice as much consumption in 2010. A number of factors could explain low consumption levels on island sites including species composition and low tree density, as well as energy expenditure from swimming, exposure to predators, unstable winter ice, etc.

Another site-level factor influencing herbivory was tree density. Consumption generally increased with higher tree densities. This suggests that as forest restoration efforts become successful in terms of seedling establishment, managers may need to consider increased deer herbivory, especially on mainland sites within easy access to deer. However, we found that consumption leveled off at high tree densities, consistent with other studies of consumer foraging (Holling 1959, Spalinger and Hobbs 1992). Herbivory often levels off at high forage availability because many of the mechanisms that regulate plant intake are mutually exclusive (e.g. biting, chewing and searching for food) (Spalinger and Hobbs 1992). In our study, consumption leveled off at roughly 55% when tree densities were greater than four trees/m². This response suggests that when control of deer herbivory is not feasible at a site, managers could dissipate the effects of browsing by establishing high seedling densities.

Consumption was always low (<20% of available stems) at sites with densities less than two trees/m². Effects of high levels of browsing at sites with low plant densities can have large effects on plant growth and community composition (Augustine *et al.* 1998, Ruzicka *et al.* 2010). Ruzicka *et al.* (2010) showed that herbivory in areas of low tree density further slowed canopy closure by reducing tree height growth and allowed some encroachment of invasive species. Augustine *et al.* (1998) more generally showed that high browsing levels at sites with low plant density can lead to complete extirpation

of some plant species, causing shifts to entirely new community compositions.

Restoration sites in the UMR with low tree densities do not appear to be subject to similar dynamics.

Tree density was negatively related to other herbaceous cover in 2010, which may be explained by consumption-related limitation of tree height (Horsley *et al.* 2003) and subsequent resource competition from fast growing, less-browsed herbaceous plants. Horsley *et al.* (2003) found that percent cover of ferns, sedges and grasses increased with increasing deer density in areas of logged upland forest. Deer avoided certain herbaceous plants while browsing preferable tree species. However, the low browsing estimates observed at sites with low plant densities indicate that deer may not become problematic in forest restoration sites until higher plant densities are achieved.

Another factor that influenced deer herbivory in floodplain forest restorations was tree species composition which is a function of propagule supply (flooding, seed trees, etc.) as well as management activity (seeding and planting). We found evidence of deer forage preference among floodplain tree species, similar to nonrandom foraging behavior observed in the upland forests (Brown and Doucet 1991). Although not all forage selection was significantly different from forage abundance, we found that in the greater UMR, silver maple was highly preferred ($E=1.5$) while oak ($E=-0.8$) and willow spp. ($E=-1.7$) were strongly avoided. Electivity only reflects deer preference among an assemblage of species at a site and variability may be explained by site specific composition and other external factors. Certain electivities calculated from a bottomland forest restoration study in southern Illinois (Ruzicka *et al.* 2010) were similar to our findings, suggesting a preference for American elm and silver maple and an avoidance of

box elder. However, while we found avoidance, oak spp., were strongly preferred or heavily browsed in bottomland restorations described by Stewart *et al.* (2008) and Ruzicka *et al.* (2010). The low browsing rates we observed on oak spp. might have been due to the relatively low oak densities at our sites, tree age, or the inclusion of different oak species included in these other studies. Electivity in upland sites is also highly variable. For example, oak spp. have been described as a preferred or highly browsed species in some sites (Strole and Anderson 1992, Hygnstrom *et al.* 2009, Wakeland and Swihart 2009), or in some cases browsed in proportion to its abundance (Kittredge 1995, Crimmens *et al.* 2010). Maples are generally a preferred food source in upland forests (Horsley *et al.* 2003) while silver maple, more commonly a bottomland species, has also been found to be preferred in forests of Indiana (Wakeland and Swihart 2009). Although Strole and Anderson (1992) found that sugar maple (*Acer saccharum*) is avoided. Willow has also been found to be a preferred forage species in some upland settings (Gill 1992, Bergman *et al.* 2005), while electivity calculated from Brown and Doucet (1991) indicated deer avoided, remained neutral and preferred pussy willow (*Salix discolor*) in each of the three years they sampled, respectively.

Selective foraging can lead to shifts in species composition in upland forests (Horsley *et al.* 2003), with species that are avoided or tolerant of browsing increasing relative to heavily browsed or species tolerant of browsing. Similar patterns may occur in floodplain forests as deer selectively forage in this system, providing a relative benefit to less heavily browsed species such as willow and oak. We never observed browsing of *Phalaris* and it is possible that high browsing rates at some sites could promote invasion or reinvasion by the grass. Control of *Phalaris* must continue to be a management

priority as tree density was lower in sites that contained *Phalaris*, potentially a result of decreased tree seedling survival (Hovick and Reinhartz 2007). Given that the impact of deer on plant growth and species composition depends on both the preference for and amount of plant tissue removed by deer from specific species as well as the ability of different species to compensate for lost tissue, future research is needed to determine consumption levels sufficient to decrease tree height growth and survival in floodplain forests.

CHAPTER III

**THE INTERACTIVE EFFECTS OF DEER HERBIVORY AND FLOODING ON
TREE RECRUITMENT IN FLOODPLAIN FORESTS**

Introduction

Floodplain forest ecosystems are among the most diverse and productive in the world. Spatial and temporal heterogeneity in flooding creates a mosaic of environmental conditions and plant species (Conner and Day 1976, Naimen *et al.* 1993, Yin and Nelson 1996, Clawson *et al.* 2001). A complex set of abiotic and biotic dynamics in the aquatic-terrestrial transition zone (i.e. the floodplain) regulate the exchange of materials between rivers and uplands (Junk *et al.* 1989) as well as plant community composition and structure (Yin *et al.* 2009). Ecosystem dynamics in the river floodplain forest are highly influenced by abiotic factors associated with periodic flooding such as sedimentation, erosion, scour, nutrient fluxes and increased soil moisture (Barnes 1985, Naimen *et al.* 1993, Bayley 1995, Hughes and Cass 1997, Richter and Richter 2000, Whited *et al.* 2007). Prolonged inundation reduces soil redox potentials affecting plant performance through decreased rates of photosynthesis, and increased costs associated with resource reallocation and morphological changes (Pezeshki 2001).

Although abiotic factors (flooding and its effects) in the floodplain have long been recognized as strong drivers of successional patterns and species composition, less consideration has been given to the effects of biotic factors or the interaction of biotic and

abiotic factors on plant species performance. In upland forests, plant performance is strongly influenced by large herbivores, often leading to changes in, productivity and nutrient cycling (Coté *et al.* 2004) and initiating shifts in community structure through high levels of herbivory (Augustine *et al.* 1998). Large herbivores can also alter plant architecture (De Jager and Pastor 2010). Trees that experience repeated browsing often remain shorter and become bushier, providing unbrowsed species a competitive advantage (Bergström and Danell 1987, Anderson and Katz 1993, De Jager and Pastor 2010). Trees may respond differently to browsing in periodically flooded areas where flooding related subsidies result in high productivity (Mitsch *et al.* 1991). In resource rich conditions, plants may overcompensate in response to herbivory (Gao *et al.* 2008) often with increased growth or biomass accrual that more than compensates for lost tissue (McNaughton 1983, Christel and Bergström 2006).

Angell and Kielland (2009) found that herbivory and moisture-related effects can influence the performance of individual trees in boreal floodplain ecosystems; larger-scale analyses have also shown that flooding and herbivory influence successional trajectories in boreal floodplains (Butler *et al.* 2007). Furthermore, herbivory by white-tailed deer (*Odocoileus virginianus*) has been found to limit the success of efforts to restore floodplain forests in temperate regions (Sweeney *et al.* 2002, Ruzicka *et al.* 2010, Thomsen *et al. in review*). However, no study has accounted for possible interactive effects of flooding and herbivory on plant growth and recruitment in temperate floodplain forests. Deer exclosures have been used extensively to research plant response to a release from herbivory (Hester *et al.* 2000), however few studies have examined the

effectiveness and cost of alternative enclosure fence types in a periodically inundated setting.

The goal of this study was to quantify the effects of flooding and white-tailed deer browsing on tree recruitment within a temperate hardwood forest in the Upper Mississippi River (UMR) floodplain. The UMR extends from Lake Itasca, MN to Cairo, IL and has been recognized by Congress as “a nationally significant ecosystem” (U.S. Congress 1986). However, navigational dams, logging, agriculture and development have resulted in a loss of up to 75% of the historic floodplain forest (Yin and Nelson 1996, Knutson and Klaas 1998). Navigation dams have altered the natural flooding regime in this reach, reducing low flow conditions and increasing inundation both spatially and temporally (Theiling 1996). Although the floodplain forests of the UMR are home to an array of native plant species adapted to periodic flooding, altered hydrology may be responsible for a recent shift in tree species dominance as well as a decline in diversity (Theiling 1996, Yin and Nelson 1996, Yin *et al.* 2009). Loss of forest has affected the numerous bird species that use the UMR as a migratory corridor as well as the availability of food, shelter, breeding grounds, and nursery habitat for a multitude of other animal species (De Calesta 1994, Smith 1996). As a consequence, floodplain forest restoration has become a goal of UMR managers (Romano 2010). Efforts to restore floodplain forests currently suffer from a lack of information regarding the role both biotic and abiotic factors play in limiting tree recruitment.

We established a series of enclosures along an elevation gradient in a UMR floodplain forest site to determine 1) whether trees require protection from herbivory in highly productive floodplain forests, 2) what type of enclosures provides the best

protection from browsing, and 3) how tree height growth, survival and community composition are affected by browsing and/or elevational differences in flood duration. We predicted that trees protected from browsing (those in exclosures of high quality) would experience lower rates of browsing by deer, that increasing browsing rates in poor quality exclosures or controls would lead to decreased height growth and increased mortality, and that the effects of deer browsing would be more pronounced at lower elevation sites that experience deeper water levels and longer durations of inundation during the flood pulse. We further predicted that the combined effects of browsing and flood inundation would lead to changes in tree species composition through time and across the elevational gradient present in our site.

Methods

Study Site

To evaluate the effects of herbivory and flooding on tree recruitment, we constructed a series of deer exclosures along an elevation gradient at a floodplain forest restoration site adjacent to the Mississippi River (43°44.3' N, 91°12.6' W) south of La Crosse, WI on land owned by the US Army Corps of Engineers (USACE) (Fig. 1). Restoration efforts at the site began in 1998 after straight-line winds blew down ~4.2 ha of floodplain forest. The site was salvaged logged and subsequently invaded by reed canary grass (*Phalaris arundinacea*) despite management efforts to promote tree seedling establishment. In the fall of 2006, a new round of restoration treatments including mowing, tilling, and herbicide were initiated. Natural seedfall from surrounding trees and some hand-seeding of native tree species followed herbicide applications. The restoration strategy successfully controlled reed canary grass by August 2009 (Thomsen *et al.* in

review). A dense seedling bed of 2-3 year old silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvaticus*), willow (*Salix* spp.) and eastern cottonwood (*Populus deltoides*) was present at the site at the commencement of the study described here.

Deer Exclosures

The research site lies on the border of two deer management units, and deer densities in these units were comparable to Wisconsin state averages with approximately 11.1 deer/km² in fall 2010 and 8.4 deer/km² in winter 2011 (Wisconsin Department of Natural Resources 2011). Densities at the site were thus higher than the estimated sustainable density of 2-4 deer/km² suggested for Wisconsin, based on historic deer densities and tolerances of trees susceptible to browse (Alverson *et al.* 1988).

In late November 2009 we constructed fifteen 300 m² exclosure fences in the restoration area to determine the best method for reducing deer browsing. We compared three fence types:

- 1) 2.4 m polypropylene mesh fence (Kencove Farm Fence Inc., Blairsville, PA),
- 2) 2.4 m solar-powered six-strand electrical fencing (1.2 cm electric ribbon; Stafix®, Mineral Wells, TX; Magnum 12 V fence charger; Parmak®, Kansas City, MO), and
- 3) Plotsaver™ (Messina Wildlife Management, Washington, NJ), a strong-smelling chemical deer repellent.

The polypropylene mesh (hereafter “mesh fence”) and electrical fencing (hereafter “electric fence”) were strung on 2.4 m tall metal fence posts spaced approximately 5 m apart. The mesh fences were further supported by a 3.26 mm nylon cable wire affixed to post tops. To prevent sub-fence entry, a 1.94 mm high tensile wire was woven through the base of the mesh fence and secured with ground staples. Plotsaver™ (hereafter

“chemical fence”) was applied monthly to a 1.78 cm woven plastic fabric ribbon strung on plastic fence posts approximately 1 m tall, spaced every 5 m. Each enclosure method was replicated five times and applied to randomly assigned treatment plots located in the area where *Phalaris* had previously been controlled (Figure 1). Five additional plots of equal size with no barriers served as controls, for a total of 20 plots.

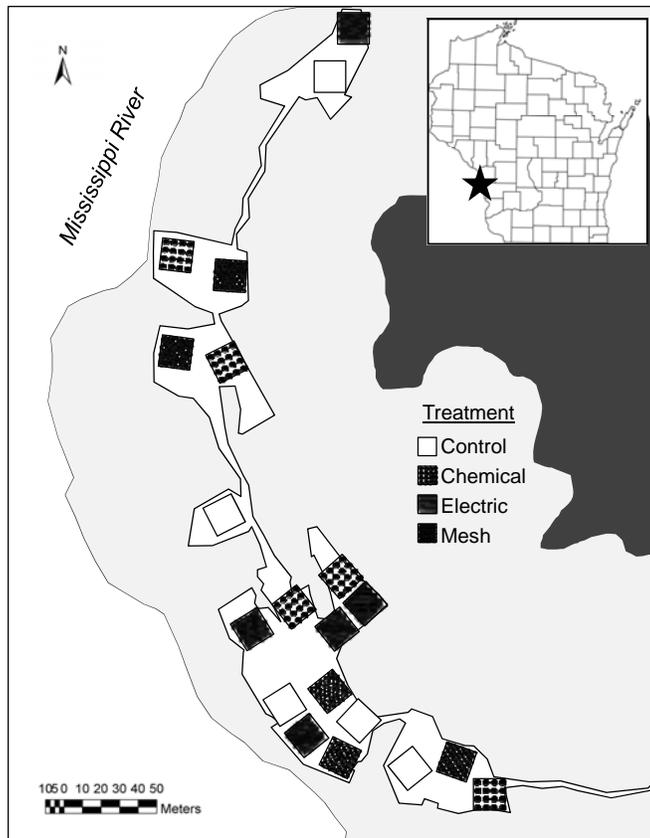


Figure 1. Floodplain forest research site managed by the US Army Corps of Engineers, located along the Mississippi River near La Crosse, WI. Twenty plots were established in a 4.2 ha restoration area in which *Phalaris* had previously been controlled (white areas within black outline). The restoration area was separated from a field of untreated *Phalaris* (dark gray) by intact floodplain forest (light gray).

Plant Growth and Browsing Measurements

Winter deer track surveys were conducted to estimate the effectiveness of enclosure fences when snow was present. Sampling occurred during the winters of 2009-

10 and 2010-11 (hereafter referred to as winter 2010 and 2011) preceding predicted snowfall. We counted the number of deer tracks in a 1 m² area at three points along three evenly spaced transects in each plot. Track density was determined by dividing mean number of tracks/m² per plot by days since last snow fall to obtain an estimate of the number of tracks/m²/week.

In March 2010 we established five permanent sampling points within each enclosure and control plot to monitor browse levels as well as tree performance (Figure 2). The sampling points used in previous work conducted at the site (Thomsen *et al. in review*) were used whenever they occurred within the exclosures. Additional subplots were established to create a rough checkerboard of sampling points within each enclosure, as shown in Figure 2.

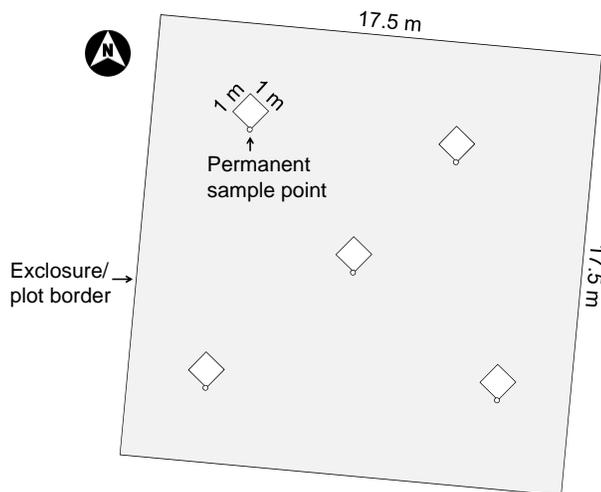


Figure 2. Schematic of enclosure and control plot layout; five permanent sampling points were marked within each 300 m² plot. Sampling was conducted within 1 m² quadrats located to the north of each permanent point. Plot-level averages calculated from the five subplot measurements were used for all analyses reported here.

Plant growth and browse measurements were made twice yearly, first in the early spring following snowmelt and again near the end of the growing season in 2010 and 2011. winter 2011 data was not recorded at the species level due to a very short sampling

window between snowmelt and flooding. To quantify browsing and its effects, we sampled a 0.25 m² subplot at each permanent sample point; when tree densities were fewer than 12 stems/m², the sampling area was expanded to 1 m². Within each subplot, tree species, height, and number of stems browsed and unbrowsed by deer were recorded for each individual. Tree density in a plot was calculated by dividing the sum of individuals within subplots by the sum of subplot areas. Percent change in density was calculated as the change in tree densities between winter 2010 and summer 2011. The total number of stems available in a plot was divided by total subplot area to determine stems available/m². Tree height was estimated in winter 2010 by selecting three trees of each species (ash, cottonwood, silver maple, willow spp.) as available at three corners of each subplot. During subsequent sampling periods height was measured for all trees within a subplot. Height was measured with a meter stick or a 2 m plastic pole with height markings on it to the nearest 1 cm in winter 2010 and summer 2010 and nearest 5 cm in summer 2011. Mean tree height was calculated as the average of heights of all trees or trees of a species measured in a plot. Annual tree height growth rate was calculated as the change in height from the spring sampling period (early May) to the fall sampling period (early October), and overall growth during the experimental period was calculated as the change in height from winter 2010 until summer 2011 per plot. Percent of trees escaping herbivory was calculated as the proportion of all measured trees within a plot that were >200 cm tall which has been considered to be beyond the reach of a deer (Ross *et al.* 1970).

All browsing estimates were conducted by a single researcher throughout the course of the experiment. The number of stems available for deer browsing was

quantified based on stem position and typical deer browsing behavior and maw size. Browsed stems in winter were quantified by counting the number of terminal buds removed whereas in the summer, browsed leaves originating from a single stem constituted a bite. Deer browsing was identified and tallied separately from occasional muskrat (*Ondatra zibethicus*) and North American beaver (*Castor canadensis*) herbivory at the site, distinguishable by the jagged and frayed versus cleanly chiseled appearance of bites typical of deer and rodents, respectively.

Percent consumption by deer was calculated as the proportion of stems removed relative to the total stems available in a plot from summed subplot data. Stems higher than 200 cm were excluded from consumption measurements. Mean percent consumption by treatment was determined by averaging plot level consumption across the site by treatment. Mean percent consumption by tree species was determined by averaging plot-level data by species. Proportion of diet each tree species represented was calculated by dividing the sum of a browsed stems of a species within a plot by the total number of stems browsed in that plot.

Deer preference for or avoidance of the four most common woody species in the site (ash, cottonwood, silver maple and willow spp.) were determined using an electivity index:

$$E_i = \ln \left[\frac{r_i(1 - p_i)}{p_i(1 - r_i)} \right] \quad \text{Eq. 1}$$

where r_i is the proportion of stems browsed from species i and p_i is the proportion of stems of species i that are available. This calculation standardizes for unequal stem abundances. Index values less than zero indicate avoidance, whereas values greater than zero suggest a preference for a given species. The total number of stems browsed and

available by species in winter 2010, summer 2010 and summer 2011 from across the site, excluding mesh fences, were summed to determine electivity. X^2 values were calculated to evaluate the statistical significance of E_i based on one degree of freedom (Jenkins 1979):

$$X^2 = \frac{E_i^2}{\left(\frac{1}{x_i} + \frac{1}{m - x_i}\right) + \left(\frac{1}{y_i} + \frac{1}{n - y_i}\right)} \quad \text{Eq. 2}$$

where E_i is electivity for species i , x_i is the number of stems browsed of species i , y_i is the number of stems of species i available, m is the number of stems browsed across all species and n is the number of stems available across all species.

Elevation and Flooding Measurements

We determined plot elevations by recording water depth at the five permanent sample points within each exclosure and control plot during a single period of inundation during spring 2010. Hourly river gage heights (USACE 2011) were used to estimate water surface elevation at the study site when the water depth measurements were taken. Sample point elevations were then determined by calculating the difference between measured water depths and estimated water surface elevation. Plot elevation was calculated as the mean of the five permanent sample point elevations within each plot, which revealed a gradient of elevations within each browsing treatment (Figure 3). Relative plot elevations were also calculated as the difference of each plot elevation from the average of all plot elevations. Finally, daily river stage estimates from the same gages were used to calculate the number of growing season days that each treatment plot was flooded during the study. Plot elevation and mean tree height winter 2010-summer 2011

were summed and then used to calculate the proportion of the two growing seasons that the top shoot of trees, or tree-top was submerged.

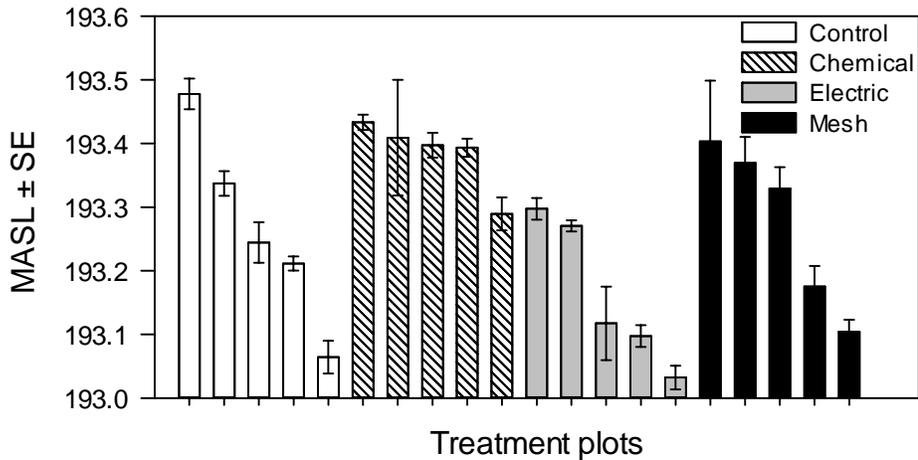


Figure 3. Elevations of five permanent sample points within a plot were pooled to determine mean plot elevation in meters above sea level (MASL). An elevational gradient existed within and among treatments to allow for evaluation of flooding effects while considering herbivory levels. There was a difference of 44.6 cm between the lowest and highest plots.

Analysis

Over the course of the study, we observed very high rates of plant mortality, which substantially reduced the number of individual trees for each of the most dominant species (ash, cottonwood, silver maple, willow spp.). Consequently our analyses focus on changes in tree height and change in density across all species. Data analysis was performed with JMP[®] 9.0.2 (SAS Institute Inc., Cary North Carolina). Plot level data were transformed as necessary to improve their normality and equality of variances. The effects of exclosure type on track density and percent consumption of available stems by deer were evaluated with one-way ANOVA; Tukey-Kramer post-hoc analyses were used to evaluate pairwise differences. The effects of winter 2010 percent consumed, plot

elevation and the interaction between consumption and elevation on tree height, annual vs. total height growth, change in tree density, and percent of trees escaping browse height were analyzed using backwards stepwise multiple linear regression. Changes in density were also examined as a function of the percent of the growing season that the tree-tops were submerged. Finally, relative abundance of each species was estimated for winter 2010, summer 2010 and summer 2011 within each plot and then grouped by both percent consumption and elevation quantiles.

Results

Deer Browsing and Flooding

Winter deer track surveys indicated that enclosure effectiveness was significantly different among fence types (Table 1, Figure 4). Mesh fences completely excluded deer and electric fences provided moderate protection, whereas no significant difference between chemical and control plots was found. Although a gradient of track density was found among the treatments, only the mesh fence significantly reduced percent consumed in winter 2010 (Table 1, Figure 5). Consumption was high in all but the mesh enclosures during winter 2010, with 40-75% of available stems browsed, compared to 20% consumed in the mesh fence plots (browsing that occurred prior to fence construction). Trees were browsed differently in winter versus summer months. Winter herbivory usually involved complete removal of apical buds whereas summer herbivory usually involved tissue removal from young leaves near the top of the tree.

A large decrease in percent consumption was found in all enclosure types during the remainder of the study, corresponding with unusually high water levels on the Upper Mississippi River (Figure 6). From 2005-2009, the mean site elevation was inundated on

average 8.8% of the growing season and 14.9% of the growing season the lowest plot was flooded. During the growing seasons of 2010 and 2011 the mean plot elevation was submerged 28.8% and 90.2% respectively, while the lowest plot was inundated 45.1% and 100%. During these two years of high water, very little browsing occurred across the plots so the winter 2010 browsing estimates were used as the main metric of browse intensity in subsequent analyses.

Table 1. One-way ANOVA results of the effects of exclosure type on deer track density and percentage of plant tissue consumed by deer during winter 2010.

Measure	F	P
Tracks/m ² /wk	F _{3,16} =14.65	<0.0001
Mean % consumed	F _{3,16} =10.58	<0.0005

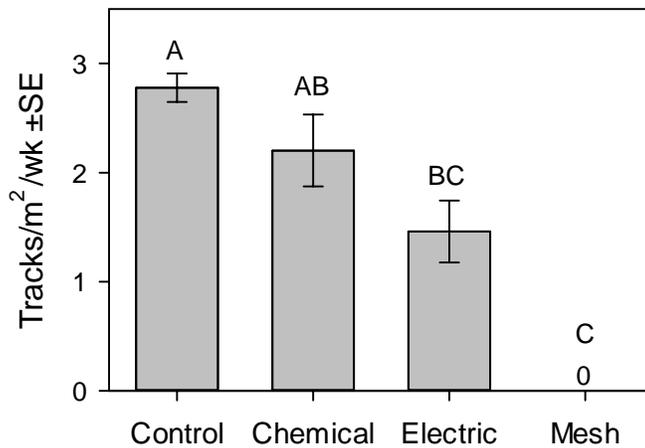


Figure 4. Winter 2010 fence effectiveness as measured by mean deer track densities. Track densities differed significantly among exclosure types (see Table 1 for ANOVA statistics). Letters indicate significant differences among treatments (Tukey-Kramer HSD post-hoc tests).

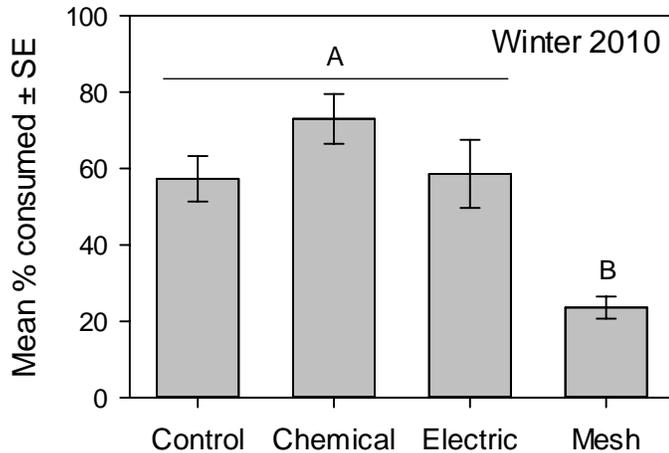


Figure 5. Mean percent consumption of tree seedlings during winter 2010 across the four enclosure types. Browsing in mesh fences likely occurred prior to fence construction in November 2009, since deer tracks were never observed in those plots (see Figure 4). Consumption estimates differed significantly among fence types (see Table 1 for ANOVA statistics), but only mesh fences significantly reduced browse levels relative to unfenced controls. Letters indicate significant differences among treatments (Tukey-Kramer HSD post-hoc tests).

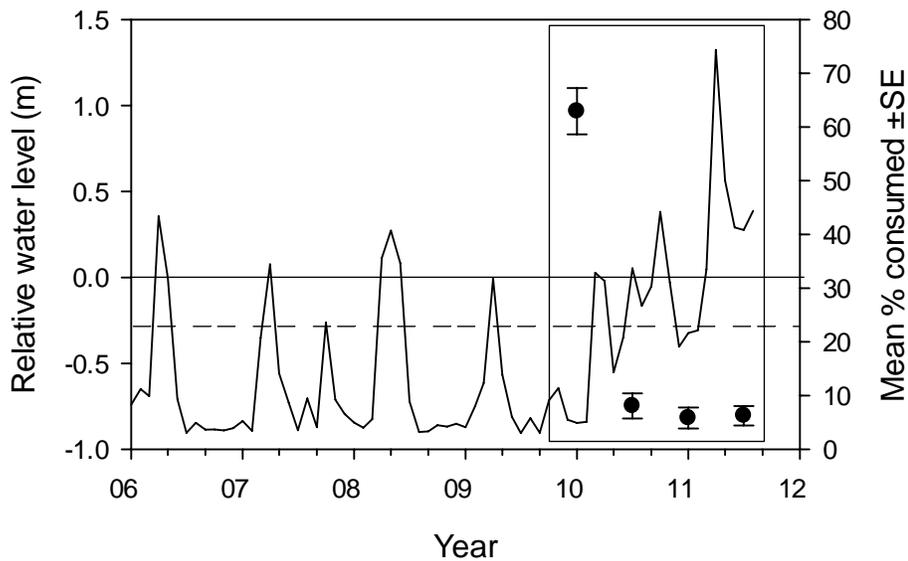


Figure 6. Hydrograph of Mississippi River water levels at the research site south of La Crosse, WI, January 2006-August 2011. Solid horizontal line indicates mean plot elevation (193.27 m above sea level), whereas dashed line is the lowest plot (0.24 m lower than mean elevation). Study period is enclosed in rectangle. Mean percent consumption over the course of the study is shown for all plots excluding mesh enclosures.

Across the site, silver maple was dominant winter 2010-summer 2011 while cottonwood was the least abundant (Figure 7a). Cottonwood densities were 0.6 trees/m² and willow 1.3 trees/m² but cottonwood experienced consumption levels three times as high as willow and was the most heavily browsed species at the site relative to its availability (Figure 7b). Electivity values for each species based on the total number of stems available during the study period indicate, however, that deer were selectively browsing (Figure 7d). Silver maple was significantly preferred while ash and willow were avoided (Table 2). No significant preference or avoidance was found for cottonwood, but a positive electivity value suggests a weak preference for the species.

Table 2. Electivity χ^2 statistics calculated from winter 2010-summer 2011 data for all plots excluding mesh exclosures.

Tree	χ^2	<i>P</i>
Ash	16.00	<0.001
Cottonwood	2.53	>0.05
Silver maple	30.21	<0.001
Willow	11.83	<0.001

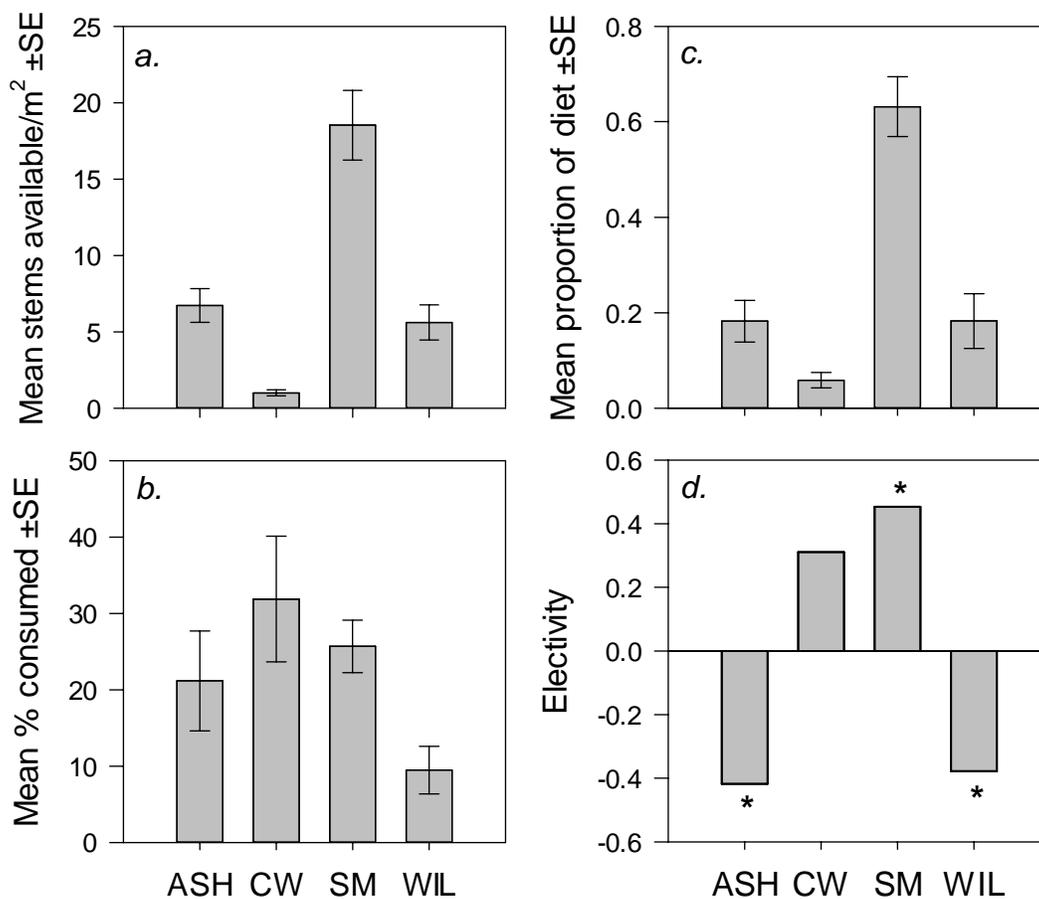


Figure 7. Comparison of green ash (ASH), cottonwood (CW), silver maple (SM) and willow (WIL) a) mean available stem density, b) mean percent consumed, and c) mean proportion of diet from winter 2010–summer 2011. d) Electivity values (based on the total number of stems available across winter 2010, summer 2010 and summer 2011) varied among tree species. Avoidance of ash and willow and preference of cottonwood and silver maple were significant (see Table 2 for statistics).

Effects of Browsing and Flooding on Tree Recruitment

Tree height following winter 2010 was negatively related to percent consumed during the winter 2010 (Table 3, Figure 8a); trees in plots that received the greatest amount of deer browsing (>80%) were on average 20 cm shorter than those that received the least (approximately 20%). Neither plot elevation ($F_{1,16}=0.51$, $P>0.48$) nor the interaction between consumption and elevation ($F_{1,16}=3.01$, $P>0.10$) significantly affected

tree height at the end of winter 2010. By the end of summer 2011, trees in plots that had experienced little or no browsing in winter 2010 were nearly a meter taller than those in plots that were browsed heavily (Figure 8b) and the relationship between percent consumed winter 2010 and height summer 2011 was significant (Table 3). Neither plot elevation ($F_{1,16}=1.05$, $P>0.31$) nor the interaction between consumption and elevation ($F_{1,16}=1.45$, $P>0.24$) significantly affected tree height growth or estimated height in summer 2011. Tree height growth rates, the difference between mean heights winter 2010 and summer 2011, were significantly affected by percent consumed in winter 2010 (Table 3, Figure 8c), but not by plot elevation ($F_{1,16}=0.84$, $P>0.37$) or the interaction between consumption and elevation ($F_{1,16}=0.71$, $P>0.41$). Trees that were protected from browsing grew approximately 80 cm per year compared to 40 cm per year in plots with the highest levels of consumption.

Table 3. Linear regression statistics for the response of tree heights in winter 2010 and summer 2011 and growth rates between winter 2010 and summer 2011 to percent consumed winter 2010.

Measure	R ²	F	P
Height winter 2010	0.48	$F_{1,18}=16.82$	<0.0008
Height summer 2011	0.49	$F_{1,18}=17.46$	<0.0007
Height growth	0.40	$F_{1,18}=11.93$	<0.0001

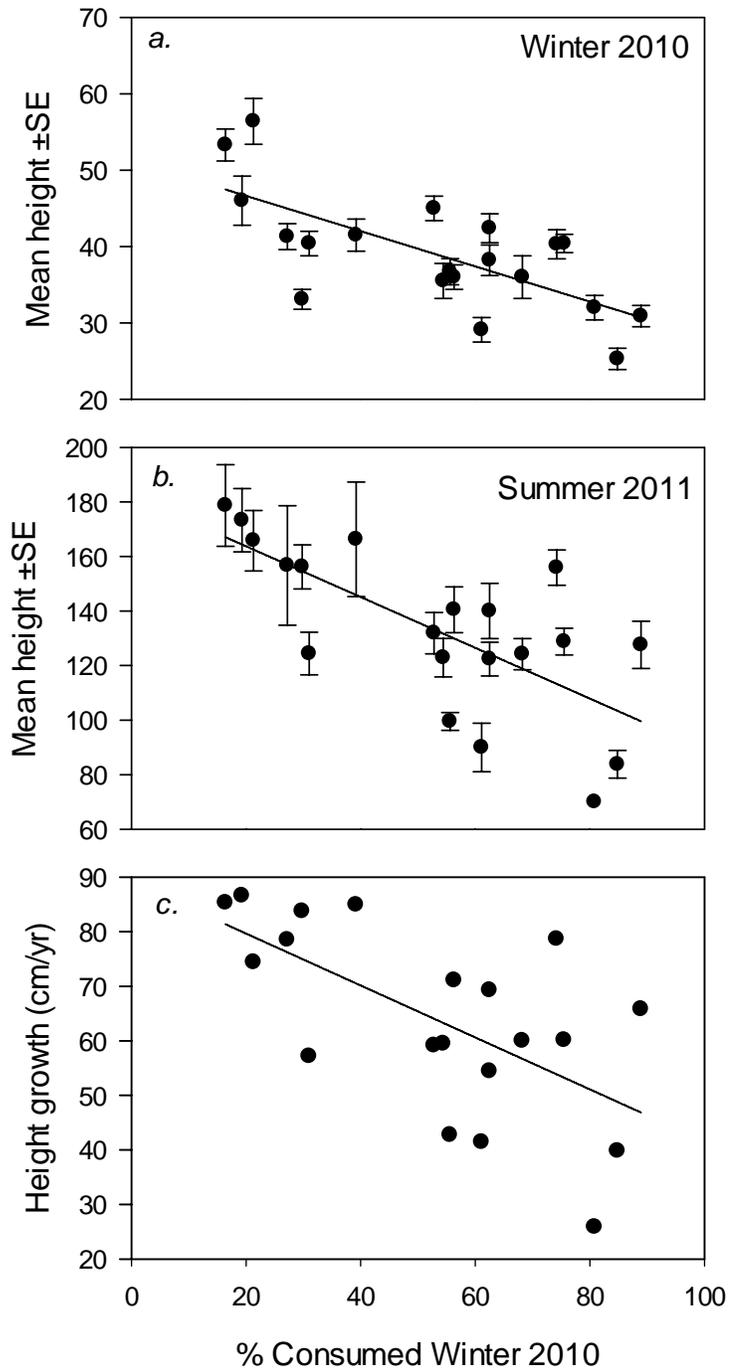


Figure 8. Consumption in winter 2010 significantly reduced a) tree height in winter 2010, b) tree height in summer 2011, and c) tree height growth between winter 2010 and summer 2011 (see Table 3 for regression statistics).

Percent change in tree density was related to plot elevation (Table 4, Figure 9), but not percent consumption ($F_{1,16}=1.91$, $P>0.19$) or the interaction between elevation and consumption ($F_{1,16}=1.22$, $P>0.28$). Changes in tree densities ranged from -20% in the highest elevation plots to -100% in the lowest elevation plots (100% mortality). Percent change in density was also significantly related to mean tree-top elevation (the sum of mean plot elevation and mean tree height) (Table 4, Figure 10), indicating that tree survival was greater in plots where there were more trees above the flooding depth. Declines in density were greater (approaching 100%) among shorter trees in low areas. Again, no significant relationship was found in response to percent consumption ($F_{1,16}=0.30$, $P>0.59$) or the interaction between elevation and consumption ($F_{1,16}=0.002$, $P>0.96$).

Table 4. Linear regression statistics for the percent change in tree density winter 2010-summer 2011 as explained by plot elevation and percent of growing season (GS) plot and mean tree-top heights were submerged.

Explanatory variable	R ²	F _{1,18}	P
Plot elevation	0.44	14.16	<0.002
% GS plot flooded	0.43	15.20	<0.001
% GS tree-top flooded	0.46	15.20	<0.0001

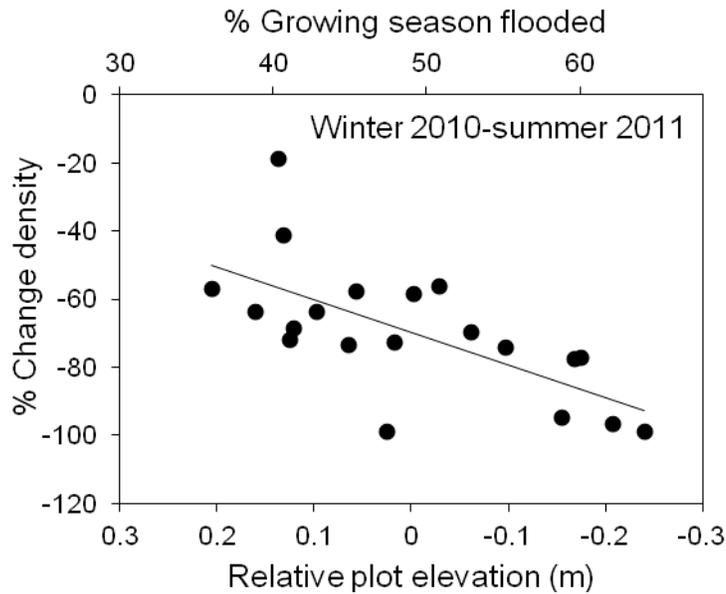


Figure 9. Percentage change in plot mean tree density from winter 2010-summer 2011 was significantly related to plot elevation and total percent of growing season in which plot was flooded. Elevation of zero indicates mean plot elevation of the research site (see Table 4 for regression statistics).

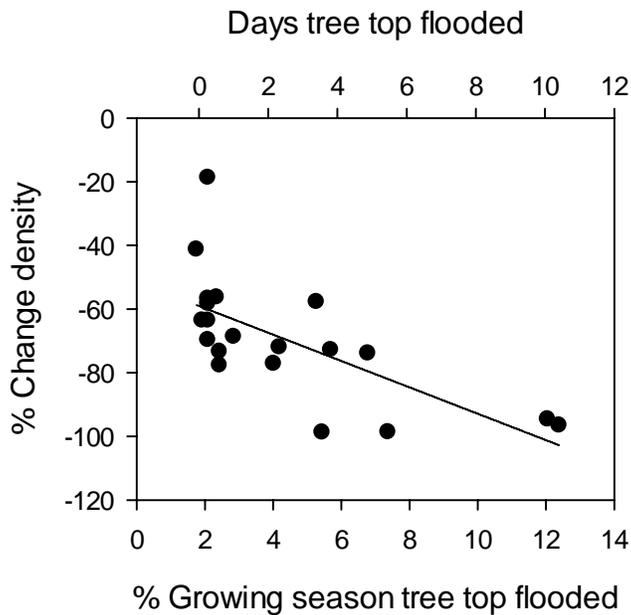


Figure 10. Tree mortality was significantly related to a plot's topographic position and mean tree height within the plot. Mean plot elevation and mean tree height winter 2010-summer 2011 were summed and then used to calculate the proportion of the two growing seasons that tree-top height was submerged (see Table 4 for regression statistics).

No trees had escaped potential deer browse (>200 cm) in winter 2010. After summer 2010, 1.5% of all measured trees had escaped, and by summer 2011, 12.5% of all surviving trees had reached escape height. Although there was a trend towards greater percent escape in mesh enclosures (25%) compared to the other plots (9%), this difference was not significant. However, percent escape was significantly affected by percent consumed winter 2010 (Figure 11; $R^2=0.57$, $F_{1,18}=23.63$, $P<0.0001$), such that 30% of the trees escaped in plots in which <40% of available stems were browsed, compared to >9% in those experiencing >75% consumption. The effects of elevation ($F_{1,16}=0.04$, $P>0.85$) and the interaction ($F_{1,16}=2.64$, $P>0.12$) had no significant effect on the number of trees >200 cm tall.

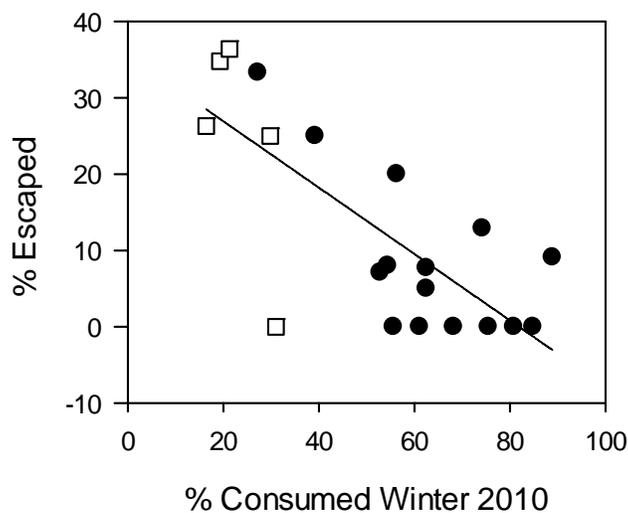


Figure 11. Winter 2010 consumption was significantly related to the likelihood of a tree reaching escape height (>200 cm) by summer 2011. Generally, the proportion of trees escaped by summer 2011 was higher in mesh enclosures (□) versus other plots (●).

Community-level Effects

Relative abundances of tree species at the site level changed over the course of the study. Density changes among species were relatively uniform independent of protection; no significant difference was found in percent change in density from winter 2010 to

summer 2011 by treatment ($F_{3,16}=2.08$, $P>0.14$). Over the course of the study (winter 2010-summer 2011), ash and willow densities decreased by <40% compared to a >75% reduction in cottonwood and silver maple. Total tree densities across the site decreased from a high of 27.9 trees/m² in the winter 2010 to 8.2 trees/m² by summer 2011. Similar changes in abundance among protected versus unprotected plots suggests that topographical position influenced shifts in species composition more significantly than protection from herbivory (Figure 12).

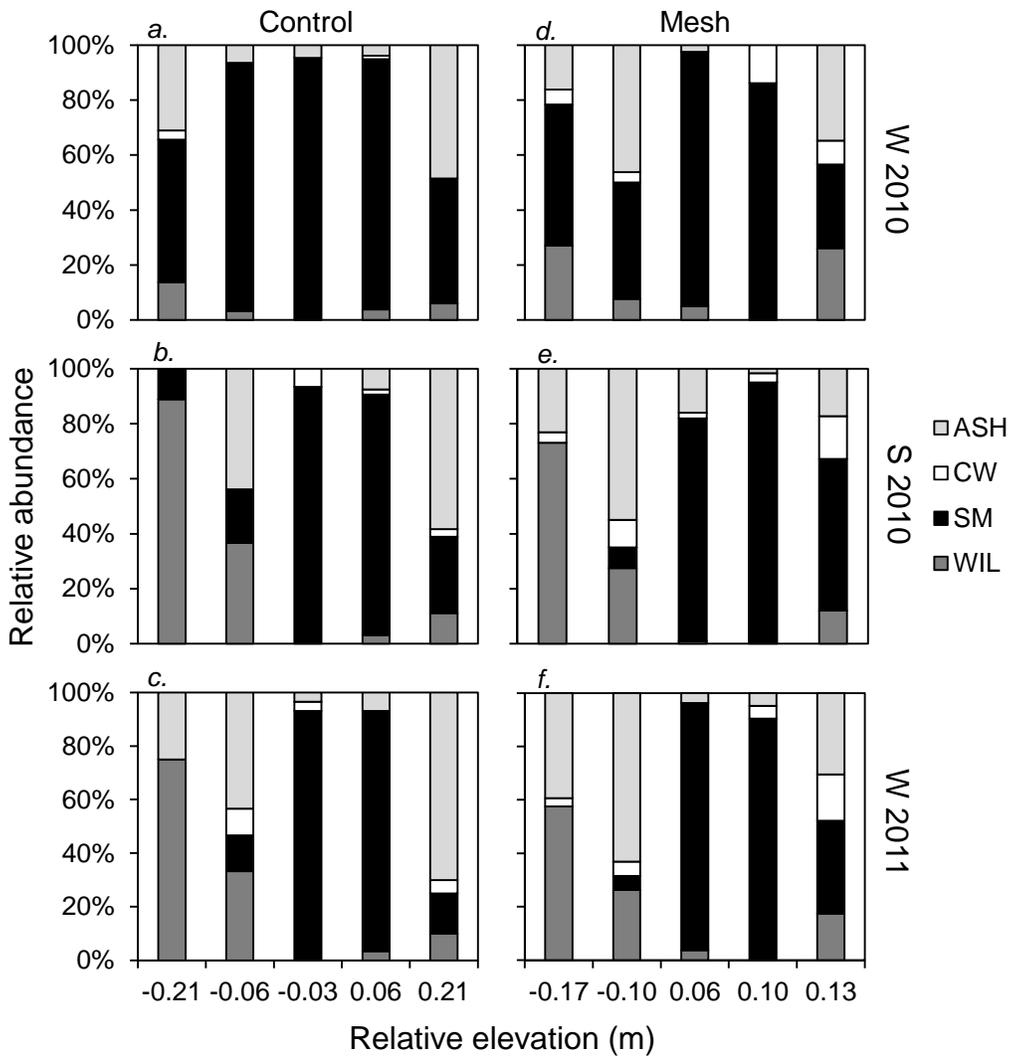


Figure 12. Changes in mean tree species composition from winter 2010-summer 2011 in all control and mesh plots arranged by elevation.

During winter 2010, the lowest control and mesh plots were similar in composition; 51% silver maple and 14-27% willow (Figure 12a,d). By summer 2011, no silver maple remained in either plot (Figure 12c,f). Mid-elevation control and mesh plots were also similar, silver maple represented 86-95% of the population initially in winter 2010 and similar proportion (92-96%) remained in summer 2011 (Figure 12a,c,d,f).

A comparison of changes in relative abundances of all plots grouped by elevation suggests that compositional shifts were not uniform across the site's elevational gradient. The five lowest plots (Figure 13a) experienced a shift from silver maple dominance in winter 2010 to ash (52%) and willow (40%) dominance by summer 2011. Willow and ash increased in abundance as well in the five lower-mid plots (Figure 13b), but silver maple remained dominant (54%) in these plots by summer 2011. The third group of plots (Figure 13c) remained relatively unchanged with silver maple representing >84 % of all trees at all sample points. The final group (Figure 13d) also remained relatively unchanged, again silver maple was dominant (>50%) and ash increased slightly from 24-27%.

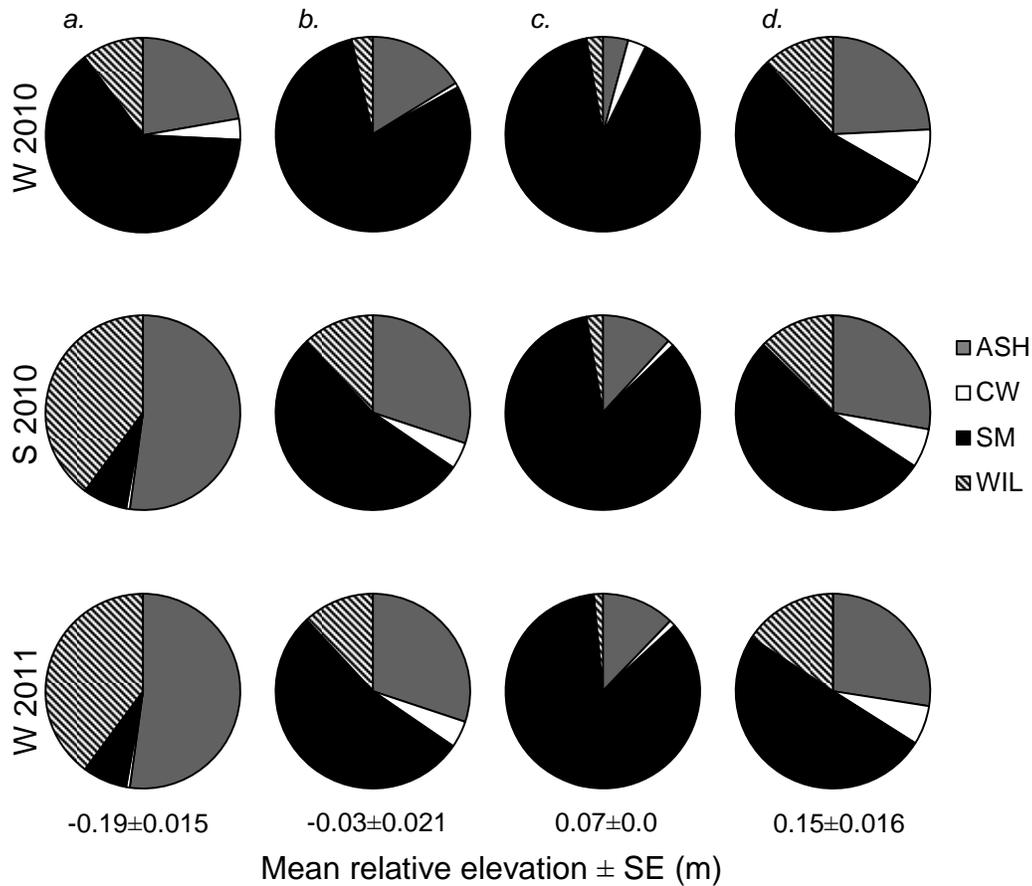


Figure 13. Changes in mean tree species composition from winter 2010-summer 2011 across all plots based on plot elevation. Five of the 20 total plots were assigned to each quarter; a) the lowest quarter, b) the lower-mid quarter, c) the upper-mid quarter, and d) the highest quarter.

Discussion

Excluding Deer and Effects of Browsing

Butler *et al.* (2007) demonstrated the importance of interactions between biotic and abiotic factors in determining plant composition at a landscape scale in boreal floodplain systems. We too have shown that biotic and abiotic factors, in the form of white-tailed deer herbivory and flooding, interact to influence plant growth and recruitment in a young temperate floodplain forest.

In our study, we documented high rates of deer browsing during winter 2010, in keeping with previous work at the same site (Thomsen *et al. in review*) and studies in other floodplain forests (Sweeney *et al.* 2002, Ruzicka *et al.* 2010). Consumption by large herbivores has been found to alter ecosystem structure and function in temperate upland forests (Côté *et al.* 1994, Augustine *et al.* 1998, Hobbs 1996, Liang and Seagle 2002, Horsley *et al.* 2003), but in floodplain forests, levels of herbivory may be influenced by flooding. Higher water levels during summer 2010-2011 likely restricted deer access to the site, leading to a decline in herbivory. During winter 2011 there was little browsing at the site though regional deer densities were similar in winters 2010 and 2011. It is possible that deer were forced out of the area by summer flooding and had established new feeding areas for winter 2011. However, Bowman *et al.* (1998) found that periodic flooding may in fact reduce predation and increase fawn survival likelihood, creating potential refuges. The floods that our study site experienced during 2010 and 2011 were apparently long enough to limit deer activity. Our data and observations suggest that deer activity and plant tissue consumption in floodplain forests can be extremely high, but modified by flood frequency and duration.

Just as large herbivores are influenced by the unique characteristics of the floodplain ecosystem, restoration practitioners in floodplain forests face unique challenges in protecting young trees from deer browsing. Similar to other settings where mesh-style fences have been found to provide the best long-term deer protection (Ver Cauteran *et al.* 2006), the mesh fences in our study were the most effective. We never found evidence of deer herbivory within mesh exclosures post construction, whereas all other fence types were breached. However, the mesh fence we used was the most costly

in terms of materials and construction labor, and post-flood maintenance was often required on these fences as debris accumulated on the upstream sides. An unintended consequence of the mesh fences was the netting of certain fish species that enter the floodplain to spawn or forage during spring floods (Starrett 1951). Several northern pike (*Esox lucius*), longnose gar (*Lepisosteus osseus*) and channel catfish (*Ictalurus punctatus*) were among fish netted. Although we attempted to visit the site frequently during high waters to release fish, frequent mortality still resulted. Furthermore, mesh fences did not offer protection from beaver or muskrats that occasionally swam or pushed themselves under fences (*pers. observation*) and severed some saplings at the waterline.

Electric fences have been used as an effective method to exclude deer and are cost efficient and effective in both upland and agricultural settings (Craven and Hygnstrom 1994, Ver Cauteran *et al.* 2006). Although these fences were relatively inexpensive and easy to construct, they required frequent maintenance and were not well suited to the floodplain. During periods of high water, the fences tended to short out and had to be disconnected from chargers when water levels submerged the lower wires. Floods carried woody debris that settled on the fences, pulling down wires as the water receded. The resulting fence power loss and disrepair may have led to the lack of effectiveness of the electric fences in the floodplain. The chemical fence was easy to construct and maintain and was the least costly of the three fence types, but it appeared to offer trees little protection. Possible explanations for this include lack of volatility of scent compounds in sub-freezing conditions in the winter months and loss of scent following occasional submersion during periods of high water.

Successful recruitment in floodplain forests appears to be driven by a tree's ability to grow tall as fast as possible to avoid the effects of herbivory and flooding. We never observed apical meristem herbivory on trees taller than 200 cm, and these trees were also less likely to be inundated during floods. Protection from herbivory for one winter (2010) increased the chances of a tree reaching escape height, the highest proportion of which were in mesh exclosures. This has direct floodplain forest management implications: where deer consume a large proportion of available plant tissue, short term protection of plant stems may be enough to ensure restoration success. It is worth noting that defining success and projecting mature forest density and composition based on early protection is difficult. Mature tree densities in temperate floodplain forests have been estimated at 0.037 trees/m² in the Black River floodplain near our site (Kordiyak 1981) to 0.040 trees/m² in southwestern Illinois (Taft 2003). These are comparatively low relative to our site of ~5 year old trees (8.2 trees/m²). In our study, numerous trees had reached escape height by summer 2011, we found up to 36% of trees escaped in one mesh exclosure after two years of protection. Presumably only 11-12 trees/plot would need to survive to maturity to achieve densities similar to mature regional floodplain forests.

We tested just three of the myriad deer protection techniques, only one of which appeared to meet our basic restoration goals. When faced with high deer densities or browse, restoration managers may also find one of the several alternatives such as low-cost tree shelters (Craven and Hygnstrom 1994), herd culling, etc. sufficient to meet the control needs in other floodplain settings.

The Effects of Browsing and Flooding on Tree Recruitment

Consumption that occurred in during winter 2010 had effects on tree height and growth rate that were still apparent nearly two years later. Ruzicka *et al.* (2010) found similar effects of deer herbivory in floodplain restoration efforts in southern Illinois, where browsed tree saplings were on average >35 cm shorter than unbrowsed over a two year period. winter browsing typically involved the removal of the apical bud which has been found to reduce hormonal suppression of lateral buds lower on plant stems (Haukioja *et al.* 1990) leading to bushier and shorter plant architecture in many tree species (Bergström and Danell 1987, Lehtilä *et al.* 2000 De Jager and Pastor 2008). The lower growth rates and lower height we found in browsed trees could be a result of resource reallocation to promote axillary growth as well as compensation for tissue removal. Though summer percent consumption was low both 2010 and 2011, trees that had been browsed winter 2010 were shorter, making them more susceptible re-browse and top shoot inundation. Tissue consumption patterns we observed were similar to what Rose and Harder (1985) found in a wooded grassland in Ohio where deer herbivory on trees consisted of woody plant material only in winter months and leaf tissue in the summer. Removal of leaf and stem material during the growing season would have reduced total leaf area and presumably resulted in a loss of photosynthetic capacity, and may have reduced the mass and reproductive ability of shoots originating from the previously browsed stem in subsequent years (Ruohomäki *et al.* 1997). As a consequence of these morphological changes, the percentage of trees escaping browse height at the completion of our study declined strongly and significantly with increased browsing.

Whereas browsing had a strong effect on plant height growth, plot elevation and flood duration had a significant effect on plant mortality. Soil saturation has been found to decrease soil redox potentials and result in a rapid depletion of oxygen by the metabolic demands of roots and soil microbes (Pezeshki 2001, Parent *et al.* 2008). Rather than investing in vertical growth, trees may have elaborated structures such as adventitious roots, hypertrophied lenticels and aerenchyma tissue to supply below ground oxygen respiratory needs in roots to metabolize stored carbohydrates (Sena Gomes and Kozlowski 1980, Armstrong *et al.* 1991). However, short trees growing in low elevation areas were completely submerged for up to 12% of the growing season, potentially limiting any belowground transfer of oxygen, and leading to significant tree mortality.

Tolerance to flood-related stresses may explain in part patterns of mortality we found in our study. The least flood tolerant species was silver maples whose seedlings have been found to experience complete mortality in just 2-4 days of submersion (Hosner 1958). Cottonwood seedlings can tolerate submersion for up to 16 days, while ash can persist up to 32 days underwater. Willow seedlings have been found to be very robust and withstand total submersion for at least 32 days (Hosner 1958). The published estimates of flood tolerance correlate broadly with the patterns of compositional change we observed in the lowest quartile of plots (Fig. 12a), where green ash and willow increased in proportional abundance at the expense of silver maple.

Although herbivory was not a significant predictor of change in density, suggesting that browsing did not result in tree mortality, shorter trees in lower elevation plots had a higher probability of mortality than taller trees growing on higher elevation sites. Thus, heavy browsing in lower elevation sites may leave trees vulnerable to

mortality as the result of their experiencing a longer period of inundation, an indication of how biotic and abiotic factors interact in the floodplain to influence tree recruitment. The biotic-abiotic interaction we found between herbivory-related height limitation and flood-related mortality offers an explanation of factors influencing tree recruitment in temperate floodplain forests.

Conclusions

Large herbivores have been identified as major drivers of terrestrial ecosystem function and plant performance in upland forests, but there has been little research on the effects of herbivores in aquatic-terrestrial transition zones (i.e. floodplains). We found that flooding may influence where and to what degree herbivory occurs in a floodplain forest of the Upper Mississippi River floodplain. We found high rates of browsing led to significant declines in tree height growth. Shorter trees growing in lower elevation areas experienced significant mortality (up to 100%). Our results suggest that management efforts in floodplain forest restorations should focus on protection when trees are young and susceptible to herbivory and inundation. Complex interactions among flooding, herbivory and related tree growth responses limit tree regeneration and influence species composition in this young floodplain forest site.

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