ORIGINAL ARTICLE

Intraspecific drought tolerance of *Betula pendula* genotypes: an evaluation using leaf turgor loss in a botanical collection

Simon Hannus[1] · Andrew Hirons[2] · Timothy Baxter[3] · Hugh A. McAllister[3] · Björn Wiström[1] · Henrik Sjöman[1,4,5]

Abstract

Key message **The results showed a significant relationship between the potential evapotranspiration of the provenance collection site and the leaf turgor loss point and significant positive differences in drought tolerance between provenances and subspecies of *B. pendula*.**

Abstract The ecosystem services provided by urban trees make substantial contributions to the quality of urban living and securing resilience towards the challenges posed by a changing climate. Water deficits are a major abiotic stress for trees in urban environments and, in many regions, this stress is likely to be amplified under future climate scenarios. Although wide variation in drought tolerance exists at the species level, many species also show substantial intraspecific variation in drought tolerance. The aim of this study is to evaluate how drought tolerance, inferred from the *water potential at leaf turgor loss point* (Ψ_{P0}), varies in *Betula pendula* from different geographical origins and determine if the observed drought tolerance can be related to the local climate and seasonal water balance from the provenance of origin, despite the trees now being established in similar soil and climatic conditions within a single botanical collection. Six subsp. *betula*, five subsp. *mandshurica* and two subsp. *szechuanica were evaluated*, giving a total of 12 different provenances. The results showed a significant relationship between the potential evapotranspiration of the provenance collection site and the leaf turgor loss point and significant positive differences in drought tolerance between provenances and subspecies of *B. pendula*. By directing efforts towards identifying more drought-tolerant genotypes, it will be possible to diversify the palette of trees that could confidently be integrated by urban tree planners and landscape architects into the urban landscape. The results of this study on different ecotypes of *B. pendula* clearly show that it is possible to find more drought-tolerant plant material.

Communicated by Buckeridge.

✉ Henrik Sjöman
henrik.sjoman@slu.se

1 Faculty of Landscape Planning, Horticulture and Agricultural Science, Department of Landscape Architecture, Planning and Management, Swedish University of Agricultural Science, PO-Box 66, 23053 Alnarp, Sweden

2 University Centre Myerscough, Bilsborrow, Preston PR3 0RY, Lancashire, UK

3 Ness Botanic Gardens, University of Liverpool, Neston Road. Ness, Cheshire, UK

4 Gothenburg Botanical Garden, Carl Skottsbergs Gata 22A, 413 19 Gothenburg, Sweden

5 Gothenburg Global Biodiversity Centre, Gothenburg, Sweden

Introduction

Societal benefits from trees are positively related to the size and health of the tree (Hirons and Sjöman 2019). For example, important ecosystem services, such as cooling, rely on expansive crowns to intercept solar radiation (Bowler et al. 2010; Sanusi et al. 2017). Similarly, large healthy trees are more effective at intercepting rainfall and mitigating flood risk (Berland et al. 2017). Those seeking to maximize the value of the urban forest, therefore, need to preserve space for large, mature trees, and diligently specify species that are capable of performing well on those sites.

Water deficits are a major abiotic stress for trees in urban environments (Sieghardt et al. 2005; Hirons and Thomas 2018) and, in many regions, this stress is likely to be amplified under future climate scenarios (Allen et al. 2010; Ruosteenoja et al. 2018). Consequently, drought tolerance should

be a fundamental consideration of those selecting trees for urban environments. Although wide variation in drought tolerance exists at the species level (Niinemets and Valladares 2006; Choat et al. 2012; Sjöman et al. 2018), many species also show substantial intraspecific variation in drought tolerance. For example, Bauerle (2003) and Sjöman et al. (2015) showed significant differences in drought tolerance between contrasting genotypes of red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*). Variation in seasonal precipitation and evapotranspiration has also been shown to influence the genotypic drought tolerance of holm oak (*Quercus ilex*) (Valero-Galván et al. 2013). Therefore, for species with an extensive natural distribution, understanding how the species' provenance and/or ecotype interacts with important selection criteria, such as drought tolerance, may be fundamental to securing the most appropriate genotype for a planting site. It is vital to understand if differences in climate observed within plant provenance and ecotype can be related to functional characteristics when plants are brought into cultivation. This study seeks to evaluate if a functional trait relating to drought tolerance—leaf turgor loss point—differs when plant material sourced from across an aridity gradient is established on a single site.

Despite knowledge about the variation in genotypic tolerance to environmental variables being well established, information on the provenance of a cultivar is rarely reported or even known by tree nurseries. It is not uncommon for nurseries to unwittingly proliferate genotypes of wholly inappropriate provenances for their purpose, instead favouring well-established cultivar names or whatever material that is most easily available. An example of this is many British nurseries growing Birch seedlings from local stock and selling them as Silver birch, *Betula pendula* Roth., even though these are often Downy birch *B. pubescens*, or Paper birch *B. papyrifera* hybrids. Given the potential importance of genotypic differences, it is important to evaluate the plasticity of a species to determine if the most appropriate plant material currently exists within commercial production, or if more suitable genetic material is likely to be found from a wild source or in situ population already established in a botanic collection.

Understanding the potential variation within a single species warrants more detailed investigations as integrating provenance-scale information into selection decisions may be crucial when identifying plant material for future climate scenarios. Furthermore, there is increasing interest in using species' traits to predict ecotypic responses to environmental change (Niinemets 2015; Cavender-Bares et al. 2016). It has been proposed that attention be focused on plant organs such as leaves to facilitate functional comparisons of plants, since leaves are the most well-studied plant organs (Wright et al. 2004; Perez-Harguindeguy et al. 2013). 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. 2018) and has subsequently helped to inform tree species selection guidance for green infrastructure (Hirons and Sjöman 2019). This analysis supports previous studies from plant collections in *Acer* (Sjöman et al. 2015) that the technique of using vapour pressure osmometry to predict Ψ_{P0} (via osmotic potential at full turgor ($\Psi\pi100$)) 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 2012b) and more sensitive than pressure–volume curves (Banks and Hirons 2019): a more traditional technique used to determine Ψ_{P0} in leaves.

Silver birch, *Betula pendula* Roth. is a temperate tree species with an enormous distribution in Europe, Asia and North America (Atkinson 1992; Ashburner and McAllister 2013). It is also one of the most widely planted species in urban environments and firmly embedded into the species palette of tree specifiers (Sjöman and Östberg 2019). Therefore, the overall aim of this study is to evaluate how drought tolerance, inferred from the *water potential at leaf turgor loss point* (Ψ_{P0}), varies in *Betula pendula* from different geographical origins and determine if the observed drought tolerance can be related to the local climate and seasonal water balance from the provenance of origin, despite the trees now being established in similar soil and climatic conditions within a single botanical collection.

Materials and methods

Plant materials

Birch are deciduous shrubs and trees of the genus *Betula* native to the northern hemisphere and a common element in subtropical, temperate and boreal forests throughout Eurasia, as well as North America (Ashburner and McAllister 2013). Silver birch (*B. pendula*) was selected as species of investigation due to its large geographical and habitat distribution and morphological and physiological variation. According to the latest compilation of the genus *Betula*, Ashburner and McAllister (2016) proposed three subspecies of *B. pendula* sensu lato: subsp. *betula*, subsp. *mandshurica* and subsp. *szechuanica*, representing the extremities of the contiguous populations of Europe, East Asia and Southwest China respectively.

Plant material for the study was collected in August 2016, at Ness Botanical Gardens (NBG), located near Liverpool, in northwestern England. NBG hosts a collection of over 200 living accessions of birch with documented origins sourced from their own botanical expeditions as well as seed

exchange programs with other botanic gardens and collectors. Due to earlier research (e.g. Sjöman et al. 2015) collection of samples for turgor loss measurement is carried out in August to allow seasonal osmotic adjustment to occur. The chosen specimens represented the width of the species' distribution across the northern hemisphere (Fig. 1), which included six subsp. *betula*, five subsp. *mandshurica* and two subsp. *szechuanica*, for a total of 12 different provenances (Table 1). NBG have a fully humid temperate climate with warm summers (Cfb and Dfb of the Köppen–Geiger climate classification system; Kottek et al. 2006) with a yearly mean temperature of 10.9 °C and yearly mean precipitation of 622.6 mm.

In order to compare the tree to each other the trees need to be growing under similar conditions. The birch were situated in a park landscape as well-established trees in various group plantings with separate clones of birch of the same origin often clustered together, the understory generally consisted of grass and/or shrub borders. The below-ground conditions were typical of a park environment; they had no apparent

Fig. 1 Locations of the different *Betula pendula* provenances used in this study. Seed collected from these sites was grown, and the trees established, at Ness Botanic Gardens

Table 1 Provenance information of the *Betula pendula* evaluated in this trial

Provenance	Country	Subspecies	Coordinates	n	Elevation (m.a.s.l.)	Yearly mean precipitation (mm)
Listvyanka	Russia	*mandshurica*	51.86°N 104.87°E	3	550	467.2
Kuril Islands	Russia	*mandshurica*	45.10°N 147.88°E	3	n.a	1244.6
Furano	Japan	*mandshurica*	43.33°N 142.35°E	5	300	1090.7
Alberta	Canada	*mandshurica*	52.68°N 113.49°W	3	800	470.2
Gonggashan Xiang	China	*mandshurica*	29.47°N 101.54°E	3	3500	1009.9
Basongtso	China	*szechuanica*	29.99°N 94.01°E	3	3900	747.8
Paoma Shan	China	*szechuanica*	30.04°N 101.97°E	5	2910	958.4
Novosibirsk	Russia	*pendula*	54.82°N 83.11°E	2	150	460
Valais	Switzerland	*pendula*	46.19°N 7.31°E	2	n.a	680
Carmolangan	Italy	*pendula*	43.96°N 7.74°E	2	1130	1285.9
Horní Bečva	Czech Republic	*pendula*	49.44°N 18.30°E	3	600	701.8
Hauho	Finland	*pendula*	61.15°N 24.59°E	2	100	652.9

constraints to the available soil volume and trees had no visual indications of nutrient or water deficits. The soil on site is free draining sandy soils of 0552a Kexby and 0552b Ollerton types with a mean pH of 5.6.

Leaf turgor loss

In this study, leaf water potential at leaf turgor loss (Ψ_{P0}) was chosen to estimate drought tolerance. Ψ_{P0} provides a robust measure of plant drought tolerance as a more negative Ψ_{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) Ψ_{P0} tend to maintain leaf gas exchange, hydraulic conductance and growth at lower soil water potentials (Ψ_{soil}) so are at an advantage where soil water deficits occur during the growth season (Mitchell et al. 2008; Blackman et al. 2010). The Ψ_{P0} also provides a surrogate for the soil water potential (Ψ_{soil}) below which the plant cannot recover from wilting (Bartlett et al. 2012a). Additionally, Ψ_{P0} is related to leaf and stem conductivity—hydraulic traits relating to drought that impact on the water supply for transpiration and photosynthesis (Bartlett et al. 2016). Therefore, Ψ_{P0} is a trait that provides information about a species´ capacity to grow in water-scarce environments and is particularly relevant for inner-city conditions, characterised by restricted soil volumes and impermeable surfaces (Sjöman et al. 2015, 2018).

One sun-exposed branch with no symptoms of abiotic or biotic damage was collected on 2–5 individual trees during early evening when transpiration was relatively low (Table 1). The branches were thereafter cut again, under water, in order to remove any stem embolism caused by the introduction of air due to the equalisation of pressure, as well as to prevent formation of air bubbles that could obstruct the vascular flow of the excised shoot. This was performed at least two nodes, or 20 cm, distal to the initial cut. While still submerged the shoots were placed in water-filled vials and placed in a dark chamber with > 90% relative humidity overnight to rehydrate. All samples were harvested during a single 2-h period.

Leaf discs (one per leaf—the leaf was the first (lowest) on the year shoot to use leaves produced in same period between samples) were taken from fully expanded leaves using a 7-mm cork borer from the mid-lamina region between the mid-rib and leaf margin. A total of 8 replicates for each birch provenance were processed in this manner, across 2–5 individuals (Table 1). To minimise 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 vapour pressure osmometer (Vapro 5600, Westcor, Logan, UT, USA) using a standard 10-µl chamber. Initial solute concentration (cs (in mmol kg^{-1})) readings were taken after 10 min equilibration time: cs was recorded when repeat readings at ~ 2-min intervals were < 5 mmol kg^{-1} apart. Solute concentration was converted to osmotic potential ($\Psi\pi$) using Van't Hoff's relation (Eq. 1), where R is the ideal gas constant, T is temperature in Kelvin and c_s is the solute concentration:

$$\psi_\pi = -RTc_s. \tag{1}$$

This osmotic potential was used to estimate the leaf turgor loss point (Ψ_{P0}) through the equation developed by Sjöman et al. (2015) for temperate tree species (Eq. 2)), which was based on the original regression by Bartlett et al. (2012b). Although Bartlett et al. (2012b) 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. (2012a) was used to generate a new equation for deriving Ψ_{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 Ψ_{P0}.

$$\psi_{P0} = -0.2554 + 1.1243 \times \psi_{\pi100}. \tag{2}$$

Climate evaluation

To attain climate data for the different collection sites, we used the WorldClim 2 database, which holds monthly climate normals for the period 1970–2000, with grid resolution of 30 arc-seconds (~ 1 km at the equator) (Fick and Hijmans 2017; WorldClim 2017). Since exact location for the collection site was not generally known, except the collection altitude, the following sampling approach was used to extract monthly average temperature and precipitation, as well as 19 standard WorldClim variables from the raster. Based on the collection site descriptions and digital maps, we estimated a position, and from that extracted the average values of the raster within a radius of 10 km for all points at an altitude of ± 100 m from the collection notation using the Zonal Statistics toolset in ArcMap v10.2.2 and the digital elevation model (DEM) *ALOS World 3D model* with a grid resolution of 1 arc-second (~ 30 m at the equator) for the altitude (JAXA 2018). To evaluate and compare the sites from where the *Betula* provenance origins from the site's potential

evapotranspiration (PET) have been calculated. Through this calculation it is possible to view the water balance over the year where loss of water through evapotranspiration is compared with precipitation, thus giving an indication of when a water deficit during the season is likely to occur and how significant it will be. In calculating PET, the regression presented by Thornthwaite (1948) was used (Eq. 3), with monthly potential evapotranspiration based on the values of temperature, number of sunshine hours per day, water runoff, and cloudiness. Accurate length of daylight was calculated using the method established by Meeus (1991), facilitated by spreadsheet provided by *The National Oceanic and Atmospheric Administration* (NOAA 2019).

The potential evapotranspiration (or reference evapotranspiration, mm per month) for a typical month of N days with an L-hour average photoperiod/day was modelled with an average temperature (T, ^oC) using the scheme proposed by Thornthwaite (1948) as

$$ET_M = 16\left(\frac{L}{12}\right)\left(\frac{N}{30}\right)\left(10\frac{T}{I}\right)^{\alpha}, T > 0^oC, \qquad (3)$$

where I is a thermal index imposed by the local normal climate temperature regime (Tn, ^oC) and the exponent a is a function of I, both computed by

$$I = \sum_{n=1}^{12}\left(0.2T_n\right)^{1.514}, T_n > 0^oC,$$

$$a = 6.75x10^{-7}I^3 - 7.71x10^{-5}I^2 + 1.7912x10^{-2}I + 0.49239.$$

Statistical analyses

We explored relations between the all the different climatic variable mentioned above using principal component analysis (PCA) on the scaled matrix of the variables (Oksanen 2019). Based on the Kaiser–Guttman criterion and a broken stick model, the top three components where chosen for further analysis (Borcard et al. 2011). Those climatic variables loading the highest on these three different axes where chosen for inclusion in forthcoming modelling of the relation between Ψ_{P0} and climate.

All univariate analysis used the lme function in package nlme (Pinheiro et al 2019) in programme R (R Core Team 2019) and significance level of 0.05. Comparison of models was based on Maximum Likelihood estimates and final reported models on REML estimates in accordance with Zuur et al. (2009).

To test if the different collection site differed in Ψ_{P0}, we used a mixed general linear model with collection *Site* as explanatory variable and the different sampled trees

as random variable. Allowing different residual variation among the site through the varIndent weight argument did not improve the model significantly and therefore the covariance was modelled as fixed. To test for differences between subspecies, a mixed general model was used with Ψ_{P0} as response and subspecies as fixed factor and *Site* and *Tree* as random variables with Tree nested under Site. Additionally, the different climate variables selected based on the PCA were individually tested as explanatory variables for Ψ_{P0} as well as together with subspecies as explanatory variables using the same approach as above.

Results

Turgor loss point

There was a significant effect on Ψ_{P0} for inclusion of the different sites (L = 38.22, df = 1, $p < 0.0001$) and Ψ_{P0} varied from -2.07 to -2.94 MPa across the examined *B. pendula* (see Table 2). The differences between the individual sites can be seen in Fig. 2. For the different subspecies there was also a significant inclusion effect (L = 16.08, df = 1, $p < 0.0001$) where subspecies *pendula* differed from *mandshurica* and *szechuanica* as seen in the boxplot of Fig. 3 and Table 2. In subsp. *pendula* it varied between -2.32 and -2.94 MPa, in subsp. *mandshurica* -2.07 and -2.46 MPa, and in subsp. *szechuanica* -2.18 and -2.34 MPa (Fig. 3; Table 2). The mean Ψ_{P0} for all *B. pendula* genotypes in this study was -2.47 MPa (± 0.03).

Drought tolerance correlations

For the tested climate variables, PET calculated according to Thornthwaite and the 15 Bioclim variables had a significant relation towards Ψ_{P0}, see Table 2 for model information. None of the significant climate variables improved the models when the subspecies variable was already included in or had any significant interaction effects. Generally, as seen in Fig. 4, the clear differences between the subspecies seems to capture the significant climatic gradients sampled in the study as the subspecies are located towards the extremes of the range of the different significant climatic variables. For a full test of the correlations between climate variables and subspecies, a larger sample size would be needed with more overlapping collection sites concerning the climatic range.

To further analyse the effect of precipitation seasonality and PET, we plotted the regional water balance for the twelve provenances. This showed the diverse large-scale hydrological conditions under which silver birch grows (Fig. 5). The onset of negative water balance under zero surface runoff happens in late spring in most instances, such

Table 2 Model summary for the different final mixed general linear models with Ψ_{P0} as response variable

Random effect	Intercept	Residuals			
StdDev	0.1778974	0.2097239			

Fixed effect	Value	Std.Error	DF	t value	p value
Intercept	−2.3193	0.1242	61	−18.6680	0.0000
Basongtso	0.0963	0.1778	23	0.5414	0.5934
Carmolangan	−0.5619	0.1917	23	−2.9309	0.0075
Furano	0.0728	0.1658	23	0.4358	0.6671
Gonggashan Xiang	−0.0269	0.1778	23	−0.1515	0.8809
Hauho	−0.6186	0.1917	23	−3.2265	0.0037
Horní Bečva	−0.4904	0.1778	23	−2.7585	0.0112
Kuril Islands	−0.1520	0.1778	23	−0.8552	0.4012
Listvyanka	0.2413	0.1801	23	1.3403	0.1932
Novosibirsk	−0.3061	0.1940	23	−1.5777	0.1283
Paoma Shan	−0.0191	0.1712	23	−0.1116	0.9121
Valais	−0.1454	0.1917	23	−0.7581	0.4561

Random effect	Intercept	Residuals			
StdDev	0.1842343	0.2092698			

Fixed effect	Value	Std.Error	DF	t value	p value
Intercept	−2.2923	0.0645	61	−35.5294	0.0000
ssp. pendula	−0.4552	0.0970	9	−4.6933	0.0011
ssp. szechuanica	0.0079	0.1201	9	0.0660	0.9488

Random effect	Intercept	Residuals			
StdDev	0.1775663	0.2094819			

Fixed effect	Value	Std.Error	DF	t value	p value
Intercept	−1.0185	0.6220	61	−1.6376	0.1067
PET_Thornthwaite	−0.0028	0.0012	10	−2.3461	0.0409

Random effect	Intercept	Residuals			
StdDev	0.1804197	0.2090407			

Fixed effect	Value	Std.Error	DF	t value	p value
Intercept	−2.8097	0.1398	61	−20.0918	0.0000
PET_Thornthwaite	−0.0059	0.0022	10	−2.7390	0.0209

The first model shows the relation between collection site and Ψ_{P0} with sampled trees as random variable. The following models shows the individual relation between Ψ_{P0} and subspecies, PET and precipitation seasonality, modelled with sampled trees nested under collection site as random variables

as Listvyanka, Alberta, Novosibirsk, Valais, Hauho and Furano, while precipitation patterns delays this drought in Horní Bečva and Carmolangan. This contrasts with the Asiatic weather patterns of Basongtso and Gonggashan Xian, Paoma Shan, and to a certain degree The Kuril Islands, where seasonal rain seemingly prevents negative water balance from being caused by evapotranspirational factors alone (Fig. 5). The role of surface runoff can be elucidated from the same plots, as a large runoff coefficient is necessary to cause drought conditions for the Asian provenances (excluding Furano), while the same conditions would cause water stress earlier in the vegetation period for the already precipitation-deficient provenances in Europe and Russia; this suggests that water balance in the latter case is strongly dependent on soil conditions and topography in the way it affects distribution of local plant life.

Discussion

Arguments and other site-related guidance published in dendrological literature are focused on the whole species level (Sjöman et al. 2018) without acknowledging the variation within the species. This is despite the fact that tree
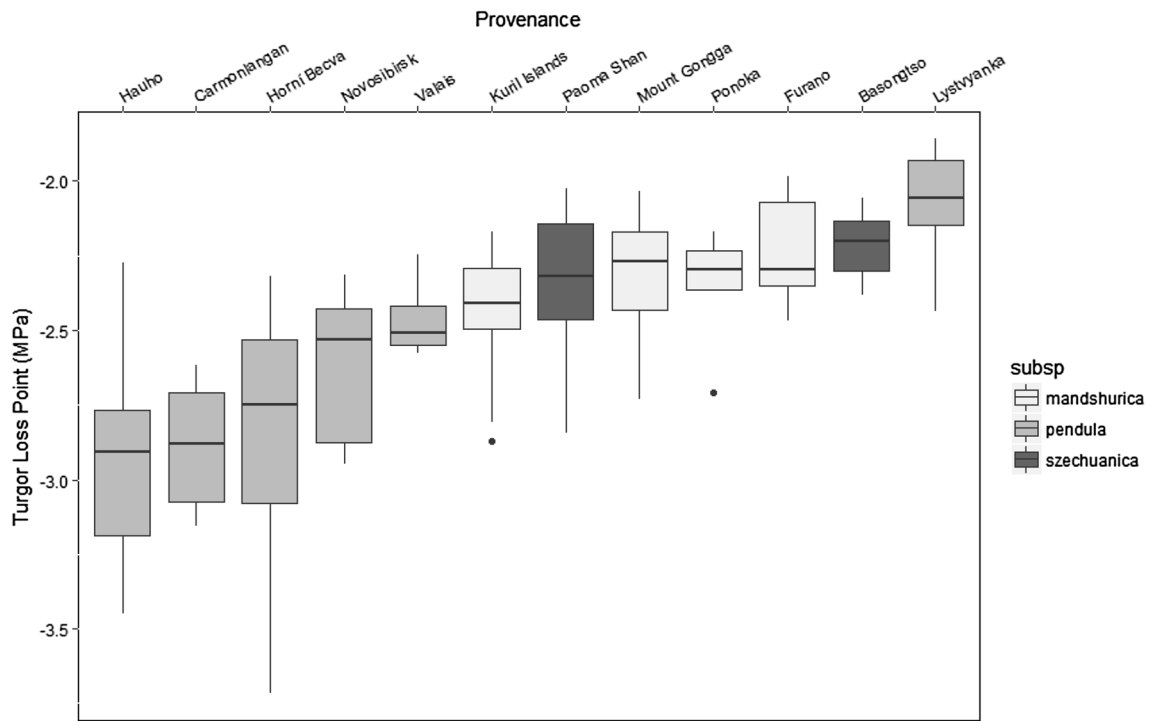
Fig. 2 Boxplot of the estimated leaf turgor loss point from the different *Betula pendula* provenances. Boxplot shows the median (central line), inter-quartile ranges, the range of data found within 1.5×the inter-quartile ranges (whiskers) and extreme values (dots). The subspecies is denoted in different tones of grey

Fig. 3 Boxplot of the estimated leaf turgor loss point between the different subspecies. All data for the sub-species have been pooled, regardless of provenance. Boxplot shows the median (central line within box), inter-quartile ranges (box), the range of data found within 1.5×the inter-quartile ranges (whiskers) and extreme values (dots)
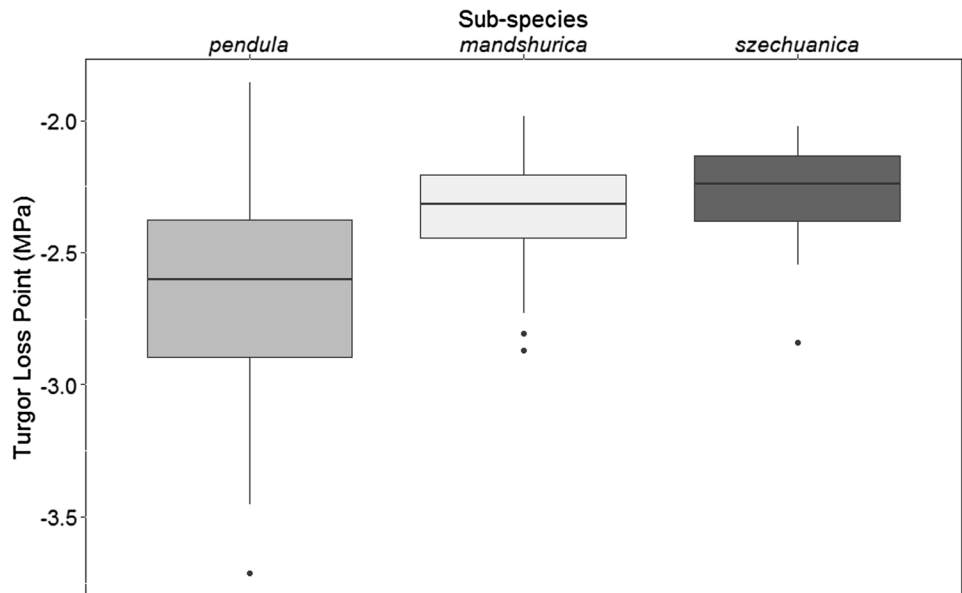
performance in the urban landscape may be greatly improved by the selection of trees from particular provenances. The primary purpose of this study was to assess the variation of Ψ_{P0} in *B. pendula* sourced from a wide geographical distribution and to investigate if variation between tree provenance and sub-species are measurable within a tree collection to evaluate this method as a screening technique for urban trees and future climate scenarios. Using Ψ_{P0} as a key trait, differences emerged across different provenances and subspecies (Figs. 2 and 3), where the European subspecies *pendula* was indicated to have a lower turgor loss point on average than the two Asiatic subspecies *szechuanica* and

Fig. 4 Illustration of relationship between site, subspecies, estimated leaf turgor loss point (TLP) and climate variables using ordinary regression with 95% confidence intervals. The regression is based on Ψ_{P0} site mean and the different climate variables found significant through mixed modelling
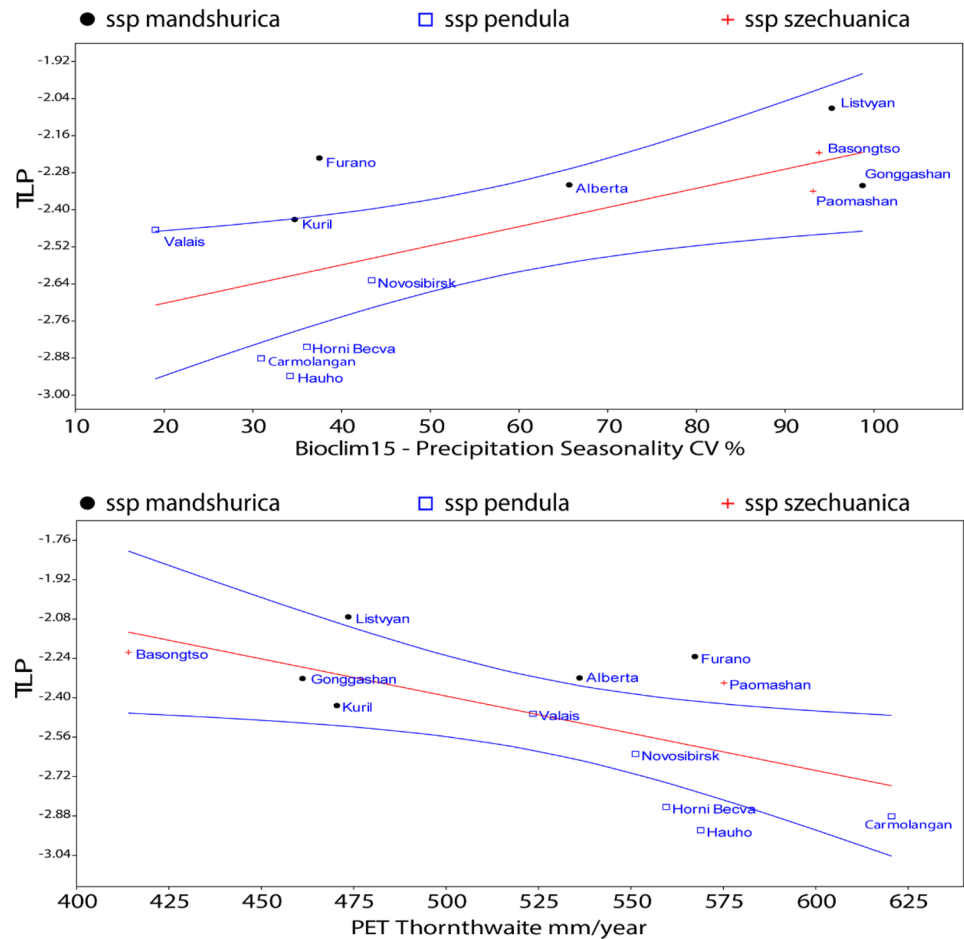
mandshurica (Fig. 3). The results confirm earlier studies evaluating drought tolerance between different species and genotypes of Betula. Aspelmeier and Leuschner (2006) evaluated morphology and carbon investments in leaves and roots between provenances of *Betula pendula*, with significant differences between ecotypes. Ranney et al. (1991) also used Ψ_{P0} as a key trait to demonstrate a contrast in drought tolerance between *Betula*, showing significant difference between six species and cultivars. It is surprising that the urban forestry industry has not embraced the fact that tolerance for a warmer and dryer climate differ greatly between ecotypes of the same species—especially among species with a large natural distribution, such as *Betula pendula*. One cause may be that this knowledge has not been communicated effectively enough in urban forestry communities and in horticultural groups despite its prominence in ecological and biological communities as well as for forestry where this knowledge is available. For example, drought adaptive traits in tree species such as *Acer grandidentatum* Nutt., *Acer rubrum* L., *Acer saccharum*, *Fraxinus americana* L. and *Quercus rubra* L., have been shown to differ across environmental gradients relating to habitat type and precipitation (Kubiske and Abrams 1992; Alder et al. 1996; Bauerle

et al. 2003; Marchin et al. 2008; Sjöman et al. 2015; Schuldt et al. 2016). Moreover, strong evidence has also been found in *Fagus sylvatica* with spatial gradient of ecotypes, from drought sensitive in north-central Europe, to more drought tolerant in the southern populations (Cavin and Jump 2017; Stojnić et al. 2017). Growth in *Fagus sylvatica* is significantly associated with PET, levels of precipitation and aridity (Hacket-Pain et al. 2016). Even though *F. sylvatica* is not part of the more warm-climate South-European populations, East European marginal populations indicated to be more drought tolerant than the nearest latitudinal central counterparts, a property assumed to be linked with the drier summers of the eastern continental climate (Rose et al. 2009; Thiel et al. 2014). The results from this study on *Betula pendula* provide further evidence of substantive intraspecific variation in stress tolerance as function of provenance.

In general, the genus *Betula* has been noted to lack tolerance for low soil water potentials, while opting for avoidance strategies such as deep roots, stomatal regulation, premature leaf senescence and abscission in response to prolonged drought (Ranney et al. 1990; Gu et al. 2007). Even *B. pendula*, which has been described to be typically preferring of well-drained soils, employs such avoidance strategies
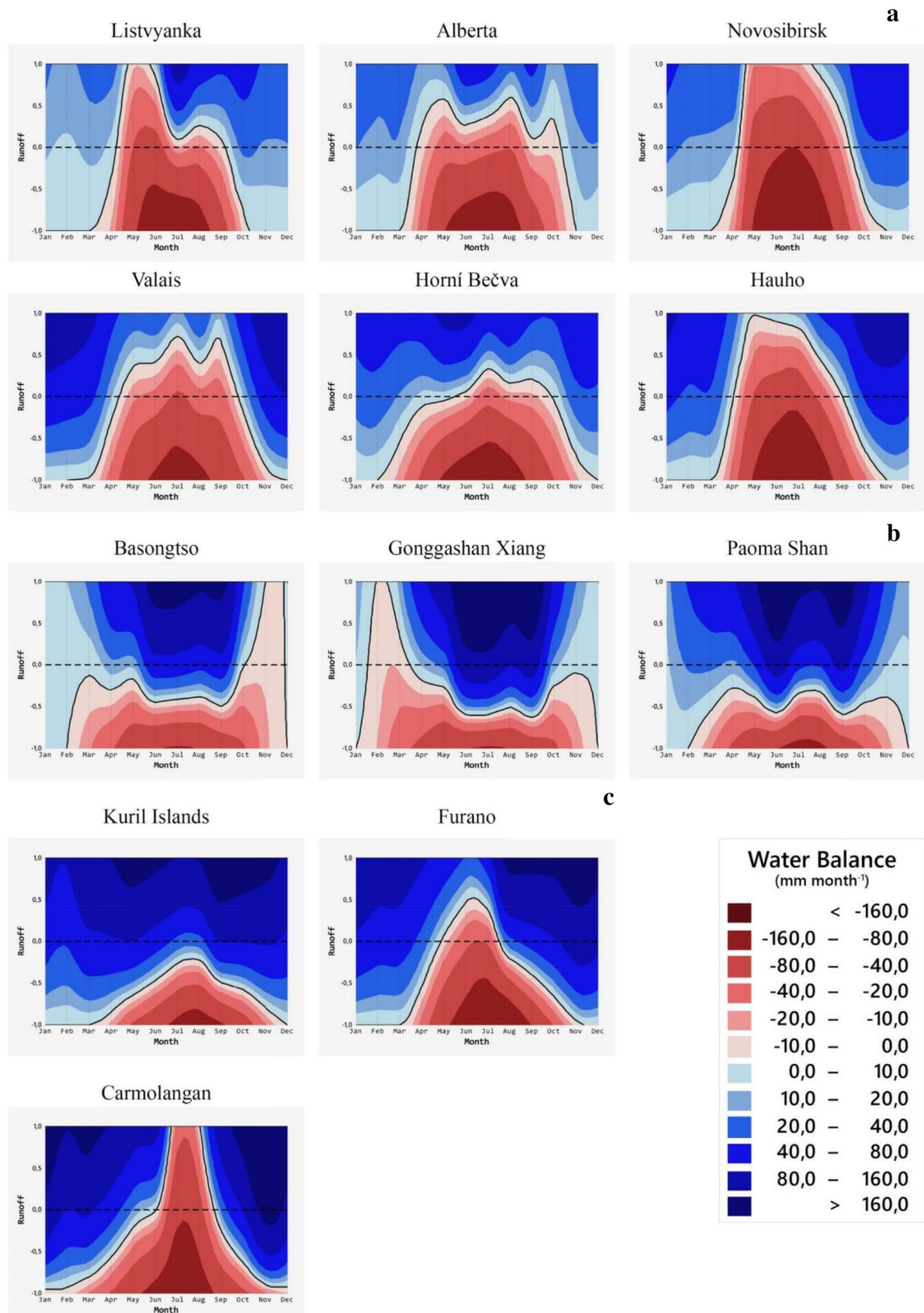
Fig. 5 Contour plot of the monthly water net differences (mm month^{-1}) for each birch provenance. *Y*-axis denotes positive and negative water net differences. Dashed line represents zero runoff, and solid line indicates water balance equilibrium over the year. Plots are grouped according to geographical location **a** Western-Europe/North America, **b** China, **c** East Asia

(Wendler and Millard 1996; Aspelmeier and Leuschner 2006; Possen et al. 2011). Avoidance strategies can be effective in their own right, as abscission effective prevents fatal water-loss by reducing total leaf area, but ecotypic adaptation towards drought tolerance strategies would allow for maintained physiological integrity and metabolic functioning over a wider span of soil- and plant-water potentials (Marchin et al. 2010). However, avoidance strategies will decrease the tree's capacity to deliver several ecosystem services. For example, a tree displaying drought-induced defoliation will transpire (and cool) less, shade less and intercept rainfall less than the same tree with a full leaved crown. Furthermore, drought tolerance traits allow the tree to maintain physiological function at a lower water potential (Bartlett et al. 2016). Therefore, Ψ_{P0} is a highly relevant trait to consider when evaluating potential genotypes for the urban landscape, as the trait will help segregate species that are adapted to perform well in habitats that experience periodic low leaf and soil water potentials (Corcuera et al. 2002; Sjöman et al. 2015; Nolan et al. 2017).

The rationale for this is the increased proficiency of genotypes with low Ψ_{P0} to tolerate drought whilst maintaining physiological leaf function during periods of water scarcity. By integrating this trait to selection decisions, those specifying trees can be more certain of good ecosystem service performance. Furthermore, as a positive carbon balance is aided by more sustained photosynthesis, it improves the long-term prospects of an urban tree's vitality and development into mature size, thus maximising its potential benefits. Increased vitality is not only desirable from an aesthetic perspective by promoting cultural ecosystem services, but a weakened state caused by low vitality makes the tree susceptible to biotic threats, thus reducing the resilience of the urban forest more generally (Raupp and Gonthier 2017).

Seasonal plasticity in osmotic potential at full turgor has been shown to vary across a wide range of species, as a function of osmotic adjustment (Kozlowski and Pallardy 2002). Preceding studies have demonstrated how this trait varies with drought and time within growing season, typically reaching a minimum in late summer when potential evapotranspiration and atmospheric drought would reach their peak (Sjöman et al. 2015; Bartlett et al. 2014). For this reason, sampling took place at NBG in August. Errors due to plasticity in osmotic potential are estimated to be small as *B. pendula* is not known to substantially adjust its leaf osmotic potential in response to water deficits (Osnubi and Davies 1978). Further, more systematic data collection combining a common garden experiment across a climate gradient with controlled environment studies would help determine the absolute minimum turgor loss for any given species, if this was of inherent interest. Whilst indications of likely Ψ_{P0} minima is valuable for segregating species tolerance to drought, understanding the plasticity of the water potential

at leaf turgor loss within a wide range of species will also be essential if species' responses to a warmer, drier climate are to be accurately predicted. Furthermore, if genotypes (or ecotypes) of a certain species are found to exhibit a much greater ability to osmotically adjust, then these may prove valuable for breeding programmes and cultivar selection.

This study provides further evidence for intraspecific variation in environmental tolerance, based on provenance. However, the scarcity of information relating to the provenance of plant material in the nursery sector makes it almost impossible for those specifying trees to consider genotypes with enhanced environmental tolerance within their selection decisions. No information relating to the genetic or ecological background of cultivars was found in any of the public-facing literature of the larger tree nurseries in Europe and North America. As a result of this knowledge deficit, available tree cultivars may not represent optimally adapted phenotypes, since they are typically selected for their aesthetic properties, such as flowers, autumn colour and crown form (Tyrväinen et al. 2005). In the plant hunting literature (focused on trees), attention to date has been driven by purely botanical interest—i.e. the introduction of a new species to science—or horticultural—i.e. the introduction of species with exceptional flowers, autumn colour, bark, etc. (Musgrave et al. 1998; Lancaster 2008; Kilpatrick 2014). Historical interest in finding trees tolerant to the various stresses that occur in urban environments has been almost non-existent. As the necessity to build resilience into gardens and public green infrastructure becomes more prominent, it will become essential to equip those specifying trees with evidence-based information relating to key environmental tolerances, such as drought. Therefore, new approaches that consider stress tolerance and the capacity to deliver ecosystem services need to be integrated with the more traditional horticultural and botanical interests in objectives of future plant hunting expeditions.

By directing efforts towards identifying more drought-tolerant genotypes, it will be possible to diversify the palette of trees that could confidently be integrated by urban tree planners and landscape architects into the urban fabric to improve urban resilience. The results of this study on different ecotypes of *Betula pendula* clearly shows that it is possible to find a more drought-tolerant plant material, even within a species that is presented as rather sensitive to drought. This should enhance confidence amongst those engaged in the hunt for trees, suitable for future urban environments.

It is important to see this study as an indication of the genotypic variation in drought tolerance within the species and sub-species of *Betula pendula.* As this was a study of plant material based in a single botanic garden, there was an inevitable limitation in the number of provenances (in this study 12 provenances were included) and replication of each

provenance. A more systematic trial with increased representation of wild provenances and greater replication would enhance the rigor of these conclusions. Additionally, a more systematic evaluation of drought tolerance using a controlled environment experiment and a wider range of traits such as vulnerability to drought-induced embolism would also help to confirm these findings. Nevertheless, this study gives good evidence of intraspecific variation in drought tolerance of an important temperate tree and provides a model for future studies designed to advance the ecotypic selection of trees using tree collections (arboretums) and botanical gardens.

Author contribution statement All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Simon Hannus, Andrew Hirons, Timothy Baxter, Björn Wiströn and Henrik Sjöman. The first draft of the manuscript was written by imon Hannus, Andrew Hirons, Timothy Baxter, Hugh McAllister, Björn Wiströn and Henrik Sjöman and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

References

Alder N, Sperry J, Pockman W (1996) Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. Oecologia 105(3):293–301

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Ashburner K, McAllister HA (2013) The genus Betula: a taxonomic revision of birches. Kew Publishing, London

Ashburner K, McAllister HA (2016) The genus Betula: a taxonomic revision of birches. Reprinted with corrections 2016. London: Kew Publishing

Aspelmeier S, Leuschner C (2006) Genotypic variation in drought response of silver birch (*Betula pendula* Roth): leaf and root morphology and carbon partitioning. Trees 20(1):42–52

Banks J, Hirons A (2019) Alternative methods of estimating the water potential at turgor loss point in Acer genotypes. Plant Methods 15:34

Bartlett MK, Scoffoni C, Sack L (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a globalmeta-analysis. Ecol Lett 15:393–405

Bartlett MK, Scoffoni C, Ardy R, Zhang Y, Sun S, Cao K, Sack L (2012) Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. Methods Ecol Evol 3:880–888

Bartlett MK, Zhang Y, Kreidler N, Sun S, Ardy R, Cao K, Sack L (2014) Global analysis of plasticity in turgor loss point, a key drought tolerance trait. Ecol Lett 17(12):1580–1590

Bartlett MK, Klein T, Jansen S, Choat B, Sack L (2016) The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. Proc Natl Acad Sci 113(46):13098–13103

Bauerle WL, Whitlow TH, Setter TL, Bauerle TL, Vermeylen FM (2003) Ecophysiology of Acer rubrum seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. Tree Physiol 23(12):841–850

Berland A, Shiflett SA, Shuster WD, Garmestani AS, Goddard HC, Herrmann DL, Hopton ME (2017) The role of trees in urban stormwater management. Landscape Urban Plan 162:167–177

Blackman CJ, Brodribb TJ, Jordan GJ (2010) Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. New Phytol 188:1113–1123

Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer, New York

Bowler DE, Buyung-Ali L, Knight TM, Pullin AS (2010) Urban greening to cool towns and cities: A systematic review of the empirical evidence. Landscape Urban Plan 97(3):147–155

Cavender-Bares J, Meireles JE, Couture JJ, Kaproth MA, Kingdon CC, Singh A, Serbin SP, Center A, Zuniga E, Pilz G, Townsend PA (2016) Associations of Leaf Spectra with Genetic and Phylogenetic Variation in Oaks: Prospects for Remote Detection of Biodiversity. Remote Sens 8(3):221

Cavin L, Jump AS (2017) Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Global Change Biol 23(1):362–379

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R et al (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–756

Corcuera L, Camarero J, Gil-Pelegrín E (2002) Functional groups in Quercus species derived from the analysis of pressure–volume curves. Trees 16(7):465–472

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Gu M, Rom CR, Robbins JA, Oosterhuis DM (2007) Effect of water deficit on gas exchange, osmotic solutes, leaf abscission, and growth of four birch genotypes (Betula L.) under a controlled environment. Hort Science 42(6):1383–1391

Hacket-Pain AJ, Cavin L, Friend AD, Jump A (2016) Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. Eur J Forest Res 135(5):897–909

Hirons AD, Sjöman H (2019) Tree Species Selection for Green Infrastructure: A Guide for Specifiers. Issue 1.3. Trees & Design Action Group

Hirons AD, Thomas PA (2018) Applied Tree Biology. Wiley Blackwell, Chichester

JAXA (2018) Japan aerospace exploration agency. https://global.jaxa.jp/

Kikuta SB, Richter H (1992) Leaf disks or press saps? A comparison of techniques for the determination of osmotic potentials in freeze thawed leaf materials. J Exp Bot 43:1039–1044

Kilpatrick J (2014) Fathers of Botany – the discovery of Chinese plants by European missionaries. Kew Publishing Royal Botanic Gardens, Kew, UK

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of 630 the Köppen-Geiger climate classification updated. Meteorologische 631 Zeitschrift 15(3):259–263

Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. Botan Rev 68(2):270–334

Kubiske ME, Abrams MD (1992) Photosynthesis, water relations, and leaf morphology of xeric versus mesic Quercus rubra ecotypes in central Pennsylvania in relation to moisture stress. Can J For Res 22(9):1402–1407

Lancaster R (2008) Plantsman´s Paradise – travels in China, 2nd edn. Garden Art Press, Suffolk, UK

Lenz TI, Wright IJ, Westoby M (2006) Interrelations among pressure–volume curve traits across species and water availability gradients. Physiol Plant 127:423–433

Marchin RM, Sage EL, Ward JK (2008) Population-level variation of Fraxinus americana (white ash) is influenced by precipitation differences across the native range. Tree Physiol 28(1):151–159

Marchin R, Zeng H, Hoffmann W (2010) Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. Oecologia 163(4):845–854

Meeus J (1991) Astronomical Algorithms. Willmann-Bell, Richmond

Mitchell PJ, Veneklaas EJ, Lambers H, Burgess SSO (2008) Leaf water relations during summer water deficit: differential responses in turgor maintenance and variations in leaf structure among different plant communities in south western Australia. Plant Cell Environ 31:1791–1802

Musgrave T, Gardner C, Musgrave W (1998) The plant hunters – two hundred years of adventure and discovery around the world. Ward Lock, England

Niinemets U (2015) Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll Quercus ilex. New Phytol 205(1):79–96

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol Monogr 76:521–547

NOAA (2019) The National Oceanic and Atmospheric Administration – Solar Calculation. https://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html

Nolan RH, Tarin T, Santini NS, McAdam SA, Ruman R, Eamus D (2017) Differences in osmotic adjustment, foliar abscisic acid dynamics, and stomatal regulation between an isohydric and anisohydric woody angiosperm during drought. Plant Cell Environ 40(12):3122–3134

Oksanen J, Guillaume BF, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Vegan: Community Ecology Package. R package version 2.5–5

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Hart MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, de Pausas JG, Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, ter Morgan HD, van der Steege H, Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–141

Possen BJ, Oksanen E, Rousi M, Ruhanen H, Ahonen V, Tervahauta A, Heinonen J, Heiskanen J, Kärenlampi S, Vapaavuori E (2011) Adaptability of birch (Betula pendula Roth) and aspen (Populus tremula L.) genotypes to different soil moisture conditions. Forest Ecol Manag 262(8):1387–1399

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ranney T, Whitlow T, Bassuk N (1990) Response of five temperate deciduous tree species to water stress. Tree Physiol 6(4):439–448

Ranney TG, Bir RE, Skroch WA (1991) Comparative drought resistance among six species of birch (Betula): influence of mild water stress on water relations and leaf gas exchange. Tree Physiol 8(4):351–360

Raupp MJ, Gonthier P (2017) Biotic factors: pests and diseases. In: Ferrini F, Van Den Bosch CCK, Fini A (eds) Routledge Handbook of Urban Forestry. Routledge, New York, pp 251–272

Rose L, Leuschner C, Köckemann B, Buschmann H (2009) Are marginal beech (Fagus sylvatica L.) provenances a source for drought tolerant ecotypes? Eur J Forest Res 128(4):335–343

Ruosteenoja K, Markkanen T, Venäläinen A, Räisänen P, Peltola H (2018) Seasonal soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st century. Clim Dyn 50(3–4):1177–1192

Sack L, Cowan PD, Jaikumar N, Holbrook NM (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant Cell Environ 26:1343–1356

Sanusi R, Johnstone D, May P, Livesley SJ (2017) Microclimate benefits that different street tree species provide to sidewalk pedestrians relate to differences in Plant Area Index. Landscape Urban Plan 157:502–511

Schuldt B, Knutzen F, Delzon S, Jansen S, Müller-Haubold H, Burlett R, Clough Y, Leuschner C (2016) How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? New Phytol 210(2):443–458

Sieghardt M, Mursch-Radlgruber E, Paoletti E, Couenberg E, Dimitrakopoulus A, Rego F, Hatzistatthis A, Randrup TB (2005) The abiotic urban environment: Impact of urban growing conditions on urban vegetation. In: Konijnendijk CC, Nilsson K, Randrup TB, Schipperijn J (eds) Urban Forests and Trees. Springer, Berlin, pp 281–323

Sjöman H, Östberg J (2019) Vulnerability of ten major Nordic cities to potential tree losses caused by longhorned beetles. Urban Ecosyst 22(2):385–395

Sjöman H, Hirons A, Bassuk NL (2015) Urban forest resilience through tree selection —Variation in drought tolerance in Acer. Urban Forestry Urban Green 14:858–865

Sjöman H, Hirons AD, Bassuk NL (2018) Improving confidence in tree species selection for challenging urban sites: a role for leaf turgor loss. Urban Ecosyst 21(6):1171–1188

Stojnić S, Suchocka M, Benito-Garzón M, Torres-Ruiz J, Cochard H, Bolte A, Cocozza C, Cvjetković B, De Luis M, Martinez-Vilalta J

(2017) Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. Tree Physiol 38(2):173–185

Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, Huber G, Konnert M, Nagy L, Jentsch A (2014) Different reactions of central and marginal provenances of Fagus sylvatica to experimental drought. Eur J Forest Res 133(2):247–260

Thornthwaite CW (1948) An approach toward a rational classification of climate. Geogr Rev 38(1):55–94

Tyrväinen L, Mäkinen L, Schipperijn J (2005) Tools for mapping social values for urban woodlands and of other green spaces. Landscape Urban Plan 79(1):5–19

Valero-Galván J, González-Fernández R, Navarro-Cerrillo RM, Gil-Pelegrín E, Jorrín-Novo JV (2013) Physiological and proteomic analyses of drought stress response in Holm Oak Provenances. J Proteome Res 12(11):5110–5123

Wendler R, Millard P (1996) Impacts of water and nitrogen supplies on the physiology, leaf demography and nitrogen dynamics of Betula pendula. Tree Physiol 16(1–2):153–159

WorldClim (2017) Bioclimatic variables. Available at: http://www.worldclim.org/bioclim [2019–02–13]

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York