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Ecology and Phenotypic Variation of *Leitneria floridana* (Leitneriaceae) in Disjunct Native Habitats

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ABSTRACT *Leitneria floridana* is a rare woody species with a disjunct distribution in the southeastern and south-central United States. Although the distribution of *L. floridana* is well established, little is known about the comparative biology of its disjunct populations or the factors contributing to its rarity. We studied populations of *L. floridana* in Missouri, Arkansas, Texas, and Florida to characterize and compare population density, habitat, ecophysiology, morphology, and growth. Our results show that plants of the Missouri provenance are the most unique phenotypically, plants in Texas are the fastest growing, and plants in Arkansas seem particularly adapted to shade. We found that *L. floridana* grows in chemically and physically diverse soils and under a broad range of insolation. Soil moisture content appears to be the most important environmental factor governing the occurrence of *L. floridana*, with soil moisture and distribution density positively correlated.

INTRODUCTION *Leitneria floridana* Chapm. (corkwood) is a rare shrub or small tree with a disjunct distribution in southern Georgia, northwestern coastal Florida, southeastern Texas, northeastern and east-central Arkansas, and southeastern Missouri (Figure 1). In Florida, *L. floridana* occurs in hydric hammocks in areas with approximately 15–25 cm of soil above limestone bedrock. Palynological data suggest continuous presence of hammock species in these habitats of northern Florida since the Altonian stadial of the early Wisconsonian glaciation, 80,000 - 30,000 yr before present (YBP) (Platt and Schwartz 1990). Throughout its range, *L. floridana* occurs almost exclusively in: wet soils of coastal marshes and woodlands; tidal, estuarine shores; swampy woodlands; and swampy prairies. Because it is localized to wet habitats, activities such as draining, removing, and destructing wetlands and marshes are a threat to the natural populations of the species. Alteration of the hydrology of the habitat resulting from road construction or off-road vehicles can also threaten stands of *L. floridana*, including the populations in national forests. Other threats include invasion of suitable habitat by non-native, aggressive plants such as *Triadica sebifera* (L.) Small, rising sea level in the Gulf, herbicide spraying of adjacent areas for timber management, and urban development (Kelly McPherson [Waccasassa Bay Preserve State Park, Florida Department of Environmental Protection] and Thomas Adams [Brazoria National Wildlife Refuge, U.S. Fish and Wildlife Service], pers. comm.).

The systematics of *L. floridana* has been debated over the years, but in recent decades it has usually been considered as constituting the monotypic family, Leitneriaceae Bentham, in the Sapindales, near the Simaroubaceae DC. (Petersen and Fairbrothers 1983, Qui et al. 1998). More recently, *Leitneria* has sometimes been merged into the primarily tropical Simaroubaceae (Angiosperm Phylogeny Group 1998, 2003). *Leitneria floridana* is rare in nature, with a global conservation rank of G3 (vulnerable; either very rare and local throughout its range or found locally in a restricted range) and state ranks of S3 (very rare and local or found locally in a restricted range) in Arkansas and Florida, S2 (imperiled because of rarity) in Missouri, and S1 (critically imperiled because of extreme rarity) in Georgia and Texas (NatureServe 2007). Information concerning the ecology, ecophysiolo-

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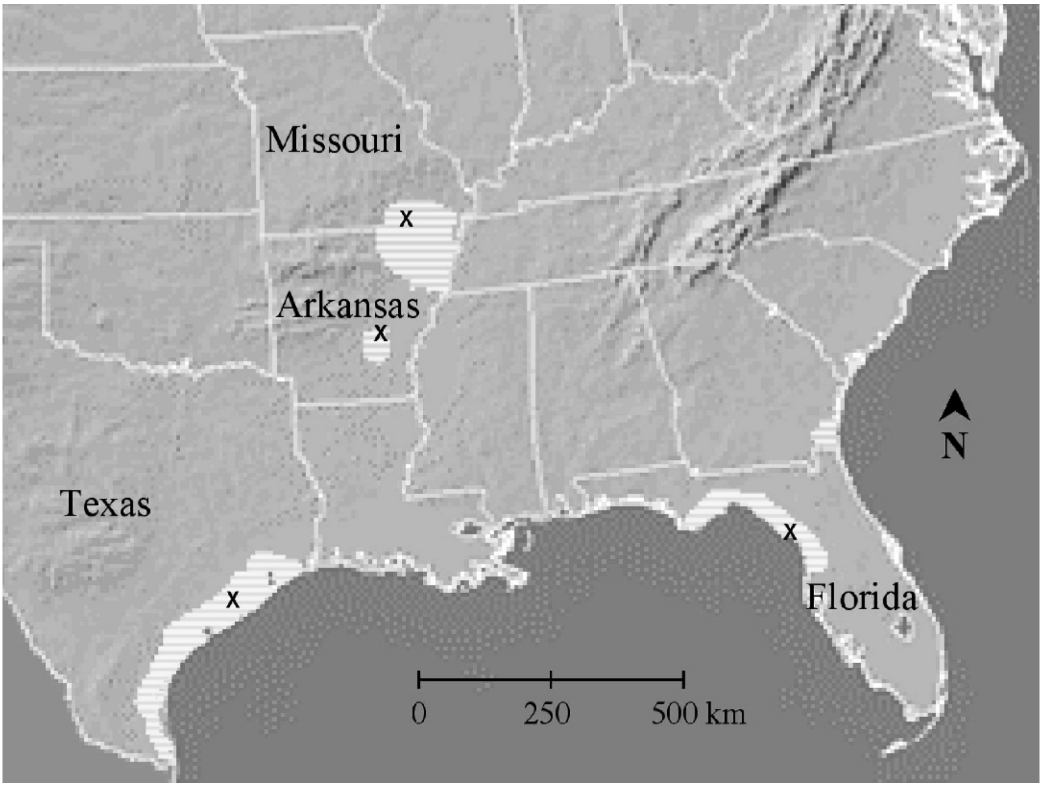

Figure 1. Disjunct distribution of *Leitneria floridana* ▤ and location of four indigenous populations assessed in this study (x): in Arkansas (Bayou Meto Wildlife Management Area, Arkansas County), Florida (Waccasassa Bay Preserve, Levy County), Missouri (Corkwood Natural Area, Butler County), and Texas (San Bernard National Wildlife Refuge, Brazoria County).

gy, and population biology of this species is needed to better understand its ecological status and to develop proper conservation strategies, but to date this information is lacking or has been based on limited observation.

We assessed *L. floridana* in its natural habitat in Missouri, Arkansas, Texas, and Florida (Figure 1) and tested the physical and chemical properties of the soil at the study sites. Our objectives were to: 1) describe and compare the morphology and ecophysiology of *L. floridana* from the four disjunct provenances; 2) characterize the habitat of *L. floridana* in the four provenances; and 3) compare the distribution density of plants in the four provenances and determine how photosynthetically active radiation (PAR) and soil moisture relate to plant distribution. Results from these assessments provide insights concerning the ecology and ecological history of *L. floridana* and help define strategies for its conservation.

MATERIALS AND METHODS In late June and early July of 2003 we assessed *Leitneria floridana* at sites representing four of its five disjunct populations (Figure 1). The four sampling sites/provenances were: Corkwood Natural Area, Butler County, Missouri (36°33.70N; 90°32.58W); Bayou Meto Wildlife Management Area, Arkansas County, Arkansas (34°17.17N; 91°37.83W); San Bernard National Wildlife Refuge, Brazoria County, Texas (29°08.21N; 95°47.66W); and Waccasassa Bay Preserve, Levy County, Florida (29°11.68N; 82°54.81W). At each site, three 50-m transects were established 30 m apart. Along each transect, six 4-m^2 sampling plots were established at 10-m intervals. Within each sampling plot we recorded: the number of *L. floridana* plants; morphology, growth, and photosynthesis measures of up to 10 randomly selected plants; soil moisture percentage; and occurrence of other woody taxa with trunk diameter at breast height (dbh) $>$ 5 cm (sight identification only). Measures at all sites were made within 14 d.

Morphological measurements included: plant height; trunk diameter at root collar; number of branches in the canopy of each plant (excluding the primary stem); number of leaves per branch; plant growth (length of the current season's growth on the primary stem); and length, width, and area of the youngest fully expanded leaf. A LI-COR 6400 Portable Photosynthesis System (LI-COR, Lincoln, Nebraska) was used to measure photosynthesis of the youngest fully expanded leaf at the top of the canopy of 180 plants per provenance. Ambient PAR for each measured leaf was recorded simultaneously with photosynthesis readings, and variation in PAR reflected the degree of shading by other plant taxa. Photosynthesis and PAR were measured between 1200 and 1330 HR under cloudless conditions for all plants in all provenances ($N = 180$). Immediately after taking the photosynthesis measurement for a plant, the measured leaf was collected from the plant, measured for length and width, pressed, and stored for area measurement, which was performed by using a Model 3100 leaf area meter (LI-COR, Lincoln, Nebraska). Volumetric soil moisture percentage in the upper 6 cm of soil was measured with a model HH1 Theta Probe (Delta-T Services, Cambridge, England) at the center of each 4-m^2 plot to help determine if the distribution of *L. floridana* is correlated with soil moisture.

These measurements were used to calculate the parameters of leaf length:width ratio, branches per meter of plant height, trunk shape (trunk diameter [cm] ÷ plant height [m]), leaf efficiency (photosynthesis ÷ PAR), peak photosynthesis (from regression of photosynthesis as a function of PAR), PAR at peak photosynthesis (according to regression analysis), percentage of plants per provenance that were growing in low PAR (plants growing in mid-day ambient PAR $< 290\ \mu mol \cdot m^{-2} \cdot s^{-1}$ [Givnish 1988]), mean PAR per plot, and percentage of full PAR (percentage of mean PAR compared to PAR under open sky). At each of the four sites, soil samples were collected from the first and sixth plots at each of the three 50-m transects; aggregate samples obtained by combining individual samples from the three first and the three last sampling plots were used for analyses. Samples were assessed for content of phosphorous (P), potassium (K), calcium (Ca), and magnesium (Mg) by using a Mehlich-3 extraction method (Mehlich 1984), and for ammonium (NH_4^+) and nitrate (NO_3^-) content by using a colorimetric method (Lachat Instruments, Milwaukee, Wisconsin). Soil texture and pH were assessed, and percentage organic matter was determined by using combustion analysis. Climate data (annual maximum and minimum temperatures, annual # days $> 32.2°C$, annual # days $< 0°C$, mean wind speed, percentage of possible sunshine, mean morning and afternoon RH percentages, and annual precipitation) were means from 1971 through 2000, and were obtained from the National Climatic Data Center (www.ncdc.noaa.gov/oa/ncdc.html) for monitoring stations closest to the assessment sites (Poplar Bluff, Missouri; Stuttgart, Arkansas; Bay City, Texas; and Cross City, Florida).

Morphological and physiological data were analyzed by using the general linear models (GLM) procedure and the least significant difference (LSD) option of SAS/STAT®, Version 8.2 (1999–2000). A correlation procedure (Pearson correlation) was used to examine the importance of soil moisture, PAR, and other environmental conditions as factors associated with plant growth and distribution. A neighbor-joining analysis was performed and a proportional dendrogram produced by using PHYLIP (Phylogeny Inference Package; Felsenstein 1995). Phenotypic distances for the neighbor-joining analysis were Euclidean distances (Sneath and Sokal 1973) based on 13 unweighted measures of morphology, physiology, and growth habit (plant height; trunk diameter; number of branches; number of leaves per branch; plant growth; thickness, length, width, and area of the youngest fully expanded leaf; trunk shape; branches per meter of plant height; leaf length:width ratio; leaf efficiency). Unweighted environmental (Euclidean), floristic (complement of the Sorenson index [1-Cs], Sorenson 1948), and geographic (km) distances among the provenances were calculated, and the four distance measures (including phenotypic) were compared by using the Mantel test (Mantel 1967).

RESULTS Morphology and growth habit of *Leitneria floridana* varied among the four sampled populations. Plants in Missouri were taller than those in the other three provenances and had a greater trunk diameter and stouter trunk shape than plants in Texas and

Table 1. Morphology and growth habit of *Leitneria floridana* sampled at disjunct sites in Missouri, Texas, Arkansas, and Florida

	Provenance				
Measure	Missouri	Arkansas	Texas	Florida	Species mean
Plant height (m)	1.46 a[1]	1.04 b	1.24 b	1.19 b	1.23
Trunk diameter[2] (cm)	1.60 a	0.90 b	0.89 b	1.45 a	1.23
Trunk shape[3] ($cm \cdot m^{-1}$)	1.11 a	0.90 b	0.72 c	1.19 a	0.99
Branch count	2.9 a	1.8 b	1.9 b	1.5 b	2.0
Branches per meter of plant height	1.9 a	1.7 a	1.5 b	1.4 b	1.6
Leaf area[4] (cm^2)	21.4 c	33.1 b	20.0 c	37.9 a	28.6
Leaf length (cm)	10.1 b	13.3 a	10.0 b	14.1 a	12.0
Leaf width (cm)	3.2 c	3.5 b	2.9 c	4.0 a	3.4
Leaf length:width ratio	3.21 c	3.86 a	3.61 b	3.64 ab	3.58
Leaves per branch	10.5 b	11.8 b	14.4 a	11.1 b	11.9
Distribution density ($plants \cdot m^{-2}$)	5.3 a	7.5 a	8.8 a	4.7 a	5.9

[1] Means in a row followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's least significant difference test.
[2] Diameter of trunk at base.
[3] Trunk diameter ÷ plant height.
[4] Blade area of first fully expanded leaf at the top of the canopy.

Arkansas (Table 1). Plants in Missouri also had more branches than plants in the other three provenances and had more branches per meter of plant height than plants in Texas and Florida. Plants in Florida were stout (large trunk diameter and trunk shape) with sparse lateral growth (branch count and branches per meter of plant height below the species mean) (Table 1), while plants in Texas were slender and wispy (small trunk diameter and shape, and low number of branches per meter). Plants in Arkansas were short (shoot height below the species mean), but showed greater lateral branching (branches per meter of plant height) than plants in Texas and Florida (Table 1). Plants in Arkansas and Florida had larger leaves (leaf area, length, and width) than those of the other two provenances, and plants in Arkansas had leaves that were more elongated (larger length-to-width ratio) than the mean. Leaves of plants in Missouri and Texas were comparatively small (leaf area, length, and width), and leaves of plants in Missouri were more elliptic (lower length to width ratio) than those of the other three provenances. Plants in Texas had the most leaves per branch, and plants in Missouri had fewer than the mean number of leaves per branch for the species.

The growth and photosynthetic physiology of *L. floridana* also varied among the four provenances. Plants in Texas showed the greatest growth in 2003 (Table 2). Plants in Missouri had the least current-season growth, the lowest peak photosynthesis, and showed below-average leaf efficiency. Although plants in Arkansas showed below-average current-season growth, they had the greatest leaf efficiency and the greatest peak photosynthesis, which was achieved at the lowest PAR among provenances (Table 2). There were no differences in the distribution density of *L. floridana* among the four provenances (Table 1), but provenance differences were found in the percentage of plants growing in low PAR (greatest percentage in Arkansas and lowest percentage in Missouri), the mean PAR (greatest in Missouri and below average in Arkansas), and percentage of full PAR (greatest in Missouri and lowest in Arkansas) (Table 2). There was no correlation between PAR and distribution density ($r = 0.13$, $P = 0.48$) nor between PAR and plant growth ($r = -0.01$, $P = 0.82$) when assessed across the four provenances. Therefore, there is no evidence that distribution and growth of *L. floridana* are affected by PAR within the range of PAR under which the species occurs.

Environmental characteristics of the four provenances varied widely. Soil texture ranged from clay loam in Arkansas to fine sandy loam in Missouri, and soil pH across provenances ranged from 4.6 in Arkansas to 6.4 in Florida (Table 3). Soil organic matter ranged from 5.3% (Missouri) to 34% (Florida), and while the soil was relatively dry at the Missouri and Texas sites (soil moisture

Table 2. Growth and photosynthetic physiology of *Leitneria floridana* sampled at disjunct sites in Missouri, Texas, Arkansas, and Florida

	Provenance				Species
Measure	Missouri	Arkansas	Texas	Florida	mean
Plant growth in 2003[1] (cm)	7.1 d[2]	10.3 c	20.4 a	16.5 b	13.6
Leaf efficiency[3]	0.011 b	0.019 a	0.013 b	0.014 b	0.014
Peak photosynthesis[4] (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	7.75	13.93	12.75	10.47	
PAR at peak photosynthesis[5] ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1,402	1,198	1,500	1,458	
Percentage growing in low PAR[6] (%)	41.3 c	86.7 a	67.8 b	69.3 b	66.3
Mean PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	718 a	197 b	330 b	318 b	391
Percentage of full PAR (%)	42.3 a	11.2 c	23.2 b	20.0 b	24.2

[1] Vertical growth of primary shoot during 2003 growing season.

[2] Means in a row followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's least significant difference test.

[3] Photosynthesis ÷ PAR (photosynthetically active radiation).

[4] Maximum photosynthesis calculated from regression analysis of photosynthesis as a function of PAR.

[5] PAR level at peak photosynthesis according to regression analysis.

[6] Percentage of plants growing in intermediate to low PAR levels ($<$290 $\mu mol \cdot m^{-2} \cdot s^{-1}$; Givnish 1988) measured between 1200 and 1330 HR under cloudless conditions.

$<$ 20%), soil at the Florida provenance was saturated (Table 3) and the root zones of all *L. floridana* there were submersed in standing water. Soil at the Missouri site had the lowest concentrations of K, Ca, Mg, and NH_4^+, while the soil in Florida had the highest concentration of Ca, Mg, NH_4^+, and NO_3^-, and therefore the highest concentration of available N (Table 3). The P concentration was lowest in soil at the site in Texas, but K concentration was highest there. The soil in Arkansas had the lowest concentration of NO_3^-, but NH_4^+ concentration was relatively high. Correlation analysis indicated that distribution density increased with soil moisture (r = 0.39, P = 0.03), but there was no

Table 3. Environmental characteristics at sampling sites for *Leitneria floridana* in Missouri, Texas, Arkansas, and Florida

	Provenance			
Environmental parameter	Missouri	Arkansas	Texas	Florida
Soil[1]				
Texture	fine sandy loam	clay loam	silty clay loam	loam
pH	5.4	4.6	5.1	6.4
Organic matter (%)	5.3	8.5	12.5	34.0
Moisture[2] (% vol)	19.5	-	15.3	100.0
P (ppm)	14	20	8	11
K (ppm)	7	19	55	35
Ca (ppm)	680	1,257	5,187	5,508
Mg (ppm)	130	620	754	1,701
NH_4^+ (ppm)	9	21	16	76
NO_3^- (ppm)	7	1	12	15
Climate				
Mean annual Max. Temp. (°C)	19.7	22.5	24.8	26.6
Mean annual Min. Temp. (°C)	7.2	11.7	18.7	14.0
Annual # days > 32.2°C	41	72	100	80
Annual # days < 0°C	95	56	3	15
Mean wind speed (km/hr)	16.7	12.7	17.7	10.3
Sunshine (% of possible)	60	62	62	63
Mean RH morning (%)	82	82	83	91
Mean RH afternoon (%)	64	62	72	57
Annual precipitation (cm)	114	129	111	123

[1] N = 3 for Missouri values; N = 2 for Texas, Arkansas, and Florida.

[2] N = 63 for Missouri, N = 59 for Texas, and N = 75 for Florida. Result for Arkansas was omitted due to equipment malfunction.

Table 4. Presence (X) of woody species growing in association with *Leitneria floridana* at sampling sites in Missouri, Texas, Arkansas, and Florida

	Provenance			
Species	**Missouri**	**Arkansas**	**Texas**	**Florida**
Acer rubrum L.	X	X		
Amorpha fruticosa L.		X		
Berchemia scandens (Hill) K.Koch		X		
Brunnichia ovata (Walter) Shinners		X		
Campsis radicans (L.) Seem.	X	X		
Carya illinoinensis (Wangenh.) K.Koch		X	X	
Cephalanthus occidentalis L.	X	X	X	
Cornus foemina Mill.		X		
Diospyros virginiana L.	X	X		X
Forestiera acuminata (Michx.) Poir.		X		
Fraxinus pennsylvanica Marshall	X	X	X	X
Gleditsia triacanthos L.	X			
Ilex decidua Walter		X		
Juniperus virginiana L.				X
Myrica cerifera L.				X
Quercus hemisphaerica Bartram ex Willd.				X
Quercus lyrata Walter		X		
Quercus phellos L.	X	X		
Quercus rubra L.	X			
Quercus texana Buckley		X		
Quercus virginiana Mill.				X
Sabal palmetto (Walter) Lodd. ex Schult.				X
Sesbania drummondii (Rydb.) Cory			X	
Smilax L. sp.	X			
Sparganium americanum Nutt.			X	
Styrax americanus Lam.		X		
Toxicodendron radicans (L.) Kuntze		X		
Ulmus alata Michx.				X
Ulmus americana L.		X		
Ulmus americana L. var. *floridana* (Chapm.) Little				X
Ulmus crassifolia Nutt.		X		X
Ulmus rubra Muhl.	X			
Vitis palmata Vahl		X		
Wisteria frutescens (L.) Poir.		X		
Total: 34	10	21	5	10

correlation between soil moisture and plant growth ($r = 0.02$, $P = 0.83$). The correlation between distribution density and soil moisture was especially evident in dry soils ($\leq$10% soil moisture by volume) because only 1.2% of plants in the survey were found in soils with moisture contents $\leq$ 10% (data not shown).

Climatic characteristics of the four provenances also varied. The mean annual maximum and minimum temperatures ranged from 19.7 and 7.2°C, respectively, in Missouri to 26.6 and 14.0°C, respectively, in Florida (Table 3). The Texas provenance had the most days with temperatures above 32.2°C and the fewest days below 0°C, while the Missouri provenance had the fewest and most, respectively. Average wind speed was greater in Texas and Missouri than in the other two provenances, and the percentage of possible sunshine was similar among the four provenances. Morning mean RH ranged from 82 to 91% and was highest in Florida, while afternoon mean RH was highest in Texas. Annual precipitation was greatest in Arkansas and was $>$ 100 cm for all four provenances (Table 3).

The floristic character of the provenances was diverse. *Fraxinus pennsylvanica* Marshall was the only woody species present at all four provenances, and *Cephalanthus occidentalis* L. was the only other species present at more than two of the provenances (Table 4). The Arkansas provenance showed the greatest diversity of woody species (21 total), and the Texas provenance showed the least. Across the four provenances, *Quercus* L. and *Ulmus* L. were well represented and were the only genera with multiple species present within the four study sites (Table 4).

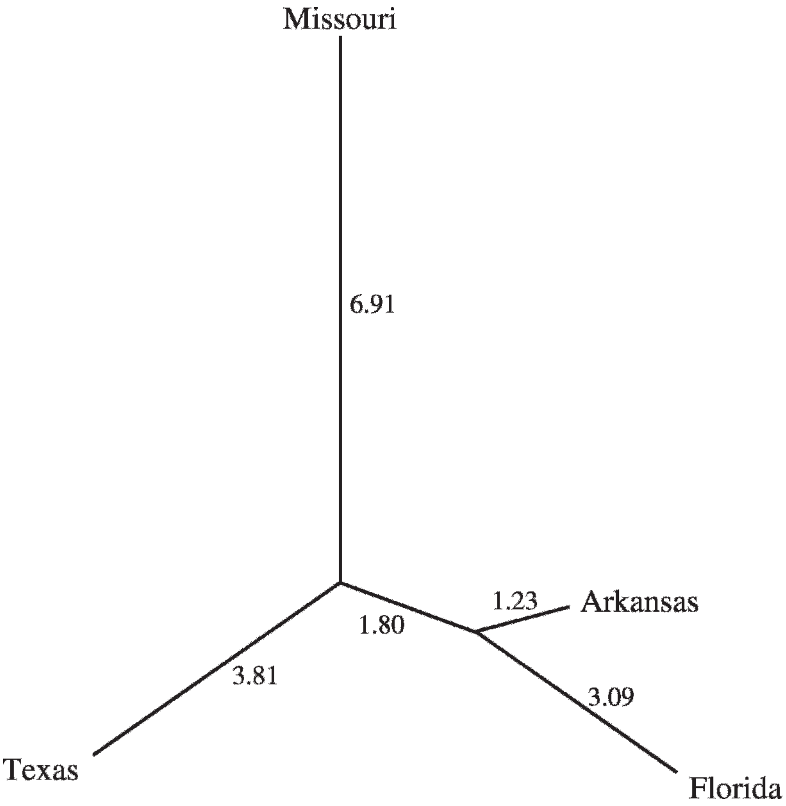

Figure 2. Neighbor-joining dendrogram illustrating the phenotypic relationship among four provenances of *Leitneria floridana* based on 13 unweighted measures of morphology, physiology, and growth habit. The phenotypic distances are Euclidean distances (Sneath and Sokal 1973).

Analysis of phenotypic distances and neighbor-joining analysis of the four provenances of *L. floridana* indicated that plants of the Missouri provenance were the most unique (Figure 2). Although the geographic distance between Missouri and Arkansas was the least of the four provenances (Figure 1, Table 5), the phenotypic distance between plants of the two provenances was large, and plants in Arkansas were more similar to those in Texas and Florida than they were to those in Missouri (Figure 2, Table 5). Plants of the Florida and Missouri provenances were the most phenotypically divergent, and plants of the Florida and Arkansas provenances were the most phenotypically similar (Figure 2).

While the phenotypic distance between *L. floridana* in Missouri and Arkansas was relatively large, the environmental and floristic distances between the two provenances were more consistent with the geographic distance (Table 5). Missouri and Arkansas were the most similar among the four provenances in both environmental and floristic character, but the environmental distances between Missouri and each of the other two provenances were large. Although the Arkansas provenance showed the greatest floristic diversity (Table 4), the floristics of the Florida provenance were the most unique, showing the greatest distances from the other three provenances (Table 5). Mantel correlation analyses showed no correlation between phenotypic distance and the other three distance measures (environmental, floristic, or geographic) and no correlation between environmental and floristic distances (Table 5). However, environmental and geographic distances were positively correlated, and there was a strong positive correlation between the geographic and floristic distances of the four provenances.

DISCUSSION Although phenotypic differences among populations of the same species can often be attributed to ontogenetic or environmental factors, they may also repre-

Table 5. Phenotypic, environmental, floristic and geographic distances among the four provenances of *Leitneria floridana*. The upper portion of the table lists the calculated distances among the provenances; the lower portion summarizes the correlation relationships among the distance parameters

	Distance			
Provenance comparison	**Phenotypic**[1]	**Environmental**[1]	**Floristic**[2]	**Geographic (km)**
Missouri - Arkansas	10.47	1.48	0.576	271
Missouri - Texas	10.72	5.28	0.647	958
Missouri - Florida	11.27	5.29	0.727	1083
Arkansas - Texas	6.31	2.91	0.714	693
Arkansas - Florida	4.32	3.76	0.758	999
Texas - Florida	9.23	2.46	0.765	1251

Distance comparison	**Mantel correlation (R_{xy})**	**$P > R$**
Phenotypic vs -		
Environmental	−0.20	0.44[3]
Floristic	−0.50	0.21
Geographic	−0.06	0.52
Environmental vs -		
Floristic	0.26	0.35
Geographic	0.55	0.04
Floristic vs -		
Geographic	0.83	0.04

[1] Phenotypic and environmental distances are Euclidean distances.

[2] Floristic distance is the complement of the Sorenson similarity index (1-Cs).

[3] P-values based on 999 random permutations.

sent true genotypic variation (Clausen et al. 1940, Turesson 1922, Wright and McConnaughay 2002). Our assessment of phenotypic differences among the four disjunct provenances of *Leitneria floridana* suggests that genetic divergence may have taken place since their isolation. In light of our results from this study, some of the differences in morphology and growth of *L. floridana* may be attributed to plant size or ontogeny. Plants in Missouri were the largest (Table 1) and likely the most developmentally advanced, a factor that may have contributed to the lower growth of plants in Missouri (Table 2). Other differences cannot be explained by plant size or ontogeny. While plants in Florida were not as tall as those in Missouri and had fewer branches per meter of plant height, they had similar trunk diameter and shape, suggesting genetic divergence in plant growth habit. Likewise, environmental variation across the four provenances may explain some of the phenotypic differences we observed. Adaptation of plants in Arkansas to low mean PAR is likely a factor contributing to their greater leaf efficiency and peak photosynthesis compared to plants in Missouri (Table 2), but morphological and growth differences between plants in Arkansas and Texas suggest different genetically determined responses to shade stress. Mean PAR was low for both the Arkansas and Texas provenances (Table 2), but plant character differed between the two populations. Plants in Texas exhibited typical shade-avoidance responses (rapid vertical growth, low leaf efficiency, thin and wispy trunks with few branches, and sun and shade leaves that were similar; Ballaré et al. 1997, Henry and Aarssen 2001, Schmitt 1997), but plants in Arkansas demonstrated tolerance to shade (slow growth, high leaf efficiency, high percentage growing in shade, high number of branches, and shade leaves that were larger than sun leaves; Givnish 1988, Henry and Aarssen 2001, Veneklaas and Poorter 1998). A thorough cladistic analysis with molecular markers should be performed to assess the genetic relationships among the populations of *L. floridana*.

The pattern of phenotypic divergence among the four provenances of *L. floridana* (Figure 2) is difficult to explain. While the lack of correlation between phenotypic distance and the other distance measures (environmental, floristic, and geographic; Table 5) seems to support the likelihood that genetic divergence has taken place, the lack of correlation also suggests that it may be difficult to determine genecological factors (Donselman and Flint 1982) that have contributed to this divergence. If the phenotypic character of the four provenances reflects their genotypic character, common theory would suggest that the Missouri population was the first of the four to become reproductively isolated even though environmentally, floristically, and geographically the populations in Missouri and Arkansas are the closest of the four. Palynological evidence indicates that *L. floridana* was once more widespread and that the present disjunct distribution likely resulted from reduction and fragmentation of a large, ubiquitous distribution (Delcourt and Delcourt 1996, Jarvis 1989, Trelease 1895, Williams et al. 1999). Our data suggest that the divergent phenotypic character of the Missouri population may be the result of a founder effect (migration, long-distance dispersal, or isolation of a limited number of founder genotypes; Barton and Charlesworth 1984, Giddings et al. 1989), a genetic bottleneck (reduction in the effective size of a population, followed by recovery with a limited genepool; Nei et al. 1975), or perhaps it was the result of the differentiation that can take place when asexual reproduction is the primary mechanism for range expansion into areas that are marginal for a species (Haag and Ebert 2004, Vrijenhoek and Pfeiler 1997). Although *L. floridana* can reproduce by seed, germination percentages can be very low (Sharma and Graves 2004a), and its propensity for rhizomatous reproduction (Bogle 1997) could result in populations with little or no gene flow and limited genetic diversity. A study of the molecular-genetic character of the disjunct populations should help clarify the phylogenetic history of extant *L. floridana* and help determine if genetic diversity is lacking within populations.

The phytogeography of *L. floridana* is unusual in two ways: it is an archaic species endemic to the Southeastern Coastal Plain (Martin et al. 1993, Sorrie and Weakley 2001), and it is rare with a widely disjunct distribution (Bogle 1997). As illustrated by Sorrie and Weakley (2001), the existence of relict species endemic to a geologically young terrain is an enigma that begs explanation. The most widely accepted paleofloristic account emphasizes invasion and widespread speciation following Tertiary recession of seawaters that covered the entire Southeastern Coastal Plain during the late Cretaceous (≈65 million yr before present [MYBP], Graham 1993). It is plausible that *L. floridana* was among the first taxa to colonize the Southeastern Coastal Plain; a notion supported by the presence of fossil *Leitneria* in the Eocene (55 - 34 MYBP) flora of northern Mississippi, southwestern Kentucky, and northwestern Tennessee (Brown 1960). Its early presence on the northern margin of the Coastal Plain and the fact that *L. floridana* is deciduous and cold hardy well beyond its range (Sharma and Graves 2004b) suggest that it invaded the Coastal Plain from a northern temperate region. While we have found phenotypic differences among the disjunct populations of *L. floridana*, its isolated taxonomic position (as the only extant member of a monotypic genus and, perhaps, family) indicates that it colonized the Coastal Plain while undergoing little evolutionary change. The hydrophilic character of the species and its tolerance of diverse edaphic conditions (Table 3) and moderate salinity (Duncan 1974) would have made it quite competitive from the Eocene through the Pleistocene (1.8 MYBP to 10,000 YBP) as sea levels receded and the coastal plains were disturbed by repeated inundations (Thorne 1993).

The cause of the rarity and disjunct distribution of *L. floridana* is less clear. If, as palynological evidence suggests (Delcourt and Delcourt 1996, Jarvis 1989, Williams et al. 1999), *L. floridana* was once ubiquitous on the Coastal Plain, what factors were responsible for its dramatic decline? Its tolerance of diverse edaphic, solar, and climatic conditions (Tables 2 and 3) indicates that *L. floridana* has a broad fundamental niche, and the diverse, impinging character of the sympatric flora of the Arkansas provenance (Table 4) suggests that interspecies competition does not restrict the species. Our results suggest that drought intolerance may be an important factor in the decline of *L. floridana*. The positive correlation between soil moisture and distribution density ($r = 0.39$, $P = 0.03$) and the very low percentage of plants in the survey found growing in soils with low moisture content (only 1.2% growing in soils with $\leq$ 10% moisture) indicate that *L. floridana* is not highly tolerant of dry soils, at least during some part of its life cycle. Even though areas of apparently suitable habitat are present across the Coastal Plain, occasional drought and drying of such sites, a common occurrence since the close of the

Pleistocene Epoch (≈10,000 YBP; Delcourt and Delcourt 1993), likely contributed to the early decline of the species. More recently, alteration of hydrology (ditching and draining of wetlands) for agriculture, forestry, and development has increased habitat fragmentation, further restricting the distribution of *L. floridana*. This anthropogenic impact on the habitat of *L. floridana* was observed in Missouri as early as 1895 (Trelease 1895).

Another factor that may be limiting the success of *L. floridana* is insufficient long-distance seed dispersal (Bohrer et al. 2005, Trakhtenbrot et al. 2005). Because the fruits of *L. floridana* float, long distance dispersal may have been mainly by water historically. If this is true, the discontinuous hydrology that has resulted from agriculture and rural development may be severely limiting the genetic diversity of extant colonies of *L. floridana* (Harrison and Bruna 1999, Trakhtenbrot et al. 2005) and may have eliminated opportunities for range expansion or colonization of suitable sites (Harrison and Bruna 1999). A formal investigation of the seed dispersal and seedling establishment of *L. floridana* would be valuable for determining the overall impact of fragmentation on this species.

A consequence of limited biological surveys is that many natural areas are currently under-surveyed. It is likely that populations of *L. floridana* exist but have not been documented in the recent past. During the course of this research, a new colony was discovered in Arkansas (sub-element occurrence for the Element Occurrence Record #PDLEI01010.025 [Arkansas Natural Heritage Commission]; Voucher Specimens - *Theo Witsell & Jyotsna Sharma #03-602* and *#03-603*) within the Bayou Meto WMA metapopulation of *L. floridana*. The possibility exists that known metapopulations are larger than previously expected, and additional searches could lead to the discovery of additional plants. Because it is localized to wetland habitats, the natural populations of *L. floridana* remain vulnerable to activities that alter local hydrology. With its broad fundamental niche, adequate soil moisture and local hydrology may be the most important barriers to long-term conservation of *L. floridana*. Restoration efforts should focus on wet sites where the likelihood of extended periods of drought is low. Managed plantings of appropriate plant communities, including *L. floridana*, on wet sites and management of site hydrology should aid its recovery.

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LITERATURE CITED

Angiosperm Phylogeny Group. 1998. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85:531–553.

Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders of flowering plants: APG II. Bot. J. Linn. Soc. 141:399–436.

Ballaré, C.L., A.L. Scopel, and R.A. Sánchez. 1997. Foraging for light: photosensory ecology and agricultural implications. Pl. Cell Environ. 20:820–825.

Barton, N.H. and B. Charlesworth. 1984. Genetic revolutions, founder effects, and speciation. Annual Rev. Ecol. Syst. 15:133–164.

Bogle, A.L. 1997. Leitneriaceae. Volume 3. *In:* Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. Oxford University Press, New York, New York.

Bohrer, G., R. Nathan, and S. Volis. 2005. Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. J. Ecol. 93:1029–1040.

Brown, R.W. 1960. Corkwood in the Eocene flora of the southeastern United States. J. Paleontol. 34:429–432.

Clausen, J., D.D. Keck, and W.M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institute Publication 520. Washington D.C.

Delcourt, P.A. and H.R. Delcourt. 1993. Paleoclimates, paleovegetation, and paleofloras of North America north of Mexico during the late Quaternary. Volume 1. p. 71–94. *In:* Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. Oxford University Press, New York, New York.

Delcourt, P.A. and H.R. Delcourt. 1996. Quaternary paleoecology of the Lower Mississippi Valley. Engineering Geol. 45:219–242.

Donselman, H.M. and H.L. Flint. 1982. Genecology of eastern redbud (*Cercis canadensis*). Ecology 63:962–971.

Duncan, W.H. 1974. Vascular halophytes of the Atlantic and Gulf Coasts of North America North of Mexico. p. 23–50. *In:* Reimold, R.J. and W.H. Queen (eds.). Ecology of Halophytes. Academic Press, New York, New York.

Felsenstein, J. 1995. PHYLIP (Phylogeny Inference Package) Version 3.57c. Distributed by the author. Department of Genetics, University of Washington, Seattle, Washington.

Giddings, L.V., K.Y. Kaneshiro, and W.W. Anderson (eds.). 1989. Genetics, speciation, and the founder principle. Oxford University Press, New York, New York.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. Austral. J. Pl. Physiol. 15:63–92.

Graham, A. 1993. History of the vegetation: Cretaceous (Maastrichtian) - Tertiary. Volume 1. p. 57–70. *In:* Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. Oxford University Press, New York, New York.

Haag, C.R. and D. Ebert. 2004. A new hypothesis to explain geographic parthenogenesis. Ann. Zool. Fenn. 41:539–544.

Harrison, S. and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225–232.

Henry, H. and L. Aarssen. 2001. Inter- and intraspecific relationships between shade tolerance and shade avoidance in temperate species. Oikos 93:477–487.

Jarvis, C.E. 1989. A review of the order Leitneriales Engler. p. 189–192. *In:* Crane, P.R. and S. Blackmore (eds.). Evolution, systematics, and fossil history of Hamamelidae. Volume 2. Oxford University Press, New York, New York.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

Martin, W.H., S.G. Boyce, and A.C. Echternact (eds.). 1993. Biodiversity of the Southeastern United States: lowland terrestrial communities. John Wiley and Sons, New York, New York.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Comm. Soil Sci. Pl. Anal. 15:1409–1416.

NatureServe. 2007. NatureServe Explorer: an online encyclopedia of life [web application]. Version 6.2. (http://www.natureserve.org/explorer, 19 December 2007). NatureServe, Arlington, Virginia.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

Petersen, F.P. and D.E. Fairbrothers. 1983. A serotaxonomic appraisal of *Amphipterygium* and *Leitneria*: two amentiferous taxa of Rutiflorae (Rosidae). Syst. Bot. 8:134–148.

Platt, W.J. and M.W. Schwartz. 1990. Temperate hardwood forests. p. 194–229. *In:* Myers, R.L. and J.J. Ewel (eds.). Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

Qiu, Y.L., M.W. Chase, S.B. Hoot, E. Conti, P.R. Crane, K.J. Sytsma, and C.R. Parks. 1998. Phylogenetics of the Hamamelidae and their allies: parsimony analyses of nucleotide sequences of the plastid gene *rbcL*. Intl. J. Pl. Sci. 159:891–905.

SAS/STAT® Software. Version 8.2 of the SAS System for Windows. Copyright© 1999–2000. SAS Inst Inc, Cary, North Carolina.

Schmitt, J. 1997. Is photomorphogenic shade avoidance adaptive? Perspectives from population biology. Pl. Cell Environ. 20:826–830.

Sharma, J. and W.R. Graves. 2004a. Germination of *Leitneria floridana* seeds from disjunct populations. HortScience 39:1695–1699.

Sharma, J. and W.R. Graves. 2004b. Midwinter cold tolerance of *Leitneria floridana* (Leitneriaceae) from three provenances. J. Environ. Hort. 22:88–92.

Sneath, P.H. and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Company, San Francisco, California.

Sorenson, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based similarity of species content. Biol. Skr. K. Dan Vidensk. Selsk. 5:1–34.

Sorrie, B.A. and A.S. Weakley. 2001. Coastal plain vascular plant endemics: phytogeographic patterns. Castanea 66:50–82.

Thorne, R.F. 1993. Phytogeography. Volume 1. p. 132–153. *In:* Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. Oxford University Press, New York, New York.

Trakhtenbrot, A., R. Nathan, G. Perry, and D.M. Richardson. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity Distrib. 11:173–181.

Trelease, W. 1895. *Leitneria floridana*. Rep. (Annual) Missouri Bot. Gard. 6:65–90.

Turesson, G. 1922. The genotypic response of the plant species to the habitat. Hereditas (Lund) 3:211–350.

Veneklaas, E.J. and L. Poorter. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. p. 337–362. *In:* Lambers, H., H. Poorter, and M. Van Vuuren (eds.). Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, Netherlands.

Vrijenhoek, R.C. and E. Pfeiler. 1997. Differential survival of sexual and asexual *Poeciliopsis* during environmental stress. Evolution 51:1593–1600.

Williams, K., Z.S. Pinzon, R.P. Stumpf, and E.A. Raabe. 1999. Sea-level rise and coastal forests on the Gulf of Mexico. U.S. Geological Survey Open Report 99-441.

Wright, S.D. and K.D.M. McConnaughay. 2002. Interpreting phenotypic plasticity: the importance of ontogeny. Pl. Spec. Biol. 17:119–131.