The Endangered Pondberry (*Lindera melissifolia* [Walter] Blume, Lauraceae)

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CONSERVATION ISSUES

The Endangered Pondberry (*Lindera melissifolia* [Walter] Blume, Lauraceae)

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ABSTRACT: Pondberry (*Lindera melissifolia*) is an endangered plant species that occurs in seven southern states. It is a rhizomatous, clonal shrub that usually grows in colonies and has numerous stems with few branches and drooping leaves that give off a spicy odor when crushed. Pondberry is dioecious, with small yellow flowers that bloom in spring and have scarlet drupes that mature in late summer or fall. The species grows in low areas within bottomland hardwood forests in the western part of its range and on the margins of limestone sinks and wet depressions in pine forests in the eastern part. Pondberry has probably always been a rare species, but its distribution and abundance have been affected by habitat destruction and alteration, such as timber cutting, clearing of land, and local drainage or flooding of wetlands. Until recently research on pondberry has been sparse; but because of proposed flood control measures for the area in which the species occurs in Mississippi, interest in research has increased. This review will be helpful to land managers and scientists because it provides information about all known current research on the species.

Index terms: endangered species, Lauraceae, *Lindera melissifolia*, pondberry

INTRODUCTION

Pondberry (*Lindera melissifolia* [Walt] Blume, Lauraceae) was listed as an endangered species in 1986 (USFWS 1986) because habitat destruction and alteration, such as timber cutting, clearing of land, and local drainage or flooding of wetlands had affected its distribution and abundance (Klomps 1980; Devall et al. 2001). Pondberry has probably always been a rare species; Steyermark discovered the plant in Ripley Co., Missouri, in 1948 and stated 'So far as I know it's one of the rarest shrubs in the United States' (Steyermark 1984). Although much of the formerly available habitat has become agricultural land, present pondberry colonies are small and occupy only a part of the apparently suitable habitat. A Recovery Plan was completed in 1993 (USFWS 1993), but little was known about the species to inform management. In the past, little published information was available and the articles that existed contained scant quantitative data.

Until recently, there has not been an intensive effort to carry out comprehensive research on the biology, ecology, and effects of forest management on the species (Devall et al. 2001; Aleric and Kirkman 2005b; Lockhart et al. 2006, 2009). Interest in pondberry research increased after the release of the Reformulation Report for the Yazoo Backwater Area in Mississippi (U.S. Army Corps of Engineers 2000; Lockhart et al. 2009). The report included plans to build a large pumping station with a year-round pump operation elevation of 26.5 m adjacent to the Steele Bayou flood control structure (32.72° N latitude, 91.01° W longitude) (Lockhart et al. 2009). Because of the proposed flood control measures, there was concern about the welfare of pondberry in the area. Studies were designed to address these concerns, including controlled experiments in a greenhouse and in a water impoundment facility, and ecological studies to understand the ecosystem dynamics and sustainability of pondberry colonies in the Lower Mississippi Alluvial Valley (LMAV). An interagency agreement was signed in September 2002 by the U.S. Army Corps of Engineers, the U.S. Fish and Wildlife Service, the U.S. Forest Service National Forest system, and the U.S. Forest Service Research and Development, concerning funding and performance of pondberry research (Lockhart et al. 2009). The purpose of this paper is to review all published research articles on the species so that management recommendations resulting from the research will be available in one place.

Pondberry is a rhizomatous, clonal shrub that occurs in seasonally flooded wetlands and on the wet edges of sinks, ponds, and depressions in the southeastern United States (Figure 1, Radford et al. 1968; Devall and Schiff 2002). The species usually occurs in colonies of erect or ascending shoots (Figure 2). Clones usually consist of numerous stems with few branches and drooping leaves that have a spicy odor when crushed (Devall et al. 2001; Devall and Schiff 2004a). The leaves are subcordate at the base with prominent veins on the lower pubescent surface (Klomps 1980). Pondberry is dioecious, with small yellow flowers that bloom in spring before leaf-out occurs (Tucker 1984). The fruit is a scarlet

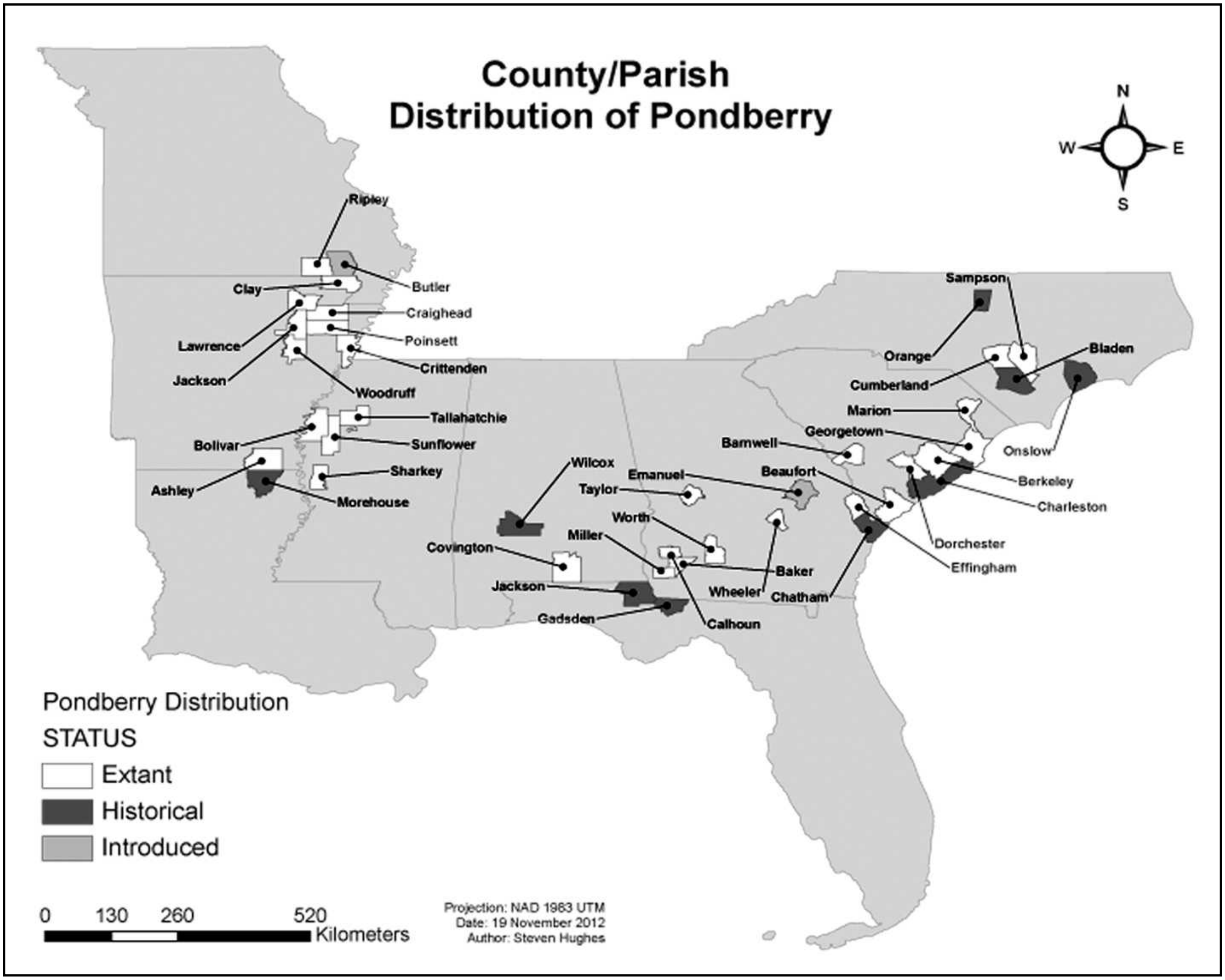

Figure 1. Distribution map of pondberry (*Lindera melissifolia*, Lauraceae) in the southeastern U.S.

drupe about 1 cm long that matures in late summer or fall (Devall et al. 2001; Devall and Schiff 2004a) (Figure 3). The species has a shallow root system, with rhizomes and most roots in the upper 20 cm of soil (Wright 1989a, 1989b).

DISTRIBUTION

Thomas Walter discovered pondberry in South Carolina in 1788 and described it as *Laurus melissaefolia* (Tucker 1984). A few early naturalists (Michaux, Pursh, Nuttall, and Nees ab Eisenbeck) also collected pondberry from southern states during the next 160 years (Steyermark 1949; McCartney et al. 1989). At present, there are populations in Alabama, Arkansas, Georgia, Mississippi, Missouri, North Carolina, and South Carolina (USFWS 2012). The species was collected in Louisiana before the twentieth century (Tucker 1984; Wurdack 1989) and recorded in Florida (Chapman 1845), but is no longer found in those states.

In Mississippi, a number of pondberry colonies occur in the Delta National Forest, a bottomland hardwood forest in Sharkey County. The forest is crisscrossed by drainages and sloughs, and seasonal flooding occurs from late fall to spring. Soils belong to the Sharkey-Dowling-Alligator associations (Pettry and Switzer 1996). Dominant species in the forest are sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.), red maple (*Acer rubrum* L.), Nuttall oak (*Quercus nuttallii* Palmer), and box elder (*A. negundo* L.) (Hawkins et al. 2009a).

Small pondberry populations also occur in Bolivar County, Sunflower County (Morris 1987), and Tallahatchee County (Heather Sullivan, Mississippi Natural Heritage Program botanist, pers. observation) in minor wooded areas surrounded by agricultural land. Dominant tree species at these sites

Figure 2. Pondberry (*Lindera melissifolia*, Lauraceae) colony in the Delta National Forest, MS.

include water oak (*Q nigra* L.), sugarberry, and hickories (*Carya* Nutt. spp.). Poison ivy (*Toxicodendron radicans* L. Kuntze) is an abundant understory species, and greenbriars (*Smilax* L. spp.), ladies eardrops (*Brunnichia ovata* [Walt.] Shinners), and swamp milkweed (*Asclepias perennis* Walter) also occur (Devall et al. 2001).

In northeastern Arkansas, pondberry grows in small single-sex clones (Wright 1994). It occurs around the bottoms and edges of small seasonal ponds in bottomland hardwood forests dominated by pin oak (*Q. palustris* Muenchh), willow oak (*Q. phellos* L.), swamp red maple (*A. rubrum* L. var. *drummondi* Hook & Arn. Ex Nutt.) Sarg.), and sweetgum (Morgan 1983). The ponds are located in depressions between old dunes that were formed from glacial outwash (Saucier 1978), and which fill with water during winter rains to a depth of < 50 cm. The water remains until after leafing-out occurs in spring (Wright 1990). Most of the surrounding land is farmed. Soils are loams and silty loams of the Boskett-Tuckermann series (USFWS 1993). The pondberry population in southeastern Missouri is contiguous with the population in northeastern Arkansas, and is the only natural occurrence in Missouri (Klomps 1980; Smith 2003). During the early 1900s, many bottomland hardwood forests in Missouri were cleared and other pondberry populations may have previously existed (Klomps 1980; Smith 2003). A planted population exists in Butler County (Smith 2003).

Pondberry was discovered by Samuel Buckley in Wilcox County, Alabama, in 1840 and was thought to be extirpated from the state until a population of several hundred stems was discovered in Covington County in 2004 (Schotz 2005), growing along the western side of a shallow depression forested with *Nyssa biflora* Walt. A second population was soon discovered less than 1 km away (Schotz 2005).

On the coastal plain in North Carolina, pondberry occurs in a different habitat, at the northeastern limit of its range, on the margins of Carolina bays and wet depressions (Morgan 1983). These ponds have a sandy substrate and tend to be fairly open with pondcypress (*Taxodium ascendens* Brongr.), red maple, loblolly pine (*Pinus taeda* L.), pond pine (*P. serotina* Michx.), and swamp blackgum (*Nyssa sylvatica* Marshall). Pond spice (*Litsea aestivalis* (L.) Fernald), another rare species, also occurs here (Leonard, unpubl. data). Pondberry populations currently exist in Cumberland and Sampson Counties and it historically occurred in Bladen, Onslow, and Orange Counties (North Carolina Natural Heritage Program 2008).

In South Carolina, pondberry grows along the edges of limestone sinks and wet depressions, in pine forests, and more open areas (Morgan 1983). The State's largest population occurs within an extensive depression area, the Honey Hill Lime-Sinks in the Francis Marion National Forest. The previously large pondberry population had decreased considerably but has been recovering after gaps were cleared around colonies (Glitzenstein 2007). Populations occur in Barnwell, Berkeley, Charleston, Dorchester, and Georgetown Counties (Jeff Glitzenstein, research associate/Beadel Fellow at the Tall Timbers Research Station, pers. observation).

In Georgia, as in other states in the southeastern coastal plain, pondberry occurs around the edges of limestone sinks, ponds, and other depressional wetlands (Wurdack 1989; Aleric and Kirkman 2005b). Populations occur in Baker, Calhoun, Effingham, Miller, Taylor, Screven, Wheeler, and Worth Counties (Georgia Department of Natural Resources 2008; Tom Patrick, Georgia Dept. of Natural Resources botanist, pers. observation), where the mostly male plants often grow together with pond spice (Patrick et al. 1995).

Pondberry reportedly occurred in Florida, where Chapman included the species in a list of plants growing around Quincy in 1845 (McCartney et al. 1989). He sent two undated specimens to the New York Botanical Garden, one labeled 'Florida' and the other 'West Florida,' which historically extended to the Mississippi River (Devall et al. 2001). Pondberry has not been seen in Florida since then.

Pondberry has not been found in Louisiana in around 200 years, although it was collected near the Ouachita River close to the Arkansas state line in Moorehouse and West Carroll Parishes, where it grew around 'spicebush ponds,' likely named for pondberry (Louisiana Department of Wildlife and Fisheries 2008). The species probably occurred at additional locations in the past, but many forested wetlands in the LMAV have been converted to other uses. Since the 1780s, 30% of wetlands in the United States have been lost (National Research Council 1992).

ASSOCIATED FORESTS

Pondberry populations occur in two general types of habitat: in low areas within bottomland hardwood forests in the western part of its range, and on the margins of limestone sinks and wet depressions in pine forests in the eastern part.

Hawkins et al. (2009a) collected pondberry data on five bottomland hardwood forests in the LMAV in Mississippi, Arkansas, and Missouri. The studied portion of the St. Francis Sunken Lands had been commercially logged, with a diameter limit cut, in the late 1970s. All the other forests had been previously cut, but the silvicultural prescriptions used were not stated. All had hydric soils and experienced seasonal flooding in late winter and early spring, and were without recent anthropological disturbance. Tree stem density and mean dbh were not significantly different between plots with or without pondberry. The sites included many flood-tolerant species and similar canopy and subcanopy species, although they differed in relative importance. Canopy species at all sites included sweetgum, Nuttall oak, overcup oak (*Q. lyrata* Walt), water oak, American elm (*Ulmus americana* L.), and persimmon (*Diospyros virginiana* L.). Two subcanopy species occurred at all five sites: green ash (*F. pennsylvanica* Marsh.) and American elm. Pondberry colonies were not associated with shade tolerant or intolerant tree species or with flood tolerant or intolerant species, supporting Wright's (1990) suggestion that both light from canopy gaps and periodic inundation together promote colony establishment and successful growth.

Pondberry also exists in an ecotonal zone in the southeastern Coastal Plain, between fire-maintained uplands and depressional wetlands (Aleric and Kirkman 2005b). Dominant species in the seasonally flooded depressions that Aleric and Kirkman (2005b) studied were *Nyssa sylvatica* var. *biflora* (Walt.) Sarg. and *Taxodium ascendens* Brongn. One population grew under laurel oak (*Quercus laurifolia* Michx.), red maple, and sweetgum. Some populations occurred across a gradient from full sun to full shade. In the Francis Marion National Forest, South Carolina, pondberry occupies a rather narrow zone interior to larger, less flood-tolerant shrubs, fetterbush (*Lyonia lucida* Lam. K. Koch.), red bay (*Persea palustris* Raf. Sarg.), and white bay (*Magnolia virginiana* L.) (Glitzenstein 2007).

Figure 3. Pondberry (*Lindera melissifolia*, Lauraceae) fruit.

LIGHT ENVIRONMENT

Pondberry colonies occur in a range of habitats from deep shade to full sun. Although Wright (1989a,b) and Klomps (1980) suggested that it requires shade, this was untested until recently. Wright (1990) investigated pondberry net photosynthesis at a dune pond in northeastern Arkansas. He found that the species was photosynthetically competent at light levels typical of shaded conditions, compared to competing understory plants such as ladies eardrops, sassafras *(Sassafras albidum* (Nutt) Nees), American beautyberry (*Callicarpa americana* L.), and catbriar (*S. glauca* Walter), and suggested that pondberry possesses the characteristics of shade plants. Wright (1990) demonstrated that pondberry growing around dune ponds had high water use efficiency, which was marginally beneficial there. He concluded that pondberry possesses physiological adaptations appropriate to its habitat in Arkansas and is not at these sites by chance. The dune ponds are a benign environment where pondberry is buffered against several potential stresses, such as lack of water and competition.

In the late 1980s, 8000 pondberry stems occurred in more than 50 depressions in the Honey Hill Lime-Sinks, in the Francis Marion National Forest, South Carolina; but in a 2001 survey, only 300 stems were found. In 2002, gaps were cleared around surviving pondberry colonies. Three years later, the total number of stems had increased by 9% and total stem length had increased 119% in response to the treatment (Glitzenstein 2007).

Aleric and Kirkman (2005b) compared photosynthetic and growth responses of rooted cuttings in a greenhouse study under 100%, 42%, and 19% of full sunlight and carried out a field study of four pondberry populations in the southeastern coastal plain. In the greenhouse study, growth was 30% less in full sun than in the other two light environments. As light decreased, there was decreased stomatal density, increased specific leaf area, and increased leaf area ratio. Patterns of photosynthetic responses to different light conditions at field sites were usually similar to those in the greenhouse study. Photosynthetic capacity was similar to that of other shade tolerant species. The authors suggested that levels of sunlight < 40% are preferred, although the species has the ability to adjust to a range of light environments, and this should be taken into account in management of existing populations and reintroduction of the species.

The Flooding Research Facility on the Theodore Roosevelt National Wildlife Refuge Complex in Sharkey County, MS, was constructed in 1994 on land that was a bottomland hardwood forest before being cleared for agriculture. The facility was recently upgraded and has 12 one-acre impoundments that can be independently flooded or drained; the bottom of each impoundment is the soil surface that was present when agriculture ceased (Lockhart et al. 2006). It was used for a three-year study of the effects of flooding and light availability on stecklings (young male and female pondberry plants produced by micropropagation), including three hydrologic regimes and three light availability treatments, with four replications. The stecklings were planted in 2005 and flooding treatments began in 2006 (Lockhart et al. 2006). Steckling survival, stem length, and stem diameter growth were only slightly affected by hydroperiod, but soil flooding may be important for reduction of interspecific competition. Survival and stem length growth were best with 37% light, and stem diameter growth was greatest with 70% light. In addition, female clones produced more ramets as light availability increased. These results suggest that active management to increase light availability would be beneficial to the species (Lockhart et al. 2013).

Lockhart et al. (2007) used the product of blade length and width as the independent variable to develop and test a predictor of pondberry leaf blade area. They showed that these simple dimensions, obtained nondestructively, can be used to make dependable predictions about how factors such as light availability, soil moisture, and response to competition would affect plant growth. The model should facilitate future ecological and physiological studies, leading to better understanding of the environmental requirements for pondberry growth and development (Lockhart et al. 2007).

Lockhart et al. (2012) raised pondberry seedlings in a growth chamber to determine effects of light availability on shoot growth pattern, and leaf and stem growth. Seedlings grown in low light were 76% taller than those receiving high light, and had larger leaf blade dimensions, blade area, seedling leaf area, and greater mass. Seedlings exhibited a brief period of phenotypic plasticity followed by ontogenic plasticity. The authors suggested that this quality may be important in efforts to conserve and recover the species. It may allow the seedlings to respond rapidly to a brief period of increased resources and maintain the gain through ontogenic plasticity, resulting in greater competitiveness.

Hawkins et al. (2009b) found that a handheld chlorophyll meter could be an effective tool for estimating foliar chlorophyll concentration and content, providing a rapid, non-destructive assessment.

COMPETITION, FLOODING, AND OTHER DISTURBANCE

Pondberry is exposed to inundation from flooding, but little is known about the hydrological characteristics of its habitat. Priest and Wright (1991) used piezometers to study the groundwater hydrology of a pondberry colony in Arkansas, in an area with low ancient dunes and seasonally flooded depressions, with pondberry growing around one of the depressions. Their study demonstrated that a subsurface hydrologic gradient existed between the dune slopes and pond bottom, so groundwater was delivered to the pond following rain events. A continuous clay lens under the depression resulted in the water ponding above it.

It has long been thought that flooding is not a physiological requirement of pondberry but that it helps to lessen competition, because less flood-tolerant species would be at a disadvantage (Wright 1990; Hawkins et al. 2009c). Also, the shaded habitat in which pondberry often occurs was thought to lessen competition (Wright 1990). Wright (1989b) found that pondberry plants that burned during the dormant season resprouted in late May. One colony with 109 stems before the fire produced 134 new stems, but in a colony extending up a pond bank, shrubby and herbaceous stem elongation of other species was twice the rate of pondberry, suggesting that flooding is helpful regarding competition.

First-year pondberry plants in pots at varied densities and with different mixtures of male and female plants were subjected to three different treatments: (1) no flooding, (2) 30 day flooding, and (3) 60 day flooding (Hawkins et al. 2009c). With the first two treatments, stem height, stem diameter, and total leaf area were significantly greater for male plants at lower than at higher densities or for female plants regardless of density. In plantings of 6, 9, and 12 individuals, biomass accumulation, leaf variables, stem height, and stem diameter did not differ between genders. Once flooding started, both male and female plants stopped stem growth and soon abscised some leaves. Single male plants were taller and had greater leaf biomass than females and seemed better adapted to colonize suitable habitat, which may contribute to the male-biased colonies seen in nature. However, the authors found no evidence that competitive exclusion occurred during the pre-reproductive growth stage. In high density plantings (≥ 6 plants), no difference was recorded in size or growth variables in male and female plants.

The most numerous pondberry populations occur in bottomland forests of the LMAV, which generally flood from late winter to early spring, with no apparent ill effects to mature plants (Wright 1990; Hawkins et al. 2009c). The species may be ecologically adapted to flooding when the plants are dormant. Hawkins et al. (2009c) demonstrated that first-year, metabolically active plants are not adapted to endure extended (≥ 30 days) flooding. Little height growth occurred after flooding began, leaf turgor declined, and some leaf abscission occurred after 10 – 14 days. Wright (1990) suggested that since flooding of 7 – 10 days during the growing season promotes ramet production; short-term flooding may promote colony expansion.

Hawkins et al. (2010) also studied the hydrologic regime and floristic composition of pondberry colonies in three populations in Mississippi. They identified 69 plant species that occurred within colonies. Although floods and their duration varied among the three populations, plant composition of the colonies and the ratio of pondberry to other plants remained fairly stable during the three-year study. They concluded that vines capable of growing over the pondberry plants (*Smilax* spp. and *Vitis* spp.) have the greatest potential to become strong competitors in this area.

These studies suggest that, like baldcypress (*Taxodium distichum* (L.) Rich**)**, seedlings that can only tolerate submergence for a short period (Demaree 1932), pondberry seedlings should survive and grow better in the field in a year with less than average flooding, but a colony benefits from annual flooding to reduce competition.

REPRODUCTIVE BIOLOGY

Information about reproductive biology would help to recover an endangered species, but very little was known about pondberry reproductive biology until Wright began to carry out research. Wright (1989a) found that fruit set (when one can see which flowers have at least temporarily produced a fruit) in several populations of pondberry was erratic, abundant in one year, and scarce the next two years, and stems that fruited heavily seemed prone to dieback. He found no effective seed bank, even where fruit production had been heavy. Wright (1994) recorded a male/female ratio of 7:1, and found that male stems had 20% higher stomatal conductance. Richardson et al. (1990) reported that female pondberry stems in Jackson Co., Arkansas, produced significantly fewer flowers (29.5 ± 4.3 ♀, 62 ± 7.9 ♂) and leaves per branch than males (6.1 ± 0.1 ♀, 6.6 ± 0.1 ♂), but exhibited no other difference in morphology. The sex ratio was male-biased, and female clones covered less area and had lower stem density. They marked and reexamined female stems and found no evidence of sex change. Two spicebush (*Lindera benzoin*) plants that produced only male flowers in 1980 and 1982 produced both male and female plants in 1983 and 1984 (Primack 1985).

Devall et al. (2001) investigated pondberry reproductive biology in Mississippi and Arkansas. At the Delta National Forest, male stems produced a mean of 10.9 flower clusters and female stems produced 6.4 flower clusters with 4.0 flowers per cluster in early March. In early October, there were 0.8 mature fruits per female stem (3.2% fruit set). Six flower clusters covered with mesh bags produced no fruit, indicating that pollen is not moved by wind. Flowers supplemented with pollination via an artist's brush did not produce significantly more fruit than open pollinated flowers. At Corning, Arkansas, male stems produced 15.0 clusters and 6.8 flowers per cluster. Females produced 12.3 clusters and 5.8 flowers per cluster. Female stems produced 11.5 mature fruit per stem (16.2% fruit set).

FRUIT AND SEED CHARACTERISTICS

Information on the best methods of planting pondberry seeds has been lacking, and nothing was known about seed storage. Aleric and Kirkman (2005a) tested germination of seeds placed on the soil surface with litter and no litter, pulp and no pulp, and cage and no cage, using a three-factor design, including two additional treatments (with litter, no pulp, and no cage) of different planting depths (2.5 cm and 5.0 cm). A 10-m^2 plot was established along a wetland margin. Each treatment was randomly assigned to a 1.0-m^2 subplot with five seeds per treatment and no replication due to flooding of some plots. Neither litter presence nor sowing depth influenced seed germination, but more caged seeds germinated when pulp was removed. In a shade-house study, there was no difference in germination of seeds in a flooded treatment planted 2.5 cm deep and non-flooded treatments at 2.5 cm and 5.0 cm.

Connor et al. (2006, 2007) investigated the early physical and biochemical characteristics of maturing pondberry fruit. Over half of the fruit were aborted during the first three months, and then loss decreased. Three months after flowering, drupes reached mature size; and seeds reached mature size a month later. Average seed diameter was 6.6 mm and weight was 0.18 g. The dominant fatty acid in the seeds was lauric acid. Oleic and linolenic acids were present in fairly large quantities and there were traces of palmitic, stearic, and linolenic fatty acids. Seeds without pulp, buried for two months, and kept in an incubator for eight weeks, had 53% germination. Seeds do not germinate immediately after dispersal (Connor 2007). Fully hydrated seeds could be stored successfully for 16 months at both 4 ºC and 2 ºC. Dried seed showed low levels of germination compared to fully hydrated seeds when conventionally stored at 4 ºC, but they could be successfully stored in liquid nitrogen, which is encouraging for long-term germplasm conservation. The authors suggested that pondberry seeds are 'sub-orthodox,' intermediate between 'orthodox' seeds, which can be dried to moisture content of < 12% and 'recalcitrant' seeds, which must be stored fully hydrated. Although pondberry may increase more by vegetative reproduction, Connor et al. (2007) concluded that fruit and seed production may be important in the survival of the species. With sufficient light and moisture and no late frosts, a stem can produce several hundred fruits. Morgan (1983) and others (M. Devall, pers. observation) never observed seedlings in the field although seed production was successful.

Connor et al. (2012) examined the survival of seeds in mesh bags kept in a soil seed bank for up to a year. They found that the presence or absence of fruit pulp did not significantly affect seed survival, but buried seeds were seven times more likely to produce seedlings in the field than seeds left on the soil surface. They suggested that it is environmental conditions or other biotic factors that limit the presence of pondberry seedlings in the field.

Hawkins et al. (2011) investigated pondberry seed ecology to determine if it contributes to the species' rarity. They found that the absence of a persistent soil bank, no obvious long-distance dispersal, and late-season germination that affects survival during floods and in the following winter may contribute to the continued rarity.

Oh et al. (2012) found that essential oil from pondberry drupes has a significant tick repellent effect and a moderate mosquito-repellent effect. Plant-based repellents may have less harmful side effects than other repellents (Oh et al. 2012).

DISPERSAL

After Steyermark found pondberry in southeastern Missouri, 643.6 km from the nearest pondberry population, Cora Steyermark asked: "How do you account for this berry bouncing 400 miles? It wasn't dropped here from a plane" (Steyermark 1984). Ridley (1930) stated that many plant species that grow near lakes and ponds, but not in running water, are widely scattered, often over a large area, similar to pondberry distribution. Passive dispersal of pondberry seeds by water may have occurred in the past (Smith et al. 2004), but flood control projects have thoroughly altered Mississippi Alluvial Valley hydrological cycles (Sharitz 1992; Stanturf et al. 2000), so water probably has little opportunity to disperse pondberry in that area today. Smith et al. (2004) suggested that the combination of showy fruits and persistence on the stem suggested that animals, especially birds, may be dispersers of the fruit. Smith et al. (2004) observed fruiting colonies of pondberry and recorded 82 bird species in the vicinity of colonies and 12 species on pondberry plants. The hermit thrush (*Catharus guttatus* Pallas) and the northern cardinal (*Cardinalis cardinalis* L.) were observed eating the fruits. Northern cardinals, pondberry seed predators, were observed crushing seeds before eating them. Hermit thrushes ate whole seeds and soon regurgitated them, but other birds and mammals, such as the raccoon (*Procyon lotor* (L.)), black bear (*Ursus americanus* Pallas), and Virginia opossum (*Didelphis marsupialis* (L.)) may be pondberry dispersers as well (Smith et al. 2004).

Abilio et al. (2008) used a recording video camera with infrared illumination to monitor animal visitors to seed plots in or near the Delta National Forest. At each location, a one-meter^2 plot was established and 25 pondberry seeds were arranged on the soil surface inside the plot. The animals identified as possible pondberry seed predators were the northern cardinal, brown thrasher (*Toxostoma rufum* Linn.), swamp rabbit (*Sylvilagus* sp.), nine-banded armadillo (*Dasypus novemcintus* L.), and gray squirrel (*Sciurus carolinensis* Gmelin).

EXPERIMENTAL PLANTING

Tucker (1984) reported that no controlled propagation techniques for pondberry were known. In order to advance protection of the species, several scientists have attempted to propagate the species. Wright (1989a) sowed pondberry seeds in the greenhouse in the fall and transplanted 64 seedlings to an existing colony around a pond in Arkansas between April and June. Survival after 4 – 5 months ranged from 10% – 89%. The author did not publish subsequent survival data.

The Missouri Department of Conservation planted first-year pondberry seedlings in a protected forest in Butler Co., near the naturally occurring population in 1990, and sowed seeds from the Sand Ponds plants at both sites in 1993 (Smith 2003). Seed handling included removal of the fruit pericarps and seed stratification. For field-sown seeds, pericarps of the fruits were removed, the seeds were washed in water, and then planted 1 – 3 cm deep within one day of collection. Eleven (7.1%) planted seedlings survived from 1990 to 2000 and their average height was slightly shorter than their height at planting due to dieback and resprouting. By the third year, 44.2% of planted seeds had germinated and 53.6% by the seventh year, but survival was very low. By 2000, three of five cohorts (seedlings that germinated in a calendar year) had not survived and survival of the other two cohorts was < 10%.

PROPAGATION

Large numbers of plants of similar physiological age and size are needed for some studies, but are often unavailable, especially with an endangered species. Hawkins et al. (2007) describe a pondberry micropropagation protocol developed by Deborah McCown at Knight Hollow Nursery using shoot cultures under the auspices of the U.S. Forest Service Center for Bottomland Hardwoods Research, Stoneville, MS. The protocol was successful and more than 10,000 stecklings representing 20 male and female genotypes were produced and used in field and controlled studies. This protocol was necessary in order to avoid depleting natural populations and to provide plants representing a cross-section of genotypes from the area, allowing for more uniform experimental materials.

Devall et al. (2004b) translocated young male and female pondberry stems from a natural population as an aid in conserving the species. They planted the stems in pots and introduced them to five protected locations in the field, on National Wildlife Refuges, and in a State Park. After a year, 69% of the plants survived, with male and female plants having equal survival rates. More than 90% of the surviving plants had increased height, although the height of the tallest stems decreased. Many of the plants produced new stems, but some older stems died during the year. However the long-term survival after three years was poor, and by 2011 only two plants survived (M. Devall, pers. observation).

GENETIC DIVERSITY

Knowledge of the genetic structure of a species can aid conservation and management strategies. Rare and endangered species often have low levels of genetic diversity due to historical or ecological causes (Godt and Hamrick 1996). Allozyme diversity of 15 pondberry populations from Missouri to the Carolinas was evaluated by Godt and Hamrick (1996). The species exhibited low levels of allozyme diversity and little genetic variation at 27 loci. Nine of the 27 loci were polymorphic, but genetic diversity at these loci was low and not many were polymorphic within populations. The results indicated that pondberry is genetically depauperate compared to spicebush and other woody species, which often maintain high levels of genetic diversity. The family Lauraceae is not genetically depauperate, and diversity occurs in avocado (*Persea americana*) Torres et al (1978). Many of the populations consisted of only one or a few genets (genetically identical individuals) with mostly or all male clones. The authors suggested that the low genetic diversity of pondberry may be caused mainly by bottlenecks during its evolutionary history and recommended that genetic diversity within populations be increased by increasing population sizes and enhancing sexual reproduction to lessen the risk of extinction, but did not specify how this should be done.

Echt et al. (2006) developed microsatellite markers for genetic studies of pondberry. Information on gene flow, inbreeding, and genetic structure within and among colonies is scarce or nonexistent, and it is not known whether genetic diversity is declining. This information would be helpful for determining if the self-sustaining populations that are required for delisting under the USFWS Recovery Plan (1993) exist and in establishing best conservation practices (Echt et al. 2006).

Echt et al. (2011) quantified population genetic differentiation and diversity among 450 genets in 10 locations across the range of pondberry (all states except Missouri) using 11 microsatellite loci. They determined that the largest pairwise regional difference occurred between eastern and western population groups, and the northern population groups in each region diverged more from each other than the southern groups. Genetic diversity was the lowest in the Sand Pond Natural Area and highest in the Francis Marion National Forest. They found no evidence for inbreeding and found heterozygote excess in four of the eastern populations. This occurs in clonal populations, and is a result of self-incompatibility in dioecious species and in obligate outcrossing hermaphrodites (Balloux 2004). It can also occur in populations that have experienced a recent population bottleneck, a severe reduction in size (Cornuet and Luikart 1996). The authors suggested that a conservative plan for increasing biological diversity in pondberry populations would be to limit germplasm transfers to within a region. They recommended that pondberry seed nurseries be established to allow crossing among a wide variety of regional genotypes, which could provide the diverse seed sources necessary for restoration programs. They cautioned that propagating vegetative cuttings from existing colonies would not increase total genet diversity.

DISEASES AND HERBIVORES

Dead stems and live stems with dead tops may be observed scattered through many pondberry populations. It was thought that a fungus might be responsible, but no information was available on the actual cause. Devall et al. (2001) recorded dead stems (7.1% to 57.9%) or stems with dieback (7.4% to 33.8%), in 20 visits to four pondberry populations in Mississippi and Arkansas. They isolated eight fungal species from pondberry stems, three of which had been previously reported from Lindera: *Cercospora, Diaporthe* and *Colletotrichum* (= *Gloesporium*). Morgan (1983) noted that 56% of flowering stems in a population in Missouri died back during the growing season, partially due to an abnormally dry summer. Twenty years later, 14.5% to 31.3% of dead stems occurred in the contiguous Arkansas population, and it was growing vigorously (Devall et al. 2001), suggesting that the die-back does not completely kill a colony.

Several insects are known to feed on pondberry, but most do not cause severe damage. The common swallowtail (*Papilio troilus*) uses pondberry as a larval food in the Sunflower County, MS, population (Morris 1989), but only damages a few leaves (M. Devall, pers. observation). Leafcutter bees (Megachilidae) cut circular sections from the edges of pondberry leaves, and Smith (2003) noted that in some years they remove the majority of leaf tissue from a stem. These bees are also present in the Delta National Forest, Mississippi, but they have not caused extensive damage at that location (M. Devall, pers. observation).

The Asian redbay ambrosia beetle (*Xyleborus glabratus* Eichoff) was first detected near Savannah, Georgia in 2002, and mortality of redbay (*Persea borbonea* (L.) Spreng) occurred nearby soon after. The beetle carries the laurel wilt pathogen (*Raffaelea lauricola* (TC Harr., Fraedrich & Aghayeva sp. nov.), which causes a vascular wilt disease in members of Lauraceae. Fraedrich et al. (2011) demonstrated that pondberry and pondspice were highly susceptible and isolated the pathogen from some diseased pondberry plants in the field. The authors suggested that pondberry and pondspice may not be attacked frequently by the beetles because they are shrubs with small diameter stems.

CONCLUSION

A lot has been learned about pondberry as a result of the recent studies. Although the species can adjust to a range of light environments, Aleric and Kirkman (2005b) and Lockhart et al. (2013) suggested that levels of sunlight around 40% seem to be best in management and reintroduction of the species. Wright's studies indicated that some flooding is helpful in reducing competition, and he suggested it may even promote colony expansion through ramet production. While flooding in late winter and spring has no apparent ill effects on mature plants, Hawkins et al. (2009c) found that introduced young plants should be protected from extended flooding. Regarding competition, vines that grow over pondberry plants are the worst competitors (Hawkins et al. 2010). Connor et al. (2007) found that seeds do not germinate immediately after dispersal, and fully hydrated seeds can be stored successfully for 16 months at both 4 ºC and 2 ºC. Connor et al. (2012) found that buried seeds were significantly more likely to produce seedlings than seeds on the soil surface, and suggested that environmental conditions or other biotic factors limit the presence of pondberry seedlings in the field.

Echt et al. (2011) suggested limiting germplasm transfers within a region. They recommended establishment of seed nurseries rather than propagation of vegetative cuttings to increase genetic diversity. Although some information is available, more research on fruit dispersal, seed banks, and seed germination is needed. Active vegetation removal or other management prescriptions may be essential for maintaining the existence of some colonies. Some monitoring of pondberry populations is being carried out by Natural Heritage Commissions and by interested scientists, but a better coordinated effort to monitor the species would be helpful. The U.S. Fish and Wildlife Service serves as a clearinghouse of information on pondberry and conducts 5-year reviews based on the best available information.

Pondberry is a difficult species to evaluate for change in its status as endangered. Numerous ramets may be present in a colony, but this can be deceptive because they all may be male or all female, or they may be part of a single genet or a very few. The Recovery Plan for pondberry (USFWS 1993) states that its status will be changed from endangered to threatened "when there are 15 protected, self-sustaining populations distributed throughout the species' historic range." New populations have been discovered, but it is unclear if recovery is progressing. The Plan does not define a self-sustaining population or the specific geographic distribution required, but this information should be part of the plan. We suggest a definition of a self-sustaining population: as an area of at least 1 km^2 containing at least 50 distinct and unrelated pondberry genets distributed across its extent, having a female:male sex ratio between 0.75 and 1.25 (ideally 1.0), and with each genet at reproductive maturity growing either singly or clonally. Under this definition, populations are distinct when situated farther than 2 km from the edge of next nearest pondberry population.

This review of all published research articles on pondberry, and the recommendations provided, should be helpful to land managers and scientists working on pondberry maintenance and recovery.

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