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Cold Hardiness of the Rare *Dirca occidentalis*: Comparisons to *Dirca palustris* from Disparate Provenances[1]

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Abstract

We determined the cold hardiness of *Dirca occidentalis* (western leatherwood) within its restricted natural distribution in northern California and made comparisons to *Dirca palustris* (eastern leatherwood) from northern (Iowa) and southern (Florida) provenances. Stems of western leatherwood were sampled twice while all or some plants were dormant (October 27 and December 8, 2004, respectively) and again on January 19, 2005, when flowering and incipient vegetative shoot growth of most plants had begun. Stems of *D. palustris* were sampled on the same schedule and on March 2, 2005 (Iowa and Florida) and April 13, 2005 (Iowa) such that the last sampling date coincided with flowering and incipient vegetative shoot growth. Lowest survival temperature was determined based on visual assessments of the viability of cambium and phloem of stems exposed to progressively lower temperatures in a freezer. Lowest survival temperature of western leatherwood was –6 to –3C (21 to 27F) regardless of date. Eastern leatherwood accrued hardiness through mid-winter and then deacclimated; minimal lowest survival temperature of eastern leatherwood was –33C (–27F) in Iowa and –17C (1F) in Florida. The minimal cold hardiness of western leatherwood is consistent with its natural distribution in specialized niches within a Mediterranean climate. Unless western leatherwood accrues increased hardiness when planted where winters are harsh, its horticultural use will be restricted to areas with mild winters. In contrast, widespread use of eastern leatherwood is feasible if production challenges are resolved and selections from climatically appropriate provenances are used.

Index words: Thymelaeaceae, leatherwood, native plants.

Significance to the Nursery Industry

Shrubs in the genus *Dirca* (leatherwoods) develop distinctive habits, reliably form unique flowers during winter and very early spring, display uniformly yellow foliage during autumn, and thrive in shade. These traits invite interest in using the three species of leatherwood (*Dirca* spp.) in managed landscapes, but culturing leatherwoods is challenging, and their resistance to potential environmental stressors, including temperature, is not known. Especially lacking are data on the rare western leatherwood, which is endemic to small, specialized niches within six counties near the San Francisco Bay. Our results show that, unlike some woody plants that accumulate more cold hardiness than required by the local climate where they are native, western leatherwood accrues only slightly more cold hardiness than necessary to persist in its Mediterranean niche. If challenges related to the propagation and culture of western leatherwood were overcome, our data suggest that planting would need to be restricted to areas where annual minima rarely are below –5C (23F). Our results also provide new information on eastern leatherwood. Differences in cold hardiness between indigenous plants in a northern and southern provenance were demonstrated, suggesting that selection of genotypes from specific native origins will be critical for more widespread horticultural use of the species.

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Introduction

While all three species of deciduous shrubs in the genus *Dirca* L. are North American, only two are native to the United States (3, 10). *Dirca palustris* L. (eastern leatherwood) occurs within an extensive portion of the eastern United States and in southeastern Canada (14). While its distribution is broad, shrubs of eastern leatherwood typically are uncommon locally but may be found cloistered within understory niches on moist soils along wooded slopes (7). *Dirca occidentalis* Gray (western leatherwood) also occurs on slopes (9), but its distribution is extremely restricted. Occurrence of western leatherwood has been documented exclusively in the Mediterranean climate near the San Francisco Bay, often in foggy niches (6) where taller neighboring plants or more distant landforms provide shade (4). Its status as the sole member of the Thymelaeaceae plant family native to California undoubtedly would be enough to attract attention from botanists; but the species has additional enthusiasts, including local nursery personnel and gardeners who favor native species and value western leatherwood for its dainty yellow flowers that are among the first signs of rejuvenation after the summer dry season is broken by autumnal rains. We have documented flowers opening as early as mid-November, but anthesis is in late December, January, or February for most plants of western leatherwood (4). Eastern leatherwood also blooms early. While flowers appear in February in the southern-most portion of the natural distribution in the central panhandle of Florida, herbarium specimens at Lakehead University in Thunder Bay, ON, show that plants within the northern-most populations of the species in Ontario bloom in late May.

Morphological traits of *Dirca* spp. have been compared (10, 14), and protocols to induce seed germination have been defined (12), but no comparisons of physiology among species have been reported. Resistance to low temperature is a primary determinant of where a perennial species can be grown. Some plants accrue only slightly more hardiness than

needed to persist where they are native, while others become much hardier than necessary (11). Therefore, the restricted distribution of western leatherwood in a small region where temperatures rarely are below –5C (23F) is not convincing evidence that the shrubs could not withstand colder winters. Populations of eastern leatherwood in the northern United States and eastern Canada resist harsh temperatures during winter, but the extent of hardiness they accrue has not been determined. Low-temperature resistance of eastern leatherwood in the southern U.S. is unknown and would be relevant if germplasm for production of the species in nurseries is obtained from southern populations.

Our main objective was to determine the lowest temperature that stems of western leatherwood collected from plants in their natural habitat in California could survive on three dates during late 2004 and early 2005. A secondary objective was to quantify stem hardiness of indigenous eastern leatherwood from two provenances. The eastern species allowed us to confirm the validity of our methods with tissue we hypothesized would be more hardy than our samples of western leatherwood. We sampled eastern leatherwood indigenous to Iowa and Florida to compare widely separated populations in different climates. For both species, stem tissue formed in 2004 was sampled because flowering, an important ornamental feature of the species, occurs on wood formed during the previous growth season.

Materials and Methods

We collected stem samples from indigenous plants of western leatherwood at Stanford University's Jasper Ridge Biological Preserve in Woodside, CA. Three different plants were chosen on each of three dates. The dates were six weeks apart and were selected to represent the early dormant period several weeks before bud break and flowering, the late dormant period at or shortly before the time when flowers begin to open, and the period when most plants in the population sampled were at anthesis. Plants of western leatherwood vary in the timing of flowering and resumption of vegetative growth. We selected plants to represent the range of developmental stages we observed in this population on the three dates. Plants sampled on October 27, 2004, had lost all or most of their leaves due to the recent onset of cold-season dormancy, or earlier due to the drought-induced summer dormancy that affects western leatherwood in relatively exposed, dry sites (1). Only one of the three plants had leaves; they were few and had yellowed and appeared nearly ready to abscise. The three plants sampled on December 8, 2004, had defoliated completely, and flowers had begun to open on one plant. On January 19, 2005, one of the three plants had recently passed anthesis and vegetative shoot growth had begun, the second plant was near anthesis and had not initiated vegetative shoot growth, and the third showed bud swelling but had not begun to flower. The individuals selected on each date were at disparate locations within the preserve [total land area = 481 hectares (1,189-acres)] to ensure the plants were not clones of one another (4, 9). Sampling consisted of removing terminal stem sections that were 20 to 36 cm (8 to 14 in) long. These were wrapped in damp paper, enclosed in plastic, and transported overnight with ice in an insulated box to Iowa State University, Ames.

The same procedures were followed for eastern leatherwood. Plants in Boone Co., IA, and Liberty Co., FL, were sampled. Autumnal defoliation was complete among plants in Iowa on October 27, 2004, but had not begun among plants in Florida. Plants in both provenances had defoliated and there was no evidence of flowering when samples were obtained on December 8, 2004, and January 19, 2005. All plants at the site in Florida were blooming six weeks later on March 2, 2005, which therefore was designated the final sampling date for that provenance. No plants at the site in Iowa were blooming on March 2, 2005, but all plants were at or slightly past anthesis when the last set of samples was collected six weeks later on April 13, 2005.

Stem samples were prepared for analysis and treated based on previous successful assessments of tissue hardiness (8, 11, 13). The terminal 6 cm (2.4 in) of each sample was removed and wrapped individually in moist paper toweling. Each wrapped stem segment was placed in a glass culture tube. The tubes were held for 12 hr at 5C (41F) until we initiated their exposure to a ramped temperature treatment within a programmable freezer (Scientemp, Adrian, MI). Immediately before the ramp treatment began, tubes with control stems were removed and placed in a refrigerator at 4C (39F). Temperature in the freezer then was lowered and held at –1C (30F) for 1 hr, each sample was nucleated with ice crystals, and temperature was lowered progressively at 2C (3.6F) per hour. Four thermocouple probes attached to a CR23X datalogger (Campbell Scientific, Logan, UT) were used to monitor temperature within culture tubes in different locations within the freezer.

Four replicate stem segments from each plant were removed at each interval of 3C (5.4F). Removed segments were thawed slowly by holding them at 4C (39F) for 12 hr. Tubes then were covered with parafilm and incubated in the dark at 22C (72F) for 12 days. Each stem segment then was sectioned longitudinally and examined for tissue discoloration under a dissecting microscope. Segments were rated as alive if the cambium and phloem appeared light green or free of pigment. Segments were judged dead if ≥60% of the surface of the cambium and phloem was brown. The lowest survival temperature was determined for each plant as the minimum treatment temperature at which ≥75% (three out of four) of the replicate stem segments survived (2, 5). Data were analyzed by using the general linear models (GLM) procedure of SAS/STAT® software, Version 6.12 (1989–96). The least significant difference (LSD) option was used within dates of sample collection to compare mean lowest survival temperature among species and/or populations of *Dirca*. Daily minimum air temperatures during the study period, and historical minima from 1997–2005 for Jasper Ridge Biological Preserve were obtained from an on-site weather station. We obtained minima (100-year records) from monitoring stations of the National Weather Service near the sampled plants in Iowa and Florida.

Results and Discussion

Stems of western leatherwood and eastern leatherwood in Florida survived to a similar temperature [–6C and –7C (21F and 19F), respectively] on October 27, 2004, while eastern leatherwood in Iowa was hardy to –21C (–6F) (Fig. 1). The lowest temperature at which western leatherwood survived had changed little on December 8, 2004, [–4C (25F)] and January 19, 2005 [–3C (27F)]. The lowest temperature at which eastern leatherwood from Florida survived during the dormant season was –17C (1F) on January 19, 2005, while eastern leatherwood from Iowa survived at –33C (–27F) on

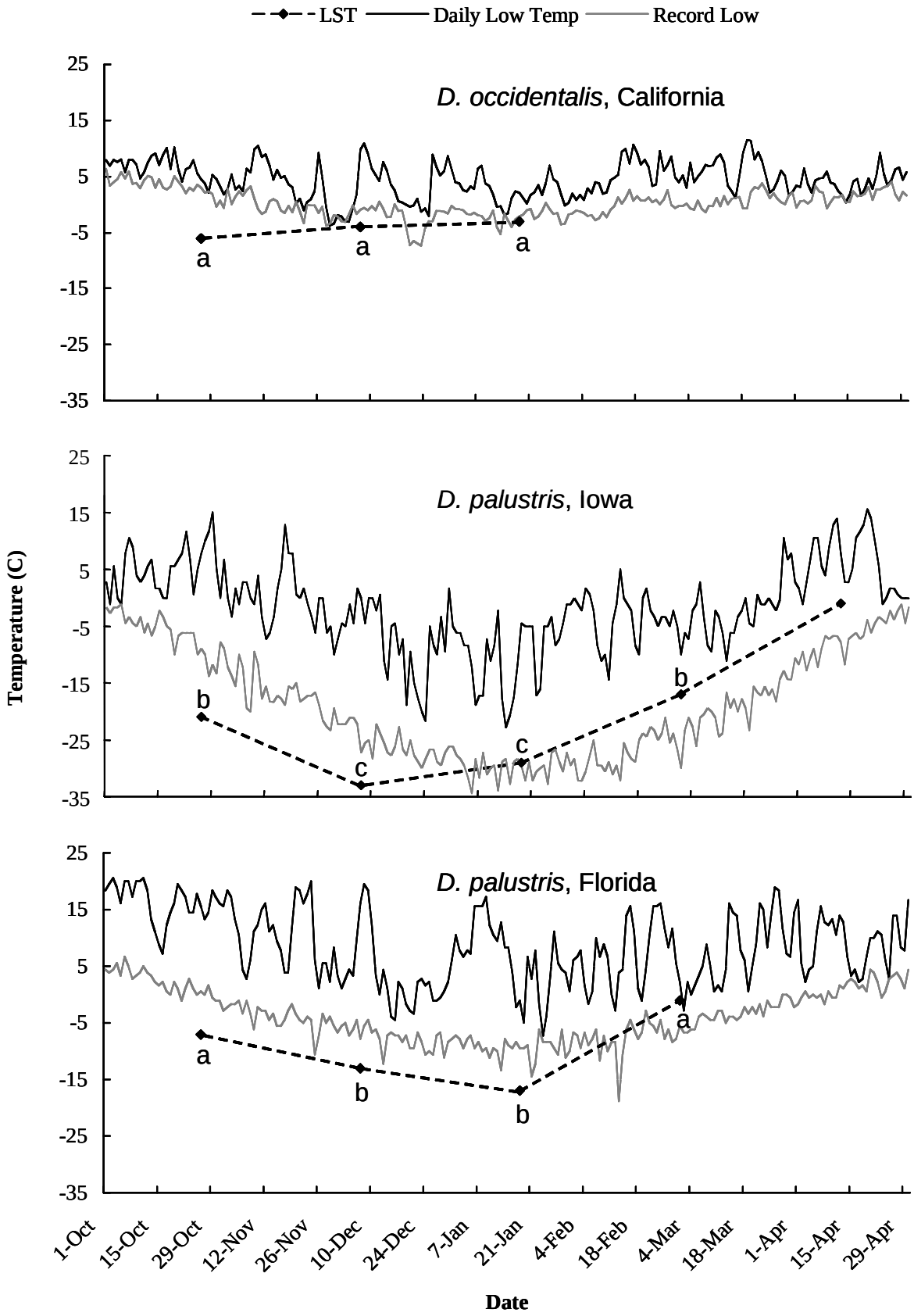

Fig. 1. **Lowest survival temperature (LST) of stems of *Dirca occidentalis* and *Dirca palustris* over selected dates in 2004 and 2005. All data were obtained from assays with stem samples performed in a laboratory freezer. Stems were obtained from plants in their native habitats in California (*D. occidentalis*, top panel), Iowa (*D. palustris*, middle panel), and Florida (*D. palustris*, bottom panel). Each LST datum is the mean of multiple stem samples from three replicate plants per sampling date. Within dates, mean LST values not labeled with the same letter differ according to the least significant difference test ($\alpha = 0.05$). For each location, daily minimum air temperatures during the study (black line) and historically (gray line) are shown.**

December 8, 2004 (Fig. 1). Eastern leatherwood in Florida had deacclimated by March 2, 2005. Eastern leatherwood in Iowa had begun to deacclimate on that date but remained capable of surviving –17C (1F); plants in Iowa were deacclimated on April 13, 2005, when they could survive only to –1C (30F) (Fig. 1).

The three replicate plants of western leatherwood selected for sampling on each date were chosen to represent the range of stages of dormancy, flowering, and resumption of vegetative growth we observed within that population. Data in Fig. 1 are means of the replicates and estimate hardiness for western leatherwood at the typical seasonal state of development within that population for each date. The various developmental states within each sampling date were not replicated over multiple plants and therefore cannot be subjected to formal comparison. Nonetheless, trends we observed in hardiness among replicate plants may influence future research. Over sampling dates, there was a consistent pattern of a slight difference in hardiness depending on whether the replicate plant had begun to bloom. For example, stems of the two plants sampled on December 8, 2004, that had not begun to flower survived to –7C (19F), while stems of the one plant that had begun to bloom on that date were damaged at <2C (36F). Likewise, on January 19, 2005, stems of the plant that had not begun to bloom survived to –7C (19F), while stems of plants near and beyond anthesis were hardy to only –1C (30F). This suggests that the onset of flowering, which immediately precedes leaf emergence of western leatherwood, coincides with a slight loss of hardiness. Similarly, stems of *D. palustris* were deacclimated on March 2 (Florida) and April 13, 2005, (Iowa), when blooming had begun. Blooming of *D. palustris* in Iowa had not begun on January 19 and March 2, 2005, but stems had started to deacclimate. This indicates that flowering does not coincide with a sudden loss of hardiness but rather follows an extended period of gradual deacclimation.

The nearly constant extent of cold hardiness of western leatherwood was sufficient by several degrees Celsius to ensure survival of stems early during the dormant season (October 27) but not later (Fig. 1). Predicted lowest survival temperature was within ≈1C (2F) of the daily low on several dates between late November and mid-January (Fig. 1). Historical data available for the site, though limited (back only to 1997), reveal daily minima below the estimates of lowest survival temperature we obtained (Fig. 1). If western leatherwood is incapable of accruing greater hardiness than we observed, plants at this site probably suffer damage from low temperatures occasionally during their life spans. Thermal sensitivity also might be among the factors that have led to the extremely restricted natural distribution of the species (4, 6). It is possible, however, that lowest survival temperature varies from year to year subject to short-term trends in ambient temperature. This issue merits resolution through future research and would have significant horticultural implications. If western leatherwood cannot become more resistant to low temperature, its geographical range of usefulness as a nursery crop would be extremely restricted. There would be greater commercial potential if hardiness can increase among plants installed in colder climates, a phenomenon demonstrated for other woody species (11). We planted three seedlings of western leatherwood in a protected location on the campus of Iowa State University in Ames during 2004. All survived their first winter in the landscape without obvious stem damage despite minima ≈10C (18F) lower than the minimum lowest survival temperature we documented for stem samples from indigenous plants in their Mediterranean niche in California (Fig. 1). Research is needed to define the potential hardiness of western leatherwood when planted outside of its native range.

In contrast to western leatherwood, eastern leatherwood showed a marked accrual and loss of hardiness between October and April, and our data provide lowest survival temperatures for both a southern and a northern population of this broadly distributed species (Fig. 1). Values of lowest survival temperature were at or below the daily local minima during our study but were higher than record minima on March 2 and April 13, 2005, in Iowa, and on March 2, 2005, in Florida (Fig. 1). Subsequent research is needed to determine the extent to which lowest survival temperature of eastern leatherwood fluctuates based on the temperatures to which plants are exposed within each dormant season. Such fluctuation would appear necessary for plants of eastern leatherwood to avoid cold injury over a life span. Another topic for further research should be the acclimation, mid-winter hardiness, and deacclimation of eastern leatherwood derived from southern populations after planting in regions with harsh winters. We have observed during informal trials that seedlings of eastern leatherwood from the South are more easily and rapidly grown in containers than are seedlings from northern sources. Eastern leatherwood from southern provenances therefore may be of particular value for horticulture, but hardiness-related limits on their use outside of their native habitat should be defined.

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