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DROUGHT TOLERANCE OF CANDIDATE URBAN TREE SPECIES

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Abstract

Global climate change is increasing the frequency and intensity of extreme events such as drought and the effect is exacerbated in urban environment, threatning urban tree health and survival. In this study, we conducted a pot experiment using 15 candidate urban tree species (267 trees in total) diverse in origin but broadly categorized as native and exotic. Three treatment groups were established: control (regular watering), moderate drought (short-term water withholding followed by rewatering), and extreme drought (water withholding until visible leaf damage, then rewatering). Key physiological parameters were measured every week at regular intervals throughout the experiment: photosynthetic rate, stomatal conductance, chlorophyll fluorescence, and predawn and midday leaf water potentials. We examined whether physiological traits decline in parallel or independently during drought, assessed recovery capacity at different drought intensities, compared drought tolerance between native and exotic species, and identified species-specific drought tolerance characteristics. Results revealed parallel declines in all physiological parameters during both moderate and extreme drought, with decline severity increasing with drought intensity and duration. Recovery patterns exhibited threshold behavior, with physiological functions failing to recover after predawn leaf water potentials dropped below -2.3 Mpa and F_v/F_m below 4, indicating permanent/irreversible damage after the point. Thus, substantial recovery was observed in moderately stressed trees while extremely stressed trees didn't show any signs of recovery. Native species were less sensitive to moderate drought than exotic species while the opposite was true under extreme drought. Species-specific responses revealed *Ostrya carpinifolia* (European Hop-hornbeam) as consistently drought-tolerant, while *Koelreuteria paniculata* (Goldenrain tree) demonstrated remarkable recovery capacity despite intermediate drought sensitivity. *Nyssa sylvatica* (Black gum) and *Acer saccharinum* (Silver maple) were consistently the most drought-sensitive species. Our findings highlight the complex, coordinated nature of physiological responses to drought and the importance of considering both drought resistance and recovery capacity when selecting urban tree species for climate resilience, particularly as extreme drought events become more common under climate change.

Abstrakt

Global klimatförändring ökar frekvensen och intensiteten av extrema händelser som torka, och effekten förvärras i urbana miljöer, vilket hotar stadsträdens hälsa och överlevnad. I denna studie genomförde vi ett krukexperiment med 15 potentiella stadsträdarter (totalt 267 träd) med varierande ursprung, men grovt indelade i inhemska och exotiska arter. Tre behandlingsgrupper etablerades: kontroll (regelbunden vattning), måttlig torka (kortvarig vattenbrist följt av återvattning) och extrem torka (vattenbrist tills synlig bladskada uppstod, därefter återvattning). Viktiga fysiologiska parametrar mättes varje vecka under hela experimentets gång: fotosynteshastighet, stomatal ledningsförmåga, klorofyllfluorescens samt förgrynings- och middagstidens bladvattenpotentialer. Vi undersökte om fysiologiska egenskaper försämras parallellt eller oberoende under torka, utvärderade återhämtningsförmåga vid olika torkintensiteter, jämförde torktolerans mellan inhemska och exotiska arter, samt identifierade artsspecifika egenskaper kopplade till torktolerans. Resultaten visade på parallella nedgångar i alla fysiologiska parametrar vid både måttlig och extrem torka, där försämringens allvar ökade med torkans intensitet och varaktighet. Återhämtningsmönstren visade tröskeleffekter: fysiologiska funktioner återhämtade sig inte om förgryningsbladvattenpotentialen sjönk under -2,3 MPa och Fv/Fm under 4, vilket indikerar permanent/irreversibel skada vid denna punkt. Betydande återhämtning observerades hos träd som utsatts för måttlig torka, medan extremt stressade träd inte visade några tecken på återhämtning. Inhemska arter var mindre känsliga för måttlig torka än exotiska arter, medan motsatsen gällde vid extrem torka. Artsspecifika svar visade att Ostrya carpinifolia (europeisk hopphassel) var konsekvent torktålig, medan Koelreuteria paniculata (gyllenträd) uppvisade anmärkningsvärd återhämtningsförmåga trots måttlig torkkänslighet. Nyssa sylvatica (svarttupel) och Acer saccharinum (silverlönn) var konsekvent de mest torkkänsliga arterna. Våra resultat belyser den komplexa, samordnade naturen hos fysiologiska svar på torka och vikten av att beakta både torkresistens och återhämtningsförmåga vid val av stadsträd för klimatanpassning, särskilt eftersom extrema torkhändelser blir allt vanligare i takt med klimatförändringarna.

Popular science summary

What does studying the ecophysiology of the complete drought cycle in urban trees tell us about drought sensitivity and how can it guide the selection of tree species for cities facing climate change?

Drought is predicted to be more frequent and intense due to climate change, and with pre-existing stressors like soil compaction and low surface permeability in urban environment, urban trees face exacerbated challenges. Therefore, it is necessary to understand the ecophysiology of trees for selecting the right trees in context of global climate change. In our open field pot experiment, we studied 15 different urban tree species under both moderate and extreme drought treatments. We measured how their key physiological processes such as photosynthesis, stomatal conductance, water status, etc changed during drought and after rewatering. Our results showed that all trees experienced a coordinated decline in their physiological function as drought intensified. However, recovery after drought varied: trees could bounce back if their stress hadn’t crossed a certain threshold point and beyond the point irreversible damages occured on tissues. Additionally, both decline and recovery varied among species. Some species performed better while some perfomed poorly under both conditions, where as some other species showed remarkable recovery capacity. Analysing these species-specific behavior during drought and post-drought helps to identify tree species that are not only good at surviving dry periods but are also able to recover when water returns. Urban planners can use the knowledge from similar studies for the selection of tree species that is resilient to urban stressors and climate change.

It should be noted that our study mainly focused on leaf-level physiological responses, allowed only a short recovery period after extreme drought and evaluated species performance through rankings, which may limit a full understanding of long-term or whole-tree resilience under different drought intensity and at species level.

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1. Introduction

Global climate change threatens plant growth and survival worldwide as rising temperature increases the severity and frequency of droughts and heatwaves through accelerated evaporation and altered precipitation patterns, leading to documented tree mortality and forest decline in past few decades (IPCC, 2023; Anderegg et al., 2016; Zscheischler et al., 2018; Allen et al., 2010). While most prevalent in arid regions, drought-induced mortality also occurs in temperate and high-latitude European forests, as evidenced by direct tree deaths during the severe soil moisture deficits and heat of the 2018 drought in Europe (Brodribb et al., 2020). Urban trees are particularly vulnerable to these stresses, with climate change exacerbating drought conditions in city environments (Rötzer et al., 2021). Studies conducted in Melbourne, Australia and Helsinki, Finland documented drought-induced tree health decline and mortality in urban landscapes (Nitschke et al., 2017). The vulnerability in urban tree health is driven by complex interactions between climate variability and anthropogenic factors like soil compaction and ground surface permeability, and restricted rooting space which allow limited ground water infiltration- enhance water scarcity and disrupts the trees' physiological processes. Therefore, accurately exploring and analyzing the responses and post-recovery of urban trees' physiological mechanisms following hot drought events are critical to obtaining a better understanding of their growth and survival under future climate change scenarios (Wang et al., 2023).

Drought is a major abiotic factor which when coupled with high air temperatures and high vapor pressure deficit negatively affects tree functioning through perturbations on interconnected processes, primarily driven by water potential decline and hydraulic dysfunction (Wang et al., 2023). These processes, however, exhibit species-specific drought strategies with species falling along an isohydric-anisohydric continuum, as species vary in the sensitivity of stomatal conductance (g_s) to leaf-to-air vapour pressure deficit (Domec & Johnson, 2012). As soil moisture depletes, reduced water uptake in tree increases xylem (vascular system in woody plants for long-distance water transportation) tension, with early stomatal closure, reduced carbon assimilation (photosynthesis) and maintenance of a sufficiently high leaf water potential to avoid hydraulic failure in isohydric species. In contrast, anisohydric species opens stomata, sustaining photosynthesis (A) at the risk of hydraulic dysfunction. Hydraulic failure and carbon starvation in trees are known to primarily drive drought-induced tree mortality (McDowell et al., 2008). Intense drought coupled with high evaporative demand increases xylem pressure and causes embolism (meaning it becomes air-filled), leading to desiccation of the shoot or the whole tree (McDowell et al., 2008). The process may be exacerbated by photoinhibition and associated damage to photosystem II (PSII). Overall, the physiological mechanisms are assumed to influence each other and to be related to the quantity, intensity and duration of stress-impact (McDowell et al., 2008). Therefore, integrated monitoring of physiological traits is critical in quantifying species-specific vulnerability of urban trees to hot drought and to inform climate-resilient forestry strategies (Wang et al., 2023).

1.1 Physiological responses of plants to drought stress: integrating water potential, gas exchange, and chlorophyll fluorescence as indicators of drought response

Water potential (Ψ) reflects the water status of a plant and its ability to transport water from the roots to the canopy by a cohesion-tension mechanism. Ψ is generally negative in plants due to the tension created by transpiration and pulling up water from the soil. Under drought conditions, water becomes less available for uptake by roots so, internal water potential in plant tissues (leaf and stem) becomes more negative to extract water from the soil triggering physiological adjustments such as stomatal closure and reduced photosynthesis (Taiz & Zeiger, 2010). Initially the cell turgor pressure declines and causes visible wilting along with inhibition of cell expansion, a key driver of plant growth. Water stress further reduces leaf number by limiting branch growth and accelerating leaf senescence. As drought persists, temporary wilting converts to permanent wilting, followed by leaf abscission- the shedding o stressed leaves to conserve water-which, if severe can ultimately result in tree mortality (Taiz & Zeiger, 2010). Here, Ψ becomes extremely negative potentially causing the formation and spread of embolisms that disrupt the transport of water. The propagation of embolisms can cause hydraulic failure and the irreversible desiccation of downstream tissues, which if widespread leads to whole tree mortality (McDowell et al., 2008; Choat et al., 2018; Arend et al., 2021).

The earliest response in leaves to water deficit is stomatal regulation to maintain hydraulic integrity and prevent desiccation, with stomatal conductance reflecting the measure of stomatal opening in plants (Yan et al., 2017; Wankmüller & Carminati, 2022). Stomatal conductance (g_s) is a measure of the diffusive conductance of entry of CO_2 or exit of H_2O through stomata (microscopic pores located on leaf under surface). Therefore, it is a key physiological parameter that integrates photosynthetic activity and plant water relations. When water is available the stomata opens and conductance increases, increasing both carbon assimilation and water loss, whereas, under drought stomata closes and conductance decreases to reduce water loss (Yan et al., 2017). This protective mechanism in plants under water stressed condition restricts diffusion of CO_2 into the plants inhibiting the photosynthetic activity and reducing carbohydrate production (Taiz & Zeiger, 2010). Under extended drought condition dependency on limited carbon reserves and continued respiration may leads to plant mortality from carbon starvation (McDowell et al., 2008).

In addition to disruption in stomatal processes, drought-induced suppression of photosynthesis is accompanied by a downregulation or irreversible damage of the photosynthetic apparatus, particularly photosystem II (PSII) which inturns inhibits photosynthetic electron transport (Hu et al., 2023). When light is absorbed by chlorophyll molecules in leaf, it undergoes one of three fates: drive photosynthesis, be dissipated as heat, or be re-emitted as light in the form of chlorophyll fluorescence (ChlF). These processes occur in close competition; therefore, measuring ChlF yield provides insight into the plant's photosynthetic performance and stress responses. The most widely used parameter is F_v/F_m ratio, which represents the maximum quantum efficiency of PSII in a dark-adapted state. The dark adaptation of leaves at first opens all PSII reaction centers and the application of weak light that doesn't drive photosynthesis measures minimum fluorescence (F_o). Then a saturating pulse of light is applied to close all PSII centers and the maximum fluorescence (F_m) is recorded. The difference between F_m and F_o is variable fluorescence (F_v). In healthy unstressed plants F_v/F_m typically ranges from 0.79 to 0.84, indicating optimal PSII function whereas the value below that indicates that the plant is under stress. F_v/F_m often decreases before visible symptoms appear and therefore; it is used as non-destructive method and as an early indicator of stress (Maxwell and Johnson, 2000).

1.2. Physiological responses of trees to drought: patterns of decline, recovery dynamics, native and exotic species and species-specific traits for climate resilience

Plants respond to water deficit through a complex interplay of physiological adjustments across multiple scales, from cellular processes to whole-plant coordination (Kim et al., 2024). Traditional perspectives conceptualized drought responses as a series of independent physiological adjustments with different sensitivity thresholds (Tardieu and Simonneau, 1998). However, emerging evidence suggests that physiological processes may decline in a more coordinated fashion across drought severity gradients (Bartlett et al., 2016; Brodribb et al., 2020). Therefore, understanding whether different physiological traits respond in parallel or independently during both moderate and extreme drought conditions is crucial for accurately modeling plant drought responses and predicting trees vulnerability under climate change.

Trees not only vary in their responses to drought stress, but also show significant variation in recovery pattern once water becomes available again (Gebauer et al., 2023). The rate of recovery is determined by trees capacity to restore functioning to pre-stress level. This depends on several factors, including the timing, duration, and severity of the drought, as well as the tree's traits and taxonomic group (Gebauer et al., 2023; Gessler et al., 2020). Generally, mild drought-stressed trees have been found to recover earlier and faster than the trees subjected to severe drought, likely due to less impaired tissues/reversible damages (Gallé & Feller, 2007). While numerous studies exist on responses of trees during prolonged drought stress, only limited information is available about the processes during subsequent recovery, specifically examining different drought durations. Therefore, it is crucial to understand, assess and compare the tree physiological recovery processes after varying intensity of drought stress (Zhang et al., 2024; Gebauer et al., 2023; Gallé & Feller, 2007).

In the face of the urban heat island (UHI) effect (cities having higher temperature than surroundings) and climate change, native tree species are expected to suffer greater mortality rates than more warm-adapted exotic species. A recommended adaptation measure by experts is to incorporate exotic species into urban forestry plans to create more resilient and sustainable urban forests (Schlaepfer et al., 2020; Sjöman et al., 2016). Resilient forests must be adapted to a range of stressors that climate change intensifies in severity and frequency, such as droughts. Currently native tree species are prioritized in many urban planning programs like Sweden's Green Area Factor where native species receive higher quality marks due to assumption about their superior adaptation and function to local conditions (Broadmeadow et al., 2005). Papers debate that the assumption may not apply to harsh urban environments and future climate scenarios suggesting the strategic introduction of exotic tree species as potentially valuable approach to urban forest construction and structural complexity across different scales (Sjöman et al., 2016). However, selecting exotic species for urban forest requires thorough evaluation of their adaptation to local conditions and drought tolerance. It is especially important to assess species-specific drought tolerant traits to prevent mortality. Therefore comprehensive and comparative analysis of how exotic and native trees respond physiologically to water limitation is essential for developing evidence-based urban forestry policies that ensure sustainable urban forest development under changing climatic conditions (Bueno et al., 2021; Broadmeadow et al. , 2005).

As repeatedly mentioned earlier, the urban environment poses additional challenges to tree survival, yet selection of trees planted in urban landscapes is primarily based on their aesthetic qualities and little information exists concerning their drought tolerance (Percival & Sheriffs, 2002). Identifying the physiological characteristics that enable certain tree species to withstand water limitation is essential for creating resilient urban forests. Plant physiological traits describe multiple functional features among species, which can be used to assess species-specific diversity in response to drought stress. Hence, the interest in a better understanding of traits that lead to survival during and after drought has increased, to allow predictions of plant vulnerability on a species-specific level (Wang et al., 2023). At the leaf level, species with rapid stomatal closure in response to decreasing soil moisture can effectively reduce water loss during drought periods, though this strategy comes with the trade-off of reduced carbon assimilation (McDowell et al., 2008). At the xylem level, wood anatomical traits of species such as resistance to cavitation play a crucial role in determining drought vulnerability (Choat et al., 2018). Furthermore, the hydraulic safety margin which is the buffer between typical operating water potentials and causing hydraulic failure has emerged as a particularly important predictor of drought survival (Anderegg et al., 2016).

Ecophysiological information has proven useful in selecting tree species for reforestation projects (Liu et al., 2011). However, projects lack basic information on the ecophysiological aspects of the tree species used for reforesting the city, particularly regarding their drought tolerance. Franceschi et al. (2023) highlights on the longstanding study of drought impacts on tree growth in natural forests and the limited- recent research in urban areas. Additionally, field experiment on urban trees physiological responses to drought are essential due to exposure of urban trees to unique and severe stressors (Gillner et al., 2015). Furthermore, tracking both resistance (during stress) and resilience (post-stress recovery) of hydraulic and photosynthetic functions in urban trees provides crucial data for assessing species vulnerability and informs climate-adaptive urban forestry strategies (Wang et al., 2023). Comprehensive and comparative analysis of physiological responses of exotic and native species to drought stress is essential before integrating exotic species into urban forestry planning (Bueno et al., 2021).

1.2. Aims:

This study aims to investigate and identify the critical physiological traits, recovery patterns and species-specific vulnerabilities of diverse urban tree species under varying drought intensities to inform climate-resilient urban forestry strategies.

Specifically, this study aims to answer the following research questions:

1. Do different physiological traits and processes decline in parallel under both moderate and extreme drought?
2. To what extent can physiological processes recover after moderate and extreme drought treatment, and is recovery a simple reversal of negative drought effects?
3. Are native tree species more drought-sensitive compared to exotic species originating from warmer and/or drier areas?
4. Which species are most/least drought sensitive and what traits characterize these species?

2. Materials and methods

2.1 Study area and plant materials

The experiment was conducted in a privately owned nursery, Essunga Plantskola (58.19N, 12.78E), located in the southwestern Sweden, approximately 90 km northeast of Gothenburg city. The study was conducted during the growing season of summer 2024, from July 1 to September 1.

Six three-year-old saplings of 15 broadleaf candidate urban tree species (except *Magnolia kobus* with 5 replicates) were collected from Splendor Plant Skola, located around 295 km south from study area and transferred to the nursery on May 17. The trees were grown in black plastic pots of size 7.5 Litre, outdoors in the field of the nursery and subjected to three different treatments (control, moderate drought, and extreme drought) to simulate different levels of drought stress. The growing medium for all trees were the same, the planting soil consisted mostly of peat, clay and compost. Among the tree species, 6 were native to Sweden, while 9 were exotic species, diverse in geographical origin and leaf morphology. All pots were adequately irrigated until the first week of July 2024 to ensure that all trees were well established in the study site.

In total, 267 trees were studied for the experiment. Saplings of the following tree species were used in the study:

Table 1. Overview of tree species used in the study, including scientific and common names, natural distribution, average tree size (cm) per treatment group, and native or exotic status.

Scientific name	Common name	Natural distribution	Tree size in experiment (Mean±S.D.)			Status (Native/ Exotic)
			Control	Moderate Drought	Extreme drought	
Acer platanoides	Norway maple	Europe and western Asia	137.2±21	117.8±11.1	118.2±33.8	Native
Acer saccharinum	Silver maple	Eastern and central North America	202.3±10.3	196.2±21.8	204.7±25.3	Exotic
Betula pendula	Silver birch	Europe and Asia	160.3±11.0	132.2±14.8	150.8±16.8	Native
Carpinus betulus	Hornbeam	Europe and western Asia	147.8±17.2	135.3±23.3	143±21.5	Native
Celtis occidentalis	Common hackberry	Central and eastern North America	202.2±11.4	204±26.8	210.2±16.3	Exotic
Koelreuteria paniculata	Goldenrain tree	China and Korea	150.8±9.9	157.8±12.6	154.2±9.5	Exotic
Liquidambar styraciflua	Sweetgum	Eastern North America	224.7±9.0	239.8±17.6	237.3±13.6	Exotic
Liriodendron tulipifera	Tulip tree	Eastern North America	213.2±24.6	213.2±20.2	221.3±13.9	Exotic
Magnolia kobus	Kobus magnolia	Japan and Korea	145.6±8.8	135.6±20.8	147.8±11.9	Exotic
Nyssa sylvatica	Black gum	Eastern North America	189±9.5	164.7±12.2	171.5±14.9	Exotic
Ostrya carpinifolia	European hop-hornbeam	Southern and central Europe	139.8±12.4	135.2±3.9	129.3±2.7	Exotic
Prunus avium	Sweetcherry	Europe, western Asia	161.3±24.1	164.7±23.0	166.5±28.0	Native
Sorbus intermedia	Swedish whitebeam	Southern Scandinavia	109.2±4.4	104.3±16.1	106.7±9.0	Native
Sorbus torminalis	Wild Service-tree	Europe, northwestern Africa, and western Asia	129.8±11.6	116.3±14.4	144.5±46.5	Exotic
Tilia cordata	Small-leaved lime	Europe and western Asia	94.8±15.3	90.8±15.6	84±13.8	Native

2.2 Experimental Setup

Each tree was assigned a unique Plant ID, and all individuals were arranged in 12 rows: 4 randomly assigned rows for each treatment (control, moderate drought and extreme drought). The drought treatments began in the second week of July. To prevent unintended water from reaching the soil during the drought treatments, the pots were wrapped with plastic skirts and secured with tape. Additionally, the pots were placed on a stand 5 cm above the ground to prevent water absorption from below. This ensured a controlled environment for simulating drought stress in respective treatments. Prior to the start of the treatments, healthy trees were selected and were randomized to each treatment and row. To mitigate the edge effects extra trees were added at all corners. This ensured similar growing conditions for all trees. Since different tree species reached moderate drought and extreme drought points at different times due to variations in size and leaf gas exchange, each tree's vitality, physiology, and soil VWC was monitored regularly to assess its status.

The control group received proper watering to ensure ample water availability throughout the study. In the moderate drought treatment, watering was withheld until soil moisture sensors indicated extreme dryness in soil, followed by re-watering after 7–10 days. Re-watering was solely based on soil moisture measurements for the moderate drought treatment. Soil moisture levels were monitored at consistent depth across all pots twice a week using a ML3 ThetaProbe (Delta-T Devices, Cambridge, UK). When a volumetric water content (VWC) of less than 11% was recorded on two consecutive occasions, indicating low soil moisture, the affected trees on drought treatment were re-watered the following week. In the extreme drought treatment, drought was prolonged until complete loss of green leaves. For rewatering the extreme drought-treated trees similar soil moisture measurements were performed as moderate drought treatment, followed by plant vitality (tree health) check. If the soil moisture and plant vitality was recorded low, then the pots were marked to be watered the next week.

2.3 Physiological measurements to assess drought response

To assess the physiological responses of trees to different treatments, we measured several variables, including leaf chlorophyll-*a* fluorescence, gas exchange, water potential, and number of leaves.

2.3.1 Number of Leaves

To estimate the relative temporal development of the number of leaves, we selected one branch per trees and counted all leaves on the branch everyweek throughout the experiment.

2.3.2 Chlorophyll fluorescence measurement

A portable Pocket-PEA fluorimeter (Hansatech, King's Lynn, UK) with a light pulse of 3500 μmol photons $m^{-2}s^{-1}$ and duration of 1 s was used to measure chlorophyll *a* fluorescence. The instrument records data every 10 μs during measurement. Measurements were taken on the adaxial side of randomly selected, fully expanded, healthy/stressed leaves on the outside of the tree crown. Prior to measurements, leaves were dark adapted for ≥ 30 min using light-withholding clips. Measurements were conducted before noon once a week throughout the study period. A widely used parameter (F_v/F_m) was measured using Murchie & Lawson, 2013 methodology, to indicate the maximum quantum efficiency of PS II.

2.3.3 Gas exchange measurements

A portable photosynthesis system (LI-6800; Li-Cor Inc., Lincoln, NE, USA) was used to monitor the gas exchange parameters: photosynthesis (*A*) and leaf stomatal conductance to water vapour (g_s). A healthy branch located on the outside of the tree crowns with typical number of leaves was selected in all trees and leaves from that branch were used for gas exchange measurements throughout the study period. Gas exchange measurements were conducted on all trees on two consequent days every week at the day time (10:00 – 17:00). If trees in the drought treatments wilted or dropped their leaves no further measurements were made until fresh leaves developed after irrigation. For each measurement, the leaf was subjected to an optimal chamber setting of CO_2 concentration (430ppm), ambient temperature, light intensity (1800 µmol m^{-2} s^{-1}), and relative humidity (full bypass: if wet Rhair = 60%). Leaves were measured when technical stability was reached or after a maximum of two minutes; then three measurements were taken 10 seconds apart. This fast measurements allowed minimal time for stomata to respond to leaf chamber conditions, with data reflecting stomatal conductance under ambient conditions.

2.3.4 Leaf water potential measurements

Leaf water potential (Ψ_L) is an indicator of plant water status that can be measured quickly and easily. The Ψ_L at any time is a combined result of the interactions between soil water availability, evaporative demand, and plant water transport and storage processes. It is expressed in pressure units, preferably MPa (Kramer & Boyer, 1995). Leaf water potential at predawn (Ψ_{pdl}) is taken when transpiration is at its minimum and the water potential of the plant is closest to equilibration with that of the soil. Leaf water potential at midday (Ψ_{mdl}) is affected by plant transpiration and thus, broadly captures the integrated effects of plant traits and the environment on the minimum daily water potential a plant reaches in natural conditions (Barlett et al., 2016).

Ψ_L is commonly measured using a pressure chamber (also known as Scholander-type pressure chamber). The samples were measured within 10 minutes of collection using the Model 3115 Pressure Extractor (Soilmoisture Equipment Corp, Santa Barbara, California, USA), designed for plant water status measurements. A complete leaf was placed inside a sealed chamber and was subjected to increasing pressure until water emerged from the cut petiole. This positive pressure, indicates the negative Ψ_L of the leaf prior to abscission (Scholander et al., 1965). We used magnifying glass to closely observe the emergence of the first water from the cut petiol. For the Ψ_{pdl} and Ψ_{mdl}, we collected three leaves per species and treatment before sunrise for the former and four leaves per species and treatment between 10:00 and 17:00 for the later (Local standard times in all cases). Mature leaves with the complete petiole were excised using a razor blade (for Ψ_{mdl}, the same leaf previously used for gas exchange measurements). After excision, the leaves were placed in a zip-lock plastic bag with a moistened paper towel to maintain a humid environment and kept in a cool box.

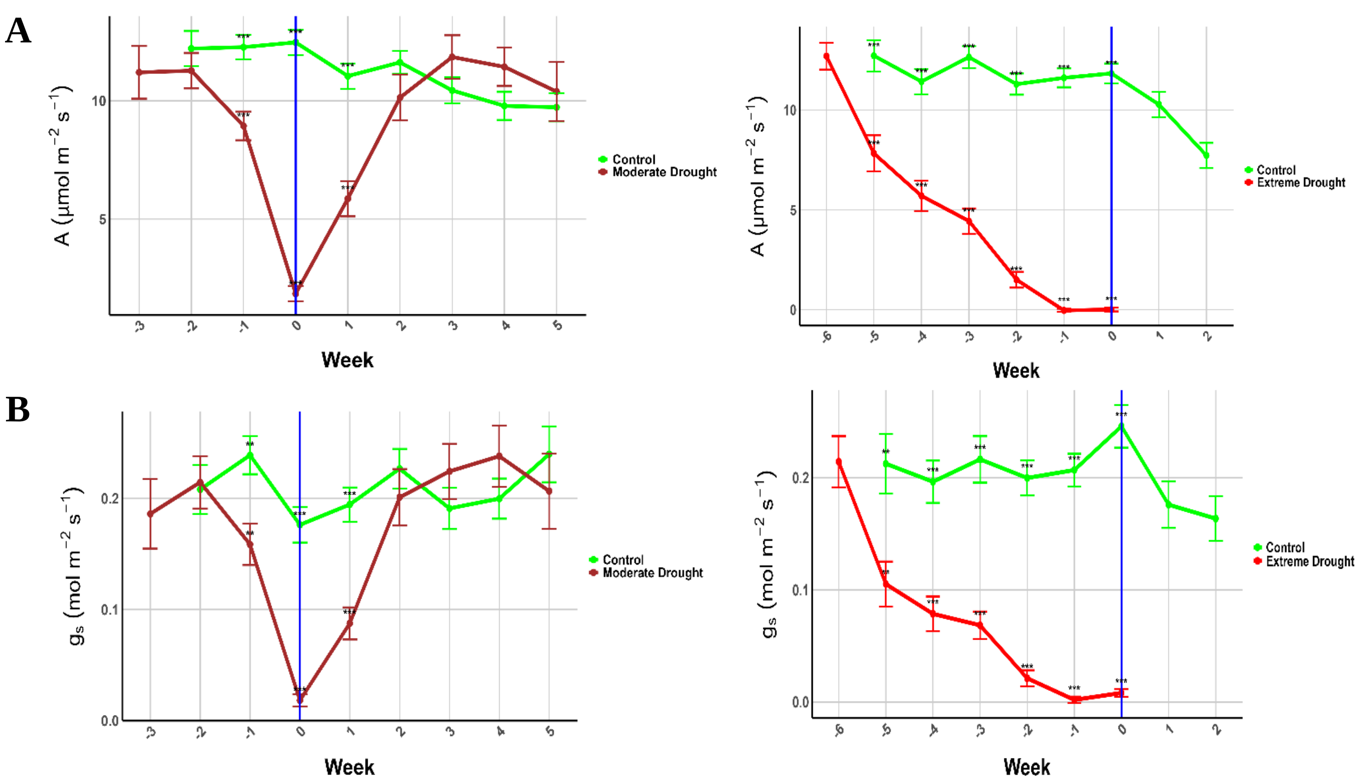
2.4 Data analysis

Data analysis was performed using Microsoft Excel and R version 4.3.3 (R Core Team, 2024**.** In Excel, raw data were organized and cleaned, and preliminary calculations (such as averages, summation, etc) were performed. R was used for more advanced statistical analyses, including data visualization and statistical testing. Temporal changes in physiological responses were visualized using line charts expressed as mean ± standard error (SE) for each treatment and species broadly grouped as native and exotic. For the NrL, we used normalized data by converting all measurements every week to percentages relative to the first day value. Statistical significance was assessed using an independent two-sample t-test to compare treatment means and species group for each week. A Pearson correlation matrix was calculated to explore relationships among physiological parameters, highlighting significant correlations ($p < 0.05$). This analysis was based on response ratios (RR) calculated for each individual tree as the ratio of the drought-treated value to the control value for Weeks 0 and 2. The RR values were then averaged across replicates to yield a single response ratio per species per variable. The statistical significance was determined using the Hmisc package in R. Finally a Drought Sensitivity Index (DSI) was created to rank species based on their physiological responses to drought. This index was calculated using the same dataset as the correlation matrix. For each significantly correlated variable ($p<0.05$), species were ranked from 1 (best performing/least sensitive) to 15 (least performing/highly sensitive). The ranks were then summed and averaged across all significant variables to generate a composite RPI score for each species. This was done separately for week 0 and week 2, depending on the variables identified as significantly correlated at each time point.

3. Results

The graphs for leaf water potentials (Ψ_{pdl} and Ψ_{mdl}), gas exchange (A and g_s), and chlorophyll fluorescence (F_v/F_m) demonstrated remarkably consistent trends across measured variables (Figure 1, A-E). Urban trees subjected to drought stress demonstrated a systematic decline with increasing intensity in most physiological parameters, with the most pronounced reductions observed at Week 0 prior to irrigation. Progressive recovery post-irrigation was observed in moderate drought-treated trees, while no signs of recovery were evident for extreme drought-treated trees. The Ψ_{mdl} curve is positioned approximately 0.5 MPa lower than the Ψ_{pdl} curve during the entire experiment.

Under moderate drought conditions, leaf water potentials declined to below -2 MPa, while extreme drought treatments resulted in potentials dropping below -3 MPa at Week 0. The partial recovery of Ψ_L especially Ψ_{pdl}, in spite of the soil being wet after irrigation is noteworthy. Gas exchange variables exhibited more pronounced declines towards zero and subsequent recovery up to control levels after Week 2, though these recoveries were statistically insignificant. Chlorophyll fluorescence (F_v/F_m) continued to decrease until the first week post-irrigation, reaching approximately 0.4 in the moderate drought treatment and recovered to 0.6. In contrast, the extreme drought treatment showed no recovery, with F_v/F_m remaining effectively zero.



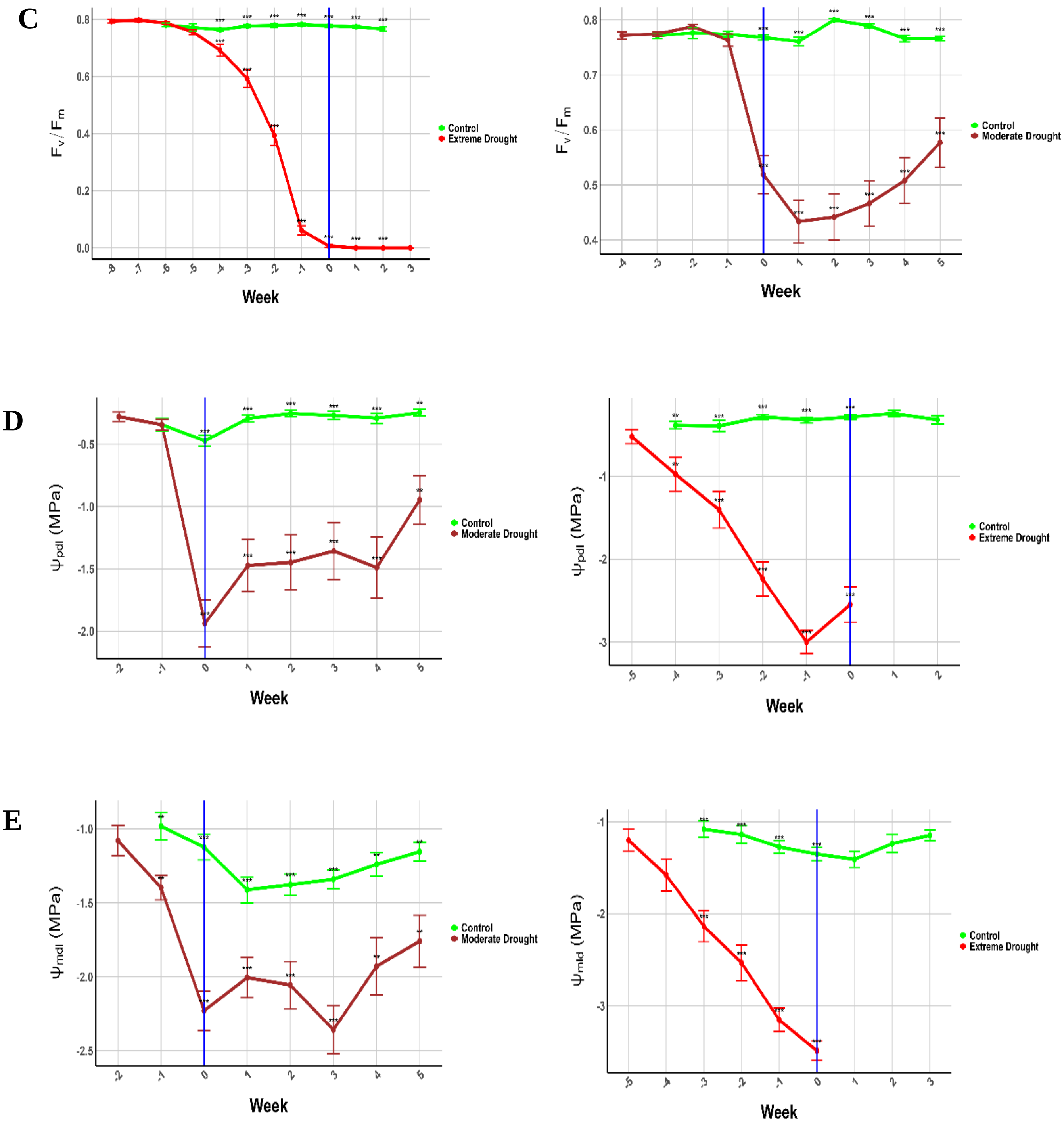


Figure 1. Comparison of net photosynthesis (*A*, A), stomatal conductance (g_S, B), maximal quantum yield of PS II (F_v/F_m, C), predawn leaf water potential (Ψ_{pdl}, D) and midday leaf water potential (Ψ_{mdl}, E) in 15 urban tree species subjected to varied intensity of drought (severe drought – brown line and extreme drought – red line). Data points with error bars represent mean ± S.E. when data is available for at least 8 out of 15 species to ensure adequate data representation. Asterisks indicate significant differences between drought-stressed and control trees: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Blue line indicates start of irrigation week, negative weeks are dry period and positive weeks are re-watered period.

The number of leaves (NrL) demonstrated a divergent response compared to other physiological parameters. Initially, NrL slightly increased during the first three weeks of drought treatment before initiating a significant decline post-irrigation. Partial recovery was observed in the moderate drought treatment after the third week of re-watering, while the extreme drought treatment showed no such recovery response (Figure 1, F).

F

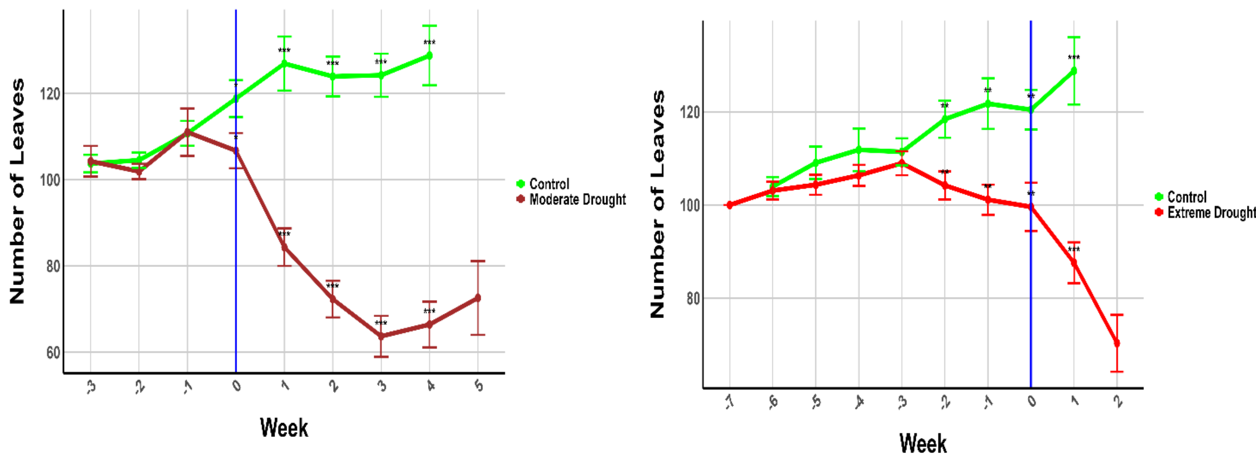


Figure 1. Change in number of leaves under varied intensity of drought stress. Data points with error bars represent normalized mean ± S.E. with thresholds of 8 unique species count to ensure adequate data representation. Asterisks indicate significant differences between drought-stressed and control trees: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Blue line indicates irrigated week, negative weeks are dry period and positive weeks are re-watered period.

The pearson correlation matrix created using the response ratios of different variables, revealed several statistically significant relationships (p<0.05) among physiological parameters during both drought (Week 0) and recovery (Week 2) phases (Fig. 2). At the peak drought (Week 0), A exhibited a strong positive correlation with g_s (r = 0.76, p<0.05) and moderately strong positive correlations with F_v/F_m (r = 0.55, p<0.05) and Ψ_{mdl} (r = 0.56, p<0.05), indicating coordinated physiological responses to water limitation. Ψ_{mdl} showed moderately strong positive correlations with g_s (r = 0.57), F_v/F_m (r = 0.54, p<0.05) and Ψ_{pdl} (r = 0.57, p<0.05). During the recovery phase (Week 2), the relationship between *A* and g_s remained very strong (r = 0.94, p<0.05), while *A* and F_v/F_m maintained the moderate positive correlation (r = 0.55, p<0.05). Notably, the correlation between Ψ_{pdl} and Ψ_{mdl} became insignificant whereas the correlation between Ψ_{mdl} and g_s strengthened (r = 0.62, p<0.05). A new positive correlation was found between F_v/F_m and Ψ_{pdl} (r = 0.65, p<0.05). The relationships between NrL and other parameters were statistically insignificant during drought (p>0.05) however, it is noteworthy that NrL correlation, initially negative, became positive and stronger with *A*, F_v/F_m and Ψ_{pdl} as water availability increased.

Under control conditions (Fig. 3, a-i), native species consistently exhibited significantly higher values (p < 0.05) than exotic species across all depicted physiological parameters throughout the experimental period. For moderate drought-treated trees (Fig. 3 a-f), drought responses and recovery patterns were similar in both species groups. However, a difference is observed in recovery in F_v/F_m (Fig. 3, d) where native species maintained values around 0.6 while exotic species dropped to approximately 0.3 at week 1 and recovered progressively. By weeks 4-5, exotic species had largely recovered, with values becoming statistically indistinguishable from native species for all variables. In case of extreme drought conditions (Fig. 3, g-i), both native and exotic species showed moderate physiological impairment with no significant recovery observed. Native species consistently started from higher baseline values in all measured variables prior to drought implementation but showed steeper decline later- statistically significant for F_v/F_m (p>0.05) while insignificant for rest. Results from other measured variables (not shown in Fig. 3) did not reveal distinct patterns regarding which group performed better under drought stress.

The integrated drought performance assessment, based on the Drought Sensitivity Index (DSI; low number indicating good performance/less sensitivity) calculated from all physiological parameters, identified substantial differences among the 15 studied species (Table 2). During acute drought conditions (Week 0), *Ostrya carpinifolia* demonstrated superior drought performance (DSI = 1.6), followed by *Magnolia kobus* (DSI = 4.4) and Betula pendula (DSI = 5.4) but with a big-jump in the RPI value compared to *O. carpinifolia*. In contrast, *Carpinus betulus* (DSI = 13.2), *Acer saccharinum* (DSI = 12.8), and *Nyssa sylvatica* (DSI = 12.4) displayed the lowest drought performance. Assessment after two weeks of recovery revealed shifts in species rankings. While *O. carpinifolia* maintained its top position (DSI = 2.6), *Koelreuteria paniculata* showed remarkable recovery, improving from rank 11 during drought to rank 2 during recovery (DSI = 2.8). Conversely, *Prunus avium* exhibited poor recovery, dropping from rank 4 to rank 12. *N. sylvatica* and *A. saccharinum* remained among the underperformer during both phases.

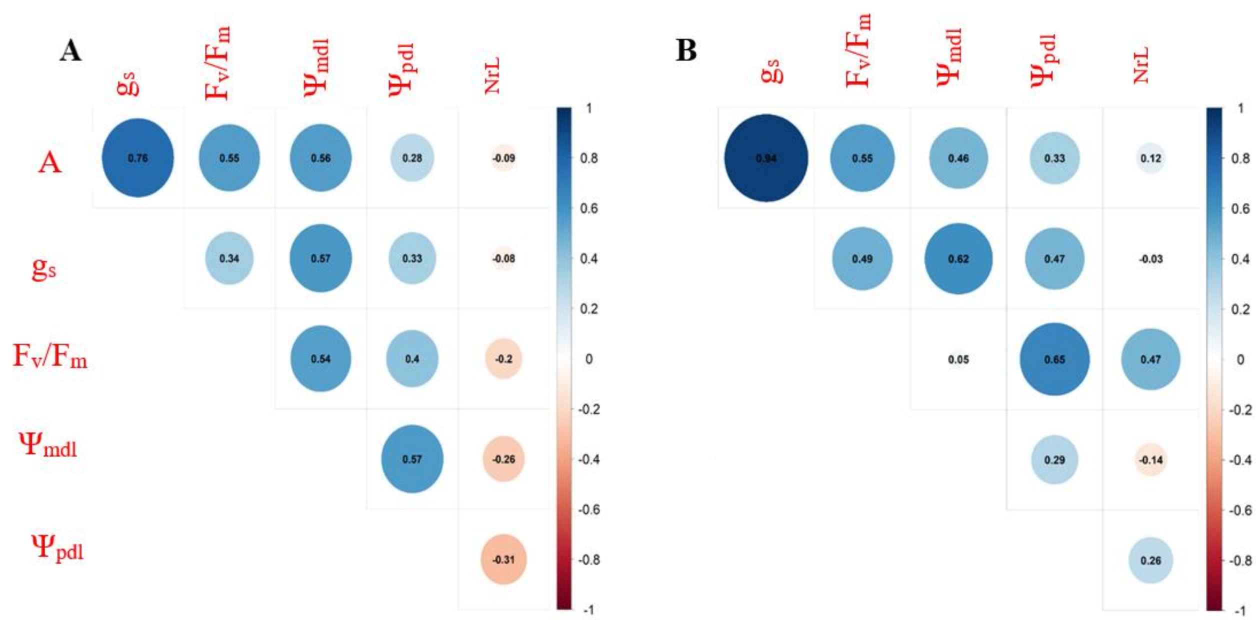


Figure 2. Pearson correlation matrices illustrating relationships among response ratios of physiological parameters at Week 0 (peak drought- A) and Week 2 (recovery phase- B). Blue shades represent positive correlations and red shades indicate negative correlations. The size of the circles corresponds to the strength of the correlation, with larger circles denoting stronger relationships. Value above 0.50 are significant correlations (p<0.05). The matrix allows the comparison between the peak dry event and the recovery phase of moderate drought treatment.

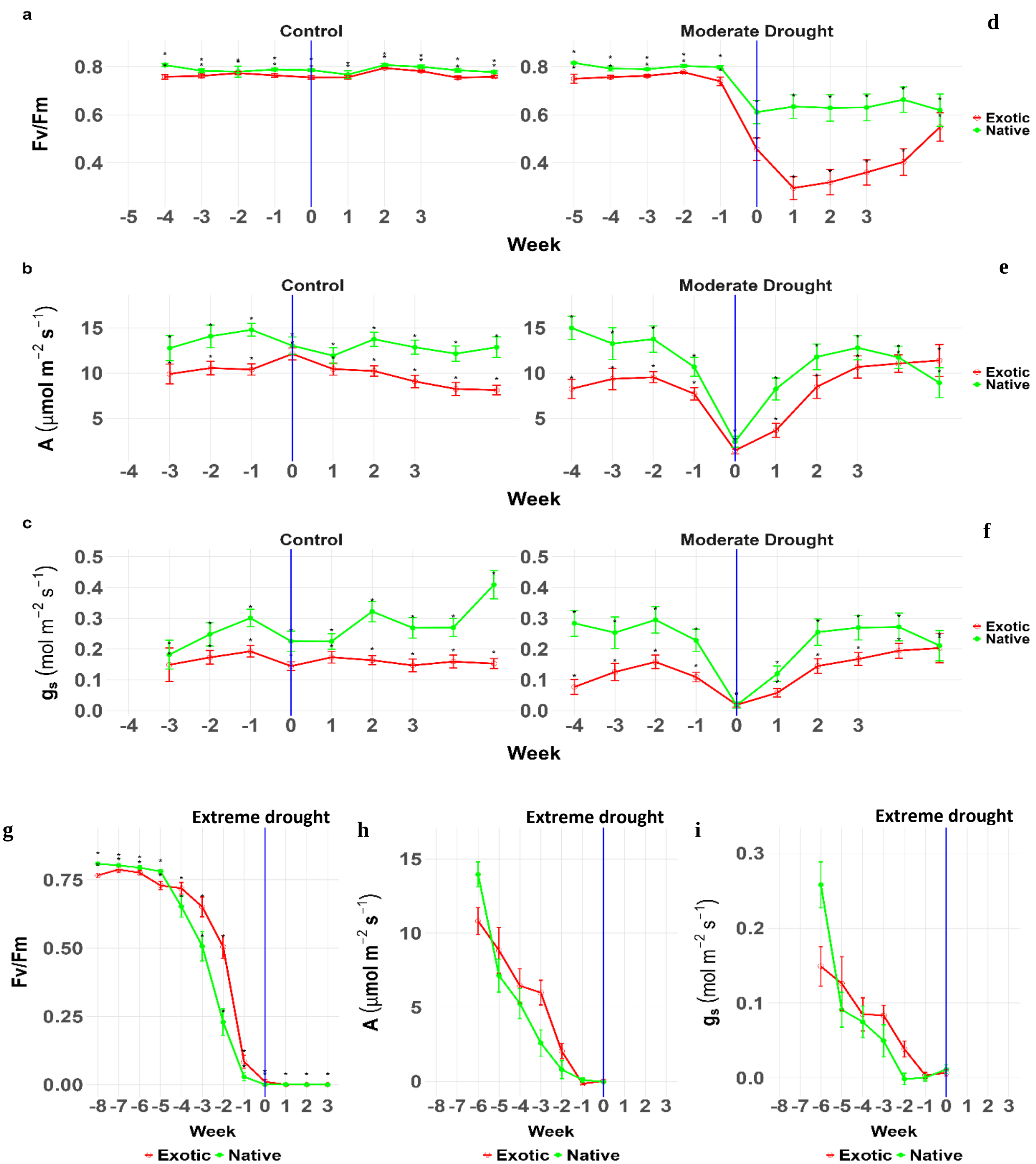


Figure 3. Dynamics of chlorophyll fluorescence (F_v/F_m), net photosynthesis (A), and stomatal conductance (g_s) in native and exotic urban tree species, subjected to different treatments (control, moderate drought and extreme drought – bottom panel) during experimental period (. Data points represent mean ± S.E. Hollow symbols (○) with solid green line represents measurement for native species, while filled symbols (●) with solid red line represents measurement for exotic species. Asterisks (*) indicate statistically significant differences (p<0.05) between native and exotic species at specific time points. For visually sufficient data representation, the number of selected data were filtered: for native

species a threshold of 5 species per week was applied, while for exotic species a threshold of 3 species was used. The vertical blue line at week 0 divides the dry period before irrigation (negative values of weeks) from the wet period that represent the recovery phase after irrigation.

Table 2. Drought Sensitivity Index (DSI) of species based on physiological responses (A, g_s, Ψ_{pdl}, Ψ_{mdl} and F_v/F_m) to moderate drought and recovery. Species were ranked from 1 (most drought-tolerant) to 15 (most drought-sensitive) using significantly correlated physiological variables ($p<0.05$). The DSI was calculated by determining the response ratio (treatment/control) for each variable, ranking species accordingly, averaging ranks across variables, and re-ranking the final values to classify drought tolerance.

	Drought (Week 0)			Recovery (Week 2)	
DSI	Species	Rank	DSI	Species	Rank
1.6	Ostrya carpinifolia	1	2.6	Ostrya carpinifolia	1
4.4	Magnolia kobus	2	2.8	Koelreuteria paniculata	2
5.4	Betula pendula	3	5.2	Betula pendula	3
5.8	Prunus avium	4	5.6	Magnolia kobus	4
5.8	Sorbus torminalis	5	6.6	Sorbus intermedia	5
6	Liquidambar styraciflua	6	7	Acer platanoides	6
6.6	Tilia cordata	7	7.2	Celtis occidentalis	7
7.4	Acer platanoides	8	7.4	Tilia cordata	8
8.8	Celtis occidentalis	9	8	Liriodendron tulipifera	9
9.4	Sorbus intermedia	10	9.2	Carpinus betulus	10
9.6	Koelreuteria paniculata	11	9.8	Sorbus torminalis	11
10.8	Liriodendron tulipifera	12	10.2	Prunus avium	12
12.4	Nyssa sylvatica	13	11.2	Liquidambar styraciflua	13
12.8	Acer saccharinum	14	13.2	Acer saccharinum	14
13.2	Carpinus betulus	15	14	Nyssa sylvatica	15

4. Discussion

We examined whether physiological traits decline in parallel or independently during moderate and extreme drought, assessed recovery capacity across different drought intensities, compared drought tolerance between native and exotic species, and identified which species was more/less sensitive to drought.

4.1 Coordinated decline of physiological parameters under progressive drought stress

Our results demonstrate that the studied physiological traits (A, g_s, Ψ_{pdl}, Ψ_{mdl}, and F_v/F_m) decline in parallel under both moderate and extreme drought conditions with decline accelerated as drought extends in duration (Figure 1). It aligns with the continuum perspective proposed by Zhou et al. (2013), where physiological responses decline gradually and proportionally as water limitation increases pointing towards integrated whole-plant responses. The parallel decline in gas exchange parameters (A and g_s) observed in our study aligns with findings from Flexas et al. (2006), who demonstrated strong coordination between photosynthesis and stomatal conductance across drought intensities. Similarly, the synchronized reduction in water potential (both Ψ_{pdl} and Ψ_{mdl}) and gas exchange parameters supports the hydraulic-photosynthetic coordination theory proposed by (Brodribb & Cochard, 2009). They suggested that stomatal regulation during water deficit is tightly coupled to plant hydraulic status to prevent catastrophic embolism. Additionally, the higher decline rate in gas exchange parameters under moderate drought compared to Ψ_{pdl} and Ψ_{mdl} suggests that stomatal regulation dominates to preserve hydraulic safety under mild drought which aligns with results from Yan et al. (2017) who found that the reduction in g_s could explain major percentage of reduction in other response variables such as leaf water potential. The parallel decline in F_v/F_m alongside other parameters contrasts with results of Genty et al. (1989), who found that photosystem II integrity remained relatively stable during moderate drought while net photosynthesis declined, with F_v/F_m only decreasing significantly under severe water limitation. This suggest that in addition to stomatal limitation, also non-stomatal limitation acts to inhibit photosynthesis as drought intensifies. The parallel nature of these declines is further supported by our correlation analysis (Figure 2, A), which revealed statistically significant relationships ($p<0.05$) among the responses of measured parameters. The strong correlations between g_s and A, g_s and Ψ_{mdl}, and Ψ_{pdl} and Ψ_{mdl} during peak drought demonstrate the tight coupling of stomatal regulation, photosynthetic capacity, and plant water status. Furthermore, the steep decline in variables under extreme drought, the limited recovery of Ψ_{pdl} and leaf loss supports the hyraulic-failure theory by McDowell et al. (2008), suggesting cavitation in trees under severe stress which lead to irreversible damages in trees tissues.

4.2 Threshold response in recovery after rewatering post-drought

The recovery results from our study for physiological processes suggest that drought is not a simple reversal of drought effects, but rather depends critically on drought severity and duration. Figure 1 reveals distinct recovery patterns across the measured physiological parameters following drought treatments of varying intensity. Under moderate drought conditions, physiological parameters showed substantial capacity for recovery. As evidenced in panels A-E of Figure 1, trees subjected to moderate drought stress maintained sufficient physiological integrity to recover their functions when rewatered. The full recovery of g_s and A to initial levels after two weeks of rewatering observed in our study aligns with an example mentioned in Xu et al. (2010) on *Populus nigra* L in which A completely recovered after A fell to almost zero. This suggests that gas exchange parameters contribute to drought-tolerance and have high recovery capacity in variables to moderate drought thanks to stomatal regulation of water losses. As shown by correlation matrix (Fig. 2, B) where the Ψ_{mdl}, and Ψ_{pdl} relationship (hydraulic regualtion) becomes insignificant with water availability meaning stomatal opening and photosynthetic apparatus repairment is regulating the recovery processes.

In contrasts, under extreme drought conditions trees exhibited permanent physiological damage with zero recovery despite rewatering. This threshold response is clearly visible in all panels, where physiological functions remained severely depressed even after drought alleviation and in major cases measurements couldn't be done due to permanent leaf wilting or complete leaf loss. This suggests that as drought intensify and a critical threshold is crossed ($\Psi_L < -2.3$ MPa and $F_v/F_m < 4$), irreversible damage occurs in tissues: hydraulic failure, permanent stomtatal closure and damages in photosynthetic apparatus. Such damage may lead to tree mortality under extreme drought condition but this was not investigated in the present experiment. Our observations align with results from several studies: Choat et al. (2018) stated that embolism spread rapidly below $\Psi_L = -2.5$ MPa in some species, which limits hydraulic conductivity and prevents recovery. Similarly, according to hydraulic failure model proposed by Brodribb and Cochard (2009), once xylem cavitation exceeds certain thresholds, recovery becomes progressively limited even when water availability is restored. The model supports our result from moderate drought treatment and suggest that the trees had partial xylem embolism which prevented the Ψ_{pdl} from fully recovering even when the soil was fully hydrated. Likewise Zhou et al. (2013) marked $F_v/F_m < 4$ as the transition from reversible photoprotection to irreversible PSII inactivation (likely due to oxidative stress and photoinhibition) under prolonged water limitation (Genty et al., 1989). These results support the concept of physiological "legacy effects" described by Anderegg et al. (2016), where extreme drought events can cause lasting impairment to plant function that persists long after the stress has been removed.

The threshold response observed in recovery capacity despite the continuous nature of initial physiological declines highlights the complexity of plant drought responses and emphasizes the importance of considering both decline and recovery dynamics when assessing drought impacts on urban trees. The correlation analysis further supports differential recovery patterns, with Ψ_{pdl} demonstrating stronger correlations with A and g_s during drought than during recovery phases. This hysteresis effect, where the pathway of decline differs from the pathway of recovery, indicates that recovery is not simply the reverse of drought-induced damage but involves distinct physiological mechanisms.

The coordinated physiological responses across multiple processes and drought intensities suggest that there is an integrated whole-plant response to water limitation rather than independent responses (Bartlett et al., 2016). However, our study focused exclusively on leaf-level measurements and therefore cannot say how these coordinated leaf responses might align with concurrent changes in stem hydraulics and root function during drought progression. Additionally, the limited recovery period provided in our experimental design, particularly following extreme drought treatments, may not have allowed sufficient time for potential long-term recovery processes to manifest. What appears as irreversible damage in our timeframe might show partial recovery over extended periods, as demonstrated by Zeppel et al. (2019) who found significant physiological recovery in some species months after severe drought when conventional short-term recovery metrics suggested permanent impairment. Furthermore, the leaves might die but new buds and leaves can be produced post-drought provided the time as long as the stem/branch meristematic tissues (cell dividing tissue) survive. Future research incorporating simultaneous measurements across all plant organs (leaves, stems, and roots), coupled with extended recovery monitoring periods, would provide a more comprehensive understanding of whole-plant integration during drought stress and the true recovery potential following severe water limitation events.

4.3 Local adaptation of native species under moderate drought and higher sensitivity under extreme drought

Both native and exotic species in our study exhibited parallel physiological down regulation to drought conditions (Figure 4), suggesting similar underlying drought sensitivity mechanisms, despite their differing evolutionary origins. This result is consistent with numerous earlier studies showing that, when non-native and native plant species of various growth forms are subjected to simulated drought stress, they decrease their physiological functions, including photosynthetic carbon assimilation and stomatal conductance (Garcia-Serrano et al. 2009; Molina-Montenegro et al. 2011; Ding et al. 2021). However, our result from key physiological variables (F_v/F_m, A and g_s) indicates that native species demonstrate significantly better performance under moderate drought conditions likely reflecting local adaptation to the prevailing climate conditions of the study region. This higher performance of native species aligns with findings by Pimienta-Barrios et al. (2012), who observed greater drought tolerance in native urban trees compared to exotics. However, in our study exotic species showed remarkable recovery capacity, matching the physiological performance levels of native species within four weeks after irrigation, this contrasts the findings by Pimienta-Barrios et al. (2012) who found better post-rainfall recovery in natives than exotics and mentioned no such recovery potentials in exotics.

Contrary to responses to moderate drought, exotic species exhibited a shallower decline in physiological parameters compared to natives under extreme drought conditions. This suggests that our exotic species originating from warmer and drier climates than the native species, have adaptive mechanisms that better buffer against severe water limitation stress. This performance reversal under extreme conditions may reflect the evolutionary history of these exotic species in warmer/drier climates, where selection pressures may have favored traits conferring resilience to severe water limitation, such as xylem anatomy resistant to embolism formation (Lens et al., 2016). Taken together, our results challenge the conventional assumption that exotic species from warmer or drier climates inherently possess superior drought tolerance compared to native species (Ashbacher & Cleland, 2015). In our study, native species were less sensitive to moderate drought while the opposite was true under extreme drought. Therefore, under the projected intensification of drought events in a warming climate, certain exotic species with adaptations to extreme water limitation may be favored, and integrating exotic species in planning of urban landscapes will be important in context of future climate change.

4.4 Differential drought sensitivity and recovery capacities among urban tree species

Our results (Table 2) reveal species-specific responses to drought stress and recovery, with considerable variation in drought sensitivity rankings depending on drought phase. Among the 15 studied species, *O.carpinifolia* (European hop-hornbeam) emerged as the best performer/least sensitive across both drought and recovery periods, maintaining superior physiological function even under peak water limitation. The native range of *O. carpinifolia* includes Middle Europe, Southern Europe and the Balkan area, Western Asia and Caucasian countries. In the northernmost part of its range it behaves as a light-demanding pioneer which prefers sunny and warm places (Pasta et al., 2016). Its moderate to good drought-resistance and tolerance to poorly developed and dry soils (Piškur et al., 2011), makes it suitable for use in urbanised environments where pavement and limited water availability are common. Studies have found that *O.carpinifolia* maintains physiological integrity under extended water limitation (Petruzzellis et al., 2020) and Aichner, N. (2017). One study found that during drought *O. carpinifolia* showed tight stomatal regualtion (isohydric behavior), preserving hydraulic safety and thus found no hydraulic damage even under prolonged drought in the species.

Interestingly, our results revealed dynamic shifts in species rankings under peak drought and during recovery. *C. betulus*, the most sensitive during peak drought condition improved its ranking (from rank 15 to rank 10) after getting watered and *Koelreuteria paniculata* transformed from moderately sensitive during drought to becoming the second best performer/least sensitive during recovery. This improvement during recovery suggests specialized repair mechanisms that enable rapid restoration of hydraulic conductivity and photosynthetic capacity following water stress alleviation. Such recovery capacity may reflect adaptations like efficient vessel refilling capabilities, rapid formation of new functional xylem, or effective antioxidant systems that minimize lasting damage from drought-induced oxidative stress (Brodribb and Cochard, 2009; Klein et al., 2018). Similarly, such strong drought sensitivity and high recovery can also be the result of an isohydric behaviour, where stomata close much under drought to prevent hydraulic damage which in turn facilitates recovery (Domec & Johnson, 2012).

The responses of *N. sylvatica* and *A. saccharinum*, which remained sensitive throughout both drought and recovery phases, may reflect their evolutionary history in mesic environments with reliable water availability. *N. sylvatica's* natural distribution in moist lowlands and its association with aquatic habitats (*Nyssa* named after Greek water nymph) reflect its adaptation to wet environments. Likewise *A. saccharinum* has been found useful in wet areas with standing water for several weeks at a time. Characteristics potentially contributing to their drought sensitivity include vulnerable xylem anatomy with large vessel diameters, limited capacitance in stem and leaf tissues, and inefficient stomatal regulation during water stress (Hacke et al., 2006). These species-specific patterns highlight the importance of considering both resistance to drought and resilience following drought when evaluating overall drought tolerance. Species like *K. paniculata* demonstrate that drought recovery capacity can be somewhat decoupled from drought resistance, suggesting these traits may be under different selective pressures and controlled by distinct physiological mechanisms. This has important implications for species selection in urban greening under climate change scenarios, where both the ability to survive drought events and recover quickly afterward will be valuable traits.

5. Conclusion

Our comprehensive investigation into plant physiological responses to varied drought intensities across multiple species reveals several important insights with implications for understanding and managing vegetation under changing climate conditions. First, our findings demonstrate that physiological traits and processes decline in parallel under both moderate and extreme drought conditions, supporting a continuous response model rather than discrete breakpoints for individual processes. However, our second result reveal significant hysteresis, where the pathway of decline differs from the pathway of recovery. While moderate drought allowed substantial physiological recovery, extreme drought conditions induced lasting impairment despite rewatering, suggesting that while decline patterns may be predictably coordinated, recovery dynamics involve complex thresholds that determine tree resilience thus, recovery of physiological processes after drought is not a simple reversal of negative drought effects. Thirdly, the conventional assumption that exotic species from warmer or drier climates inherently possess superior drought tolerance compared to native species is only partially supported. Native species demonstrated superior performance under moderate drought conditions, while exotic species were less sensitive to extreme drought. Exotic species matched native species with respect to recovery. This performance reversal suggests that as climate change intensifies drought events, certain exotic species may gain competitive advantage. Therefore, including drought-adapted exotic species alongside natives in urban landscapes will be essential for maintaining resilient green spaces under future climate conditions. Finally, we identified significant species-specific variation in drought sensitivity and recovery capacity. *O. carpinifolia* consistently demonstrated superior drought performance/least sensitive, while *N. sylvatica and A. saccharinum* exhibited persistent drought sensitivity. Species like *K. paniculata* and *C. betulus* on the other hand showed remarkable improvement in sensitivity rankings during recovery despite their drought sensitivity. These patterns indicate that drought resistance and resilience may be somewhat decoupled processes and mechanisms under different selective pressures. Collectively, these findings highlight the complex and dynamic nature of plant drought responses and emphasize the importance of considering the entire drought cycle on species level. As climate change intensifies drought frequency and severity, understanding these coordinated physiological responses, recovery thresholds, and species-specific response will be crucial for selecting urban trees that cope with water stress.

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