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INFLUENCE OF FLOODING, GAP SIZE, AND SURROUNDING FOREST CHARACTERISTICS ON THE FATE OF UMRS FLOODPLAIN FOREST CANOPY GAPS

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INFLUENCE OF FLOODING, GAP SIZE, AND SURROUNDING FOREST CHARACTERISTICS ON THE FATE OF UMRS FLOODPLAIN FOREST CANOPY GAPS

By Alexandra Oines

We recommend acceptance of this thesis in partial fulfillment of the candidate's requirements for the degree of Master of Science, Biology: Environmental Science.

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ABSTRACT

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A natural loss of forest canopy creates gaps that can serve as locations for the growth of new cohorts of seedlings. However, adverse environmental conditions (e.g. change in flood regime, invasive species) may inhibit typical successional patterns and prevent gap closure. This project aims to improve our understanding of factors that determine the fate of canopy gaps in the Upper Mississippi River System floodplain forests. Collaborators identified forest gaps with GIS data and LiDAR imagery. We surveyed a subset of 20 gaps across a range of sizes and flood conditions in Pools 8 and 9 of the Mississippi River in summer 2019. Across all surveyed gaps, the presence of tree seedlings < 50 cm tall declined as the presence of reed canarygrass increased. Tree saplings > 50 cm in height were only recorded within 45% of sites, suggesting a lack of natural regeneration. Statistical modeling suggests that multiple environmental factors may interact to influence the vegetation that grows within canopy gap sites, including gap size, flood period, and forest buffer percentage. This insight may be used to select project areas that are suitable for forest management and for the design of management plans to most effectively conserve our forests.

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INTRODUCTION

Canopy Gaps and Forest Succession

Forested systems develop canopy gaps when mature trees are lost from the canopy layer, leaving a hole or gap in their absence. The creation of gaps may be the most common form of disturbance in forests throughout the world (Muscolo et al., 2014). Depending on the forest, natural causes of tree loss may include mortality due to old age, windstorms, intense flooding, insects, disease, beaver activity, or localized fires (Kern et al., 2017). Canopy gaps may also be caused by timber harvesting in managed areas of forest. The scale and type of the disturbance influences the size and shape of the gap, as well as how the gap changes over time (Sousa, 1984; Muscolo et al., 2014).

Canopy gaps are an important natural component of mature forests. Canopy gaps often play a role in nutrient cycling and help forests to maintain a complex structure of tree size and age (Muscolo et al., 2014). Gaps can also preserve biodiversity by promoting the growth of new and/or young trees of different species. When large trees fall from the canopy, the resulting gap has more light, space, and nutrients available, which means that species with varying tolerances and requirements for growth may become established. Because these conditions promote both plant reproduction and growth, canopy gaps can serve as locations for forest succession (Oliver, 1980; Muscolo et al., 2014).

The development of a new stand of trees in a canopy gap with available sunlight and limited competition from larger trees typically follows a four-step pattern of succession: stand initiation, stem exclusion, understory reinitiation, and old growth (Oliver, 1980). If a significant disturbance occurs and the understory is destroyed along with the overstory, then succession may restart back at an earlier stage as a new gap is formed (Oliver, 1980). When new trees fill in the canopy gaps that are created by the death of old trees, the natural loss of forest promotes the growth of new seedlings. However, adverse environmental conditions may prevent stand initiation from occurring. If tree regeneration ability is weak within canopy gaps, so that lost trees are not replaced, the forest structure could change drastically, and gaps may even fail to regenerate trees and instead convert to non-forested systems (Guyon & Battaglia, 2018; Bouska et al., 2019).

Ecological conditions within canopy gaps vary depending on their size in ways that can influence stand initiation. Larger gaps typically experience more sunlight than smaller gaps due to the angle of the sun in the sky. A higher level of sunlight is associated with warmer soil temperatures and a higher rate of evaporation of water from the soil. Warmer soil temperatures can also promote soil microbial activity, which influences nutrient cycling (Muscolo et al., 2014). Conditions may vary across locations within the gap, as well. More sunlight is experienced in the center of the gap interior as compared to locations along the edge with partial canopy cover, which can allow soil to retain more moisture and maintain a cooler temperature at the edges of gaps. Variation in these conditions may make certain gaps more suitable for different types of vegetation to flourish, which may or may not include new cohorts of trees.

Different reproductive mechanisms may also vary in success rate across gaps of different sizes, as well as across different locations within a gap. For example, shade-tolerant species that use advance regeneration are typically more successful competitors within small gaps compared to species that rely on the seed bank (Muscolo et al., 2014). In large gaps, species with lower dispersal ability may not be able to reach or become established within the gap interior and remain confined to the edges of the gaps. Many trees have restricted dispersal of propagules, meaning local recruitment of new seedlings will occur closer to the mature trees that produce the propagules (Connell, 1978). Of course, for any species to have a chance to become established within or adjacent to canopy gaps, a healthy propagule supply is required. If a species has limited propagule availability, establishment will likely be limited even if environmental conditions are ideal (Sousa, 1984).

The UMRS Floodplain Forest

The Upper Mississippi River System (UMRS) ranges from central Wisconsin and southeast Minnesota to the southern part of Illinois (Romano, 2010). The UMRS floodplain forest is located on the primary and secondary terraces of the river's floodplain, meaning that it becomes flooded when river levels are high. It is commonly defined as the Elm-Ash-Cottonwood forest cover type or as the Silver Maple-American Elm forest cover type. The flood tolerant silver maple (*Acer saccharinum*) currently dominates the canopy, but stand level average ages of these trees range from 60-82 years, meaning they are expected to senesce and die within the next 50 years (Kirsch and Gray, 2017; Nielsen, 2020). American elm (*Ulmus americana*) was a major component of the forest system prior to the arrival of the fungal Dutch elm disease (*Ophiostoma ulmi*); although the species remains present in the midstory level, its ecological role has substantially changed (Romano, 2010). Green ash (*Fraxinus pennsylvanica*), which is dominant in the understory of the UMRS floodplain forest, is currently threatened by the emerald ash borer (*Agrilus planipennis*). The coverage of the floodplain forest has also been reduced due to human activities, such as conversion of forested area to farmland, urbanization, the implementation of lock and dam systems, and timber harvesting (Kirsch & Gray, 2017; Bouska et al., 2018; Guyon & Battaglia, 2018).

The UMRS floodplain forest serves several important ecological roles, including serving as a carbon source for the river ecosystem; providing habitat for wildlife, including both native and migratory birds; and performing water and nutrient cycling (Romano, 2010; Kirsch & Gray, 2017; Bouska et al., 2019). In addition to providing carbon for food webs, the floodplain forest is important in terms of carbon storage: large amounts of carbon are stored both in the biomass of trees and in the soil in the form of organic matter (Hanberry et al., 2015). Because the floodplain forest is able to store large amounts of carbon, this keeps it out of the atmosphere where it would otherwise contribute to the greenhouse effect associated with global climate change. Additionally, floodplains often act as buffers against high concentrations of nitrogen within river systems (De Jager et al., 2015). Floodplains can provide storage for excess nitrogen in organic matter and also increase the rate of biogeochemical cycling via seasonal flooding (Swanson et al., 2017). Microbial processes decrease the amount of nitrogen that is transported downstream, which helps to prevent eutrophication and “dead zones” in coastal areas (Pinay et al., 2000). As mature trees are lost due to old age, disease, and invasive pests, the forests decline in their ability to perform these important ecological functions. If canopy gaps convert to non-forested areas, both local ecosystems and ecosystems further downstream may be impacted.

Currently, data suggest that the UMRS has insufficient natural forest regeneration, a situation that may result in the failure to recruit new generations of trees and the consequent loss of floodplain forest habitat over time (Guyon & Battaglia, 2018). Some major factors of concern regarding tree regeneration within UMRS floodplain forest canopy gaps include altered flooding patterns influenced by climate change, the growing presence of invasive species, and selective herbivory.

In the Midwest region of the United States, extreme rainfall events have increased throughout the past century and are expected to continue to increase with time (U.S. Global Change Research Program, 2017). Furthermore, the lock-and-dam system, which raises the water level throughout most of each navigation pool, has increased periods of flooding within the UMRS (Kirsch & Gray, 2017). It is universally understood that flood duration and intensity can alter species composition within plant communities. For example, a tree's tolerance to flooding depends upon its species, its developmental stage, and the length and depth of the flood (Romano, 2010). Extended flooding during the spring growing season may lead to the death of small trees that cannot survive in the anaerobic conditions beneath the water, and it may instead facilitate the invasion of wetland plants with greater flood tolerance (De Jager et al., 2013; Bouska et al., 2019). Because flood duration is related to elevation thresholds, different locations may be more impacted as flood regimes change in response to climate change. In particular, low-lying areas that experience frequent flooding may potentially transition to wet meadows that consist of invasive grasses that thrive in disturbed sites (Bouska et al., 2019).

One specific invasive species of concern is reed canarygrass (*Phalaris arundinacea)*, which frequently becomes established in locations of canopy disturbance in the UMRS. Reed canarygrass is a cool-season, perennial plant that is native to Eurasia and North America (Lavergne & Molofsky, 2004). Non-native strains were introduced in North America as early as the 1850s for agricultural purposes, such as providing soil stabilization and serving as a food source for livestock (Lavergne & Molofsky, 2004). It now commonly takes over naturally wet prairies, banks of streams, and wetland areas, such as the floodplain. This invasive grass has the capacity to grow early in the season, spread rapidly via rhizomatic growth, and produce high numbers of seeds (Lavergne & Molofsky, 2004; Thomsen et al., 2012). These features give reed canarygrass the ability to outcompete young tree seedlings in the UMRS floodplain (Reinhardt Adams et al., 2011; Thomsen et al., 2012). Lower rates of tree seedling establishment during the stand initiation phase will in turn lead to decreased dominance by woody species and decreased species richness in the system.

Reed canarygrass may also have an advantage relative to young tree seedlings during the stand initiation phase due to selective herbivory. Reed canarygrass is frequently avoided by herbivores due to its high alkaloid content and low level of digestibility, and when it is browsed, it remains more resilient than other species (Kellogg & Bridgham, 2004). White-tailed deer (*Odocoileus virginianus*) browsing activity typically leads to reduced tree seedling height growth (De Jager et al., 2013). Shorter stature may be detrimental during flood events because longer durations of complete submergence are linked to an increased likelihood of tree mortality, especially when water depth limits light availability (Siebel et al., 1998). The interactive effects of deer herbivory and flooding can therefore alter the community composition of trees if browsing is selective or if flooding is chronically deeper than browsed seedling height (De Jager et al., 2013). Heavy herbivory of smaller trees by abundant populations of white-tailed deer may lead to longer periods of open canopy space (Cogger et al., 2014). This lag can facilitate the invasion of other plant species, such as reed canarygrass, which alters the community structure.

Though we know that there are several factors that likely influence tree regeneration (or lack thereof) within floodplain forest canopy gaps, there is a lack of research specific to disturbance dynamics in the UMRS. Improving our understanding of processes within the UMRS floodplain forest will allow natural resource managers to further understand the ecosystem’s resilience (Bouska et al., 2018). Furthermore, several factors threaten the long-term stability of the UMRS floodplain forests, including a low diversity of tree species, a loss of forest habitat, declining forest health, and limited regeneration success in many areas (Guyon & Battaglia, 2018). These changes have led to a higher importance of floodplain forest restoration efforts, which require research and the assessment of forest conditions so that future efforts can be appropriately targeted. For example, understanding which conditions promote tree seedling survival within canopy gaps can allow forest managers to try to recreate the same conditions in sites where restoration projects are implemented. We aim to determine drivers of forest regeneration success or failure within and adjacent to canopy gaps within the UMRS floodplain forest.

Objectives

1. To evaluate the plant community composition within floodplain forest canopy gaps with an emphasis on the metrics related to forest regeneration and on the relationship between reed canarygrass and other types of plants.

2. To determine which variables (e.g. gap size, annual flood dynamics, location within the gap, and surrounding forest characteristics) best predict the cover of different vegetation types.

METHODS

Study Sites

Canopy gaps throughout UMRS floodplain forests were identified by collaborators at the USGS Upper Midwest Environmental Sciences Center. Data sources used included land cover layer maps, LiDAR imagery, and image interpretation (USACE Long Term Resource Monitoring Program, 2011). The LiDAR imagery was collected in 2010, so the gaps identified were at least nine years old when sampled in 2019. Gaps were stratified based on size (small: 0.04-0.10 ha / 0.10-0.25 ac, medium: 0.10-0.30 ha / 0.25-0.75 ac, or large: 0.30-0.81 ha / 0.75-2.00 ac) and average annual duration of flood period (low: 1-20 days, medium: 20-40 days, or high: 40-100 days). Flood period was based on the 30 year average during the growing season (April 1 – September 30 from 1972 to 2011), averaged across the entire gap area, as determined by the UMRS Inundation Model (De Jager et al., 2018; Van Appledorn et al., 2020). A total of nine different gap type combinations were possible. A large subset of gaps representing each combination of size and flood period were randomly selected within navigation pools 8 and 9 of the UMRS.

From this list, we randomly selected three gaps within each of the nine categories for field sampling, equaling 27 gaps in total. Gaps were excluded from sampling if they were within 0.5 km of another selected gap within the same category of conditions. We also omitted gaps if they were the third gap of a given type within the same pool (i.e. selections were stratified so that we had at least one gap from each pool within each gap type category). When gaps had to be omitted for this reason, accessibility was considered when selecting which one to sample. Land ownership maps were used during this process to avoid potential trespassing when determining access plans. One site was omitted due to extreme difficulty of access (a long distance from passable river channels and blocked by private property). Selected gaps were then examined by collaborators using aerial imagery to verify that they contained terrestrial vegetation rather than open water (e.g. permanent ponds). When gaps were removed from consideration, suitable replacement gaps were selected randomly and evaluated as described above.

Gap sites were sampled between June 25 and September 30, 2019. A handheld Garmin GPSMAP66i unit and a Trimble Geo 7X Handheld Data Collector were used in combination when navigating to canopy gap field sites. When gaps were located, the general vegetation composition and current flood conditions were assessed. If gaps were dominated by more than 50% emergent aquatic vegetation, such as arrowhead (*Sagittaria latifolia*), cattail (*Typha spp.*), or bulrush (*Schoenoplectus tabernaemontani*), they were deemed to be wetland openings within the forest rather than canopy gaps and were not sampled. Additionally, if sites were too flooded for accurate sampling at that time, they were not sampled. Replacement sites were assigned when possible. Due to the long duration of flooding during the summer of 2019 and a lack of suitable sites, we did not sample the total of 27 sites that we had aimed for and were limited to 20 sites (Figure 1). The following types of gaps were not sampled: 3 large, high flood period gaps; 2 medium, high flood period gaps; 1 small, high flood period gap; and 1 medium, low flood period gap. Due to our inability to sample many gaps greater than 1 acre in size (Figure

1), any analyses indicating a significant effect of gap size were repeated without data from the two largest gaps in order to evaluate the influence of the patterns detected.

When sites were deemed suitable for sampling, we visually identified the gap centroid and marked it with a metal t-post. We used the handheld GPS to collect and record the centroid coordinates. Prior to sampling, four photographs were taken at one-meter distances from the t-post, facing each cardinal direction (0°, 90°, 180°, and 270°) and including the t-post in the photograph for reference. Image file numbers were recorded to document which photo corresponded to which cardinal direction. Images were sent to the USACE to be archived for future use.

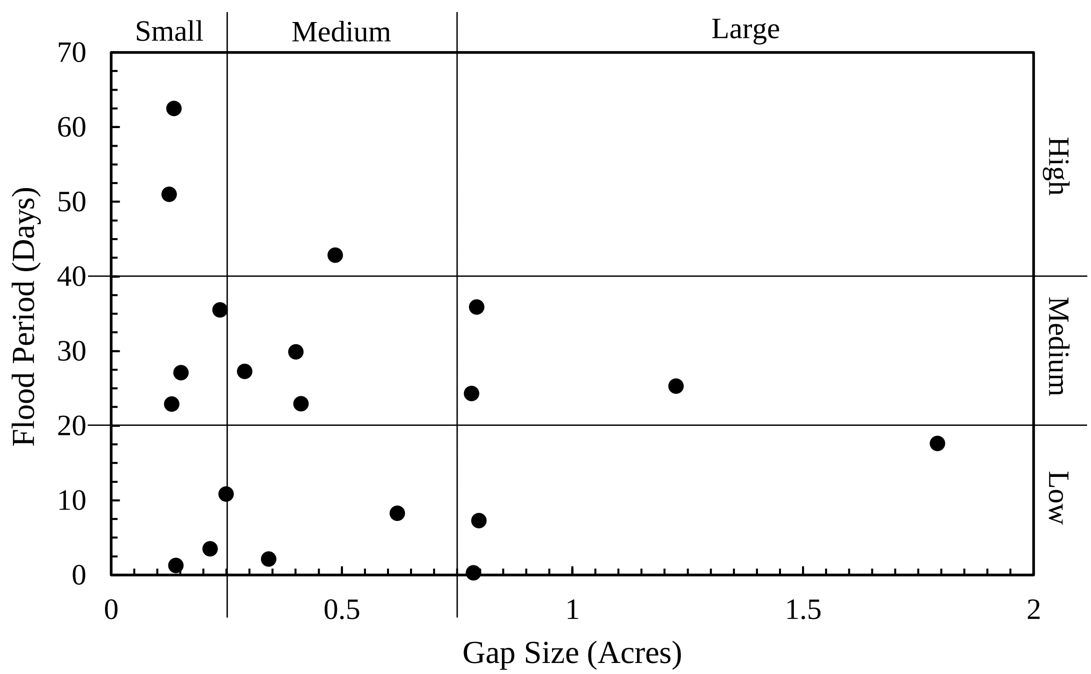

Figure 1. Distribution of the canopy gap sites that were sampled for this project (N = 20). Original gap size and flood level categories are included to demonstrate how sampling success varied across gap types.

Data Collection

From the centroid t-post, transects were placed along the four cardinal directions using reel tape measures and a sighting compass. Six locations for herbaceous layer sampling were temporarily marked along each transect with fluorescent pin flags (Figure 2). Placement of sample points within the gap interior was determined by measuring the distance from the centroid to the "canopy edge," defined as the location where the individual waking along the transect first stood beneath continuous canopy cover. That distance was divided by three to determine the spacing for quadrats #1 and #2 (e.g. a 60-meter distance from the centroid to canopy edge would have quadrats #1 and #2 placed at 20 meters and 40 meters from the gap centroid). Quadrat #3 was placed at the canopy edge. The "tree edge," defined as the area where large tree trunks of canopy trees were in line with the individual running the transect, was used for the placement of quadrat #4. From the tree edge, one sample location was marked 5 meters into the surrounding forest cover (quadrat #5), and the final location was at the end of the transect, 25 meters beyond the tree edge into the surrounding forest cover (quadrat #6). All quadrat distances from the gap center were recorded to the nearest 0.25 meter. One additional sampling location associated with the centroid was placed on the ground at a randomly determined azimuth where the northwest corner of the quadrat was two meters from the metal t-post (quadrat C). In total, there were 25 vegetation sampling points at each study site. We defined quadrats C, #1, and #2 as "interior," quadrats #3 and #4 as "edge," and quadrats #5 and #6 as "forest" for analysis of location effects.

The quadrat edge that was aligned with the marking flag at each location was the edge associated with the azimuth (e.g. the 90° quadrats had the 0.5-meter mark on the east edge placed at the quadrat marker). When standing and/or fallen trees were located in sampling locations, quadrats were moved directly perpendicular to the transect to a location where there was no woody debris greater than 6 inches in diameter within the 1 m^2 sampling plot. Sample points were excluded from data collection if the gap was too narrow to avoid overlap of quadrat placement along the transect or if deep water prevented accurate sampling. Forest sampling points were excluded or relocated to alternate azimuths for 21 transects (out of 80 total transects) that extended into another canopy gap or marsh area rather than forest. If it was possible to survey closed canopy conditions at the same distance from the gap edge along another azimuth without re-sampling an area that was already sampled on one of the other transects, a substitute azimuth was randomly selected, and the inventory was performed 25 meters from the tree edge on the new azimuth. In 9 cases, it was impossible to shift the transect location in this way, and this led to fewer forest sample locations for the impacted gaps.

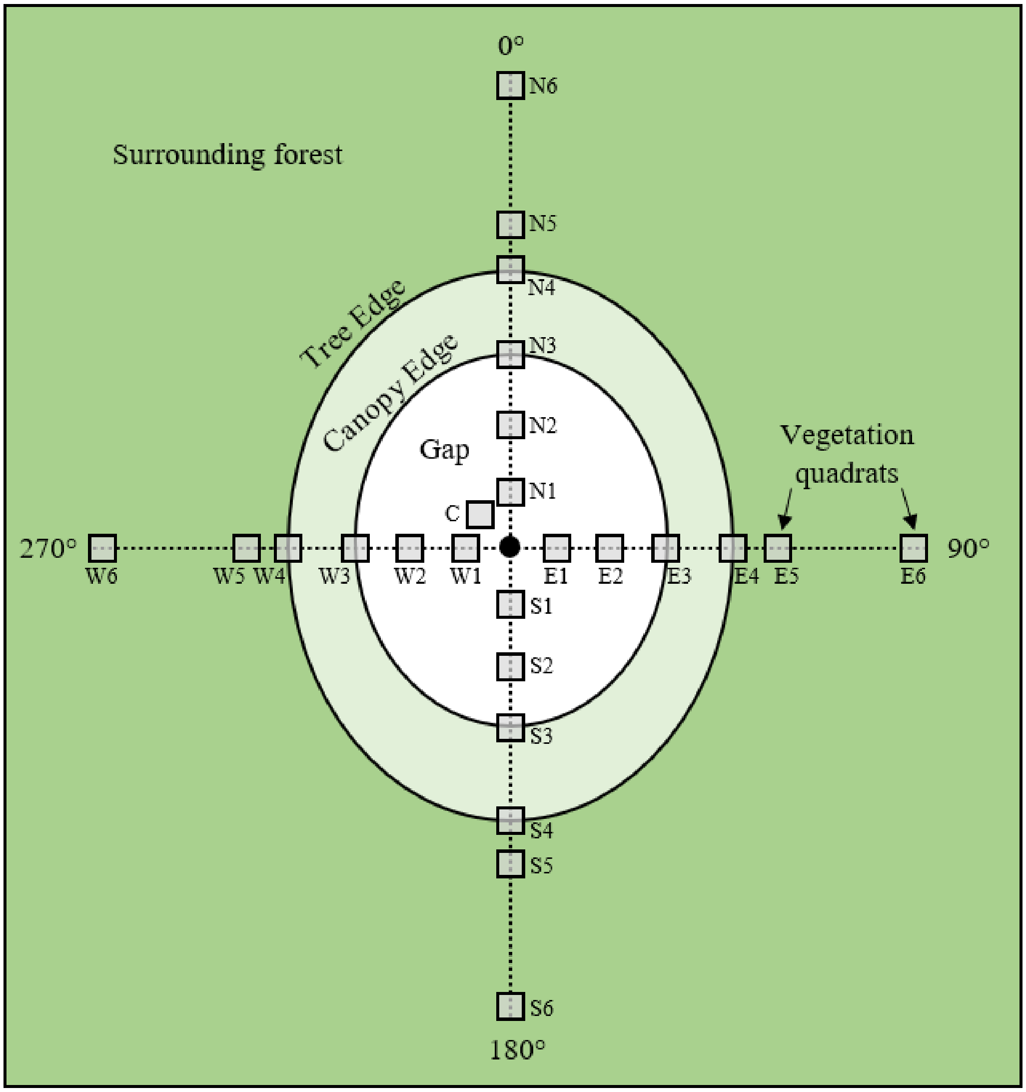

Figure 2. Location of sampling quadrats within a hypothetical gap site. We defined quadrats C, #1, and #2 as “interior,” quadrats #3 and #4 as “edge,” and quadrats #5 and #6 as “forest” for analysis of location effects.

Vegetation Sampling: Herbaceous Layer

Within each sampling quadrat, all herbaceous vegetation (including woody vines and tree seedlings less than 0.5 meters tall) was identified and recorded. The percent cover was recorded for plants within four broad groups: graminoids, forbs, tree seedlings, and non-invasive vines. We also recorded the percent cover for species of forest management concern, including reed canarygrass, wood nettle (*Laportea canadensis*), stinging nettle (*Urtica doica*), Japanese hops (*Humulus japonicus*), giant ragweed (*Ambrosia trifida*), wild grape (*Vitis vinifera*), burr cucumber (*Sicyos angulatus*), and trumpet creeper (*Campsis radicans*). For each species or group, the visually estimated cover class (1-6) was recorded (1: > 0-5%, 2: 6-25%, 3: 26-50%, 4: 51-75%, 5: 76-95%, 6: 96-100%). With this method, it was possible for the total percent cover for all species/groups in a quadrat to be greater than 100%. Throughout the gap, a species roll call for the types of tree seedlings that we observed within the quadrats was recorded.

Vegetation Sampling: Woody Stems

Within each quadrat, if any woody stem greater than 50 cm was present, we identified the tallest individual and recorded the species name. Height was measured to the nearest centimeter if the stem was less than 1.5 m tall and was measured to the nearest 5 cm if the stem was greater than 1.5 m tall. We also assessed and recorded a browsing severity index value for the tallest woody stems. Browsing was scored from 0-3 as follows:

0: no browsing or girdling;

1: some browsing and/or girdling but > 25% of available forage or stem circumference has been browsed and plant growth is unaffected;

2: 25-75% of available forage has been browsed and/or 25-75% of circumference has been girdled and plant growth if affected;

3: > 75% of available forage has been browsed and/or >75% of stem circumference has been girdled and growth has been affected enough that plant survival is questionable.

For other woody stems present within the quadrat, we recorded the number of individuals present by species and height class (1: 0.5-1.5 m, 2: 1.5-3.0 m, 3: > 3.0 m) for all stems by species.

Canopy Cover

In addition to surveying the herb layer and woody stems, quantitative and/or qualitative measurements of canopy cover were taken at each quadrat location. A spherical densiometer was used to determine canopy density above the centroid quadrat and quadrats 3 (canopy edge) and 6 (furthest into interior forest) along each transect. A total of four densiometer readings were recorded per quadrat location; a measurement was taken facing each cardinal direction when standing in the center of the quadrat. At all quadrat locations, a qualitative canopy measure was recorded based on visual assessment of the 1 m^2 area of canopy directly above the quadrat (O = open canopy, P = partially closed, C = closed canopy cover).

Forest Inventory

An inventory of forest matrix health was taken at quadrat #6 on each transect (25 m from the tree edge of the gap). Methods used for this portion matched those of the US Army Corps of Engineers St. Paul District Phase II Forest Inventory Protocol. Quadrat #6 was used as the temporary center point for a visual 5 radial meter circle representing approximately 1/50th of an acre (Figure 3). From the center point, we determined a regeneration rating by first noting the presence (1 point) or absence (0 points) of trees at least 0.5 meters tall and less than or equal to 10 cm DBH. We then used four 1/1000th acre plots (1.12 radial meters) located at the end of each visual cardinal transect surrounding the center and made a tally (0 to 4 points) of how many contained trees of at least 0.5 meters tall and less than or equal to 10 cm DBH. To calculate the regeneration rating for the forest location, we summed the scores for the 1/50th and 1/1000th acre plots and determined a total score between 0 and 5, with 5 being the best possible score.

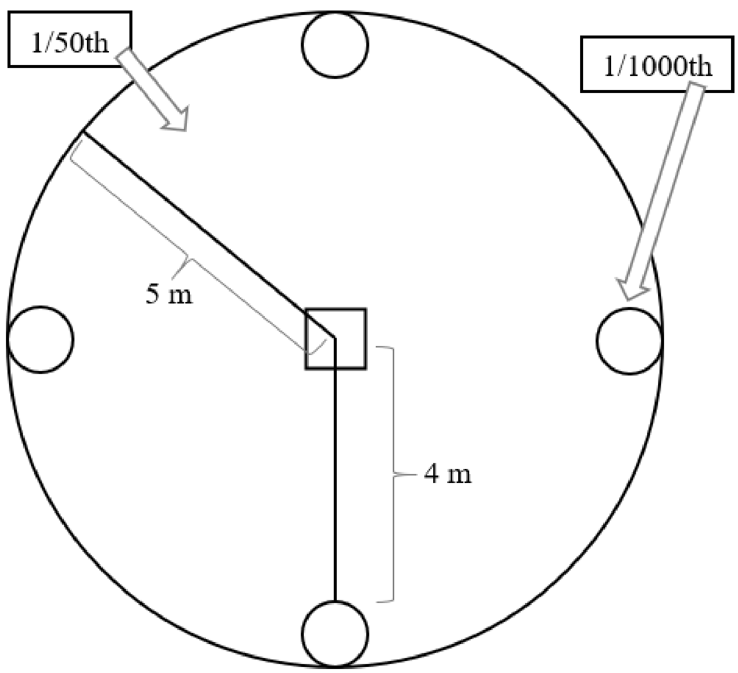

Figure 3. Layout of a forest inventory point surrounding quadrat #6 (square).

In addition to calculating the regeneration rating, we recorded the three most dominant species of tree regeneration within the 1/50th acre tree regeneration area that were at least 0.5 meters tall and less than or equal to 10 cm DBH. The species were recorded in order of dominance, with the first species listed being the most numerous. We also recorded the three most dominant woody invasive species and herbaceous invasive species within the regeneration area, if present. These species were also recorded in order of dominance.

Finally, a 10 square feet basal area glass prism was used to take a tally of large, living trees in the surrounding forest cover to be included with the calculation of basal area following protocol used by the U.S. Army Corps of Engineers (Wisconsin Department of Natural Resources, 1970). While standing in the location of the vegetation quadrat, the glass prism was held out an arm's length at eye level. While slowly rotating a full 360°, tallies were taken of the number of trees that were "hits" (e.g. where the trunk of the actual tree connected to the portion of the tree viewed through the prism). Tallies were recorded by species and then summed together and multiplied by 10 to get a single basal area measure for each azimuth.

Data Analysis

Geospatial data collected from by collaborators was used to assess environmental conditions in the area directly surrounding the gaps. LiDAR imaging and land cover layer maps were used to determine each gap's area to perimeter ratio and % forest buffer (percentage of a 150 m buffer area around each canopy gap that was classified as forest in the land cover assessment). The gap layer map was used in combination with the UMRS Inundation Model (De Jager et al., 2018; Van Appledorn et al., 2020) to determine the number of days of the 2019 growing season that each site was dry prior to the date it was sampled in order to control for seasonal variation. However, evaluation of models with and without this metric led us to conclude that it did not significantly impact results, and it was excluded from final models.

We determined the proportion of quadrats where each vegetation type was present at each gap. Proportion values were Arcsine square root transformed for correlational analyses between vegetation types. Chi square tests were used to evaluate patterns in the occurrence of tree seedlings and saplings across gap interior, canopy edge, and forest quadrats. We calculated mean canopy openness for the centroid, canopy edge, and closed forest locations along the four transects for each gap based on densiometer data. An ANOVA with post-hoc analysis was completed to confirm that densiometer canopy openness ratings varied between the gap centroid, canopy edge, and forest inventory locations. Chi square analyses were performed to confirm that the location designations of “interior,” “edge,” and “forest” were associated with qualitative canopy cover measurements that varied from the null hypothesis.

Members of the University of Wisconsin – La Crosse Statistical Consulting Center were involved with data analysis. These collaborators performed a model-building process using linear mixed effects models to determine the most suitable model to describe the relationship between each particular response variable (e.g. mean percent cover of a vegetation type) and the pool of possible fixed effects, which were due to the following: location (interior, edge, forest), gap area, flood period, dry days, percent forest buffer, regeneration score average, basal area average, total species richness (for large trees), and any interaction effects among them. For these analyses, we transformed cover class data to the midpoint and calculated the mean percent cover of each vegetation type across the gap interior, gap edge, and forest quadrats for each gap, so there were three data points included for each gap site. We similarly calculated the mean values of the forest inventory data collected at quadrat #6 for the four transects within each gap, including the species richness of mature trees listed during the basal area count. Data analysis programs utilized for this project included *JMP* (SAS, 2020) and *R* (R Core Team, 2020) in combination with *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), *ggplot2* (Wickham, 2016), and *emmeans* (Lenth, 2019).

Random intercepts were allowed on each model to account for the random effects due to repeated measures on gaps. The *P*-values for fixed effects factors were obtained using *F*-tests with Satterthwaite's method for estimating degrees of freedom. The model-building approach used a 5% significant level to determine which variable should remain within each of the models, as well as retaining all lower order terms that were involved in significant higher order interactions. Rank, logarithm, and square root transformation were examined to find the best models that satisfied linear mixed model conditions of normally distributed and homoscedastic residuals due to severe right skewness and outliers within the response variables. These transformations were assessed with the use of residual plots, boxplots, histograms, normal probability plots, and the Shapiro-Wilk normality test. The marginal and conditional Nakagawa R^2 was utilized to explain variation within the model (Nakagawa et al., 2017). We further compared model outputs based on the full data set as compared to those when the two largest gaps were omitted from the analysis, due to our concerns that the lack of gaps larger than 1 acre in size might give the two largest gaps undue influence over results.

The fitted models were used to compute predicted values for percent cover of vegetation groups/species and then back-transformed to match the units used when measuring these variables originally. To avoid extrapolation, only the back-transformed values that fell between 0 and 100 were retained for plotting because, as percentages, values outside of that range are not possible. The predicted values were averaged over gaps because random intercepts were originally used for each gap within the mixed model. The predicted values were also averaged over the variables that were not used in the graph.

RESULTS

General Findings Across Gap Sites

Vegetation varied considerably across the 20 sample sites (Table 1). Tree seedlings and native forbs were recorded at all sites that we sampled. Native graminoids were present in all but one canopy gap location, and reed canarygrass was present in all but three sites. Finally, both vines and tree saplings or other woody stems greater than 50 cm tall were present in only 9 of the 20 sites. When present at sites, the percent of quadrats per site where the species or groups of vegetation were present varied from an average of approximately 80% for forbs to just below 12% for tree saplings.

Table 1. Presence of different plants across 20 canopy gap sites.

Species/Group	**% of sites**	**Mean % of quadrats per site when present**
Tree Seedlings < 50 cm	100	48.3
Tree Saplings > 50 cm	45	11.7
Forbs	100	79.6
Graminoids	95	58.8
Reed Canarygrass	85	46.2
Non-Invasive Vines	45	20.9

Several species of management concern were occasionally seen throughout the study sites (Table 2). The most commonly seen species of management concern was wood nettle, which was present in a total of 46 quadrats across 6 of the gap sites. Wild grape was recorded in 5 sites, burr cucumber was recorded in 4 sites, and both stinging nettle and giant ragweed were recorded in 2 gap sites. Finally, Japanese hops was present in only one site, and we did not record the presence of trumpet creeper in any of our vegetation surveys. Average percent cover of these species of interest based on cover class midpoint values ranged from 4.6% (burr cucumber) to 27.7% (wood nettle).

Table 2. Presence of species of management concern across 20 sites.

Species	**% of gaps**	**Total quadrats where present**	**Mean % cover when present**
Wood Nettle	30	46	27.7
Stinging Nettle	10	11	10.4
Japanese Hops	5	18	13.2
Giant Ragweed	10	7	26.9
Wild Grape	25	5	9.1
Burr Cucumber	20	6	4.6
Trumpet Creeper	0	-	-

When comparing the presence of reed canarygrass to the presence of tree seedlings, as defined by the proportion of quadrats across a site in which they were present, it was found that the presence of reed canarygrass is negatively correlated with the presence of tree seedlings within canopy gap sites (Figure 4a). As reed canarygrass presence increased, the presence of tree seedlings decreased from approximately 60% of quadrats in sites lacking reed canarygrass to about 20% of quadrats in sites where reed canarygrass occurred the most frequently (r = -0.448, N = 20, P = 0.048). Reed canarygrass also showed a negative correlation against graminoids across gaps, (Figure 4b). As the presence of reed canarygrass increased, presence of other graminoids significantly decreased from nearly 100% of quadrats in sites lacking reed canarygrass down to less than 20% where reed canarygrass appeared most frequently (r = -0.694, N = 20, P = 0.0007). No relationship was seen between reed canarygrass and forb presence (r = -0.400, N = 20, P = 0.0807).

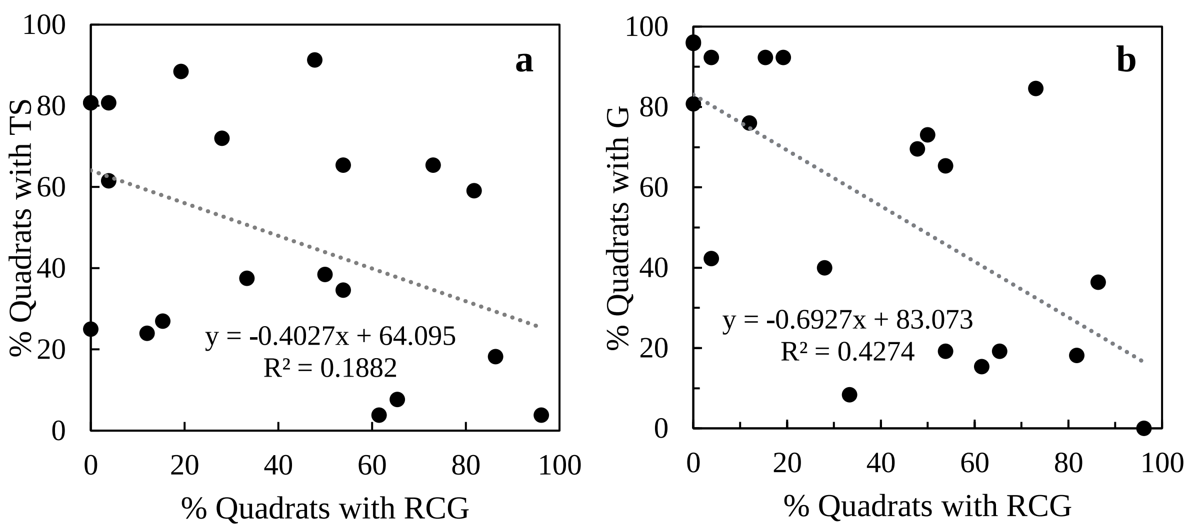

Figure 4. Correlations involving the presence of reed canarygrass. Correlations are between the presence of reed canarygrass and the presence of tree seedlings (a) and other graminoids (b) across sampled canopy gap sites (N = 20).

We recorded the presence of eight different species of tree seedlings, with silver maple seedlings being seen the most frequently (Table 3). Silver maple seedlings were recorded in 18 of the 20 sites. The next two most frequently observed species included green ash and American elm, which were seen in 10 and 7 sites, respectively. Of all quadrats with tree seedlings recorded in them, 30% were located within the gap interior, 35% were located at the edge of the gaps, and 35% were out in the forest area adjacent to the canopy gaps. The frequency at which tree seedlings were found in interior, edge, and forest quadrats was proportional to the abundance of those quadrat types ($X^2 = 1.2$, $P = 0.546$).

Table 3. Presence of tree seedling species across 20 canopy gap sites.

Species	**Number of sites**
Silver Maple	18
Green Ash	10
American Elm	7
River Birch	4
Swamp White Oak	3
Hackberry	3
Boxelder	3
Buckthorn	1

Across the 9 gaps in which saplings (woody stems greater than 50 cm tall) were recorded, a total of 54 individuals were counted, representing 7 species (Table 4). Of the observed woody stems, green ash saplings were the most commonly recorded and represented 50% of the individuals counted. Thirty of these individuals were recorded as being the tallest woody stems within sampling quadrats. Browsing activity was seen on the tallest woody stems within 7 of the 9 gaps (78%), impacting 13 of the 30 individual saplings (43%) considered in this analysis. All browsing was within browsing class 1, meaning some evidence of browsing was seen but less than 25% of available forage had been browsed and plant growth was unaffected. We saw no sign of girdling on any of the tallest woody stems.

Table 4. Summary of woody stems greater than 50 cm in height. Stems were observed during our vegetation sampling in quadrats across 20 canopy gap sites (N = 54). Tallest woody stems (TWS) are described by species (N = 30). Average height measurements and browsing by species columns refer only to stems that were measured at TWS.

Species	**Total # Observed**	**# Observed as TWS**	**Avg Height (cm)**	**# Browsed**
Green Ash	27	16	90	8
Sandbar Willow	19	6	236	1
Buttonbush	3	3	143	1
Buckthorn	2	2	280	0
Silver Maple	1	1	130	1
Hackberry	1	1	65	1
Boxelder	1	1	400	1

Of all individual recorded woody stems greater than 50 cm in height, 45% were located within the gap interior, 24% were located at the edge of gaps, and 28% were in the forest area adjacent to canopy gaps. The frequency at which tree woody stems were found in interior, edge, and forest quadrats was proportional to the abundance of those quadrat types (X^2 = 0.741, P = 0.600).

Within our forest inventory basal area counts, we recorded a total of 737 large trees across the 20 gap sites (Table 5). Ten different species of trees were represented; silver maple was the dominant species and composed 75% of the individuals recorded. The next most counted species was the cottonwood, and it represented just 7% of the total. The average basal area score per site ranged from 45-190 ft^2/ac with an average measurement of 108.3 ft^2/ac. The greatest species richness observed was 7 species in the forest around one canopy gap; the average total richness value was 3.2 species per site.

Table 5. Summary of large trees recorded in basal area counts by species (N = 737).

Species	Total Counted
Silver Maple	556
Cottonwood	51
Swamp White Oak	29
Green Ash	25
American Elm	21
Bitternut Hickory	15
Common Hackberry	15
Boxelder	13
River Birch	9
Black Willow	6

Site average regeneration scores within the entire $1/50^{th}$ acre plot ranged from 0-2 out of 5 possible points with a mean score of 0.8. A total of 12 species were recorded as part of the regeneration assessment, with green ash being the mostly commonly observed species (Table 6). The three most commonly recorded invasive species observed during the forest inventory were reed canarygrass, wood nettle, and wild grape. Forest buffer values surrounding the gaps were provided by the USGS; values ranged from 62.1-100% with an average of 78.7%.

Table 6. Summary of woody species included when scoring regeneration within forest inventories across 20 sites (N = 53).

Species	# times recorded	# of sites where present
Green Ash	22	14
American Elm	9	4
Silver Maple	9	7
Bitternut Hickory	2	1
Boxelder	2	2
Buttonbush	2	1
Buckthorn	2	1
Swamp White Oak	1	1
Black Willow	1	1
Hackberry	1	1
River Birch	1	1
Prickly Ash	1	1

Densiometer readings at the gap centroid had an average value of 63.1% openness across all 20 gaps. One small gap was well developed at the pole stage and had a centroid canopy with only 0.5% openness, while 10 gaps had 100% canopy openness at the centroid. Densiometer readings at quadrat #3 (the canopy edge) ranged from 0.3-78.8% openness with a mean score of 34.4% openness. The average canopy openness above the forest inventory plots (quadrat #6) as determined by densiometer calculations was 11.0% open. Openness values ranged from 0.0% (fully closed canopy) to 42.5% open across all forest inventory locations. An ANOVA with post-hoc analyses determined that average canopy openness percentages varied significantly between the gap centroid, canopy edge, and forest samplings points ($F_{2,57} = 20.541$, $P < 0.0001$).

The numbers of “open,” “partial,” and “closed” ratings that were recorded for all interior, edge, and forest quadrats were also significantly different from one another, further confirming that canopy cover and associated conditions varied at different locations throughout the gaps. In the gap interior, canopy cover was most frequently rated as being open and very rarely considered closed (X^2 = 135.1, df = 2, P < 0.0001). At the canopy edge, partial canopy cover was recorded most often (X^2 = 73.5, df = 2, P < 0.0001). In the surrounding forest, closed and partial ratings were recorded more often than open ratings (X^2 = 47.8, df = 2, P < 0.0001).

Tree Seedling Cover

Model-building indicated that the log-transformed tree seedling percent cover was significantly influenced by an interaction between location and flooding, ($F_{2,36}$ = 4.75, P = 0.015; Table 7). Specifically, tree seedling percent cover in the surrounding forest did not decrease with increasing flood period as it did in the gap interior and edge locations (Figure 5). While tree seedlings are predicted to have between 2.5-3.5% cover within all gap locations at low flood duration, predicted cover in edge and interior quadrat locations drops to around 1% at the longest flood durations.

Table 7. Summary of the linear mixed model that was deemed to be the best fit for tree seedling percent cover values. The random effect of Gap ID was included in models to account for the repeated measurements made on each gap (mean values for interior, edge, and forest quadrats).

	log(TS Percent Cover + 0.5)		
Predictor	**Estimate**	**95% CI**	***P***
Location [Edge]	0.249	-0.399 – 0.898	0.456
Location [Forest]	-0.097	-0.745 – 0.551	0.771
Flood Days	-0.025	-0.055 – 0.005	0.117
Gap Area	-3.209	-5.635 – -0.784	**0.020**
Mean Basal Area	0.015	0.003 – 0.027	**0.026**
Location [Edge]*Flood Days	-0.004	-0.027 – 0.019	0.716
Location [Forest]*Flood Days	0.029	0.006 – 0.052	**0.019**
Random Effects			
σ^2	0.38		
$\tau_{00\ \mathrm{Gap\_ID}}$	0.53		
$n_{\mathrm{Gap\_ID}}$	20		
Observations	60		
Marginal R^2 / Conditional R^2	0.315 / 0.713		

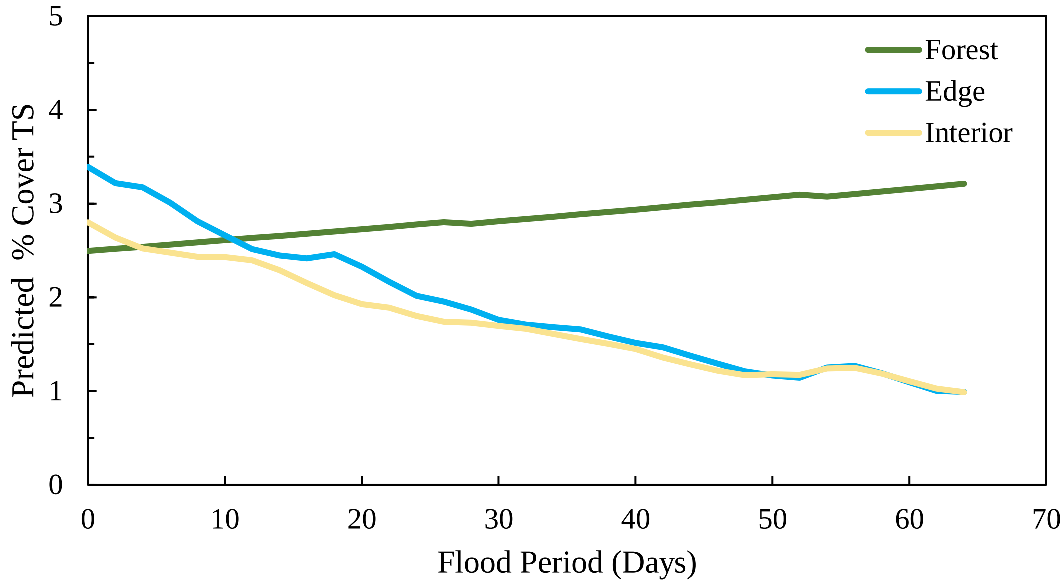

Figure 5. Predicted response of tree seedlings to flood period by location. Patterns show how tree seedling percent cover is predicted to respond to flood period in different locations within and adjacent to canopy gaps. Model is based on 60 values obtained from field data (one interior, edge, and forest value per sampled gap).

The model also predicts a small decrease in tree seedling percent cover (from 4% to 1%) with increasing gap area ($F_{1,16}$ = 6.73, P = 0.020; Figure 6). However, the significance of this effect disappeared when the two largest gaps were omitted from the analysis. Tree seedling percent cover is predicted to increase by a similar magnitude (from 1% to 4%) with an increasing mean basal area within the forest surrounding the gap ($F_{1,16}$ = 5.97, P = 0.026; Figure 7).

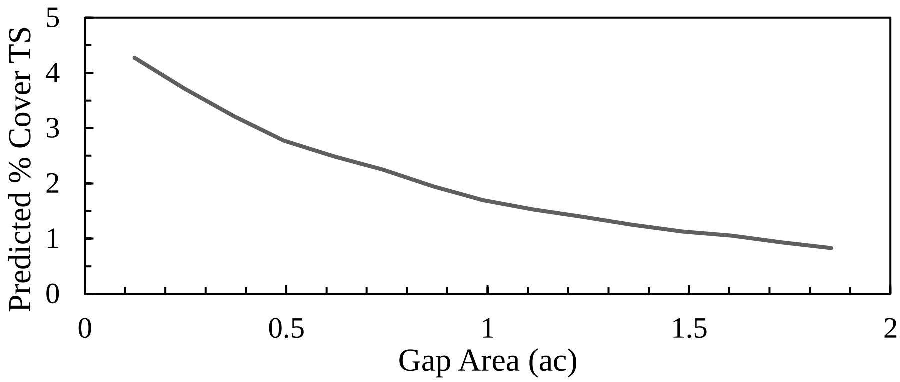

Figure 6. Predicted response of tree seedlings to gap size. Model is based on 60 values obtained from field sampling (one interior, edge, and forest value per sampled gap). However, the significance of this pattern does not hold when it is evaluated only for gaps smaller than 1 acre in size.

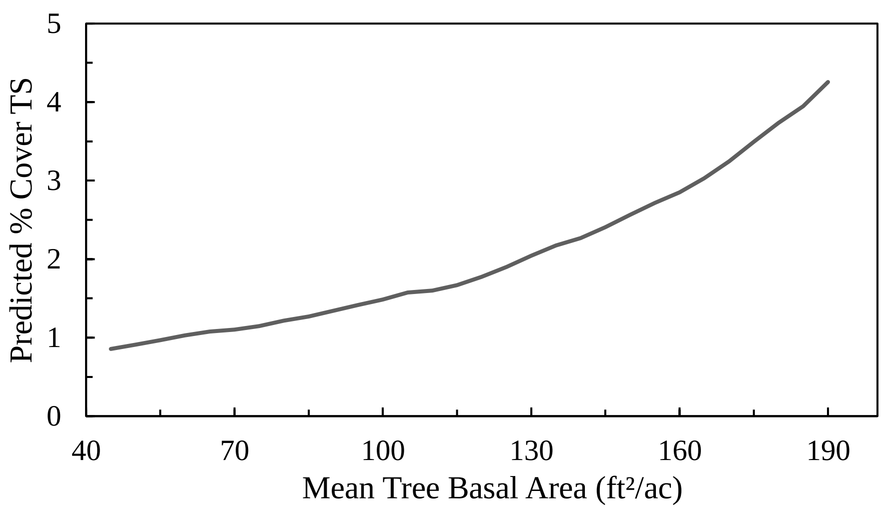

Figure 7. Predicted response of tree seedlings to tree basal area. Model is based on 60 values obtained from field data (one interior, edge, and forest value per sampled gap).

Reed Canarygrass Cover

The final model that best fit the log-transformed values for reed canarygrass percent cover included multiple predicting factors, as well as a significant three-way interaction (Table 8).

Table 8. Summary of the linear mixed model that was deemed to be the best fit for reed canarygrass percent cover values. The random effect of Gap ID was included in models to account for the repeated measurements made on each gap (mean values for interior, edge, and forest quadrats).

	log(RCG Percent Cover + 0.5)		
Predictor	**Estimate**	**95% CI**	***P***
Location [Edge]	-0.360	-0.855 – 0.136	0.163
Location [Forest]	-1.236	-1.732 – -0.741	**<0.001**
Gap Area	-15.851	-61.551 – 29.848	0.510
Flood Days	-0.347	-0.715 – 0.022	0.090
Percent Forest Buffer	0.019	-0.101 – 0.138	0.764
Gap Area*Flood Days	3.164	0.910 – 5.419	**0.018**
Gap Area*Forest Buffer	0.398	-0.184 – 0.980	0.205
Flood Days*Percent Forest Buffer	0.005	0.000 – 0.010	0.066
Gap Area*Flood Days*%Forest Buffer	-0.048	-0.077 – -0.018	**0.008**
Random Effects			
σ^2	0.64		
$\tau_{00\ Gap\_ID}$	0.59		
n_{Gap_ID}	20		
Observations	60		
Marginal R^2 / Conditional R^2	0.666 / 0.826		

There was a significant three-way interaction on the log-transformed reed canarygrass percent cover between gap area, flood days, and percent forest buffer ($F_{1,12}$ = 9.98, P = 0.008). This three-way interaction remained significant when the two largest gaps were omitted from the analysis. The percent cover of reed canarygrass is expected to increase from 0% to ≥ 60% cover with an increasing gap size for all flood periods when the forest buffer is relatively low (60%), but when the forest buffer is higher (80% and 100%), the increasing trend is only seen for locations with a lower flood period (Figure 8). The model also predicted a significantly higher mean percent cover of reed canarygrass within the gap interior (approximately 5% cover) than within the surrounding forest (just above 1% cover) (t_{38} = 43.9, P < 0.001).

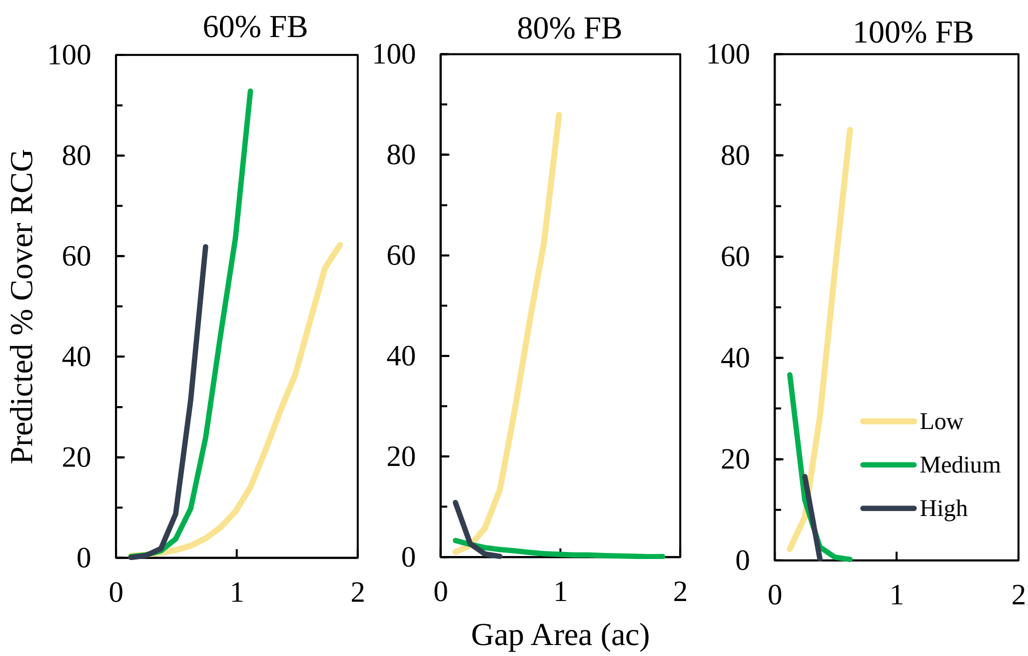

Figure 8. Predicted percent cover of reed canarygrass in response to the interactive effects of flooding, gap size, and forest buffer percentage. The different colored lines represent different periods of flooding, depicted in the legend within the third panel.

Forb Cover

The final model that best fit the values for forb percent cover was for the rank-transformed values and included a variety of predicting factors and the same three-way interaction that was observed for reed canarygrass ($F_{1,10}$ = 5.20, P = 0.046, Table 9). The significant three-way interaction suggests that the percent cover of forbs decreases from approximately 40% cover down to nearly 0% cover as gap size increases within all flood periods when the forest buffer is relatively low (60%), but as the forest buffer increases (to 80%, 100%), forb cover begins to increase with gap size in sites with medium and high flood periods, reaching upwards of 50% cover in areas with the most intact forest buffer (Figure 9). However, we note that this three-way interaction did not hold when the two largest gaps were eliminated from the analysis. Forb percent cover is also predicted to be significantly related to both the average regeneration score ($F_{1,10}$ = 8.65, P = 0.015) and the total species richness of large trees within the surrounding forest ($F_{1,10}$ = 6.83, P = 0.026). The generated model suggests that the predicted percent cover of forbs increases gradually from approximately 26% to near 35% as the regeneration score of younger trees within the surrounding forest increases (Figure 10). In contrast, the model found a negative relationship between the species richness of mature trees and predicted forb percent cover, impacting the predicted percent cover to a similar extent in the opposite direction (Figure 11).

Table 9. Summary of the linear mixed model that was deemed to be the best fit for forb percent cover values. The random effect of Gap ID was included in models to account for the repeated measurements made on each gap (mean values for interior, edge, and forest quadrats).

Predictor	F Percent Cover Rank Estimate	 95% CI	 *P*
Gap Area	270.045	-236.186 – 776.276	0.320
Flood Days	2.192	-2.093 – 6.477	0.340
% Forest Buffer	0.343	-1.214 – 1.900	0.675
Regen Score	16.718	5.575 – 27.860	**0.015**
Total Richness	-5.615	-9.827 – -1.403	**0.026**
Gap Area*Flood Days	-26.788	-52.018 – -1.557	0.064
Gap Area*%Forest Buffer	-4.844	-11.269 – 1.581	0.170
Flood Days*%Forest Buffer	-0.042	-0.100 – 0.016	0.186
Gap Area*Flood Days*%Forest Buffer	0.383	0.054 – 0.712	**0.046**
Random Effects			
σ^2	96.83		
$\tau_{00\ \mathrm{Gap\_ID}}$	64.17		
$n_{\mathrm{Gap\_ID}}$	20		
Observations	60		
Marginal R^2 / Conditional R^2	0.542 / 0.724		

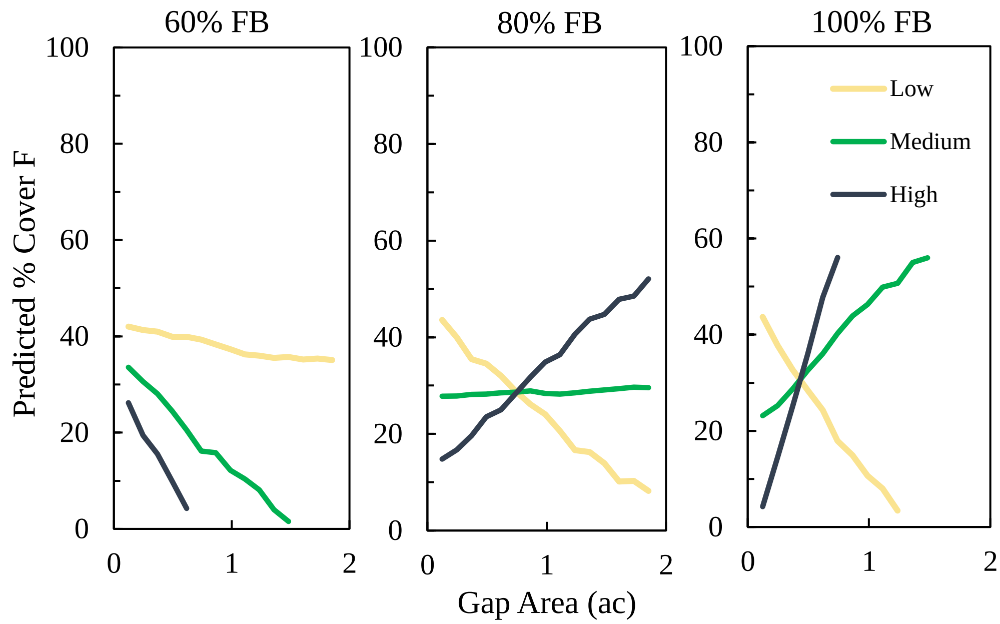

Figure 9. Predicted percent cover of forbs in response to the interactive effects of flooding, gap size, and forest buffer percentage. The different colored lines represent different periods of flooding, depicted in the legend within the third panel.

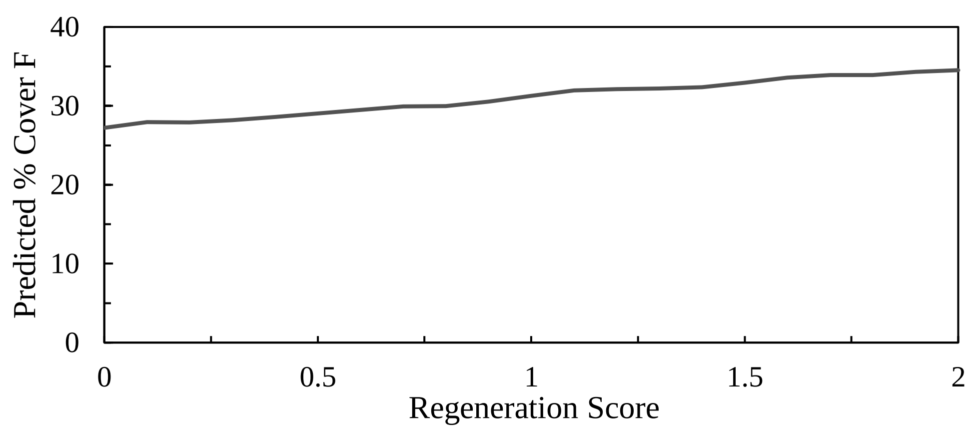

Figure 10. Predicted response of forbs to regeneration in surrounding forest. Model is based on 60 values obtained from field data (one interior, edge, and forest value per sampled gap).

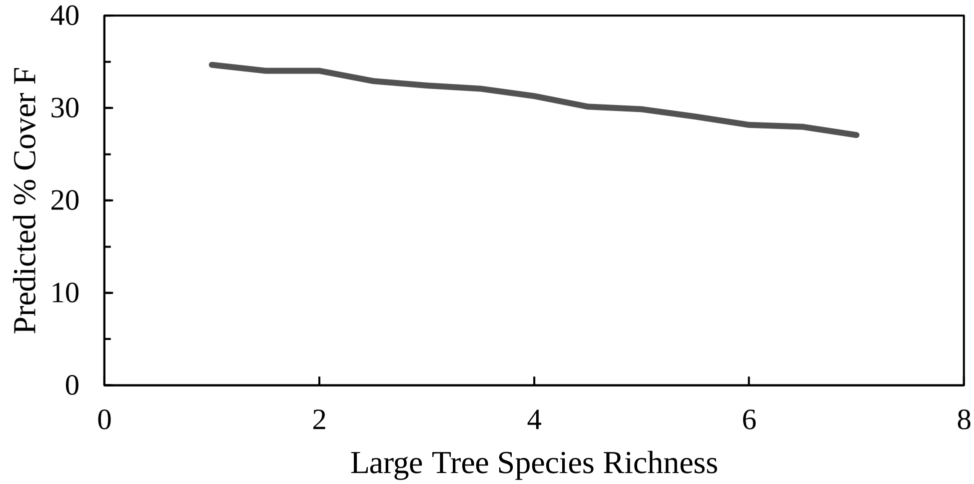

Figure 11. Predicted response of forbs to species richness of canopy trees. Model is based on 60 values obtained from field data (one interior, edge, and forest value per sampled gap).

Graminoid Cover

Robust linear mixed modeling found that the best model to fit and describe the percent cover values of graminoids included several predicting factors and interactions (Table 10). The same significant three-way interaction between gap area, flood days, and percent forest buffer was identified for predicted graminoid percent cover ($F_{1,10}$ = 7.20, P = 0.021). The model suggests that when forest buffer is relatively low (60%), percent cover of graminoids increases from approximately 20-80% in low flood conditions while maintaining an average of around 30% in medium flood conditions, but as forest buffer increases (to 80%, 100%), percent cover increases to nearly 100% in medium and high flood conditions but remains low for low flood periods (Figure 12). However, we note that significance was lost when the two largest gaps were removed from the model.

Table 10. Summary of the linear mixed model that was deemed to be the best fit for graminoid percent cover values. The random effect of Gap ID was included in models to account for the repeated measurements made on each gap (mean values for interior, edge, and forest quadrats).

		G Percent Cover	
Predictor	**Estimate**	**95% CI**	***P***
Location [Edge]	-3.961	-13.544 – 5.622	0.423
Location [Forest]	-13.325	-22.908 – -3.742	**0.010**
Gap Area	793.289	80.967 – 1505.612	0.052
Flood Days	3.713	-1.816 – 9.241	0.215
% Forest Buffer	0.268	-1.511 – 2.047	0.774
Basal Area	-0.389	-0.652 – -0.125	**0.015**
Gap Area*Flood Days	-42.114	-77.122 – -7.107	**0.038**
Gap Area*%Forest Buffer	-10.934	-20.034 – -1.833	**0.038**
Flood Days*%Forest Buffer	-0.052	-0.127 – 0.022	0.197
Gap Area*Flood Days*% Forest Buffer	0.638	0.172 – 1.104	**0.021**
Random Effects			
σ^2	239.07		
$\tau_{00\ \mathrm{Gap\_ID}}$	96.76		
$n_{\mathrm{Gap\_ID}}$	20		
Observations	60		
Marginal R^2 / Conditional R^2	0.437 / 0.599		

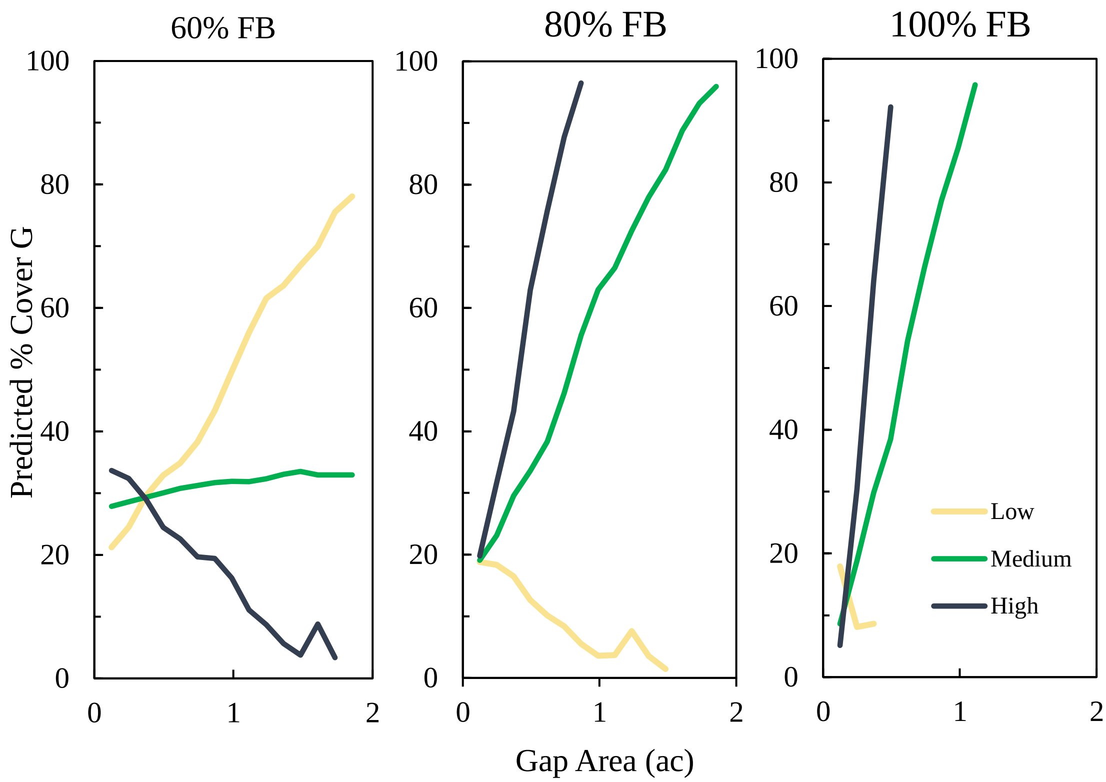

Figure 12. Predicted percent cover of graminoids in response to the interactive effects of flooding, gap size, and forest buffer percentage. The different colored lines represent different periods of flooding, depicted in the legend within the third panel.

The model also suggested that location significantly influences graminoid percent cover ($F_{2,38}$ =3.92, P = 0.028). Specifically, the model predicts graminoid percent cover will be significantly higher in the gap interior (estimated 35% cover) than in the surrounding forest (estimated 22% cover), with no significant difference in cover between the gap interior and gap edge. In addition to the influence of location, the model found a significant relationship between basal area in the surrounding forest and graminoid percent cover ($F_{1,11}$ =8.34, P = 0.015). The significant relationship between graminoid percent cover and basal area is overall positive when the trendline is examined (m = 0.0716), though it appears to decrease before increasing (Figure 13).

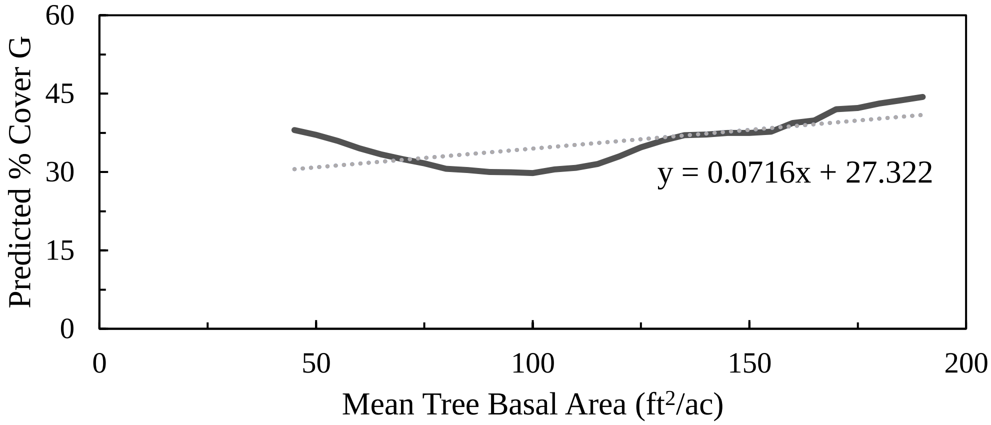

Figure 13. Predicted response of graminoids to tree basal area. A linear trendline is included; its equation is provided on the figure. Model is based on 60 values obtained from field data (one interior, edge, and forest value per sampled gap).

DISCUSSION

The floodplain forests of the UMRS are dynamic ecosystems with a variety of biotic and abiotic environmental factors that interact and influence the creation of canopy gaps, as well as whether the gaps serve as locations for forest regeneration or are instead invaded by herbaceous plant species. Our field study allowed us to examine the plant communities that are currently present within and adjacent to 20 canopy gaps representing a range of sizes and flood periods in floodplain forests of pools 8 and 9 of the UMRS, and to examine how gap communities are influenced by environmental factors. We hope that the data that we collected and the trends that we identified can be used as a resource for the formation of future management plans that will allow for the most effective conservation of these forests.

Regeneration

Our data analyses showed that there is a lack of successful forest regeneration across canopy gap sites. Because the LiDAR imagery used to identify the gaps for this study was from 2010, we know that these gaps had been present for at least nine years before they were sampled. While tree seedlings were present at all 20 sites, their average percent cover was relatively low overall, with models predicting only around 5% cover. Additionally, saplings greater than 50 cm in height were present in fewer than half of the sites that we surveyed, and only one gap was at the pole stage when sampled. We also recorded low regeneration ratings for the forest inventory plots, with all scores ranging from 0-2 out of 5 possible points. These data raise questions as to what is preventing seedlings from surviving for multiple growing seasons and reaching the sapling or pole stage needed for the stand initiation phase of forest succession. A previous assessment of regional floodplain forests also noted a limited to nearly absent understory layer as a characteristic seen throughout the UMRS (Guyon & Battaglia, 2018), suggesting the same uncertainty regarding future canopy tree recruitment.

We also noted evidence of the effects of the emerald ash borer during our study. Multiple gaps had dead and/or dying ash trees present at the canopy edge, which meant that the gaps were slightly larger than when they had originally been mapped. Despite the loss of mature green ash, we noted green ash seedlings in half of our study sites. Green ash was also the most commonly recorded species at the sapling stage and when measuring regeneration within the forest inventory. While green ash still remains present within UMRS floodplain forests, the threat of the emerald ash borer may cause it to play a different functional role if some individuals are able to persist in isolated areas (Romano, 2010). This has implications for overall forest structure if the main species showing advance regeneration is not likely to reach full maturity in most areas.

In addition to finding that some sites were larger than expected, we also found that other sites were wetter than expected. Certainly, this is due in part to the high flood year; sites that were categorizes as having a high flood period (40-100 days) maintained standing water through the summer 2019 field season (143+ days). Of all of the large (0.75-2.00 ac) gaps with a high flood period, none were appropriate for our study: they were either dominated by more than 50% emergent aquatic vegetation or were too flooded for accurate sampling. It is understood that current flood conditions are different than conditions that were present when mature trees became established (Romano, 2010; Guyon & Battaglia, 2018). If extreme rainfall events continue to increase as the climate changes, it is possible that areas of the understory- both beneath the canopy and within canopy gaps- may no longer support the recruitment of new generations of tree species that are currently key components of the system (Guyon & Battaglia, 2018).

Reed Canarygrass

Our results confirm the idea that reed canarygrass is widespread in canopy gaps of pools 8 and 9 of the UMRS, and that it could be inhibiting the establishment of tree seedlings. We observed reed canarygrass within a majority (85%) of the gap sites that we surveyed. Furthermore, our model for reed canarygrass predicted a significantly higher percent cover within the gap interior, and our correlational analysis identified a significant negative relationship between reed canarygrass presence and the presence of tree seedlings and other graminoids. Previous studies have shown that reed canarygrass is a strong competitor against floodplain tree seedlings (Reinhardt Adams et al., 2011; Thomsen et al., 2012), so it comes as no surprise that this invasive grass is able to inhibit the establishment of tree seedlings within UMRS floodplain forest canopy gaps.

Our analyses suggest one avenue to explore in terms of locations where reed canarygrass may be easier to control, in that the percent cover of reed canarygrass is predicted to be significantly lower beneath the surrounding forest cover than within the gap interior. Reed canarygrass has been shown to be inhibited by shading in other studies (Lavergne & Molofsky, 2004). However, the grass does appear to be able to infiltrate the edge areas immediately adjacent to the canopy gap, and if the forest canopy is somewhat broken, patches of sunlight may allow it to persist further away from canopy gaps, as well. Additionally, our models suggest that when the forest buffer is low (60%), reed canarygrass percent cover increases as gap size increases across all flood periods. This means that it is able to successfully remain established under harsh environmental conditions and exert further pressure on other plant species that are present, especially in areas with a lot of sunlight available. Reed canarygrass becomes less successful when the forest buffer is more complete (80%, 100%), further showing how important it is to maintain canopy cover and/or to re-establish it where it has been lost.

New Generations of Trees

To successfully manage the UMRS floodplain forest, we need to know where tree seedlings are the most successful. In our study, the best fit model predicted that tree seedling percent cover would be lower in larger gaps than in smaller ones. This may be due to a lack of successful transport of propagules from the forest to the interior of the canopy gap (Connell, 1978). However, it may also relate to the likelihood of increased competition within larger gaps. Resources such as light and space are more readily available in larger gaps, and the soil conditions associated with higher levels of sunlight may promote the growth of other herbaceous species in these locations, including reed canarygrass and other graminoids, as seen in our results. For example, reed canarygrass is predicted to have a high percent cover in large gaps when the forest buffer is approximately 60% or when the flood period is relatively low (ranging from 60% to 90% cover). In contrast, graminoid percent cover is higher (reaching nearly 100% cover) in large canopy gaps when the flood period is longer (medium, high) and when the forest buffer is higher (80%, 100%), meaning nearly all conditions have the potential to promote the establishment of herbaceous species in large canopy gaps.

Our model-building provides some additional insight as to what environmental conditions promote tree seedling establishment. First, we found that flood period influences tree seedling percent cover differently within the surrounding forest than it does within the gap interior or locations along the gap edge. Within the gap interior and at the gap edge, tree seedling percent cover was predicted to decrease as flood period increases, as predicted by the idea that flood period is a critical factor that influences the performance and survival of tree seedlings within the floodplain forest (Romano, 2010; De Jager et al., 2013; Bouska et al., 2018). In contrast, percent cover of tree seedlings did not decrease within the surrounding forest as flood period increased. This result could be an artifact of our metric of flood period being based on the conditions within the gap, meaning that the values may not accurately describe conditions within the forest that was adjacent to the gaps. All things being equal, we assume that the forest surrounding a gap has a similar elevation and flood duration, but this is not necessarily the case. It is possible that the areas where gaps had formed were low-lying, meaning they remained inundated for longer periods of time than the higher surrounding forest and may be at a greater risk of herbaceous invasion (Bouska et al., 2019). Additionally, our limited ability to sample areas where standing water prevented accurate sampling along transects within the forest may mean that we under-sampled the wettest forest areas around gaps with longer flood periods.

Tree basal area in the surrounding forest was also found to significantly influence the predicted percent cover of tree seedlings, which may reflect the importance of propagule supply in the establishment of future generations of trees. In our forest inventories, we saw that the silver maple dominated the canopy in the forest area surrounding the canopy gaps and represented 75% of the individuals recorded in our basal area measurements. We also noted the presence of silver maple seedlings at 18 of the 20 gaps. Clearly, there is an ample supply of viable silver maple seeds within the floodplain forest spanning pools 8 and 9 of the UMRS. However, we only recorded one silver maple at the sapling stage during our vegetation sampling. If a majority of the silver maple within the canopy of the UMRS are 60-82 years old and expected to die within the next 50 years (Kirsch & Gray, 2017), but the seedlings are failing to reach the sapling stage, this suggests that the structure of the forest has the potential to change if lost trees are not replaced. Previous research has mentioned that a lack of tree species diversity and successful regeneration are threats to the long-term stability of UMRS floodplain forests (Guyon & Battaglia, 2018).

While selective browsing pressure by herbivores, such as the white-tailed deer, has been shown to interact with flooding to negatively impact tree seedling and sapling survival (De Jager et al., 2013), we did not observe a severe level of browsing on woody stems throughout our sites. The browsing we saw impacted fewer than half of the observed woody stems greater than 50 cm in height, and the browsing intensity was low and therefore did not affect the survival of the stems. Other studies have shown similar rates of deer browse occurrence, but greater browsing severity, in UMRS floodplain forest sites. A study that utilized the same scale to measure browse intensity on planted stems calculated average browse ratings ranging from 1 to roughly 2.5 after one growing season, which varied depending on the species of the woody stem (DeLaundreau, 2019).

Another study found that approximately 48% of planted stems were browsed, and browsing was severe enough that it was linked to a higher risk of mortality by the following year (Miller-Adamany et al., 2019). Finally, one other field study recorded a typical browsing intensity that impacted ~46% of available forage on tree saplings, with even more intense browsing on preferred species (Cogger et al., 2014). While it is possible that browsing may be inhibiting tree regeneration within some canopy gaps present throughout the UMRS floodplain forests, we did not necessarily observe it to be a detrimental factor in the gap sites that we surveyed for this study.

Conclusion

The floodplain forests of the UMRS are dynamic ecosystems that provide important ecosystem services. However, our study suggests that tree regeneration is not occurring within canopy gaps as we would expect, suggesting the potential for future loss of forest cover. The composition of the plant communities that we saw within the canopy gaps that we sampled was typically dominated by herbaceous species. While tree seedlings were present throughout all sites, less than half of the canopy gaps had tree saplings that were greater than 50 cm in height. We found that the increasing presence of reed canarygrass within our sites was correlated with a significant decrease in the presence of both tree seedlings and native graminoids. Physical management intervention may be required to remove this invasive grass from the system before it spreads further through disturbed areas of the floodplain forest.

Our results suggest that flooding may also be inhibiting the survival and growth of tree seedlings into larger size classes within canopy gaps, especially in larger gaps where competition with other species may be limiting seedling establishment. Repeated surveys will be needed to provide further insight into how plant communities within canopy gaps change over time under different environmental conditions, as the results of our study only describe communities at a single time point. When considering our results, future management efforts may need to focus on either promoting the survival of tree seedlings that are naturally being recruited or to plant larger saplings within gaps and other understory areas where natural tree recruitment is lacking. In particular, large canopy gaps may require more attention, especially if the forest buffer surrounding them is low. It is also important to determine a successful way to remove competitive invasives such as reed canarygrass from the floodplain forest before it becomes converted to another plant community type and loses the ability to perform important ecological functions.

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