Tree Root Ecology in the Urban Environment and Implications for a Sustainable Rhizosphere

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Abstract. This review examines current understandings of how the belowground characteristics of urban settings affect tree roots as well as how tree roots contribute to biogeochemical processes in this belowground environment. Soil characteristics common to the urban environment include soil compaction and other physical impediments to root exploration, elevated pH, altered temperature and moisture patterns, and the presence of contaminants. These conditions may alter the growth dynamics, morphology, and physiology of roots. At the same time, roots have a profound effect on the soil environment, with trees directing 40%–73% of assimilated carbon below ground. Urban rhizosphere ecology is a topic of renewed interest for research not only because of its critical role in the urban ecosystem, but also because of its role in global environmental issues. In addition to its obvious contribution to aboveground growth, root exploration of the soil environment can influence environmental sustainability through root contributions to soil structure and drainage. Root influence is further mediated by the intimate role of roots in soil biological activity and thus carbon storage and nutrient cycling. Current advances and implications for emerging research are discussed.

Key Words. Heavy Metals; Road Salt; Root Periodicity; Soil Compaction; Soil Structure; Urban Hydrology; Urban Infrastructure.

The root-soil environment—the urban rhizosphere—is critical not only to tree health, but to urban ecosystem function as well. The performance of urban trees depends upon the ability of their root systems to acquire resources and provide anchorage. However, conditions prevalent in the built environment, such as compacted soils, underground infrastructure, chemical contamination, and excessive heat, create a unique and often unaccommodating environment that may impair root growth and development. In addition, practices associated with establishing and maintaining a landscape, such as transplanting large trees and employing irrigation systems, can alter tree root growth dynamics. In turn, tree roots alter the belowground environment through their influence on biological, physical, and chemical soil properties. This urban rhizosphere ecology has implications for both establishing trees in cities, and for assessing potential ecosystem services that trees, and their root systems in particular, provide to society. The scope of this review includes root responses to environmental elements typical of urban settings (for example, soil compaction) and root interactions with that environment through carbon deposition and other means. This paper avoids discussion of root architecture and specific root management practices (e.g., directing roots with barriers or planting space designs, root pruning, fertilization), and instead focuses on root ecological interactions with the environment. These interactions include growth periodicity; root response to physical constraints and soil chemical and biological properties; and root contributions to characteristics of the belowground environment that relate to contemporary discussions of environmental sustainability, such as carbon sequestration, erosion control, and soil hydrological processes. The purpose of this paper is to provide a review of the literature in this emerging area of inquiry in the context of arboriculture and urban forestry that will help identify knowledge gaps and inform future research.

ROOT GROWTH PERIODICITY—RESPONSES TO TRANSPLANTING, SOIL TEMPERATURE, AND SEASON

Root growth, especially fine root production and mortality, is a dominant feature of the belowground ecosystem where trees are present. In arboriculture and urban forestry, the question "When do tree roots grow?" has been largely addressed in the context of transplanting (Harris et al. 2001; Harris et al. 2002; Richardson-Calfee et al. 2007; Richardson-Calfee et al. 2008), where tree establishment depends upon root exploration of the new site (Harris 2007) and can be influenced considerably by transplant time (Richardson-Calfee et al. 2004).

Mathematical modeling of root growth periodicity has shown that resource limitation feedback between shoot and root growth results in a balance between the two processes that is favorable to tree growth in the particular environment where it is located (Thornley 1972; Thaler and Pagés 1998). Investigators have reported that many temperate woody plants exhibit pronounced periods of root elongation in autumn and spring, although activity level will decline during shoot expansion as resources are allocated to aboveground parts (Stone and Schubert 1959; Stone et al. 1962; Cripps 1970 Roberts 1976; Deans 1979; Dell and Wallace 1983; Wargo 1983; Deans and Ford 1986; Harris et al. 1995; Harris and Fanelli 1999). Although root growth is clearly linked to shoot growth by endogenous signals (Richardson 1958; Larson and Whitmore 1970; Farmer 1975), climate, local weather, and soil conditions are key factors controlling these root growth periods. In particular, root growth is strongly influenced by soil temperature and moisture (Lyr and Hoffman 1967). Each species has a different amplitude, or "ideal" range, of soil temperature that is suitable for root growth. This range usually corresponds to the climate of the region where the species (or species ecotype) is native. The typical temperature range that permits root growth

for temperate zone species is between 2°C and 25°C (Lyr and Hoffman 1967). Root elongation of many temperate species is severely limited when soil temperatures fall below 10°C (Harris et al. 1995; Harris et al. 1996). In contrast to their shoots, which have a dormant period that can only be overcome by chilling, the roots of many temperate zone trees do not exhibit an easily identified period of innate dormancy (Richardson 1958; Taylor and Dumbroff 1975), and can respond quickly to warming soil. However, Arnold and Young (1990) found evidence with several *Malus* (apple) species that an innate root dormancy satisfied by low temperature exposure may exist in some tree species. Lack of moisture suppresses root growth in two ways: first by restricting water uptake that drives cell expansion, and second by increasing soil strength (see *Compacted Soil as a Permeable Impediment*). For trees in tropical areas, water availability is the main environmental determinant for periodic root growth patterns (Borchert 1994), and root biomass is strongly correlated with soil moisture across tropical moisture gradients (Green et al. 2005; McGroddy and Silver 2009). In temperate species, soil moisture dynamics influence root growth periodicity within the confines of temperature controls (Tesky and Hinkley 1981; Kuhns et al. 1985).

ROOT RESPONSE TO PHYSICAL CONSTRAINTS
The ability of roots to explore the belowground environment in urban settings influences tree health, stability, and longevity. However, few studies have addressed rooting response of urban trees to specific characteristics of the belowground environment (for a general view of root architecture in urban settings, see Day et al. 2010). In a study encompassing seven German cities, 20- to 40-year-old *Tilia* spp. (lindens, species not identified) were excavated in an attempt to identify belowground factors that influenced root penetration and proliferation (Krieter 1986). One unusual facet of this large-scale study was the excavation of potential rooting spaces under streets and sidewalks. Root penetration and fine root proliferation were influenced by soil type. Both pure sands and gravel layers (no fine materials) as well as highly compacted loamy and clayey soils restricted or prevented root penetration (see also *Soil Compaction*). Greater fine root proliferation was observed within irrigated areas, around utility and irrigation lines, in areas with coarse gravel and debris mixed with finer materials (clay and silt), and at curb interfaces and similar structures where a physical "dam" was created that may have collected water. Even with this large-scale study, however, variation was considerable, and the root responses observed may have been unique to German street tree installation practices, to the northern European climate, or to the particular tree species.

As this study demonstrates, there are multiple physical constraints that dictate root exploration of the subterranean urban environment. These constraints can be broadly classified into two types: solid impediments such as building foundations, roads, and rocks; and permeable impediments, such as compacted soils. Root exploration of these physical obstructions may further depend upon moisture content.

Urban Infrastructure as a Solid Impediment
In urban conditions, tree root systems may be confined by belowground infrastructure that is essentially impenetrable unless seams, cracks, or other openings are present. Studies in urban and landscape settings documenting tree root growth in and around this infrastructure are extremely limited. Nonetheless, the following examples illustrate the potential for roots to navigate minute fissures in the urban underground complex. In a case study describing management of root–infrastructure conflicts, Schroeder (2005) published a photo of *Acer pseudoplatanus* (sycamore maple) fibrous roots penetrating through mortar joints into an underground utility room and extending 1 m or more through the air inside the chamber. Root interactions with sewer pipes have been reviewed by Randrup et al. (2001), who documented numerous intrusions by roots into unsealed pipes. Although tree roots may successfully explore belowground urban infrastructure, this does not necessarily mean that adequate nutrients and water can be obtained, and spatial availability of these resources can have a profound effect on root distribution (Mou et al. 1997).

Because research in urban settings is limited, we must rely on studies in analogous situations to provide additional insight into root response to physical constraints. For example, trees adapted to arid, rocky conditions may grow roots through very small cracks (less than 0.3 cm wide) in rock up to 9 m deep in order to access the water table (Saunier and Wagle 1967). In southwestern Oregon, U.S., roots were found in rock fissures as small as 100 µm (Zwieniecki and Newton 1995). While the stele retains its regular shape under such confined conditions, the root cortex may become flat, creating wing-like structures on the sides of the stele (Saunier and Wagle 1967; Stone and Kalisz 1991; Zwieniecki and Newton 1995). These structures have been measured at up to 0.75 mm across with root hairs only occurring on the edges of the structures (Zwieniecki and Newton 1995). These studies illustrate how roots might penetrate minute fissures in concrete, masonry, or other urban infrastructure and adapt anatomically to the space. Documented observations in urban environments are few, and the conditions necessary for this adaptive growth are unknown. In some cases, tree roots will grow around physical obstacles. For example, *Platanus × acerifolia* roots were observed to partially or completely encapsulate 2 cm limestone gravel that was a component of a structural soil mix (Bassuk 2008).

Compacted Soil as a Permeable Impediment
Soil compaction arising from urban land development and use is a more pervasive cause of root restriction for landscape trees. Compaction occurs as soil is compressed, which degrades structure, diminishes porosity, and increases strength—the soil's physical resistance to penetration. Soil compaction in urban areas is widespread. In a study of 48 sites in Moscow, Idaho, and Pullman, Washington, recently developed sites were found to have higher soil bulk densities than older sites (Scharenbroch et al. 2005), presumably due to more stringent engineering standards and more effective compaction equipment. Site development practices often entail removal of upper soil horizons (especially O and A) during grading (Jim 1998), leaving denser subsoil at the surface, and the soil underlying pavement is typically compacted to provide structural support. Thus urban tree root systems are likely to encounter compacted soil. These restricted root systems are commonly shallower, confined by dense soil underlying pavement or planting pits, or exhibit less extensive soil exploration than would be possible in uncompacted soil. Root systems in compacted soil are more highly branched and consist of thicker, stubbier roots, which often results in shallower rooting depth (Tackett and Pearson 1964; Voorhees et al. 1975; Gilman et al. 1987; Materechera et al. 1991).

Although bulk density indicates the degree of compaction for a particular soil, it does not provide a complete picture of root inhibition for that soil. Soil texture and moisture must also be considered along with bulk density, because these properties in combination determine soil strength (Taylor and Gardner 1963; Taylor and Ratliff 1969; Zisa et al. 1980; Daddow and Warrington 1983; Day et al. 2000). In their classic study, Daddow and Warrington (1983) used an in-depth survey of forest soil compaction research to create a chart depicting root-growth-limiting bulk density for each soil texture (i.e., the bulk density at which root growth would essentially halt for a given soil texture). As they note, this serves as a useful proxy for soil resistance to penetration, but does not account for other factors that affect soil strength, particularly moisture.

Soil strength is a function of bulk density and moisture content. As bulk density increases due to compaction, the frictional and cohesive forces between soil particles increase and thus soil strength increases (Greacen and Sands 1980). As soil strength increases, root elongation rate decreases due to resistance of soil particles to displacement (Clark et al. 2003). The critical soil strength (measured with a cone penetrometer) above which woody plant root elongation is severely restricted is in the vicinity of 2.3 MPa, depending on soil type and plant species (Day and Bassuk 1994). Soil moisture can alleviate excessive soil strength by lubricating soil particles and the elongating root tip. However, the moisture content required to alleviate excessive soil strength is progressively greater as bulk density increases. In sandy loam soil, the volumetric moisture content at which soil strength fell below the critical limit was about 20% at a bulk density of 1.18 g/cm^3 versus about 30% at a bulk density of 1.26 g/cm^3 (Siegel-Issem et al. 2005).

In compacted soil, the combination of increased volumetric water content, and decreased macroporosity limits gas diffusion and may cause root aeration stress. In silty loam soil compacted to 1.44 g/cm^3, root growth of shortleaf pine (*Pinus echinata*) is limited above 35% volumetric water content due to poor aeration (Siegel-Issem et al. 2005). In a loam soil compacted to 1.5 g/cm^3, root growth of *Cornus florida* (flowering dogwood) is depressed in very moist soils (matric tension of 0.006 MPa and oxygen diffusion rates <0.5 mg cm^{-2} min), while roots of *Acer saccharinum* (silver maple) are not (Day et al. 2000). However, poor aeration due to low macroporosity in compacted soil may not be an issue in unsaturated soil (Day et al. 1995; Aust et al. 1998; Day et al. 2000).

Species vary in their ability to elongate roots in compacted soils. This is not simply attributable to differential ability to exert pressure on the soil, although slight differences have been demonstrated among species in controlled laboratory environments. For example, Materechera et al. (1991) evaluated root penetration of 22 crop species at an extreme soil strength of 4.2 MPa and found that all species had root elongation reduced between 92 and 98% and that the ability of a given species to penetrate strong soil was positively correlated with root diameter. At lower soil strength levels, species differences in root response to compaction can be easier to discern. For example, when soil strength is increased from 0 to 1.0 MPa, root elongation of peanuts is reduced by only 29% while elongation of cotton roots is reduced by 62% (Taylor and Ratliff (1969). However, low soil strengths such as these are unlikely to be encountered in the field except under wet conditions. These data illustrate that root growth of woody plants will be restricted with *any* increase

in soil strength, rather than growing "normally" until a certain threshold is reached. In a recent study with native Australian *Eucalyptus* spp., root penetration decreased linearly as soil bulk density was increased from 1.0 to 1.4 g/cm^3 (soil texture not described), further demonstrating the immediate reduction in root penetration when soil compaction increases (Skinner et al. 2009).

Variation in species tolerance of soil compaction is currently conceived to be a complex response to the whole rooting environment. The strongest hypothesis for explaining the ability of certain tree species to tolerate compacted soil is the "root growth opportunity" hypothesis, which states that tree species tolerant of wet soils (e.g., bottomland species) can grow roots during wet periods when soil strength is low, while species less tolerant of wet soils (i.e., soil hypoxia) cannot. Thus bottomland species may be expected to have a greater root growth opportunity when soil strength is low, and thus be more adapted to soil compaction, such as is found in urban areas. Generalized models addressing this root growth opportunity were initially developed to integrate the limits of soil strength with the limits of soil water content into a single descriptor for evaluating soil quality for crop production (Letey 1985), and were eventually described as the Least Limiting Water Range (da Silva et al. 1994). Day et al. (2000) presented a similar hypothesis for urban trees and evaluated the root growth opportunity in the context of species tolerances via a study of silver maple (*Acer sacharrinum*) and flowering dogwood (*Cornus florida*). Siegel-Issem et al. (2005) further developed this approach as a measure of forest soil productivity. These last experiments evaluated the influence of soil strength, bulk density, soil moisture, and oxygen diffusion rate on seedling root growth, providing support for this hypothesis as an explanation for species response to compacted soils (Day et al. 2000; Siegel-Issem et al. 2005). Yet, response to compacted soils is influenced by a host of environmental and genetic factors and species differences are not always easily explained (Bassett et al. 2005).

ROOT RESPONSE TO SOIL CHEMISTRY AND CONTAMINANTS

Urban soils typically have very different environmental inputs than rural or forested landscapes. These include anything related to intense human activity, such as de-icing salts, tire residue, engine oil, construction debris, landscape mulches, and lawn clippings. Many of these items alter soil chemistry. In addition, brownfields—land previously used for industrial, or sometimes other commercial, purposes that may have environmental contaminants—are prevalent in many countries (Oliver et al. 2005). Decisions concerning brownfield development receive more attention as land becomes more scarce (e.g., Altherr et al. 2007), and the numerous economic, social, and environmental benefits of urban greenspaces are better appreciated. In a Canadian study, uncertainty about the effects of soil contamination and approaches to its mitigation was ranked as the most important noneconomic barrier to developing these areas as greenspace (De Sousa 2003). Chemical contaminants are also common beyond brownfields. These include de-icing salt as well as heavy metals such as Cu, Pb, and Zn that are by-products of automobile traffic (Pouyat et al. 1995; Irvine et al. 2009). Thus, there is increasing need to broaden our knowledge of root interactions with chemically altered urban soils.

Adverse Soil pH

While some instances of slightly lower pH in forested lands near urban cores have been documented (Pouyat et al. 1995), disturbed urban soils are rarely too acidic for satisfactory tree growth. Instead, soil alkalinity is a more common consequence of urbanization and therefore a more common impediment to tree health. The use of concrete and other calcareous construction materials is nearly universal in urban areas and the removal of topsoil and horizon mixing facilitates the increase in soil pH. In Hong Kong, China, soils sampled from 100 locations around the city core had a mean pH of 8.68 (Jim 1998). Sampling of soil pH in the top 10 cm of mineral soil around the Virginia Tech central campus in Blacksburg, VA, by students during laboratory exercises in horticulture and forestry classes taught by two authors of this review revealed soil pH is always above 7.0 and as high as 8.3, whereas nearby relatively undisturbed sites has surface soil pH of 5.9–6.2 and nearby disturbed roadside ditches a pH of 6.8–7.3 (Harris et al. 2008). A study of six urban landscapes in Moscow, ID, and Pullman, WA, found average pH ranges from 6.64 to 7.32 (Scharenbroch et al. 2005).

At higher soil pH, many tree species suffer from micronutrient deficiencies (B, Cu, Fe, Mn, and Zn) because these nutrients exist in insoluble forms that are unavailable to the plant (Mengel and Kirkby 2001). Availability of P is also reduced in alkaline soil. Elevated pH may also alter the composition and abundance of endomycorrhizal fungi that inhabit soil (Porter et al. 1987), which could influence root system colonization and therefore nutrient uptake capacity. On the other hand, soil alkalinity also reduces the solubility of certain elements such as Al and Pb, which are toxic to tree roots.

Sensitivity to alkalinity-induced nutrient deficiencies differs among tree species. In even slightly alkaline soils, sensitive species such as *Quercus palustris* (pin oak) and *Quercus phellos* (willow oak) may develop interveinal chlorosis in response to Fe and Mn deficiency while others remain unaffected [e.g., *Ulmus americana* (American elm) and *Platanus* × *acerifolia* (London plane)] (Dirr 1998). Root adaptations have been identified in some tolerant species that enhance Fe uptake, one example being the production of a specialized enzyme to reduce Fe (Moog and Brüggemann 1994). An evaluation of olive tree cultivars and rootstocks indicated that tolerance of calcareous soils was conferred by the rootstock rather than the scion (Alcántara et al. 2003).

Because of the ubiquity of alkaline soils in urban settings and the varied sensitivity of tree species to these soils, lists have been published to assist practitioners in selecting tree species and cultivars that tolerate particular soil pH levels (e.g., Appleton and Chaplin 2001; Bassuk et al. 2009). These lists are based partly, although certainly not exclusively, on practitioner experience since research reports are limited on many trees. In orchard trees, a clear asymptotic relationship is apparent between extractable Fe in the soil and leaf chlorosis: leaf greenness increases rapidly with increasing extractable Fe until a maximum level is reached, at which point the relationship levels off (de Santiago et al. 2008). However, in some urban trees, iron deficiency chlorosis has not shown a strong relationship with soil pH (Watson and Himelick 2004) and therefore likely not with the associated variable of extractable soil Fe either, although this last relationship has not been reported. A host of root system stresses – including root severance can negatively affect Fe uptake by urban tree roots. This has real consequences for urban trees since Fe or Mn deficiency impairs photosynthetic capacity (Abadía et al. 1999), which may diminish tree growth and stress tolerance.

Salt Contamination

Salt contamination of soils can stunt or kill tree roots depending upon species sensitivity, environmental variables (soil physical and chemical properties, precipitation, light intensity, temperature), duration and timing of exposure, and severity of contamination (Headley and Bassuk 1991; Bernstein and Kafkafi 2002). Salt contamination can arise from meltwater or spray from de-icing salts (Kayama et al. 2003), from saltwater intrusion into groundwater, from sea salt blown ashore in coastal areas, or even from repeated applications of sewage sludge (Usman et al. 2004). De-icing salt is a common soil contaminant in colder climates. NaCl is the most widely-available, cost-effective material for de-icing streets, sidewalks, and parking lots, although other formulations such as $CaCl_2$ and K_2CO_3 are used. In Denmark, high road salt concentrations were found in soils within 2 m of roadways, but quickly dissipated at greater distances (Pedersen et al. 2000). When precipitation is abundant, salt does not persist in the top layers of soil and eventually leaches down to subsoil horizons and groundwater (for a review of the environmental effects road salt, including effects on vegetation, see Priority Substances List Assessment: Road Salt 2001).

Because of its agronomic importance, salt stress has been the subject of considerable research. Nonetheless, the physiological mechanisms for tolerance are varied and complex and likely represent expressions of multiple genes as well as other adaptive responses (for reviews, see Cheeseman 1988). Root growth is usually less sensitive to salt stress than shoot growth, resulting in a higher root:shoot ratio in salt-stressed plants (Cheeseman 1988). However, in landscape situations, tree roots can be subjected to acute salt shock when large amounts of roadside deicing salt are applied (Headley and Bassuk 1991). High levels of salinity impose two types of stress on roots; first, osmotic stress results from lowered water potential in the soil solution (desiccation), and second, ionic stress results from changes in concentrations of specific ions in the soil solution and inside growing tissues (toxicity). Root systems vary in their ability to tolerate salts; tolerant species may be able to selectively exclude salt ion uptake (Lloyd et al. 1987). However, few generalizations can be made. For example, in a study of grafted *Citrus* spp. (lemon trees), salinity reduced growth of some rootstocks more than others and in some cases physiological stress was governed primarily by toxic levels of Na^+ and Cl^- in leaf tissue (Gimeno et al. 2009). Salinity can also alter the symbiotic relationship between the roots of woody plants and mycorrhizal fungi, but this is not well understood at this time (Tian et al. 2004; Porras-Soriano et al. 2009). Because of the economic importance of salt tolerance in food crops, research is quickly identifying plant mechanisms of salt tolerance and their genetic control (e.g., Papdi et al. 2009).

Trace Elements and Heavy Metals

Numerous trace elements are essential or beneficial for plant function, including B, Cu, Fe, Mn, Mo, and Zn (essential); Cl and Ni (sometimes essential); and Co, I, Na, Si, and V (beneficial) (Marschner 1996; Mengel and Kirkby 2001). However, all these elements can be toxic when their concentrations are too high (Hagemeyer and Breckle 2002). Heavy metals are commonly

found in urban soils. They persist in the environment and can accumulate over time to levels toxic to plants. Besides industry, vehicular traffic is the main source of metal pollutants. The highest levels occur near roads (Jim 1998) and levels decrease with distance from the roadside (Birch and Scollen 2003; Fakayode and Olu-Owolabi 2003). Although modern regulations have reduced Pb emitted from vehicles, it persists in the environment and may remain elevated in roadsides. Zinc from tires is another major contaminant associated with vehicular traffic (Roberts et al. 2006).

Excessive concentrations of trace elements or heavy metals cause phytotoxicity through several mechanisms, including changes in cell membrane permeability, interference with metabolic processes, and replacement of essential ions (Patra et al. 2004). In roots, metals inhibit growth by interfering with cell division or cell elongation (Hagemeyer and Breckle 2002). These negative effects on roots may translate directly to negative effects on aboveground physiological function. For example, Hg toxicity symptoms of spruce seedlings such as decreased transpiration and lowered chlorophyll content were attributed primarily to root injury (Godbold and Hutterman 1988). Enhanced lateral root formation and compact, dense root branching habit have been observed in response to increasing concentrations of Pb, Zn, Mn, Cd, and Cu (Kahle 1993; Hagemeyer and Breckle 2002). It is thought that injury to the root apex by metals diminishes apical dominance, thereby increasing lateral root primordia. Lead also interferes with root hair formation. For example, root hair formation in *Fagus sylvatica* (European beech) was strongly inhibited by Pb at a concentration of 44 ppm and was completely eliminated at 283 ppm (Kahle 1993). Although a reduction in root hair density is an adaptive response for decreasing absorption of heavy metals, absorption of water and nutrients will also likely be reduced. In addition, nutrient uptake may be further reduced because of direct ion competition from heavy metals. For example, Kahle (1993) found lower nutrient concentrations in roots of numerous tree species exposed to heavy metals due to both reduced uptake and increased membrane leakage. Thus heavy metals commonly found in urban areas may both reduce root exploration of the soil and restrict uptake of nutrients and water. For a discussion of heavy metal threshold concentrations that reduce root growth, see Kahle (1993). Metal phytotoxicity is tempered in soils with high pH, CEC, clay content, and organic matter because these conditions lower metal bioavailability (for reviews, see Kahle 1993; Sieghardt et al. 2005).

Tolerance of heavy metals

Plant tolerance of heavy metal toxicity varies among species and genotypes, and tolerance of one metal does not imply tolerance of all metals. Because of their relatively long life span, trees can accumulate large amounts of toxic elements when growing on contaminated soils. Moreover, they often lack the morphological and physiological adaptations possessed by herbaceous plants that regulate internal concentrations of toxic trace elements (Hagemeyer and Breckle 2002). Heavy metals are likely not uniformly accumulated in the root system. Violina et al. (1999), for example, found that Pb concentrations in grapevine (*Vitis* spp.) were highest in fine absorbing roots and much lower in older, woody roots. Trees that can survive on metal-rich sites may rely on phenotypic plasticity, which enables roots to avoid areas of high contamination (Lepp 1991; Turner and Dickinson 1993; Hagemeyer and Breckle 2002). On the other hand, tolerant ecotypes of

some genera, such as *Betula* spp. (birch) and *Salix* spp. (willow), may exhibit multiple survival strategies, including synthesis of phytochelatins that immobilize metal ions within the plant, rapid root turnover, and metal ion exclusion (Kahle 1993), and can become dominant species on metal contaminated sites (Gallagher et al. 2008). *Salix* spp. are frequently employed in phytoremediation of soils, where plants are selected for their ability to accumulate heavy metals or other contaminants from the soil and later harvested and safely disposed (Pulford and Watson 2003).

Organic Pollutants and Pesticides

There are a number of synthetic organic compounds (commonly pesticides and industrial compounds/by-products) that are potential pollutants in urban settings, and some may persist in the environment. Toxic levels of industrial organics usually are a concern on sites that have historic industrial activity, but may also occur at accident "hotspots" such as along roadways and railways. Some pesticides can have a negative impact on nontarget soil organisms (Bunemann et al. 2006) and may therefore adversely affect root growth. Mycorrhizae, for example, are sensitive to certain pesticides, particularly fungicides. Container-grown *Liriodendron tulipifera* (tulip-poplar) inoculated with arbuscular mycorrhizal fungi and subsequently soil-drenched with benomyl fungicide had reduced growth and mycorrhizal colonization compared to their non-drenched counterparts (Verkade and Hamilton 1983).

ROOT CONTRIBUTIONS TO ENVIRONMENTAL SUSTAINABILITY

Tree roots have the potential to positively influence soil quality, hydrology, and biogeochemistry in urban settings. More specifically, the roots of trees improve soil physical properties; maintain or enhance soil organic matter, N_2 fixation, and nutrient uptake from below the reach of crop roots; increase water infiltration and storage; decrease loss of nutrients to erosion and leaching; decrease soil acidity; and improve soil biological activity (Young 1997).

Soil Structure

There are many factors in the urban environment that contribute to degradation of soils and in particular, soil structure (see *Compacted Soil as a Permeable Impediment*). Thus, the potential of tree roots to influence soil structure is of considerable interest. Tree roots are primary contributors to the development of soil structure and, in the longer term, soil formation. This new appreciation of the influence of roots on soil is redefining and enlarging our concept of rhizosphere: the area where soil interacts directly with living roots (Richter et al. 2007). Tree root contributions to soil structure not only affect plant growth, but a host of other soil functions that provide ecosystem services such as stormwater runoff mitigation through enhanced soil permeability (Bramley et al. 2003; Bartens et al. 2008).

Tree roots form soil macropores

Tree roots aid in improving soil structure in several ways. One of the most significant plant-induced changes in soil structure is the formation of continuous macropores (i.e., channels) by penetrating roots (Angers and Caron 1998). A large proportion of pores formed by roots fall into the macropore range (>30 μm) (Gibbs and Reid 1988). These macropores facilitate soil aera-

tion and water percolation and storage as well as create zones of failure, which help fragment the soil, form aggregates, and decrease resistance for further root growth. Roots form macropores by creating compressive and shear stresses when growing through the soil matrix (Goss 1991). Radial pressure exerted by growing roots compresses adjacent soil (Dexter 1987), which enlarges existing pores and creates new ones. Bartens et al. (2008) demonstrated that live roots can create channels through compacted soils and vastly increase water infiltration, although flow may be greater once roots die and decay (Mitchell et al. 1995). As root decay occurs, tissue remnants and associated microflora coat pore walls, which may enhance water transport efficiency (Barley 1954; Yunusa et al. 2002).

Tree roots aid in soil aggregate formation

Aggregate stability, an indicator of soil structure, results from soil particle rearrangement, flocculation, and cementation; it is mediated by soil organic carbon, biota, ionic bridging, clay, and carbonates (Bronick and Lal 2005). Rhizosphere soil has been found to have greater aggregate stability than nonrhizosphere soil (Angers and Caron 1998), and is influenced by rhizosphere deposition as well as a number of root system attributes, including root length, mass, density, size distribution, turnover rate, and hyphal growth (Caravaca et al. 2002). Dorioz et al. (1993) observed that adsorption of water by roots promoted reorganization of the clay, characterized by oriented and compacted clay particles, and that this environment was very rich in root mucilage. "The outstanding effect of the rhizosphere on soil structure can be related to the rhizosphere as being the privileged site for growth for a wide range of microorganisms at various sizes, each of them organizing the material at its own scale" (Dorioz et al. 1993).

Tree roots can directly enhance aggregation by releasing a variety of compounds that have a cementing effect on soil particles (Bronick and Lal 2005). For example, polysaccharides from root tips can penetrate and impregnate surrounding soil up to 50 μm while bacteria polysaccharides penetrate less than 1 μm (Dorioz et al. 1993). Research suggests that the root exudate polygalaturonic acid (PGA) stabilizes soil by increasing strength of bonds between particles and decreasing wetting rate of soil via water repellency at the soil surface (Czarnes et al. 2000). Tree roots also indirectly contribute to soil aggregate formation and stability because their exudates are a food source for soil organisms, which in turn release their own exudates that contribute to soil aggregation (Tisdall et al. 1978). These exudates are also a food source for earthworms (Angers and Caron 1998), which create macropores as they burrow through the soil (Edwards et al. 1989).

Soil strength and stability

Tree root systems form part of a complex matrix that can stabilize soil and reduce erosion, both important contributions to environmental sustainability. Soil inhabited by plants dries more quickly due to transpiration; as a result, the soil has greater shear and tensile strength and the root/soil tangential resistance to slipping will be increased (Waldron and Dakessian 1982). Lower soil water content resulting from the presence of plants may also help soils resist compaction (Horn and Dexter 1989; Lafond et al. 1992). Deep-rooted woody vegetation extracts more water from greater soil depths than grassy vegetation (Bethlahmy 1962; Rogerson 1976; McColl 1977).

This deep water extraction and resulting wetting and drying cycles can cause shrinkage and strengthening of the soil.

In addition to drying soil, tree roots increase soil stability via mechanical reinforcement (Waldron and Dakessian 1981; Waldron and Dakessian 1982; Abe and Iwamoto 1986; Mamo and Bubenzer 2001a; Mamo and Bubenzer 2001b; Wynn and Mostaghimi 2006). Construction of highways and other infrastructure alters the natural terrain, often resulting in steep, barren slopes that pose a landslide hazard. Tree roots have been used as tools for slope reinforcement, either alone (Norris 2005), or in combination with engineered approaches (Naoto et al. 2008). Although herbaceous vegetation may provide more immediate cover and soil stabilization, woody plants may provide greater reinforcement strength. In a study comparing the shear resistance of soil inhabited by different plants, alfalfa and grass had a more immediate effect on sheer resistance than yellow pine, but the older pine roots were clearly superior to young alfalfa roots, and shearing resistance was proportional to the number and diameter of pine roots (Waldron and Dakessian; Waldron et al. 1983).

Trees can also play an important role in stream bank stabilization (Docker and Hubble 2008; Pollen-Bankhead et al. 2009). In urban areas, stormwater runoff results in widely fluctuating water levels in streams, leading to channel erosion and impaired water quality (Schoonover et al. 2006). An *in situ* study of vegetated stream banks showed that an increase in the volume of roots with diameters of 2–20 mm was correlated with reduced soil erodability (Wynn and Mostaghimi 2006). Wynn et al. (2004) compared root distribution and density in stream banks inhabited by both herbaceous and woody vegetation. Their findings suggest riparian forests may provide better protection against stream bank erosion than herbaceous buffers.

Hydrology

Impervious surfaces, soil compaction, and stormwater drains prevent dispersed infiltration of stormwater in the built environment, decreasing groundwater levels and stream baseflow (Kaye et al. 2006). Even unpaved urban soils can have much reduced infiltration rates compared to undeveloped land (Gregory et al. 2006). In vegetated areas, only 5%–15% of rainwater runs off the ground and the rest evaporates or infiltrates into the soil, whereas about 60% of rainfall in urban areas is exported through storm drains (Bolund and Hunhammar 1999). Older stormwater systems are often connected to sewers and when these stormwater systems overflow, untreated sewage pollutes surface waters. Even if storm drains are not connected to sewers, stormwater is still concentrated and not allowed to infiltrate in a dispersed fashion, thereby reducing the influence of plants and soil on water chemistry and increasing stream temperatures when stormwater is directly deposited into surface waters (Kaye et al. 2006).

Urban trees are well recognized as effective tools for mitigating urban runoff (Xiao et al. 2000; Xiao and McPherson 2003), but the specific role of the root system is largely unrecognized. Root systems aid in dispersal of stormwater into the soil by guiding stormwater along root channels, playing a primary role in base flow (Dasgupta et al. 2006; Johnson and Lehmann 2006), aiding in water infiltration (Bramley et al. 2003; Bartens et al. 2008), and absorbing water (Wullschleger et al. 1998; Szabo et al. 2001). In addition, hydraulic lift by tree roots may improve survival of other plant species in dry climates, thus enhancing the contribution of

the plant community as a whole (Dawson 1993; Dawson 1996). In addition to "lifting" water, trees may redistribute water into deeper soil regions, possibly improving groundwater recharge (Burgess et al. 1998; Burgess et al. 2001). Tree roots may also have indirect effects on the hydrologic cycle through their role in nutrient and carbon cycling and improvements in soil structure.

Nutrient Cycling

Plant nutrient content of urban soils can range from highly deficient due to interrupted nutrient cycles and disturbed soils to overly abundant due to misapplication of fertilizers and other anthropogenic sources. Nitrogen deposition from the atmosphere has increased considerably over the past 150 years, and the consequences of this change are still uncertain (Holland et al. 2005). Urban ecosystems have been identified as sources of nutrient pollution to receiving waters (Boyer et al. 2002), particularly N and P. Urban and suburban watersheds have much higher N losses than completely forested watersheds (Groffman et al. 2004). The input of reactive N compounds in urban areas is also much higher than surrounding, less populated areas, with sources ranging from automobile engines and excessive N fertilization to pet urine and feces (Zhu et al. 2004). Rates of denitrification in urban areas can be very high compared to other ecosystems and N distribution is influenced by stormwater capture systems (Zhu et al. 2004). The effect of such nutrient hotspots on urban tree root systems is poorly documented. However, tree roots can help regulate nutrient cycles by influencing the supply and availability of nutrients in the soil via root turnover, root exudates, and nutrient uptake.

Trees can affect nutrient export by reducing stormwater runoff and soil erosion (see *Hydrology*); stormwater may carry nutrients as well as sediment laden with nutrients that may be tightly bound to soil (e.g., P). Trees can influence nutrient supply in the rhizosphere by biological N fixation, extracting nutrients – especially nitrate – from below the root zone of other plants, and reducing nutrient losses from processes such as leaching and erosion (Buresh and Tian 1997; Jama et al. 1998). Roots influence a complex set of nitrogen transformations that regulate production, flow, and loss of N in ecosystems (Fornara et al. 2009). In a Jamaican study, proximity to *Casuarina cunninghamiana* (river sheoak) trees increased N, NO_3, organic matter, P, Mg, K, Ca, pH, and CEC (Zimpfer et al. 1999). The researchers attributed this response to a complex symbiotic relationship with particular mycorrhizal species. On a global scale, nutrient cycling by plants alters vertical distribution of nutrients within the soil profile, keeping nutrients available nearer the soil surface (Jobbágy and Jackson 2001). For example, sloughed root cells and mucilage contain substantial amounts of soluble C and N (Jones et al. 2004), which is a source of energy for rhizosphere flora and fauna that in turn contribute to a consistent supply of N for plants.

Carbon Cycling, Soil Organic Material, and C Sequestration

Urban regions are large contributors to atmospheric CO_2 enrichment because of both high emissions and fuel use and minimal C sequestration (Kaye et al. 2006). In addition, daily average atmospheric CO_2 concentrations in city centers can exceed 500 ppm, whereas global mean concentrations are 379 ppm (Pataki et al. 2007; Lorenz and Lal 2009). Higher CO_2 concentrations enhance plant growth (Gregg et al. 2003), and trees fix this CO_2 via photosynthesis and sequester it into the soil through litter and root inputs. Urban soils have the potential to store large amounts of root-supplied soil organic carbon (SOC) and therefore to contribute to mitigation of increased atmospheric CO_2 concentrations (Lorenz and Lal 2009). The amount of SOC that can be stored is highly variable – the SOC pool at 0.3-m depth may range between 16 and 232 Mg/ha and between 15 and 285 Mg/ha at 1-m depth (Lorenz and Lal 2009). SOC storage is also dependent on the local climate, land use, and parent material. For example, the cool, wet climate of northeastern United States favors higher accumulation of soil organic carbon than dry, rocky, arid climates (Pouyat et al. 2006).

The role of urban tree root systems in carbon storage has received limited attention, and research rests primarily on results from other ecosystems and laboratory studies. However, the potential for carbon storage through root deposition is considerable. Besides the deliberate incorporation of organic matter, carbon enters soil from plant litter, the release of carbon-rich root exudates, and root death along with associated mycorrhizae (i.e., turnover) (Grayston et al. 1997; Young 1998; Farrar et al. 2003). It has been estimated 2%–4% of net fixed C in plants may be directly deposited into the soil via root exudates (for a review, see Jones et al. 2004). These carbon compounds can also be taken back up by the plant in a controlled fashion (Farrar et al. 2003). Trees direct a greater proportion of their fixed carbon below ground when compared to annual plants, with rates from 40%–73% of assimilated C being demonstrated in studies with trees (Grayston et al. 1997). Up to 47% of carbon allocated to fine roots and mycorrhizae is deposited into soils through root turnover (Fogel and Hunt 1983). Not only does SOC increase activity of microorganisms, but the presence of the microorganisms can initiate a feedback system that increases root exudation (Meharg and Killham 1991). Carbon from plant roots therefore exerts a large control on the soil microbial community and consequently on overall soil health (Brant and Myrold 2006).

As previously discussed, urban soils are often very inhospitable to root growth. Stripping urban land of its vegetation and topsoil, coupled with elevated temperatures, also depletes soil organic matter and consequently decreases soil microbial populations, particularly in newly disturbed soils (McDonnell et al. 1997; Scharenbroch et al. 2005). Soil microorganisms are very important to tree growth because they are critical drivers of nutrient cycling, N fixation, nitrification, and the aggregation of clay particles (i.e., building of soil structure) (Lee and Pankhurst 1992). Urban sites in Colorado, U.S., that were fertilized and irrigated had greater microbial biomass than adjacent agricultural land that was not fertilized or irrigated (Kaye et al. 2005). Takahashi et al. (2008) compared soil C concentrations of different land uses [turf, trees "with management" (weed and litter removal), and trees "without management" in urban parks], and found that at 0–10 cm soil depth there were similar soil C concentrations, but at 10–30 cm, average C concentrations were lower for turf than they were for trees "with management." Trees "without management" resulted in far greater soil C concentrations than the other land uses.

CONCLUSIONS AND FUTURE RESEARCH

This review has focused on the ecophysiology of tree roots in the urban environment and how they interact with this human-dominated world. There are many unanswered questions that relate to management of urban tree root systems,

but comments here are confined to basic research questions that can provide a greater understanding of the role of the tree root system in the ecology of the urban rhizosphere. The following are proposed as possible areas of future research:

1. Biological community in the larger rhizosphere. Evidence is abundant that tree root systems cannot be fully understood separately from the microorganisms that inhabit the larger rhizosphere. Yet, we know little about these communities and how they develop in urbanized settings. The interactions that occur within the larger rhizosphere may not only influence tree growth, but also play a role in certain ecosystem services that trees provide, such as treatment of stormwater, that are now taking on a heightened importance.

2. Soil contamination. Urban infill development is growing in importance as societies seek to protect increasingly scarce agricultural and forested land from development and to rehabilitate previously developed land. Thus, professionals who work with urban trees will be increasingly faced with managing trees on sites that are undergoing rehabilitation, such as brownfields. Although considerable information concerning tree roots and contaminated soils is available from phytoremediation and mine spoils research, this work focuses on maximizing extraction of contaminants by trees and other plants with the intention of eventually harvesting the plant and safely disposing of it. Little is known about long-term challenges to growing trees in contaminated soils and the long-term effects of tree roots on contaminated soils.

3. Climate change. There is a growing body of scientific evidence demonstrating that global temperature is increasing, atmospheric CO_2 levels are rising, N deposition from the atmosphere is increasing, and urban heat islands are generating ground-level ozone. All of these factors affect root growth and development either directly or indirectly through mediation from the aboveground portion of the plant. What will be the responses of tree root systems in this altered environment?

The urban ecosystem is under increasing scrutiny as society strives to manage the environment in a sustainable way. Urban trees play a critical role in the urban environment on many levels. As we increase our understanding of the complex processes at play in the rhizosphere, we will not only be able to better manage landscape trees, but also more fully benefit from their role in urban ecosystem processes.

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