



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



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## 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 ( $\Psi_{P0}$ ) provides a robust measure of drought tolerance since a more negative  $\Psi_{P0}$  allows the leaf to maintain physiological function over a wider range of leaf water potentials and, by implication, soil matric potentials ( $\Psi_{soil}$ ). In this study,  $\Psi_{P0}$  was calculated for 27 maple (*Acer*) genotypes based on a known linear relationship between the osmotic potential at full turgor ( $\Psi_{\pi100}$ ) and  $\Psi_{P0}$ . In spring,  $\Psi_{P0}$  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  $\Psi_{P0}$  at  $-1.6$  MPa and *Acer monspessulanum* had the lowest  $\Psi_{P0}$  at  $-4.3$  MPa. Significant differences in  $\Psi_{P0}$  were found between cultivars of *A. rubrum* and *Acer saccharum*. A highly significant relationship was found between seasonal osmotic adjustment and summer  $\Psi_{P0}$  suggesting that osmotic adjustment is a driving force for summer  $\Psi_{P0}$  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).

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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

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  $\sim 3$  and  $\sim 4$  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 ( $\Psi_{p0}$ ) provides a robust measure of plant drought tolerance since a more negative  $\Psi_{p0}$  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  $\Psi_{p0}$  tend to maintain leaf gas exchange, hydraulic conductance and growth at lower soil matric potentials ( $\Psi_{soil}$ ) so are at a competitive advantage where soil water deficits occur during the growth season (Mitchell et al., 2008; Blackman et al., 2010). The  $\Psi_{p0}$  also provides a surrogate for the  $\Psi_{soil}$  below which the plant cannot recover from wilting (Bartlett et al., 2012a). Consequently,  $\Psi_{p0}$  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  $\Psi_{p0}$  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  $\Psi_{p0}$  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

**Table 1**  
 Compilation of site related information of 27 genotype of maples with regards to information concerning perceived drought tolerance. Sources include recent publications and standard literature. Niinemets and Valladares (2006) scale: 1 = least tolerant, 5 = most tolerant. Section nomenclature in accordance with van Gelderen et al. (1994). n = number of individual trees in the study. \* = Summer reading only.

Species	Section	Described ecology and drought tolerance
<i>Acer campestre</i> L. (n = 4)	Platanoidea	<ul style="list-style-type: none"> <li>• Likes sandy clay soil. Heat tolerant (Krüssmann, 1986)</li> <li>• Tolerant of dry soil and compaction (Stoecklein, 2001)</li> <li>• 2.93 (<math>\pm 0.32</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Tolerate prolonged periods of dry soil (Bassuk et al., 2009)</li> <li>• Drought tolerant (Dirr, 2009)</li> <li>• Growing well in warm and dry steppe forests (Sjöman et al., 2012b)</li> </ul>
<i>Acer cappadocicum</i> Gled. (n = 3)	Platanoidea	<ul style="list-style-type: none"> <li>• Adaptable to any well-drained soil (van Gelderen et al., 1994)</li> <li>• Might be considered for difficult sites (Dirr, 2009)</li> </ul>
<i>Acer carpinifolium</i> Sieb. & Zucc. (n = 4)	Indivisa	<ul style="list-style-type: none"> <li>• It grows on all types of soil (van Gelderen et al., 1994)</li> <li>• Grows well in all soils (Beaulieu, 2003)</li> <li>• 1 out of 5 (Niinemets and Valladares, 2006)</li> <li>• Prefer moist soil (Dirr, 2009)</li> </ul>
<i>Acer x freemanii</i> 'Autumn Blaze' (n = 6)	Rubra x Rubra	<ul style="list-style-type: none"> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> </ul>
<i>Acer grandidentatum</i> Nutt. (n = 3)	<i>Acer</i> (Series Saccharodendron)	<ul style="list-style-type: none"> <li>• Grows along mountain streams (Krüssmann, 1986)</li> <li>• Grows on sunny dry slopes (van Gelderen et al., 1994)</li> <li>• Prefer dry soil and sunny locations (Beaulieu, 2003)</li> <li>• 2.63 (<math>\pm 0.13</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Grows in moist mountain areas (Spellenberg et al., 2014)</li> </ul>
<i>Acer griseum</i> (Franchet) Pax (n = 5)	Trifoliata (Series Grisea)	<ul style="list-style-type: none"> <li>• 1.53 out of 5 (Niinemets and Valladares, 2006)</li> <li>• Prefer moist and well-drained soil (Dirr, 2009)</li> </ul>
<i>Acer heldreichii</i> Orph. ex Boiss. (n = 3)	<i>Acer</i> (Series Acer)	<ul style="list-style-type: none"> <li>• No source available</li> </ul>
<i>Acer mandshuricum</i> Maxim. (n = 4)		<ul style="list-style-type: none"> <li>• No source available</li> </ul>
<i>Acer miyabei</i> Maxim. (n = 5)	Platanoidea	<ul style="list-style-type: none"> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> <li>• Prefer moist and well-drained soil (Dirr, 2009)</li> </ul>
<i>Acer monspessulanum</i> L. (n = 3)	<i>Acer</i> (Series Monspessulana)	<ul style="list-style-type: none"> <li>• Grows in dry gravelly slopes (Krüssmann, 1986)</li> <li>• Grows in dry and stony places (van Gelderen et al., 1994)</li> <li>• Adapted to a warm climate and stony soil (Beaulieu, 2003)</li> <li>• 4.31 (<math>\pm 0.41</math>) out of 5 (Niinemets and Valladares, 2006)</li> </ul>
<i>Acer negundo</i> L. (n = 6)	Negundo	<ul style="list-style-type: none"> <li>• Useful for sandy, dry to sterile soil (Krüssmann, 1982)</li> <li>• Grows along shores of permanent bodies of water (Krüssmann, 1986)</li> <li>• Very heat and drought tolerant (Hightshoe, 1988)</li> <li>• Drought tolerant (Stoecklein, 2001)</li> <li>• Its native habitat is along streams and ponds (Grimm, 2002)</li> <li>• Like humid areas (Beaulieu, 2003)</li> <li>• 3.03 (<math>\pm 0.82</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Native in moist habitats but perform well also in poor, wet, or dry habitats (Dirr, 2009)</li> <li>• Grows along stream banks, flood plains, swamps (Spellenberg et al., 2014)</li> </ul>
<i>Acer nigrum</i> Michx. f. (n = 1)	<i>Acer</i> (Series Saccharodendron)	<ul style="list-style-type: none"> <li>• Sensitive for heat and drought (Hightshoe, 1988)</li> <li>• Prefers sites that are more humid (Beaulieu, 2003)</li> <li>• 3.35 (<math>\pm 0.35</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Has a higher drought tolerance than sugar maple (Bassuk et al., 2009)</li> <li>• Heat and drought tolerant (Dirr, 2009)</li> </ul>
<i>Acer pensylvanicum</i> L. (n = 6)	Macrantha	<ul style="list-style-type: none"> <li>• Grows usually near water (Krüssmann, 1986)</li> <li>• Sensitive for heat and drought (Hightshoe, 1988)</li> <li>• Are found in cool, moist woods as understory (Grimm, 2002)</li> <li>• Prefers moderately moist soil (Beaulieu, 2003)</li> <li>• 2 out of 5 (Niinemets and Valladares, 2006)</li> <li>• Needs cool climates and moist and well-drained soil (Dirr, 2009)</li> </ul>
<i>Acer platanoides</i> L. (n = 5)	Platanoidea	<ul style="list-style-type: none"> <li>• It thrives on almost any soil, and even in the poor sandy soils at Kew it grows rapidly (Bean, 1980)</li> <li>• Has moderate drought tolerance (Gilman, 1997)</li> <li>• High demands of moist and cool growing conditions (Almgren et al., 2003)</li> <li>• Drought tolerant (Stoecklein, 2001)</li> <li>• It resist drought (Beaulieu, 2003)</li> <li>• 2.73 (<math>\pm 0.16</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Is tolerant to prolonged periods of dry soil (Trowbridge and Bassuk, 2004)</li> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> <li>• Withstands hot and dry conditions better than sugar maple (Dirr, 2009)</li> <li>• Drought tolerant (Roloff et al., 2009)</li> </ul>
<i>Acer pseudoplatanus</i> L. (n = 3)	<i>Acer</i> (Series Acer)	<ul style="list-style-type: none"> <li>• Dislikes excessive moisture and dryness (Krüssmann, 1986)</li> <li>• High demands of moist and cool growing conditions (Almgren et al., 2003)</li> <li>• Prefers deep well-drained soils (Beaulieu, 2003)</li> <li>• 2.75 (<math>\pm 0.16</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> <li>• Very adaptable to soil types (Dirr, 2009)</li> </ul>

Table 1 (Continued)

Species	Section	Described ecology and drought tolerance
<i>Acer rubrum</i> 'Northwood' (n=4)	Rubra	<ul style="list-style-type: none"> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> </ul>
<i>Acer rubrum</i> 'October Glory' (n=4)	Rubra	<ul style="list-style-type: none"> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> </ul>
<i>Acer rubrum</i> 'Red Sunset' (n=5)	Rubra	<ul style="list-style-type: none"> <li>• Tolerate occasional periods of dry soil (Bassuk et al., 2009)</li> </ul>
<i>Acer saccharinum</i> L. (n=5)	Rubra	<ul style="list-style-type: none"> <li>• A river bank tree (Grimm, 2002)</li> <li>• Occurs in flood plains (Krüssmann, 1986)</li> <li>• Tolerant of wide variety of soils (Dirr, 2009)</li> <li>• Very heat and drought tolerant (Hightshoe, 1988)</li> <li>• It prefer rich, moist soils (Beaulieu, 2003)</li> <li>• 2.88 (<math>\pm 0.12</math>) out of 5 (Niinemets and Valladares, 2006)</li> </ul>
<i>Acer saccharum</i> 'Caddo' (n=1)	<i>Acer</i> (Series <i>Saccharodendron</i> )	<ul style="list-style-type: none"> <li>• Extremely drought tolerant (Bassuk et al., 2009)</li> <li>• Extremely heat and drought tolerant (Dirr, 2009)</li> </ul>
<i>Acer saccharum</i> 'Green Column' (n=1)	<i>Acer</i> (Series <i>Saccharodendron</i> )	<ul style="list-style-type: none"> <li>• Well adapted to dry conditions (Beaulieu, 2003)</li> <li>• Drought tolerant (Stoocklein, 2001)</li> </ul>
<i>Acer saccharum</i> 'Green Mountain' (n=1)	<i>Acer</i> (Series <i>Saccharodendron</i> )	<ul style="list-style-type: none"> <li>• Perform better than the species in dry areas (Dirr, 2009)</li> </ul>
<i>Acer spicatum</i> Lam. (n=5)*	Caudata	<ul style="list-style-type: none"> <li>• Grows in forest, usually moist, rocky areas all over the east (N. America) near water (Krüssmann, 1986)</li> <li>• Drought and heat sensitive (Hightshoe, 1988)</li> <li>• Grows in forest borders in rocky and moist situations (van Gelderen et al., 1994)</li> <li>• Mostly an understory tree but withstands full sun without problem, as long as it has a good water supply. It favours the moist soil near a river (Beaulieu, 2003)</li> <li>• Grows in cool moist deciduous forests, swamp margins, often along streams (Nelson et al., 2014)</li> </ul>
<i>Acer tataricum</i> L. (n=3)	Ginnala	<ul style="list-style-type: none"> <li>• Prefers sunny, dry situations in forest undergrowth (van Gelderen et al., 1994)</li> <li>• Drought tolerant (Stoocklein, 2001)</li> <li>• 3.37 (<math>\pm 0.32</math>) out of 5 (Niinemets and Valladares, 2006)</li> <li>• Tolerate prolonged periods of dry soil (Bassuk et al., 2009)</li> <li>• Drought tolerant (Dirr, 2009)</li> </ul>
<i>Acer tegmentosum</i> Maxim. (n=4)	Macrantha	<ul style="list-style-type: none"> <li>• Grows in moist locations along river banks (van Gelderen et al., 1994)</li> </ul>
<i>Acer truncatum</i> Bunge. (n=4)	Platanoidea	<ul style="list-style-type: none"> <li>• Grows in average soils (Beaulieu, 2003)</li> <li>• Tolerate prolonged periods of dry soil (Bassuk et al., 2009)</li> <li>• Heat and drought tolerant (Dirr, 2009)</li> </ul>
<i>Acer x zoechense</i> Pax. (n=3)	Platanoidea $\times$ Platanoidea	<ul style="list-style-type: none"> <li>• No source available</li> </ul>

this study was to evaluate a wide range of traditional and less conventional *Acer* genotypes for their drought tolerance and, therefore, their potential for a wide range of urban sites.

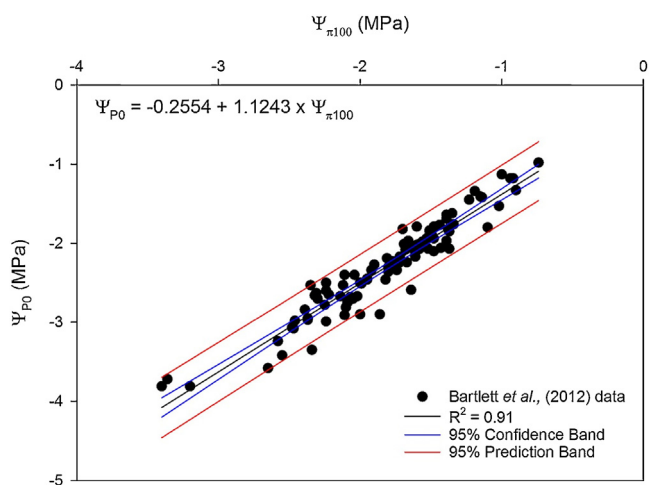
## 2. Materials and methods

The study included 27 species and genotypes of maples, all found at the F.R. Newman Arboretum at Cornell University, New York State (42°27'0N, 76°28'19W) and at the surrounding north campus of Cornell University except *Acer spicatum* Lam. which were collected at the nearby Treman State Park (42°24'00N, 76°34'26W) (Table 1). The trees used in the study were all well-established trees growing as solitary trees in park environments (which include mixed plantations with shrubs or in cut grass lawns) with unlimited rooting space except *A. spicatum*. Since *A. spicatum* grows naturally as an understory tree, this species was collected from a shaded position in a forest environment. Table 1 also describes published information on drought tolerance for those genotypes used in the study and confirms a wide range of drought tolerance across the selected genotypes.

In accordance with Bartlett et al. (2012b) sun exposed branches three to 5 m above ground (<20 mm in diameter) with no symptoms of abiotic or biotic damage (such as leaf fungal pathogens, leaf defoliation or leaf chlorosis) were selected from each species/genotype. Depending on the availability of trees within the collection, leaf material was collected from one to six individual trees between

18:00 and 20:00 h. In the few species/genotypes which only existed with one specimen (*Acer nigrum* and three *A. saccharum* cultivars), three branches of same tree where collected. Excised branches were immediately placed in a humid bag and taken to the laboratory within 20 min. At the laboratory, branches were recut under water at least two nodes distal to the original cut and placed in a tube of water without exposing the cut surface to the air. Branches were rehydrated overnight in a dark chamber with >75% relative humidity as measured by a wet–dry bulb thermometer (wet bulb 15 °C/dry bulb 17 °C). The following day, leaf discs (one per leaf) were taken from fully expanded leaves using a 7 mm cork borer from the mid-lamina region between the mid-rib and leaf margin. To minimize potential sources of error, no leaf discs were taken from lamina regions with first and second order veins. All discs were tightly wrapped in foil to limit condensation or frost after freezing. Foil-wrapped leaf discs were then submerged in liquid nitrogen for 2 min to fracture the cell membrane and walls. The time from harvesting the fully hydrated leaf discs to submergence in liquid nitrogen was less than 40 s. Upon removal from the liquid nitrogen, leaf discs were punctured 10–15 times with sharp tipped forceps to facilitate evaporation through the cuticle and decrease equilibration time (Kikuta and Richter, 1992) before sealing the leaf disc in the vapour pressure osmometer (Vapro 5600, Wescor, Logan, UT, USA) using a standard 10  $\mu$ l chamber. Initial solute concentration ( $c_s$  (in  $\text{mmol kg}^{-1}$ )) readings were taken after 10 min equilibration time,  $c_s$  was recorded when repeat readings at 2 min intervals was





**Fig. 1.** Meta-analysis based on a subset of paired variables ( $\Psi_{\pi 100}$ ,  $\Psi_{P0}$ ) for woody temperate, Mediterranean/temperate-dry and temperate conifer species from Bartlett et al. (2012a) supplementary data. The equation generated (see graph panel) was used in this study to calculate the turgor loss point  $n = 116$ .

$<5 \text{ mmol kg}^{-1}$ . Solute concentration was converted to  $\Psi_{P0}$  using Van't Hoff's relation (Eq. (1)):

$$\psi_{P0} = -RTc_s \quad (1)$$

where  $R$  is a gas constant,  $T$  is temperature in Kelvin and  $c_s$  is the solute concentration. Eight leaf discs were analyzed per species/genotype during two periods of data collection 19th–30th May (spring dataset) and 1st–10th August 2014 (summer dataset), except for *A. spicatum* which is only represented by a summer reading.

Although Bartlett et al. (2012a) published an equation allowing the prediction of  $\Psi_{P0}$  from  $\Psi_{\pi 100}$ , this was based on a global dataset that included data from tropical biomes. Since the current study is limited to the temperate biome, a subset (i.e. woody temperate, Mediterranean/temperate-dry and temperate conifer species) of the supplementary data published by Bartlett et al. (2012a) was used to generate a new equation for deriving  $\Psi_{P0}$  from  $\Psi_{\pi 100}$  in temperate tree species (Fig. 1 and Eq. (2)). This new equation was used as it provided a higher coefficient of determination ( $R^2$  0.91 vs. 0.86) so provided a more reliable means of calculating  $\Psi_{P0}$ .

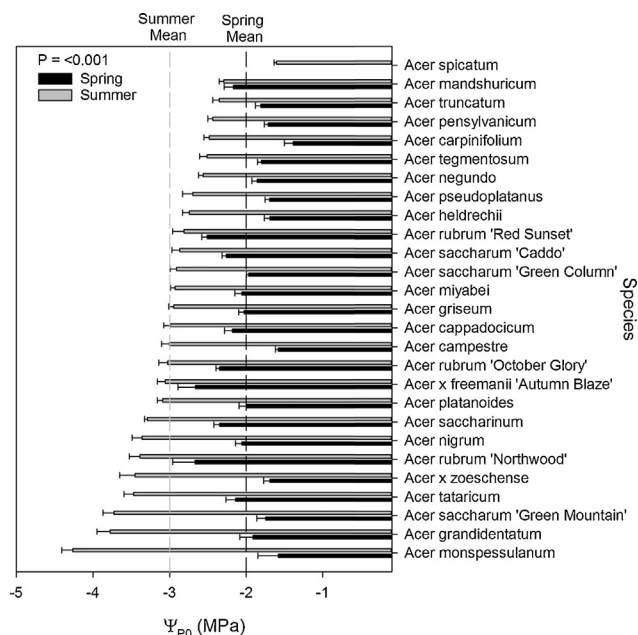
$$\psi_{P0} = -0.2554 + 1.1243 \times \psi_{\pi 100} \quad (2)$$

Osmotic adjustment ( $\Delta\Psi_{\pi 100}$ ) was calculated as the difference between the spring and the summer datasets.

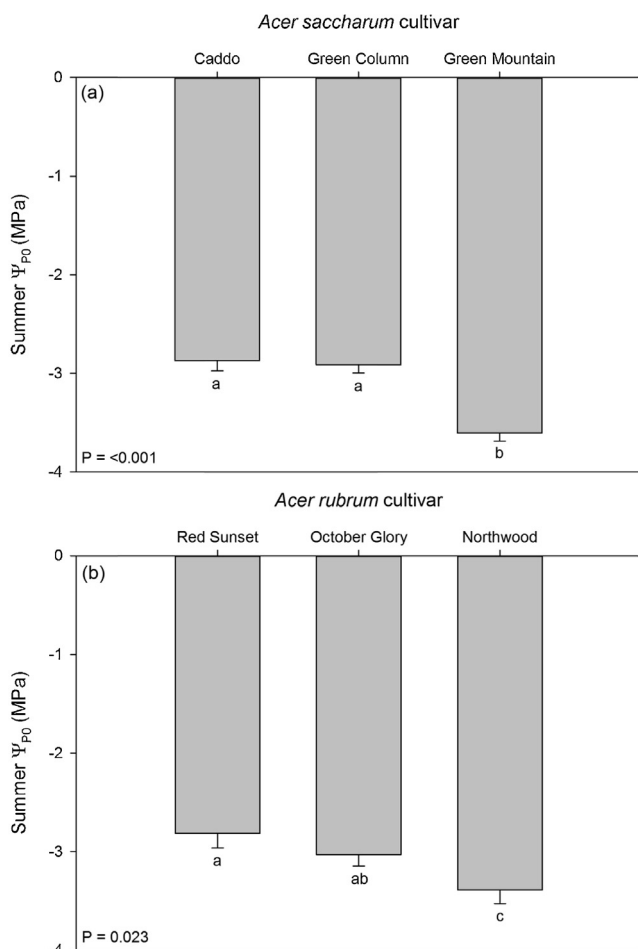
Statistical analysis was conducted using Minitab v17 (Minitab Ltd., Coventry, UK). A general linear model (GLM) was used to determine differences across multiple levels. One-way analysis of variance (ANOVA) was used when comparing differences across a single level, a Tukey's post hoc analysis was then applied to determine where these differences occurred, as indicated by letters of homogeneity. Linear regression was used to describe relationships between variables. All data was plotted using SigmaPlot v13 (Systat Software Inc. San Jose, California, USA).

### 3. Results

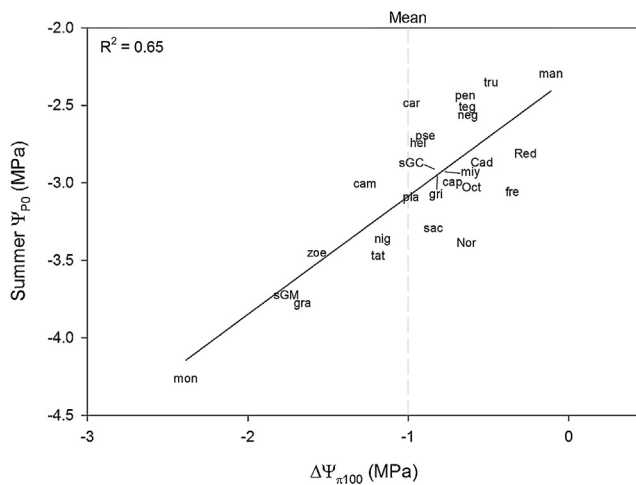
Dendrological literature and publications on plant use for urban environments gives inconsistent and rather limited advice (Table 1). For example, Dirr (2009) describes *A. nigrum* as a heat and drought tolerant tree, while Hightshoe (1988) and Beaulieu (2003) argue that the species is sensitive for heat and drought, and prefers sites that are humid. This variation in opinion is most likely explained by the contrasting experience of the authors. Niinemets



**Fig. 2.** Predicted turgor loss of leaves in summer based on the assessment of osmotic potential at full turgor of 27 *Acer* genotypes. Dashed lines represent mean for all genotypes. Bars show SE,  $P < 0.001$  across species for spring and summer datasets as determined by the GLM,  $n =$  see Table 1. Genotypes have been ranked by summer  $\Psi_{P0}$ .



**Fig. 3.** Predicted turgor loss of leaves in summer of (a) *A. saccharum* and (b) *A. rubrum* cultivars. Bars show SE, letters indicate where significant differences ( $P < 0.05$ ) occur between cultivars as indicated by a one-way ANOVA,  $n =$  see Table 1.



**Fig. 4.** Relationship between the seasonal osmotic adjustment of genotypes ( $x$  axis) and their calculated summer turgor loss point ( $y$  axis). Solid line represents a highly significant ( $R^2 = 0.65$ ;  $P < 0.001$ ) linear regression,  $n = 26$ . Dashed line represents mean seasonal osmotic adjustment for all genotypes. Abbreviations: *Acer campestre* (cam); *A. cappadocicum* (cap); *A. carpinifolium* (car); *A. grandidentatum* (gra); *A. griseum* (gri); *A. heldreichii* (hel); *A. mandshuricum* (man); *A. miyabei* (miy); *A. monspessulanum* (mon); *A. negundo* (neg); *A. nigrum* (nig); *A. pensylvanicum* (pen); *A. platanoides* (pla); *A. pseudoplatanus* (pse); *A. rubrum* 'Northwood' (Nor); *A. rubrum* 'October Glory' (Oct); *A. rubrum* 'Red Sunset' (Red); *A. saccharinum* (sac); *A. saccharum* 'Caddo' (Cad); *A. saccharum* 'Green Column' (sGC); *A. saccharum* 'Green Mountain'; (sGM); *A. tataricum* (tat); *A. tegmentosum* (teg); *A. truncatum* (tru); *A. x freemanii* 'Autumn Blaze' (fre); *A. x zoeschense* (zoe).

and Valladares (2006) are the only authors to attempt a quantitative scale (1–5) based on environmental variables, although a qualitative scale (1–12) is used by Bassuk et al. (2009) to help guide tree selection choices. None of the literature reviewed contained a quantitative scale based on leaf turgor loss or analogous physiological criteria. While many scientific studies evaluating maples and drought do exist, these focus on well-known species such as *A. rubrum*, *A. saccharum*, *A. platanoides* and *A. pseudoplatanus* (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). Less traditionally used *Acer* species are very poorly represented in the literature. Indeed, this paper is the first to describe any measure of drought tolerance in *Acer heldreichii*, *Acer mandshuricum* and *Acer x zoeschense*.

Leaf turgor loss point varied widely across *Acer* genotypes in both spring and summer (Fig. 2). In spring, the grand mean of all species evaluated was  $-2.0$  ( $SE \pm 0.07$ ) MPa and ranged 1.3 MPa between  $-1.4$  MPa in *Acer carpinifolium* and  $-2.7$  MPa in both *A. rubrum* 'Northwood' and *Acer x freemanii* 'Autumn Blaze'. In summer, the grand mean increased to  $-3.0$  ( $SE \pm 0.10$ ) MPa and ranged 2.7 MPa from  $-1.6$  MPa for *A. spicatum* to  $-4.3$  MPa for *Acer monspessulanum*. This reveals an average seasonal osmotic adjustment of 1 MPa across the *Acer* sp. evaluated in this study. Differences in  $\Psi_{P0}$  across all genotypes were highly significant ( $P < 0.001$ ) for both the spring and the summer datasets. Significant differences in  $\Psi_{P0}$  also occurred across cultivars of the same species: *A. saccharum* and *A. rubrum* showed significant differences ( $P < 0.05$ ) across their cultivars (Fig. 3). A highly significant ( $P < 0.001$ ) relationship was shown between seasonal osmotic adjustment and the summer  $\Psi_{P0}$ . Species exhibiting the lowest (most negative) summer  $\Psi_{P0}$  showed the greatest seasonal adjustment in  $\Psi_{\pi 100}$  (Fig. 4). For example, *A. monspessulanum* and *A. saccharum* 'Green Mountain' displayed a spring  $\Psi_{P0}$  of  $-1.6$  MPa and  $-1.7$  MPa, respectively, while their summer  $\Psi_{P0}$  was recorded at  $-4.3$  MPa and  $-3.7$  MPa, respectively. By comparison, species with a less negative summer  $\Psi_{P0}$  displayed seasonal adjustment in their  $\Psi_{\pi 100}$  below the average value of 1 MPa. At the extremes of this dataset, *A. mandshuricum*

only differed 0.1 MPa between spring and summer readings while *A. monspessulanum* changed by 2.4 MPa. The variable magnitude of seasonal osmotic adjustment resulting in changes in the ranking of  $\Psi_{P0}$  across genotypes varied by season. This suggests that those species that have the lowest leaf turgor loss points in summer are not necessarily those that display the greatest resilience to water deficits in spring.

#### 4. Discussion

The *Acer* genus makes a significant contribution to the urban forest with its variety of aesthetic qualities and its potential to deliver ecosystem services such as the regulation of microclimate and mitigating the urban heat island effect (Deak Sjöman et al., 2015). However, such qualities and ecosystem services are dependent on the establishment and long-term development of the trees in question. This makes site adapted plant selection an essential component in the design and development of a resilient urban forest. Since water stress is a major constraint for trees in urban environments (Sieghardt et al., 2005) and, in many regions, it is likely to increase under future climate scenarios (Allen et al., 2010), the quantitative drought tolerance of a genotype should be a fundamental consideration in tree selection for urban environments. Climate change also heightens the risk of pest and disease outbreaks (Tubby and Webber, 2010). This may lead to substantial canopy loss, especially in cities in the northern hemisphere where a limited range of species makes up the urban forest (Raupp et al., 2006; Sjöman et al., 2012a; Cowett and Bassuk, 2014). Increasing species diversity through the use of untraditional species is, consequently, of strategic importance to securing a resilient urban forest. Information regarding species selection and stress tolerance in different growing conditions will become increasingly relevant, particularly for the daily practice of urban tree planners and landscape architects.

In this paper, we classified the drought tolerance for 27 genotypes of maples, the majority could be considered as rare or untraditionally used for urban environments in northern temperate regions. The predicted leaf water potential at turgor loss ( $\Psi_{P0}$ ) was chosen as an indicator to quantify the level of drought tolerance amongst the genotypes. By extension, assessing  $\Psi_{P0}$  provides quantitative data that resolves which genotypes can maintain physiological function more effectively in drying soil (Sack et al., 2003; Lenz et al., 2006). In summer, the point of leaf turgor loss differed by approximately 2.7 MPa ( $-1.6$  to  $-4.3$  MPa) across the 27 *Acer* genotypes described here revealing substantial differences in tolerance to water deficits at both species and cultivar level. Consequently, it is now possible to anticipate which maples are likely to perform well in challenging urban sites as well as identifying those that are only likely to perform well in park environments.

Maples with a higher summer  $\Psi_{P0}$  such as *A. spicatum*, *A. mandshuricum* and *A. truncatum* ( $-1.6$ ,  $-2.3$  and  $-2.4$  MPa, respectively) are most suitable for sites with large soil volumes and greater water holding capacity. Genotypes with lower summer  $\Psi_{P0}$  such as *Acer grandidentatum* and *A. monspessulanum* ( $-3.8$  and  $-4.3$  MPa, respectively) should perform better in sites with more limited soil volume and sites with reduced water availability. Lower  $\Psi_{P0}$  is also likely to confer a resilience to water deficits imposed by root loss during tree transplantation.

Data collected in this study also supports observations relating to the natural habitat of contrasting maple species. For example, *A. spicatum*, *A. mandshuricum*, *A. carpinifolium* and *A. tegmentosum* are found predominantly in moist, understory forest habitats (van Gelderen et al., 1994) and display higher  $\Psi_{P0}$  indicating lower tolerance to dry conditions. In contrast, species with the lowest  $\Psi_{P0}$  in this study e.g. *A. monspessulanum*, *A. grandidentatum* and

*A. tataricum* grow naturally in warm and periodically dry habitats (van Gelderen et al., 1994; Sjöman et al., 2012b). However, in the most drought tolerant maples, a reduced summer  $\Psi_{P0}$  was driven by substantial seasonal osmotic adjustment. As a result, the timing and velocity of soil drying will be relevant for all species as even those with the lowest summer  $\Psi_{P0}$  may still be sensitive to relatively mild water deficits early in the growth season. Therefore, from a tree management perspective, selection of species with a low  $\Psi_{P0}$  may not remove the requirement to irrigate if soil water deficits develop shortly after leaf emergence.

The magnitude of seasonal osmotic adjustment can be used as a measure of the species 'plasticity' to changing soil water status (Bartlett et al., 2014). Those species showing high variation in their  $\Psi_{\pi 100}$  across the growing season can be expected to possess a greater capacity to maintain physiological function across a wide range of soil moisture levels. In a review of global data, Bartlett et al. (2014) show that plasticity in  $\Psi_{P0}$  could be as much as  $-2$  MPa, this value was exceeded by the seasonal change of  $2.7$  MPa in *A. monspessulanum* suggesting exceptional plasticity in this species. Evaluating the plasticity of tree response to soil drying is likely to be instructive for those recommending trees for particular sites. Genotypes showing little plasticity in  $\Psi_{P0}$  are likely to perform well only in a narrow range of soil moisture conditions, whereas, those with a high degree of plasticity will have the capacity to adapt to more variable conditions. Further, species with greater plasticity are also likely to be more resilient to the changing precipitation patterns indicated by some future climate scenarios (Allen et al., 2010). Seasonal plasticity of  $\Psi_{P0}$  is also likely to explain why levels of  $\Psi_{P0}$  can differ for same species between different studies and underscores the need to develop a protocol for data collection that will make comparative studies more robust.

A further reason for differences in  $\Psi_{P0}$  between studies seems to be intra-specific genetic variation. This study showed significant differences in  $\Psi_{P0}$  occur between genotypes of *A. saccharum* and *A. rubrum* cultivars highlighting the challenges in assessing a single species' tolerance for drought. In fact, these data also contrast with previously published  $\Psi_{P0}$  values for *A. rubrum* (e.g. Tschaplinski and Gebre, 2003; Burghardt and Riederer, 2003) confirming the potential variation across a single species on the basis of provenance, genotype or ecotype, season of data collection or a combination of both. Ultimately, evaluation of single genotypes will be more instructive than a single value representing a species. Indeed, understanding the potential magnitude of genotypic differences in  $\Psi_{P0}$  within a single species is an important question for further research and pertinent for species with a large natural distribution that shows marked variation in climate and other site conditions.

Despite the potential limitation caused by variation across genotypes of a single species (e.g. cultivars), this study demonstrates that evaluation of  $\Psi_{P0}$  can give a valuable insight into the potential of species to tolerate periods of low water availability and their capacity to respond to environmental change. Clearly, measured rather than predicted leaf turgor loss data would be even more robust, however, the highly significant linear relationship between osmotic potential at full turgor and leaf turgor loss (Fig. 1) should provide confidence in the data. Indeed, the same technique has successfully been used to evaluate the drought tolerance of 71 tree species within the Amazonian forest (Maréchaux et al., 2015). Further, the relative speed of the technique advocates the method as a potential screening tool for the physiological drought tolerance of new and traditional plant material for the urban forest.

The trees chosen for this study have all established in the same climate within an unconstrained rooting environment of similar soil conditions (silt loam). Although a more robust experimental design may have been achieved with a pot-plant or field trial, the range of species evaluated would have been limited

to those currently in cultivation. Further, data would have been restricted to younger plants not established in the landscape. Since a major motivation of the study was to acquire information on the drought tolerance of rare or untraditionally species, a methodological approach utilising an established collection was favoured. Three clonal cultivars of *A. saccharum* and *A. nigrum* were represented by one individual tree; consequently, these data should be interpreted with caution. More robust data exists for the remaining 23 maple genotypes that were represented by at least three established specimens (Table 1). Despite presenting occasional problems with replication, botanical gardens and arboreta have highly diverse landscapes with the potential to yield hugely valuable information on currently under-utilized species. Therefore, the use of established tree collections should be facilitated where possible. Datasets extending this study will be valuable for those specifying trees and should provide excellent guidance to tree nurseries seeking to introduce new genotypes to market or evaluate the use-potential of their current stock.

Many urban planting sites require tree species that are capable of surviving prolonged periods of water deficit. Current guidance in the dendrological and nursery literature does not provide quantitative data that enables robust decisions to be made when matching tree species to particular urban sites. This frequently leads to unsuitable trees being planted in some sites and a reluctance to plant untraditional genotypes. As a consequence, the resilience of the urban forest is diminished by reduced performance of individual trees and reduced genotypic diversity.

This study provides guidance on both traditional and rarely used maples that will help match the assessed genotypes to particular sites. Further, the methodology used describes a framework for the evaluation of a plant trait that is of inherent interest to those specifying trees for the urban environment.

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