

# Sprouting capacity of *Persea borbonia* and maritime forest community response to simulated laurel wilt disease

Adam D. Chupp  · Loretta L. Battaglia

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**Abstract** There are numerous examples of how exotic insect pests and pathogens have altered the dominance of native tree species. Changes to the structure of associated communities will depend on whether the affected species survives and if so, the degree to which it is diminished. In the southeastern USA, *Persea borbonia*, a common tree found in many coastal plain habitats, is the primary host of laurel wilt disease (LWD); infection rates and main-stem mortality are catastrophically high (>90%) in invaded populations. We simulated the effects of LWD prior to its arrival in coastal Mississippi by girdling and then removing the main stems of *P. borbonia* trees. Over a 2-year period, we monitored *P. borbonia* persistence via basal resprouts, understory light availability, and community structure. Removal of *P. borbonia* main stems resulted in a 50% increase in light transmission (measured at 1 m above ground level). All treated individuals produced basal resprouts, the size and number of which were positively related to initial tree girth. Post-treatment increases in basal area were greatest for the sub-canopy species, *Ilex vomitoria*, and were significantly higher in treatment versus

control plots. Woody seedlings and herbaceous plants showed no significant trends in composition and abundance over time or between control and treatment plots. Our results suggest that removal of *P. borbonia* and subsequent resprouting causes shifts in *P. borbonia* size class frequencies and sub-canopy species dominance but has negligible impacts on understory plant community dynamics.

**Keywords** Biological invasion · Forest insect pests and disease · Persistence · Plant community dynamics · Vegetative reproduction

## Introduction

In North America, invasions by exotic forest pathogens have dramatically reduced the dominance of native trees, e.g., Dutch elm disease (Dunn 1986), beech bark disease (Houston et al. 1979), and chestnut blight (Anagnostakis 1987). While declines of host species have been well documented, the American chestnut (*Castanea dentata*), American elm (*Ulmus americana*), and American beech (*Fagus grandifolia*) are all known to persist via the production of vegetative resprouts (Barnes 1976; Griffin 1989; Forrester et al. 2003). In northern New York, mortality of large *F. grandifolia* stems due to beech bark disease produced canopy gaps that were quickly filled by resprouting of smaller stems. Although the relative importance values of smaller *F. grandifolia* size

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A. D. Chupp (✉) · L. L. Battaglia  
Department of Plant Biology, Life Sciences II, Southern Illinois University, Mail Code 6509, Carbondale, IL 62901, USA  
e-mail: adam.chupp@gmail.com

classes became greater than those of larger size classes, canopy composition and species densities remain relatively unchanged and shade-tolerant species continued to dominate the canopy layer (Forrester et al. 2003). In the wake of emerging insect pests and diseases, the ecological impacts of persistence by affected species and resultant community dynamics remain unclear.

The capacity of forest canopy species to avoid or tolerate disturbance can affect conditions for under-story species regeneration. For example, in forested ecosystems, perturbation from crown dieback and canopy gap formation alter light availability, temperature, and moisture, affecting seedling emergence, growth, and survival (e.g., Bazzaz and Miao 1993; Pacala et al. 1994; Canham et al. 1996; Battaglia and Sharitz 2006). Studies of regeneration from seed and seedling have been central to traditional concepts of gap dynamics (e.g., Grubb 1977). Conversely, the role of non-seed regeneration (i.e., vegetative sprouting) had been largely overlooked until the early 2000s (Bellingham and Sparrow 2000; Bond and Midgley 2001; Garcia and Zamora 2003; Knox and Clarke 2005; Clarke et al. 2010). Forecasting the impacts of emerging forest pests and pathogens will require an integrated approach that examines the capacity for targeted species to persist and how these responses may influence regeneration, community dynamics, and other ecological processes.

In the southeastern US, laurel wilt disease (LWD) continues to cause widespread mortality of several Lauraceae species since its introduction to Savannah, GA in 2002 (USDA Forest Service 2015). The disease is caused by a fungal pathogen (*Raffaelea lauricola*), vectored by an exotic stem-boring ambrosia beetle (*Xyleborus glabratus*); once introduced, the fungus spreads throughout the xylem, resulting in the wilting and mortality of main stems within a few months of infection (Fraedrich et al. 2008; Mayfield 2008). Among the species in which LWD has been identified, infection rate is highest in *Persea borbonia*, a common sub-canopy species and integral component of Atlantic and Gulf Coastal Plain communities (Brendemuehl 1990; Van Deelen 1991; Fraedrich et al. 2008; Chupp and Battaglia 2014, 2016; Chupp et al. 2015). In populations of *P. borbonia* on the Atlantic Coastal Plain, LWD-induced mortality rates are as high as 97% (Fraedrich et al. 2008; Spiegel and Leege 2013). However, basal resprouting has been observed in

infected *P. borbonia* on the Atlantic and Gulf Coastal Plain (Fraedrich et al. 2008; Spiegel and Leege 2013; Evans et al. 2013). On the Coastal Plain of southeastern Georgia, 87% of infected trees produced basal resprouts (Spiegel and Leege 2013). On St. Catherine's Island, GA, a large percentage of trees produced resprouts but only 21% of basal resprouts survived after 5 years; deer browsing appeared to severely reduce sprout survival (Evans et al. 2013).

Inherent and environmentally induced differences in the capacity for resprouting and sprout persistence are well documented (e.g., Bellingham and Sparrow 2000; Bond and Midgley 2001; Clarke et al. 2013; Poorter et al. 2012). Resprouting is influenced by the ability of plants to accumulate non-structural carbohydrates and by the patterns of allocation to different parts of the plant (Poorter et al. 2012). Other factors influencing resprouting responses include the type and severity of disturbance, size class, growth form, site productivity, and type of resprouter as indicated by the anatomical location of sprout production (i.e., aerial, epicormic, basal, lignotuber, root) (Clarke et al. 2013). A meta-analysis of size class and resprouting suggested that the capacity of trees incapable of avoiding damage through growth (e.g., *P. borbonia*) should remain consistent across all size classes (Vesk 2006). A survey of tree species with broken and sprouted trunks on Barro Colorado Island, Panama, indicated that the number and persistence of resprouts was highest in the smallest size class [10–20 diameter at breast height (DBH)] and dramatically decreased in larger size classes (Putz and Brokaw 1989). Quantifying sprouting responses of LWD-susceptible trees across a range of size classes and habitats is crucial for understanding the impacts of this emerging disease.

Recent studies have quantified LWD-induced mortality in *P. borbonia* populations and persistence via resprouting on the Atlantic Coastal Plain (Evans et al. 2013; Spiegel and Leege 2013). However, the capacity for resprouting has not been examined on the Gulf Coast, but recent field surveys of LWD-infected trees on the Mississippi Gulf Coast suggest that basal resprouting is common (Chupp, pers. obs.). In addition, effects of LWD on the composition of Gulf Coast plant communities have not been evaluated. Our study was designed around the following key hypotheses. First, we hypothesized that simulation of LWD (main-stem removal causing loss of apical dominance) would cause initial basal resprouting that differed among tree

size classes, followed by increased variability in multi-year survival of resprouts. Therefore, we predict a slight decline in the abundance of *P. borbonia* and a shift towards dominance of smaller size classes. We also hypothesized that experimental removal of *P. borbonia* (i.e., LWD simulation) would increase light availability, leading to shifts in understory plant composition. Specifically, we expect establishment of new species and shifts towards more shade-intolerant assemblages. Alternatively, shifts may be minimal if species already present opportunistically increase in abundance.

## Methods

### Study site

The study site ( $\sim 5$  ha) was located in the Grand Bay National Estuarine Research Reserve (GBNERR), which encompasses 7446 ha of Jackson County in coastal Mississippi, USA. Within this reserve, *P. borbonia* is often a common sub-canopy component of maritime forests; density of *P. borbonia* at our study site was 325 trees ( $\geq 2.5$  DBH)  $ha^{-1}$  [determined from point-centered quarter method (Mitchell 2001)]. Laurel wilt disease was first reported in Jackson County, Mississippi in 2009 near Sandhill Crane National Wildlife Refuge (Riggins et al. 2010) and infected trees were first observed on the GBNERR in early 2014. We targeted an area within GBNERR where *P. borbonia* was abundant and the invasion of LWD imminent. The habitat at this location is typified by Gulf Coast wet pine forest with a slash pine (*Pinus elliottii*) overstory, a sub-canopy and understory dominated by *P. borbonia* and several woody shrubs (e.g., *Morella cerifera*, *Ilex vomitoria*, and *Ilex glabra*), and a patchy herbaceous layer that includes a mixture of marsh and pine savanna species. At the end of the study, no *P. borbonia* trees at the study site had shown symptoms of LWD.

### Experimental transect and plot establishment

Two parallel east–west transects (transect 1 = 210 m, transect 2 = 270 m) were established within our 5-ha field site in November 2010; the transects were 50 m apart and formed the baseline along which plots were located. Transect points were marked at 10 m

intervals. At each 10-m point, a line perpendicular to the transect created four quadrants (NE, NW, SE, SW). In each quadrant, the nearest *P. borbonia* tree  $\geq 2.5$  cm DBH was tagged and measured for DBH and distance to point-marker.

Treatment and control plots were established along transects 1 and 2, respectively. Along each transect, we randomly selected six previously tagged *P. borbonia* trees. These trees were used as center points for circular treatment and control plots, each with a 17.5 m radius ( $110 m^2$ ). As such, there were six experimental plots along each transect for a total of 12 plots. Experimental plot locations were ground-truthed to ensure there was no overlap among plots and that plots contained a density of *P. borbonia* comparable to the overall density of *P. borbonia* within the community. All *P. borbonia*  $\geq 2.5$  cm DBH within each plot were tagged, totaling 86 and 130 tagged *P. borbonia* trees in treatment and control plots, respectively.

We also established three 4  $m^2$  survey plots within each treatment and control plot (36 total survey plots). Each plot was subdivided into two 1  $m^2$  composition plots located in opposite corners of the survey plot ( $n = 72$  composition plots). Survey plots were located within experimental plots using randomly selected tagged *P. borbonia* trees as center points.

### LWD simulation, resprouting, and light transmission

To simulate LWD at the study site, we girdled all tagged *P. borbonia* trees along transect 1, including all treatment plots, in March 2011. For girdling, an axe was used to make a double cut around the circumference of the main trunk between 0.5 and 1.0 m above ground level. A 2- to 3-cm-deep layer of tissue was removed from between the double cut (Kilroy and Keith 1999). The DBH of each girdled tree was recorded and all stems (seedlings or resprouts  $< 1$  m above ground) within a 0.5 m radius of each tree's base were counted and flagged. We completely removed all previously girdled main stems nine months after girdling (January 2012). Main stems were cut with a chainsaw at the point of girdling, leaving behind stumps and all resprouts that had emerged in response to girdling. All portions of above-ground material were removed  $> 20$  m from the plot center. On control plots, the DBH of each *P. borbonia* ( $\geq 2.5$  cm DBH) was also recorded at this time.

Following the complete removal of *P. borbonia* main stems from treatment plots, we recorded the number of resprouts that had emerged from the trunk of the tree (below point of girdling) and from the ground within 0.5 m of the base of the tree. We also measured the basal diameter and DBH (if applicable) of the tallest sprout. These measurements, collected only from treatment plots, were repeated in January 2013 and 2014.

Immediately following the removal of *P. borbonia* and again in January 2014, we took canopy photos in all 4 m<sup>2</sup> survey plots ( $n = 36$ ). Canopy photos were taken from a point 1 m above the ground using a Nikon Coolpix 4500 with Nikon FC-E8 fisheye converter lens. Canopy photos were analyzed and converted to percent light transmission using the Gap Light Analyzer (GLA) imaging processing software (Frazer et al. 1999). The program determines the amount of direct and diffuse solar radiation on a horizontal surface while accounting for the topographic mask at that location (Frazer et al. 1999). Preliminary canopy photos were also taken along transects 1 and 2 in 2011 prior to the girdling and removal of *P. borbonia*.

### Composition surveys

In July 2011, all 1 m<sup>2</sup> composition plots were surveyed for the percent cover of all herbaceous species and the density of woody seedlings (height <1.5 m). In addition, we used the entire 2 m<sup>2</sup> survey plots to record the basal diameter of woody shrubs (multiple main stems ≥1.5 m above ground level) and the DBH of all trees (single main stem ≥1.5 m above ground level); DBH was subsequently converted to basal area. Composition surveys were repeated in 2012 and 2013 during the peak of the growing season (July–September).

### Statistical analysis

Differences in the mean basal area of *P. borbonia* between control and treatment plots were compared with a *t* test. A repeated measures analysis of variance (ANOVA) was used to test for differences in percent light transmission due to plot type (control vs. treatment), time (2012 vs. 2014), and interactions between the two factors. For *P. borbonia* trees in treatment plots, we used linear regressions to examine

the relationships between sprouting responses (number of sprouts and basal diameter of tallest sprout) and initial tree basal area. For both measures of sprouting response, we compared survey years using repeated measures ANOVA. Sprouting data were graphically examined for normality and homoscedasticity; log transformations corrected for violations of these assumptions and the Satterthwaite approximation were used in cases where heteroscedasticity persisted.

We compared woody seedling species densities in control versus treatment plots over time using repeated measures ANOVA. The same comparison was conducted for woody species basal area (calculated from DBH). All pairwise comparisons were conducted using both the Tukey's post hoc least square means and the slice approach for simple effects. As with herbaceous species, seedling estimates were averaged between composition plots that occurred within the same survey plot (i.e., density = individuals/m<sup>2</sup>).

We used a permutational multivariate analysis of variance (PERMANOVA) to examine differences in herbaceous species composition due to plot type, year, and interactions between these two factors. Bray–Curtis dissimilarities, based on abundances of species, were used for this analysis and for constructing an ordination of the sample units (Bray and Curtis 1957). We used the percent cover of herbaceous species in each year of the surveys (2011, 2012, and 2013) to create an ordination of control and treatment survey plots (sample units); percent cover for each species was an average of both composition plots that occurred within the same survey plot. The ordination was created using non-metric multidimensional scaling with the DECODA software package (Minchin 1989). The PERMANOVA was conducted using the PRIMER software package version 6 with PERMANOVA add-on (Anderson et al. 2008). We also conducted an indicator species analysis across plot types and survey years (Dufrêne and Legendre 1997). Indicator values were calculated from the relative abundance and frequency of occurrence for individual herbaceous species. Faithful occurrence and/or concentrated abundance within a single group of sample units (i.e., plot type and year) generate a greater indicator value for a given species (McCune and Grace 2002). Indicator species analyses were conducted with the PC-ORD software package version 4 (McCune and Mefford 1999).

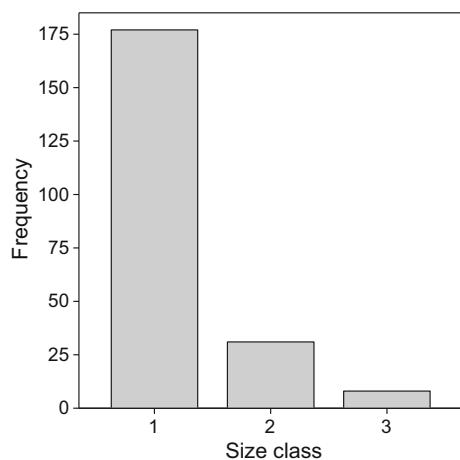
For all groups of vegetation, we tested for quantitative differences between control and treatment survey plots as well as for trends in individual target species over time. All data were tested for normality and homoscedasticity. Percentages were log-transformed to better approximate a normal distribution. We used the SAS software package version 9.3 (SAS Institute Inc. 2011) to conduct all univariate analyses and data transformations.

## Results

### LWD simulation, resprouting, and light transmission

Across control and treatment plots, tagged *P. borbonia* trees ranged between 2.5 and 19.8 DBH ( $n = 216$ ). The smallest and largest trees tagged were used as endpoints for three evenly sized classes (Fig. 1). Eighty-two percent of tagged *P. borbonia* trees fell into size class 1.

On 2 m<sup>2</sup> survey plots, there was no initial difference in per plot basal area of *P. borbonia* between control and treatment ( $t = -0.09, P = 0.934$ ). Basal area of *P. elliottii* was considerably higher in control plots due to the presence of three large individuals (>40 DBH) (Table 1). However, light transmission calculated from preliminary canopy photos captured in 2011 (prior to *P. borbonia* stem removal) showed



**Fig. 1** Frequency histogram representing all tagged *P. borbonia* trees in treatment and control plots ( $n = 216$ ). DBH size classes are defined as follows: 1 = 2.5–8.2, 2 = 8.3–14.0, 3 ≥ 14.1

only slightly higher values (mean ± standard error) along transect 2 [control ( $35.2 \pm 1.0$ )] compared to transect 1 [treatment ( $30.8 \pm 0.9$ )].

Within treatment plots, all 86 trees whose main stems were girdled and removed subsequently produced resprouts that were alive during the final survey in 2014. Over the course of our surveys, the average number of resprouts per tree significantly declined ( $F_{2,170} = 27.32, P < 0.0001$ ) from  $13.6 \pm 1.1$  in 2012 to  $11.7 \pm 0.8$  in 2013 and  $8.9 \pm 0.6$  in 2014. Pairwise tests indicated a significant decline between each survey period. There was a significant positive effect of initial tree basal area (i.e., stump basal area) on the number of resprouts produced (2012,  $F_{1,84} = 10.52, P = 0.002$ ; 2013,  $F_{1,84} = 7.11, P = 0.009$ ; 2014,  $F_{1,84} = 5.06, P = 0.027$ ) (Fig. 2).

The average basal diameter of the tallest sprout increased significantly during each year of the survey ( $F_{2,254} = 112.08, P < 0.001$ ) from  $0.74 \pm 0.03$  cm in 2012 to  $1.35 \pm 0.06$  cm in 2013 and  $1.95 \pm 0.08$  cm in 2014. There was a positive effect of initial tree basal area on the basal diameter of the tallest sprout during each year of our survey; this effect was significant in 2012 ( $F_{1,84} = 18.61, r^2 = 0.18, P < 0.001$ ), 2013 ( $F_{1,84} = 44.07, r^2 = 0.35, P < 0.001$ ) and 2014 ( $F_{1,84} = 42.10, r^2 = 0.34, P < 0.001$ ) (Fig. 2).

In 2012, 9 months after girdling, only 42% of the tallest resprouts had reached breast height (1.5 m) compared to 80% in 2013 and 92% in 2014. Because less than half of the tallest resprouts on each tree had reached breast height by 2012, we omitted this year of data from the analyses. The average DBH of tallest resprout main stems was significantly greater in 2014 ( $1.20 \pm 0.06$ ) compared to 2013 ( $0.68 \pm 0.04$ ) ( $t = 7.90, P < 0.0001$ ).

Light transmission was significantly affected by plot type with 50% higher levels on removal plots compared to control plots, a trend that was consistent across years ( $F_{1,34} = 94.73, P < 0.001$ ) (Fig. 3).

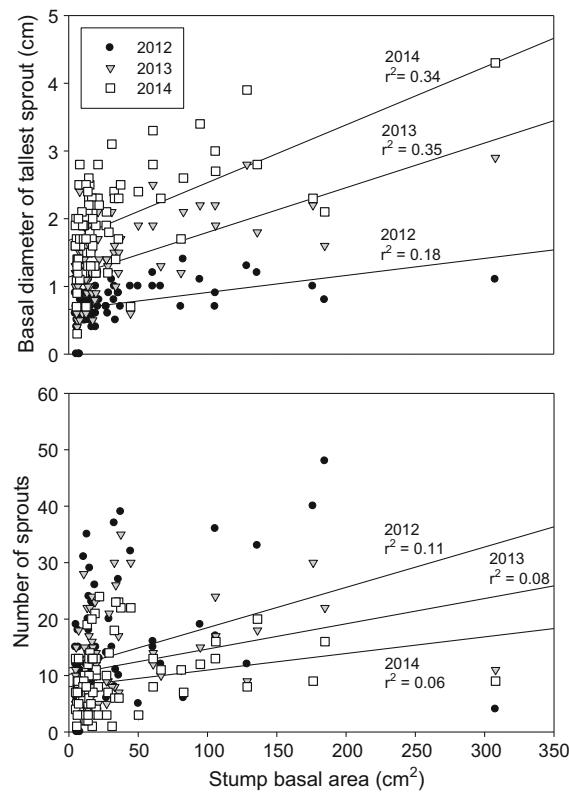
### Composition surveys

Analyses of the percent cover of herbaceous species suggest significant interactions between plot type (control vs. treatment) and survey year (2011, 2012, and 2013) (Pseudo- $F_{2,64} = 2.03, P = 0.046$ ) but no obvious patterns due to *P. borbonia* removal over time. Differences between treatment and control plots were only significant in 2012 ( $t = 1.60, P = 0.017$ ).

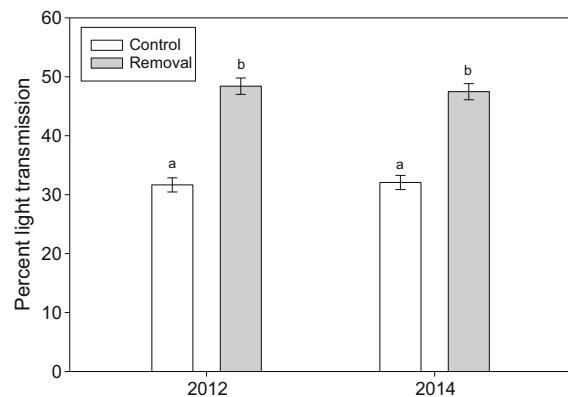
**Table 1** Average basal area for woody species (cm per 12 m<sup>2</sup> ± standard error) observed on control and treatment plots during each year of study

|                                 | 2011                        | 2012                     | 2013                      |
|---------------------------------|-----------------------------|--------------------------|---------------------------|
| Control plots ( <i>n</i> = 6)   |                             |                          |                           |
| <i>Ilex glabra</i>              | 2.82 ± 1.68                 | 4.17 ± 2.15              | 4.18 ± 1.63               |
| <i>Ilex vomitoria</i>           | 3.96 ± 2.55                 | 5.95 ± 3.65              | 7.57 ± 4.29               |
| <i>Morella cerifera</i>         | 14.16 ± 7.02                | 14.80 ± 7.33             | 19.47 ± 8.37              |
| <i>Persea borbonia</i>          | 78.48 ± 10.76               | 90.39 ± 11.51            | 91.74 ± 10.29             |
| <i>Pinus elliottii</i>          | 1145.62 ± 271.80            | 1191.55 ± 284.80         | 1205.79 ± 290.22          |
| Treatment plots ( <i>n</i> = 6) |                             |                          |                           |
| <i>Baccharis halimifolia</i>    | 0.58 ± 0.58                 | 0.00                     | 0.00                      |
| <i>Ilex glabra</i>              | 1.97 ± 1.34                 | 1.28 ± 0.91              | 1.63 ± 1.04               |
| <i>Ilex vomitoria</i>           | 3.57 ± 2.12 <sup>a</sup>    | 7.00 ± 3.84 <sup>b</sup> | 12.50 ± 5.46 <sup>c</sup> |
| <i>Morella cerifera</i>         | 5.00 ± 4.81                 | 5.95 ± 5.56              | 6.96 ± 6.52               |
| <i>Persea borbonia</i>          | 113.47 ± 25.03 <sup>a</sup> | 5.59 ± 1.58 <sup>b</sup> | 9.80 ± 2.26 <sup>b</sup>  |
| <i>Pinus elliottii</i>          | 230.25 ± 189.64             | 237.25 ± 191.72          | 250.57 ± 199.64           |

Different letters indicate significant differences among survey years

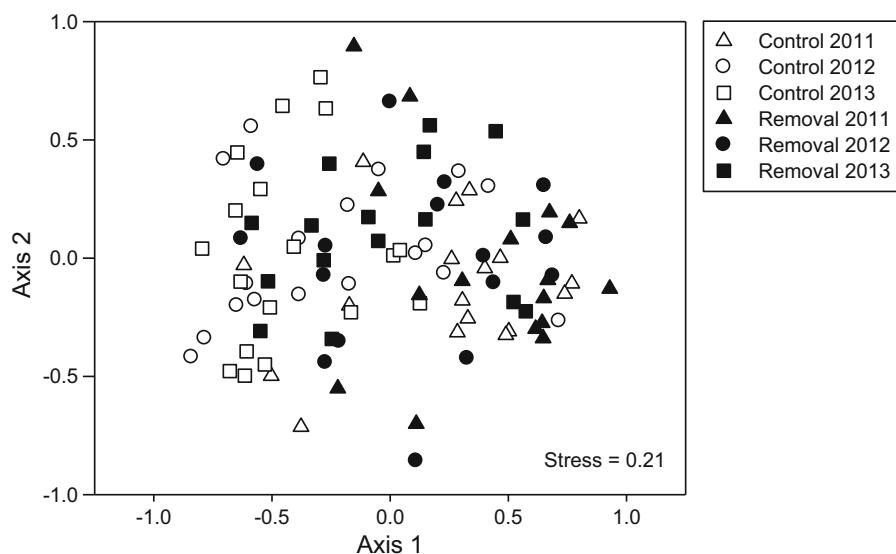


**Fig. 2** Relationship between stump basal area and the number of basal sprouts (bottom) and basal diameter of the tallest sprout (top) during each year of the survey. The 2012 survey was conducted 9 months after trees were girdled and just prior to complete stem removal. The same 86 trees were surveyed each year. All  $r^2$  values are significant ( $P < 0.05$ )



**Fig. 3** Percent light transmission on vegetation survey plots in 2012 and 2014. Values are based on analyses of canopy photos using GLA. Bars that do not share the same letter are significantly different from one another ( $P < 0.05$ ). Error bars represent one standard error

A two-dimensional ordination of understory species composition illustrates this pattern; control (white circles) and treatment plots (black circles) tend to cluster on the left and right sides of the ordination, respectively (Fig. 4). Species that were common to both control and treatment plots included *Andropogon virginicus*, *Juncus roemarianus*, *Panicum virgatum*, *Rubus argutus*, and *Spartina patens*. All of these species had relatively high indicator values for both plot types and no significant differences in percent cover occurred between plot types for any of these

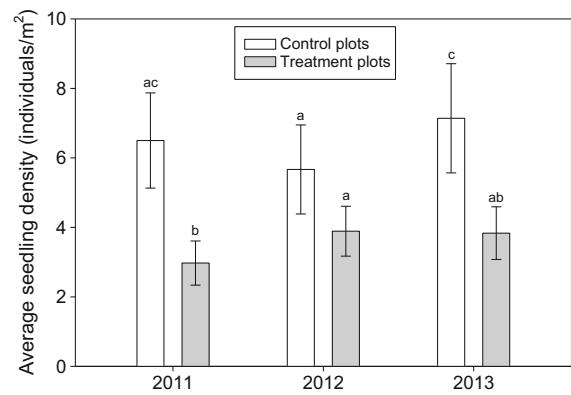


**Fig. 4** Non-metric multidimensional scaling ordination of herbaceous communities in control and removal plots ( $n = 36$ ) across 3 years. The ordination was constructed using the percent cover of each plant species in each year of the survey

species ( $P > 0.05$ ). Although *Toxicodendron radicans* was a significant indicator of treatment plots ( $IV = 55.3$ ,  $P = 0.001$ ), its indicator value was highest in 2011 and declined in 2012 and 2013 following *P. borbonia* removal. *Imperata cylindrica* (exotic invasive), *Ipomoea sagittata*, and *Dichanthelium* sp. were also significant indicators of treatment plots but showed no differences among survey years.

Overall, analysis of woody seedling densities indicated interacting effects between plot type and survey year (ANOVA:  $F_{2,34} = 6.07$ ,  $P = 0.006$ ). On treatment plots, the average number of seedlings significantly increased in the first year following the girdling and removal of *P. borbonia* (2012:  $t = 2.08$ ,  $P = 0.045$ ) but increases were not significant in 2013. Conversely, seedling densities on control plots did not significantly differ between 2011 and 2012 but showed a significant increase between 2012 and 2013 ( $t = 3.50$ ,  $P = 0.001$ ) (Fig. 5). Across control and treatment plots, four species (*I. glabra*, *I. vomitoria*, *M. cerifera*, and *P. borbonia*) represented approximately 90% of all seedlings during each year of the survey (Table 2). However, no individual species showed significant changes among survey years on either plot type.

Among shrub species, *Ilex vomitoria* was the only one to show a significant increase in basal area across survey years (ANOVA:  $F_{2,18} = 11.80$ ,  $P < 0.001$ ), a



**Fig. 5** Average seedling density ( $\pm$  standard error) in control and removal plots ( $n = 36$ ) during each year of our composition survey. There was a significant plot type by time interaction (ANOVA:  $F_{2,34} = 6.07$ ,  $P = 0.006$ ). Bars that do not share the same letter are significantly different from one another ( $P < 0.05$ )

pattern that was found only in treatment plots (Table 1).

## Discussion

Simulation of LWD resulted in consistent basal resprouting of *P. borbonia* across all size classes. The sprouting of *P. borbonia* in response to the loss of apical dominance is consistent with prior observations

**Table 2** Average density of seedlings (cm per 12 m<sup>2</sup> ± standard error) for each species that was observed on control and treatment (*P. borbonia* removal) plots during each year of our composition survey

|                                 | 2011         | 2012         | 2013         |
|---------------------------------|--------------|--------------|--------------|
| Control plots ( <i>n</i> = 6)   |              |              |              |
| <i>Acer rubrum</i>              | 0.67 ± 0.49  | 0.33 ± 0.33  | 1.83 ± 1.83  |
| <i>Baccharis halimifolia</i>    | 0.17 ± 0.17  | 0.00         | 0.00         |
| <i>Cinnamomum camphora</i>      | 0.00         | 0.00         | 0.17 ± 0.17  |
| <i>Ilex glabra</i>              | 18.67 ± 6.32 | 15.83 ± 7.65 | 18.50 ± 8.72 |
| <i>Ilex vomitoria</i>           | 7.00 ± 1.51  | 6.00 ± 1.24  | 7.50 ± 1.43  |
| <i>Morella cerifera</i>         | 5.17 ± 2.50  | 3.83 ± 1.42  | 6.00 ± 2.46  |
| <i>Persea borbonia</i>          | 6.00 ± 1.68  | 6.50 ± 1.77  | 7.33 ± 1.50  |
| <i>Pinus elliottii</i>          | 1.17 ± 0.65  | 1.00 ± 0.82  | 1.00 ± 0.63  |
| <i>Quercus virginiana</i>       | 0.17 ± 0.17  | 0.50 ± 0.50  | 0.50 ± 0.50  |
| Treatment plots ( <i>n</i> = 6) |              |              |              |
| <i>Acer rubrum</i>              | 0.00         | 0.00         | 0.50 ± 0.34  |
| <i>Ba ccharis halimifolia</i>   | 0.67 ± 0.42  | 0.33 ± 0.33  | 0.17 ± 0.17  |
| <i>Cinnamomum camphora</i>      | 0.00         | 0.33 ± 0.33  | 0.33 ± 0.33  |
| <i>Ilex glabra</i>              | 5.50 ± 3.72  | 6.00 ± 3.93  | 6.00 ± 4.12  |
| <i>Ilex vomitoria</i>           | 3.00 ± 0.77  | 3.17 ± 0.75  | 4.83 ± 1.08  |
| <i>Morella cerifera</i>         | 2.67 ± 1.20  | 2.67 ± 1.73  | 2.67 ± 1.78  |
| <i>Persea borbonia</i>          | 4.67 ± 1.23  | 9.17 ± 2.59  | 6.83 ± 2.47  |
| <i>Photinia pyrifolia</i>       | 0.17 ± 0.17  | 0.00         | 0.17 ± 0.17  |
| <i>Pinus elliottii</i>          | 0.50 ± 0.34  | 1.50 ± 0.50  | 1.17 ± 0.79  |
| <i>Quercus virginiana</i>       | 0.33 ± 0.33  | 0.00         | 0.17 ± 0.17  |
| <i>Triadica sebifera</i>        | 0.33 ± 0.21  | 0.17 ± 0.17  | 0.17 ± 0.17  |

of LWD-infected populations (Evans et al. 2013; Spiegel and Leege 2013; Cameron et al. 2015); however, it should be noted that temporal trends in resprout production could be influenced by the presence of disease in trees. In southeastern Georgia, LWD-induced basal resprouting increased during the 2-year period after tree infection (mean 3.7 resprouts after 2 years), although there appeared to be constant mortality and replacement of basal resprouts between assessment periods. In the present study, there was a large production of basal resprouts after 1 year (mean = 13.6) but numbers of resprouts declined significantly over the next 2 years. In Jackson County, Mississippi, we have observed numerous LWD-infected individuals that failed to produce resprouts at least 2 years after infection. It is possible that variable spread through the roots and stumps can impact resprouting. Altogether, it is unclear how biological and environmental factors combine to regulate resprouting responses in *P. borbonia* and other species affected by LWD.

Despite high density of *P. borbonia* (325 trees ha<sup>-1</sup>) and consistent basal resprouting, few resprouts

had reached the sub-canopy layer by the final year of our survey and thus resulted in minimal influence on light transmission. Instead, the 50% increases in light transmission on treatment plots persisted across yearly surveys. Such increases in light availability are expected with rapid declines in species that contribute greatly to sub-canopy and canopy structure. In the Coastal Plain of South Carolina, where average *P. borbonia* densities range from 200 to 400 trees ha<sup>-1</sup>, infestations of LWD and subsequent high levels of *P. borbonia* mortality have led to as much as 5-fold increases in photosynthetically active radiation (PAR) (Hanula et al. 2008; Spiegel and Leege 2013). Spiegel and Leege (2013) suggested that the opening of canopy gaps and associated increases in PAR within 2–4 years of LWD infestation have altered community composition and structure. At the very least, the removal of a common and often densely populated species of southeastern Coastal Plain habitats is dramatically increasing understory light availability in these communities.

Although LWD simulation caused substantial increases in understory light availability, our results

failed to detect changes in woody species composition due to establishment of new species. Instead, we agree with previous findings that suggest LWD-induced changes in species composition are due to dramatic declines of *P. borbonia* and subsequent niche-space replacement by other co-occurring sub-canopy species (Goldberg and Heine 2009; Gramling 2010; Shields et al. 2011; Evans et al. 2013; Spiegel and Leege 2013). For example, on the Coastal Plain of Georgia, USA, sub-canopy species *Magnolia virginiana* and *Gordonia lasianthus* showed higher importance values due to increased relative frequency and density in LWD-infested sites (2–4 years after infestation) versus uninhabited sites (Spiegel and Leege 2013). However, it would be valuable to know if these differences existed prior to LWD infestation; infested communities were not sampled prior to the arrival of LWD. In a Florida maritime hammock, results from sites that were sampled pre- and post-LWD invasion suggested that *P. borbonia* was replaced in the canopy by *Juniperus virginiana* (Goldberg and Heine 2009). Here, on the Gulf Coastal Plain, removal of *P. borbonia* was accompanied by significant increases in the basal area of *I. vomitoria*, a result not observed on control plots. Relative contributions to total basal area were also higher for *M. cerifera* on treatment plots; however, increases in basal area across years did not differ between control and treatment plots. While it is unclear if the removal of *P. borbonia* main stems and associated increases in light availability are responsible for greater increases in *I. vomitoria* on treatment plots, it is evident that already present species of similar growth form will show increases in relative basal area as they rapidly fill vacated niche space and leave little opportunity for the establishment of new species.

In the understory layer, herbaceous species *Toxicodendron radicans*, *Imperata cylindrica*, *Ipomea sagittata*, and *Dichanthelium* sp. were all indicators of treatment plots; however, there were no obvious trends in their abundances over time that would indicate a response due to the removal of *P. borbonia*. Overall, comparisons between control and treatment plots suggested that observed increases in light availability due to the removal of *P. borbonia* had minimal effect on the regeneration and/or recruitment of understory plants after 2 years. This was the case for both woody seedlings and herbaceous species. We should note that the experimental removal of *P. borbonia* and associated changes in light availability

was expedited compared to the natural progression of main-stem decomposition and subsequent canopy collapse. If the abrupt changes to light conditions during our LWD simulation failed to produce detectable changes in understory plant composition/abundance, we submit that such shifts are unlikely under more natural conditions.

We know very little about the impacts of LWD on associated communities. Although mortality rates of *P. borbonia* main stems have been well documented, it is unclear what regulates both the initial production and long-term persistence of basal resprouts and how this response will affect understory communities. We encourage the initiation of long-term surveys that encompass periods of pre- and post-LWD invasion in habitats across the distributional range of *P. borbonia*. These investigations will be crucial towards understanding how outbreaks of exotic plant pathogens have shaped and will continue to shape native ecosystems.

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