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Variations in seasonal drought tolerance rankings

Jonathan M. Banks^{1,2} · Glynn C. Percival¹ · Gillian Rose²

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Abstract

Key message Cultivars of *Acer platanoides*, *A. pseudoplatanus* and *A. campestre* show significant seasonal drought tolerance variation, identified by in vitro desiccation a whole-tree drought and water potential at turgor-loss-point.

Abstract Drought is one of the most common and significant disorders affecting tree establishment and growth, in the urban environment. Consequently, improving tree selection by the provision of quantifiable tolerance data by which to evaluate genotypes is an important area of scientific research. A number of in vitro studies address drought tolerance in isolation, at a single time point during the growing season. Using an in vitro foliar dehydration method to evaluate closely related genotypes of *Acer platanoides*, *A. pseudoplatanus* and *A. campestre*, drought tolerance rankings were not found to be consistent throughout the growing season (spring, summer and autumn). i.e., *A. pseudoplatanus* ‘Negenia’ was found to be comparatively drought tolerant in spring, but displayed moderate to low comparative tolerance in summer and autumn; as measured using in vitro foliar dehydration as a proxy for drought tolerance. Drought conditions are most severe and common in summer; however, this study discusses the need to consider spring tolerance in addition to summer or autumn, particularly when selecting trees for tough urban sites, prone to drought stress across all three seasons.

Keywords Drought · Drought tolerance · Foliar dehydration · Turgor loss point · *Acer*

Introduction

Drought is one of the most common and significant disorders affecting tree establishment and growth (Aranda et al. 2012). The frequency and intensity of drought events is likely to increase with climate change (IPCC 2007; Bartlett et al. 2014; Pflug et al. 2018); this is particularly true within urban areas, where root zone limitations (Kopinga 1991; Volder et al. 2009) and the urban heat island effect (Cregg and Dix 2001) decrease water availability and increase vapour pressure deficit and evapotranspiration, respectively. Species selection can significantly affect survival prospects (Roman et al. 2014). Low-value and short-lived plants can be rapidly replaced with plant material that exhibits more appropriate tolerance characteristics. However, for longer-lived and higher-value plants, such as urban trees, replacement is

undesirable. Appropriate tree selection for future climatic conditions is, therefore, of increasing importance to prevent tree losses and reduce intensifying demand on water-use due to inappropriate selection (Roman et al. 2014). Tree selectors, however, have been criticised for selecting trees based on aesthetic criteria, rather than tolerance traits (Vaz Monteiro et al. 2017). Additionally, the information available to tree selectors is often ambiguous, conflicting and lacking in appropriate specificity (Sjöman et al. 2015). In vitro empirical methods (namely, chlorophyll fluorescence on dehydrating foliage and measurements of turgor loss point) are available which can address some of the problems associated with the current paradigm of tree selection. However, the seasonal specificity of such tolerance evaluation methods requires further study. Drought tolerance has many components some of which are static and may be determined by the genotype others are plastic and can shift in response to water deficit events or during seasonal development. Tolerance is known to develop as water deficit events increase during the season (Sjöman et al. 2015). However, it is not yet clear if, or at what point, tolerance rankings within a group of genotypes maintain consistency throughout the course of a growing season.

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Large-scale drought trials are important (Ryan 2011) but not generally practical to undertake on a wide range of trees owing to cost and time needed to reach maturity in comparison to most crop plants. In vitro experimentation is, therefore, essential to evaluate whole-tree genotypic drought tolerance without undertaking whole-tree drought trials. Percival and Sheriffs (2002) and Faraloni et al. (2011) show dehydration of excised foliage can act as a viable proxy for whole-plant drought experiments. Plant root detachment and dehydration has also been used to represent drought stress in *Arabidopsis* rosettes (Catala et al. 2007). Leaf dehydration studies account for foliar anatomical and morphological adaptations such as trichomes, sunken stomata, thick cuticles and reduced leaf size. Another method currently gaining attention is the measurement or estimation of water potential at the turgor loss point (π_{tlp}) (Maréchaux et al. 2015; Sjöman et al. 2015, 2018b); this measure is indicative of the permanent wilting point (Bartlett et al. 2012b). The π_{tlp} is known also to reflect the point below which a plant cannot take up sufficient soil water, and is, therefore, considered a ‘higher-level’ drought tolerance trait (Bartlett et al. 2014). Foliar-focused measurements are unlikely to account for whole-plant adaptations, such as foliage shedding, stem water storage mechanisms or structures (e.g., succulents or cacti) and deep rooting strategies, further discussed by Bartlett et al. (2012a, b). Experimentation has, however, revealed the validity of foliar-focused measurement’s when compared against whole-plant studies, either directly or via meta-analysis (Percival and Sheriffs 2002; Bartlett et al. 2012b, 2014). Additionally, many drought avoidance mechanisms (foliage shedding) are undesirable for trees planted in the urban environment (Sjöman et al. 2015). Measurements which exclude these avoidance factors, such as measurements of π_{tlp} and foliar dehydration studies, are, therefore, of potential benefit to those involved in the selection of urban trees.

A tree’s ability to adapt to drought stress events throughout a season facilitates a balance between the costs and benefits of maintaining tolerance traits (Postma and Jaramillo 2008; Bigler 2016). Most water is lost from the leaves of woody plants (Pallardy 2007); therefore, adaptations are primarily located in the foliage. Stomatal closure is the primary means of reducing water loss, maintaining turgor and extending the range of foliar function under minor to moderate drought (Arndt et al. 2001). However, this reduces the rate of photosynthesis while increasing the risk of photoinhibition (Takahashi and Murata 2008). Under more severe drought, developmental water deficit tolerance mechanisms involve the maintenance, and extension of cellular tolerance to reduced relative water content (RWC). Plants can alter their drought tolerance by reallocation of root/shoot dry matter and other molecular changes (Kozłowski and Pallardy 2002). True tolerance mechanisms, however, involve the maintenance of cellular turgidity through cellular osmotic

potential (osmoregulation) and tissue elasticity (Kozłowski and Pallardy 2002), both mechanisms and are capable of fluctuating throughout the course of a season.

Osmoregulation involves the local synthesis of osmotically active metabolites, resulting in osmotic adjustment (Arndt et al. 2001; Burg and Ferraris 2008), increasing osmotic gradients and maintaining cellular turgidity (Farooq et al. 2012). Turgor maintenance is required for growth to continue during drought events (Clifford 1998). Increases in inorganic ion concentrations (sodium, calcium and potassium) for this purpose, however, can perturb protein function (Burg and Ferraris 2008). Therefore organic osmolytes are also used, such as proline and glycine betaine (Bohnert 1995). Significant growth period, seasonal, environmental and species-specific fluctuations in osmolytes are known to occur (Bohnert and Jensen 1996; Murakeözy et al. 2003; Regier et al. 2010; Ryan 2011). Current evidence suggests osmolyte levels in foliage are highest in spring and lowest in the summer months (Lansac et al. 1994; Murakeözy et al. 2003; Bandurska et al. 2009). Conversely, inorganic ions and carbohydrates tend to accumulate across the seasons (Murakeözy et al. 2003); however, significant seasonal and intraspecific variations in stored and utilised carbohydrates in response to drought are known to occur (Regier et al. 2010; McDowell 2011; Ryan 2011; Brunner et al. 2015). Osmoregulation is not, however, a universal strategy (Pallardy 2007); *Acer saccharum* (Bahari et al. 1985; Sjöman et al. 2015), *Fagus sylvatica* and *Quercus petraea* (Backes and Leuschner 2000), for example, were reported to exhibit little or no osmotic adjustment.

Tissue elasticity or elastic modulus (ϵ) can also influence drought tolerance variation throughout a season as leaves become more rigid. Elastic modulus is defined as the pressure required to cause a unit change in cell volume (Verslues et al. 2006). It is well documented that (other variables being equal) a more elastic tissue, low ϵ , is more capable of maintaining turgor under relatively large water losses (Kozłowski and Pallardy 2002; Verslues et al. 2006; Pallardy 2007). However, highly elastic cells which exhibit significant osmotic adjustment may be at risk of damage upon rehydration (Clifford 1998). Decreased elasticity (greater rigidity, high ϵ) tends to maintain RWC as water potential declines and cell volume is maintained (Clifford 1998; Pallardy 2007). This is observed in scleromorphic and coriaceous (texture of leather) leaves which are often considered drought resistant (Ogaya and Peñuelas 2006; De Micco and Aronne 2012). Both increases and decreases in elasticity, therefore, have been associated with tolerance to drought (Clifford 1998; Pallardy 2007). *Acer saccharum* trees have been shown to display seasonal variations in ϵ from ca. 5 MPa in mid-May to 18 MPa in July, lowering again to 7 MPa in October (Tyree et al. 1978). However, differences in elastic response to drought have been noted

to diverge even in closely related species of the same genus (Pallardy 2007). Divergence may in some cases, however, be as a result of other ecological strategies such as resistance to herbivory (Powell et al. 2017).

Acer saccharum also exhibits seasonal variations in π_{tip} (incipient plasmolysis), identifying values ca. 1 MPa in May rising rapidly to ca. 1.8 MPa by June before gradually rising to ca. 2 MPa by October (Tyree et al. 1978). Sjöman et al. (2015, 2018) also identify seasonal change in π_{tip} within a range of *Acer* and *Magnolia* species and cultivars. They identify that spring tolerance is lower and the species tested rank differently in comparison to summer tolerance (Sjöman et al. 2015, 2018b). Little information is, however, available to suggest if tolerance levels are maintained or decline following summer tolerance acquisition. Additional data regarding seasonal variation is not available for other species and cultivars within the *Acer* genus. A range of information is important as differences in both osmoregulation and elastic adjustment have been noted in closely related species (Pallardy 2007). This study uses species and cultivars from the *Acer* genus as a model for the drought tolerance of very closely related deciduous tree species. The seasonal consistency of foliar desiccation is determined and compared to summer measurements of π_{tip} and whole-tree drought tolerance.

Materials and methods

Plant material

All *Acer* species represented within this trial are commonly utilised as urban street trees. A range of genotypes with contrasting intraspecific foliar and crown characteristics were selected. All genotypes used were grafted onto their respective species-type rootstocks. 87-year-old 4.2 m (± 0.3) tall trees with a DBH of 50.7 mm (± 7.9) growing in 45 L Light Pots™ (white, mypex woven grow bags) grafted onto their respective species-type rootstocks were used for this experiment. The potting substrate consisted of a 50:50 green waste and pine bark compost mix, with a pH of 7.7. Ten trees from each of the following genotypes were used: *A. campestre*, *A. campestre* ‘Louisa Red Shine’, *A. platanoides* ‘Drummondii’, *A. platanoides* ‘Emerald Queen’, *A. platanoides* ‘Princeton Gold’, *A. platanoides* ‘Royal Red’, *A. pseudoplatanus* ‘Negenia’, and *A. pseudoplatanus* ‘Spaethii’. Further information on the selected genotypes is displayed in Table 1. For the duration of this experiment, all trees were kept outside, at Barcham Trees nursery, Ely, Cambridgeshire (52.366923°N, 0.315864°W). All experimental trees were arranged in a single row, either side of which was bordered by two rows of nursery trees of equal size to minimise edge effects.

Experimental trees were arranged in 5 repeat blocks, each containing 16 randomly placed specimens representing all aforementioned *Acer* genotypes for both the droughted and watered treatment.

Whole-tree drought treatment

A watering treatment (irrigated or non-irrigated) was alternated between blocks, and all trees allocated to the irrigated treatment were drip-irrigated with ca. 5 l of water per day. Drought treatment was initiated by detaching irrigation lines from non-irrigated trees. Drought was augmented by installing black plastic rain covers over all root balls (irrigated and non-irrigated) to exclude rainfall and by raising all pots ca. 75 mm off the ground to avoid water uptake from the ground, which was covered in pea gravel.

Drought was initiated on the 27th July 2016 and continued until the 9th of August. Chlorophyll fluorescence and soil moisture measurements were made on three leaves per tree on the 18th July (-216 h prior to irrigation removal), 4th August (192 h) and 9th August (310 h).

Environmental conditions were monitored using a Tiny Tag (TGP-4500) temperature and relative humidity sensor. The conditions during the drought trial were 18.1 °C (± 3.6), 63% RH (± 34.5), VPD 0.78 kPa (± 0.69).

Percent volumetric water content (VWC) was measured at each timepoint using a Delta-T Devices SM150 soil moisture sensor kit (Delta-T Devices Ltd, Cambridge) generating volumetric soil moisture content (VMC) data with $\pm 3\%$ accuracy. The probe permits soil moisture readings to be taken with minimal root or soil disturbance by gently pushing the two 51 \times 2.5 mm probes through the Light Pots™ 10–15 cm from the base of the pot. Soil moisture data were used to confirm a significant difference occurred between watered and droughted trees ($p \leq 0.001$) (Fig. 1).

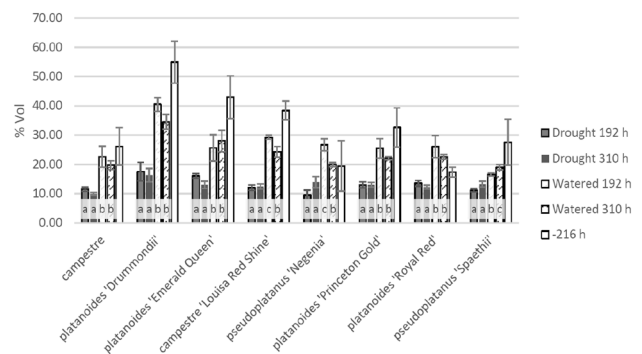


Fig. 1 Percent volumetric water content for droughted and control genotypes, 192 h and 310 h following irrigation removal. Error bars show standard error, letters denote significant differences within genotypes ($n=5$). -216 h prior to drought initiation includes both droughted and watered groups; it is included for comparison but omitted from statistical analysis ($n=2$)

Table 1 Available information on the species used within this study

Species 'Cultivar'	Common Name	Key Features	Ecology/Drought tolerance
<i>A. pseudoplatanus</i>	Sycamore	Fast growing deciduous spreading tree Considered a British non-native, introduced to the UK in ca. 1250 (Southwood 1961).	Recommended for an exposed position (Brickell 1989). Drought sensitive in comparison to <i>F. sylvatica</i> , <i>F. excelsior</i> , <i>Q. petraea</i> , <i>T. platyphyllos</i> and <i>P. avium</i> . Scherrer et al. (2011). Tolerant of prolonged periods of dry (cat. 10) and very wet soil (cat. 3) (Bassuk et al. 2009). Very adaptable to soil types, preferably well drained (Dirr 1990). 2.75 ± 0.16 (Niinemets and Valladares 2006). π_{TLP} -2.70MPa (permanent wilting point) (Sjöman et al. 2015)
'Spaethii' 'Atropurpureum', 'Purpureum'		Leaves dark green above, rich purple below (Dirr 1990)	Thought to be less tolerant than the straight species to insect and disease factors, leaf scorch, sunscald and borer infestations (Bassuk et al. 2009).
'Negenia'		Vigorous conical shaped tree with red-stalked, large dark green leaves (Hillier 1993).	Tolerant to poor soil conditions (van den Berk and van den Berk 2015).
<i>A. campestre</i>	Field Maple	Low branching compact tree commonly found in field hedgerows and brownfield sites Native to the UK (Southwood 1961).	Tolerant of prolonged periods of dry (cat. 12), and consistently moist soil (cat. 4). (Bassuk et al. 2009). Cat. 2.93 ± 0.32 (Niinemets and Valladares 2006). Tolerant of any soil except dry infertile and sandy (van den Berk and van den Berk 2015). π_{TLP} -3.00MPa (permanent wilting point) (Sjöman et al. 2015)
'Louisa Red Shine'		Leaves have a slight red coloration in spring.	Tolerant to all soil types except dry infertile and sandy (van den Berk and van den Berk 2015).
<i>A. platanoides</i>	Norway Maple	Vigorous deciduous spreading tree with clusters of yellow flowers in mid spring, before leaves appear. Considered an invasive plant in parts of the United States of America (Martin 1999). Considered a British non-native. Native to continental Europe (Webb and Kaunzinger 1993).	Tolerant of prolonged periods of dry (cat. 10) and very wet soil (cat. 3) (Bassuk et al. 2009). Cat. 2.73 ± 0.16 (Niinemets and Valladares 2006). π_{TLP} -3.09MPa (permanent wilting point) (Sjöman et al. 2015)
'Drummondii'		Variiegated cultivar, leaves have creamy-white edges turning yellowish in autumn (Brickell 1989; Bassuk et al. 2009).	Supposedly the best of its class (Dirr 1990).
'Emerald Queen'		Upright when young, leaves have a reddish tint in spring and are bright yellow in autumn (Hillier 1993)	Less tolerant than 'Summershade' similar to 'Deborah' (Fini et al. 2009). One of the best Norway Maples for urban plantings (Dirr 1990).
'Royal Red'		Deep reddish-purple leaves (Brickell 1989) Underlying suspicion that 'Royal Red' and 'Crimson King' are the same tree (Dirr 1990)	Considered more susceptible to pest problems than the straight species, but more tolerant and slower growing than 'Crimson King' (Bassuk et al. 2009). Supposedly harder than 'Crimson King' (Dirr 1990).
'Princeton Gold'		Shows yellow spring and summer foliage and may fade to a darker yellow in autumn (Bassuk et al. 2009).	No source available

In vitro dehydration treatment

Three leaves from each of the 80 experimental trees were collected. Leaves were collected from the second and third node region as these displayed appropriate maturity and would putatively provide greater consistency. Spring foliage collection commenced once foliage was deemed to have reached maturity following leaf flush, i.e., developed mature colouration and structure. This occurred on the 11th May 2016 (hereafter referred to as spring). Summer foliage collection took place on 20th June 2016 (summer). Autumn collection occurred immediately as the first signs of senescence [leaf colour change (Ougham et al. 2005)] were visible in nearby healthy early indicator species (*Prunus* spp.), this occurred on the 23rd September 2015 (autumn). Initial measurements for each season were confirmed to demonstrate a "normal" polyphasic OJIP fluorescence rise to ensure immaturity or senescence would not influence results (data not shown) (Holland et al. 2014). Immediately after removal, all leaves were sealed in Ziploc plastic bags and kept in the dark while being transferred to the laboratory. Chlorophyll fluorescence (CF) was measured on these leaves between 11th and 16th May 2016 (spring), 21st and 29th June 2016 (summer), 23rd and 26th September 2015 (autumn). Measurements were initiated immediately upon arrival at the laboratory. Immediately after the first measurements, leaves were laid out across the laboratory bench

and left to dehydrate. Leaves were arranged in a completely randomised block design ensuring each leaf had > 1 cm peripheral zone to reduce effects on nearby leaves. Laboratory conditions were measured using Tinytag plus TGP-4500 (Gemini Data Loggers Ltd. Chichester, West Sussex, UK). Vapour pressure deficit (VPD) was calculated in accordance with Kirkham (2014) and Shamshiri et al. (2017).

The laboratory was kept at an average VPD of: 0.34 (± 0.13) spring, 0.57 (± 0.14) summer, and 0.34 (± 0.15) autumn. The windowless laboratory was kept in darkness at all times apart from when measurements were taking place (< 3 h per day). Measurements of CF were taken each day at: 8, 22, 30, 46, 72 and 120 h after removal from the trees (spring); 20, 43, 67, 91, 163 and 211 h (summer); 5, 25, 29, 46 and 79 h (autumn).

Pressure–volume curves

Pressure–volume (P–V) curves were calculated between the 12th and 22nd of July 2016 in accordance with the sap expression method; similar to that used by Parker and Pallardy (1988). Six healthy, representative leaves were collected from each genotype at random from the 80 experimental trees throughout the measurement period. Leaves were collected and taken to the laboratory in sealed plastic bags within 15 min. Petioles were re-cut underwater and left to rehydrate overnight (15–20 h). Leaves were then

sealed inside a pressure chamber (model 1505D EXP, PMS instruments Co., Albany, USA). The average initial balance pressure was -0.07 MPa (± 0.017). Leaves which did not hydrate to an initial water potential of > -0.2 MPa were discarded (Lenz et al. 2006). Incremental pressures of 0.2 MPa were applied to the leaf, beginning at 0.2 MPa. P–V curves were halted at 2.2 MPa if at least three data points were in the linear portion of the graph. Total expressed sap at each pressure was absorbed in pre-weighed 1.5 ml Eppendorf tubes filled with dry low-lint absorbent tissue paper (Kimtech Science, Kent, UK). Tubes were handled and opened for the minimum possible time during sap collection to prevent evaporation. P–V curves were plotted as accumulated expressed sap on the x -axis, against $-1/\text{applied pressure (MPa)}$ (y -axis). Osmotic potential at full turgor (π_0) was determined by extrapolation of the linear portion of the graph to zero expressed sap (Tyree and Hammel 1972). Water potential at the turgor loss point (π_{tlp}) was calculated as the Y axis value at the intersection point of the linear and exponential models (i.e., $Y = \text{when } \Delta x\text{-axis lin. and exp.} = 0$) (Jane and Green 1983) (Fig. 2).

Chlorophyll fluorescence

Chlorophyll fluorescence has been shown to be a viable quantitative indicator of drought stress and survival (Woo et al. 2008; Jedmowski et al. 2015; Kalaji et al. 2017; Banks 2018). Measurements were performed on leaf material from both the whole-tree drought and foliar dehydration. Following dark adaptation (30 min) measurements were performed using a Pocket Plant Efficiency Analyser (PEA) device (Hansatech instruments Ltd., Norfolk). Dark adaptation was still necessary despite the laboratory being kept in near-complete darkness as light was necessary when working in the laboratory. Chlorophyll fluorescence was induced by a 1 s flash of light (650 nm, $1500 \mu\text{mol}/\text{m}^2/\text{s}$) provided by an array of three light-emitting diodes over a 4 mm diameter of leaf surface. The ratio of variable ($F_v = F_M - F_0$) to maximal fluorescence (F_M) was calculated. F_0 at T_0 was used during this study (Banks 2017). The sensitivity of F_v/F_m is known to vary in response to drought stress (Banks 2018),

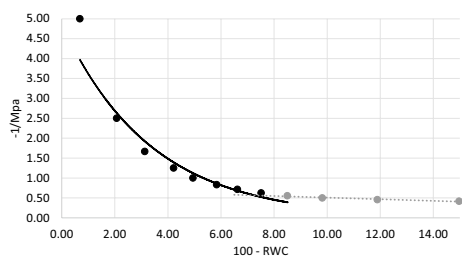


Fig. 2 An example pressure–volume (P–V) curve. Linear portion $y = -0.0205x + 0.7131$ $R^2 = 0.9307$, exponential $y = 4.8672e^{-0.297x}$ $R^2 = 0.9609$

researchers should use caution relying on this parameter alone for drought trials particularly when stress is not severe.

Time for the chlorophyll fluorescence parameter F_v/F_m to decline by 50% was calculated per tree, using a linear regression and results per tree were subsequently analysed (Drought $n = 5$ $R^2 = 0.85 \pm 0.21$, Dehydrated $n = 10$ average $R^2 = 0.79 \pm 0.11$).

Relative water content

Due to the size of the trial, it was not possible to measure relative water content for each leaf. Time was, therefore, used as a substitute for relative water content (RWC). To confirm this was an appropriate assumption in a subset of this trial ($n = 15$), RWC was plotted against time and a strong correlation was observed, this was in agreement with data displayed by Rastogi et al. (2002) and Faraloni et al. (2011). These data confirm time can be used as a proxy in this experiment, it is important to note, however, that RWC should not be predicted using these data (Fig. 3).

Statistical analysis

Statistical analysis was performed using GenStat 17. Time series data were analysed using a residual maximum likelihood (REML) model. Following this, analysis of variance (ANOVA) was performed on transformed data (time for 50% reduction in F_v/F_m) to assess for differences between *Acer* genotypes for each measurement season individually. Post hoc analysis was performed using a Tukey's multiple comparison test at the 95% level.

Spearman's rank correlation coefficient [ρ (rho) or r_s] was calculated to determine the similarity in ranking between each categorical variable on a per tree basis. The strength of rank correlations was interpreted using the following thresholds (Table 2).

Results

Significant differences ($p \leq 0.05$) were observed within whole-tree drought, π_{tlp} , and dehydration for all seasons between the *Acer* genotypes evaluated. Table 3 identifies the time taken for *Acer* genotypes to decline by 50% , with π_{tlp} included for comparison. It was not possible to achieve consistent environmental conditions between seasons, resulting in dehydration occurring more rapidly in summer owing to a higher VPD (ca. $+4$ °C in comparison to autumn and spring), this difference prevents direct comparison of raw values. However, ranking genotypes, relative to the rank-position within the other seasons facilitates comparison between seasons. To provide this, a Spearman's rank correlation coefficient (r_s) was performed (Table 4) on the data

displayed in Table 3. This allows the relative rank of each season to be compared. Results identify a progression in conformity towards the drought tolerance ranking; a negative weak ($r_s = -0.21$), strong (0.62) to moderate (0.52) rank correlation (Table 4) can be observed developing from spring to summer and autumn, respectively, in comparison to the rank observed in the summer whole-tree drought.

A more negative π_{tlp} infers greater drought tolerance, therefore, the corresponding r_s values are negative. In this study, the π_{tlp} conforms strongly to the rankings achieved for summer and autumn foliar dehydration (-0.64 and -0.74 r_s , respectively) and summer drought (-0.6 r_s) (Table 4). Very strong similarity exists between summer and autumn (r_s 0.81) suggesting that in this trial tolerance is maintained from autumn into summer the following year.

Discussion

Spring drought tolerance is lower in both annual plants (Farooq et al. 2012) and deciduous trees (Sjöman et al. 2015, 2018a, b) when compared to summer tolerance. Sjöman et al. (2015, 2018a) identifies, however, that *Acer* species which are most drought tolerant in spring are not necessarily the most tolerant in summer. It is, therefore, important to clarify if tolerance ranks are maintained throughout the season. This will determine the applicable seasonal range for this type of categorical data.

Data presented here adds further evidence that foliar dehydration and π_{tlp} can identify whole-plant drought tolerance (Jane and Green 1983; Percival and Sheriffs 2002; Baltzer et al. 2008; Faraloni et al. 2011; Bartlett et al. 2012a; Sjöman et al. 2015, 2018b). However, the timing of dehydration studies is highly important. Spring dehydration tolerance is not concurrent with summer π_{tlp} , drought or summer dehydration tolerance (Table 4). Tolerance ranks approach parity with whole-tree summer drought tolerance

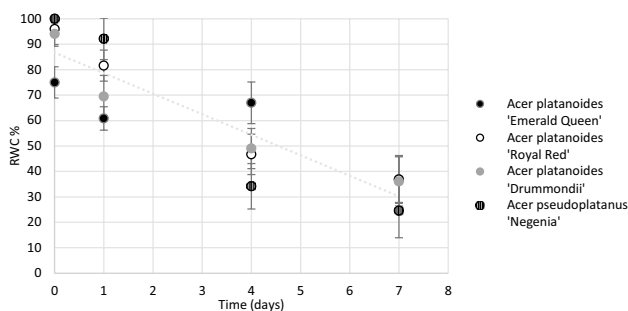


Fig. 3 Relative water content (RWC) (%) plotted against time (days) for four selected species. $n=15$. Error bars show standard error. Linear regression expressed for all four species was $y = -8.0701x + 86.733$ $R^2 = 0.808$

and π_{tlp} after the spring season. A very strong correspondence exists between autumn and summer dehydration ranks, suggesting tolerance levels are maintained into the autumn. The autumn dehydration experiment, however, occurred during the previous year, and, therefore, these data suggest that consistency of rank is present in successive years, further work under differing drought exposure is nevertheless required to fully confirm this. The timing of drought events in perennial plants is clearly an important factor determining species tolerance or survival. Sjöman et al. (2015) rank tolerance based on summer estimates of π_{tlp} while also reporting spring values. Water deficit is most severe in summer (Lansac et al. 1994), therefore, species with a greater summer tolerance are likely more desirable. However, a combined high spring and summer tolerance is also desirable if a risk of spring drought is present. Drought stress is more likely to occur in all seasons in urban areas where limited rooting volumes and increased root injury are likely (Clark and Kjelgren 1990; Savi et al. 2015). Data presented by Sjöman et al. (2015) identify *Acer monspessulanum* as the most summer drought tolerant (π_{tlp} ca. -4.2 MPa) species in comparison to the 27 other *Acer* genotypes evaluated. However, *Acer rubrum* 'Northwood' would be significantly more tolerant in a spring drought event, π_{tlp} ca. -2.6 MPa vs -1.7 MPa for *A. monspessulanum* while also maintaining a relatively low summer π_{tlp} of ca. -3.5 MPa (Sjöman et al. 2015). In urban areas, therefore, *A. rubrum* 'Northwood' may be recommended over the more summer drought tolerant *A. monspessulanum*. In this study, *A. platanoides* 'Princeton Gold' was consistently the most dehydration tolerant (Table 3). However, in the whole-tree drought study the variegated *A. platanoides* 'Drummondii' was significantly more drought tolerant (Table 3). Soluble carbohydrates in white non-photosynthetic tissue have been shown to not respond to drought to the same degree as green tissue (Pattanagul and Madore 1999). Additionally, white foliage has a lower stomatal conductance (Aphalo and Sánchez 1986) and higher reflectance (Smith 1986) than its green counterpart, irrespective of drought treatments. This putatively suggests that the variegation in this genotype facilitates an avoidance mechanism which was not identified in detached leaves or when using π_{tlp} . Variegation may have reduced total photoinhibition because of the lack of photosynthetic activity and reduced water loss because of

Table 2 Spearman's rank correlation coefficient interpretations (Weir 2018)

r_s	Interpretation
0.00–0.19	Very weak
0.20–0.39	Weak
0.40–0.59	Moderate
0.60–0.79	Strong
0.80–1.0	Very strong

Table 3 Summary of means including, time (hours) for 50% reduction in F_v/F_m and mean π_{tip} (MPa) for the *Acer* genotypes tested

Sp. cultivar	In vitro				Whole tree
	Spring dehydration (h, F_v/F_m)	Summer dehydration (h, F_v/F_m)	Autumn dehydration (h, F_v/F_m)	π_{tip} (MPa)	Drought (h)
<i>pseudoplatanus</i> ‘ <i>Spaethii</i> ’	146.7a	94.0a	71.6ab	− 1.45ab	269.7a
<i>campestre</i> ‘ <i>Louisa Red Shine</i> ’	85.8a	96.9a	49.5a	− 1.33ab	259.3a
<i>campestre</i>	177.4ab	106.0ab	56.9ab	− 1.28a	260.4a
<i>pseudoplatanus</i> ‘ <i>Negenia</i> ’	301.4bc	112.4b	84.5ab	− 1.44ab	265.8a
<i>platanoides</i> ‘ <i>Drummondii</i> ’	94.3a	121.4bc	64.9ab	− 1.49ab	449.7c
<i>platanoides</i> ‘ <i>Royal Red</i> ’	113.1a	127.9cd	103.0b	− 1.39ab	382.7bc
<i>platanoides</i> ‘ <i>Emerald Queen</i> ’	134.4a	130.7cd	96.7ab	− 1.55ab	342.9abc
<i>platanoides</i> ‘ <i>Princeton Gold</i> ’	346.7c	140.5d	219.9c	− 1.67b	286.7ab
<i>p</i>	<0.001	<0.001	<0.001	0.031	<0.001

Letters denote significant differences between genotypes at the 95% confidence interval

Note that comparison between measurement methods should not be attempted using raw data, rather, comparing relative genotype positions facilitates assessment between seasons and methods

Table 4 Spearman’s rank correlation coefficient matrix comparing the time for 50% reduction in F_v/F_m between dehydration seasons, π_{tip} and a controlled drought event

	1	2	3	4	5
Leaf dehydration (spring)	1				
Leaf dehydration (summer)	0.17	1			
Leaf dehydration (autumn)	0.45	0.81	1		
π_{tip}	− 0.19	− 0.64	− 0.74	1	
Whole-tree drought	− 0.21	0.62	0.52	− 0.60	1

All trials conducted during the 2016 season with the exception of the autumn dehydration conducted in 2015

the lower stomatal aperture and higher reflectance in the white portions of these leaves. Ecological evidence supports this assumption; Smith (1986) identifies an advantage of increased variegation in clearings with higher drought risks but additionally high availability of photosynthetically active radiation.

The progression in conformity to the summer drought rank observed here suggests that drought tolerance is required to develop, to provide an accurate summer ranking. However, some evidence from well-watered experiments suggests tolerance acclimation may be genetically “programmed” (Bahari et al. 1985; Kozlowski and Pallardy 2002) and not necessarily as a result of the plant’s water deficit history. It is clear from these data, however, that there is a seasonal or developmental element for tolerance acclimation. Later season evaluations may provide more opportunity for drought exposure or tolerance development; however, an undesirable, slight reduction in conformity to a summer drought rank would be expected to be observed later in the season. Seasonal tolerance patterns within evergreen plants are an area requiring further study.

Conclusion

This study adds to evidence suggesting that foliar dehydration tolerance can act as a proxy for whole-tree drought tolerance, evaluated in this study using deciduous genotypes from the genus *Acer*. We suggest species which exhibit both high spring and summer drought tolerances are more suitable for planting in urban areas than species which only exhibit summer tolerance. Caution is, however, recommended as other factors are associated with drought tolerance and tree selection more generally. However, the increase in measurements detailing drought tolerance selection metrics is essential to progress from the current paradigm of tree selection.

Author contribution statement JB performed the field work and laboratory analysis, prepared figures, and wrote the manuscript. GP and GR provided supervisory support during the experiment and commented on the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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