RESEARCH ARTICLE

Plants People Planet PPP

Using botanic gardens and arboreta to help identify urban trees for the future

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Societal Impact Statement

Diversification of urban forests is essential to enhance their resilience to future biotic threats as well as those posed by a changing climate. Arboreta and botanic gardens host a wide range of plant material that can be evaluated to inform tree selection policy. This study demonstrates that plant functional traits, such as the water potential at leaf turgor loss, can be highly instructive when developing evidence-based recommendations for urban environments. However, if botanic collections are to fulfil a critical role in understanding plant response to environment, they should not be managed solely as visitor attractions but must have scientific objectives at the forefront of management policy.

Summary

- Arboreta and botanic gardens host a multitude of species that can be utilized in research focused on improving diversity within urban forests. Higher tree species diversity will enhance the resilience of urban forests to abiotic and biotic threats and help deliver strategies that foster sustainable communities. Consequently, this study aims to demonstrate the value of botanic collections as a resource for research into tree species selection for more resilient urban landscapes.

- As water stress is a major constraint for trees in urban environments, understanding the drought tolerance of species is essential for urban tree selection. This study evaluates a key functional trait relating to drought tolerance. Using vapor pressure osmometry, the water potential at leaf turgor loss was evaluated for 96 species using plant material from seven botanic collections in North America and Europe.

- Leaf turgor loss contrasted widely in the temperate deciduous trees evaluated and, in summer, ranged from −1.7 MPa to −3.9 MPa. Significant differences in drought tolerance were also apparent across genera and closely related cultivars. Osmotic adjustment was shown to be a major physiological factor driving leaf turgor loss. A meta-analysis also demonstrated that leaf turgor loss was closely

related to a drought-tolerance scale based on observations of tree performance under drought.

- Arboreta and botanic collections can play a vital role in the evaluation of plant material for urban environments, provided they are curated with scientific objectives at the forefront of management policy and are not managed purely as visitor attractions.

1 | INTRODUCTION

Trees established in our towns and cities enrich the lives of those who encounter them. Evidence for the positive contribution trees make to society is extensive. Thermal comfort of urban areas can be improved as a result of the increased shelter, shading, and transpirational cooling provided by trees (Deak Sjöman et al., 2016; Moss et al., 2019; Rahman et al., 2020). The interception and storage of rainfall associated with trees alleviates flood events in areas with extensive canopy cover (Berland et al., 2017). The presence of trees can enhance numerous aspects of our social relationships (Wolf, 2017), mental health, and well-being (Triguero-Mas et al., 2015; Bratman et al., 2019). Intriguingly, substantive loss in tree cover has even been shown to increase human mortality rates as a result of higher incidence of cardiovascular and respiratory disease (Donovan et al., 2013). Beyond human society, a host of wildlife also benefits from trees established within the urban landscape (Le Roux et al., 2018; Somme et al., 2016). The multiplicity of benefits that trees bring to society is, therefore, without question. Furthermore, a well-placed, healthy, mature tree may well be one of the few elements of our urban realm which has an asset value that actually increases over time, independently of macro-economic forces. Resilient urban forests are also likely to be an essential component of local and regional strategies to meet the Sustainable Development Goals established by the UN, in particular, Goal 11 – Sustainable Cities and Communities (Turner-Skoff & Cavender, 2019). Given the potential magnitude of their value, it is essential that professionals engaged with growing, specifying, and establishing trees in our urban landscapes are equipped to make strategic decisions that will enhance the quality and resilience of our urban forests for future generations.

There is general agreement that higher species diversity increases the resilience of ecosystems to future biotic and abiotic threats (Hooper et al., 2005; Smith et al., 2017). In the context of the urban forest, this assumes that the greater the range of species (and genotypes within a species), the more likely it is that the health of fewer trees will be compromised by any single threat. Thus, diversification helps to provide an insurance policy against

future threats. Urban forests, or sectors of the urban forest, become more vulnerable if they are comprised of only a few dominant species, as a significant climatic event, pest or pathogen outbreak may make it necessary to remove a high percentage of the trees. However, tree inventories from across the world demonstrate that poor trees species diversity is widespread in urban forests (Breuste, 2012; Bühler et al., 2007; Cowett & Bassuk, 2017, 2020; Pauleit et al., 2002; Roloff et al., 2009; Sæbø et al., 2005; Sjöman & Östberg, 2019; Thomsen et al., 2016; Yan & Yang, 2017). Therefore, limited genotypic diversity in urban tree populations is a prevailing international issue and strategic diversification is critical for building resilience into the urban forest and its associated green infrastructure.

Species diversification should be done strategically, so that a breadth of well-suited trees is established: there is little value in increasing diversity simply to meet an arbitrary target. Consideration of a species' (or genotypes') ability to perform well within the likely environmental envelope anticipated by changes to local climates is of central importance to the selection of future urban trees. Therefore, developing approaches that are capable of assessing the suitability of a species or cultivar/genotype to a future climate is essential if robust and resilient species palettes are to be advocated to urban planners.

Arboreta and other botanic collections generally have a wide range of species that are taxonomically, functionally and biogeographically diverse. Often these collections of species are not found in close proximity in natural environments and have high representation from particular genera. Climatic variables are similar across a single collection and planting conditions are typically favorable to good plant development. These characteristics combined with diligent record keeping of plant origins, phenology (*e.g.*, flowering periods), and horticultural requirements make them exceptional resources for scientific research (Chen & Sun, 2018; Dosmann, 2006; Primark & Miller-Rushing, 2009). However, while much of the research in botanic gardens has focused on conservation, economic botany, and taxonomy, these living collections should be used to address challenges such as water scarcity, human health, and climate change (amongst others) (Smith, 2019). As such, well-curated, diverse collections of species represent a key resource for research that is intended to inform the design

and management of green infrastructure (Cannon & Kua, 2017). In particular, the range of tree species found in botanic collections can be used as an asset to facilitate research into species selection in order to improve diversity within urban forests (Cavender & Donnelly, 2019).

ne approach that warrants attention from those tasked with specifying trees for green infrastructure projects is the use of plant functional traits (Violle et al., 2007) to help characterize the likely performance of a species (or genotype) under key environmental perturbations found in urban landscapes.

As water stress is the main constraint for trees in urban environments (Hirons & Thomas, 2018; Sieghardt et al., 2005) and, in many regions, is likely to increase under future climate scenarios (Allen et al., 2010; Naumann et al., 2018; Trenberth et al., 2014; Vicente-Serrano et al., 2020), a robust indication of tree drought tolerance is an essential criteria for urban tree selection, particularly when considering sites with paved surfaces and those subjected to higher evaporative demand as a result of the urban heat island effect.

In natural environments, trees have evolved a range of strategies to cope with periodically dry conditions. These generally equip the tree either to avoid low (more negative) water potentials developing in its tissues or to tolerate low water potential arising from water deficits (Bacelar et al., 2012; Choat et al., 2018; Kozlowski & Pallardy, 2002; Levitt, 1980).

Avoidance of tree water deficits can be mediated either by traits that maximize water acquisition or reduce water use. For example, by developing roots deep within the soil profile, groundwater sources can supply water during extended periods without notable precipitation and thereby help the tree avoid the development of low water potentials (Canadell et al., 1996). Reducing water use through early stomatal closure can also help to postpone drought-related damage to stems (*e.g.*, embolism) and maintain the water status of the leaf (Martínez-Vilalta & Garcia-Forner, 2017). This involves the dynamic control of stomata provided by both hydraulic and non-hydraulic mechanisms (Augé et al., 2000).

In contrast, traits that enable a degree of drought tolerance allow the tree to maintain physiological function at lower water potentials and for longer periods during the drying cycle. This is advantageous on urban sites where restricted soil volume and depth accelerate the development of water deficits. The water potential at turgor loss point (Ψ_{P0}) is a highly instructive trait as it represents a quantifiable measure of physiological drought tolerance. Furthermore, it has been demonstrated to segregate a wide range of species and cultivars in relation to their drought tolerance (Sjöman et al., 2015, 2018a, 2018b) and has subsequently helped to inform tree species selection guidance for green infrastructure (Hirons & Sjöman, 2019).

The overall aim of this study is to demonstrate the value of arboreta and botanic gardens as a resource for research into tree species selection for more resilient urban landscapes. More specifically, we aimed to use multiple collections to increase our understanding of both widely available and underutilized species in relation to their drought tolerance by evaluating the water potential at leaf turgor loss. Where extensive collections of one genus were available, these provided a focus for our research efforts.

2 | MATERIALS AND METHODS

2.1 | Plant material

Plant material was taken from seven different temperate botanic collections: Alnarp (Swedish University of Agricultural Sciences (SLU) (Alnarp); Arboretum Wespelaar (Wespelaar); the F.R. Newman Arboretum at Cornell University (Cornell); Royal Botanic Gardens, Kew (Kew); The Morton Arboretum (Morton); Ness Botanic Garden (Ness); and Savill Garden, Windsor Great Park (Savill). The trees used in the study were all trees established for over 10 years in unconstrained rooting space, growing in full sun or only subjected to short periods of partial shade, with no visual symptoms of stress indicating that the tree was fit for purpose within the climate being evaluated.

2.2 | Climate analysis

Alnarp, Kew, Ness, Savill, and Wespelaar are considered to have a fully humid, oceanic temperate climate with a warm summer, while Cornell and Morton are considered to have a fully humid, snow climate with a warm summer (Cfb and Dfb of the Köppen–Geiger climate classification system, respectively; Kottek et al., 2006). Climate data for each of the study sites were assessed using R (R Core Team, 2020) and the *ggspatial*, *ggplot2*, and *raster* packages. Data for Annual precipitation and Maximum temperature were gathered from World Clim 2 based on aggregated data from 1970 to 2000 (Fick & Hijmans, 2017). Data for the Aridity Index were derived from the ENVIREM dataset (Title & Bemmels, 2018), the index expresses the water deficiency as a percentage of potential evapotranspiration with a higher percentage describing a climate that has higher levels of aridity (Thornthwaite, 1948). Warmth Index indicates the accumulated warmth found across a growing season by summing the monthly mean temperatures where the mean temperature is > 5°C (Yim & Kira, 1975). In combination, these data provide an effective characterization of the growth environment at the botanic gardens in this study and their regional contexts. Maps of the study areas (Figure 1) were plotted using *Rmaps*, *Rnaturalearth*, and *RColorBrewer* packages.

2.3 | Leaf water potential at turgor loss

In accordance with Bartlett, et al. (2012), one sun exposed branch 3–5 m above ground level with no symptoms of abiotic or biotic damage was collected on 3–8 individual trees during early evening when transpiration was relatively low. Excised branches were
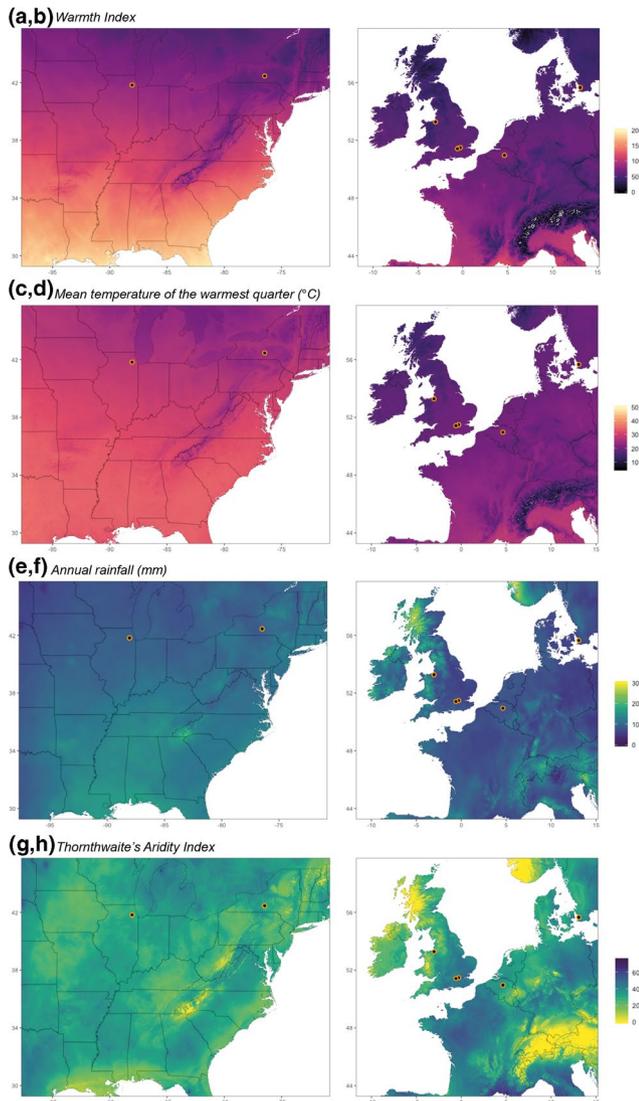
(a,b) *Warmth Index*

(c,d) *Mean temperature of the warmest quarter (°C)*

(e,f) *Annual rainfall (mm)*

(g,h) *Thornthwaite's Aridity Index*

FIGURE 1 Climate conditions relating to heat and precipitation experienced by the seven study sites in North America (left-hand panels) and Europe (right-hand panels). a, b; Warmth Index. c, d; mean temperature of the warmest quarter. e, f; annual rainfall. g, h; Thornthwaite's Aridity Index. Actual values presented in Table 2

immediately 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. Shoot material was then rehydrated overnight in a dark chamber with > 95% relative humidity. 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 at least 2 min to fracture the cell membrane 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 & Richter, 1992)
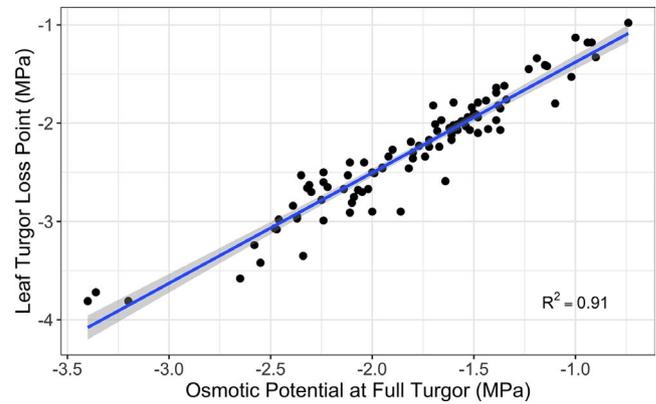

FIGURE 2 Meta-analysis based on a subset of paired data (Osmotic potential at full turgor, leaf turgor loss point) for woody temperate, Mediterranean/temperate-dry and temperate conifer species from Bartlett et al., 2012 supplementary data. The resulting equation (Equation 2) was used in this study to calculate the water potential at turgor loss point (Sjöman et al., 2015). $n = 93$

before sealing the leaf disc in the vapor pressure osmometer (Vapro 5,600, Westcor) using a standard 10-μl chamber. Initial solute concentration (c_s (in mmol/kg)) readings were taken after 10-min equilibration time: c_s was recorded when repeat readings at ~2 min intervals were < 5 mmol/kg. Solute concentration was converted into osmotic potential (Ψ_π) using Van't Hoff's relation (Equation 1):

$$\Psi_\pi = -RTc_s, \qquad (1)$$

where R is a gas constant, T is temperature in Kelvin, and c_s is the solute concentration. Eight replicates were analyzed per species/cultivar. Where possible, two datasets were collected; a spring dataset at the end of May and a summer dataset at the end of July or beginning of August. In spring, all leaves had fully expanded before being collected and analyzed.

Although Bartlett et al. (2012) published an equation allowing the prediction of Ψ_{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. (2012) were used to generate a new equation for deriving Ψ_{P0} from $\Psi_{\pi100}$ in temperate tree species (Figure 2 and Equation 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 Ψ_{P0}.

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

Osmotic adjustment ($\Delta\Psi_{\pi100}$) was calculated as the difference between the spring and the summer datasets. Statistical analysis and plotting were conducted using R Core Team (2019).

TABLE 1 Approximate environmental characteristics aligned with the Niinemets and Valladares (2006) drought-tolerance scale. The distribution of precipitation is founded on the coefficient of variation (ratio of standard deviation to the mean (CV)) of annual precipitation: where a low percentage indicates that precipitation is distributed evenly throughout the year and a higher percentage indicates a greater degree of seasonality in precipitation

Scale ranking	Annual precipitation (mm)	Distribution of precipitation (CV)	P:PET ratio	Soil water potential (MPa)	Duration of dry period
1	>600	Minimal	>3.0	> −0.3	A few days
2	500–600	<10%	1.5:3	−0.3 to −0.8	A few weeks
3	400–500	10%–15%	0.8–1.5	−0.8 to −1.5	Up to a month
4	300–400	20%–25%	0.5:0.8	−1.5 to −3	2 to 3 months
5	<300	>25%	<0.5	< −3	More than three months

TABLE 2 Climatic conditions relating to heat and precipitation of the gardens used in this study. These values are presented in their regional context in Figure 1

Site	Warmth Index	Mean temperature of the warmest quarter (°C)	Annual precipitation (mm)	Aridity index
Alnarp	54.7	19.4	578	39.8
Cornell	72.8	25.7	930	31.8
Kew	71.1	21.1	606	48.1
Morton	85.8	27.8	937	30.6
Ness	58.0	19.0	697	33.6
Savill	63.3	20.2	648	44.8
Wespelaar	70.1	21.3	759	38.0

2.4 | Meta-analysis with ecological stress tolerance scale

In order to evaluate the relationship between drought tolerance and the water potential at leaf turgor loss, the leaf turgor loss data from this study were supplemented by previously published data (Sjöman et al., 2015, 2018a, 2018b) and compared with the Niinemets and Valladares (2006) drought-tolerance scale for shared species. In accordance with Niinemets and Valladares (2006), Table 1 describes the environmental characteristics linked to the 5-point tolerance scale (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; and 5, very tolerant) used. To be assigned a particular rank, tree species were assessed by their ability to be able to persist within the described conditions with <50% foliage damage or crown dieback.

2.5 | Statistics

Differences in genera, species, and genotypes were evaluated using a one-way ANOVA and a linear regression employing the ordinary least squares method was used to evaluate paired relationships. All analysis was conducted using the R software (R Core Team, 2020).

3 | RESULTS

Long-term global climate data have been used to describe key growing conditions found at the botanical collections in this study

(Table 2, Figure 1). The Warmth Index and mean temperature of the warmest quarter show that the US gardens (Cornell and Morton) had the highest degree of warmth in the growing season while the west coast European gardens (Alnarp and Ness) were the coolest. The US gardens also had the higher levels of annual precipitation and consequently lowest Aridity Index. The two gardens in the southeast of the UK (Kew and Savill) were shown to be the driest sites, according to long-term averages.

A wide range of estimated leaf water potential at turgor loss (Ψ_{P0}) was found in each botanic collection (Figure 3). At a species level, these differences were highly significant ($p = <.001$). The mean summer Ψ_{P0} for the 116 species and cultivars represented in this study was −2.6 (SE ± 0.02) MPa and ranged from *Magnolia sinensis* at −1.7 (SE ± 0.05) MPa to *Quercus prinoides* at −3.9 (SE ± 0.25) MPa. For the 49 species that included a spring dataset, the overall species spring Ψ_{P0} mean was −2.2 (SE ± 0.02) MPa and ranged from *Betula utilis* subsp. *utilis* at −1.2 (SE ± 0.07) MPa to *Quercus palustris* at −3.5 (SE ± 0.12) MPa.

Differences between genera were also found to be highly significant ($p = <0.001$) (Figure 4). The mean Ψ_{P0} for all genera was −2.7 (SE ± 0.15). *Magnolia* had the highest Ψ_{P0}, with a mean of −2.02 (SE ± 0.02) MPa, and *Quercus* had the lowest Ψ_{P0}, with a mean of −3.42 (SE ± 0.03) MPa.

To illustrate the sensitivity of the technique within closely related cultivars, Figure 5 shows an evaluation of *Ulmus* cultivars based at The Morton Arboretum. The mean Ψ_{P0} for all *Ulmus* cultivars was −2.7 (SE ± 0.06). *Ulmus* 'New Horizon' was found to have the lowest Ψ_{P0} at −2.9 (SE ± 0.10) MPa. This differed significantly ($p < .05$) from *Ulmus* 'Validation' which had the highest Ψ_{P0} at −2.5
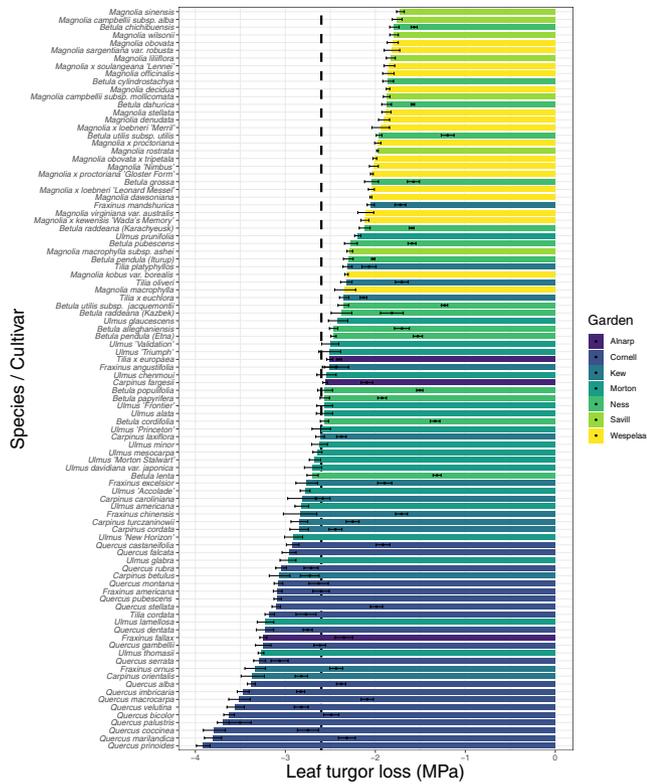
FIGURE 3 Estimated summer water potential at leaf turgor loss for 96 species and cultivars found within seven botanic collections. Where species data were available from multiple botanic gardens, the lowest value (most negative) was represented in this figure (see also Figure 6). Species differences are highly significant (p =< .001) and are ranked here by the mean leaf turgor loss values. Error bars show *SE* of mean. Points and error bars held internally within the bar indicate the spring mean leaf turgor loss values with corresponding *SE*, where these are available. Vertical dashed line indicates the overall summer leaf turgor loss mean

(*SE* ± 0. 09) MPa but was not found to be statistically distinct from the other cultivars.

A comparison of the equivalent species found in contrasting botanic gardens was conducted for the 13 species that had a dataset for two or more gardens. *Carpinus caroliniana*, *C. turczaninowii*, *Fraxinus excelsior*, *Magnolia macrophylla* var. *ashei*, *M. wilsonii*, and *M.* x *loebneri* 'Leonard Messel' showed no statistically significant (p > .05) variation in leaf turgor loss across gardens. However, *C. orientalis*, *F. americana*, *M. denudata*, *Tilia cordata*, *T. tomentosa*, and *Ulmus parvifolia* all displayed significant differences (p < .05) across different gardens (Figure 6). Cornell was the garden that most frequently yielded the lowest (most negative) Ψ_{P0} of any given species, it was also associated with a higher degree of warmth than Alnarp and Kew (see Table 2)).

An estimation of seasonal osmotic adjustment ($\Delta\Psi_{\pi100}$) was made for 53 species in this study. To increase the quality of the analysis, these data were supplemented by data reported in Sjöman et al. (2015), Sjöman et al. (2018a), Sjöman et al. (2018b) to give the $\Delta\Psi_{\pi100}$ for 115 species in total. Regression analysis confirms a highly
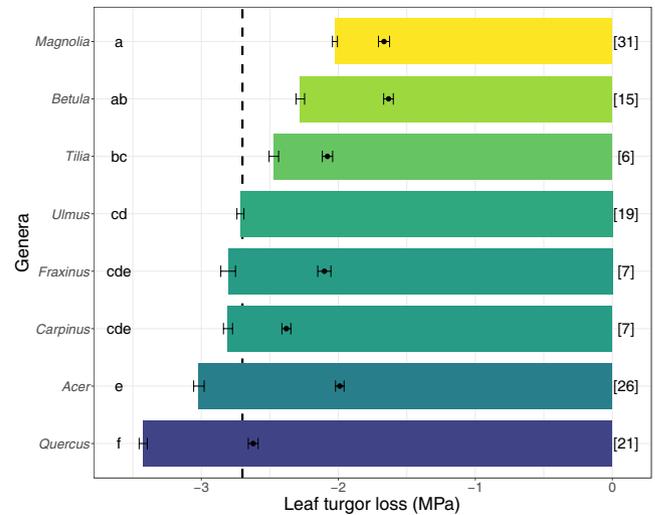

FIGURE 4 Estimated water potential at leaf turgor loss during summer of the major genera featured in this study, supplemented by data from Sjöman et al. (2015, 2018a, 2018b) to improve the analysis. Vertical dashed line represents the mean of all genera. Highly significant differences (p < .001) were found between genera. Letters of heterogeneity indicate where significant differences (p =<0.05) occur between genera as a result of a one-way ANOVA; points and error bars held internally within the bar indicate the spring mean leaf turgor loss values with corresponding *SE*, where these are available. Numbers in square brackets ([x]) show the number of species and cultivars contributing to the analysis

significant relationship (p = <0.001, R^2 = 0.32) between the magnitude of species' $\Delta\Psi_{\pi100}$ and the estimated summer leaf Ψ_{P0} (Figure 7).

Leaf turgor loss is a plant trait that provides quantitative information on the inherent species tolerance to low water potential. This is a key characteristic of drought tolerance so was compared with a previously published (Niinemets & Valladares, 2006) qualitative drought-tolerance scale, where species in common were found. In the current study, 46 species were shared between the datasets; to increase the quality of the analysis, data were supplemented by data reported in Sjöman et al. (2015, 2018a, 2018b)) to provide 100 species for analysis. A highly significant (p = <0.001, R^2 = 0.30) relationship was found between the qualitative drought-tolerance score (between 1–5) and the estimated summer water potential at leaf turgor loss (Figure 8).

4 | DISCUSSION

Tree species selection is a vital component of any strategy employed to enhance the resilience of our urban forests. Despite the recognition that many trees in urban environments are vulnerable to a changing climate, practitioners express uncertainty about how to make robust species selection decisions for future environments (Khan & Conway, 2020). Therefore, advancing our understanding of tree performance thresholds under relevant abiotic stresses should be a focus of those seeking to provide species (and cultivar) selection guidance to urban forest planners and the
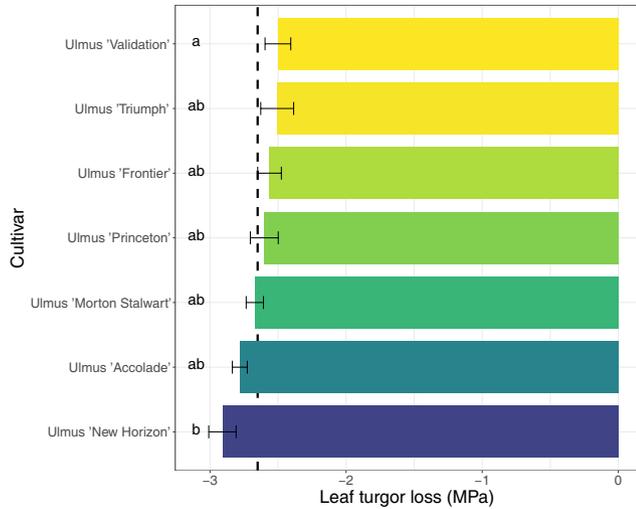
FIGURE 5 Example of how the estimated water potential at leaf turgor loss can be used to evaluate the performance of trees in relation to drought across closely related cultivars. Vertical dashed line represents the mean of all cultivars. Significant differences (*p* < .01) were found between cultivars. Letters of heterogeneity indicate where significant differences (*p* =< .05) occur between cultivars as a result of a one-way ANOVA. Error bars indicate *SE* of mean. Letters of heterogeneity indicate where significant differences (*p* =< .05) occur between cultivars

FIGURE 7 The magnitude of leaf osmotic adjustment in relation to the estimated water potential at leaf turgor loss point. Data from the current study are supplemented by that of three other previously published studies (Sjöman et al., 2015, 2018a, 2018b) to increase the power of analysis. The relationship is highly significant ($p =< 0.001$, $R^2 = 0.32$) $n = 115$

FIGURE 8 The relationship between the drought-tolerance scale derived by Niinemets and Valladares (2006) and the estimated water potential at leaf turgor loss. The drought-tolerance scale runs from 1; Least tolerant to 5; most tolerant. Analysis is based on data from the current study and supplemented by data from three other previously published studies to increase the power of analysis. The relationship is highly significant ($p =< 0.001$ $R^2 = 0.3$) $n = 100$
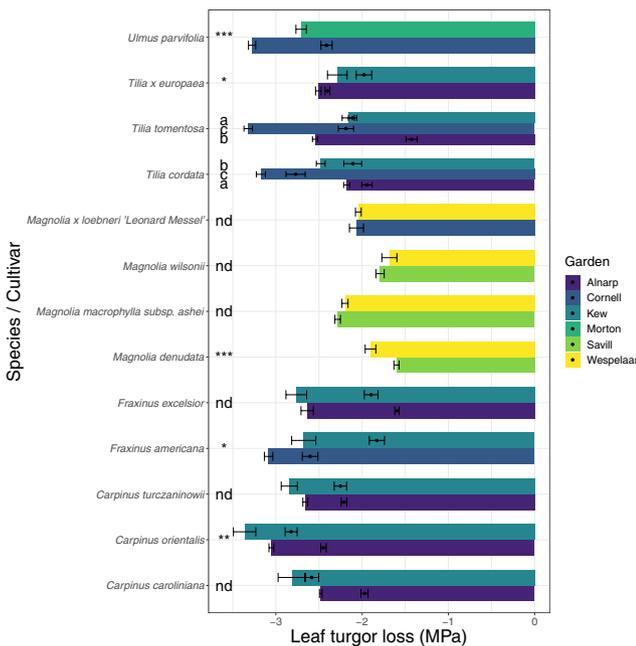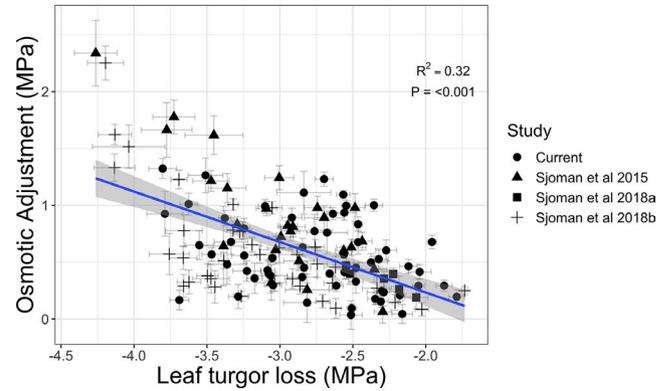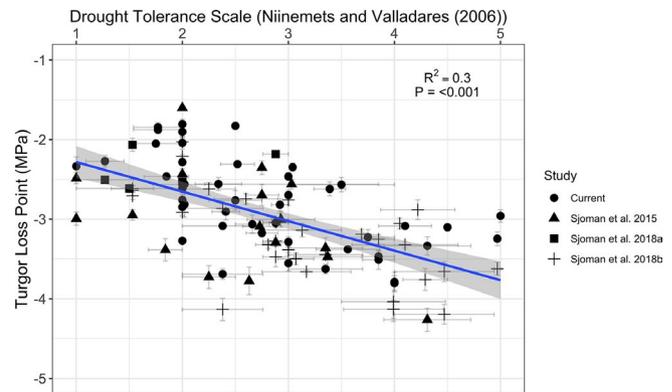

FIGURE 6 Estimated water potential at leaf turgor loss of the same species at different botanic collections. Error bars show *SE* of mean, error bars held internally indicate the spring leaf turgor loss values, where these are available. Where two gardens are compared, the significance level is indicated by * =*p* < .05, ** =*p* < .01, and *** = *p* < .001. Letters of heterogeneity indicate differences where three gardens are compared. nd = no significant difference

landscape community. Tolerance to drought stress is critical to the performance of many urban trees as it is relevant to sites with small soil volumes and those with impermeable surfaces (Hirons & Thomas, 2018; Wang et al., 2019), those subjected to the urban heat island (Orlandini et al., 2017), as well as future climate scenarios, characterized by reduced summer precipitation and increased frequency of heat waves (Naumann et al., 2018; Teskey et al., 2015; Webster et al., 2017). Assessments of species that are currently widespread in urban green infrastructure demonstrate their vulnerability to projected changes in climate (Khan & Conway, 2020; Nitschke et al., 2017). Consequently, selection of species based on hierarchical filters that place key biophysical climate variables (*e.g.*, drought) as fundamental criteria for selection is likely to substantially improve outcomes for those tasked

with establishing the urban forest (Burley et al., 2019; Hirons & Sjöman, 2019).

Arboreta and botanic gardens provide a diverse range of plant material, suited to local and regional climates. Where sufficient replication of species occurs within the same garden, such species diversity presents an opportunity to systematically evaluate key plant traits to better inform species-level guidance for the plant-user community as well as growers producing trees for future landscapes. This study contributes data on the leaf water potential at turgor loss (Ψ_{P0}) for 96 species (Figure 3). These data were combined with species-level data previously published (Sjöman et al., 2015, 2018a, 2018b) to evaluate eight important genera widely found in temperate urban forests (Figure 4).

Consistent with other inter-specific studies (Bartlett, et al., 2012; Maréchaux et al., 2015, 2019; Sjöman et al., 2015, 2018a), this research confirms that tree species can differ by > 2 MPa in the leaf turgor loss point during summer. This study showed a range from −1.7 MPa (*Magnolia sinensis*) to −3.9 MPa (*Quercus prinoides*), similar ranges have been shown even within an evaluation of one genus, *Acer* (Sjöman et al., 2015). This range demonstrates that across an array of species there is a profound difference in tolerance to water deficits and the concomitant ability of species to maintain physiological performance under stress. Of the genera evaluated in this study, *Magnolia* were the least tolerant to drought. This sensitivity to drought is consistent with observations that *Magnolia* are predominately from cool, moist, forest habitats (Sjöman et al., 2018a) and require ample moisture throughout the growing season in cultivation (Grimshaw & Bayton, 2009). *Quercus* were the most tolerant to drought, while *Betula*, *Tilia*, *Ulmus*, *Fraxinus*, *Carpinus*, and *Acer* occupy intermediate positions. Importantly, as the position of each genus is a function of the underlying species-level evaluations, they should be taken as an indicative estimate of the generic-level Ψ_{P0} as it is impracticable to evaluate every species within a genus. However, this still represents the most comprehensive analysis of temperate tree turgor loss at the generic level. It can, therefore, act as a benchmark for the relative drought tolerance of temperate trees.

A substantial limitation of evaluating species and cultivars in botanic gardens and arboreta is that there is likely to be a much wider range of genotypes growing in the wild than is represented in gardens (Hoban et al., 2020). This is likely to bias the evaluation of species in specialist horticultural texts (heuristic literature), particularly for taxonomic groups that are not well studied. As demonstrated in the genus *Magnolia*, the use of species distribution models (SDMs) that integrate observational and climate data offer opportunities to identify new species' ecotypes (provenances) from which to recruit plant material for urban forestry (Watkins et al., 2020). These models in combination with plant functional trait data offer exciting opportunities to evaluate woody flora for future climate scenarios. Indeed, arboreta and botanic collections should play a central role on building the future resilience of the landscape beyond their immediate boundaries and not just in far-flung places associated with conservation priorities.

Where tree species selection guidance is developed, it is clear that the summer leaf Ψ_{P0} should be considered as a fundamental trait that can help inform advice relating to drought tolerance. For example, a four-point qualitative scale (sensitive, moderately sensitive, moderately tolerant, and tolerant) could be underpinned with quantitative Ψ_{P0} data, where: sensitive => −2.5 MPa; moderately sensitive = −2.5 MPa to −3 MPa; moderately tolerant = −3 MPa to −3.5 MPa; and tolerant = <−3.5 MPa (Hirons & Sjöman, 2019). This approach should always be applied with discretion and allocation of a tolerance rating can be given increased confidence when combined with other trait data such as that relating to the vulnerability of xylem to drought-induced embolism. Clearly, the use of traits to underpin plant-user guidance has great potential to increase the confidence that amateurs and professionals have in plant specifications, something that will be essential as designers seek to increase the resilience of landscapes to climate projections that encompass increased drought.

As the use of cultivars is so widespread in amenity landscape specifications, it is important that evaluative tools used to screen functional differences between genotypes are sufficiently sensitive. To help confirm that leaf Ψ_{P0} is sensitive enough to resolve differences between closely related cultivars, a number of *Ulmus* cultivars, developed as part of the long-term breeding program at The Morton Arboretum was evaluated. While most cultivars were not statistically distinct from each other, the *Ulmus* 'New Horizon' was found to be significantly more drought tolerant than *Ulmus* 'Validation' (Figure 5). This analysis supports previous studies conducted with *Acer* (Sjöman et al., 2015) that the technique of using vapor pressure osmometry to predict Ψ_{P0} (via $\Psi_{\pi 100}$) is sensitive enough to resolve differences in drought tolerance between closely related genotypes. From a practical perspective, the technique has been proven to be more time efficient (Bartlett, et al., 2012) and more sensitive than pressure-volume curves (Banks & Hirons, 2019): a more traditional technique used to determine Ψ_{P0} in leaves. Therefore, it is likely to be a useful technique to identify which plant lineages are likely to be contributing to drought tolerance within novel breeding programs. Collections that host a range of plant provenances and ecotypes in cultivation will be especially well placed to carry out this type of research.

In natural ecosystems and managed landscapes, there is evidence of intraspecific variation in Ψ_{P0} along a water availability gradient, with lower (more negative) Ψ_{P0} being expressed by trees growing in warmer, drier conditions (Esperon-Rodriguez et al., 2020; Rosas et al., 2019). Furthermore, the observation that Ψ_{P0} of leaves is not closely related to other leaf traits (Maréchaux et al., 2015, 2019) also suggests that more widely available traits (e.g., leaf mass per area (LMA) via the TRY database (Kattge et al., 2020)) are not good surrogates for tree drought tolerance and, therefore, should not be substituted for Ψ_{P0} to inform tree selection guidance. Data demonstrating that tree species with a lower (more negative) Ψ_{P0} are able to maintain stomatal conductance (Bartlett et al., 2016) and sap flow (Maréchaux et al., 2018) for longer during a soil drying cycle also suggests that these species will maintain key ecosystem services,

such as evapotranspirational cooling, more effectively than species with a higher (less negative) Ψ_{P0}. Additionally, growth resilience to non-lethal drought has been shown to reduce mortality risk under subsequent drought events (De Soto et al., 2020) underscoring the value of drought tolerance as a fundamental criterion for tree selection. Therefore, Ψ_{P0} should be a core trait when seeking to screen species and cultivars to support plant selection guidance or to provide data for ecological models seeking to assess plant-community response to drought.

Evaluation of the same species in multiple gardens confirms that there can be highly significant intraspecific variation in leaf Ψ_{P0} according to site. Although this was not a systematic analysis of the potential of climate to influence leaf Ψ_{P0}, it does provide evidence that Ψ_{P0} is a trait that could help define the ecological plasticity of a species in relation to drought. However, while this meta-analysis does not provide sufficient resolution of (micro-) climatic conditions to confirm that summer Ψ_{P0} is a function of water availability, the clear evidence of intraspecific variability according to site does suggest that more controlled, mechanistic studies involving a wide range of species are warranted. It also suggests that some species are likely to have a much lower capacity to reduce their Ψ_{P0} in response to site conditions. In such cases, this is likely to be because of a limited ability to osmotically adjust. Figure 7 shows that, in general, species with a higher (less negative) Ψ_{P0} during summer show a more limited ability to osmotically adjust than those with a lower (more negative) Ψ_{P0}. Indeed, the meta-analysis based on 115 species relating osmotic adjustment to summer Ψ_{P0} (Figure 7) provides some of the best evidence to date that a tree's ability to osmotically adjust is a fundamental attribute leading to drought tolerance during summer. However, a few species, for example, *Quercus palustris, Q. muhlenbergii, Cornus mas, Ostrya carpinifolia, Prunus sargentii,* and *Eucommia ulmoides,* show relatively low levels of OA (<0.5 MPa) but are considered tolerant to drought (Ψ_{P0} < −3.5 MPa) indicating that some species have good tolerance to drought throughout the growing season and might, therefore, be less vulnerable to water deficits early in the growing season. Two species, *Acer monspessulanum* and *Koelreuteria paniculata,* show osmotic adjustment > 2 MPa, such a profound capacity for physiological adjustment is likely to make these species highly resilient to future scenarios that predict a reduced water availability.

Evidence that summer leaf Ψ_{P0} is an appropriate surrogate for overall drought tolerance is provided by the highly significant relationship between species in the Niinemets and Valladares (2006) dataset that are shared with this study (Figure 8). However, it is clear that some outliers do exist; for example, *Syringa reticulata* was rated as 2.38 on a 5-point scale according to Niinemets and Valladares (2006) (see Table 1) but is reported to have a Ψ_{P0} of −4.13 MPa. This apparent contradiction between the Niinemets and Valladares (2006) dataset and the leaf Ψ_{P0} may be because information for some species, including *S. reticulata,* came from heuristic university extension literature, so is perhaps less robust than primary literature sources, or trait evaluation. For other species, discrepancies between the apparent drought tolerance indicated by summer leaf Ψ_{P0}

and the tolerance index based on crown condition may be that those species that avoid drought through isohydric behavior (Martínez-Vilalta & Garcia-Forner, 2017) or deep rooting strategies (Canadell et al., 1996) do not necessarily have an ability to cope with low leaf water potential. Variation in putative drought tolerance may also arise as a function of data being derived from different ecotypes or provenances (Watkins et al., 2020).

Botanic gardens and arboreta can provide a rich source of plant material that can be evaluated to inform the selection of trees for current and future climates. This analysis is the first to pool data from multiple botanic collections to facilitate a multi-genera overview of drought tolerance in temperate trees. It demonstrates that it is now feasible to efficiently and sensitively screen a wide range of species and genotypes for a key trait that can meaningfully inform ecological models and plant-user guidance. However, this type of research is only possible if curators of collections consider facilitating future research opportunities as a key objective when introducing plant material to a garden. Consideration should also be given to the sampling design of plant collection trips so that a breadth of genetic material is represented in cultivation (Hoban et al., 2020). This will not only support conservation goals but will also facilitate the evaluation of intraspecific trait variability and help provide focus for plant selection. Furthermore, more than six individuals per species or genotype should be planted to grant sufficient replication for statistically valid research. Clearly, space constraints may limit this in some circumstances, in which case, curators are encouraged to achieve this for core collections and to collaborate with allied botanic collections. Arboreta and botanic gardens are uniquely placed to support the evaluation of a range of landscape plants – including trees – because they are intended to be long-term custodians of plants, have substantial expertise in the management of living collections, and precise records of plant origins. However, without an emphasis on future research, many botanic collections may be in danger of becoming botanical zoos that serve spectators but not scientists.

AUTHOR CONTRIBUTION

ADH led the writing of the manuscript, data analysis, and data collection at Royal Botanic Gardens, Kew and Ness Botanic Gardens. JHRW led the collection data at Savill Gardens and Arboretum Wespelaar as well as leading the presentation of climate data characterizing the gardens and revision of the manuscript. TJB assisted with data collection at Ness Botanic Gardens and revision of the manuscript. JWM led the data collection at The Morton Arboretum and helped revise the manuscript. AM-M assisted with data collection at The Morton Arboretum. KWEM assisted

with data collection at Royal Botanic Gardens, Kew. NLB assisted with data collection at the F.R. Newman Arboretum at Cornell University and with revision of the manuscript. HS led the data collection at the F.R. Newman Arboretum and Alnarp as well as helping to revise the manuscript.

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