



Species-specific evaluation of growth and environmental tolerance for ecosystem services – evaluation from a botanic tree collection

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Abstract

The planting of trees in urban environments is a challenging endeavor, largely due to the limited space available. It is therefore essential to select species that can deliver essential ecosystem services in an effective manner. This study presents a novel screening technique for identifying tree species with high potential for urban settings, with a particular focus on drought tolerance and rapid growth as key factors for success. The utilization of non-destructive data collection in a botanical tree collection enables the highlighting of variations in environmental tolerance and growth strategies among species. It is noteworthy that a subset of species exhibited a distinctive combination of high drought tolerance and robust growth, distinguishing them from the majority. These findings highlight the value of preliminary screening to identify promising candidates for more detailed and resource-intensive studies, such as greenhouse trials. Additionally, the study underscores the crucial role of botanical collections as repositories of distinctive genetic material, offering avenues to discover unconventional species suitable for urban greening. Further advancement of screening methodologies will enhance our capacity to select resilient tree species capable of flourishing in urban environments and providing multifunctional ecosystem benefits.

Keywords Urban trees · Climate change · Ecosystem services · Drought tolerance · Tree selection · Botanic garden

Introduction

It is widely acknowledged that global warming is a consequence of the emission of greenhouse gases and the subsequent climate change. It is predicted that climate change will increase the frequency of extreme weather events, natural disasters, and droughts, which will have a significant impact

on human living conditions, ecosystems, and biodiversity (Lyon et al. 2022). The global temperature has increased by approximately 1.0 °C in comparison to the mean global temperature observed between the years 1850 and 1900 (WMO 2022). The mean global temperature is increasing at a rate of approximately 0.2 °C per decade, due to past and current global emissions. However, the rate of global warming in Europe has been more rapid than previously predicted, with an average increase of 0.5 °C per decade over the past 30 years (WMO 2022). As urban populations continue to expand and rural-to-urban migration persists for enhanced opportunities in education, employment, and quality of life, where projections indicate a staggering addition of 2.5 billion people to the global population by 2050 (Aslam and Rana 2022). This surge in population results in increased demand for housing and infrastructure, which exacerbates existing environmental challenges and leads to accelerated urbanisation and the growth of slums. The significant climate impact of anthropogenic activities is set to further compound challenges, rendering highly populated areas increasingly inhospitable and precarious. However, it has been established that the presence of urban greenery

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plays a significant role in mitigating incidents associated with urbanisation and extreme weather events (Aslam and Rana 2022).

Urban green infrastructure and especially trees are of crucial importance to deliver different types of ecosystem services. These services are defined in this paper as the benefits that people and society receive from an ecosystem (Leemans and De Grot 2003). The potential benefits of trees for human well-being and the environment are manifold. They include the regulation of temperature through shading and transpiration (Rötzer et al. 2019; Zölch et al. 2016), the storage and sequestration of carbon (Davies et al. 2011), the regulation of the water balance in urban areas, reduced risk of flooding (Rötzer et al. 2019), filtering of air pollutants (Klingberg et al. 2022), noise and wind buffer (Roy et al. 2012), habitats for biodiversity, and areas of human

recreation (Fischer et al. 2018). The extensive range of functions and services that urban trees provide is of paramount importance for the development of resilience to future challenges. Consequently, the implementation of high-quality tree planting is a crucial factor. However, many of the functions and services mentioned are linked to large and healthy trees, where tree size, leaf and branch density are of crucial importance and linked to vitality (Rötzer et al. 2021). In a review by Liang and Huang (2023), leaf area, crown size, crown and leaf thickness, and total height are highlighted as key characteristics for a high delivery quality of ecosystem services (Fig. 1).

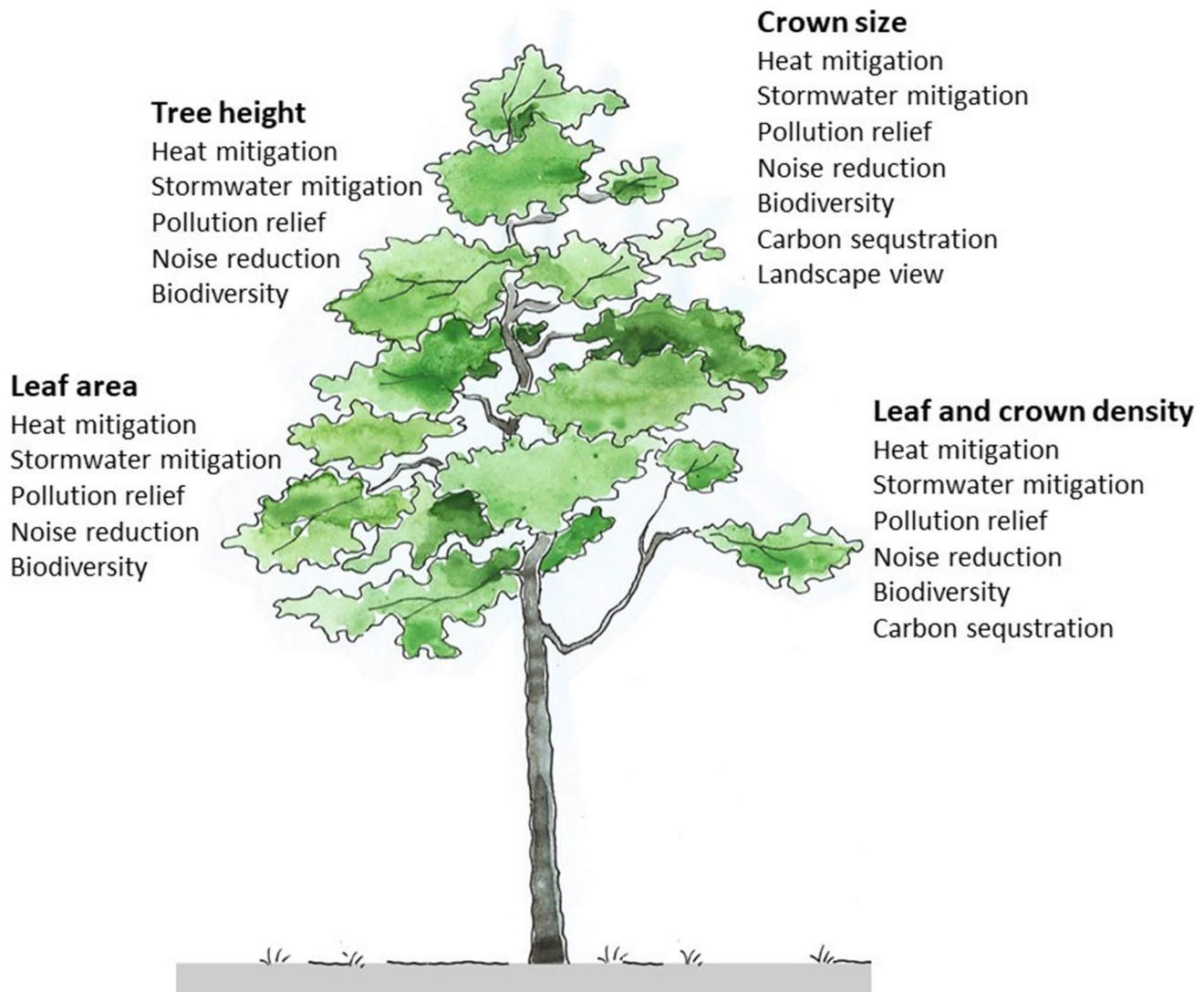


Fig. 1 A significant proportion of the ecosystem services that trees can provide are associated with canopy size and density, leaf and branch density, and leaf area. An increase in these traits is linked to an enhanced capacity, as demonstrated by Liang and Huang (2023) and Rötzer et al. (2021)

Tree growth and functional traits

The growth rate of trees is a key determinant of their capacity to deliver ecosystem services, particularly in urban environments (Rötzer et al. 2021; Scharenbroch 2012). A substantial body of previous research provides evidence that the provisioning of multiple ecosystem services is linked to interspecific variation in traits associated with the carbon and nutrient economy of plants. This forms the plant economic spectrum (Díaz et al. 2016) and the resource economic spectrum. Across species, fast growth and decomposition cycles are linked with large specific leaf area and high concentrations of nitrogen (N) and phosphorus (P) in living plant parts involved in photosynthesis and nutrient acquisition. In contrast, slow growth and decomposition cycles are linked to high tissue dry matter content (DMC) and high lignin content (Freschet et al. 2012; Guo et al. 2020, 2021).

A comprehensive review by Reich (2014) identified a correlation between the investment of plants in their leaves, stems, and roots to cope with varying resource availability and climatic conditions. In the same study, Reich (2014) concluded that leaf investments provide a framework for assessing the ability of different species to cope with different habitats and provide guidance on their investment priorities and thus their growth rate. The recent research conducted by Simovic et al. (2024) provides further support for the argument that the unique functional traits of tree species must be evaluated to assess their growth rate. This will assist in determining how species can achieve robust growth where wood and leaf density can influence tree growth and hydraulic functions, with species with lower wood density achieving rapid growth through more efficient water transport and volumetric expansion of tissues (Gleason et al. 2016), or low leaf dry matter content indicate a fast spectrum of resource use (Craine 2009).

Growth challenges: drought tolerance

One consequence of favorable growth is site tolerance, whereby stressors exert a detrimental impact on trees when they are engaged in the acquisition of essential resources. This is particularly evident in instances where photosynthetic capacity is significantly compromised under conditions of elevated temperatures and low humidity. In a study conducted by Meineke et al. (2016), *Quercus phellos* was observed to demonstrate a 12% reduction in carbon storage (impaired photosynthetic capacity) when subjected to conditions of elevated heat stress. Similarly, studies conducted in Tokyo and China have demonstrated a reduction in photosynthetic activity during periods of elevated temperatures and low humidity (Fares et al. 2017; Wang et al. 2019). Furthermore, the presence of impervious ground intensifies

these challenges by elevating surface and air temperatures while reducing humidity, thereby impeding photosynthetic activity in urban trees (Wang et al. 2019).

In a related study, Martínez-Sancho et al. (2022) sought to enhance the comprehension of the intricate physiological processes and structural adaptations associated with tree water use and photosynthetic capacity. The study employed a tree-centred approach to accurately identify the onset and severity of physiological drought. The study revealed that a reduction in wood-forming capacity, as indicated by alterations in wood structure, led to a considerable decline in stored carbon by 67% during drought periods in comparison to typical years. This finding emphasises the substantial influence that drought-induced constraints exert on photosynthetic capacity and indirect growth rate in trees, while also underscoring the intricate dynamics of urban forest ecosystems under stress (Martínez-Sancho et al. 2022). It is therefore evident that water stress represents a significant factor capable of impeding urban tree growth (Meineke and Frank 2018).

When temperatures exceed the species-specific thermal limits and extreme events, such as droughts, become more frequent and intense, adverse effects on tree growth can be observed which makes drought tolerance one of the most important factors to be included when selecting urban trees for ecosystem services in a future climate. Trees have evolved a variety of strategies and traits to enable them to cope with limited water availability. Such avoidance strategies include the reduction of leaf area through defoliation, which limits the surface area from which water is transpired (Laughlin 2023). However, this is not a sustainable approach, as many ecosystem services are linked to leaf mass density and total leaf area. Conversely, tolerant strategies are to be preferred, such as water potential at turgor loss point (Ψ_{p0}), which constitutes a principal trait for assessing drought tolerance in diverse species of trees. Ψ_{p0} is a highly instructive trait, as it represents a quantifiable measure of physiological drought tolerance. A negative Ψ_{p0} value is indicative of enhanced drought tolerance, as it enables the leaf to sustain its physiological function across a broader range of leaf water potentials (Sack et al. 2006; Lenz et al. 2006). Moreover, Ψ_{p0} has been demonstrated to distinguish a diverse array of species and cultivars with regard to their drought tolerance, thereby providing insights into the selection of plant species for green infrastructure (Sjöman and Anderson 2023).

Balancing growth and drought tolerance

To provide ecosystem services effectively, urban trees must tolerate challenging environmental conditions while maintaining healthy, rapid growth. However, these two aspects

are often contradictory, as drought-tolerant strategies require resource investment in dense, persistent tissues, which limits growth (Grime and Pierce 2012). Understanding the trade-off between growth and drought tolerance among species is crucial for selecting appropriate trees for urban environments and predicting their performance under site-specific conditions and facilitate the estimation of expected growth.

This study aims to examine the correlation between drought tolerance (defined by Ψ_{p0}) and growth rate (characterized by leaf and wood traits) across 29 tree species, including several underutilized species for urban environments. We hypothesize that species exhibiting ‘fast’ growth strategies – such as high specific leaf area, low leaf dry matter content, and low wood density – are more sensitive to drought, while species with ‘slow’ growth strategies demonstrate greater drought tolerance. This work also highlights and aim to discuss the research potential of botanical tree collections for screening and evaluating species for future urban climates. Identifying additional tree species with robust drought tolerance and growth potential can enhance the resilience and diversity of urban forests, reducing vulnerability to pests, diseases, and climate impacts (Sjöman and Martin 2025; Watkins et al. 2021).

Arboreta and other botanic collections are characterized by an extensive array of species exhibiting a diverse spectrum of taxonomic, functional, and biogeographical characteristics. These characteristics, when coupled with the meticulous documentation of plant origins, phenology (e.g., flowering periods), and horticultural requirements, position these collections as exceptional resources for scientific research (Chen and Sun 2018; Primack and Miller-Rushing 2009). However, while most research in botanic gardens was focused on conservation, economic botany, and taxonomy, it is crucial to utilise these living collections to address pressing challenges, including water scarcity, human health, and climate change (Smith 2019). In this regard, the curation of diverse collections of species emerges as a pivotal resource for research endeavors aimed at informing the design and management of green infrastructure (Cannon and Kua 2017). Notably, the extensive range of tree species represented in botanic collections can serve as an asset in facilitating research into species selection, with the objective of enhancing biodiversity within urban forests (Hirons et al. 2020). A particular approach that merits 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 which is the aim of this study.

Method and materials

Plant material

Plant material was taken from Royal Botanic Gardens, Kew, London, UK (51°28′41.8728″ N and 0°17′52.6344″ W). The species 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. Kew are considered to have a fully humid, oceanic temperate climate with a warm summer (Cfb of the Köppen–Geiger climate classification system; Kottek et al. 2006). A total of 29 species were evaluated (Table 1); the number of replicates (number of individuals in the collection at Kew) varied among species by 5–7 trees.

Drought evaluation

The current technique for determining Ψ_{p0} employs vapor pressure osmometry to predict osmotic potential at full turgor ($\Psi_{\pi100}$) and is sufficiently sensitive to discern differences in drought tolerance between closely related genotypes (Hannus et al. 2021). The methodology is based on the protocol developed by Bartlett et al. (2012a). Data collection was carried out during July–August were one sun-exposed branch exhibiting no symptoms of abiotic or biotic damage was collected from 5 to 7 trees of each species during the early evening, when transpiration was minimal. The excised branches were promptly recut at a minimum of two nodes distal to the original incision and placed in a tube of water, ensuring that the cut surface was not exposed to the air.

Subsequently, the shoot material was rehydrated for a period of 24 h in a dark chamber with a relative humidity > 95%. Following an overnight rehydration period, one leaf disc was taken from each fully expanded leaf using an 8-mm cork borer. All discs were tightly wrapped in aluminum foil to prevent condensation or frost formation following freezing. The foil-wrapped leaf discs were then submerged in liquid nitrogen for 2 min to fracture cell membranes and walls. Next, the leaf discs were punctured 10–15 times with sharp-tipped forceps to allow evaporation through the cuticle and decrease equilibration time (Kikuta and Richter 1992). Then, each leaf disc was sealed in a vapor pressure osmometer (Vapro 5600, Westcor, Logan, UT, USA) utilizing a standard 10 μ L chamber. The initial readings of solute concentration (CS, mmol kg⁻¹) were taken after 10 min of equilibration time. Thereafter, CS was recorded in repeated readings at approximately two-minute intervals while the value remained below 5 mmol kg⁻¹.

Table 1 Compilation of collected data for 29 tree species at RBG Kew showing mean wood density (WD), mean leaf area (LA), mean leaf dry matter content (LDMC), mean specific leaf area (SLA), the percentage distribution between competitors, stress-tolerators and ruderals resulting in their strategy class, and the mean water potential at turgor loss point (Ψ_{p0})

Species	Mean WD [mg mm ⁻³]	Mean LA (mm ²)	Mean LDMC (%)	Mean SLA (mm ² mg ⁻¹)	C: S: R	Mean Ψ_{p0} (MPa)
<i>Acer platanoides</i>	0.75	15,845	41.4	11.3	57: 40: 3%	-1.99
<i>Carpinus betulus</i>	0.86	4472.4	45.8	16.9	34: 53: 13%	-3.10
<i>Carpinus orientalis</i>	0.912	567.1	48.9	13.2	14: 76: 10%	-3.50
<i>Celtis chinensis</i>	0.756	2866.3	37.8	16.9	32: 51: 16%	-2.67
<i>Celtis occidentalis</i>	0.83	3491.7	40.7	12.6	36: 56: 8%	-3.10
<i>Celtis sinensis</i>	0.77	3161.3	38.2	15.8	34: 52: 14%	-3.00
<i>Cercidiphyllum japonica</i>	0.721	4220	39.4	11.4	41: 55: 5%	-1.95
<i>Eucommia ulmoides</i>	0.826	7078.9	36.2	12.1	49: 45: 6%	-3.16
<i>Fraxinus americana</i>	0.802	37,223	41.4	14.3	65: 30: 6%	-2.60
<i>Fraxinus angustifolia</i>	0.842	5944.2	33	13	48: 43: 9%	-2.60
<i>Fraxinus excelsior</i>	0.798	27,178	34.8	11.9	67: 29: 4%	-2.07
<i>Fraxinus ornus</i>	0.898	10836.3	31	18.9	53: 31: 16%	-2.58
<i>Koeleria paniculata</i>	0.857	21258.9	39.5	10.9	62: 36: 2%	-4.56
<i>Liriodendron tulipifera</i>	0.646	19481.9	29.7	15.4	64: 26: 10%	-2.47
<i>Magonia acuminata</i>	0.68	22936.3	32.5	12.9	66: 28: 6%	-2.85
<i>Magonia salicifolia</i>	0.718	5163.8	35.9	21.3	39: 41: 20%	-2.57
<i>Ostrya carpinifolia</i>	0.988	3392.9	46.5	14.1	32: 58: 10%	-2.69
<i>Ostrya virginiana</i>	1.005	3058.8	48.9	16.4	29: 58: 13%	-3.51
<i>Parrotia persica</i>	0.889	6658.8	51.2	10.4	41: 58: 2%	-4.48
<i>Platanus orientalis</i>	0.719	19,201	40.3	11.6	60: 37: 3%	-2.50
<i>Tilia cordata</i>	0.584	6277.8	37.7	13.4	45: 47: 8%	-1.90
<i>Tilia dasystyla</i>	0.596	4987.5	33.3	15.3	44: 43: 13%	-3.52
<i>Tilia euchlora</i>	0.529	4758.8	32.9	14.2	44: 44: 12%	-2.39
<i>Tilia heterophylla</i>	0.54	7165	40.1	14.6	44: 46: 10%	-2.31
<i>Tilia platyphyllos</i>	0.601	8120	38.7	15	46: 43: 10%	-2.35
<i>Tilia tomentosa</i>	0.61	9717	37.4	12.3	52: 42: 6%	-4.36
<i>Tilia x europaea</i>	0.635	6607.9	38.5	16.2	43: 44: 13%	-1.80
<i>Zelkova carpinifolia</i>	0.974	2325.8	46.6	8.7	31: 69: 0%	-3.32
<i>Zelkova serrata</i>	0.888	3416.1	473	11.5	33: 62: 5%	-3.01

The solute concentration values were converted to osmotic potential (Ψ_{p0}) using Van 't Hoff equation:

$$\Psi_{p0} = -RTc_s$$

where R is the gas constant, T is temperature in Kelvin, and c_s is solute concentration in the leaf disc.

An equation developed by Bartlett et al. (2012b) allowing prediction of Ψ_{p0} from osmotic potential at full turgor ($\Psi_{\pi100}$) is based on a global dataset that includes data from tropical biomes. Since the present study was limited to the temperate biome, an equation developed by Sjöman et al. (2015) for deriving Ψ_{p0} from $\Psi_{\pi100}$ in temperate species, based on a subset (woody temperate, Mediterranean/temperate-dry and temperate conifer species) of the supplementary data provided by Bartlett et al. (2012a), was used here:

$$\Psi_{p0} = -0.2554 + 1.1243 \times \Psi_{\pi100}$$

This equation provided a higher coefficient of determination ($R^2=0.91$) than the Bartlett et al. equation ($R^2=0.86$), and therefore provided a more reliable means of predicting Ψ_{p0} .

Leaf trait evaluation

Pierce et al. (2017) evaluated different traits linked to resource investments and environmental adaptations. The study found that there was relatively little loss of information when only three leaf traits were used, instead of 14 traits, and that the multivariate plant functional space described by leaf traits alone was representative of whole-plant functional variation. These three leaf traits are leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) (representing interspecific variation in plant size, conservative resource economics and acquisitive resource economics, respectively). Combining these traits gives a strong indication about the classification of the different species, which in turn makes it possible to create an overview of a species

and its plant economic investments, and thus their potential for use in e.g., urban environments and its growth rate.

The methodology used for collecting leaf trait data followed the standard presented in Pérez-Harguindeguy et al. (2013). Specific leaf area was calculated as the ratio of one-sided area of a fresh leaf to its oven-dry mass, and thus indicated how much leaf area a plant builds with a given amount of leaf biomass:

$$SLA = \frac{A}{M_L}$$

where A is the area of a given leaf and M_L is oven-dry mass of that leaf. Typical units are $\text{m}^2 \text{kg}^{-1}$ or $\text{mm}^2 \text{mg}^{-1}$.

Leaf area is the most used metric for leaf size and is defined as the one-sided or projected area of an individual leaf, expressed in mm^2 . Heat stress, cold stress, drought stress, nutrient stress and high-radiation stress all tend to select for relatively small leaves, which makes LA a strong trait in the plant economic spectrum.

Leaf dry-matter content is the oven-dry mass (mg) of a leaf divided by its water-saturated fresh mass (g), expressed in mg g^{-1} . LDMC is widely used as an indicator of plant resource use and has been shown to correlate positively with the leaf lifespan.

In the study, the leaf area of the species under investigation was measured using a LI-3100 C Leaf Area Meter, which calculated the ratio of the one-sided area of a fresh leaf to its oven-dry mass. After the measurement of leaf area, the individual leaf (15 leaves per species) was placed in a drying oven set at 70 °C for a minimum of 72 h to reach the dry mass.

An easy-to-understand method for classifying plant investments, and thereby their tolerance to different plant environments, and for gaining insights into growth rate is the CSR classification system (Hodgson et al. 1999; Pierce et al. 2013) based on Grime's theory of competitor–stress-tolerator–ruderal (CSR) plant strategies (Grime and Pierce 2012). In the CSR system, the three principal strategies represent viable trait combinations arising under conditions of competition, abiotic limitation to growth or periodic biomass destruction.

Data collection was carried out during July–August on a sun-exposed branch with no symptoms of abiotic or biotic damage (such as leaf fungal pathogens, leaf defoliation or leaf chlorosis) from 5 to 7 trees per species. Leaf material was collected from between 18:00 and 20:00. Excised branches were immediately placed in a humid bag and taken to the laboratory within 20 min. In the laboratory, branches were recut under water at least two nodes distal to the original cut and placed in a tube of water without exposing the cut surface to the air. Branches were rehydrated overnight in

a dark chamber with >75% relative humidity as measured by a wet-dry bulb thermometer (wet bulb 15 °C/dry bulb 17 °C) to achieve full turgor. Through this procedure, it was possible to compare different species and genotypes. Mean trait values were then calculated for each species.

Wood density

For the collection of wood density (the ratio between the dry weight of wood divided by the green volume of the same wood) we have followed the standard presented in Pérez-Harguindeguy et al. (2013) by taking samples via increment borer from trees in the collection at Kew taken at ca. 1.3 m above ground ('breast height'). After the core is extracted, it was stored in a plastic drinking straw, with the ends of the straw sealed before being transported to the laboratory where they were placed at 90 °C for at least 72 h. The volume of a cylindrical sample is determined by measuring its total length (L) of the core, and its diameter (D), and calculating the volume (V) of the cylinder as

$$V = (0,5D)^2 \times \pi \times L$$

Statistical analysis

Linear regression was used to assess the relationship between SSD and SLA, LA, LDMC, and Ψ_{po} . The confidence limits of the regression slope were used to assess if the regression slope coefficient was significantly different from a hypothetical 1:1 relationship representing no difference between the variables. The coefficient of determination R^2 and p were calculated via simple linear regression and included the strength and statistical significance of the correlation between the variables.

To calculate CSR, we were using the StrateFy tool (Pierce et al. 2017), which were plotted in ternary plots. The StrateFy tool, as described by Pierce et al. (2013, 2017), employs mean trait values for each species to generate a principal components analysis (PCA) utilizing XLSTAT 10 software (Kovach Computing Services, Anglesey, Wales). The resulting PCA was rotated via standard Varimax rotation, also using XLSTAT. Based on the outcome of the PCA, the values of LA were regressed against PCA axis 2, LDMC was regressed against PCA 1 (a positive correlation), and SLA against PCA 1 (a negative correlation), to produce three regression equations. The resulting curves of best fit, derived from a range of models in the SigmaPlot 10 database (Systat Software, Chicago, IL, USA), were fitted and those with the highest R^2 values were selected. Subsequently, the regression equations were employed to generate functions within a Microsoft Excel spreadsheet, thereby

enabling the prediction of PCA 1 and 2 coordinates derived from values of LA, LDMC, and SLA. Three dimensions were thus assigned to the target species: a ‘LA dimension’ based on PCA2, a ‘LDMC dimension’ based on positive variability along PCA1, and a ‘SLA dimension’ based on negative position along PCA1. Given that PCA values may be either positive or negative, the minimum values along each PCA axis were identified and used as a constant to be added to all values of each trait. This was done to translate the LA, LDMC, and SLA dimensions into an entirely positive space (Pierce et al. 2013).

The subsequent function established the maximum values, thereby defining the range of values for each trait. To produce ternary coordinates (i.e., three coordinates for a triangular graph), a function was then added to the spreadsheet that summed the three dimensions and divided by 100. This allowed for the determination of the proportional contributions of LA, LDMC, and SLA for each species. The resulting ternary coordinates represent a trade-off between three competing functional traits and thus three competing ecological functions. It is necessary for all species to have a minimal capacity for competition, stress tolerance, and survival of disturbance (Grime and Pierce 2012). Furthermore, no leaves were characterized by zero area or zero mass. Therefore, the resulting triangular ordination of species represented a ‘trade-off triangle’. The ternary plots were produced separately using SigmaPlot. A spreadsheet function was used for all three dimensions, resulting in space occupied by species filling the entire ternary plot and thus achieving a CSR classification. This was achieved by multiplying all values by a rescaling constant that allowed the maximum and minimum values along the axis exhibiting the least variability to occupy 100% of the range of the x-axis of a ternary plot (Pierce et al. 2013, 2017). The calculations and plot creation were carried out using R software (R Core Team 2022) complemented by the Tidyverse and ggtern packages (Hamilton and Ferry 2018).

Results

The wood density exhibited distinguished variation between the studied species, with values ranging from 0.529 mg mm⁻³ in *Tilia euchlora* to 1.005 mg mm⁻³ in *Ostrya virginiana*. All *Tilia* species, in conjunction with *Magnolia* and *Liriodendron*, exhibited the lowest levels of wood density (Table 1). The evaluation of drought tolerance based on the species Ψ_{p0} revealed a considerable range, from -4.56 MPa for *Koeleruteria paniculata* to -1.8 MPa for *Tilia x europaea* (Fig. 3). However, the data set from the study demonstrates a significant discrepancy between the various species of *Tilia*. *Tilia tomentosa* and *Tilia dasystyla* exhibit notable

drought tolerance, with Ψ_{p0} values of -4.36 and -3.52 MPa respectively, while *Tilia x europaea* and *Tilia cordata* exhibited the weakest drought tolerance, with Ψ_{p0} values of -1.80 MPa and -1.90 MPa, respectively.

When the relationship between different traits of the studied species is evaluated, a clear significance emerges when comparing Ψ_{p0} and leaf dry matter content with wood density (Fig. 2, $p=0.04$ and 0.003, respectively). The relationship was less significant when leaf area and specific leaf area were compared with wood density ($p=0.65$ and 0.08, respectively). The poorer relationship can be attributed to the fact that two species, *Tilia dasystyla* and *Tilia tomentosa*, stand out when other factors in the study are analyzed. These species have a very high drought tolerance ($\Psi_{p0} = -3.51$ and -4.36 MPa, respectively) while their wood density is among the lowest in the study (0.60 and 0.61 mg mm⁻³, respectively).

Except for the two aforementioned *Tilia* species, a distinct pattern emerges, characterized by species with high wood density and drought tolerance. This is exemplified by *Koeleruteria paniculata*, *Ostrya virginiana*, and *Zelkova carpinifolia*, which demonstrate high drought tolerance and exhibit high investments in wood structures and wood density (Figs. 3 and 4). Regarding growth rate based on leaf economy (SLA, LDMA, LA), the ordination within the CSR model revealed that the study taxa were distributed along the Competitor-Stress Tolerator (CS) axis of the ternary plots. The data gathered at Kew revealed that a significant proportion of the species acted as CS strategists, exhibiting a tendency towards C or S. Those with a more stress-tolerant strategy invest more heavily in their leaves, which limits their growth potential. Consequently, they are classified as stress strategists (Table 1; Fig. 5). An exception to this conclusion is *Koeleruteria paniculata*, which, based on the trees evaluated at Kew, exhibits a high tolerance for drought (-4.56 MPa) and a high wood density (0.86 mg mm⁻³). However, it is classified as a competitive strategist (62% C strategist) due to less safely invested leaves, indicating a fast growth despite a high tolerance for drought and a high wood density (Table 1).

The dataset contained some interesting outliers, although there are a close correlation between a more defensive growth rate and high drought tolerance in species of *Zelkova* and *Ostrya*, and *Carpinus orientalis*, and a strong correlation between a more rapid growth rate and limited environmental tolerance in *Fraxinus americana*, *Liriodendron tulipifera* and *Magnolia acuminata*. *Tilia dasystyla* and *Tilia tomentosa* show high drought tolerance with Ψ_{p0} values of -3.51 and -4.36 MPa respectively. However, they are classified as Competitor Stress Tolerators (CS) and Competitors (C) in the CSR model and have low wood densities (0.60 and

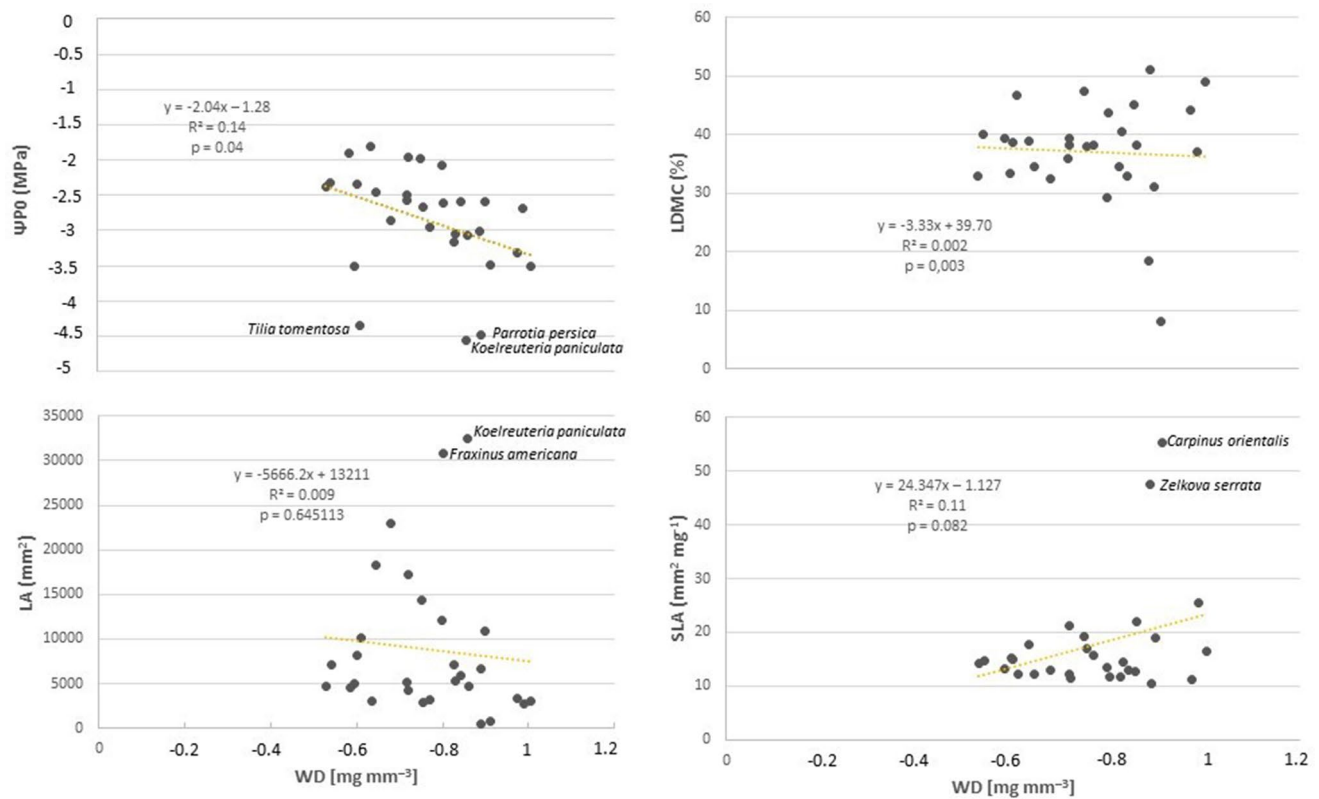


Fig. 2 Scatterplots showing the relationship between leaf economical traits (SLA, LDMA, LA) with wood density (WD), and between Ψ_{p0} and wood density from 29 broadleaved tree species growing at Kew.

0.61 mg mm⁻³, respectively). This suggests that they are fast growing species with high environmental tolerance.

Discussion

Environmental tolerance

The findings of this study indicate a significant variation in drought tolerance among different species, as evidenced by their turgor loss point (Ψ_{p0}). This parameter is closely linked to wood density, a correlation that has been corroborated by other studies (e.g., Liang et al. 2021), where wood density plays a critical role in determining species' hydraulic safety and drought tolerance. Higher wood density enhances resistance to xylem cavitation, a key mechanism for preventing air embolisms under water stress (Hacke et al. 2001a, b; Nardini et al. 2013a). This structural investment ensures the integrity of the plant water transport system, which is crucial in drought-prone or water-limited environments. This phenomenon is also observable on a global scale, where tree species with higher wood density tend to exhibit lower mortality rates during drought conditions (Nardini et al. 2013b; Greenwood et al. 2017). A further point of comparison

The coefficient of determination R^2 and p were calculated via simple linear regression and included the strength and statistical significance of the correlation between the variables

between this study and others is the way trees invest in their leaves, either to gain an advantage through vigorous growth or to develop resilience in the face of challenging and resource-limited habitats. The studies by Petruzzellis et al. (2019) and Simovic et al. (2024) demonstrate that leaf dry matter content (LDMC) is a more valuable indicator than other leaf traits for assessing the capacity of different tree species to take up carbon under more resource-limited habitats. This is because high LDMC constrains growth rates. Denser leaves, which are more costly to construct and maintain, may nevertheless confer advantages in certain circumstances. For instance, high leaf dry matter content (LDMC) could confer greater tolerance of leaf desiccation (Petruzzellis et al. 2019), which could sustain photosynthetic rates through 'dry' periods and thus have a greater role in more stressful environments. The findings of this study indicate that Ψ_{p0} , in conjunction with wood density and LDMC, constitutes a robust trait combination for predicting a species' capacity to maintain active and prolonged photosynthesis, even in the face of more challenging and resource-limited habitats. This underscores the importance of integrating wood and leaf-related traits in such assessments.

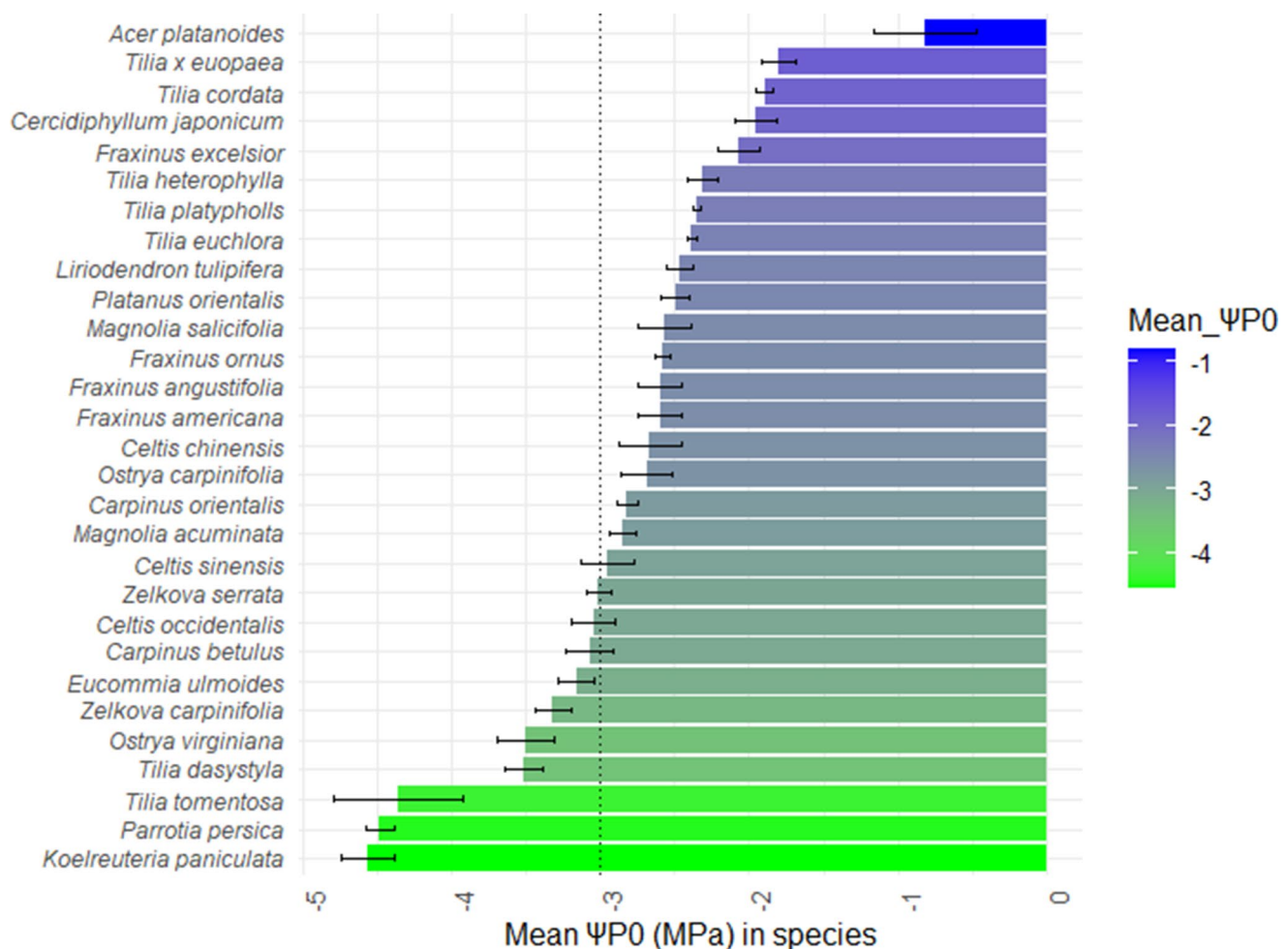


Fig. 3 Mean Ψ_{P0} point of 29 tree species at Royal Botanic Garden Kew ranked by summer Ψ_{P0} values where an increasing negative value (MPa) indicates increasing drought tolerance. The error bars repre-

sent the standard error of collected Ψ_{P0} data. The vertical dashed line denotes the mean value of the dataset

Tree growth and functional traits

In addition to environmental tolerance, the growth rate of a tree species is an important factor in determining its capacity to deliver ecosystem services in urban environments. In this study, functional traits have been employed to gain insight into plant growth strategies (Westoby et al. 2002), as well as to elucidate community composition (Lavorel and Garnier 2002; Shipley 2010), and ecosystem processes (Lavorel and Garnier 2002). At present, two principal spectra of trait variation are frequently cited as the underlying basis for differences in vegetative growth rates between species, i.e., the leaf economic spectrum (Wright et al. 2004) and the wood economic spectrum (Chave et al. 2009) which reflect the costs of tissue construction, namely leaf area and wood volume, respectively. These costs are traded off with rates of tissue turnover or mortality. It has been widely anticipated that species with low tissue construction costs will typically exhibit fast growth rates, particularly in favorable

physical environments (e.g., Iida et al. 2014; Paine et al. 2015). There is compelling evidence that plant economics is a primary determinant of the ability of different species to compete within diverse plant environments (Diaz et al. 2016). Functional traits have been employed as the primary basis for constructing classifications, identifying ecological strategies that illustrate how species cope with environmental factors and are assembled in a given community (Grime 1977; Westoby 1998; Westoby et al. 2002; Reich 2014; Pierce et al. 2017).

In this study we used the CSR theory to communicate the leaf economical spectrum which has been proven to be powerful because of its efficiency (Caccianiga et al. 2006; Cerabolini et al. 2010; Negreiros et al. 2014; de Paula et al. 2015). The CSR analysis tool proposed by Pierce et al. (2017) can therefore be considered a valuable way to clarify some of the mechanisms explaining plant community assembly and environmental filtering across scales. Our analysis of 29 species revealed that the C-strategists

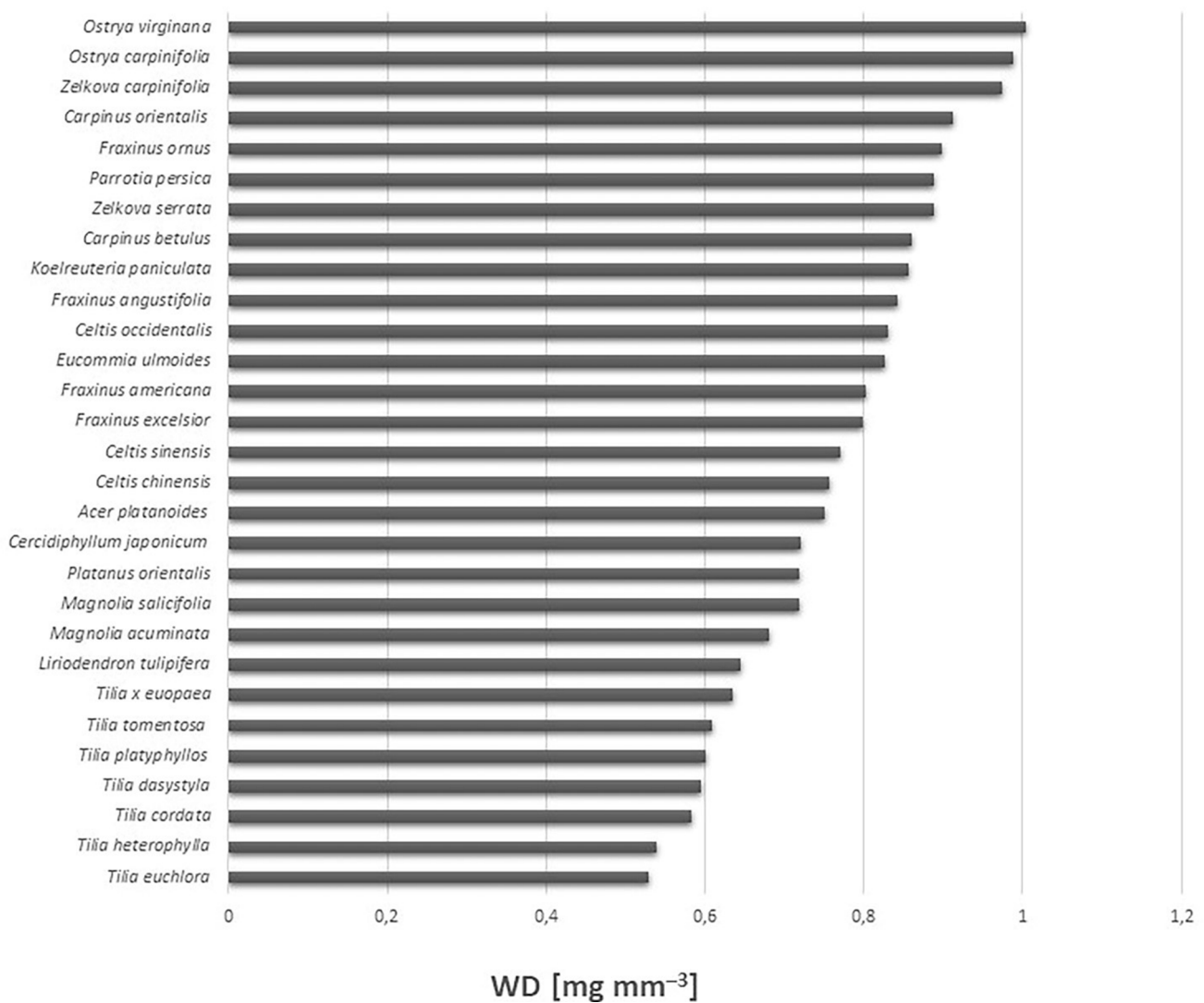


Fig. 4 Mean wood density (WD) levels of 29 tree species at royal botanic garden kew

comprised many species that have their natural origin as pioneers in resource-rich habitats, i.e., environments with a very good supply of water, nutrients, and sunlight. They included *Liriodendron tulipifera* and *Magnolia acuminata* which originate from resource-rich terrain with a good supply of nutrients and water, and more or less unlimited supply of sunlight in the early phases of the succession (Kress 2024; Farrar 1995). This confirms the reliability of the CSR model in positioning these species as distinct C-strategists, as both in nature and in cultivation they show very strong growth in resource-rich habitats (Dirr 2011). Even if the CSR-model is based on natural environments with competition compared to trees growing in a botanical garden, the evaluation can be a strong tool. In a landmark study by Grime and Hunt (1975) it is shown that species originating from resource-limited habitats (S-strategists) maintained lower growth even in cultivation under ‘optimal’ conditions, which has

since been confirmed by numerous studies (Laughlin 2023) which indicate that evaluation within favorable tree collection can give good guidance. Moreover, the study concludes that trees which employ a fast-growing strategy are unable to mount a defense against conditions which are more resource-limiting when comparing drought tolerance and plant economic spectrum based on leaf and wood economics. Regarding growth, trees such as *Fraxinus excelsior*, *Liriodendron tulipifera*, *Magnolia acuminata* and *Fraxinus americana* are only capable of efficient growth under conditions of resource abundance. This indicates that they are best suited to parks and gardens, where their photosynthetic capacity is most efficient. However, their ability to cope with more resource-limited habitats, such as dry street environments with efficient surface runoff, is significantly reduced. Slow-growing species with high wood density and expensive leaf (e.g., *Carpinus orientalis*, *Parrotia persica*,

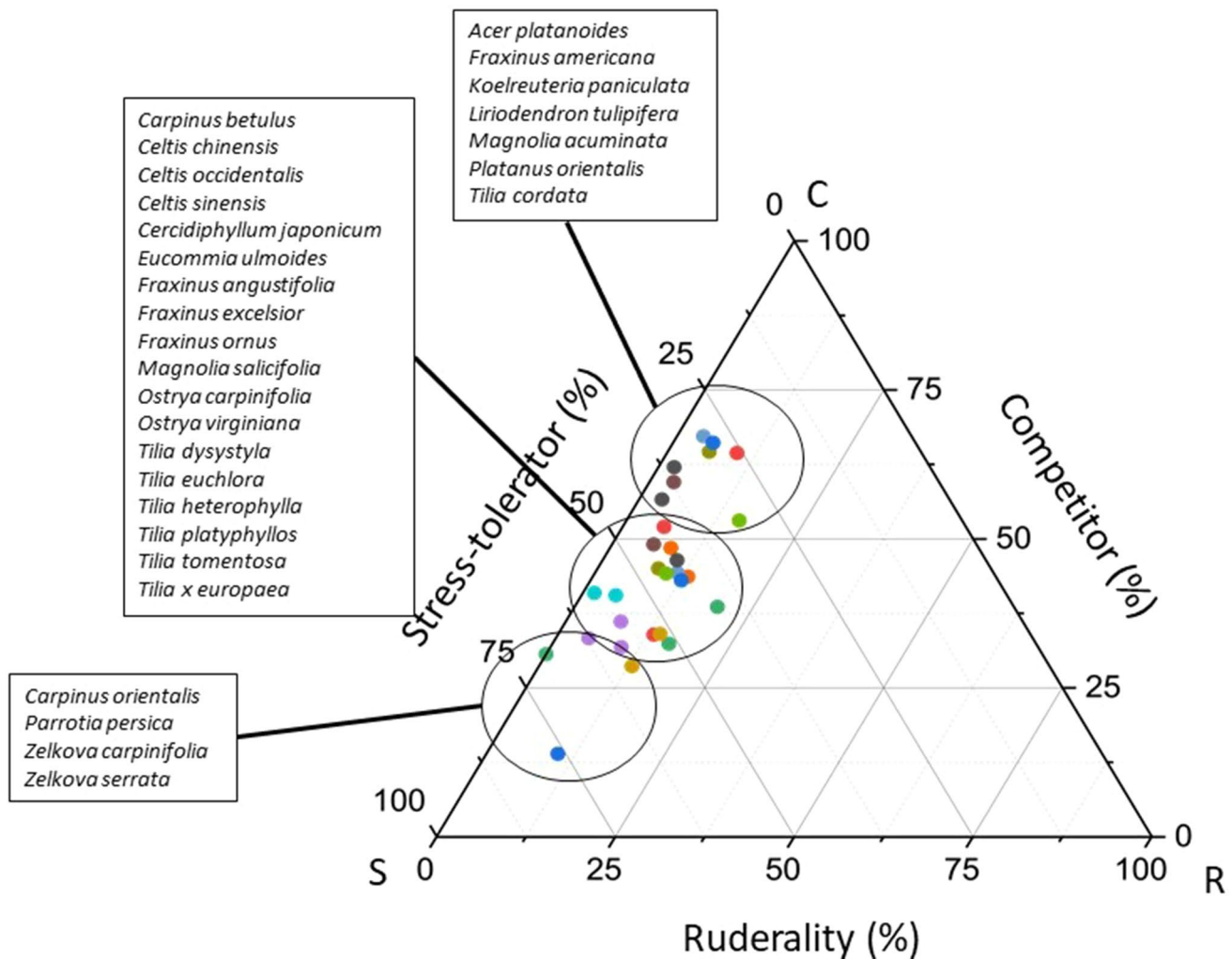


Fig. 5 Ordination of studied tree species of the Royal Botanic Gardens Kew. In this assessment, the study taxa were distributed along the Competitor–Stress tolerator (CS) axis of the ternary plots. It indicates that long-lived organisms such as trees have a limited tolerance

Zelkova carpinifolia, *Zelkova serrata*) invest in structural resilience, providing a competitive advantage in resource-limited environments which is also visible when including Ψ_{p0} .

Trade-off in growth and environmental tolerance

The relationship between SLA and wood density had a weak significance in our study contrasting to other publications (e.g., Reich 2014; Laughlin 2023). This is largely due to the inclusion of two outliers, namely *Carpinus orientalis* and *Zelkova serrata*. It can be reasonably assumed that the significance would be more pronounced if these two species were not part of the dataset. However, it is of particular interest to focus on the outliers in the dataset of this study, as these species possess distinctive characteristics that render them invaluable for the more challenging urban

environments with extensive biomass losses. The position of the different species is based on leaf economic values (Pierce et al. 2017), where the different values are further presented in Table 1

to recurrent disturbances with extensive biomass losses. The position of the different species is based on leaf economic values (Pierce et al. 2017), where the different values are further presented in Table 1

environments, despite their ability to provide crucial ecosystem services. *Tilia dysstylis* and *T. tomentosa*, in conjunction with *Koelreuteria paniculata*, exhibit a relatively high SLA from a leaf economic perspective, indicative of a CS strategist classification. However, they also demonstrate the highest levels of Ψ_{p0} , at -3.51 , -4.36 and -4.56 MPa, respectively. This suggests a robust growth pattern with a high environmental tolerance which is also evident when wood density is compared between the species where the two *Tilia* species in question have the lowest wood density.

We also sought to test an overreaching hypothesis that higher growth rates are observed for species with a ‘fast’ strategy (e.g., high specific large leaf area, high leaf dry matter content, low wood density) and that species with a ‘slower’ strategy are more drought tolerant (low turgor loss point). This hypothesis is confirmed by the results of the study. However, the species who do not follow the general

trend in the study demonstrate a distinct pattern in their investment in leaves and wood, which is not correlated with growth. Conversely, their investments facilitate a more rapid growth process, yet they continue to invest in, for instance, cell structure in the leaves to cope with periods of drought (Ψ_{p0}), thereby ensuring the maintenance of good development, a preserved photosynthetic capacity even under more challenging conditions.

Although being a pilot study with only 29 species included, several outliers can be identified in this data set. These represent an interesting combination of investments that make them relatively fast-growing (plant economic) but with a high tolerance to drought (Ψ_{p0}). Despite challenging conditions, these trees can offer good growth and quickly become important trees with a high capacity to deliver important ecosystem services. It would be of interest to investigate what other outliers could occur if another and larger dataset were studied. It may be that these outliers represent the study's most interesting findings, as it is precisely those who do not follow the stream that may be of importance in the work of matching trees for a future climate and with a high capacity to deliver important ecosystem services.

Using botanical tree collections

The study was based on a botanical plant collection (RBG Kew), which offers considerable scope for investigation, comprising a wide range of tree species, many of which are non-traditional in public plantings, and where studies on their capacity as urban trees are either very limited or completely excluded (e.g., Yan and Yang 2017; Sjöman and Östberg 2019; Cowett and Bassuk 2020). The study encompassed a range of commonly utilised species commonly found in urban environments within the northern hemisphere, including *Acer platanoides*, *Fraxinus americana*, and *Tilia x europaea* (Sjöman and Östberg 2019; Cowett and Bassuk 2020). The study also included more unusual species, such as *Celtis sinensis*, *Parrotia persica*, and *Zelkova carpinifolia*, with the intention of facilitating a comparison between a standard range and a more unconventional plant material in the same study, thereby facilitating a more comprehensive comparison of promising candidates.

The inclusion of unique plant material in studies conducted in a botanical garden presents several opportunities but also raises some limitations. One of the principal challenges is the number of replicates available for the different species many botanical tree collections desire to include a diverse range of species, which inevitably impacts the number of individuals of a single species in the collection due to limited space. In this study, the number of species included was limited by the number of replicates required to conduct

the study. A further challenge was to identify a methodology that did not compromise the integrity of the unique collection. This necessitates a data collection process that causes minimal damage to the trees, while still yielding robust data. An alternative approach would be to propagate the desired species from seed or woody material for more detailed studies in greenhouses. This would facilitate a more detailed examination of their capacity to deal with stress. It should be noted that this process is inherently more time-consuming, given that the cultivation of the desired species to the requisite final size for evaluation can span over several years. It is therefore useful that an initial screening be conducted, as presented in this study, to obtain robust indications of which species should be proceeded with more detailed greenhouse trials. In the absence of this preliminary screening, there is a significant risk of including species in the more detailed studies in greenhouses that lack the requisite potential, thereby precluding the inclusion of other, more promising candidates that could ultimately become the urban trees of tomorrow.

Furthermore, recent research findings indicate that there is notable intraspecific variation within a given species regarding, for instance, drought tolerance (Hirons et al. 2020; Hannus et al. 2021) which means that the result from this study can differ if different genetic material of same species are evaluated. From a future climate perspective, this is crucial to enhance the precision of tree selection for specific locations and functions. However, in a considerable number of botanical plant collections, the number of replicates of a single collection is often inadequate. Instead, collections are represented by a very limited number of individuals, which complicates the evaluation of ecotype-related research. This limitation of individuals from a single ecotype represents a significant future challenge for these plant collections, as they seek to establish themselves as essential research infrastructure on trees for urban environments in a future climate.

It is of the utmost importance that future research on the selection of trees for specific locations and functions takes intraspecific variation into account where botanical tree collection can be of great value – they facilitate the comparison of different genetic types of the same species across diverse collections and they offer unique insights into the provenance of the plant material included in the collections, which is often meticulously documented in their databases. This represents a significant advantage over study plants from the horticultural trade, where such information is often lacking (Sjöman et al. 2024). This approach will undoubtedly facilitate a deeper comprehension of the urban trees of the future. Therefore, the result from this study have to be seen as an contribution to the search for the best species and

the best genetic material for future cities when comparing different plant collections.

Conclusion

In current urban environments, where the availability of space for tree planting is limited, it is of paramount importance to acknowledge the multifunctional roles that trees can fulfil. Nevertheless, for the successful delivery of vital ecosystem services, size and well-being remain fundamental factors. This suggests that site tolerance, such as drought tolerance and rapid growth to reach a significant size as fast as possible, is of great importance. This study has identified an intriguing variation in the combination of environmental tolerance and growth rate based on non-destructive data collection in a botanical tree collection.

Our findings have significant implications for urban forestry in the context of climate change where species with high wood density and moderate to high drought tolerance (e.g., *Carpinus orientalis*, *Zelkova serrata*) are ideal for dry or water-limited urban habitats. Fast-growing species such as *Liriodendron tulipifera* and *Magnolia acuminata* may thrive in parks or resource-abundant environments but are less suitable for drought-prone areas. Outlier species in the study (*Tilia dasystyla*, *T. tomentosa* and *Koeleruteria paniculata*) provide a unique opportunity for urban programs, balancing growth and resilience to deliver long-term ecosystem services. The integration of functional traits (e.g., wood density, ΨP0, LDMC) into tree selection frameworks will enable urban planners to optimize tree performance, ensuring climate resilience, improved shading, and carbon sequestration. The study also demonstrates the potential, but also the challenge, of conducting this type of screening in a botanical tree collection. The development of a unique methodology is crucial in this context, as these tree collections harbor unique genetic material of an unconventional plant material with the potential to contribute to the greening of our future cities.

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Author contributions All authors have agreed to re-submit this version and have also have equal responsibility in the planning, data collection, analyses and writing of the study.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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