

From Forest Nursery Notes, Winter 2010

46. Variation in development and response to root-zone pH among seedlings of *Dirca palustris* (Thymelaeaceae) from three provenances. Peterson, B. J. and Graves, W. R. HortScience 44(5):1319-1322. 2009.

Variation in Development and Response to Root-zone pH Among Seedlings of *Dirca palustris* (Thymelaeaceae) from Three Provenances

Bryan J. Peterson and William R. Graves¹

Department of Horticulture, Iowa State University, 106 Horticulture Hall, Ames, IA 50011-1100

Additional index words. eastern leatherwood, phenotypic and intraspecific variation, SPAD, micronutrient, biomass allocation, native landscape plants, acidic, alkaline

Abstract. Horticulturists have not promoted use of *Dirca palustris* L. (eastern leatherwood) despite its suite of traits valued by gardeners and landscapers. Horticultural production of *D. palustris* may be hindered by slow shoot growth and sensitivity of plants to edaphic conditions. Because of discrepancies in reported tolerances of *D. palustris* to root-zone pH, we assessed whether pH of soils supporting indigenous populations in Florida, Maine, and North Dakota corresponded to responses of seedlings from the three provenances to root-zone pH of 4.5 to 7.3 in soilless media. Regression showed that root zones at pH 5.8 promoted maximum stem length of seedlings from Florida and North Dakota, whereas root zones at pH 4.5 led to maximum stem length of seedlings from Maine. Root-zone pH 5.6 and 5.5 fostered maximum root and shoot dry weight, respectively, for seedlings from Florida, whereas root zones at pH 4.5 promoted maximum root and shoot dry weights of seedlings from Maine and North Dakota. Averaged over provenance, relative leaf greenness decreased by 62%, and foliar nitrogen, iron, manganese, and zinc decreased by 49%, 70%, 95%, and 48%, respectively, as root-zone pH increased from 4.5 to 7.3. Foliar phosphorus decreased at both low and high pH. The pH of soils where seeds were collected did not predict optimal root-zone pH for stem length or biomass accrual in soilless media; genotypes from soils with a pH of 7.4 in North Dakota did not exhibit greater tolerance to high pH than genotypes from Maine or Florida, where pH of indigenous soil was 6.1 and 5.2, respectively. Averaged over pH treatments, seedlings from Florida showed the greatest stem length and formed the most shoot biomass, whereas seedlings from North Dakota had stouter stems, greater root biomass, and greater root-to-shoot ratios than did seedlings from Florida and Maine. Our results illustrate that acidic media facilitate horticultural production of *D. palustris*, that further evaluation of provenance differences could facilitate selection of genotypes for horticulture, and that tolerances of genotypes to root-zone pH do not strictly correspond to the pH of soils on which they were indigenous.

Dirca palustris L. occurs sporadically as an understory shrub in rich mesic forests from Nova Scotia west to North Dakota, and south to Oklahoma and Florida (Nevling, 1962; Peterson et al., 2009). Known commonly as eastern leatherwood, the species has received little attention from horticulturists despite its suite of traits valued by gardeners and landscapers, including its flowers in early spring, unique and upright growth habit, rich yellow foliage in fall, and shade tolerance (Anderson, 1933; Del Tredici, 1984; Esson,

1949). Our observations indicate that limitations to commercial production of *D. palustris* include its sensitivity to edaphic conditions and slow shoot growth (5 to 10 cm annually). Overcoming these challenges could facilitate the use of *D. palustris* as a commercially viable shrub for horticulture. Our broad goal is to determine how horticulturists can manage the root-zone environment during production and use of *D. palustris* to promote growth and plant health.

Responses of *D. palustris* to pH of substrates used for horticultural production are unknown, and discrepancies exist in the reported pH affinities of the species in the wild. Del Tredici (1984) reported that *D. palustris* performs best in moist areas that have high limestone content, and Cooperrider (1962) found occurrence of the species in eastern Iowa to be limited to sites over limestone bedrock. Clark (1971) asserted that

D. palustris occurs over circumneutral or basic soils in the southeastern United States. Nevling (1962) characterized *D. palustris* as a facultative calciphile, whereas Anderson (1933) claimed it grows in a range of environments but avoids limestone. A survey of *D. palustris* in South Carolina demonstrated that it occurs on acidic soils (Ward and Horn, 1998), and Dirr (1997) stated that the species prefers acidity. Conflicting information on soil-pH tolerances of *D. palustris* might indicate either that the species is inherently adapted to a wide range of soil pH or that ecotypic adaptation to localized soil pH has occurred (Dawson et al., 2007; Rajakaruna, 2004; Snaydon, 1970). If the latter is true, genotypes of *D. palustris* from disparate provenances may respond differently to root-zone pH, which could influence strategies for selecting and using genotypes for horticulture. Researchers have demonstrated that genotypes of the same species from contrasting edaphic environments may vary in response to root-zone pH (Anderson and Ladiges, 1978; Dawson et al., 2007; Kerley et al., 2002; Snaydon, 1970). Nevertheless, the degree to which the pH of soil where a genotype is indigenous predicts responses of propagules of that genotype to pH of horticultural substrates likely varies among species according to their evolutionary histories (Bounejmame and Robson, 1992; Snaydon, 1970; Symonds et al., 2001).

We evaluated responses of seedlings of *D. palustris* from diverse provenances to pH of a soilless medium. We studied seedlings indigenous to Florida, Maine, and North Dakota because our assessments of wild populations showed that the pH of soils supporting these populations differs. Our specific objectives were to 1) evaluate growth of first-year seedlings of *D. palustris* in soilless media across a range of pH; 2) assess whether pH of soils where the genotypes were native corresponds to early responses of seedlings to pH in a horticultural substrate; and 3) characterize phenotypic differences of horticultural utility among seedlings from the three provenances.

Materials and Methods

Plant materials and handling. *Dirca palustris* was propagated from seeds harvested within three populations in 2007. Drupes were collected in April from Torreya State Park in Liberty Co., Florida (long. 30°34'632" N, lat. 84°56'747" W) from a minimum of 30 maternal parents. In July, drupes were collected near Sherman Mills in Aroostook Co., Maine (long. 45°56'056" N, lat. 68°19'357" W) and near the Little Pembina River in Cavalier Co., North Dakota (long. 48°57'892" N, lat. 098°06'031" W) from a minimum of 10 maternal parents and 30 maternal parents, respectively. A composite soil sample comprising 10 subsamples was collected from each site where drupes were obtained. Soil pH was measured by the Soil and Plant Analysis Laboratory, Iowa State University, Ames, IA, using the 1:1 soil:water suspension method. Drupes were

Received for publication 3 Apr. 2009. Accepted for publication 28 May 2009.

We thank Candy McKellar, Jyotsna Sharma, and the staff of Torreya State Park, Bristol, FL, for helpful assistance.

¹To whom reprint requests should be addressed; e-mail graves@iastate.edu.

sown in flats filled with a soilless, peatmoss-based medium (Fafard[®] 52; Fafard[®], Inc., Agawam, MA) within 1 week after collection. Flats were held in a minimally heated greenhouse until seeds germinated during Spring 2008 after exposure to warm and cold stratification under ambient conditions.

Plants from each provenance were randomly assigned to one of five pH treatments when seedlings had three to four true leaves. The experiment was conducted on a shaded bench in a glass-glazed greenhouse where photosynthetically active radiation (PAR) at canopy level at solar noon was measured on 10 dates during the experiment. Mean PAR was 245 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 11.6). Temperatures in the greenhouse were logged with an iButton Data Logger (Maxim Integrated Products, Sunnyvale, CA). The mean daily temperature during the experiment was 22 °C; mean daily minimum and maximum were 17 and 32.5 °C.

Treatments and experimental design. We adjusted pH of a soilless, peatmoss-based medium (Fafard[®] 52) to 4.5, 5.3, 5.9, 6.5, and 7.3 with 1-M sulfuric acid (H₂SO₄) or reagent-grade calcium carbonate (CaCO₃) (Table 1). These chemicals were chosen because injection of H₂SO₄ into irrigation water and addition of CaCO₃ to container substrates are common methods for lowering or raising pH of horticultural media. Distilled water was then added to each adjusted medium to ensure uniform moisture content among treatments. Seedlings from each provenance were transplanted singly into square band pots with a diameter of 6 cm and a height of 12.5 cm (Anderson Die & Mfg. Co., Portland, OR) filled with the media.

The experiment was designed as a two-way factorial, randomized complete block with three blocks. Six replicates were used for each combination of provenance and root-zone pH within each block (N = 270; 90 per block). Seedlings were irrigated with tap water to container capacity every 5 to 9 d. Root-zone pH was measured every 7 to 14 d (Cavins et al., 2000). Leachate from two pots per treatment per block was collected and its pH determined with an IQ160 pH meter (IQ Scientific Instruments, Carlsbad, CA) with an IFSET probe.

Harvest and data analysis. Responses of plants were assessed after 15 weeks. Relative greenness, a presumed measure of relative chlorophyll content (Netto et al., 2005), was

measured on the youngest fully expanded leaf of each plant with a handheld SPAD-502 Chlorophyll Meter (Konica Minolta Sensing, Tokyo, Japan). Length of the single stem of every seedling was determined from the cotyledon scars to the youngest node. Stem diameter was measured immediately below the cotyledon scars with handheld calipers. Shoot and root tissue was harvested from every plant, media were washed from the roots, and both shoots and roots were dried at 67 °C for 5 to 7 d. Roots included all biomass below the cotyledon scars. Shoots and roots were weighed, and a root-to-shoot ratio was calculated for each seedling.

Leaves of plants from each treatment were analyzed for nutrient content by the Soil and Plant Analysis Laboratory, Iowa State University, Ames, IA. Because we had limited material for analysis, one sample was created for each combination of provenance and pH by combining leaves from multiple plants until there was enough biomass for the analyses. This allowed three analyses from each of the five pH treatments, with one sample from each of the three seedling provenances (N = 15). Total nitrogen (N) was measured by combustion analysis, and iron (Fe), manganese (Mn), zinc (Zn), and phosphorus (P) were measured by microwave digestion.

Data were analyzed with the Statistical Analysis System 9.1.3 (SAS Institute Inc., Cary, NC). Treatment responses were natural log-transformed when necessary to normalize variances. The regression procedure and F-tests were used to test the significance of linear and quadratic models for responses of seedlings to root-zone pH. The LSMEANS option of the general linear models procedure was used with Tukey adjustment for multiple comparisons to generate means-separation statistics. Main effects of root-zone pH and seedling provenance were tested, as were their interactions.

Results

The pH of soils supporting the populations from which drupes were collected varied from acidic (5.2 in Florida and 6.1 in Maine) to basic (7.4 in North Dakota). In containers, acidic root zones enhanced stem length and root and shoot dry weights of seedlings from all three provenances, although interactions existed between root-zone pH and provenance for all three responses (interactions: $P = 0.0002$, $P < 0.0001$, and $P = 0.0122$, respectively). Stem length of seedlings from Maine decreased linearly with increasing pH, whereas stem length of seedlings from Florida and North Dakota was best described by quadratic functions with predicted maxima at pH 5.8 (Fig. 1). Both root (Fig. 2A) and shoot (Fig. 2B) dry weight of seedlings from Maine and North Dakota decreased linearly with increasing pH. Quadratic functions best described responses of seedlings from Florida, with predicted maxima at pH 5.6 and pH 5.5 for root (Fig. 2A) and shoot (Fig. 2B) dry

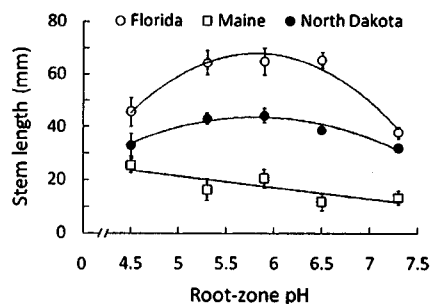


Fig. 1. Interaction of root-zone pH and provenance for stem length of seedlings of *Dirca palustris*. Symbols represent means of 18 single-plant replications \pm SE. Regression models were determined based on log-transformed data, but plot depicts untransformed data for clarity. Regression functions are: Florida: stem length = $-13.1(\text{pH}^2) + 152.7(\text{pH}) - 376.0$, $r^2 = 0.93$; Maine: stem length = $-4.3(\text{pH}) + 43.0$, $r^2 = 0.57$; North Dakota: stem length = $-5.7(\text{pH}^2) + 66.0(\text{pH}) - 148.2$, $r^2 = 0.88$.

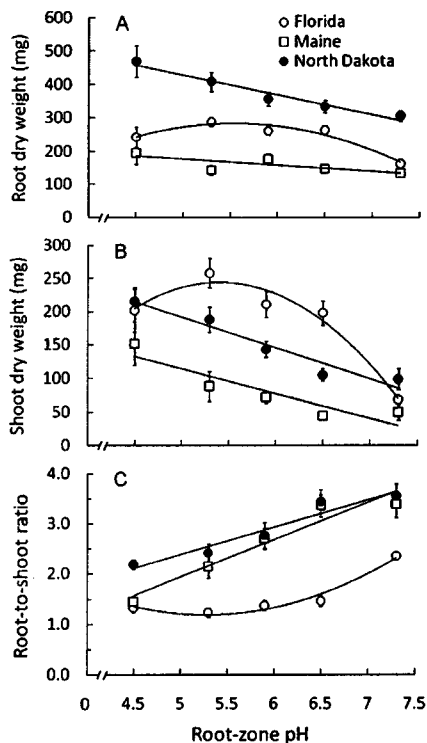


Fig. 2. Interactions of root-zone pH and provenance for root dry weight, shoot dry weight, and root-to-shoot ratio of seedlings of *Dirca palustris*. Symbols represent means of 18 single-plant replications \pm SE. Regression models were selected based on log-transformed data, but plots depict untransformed data for clarity. Regression functions for root dry weight are: Florida: weight = $-37.7(\text{pH}^2) + 418.2(\text{pH}) - 874.3$, $r^2 = 0.87$; Maine: weight = $-18.5(\text{pH}) + 269.9$, $r^2 = 0.43$; North Dakota: weight = $-59.3(\text{pH}) + 725.2$, $r^2 = 0.95$. Functions for shoot dry weight are: Florida: weight = $-48.5(\text{pH}^2) + 524.2(\text{pH}) - 1171.8$, $r^2 = 0.92$; Maine: weight = $-37.0(\text{pH}) + 299.8$, $r^2 = 0.77$; North Dakota: weight = $-46.5(\text{pH}) + 424.6$, $r^2 = 0.92$. Functions for root-to-shoot ratio are: Florida: ratio = $0.3(\text{pH}^2) - 2.9(\text{pH}) + 8.9$, $r^2 = 0.93$; Maine: ratio = $0.8(\text{pH}) - 1.8$, $r^2 = 0.91$; North Dakota: ratio = $0.6(\text{pH}) - 0.4$, $r^2 = 0.92$.

Table 1. Addition of 1-M H₂SO₄ and reagent-grade CaCO₃ to a soilless, peatmoss-based medium to achieve pH treatments.

| Amendment | Amount added/L medium | Mean pH ^a | SE of mean pH |
|------------------------------------|-----------------------|----------------------|---------------|
| 1-M H ₂ SO ₄ | 35 mL | 4.5 | 0.06 |
| 1-M H ₂ SO ₄ | 23 mL | 5.3 | 0.06 |
| 1-M H ₂ SO ₄ | 14 mL | 5.9 | 0.07 |
| None | — | 6.5 | 0.07 |
| CaCO ₃ | 5 g | 7.3 | 0.05 |

^aValues represent average measures of leachate pH taken every 7 to 14 d.

weight, respectively. Root-to-shoot ratios of seedlings from Maine and North Dakota increased linearly with increasing root-zone pH, whereas a quadratic function described the root-to-shoot ratios of seedlings from Florida (Fig. 2C).

Relative greenness of leaves on plants from all provenances decreased linearly with increasing pH (Fig. 3), and analysis of variance showed no evidence of differences among provenances in this response ($P = 0.1942$). Foliar concentrations of N, Fe, and Zn decreased linearly with increasing root-zone pH (Table 2), whereas concentration of Mn decreased quadratically with increasing root-zone pH. In contrast, regression of leaf P concentration with pH revealed a quadratic response with a predicted maximum P concentration at pH 5.5 (Table 2).

Differences in growth were found among seedlings from the three provenances, averaged across pH treatments (Table 3). Seedlings from Florida formed stems 48% longer than seedlings from North Dakota and 211% longer than seedlings from Maine (Table 3). Seedlings from North Dakota and Maine had the thickest and thinnest stems, respectively (Table 3). Mean shoot dry weight of seedlings from Florida was 25% greater than that of seedlings from North Dakota and 129% greater than that of seedlings from Maine (Table 3). Root dry weight of seedlings from North Dakota averaged 53% and 134% greater than mean root dry weights of seedlings from Florida and Maine, respectively (Table 3). Root-to-shoot ratios of seedlings from North Dakota exceeded the root-to-shoot ratios of seedlings from Florida and Maine by 93% and 12%, respectively (Table 3).

Discussion

Seedlings of *D. palustris* were sensitive to the pH of a soilless, horticultural medium under greenhouse conditions. Regression statistics predicted that stem length and root and shoot dry weights of seedlings from all three

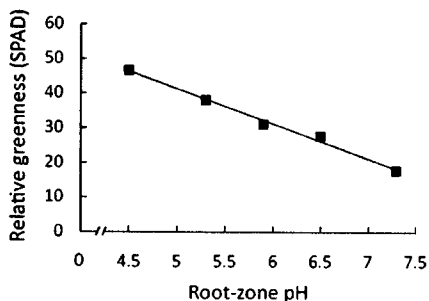


Fig. 3. Relative greenness of leaves of *Dirca palustris* grown in a soilless medium adjusted to five pH levels. The unitless values were obtained as measures from a SPAD-502 Chlorophyll Meter. Symbols represent means of 54 single-plant replicates, 18 from each of Florida, Maine, and North Dakota. For all means, SE bars fell within the areas of the filled symbols. The regression function is: $SPAD = -10.1(pH) + 91.8$, $r^2 = 0.99$.

provenances were maximized by root-zone pH less than 6.0; some measures of growth were maximal at pH 4.5, the lowest root-zone pH we evaluated (Figs. 1 and 2A–B). These results demonstrate that use of acidic media facilitates cultivation of this species. Furthermore, the positive relationship between root-to-shoot ratio and root-zone pH (Fig. 2C) indicates that low-nutrient stress of seedlings increased as pH increased. This conclusion is based on numerous reports that relative allocations of biomass to roots increase as the nutrients available to a plant decrease (Gutschick and Kay, 1995; Huante et al., 1995). Also supporting this conclusion are data on relative greenness of leaves (Fig. 3) and foliar concentrations of N, Fe, Mn, Zn, and P (Table 2), which were greatest among plants in acidic media. These nutrient analyses support the assertion that root zones with pH less than 6.0 promote the health of *D. palustris*. However, curling and puckering was noted on lamina of some seedlings from all three provenances when grown in media at pH 4.5. This symptom and the high Mn concentrations in leaves of plants in media at pH 4.5 (Table 2) suggest that seedlings from all three provenances may be sensitive to Mn availability in highly acidic media (Handreck and Black, 2002). Collectively, these results do not support the contention that *D. palustris* is insensitive to root-zone pH nor the possibility that extensive local adaptation to root-zone pH has occurred. Some researchers have stated that the species is restricted primarily

to limestone soils (Clark, 1971; Cooperrider, 1962; Del Tredici, 1984), whereas others have reported that *D. palustris* is typically found on or prefers acidic soils (Anderson, 1933; Dirr, 1997; Ward and Horn, 1998). Our results provide clarification for horticulturists by demonstrating that seedlings of *D. palustris* in horticultural media prefer acidic root zones.

Despite their general preference for acidic media, seedlings from the three provenances varied in some ways in their responses to the wide range of root-zone pH we used. Stem length and root and shoot dry weight of seedlings from Florida were diminished by both low-pH and high-pH root zones (Figs. 1 and 2A–B). In contrast, stem length and root and shoot dry weight of seedlings from Maine were greatest at pH 4.5 and diminished with increasing pH (Figs. 1 and 2A–B). Responses of seedlings from North Dakota were less consistent. Stem length was reduced by both low-pH and high-pH root zones (Fig. 1), whereas dry weights were greatest in the low-pH root zone of 4.5 (Fig. 2A–B). The reason for these differential responses to root-zone pH among the provenances is unclear, although they may represent divergent tolerances to micronutrient limitation or toxicity. Regardless, the varied responses of seedlings from the three provenances to root-zone pH suggest that comprehensive assessments of edaphic tolerances may facilitate horticultural selection for specific responses to root-zone pH.

Table 2. Mean foliar nutrient concentration of *Dirca palustris* after 15 weeks of growth.^a

| Root-zone pH | N (%) | Fe (mg·kg ⁻¹) | Mn (mg·kg ⁻¹) | Zn (mg·kg ⁻¹) | P (mg·kg ⁻¹) |
|--------------|-----------------|---------------------------|---------------------------|---------------------------|--------------------------|
| 4.5 | 3.5 | 247 | 1,979 | 65 | 2,381 |
| 5.3 | 3.0 | 186 | 1,313 | 65 | 3,221 |
| 5.9 | 2.5 | 103 | 284 | 52 | 2,684 |
| 6.5 | 2.1 | 91 | 165 | 59 | 2,271 |
| 7.3 | 1.8 | 74 | 101 | 34 | 1,369 |
| Model | | | | | |
| Linear | <0.0001 | 0.0002 | <0.0001 | 0.0492 | 0.0251 |
| Quadratic | NS ^b | NS | 0.0092 | NS | 0.0059 |

^aMeans are of three replicates for each pH treatment, one from each of three provenances. Regression functions for foliar nutrients are: % nitrogen (N) = $-0.6(pH) + 6.4$, $r^2 = 0.87$; mg·kg⁻¹ iron (Fe) = $-64.5(pH) + 520.6$, $r^2 = 0.51$; mg·kg⁻¹ manganese (Mn) = $287.2(pH^2) - 4104.6(pH) + 14720$, $r^2 = 0.86$; mg·kg⁻¹ zinc (Zn) = $-10.2(pH) + 115.2$, $r^2 = 0.16$; mg·kg⁻¹ phosphorus (P) = $-478.5(pH^2) + 5218.3(pH) - 11301$, $r^2 = 0.59$.

^bNonsignificant at $P \leq 0.05$.

Table 3. Mean stem length, stem diameter, shoot dry weight, root dry weight, and root-to-shoot ratio of seedlings of *Dirca palustris* from three provenances after 15 weeks of growth.^a

| Provenance | Stem (mm) | | Dry wt (mg) | | Root-to-shoot ratio |
|--------------|-------------------|-------|-------------|-------|---------------------|
| | Length | Diam | Shoot | Root | |
| Florida | 56 a ^b | 2.2 b | 188 a | 245 b | 1.6 c |
| Maine | 18 c | 2.1 c | 82 c | 161 c | 2.6 b |
| North Dakota | 38 b | 2.4 a | 151 b | 376 a | 2.9 a |

^aProvenance means are of 90 replicates, 18 each of five pH treatments (N = 270). Interactions between provenance and root-zone pH existed for some variables; an assessment of the sources of the interactions showed that they did not preclude consideration of provenance main effects. Means for the main effect of provenance therefore are shown. Interaction means for stem length are depicted in Figure 1, and interaction means for shoot dry weight, root dry weight, and root-to-shoot ratio are depicted in Figure 2. Interaction means for stem diameter (mm) of seedlings grown in root-zone pH 4.5, 5.3, 5.9, 6.5, and 7.3: Florida: 2.3, 2.5, 2.3, 2.3, and 1.7, respectively; Maine: 2.5, 2.0, 2.1, 1.9, and 1.8, respectively; North Dakota: 2.9, 2.5, 2.4, 2.2, and 2.0, respectively.

^bMeans within each column followed by the same letter are not different at $P \leq 0.05$ according to Tukey's honestly significant difference test.

The pH of soils that supported the indigenous plants from which we collected seeds did not predict optimal root-zone pH for stem length or biomass accrual in soilless media. This contrasts with previous work in which populations within a species occurring on soils of divergent pH demonstrated localized adaptation to disparate root-zone conditions (Kerley et al., 2002; Snaydon, 1970). In our experiment, responses of seedlings of *D. palustris* to root-zone pH were independent of indigenous soil pH at the three provenances. Although the populations from which seeds were collected in North Dakota and Maine were supported by slightly basic soils (pH 7.4) and acidic soils (pH 6.1), respectively, seedlings from these provenances produced greatest biomass in strongly acidic media at pH 4.5 (Fig. 2A–B). In contrast, soil supporting the population in Florida was the most acidic of the three provenances (pH 5.2), but regression predicted a root-zone pH near 5.5 would promote the greatest dry weight of seedlings from Florida (Fig. 2A–B). This root-zone pH is higher than that which maximized dry weights among seedlings from both North Dakota and Maine. Similarly, stem-length responses of seedlings from the three provenances did not correspond to indigenous soil pH. Stem length was maximal for seedlings from Maine when grown at pH 4.5 in the root zone, whereas seedlings from Florida and North Dakota had the longest stems at a pH near 5.8 (Fig. 1). We conclude that efforts to select genotypes for specific adaptation to acidic or basic root zones should not be restricted to populations occurring on soils with the pH range of interest.

Evidence from *D. palustris* in the wild and results from other species demonstrate that our results should not be extrapolated to the ecology of *D. palustris* in its native habitats or horticultural landscapes. Although we observed that *D. palustris* preferred an acidic horticultural substrate, the wild population on a basic soil in North Dakota grows more vigorously than the population in Florida on an acidic soil (Peterson, 2009). We recognize that other factors might explain the difference in growth of plants in these populations. Nonetheless, it is apparent that *D. palustris* can grow vigorously in field soils that are mildly basic. Our use of a soilless medium may account for the relatively poor response we observed among seedlings as pH increased (Figs. 1 and 2A–B). Plants often tolerate a higher root-zone pH in mineral soils than in soilless media, attributable in part to the greater cation exchange capacity and micronutrient availability of many field soils (Handreck and Black, 2002). Our results are consistent with those of Symonds et al. (2001), who found that growth of species of *Eucalyptus* Labill. indigenous to either acidic or alkaline soils was maximized by an acidic container medium. Trials in horticultural

landscapes could extend our knowledge of the responses of *D. palustris* to soil pH.

Phenotypic differences were observed among seedlings from the three provenances (Table 3), suggesting that further evaluation of provenance differences may facilitate selection of genotypes for horticulture. Annual stem elongation should be a selection trait of primary interest because the species typically grows slowly (Steyermark, 1963). The population in Florida is promising in this regard; seedlings from Florida showed the greatest stem length and shoot dry weight (Table 3). Other traits of potential concern to those interested in selecting genotypes for horticulture include stem diameter, root biomass, and root-to-shoot ratios. Seedlings from the population in North Dakota had stouter stems, greater root dry weight, and greater root-to-shoot ratios than did seedlings from Florida or Maine (Table 3). Adaptation for enhanced foraging of soil among plants from North Dakota represents a plausible explanation for the greater allocation of biomass to root-system development by seedlings from this provenance. Low available soil moisture can favor the evolution of increased root-to-shoot ratios (Markesteyn and Poorter, 2009; Zhang et al., 2005), and mean annual precipitation near the population of *D. palustris* in North Dakota is less than 40% of the annual precipitation near the population in Florida (U.S. Department of Commerce, 2007). The horticultural implications of these provenance differences merit further investigation. If the trait remains stable in different environments and as plants age, the high root-to-shoot ratio of seedlings from North Dakota may impart increased drought avoidance and an enhanced capacity to sequester nutrients in horticultural landscapes.

Literature Cited

- Anderson, C.A. and P.Y. Ladiges. 1978. A comparison of three populations of *Eucalyptus obliqua* L'Hérit. growing on acid and calcareous soils in southern Victoria. *Aust. J. Bot.* 26:93–109.
- Anderson, E. 1933. Leatherwood (*Dirca palustris*). *Arnold Arboretum Bul. Popular Info.* 1:25–27.
- Bounejmate, M. and A.D. Robson. 1992. Differential tolerance of genotypes of *Medicago truncatula* to low pH. *Aust. J. Agr. Res.* 43:731–737.
- Cavins, T.J., B.E. Whipker, W.C. Fonteno, B. Harden, I. McCall, and J.L. Gibson. 2000. Monitoring and managing pH and EC using the PourThru extraction method. *North Carolina State University Hort. Info. Lft.* 590.
- Clark, R.C. 1971. The woody plants of Alabama. *Ann. Mo. Bot. Gard.* 58:99–242.
- Cooperrider, T.S. 1962. The flora of north-facing slopes compared to that of the surrounding area in eastern Iowa. *Amer. Midl. Nat.* 67:368–372.
- Dawson, K., K.E. Veblen, and T.P. Young. 2007. Experimental evidence for an alkali ecotype of *Lolium multiflorum*, an exotic invasive annual grass in the Central Valley, CA, USA. *Biol. Invasions* 9:327–334.
- Del Tredici, P. 1984. Propagating leatherwood: A lesson in humility. *Arnoldia* 44:20–23.
- Dirr, M.A. 1997. *Dirr's hardy trees and shrubs: An illustrated encyclopedia.* Timber Press, Portland, OR.
- Esson, J.G. 1949. Leatherwood for early spring bloom. *J. New York Bot. Garden* 50:57–59.
- Gutschick, V.P. and L.E. Kay. 1995. Nutrient-limited growth rates: Quantitative benefits of stress responses and some aspects of regulation. *J. Expt. Bot.* 46:995–1009.
- Handreck, K. and N. Black. 2002. *Growing media for ornamental plants and turf.* Univ. of New South Wales Press, Sydney, Australia.
- Huante, P., E. Rincón, and I. Acosta. 1995. Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Funct. Ecol.* 9:849–858.
- Kerley, S.J., C. Norgaard, J.E. Leach, J.L. Christiansen, C. Huyghe, and P. Römer. 2002. The development of potential screens based on shoot calcium and iron concentrations for the evaluation of tolerance in Egyptian genotypes of white lupin (*Lupinus albus* L.) to limed soils. *Ann. Bot. (Lond.)* 89:341–349.
- Markesteyn, L. and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J. Ecol.* 97:311–325.
- Netto, A.T., E. Camprostrini, J.G. de Oliveira, and R.E. Bressan-Smith. 2005. Photosynthetic pigments, nitrogen, chlorophyll *a* fluorescence and SPAD-502 readings in coffee leaves. *Scientia Hort.* 104:199–209.
- Nevling, L.I. 1962. The Thymelaeaceae in the southeastern United States. *J. Arnold Arbor.* 43:428–434.
- Peterson, B.J. 2009. Ecology and horticultural potential of *Dirca palustris*. MS Thesis, Iowa State Univ., Ames, IA.
- Peterson, B.J., W.R. Graves, and J. Sharma. 2009. Color of pubescence on bud scales conflicts with taxonomic keys for identifying species of *Dirca* L. (Thymelaeaceae). *Rhodora* 111: 126–130.
- Rajakaruna, N. 2004. The edaphic factor in the origin of plant species. *Int. Geol. Rev.* 46:471–478.
- Snaydon, R.W. 1970. Rapid population differentiation in a mosaic environment. I. The response of *Anthoxanthum odoratum* populations to soils. *Evolution* 24:257–269.
- Steyermark, J.A. 1963. *Flora of Missouri.* Iowa State Univ. Press, Ames, IA.
- Symonds, W.L., L.C. Campbell, and J. Clemens. 2001. Response of ornamental *Eucalyptus* from acidic and alkaline habitats to potting medium pH. *Scientia Hort.* 88:121–131.
- U.S. Department of Commerce. 2007. National Climatic Data Center. 15 Jan. 2009. <<http://www.ncdc.noaa.gov>>.
- Ward, A.B. and C.N. Horn. 1998. A status survey of *Dirca palustris* L. (leatherwood, Thymelaeaceae) in South Carolina. *Castanea* 63:165–173.
- Zhang, X., N. Wu, and C. Li. 2005. Physiological and growth responses of *Populus davidiana* ecotypes to different soil water contents. *J. Arid Environ.* 60:567–579.