Urban Forestry & Urban Greening 14 (2015) 858–865

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

journal homepage: www.elsevier.com/locate/ufug

Urban forest resilience through tree selection—Variation in drought tolerance in *Acer*

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ARTICLE INFO

Article history:
Received 6 March 2015
Received in revised form 19 July 2015
Accepted 8 August 2015

Keywords:
Ecosystem services
Leaf turgor loss point
Maples
Osmotic adjustment
Urban trees

ABSTRACT

It is widely recognized that trees contribute a range of ecosystem services in urban environments. However, the magnitude of their contribution is closely related to their physiological condition and capacity to persist within our towns and cities. Root loss during transplanting, limited soil volume, disruption to soil hydrological processes and impermeable surfaces result in water deficits being major physiological stress limiting the performance of urban trees. The leaf water potential at turgor loss (Ψ_{P0}) provides a robust measure of drought tolerance since a more negative Ψ_{P0} allows the leaf to maintain physiological function over a wider range of leaf water potentials and, by implication, soil matric potentials (Ψ_{soil}). In this study, Ψ_{P0} was calculated for 27 maple (*Acer*) genotypes based on a known linear relationship between the osmotic potential at full turgor ($\Psi_{\pi 100}$) and Ψ_{P0}. In spring, Ψ_{P0} varied between −1.4 MPa in *Acer carpinifolium* and −2.7 in both *Acer rubrum* 'Northwood' and *Acer x freemanii* 'Autumn Blaze'. During summer, *Acer spicatum* had the highest Ψ_{P0} at −1.6 MPa and *Acer monspessulanum* had the lowest Ψ_{P0} at −4.3 MPa. Significant differences in Ψ_{P0} were found between cultivars of *A. rubrum* and *Acer saccharum*. A highly significant relationship was found between seasonal osmotic adjustment and summer Ψ_{P0} suggesting that osmotic adjustment is a driving force for summer Ψ_{P0} in *Acer* leaves. These data confirm the wide range of tolerance to water deficits in *Acer* and give important insight into the potential of species to tolerate periods of low water availability by providing quantitative data not previously available. The technique shows great promise as a screening tool for the drought tolerance of new and traditional plant material. This data will be highly relevant for those selecting trees for urban sites as well as for nurseries seeking to evaluate genotypes for production purposes.

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1. Introduction

Trees are major components of the green infrastructure in urban environments and their contribution to a range of ecosystem services is widely recognized. These services include mitigation of flood risk, reduced energy use in buildings, increased thermal comfort, mitigation of the urban heat island effect, recreational values, and the enhancement of cultural and aesthetic qualities, etc. (in e.g. Akbari et al., 2001; Xiao and McPherson, 2002; Grahn and Stigsdotter, 2003; Gill et al., 2007; Tyrväinen et al., 2005; Tzoulas et al., 2007).

Since the provision of these services is reliant on healthy trees, assessments of projected ecosystem services frequently assume large, mature trees with good growth rates (Gómez-Muñoz et al., 2010). This assumption is misguided as many urban sites do not provide a high quality growth environment. Variation in the rooting environment of *Pyrus calleryana* Decne. trees lead to an approximately 80% reduction in evapotranspirational cooling as a result of suppressed stomatal conductance (Rahman et al., 2011). Tree height and girth (DBH at 1.3 m) of *Quercus robur* L. showed marked variation across urban sites with different levels of soil aeration (Weltecke and Gaertig, 2012) suggesting carbon sequestration is reduced where soil gas diffusivity is reduced. These data provide evidence that the magnitude of at least some ecosystem services provided by trees will be closely related to their physiological performance and condition.

Water deficits in trees develop when root uptake of water does not meet the evapotranspirational demand from the crown. In

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http://dx.doi.org/10.1016/j.ufug.2015.08.004
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newly planted trees, root loss during transplanting reduces the tree's capacity to take up water even where there is ample water within the bulk soil (e.g. soil matric potential >−0.05 MPa). Consequently, in recently planted trees, water demand from transpiration can rapidly exceed the supply from the root system (Watson and Kupkowski, 1991). If this condition persists, tree decline results from a combination of water supply limiting tree growth, loss of hydraulic conductance, nutrient deficiency and reduced photosynthesis. Moreover, established trees that are well coupled to bulk soil can develop water deficits as a result of climate, restricted soil (rooting) volume, disruption to soil hydrological processes as a result of below-ground urban infrastructure or a combination of the above. Impermeable surfaces may further accelerate the development of water deficits (Craul, 1999; Sieghardt et al., 2005; Morgenroth and Visser, 2011). As a result, 'drought' is often cited as being a major stress in urban landscapes and a primary cause of premature mortality in landscape plants (Bradshaw et al., 1995; Cameron, 2003). Indeed, despite the genetic potential to grow decades and centuries in their natural environments, the average lifespan of trees planted in paved sites rarely exceeds 10 years (Foster and Blaine, 1977; Gilbertson and Bradshaw, 1990; Nowak et al., 1990). If these trends continue, urban forests will be confined to perpetual immaturity with little realization of their potential ecosystem services.

Tree inventories in northern Europe and northeastern North America reveal that the majority of trees in street environments originate from rich and moist forest habitats and consequently have a limited capacity to tolerate water deficits that frequently occur in paved sites (Raupp et al., 2006; Sjöman et al., 2012a; Cowett and Bassuk, 2014). Dendroecological studies show that trees from warm and periodically dry steppe environments, or rocky mountain sites, have greater potential to develop into mature specimens in paved environments (Sjöman et al., 2010, 2012b). Further, many of the selection pressures faced in these environments have resulted in plant strategies and traits that are likely to enable these species to persist in challenging urban sites (Ware, 1994).

1.1. Ecological strategies and the urban environment

Drought tolerance indices based on the persistence of species under a defined set of environmental conditions are valuable in describing the tolerance of species under natural conditions. Niinemets and Valladares (2006) developed a five-point scale (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant) for the drought tolerance of temperate trees. Trees that require >600 mm of precipitation (P) distributed relatively evenly throughout the year with a potential evapotranspiration (PET) ratio (P:PET) of >3.0, a dry period of just a few days with minimum soil water potentials of >−0.3 MPa were ranked 'very intolerant' (1). Species that can persist in regions with a very low (<0.5) P:PET, annual precipitation of <300 mm unevenly distributed throughout the year with dry periods of more than three months and minimum soil water potentials of <−3 MPa were ranked as 'very tolerant' (5). Intermediate values for these criteria were given for the other points on the scale (Niinemets and Valladares, 2006). However, since 'drought tolerance' can be conferred either by the avoidance or tolerance of water deficits (e.g. Levitt, 1980; Ludlow, 1989; Larcher, 2003; Schulze et al., 2005; Lamberts et al., 2008; Aranda et al., 2012) species with the same ranking using the Niinemets and Valladares (2006) scale may have widely contrasting plant traits. Species that rely on root architectural or morphological adaptations to avoid water deficits may not have developed physiological tolerance to low water potential. For example, species with a drought tolerance ranking of ∼3 and ∼4 varied in their turgor loss point by over 1 MPa and 2 MPa, respectively (Niinemets and Valladares, 2006; Bartlett et al., 2012a). Therefore, the use of such a scale to select 'drought tolerant' species for the urban environment is potentially problematic. Limited soil depth and volume is likely to limit the value of many avoidance strategies leaving these species vulnerable to soil drying. Many routine cultural practices such as root pruning, transplanting and containerization (Watson and Himelick, 2013) used in the production of amenity trees will further diminish the value of avoidance strategies (Hirons, 2013). Traits that provide tolerance of water deficits confer an advantage even in restricted soil volumes and after root severance. As a result, these species are likely to provide better candidates for planting in challenging urban sites.

The water potential at turgor loss (Ψ_{P0}) provides a robust measure of plant drought tolerance since a more negative Ψ_{P0} allows the leaf to maintain physiological function over an increased range of leaf water potential (Sack et al., 2003; Lenz et al., 2006). Plant genotypes that have a more negative Ψ_{P0} tend to maintain leaf gas exchange, hydraulic conductance and growth at lower soil matric potentials (Ψ_{soil}) so are at a competitive advantage where soil water deficits occur during the growth season (Mitchell et al., 2008; Blackman et al., 2010). The Ψ_{P0} also provides a surrogate for the Ψ_{soil} below which the plant cannot recover from wilting (Bartlett et al., 2012a). Consequently, Ψ_{P0} is a highly instructive plant trait to measure when actual tolerance of water deficits is required rather than information on the persistence of a species under a particular amalgamation of climatic conditions.

Traditionally, the Ψ_{P0} is assessed using pressure–volume curves (Tyree and Hammel, 1972; Tyree and Richter, 1982; Turner, 1988) but these are highly time-consuming, particularly if a large dataset is to be produced. Meta-analysis of pressure–volume curve data (Bartlett et al., 2012a) have demonstrated that the osmotic potential at full turgor ($\Psi_{\pi 100}$) is a key variable driving Ψ_{P0} across species and can, therefore, be used to predict physiological drought tolerance in plants. A major advantage of assessing $\Psi_{\pi 100}$ is that it can be determined using techniques that are much more rapid than pressure–volume curves (Bartlett et al., 2012b) facilitating the collection of larger datasets. Consequently, it is now possible to efficiently screen traditional and novel tree species for a drought tolerance trait that is highly relevant for the urban environment.

1.2. Maples as urban trees

The *Acer* genus consists of 120–156 species, including deciduous and evergreen species (van Gelderen et al., 1994; Dirr, 2009; Grimshaw and Bayton, 2009). Maple species are found in many types of climates and landscape types in Europe, Asia and North America—from dry steppe environments in southeast Europe to moist and rich forest habitats in China and eastern North America. Several species are endowed with the aesthetic qualities (e.g. leaf texture, flowers, attractive bark, autumn colour) sought in amenity tree planting schemes. Published inventories (Raupp et al., 2006; Sjöman et al., 2012a; Cowett and Bassuk, 2014) indicate that *Acer* are routinely used across the temperate world but the range of species used is commonly restricted to just a few traditional species. Scientific studies also seem limited to a narrow range of *Acer* such as *A. rubrum* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Acer saccharum* Marshall. and *Acer saccharinum* L. (e.g. Loewenstein and Pallardy, 1998; Tschaplinski et al., 1998; Bauerle et al., 2003; Fini et al., 2009; Köcher et al., 2009; Scherrer et al., 2011). Where information does exist on a wide range *Acer* species, limited experience of their development frequently results in inconsistency between sources (Table 1).

A central challenge for those tasked with securing the resilience of the urban tree population is to select and plant trees that can tolerate the urban environment, reach maturity and maintain a capacity to deliver a wide range of ecosystem services. The aim of

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