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# Mortality patterns following a hickory decline event – Is density reduction key to maintaining bitternut hickory?

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ABSTRACT

Bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) is an important component of many hardwood forest systems in the northern hardwood forests of the Lake States. Extensive mortality of the species was observed in a long-term field experimental site in a second growth northern hardwood forest of Wisconsin between 2010 and 2016. We quantified and documented the characteristics of the mortality, investigated the relationship between bitternut hickory density and mortality patterns, and assessed the persistence of hickory regeneration. The presence of a pathogenic fungus (*Ceratocystis smalleyi* Johnson and Harrington) and hickory bark beetle (*Scolytus quadrispinosus* Say) were identified as the main cause of mortality in other instances of hickory decline during a similar time period in the Midwest and Northeast. We investigated the role of these agents through *post hoc* analysis. Tree surveys of mapped stems ≥10 cm dbh conducted periodically from 2005 to 2016 indicated mortality of hickory rose sharply to 35% year$^{-1}$ from 2010 to 2016. This is a substantial increase in mortality relative to the dominant species at the site (*Acer saccharum* Marshall, *Tilia americana* L., and *Fraxinus* spp.) which was 1.11% year$^{-1}$ in the same time period. Mortality rates were higher in larger stems (≥20 cm dbh) than smaller stems (10 < 20 cm dbh). Additional analyses evaluated whether mortality rates were affected by localized species composition, using the proportion of hickory stems among neighboring trees. Proportion of hickory stems, diameter, and crown class proved to be statistically important in predicting mortality in individual hickory stems. The density of hickory regeneration in the <30 cm tall height class decreased from 2010 to 2016. Overall the bitternut hickory population significantly declined, especially the larger sized trees, and this decline will have lasting consequences on the persistence of the species in the area. Potential management actions for mitigating impacts of such rapid hickory decline events, mainly selective thinning, are discussed. Methods for maintaining this co-occurring species is increasingly important as several other codominant species in northern hardwood forests are also decreasing.

## 1. Introduction

Forests in the U.S. Lake States (Minnesota, Wisconsin, and Michigan) have historically undergone immense changes following intense exploitation from the lumber industry in the late 1800s to very early 1900s, where around 20 million hectares were deforested (Williams, 1992). Before Euro-American settlement, the region was mostly dominated by mature and old conifer forests, especially by red (*Pinus resinosa* Sol. Ex Aiton), Eastern white (*Pinus strobus* L.), and jack pine (*Pinus banksiana* Lamb) on sandy soils, and east of Minnesota, by Eastern hemlock (*Tsuga canadensis* (L.)) Carriere) and hardwoods on mesic soils (Schulte et al. 2007). After extensive cutting, which left much of the region bare and subject to slash fires, the Lake States became hardwood dominated, especially by aspen (*Populus* spp.), and succeeding increasingly to the shade tolerant sugar maple (*Acer saccharum* Marshall) which is dominant in this region. This has also resulted in a reduction of biodiversity and structural complexity (Schulte et al. 2007). Sugar maple dominance specifically has almost doubled, which is most likely due to fire suppression, tolerance of white-tail deer herbivory, and to the predominance of single tree selection harvesting in the region (Schulte et al. 2007). The disturbance regime is dominated by small to moderate (average of about 40% basal area removal) disturbances caused by

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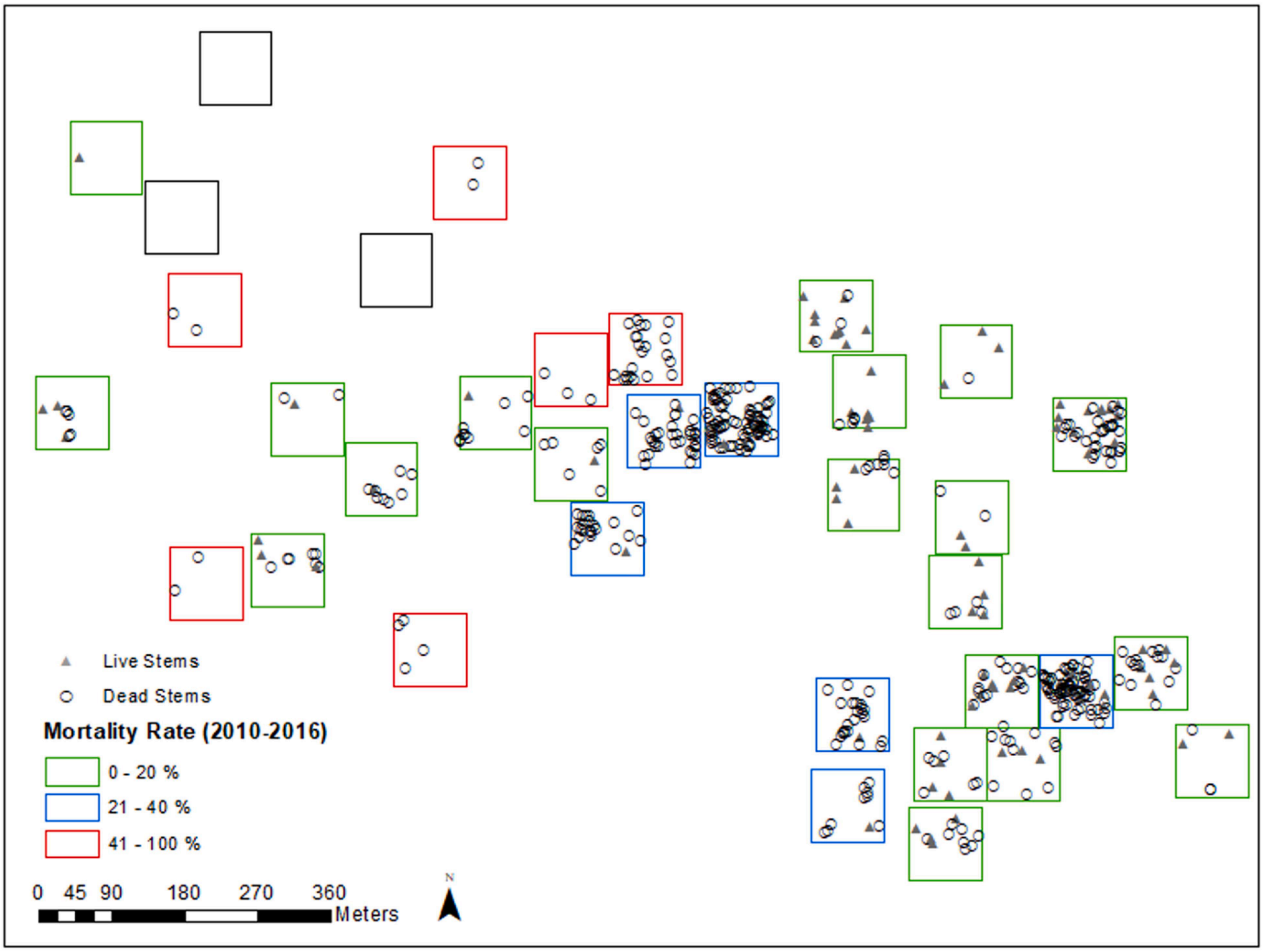


**Fig. 1.** Map of bitternut hickory stem locations and status in 2016 within the 35 80 × 80 m plots at the experimental site, located in the Flambeau River State Forest. Hollow circles are dead hickory stems, gray triangles are living hickory stems. Outline color of plots (squares) are indicative of intensity of mortality. Three plots with solid black outlines in NW corner contain no hickory stems. Experimental site located in north-central Wisconsin. (n = 393 dead stems, n = 76 living stems).

windstorms (Lorimer and Frelich 1994, Frelich and Lorimer 1991, Hanson and Lorimer 2007).

Bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) is an important component of many hardwood forest systems, such as sugar maple and sugar maple-basswood forests (Society of American Foresters Type 27 and Type 26) in the northern hardwood forests of the Lake States (Burns et al. 1990). Bitternut hickory exists in a large range in eastern North America, extending from Quebec to Minnesota, and south to Georgia and Texas. Bitternut hickory is a shade-intolerant species as a mature tree, although shows some tolerance as a seedling (Burns et al. 1990, Curtis 1959). It is an important species for biodiversity and soil-improvement due to the high calcium content in the foliage (Juzwik et al. 2008, Burns et al. 1990).

Periodic severe mortality of bitternut hickory has historically been reported across its range. Widespread mortality from Wisconsin east to Vermont, and south into Georgia was reported in the early 1900s (Hopkins 1912). Smaller areas of mortality were reported in Illinois in 1878 (Anonymous 1878), and in North Carolina and Michigan in the 1920's (St. George 1929, 1930). Many of these occurrences of periodic and intensive bitternut hickory mortality were at that time attributed to attacks from the native hickory bark beetle (*Scolytus quadrispinosus* Say) following drought conditions (St. George 1929, 1930).

Extensive mortality of bitternut hickory occurred in a long-term research site in the Flambeau River State Forest, Northern Wisconsin between 2010 and 2016, but the cause of mortality was not determined at that time. The tree population had been monitored for over a decade in a long-term experiment on forest structure manipulation (Forrester et al. 2013, 2014) providing a record of individuals before and after the mortality event. Similar rapid crown declines of hickory were seen in New York and the Midwest between 2006 and 2011 and were investigated (Juzwik et al., 2012). The decline and mortality observed were attributed to an interaction between the hickory bark beetle and the canker pathogen *Ceratocystis smalleyi* J.A. Johnson and Harrington) (Park et al. 2010, 2013; Park and Juzwik 2014). Interactions like these are common in declines, which is a category of plant disease involving a combination of factors, being predisposing, inciting, and contributing factors which lead to the eventual death of a tree (Manion 1991). However, quantitative description of the effects and implications of extensive bitternut hickory mortality in the affected stands is lacking. The loss of a species in a system, even an infrequent tree species, can affect ecosystem structure and processes, including the ability to recover after a disturbance event. Understanding and documenting the effects of intense bitternut hickory mortality on stand structure and regeneration patterns in a northern hardwood forest is necessary to develop methods or management strategies to maintain the species as part of the system.

The purpose of this study is to describe the rapid mortality of bitternut hickory and the stand characteristics associated with the decline, and to identify possible predisposing factors. The specific objectives are to (1) quantify and characterize the extent of mortality in the mature bitternut hickory population, (2) test the hypothesis that mortality patterns are influenced by tree competition and stem density, and (3) assess the persistence of hickory regeneration. The study results can

**Table 1**
Importance Values ((Relative Basal Area + Relative Density)/2) of tree species (stems ≥10 cm dbh) in the Flambeau Experimental Area in 2010 and 2016 (relative referring to percentage of total BA or density at site). Total stand density was 404.0 stems hectare$^{-1}$ and total BA was 28.7 m$^2$ hectare$^{-1}$ in 2010.

| | IV | | Relative BA (%) | | Relative Density (%) | |
|---|---|---|---|---|---|---|
| **Species** | **2010** | **2016** | **2010** | **2016** | **2010** | **2016** |
| **Sugar maple** | 61.2 | 64.4 | 57.1 | 59.8 | 65.3 | 69.0 |
| **Ash species** | 13.7 | 14.8 | 16.6 | 18.4 | 10.7 | 11.1 |
| **American basswood** | 13.0 | 13.5 | 15.3 | 15.8 | 10.8 | 11.1 |
| **Bitternut hickory** | 4.5 | 0.6 | 4.0 | 0.3 | 5.0 | 1.0 |
| **Northern red oak** | 1.7 | 1.8 | 2.3 | 2.5 | 1.0 | 1.1 |
| **Other** | 6.3 | 6.1 | 5.4 | 5.6 | 7.2 | 6.7 |

inform how extensive bitternut hickory mortality affects stand structure and regeneration of bitternut hickory, and what conditions may increase the likelihood of that mortality. *Post hoc* sampling for occurrence of the hickory bark beetle and *C. smalleyi* from declining and dead trees was conducted to support our hypothesis of the most likely cause of the extensive mortality, hickory decline.

## 2. Methods

### 2.1. Site description

The 300 ha study site is in the southern edge of the Flambeau River State Forest (45°37.4 N, 90°47.8 W), in northern Wisconsin (Fig. 1). The site is an even-aged, second-growth hardwood forest that is dominated by sugar maple (Table 1). Other overstory species within the site are American basswood (*Tilia americana* L.*)*, white, green, and black ash (*Fraxinus* spp.*)*, bitternut hickory, and northern red oak (*Quercus rubra* L.). To a lesser extent, other overstory trees are Eastern hemlock*,* black cherry (*Prunus serotina* Ehrh.*)*, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britt.), and aspen.

Average temperature for January and July is 10.3 °C and 19.1 °C, respectively (2010–2018) (Midwestern Regional Climate Center 2019). Average annual precipitation from 2010 to 2018 is 967 mm. The soils at the site are mostly well-drained silt loams (glossdalfs) of Magnor and Freeon series, over glacial till (Forrester et al. 2013).

The Flambeau Experiment was established to test the role of forest structural features on forest productivity, diversity, and carbon and nutrient cycling (Forrester et al. 2013). Thirty-five 80x80m (0.64 ha) permanent plots were established, to test seven treatment levels, with five replicates of each experimental level. Treatment types include woody debris addition, gap creation, gap creation and woody debris addition, gap creation with deer exclusion, deer exclusion, mechanical, and control (Forrester et al. 2013). In January 2007, variable sized gaps (50 m$^2$, 200 m$^2$, and 380 m$^2$) were created in each whole plot for a split-plot design. These sizes were chosen to represent the range of gaps that are often found in old-growth northern hardwood forests. Deer exclosure fences were installed in fall 2007 around five gap and five control plots to study the effect of white-tail deer. The mechanical treatments were controls included to account for any influence of harvest equipment. The three variable sized central zones (where trees were harvested in gap creation treatment plots) and associated transition zones together compose the three subplot areas of each plot, where more intensive surveys were completed. Permanent vegetation quadrats (n = 42, 2 × 2 m) were established within each plot, distributed along cardinal and sub-cardinal directions from each subplot center (Fig. A.1). For more information on the experimental design see Forrester et al. (2013).

### 2.2. Stem inventory

All trees ≥10 cm within the thirty-five, 0.64 ha plots were permanently tagged, identified, and mapped using a survey grade total station initially, and ingrowth was subsequently mapped with laser rangefinders. Trees were measured annually in fall from 2005 to 2010 and in 2016. Diameter at breast height (dbh) was measured with diameter tape, status (living or dead), and crown class (dominant, codominant, intermediate, and suppressed) was recorded for each stem.

Saplings (0.5 < 10 cm dbh, > 1.4 m in height) in subplots were surveyed beginning in 2005 and in 2010, 2013, and 2016. Species was recorded, and dbh was measured to the nearest 0.1 cm using calipers and diameter tape. Heights were measured to the nearest 0.01 m with a height pole or clinometer. Woody understory in 2 × 2 m quadrats were surveyed in 2010, 2013, and 2016. Understory was divided into the following height classes; seedling (0–30 cm), small sapling (30.1–100 cm), and intermediate sapling (100.1–140 cm). Species and stem count were recorded in these height classes, as well as age (1 year or 2+ years) for the seedling height class. Understory and sapling surveys were completed in 30 of the 35 plots, which includes all treatment types excluding mechanical treatment plots which were not resampled in 2010 and 2016.

### 2.3. Statistical analysis

#### 2.3.1. Tree population dynamics

Mortality rates were calculated over 1 year time periods from 2005 to 2010, and over a six year period between 2010 and 2016, following inventory data availability. The mortality rates were calculated using a standard mortality equation based on a negative compound interest rate formula (from Lorimer et al. 2001):

$$mortality = (1 - \left(\frac{N_t}{N_o}\right)^{\left(\frac{1}{t}\right)}) \cdot 100$$

where $N_o$ = number of stems at first measurement, $N_t$ = number of surviving stems at next measurement, t = time between measurements..

Mortality rates for the hickory tree population were calculated for 5 cm diameter classes, starting at 10 cm dbh. Hickory stems ≥40 cm were combined into one 40+ cm diameter class for the analysis of mortality rates because only three trees at the site were larger than 45 cm. Mortality rates of bitternut hickory were tested using one-way analysis of variance (ANOVA)) with diameter class as main effects and a Tukey's test to test for difference in mortality rates by diameter class. All statistical analyses were completed in SAS statistical software (SAS version 9.0, SAS institute, Cary, NC) unless noted otherwise. Treatment was not included in mortality rate testing as deer do not influence stems at this site over 10 cm dbh. Density (stems per ha) was calculated for 2010 (pre-mortality) and 2016 (post-mortality) by dbh class and plot, then averaged across the entire site.

To test the role of tree competition in influencing mortality, the spatial distribution of bitternut hickory was tested with an average nearest neighbor (ANN) analysis in ArcMap (ESRI, 10.6.1). This analysis compares the average distance between points to a hypothetical random distribution, which produces a unitless ratio. That ratio reveals information on whether those spatial points are clustered (value less than 1), random (value close to 1), or dispersed (value greater than 1). The analysis was based on the mapped trees 10 cm dbh and larger (live and dead, in the 2010 inventory) in plots with 10 or more hickory individuals so as to better represent the spatial distribution of the hickory population. This was completed using the ARCGIS ANN tool within each plot, and then averaged separately for plots with and without gap treatment. These plots were calculated separately because the gap treatment plots have gap areas in which all trees were removed, which may change the outcome of the ANN analysis.

Temporal differences for hickory regeneration were assessed by the four height classes (≤30 cm, 30 < 100 cm, 100 < 140 cm, and >140 cm < 10 cm dbh) defined in the woody understory and sapling surveys. Density in stems per hectare was calculated by height class and plot and averaged across the site for 2010 and 2016. The difference in stems per hectare (square root transformed as needed) was analyzed with a multiway ANOVA (using PROC GLM in SAS statistical software) and Tukey's means comparison test to evaluate the differences of density between height classes. The main effects in this model were height class, year, and treatment, and interactions were included for all variables. An analysis of simple effects using least squares means comparisons was completed to test the significance of the interaction of year by height class to evaluate if density differed between time periods within each height class. The distribution of the seedling data was assessed using residual and Q-Q plot diagnostics, and a square-root transformed density variable was included in the simplified analysis. The treatment variable was included in this analysis to check for any effect of experimental treatment on regeneration persistence between years.

### 2.3.2. Testing for stem density dependence at multiple scales

The strength of the relationship between hickory mortality and stem density was evaluated on a plot-level and an individual tree-level. Plot-level relationships were evaluated using a simple linear regression of mortality and explanatory values individually. Explanatory variables used were basal area of all species, basal area of bitternut hickory stems, trees per hectare (tph) of bitternut hickory, tph of all species, and percent bitternut hickory relative to all species. These variables along with mortality of bitternut hickory between 2010 and 2016 were calculated for each of the 35 plots at the site.

Individual tree-level relationships were evaluated to test if the likelihood of mortality of an individual stem was related to the density within its immediate neighborhood. Using ArcMap to estimate tree-level density, a circular buffer was created around all hickory trees (live and dead, n = 469) and clipped to the extent of the 35 mapped plots. Geometry was calculated and a count of hickory stems and a count of trees of all species were output and scaled to stems per hectare for each buffer around all hickory stems within the experimental plots. Four buffer sizes were generated, ranging from 50 $m^2$ to 1964 $m^2$ (Fig. A.4). A 25 m radius (1964 $m^2$) represents the height of the forest canopy, and 11 m, 8 m and 4 m radii span the range of large to individual size gaps (380–50 $m^2$) characteristic of variation in the forest type (Goodburn and Lorimer 1998).

Logistic regression was used to estimate the probability of individual bitternut hickory stem mortality using density variables, diameter, and crown class (Proc Logistic in SAS statistical software) (Table A.1, Table A.2). Density variables tested were tree-level density values scaled to stems per hectare of all species, stems per hectare of only hickory stems, and percentage of stems that are hickory all within a defined radius. Crown class was defined as canopy "D" (combined dominant and codominant classes) and sub canopy "S" (combined intermediate and suppressed classes) trees not only to simplify the model but also to increase the ease of interpretation of this variable. Density variables were not used in the same model to avoid multicolinearity and correlations among variables that were included in all models were evaluated (Table A.4).

The logistic regression model follows:

$$M = \ln(m/(1-m)) = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$$

where M is the log-odds of the probability of hickory tree mortality, and $\beta_o$ through $\beta_3$ are model coefficient estimates. Crown class is included as a categorical variable with canopy crown class valued at 1, and subcanopy valued at −1. Four models were created using the density values from the four different buffer sizes, in addition to diameter and crown class. The variables for the best fit were selected based on within model comparisons using AIC (Akaike Information Criterion).

## 2.4. Identification of biotic decline agents

In the summer of 2018 a subset of dead and dying hickory stems (n = 53) were surveyed for signs of decline agents, including stem lesions and cankers, and beetle holes and galleries (Fig. A.2, Fig. A.3). In July of 2019, three trees larger than 10 cm dbh were selected for subsampling and confirmation of decline agents based on similar signs of decline as listed above. Trees selected were found between, but not within, the permanent plots of the Flambeau Experiment. Selected trees were felled, and stem cross-sections were harvested at the locations of beetle entry holes and visible sunken cankers. Bark was stripped and stems were surveyed for colonization by hickory bark beetles (i.e. the presence of beetles, unique centipede-shaped galleries, or bark beetle entrance holes). Any visible cankers or xylem lesions, and the extent of such, were recorded.

Wood samples were transported to the laboratory (USFS Northern Research Station in St. Paul, Minnesota). Small cubes approximately 2 × 2 cm were cut at the margin of putative fungal infection, indicated by the edge of sapwood discoloration. Cubes (n = 10–25) were placed in moist chambers using glass Petri dishes and kept at about 25 °C. At 10 and 20 days the samples were examined for *C. smalleyi* perithecia, and

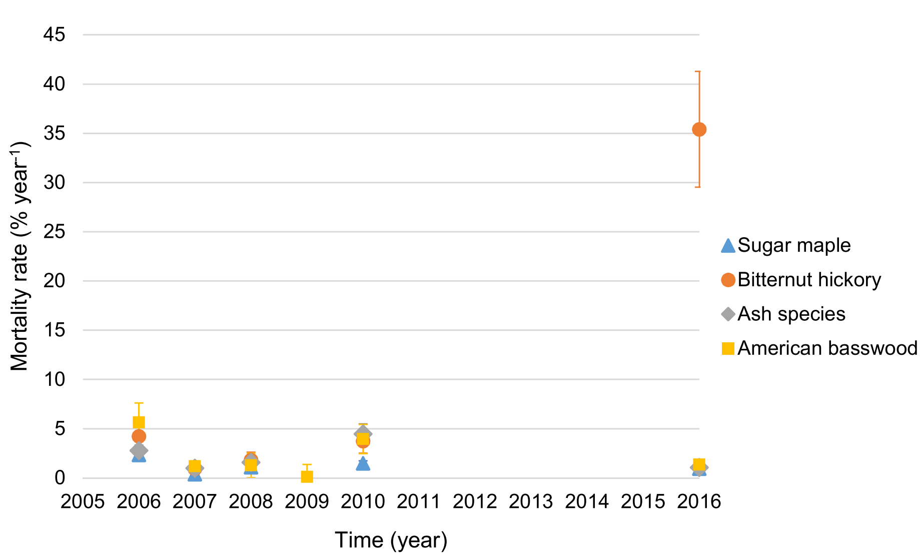


**Fig. 2.** Mortality (% year$^{-1}$) of the four most dominant species in the Flambeau Experimental Area monitored from 2005 through 2016 (stems ≥ 10 cm dbh). Mortality values calculated annually from 2006 to 2010 and between 2010 and 2016 using equation from Lorimer et al. (2001). Ash species includes *Fraxinus americana, F. nigra, and F. pennsylvanica.* Sample size ranges from 94 to 6384 stems per species per year.

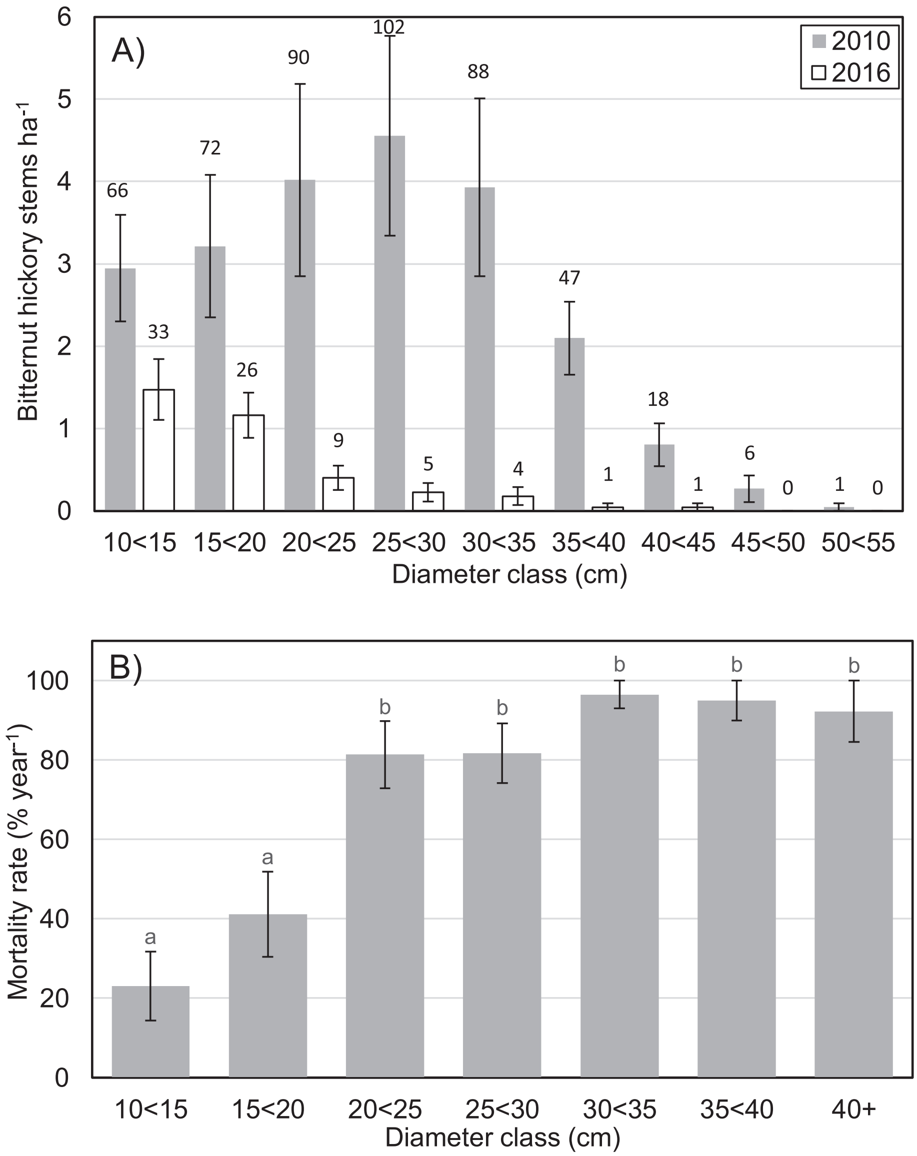


**Fig. 3.** A) Diameter distribution of bitternut hickory (trees ≥ 10 cm dbh). Stem counts per diameter class are indicated above each bar in density distribution. B) Mean mortality rates of bitternut hickory (trees ≥ 10 cm dbh). Results from an ANOVA with a Tukey's test show statistically significant differences in mortality rates between diameter classes, which are indicated with letters a and b. Mean mortality rates by diameter class from 2010 to 2016. Significance shown on $\alpha = 0.05$ level. Error bars indicate ± 1 standard error from plot variability.

ascospore masses were transferred to Petri dishes with 2% malt yeast agar extract agar (MYEA) amended with streptomycin sulfate (100 ppm) for fungal isolate collection. Pure isolates were obtained and then maintained on MYEA at 4 C until further processed.

A small amount of mycelia was obtained from the outer margin of a 7-day old culture growing under ambient lab conditions and mycelia placed in 200 µl CTAB lysis buffer (1.4 M NaCl 0.1 M Tris-HCL, 20 mM EDTA, 2% CTAB). The protocol described by Lindner and Banik (2009) was used with components of a commercial DNA extraction kit (Gene Clean III, Obiogene, www.qbiogene.com) to extract purified DNA from the fungal isolates. Amplification of DNA was performed with primer pairs (EF1F/EF2; ITS1F/ITS4) from two gene regions - translation elongation factor (tef) and internal transcribed spacer (ITS), respectively. Polymerase chain reactions (PCR) were performed in 15 µl reaction mixtures containing 3 µl DNA template, 0.3 µl of each forward and reverse primer of a pair, 5.025 µl of molecular grade water, 0.3 µl dNTP, 3 µl green GoTaq reaction buffer, 0.075 µl Go Taq DNA polymerase, 1.5 µl bovine serum albumen (0.1% solution), and 1.5 µl polyvinyl pyrroliodone-40 (1% solution). Amplification reactions were conducted in a thermocycler (Bio-Rad, Hercules CA, USA) following conditions described by Lindner and Banik (2009).

PCR products were visualized under ultraviolet light on a 2% agarose gel stained with ethidium bromide (0.5 µg/ml). The gel was flooded with Tris-borate-EDTA buffer and electrophoresis conducted at 100 V for 15 min before visualization. Sequencing reactions with the PCR products obtained from amplification of either gene region were performed following the Big Dye terminator protocol (ABI Prism). For each sample, 7 µl diluted DNA was combined with 1.8 µl molecular grade water, 25 µl 5X buffer, 0.5 µl betaine and 0.2 µl of appropriate forward 10X primer. Sequencing products were cleaned and analyzed using ABI 3730xl equipment at a commercial sequencing laboratory (Functional Biosciences, Inc. Madison, WI). The fungal sequences obtained were viewed and edited using commercial software (ChromasPro, Queensland, Australia). The resulting sequences were then aligned with sequences in the NCBI database using BLAST (www.blast.ncbi.nlm.nih.gov/).

## 3. Results

### 3.1. General mortality

Overall, tree mortality in the four most important species at the experimental site (sugar maple, bitternut hickory, ash species, and American basswood) was 1.83% year$^{-1}$ averaged from the start of the measurements in 2005 through 2010 (Fig. 2). However, from 2010 to

**Table 2**
Average nearest neighbor (±standard error) metrics of bitternut hickory stems (≥10 cm dbh) in plots with and without gap treatment.

| | Nearest Neighbor Ratio | Range | Sample Size (Plots) |
|---|---|---|---|
| Gap plots | 0.96 ± 0.11 | 0.51–1.55 | 9 |
| Non-gap plots | 0.86 ± 0.06 | 0.48–1.08 | 9 |

2016 bitternut hickory mortality increased to 35% year$^{-1}$ compared to other species at 1.11%year$^{-1}$ which reflects a reduction in bitternut hickory stem number from 21.9 stems hectare$^{-1}$ in 2010 to 3.5 stems hectare$^{-1}$ in 2016 (stems ≥ 10 cm), or an 84% reduction in stems hectare$^{-1}$.

### 3.2. Bitternut hickory distribution and mortality

The bitternut hickory population declined across all diameter classes from 2010 to 2016 (Fig. 3). The shape of the diameter distribution shifted from more larger to more smaller stems, with only two trees larger than 35 cm surviving. Mortality rates of stems (≥10 cm dbh) were high in all diameter classes, ranging from 23% year$^{-1}$ in the 10 < 15 cm diameter class up to 100% year$^{-1}$ in the largest three diameter classes (30 < 35, 35 < 40, 40+) (Fig. 3). The one-way ANOVA of the mortality rates by diameter class resulted in a p-value of <0.0001 and a F-value of 15.79. Means comparisons with the Tukey's test indicated that mortality in stems from 10 to 20 cm diameter have significantly lower mortality than stems larger than 20 cm dbh (comparisons significant at p = 0.05).

The average nearest neighbor analysis revealed that the bitternut hickory population was best characterized as randomly dispersed (values close to 1), if slightly clustered (Table 2). Hickory within gap creation treatment plots, had a slightly more clustered patterning (n = 9, mean 0.96) compared to the spatial distribution in plots where gaps had not been created (n = 9, mean = 0.86).

### 3.3. Stem density dependence patterns

Proportion of hickory stems within each plot was tested against mortality by plot (n = 25). Six plots with 100% mortality values were removed as most of these plots had fewer than 5 stems. This regression produced an r-squared value of 0.2493, p = .01, F = 7.64 (Fig. 4).

On an individual tree-level, mortality of bitternut hickory was predicted with a model and the best fit model included the following predictor variables: diameter at breast height, crown class, and percent hickory stems (Table 3). All of the predictor variables were significant (p < .05) for models of all buffer sizes. The Likelihood Ratio Chi-Square was significant for all sized buffer models (p < .0001), and the Hosmer and Lemeshow test was not significant (p > .05) for all models, revealing good model fit. The Wald's Chi-Square Test also showed that all three predictor variables were very significant to each model (P < .001). A classification matrix for observed and predicted model outputs shows that the models have an overall correction prediction of about 85% (Table A.3). All models show that the probability of mortality increases with increasing dbh, a canopy (D) crown class, and higher percentage of hickory stems in proximity to the host stem in question (see Fig. 5, showing model output for the 25 m buffer).

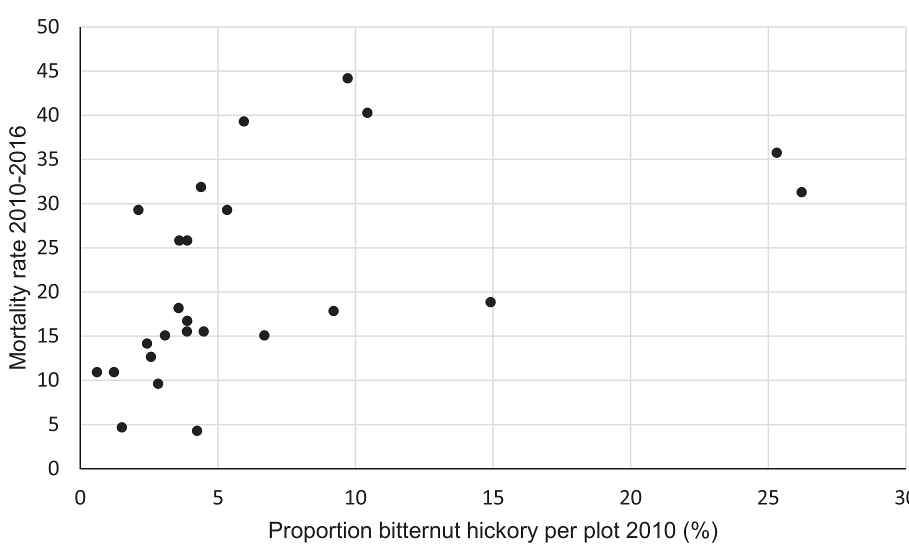


**Fig. 4.** Mortality rate of bitternut hickory stems (≥10 cm dbh) from 2010 to 2016 by proportion of hickory over all tree species within a plot in 2010. Linear regression analysis showed variables were not significantly correlated, with r-squared = 0.2493, p = .01, F = 7.64.

**Table 3**
Logistic regression models for predicting bitternut hickory mortality using four different sized buffers (all models P > Chi Sq < 0.0001 for LR ChiSq). Significance of parameter estimates from Wald's Chi-Squared test denoted by * (α=0.05) and ** (α=0.01). M is the log-odds of the probability of mortality, $\beta_i$ are model coefficient estimates, $X_1$ is crown class (Canopy (D) = 1, Sub-canopy (S) = −1), $X_2$ is % hickory (hickory stems over total stems of all tree species *100), and $X_3$ is diameter at breast height (cm). Model: $M = \ln(m/(1-m)) = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$.

| Buffer Size (radius) | $\beta_o$ | $\beta_1$ (crown class) | $\beta_2$ (% hickory) | $\beta_3$ (dbh) | LR ChiSq | H-L (df = 8) | P > ChiSq for H-L |
|---|---|---|---|---|---|---|---|
| 4 m | −1.1018 | 0.7813** | 0.0176** | 0.0920** | 105.91 | 4.5695 | 0.8024 |
| 8 m | −1.2583* | 0.8040** | 0.0367** | 0.0875** | 112.09 | 11.2861 | 0.1860 |
| 11 m | −1.1695* | 0.7821** | 0.0345** | 0.0862** | 105.85 | 7.4211 | 0.4919 |
| 25 m | −1.4728** | 0.7902** | 0.0554** | 0.0903** | 110.14 | 5.7647 | 0.6736 |

LR ChiSq = Likelihood Ratio Chi-Square statistic, H-L = Hosmer and Lemeshow statistic for model goodness of fit testing (P > ChiSq are the associated statistical significance).

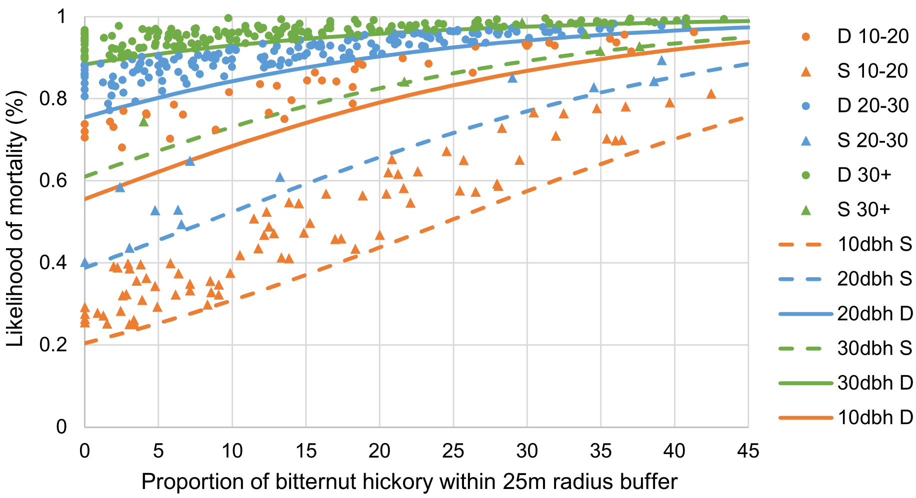


**Fig. 5.** Likelihood of mortality of bitternut hickory trees (≥10 cm dbh) by proportion of hickory stems over all species within a 25 m radius buffer, using logistic regression model. Circles and solid lines represent stems with a canopy crown class (D), triangles and dashed lines represent stems with a subcanopy (S) crown class. Orange points represent stems 10–20 cm dbh, blue points represent stems 20–30 cm dbh, and green points represent stems 30 + cm dbh. Lines are produced from model output, keeping diameter constant at 15 cm dbh (orange), 25 cm dbh (blue), and 35 cm dbh (green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

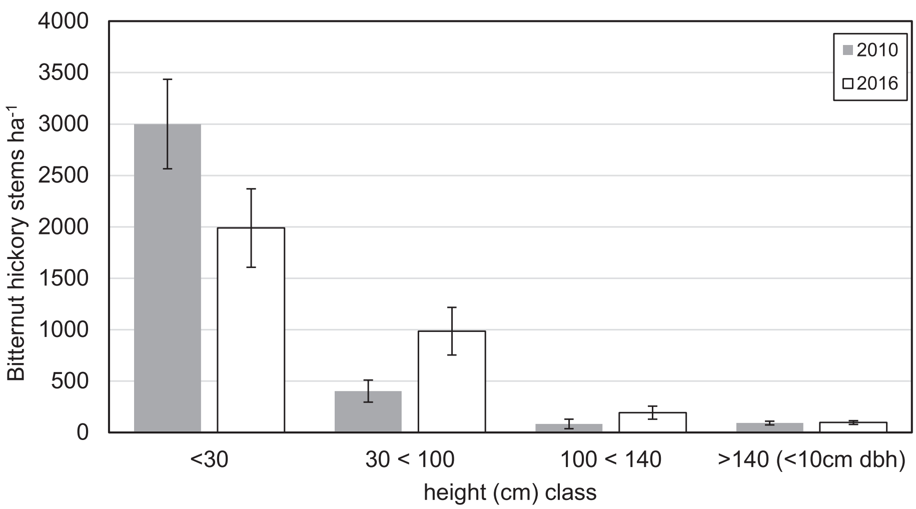


**Fig. 6.** Distribution of the mean density (stems hectare$^{-1}$) by height class of bitternut hickory regeneration layer (stems < 10 cm dbh) before (gray bars, 2010) and after (white bars, 2016) mortality. A multi-way ANOVA test with means comparisons within each height class showed significance (p < .05) in the interaction of year by height for stems per hectare for the two smallest height classes (<30 cm, p = 0.0012F-value = 10.86; 30 < 100 cm, p = 0.0247 F-value = 5.12). Error bars indicate ± 1 standard error.

**Table 4**
Mean density (stems ha$^{-1}$) of 1 year and 2+ year bitternut hickory seedlings (<30 cm tall) in seven time periods from 2004 to 2016 (n = 30 plots). Standard error of the means are displayed in parentheses.

| | 2004 | 2006 | 2008 | 2009 | 2010 | 2013 | 2016 |
|---|---|---|---|---|---|---|---|
| **1 year seedling** | 37.5 (22.3) | 68.1 (46.0) | 50.0 (39.3) | 11.1 (11.1) | 0 (0) | 47.2 (29.2) | 11.1 (11.1) |
| **2+ years seedling** | 1065.3 (237.1) | 1680.6 (232.1) | 1812.5 (251.4) | 2826.4 (384.9) | 3387.5 (563.3) | 3040.3 (666.3) | 2212.5 (767.4) |

### *3.4. Survivorship of regeneration*

The multi-way ANOVA revealed changes in density between 2010 and 2016 differed among height classes for the regeneration cohort (p < .0001, F-value = 8.82) (Fig. 6). A least squares means comparison showed that the smallest height class (<30 cm in height) decreased significantly in density between time periods (from 3000 tph in 2010 to 1989 tph in 2016: p = .0012 F-value = 10.86). The density in the 30 < 100 cm height class increased significantly between years as well (p = .0247, F-value = 5.12). Densities between time periods in the two larger height classes did not differ significantly (all p-values > 0.1953).

Seedling densities from earlier measurement dates revealed that stems ranged from approximately 1000–3000 stems ha$^{-1}$ (Table 4). Occurrence was particularly high in 2010, and though regeneration was less dense during the decline event, densities were low in the prior decade as well. Hickory made up 3% of the seedling pool in 2016, while sugar maple and ash species were dominants (70% and 24%,

**Table 5**
Composition of mean (and standard error) density (stems ha$^{-1}$) of woody stems (<30 cm tall) in 2016 (n = 30 plots).

| Species | Mean (SE) stems ha$^{-1}$ |
|---|---|
| Sugar maple | 57291.7 (12032.3) |
| Ash species | 18875.0 (4383.5) |
| Bitternut hickory | 1989.0 (382.4) |
| Black cherry | 669.4 (210.2) |
| Northern red oak | 486.1 (173.3) |
| Red maple | 347.2 (271.4) |
| Eastern hophornbeam | 294.4 (65.4) |
| Yellow birch | 97.2 (45.6) |
| Musclewood | 33.3 (20.2) |
| American basswood | 27.8 (18.0) |
| Eastern hemlock | 25.0 (19.4) |

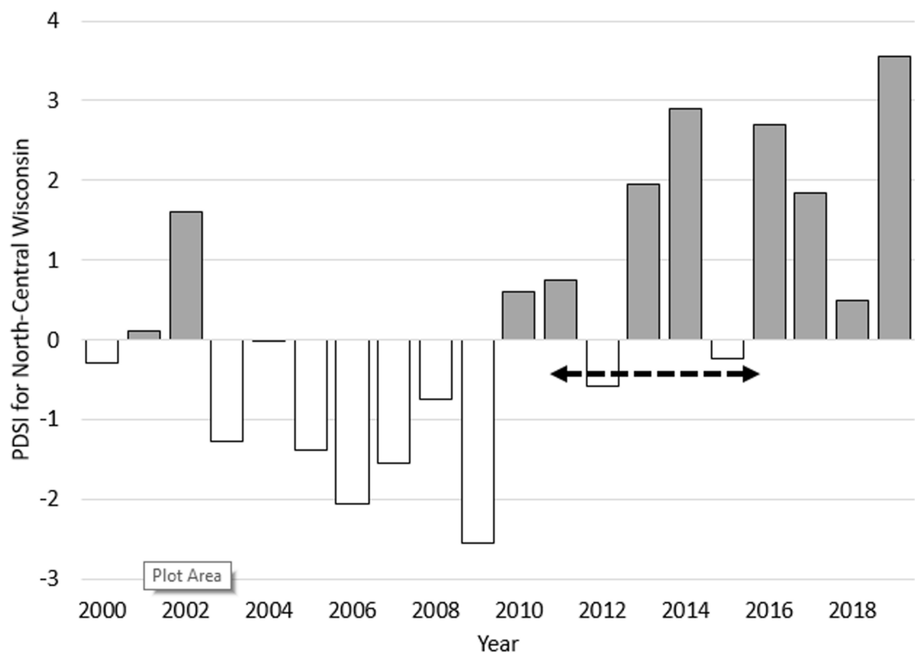


**Fig. 7.** Palmer Drought Severity Index (PDSI) for north-central Wisconsin from 2000 to 2019. The black dashed line represents time period of hickory mortality in the Flambeau Experiment. Hollow bars represent drought conditions and gra gray bars represent wet conditions. Data from https://www.ncdc.noaa.gov/.

respectively) (Table 5).

### 3.5. Identification of biotic decline agents

The survey in 2018 of the 53 dying and dead hickory stems showed that there was evidence of bark cankers and lesions, and bark beetle activity. Felling and debarking of the three selected actively declining hickory stems revealed the characteristic pattern of the larval galleries of the hickory bark beetle, confirming its presence at the site. Debarking also uncovered the presence of a hickory bark beetle within a gallery. Fourteen cankers were cut from the three sampled trees and woody tissue obtained from each were placed on agar medium. Based on presence of perithecia and asocspore morphology. One of the sub-sampled trees was tentatively confirmed for presence of *C. smalleyi*. This identification was validated by DNA sequencing which revealed four isolates to be *C. smalleyi.* Eight other isolates were tentatively identified as *Fusarium solani* based on cultural morphology and microscopic characteristics. This identification was verified using DNA sequencing.

## 4. Discussion

### 4.1. Hickory decline

There was a reduction of 84% in bitternut hickory stems ha$^{-1}$ $\geq$ 10 cm dbh within the experimental site from 2010 to 2016. The 53 surveyed stems at the site exhibited signs of fungal infection including leaf wilt and rapid crown dieback, stem cankers, and bark beetle galleries. These signs, the presence of the biotic decline agents on the three trees intensively sampled, and the observed mortality patterns consistent with the rapid crown decline of hickory reported in the Midwest and Northeast USA for the same time period all support this as the likely cause. The canker pathogen is consistently associated with galleries of the hickory bark beetle (Juzwik et al., 2013). Furthermore, the fungus is commonly associated with adult beetles and wood-boring dust created during initial attack of bitternut hickory stems. However, the ability of *S. quadrispinosus* to serve as a vector of the pathogen, and thus transmitting it to healthy bitternut hickory, has not been proven.

*Ceratocystis* is mostly insect dispersed, and *C. smalleyi* is unique in that it is associated specifically with the hickory bark beetle (Johnson et al. 2005). *Ceratocystis smalleyi* is a native fungus that causes distinct bark cankers and infects the sapwood, leading to a limited vascular dysfunction when at least 50 cankers are present (Park et al. 2013, Park and Juzwik 2014). Although other fungi have been noted to occur in stems experiencing decline symptoms, they have minimal contribution to mortality. *Fusarium solani* ((Mart.) Sacc.)*,* produces an annual canker often on the main stem or branches of a tree that may lead to top-kill (Juzwik et al., 2008). *Phomopsis* spp. (Sacc. & Roum.) produce branch galls that may girdle affected branches but usually does not lead to whole tree mortality (Juzwik et al. 2008).

Juzwik et al. (2013) hypothesized that recent (2003–2011) decline events are similar to hickory mortality events reported historically, suggesting that rapid crown decline of bitternut hickory involving the hickory bark beetle and *C. smalleyi* has been influencing hickory populations well into the past. Historically, bitternut hickory mortality has been attributed to drought induced stress and population outbreaks and increased attacks of hickory by *S. quadrispinosus* (St. George 1929, 1930). Coalescing of damage caused by bark beetle galleries was considered the cause of mortality. The north-central region of Wisconsin did indeed experience an extended drought period from about 2003 to just before 2010 (Fig. 7), to which bitternut hickory mortality in other areas of Wisconsin had also been attributed (WI DNR 2019). Although the drought ended before the mortality was documented, it is possible that the bitternut hickory trees were experiencing a lagged residual stress, and bark beetle populations were also building. Drought is well understood to be a predisposing or inciting factor in declines, but density is another predisposing factor that can also induce great stress on trees. Both of these factors reduce quality and quantity of phloem in stems and reduce the ability of a tree to defend against attacks from insects and pathogens (Ryan et al. 2015). Hickory bark beetles are attracted to stressed trees with decreased vigor due to chemical cues (Goeden and Norris 1964), so stems that are predisposed to decline by drought or high density may face more bark beetle attacks. The prolonged drought period, tree age, and the location of this population at the edge of its geographic and climatically adapted range in northern Wisconsin are proposed to be the predisposing factors in this documented mortality event.

Due to the extensive and rapid mortality, timing of surveys three years after the decline event, and the restriction for tree selection outside of established plot boundaries, trees available for felling and subsampling were limited. Although biotic decline agents were indeed identified in several sampled trees, a larger sample size for agent confirmation and conducting subsampling during an active decline event would be ideal.

### 4.2. Mortality patterns

Annual mortality rates in hemlock-hardwood forests of the Lake States range from about 0.4 to 1.7% year$^{-1}$ (Tyrell and Crow 1994). Annual mortality ranged from 0.0 to 3.7% year$^{-1}$ for species at the experimental site, with the exception of bitternut hickory mortality which was 35% year$^{-1}$. Even though hickory stems only composed about 4.5% of stems in 2010 (Table 1), the effect of their mortality was reflected in the overall mortality rate of the site of all species, which increased to 7.8% year$^{-1}$, well above the average for the region.

Individuals in the dominant and codominant crown classes were nearly eliminated as a result of the mortality event. Only 20% of trees greater than 10 cm in diameter survived, with mortality highest in the largest diameter classes. These mortality patterns are not unique, as declines often affect the older trees that are more susceptible to stress, and in other cases of hickory decline trees ≥13 cm dbh were most affected (Park et al. 2010). Larger trees are more often preferred by bark beetles (Coulson 1979) and the hickory bark beetle creates galleries in the trunks and large stems of trees (USDA 1985). Some evidence of survivorship was seen in the smaller diameter classes of the tree cohort. Although diameter is not always directly related to age, younger trees do tend to be more tolerant of stress, so may be better able to defend themselves against insect attacks and fungal infections.

The combined approach of assessing density patterns at the plot and tree level clearly indicated that the likelihood of mortality increased when more host trees comprised a greater proportion of stems in the proximate neighborhood. The likelihood of mortality also increased with higher density of either hickory or all species combined, although these variables were redundant and not included in the final model because proportion of hickory proved to be a better predictor of mortality. Crown class influenced susceptibility to mortality, with individuals in dominant or codominant crown positions being more likely to succumb to mortality. When considering density as a stressing agent or predisposing factor, these results make sense. A canopy tree may experience more competition with other canopy trees. Trees compete with each other for water and nutrient resources, so as stand density increases trees become stressed and susceptible to mortality from beetles or pathogens (Greenwood and Weisberg 2008, Ryan et al. 2015, Negron 1998, Coulson 1979). Additionally, if suitable host trees exist in high densities then bark beetles are more likely to experience an eruptive increase in their population which can in turn induce high levels of mortality in those tree species (Raffa et al. 2008).

### 4.3. Persistence of hickory regeneration

The variation of hickory seedlings over time indicates that the reduction of density from 2010 to 2016 is not necessarily due to the decline event. While there is definitely extensive mortality of overstory trees that may lead to reduced seed production it is not possible to say that that is what caused the reduction in seedling density in this case. The potential effects of the experimental treatments, including gap creation, on regeneration dynamics were evaluated for densities of the four height classes between 2010 and 2016, however neither canopy gaps nor deer exclusion was found to have any influence on hickory stem density and persistence (results not shown). In the short term there is evidence that young and advanced regeneration have persisted, and the reduction in the smallest height class may be part of natural density fluctuations. Advanced regeneration of hickory builds in the understory over time, surviving in a suppressed state (Lefland et al. 2018). Hickory seedlings establish at low densities (Table 4) relative to fast growing ash and shade tolerant sugar maple, so they are already at a competitive disadvantage (Table 5). The continued monitoring of hickory regeneration through time is important to understanding how the competitive disadvantage and reduction in overstory trees will affect the future hickory population. We show here that shortly following overstory mortality, hickory regeneration does persist.

### 4.4. Management to reduce impacts of hickory decline

Bitternut hickory in general has persisted in northern hardwood forests, even though historic droughts and mortality events have periodically occurred. Low mortality in the regeneration layer and surviving mature individuals suggest that hickory will maintain itself at the Flambeau site. The potential for increased water stress following more frequent and intense droughts could predispose the future population to another decline event, continuing and perhaps shortening the cycle of mortality events. The loss of the species reduces the potential resilience of this site, especially when another important species, ash (14.8% IV), faces a major mortality event due to the invasive emerald ash borer (*Agrilus planipennis* Fairmaire). As forests lose one tree species and is replaced by another species, the new species often faces threats of its own (Gandhi and Herms 2010).

Managing forests to encourage stand resilience to insects and pathogens and to limit stress on trees is especially important in decline diseases as a stressed tree is more likely to succumb to other inciting and contributing factors. The model developed here can be used to guide prescriptions to reduce stand density and minimize the effect of this predisposing factor on tree vigor. Although mortality is likely across diameter sizes and canopy positions, smaller stems in sub-canopy positions are less likely to die when hickory is in lower proportions (Fig. 5). Silvicultural treatments that focus on maintaining smaller diameter trees in subcanopy positions and ensure the proportion of hickory near other hickory stems is below 20% will reduce the likelihood of mortality from the decline. Density reduction reduces the availability and susceptibility of host trees to attacks (Knops et al. 1999, Bentz 2009, Fettig 2012). Thinning or more selective harvesting techniques can create heterogeneity as well in the structure of the forest and species composition, which can help reduce bark beetle attacks by keeping populations at lower levels (Fettig 2012, Knops et al. 1999). Structural diversity may also help to support populations of predatory insects which can contribute to natural control of insect insects (Knops et al. 1999). Variable intensity harvests that create uneven-aged cohorts is another management strategy for reducing loss of biodiversity and encouraging forest heterogeneity (Hanson and Lorimer 2007) which benefits mid-tolerant species like bitternut hickory to regenerate and build their populations and reduce density and tree stress.

Historic hickory mortality events were most likely due to the same decline factors that affected the stems in this study. As discussed previously, these mortality events have been a natural occurrence induced by a native pathogen and bark beetle, however the threats from climate change in terms of increased frequency of prolonged droughts could mean more intense and extensive mortality events from this rapid crown decline disease of hickory. We of course cannot manage the occurrence of droughts, but we can manage these forests by reducing density which directly increases tree vigor, which can help reduce susceptibility of trees like the bitternut hickory to the decline spiral.

## CRediT authorship contribution statement

**K.A. Bakken:** Conceptualization, Methodology, Writing - original draft, Formal analysis. **J.A. Forrester:** Conceptualization, Methodology, Writing - original draft. **D.J. Mladenoff:** Writing - review & editing, Methodology. **Z. Leggett:** Writing - review & editing. **J. Juzwik:** Methodology, Writing - review & editing. **R.M. Jetton:** Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A

**Fig. A2.** Photo of hickory bark beetle gallery on a hickory tree from the Flambeau Experimental site. Photo taken by Kelsey Bakken.

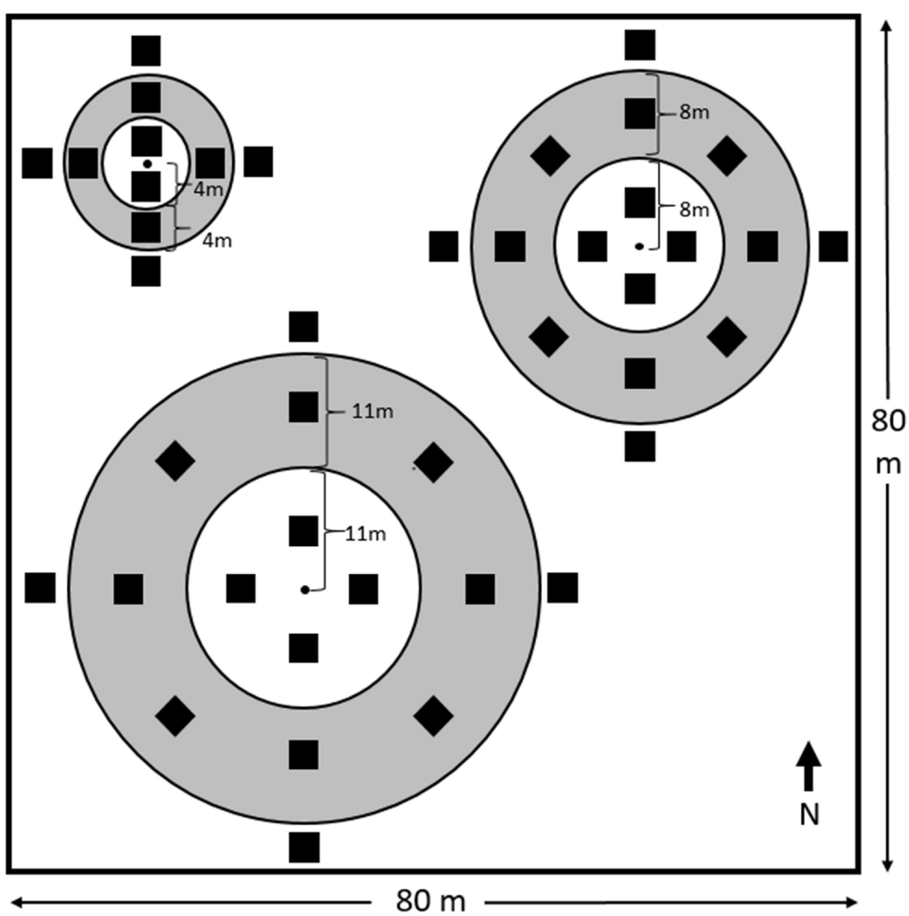


**Fig. A1.** Diagram of an 80 × 80 $m^2$ (0.64 ha) whole plot with small, medium, and large subplots. Inner white circles are central zones, where trees were removed in plots receiving gap creation treatments. Shaded areas are transitional zones, untreated. Black squares represent 2 × 2 m quadrats.

**Fig. A3.** Sapwood discoloration in an infected bitternut hickory stem from the Flambeau Experimental site. Photo taken by Kelsey Bakken.

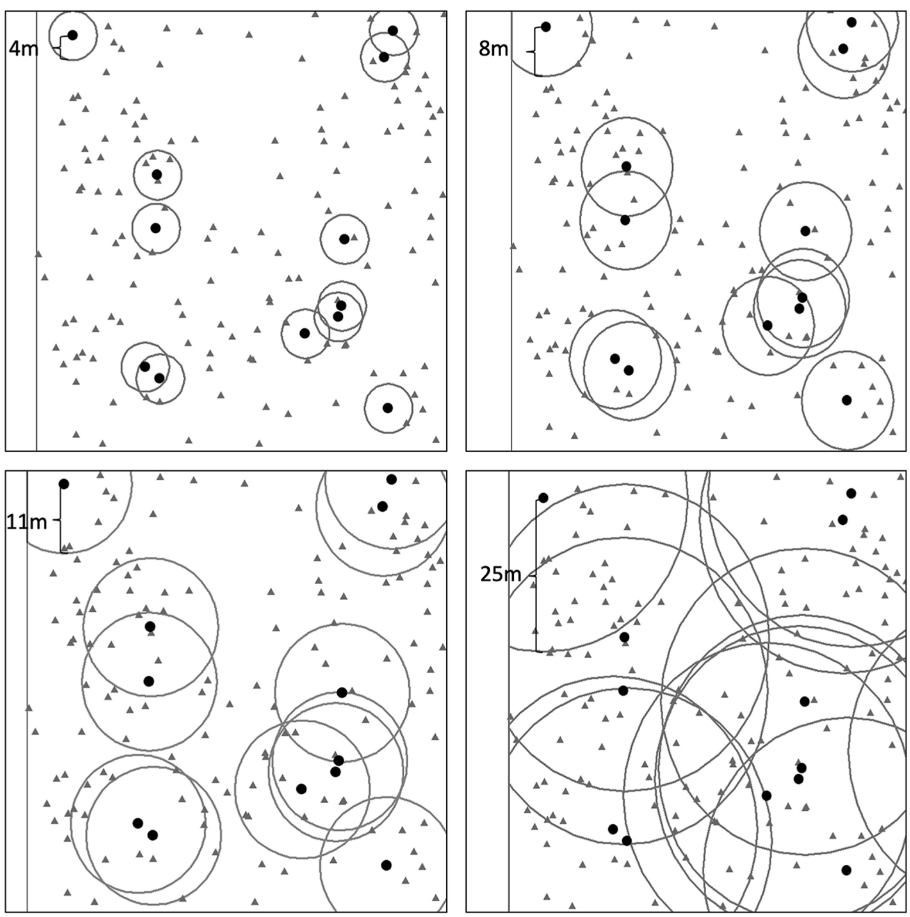


**Fig. A4.** Stem maps of *C. cordiformis* trees (black circles) and all other trees (gray triangles) with buffer area (hollow circles) around *C. cordiformis* stems used to calculate density of stems within buffer area for use in logistic regression models. Buffer sizes are 50 $m^2$ (top left), 201 $m^2$ (top right), 380 $m^2$ (bottom left), and 1964 $m^2$ (bottom right).

**Table A1**
Bitternut hickory tree characteristics (stems ≥ 10 cm dbh) used in logistic regression models to predict the probability of stem mortality.

| | Sample Size | Mean dbh (SE) | Range of dbh (cm) | Crown Class Count | |
|---|---|---|---|---|---|
| | | | | C | S |
| Dead Stems | 393 | 28.08 (0.45) | 10.9–62.0 | 342 | 51 |
| Living Stems | 76 | 19.16 (0.68) | 10.5–54.0 | 29 | 47 |

**Table A2**
Density (trees hectare$^{-1}$) characteristics of trees used in logistic regression models of varying buffer sizes to predict the probability of bitternut hickory stem mortality.

| Buffer Size (radius in m) | Mean (SE) trees hectare$^{-1}$ *C. cordiformis* | Mean (SE) trees hectare$^{-1}$ all species |
|---|---|---|
| 4 | 134.15 (10.21) | 478.10 (15.24) |
| 8 | 108.29 (6.27) | 493.40 (9.44) |
| 11 | 94.74 (4.85) | 474.81 (7.89) |
| 25 | 70.76 (2.93) | 430.57 (4.98) |

**Table A3**
Classification table for observed and predicted frequencies for logistic regression models with the cutoff of 0.50 by buffer radii (4 m, 8 m, 11 m, 25 m).

| | **Correct** | | **Incorrect** | | **Percentages (%)** | | |
|---|---|---|---|---|---|---|---|
| | **Event (dead)** | **Non-Event (Live)** | **Event (Dead)** | **Non-Event (Live)** | **Correct** | **Sensitivity** | **Specificity** |
| **4 m** | 368 | 29 | 47 | 25 | 84.6 | 93.6 | 38.2 |
| **8 m** | 369 | 31 | 45 | 24 | 85.3 | 93.9 | 40.8 |
| **11 m** | 366 | 31 | 45 | 27 | 84.6 | 93.1 | 40.8 |
| **25 m** | 370 | 29 | 47 | 23 | 85.1 | 94.1 | 38.2 |

**Table A4**
Correlation matrices to test for multicollinearity for variables included in the logistic regression models by buffer radii (4 m, 8 m, 11 m, 25 m). Variables are crown class (dominant), % hickory (proportion of hickory stems within the buffer radius), and DBH (diameter at breast height).

| **Buffer Size** | **Parameter** | **Intercept** | **Crown Class** | **% Hickory** | **DBH** |
|---|---|---|---|---|---|
| **4 m** | **Intercept** | 1 | 0.5043 | −0.2212 | −0.9462 |
| | **Crown Class** | 0.5043 | 1 | 0.1049 | −0.5782 |
| | **% Hickory** | −0.2212 | 0.1049 | 1 | 0.0541 |
| | **DBH** | −0.9462 | −0.5782 | 0.0541 | 1 |
| **8 m** | **Intercept** | 1 | 0.482 | −0.2602 | −0.9297 |
| | **Crown Class** | 0.482 | 1 | 0.1114 | −0.5765 |
| | **% Hickory** | −0.2602 | 0.1114 | 1 | 0.0172 |
| | **DBH** | −0.9297 | −0.5765 | 0.0172 | 1 |
| **11 m** | **Intercept** | 1 | 0.4938 | −0.2795 | −0.9215 |
| | **Crown Class** | 0.4938 | 1 | 0.073 | −0.5812 |
| | **% Hickory** | −0.2795 | 0.073 | 1 | 0.0035 |
| | **DBH** | −0.9215 | −0.5812 | 0.0035 | 1 |
| **25 m** | **Intercept** | 1 | 0.4791 | −0.3691 | −0.9131 |
| | **Crown Class** | 0.4791 | 1 | 0.0881 | −0.5911 |
| | **% Hickory** | −0.3691 | 0.0881 | 1 | 0.06 |
| | **DBH** | −0.9131 | −0.5911 | 0.06 | 1 |

## Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118956.

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