Lindera melissifolia Seed Bank Study in a Lower Mississippi Alluvial Valley Bottomland Forest

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ABSTRACT

***Lindera melissifolia* (Walter) Blume, or pondberry, is federally listed as an endangered shrub and grows in warm, humid lowland forests of seven states in the southeastern United States. The dioecious plants usually form clonal colonies as a result of rhizome sprouting. Although *L. melissifolia* can annually produce many bright red spicy scented drupes, information on reproduction of the species is limited to its clonal regenerative capabilities. We examined the survival of *L. melissifolia* seeds held within bags for up to 1 y in a soil seed bank. Half of the bags were buried and the other half left on the soil surface. Additionally, bags contained seeds either with the oily fruit pulp removed or with drupes left intact. Results indicated that the presence or absence of the pulp does not significantly affect seed survival. However, the viability of buried seeds was greater than 50% by the end of 1 y, whereas over 70% of the seeds left on the surface were rotten or missing. Buried seeds were seven times more likely to produce seedlings in the field than those left on the soil surface. Because *L. melissifolia* seedlings are not often observed in naturally occurring populations despite the production of viable seeds, it is likely that environmental conditions or other biotic factors limit the field distribution and sustainability of seedlings.**

INTRODUCTION

Lindera melissifolia (Walter) Blume (pondberry, Lauraceae) is a federally listed endangered shrub that grows in the warm humid lowland forests of seven southeastern states: Alabama, Arkansas, Georgia, Mississippi, Missouri, North Carolina and South Carolina.

Lindera melissifolia is dioecious and sparsely distributed within its territory, which ranges from the Lower Mississippi Alluvial Valley east to North Carolina. It usually occurs in isolated clonal colonies, the result of rhizome sprouting. In the bottomland forests typical of our study sites in the western part of *L. melissifolia*'s range, the 1 to 2 m tall plants grow in areas that commonly flood in the spring but are frequently dry in the fall (Devall and Schiff, 2004). Found in ambient light conditions of deep shade to almost full sun, Devall et al. (2001) speculated that the plant can occupy many habitats as long as there is sufficient moisture.

Lindera melissifolia may have always been scarce throughout its range (Steyermark, 1949; Radford et al., 1968; Kral, 1983). The clonal regenerative capabilities of *L. melissifolia* serve to increase colony size, but the species lacks the sexual

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reproduction and seed dispersal necessary for establishment of new colonies. In February, before leaves emerge, *L. melissifolia* produces flowers on axillary inflorescences. By October, female plants are easily identified by an often-abundant crop of bright red drupes. While the showy persistent nature of *L. melissifolia* fruit may favor dispersal by birds or other animals (Smith et al., 2004) and attract seed predators (Abilio et al., 2008), research has not yet documented animals or birds inhabiting southern bottomland forests that are capable of dispersing *L. melissifolia* seeds over distances greater than 100 m, although the hermit thrush [*Catharus guttatus* (Turdidae)] is a short-distance disperser (Smith et al., 2004).

Unlike plants that rely on vegetative or asexual reproduction, plants that produce seeds have a means of spatial dispersal, often over great distances. Terrestrial plants generally are only mobile during the seed or seedling stage and often rely on animals, wind or water for dispersal. In addition, seed dormancy facilitates temporal dispersal, delaying germination until conditions are favorable for survival and growth of the new plant. Dormant seeds are critical to community succession and to assuring a durable genetic bank of characteristics necessary for survival in changing environments (Farmer, 1997).

Roberts (1973) divided seeds into two broad categories based on their storage potential: orthodox seeds that can be dried to moisture contents of less than 10% and stored at subfreezing temperatures for long periods of time, and recalcitrant seeds that cannot be dried below moisture contents of 25–45%, and therefore cannot be stored at below freezing temperatures. Orthodox seeds are often resistant to severe environmental conditions and can persist in seed banks for long periods of time. The high-moisture recalcitrant seeds remain metabolically active and are thus susceptible to temperature and moisture fluctuations and to fungal decay. Further research has proposed additional classes of seeds based on their storage potential: true orthodox, sub-orthodox, temperate-recalcitrant, tropical-recalcitrant, and intermediate (Ellis et al., 1990; Wang and Simpson, 2006; Bonner, 2008). Sub-orthodox seeds can be stored under the same conditions as true orthodox seeds but for shorter periods of time. Suggested reasons for this reduced storage potential include high lipid content and thin seed coats (Bonner, 2008).

Mature seeds of *L. melissifolia* are approximately 10.9 mm long by 7.6 mm wide, with an average 6.6 mm diameter (Connor et al., 2007). They contain over 28% moisture (FW basis) when shed from the plant (Connor et al., 2007) and can survive drying to 8.6% moisture content but at greatly reduced viability. This suggests the seeds may be sub-orthodox. There is little information available, however, on survival of these seeds in the soil seed bank.

The fate of *L. melissifolia* fruits and seeds once shed from the plant is unknown. It is unknown if they can survive for extended periods of time in the flooded conditions on wet sites or the desiccating conditions of dry sites. It is also unknown if seeds remain on the soil surface or if they are covered by leaves and other debris after being shed from the plant, and how this might affect seed survival in the seed bank. Additionally, the fruit pulp of the seeds is rich in oleic, palmitic and linoleic acids (Connor et al., 2007), and is potentially an oil-rich food source for seed predators such as ants and birds, as well as for fungi. How such predation on the fruit pulp would affect seed survival is unknown.

This study was initiated to determine (1) the fate of *L. melissifolia* fruits and seeds deposited on the soil surface or buried in the forest floor, (2) the length of time seeds remain viable in the seed bank, and (3) the effect of retention of fleshy layers of the fruit (exocarp and mesocarp, hereafter referred to as fruit pulp) on seed survival in the soil seed bank. We also wanted to determine if and when field seed germination occured and its implications for establishing new colonies. Data from this study augments the existing life history information about *L. melissifolia*.

MATERIALS AND METHODS

Lindera melissifolia fruits were collected and studied at two sites, wet and dry, within the Delta National Forest, Sharkey County, Mississippi, in the Yazoo River Basin of the Lower Mississippi Alluvial Valley. Typical bottomland forests in this area have an overstory composed primarily of sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.) and red maple (*Acer rubrum* L.), with Nuttall oak (*Quercus texana* Buckley) and box-elder (*Acer negundo* L.) also present (Hawkins et al., 2009). Both sites were relatively flat, with soils representative of the Sharkey series, very-fine, montmorillonitic clay, nonacid, thermic Vertic Haplaquepts (Scott et al., 1975). Surface-water ponding was evident on the wet site but not on the dry site. Climate is humid and subtropical, with a growing season averaging 229 d and an average temperature of 27 °C in July and 7.5 °C in January (Scott and Carter, 1962; Scott et al., 1975).

Plastic screens were sewn into 10.2 × 10.2 cm bags which were used to loosely enclose 25 *L. melissifolia* entire fruits or peeled seeds per bag. The screen allowed free conduction of moisture, small insects and air but securely encased the fruit and seeds. To determine how long seeds remain in the soil seed bank (longevity), bags were buried 5 cm deep under two field conditions in Oct. 2004, wet and dry. The wet site flooded at least 1 month during the period after seed shedding while the dry site did not flood. On the wet site, one-half of the bags were buried (B) containing seeds with the associated fruit pulp removed (B–) while the other half were buried containing seeds with the fruit pulp intact (B+). At each sampling time, 4 bags of each treatment were collected. Limited by the number of available seeds, only the longevity B+ treatment was replicated on the dry site; at each sampling time, only 3 replications of B+ were collected from this site. All bag positions were marked with wire flags to aid in relocation. Samples were collected after 1, 2, 4, 6, 7, 9 and 12 months in the field.

We also wanted to determine the fate of seeds (persistence) after dispersal. On the wet side only, we left bags of 25 seeds on the surface (S) of the forest floor. At each sampling time, 4 bags of seeds with fruit pulp removed (S–) and 4 bags of entire drupes (S+) were collected.

At each sampling time, seeds were classified as germinated (both root and shoot emerged), ungerminated, rotten or missing. The missing category included seeds which had completely rotted or which had vanished from a torn bag. Bags were brought to the laboratory, where ungerminated seeds and those with just the root emerging were extracted from bags and placed in a germinator for 16 wk to determine if germination would occur. Seeds thus removed from bags

were germinated as 3 or 4 replications of up to 25 seeds each on moist Kimpac®. The Stultz® germination cabinet was set at 35 °C for 16 h with light and 30 °C for 8 h without light. At the end of the 16 wk period, seeds were scored as germinated, abnormally germinated (missing root or shoot), ungerminated (but potentially viable, tetrazolium-tested) or rotten.

Seeds from the 1, 4, 9 and 12 month samples that remained in the germinator at the end of the 16 wk period were stained with a 1% (w/v) tetrazolium chloride solution to determine viability (seeds from the 2 and 7 month samples were destroyed when an oven malfunctioned and through technical error). Seeds were longitudinally cut in half, with the embryo exposed, and placed in Petri dishes along with the staining solution. The dishes were covered and put in a 30 °C oven for 16 h. Seeds exhibiting dark red staining of both the embryo and cotyledon tissue were considered viable (Bonner et al., 1994).

The study was a completely randomized design with a two-way factorial treatment structure. Each month's wet site data were analyzed (SAS version 9.2-2008; SAS Institute, Inc., Cary, NC) using two factors, position (buried or surface) and fruit pulp (present or absent). If no significant interaction between the two factors was detected ($p \leq 0.05$), each factor was then tested separately using Tukey's multiple comparisons test on the two means from each factor. If the interaction was significant, then all six pairwise comparisons between the four treatment combinations were tested using Tukey's multiple comparisons test. Simple *t*-tests were used to determine if differences existed between wet site B+ and dry site B+ treatments.

RESULTS AND DISCUSSION

General

Results from the two-way factorial analyses of the germinated and rotten/missing seeds are reported in Table 1. Analyses determined significant interactions between factors (position and fruit pulp) in the 2 and 4 month germination samples and in the 4 month rotten/missing samples only. However, when no significant interaction was present, individual treatment effects within either factor were significant in all collections except month 6 for both germinated and rotten/missing seeds (Table 1). Further analysis of treatment differences determined

Table 1. Results (*p* values) for the germination and rotten/missing analyses on *Lindera melissifolia* seeds based on a completely randomized design with two factors, position (buried or surface) and fruit pulp (with or without).

	Germination			Rotten/Missing		
Month	Position (P)	Fruit pulp (FP)	P×FP	Position (P)	Fruit pulp (FP)	P×FP
1	0.3370†	0.0032	0.7446	0.0020	0.0020	0.2419
2	<0.0001	<0.0001	0.0392	0.4480	0.0365	0.7018
4	0.0022	0.3811	0.0073	1.0000	0.6347	0.0033
6	0.1484	0.3793	0.7316	0.5869	0.4187	0.1881
7	0.4370	0.1247	0.2432	0.3039	0.0158	0.8715
9	0.0003	0.7094	0.9256	<0.0001	0.3124	0.4281
12	<0.0001	0.5805	0.2097	0.0007	0.4554	0.7466

†Effects with *p* values ≤ 0.05 are statistically significant.

that presence or absence of fruit pulp was significant in the first 2 months of the study, but rarely after that (Table 2). Seed position, however, was significant for both germinated and rotten/missing seeds after 9–12 months in the field.

Seedlings (root and shoot emerged) were first observed in the field 7 months (May) after the study began. Thus, germination results reported before that time all occurred in laboratory germinators, whereas results from 7 through 12 months reflect a combination of field and laboratory germination.

Wet site study

Longevity (B+ and B– seeds). Percentages of seeds by treatment category are shown in Table 3. After the first 2 months in the field and 6 to 9 wk in the

Table 2. Least squares means for proportion of germinated and rotten/missing *Lindera melissifolia* seeds based on a completely randomized design with two factors, position (buried or surface) and fruit pulp (with or without).

	Germination				Rotten/Missing			
	Position		Fruit pulp		Position		Fruit pulp	
Month†	Buried	Surface	With	Without	Buried	Surface	With	Without
1	0.090a	0.135a	0.030a	0.195b	0.245a	0.085b	0.245a	0.085b
2	0.445a	0.710b	0.440a	0.715b	0.045a	0.065a	0.085a	0.250b
4	0.830a	0.595b	0.685a	0.740a	0.125a	0.125a	0.135a	0.115a
6	0.810a	0.590a	0.635a	0.765a	0.110a	0.090a	0.115a	0.085a
7	0.270a	0.365a	0.220a	0.415a	0.500a	0.370a	0.605a	0.265b
9	0.625a	0.105b	0.385a	0.345a	0.170a	0.770b	0.515a	0.425a
12	0.605a	0.100b	0.375a	0.330a	0.340a	0.750b	0.510a	0.580a

†There was no significant position × fruit pulp interaction for germination and rotten/missing in months 1, 6, 7, 9, and 12, and month 2 for rotten/missing, so the same letter within position or fruit pulp, within each of those months, indicates no significant difference. There was a significant position × fruit pulp interaction for germination in months 2 and 4, and for rotten/missing in month 4, so all six pairwise multiple comparisons within each of those months were performed.

Table 3. Percentage of *Lindera melissifolia* seeds germinated and rotten/missing (in parentheses) from wet and dry sites. Seeds were either buried (B) or left on the soil surface (S), with (+) or without (–) the fruit pulp removed.

	Wet site†				Dry site†
Collection month	B+	B–	S+	S–	B+
1	0 (35)	18 (14)	6 (14)	21(3)	3 (17)
2	36 (7)	53 (2)	52 (10)	90 (1)	25 (3)
4	90 (6)	76 (19)	47 (21)	72 (4)	85 (8)
6	77 (10*)	85 (12)	50 (13)	68 (5)	55 (29*)
7	10* (66)	44 (34)	34 (55)	39 (19)	31* (59)
9	64 (18)	61 (16)	13 (85)	8 (69)	46 (50)‡
12	68 (29)	53 (39)	7 (73)	13 (77)	44 (56)

†Wet site counts are from 4 bags with 25 seeds each; dry site counts are from 3 bags with 25 seeds each.

‡One bag from the dry site was destroyed; the average of two replications is shown.

*Differences in percentage of germinated or rotten/missing seeds between a wet B+ and dry B+ site, within the same collection month, are significant ($p \leq 0.05$).

germinator, B+ seeds went from 0% germination after 1 month to 36% germination after 2 months. A large unaccountable reduction in rotten seeds also occurred between the first and second collections. Germination of B– seeds increased from 18% after 1 month to 53% after 2 months, and again, a decrease in rotten seeds occurred. These initial observations suggested that B– seeds had a higher viability in the laboratory than B+ seeds, and we expected that B– seeds would move out of the seed bank by germinating at a faster rate than B+ seeds.

However, the results after 9 to 12 months did not support our initial predictions. Germination of B+ drupes peaked in 4 months at 90%, whereas B– germination peaked in 6 months at 85%. At 9 months, germination for B+ seeds was still high (64%), and the number of rotten/missing seeds had increased only slightly to 18%. The remaining 18% of the seeds either did not germinate or had abnormal germination. By 12 months, germination was still high (68%), but rotten/missing seeds now accounted for 29% of the tally. Germination of B– seeds at 9 months was 61% and 16% of seeds were rotten/missing. Ungerminated or abnormally germinated seeds accounted for 23%. By 12 months, germination had fallen to 53% for B– seeds. Rotten and missing seeds totaled 39% of the final collection.

Persistence (S+ and S– seeds). Fresh S+ seeds deposited directly on the litter layer had 6% germination after 1 month and 52% germination after 2 months (Table 3). The number of rotten/missing seeds was initially 14%, and fell to 10% after 2 months. For S– seeds, germination increased from 21% after 1 month to 90% after 2 months. The percentage of rotten/missing seeds was negligible for the first 2 months of the study. These preliminary laboratory results suggested that seeds on the soil surface might germinate and move out of the seed bank faster than buried seeds. It was also noted that, like the buried seeds, seeds with fruit pulp removed had higher laboratory germination than those with the pulp intact. However, germination for S+ seeds remained fairly constant for the 2–6 month collections. By 9 months, germination had dropped to 13% and by 12 months to 7%. Meanwhile, rotten/missing seeds accounted for 85% of the 9 month collection and 73% of the 12 month collection.

Similar results were found for S– seeds. Germination dropped to 8 and 13% for the 9 and 12 month collections, respectively, whereas rotten/missing seeds comprised 69% of the 9 month collection and 77% of the 12 month tally.

Dry site study

Longevity (B+ seeds). The dry site longevity study mimicked the wet site longevity study but because of limited seed supply included only B+ seeds. Germination on this site, as on the wet site, peaked after 4 months at a comparable 85% (Table 3). Dry site germination after 9 and 12 months tended to be lower than that on the wet site, but the differences were not significant. Unlike the wet site B+ results, the majority of B+ seeds fell into the rotten/missing category by the end of the study on the dry site, but again the difference was not significant.

A forested lowland in the southern United States may not seem the best environment for maintaining seed viability on the soil surface. In general, high

heat and humidity speed up seed metabolism, and fungal infections cause seeds to deteriorate and die. Recovery and regrowth of any endangered plant requires knowledge of the ecology of the species in its natural habitat. In particular, information on reproductive capacity is vital to recovery programs. Zedler (2000) stressed the importance of seed longevity in wetland restoration programs. Van der Valk (1981) and van der Valk and Verhoeven (1988) stated that if a desired species fails to establish in initial restoration efforts, it is often difficult to introduce later in the process. Persistence of a species' seeds in the soil seed bank should facilitate natural regeneration and the restoration and recovery of that species within an ecosystem.

Results from this study in the Lower Mississippi Alluvial Valley indicated that *L. melissifolia* seeds could survive in the seed bank for at least 12 months. While the presence or absence of fruit pulp was significant early in the study, it did not affect seed survival after 12 months in the field. However, seed position was highly significant in determining seed survival. Germination of buried seeds was greater than 50% by the end of the study whereas over 70% of the seeds left on the surface were rotten or missing.

Lindera melissifolia seed dispersal mechanisms are still largely unknown. Only the hermit thrush has been documented as a short-distance disperser of *L. melissifolia* seeds (Smith et al., 2004), and it is unknown if any bird or animal caches the seeds beneath the litter layer. With but one known consumer/disperser of the seeds, we speculate that the majority of *L. melissifolia* seeds stay in place on the soil surface after dropping from the plant. If this is the case, our results show that they would largely fall into the rotten/missing category and not contribute to the seed bank or form new colonies.

It is possible that leaf fall and silt from seasonal flooding would cover some seeds and thus aid their survival. Mississippi River depth peaked in the late winter and remained high through April during the study year. However, there is an extensive levee system in place along the Mississippi River and it is unknown how this might affect soil deposition on its flood plain. It is possible that localized rainstorms and flooding from smaller streams may deposit soil over pondberry seeds, but this has not been measured.

The month of May usually coincides with the beginning of warmer summer temperatures, and it marked the start of floodwater recession in the Lower Mississippi Alluvial Valley during the year of this study. This was also when field germination for *L. melissifolia* seeds peaked in the screen bags. A total of 109 seeds had produced plants in B+ wet site bags, 85 in B– bags, 4 in S+ bags and 22 in S– bags. Thus, after 7 months, buried seeds produced seven times the number of plants as seeds placed on the soil surface. Van der Valk (1981, 1986) and van der Valk and Davis (1978) found that, in marshes, many perennial emergent species can only become established during periods of drawdown. While this process is perhaps necessary for *L. melissifolia* seed germination, it could be that drawdown and limited or episodic summer rainfall during the study year led to scarcity of water and resulted in high seedling mortality.

It appears that any litter deposited over buried bags was not of significant depth to negatively affect *L. melissifolia* seed germination. It is possible that

seeds on the surface were more susceptible to shifts in moisture and temperature and thus less likely to survive and produce seedlings. It is more probable that our results reflect the high percentage of rotten and missing *L. melissifolia* seeds from surface bags, which by the end of the study dwarfed the number of germinating seeds. Although one S bag was torn open after 9 months in the field, none of the plastic thread seams had failed. The screen bags may have provided some initial protection against predation, but over 75% of the seeds left on the soil surface were ultimately in the rotten/missing category after 9–12 months. After this length of field exposure, the only indication of rotten seeds was usually the presence of empty seed coats. Garwood (1989) concluded that such remains implicated predators or pathogens in seed disappearance, a conclusion shared by the authors of this paper. The most probable reason the number of rotten seeds decreased after 12 months on the soil surface was that seeds had deteriorated beyond recognition and therefore fell into the missing category. It is only speculation that environmental and microsite conditions affect seedling survival; it may well be herbivore predation of seedlings that accounted for the absence of *L. melissifolia* seedlings in the field.

Sri-ngernyuang et al. (2003) buried seeds of a tropical *L. melissifolia* relative, *Lindera metcalfiana* C.K. Allen, 5 cm deep in forest soils in Thailand. They found that germination of excavated seeds peaked after being buried for approximately 6 months and that seeds experienced 26 to 48% mortality after being buried for 4 months. Additionally, they observed that none of the seeds germinated in the field during the entire 2 y experiment but that seeds buried for that long were still viable. Germination peaked at 4–6 months in the buried *L. melissifolia* seeds in our study, and over 50% of the wet site buried seeds were still viable after 1 y. Thus *L. melissifolia* maintains a sizable soil seed bank after 1 y if seeds do not remain on the soil surface. However, unlike *L. metcalfiana*, field germination of *L. melissifolia* was found to be still prevalent after 7 months.

If suitable germination conditions do not occur for a species, recruitment of new individuals into the population may be absent and the species may, like *L. melissifolia*, expand by vegetative means. Parker et al. (1989) noted that vegetative propagation is an effective means of survival in habitats with environmental fluctuations or disturbances. Burial beneath 5 cm of soil and few months of inundation at the wet site did not appear to greatly affect *L. melissifolia* seed survival, but it is not known how a second season of inundation would affect seed viability, nor is it known how many of the *L. melissifolia* seeds produced in the field remain at or near the soil surface after being shed from the plant (Abilio et al., 2008). If seeds are not buried, 1 y survival is greatly reduced, and it is likely that unless a seed germinates within 6–9 months of being shed from the plant, its long-term survival is improbable. Since greater seed longevity results in a rapidly accumulating dormant seed bank, the unknown viability of *L. melissifolia* seeds in excess of 1 y and scarcity of seedlings observed in the field may increase the importance of persistent rhizomes to its survival (Parker et al., 1989).

It is noteworthy that 274 seedlings were produced in the field, representing more than 8% germination. While this seems little enough, in some years in-

dividual female plants produce more than 250 drupes (K. F. Connor, personal observation). This, combined with high germination rates observed in the laboratory, should result in considerable natural seedling production within a colony. Since accurate counts necessitated removal of the seedlings once they germinated, results from this study could not be translated into long-term field survival. However, because *L. melissifolia* seedlings are not often observed in naturally occurring populations (Tucker, 1984; Wright, 1990; Devall et al., 2004) despite the production of viable seeds, it is likely that environmental conditions or unknown biotic factors limit the field distribution and sustainability of *L. melissifolia* via sexual reproduction. Ongoing studies in the Mississippi Alluvial Valley investigating *L. melissifolia* seed and seedling predators (Abilio et al., 2008) and seed dispersers (Smith et al., 2004) may shed light on biotic factors affecting *L. melissifolia* sustainability.

ACKNOWLEDGMENTS

The authors thank the U.S. Army Corps of Engineers, Vicksburg District, Vicksburg, MS, for underwriting a significant portion of the cost of this research. Pondberry seeds were collected under permit no. 43680-02003, issued by the U.S. Fish and Wildlife Service.

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