INITIAL RESPONSE OF PONDBERRY RELEASED FROM HEAVY SHADE

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Abstract--Pondberry [*Lindera melissifolia* (Walt.) Blume] is a federally endangered woody shrub in the Lauraceae family. The U.S. Fish and Wildlife Service developed a recovery plan in 1993 that emphasized the need to study pondberry biology and ecology and to develop management practices that would promote recovery and conservation of this species. We initiated a large-scale study in 2005 to determine the effects of soil flooding and light availability on pondberry survival and growth. The study was conducted in Sharkey County, MS in a network of research impoundments known as the Flooding Research Facility. Following the conclusion of our initial research, we implemented a release study to utilize plants which were established in 12 shade houses that provided a light availability near 5 percent of full sunlight. We randomly assigned new shade cloth densities to these 12 houses so that four provided 70 percent of full sunlight, four provided 37 percent of full sunlight, and four provided 5 percent of full sunlight. Our research objective was to quantify survival, stem length, stem diameter, and ramet production of pondberry shrubs released from a heavily shaded environment. Three growing seasons after release, shrub survival averaged 71 percent, and stem length averaged 113 cm regardless of assigned light level. Pondberry released into 70 or 37 percent light developed 58 percent larger stem diameters than those maintained under 5 percent light. Plants released into 70 or 37 percent light also produced 274 percent more ramets than those grown under 5 percent light. These results indicate pondberry growth should respond positively to silvicultural practices such as midstory or overstory canopy treatments that increase light availability in the understory of floodplain forests. However, we speculate that control of competing understory vegetation invigorated by canopy treatment may be necessary to ensure pondberry release.

INTRODUCTION

Pondberry [*Lindera melissifolia* (Walt.) Blume (Lauraceae)] is a deciduous woody shrub endemic to low-lying forests of the southeastern United States (USFWS 1986). In the Lower Mississippi Alluvial Valley (LMAV), this dioecious and rhizomatous plant grows up to 2-m tall on sites flooded for periods ranging from several days to several months. Impacts of deforestation and forest degradation have reduced potential pondberry habitat in the LMAV where it is currently found in isolated colonies within scattered forest patches (Devall and others 2001, Hawkins and others 2010). Consequently, the U.S. Fish and Wildlife Service listed this species as endangered in 1986 (USFWS 1986). A pondberry recovery plan was developed after this listing (USFWS 1993). The plan emphasized the need to study pondberry biology and ecology and to develop management practices that would promote recovery and conservation of this species.

Our knowledge of pondberry biology and ecology is increasing (Aleric and Kirkman 2005a, 2005b; Connor and others 2007; Devall and others 2001; Echt and others 2006, 2011; Fraedrich and others 2011; Godt and Hamrick 1996; Hawkins and others 2009a, 2009b, 2010, 2011; Lockhart and others 2012, 2013; Wright 1990). However, we do not know the resilience of pondberry survival and growth when plants are established in heavily shaded understories; and we do not know how established pondberry responds to release from heavily shaded conditions. Research presented in this manuscript examines: (1) a 7-year progression of survival, stem length, stem diameter, and ramet production for pondberry established under low light availability; and (2) survival, stem length, stem diameter, and ramet production for pondberry established and raised for 4 years under low light availability then subjected to release into higher light environments. An understanding of how pondberry tolerates shade and responds to release from heavily shaded environments should inform the design of silvicultural practices to recover and conserve this endangered species.

MATERIALS AND METHODS

The study was conducted in the Flooding Research Facility (FRF) in Sharkey County, MS, on the Theodore Roosevelt National Wildlife Refuge Complex (32° 58' N, 90° 44' W). The FRF is situated about 7 km from natural pondberry colonies growing on the Delta National Forest. Mean annual temperature at the FRF averages 17.3 °C with a range from 27.3 °C in July to 5.6 °C in January, and mean annual precipitation averages 1350 mm (WorldClimate 2008). The FRF was constructed on Sharkey soils (very-fine, smectitic and thermic Chromic Epiaquerts) which are shrink-swell clay soils that

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developed from alluvium deposited on slackwater areas.

The FRF is comprised of 12, 0.4-ha rectangular impoundments that can be independently flooded or drained [see Lockhart and others (2006) for more details about design and operation of the FRF]. Pondberry research conducted between 2005 and 2007 called for flooding the FRF impoundments according to three different hydroperiod regimes [see Lockhart and others (2013) for more information about the initial pondberry study]. Additionally, three rectangular shade houses (25.6-m long by 7.3-m wide by 2.4-m tall) were constructed in each impoundment to provide light levels of 70, 37, or 5 percent of full sunlight. Light availability within these shade houses was controlled using neutral density shade cloth (PAK Unlimited, Inc., Cornelia, GA). Following completion of the 2005-2007 research, established pondberry plants were maintained under their assigned light levels, but flooding treatments were suspended. Prior to the 2009 growing season, we implemented a new study (named the pondberry release study) that utilized plants established in the 12 houses assigned the 5 percent light level (one house in each of the 12 impoundments). We randomly assigned new shade-cloth densities to these 12 shade houses to emulate a release treatment such that four houses provided 70 percent of full sunlight, four houses provided 37 percent of full sunlight, and four houses provided 5 percent of full sunlight.

Pondberry plants established in the FRF included 20 LMAV genotypes that were outplanted during April 2005. Ninety-six, single-stemmed stecklings (rooted cuttings) were planted on a 1.2- by 1.2-m spacing in each shade house. Stecklings were randomly assigned in each shade house so that each genotype was well represented. Transplants were maintained free of competing vegetation for the duration of the research by hand hoeing and directed applications of herbicides.

Plants were measured immediately after planting in 2005 and at the end of each growing season through 2011. Measurements included stem length, stem diameter, and a count of ramets produced by the original steckling. Stem length was measured from the groundline to the base of the terminal bud. Stem diameter was measured 2 cm above the groundline with dial calipers. Two diameter measurements perpendicular to each other were collected to calculate an average diameter for each stem.

Data were analyzed according to a completely randomized design with light availability as a fixed-effect treatment. Analyses were conducted using PROC GLM in SAS 9.3 (SAS Institute, Inc., Cary, NC). Response variables analyzed included survival (percent), length (cm) and diameter (mm) of the longest stem, and ramet number for each shrub. Data transformation was used as needed to normalize model residual errors. Statistical significance among treatment means for each response variable was determined at $\alpha = 0.05$. Duncan's Multiple Range Test was used for mean separations and untransformed data are presented in all figures.

RESULTS

Pondberry mortality was greatest the first 3 years following planting as survival for plants declined to 73 percent (fig. 1). Mortality stabilized following the third growing season, and survival remained near 71 percent for all treatment levels 7 years after planting ($p = 0.53$; fig. 1).

Stem length of pondberry planting stock averaged 21 cm at outplanting, and increased 371 percent to 99 cm when receiving 5 percent light for seven growing seasons (fig. 2). Release of pondberry into higher light environments did not influence stem length until the third growing season after release (fig. 2). At that time, the longest stems on shrubs receiving 37 percent light were 23 percent longer than those receiving 70 or 5 percent light ($p = 0.01$; fig. 2).

Pondberry stem diameter averaged 1.5 mm at outplanting (fig. 3). Stem diameter increased 360 percent to 6.9 mm through 7 years of growth under 5 percent light (fig. 3). Pondberry stem diameter responded quickly to increased light

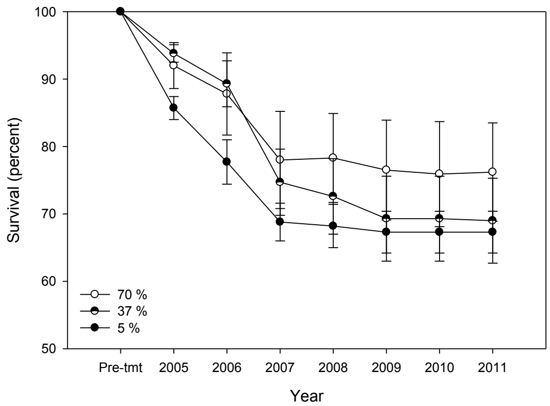

Figure 1--Pondberry survival by light availability at the Flooding Research Facility, Sharkey County, MS. Plants were grown in 5 percent light from 2005 through 2008, though they are shown by release treatments for information purposes. Vertical bars represent one standard error.

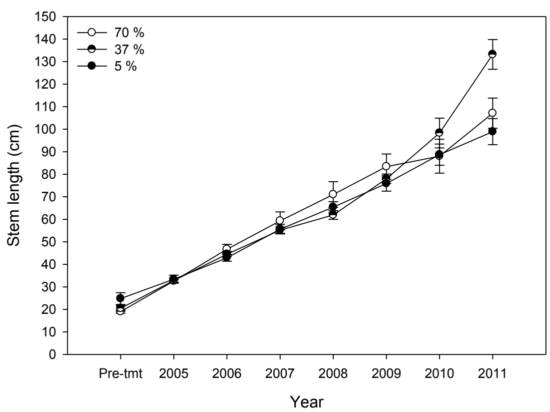

Figure 2--Pondberry stem length by light availability at the Flooding Research Facility, Sharkey County, MS. Plants were grown in 5 percent light from 2005 through 2008, though they are shown by release treatments for information purposes. Vertical bars represent one standard error.

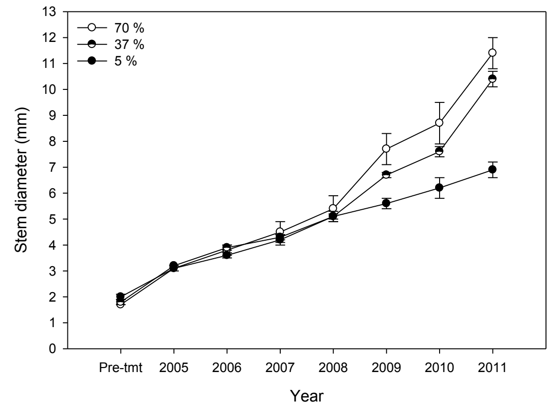

Figure 3--Pondberry stem diameter by light availability at the Flooding Research Facility, Sharkey County, MS. Plants were grown in 5 percent light from 2005 through 2008, though they are shown by release treatments for information purposes. Vertical bars represent one standard error.

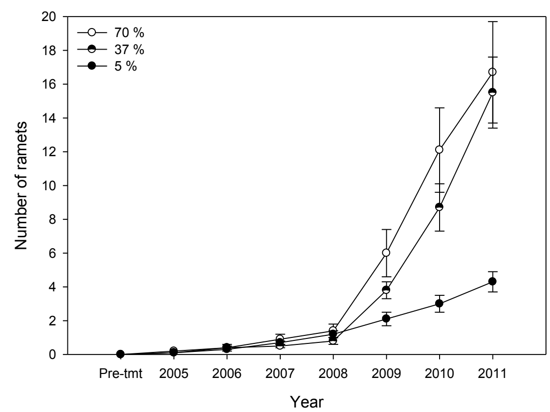

Figure 4--Number of pondberry ramets produced and maintained by light availability at the Flooding Research Facility, Sharkey County, MS. Plants were grown in 5 percent light from 2005 through 2008, though they are shown by release treatments for information purposes. Vertical bars represent one standard error.

availability, as shrubs released to 70 or 37 percent light grew 290 percent more in diameter the first year after release than those maintained under 5 percent light. Three years after release, pondberry stem diameter was 58 percent larger when receiving 70 or 37 percent light compared to shrubs receiving 5 percent light ($p < 0.01$; fig. 3).

The number of ramets produced and maintained by pondberry plants receiving 5 percent light increased from 0.1 per plant during the first growing season to 4.3 per plant by the end of the seventh growing season (fig. 4). As with stem diameter, ramet production quickly responded to increased light availability. During the first growing season after release, shrubs released into 70 or 37 percent light produced and maintained 322 percent more ramets than those maintained under 5 percent light. Three years after release, the number of ramets observed on pondberry shrubs receiving the two highest light levels had increased from an average of 1.1 to 16.1 ramets per plant. At this time, shrubs maintained under 5 percent light had 73 percent fewer ramets per plant than those released into 70 or 37 percent light ($p = 0.01$; fig. 4).

DISCUSSION

Hawkins and others (2009b) reported that pondberry colonies found in the LMAV were associated with forest compositions and structures reflective of hydrologic regime, topography, historical disturbance, and an absence of recent disturbance. Common overstory tree species found in LMAV forests supporting pondberry colonies included Nuttall oak (*Quercus nuttallii* Palmer), willow oak (*Q. phellos* L.), overcup oak (*Q. lyrata* Walt.), American elm (*Ulmus americana* L.), green ash (*Fraxinus pennsylvanica* Marsh.), sweetgum (*Liquidambar styraciflua* L.), and common persimmon (*Diospyros virginiana* L.). Red maple (*Acer rubrum* L.), sugarberry (*Celtis laevigata* Willd.), deciduous holly (*Ilex decidua* Walt.), green ash, and American elm were among the midstory species abundant in these forests (Hawkins and others 2009b). The stratified overstory and midstory canopies characteristic of these forests intercept most ambient sunlight, leaving relatively little available to understory woody plants. For example, ambient light levels less than 7 percent of full sunlight have been routinely observed in mature floodplain forest understories across the southeastern U.S. (Cunningham and others 2011, Jenkins and Chambers 1989, Lhotka and Loewenstein 2006, Lockhart and others 2000).

We found that pondberry was able to survive and grow for seven growing seasons in a low light environment. Plants receiving 5 percent light had a slow but steady increase in stem length, stem diameter, and ramet production. Pondberry acclimated to this low light environment exhibited typical shade leaf-blade characteristics, including dark green leaf blades with large surface areas and a horizontal leaf-blade display that minimizes leaf-blade overlap and maximizes light gathering capabilities (Aleric and Kirkman 2005a, Lockhart and others 2012). Other research conducted at our study site confirmed that plants receiving 5 percent light had lower total leaf mass, thinner leaf blades, lower stomatal densities, thinner palisade layers, and thinner spongy mesophyll layers than plants grown under higher light environments (data not shown). Leaves acclimated to low light availability were also able to maintain low, but positive, rates of net photosynthesis through the growing season (data not shown). Findings from this study confirmed that pondberry can survive and exhibit positive growth in light environments characteristic of heavily shaded understories in bottomland hardwood forests (Aleric and Kirkman 2005a, Lockhart and others 2012).

Research into silvicultural practices that increase the amount of ambient sunlight reaching the understory of floodplain forests has focused on applications to enhance oak reproduction (Cunningham and others 2011, Guttery and others 2011, Lhotka and Loewenstein 2006, Lockhart and others 2000). Yet results should be equally as relevant to other understory species. Deadening midstory canopy trees, through mechanical or chemical operations, will increase the amount of ambient sunlight reaching the forest understory. Researchers have shown that control of midstory canopy competition can increase light levels reaching the forest understory to between 25 and 40 percent of full sunlight (Cunningham and others 2011, Guttery and others 2011, Lockhart and others 2000).

This research documents pondberry responding favorably to increases in light availability following several years of growth suppression under low light environments. Enhanced stem diameter and ramet production were the earliest responses observed and were recorded during the first growing season for plants released into 70 or 37 percent light. Stem length also increased for plants receiving 37 percent light, but this response was not observed until three growing seasons after release from 5 percent light. The increases in stem length, stem diameter, and ramet production for pondberry plants receiving 70 or 37 percent light appeared to be supported by morphological and physiological acclimation of shrubs to the higher light environments.

Our observations of pondberry in the current experiment indicate this plant can tolerate relatively low light availability for several years then acclimate to and improve growth when released into a higher light environment. Light availability observed under the 37 percent light level of this experiment is within the range of light levels reported by researchers following deadening of midstory canopy trees in floodplain forests (Cunningham and others 2011, Guttery and others 2011, Lockhart and others 2000). Thus, our observations provide a starting point for future research aimed at developing silvicultural practices to enhance understory light availability for pondberry recovery and restoration in bottomland hardwood forests.

Glitzenstein (2007) reported on an earlier effort to restore a declining pondberry population in South Carolina. He observed a rapid increase in the number of pondberry stems and the sum of pondberry stem lengths 2 years after established shrubs were released with partial removal of overstory and midstory trees. However, practitioners understand that release of competing vegetation can be a primary concern when performing practices that increase understory light availability. Glitzenstein (2007) accounted for this by clipping competing vegetation during the release treatment, but the effects of this practice on competing vegetation were not reported.

In our study, all vegetation growing in pondberry plots was controlled with mechanical or chemical treatments, so we cannot speculate how pondberry would respond relative to competing vegetation. Natural pondberry colonies in the LMAV occur in areas subject to seasonal soil flooding, and researchers have hypothesized that the flooding likely reduces understory plant competition (Wright 1990). It is reasonable to speculate that vegetation control practices may be necessary to ensure pondberry survival and growth where soil flooding is not expected to reduce competing vegetation invigorated by canopy treatment.

Our research confirmed that pondberry is capable of tolerating the heavily shaded conditions characteristic of understories in many mature bottomland hardwood forests. Though this species was able to persist and even grow under heavy shade, we demonstrated that above-ground growth was suppressed by low light availability. Following 4 years of suppression beneath heavy shade, pondberry growth increased after simulated release into higher light environments. The responses to release we observed indicate that pondberry would likely react favorably to canopy disturbance created through silvicultural practices. Our findings support the premise that active management could be used to promote vigor and therefore sustainability of extant pondberry colonies. Future research should focus on development of silvicultural practices that provide for the biological requirements of this endangered species.

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