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Interactive effects of flooding and deer (*Odocoileus virginianus*) browsing on floodplain forest recruitment

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ABSTRACT

Floodplain forests have historically been resilient to the effects of flooding because the tree species that inhabit these ecosystems regenerate and grow quickly following disturbances. However, the intensity and selectivity of ungulate herbivory in floodplains has the potential to modify the community-level effects of flooding by delaying forest recruitment and leaving sites vulnerable to invasive species. We established a series of exclosures along an elevation gradient in an actively recruiting floodplain forest along the Upper Mississippi River prior to three large-magnitude flood events. Pre-flood browsing by *Odocoileus virginianus* (white-tailed deer) ranged from 20% to 85% of all available stems, and reduced subsequent annual tree height growth from 60 cm/yr to approximately 35 cm/yr, regardless of elevation. Tree mortality, in contrast, was positively correlated with both pre-flood browsing rates and the duration of the growing season that the ground elevation of plots was flooded. Mortality rates ranged from approximately 40% in plots that experienced low levels of deer browsing (<30% of stems) and short flood durations (<40 days) to as high as 98% in plots that experienced high levels of deer browsing (>80% of stems) and long flood durations (>50 days). Longer flood durations led to larger shifts in tree community composition, away from heavily browsed and less flood tolerant *Acer saccharinum* L. (silver maple) and *Populus deltoides* (cottonwood) and toward species that were more flood tolerant and not preferred by deer. *Phalaris arundinacea* (reed canarygrass) colonized some portions of all plots, except for those situated at high elevations and protected by exclosures.

Hence, herbivory can interact with the local flooding regime of rivers to delay recruitment of some tree species, resulting in shifts in successional trajectories, and leaving young forests vulnerable to invasion by exotic herbaceous species.

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1. Introduction

Flooding is the main driver of the structure and function of floodplain ecosystems (Junk et al., 1989). Although large magnitude floods can initially cause high rates of tree mortality, floodplain forests have historically been resilient to flooding as the tree species that inhabit these ecosystems have a high capacity to regenerate on frequently disturbed sites (Whitlow and Harris, 1979; Yin, 1998; Yin et al., 2009). However, flooding also provides a constant supply of invasive plant propagules from upstream sources, increasing the likelihood of invasion in disturbed floodplain sites (Rood et al., 2010; Eschtruth and Battles, 2011). Additionally, herbivore overabundance is now common worldwide (Côté et al., 2004; Mysterud, 2006) and selective foraging on tree species and avoidance of herbaceous species may further promote invasion (Kellogg and Bridgham, 2004). Understanding how flooding interacts with herbivory to affect the resilience of floodplain forests in the presence of invasive species is important given the potential for more frequent large magnitude floods (Watson et al., 1998; Osborn and Hulme, 2002; Robson, 2002; Knox, 2009), the broad distribution of invasive wetland species (Zedler and Kercher, 2004), and overabundant herbivore populations (Côté et al., 2004).

Effects of flooding in bottomland hardwood ecosystems are mainly determined by variation in hydroperiod (Sharitz and Mitsch, 1993; Hodges, 1997). Longer periods of soil saturation and anoxic conditions decrease plant photosynthetic rates and respiratory efficiency (Sena Gomes and Kozlowski, 1980; Pezeshki, 2001), resulting in overall higher rates of mortality at the lowest floodplain elevations. Some tree species can tolerate extended periods of anoxia by inducing the formation of morphological structures that aid in the transport of oxygen between roots and shoots (e.g. aerenchyma, lenticels, and adventitious roots (Whitlow and Harris, 1979)). Such adaptations allow flood-tolerant species to dominate in low-elevation sites (De Jager et al., 2012).

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Herbivory may alter the ability of individual trees to tolerate the effects of flooding. Browsing by large ungulates often reduces height growth via the removal of apical meristems (Danell et al., 1994) which reduces auxin levels in axillary buds, increasing cytokinin levels and thereby promoting axillary bud development (Senn and Haukioja, 1994; Tanaka et al., 2006). The result is a highly pruned, shrub-like architecture (De Jager and Pastor, 2008, 2010). Browsing-induced reductions to the height growth of young trees could contribute to mortality in floodplains because lower stature prolongs the duration of terminal bud submergence during flood events, which is known to increase the likelihood of tree mortality (Hosner, 1958, 1960). Browsing could also increase mortality rates of trees not completely submerged by altering the production and balance of auxin and cytokinin, which are thought to be responsible for the formation of aerenchyma, lenticels, and adventitious roots in response to prolonged conditions of soil anoxia (Whitlow and Harris, 1979). By selectively foraging on some tree species and avoiding others, deer could cause shifts in tree species composition. Or, by focusing their feeding activity on woody species and avoiding herbaceous plants, deer could induce community type conversion in floodplains, especially when these ecosystems face pressure from highly invasive herbaceous species (e.g. Kellogg and Bridgham, 2004).

In the winter of 2009, we established a series of exclosures to compare alternative methods to limit browsing by *Odocoileus virginianus* (white-tailed deer) along an elevation gradient in an actively recruiting forest in the floodplain of the Upper Mississippi River (UMR). The site had been successfully treated to control *Phalaris arundinacea* (reed canarygrass), but a previous study had demonstrated that deer browsing was limiting tree seedling height growth, slowing forest establishment (Thomsen et al., 2012). By chance, three large magnitude flood events occurred during the following two growing seasons, giving us the additional opportunity to examine a series of questions related to tree and reed canarygrass recruitment patterns in response to flood duration (elevation) and herbivory. The specific questions we addressed included: (1) What are patterns of plant forage selection by deer in bottomland hardwoods? (2) How do different tree species respond to lost tissue and variable flood durations? (3) Do browsing and flooding cause shifts in tree species compositions? (4) Does browsing and flooding facilitate invasion by reed canarygrass? (5) What are the implications for management actions aimed at promoting floodplain forest regeneration?

2. Methods

2.1. Study site

Deer exclosures were constructed in a Mississippi River floodplain site owned by the U.S. Army Corps of Engineers (USACE) south of La Crosse, WI (43°44.3′N, 91°12.6′W). The low head dams constructed along the UMR do not store flood waters and thus the river still experiences flood pulses; the dams do however prevent low-flow conditions during the summer growing season. In 1998, straight-line winds blew down approximately 4.2 ha of forest within the site; it was salvaged logged and subsequently invaded by *P. arundinacea* L. (reed canary grass). By the start of the study described here, a previous restoration experiment (Thomsen et al., 2012) had reduced *Phalaris* cover and resulted in a mean tree seedling density of 30 seedlings per m^2 of 2–3 year old *Acer saccharinum* L. (silver maple), *Fraxinus pennsylvaticus* Marshall (green ash), *Salix exigua* Nutt. and *S. nigra* Marshall (sandbar and black willow) and *Populus deltoides* W. Bartram ex Marshall (eastern cottonwood). White-tailed deer densities near the site during the study period were comparable to Wisconsin state averages with an estimated 11.1 deer/km^2 in fall 2010 and 8.4 deer/km^2 in winter 2011 (Wisconsin Department of Natural Resources, 2011). Densities exceed the estimated sustainable density of 2–4 deer/km^2 for Wisconsin, suggested by Alverson et al. (1988).

In late November 2009 we constructed three types of 20 × 20 m exclosures to reduce deer browsing of young trees: (1) mesh fences, (2) electric fences and (3) chemical fences. Mesh fences consisted of 2.4 m tall polypropylene mesh (Kencove Farm Fence Inc., Blairsville, PA) strung on 2.4 m tall metal fence posts spaced approximately 5 m apart. 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. Electric fences consisted of 2.4 m tall solar-powered six-strand electrical fencing (1.2 cm electric ribbon; Stafix®, Mineral Wells, TX; Magnum 12 V fence charger; Parmak®, Kansas City, MO) also strung on 2.4 m tall metal fence posts. Finally, chemical fences were constructed from 1.78 cm woven plastic fabric ribbon strung along plastic fence posts approximately 1 m tall, spaced every 5 m. Plotsaver™ (Messina Wildlife Management, Washington, NJ), a strong-smelling chemical deer repellent, was sprayed on the ribbon once a month for the duration of the study. Each exclosure type was replicated five times and applied to randomly assigned treatment plots. Five additional plots of equal size with no barriers served as controls, for a total of 20 plots. All experimental plots were located in the area in which *Phalaris* had previously been controlled and tree seedlings were abundant.

Plot elevations were determined by recording the water depth at the four corners of each plot during a single day of stable inundation during spring 2010. The river stage height of the UMR at the longitudinal position of the study site was used to estimate water surface elevation (M.A.S.L). The difference between the measured water depths at the four corners of each plot and the elevation of the water surface of the UMR was then used to estimate the elevation of each plot. Plot elevations were later confirmed with LiDAR (Light Detection and Ranging) imagery. The mean of the four corner elevations was used as a single measure of plot elevation and revealed a gradient of ground elevations within each exclosure treatment (Fig. 1a). We transformed elevation from M.A.S.L to the number of days that the ground elevation was submerged during the growing seasons of 2010 and 2011 (April 1-Sept 30) by comparing plot elevation with river stage hydrographs at the longitudinal river position of the study site Fig. 1b).

2.2. Data collection

Track surveys were conducted after snowfall events during the winter of 2009 (December 2009 – February 2010). The number of tracks was counted in a 1 m^2 area at three points along three evenly spaced transects per plot. The mean number of tracks m^{-2} in each plot was divided by the number of days since the last snowfall to estimate the number of tracks m^{-2} day^{-1}. Track densities were qualitatively inspected during 2010 because there was little evidence of deer presence at the site.

Vegetation sampling took place within five 1.5 × 1.5 m subplots within each of the 20 plots. Four subplots were located approximately 3 m from the corners of each plot and one subplot was centered within each plot. Sampling occurred during the spring (April) and late summer (August) of 2010 and 2011. Tree density was estimated within each subplot and used to estimate the percent mortality per plot over the course of the entire study period. Tree heights were measured for individuals within subplots and used to estimate mean annual height growth (cm yr^{-1}) per plot as well as the percentage of trees per plot escaping both the height reach of deer and maximum flooding depth at the site (>200 cm). Because our measure of flood duration extended past