Urban Forestry & Urban Greening 91 (2024) 128164

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

journal homepage: www.elsevier.com/locate/ufug

Using stomatal conductance capacity during water stress as a tool for tree species selection for urban stormwater control systems

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ARTICLE INFO

Handling Editor: Dr Cecil Konijnendijk van den Bosch

Keywords:
Plant stress
Plant water relations
Ecosystem services
Tree transpiration
Green infrastructure

ABSTRACT

Improving our understanding of how different tree species function in urban stormwater management systems is important, as tree pits may provide a temporary reservoir for stormwater and as trees have the potential to actively reduce stormwater runoff by transpiration. While urban tree planting pits are increasingly used for short-term water storage during stormwater runoff events, this storage can have negative effects on both tree vitality and water removal capacity, since stress from waterlogging result in stomatal closure. However, sensitivity to water stress varies by species. It is therefore important to determine which tree species can maintain long-term vitality and continued transpiration even under water stress, and thus are suitable for such locations. Here, we studied how nine different tree species, varying in expected tolerance to water stress, were affected by short-term and seasonal waterlogging, in a greenhouse experiment. The seedlings (*Magnolia* x *loebneri*, *Tilia tomentosa*, and *Sorbus torminalis* – low water logging tolerance; *Cercidiphyllum japonicum*, *Rhamnus cathartica*, and *Fraxinus ornus* – medium water logging tolerance; *Quercus palustris*, *Acer saccharinum*, and *Fraxinus pennsylvanica* – high water logging tolerance) were exposed to two days, five days and seasonal waterlogging. The treatments reflected best practice (optimal), suboptimal and total lack of tree pit drainage, using Swedish standards. Stomatal conductance and leaf water potential were determined regularly over a period of 71 days, and morphological adjustments were registered. Four of the species were affected already after two days of waterlogging, with reduced stomatal conductance either during the waterlogging or immediately after, and only the most waterlogging tolerant species were unaffected by the five-day treatment. However, all plants survived waterlogging for almost 30 days before the estimated permanent wilting was reached in some plants. We suggest that tree species selection for stormwater management systems should consider the species' capacity to maintain high stomatal conductance during waterlogging, as there were clear differences between species. The effectiveness of the selected species could have an important impact on the stormwater management capacity of cities, as well as on other aspects of ecosystem service delivery from urban trees.

1. Introduction

Stormwater control measures (SCM) for urban areas have received increased attention in recent years as a solution for problems with both water quantity and quality (Paul and Meyer, 2001, Sadeghi et al., 2018, Walsh et al., 2005). Extensive impervious surfaces and compacted soils prevent infiltration of precipitation, transforming rain into stormwater runoff (Berland et al., 2017). Increasing urbanization and prevailing densification ideals (Haaland and Van Den Bosch, 2015) exaggerate these problems as expanding cities lead to increased surface sealing, disturbing the natural hydrological cycles of formerly open land areas and parks (Emilsson and Ode Sang, 2017, Fritz, 2017). This intensification of urban areas is creating pressure on the traditional grey infrastructure that is often already at its full capacity. The combined effect of continued urbanisation and increased probability of high intensity cloudbursts as expected under current climate change scenarios will most likely increase the risk of pluvial flooding events (IPCC, 2021; Semadeni-Davies et al., 2008).

Trees have an important impact on the urban hydrological cycle through interception (Livesley et al., 2014, Nooraei Beidokhti and Moore, 2021), evapotranspiration (Zolch et al., 2017) and infiltration of stormwater through open soil surfaces surrounding trees (Baker et al., 2021). Lately, several studies have shown that redirecting rainwater into existing tree pits can have a considerable effect on the control of

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https://doi.org/10.1016/j.ufug.2023.128164
Received 21 October 2022; Received in revised form 22 November 2023; Accepted 27 November 2023

stormwater runoff (Frosi et al., 2019, Grey et al., 2018b). Furthermore, increasing attention is given to tree pits that are specifically constructed as integral parts of stormwater control management, aimed at providing short-term water storage during rain events (Bartens et al., 2009; Caplan et al., 2019; Scharenbroch et al., 2016). While such systems may be positive also for the trees (Grey et al., 2018a), which are often exposed to drought in the urban areas, there is a risk that trees planted in such systems will be negatively affected by the anaerobic conditions occurring during waterlogging (Thom et al., 2022a).

Trees respond to short-term waterlogging during the vegetative period by stomata closure, leading to altered gas exchange with lowered rates of transpiration and photosynthesis (Kozlowski, 1991, Kreuzwieser and Rennenberg, 2014). A capacity to maintain transpiration rates during waterlogging, as well as a potential for quick recovery after waterlogging, is therefore fundamental for the restoring capacity in the SCM as well as for urban temperature regulation (Bartens et al., 2009, Berland et al., 2017, Rahman et al., 2020). Furthermore, reduced oxygen availability in the root zone disturbs plant metabolism, hindering respiration, which in combination with reduced photosynthetic rates, eventually will lead to reduced shoot and root growth, visible damage on leaves and stem, and increased susceptibility to pathogens, crown dieback or death (Kozlowski and Pallardy, 2002, Leksungnoen et al., 2017). Thus, on a short-term perspective, waterlogging affect trees' transpiration capacity and thereby their capacity for active removal of detained water. Additionally it can also have a negative impact on the long-term vitality and stability of trees, severely affecting their potential to deliver a wide variety of ecosystem service over a substantial amount of time.

However, the responses to waterlogging are highly species-dependent (Glenz et al., 2006). Earlier studies have demonstrated this, though not specifically addressing the conditions in urban tree pits and related short-term recovery after waterlogging. As long-term tree survival and vitality are necessities for sustainable tree plantings, using species that can tolerate short-term water storage is also important when including planting pits in the stormwater control management.

Research on plant selection for urban areas has mainly been directed towards drought resistance, since drought is considered the main constraint for urban tree growth and vitality. Screenings of drought tolerance have been performed, to help select tree species for dry urban sites (e.g., Hirons et al., 2021, Sjöman et al., 2018). However, corresponding compilations of the waterlogging tolerance and post-flooding recovery for tree species suitable for urban plantings are less studied, especially in a northern hemisphere context. This is a critical knowledge gap, since waterlogging tolerance can be fundamental for survival and long-term vitality of urban trees, particularly in SCMs. Consequently, we need to grow the knowledge base regarding suitable tree species for urban sites, by including waterlogging tolerance as a selection criterion. This approach should help ensure that the chosen tree species are capable of enduring the expected temporal flooding exposure, and can continue to deliver ecosystem services both during a flooding event and in the immediate aftermath.

The aim of this study was to investigate how tree species from a variety of natural habitats respond in stomatal regulation to short-term waterlogging similar to those in SCMs. The knowledge gained will improve our understanding of which species are suitable for planting in SCMs and thus can continue to deliver ecosystem services even when faced with heavy rains and flooding events.

2. Materials & methods

2.1. Species selection

We used a systematic approach to identify relevant species that covered a wide spectrum of tolerance against waterlogging and drought to include in the experiment, selecting nine species, representing nine different categories of water and drought tolerance. Niinemets and Valladares (2006) dataset using a scale of 0–5, is one of the largest dataset of woody species in the Northern hemisphere that simultaneously scales drought and waterlogging tolerance (Puglielli et al., 2021). We used this dataset to select non-shrubby angiosperm species covering a wide spectrum of drought and waterlogging tolerance using the following filtering and selection process.

2.1.1. Taxonomically unresolved species

A few species that were seen as taxonomically redundant or unresolved based on the Plant list database (www.theplantlist.org) were excluded. Palmtree species *Sabal palmetto,* non-woody species (*Sambucus ebulus*, *Veronica fruticans*) and vine/climber (*Clematis alpina*) were also excluded.

2.1.2. Height and growth form

Using national digital floras (www.eFloras.org), USDA PLANTS database (www.plants.usda.gov/home), additional local floras and, when needed, dendrological databases, the average height in the wild was estimated for all species in the Niinemets and Valladares (2006) dataset. Height together with the description of growth form in the floras were used to classify species into either shrubs or trees, including shrub-trees and small trees in the latter. Species with less than five meters as expected final-height were categorised as shrubs. Shrub-trees and small trees are generally above eight meters tall and have the capacity to grow with one or few stems, whereas most shrubs are below eight meters and have multiple stems (adapted from Du Rietz (1931) and Gotmark et al., (2016)). All shrub- and conifer-species were filtered out and the deciduous trees, including shrub-trees, were kept for further selection.

2.1.3. Winter hardiness

To attain specific hardiness zones for Swedish conditions (the context of the experimental site) we used two main Swedish dendrological textbooks (Lorentzon 1996; Sjöman and Slagstedt, 2015) and the database Movium Plantarum (www.plantarum.slu.se). Additional to these records, Swedish and Finnish arboreta representing one Swedish hardiness zone each were used to attain possible hardiness information for species missing from the literature above. The arboreta were Alnarp (zone 1), Göteborg (zone 2), Uppsala (zone 3), Mustila (zone 4), Umeå (zone 5) and Enaforsholm (zones 6–7). Swedish hardiness zones are opposite to the USDA system; i.e., zone 1 is warmest and zone 8 the coldest. Additional to this, Artportalen (www.artportalen.se), a web-based species reporting-system, was used to explore field observations in Sweden. If information was still lacking, nursery and gardener websites were searched for experience and zone recommendations. Based on this, species seen as non-hardy for the experimental site, situated in Swedish zone 1, were filtered out.

2.1.4. Classification

By scatter-plotting the remaining species it was evident that almost all species were within the range of 1.5–4.5 in drought tolerance and 1–4 in waterlogging tolerance, based on the categorisation of Niinemets and Valladares (2006). We developed a classification for drought tolerance where 1.5–2.5 was Low, 2.5–3.5 was Mid and 3.5–4.5 was High drought tolerance. For waterlogging tolerance, 1–2 was classified as Low, 2–3 as Mid and 3–4 as High waterlogging tolerance. One species within each matrix of 9 categories was selected (Fig. 1). As a security measure, all selected species were checked for invasiveness in a Swedish context using the NOBANIS database (www.nobanis.org) and Tyler et al., (2015). Due to extremely few species occupying the High-High group, a borderline case concerning waterlogging tolerance - *Fraxinus pennsylvanica* - was selected in this category (Table 1).

2.2. Experimental setup

The experiment was set up at the facilities at the university campus at

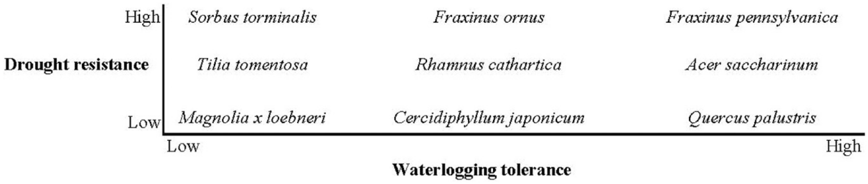

Fig. 1. The included species and their categorisation position in the matrix produced within this project, based on the data from Niinemets and Valladares (2006).

Table 1
Species included in the study with a description of their natural origin. The description of the species' natural occurrence is based on Leuschner & Ellenberg (2017); Nelson et al. (2014); Kurylo et al. (2007); Smith (1966).

Species	Description
Acer saccharinum	Grows naturally in low areas, bottomlands, and flood plains in eastern US
Cercidiphyllum japonicum	Found in resource-rich habitats where a good supply of ground water is available
Fraxinus ornus	Grows naturally on sunny dry slopes in eastern Europe
Fraxinus pennsylvanica	Native distribution in bottomlands, floodplains, riverbanks – tolerant of moving water in eastern US
Magnolia x loebneri	Hybrid between the Japanese species *M. kobus* and *M. stellata* where the latter is found naturally in wetlands. *M. kobus* is found in resource-rich deciduous forest systems.
Quercus palustris	In eastern US the species has a dominant existence in lowlands woods, river bottomlands, and swamp margins.
Rhamnus cathartica	Native in Europe and Central Asia and within this broad distribution the species are found as understorey in forests, in forest edges, and in disturbed environments in the landscape.
Sorbus torminalis	Has a wide distribution in Europe and north-western Africa, exists in mixed oak forests with varying exposure to drought.
Tilia tomentosa	Grows in eastern Europe in warm steppe forest environments

Alnarp, SLU, southern Sweden (55.66065 N, 13.08390 E) in the early spring of 2019, before the start of the vegetation season. In total, 120 bare-rooted plants of each of the species *Acer saccharinum*, *Cercidiphyllum japonicum*, *Fraxinus ornus*, *Fraxinus pensylvanica*, *Magnolia* x *loebneri*, *Quercus palustris*, *Rhamnus cathartica*, *Sorbus torminalis*, and *Tilia tomentosa* were delivered to the greenhouse in which the experiment was conducted.

The plants were 60–100 cm tall at delivery or standardised by pruning (*A. saccharinum*) of both above and belowground biomass in order to minimize the plant growth differences between species (Poorter et al., 2012). All plants were immediately planted in 10 l pots in a rain-garden substrate, consisting of pumice, sand and compost, and were kept well irrigated until the start of the experiment.

In June 2019, we selected and randomly categorised the 96 most vital plants of each species into eight different treatment groups. We used four of the groups for a parallel experiment on drought tolerance. The four remaining groups were placed in treatment-specific rows, with 6 rows per treatment. Each row consisted of two blocks, with one species per block. The species were randomly distributed within the blocks. There were 12 replicates in total per treatment. However, for time reasons, only 10 of the replicates were included in the water status determinations. All twelve were part of the evaluation of morphological adjustments at the end of the experiment.

2.2.1. *Experimental treatments*

The plants were subjected to either two days (W2) five days (W5), or seasonal (SW) waterlogging treatments as a way to test the impact of current best management practice of rain garden on plant performance (Salazar et al. 2023; USEPA, 2021). The (W2) would in this case represent an optimal rain garden design, and the treatment was based on the estimated time of flooding an urban tree will be exposed to during a heavy rain if planted in best practice management pits in Sweden, designed as integral elements of SCM. (W5) would represent a reduced infiltration or suboptimal conditions with extended retention and the treatment was based on the estimated time of waterlogging for a tree placed in a traditional system/in an inadequate storm water management system. (SW) represents a total lack of drainage of an SCM, and was included to analyse how long each species may endure waterlogging until reaching permanent wilting. After the time dedicated for each treatment (71 days for SW), the waterlogged plants were removed from their underwater state and left to drain until field capacity was reached in the pots. We then kept all plants on a well-watered schedule during the rest of the growing season.

The experimental treatments started on June 24th 2019, when cessation of the first flush of shoot growth had occurred and the plants showed high shares of fully matured leaves. The pots with the plants were placed in 50 l plastic containers, which were then filled with water until all the soil in the pots was covered. Two pots were included in each plastic container. Water was refilled when needed during the experiment period to maintain the water level at the rim of the soil in the pots. The last determinations of the water status of the SW plants was performed on September 3rd 2019.

2.2.2. *Experimental conditions*

The experiment was set up in a 100 m^2 chamber in an unheated greenhouse with natural light. A thin shading curtain was used to cover the ceiling throughout the experiment to avoid leaf damage from intense radiation. Temperature (T), in °C, and relative humidity (RH), as a % were monitored at each measuring point of stomatal conductance. Mean daily temperatures varied between 26 °C and 40 °C on the measuring occasions. Mean daily RH varied between 35 % and 54 % humidity (Fig. 2). Daily Vapour Pressure Deficit (VPD) was calculated as:

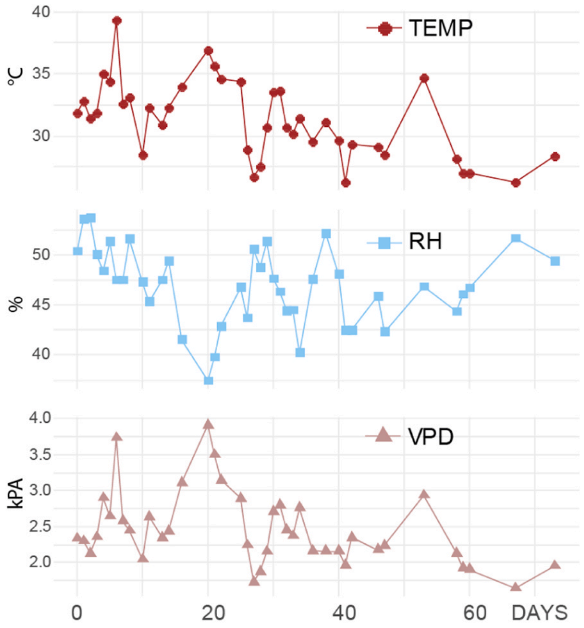

Fig. 2. Conditions in the greenhouse throughout the experiment, represented by temperature (TEMP) in Celsius (°C), relative humidity (RH) in percentage (%) and vapour pressure deficit (VPD) in kiloPascal (kPa).

$$0\cdot 6108*\exp(17\cdot 27*T/(T+237\cdot 3)) = es$$

$$VPD = es*(100-RH)/100$$

Where es is saturation vapour pressure. Calculated daily mean T and RH were used in the equations.

2.2.3. *Measurements*

Midday measurements of plant water status were performed on 18 occasions throughout the experiment to capture stress and recovery in the different treatments. W2 and W5 treatments were measured daily during the period of treatment, then the two first days of post-treatment recovery, and thereafter on a weekly schedule. SW was initially measured daily, then on a four-day schedule, and then after two weeks, weekly for the remainder of the experiment. Measurements started at 10:30 am and continued until 4:00 pm. Although this is a longer period than is standard in midday measurements, the time interval was necessary to be able to include all plants during one day, and could be motivated by the long Nordic summer days. As the sun rose at 4:24 am on the starting day of the experiment, the plants had many hours to be activated before measurements started. To further reduce the risk of confounding results due to diurnal variations, the plants were measured in the same order on each measuring occasion, with the first two blocks from each treatment in a first round, then continuing in the same pattern throughout the measurement, to ensure that all treatments were measured within a limited amount of time.

2.2.4. *Water status*

Determinations of leaf water potential (Ψ_l) and stomatal conductance (g_s) were performed to investigate plant response to the altered water conditions. Ψ_l is the most widely used parameter in estimations of water status (Gimenez et al., 2005) and g_s is related to this parameter by a feedback processes, as reductions of g_s prevent lowered Ψ_l. The g_s can be used as an estimation of transpiration rate, as reduction in conductance reduces transpiration, as well as an estimation of photosynthetic capacity (Farquhar and Wong, 1984, Miner et al., 2017). The g_s was measured by determination of vapour flux from stomata with a portable porometer (SC-1Leaf Porometer, Decagon Devices, Meter group) on one fully developed, sun-exposed leaf per plant.

Ψ_l was determined in a pressure chamber, and the flow of nitrogen gas into the chamber was set at a steady state throughout the experiment (Pressure Bomb, PMS Instruments, OR, USA). One fully developed, sun-exposed leaf per plant was cut and then instantly installed in the pressure bomb for onsite determination.

Permanent wilting was estimated and registered when the leaves showed clear signs of wilting and neither Ψ_l nor g_s could be determined with the equipment used. On such dates, the plants were considered dead.

2.2.5. *Morphological adjustments*

The occurrence of lenticels and adventitious roots, as well as regular roots that had grown up to the surface of the substrate, were registered in the SW-treatment after the water status determinations had ceased. In some species, the regular roots had developed aboveground parts, which were also registered.

2.3. *Statistical analyses*

Statistical modelling was performed in R (R Core Team, 2019) with the gglot2 package for graphical plotting. Significance level for statistical tests was $\alpha = 0.05$. The measurement-protocol for Ψ_l and g_s was designed with uneven measurement intervals to enable the study of both short-term effects (including recovery) as well long-term effects of waterlogging. The statistical modelling of the data was adapted to this by splitting the data set into two main segments to ensure correct variance estimation. The first segment was from 0 to 14 days with short measuring intervals and the second from 14 to 71 days with weekly intervals. For the latter only the SW and Control were included. The two segments were modelled using linear mixed models within the lmer function. Response variables were, respectively, the log of g_s and the square root of Ψ_l. Fixed factors were Treatment, Species and Day, including one and two-way interactions. Random factors to account for the blocking and repeated measurement structure were Treatment nested in Block, and Species nested in Individual Plant. Model assumptions were verified by plotting of the model residuals (Zuur et al., 2009). Testing of the model and its explanatory variables was done using type II ANOVA through package lmerTest. Back-transformed estimated marginal means from the models for post hoc testing and plotting were produced using function emmeans. Post-hoc testing focused on treatment differences towards the control for the different species over time, using approximate Dunnett correction for multiple testing. To aid the interpretation of change over time for each species, the relative change in response variables for each waterlogging treatment compared to the control for each block were calculated and plotted as a time series. To increase the precision we used the mean per block, where treatments W2, W5, and SW were used together for days 0–2, W5 together with SW for days 3–5, and finally only SW for the rest of the days. The relative g_s values were modelled as response in the same mixed model framework as above for Days 0–14, but without the Treatment factor since that was used to calculate the response.

Survival curves for the probability of survival for the different species were calculated using the Aalen-Johansen estimator with Fleming-Harrington correction for tied events (Fleming and Harrington, 1984). Testing for differences between the survival curves was performed using the G-rho family of tests (Harrington and Fleming, 1982).

Differences in morphological adjustment between species in the SW treatment were tested using an overall permutation test stratified by block using the coin package. Response variables, each tested separately, consisted of the number of hypertrophic lenticel, adventitious roots, re-surfacing roots and the combination of the latter, i.e., reflecting overall visible root adjustment. To explore species-specific behaviour, their ratio of each of the morphological adjustments was tested using exact binomial tests towards the ratio for that adjustment of all other species in the experiment. Holm correction was used to handle the multiple testing (Holm, 1979).

3. Results

There were clear interspecific differences in both stomatal conductance (g_s) and leaf water potential (Ψ_l) between the species included in the experiment when studying the control plants (Fig. 3). The seasonal g_s -mean for the control plants ranged from 117 mmol m^{-2} s^{-1} (*M. x loebneri*) to 324 m^{-2} s^{-1} (*F. ornus*). For Ψ_l, the seasonal mean values ranged from −0.68 MPa (*M. x loebneri*) to −2.15 MPa (*S. torminalis*).

3.1. *W2 - 2 days of waterlogging*

A waterlogging effect was observed in g_s after two days, shown as a significant reduction in g_s, when all the species were included in the analysis ($p < 0.0001$). This reduction could still be found two days after the treatment ended ($p < 0.0001$).

Species-specific analyses showed that *C. japonicum* and *T. tomentosa* both had a reduced g_s after two days ($p = 0.0204$ and $p = 0.0272$, respectively). This corresponds to a polled average of 71 % (CL 49–100 %) and 67 % (CL 47–95 %), respectively, compared to the control. This treatment effect persisted during the two first post-treatment days, when the plants had been lifted from the waterlogging and were left to drain (Fig. 4). Furthermore, *R. cathartica* and *F. ornus* showed no reaction to the treatment during the two treatment days, but had significantly lower g_s during the two first post-treatment days.

There were no consistent differences in Ψ_l between the treated plants and the controls during the first 2 days of waterlogging. However, some

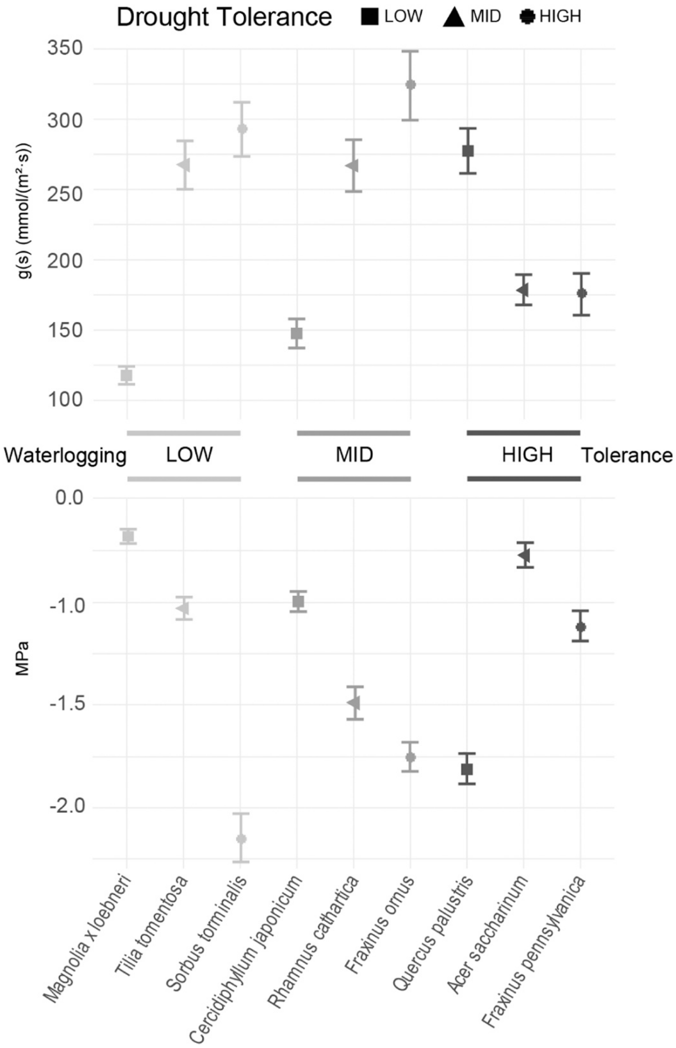

Fig. 3. Seasonal mean stomatal conductance (mmol/(m^2s)) and leaf water potential (MPa) for the nine species included in the greenhouse experiment, focusing on waterlogging tolerance. Values are based on 19 measuring occasions from June to September in the control group (bars indicate SE). Low, mid and high categories are based on the Niinemets and Valladares (2006) data.

species had significantly reduced Ψ_l during the first treatment day (*A. saccharinum*, *C. japonicum, F. ornus*, and *M x loebneri*). This reduced Ψ_l did not persist and no species had a reduced Ψ_l during the second day of treatment, or the two first post-treatment days.

3.2. W5 – 5 days of waterlogging

All species except *A. saccharinum*, *F. pennsylvanica* and *Q. palustris* (the three graded as the most waterlogging tolerant species) showed significantly reduced g_s when submerged for 5 days. *F. ornus*, *M. x loebneri* and *S. torminalis* reacted after three days and *R. cathartica* after four days. At day five this corresponds to a polled average against the control in falling order as follows: *S. torminalis* 61 % (43–86 %), *T. tomentosa* 61 % (CL 43–86 %), *R.cathartica* 59 % (CL 41–85 %), *F. ornus* 53 % (37–74 %), *M. x loebneri* 48 % (CL 34–70 %), and *C. japonicum* 41 % (CL 29–58 %). For all species, the effect was still noticeable two days after the treatment ended, and for *C. japonicum* g_s was still reduced nine days after treatment cessation. After nine days, all the other species had regained g_s values similar to the control plants.

None of the species included showed any consistent differences in Ψ_l for the W5-treatment. However, *C. japonicum* showed a tendency to reduced Ψ_l values after a few days of treatment (Fig. 5).

3.3. SW – seasonal waterlogging

Survival probabilities determined as permanent wilting of the leaves differed significantly between species ($p < 0.0001$). *C. japonicum, S. torminalis* and *T. tomentosa* significantly differed in their survival curves compared to the species that did not wilt, but showed a gradient in relation to each other, with *C. japonicum* having the lowest survival probability, followed by *S. torminalis* and *T. tomentosa* (Fig. 6). In these three species, half or more of the plants in the SW-treatment had wilted at the last measuring occasion (see Fig. 8). A majority of the *C. japonicum*-plants were registered as wilted after 28 days. For *S. torminalis*, this occurred after 42 days. Half of the plants of *T. tomentosa* were dead on the day of the last measuring occasion. In the remaining species, almost every plant survived the long waterlogging treatment.

However, only three species remained unaffected in terms of g_s when the long-term waterlogging treatment exceeded five days. *Q. palustris* had a significantly reduced g_s from day eight (Fig. 7) and onwards, with an exception at 28 days, when there was no difference. *A. saccharinum* showed occasional significant differences in g_s between the control plants and the waterlogged plants throughout the 71 days of experiment. However, the percentage deviations from the control values were small (see Fig. 8). *F. pennsylvanica* showed no effect on g_s from long-term waterlogging.

For all treatments, Ψ_l was correlated with the water potential of the control plants. However, the waterlogged plants had consistently lower values of Ψ_l and for *C. japonicum,* and for *M. x loebneri* the values were significantly lower from day 7. For *R. cathartica, S. torminalis* and *T. tomentosa* the values were significantly lower from day 21. *A. saccharinum* had clearly reduced Ψ_l on some occasions. For the three remaining species (*F. ornus, F. pennsylvanica* and *Q. palustris*), occasional significantly lower values were seen. However, these were inconsistent and with small deviations from the control plants (Fig. 8).

3.4. Morphological adjustments

No morphological adjustments were seen in the W2 and W5 treatments. In the SW treatment, where there were visible adjustments, the permutation tests showed overall differences between species for hypertrophic lenticels (maxT = 4.9036, p-value<0.001), adventitious roots (maxT = 3.8605, p-value < 0.001), resurfacing roots (maxT = 4.439, p-value<0.001) and the combination of the latter, i.e., overall visible root adjustment (maxT = 3.3925, p-value = 0.006). Species a priori ranked as most waterlogging tolerant had significantly more morphological adjustments for both hypertrophic lenticels and root adjustments; *A.saccharinium* through resurfacing roots and *F. pennsylvanica* and *Q. palustris* by adventitious roots. *C. japonicum* showed less, or total lack of, adjustments compared to other species. Also *S. torminalis* had a much lower capacity of root adjustments compared to the other species (Fig. 9).

4. Discussion

Understanding the effects of tree species selection is important in the development of sustainable cities. By recognising trees as active parts of the SCM, their planting beds can be used for short-term water storage, water can be recoupled to the hydrological cycle by transpiration from the canopy and evaporation from the surrounding surfaces, and precipitation can be captured by interception (Bartens et al., 2009, Livesley et al., 2014, Thom et al., 2022a). However, it is still unclear which species are most suitable in terms of tolerance to waterlogging, and which have the greatest capacity to deliver ecosystem services in the context of trees as a part of SCM.

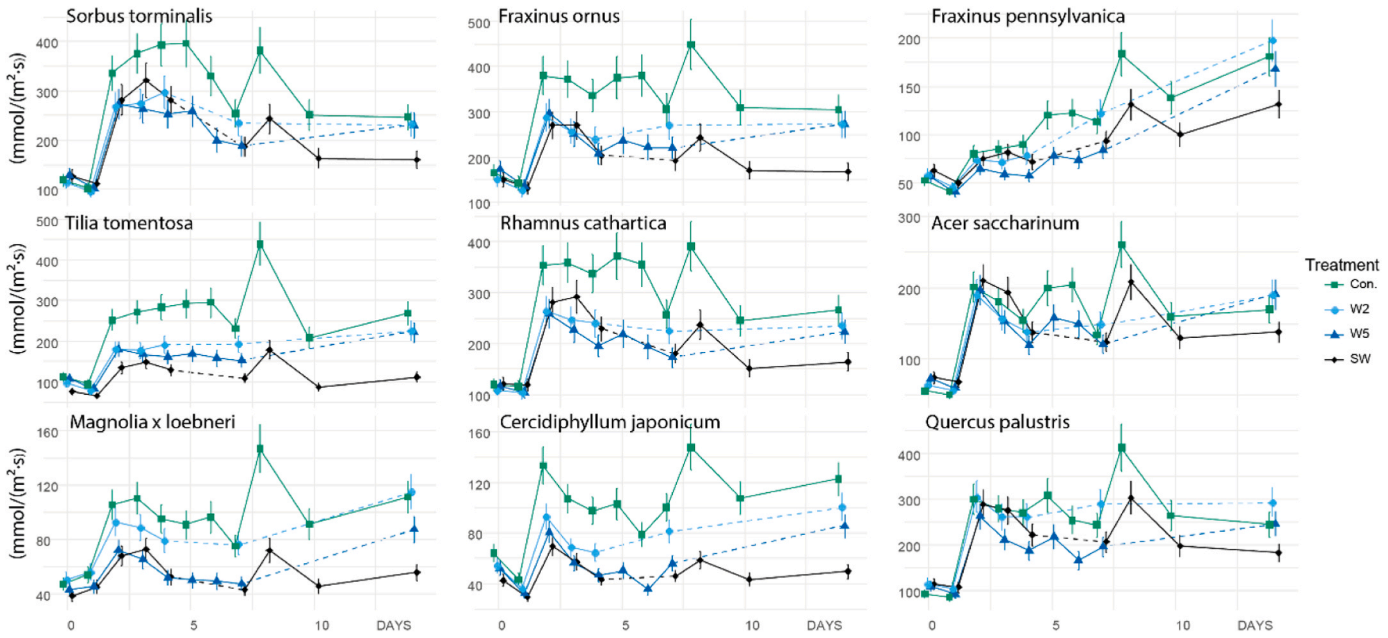

Fig. 4. Mean stomatal conductance (mmol/m^{2}s) for two days (W2), five days (W5) and seasonal waterlogging (SW) treatments, and the control plants (Con.), during the first 14 days of the greenhouse experiment of waterlogging tolerance (bars indicate SE). Each figure panel represents one of the nine species included in the experiment. Dotted lines between two measuring points indicate that there was no measurement done for that particular treatment between the points.

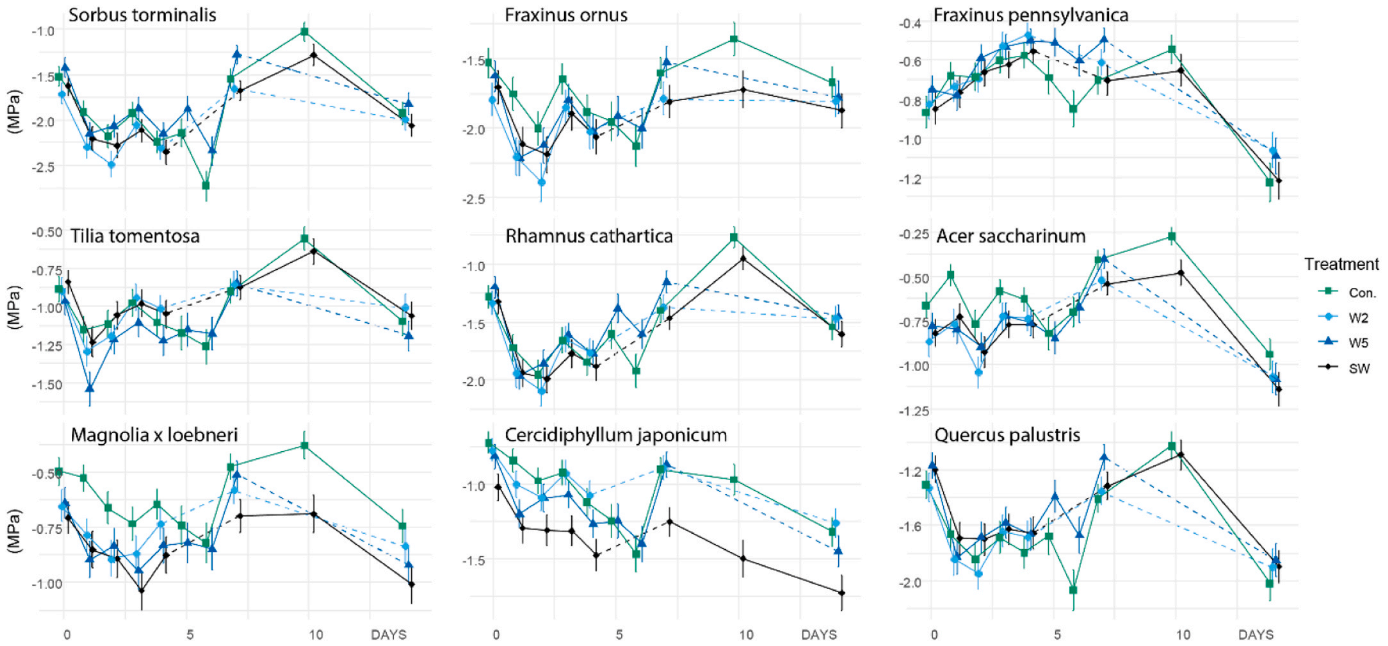

Fig. 5. Mean leaf water potential (MPa) values for the three treatments (W2 = two days waterlogging, W5 = five days waterlogging, and SW=seasonal waterlogging) and the control plants (Con.) during the first 14 days of the greenhouse experiment, studying waterlogging tolerance (bars indicate SE). Each figure panel represents one of the nine species included in the experiment. Dotted lines between two measuring points indicate that there was no measurement done for that particular treatment between the points.

4.1. Tree response to two-day waterlogging

We were able to show that there are interspecific differences in response to waterlogging. For five of the nine species included in the study, the negative effects of a two-day waterlogging were limited, as neither leaf water potential nor stomatal conductance were affected. The other four species that were negatively affected in the W2-treatment were all categorised as low-to-mid tolerant to both drought and waterlogging. However, many of the species that we use today in urban areas in the northern hemisphere fall into these categories (Cowett & Bassuk, 2020; Sjöman and Östberg, 2019; Yan & Yang, 2017). A very rough estimate, using Niinemets and Valladares (2006) dataset, and screening the availability of these species, is that only approximately 10 % of the species available in the European nursery industry belong to high tolerance groups with regards to waterlogging stress. Thus, a large part of the traditional plant material might not be fully appropriate to use as components in SCMs due to their loss of transpiration capacity during and immediately after waterlogging. This is in line with the emphasis on

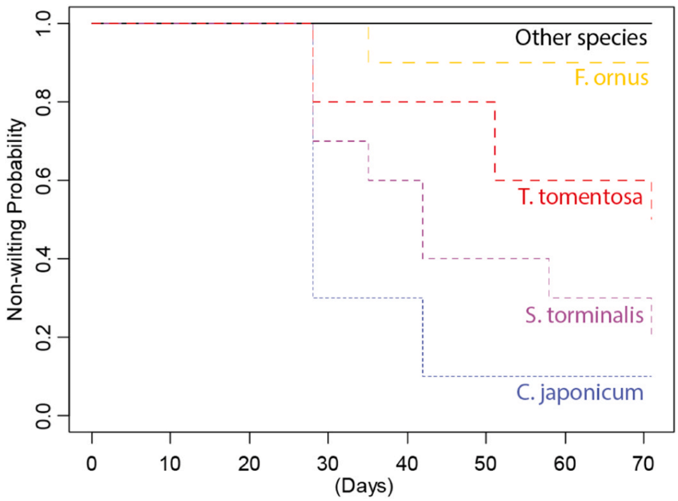

Fig. 6. Survival curves over time for the probability of survival (avoiding permanent wilting) in the SW treatment (seasonal waterlogging) for the different species. Species without any permanent wilting are grouped as Other species. In total, nine species were included in the waterlogging study.

trade-offs in the development of adaptation to different stressors formulated by Niinemets and Valladares (2006) and further developed by Puglielli et al., (2021). In this context, there is a smaller species pool available to use for more extreme urban growing environments where trees are exposed to both water stress and drought stress. Striving to maintain a high species diversity in urban forestry thus also requires thoughtful site-matching of species to avoid over-use of the most tolerant species (Cimburova and Pont, 2021; Morgenroth et al., 2016).

4.2. Tree response to five-day waterlogging

All species except the three most waterlogging tolerant ones, showed reduced stomatal conductance after three or four days, indicating that in systems where stormwater might be detained for longer than two days, there are few species that are able to maintain expected ecosystem services by transpiration. This raises concerns about using already established tree-structures as SCMs since neither plant material nor substrates have been selected for such purposes. The risk is that water will be detained for more than two days and the trees thus cannot effectively reduce the stormwater due to reduced transpiration.

4.3. Tree response to seasonal waterlogging

Surprisingly, few of the species showed signs of permanent wilting in the seasonal waterlogging treatment. Those that wilted permanently, such as *C. japonicum* and *S. torminalis,* were the species unable to maintain leaf water potential throughout the SW-treatment. The same species were very limited in making morphological adjustments, like developing adventitious roots or hypertrophic lenticels.

Stomatal conductance values in the seasonal waterlogging-treatment remained around 50 % of the value of the control plants throughout the 71 days of experiment for the majority of the species. A value of 50 % of maximum g_s, together with the Ψ_l at that value, have been used as proxies for defining species as isohydric or anisohydric (Klein, 2014). About 50 % of relative g_s compared to the control seemed to act as an important level, except for the three most waterlogging-tolerant species. Four of the other six species stabilised around approximately 50 % of maximum, after a more or less rapid decrease. The two dropping below this, *C. japonicum* and *S. torminalis,* were also the two showing clear patterns of permanent wilting in the SW treatment, and no clear adjustments by developing adventitious or resurfacing roots were observed for these two species.

4.4. Species-specific conductance capacity

As has been shown in previous studies (Caplan et al., 2019, Scharenbroch et al., 2016), there were species-specific differences in stomatal conductance for the non-water-limited control plants. Consistent with Caplan et al., (2019), we found no clear patterns as to which categories of species had the higher values. Stomatal conductance ranged from 117 to 324 m^{-2} s^{-1}, with the most water-logging tolerant species showing some of the lowest seasonal mean values. As a consequence, species that had a significantly reduced stomatal conductance due to waterlogging could still have a higher stomatal conductance value than the non-affected ones, which complicates the interpretation of the results. However, tree transpiration capacity is dependent on both vitality and the total leaf area of a tree, meaning that species with a large mature size and a dense crown, that are in good health, will likely have a higher transpiration potential. This implies that species such as *M. loebneri* and *C. japonicum*, which had low stomatal conductance values in the control plants, reduced stomatal conductance even under short periods of waterlogging, and have a limited height growth, are not appropriate for stormwater management systems. Instead, a species like *Q. palustris* could be more appropriate as this species seemed to have a high normal stomatal conductance, did not reduce stomata conductance until day eight and can become quite a large tree, with a dense crown.

Studies have shown that species characteristics affect interception capacity (Gotsch et al., 2018, Nooraei Beidokhti and Moore, 2021) and that transpiration rates vary among species under both normal and post-dry conditions (Scharenbroch et al., 2016, Thom et al., 2022b). Gotsch et al., (2018) argues that species with a time lag in sap flow after a rain event should be avoided in urban areas with high stormwater runoff. Nonetheless, it is also important to find tolerant species with capacity to maintain high stomatal conductance during short-term waterlogging, so that vitality is not compromised and transpiration can be maintained in order to restore capacity in the SCM and contribute to urban cooling.

4.5. Ranking of species tolerance based on natural occurrence

In this study, a coarse classification of species was employed using cut-off levels to create clear categories, which seen from a biological point of view can be limiting as species in natural environments are occurring and reacting to gradients as opposed to clear boundaries. However, our approach ensured that species from a wide range along these gradients of stress tolerance were selected and tested in a systematic manner. Ideally, specific traits or trait combinations that could quantify the tolerance to waterlogging could be used to categorise suitable trees for SCM, instead of only relying on coarse classification of occurrence in nature, as is standard today. Developing a trait-based approach could be a natural continuation of this study, as it would increase our confidence concerning species selection in low to mid ranges of tolerance, particularly since that group contains the bulk of trees available for use by practitioners.

Notable is that within each class of waterlogging tolerance, there was a gradient where the more drought tolerant species maintained their relative g_s better than the less drought tolerant species during the short-term waterlogging. As most SCMs will also face times of drought, these results support selecting species with both waterlogging and drought tolerance to optimize ecosystem service delivery through transpiration. Species drought tolerance is commonly assumed based on natural distributions, but occurrence in nature might not give the full picture of the species-specific stress tolerance, as seen for example in this study for *C. japonicum,* and reported for experimental evaluation of other species (Schrader et al., 2005). Natural occurrence might be a helpful first categorisation of species, but refining our knowledge using measurable plant traits could reveal tolerance capacities not evident from natural distributions, and thereby help better select plants for a given site. Thus, to increase the knowledge base regarding suitable trees to use in SCM,

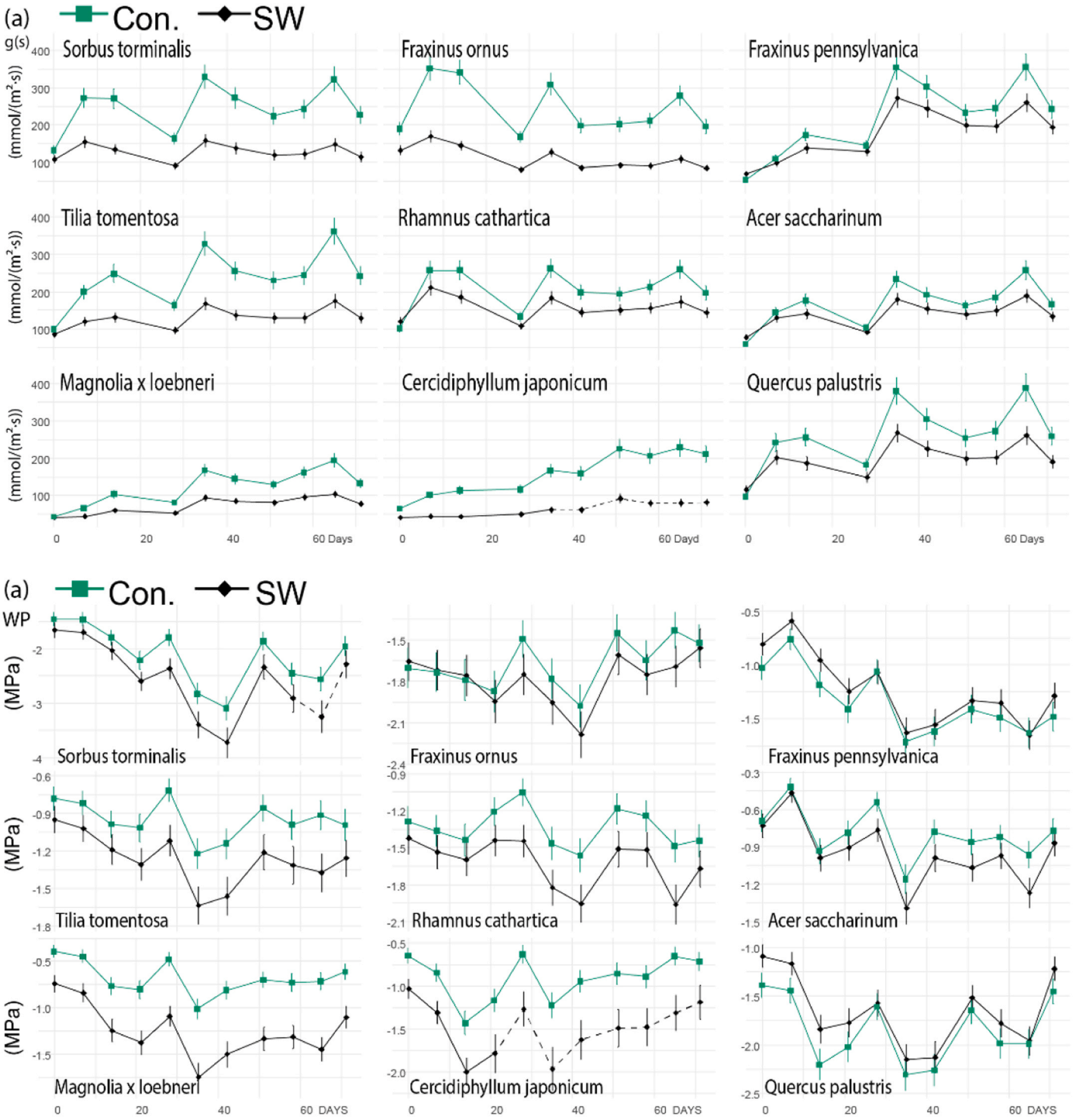

Fig. 7. Mean stomatal conductance (mmol/(m2s)) and mean leaf water potential (MPa) for the seasonal waterlogging (SW) and control treatment (Con.)over the 71 days experiment period for the nine species included in the greenhouse waterlogging experiment (bars indicate SE). Dotted lines represent values estimated with several missing data points for stomatal conductance due to permanent wilting or water potential values too negative to be recorded with the equipment used.

we propose to use species known to cope with single stressors, and to jointly test them for other stressors.

M. x loebneri and *C. japonicum* showed patterns opposite to expected in relation to the ranking values used in this study. Although ranked as a low tolerant species, *M x loebneri* showed a capacity to adapt over time to the waterlogging. This might be explained by its origin, as one of the parents of this hybrid is *Magnolia stellata,* which is naturally found in swampy habitats (Wang et al., 2013). However, most horticultural and dendrological literature consider the *Magnolia* genus sensitive in cultivation (Watkins et al., 2020), which might have affected the original ranking from Niinemets and Valladares (2006). *C. japonicum* is common in riparian forests in Japan (Ohno, 2008) and, based on natural occurrence, it can be seen as a more waterlogging-tolerant species than suggested by in Niinemets and Valladares (2006). However, studies of its recruitment ecology by Sakio et al. (2008) suggest that its abundance in riparian habitat is connected to its dispersal ecology and sprouting capacity, rather than its flooding tolerance.

Another important aspect to consider in generalizing our results is

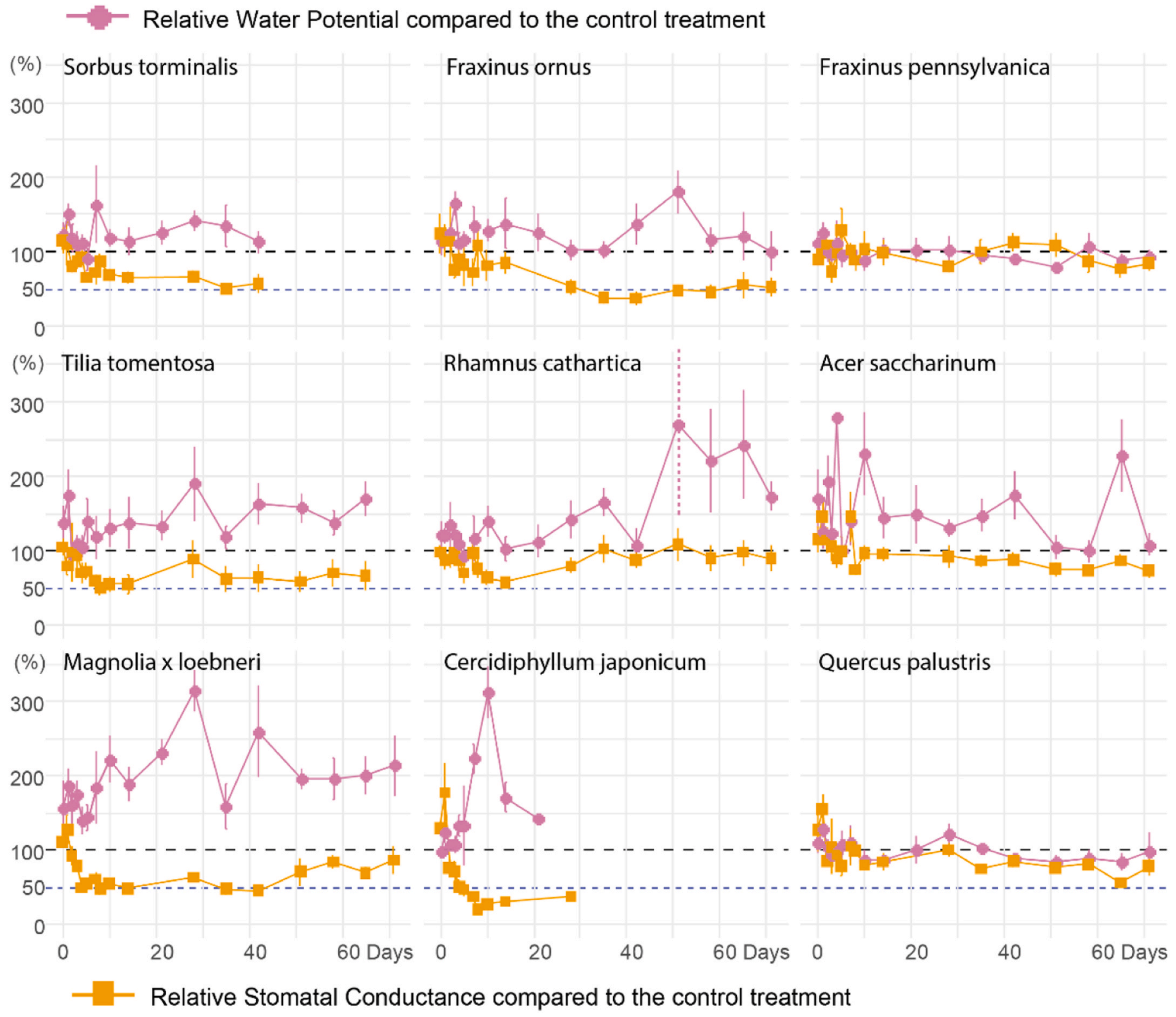

Fig. 8. The relative difference of the SW-treatment (seasonal waterlogging) from the control plants over the whole duration of the experiment, where 100 % is the daily mean value of the control. Leaf water potential values are reversed, so that higher values in the figure represent a more negative result. Cercidiphyllum japonicum and Sorbus torminalis both reached water potential values that were too low to be measured with the equipment used before the experiment was over.

that many of the species included in this study have very large geographical distributions. For example, *S. torminalis* exists from Ireland in the west to northern Iran in the east, with Denmark as its most northern distribution. Thus there might be large intraspecific variations depending on the provenance or ecotype used. The plant material in this study represent the material available today within the nursery industry and information on exact ecotype or provenance is not available, except for *F.s pennsylvanica* that was collected at Ithaca, New York State on an exposed rocky site. Ecotype differences in drought tolerance have been shown across environmental gradients relating to habitat type and precipitation for dominant tree species in mesic habitats, such as *Acer rubrum, Acer saccharum, Betula pendula, Fagus sylvatica, Fraxinus americana* and *Quercus rubra* (Bauerle et al., 2003, Hannus et al., 2021, Kubiske and Abrams, 1992, Marchin et al., 2008; Schuldt et al., 2016). The ecotype differences related to waterlogging have been less investigated, with some exceptions such as Bauerle et al. (2003), evaluating different ecotypes of *A. rubrum*. This needs to be addressed in future studies. Today, there is a limited knowledge of the origin of the plant material currently used in European nursery cultivation (Sjöman and Watkins, 2020). For more precise plant selection based on location and wanted functions, this knowledge gap also needs to be addressed.

4.6. Experimental constrains

Stomatal conductance is dependent on a complex set of environmental and physiological factors, including irradiance, CO_2, vapour pressure deficit (VPD) and leaf turgor (Jarvis and Davies, 1998, Tuzet et al., 2003). All the listed abiotic factors varied between the measurement occasions, which could explain some of the temporal variation in stomatal conductance. Furthermore, stomatal conductance is related to leaf water potential by feedback processes, as stomata close to mitigate loss of water potential, and previous studies have shown that Ψ_l was unaffected by waterlogging for several species while stomatal conductance was reduced (Blake and Reid, 1981).

In this experiment we only induced one stress pulse of flooding, and all species were allowed (and able) to recover back to full functionality

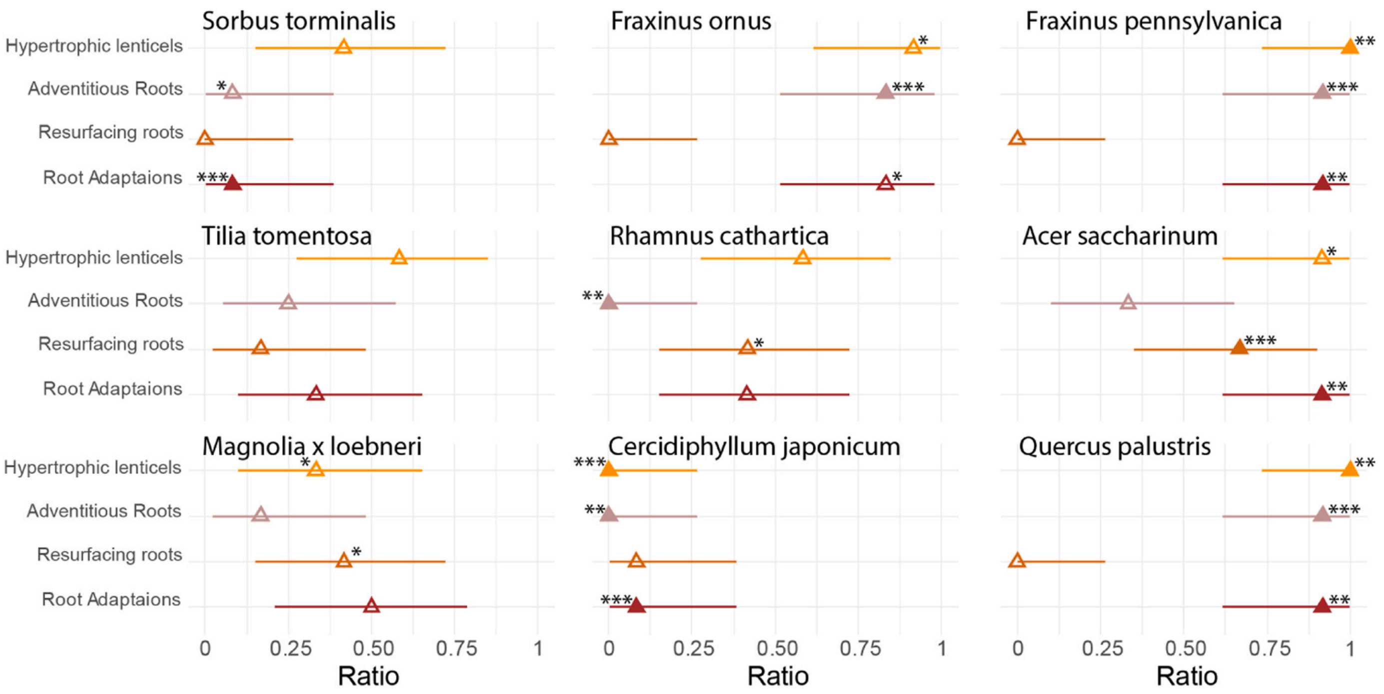

Fig. 9. Mean ratio of individual samples showing morphological adjustment in the SW treatment with 95 % confidence intervals. Significance stars indicate level of significance for unadjusted p-values against the combined mean ratio of all other species. Placement of stars in relation to the point estimate indicates the direction (lower or higher) towards other species, e.g., Sorbus torminalis has a significantly lower ratio of roots adaptions, while in contrast Fraxinus pennsylvanica has a significantly higher ratio compared to the combined ratio of all species together. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Filled triangles show that the test is also significant at $p < 0.05$ using Holm correction for multiple testing.

after the short-term waterlogging. However, trees growing in actual SCM will most likely face repeated stress pulses and this needs to be further evaluated in future studies. Being able to recover rapidly from a stressor could also be of high importance (Thom et al., 2022b). Furthermore, the growth of hypertrophic lenticels and other root adaptations require a lot of energy. High temperatures, as maintained in greenhouse experiments and in future climate changes, might affect the tree's capacity to carry out such adaptations, provided that the temperatures are within the tolerance range of the species. For the long-term survival seen in many of the species in this greenhouse experiment, caution should be used in translating the number of days to an outdoor situation. It is also important to note that the experiment was conducted on young plants and earlier studies have found that adult trees tolerate waterlogging and flooding better than seedlings from the same species (Kreuzwieser & Rennenberg, 2014).

5. Conclusion

Selecting trees based on stomatal conductance during waterlogging shows promise as a measure to identify suitable trees for SCM, since there were clear differences in transpiration capacity between the species when exposed to waterlogging. Few species could tolerate waterlogging for more than three days without a significant drop in stomatal conductance, indicating that it might be advisable to save those species for such situations, to avoid overuse of a few species and to be able to develop high species diversity in the tree population of a city. This also raises concerns regarding using already established tree-structures as SCMs since existing tree species might be suboptimal for this new context with frequent and potentially long-lasting waterlogging. Furthermore, the categorization based on natural occurrence seemed more precise for the highest tolerance groups and less for the low-and-mid tolerance groups. Based on our results, 50 % of maximum g(s) could be an interesting cut-off value to consider in future work when trying to quantify suitable trees for SCM.

CRediT authorship contribution statement

Anna Levinsson: Conceptualization, Methodology, Investigation, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Project administration, Funding acquisition. Tobias Emilsson: Conceptualization, Methodology, Investigation, Writing - Review & Editing, Funding acquisition.Henrik Sjöman: Conceptualization, Methodology, Investigation, Writing - Review & Editing, Funding acquisition.Björn Wiström: Conceptualization, Methodology, Investigation, Formal analysis, Writing - Review & Editing, Visualization, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to sincerely thank our colleagues Anna Lund, Sanna Ignell and Anne-Lii Bellan for help with data collection. This project was funded by FORMAS (Swedish research council for sustainable development), and part of the research project “Tree establishment in a future urban climate” (2016-20098).

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