



# Improving confidence in tree species selection for challenging urban sites: a role for leaf turgor loss

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## Abstract

High species diversity is argued to be the most important requisite for a resilient urban forest. In spite of this, there are many cities in the northern hemisphere that have very limited species diversity within their tree population. Consequently, there is an immense risk to urban canopy cover, if these over-used species succumb to serious pests or pathogens. Recognition of this should motivate the use of less commonly used species. Analysis of plant traits, such as the leaf water potential at turgor loss ( $\Psi_{p0}$ ), can provide useful insights into a species' capacity to grow in warm and dry urban environments. Therefore, the aim of this study was to evaluate  $\Psi_{p0}$  of 45 tree species, the majority of which are rare in urban environments. To help evaluate the potential for using  $\Psi_{p0}$  data to support future decision-making, a survey of professionals engaged with establishing trees in urban environments was also used to assess the relationship between the measured  $\Psi_{p0}$  and the perceived drought tolerance of selected species. This study demonstrates that  $\Psi_{p0}$  gives strong evidence for a species' capacity to tolerate dry growing conditions and is a trait that varies substantially across species. Furthermore,  $\Psi_{p0}$  was shown to closely relate to the experience of professionals involved in establishing trees in urban environments, thus providing evidence of its practical significance. Use of plant traits, such as  $\Psi_{p0}$ , should, therefore, give those specifying trees confidence to recommend non-traditional species for challenging urban environments.

**Keywords** Urban trees · Urban forest · Plant selection · Diversification · Trait based tree selection · Leaf turgor loss

## Introduction

The benefits of trees in urban environments are increasingly being recognised. Looking forward, the ecosystem services provided by the urban forest will be vital to urban communities (Benedict and McMahon 2006). They include

provisioning services (e.g. fuel), regulating services (e.g. storm water management, urban heat island mitigation, air pollution regulation), cultural services (e.g. recreation, physical and mental health benefits), and supporting services (e.g. wildlife habitats) (Akbari et al. 2001; Costanza et al. 1997; Gill et al. 2007; Grahn and Stigsdotter 2003; Morgenroth et al. 2016; Tyrväinen et al. 2005; Xiao and McPherson 2002). Recognition of these benefits has motivated green-infrastructure policy makers to implement ambitious tree planting programs, especially in North America. For example, Los Angeles, New York City, Houston, Salt Lake City and Denver have established planting goals of 1 million trees, while Sacramento has a planting goal of 5 million trees (Young 2011). Similar 'million tree programs' have been launched in other parts of the world, such as Shanghai (Shanghai roots and shoots 2007). Within such planting programs, it is important to be strategic in the selection of trees so that new plantings can develop into mature trees, as their contribution to ecosystem services is improved with increasing tree size (Gómez-Muñoz et al. 2010; Hiron and Sjöman 2018). This requires that species are carefully matched to their planting site and that their vulnerability to pests and pathogens is minimised.

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## Diversification of urban trees

High species diversity is vital to enhance the resilience of urban forests to abiotic and biotic challenges of the future (Alvey 2006; Hooper et al. 2005). Recognition of this should motivate the use of less commonly used species. However, the strategic value of diversifying the urban forest is compromised by the lack of familiarity that urban tree planners and nurseries have in the utilisation and production of species that are not currently well-known. Therefore, approaches must be developed to provide guidance on the use of species that are not widely observed in urban landscapes. Two further obstacles to achieving more diverse urban forests are: firstly, the unwillingness among tree planners to take risks associated with using non-traditional plant material (Sjöman and Nielsen 2010); and secondly, the availability of tree species among nurseries (Pincetl et al. 2013; Sydnor et al. 2010). Thus, the species identified in a landscape architect's initial design plans are sometimes substituted due to a lack of supply, particularly for large caliper trees required in large numbers (Conway and Vecht 2015). Consequently, clear guidance of species tolerance and potential for different urban growing conditions is vital, to give those specifying and growing trees the confidence to use less well-known plant material. Since inner-city environments and paved sites represent some of the most challenging urban planting sites, evaluating species tolerance to these environments is a particular priority.

Site related information in the literature is predominantly based on the authors' own experiences and qualitative observations from arboreta, botanical gardens and other tree collections (Sjöman and Nielsen 2010). Such guidance is not robust enough to give tree planners and nurseries confidence to specify, and produce, non-traditional species. An alternative approach is to identify plant traits that can help characterise a species' tolerance to stresses, relevant to the urban environment, thus providing evidence for site fitness (Sjöman et al. 2015).

## Trait based tree selection

Water stress is the main abiotic constraint for trees in urban environments (Sieghardt et al. 2005; Hirons and Thomas 2018) and, in many regions, it is likely to increase under future climate scenarios (Allen et al. 2010). Therefore, a quantitative indication of tree drought tolerance should always be a fundamental consideration in tree selection for urban environments.

In nature, trees have evolved a broad continuum of strategies to cope with warm and periodically dry conditions. These strategies arise from a combination of drought-avoidance and/or drought tolerance traits evolved by different species in response to water deficits of different frequencies and duration (Levitt 1980; Kozlowski and Pallardy 2002; Bacelar et al. 2012; Hirons and Thomas 2018).

Avoidance of water deficits involves either maximizing water acquisition or reducing water use. Species that would naturally avoid water deficits by rooting deeply are often thwarted in urban sites with minimal soil depth and, as a result, perform poorly. Other avoidance strategies, such as leaf isohydry are likely to diminish the ecosystem services delivered by the tree where these rely on water loss from the leaf (evapotranspirational cooling) or photosynthesis (carbon sequestration). However, drought tolerance traits allow the tree to maintain physiological function at a lower water status (potential) (Bartlett et al. 2016).

Traits that confer a tolerance to water deficits have inherent interest to those selecting trees as they allow the tree to maintain physiological processes for longer during the drying cycle.

Leaf water potential at turgor loss ( $\Psi_{P0}$ ) provides a robust measure of plant drought tolerance as a more negative  $\Psi_{P0}$  allows the leaf to maintain physiological function over an increased range of leaf water potentials (Sack et al. 2003; Lenz et al. 2006). Species that have a low (more negative)  $\Psi_{P0}$  tend to maintain leaf gas exchange, hydraulic conductance and growth at lower soil water potentials ( $\Psi_{soil}$ ) so are at an 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).  $\Psi_{P0}$  is also related to leaf and stem conductivity – hydraulic traits measuring drought impacts on the water supply for transpiration and photosynthesis (Bartlett et al. 2016). Therefore,  $\Psi_{P0}$  is a trait that provides information about a species' capacity to grow in dry environments and is particularly relevant for paved urban sites, characterised by restricted soil volumes and impermeable surfaces (Sjöman et al. 2015). Consequently,  $\Psi_{P0}$  is of significant interest as it represents a quantifiable measure of drought tolerance; species with a greater tolerance to drought may be more likely to survive in paved sites and have a greater ability to deliver the ecosystem services sought by urban forest professionals.

The evaluation of  $\Psi_{P0}$  for 45 tree species, is contextualised with the qualitative site related information that urban tree planners and nurseries can access from dendrological and plant-use literature. Furthermore, to help evaluate the potential for using  $\Psi_{P0}$  data to support future decision-making, a survey of professionals engaged with establishing trees in urban environments was used to assess the relationship between the measured  $\Psi_{P0}$  and the perceived drought tolerance of selected species.

## Material and methods

### Plant material

For the study, 45 tree species were selected (Table 2). With the exception of *Pyrus calleryana*, which is quite widely planted

in the UK and North America, tree inventory data suggests that they are all rare as urban trees in temperate regions of the northern hemisphere (Bourne and Conway 2014; Cowett and Bassuk 2014; Sjöman et al. 2012; Yang et al. 2012; Raupp et al. 2006).

All trees were found at the F.R. Newman Arboretum at Cornell University, New York State (42°27'0 N, 76°28'19 W) and at the surrounding north campus of Cornell University. The mean annual temperature of the case study area is 8.1 °C with the highest mean monthly temperature is in July with 21 °C while the lowest mean monthly temperature is in January with -5.6 °C. The study area is categorized as zone 5b according to USDA Plant Hardiness Zone Map (USDA 2012). The soil type is gravelly silt loam. The trees used in the study were all well-established trees growing as solitary trees in park environments (which include mixed plantations with shrubs and those in cut grass lawns) with apparently unconstrained rooting space. As plants can adjust their water potential at turgor loss point ( $\Psi_{P0}$ ) under different growing habitats (Bartlett et al. 2014) it is important that studied plants are grown under similar growing conditions in order to compare the results between the species and genotypes.

### Leaf water potential at turgor loss

One sun exposed branch 3–5 m above ground level with no symptoms of abiotic or biotic damage was collected on 2–6 individual trees during early evening when transpiration was relatively low. 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 of the original cut and placed in a tube of water without exposing the cut surface to the air. Branches were placed in a dark chamber with >75% relative humidity overnight to rehydrate. Leaf discs (one per leaf) were taken from fully expanded leaves using an 8 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 membranes and walls. Leaf discs were then 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 vapor pressure osmometer (Vapro 5600, Westcor, 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 were < 5  $\text{mmol kg}^{-1}$ . Solute concentration was converted to osmotic potential ( $\Psi_\pi$ ) using Van't Hoff's relation (Eq. 1):

$$\Psi_\pi = -RTc_s \quad (1)$$

where R is a gas constant, T is temperature in Kelvin and  $c_s$  is the solute concentration. Eight replicates were analyzed during two periods of data collection 19th – 30th May (spring dataset) and 1st -10th August 2014 (summer dataset). In the spring all leaves had reached full size before being collected and analyzed.

Although Bartlett et al. (2012b) published an equation allowing the prediction of  $\Psi_{P0}$  from the osmotic potential at full turgor ( $\Psi_{\pi100}$ ), 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  $\Psi_{\pi100}$  in temperate tree species (Fig. 1 and Eq. 2; Sjöman et al. 2015). 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 predicting  $\Psi_{P0}$ .

$$\Psi_{P0} = -0.2554 + 1.1243 \times \Psi_{\pi100} \quad (2)$$

Osmotic adjustment ( $\Delta\Psi_{\pi100}$ ) was calculated as the difference between the spring and the summer datasets.

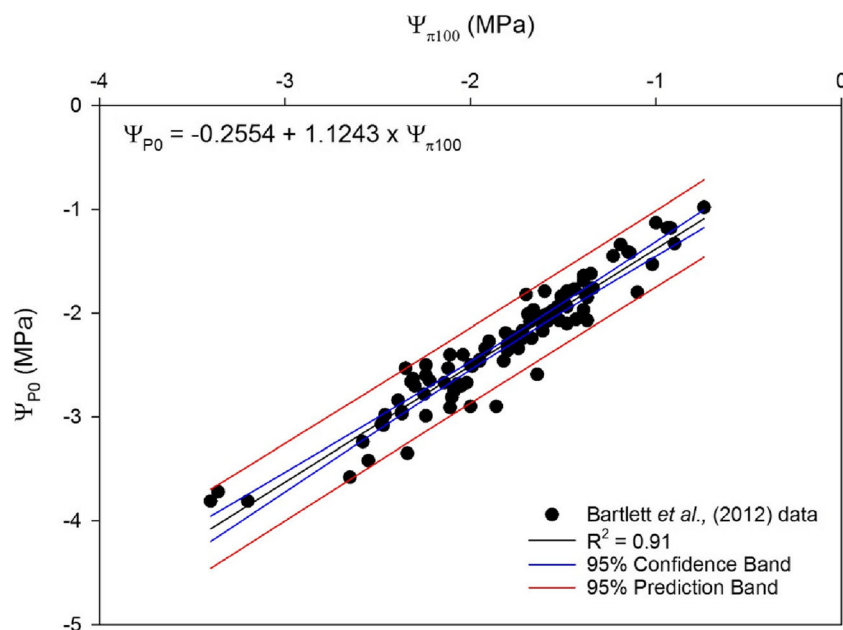
### Literature review

The plant literature reviewed fell into two main categories (Table 1). Dendrological literature (19 books) focuses mainly on species' taxonomical relationship, identification and information relating to their distribution. Site related information tends to be related to a species' natural habitat: some dendrological literature also briefly describes site related guidance for species in cultivation. Plant-use literature (14 books), focused on tree use in urban environments and contains planting recommendations for different urban sites. Many of these publications are used for teaching arboriculture, horticulture and landscape architecture students in Scandinavia, UK and USA (Table 1). Only literature in English was reviewed. The literature was analysed for information relating to species site tolerance with a particular focus on content relating to soil water requirements.

### Professional experience survey

To help establish if a relationship between the qualitative tree species performance and quantitative psychometric measurements of a single plant trait ( $\Psi_{P0}$ ) exists, landscape professionals were asked to evaluate a subset of 23 species' drought tolerance using a six-point likert scale (1, very sensitive to drought; 2, sensitive to drought; 3, moderately sensitive to

**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.  $n = 116$



drought; 4, moderately tolerant of drought; 5, tolerant of drought; 6, very tolerant of drought). These data were then compared to known measurements of  $\Psi_{P0}$ . To reduce speculative answers, respondents were only requested to allocate a drought tolerance rating for species that they were familiar with. The survey was distributed electronically to via Survey Monkey® to a wide range of landscape professionals involved with tree selection for urban environments in the UK. A linear regression ( $f = y_0 + a \cdot x$ ) was used to determine the relationship between the mean qualitative drought tolerance score and the  $\Psi_{P0}$ , previously assessed (Fig. 3). All statistical tests were done in SigmaPlot 13.0.

## Results

### Literature review

Despite the fact that the species included in the study are rarely used as urban trees, there is a large amount of site related information available for most species in this study. However, *Ostrya carpinifolia* and *Acer x zoeschense* were only found within two sources (Table 2). In many cases, the information is too general, making it difficult for the reader to ascertain the species-specific capacity to cope with dry growing conditions. For example, when reviewing information on *Phellodendron amurense* (in total, 7 sources, (Table 2)) much of the information is imprecise in its presentation with conclusions such as: “Drought tolerant” (Gilman 1997; Stoecklein 2001); “Does well in many types of soil e.g. drought” (Dirr 2009); “Tolerates occasional periods of drought” (Trowbridge and Bassuk 2004); “Tolerates occasional brief drought but not prolonged dry periods” (Flint 1983). Such information makes

it hard to interpret the potential of the species for paved sites. Important questions remain: how drought tolerant is *Phellodendron amurense* based on above sources; what is the difference between “Drought tolerant” and “Tolerates occasional periods of drought”? Furthermore, for many species the information is inconsistent. One author may state that a species is sensitive to drought and another tolerant: *Gymnocladus dioica* is described by Hightshoe (1988) to “prefer wet to average soils” and by Gilman (1997) as “Extremely drought tolerant”; *Acer grandidentatum* is said by Spellenberg et al. (2014) to grow in “moist mountain areas” while Beaulieu (2003) describe same species as preferring “dry soil and sunny locations”; *Acer miyabei* is described by Trowbridge and Bassuk (2004) as “tolerant to occasional periods of dry soil”, whilst Dirr (2009) present it as it preferring “moist and well-drained soils” (Table 2).

### Osmotic adjustment and leaf water potential at turgor loss

Species showed a mean  $\Psi_{\pi 100}$  of  $-1.86 (\pm 0.06)$  MPa with a range of 1.56 MPa in spring and a mean  $\Psi_{\pi 100}$  of  $-2.59 (\pm 0.08)$  with a range of 2.25 MPa in summer. Significant seasonal osmotic adjustment was demonstrated in most species, only *Aesculus flava*, *Betula nigra*, *Cladastris kentukea* and *Halesia monticola* did not demonstrate significant seasonal osmotic adjustment (Fig. 2; Table 2).

Highly significant differences in the predicted  $\Psi_{P0}$  existed across species in both spring and summer. The mean value for all species in spring was  $-2.38 (\pm 0.07)$  MPa and with a range of 1.75 MPa. The more critical  $\Psi_{P0}$  in summer had a mean of  $-3.17 (\pm 0.09)$  with a range of 2.53 MPa from the most drought sensitive *Stewartia*

**Table 1** Common literature used to evaluate tree growth under varying levels of soil water deficits

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Dendrological literature

- Ashburner and McAllister (2013). The genus *Betula* – a taxonomic revision of birches.
- Bean (1980) Trees and Shrubs Hardy in the British Isles.
- Beaulieu (2003) An Illustrated Guide to Maples.
- Cappiello and Shadow (2005) Dogwoods.
- Dirr (2009) Manual of Woody Landscape Plants.
- Elias (1989) Field guide to North American trees.
- Fiala (2008) Lilacs – a gardener’s encyclopedia.
- Gardiner (2000) Magnolias – a gardener’s guide.
- Gayraud (2013) Cornus.
- Grimm (2002) The illustrated book of trees.
- Kozłowski and Gratzfeld (2013) *Zelkova* – an ancient tree; global status and conservation action.
- Krüssmann (1986) Manual of Cultivated Broad-leaved Trees & Shrubs.
- Leopold (2005) Native plants of the northeast.
- Menitsky (2005) Oaks of Asia.
- Miller and Lamb (1985) Oaks of North America.
- Nelson et al. (2014) Trees of Eastern North America.
- Pigott (2012) Lime-trees and Basswoods: a biological monograph of the genus *Tilia*.
- Spellenberg et al. (2014) Trees of Western North America.
- van Gelderen et al. (1994) Maples of the World.

Literature directed at landscape plant use

- Bradshaw et al. (1995) Trees in the urban landscape.
- Carr (1979) Gardener’s Handbook; Broad-leaved trees.
- Flint (1983) Landscape plants for eastern North America.
- Forrest (2006) Landscape Trees and Shrubs – Selection, Use and Management.
- Gilman (1997) Trees for urban and suburban landscapes.

Gruffydd (1994) Tree form, size and colour – a guide to selection, planting and design.

- Hightshoe (1988) Native trees, shrubs and vines for urban and rural America.
- Krüssmann (1982) Choosing Woody Ornamentals—A Concise Manual for the correct use of woody landscape plants.
- Mitchell and Coombes (1998) The garden tree.
- Mitchell and Jobling (1984) Decorative trees for country, town and garden.
- Philips (1993) Urban trees – a guide for selection, maintenance, and master planning
- Stoecklein (2001) The complete plant selection guide for landscape design.
- Trowbridge and Bassuk (2004) Trees in the Urban Landscape – Site Assessment, Design and Installation.
- Houtman, R. (ed.) (2015) Van den Berk on Trees
- Sternberg and Wilson (2004) Native Trees for North American Landscapes

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*pseudocamelia* with a  $\Psi_{P0}$  of  $-1.73$  MPa to the most drought tolerant *Acer monspessulanum* with a  $\Psi_{P0}$  of  $-4.26$  MPa (Fig. 2).

## Professional experience survey

The professional roles represented in the survey varied, but the three major groups were landscape architects, local authority officers and arboricultural consultants. In total, 108 professionals gave their opinion on the drought tolerance of 23 different species, representing a wide range of drought tolerance. The selected spring dataset had a  $\Psi_{P0}$  variance of 0.24 MPa and a range of 3.2 MPa, from  $-0.68$  to  $-3.89$  MPa. The selected summer dataset had a variance of 0.39 MPa and a range of 3.1 MPa, from  $-1.66$  to  $-4.76$  MPa. As the respondents were only asked to categorize species that they were familiar with, the mean score was made up from between 23 and 95 responses. No significant relationship ( $p > 0.05$ ) was found between the spring  $\Psi_{P0}$  and the professional drought tolerance score. However, a significant relationship ( $R^2=0.35$ ,  $P < 0.003$ ) was found between the measured summer  $\Psi_{P0}$  value and the score derived from the professional’s experience (Fig. 3).

## Discussion

Urban trees only contribute substantial ecosystem services to society if they mature and have continued health: trees must thrive, not simply survive. At a population scale, the urban forest must have sufficient diversity – at the species, genus and family level – to be resilient to threats from pathogens and damaging insects, as well as from a changing climate. Without adequate species diversity, the long-term provision of ecosystem services from the urban forest will be compromised.

While ambitious planting programs are laudable, their success is highly dependent on the use of trees that are well-adapted to their planting sites. In this regard, species selection is integral to achievement of canopy cover targets, the future resilience of the urban forest and the expansion of ecosystem services derived from trees. As tree inventory data from across the northern hemisphere indicates that species diversity is particularly low in paved and street environments (e.g. Cowett and Bassuk 2014; Sjöman et al. 2012; Yang et al. 2012; Raupp et al. 2006), it is strategically important to use non-traditional species in new planting programs to help ensure sustainable populations of trees. For this to be achieved, it is necessary to evaluate the tolerance of a wide range of species to major threats to establishment and longevity. As water deficits are a major constraint in urban environments (Sieghardt et al. 2005; Hirons and Thomas 2018) and are clearly implicated in mortality during tree establishment (Roman et al. 2014), quantifying species’ tolerance to drought is fundamental to identifying suitable species for urban environments. Many urban tree inventories made in the northern hemisphere show that the most dominant species originate from moist and cool forest habitats and are hence less suitable for warm and dry

**Table 2** Compilation of osmotic potential at full turgor ( $\Psi_{\pi 100}$  ( $\pm$ SE)), seasonal osmotic adjustment ( $\Delta\Psi_{\pi 100}$ ) and site related information of 45 species with regard to information concerning perceived drought tolerance. Sources include dendrological literature and literature directed at landscape plant use (Table 1). n = number of individual trees in the study. \*s indicate where a significant difference between spring and summer  $\Psi_{\pi 100}$  was determined by a paired T-test; \* $P \leq 0.05$  \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
<i>Acer grandidentatum</i>	3	-1.47 ( $\pm 0.15$ )	-3.13 ( $\pm 0.15$ )	1.66***	<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>•Prefers dry soil and sunny locations (Beaulieu 2003)</li> <li>•Grows in moist mountain areas (Spellenberg et al. 2014)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Tolerates very alkaline soils and dry conditions (Sternberg and Wilson 2004)</li> </ul>
<i>Acer miyabei</i>	5	-1.60 ( $\pm 0.08$ )	-2.38 ( $\pm 0.06$ )	0.77***	<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> <li>•Grows in river banks (Krüssmann 1986)</li> <li>•Some drought tolerance (Gilman 1997)</li> </ul>
<i>Acer monspessulanum</i>	3	-1.18 ( $\pm 0.24$ )	-3.56 ( $\pm 0.13$ )	2.39***	<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>•Very drought tolerant (Houtman 2015)</li> </ul>
<i>Acer tataricum</i>	3	-1.68 ( $\pm 0.12$ )	-2.86 ( $\pm 0.11$ )	1.19***	<ul style="list-style-type: none"> <li>•Prefers sunny, dry situations in forest undergrowth (van Gelderen et al. 1994)</li> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Tolerate prolonged periods of dry soil (Bassuk et al. 2009)</li> <li>•Drought tolerant (Dirr 2009)</li> <li>•Resistant to drought (Houtman 2015)</li> <li>•Tolerate occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Some drought tolerance (Gilman 1997)</li> <li>•Very adaptable and tolerates most sites (Philips 1993)</li> </ul>
<i>Acer x zoeschense</i>	3	-1.28 ( $\pm 0.07$ )	-2.84 ( $\pm 0.18$ )	1.57***	<ul style="list-style-type: none"> <li>•Tolerate any soil (Houtman 2015)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Aesculus flava</i>	6	-1.49 ( $\pm 0.04$ )	-1.58 ( $\pm 0.04$ )	0.09 <sup>ns</sup>	<ul style="list-style-type: none"> <li>•Prefers a deep, moist, well-drained root run (Dirr 2009)</li> <li>•Good tolerance to hard surfaces (Houtman 2015)</li> <li>•Tolerate drought but prefer wet to moist soil conditions (Hightshoe 1988)</li> <li>•Grows in river valleys and hillsides (Krüssmann 1986)</li> <li>•Occurs naturally in stream valleys and lower slopes (Grimm 2002)</li> <li>•Strongly recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Moderate drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Betula nigra</i>	5	-2.01 ( $\pm 0.07$ )	-2.10 ( $\pm 0.03$ )	0.09 <sup>ns</sup>	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•The heat tolerance is legendary, however, it is not drought tolerant (Dirr 2009)</li> <li>•Originally grows in moist soil, but it also grow in drier locations (Houtman 2015)</li> <li>•Best birch for hot-dry climates, prefer wet to average (Hightshoe 1988)</li> <li>•Tolerate occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerate occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Grows naturally on streambanks and damp grounds although in cultivation it will grow perfectly well in drier habitats (Ashburner and McAllister 2013)</li> <li>•Tolerant to temporary water logging (Gruffydd 1994)</li> <li>•Not recommended for sandy dry soils (Mitchell and Jobling 1984)</li> <li>•Drought sensitive (Gilman 1997)</li> <li>•Dry to wet soil conditions (Mitchell and Coombes 1998)</li> <li>•Most vigorous with ample water but can survive on relatively dry sites once established (Sternberg and Wilson 2004)</li> </ul>
<i>Carya ovata</i>	4	-2.27 (0.06)	-2.78 ( $\pm 0.03$ )	0.51***	<ul style="list-style-type: none"> <li>•Prefers rich and well-drained loams, but is adaptable to a wide range of soils (Dirr 2009)</li> <li>•Prefers rich, well-drained soil (Houtman 2015)</li> <li>•Wet to porous droughty granular soils (Hightshoe 1988)</li> <li>•Tolerate occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerate occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Prefer rich and well-drained soils (Grimm 2002)</li> <li>•Not recommended for sandy, dry soils (Mitchell and Jobling 1984)</li> <li>•Some drought tolerance (Gilman 1997)</li> </ul>

**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
<i>Catalpa speciosa</i>	6	-1.77 ( $\pm 0.04$ )	-2.34 ( $\pm 0.11$ )	0.57***	<ul style="list-style-type: none"> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Very tolerant of most well-drained soils (Sternberg and Wilson 2004)</li> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Very tolerant of different soil conditions – moist to extremely hot, dry environments (Dirr 2009)</li> <li>•Few soil requirement, not too wet (Houtman 2015)</li> <li>•Wet soils to porous droughty granular soils (Hightshoe 1988)</li> <li>•Tolerate occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Prefer clay (Gruffydd 1994)</li> <li>•Tolerates hot, dry weather (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Can survive under very diverse circumstances, including rich and poor soils, alternate flood and drought conditions, full sun or partial shade, and basic or acidic soils (Sternberg and Wilson 2004)</li> </ul>
<i>Celtis occidentalis</i>	6	-1.89 ( $\pm 0.07$ )	-2.67 ( $\pm 0.05$ )	0.78***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Prefers rich, moist soils or very dry areas (Dirr 2009)</li> <li>•Few soil requirements (Houtman 2015)</li> <li>•From wet to dry soils (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Prefers rich moist soils, but it often grows on rich, rocky hillsides (Grimm 2002)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Excellent drought resistance (Philips 1993)</li> <li>•Will adjust to almost any cultural situation ... the best <i>C. occidentalis</i> sites are rich, deep, alluvial soils with neutral to basic pH, adequate moisture, and full sun (Sternberg and Wilson 2004)</li> </ul>
<i>Cercidiphyllum japonicum</i>	6	-2.02 (0.04)	-2.18 ( $\pm 0.04$ )	0.16*	<ul style="list-style-type: none"> <li>•Soil should be rich, moist and well-drained (Dirr 2009)</li> <li>•Prefers loose loamy soil – not too dry (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Needs consistently moist well-drained soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Requires moist soil (Philips 1993)</li> <li>•Deep moisture-retentive loam (Carr 1979)</li> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Cercis canadensis</i>	6	-1.51 ( $\pm 0.05$ )	-2.49 ( $\pm 0.06$ )	0.98***	<ul style="list-style-type: none"> <li>•Does exceedingly well in many soil types, except permanently wet ones (Dirr 2009)</li> <li>•Thrives best in fertile locations (Houtman 2015)</li> <li>•Prefers moist, tolerate dry soils (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Moderate to high drought tolerance (Gilman 1997)</li> <li>•Needs well-drained soil yet can tolerate the short-term flooding that occurs along small streams (Sternberg and Wilson 2004)</li> </ul>
<i>Cladrastis kentukea</i>	6	-1.58 ( $\pm 0.08$ )	-1.85 ( $\pm 0.09$ )	0.27 <sup>ns</sup>	<ul style="list-style-type: none"> <li>•Well-drained soil (Dirr 2009)</li> <li>•Clay and sandy soils (Houtman 2015)</li> <li>•Prefers wet to average soil moisture (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Need consistently moist, well-drained soil (Trowbridge and Bassuk 2004)</li> <li>•Prefers clay (Gruffydd 1994)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Needs rich soil with good drainage (Philips 1993)</li> <li>•Should have good drainage (Sternberg and Wilson 2004)</li> </ul>
<i>Cornus kousa</i>	6	-1.81 ( $\pm 0.03$ )	-2.12 ( $\pm 0.05$ )	0.31***	<ul style="list-style-type: none"> <li>•Well-drained soil. More drought resistant than <i>C. florida</i> (Dirr 2009)</li> <li>•Well-drained soil. Tolerate more drought than <i>C. florida</i> (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Prefers well-drained clay-silica soil (Gayraud 2013)</li> </ul>

**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
<i>Cornus mas</i>	6	-2.74 ( $\pm 0.10$ )	-3.03 ( $\pm 0.02$ )	0.29*	<ul style="list-style-type: none"> <li>•Can tolerate less favorable soil but dry, droughty soil is to pushing the limit (Cappiello and Shadow 2005)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Require moist, high-organic soil (Philips 1993)</li> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Adaptable for soil, but prefers rich, well-drained soil (Dirr 2009)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Perfectly adapted to all types of soil – dry, rich, poor, moist etc. (Gayraud 2013)</li> <li>•Takes just about any soil from dry to wet (Cappiello and Shadow 2005)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> </ul>
<i>Corylus colurna</i>	5	-2.00 ( $\pm 0.06$ )	-2.56 ( $\pm 0.08$ )	0.57***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Once established, the tree is quite drought tolerant (Dirr 2009)</li> <li>•Drought tolerant (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Recommended as a street tree (Forrest 2006)</li> <li>•Prefers loams (Gruffydd 1994)</li> <li>•Recommended for dry, sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Eucommia ulmoides</i>	6	-2.49 ( $\pm 0.04$ )	-3.03 ( $\pm 0.08$ )	0.54***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Very soil tolerant; resists drought (Dirr 2009)</li> <li>•Tolerates all soil types (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Tolerant of most soils and drought (Philips 1993)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Ginkgo biloba</i>	6	-1.80 ( $\pm 0.06$ )	-3.45 ( $\pm 0.10$ )	1.65***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Grows in almost any situation (Dirr 2009)</li> <li>•Tolerates all soil types (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Prefer loams, clay, sand (Gruffydd 1994)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Adapted to extreme urban environments (Bradshaw et al. 1995)</li> <li>•Requires moist well-drained soil (Philips 1993)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Gymnocladus dioica</i>	6	-1.96 ( $\pm 0.03$ )	-2.61 ( $\pm 0.05$ )	0.65***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Adaptable to a wide range of conditions, such as drought (Dirr 2009)</li> <li>•Well-drained soil (Houtman 2015)</li> <li>•Prefers wet to average soils (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Extreme drought tolerance (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Young trees prefer ample moisture, and a deep, rich alluvial soil (Sternberg and Wilson 2004)</li> </ul>
<i>Halesia monticola</i>	5	-1.60 ( $\pm 0.08$ )	-1.74 ( $\pm 0.02$ )	0.14 <sup>ns</sup>	<ul style="list-style-type: none"> <li>•Prefers rich, well-drained moist soils</li> <li>•Prefers humus-rich, lightly humid soil (Houtman 2015)</li> <li>•Moist to average soils (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Needs consistently moist well-drained soil (Trowbridge and Bassuk 2004)</li> <li>•Drought sensitive (Gilman 1997)</li> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Juglans nigra</i>	6	-2.03 ( $\pm 0.06$ )	-2.32 ( $\pm 0.05$ )	0.29**	<ul style="list-style-type: none"> <li>•Prefers deep, rich, moist soils – tolerates drier soils but grows much more slowly under these conditions (Dirr 2009)</li> <li>•Prefer nutritious, calcareous, drained soil (Houtman 2015)</li> </ul>



**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
					<ul style="list-style-type: none"> <li>•Prefers moist, tolerates droughty conditions (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Attains its maximum growth on deep, rich soils, being much smaller on poorer sites (Grimm 2002)</li> <li>•Prefers clay (Gruffydd 1994)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Prefers good, fertile, moist, well-drained soil (Sternberg and Wilson 2004)</li> </ul>
<i>Koelreuteria paniculata</i>	3	-1.25 ( $\pm 0.06$ )	-3.50 ( $\pm 0.11$ )	2.25***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Adaptable to a wide range of soils; withstand drought (Dirr 2009)</li> <li>•Few soil demands – stands up to dry conditions (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for sandy, dry to sterile soil (Krüssmann 1982)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Fairly easily satisfied as regards soil (Carr 1979)</li> <li>•Best on good soils, including very dry ones (Mitchell and Coombes 1998)</li> </ul>
<i>Laburnum x watereri</i>	3	-1.59 ( $\pm 0.03$ )	-2.23 ( $\pm 0.06$ )	0.63***	<ul style="list-style-type: none"> <li>•Moist, well-drained soils (Dirr 2009)</li> <li>•Prefers substantial, open and nutritious soil (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Recommended for sandy, dry to sterile soil (Krüssmann 1982)</li> <li>•Tolerates anything except waterlogging (Gruffydd 1994)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Liquidambar styraciflua</i>	5	-1.82 ( $\pm 0.08$ )	-2.45 ( $\pm 0.07$ )	0.63**	<ul style="list-style-type: none"> <li>•In the wild it occurs as a bottomland species on rich, moist, alluvial soils but is found on a great variety of sites (Dirr 2009)</li> <li>•Not resistant to long-lasting dry periods (Houtman 2015)</li> <li>•Prefers moist to average soil (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Intolerant to drought (Gruffydd 1994)</li> <li>•Not recommended for sandy dry soils (Mitchell and Jobling 1984)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Flourish on well-drained loam or moist, sandy soils (Carr 1979)</li> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Adaptable to a variety of conditions, preferring deep, moist, acidic soil and full sun ... grows more slowly on dry sites or in less idea soil (Sternberg and Wilson 2004)</li> </ul>
<i>Liriodendron tulipifera</i>	5	-1.73 ( $\pm 0.07$ )	-2.21 ( $\pm 0.06$ )	0.48**	<ul style="list-style-type: none"> <li>•Prefers deep, moist, well-drained loam (Dirr 2009)</li> <li>•Humid and rich soil (Houtman 2015)</li> <li>•Prefers moist to average (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Needs consistently moist well-drained soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•It prefers a deep, rich, moist soil – it is also occupies the rocky slopes of the mountains (Grimm 2002)</li> <li>•Prefers deep loams, clay (Gruffydd 1994)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Moderate drought tolerance in humid climates, drought sensitive elsewhere (Gilman 1997)</li> <li>•Thrives on well-drained, deep, rich loams (Carr 1979)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Likes deep, rich, well-drained soil with uniform rainfall (or supplemental irrigation) throughout the growing season (Sternberg and Wilson 2004)</li> </ul>
<i>Magnolia acuminata</i>	6	-1.62 ( $\pm 0.09$ )	-2.01 ( $\pm 0.03$ )	0.40**	<ul style="list-style-type: none"> <li>•Prefers moist to average soil moisture (Hightshoe 1988)</li> <li>•Should be planted into loamy, deep, moist well-drained soil – does not tolerate extreme drought and wetness (Dirr 2009)</li> <li>•Quite a hardy park tree (Krüssmann 1986)</li> </ul>

**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
					<ul style="list-style-type: none"> <li>•Consistently moist and well-drained (Trowbridge and Bassuk 2004)</li> <li>•Ability to grow in a wide range of soils, but is not tolerant of drought (Gardiner 2000)</li> <li>•Moist and well-drained soil (Leopold 2005)</li> <li>•Prefers moist soil conditions (Flint 1983)</li> <li>•Grows in deciduous woodlands with deep, rich soils on moist slopes along river banks (Nelson et al. 2014)</li> <li>•Grows naturally on the lower slopes along stream banks in deep, rich moist soils (Flint 1985)</li> <li>•Prefers moist, well-drained soil (Stoecklein 2001)</li> <li>•Tolerate all soil types, except alkaline soils (Houtman 2015)</li> <li>•Prefers moist to average (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•It prefers deep, moist, and fertile soils, but is often found on rather rocky slopes (Grimm 2002)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Requires deep, moist, well-drained soil ... will not take wet soil or drought conditions (Sternberg and Wilson 2004)</li> </ul>
<i>Magnolia salicifolia</i>	3	-1.45 ( $\pm 0.06$ )	-1.81 ( $\pm 0.05$ )	0.35**	<ul style="list-style-type: none"> <li>•Native in rocky granite soil by the side of forest streams (Dirr 2009)</li> <li>•Prefers moisture-retentive soil (Gardiner 2000)</li> <li>•Prefers moist soil conditions (Flint 1983)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Prefers clay (Gruffydd 1994)</li> </ul>
<i>Magnolia tripetala</i>	4	-1.57 ( $\pm 0.08$ )	-2.04 ( $\pm 0.08$ )	0.47**	<ul style="list-style-type: none"> <li>•Grows in deep, moist woody soils along streams and swamp margins (Dirr 2009)</li> <li>•Prefers humus-rich and moisture-retentive soil (Gardiner 2000)</li> <li>•Moist and well-drained soil (Leopold 2005)</li> <li>•Grows in rich woods, ravine slopes, margins of mountain streams (Nelson et al. 2014)</li> <li>•It grows naturally in deep rich forests. It occurs in moist soils high in humus in protected ravines, along streams (Elias 1989)</li> <li>•Prefer moist, well-drained soil (Stoecklein 2001)</li> <li>•Need fertile, well permeating soil (Houtman 2015)</li> <li>•Demands wet, tolerates dry soils (Hightshoe 1988)</li> </ul>
<i>Nyssa sylvatica</i>	6	-2.01 ( $\pm 0.05$ )	-2.36 ( $\pm 0.05$ )	0.35**	<ul style="list-style-type: none"> <li>•Prefers moist, well-drained deep soils, however, in the wild it is found on dry mountain ridges (Dirr 2009)</li> <li>•Prefers loamy soils, not to dry (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Best development in rich, moist bottomlands, but is often common on dry mountain ridges (Grimm 2002)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Requires moist loam (Philips 1993)</li> <li>•Dry to wet soil conditions (Mitchell and Coombes 1998)</li> <li>•Once established is resistant to both drought and short-term flooding (Sternberg and Wilson 2004)</li> </ul>
<i>Ostrya carpinifolia</i>	3	-2.50 ( $\pm 0.08$ )	-2.88 ( $\pm 0.07$ )	0.38**	<ul style="list-style-type: none"> <li>•Grows in any soil, even very dry soils (Houtman 2015)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Parrotia persica</i>	5	-2.48 ( $\pm 0.04$ )	-2.68 ( $\pm 0.05$ )	0.20**	<ul style="list-style-type: none"> <li>•Extremely tolerant once established – withstands drought, heat etc. (Dirr 2009)</li> <li>•Needs well-permeable soil (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Recommended for moist to wet soils (Krüssmann 1982)</li> <li>•Prefer loams (Gruffydd 1994)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Tolerant, once established (Philips 1993)</li> <li>•Ideal soil conditions is well-drained sandy loams (Carr 1979)</li> </ul>

**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
<i>Phellodendron amurense</i>	5	-1.95 ( $\pm 0.06$ )	-2.73 ( $\pm 0.04$ )	0.78***	<ul style="list-style-type: none"> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Does well in many types of soils e.g. drought (Dirr 2009)</li> <li>•Tolerates all soil types but prefers nutritious, humic soils (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Platanus occidentalis</i>	5	-1.65 ( $\pm 0.07$ )	-2.10 ( $\pm 0.07$ )	0.46**	<ul style="list-style-type: none"> <li>•Not as tolerant as <i>P. x hispanica</i>. Attains its greatest size in deep moist rich soils (Dirr 2009)</li> <li>•Prefer rich humid soils (Houtman 2015)</li> <li>•Prefers wet to average (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Characteristically a tree of the bottomlands (Grimm 2002)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> </ul>
<i>Prunus sargentii</i>	4	-2.51 ( $\pm 0.06$ )	-2.86 ( $\pm 0.11$ )	0.36*	<ul style="list-style-type: none"> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Prefer loams (Gruffydd 1994)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Require moist well-drained soil (Philips 1993)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Pyrus calleryana</i> 'Chanticleer'	6	-2.25 ( $\pm 0.05$ )	-3.03 ( $\pm 0.11$ )	0.78**	<ul style="list-style-type: none"> <li>•Very adaptable to many different soils, tolerates dryness (Dirr 2009)</li> <li>•Places little soil demands (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Quercus acutissima</i>	2	-1.93 ( $\pm 0.11$ )	-3.36 ( $\pm 0.22$ )	1.43**	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Quite adaptable (Dirr 2009)</li> <li>•Slightly acid and well-drained soil (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Grows better than average on suitable soils (Miller and Lamb 1985)</li> <li>•Not recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Quercus cerris</i>	3	–	-3.12 ( $\pm 0.12$ )	–	<ul style="list-style-type: none"> <li>•Great adaptability (Dirr 2009)</li> <li>•Prefers calcareous soil (Houtman 2015)</li> <li>•Drought tolerant (Gruffydd 1994)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Adapted to dry calcareous soils (Bradshaw et al. 1995)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Quercus frainetto</i>	3	-1.83 ( $\pm 0.06$ )	-3.06 ( $\pm 0.05$ )	1.23***	<ul style="list-style-type: none"> <li>•Prefers nutritious loamy soil (Houtman 2015)</li> <li>•Fast growing park tree (Krüssmann 1986)</li> <li>•A drought and frost tolerant species (Menitsky 2005)</li> <li>•Prefer sandy loams, clay (Gruffydd 1994)</li> <li>•Recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Quercus muehlenbergii</i>	4	-2.63 ( $\pm 0.06$ )	-3.00 ( $\pm 0.07$ )	0.36*	<ul style="list-style-type: none"> <li>•Is found in the wild on dry limestone outcrops – prefers rich bottomlands and there attains its greatest size (Dirr 2009)</li> <li>•Tolerates dry to droughty (Hightshoe 1988)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Considered a climax-species on dry droughty soils, and subclimax on moist sites (Miller and Lamb 1985)</li> <li>•Attains its greatest size on rich soils of the bottomlands – eastern distribution of the species occupies dry hillsides (Grimm 2002)</li> <li>•Drought tolerant (Gilman 1997)</li> </ul>

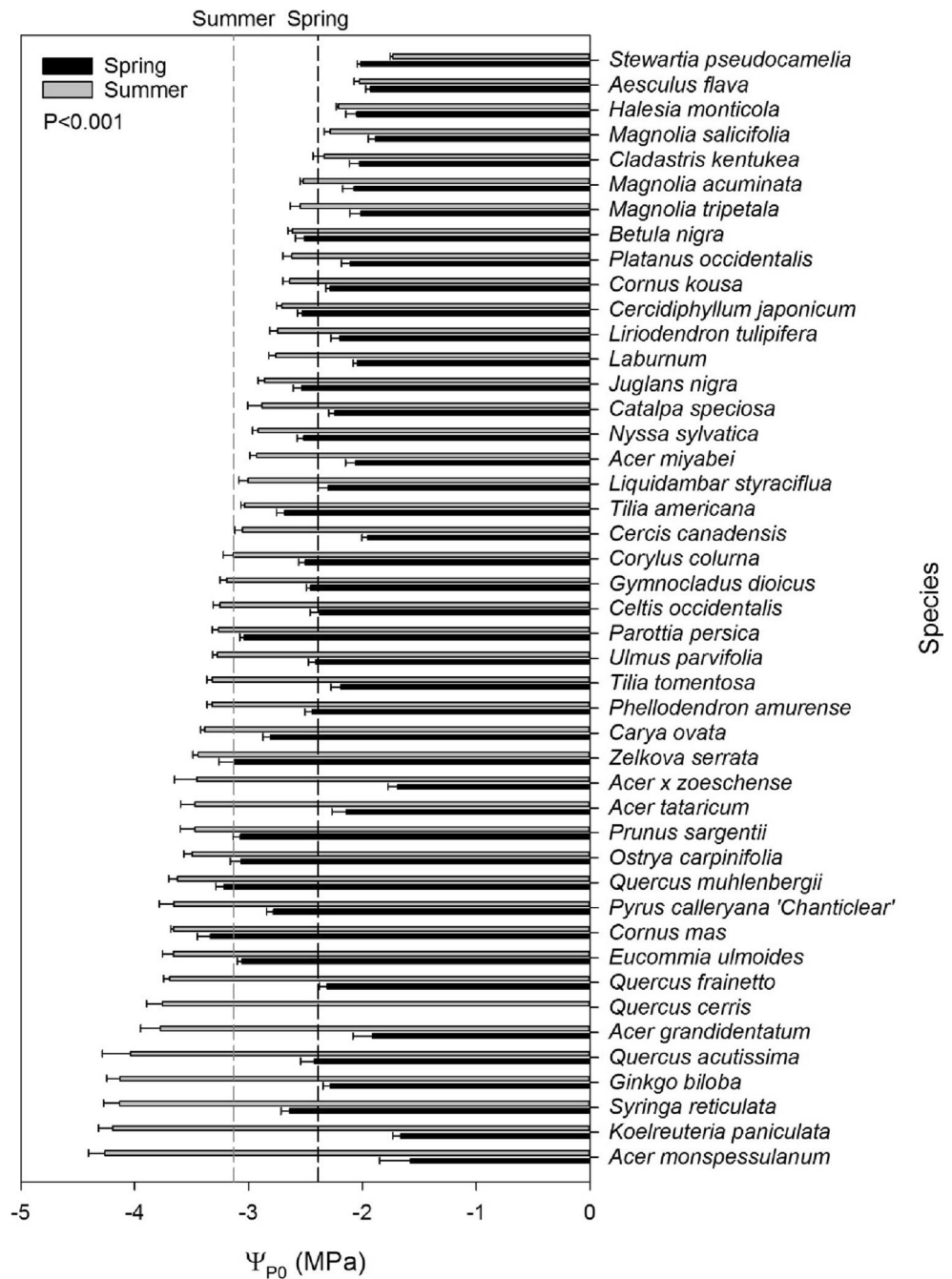
**Table 2** (continued)

Species	n	Spring $\Psi_{\pi 100}$	Summer $\Psi_{\pi 100}$	$\Delta\Psi_{\pi 100}$	Site related information from literature
<i>Stewartia pseudocamelia</i>	5	-1.56 ( $\pm 0.03$ )	-1.31 ( $\pm 0.02$ )	0.25***	<ul style="list-style-type: none"> <li>•Prefers moist (not too wet) peaty soil (Houtman 2015)</li> <li>•Tolerate occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Needs consistently moist well-drained soil (Trowbridge and Bassuk 2004)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Syringa reticulata</i>	6	-2.12 ( $\pm 0.07$ )	-3.45 ( $\pm 0.13$ )	1.33***	<ul style="list-style-type: none"> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Thrives in rich, well-drained soils (Fiala 2008)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> </ul>
<i>Tilia americana</i>	5	-2.16 ( $\pm 0.06$ )	-2.47 ( $\pm 0.03$ )	0.31**	<ul style="list-style-type: none"> <li>•Prefers deep, moist fertile soils ... but will grow on drier heavier soils (Dirr 2009)</li> <li>•Have few demands, not on soil that is too dry (Houtman 2015)</li> <li>•Prefers moist to average (Hightshoe 1988)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Attains a large size on deep, moist soils (Bean 1980)</li> <li>•The preferred habitat is bottomlands, where the soils are deep, moist and fertile (Grimm 2002)</li> <li>•Moderate drought tolerant (Gilman 1997)</li> <li>•Moist soil conditions (Mitchell and Coombes 1998)</li> <li>•Will not perform well as a landscape tree, unless given deep, moist soil (Sternberg and Wilson 2004)</li> </ul>
<i>Tilia tomentosa</i>	3	-1.72 ( $\pm 0.08$ )	-2.73 ( $\pm 0.04$ )	1.01***	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Good street tree as it tolerates heat and drought better than other lindens (Dirr 2009)</li> <li>•Tolerates dry conditions (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•The species grows normally in well-drained soils that remain moist during summer (Pigott 2012)</li> <li>•Prefers clay (Gruffydd 1994)</li> <li>•Moderate drought tolerance (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Ulmus parvifolia</i>	5	-1.92 ( $\pm 0.06$ )	-2.69 ( $\pm 0.04$ )	0.77***	<ul style="list-style-type: none"> <li>•Shows excellent urban soil tolerance (Dirr 2009)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates prolonged periods of dry soil (Trowbridge and Bassuk 2004)</li> <li>•Recommended for dry, sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>
<i>Zelkova serrata</i>	6	-2.56 ( $\pm 0.12$ )	-2.84 ( $\pm 0.04$ )	0.28 <sup>ns</sup>	<ul style="list-style-type: none"> <li>•Drought tolerant (Stoecklein 2001)</li> <li>•Once established, very wind and drought tolerant (Dirr 2009)</li> <li>•Humus, moist, loamy soil (Houtman 2015)</li> <li>•Tolerates occasional brief drought but not prolonged dry periods (Flint 1983)</li> <li>•Tolerates occasional periods of drought (Trowbridge and Bassuk 2004)</li> <li>•Grows particularly well on rich, moist soils, although it can also develop in drier environments and under poorer soils conditions (Kozłowski and Gratzfeld 2013)</li> <li>•Not recommended for dry sandy soils (Mitchell and Jobling 1984)</li> <li>•Drought tolerant (Gilman 1997)</li> <li>•Dry to moist soil conditions (Mitchell and Coombes 1998)</li> </ul>

inner-city environments. In the largest cities in the Scandinavian region *Tilia x europaea* and *Betula pendula* are the most dominant trees, in Lhasa, China, the two most used tree genera are *Populus* and *Salix*, while cities in north-east USA are dominated by maples (e.g. *Acer platanoides*, *A. saccharum*, *A. saccharinum*) (Cowett and Bassuk 2014;

Sjöman et al. 2012; Yang et al. 2012). The potential for combined water deficits and high temperature stresses are predicted to increase in a future climate and will lead to greater tree mortality, even within temperate regions (Allen et al. 2010; Teskey et al. 2015). In this paper, 45 (mostly non-traditional) species, have been analysed for their drought tolerance to infer

**Fig. 2** Predicted leaf turgor loss point in spring and summer of various species ranked by summer leaf turgor loss values. Bars represent the SE of the mean. Vertical dashed lines indicate the season mean across all species

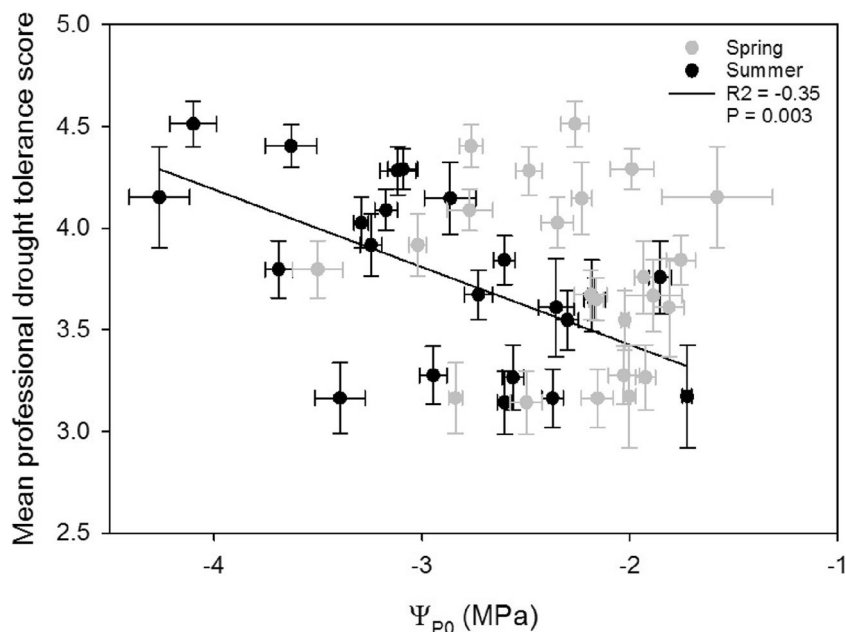


which species have the capacity to grow and perform well in dry urban sites. Furthermore, by systematically evaluating species, it is also possible to identify those species that are sensitive to dry conditions, so that they are not forced into sites where they will not develop successfully.

Professionals making species selection decisions based on existing literature (Table 1) may easily be confused by the guidance for different species' tolerance and their use-potential for urban sites. In this study, we reviewed dendrological and plant-use literature – sources of information that those in the field of urban forestry and urban planning could

use to find species selection guidance for urban sites. Much of the information is presented without references to other sources, giving the impression that the content is strongly rooted in the authors' own experience (s) and qualitative observation, rather than scientific studies (Table 2). This may be the reason why the information between sources is often contradictory. Statements such as “drought tolerant” “not resistant to long-lasting dry periods” and “tolerant of dry to moist soil conditions” do not give precise information regarding the species' capacity to tolerate drought (water deficits) as it is open to reader interpretation. However, it is possible that some trees

**Fig. 3** The relationship between mean professional drought tolerance score leaf turgor loss point predicted from the osmotic potential at full turgor. Grey circles (●) show spring data and black circles (●) show summer data. Vertical bars represent the SE of the practitioner experience and horizontal bars represent the SE of the measured  $\Psi_{P0}$  value. Linear regression for spring data not shown as it was not significant



are genuinely tolerant of both wet and dry site conditions e.g. *Quercus bicolor*, as a result of their natural heritage. Another potential reason for the inconsistency of site related information is the lack of plantations in urban environments. Most of the species in the study are not widely planted in urban landscapes and are normally found in arboreta or botanical gardens, where high quality growing environments can often obscure their tolerance to more challenging sites. Information about much more common species, such as *Acer platanoides* and *Tilia cordata*, more readily integrate plantations in e.g. paved environments, making it easier to evaluate their capacity for such sites (Sjöman and Nielsen 2010).

Currently, robust data that can be used to evaluate and rank different species' site tolerance, especially amongst rare and non-traditionally used species is scarce. In this paper, predicted leaf water potential at turgor loss ( $\Psi_{P0}$ ) was chosen as an indicator to quantify the level of drought tolerance among the species. Paved urban sites are often characterised by restricted soil volume and impermeable surfaces, so tolerance to low soil water potential can aid tree performance in these conditions (Sjöman et al. 2015). Drought avoidance strategies, such as deep rooting, are often restricted in these conditions, as such, species that rely on deep rooting to sustain water uptake and maintain a relatively high shoot water potential are unlikely to perform well on these sites. Other avoidance strategies, such as leaf isohydry are likely to diminish the ecosystem services delivered by the tree, where these rely on water loss from the leaf (evapotranspiration cooling) or photosynthesis (carbon sequestration). Reducing the leaf area of the crown is another avoidance strategy that reduces plant water use. This may either be achieved by premature leaf senescence or as part of a phenological strategy, commonly known as drought-deciduousness. Although trees may survive using avoidance

strategies, species that reduce their crown leaf area in this way during summer will not be able to contribute to the site's seasonal qualities and, consequently, have a limited capacity to deliver ecosystem services. Thus, the leaf water potential at turgor loss point ( $\Psi_{P0}$ ) is of significant interest as it represents a quantifiable measure of drought tolerance.

According to the dataset presented in this study, it is possible to identify species that have a limited capacity for drier planting sites. Examples of these drought sensitive species are *Stewartia pseudocamelia*, *Halesia monticola* and *Magnolia salicifolia* with  $\Psi_{P0}$  of  $-1.8$  MPa,  $-2.1$  MPa and  $-2.3$  MPa respectively (Table 2; Fig. 2). Those species with a  $\Psi_{P0}$  between  $-2.5$  MPa to  $-3.0$  MPa can be considered as moderately sensitive to drought. These species have their main use-potential in park and garden habitats with unconstrained rooting volumes with high quality soil. Use in paved environments can only be considered where extensive soil volumes have been engineered into the site using structural cells (e.g. Rootspace® or Silvacell) and high quality soil is provided. Species with a lower (more negative)  $\Psi_{P0}$  of  $-3.0$  MPa, such as *Syringa reticulata*, *Koelreuteria paniculata* and *Acer monspessulanum* with  $-4.0$  MPa,  $-4.2$  MPa and  $-4.3$  MPa respectively, have the capacity to tolerate prolonged periods of drought so should be favored for paved sites (Table 2; Fig. 2). Importantly, species with a low  $\Psi_{P0}$  can be considered for park and garden habitats but they also have a wider use-potential for more demanding sites such as street environments, podium plantings, roof gardens or green bridges.

Information relating to the seasonal adjustment of species will be of value when planning for future urban tree populations that may experience future climate scenarios that are likely to have warmer and drier conditions (Allen et al. 2010). Change is also likely to occur within seasons,

suggesting that drought may occur much earlier in the growing season (Benestad 2005). By assessing the seasonal change in leaf turgor loss, brought by osmotic adjustment, it is possible to identify species that have a high degree of plasticity in their drought tolerance throughout the growing season. For example, some of the most drought tolerant species in summer appear the most sensitive early in the growing season. *Acer monspessulanum* and *Koelreuteria paniculata* have a  $\Psi_{P0}$  of  $-1.7$  MPa and  $-1.8$  MPa respectively in spring, indicating sensitivity to drought early in the season; as they osmotically adjust, they become much more tolerant by summer. In contrast *Cornus mas* has a  $\Psi_{P0}$  of  $-3.3$  MPa in the spring and  $-3.6$  MPa in summer. Variation in spring phenology, particularly in relation to leaf emergence may underlie some of the variability in the spring dataset despite only fully expanded leaves being selected for evaluation. Such high plasticity in seasonal tolerance to drought is poorly explored and is likely to be important as some climate scenarios indicate dry periods even early in the season. Further, more targeted research in this area is warranted.

Assessment of  $\Psi_{P0}$  provides quantitative data that resolves which species can maintain physiological function more effectively in drying soil (Sack et al. 2003; Lenz et al. 2006). Furthermore, evaluating  $\Psi_{P0}$  can give a valuable insight into the potential of a species to tolerate periods of low water availability and their capacity to respond to environmental change. Through evaluation of  $\Psi_{P0}$  it is possible to use more robust data on species physiological tolerance to dry sites rather than more qualitative conclusions regarding tree species' capacity for dry environments typically found in dendrological and landscape plant-use literature (Table 2). As species are ranked using the same scale, it is possible to present an overview of sensitive and tolerant trees (Fig. 2). For this study we decided to conduct an initial screening of a wide range of species'  $\Psi_{P0}$  growing under similar site situations. Determining more absolute minima of  $\Psi_{P0}$  for each species will require more controlled experiments where plants undergo known degrees of water deficit. Such an approach would restrict the number of species that could be evaluated in any experimental period but will be worthwhile for species of particular interest. It is, therefore, important to see this study as an initial screening for rare or untraditionally species use-potential in urban areas. Besides, as drought tolerance is determined by multiple traits it is not possible to evaluate a single trait and anticipate a species capacity to withstand dry habitats. However, species that have a low (more negative)  $\Psi_{P0}$  tend to maintain leaf gas exchange and growth at lower soil water potential ( $\Psi_{soil}$ ) so are at an 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). Furthermore,  $\Psi_{P0}$  has also been shown to correlate to a series of other traits that confer and

advantage to plant performance during drought, including maintenance of stomatal conductance and hydraulic conductivity (Bartlett et al. 2016). Consequently, the systematic analysis of  $\Psi_{P0}$  does provide good evidence for a species' likely response to dry conditions. Further research pairing  $\Psi_{P0}$  data with other traits used as surrogates for drought tolerance, such as specific leaf area and wood density (Greenwood et al. 2017) may further improve confidence in the use of traits for plant selection purposes.

Research relating to less common tree species is necessarily reliant on the ex situ populations in arboreta and botanical gardens. The advantage of this is that trees are well tended, are grown in unconstrained rooting environments and experience the same climatic conditions. However, since space in these gardens is often at a premium, the number of individual trees represented by each species does present some limitations, particularly in terms of statistical replication. In this study, there are several species that are represented only by three individual trees and one species (*Quercus acutissima*) that was only represented by two trees (Table 2); these data should be interpreted with caution. More widely, it is important to note that significant variation can occur between different genotypes within the same species. In a study by Sjöman et al. (2015) where 27 different genotypes of maples were evaluated for their  $\Psi_{P0}$ , significant differences were found between cultivars of *Acer rubrum* and *A. saccharum*. This suggests that the results presented in this paper should not be considered as definitive descriptions of the species tolerance, but as an indication of their likely drought tolerance in relation to other species. Indeed, for species that have a large natural distribution that includes variation in climate and site conditions, such as *Liriodendron tulipifera* and *Platanus occidentalis* (Nelson et al. 2014), different genotypes are likely to exhibit different levels of drought tolerance. Further research is certainly needed in understanding the variation of drought tolerance between genotypes within the same species. Future studies should be conducted in multiple tree collections and provenances to identify both species and genotypes with potential to become the next generation urban trees.

If quantitative data relating to a species drought tolerance is to be used to convince landscape architects, municipal tree officers and other professionals engaged with species selection to plant alternative species in the urban environment, there must be coherence between their current experience of a species and the actual  $\Psi_{P0}$  of the species. The findings of the survey (Fig. 3) demonstrate that a relationship between the professional's experience of a species and its summer  $\Psi_{P0}$  does exist. This gives persuasive evidence that those species with a more negative  $\Psi_{P0}$  will perform better on sites prone to water deficits. Without this relationship, the practical significance of the  $\Psi_{P0}$  data is less certain. Variance in the experience of professionals is clear, but the average opinion from the community using trees in urban landscapes was related to

trait-based data. This demonstrates that trait data can be effectively used to supplement professional experience and give those specifying trees for urban environments confidence to recommend species that they have less personal experience of. Accordingly, evidence from selected plant traits, such as  $\Psi_{P0}$ , could help anticipate the likely performance of non-traditional species in the landscape, without the necessity of extensive landscape trials. This will enable tree nurseries to identify new candidate species for production and, over time, help expand the palette of species available for challenging urban environments. Indeed, such information could provide an additional marketing tool for certain species. Convincing those specifying trees to recommend species they are less familiar with and incentivising nurseries to grow non-traditional plant material are both strategically important to those tasked with planning resilient urban forests.

Tree selection for urban environments is complex. Those selecting trees must: evaluate key constraints relating to the site and design brief; have knowledge of tree ecophysiology, particularly in relation to species' tolerance of environmental stress; understand the species characteristics that bestow ecosystem services and have an aesthetic vision for the landscape (Sjöman et al. 2017; Hiron and Sjöman 2018). Future tree selection decisions must be made in anticipation of likely changes to local climate and the strategic provision of ecosystem services. This will require the integration of species- and cultivar-level data based on trait analysis, quantifiable relationships between species' characteristics and ecosystem services as well as planning with regard to species' vulnerability to emerging threats from pests and pathogens.

## Conclusions

The future security of the urban forest, and the ecosystem services that it provides for society, depends on trees that are well adapted for the planting site conditions. Threats from a changing climate and the spread of pathogens and damaging insects necessitate the diversification of urban forests to improve its resilience. In order to achieve more diverse urban forests, urban foresters, urban planners, landscape architects (and other related professionals) require clear guidance on species use-potential. This study shows that the current literature on tree species' site preferences can be imprecise and inconsistent across sources. Therefore, the use of quantitative plant trait data can help provide more robust data to aid selection decisions. Since water deficits are known to be a major stress for newly planted trees and trees in paved sites, the drought tolerance of a species plays an eminent role in the tree's performance. Evaluation of the leaf water potential at turgor loss ( $\Psi_{P0}$ ) gives strong evidence for a species' capacity to tolerate dry growing conditions. This was shown to vary significantly across the 45 species evaluated in this study and

shows excellent potential to underpin tree selection guidance. In particular, this trait is directly related to a species ability to perform well in paved sites and street environments. Furthermore, it was demonstrated that the  $\Psi_{P0}$  was related to the experience of professionals involved in establishing trees in urban environments, thus providing evidence of its practical significance. Use of plant traits, such as the  $\Psi_{P0}$ , should, therefore, give those specifying trees for urban environments confidence to recommend non-traditional species. This is necessary to improve species diversity and enhance the resilience of urban forests.

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