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A comparison of root growth dynamics of silver maple and flowering dogwood in compacted soil at differing soil water contents

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Summary Many bottomland tree species are tolerant of compacted soil and perform well in urban environments; however, the mechanism underlying this tolerance is unknown. Increased soil water content has been shown to alleviate some of the effects of soil compaction on plant growth, presumably because increasing soil water reduces soil strength. We hypothesized that tree species tolerant of very wet soils would have opportunities for root growth in compacted soil when high soil water contents reduced soil strength, whereas species intolerant of bottomland conditions would not. We tested this hypothesis on flowering dogwood (*Cornus florida* L.), a mesic species intolerant of inundation, and silver maple (*Acer saccharinum* L.), a bottomland species. Seedlings of both species were grown in pots for 21 and 30 days, respectively, in a growth chamber in native loam soil maintained at various combinations of soil strength and soil water tension. Downward root growth rate decreased in response to increasing soil strength in both species. At low soil strength (0.6 MPa), downward root growth rate of dogwood seedlings slowed when soil was either excessively wet or dry, whereas root growth rate of silver maple seedlings increased linearly with soil water content. In moderately compacted soil (1.5 g cm^{-3} bulk density), silver maple seedlings had greater root growth rate, root length per plant, and ratio of root length to root dry weight in wet soil (0.006 MPa soil water tension) than in moist and dry soils (0.026 and 0.06 MPa, respectively), even though mean oxygen diffusion rate (ODR) was only 0.28 µg cm^{-2} (SE = 0.05). No such effect was detected in highly compacted soil (1.7 g cm^{-3} bulk density) in either species. Mean ODR showed a weak positive correlation with soil water tension ($r = 0.40$, $P = 0.07$), but was unrelated to soil strength. We conclude that silver maple roots can grow in moderately compacted soil when high soil water content decreases soil strength, whereas dogwood is unable to take advantage of this opportunity.

Keywords: Acer saccharinum, bottomland, bulk density, Cornus florida, oxygen diffusion rate, soil compaction, soil strength, urban forestry.

Introduction

Many of the most successful street trees are bottomland species and their hybrids: e.g., American elm (*Ulmus americana* L.), London plane tree *(Platanus* × *acerifolia* (Ait.) Willd.), pin oak (*Quercus palustris* Muenchh.), willow oak (*Quercus phellos* L.), water oak (*Quercus nigra* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and many others. Urban soils are typically compacted (Patterson 1977, Alberty et al. 1984) and, therefore, in many regions, trees must be tolerant of compacted soils to function successfully as street trees. These observations suggest that there may be an association between tolerance of excessive soil water and the ability to grow in compacted soils.

Based on the limited literature available on woody plants, 2.3 MPa has been suggested as a threshold soil penetration resistance, where the reduction in tree root growth due to mechanical impedance becomes severe (Day and Bassuk 1994). In a severely compacted soil, the soil strength would probably only fall below this threshold when the soil is very wet. It is possible that the decrease in soil strength that accompanies an increase in water content in most soils (Taylor and Gardner 1963) creates an opportunity for root growth that could explain the tolerance of bottomland species for compacted soil. According to this hypothesis, a bottomland species could exploit this period of reduced soil strength for root growth, whereas the growth of an upland or mesic species would be inhibited by high soil water content and the associated impaired gas exchange. When the soil dries and gas exchange improves, the soil would once again be too hard for roots to penetrate. The upland or mesic species would, therefore, have very limited opportunity for root growth.

Although an increased water supply has been shown to alleviate some of the effects of compaction (Buttery et al. 1998), it has not been determined if tolerance of excessively wet soils provides a means by which certain species can achieve greater root growth in compacted soils. Taylor and Ratliff (1969) found that peanut and cotton roots were affected by soil strength independently of water content, but they did not evaluate growth in the nearly saturated soils required to achieve low soil strength in highly compacted soils. Wolfe et al. (1995) attributed differences among vegetable species in yield response to soil compaction, in part, to differing sensitivity to secondary effects such as poor drainage and greater pest populations.

We compared root growth dynamics of a bottomland and a mesic tree species over a range of soil strengths and water contents. Flowering dogwood (*Cornus florida* L.), a mesic species native to Eastern North America and widely planted as an ornamental, is generally considered to be intolerant of compacted soils. Silver maple (*Acer saccharinum* L.) has a similar native range, but is a bottomland species considered highly tolerant of compacted soils. According to our hypothesis, these species are similarly affected by increases in soil strength, but respond differently to changes in soil water content, even when soil strength is low. Furthermore, our hypothesis predicts that as soil water content increases in a given compacted soil, silver maple is able to take advantage of the resulting decrease in soil resistance, whereas dogwood is not.

Materials and methods

Preliminary soil analyses

Several preliminary preparations and tests of the experimental soil were conducted before the final experimental pots were prepared. A Unison loam soil (fine, mixed, semiactive, mesic Typic Hapludults; 48.5% sand, 39.4% silt, and 12.1% clay, pH 5.8) was screened through 0.6-cm wire mesh to remove organic debris and air-dried. Equal numbers of metal sleeves (about 89 cm^3 each) were packed with screened soil to each of three bulk densities (1.2 (uncompacted), 1.5 and 1.7 g cm^{-3}). A soil water-release curve was established for each bulk density based on these samples (n = 5), using a tension table and a pressure plate. These curves established the volumetric water content required to maintain specified soil water tensions for each compaction treatment. Further tests were then performed to establish soil penetration resistance–water tension relationships for each compaction treatment. For these tests, we prepared large soil samples (500 cm^3) for each compaction treatment as described below for the experimental pots. For each compaction treatment, three samples were brought to each of four (five for the uncompacted soil) soil water tensions, ranging from 0.005 to 0.06 MPa (3 replications × 3 bulk densities × 4 (5 for non-compacted) water tensions = 37 cores). Soil penetration resistance of each core was tested with a Proctor penetrometer (Model CN-433, Soiltest, Inc., Evanston, IL) complying with ASTM standard D1558 (ASTM 1999) equipped with a 1.6 cm^2 flat tip. We took measurements at four locations (subsamples) within each core. The data were fitted to establish separate soil penetration resistance–water tension curves for each of the compaction treatments. We used the information to prepare experimental pots containing soil of known penetration resistances by varying soil compaction and water content.

Preparation of experimental pots

Sifted, air-dried soil was pre-weighed, moistened to 16% gravimetric water content, and packed in pots made of polyvinyl-chloride pipe (10-cm diameter, 15-cm length), with the bottom end sealed with cellophane and secured with a rubber band. The soil was packed in three layers to one of three bulk densities (1.2 (non-compacted), 1.5 and 1.7 g cm^{-3}) with a specially designed compaction chamber and a Proctor hammer. Through several trial runs, we determined a reproducible compaction protocol, specifying the number of blows and the force of each blow required to yield the desired compaction for each layer. After compaction, all pots contained 500 cm^3 of soil. Water was added to bring each pot to the desired mean soil water tension and the top was tightly sealed to prevent water loss before the experiment began the next day. Treatments consisted of soil prepared in eight different combinations of soil water tension and soil penetration resistance (Table 1). The treatments comprised an incomplete factorial (7 missing cells) with three soil water tensions (0.006, 0.026, and 0.06 MPa) and five penetration resistances (0.6, 1.75, 2.0, 2.3, and 3.1 MPa). A complete factorial structure was not possible because of space limitations, and because soil physical properties do not allow certain soil water tension and soil strength combinations.

Plant material

Flowering dogwood (*Cornus florida*) seeds collected in Michigan were soaked in water for 24 h and stratified in moist paper for 95 days at 3 °C. Seeds were then placed on blotting paper in a 16-h photoperiod with a day/night temperature of 30/20 °C for 14 days, by which time the majority had germinated. Silver maple (*Acer saccharinum*) seeds collected from a landscape tree in Blacksburg, VA had their wings removed, were soaked in water for 24 h, and stratified at 3 °C for approximately 30 days. Seeds germinated during stratification. At the beginning of the experiment, we selected seeds at the same stage of germination (radicle emerged from 1 to 3 mm from seed coat for dogwoods, 2 to 5 mm for silver maples) and placed them in the prepared pots in small depressions on the soil surface. Three seeds were placed in each pot. Soil was pressed carefully around each seed to ensure good seed–soil contact.

Placement and maintenance of experimental pots

The open-bottomed pots were weighed and placed in a completely random design (8 treatments × 2 species × 4 replica-

Table 1. Incomplete factorial treatment structure for the experiment. Values are bulk densities (g cm^{-3}) used to create the soil water tension × soil strength combinations. Cells with “na” indicate no treatment for that factor combination. Each combination was replicated four times per species.

Soil water tension (MPa)	Soil penetration resistance (MPa)				
	0.6	1.75	2.0	2.3	3.1
0.006	1.5	1.7	na	na	na
0.026	1.2	1.5	na	1.7	na
0.06	1.2	na	1.5	na	1.7

tions = 64 pots) on large glass plates set on black corrugated plastic in a growth chamber (Conviron Model E15, Controlled Environments Ltd., Winnipeg, Manitoba, Canada). The chamber provided a 16-h photoperiod with a day/night temperature of 22/16 °C and a relative humidity of 90%. The photosynthetically active radiant flux was maintained at 400–425 μmol m^{-2} s^{-1}. This was measured occasionally during the experiment with a portable photosynthesis system (LI-6200, Li-Cor, Lincoln, NE) to ensure consistency over time. At the same time each day, we weighed the pots and added distilled water to bring each pot to its original weight. By adding water at regular and frequent intervals, soil was kept uniformly close to the target mean soil water tension. Silver maples were harvested after 21 days and the slower-growing dogwoods after 30 days. After 11 days, all the seeds in one maple pot and eight dogwood pots had died. These were replaced and allowed to grow for 21 and 30 days, respectively.

Plant measurements

At the same time each day, the glass trays were removed from the growth chamber and the bottoms of the pots examined for roots with the aid of a hand lens. We recorded each new root that appeared. The number of days needed for the first root to reach the bottom of a given pot divided by the depth of the soil was the downward root growth rate. At the end of the experiment, pots in which no roots had appeared at the bottom were carefully excavated from the lower end and the depth of the deepest root of the three plants determined. This depth was used to calculate the downward root growth rate in these pots. At harvest, the number of surviving plants in each pot was noted, and the soil was gently washed away from each plant. The root systems were spread out as a single layer, and the plants photocopied for later determination of root length. Shoots and roots were dried separately to a constant mass at 60 °C, and dry weights recorded. Total root length for each pot was determined by scanning the photocopied images with imaging software (Desk-Scan II, Hewlett Packard Co., Mountain View, CA) and an image analyzing system (Delta-T SCAN, Delta-T Devices Ltd., Cambridge, U.K.). Root and shoot dry weights and root lengths are expressed on a per-surviving-plant basis for each pot.

Oxygen diffusion rate measurements

At the end of the experiment, the soil in the remaining dogwood pots was sampled for oxygen diffusion rate. We selected the dogwood pots because they had relatively few roots that might affect measurements. We inserted eight platinum electrodes approximately 3.0 cm deep in each pot and calculated the oxygen diffusion rate to each electrode (Oxygen Diffusion Ratemeter, Model E, Jensen Instruments, Tacoma, WA).

Data analysis

Data for treatments with soil water tensions of 0.006 and 0.026 MPa and soil penetration resistances of 0.6 and 1.75 MPa formed a complete 2 × 2 factorial and were analyzed by contrast statements with the SAS statistical software package (SAS Institute, Cary, NC). We used the general linear models procedure (GLM) in SAS to determine significant trends where treatments occurred at more than two soil strengths or soil water tensions with the other factor constant. Regression analysis was used to model the relationship between soil strength and downward root growth rate, independently of other factors. In the two compacted soils, the effects of bulk density and soil water tension were analyzed separately by analysis of variance with the GLM procedure in SAS. Multiple comparisons were made by Fisher's protected least significant difference (LSD, $\alpha = 0.05$) where appropriate. Data for the two species were analyzed separately, because an initial analysis indicated compaction, soil water tension and species interacted. Subsamples of oxygen diffusion rate measurements were averaged and tested for correlation with soil water tension and soil strength with Pearson's correlation coefficient.

Results

In both species, downward root growth rate decreased with increasing soil strength (Figure 1). Because of the incomplete factorial treatment structure, interactions with soil water tension could not be calculated across the entire data set. However, in the treatments with wet soils and low penetration resistances (which made up a complete 2 × 2 factorial), there were no significant interactions between soil water content and soil strength on root growth rate for either species. Under these conditions, increased soil strength reduced root growth rate for both species ($P = 0.0002$ and $P = 0.0035$ for silver maple and dogwood, respectively), whereas increased soil water affected root growth of the dogwood seedlings only ($P = 0.02$) (Table 2). At low soil strength (0.6 MPa), root growth rate of dogwood seedlings slowed when soil became excessively wet or dry, whereas root growth rate of silver maple seedlings increased linearly with soil water content (Figure 2).

Table 2. Downward root growth rate (mm day^{-1}) for dogwood and silver maple seedlings in wet soils with low soil strengths. Standard errors are in parentheses.

Soil water tension (MPa)	Soil penetration resistance (MPa)			
	0.6		1.75	
	Dogwood	Maple	Dogwood	Maple
0.006	1.65 (0.35)	4.83 (0.43)	0.34 ($n = 1$)	1.60 (0.37)
0.026	3.22 (0.92)	5.10 (1.05)	1.21 (0.21)	2.43 (0.92)

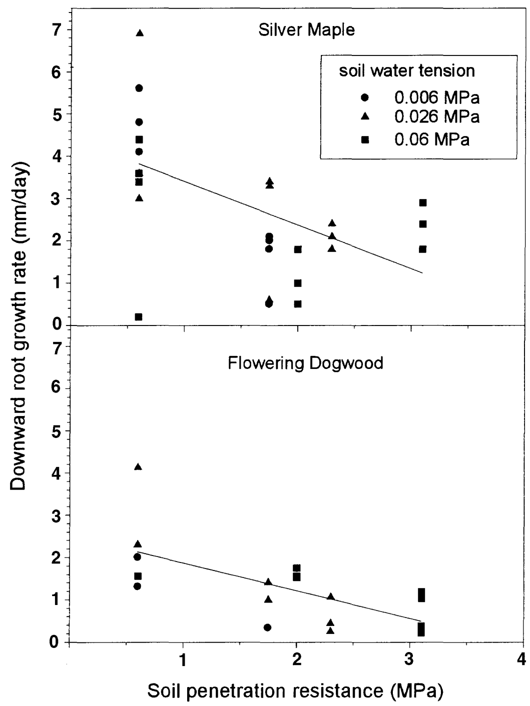

Figure 1. Downward root growth rate of dogwood and silver maple seedlings as a function of soil strength for all soil water tensions. Lines represent least squares regressions for all data points (maples: $y = 4.44 - 1.03x$, $r^2 = 0.29$; dogwoods: $y = 2.53 - 0.656x$, $r^2 = 0.42$).

Analysis of root growth in the compacted soil treatments suggested that silver maple seedlings were able to take advantage of the low soil strength that resulted when the moderately compacted soil (1.5 g cm^{-3}) was very wet (Figure 3). Dogwood seedlings did not show this response. Analysis of variance of the effects of bulk density of the compacted soils (bulk densities 1.5 and 1.7 g cm^{-3}), soil water tension, and species showed a three-way interaction for several of the root growth variables measured ($P = 0.02$ for rate of root growth, $P = 0.01$ for root length, and $P = 0.02$ for ratio of root length to root dry weight). These data indicate that the two species responded differently across the soil water content and compacted soil treatments. No such interaction was evident for root and shoot dry weights (data not shown). When species were analyzed separately, effects of bulk density and soil water content showed a strong interaction for both root growth rate and root length of silver maple seedings ($P = 0.0003$ and $P = 0.0001$, respectively) (Figure 3). Although soil water content did not affect root growth rate or root length of silver maple in the highly compacted soil (1.7 g cm^{-3}), root growth rate and root length increased rapidly with increasing soil water content in the moderately compacted soil (1.5 g cm^{-3}) ($P = 0.008$ and $P = 0.004$, respectively). Multiple comparisons with LSD at $\alpha = 0.05$ indicated that root growth rate and root length of silver maple seedlings in the wet soil (0.006 MPa) were significantly greater than in the moist (0.026 MPa) or dry (0.06 MPa) soils.

Many dogwoods died during the experiment. Although no statistically significant cause could be identified, only 38% of the pots containing soil at a water tension of 0.006 MPa had surviving plants at the end of the experiment. At soil water tensions of 0.026 and 0.06 MPa, 58% of pots had survivors. In contrast, all but one maple pot had surviving plants.

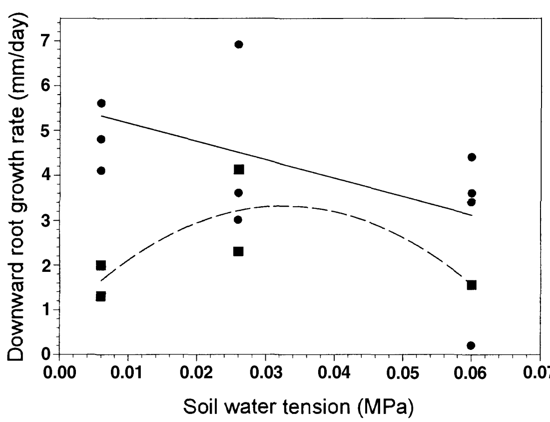

Figure 2. Downward root growth rate of silver maple (● solid line) and dogwood (■ broken line) seedlings at low soil strength (0.06 MPa) across soil water tensions. Lines are least squares regressions reflecting the significant trends identified: a linear trend for silver maple ($P = 0.011$) and a quadratic trend for dogwood ($P = 0.003$).

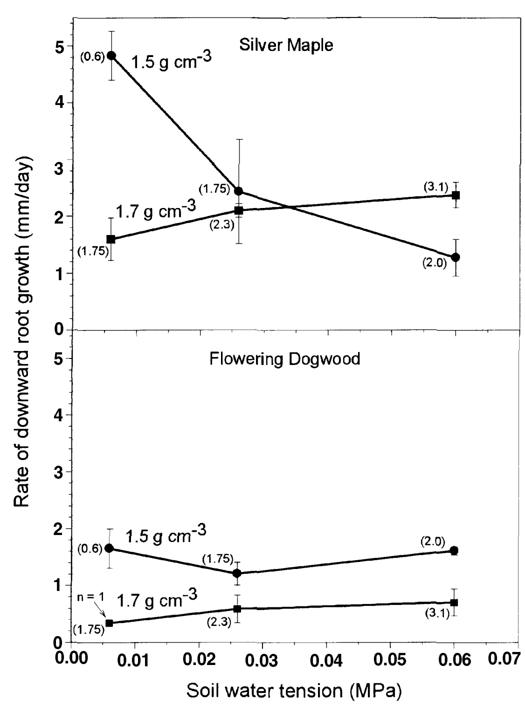

Figure 3. Downward root growth rate for dogwood and silver maple seedlings at two bulk densities (1.5 and 1.7 g cm^{-3}) across soil water tensions. Numbers in parentheses to the left of data points indicate soil strength in MPa for that treatment. Bars indicate standard error.

High bulk density (1.7 g cm^{-3}) reduced root growth rate of dogwood seedlings (P = 0.002) (Figure 3). In contrast to silver maples, however, root growth rate of dogwood seedlings was unaffected by soil water tension (P = 0.54) and no interaction was evident. No significant interactions or main effects were detected in dogwood seedlings for any of the other variables measured (root length, root and shoot dry weights, and ratio of root length to root dry weight) (data not shown).

The ratio of root length to root dry weight provides an index of root morphology. A low ratio represents a higher degree of stubbiness, a root morphology sometimes associated with roots grown in compacted soil or at low oxygen concentrations (Hook et al. 1971, Eavis 1972). Bulk density and soil water tension interacted in their effects on this ratio (P = 0.023) in silver maples, but not in dogwoods (Figure 4). In silver maples, soil water content affected root stubbiness at a bulk density 1.5 g cm^{-3}, but not in the more compacted soils. Multiple comparison by LSD at α = 0.05 showed that root stubbiness was reduced in the wet soil compared with the moist and dry soils. This corresponds with our observation that the root systems of silver maple seedlings appeared more spreading and fibrous with thinner roots in the treatment providing a 0.006 MPa water tension, a 0.6 MPa penetration resistance, and a 1.5 g cm^{-3} bulk density than in the other treatments. For dogwoods, the ratio of root length to root dry weight was not significantly affected by any factor, although there was some indication that a high bulk density (1.7 g cm^{-3}) tended to increase root thickness (P = 0.066).

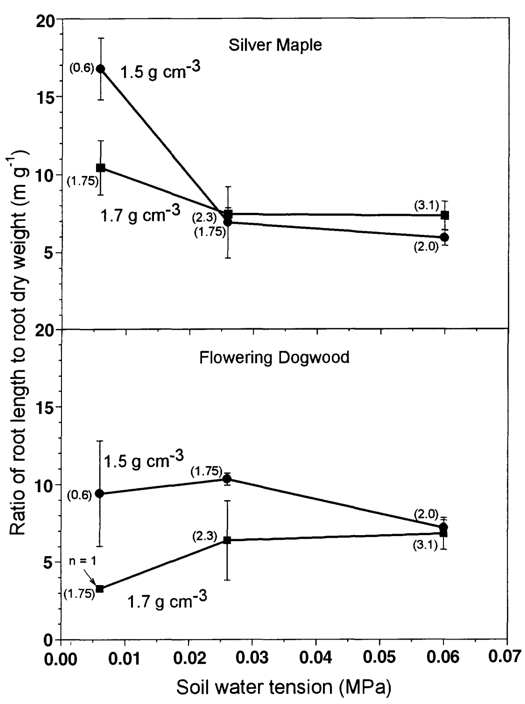

Figure 4. Ratio of root length (m) to root dry weight (g) for silver maple and dogwood seedlings at two bulk densities (1.5 and 1.7 g cm^{-3}) across soil water tensions. Numbers in parentheses to the left of data points indicate soil strength in MPa for that treatment. Bars indicate standard error.

There was a weak positive correlation (r = 0.40) between soil water content and oxygen diffusion rate (ODR) (P = 0.07). Variation among replicates was large, mainly because low ODR (< 0.4 mg cm^{-2} min) occurred at all soil water tensions. In the wet soils, mean ODRs were less than 0.5 mg cm^{-2} min for all replications, whereas values reached well above 0.8 mg cm^{-2} min in the moist soils and 1.0 mg cm^{-2} min in the dry soils. Mean ODR was unrelated to soil strength.

Discussion

Silver maple is known to be tolerant of prolonged submergence (Hosner 1960, Loucks and Keen 1973), whereas flowering dogwood shows poor survival on poorly drained soils (McLemore 1990). The greater sensitivity of dogwood to poor drainage was also evident in our experiment (Table 2 and Figure 2). In many species, root growth is severely restricted when ODR is below 0.4 mg cm^{-2} min (Erickson 1982); however, silver maple produced extensive root systems in wet soil with low resistance where mean ODR was only 0.28 mg cm^{-2} (SE = 0.05).

Downward root growth rate of both species decreased with increasing soil resistance (Figure 1), indicating that the ability to penetrate harder soils does not account for the success of silver maple in compacted soils compared with dogwood. Other researchers have also noted few differences among species in their ability to penetrate hard soil. For example, when root growth of 22 crop species was evaluated in very compacted soil (4.2 MPa), root elongation of all species was reduced between 92.2 and 97.5% (Materechera et al. 1991). At lower soil strengths, on the other hand, root elongation was somewhat less affected in peanut than in cotton by increases in soil strength from 0 to 1.0 MPa (29 versus 62%) (Taylor and Ratliff 1969). Taylor and Ratliff also found that soil strength, rather than bulk density, was the primary factor restricting root growth. This effect was independent of soil water except in dry soils. Other studies have demonstrated an interaction between aeration and soil strength on root growth (Tackett and Pearson 1964). Because of our treatment structure, we were unable to test statistically for an interaction effect across our entire range of data. Consistent with the findings of Taylor and Ratliff (1969), however, there was no interaction across the moist and wet soils at the two lowest soil strengths. Interactions may have occurred at higher soil strengths, but as root growth is already severely restricted at this point, it is not likely to be a factor in the success of particular species in compacted soils.

When wet, soil compacted to a bulk density of 1.5 g cm^{-3} had a soil strength of 0.6 MPa (a very low resistance); silver maple, but not flowering dogwood, was able to take advantage of the reduced soil strength (Figure 3). At the same soil water tension, the highly compacted soil (1.7 g cm^{-3}) maintained a soil strength of 1.75 MPa, and no increase in rate of root growth or root length occurred in response to the increase in soil water content (cf. Figure 1). This finding indicates that the highly compacted soil was not soft enough to create an opportunity for root growth when wet. Even when saturated, the soil compacted to 1.7 g cm^{-3} had a soil strength of 1.56 MPa, suggesting that opportunities for root growth would be few in most highly compacted soils regardless of soil water content.

The mechanism by which bottomland species tolerate inundation has not been identified. It has been suggested that flood tolerance is related to a plant's ability to function when oxygen concentration is low. Some flood-tolerant tree species maintain higher root starch concentrations after prolonged flooding than less tolerant species (Gravatt and Kirby 1998). In the genus *Myosotis*, wetland species were found to maintain a fructan:starch ratio that could allow roots to continue to function as a sink for photosynthate, whereas their non-wetland counterparts did not (Albrecht and Biemelt 1998). Many wetland species develop aerenchymatous tissue in response to flooding, thereby increasing root porosity as a means to improve oxygenation of the flooded root tissues, whereas most non-wetland species do not form aerenchyma (Justin and Armstrong 1987). Although flooding tends to reduce secondary thickening of roots (Justin and Armstrong 1987), the anatomical changes associated with flooding can result in increased root diameters (Hook et al. 1971). Mechanical impedance also results in increased root diameters (Tackett and Pearson 1964, Materechera et al. 1991). In our experiment, silver maple roots growing in soil of bulk density 1.5 g cm^{-3} were significantly less thickened in the wet soil, where soil strength was low, than in the dry soil (Figure 4). Similarly, Bengough and Young (1993) found that root diameters of pea seedlings only increased significantly when soil was compacted to 1.4 g cm^{-3} and soil strength was above 1.5 MPa. However, under similar conditions, dogwood root thickness was unaffected. In dogwood, the ratio of root length to root dry weight was greatest (i.e., roots were thinnest) in the moist uncompacted soil (15.67 ± 1.37 m g^{-1}), whereas silver maple seedlings produced the thinnest roots in wet soil of the same soil strength (i.e., 0.6 MPa). This may indicate differing responses of the study species to soil water tension. Greater root thickening has been associated with increased ability to exert pressure (Materechera et al. 1991), but we found no evidence of this in our experiment.

In the field, soil water content fluctuates on a daily and a seasonal basis. Soils are frequently near saturation in spring, which is also an optimum time for root growth of many species (Harris et al. 1995). Furthermore, because water moves more slowly through compacted soils than through uncompacted soils, compacted soils are more likely to remain wet, extending the opportunity for root growth for silver maple. We note that other factors may also contribute to the poor success of flowering dogwoods in urban areas. For example, dogwoods may not be able to survive long periods of wet soil. Furthermore, compacted and poorly drained soils typically result in shallower root systems (Voorhees et al. 1975, Gilman et al. 1987, Justin and Armstrong 1987), making the shallow-rooting dogwood (McLemore 1990) more susceptible to drought.

We conclude that silver maple trees, but not flowering dogwoods, would be able to take advantage of low soil strength resulting from wet soils. This could enable silver maples to achieve greater success in compacted soils in the field than flowering dogwood. Because of the role of high soil water content in limiting root extension of dogwoods, our hypothesis could be applicable to a broader range of bottomland and mesic tree species. However, we note that, although silver maple and dogwood are bottomland and mesic tree species, respectively, it is possible that the responses we observed to our experimental conditions were specific for these species and not indicative of the responses of other trees of these classes.

References

Alberty, C.A., H.M. Pellett and D.H. Taylor. 1984. Characterization of soil compaction at construction sites and woody plant response. J. Environ. Hortic. 2:48–53.

Albrecht, G. and S. Biemelt. 1998. A comparative study on carbohydrate reserves and ethanolic fermentation in the roots of two wetland and non-wetland species after commencement of hypoxia. Physiol. Plant 104:81–86.

ASTM. 1999. Standard test method for moisture content penetration resistance relationships of fine-grained soils. Annual Book of ASTM Standards. 4.08. No. D-1558-94. American Society for Testing and Materials, West Conshohocken, PA, pp 135–137.

Bengough, A.G. and I.M. Young. 1993. Root elongation of seedling peas through layered soil of different penetration resistances. Plant Soil 149:129–139.

Buttery, B.R., C.S. Tan, C.F. Drury, S.J. Park, R.J. Armstrong and K.Y. Park. 1998. The effects of soil compaction, soil moisture and soil type on growth and nodulation of soybean and common bean. Can. J. Plant Sci. 78:571–576.

Day, S.D. and N.L. Bassuk. 1994. Effects of soil compaction and amelioration treatments on landscape trees. J. Arboric. 20:9–17.

Eavis, B.W. 1972. Soil physical conditions affecting seedling root growth I. Mechanical impedance, aeration and moisture availability as influenced by bulk density and moisture levels in a sandy loam soil. Plant Soil 36:613–622.

Erickson, A.E. 1982. Tillage effects on soil aeration. *In* Predicting Tillage Effects on Soil Physical Properties and Processes. Eds. P.W. Unger and D.M. Van Doren, Jr. American Society of Agronomy and the Soil Science Society of America, Madison, WI, pp 91–104.

Gilman, E.F., I.A. Leone and F.B. Flower. 1987. Effect of soil compaction and oxygen content on vertical and horizontal root distribution. J. Environ. Hortic. 5:33–36.

Gravatt, D.A. and C.J. Kirby. 1998. Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. Tree Physiol. 18:411–417.

Harris, J.R., N.L. Bassuk, R.W. Zobel and T.H. Whitlow. 1995. Root and shoot growth periodicity of green ash, Turkish hazelnut and tree lilac. J. Am. Soc. Hortic. Sci. 120:211–216.

Hook, D.D., C.L. Brown and P. Kormanik. 1971. Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.). J. Exp. Bot. 22:78–89.

Hosner, J.F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. For. Sci. 6:246–251.

Justin, S.H.F.W. and W. Armstrong. 1987. The anatomical characteristics of roots and plant response to soil flooding. New Phytol. 106:465–495.

Loucks, W.L. and R.A. Keen. 1973. Submersion tolerance of selected seedling trees. J. For. 71:496–497.

McLemore, B.F. 1990. *Cornus florida* L. flowering dogwood. *In* Silvics of North America, Vol. 2, Hardwoods. Eds. R.M. Burns and B.H. Honkala. USDA, Forest Service, Washington, DC, pp 278–283.

Materechera, S.A., A.R. Dexter and A.M. Alston. 1991. Penetration of very strong soils by seedling roots of different plant species. Plant Soil 135:31–41.

Patterson, J.C. 1977. Soil compaction: effects on urban vegetation. J. Arboric. 3:161–167.

Tackett, J.L. and R.W. Pearson. 1964. Oxygen requirements of cotton seedling roots for penetration of compacted soil cores. Soil Sci. Soc. Am. Proc. 28:600–605.

Taylor, H.M. and H.R. Gardner. 1963. Penetration of cotton seedling taproots as influenced by bulk density, moisture content, and strength of soil. Soil Sci. 96:153–156.

Taylor, H.M. and L.F. Ratliff. 1969. Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. Soil Sci. 108:113–119.

Voorhees, W.B., D.A. Farrell and W.E. Larson. 1975. Soil strength and aeration effects on root elongation. Soil Sci. Soc. Am. Proc. 39:948–953.

Wolfe, D.W., D.T. Topoleski, N.A. Gundersheim and B.A. Ingall. 1995. Growth and yield sensitivity of four vegetable crops to soil compaction. J. Am. Soc. Hortic. Sci. 120:956–963.