DEPARTMENT OF BIOLOGICAL AND
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MINIMUM LEAF CONDUCTANCE AND BARK WATER VAPOR CONDUCTANCE IN 14 DECIDUOUS TREE SPECIES

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Abstract

How well trees handle drought varies among species, and it is well-known that trees can use different strategies to survive drought stress. One main strategy is to avoid desiccation by limiting water losses through stomatal closure. Two less studied pathways of water loss in trees is the water that is leaving the leaf through other parts of the leaves than the stomata, leaf minimal conductance (g_{min}), and through the bark, bark water vapor conductance (g_{bark}). Although the amounts of water loss through these processes are small compared to the tree's total water loss when water availability is high, recent studies have shown that they can be more important for tree health than previously known during droughts.

The aim of this study was to investigate: 1) the interspecies variation in g_{min} and g_{bark} among 14 deciduous tree species, including species that are commonly used in Swedish cities today and ones that may be planted in the future, and 2) if g_{min} and g_{bark} are linked and if g_{min} co-varies with stomatal conductance (g_{sw}) and other leaf properties. The g_{min} and g_{bark} were estimated based on measurements of the weight loss of detached leaves and branch pieces collected from well-watered trees using the "bench drying" method. To facilitate comparison between g_{min} and g_{sw}, stomatal conductance was measured for attached leaves during both well-watered and drought conditions.

Significant interspecies differences in g_{min} and g_{bark} were found. Also, species with high LMA were observed to have low g_{min}, while no significant relationship was found between g_{min} and g_{sw} or leaf water content. In addition, g_{min} and g_{bark} were not significantly correlated. However, the observed among-species differences in g_{min} and g_{bark} suggest that these traits may be useful for identifying species that are well suited for growth in situations where water availability is limited.

Keywords: minimum leaf conductance, bark water vapor conductance, tree, urban trees, drought, climate mitigation

Sammanfattning

Träds förmåga att hantera torka varierar mellan arter, och det är väl etablerat att träd kan använda olika strategier för att överleva torkstress. En central strategi är att undvika uttorkning genom att stänga klyvöppningarna för att begränsa vattenförlust. Två mindre studerade vägar för vattenförlust är det vatten som avges genom andra delar av bladet än stomata, så kallad minimal bladkonduktans (g_{min}), samt genom barken, barkkonduktans (g_{bark}). Trots att vattenförlusten via dessa vägar är liten i förhållande till trädets totala vattenförlust vid god vattentillgång, har nyare studier visat att de kan ha större betydelse för trädens hälsa under torkperioder än vad som tidigare antagits.

Syftet med denna studie var att undersöka: 1) mellanartsvariation i g_{min} och g_{bark} hos 14 lövträdarter, inklusive arter som är vanligt förekommande i svenska städer idag samt arter som potentiellt kan planteras i framtiden, och 2) huruvida g_{min} och g_{bark} är korrelerade, samt om g_{min} samvarierar med stomatakonduktans (g_{sw}) och andra bladegenskaper. g_{min} och g_{bark} uppskattades genom att mäta viktförlusten hos avskurna blad och grenar från välvattnade träd med hjälp den så kallade "bench drying"-metoden. För att möjliggöra jämförelse mellan g_{min} och g_{sw} mättes stomatakonduktans hos fästa blad under både god vattentillgång och torkförhållanden.

Betydande skillnader i g_{min} och g_{bark} mellan arter påvisades. Arter med hög bladmassa per area (LMA) uppvisade lägre g_{min}, medan ingen signifikant korrelation kunde fastställas mellan g_{min} och g_{sw} eller bladets vatteninnehåll. g_{min} och g_{bark} visade sig inte heller vara signifikant korrelerade. De observerade skillnaderna mellan arter i g_{min} och g_{bark} antyder dock att dessa egenskaper kan vara användbara indikatorer vid val av trädarter för miljöer med begränsad vattentillgång.

1. Introduction

The frequency and intensity of droughts is increasing due to climate change (IPCC, 2023). During drought, the water availability in the soil decreases, which leads to lower access to water for tree roots and can cause significant stress. This has led to an increase in drought-related tree mortality worldwide (Allen et al., 2015; Allen et al., 2010). However, different tree species respond differently to drought stress, and the different strategies they respond through can have a significant impact on how drought tolerant the tree is (Brunner et al., 2015; Chen et al., 2022; Thom et al., 2023).

1.1 Background

1.1.1 Drought tolerance in trees

The definition of drought tolerance in trees varies between different studies, but most of them refer to the tree's ability to grow and survive during and after a drought. McGregor et al. (2021) divide the definition of drought tolerance of a tree into three categories: resistance, recovery, and resilience. Resistance is the ability of the tree to preserve growth under drought; recovery is the tree's capacity to increase growth to more than minimum during drought and the resilience is how well the tree can restore the growth rate from before the drought to after the drought. Furthermore, McGregor et al. (2021) state that previous studies have found that survival is connected to resistance, recovery and resilience, and that this could imply that these three characteristics could be affected by the same factors as survival. Moran et al. (2017) defines drought tolerance of a tree as "the ability to survive, and sometimes grow, during periods of water shortage". Furthermore, Moran et al. (2017) say that often the survival is correlated with the growth because trees that have experienced growth lower than average or sudden growth declines often have a higher mortality, according to previous studies.

1.1.2 Strategies for water conservation and reduction of drought stress

Stomata are pores embedded in the cuticle, a hydrophobic wax layer located at the surface of the leaf, which regulates the influx of CO_2 into the leaf and the diffusion of water vapor into the surrounding air in a process called transpiration. The flow in each direction happens simultaneously and is regulated by opening and closing of the stomatal pores (Hillis et al., 2020). Considering the importance of CO_2 in photosynthesis, the regulation of stomatal closure is an important trade-off between gaining enough CO_2 to maintain plant functions as well as preventing hydraulic failure due to critically low water potential (and lack of turgor pressure), and ultimately death. If the input of CO_2 into the leaf gets too low, the storage of carbohydrates gradually gets depleted by a continued metabolism, eventually resulting in starvation of the plant tissues ("carbon starvation") (McDowell et al., 2008; McDowell, 2011).

The extent of stomatal closure depends on specific environmental conditions such as the atmospheric CO_2 concentration, air humidity and light intensity at the surface of the leaf (Duursma et al., 2019), and soil water status (Damour et al., 2010). During a drought, when soil water is limited, the tree needs to prioritize to conserve the remaining water inside the leaf to avoid desiccation and prevent damage on xylem conduits. Therefore, a common early response during drought is that stomata close to prevent water loss to the surrounding air by transpiration (Creek et al., 2019; Duursma et al., 2019), with the cost of gaining less CO_2.

Trees can survive drought conditions by two different physiological strategies: dehydration tolerance and dehydration avoidance (Lewitt, 1972; Liang & Ye, 2024). Dehydration tolerance is the ability of the tree to tolerate loss of water from the tissues, while dehydration avoidance is the ability to keep the moisture in the leaves (Volaire, 2018). Thereby dehydration tolerance determines how low water potential the tree can tolerate before it is lethal, and dehydration avoidance determines how fast the water potential declines (Liang & Ye, 2024). The tree's survival during drought is largely determined by a combination of these two mechanisms (Brodribb et al., 2020).

Dehydration avoidance in trees includes both water conservation and acquisition. Water conservation is largely determined on the leaf level. Overall, water conservation is the result of stomatal control (water loss in transpiration through stomata), minimum leaf conductance g_{min} (the rate of water loss from the leaf when the stomata are closed) and transpiring leaf area, while the water acquisition is determined by water storage and rooting depth (Liang & Ye, 2024). Dehydration tolerance if often described as a group of functional traits: the lethal water potential (Ψ_{lethal}), the water potential at 50% or 88% loss of xylem conductivity (P_{50} or P_{88}), leaf water potential at turgor loss point (Ψ_{tlp}) and wood density (Choat, 2013).

One way to describe plant drought physiological responses and recovery is through the isohydry-anisohydry spectrum, which describes a species' stomatal behavior during drought. Isohydric species are expected to close their stomata to save water and keep leaf water potential (Ψ_L) high and stable, but with loss of photosynthetic activity (carbon assimilation), while anisohydric species keep stomata open to maintain gas exchange and photosynthesis, while risking low leaf water potential and, consequently, hydraulic damage (Kannenberg et al., 2019; Volaire, 2018).

Morphological adaptations, such as leaf shedding and quick resprouting when water becomes available again, as a response to avoid drought stress can sometimes be more important to prevent drought-induced mortality than physiological drought tolerance traits such as more negative Ψ_{tlp}. For example, four Asian savanna tree species from two genera with different Ψ_{tlp} showed the same morphological drought-adaptive strategy of shedding the leaves when the water potential dropped below Ψ_{tlp} and resprouted vigorously after rewatering, resulting in only 2% whole-plant mortality rate for all four species (Nguyen et al., 2019).

Shedding the leaves is a way to delay desiccation but comes with the cost of regrowing the leaves later. So, while it could be an efficient survival strategy during prolonged drought, it may be dependent on a high photosynthetic rate, which likely allows for more extensive carbon storage, which in turn makes it possible for the tree to regrow the leaves once water is available again (Slot & Poorter, 2007).

Also, morphological tree traits such as leaf mass per area (LMA) and leaf water content (LWC) could influence how a tree species behaves and react to environmental stressors like drought. LMA is an important trait for leaf economics. It describes the amount of dry mass that the leaf invest in per photosynthetic area, where species with high LMA have thicker and denser leaves (Wright et al., 2004). Species that are found in areas with high drought stress often have high LMA, but the functional importance of LMA, for example how it relates to water use and drought tolerance is under debate (Sancho-Knapik et al., 2021). For example, Wu et al. (2022) found that low g_{min} together with high LMA was most important traits to decrease water loss during drought in subtropical *D. odorifera* saplings. Additionally, trees have shown to increase LMA as a response to drought stress (Wu et al., 2022). LWC is the proportion of the leaf's water mass in relation to dry mass (Wang et al., 2022). It is often used as a proxy for drought stress in trees, as it reflects the water status of the plant, which is strongly connected to turgidity, cell volume and therefore also xylem function. LWC has also shown to be important for physiological functions like stomatal conductance and photosynthesis (Li et al., 2024).

1.1.3 Influence of leaf minimum and bark vapor conductance on drought tolerance

Two physiological drought tolerance traits that have gained more attention recently are g_{min} and the loss of water through the bark (bark water vapor conductance, g_{bark}).

The minimum leaf conductance, g_{min} is the rate of water loss through other parts of the leaf, such as the cuticular wax layer, from the leaf to the surrounding air when stomata is closed (Duursma et al., 2019; Schuster et al., 2017). In earlier studies of stomatal conductance linked to drought stress and drought tolerance in trees, these pathways have been treated as unimportant due to a lack of precision in the methods for measuring g_{min} (Jarvis, 1976). In recent years, the precision in the methods has been improved, which has made it possible to study g_{min}. These studies have shown that g_{min} is more important for the drought tolerance of the tree than previously thought (Barnard & Bauerle, 2013).

When stomata are closed, g_{min}, together with the tree's total leaf surface area and VPD, affects whole-tree canopy water loss, and this is one of the most important factors for the dehydration rate (along with stored water and dehydration tolerance). The dehydration rate determines how long the tree will survive during a severe drought after the uptake of water through the roots has been restricted (Wang et al., 2024).

Previous studies have shown a large variation in g_{min} among tree species, but much of the interspecies variation in g_{min} remains unexplained (Duursma et al., 2019). Duursma et al. (2019) suggests, based on their extensive review of g_{min}, that the variation probably is explained by multiple interacting factors such as cuticular traits, stomatal traits, environmental acclimation and leaf age, rather than by single traits alone. They also suggest that the lack of standardized methods may be a reason why it is hard to find explanations.

Nevertheless, some studies have found some possible explanations to the variation. Both Burghardt and Riederer (2003) and Schuster et al. (2017) found a positive correlation between and g_{min} and cuticular permeance in several tree species. Liao et al. (2025) studied 39 subtropical woody species and found a strong negative correlation ($R^2 = 0.85$) between g_{min} and cuticle thickness and a weaker positive correlation between g_{min} and proportion of epidermis dedicated to stomata ($R^2 = 0.17$). They also observed that light demanding species had higher g_{min} than shade tolerant species, and that this was linked to their light requirement strategies. Light demanding species had a higher proportion of the epidermis dedicated to stomata, prioritizing photosynthetic capacity (stomatal conductance, photosynthetic rate and shorter leaf life span) over cuticle thickness with the cost of increased water loss and decreased dehydration tolerance.

To investigate explanations for the interspecies variation further, Duursma et al. (2019) suggests that many different tree species that have grown under the same conditions should be studied, to get a better understanding of the adaptive ability of g_{min} and decrease the possible overlapping effects coming from sampling in different habitats and conditions.

Another trait that similarly has gotten some more attention recently is g_{bark}. Despite that g_{bark} rarely is considered a functional trait, the importance for drought tolerance in trees has been shown to be larger than previously thought. Wolfe (2020) studied 14 populations of tropical tree saplings of 8 species in two different environments, one in the understory of a forest and one in a shadehouse that was exposed to extreme drought. In the forest, they found a strong correlation between g_{bark} and stem water deficit for 4 deciduous species, but not for the evergreen species. According to Wolfe, this was probably because the evergreen species still had access to the soil water during the drought, in contrast to the deciduous species. In the shadehouse, all 6 species showed a positive correlation between g_{bark} and stem water deficit as well as mortality. In other words, higher g_{bark} increased the risk of water deficit in the stem and for mortality. Therefore, that study indicated that g_{bark} potentially plays an important role for the drought tolerance of trees.

Even though the flux (pathway) of water loss through the bark is small compared to e.g., the ones through stomata, when water availability is limited, the water loss through the bark becomes more important. Especially because common drought responses involve closing of stomata, shedding of leaves as well as modifications and eventually dieback of fine roots, which decreases other sources of water loss (Wolfe, 2020).

Loram-Lourenço et al. (2022) found a connection between g_{min} and g_{bark} and the growth strategies and drought tolerance, where low g_{min} and g_{bark} were associated with slower growth and more effective prevention of lethal hydraulic failure. They also found that how much g_{min} and g_{bark} affected the water status depended on the degree of resistance to cavitation in the leaves and the stem.

1.1.4 Trees and drought in a city environment

Cities generally have higher mean air temperatures compared to rural areas. This phenomenon is called the 'urban heat island', UHI (Oke, 1987). There are several processes contributing to this phenomenon. One of them is the trapping of heat in buildings. Many materials used in city buildings, such as concrete, have a high heat capacity. This causes a high absorption of energy from solar radiation, which is stored as heat during the day and emitted at night as longwave radiation, which causes heating of the air surrounding the buildings. Also, the wind speed in cities is generally lower, mainly due to the small distances between buildings and their block-like geometry, restricting air flow, meaning that less heat leaves the city area. Additionally, cities contain a lower coverage of vegetation which restricts cooling from evapotranspiration compared to rural locations. On top of that, anthropogenic heat emissions such as waste heat from buildings and road traffic add more heat (Doick & Hutchings, 2013; Oke, 1987; Santamouris, 2015).

In addition to higher air temperatures, the soil water availability in the city is low. Less rainwater reaches the soil surrounding the tree roots due to a lot of impermeable surfaces in cities, such as asphalt, which increases runoff and decreases infiltration of rainwater into the soil. Also, often the soil in cities is compacted due to, for example lots of traffic and heavy buildings, which makes it harder for tree roots to develop and limits water movement through the soil, together decreasing absorption of water to the roots (Czaja et al., 2020). A rise in air temperature without an increase in relative humidity (RH) also increases the vapor pressure deficit (VPD) of the air. The initial reaction by plants to increased VPD, at least to a certain point, is to increase the transpiration rate, which further dries the soil and increase water stress for the tree (Grossiord et al., 2020). Due to a high level of water stress, urban trees will be especially vulnerable to further water constraint in a future climate with more extreme climate events, such as frequent and intense droughts (Esperon-Rodriguez et al., 2022).

Different tree species have different traits, responses and strategies that determine how well they cope with and adjust to environmental changes, such as increased frequency and intensity of droughts. One way to make sure the trees will grow and survive in future climates is therefore to optimize the choice of species based on traits when planting a tree. To help city planners to know which tree species that are most well suited for the urban environment it is therefore important to study the traits of different species and how they impact the tree's tolerance for different environmental challenges (Esperon-Rodriguez et al., 2020; Esperon-Rodriguez et al., 2022; Hirons et al., 2021; Watkins et al., 2021).

1.2 Aim

The aim of this study was to study minimal leaf conductance, g_{min} and the bark water vapor conductance, g_{bark} in 14 tree species, including species that are commonly used in Swedish cities today and ones that potentially may be planted in the future when more stress tolerant species may be needed. The following research questions were investigated:

- How do minimum leaf conductance and bark water vapor conductance vary between 14 species of deciduous tree saplings that have been grown under the same conditions?
- How are minimum leaf conductance and bark water vapor conductance linked, and does minimum leaf conductance co-vary with stomatal conductance and other leaf properties such as leaf mass per area, LMA and leaf water content, LWC?

2. Material and method

2.1 Experimental design

2.1.1 The design of the larger urban tree study

The leaf and branch samples used in this study were collected from young trees (three-year-old saplings) included in a larger field experiment, where the overall aim is to investigate how different tree species respond to drought, to improve species selection for Swedish urban environments. The trees had been growing outside in 7.5-liter pots during the summer of 2024, from mid of June to mid of August, at Essunga plantskola (58.19 N, 12.78 E), a plant nursery about 95 km northeast of the Swedish city of Gothenburg. In total, there were 267 trees of 15 different species in the larger study. The trees were divided into 3 groups, receiving different treatments: control, drought, and extreme drought.

The trees that were sampled for g_{min} and g_{bark} were from the control group, meaning that they were well-watered throughout the experiment (with commercial drip irrigation) and not limited by nutrients. Stomatal conductance, g_{sw} were measured on both the control group and the drought treatment group. In the drought treatment group, the trees were exposed to drought by not getting any water under two weeks before the gas exchange measurements.

2.1.2 Test organisms

The tree selection included both species that are currently common in Swedish cities today as well as species that are potentially suitable for Swedish cities in a future with warmer climate. Six of the species were native to Sweden and nine were exotic species from Southern Europe and Northern America (**Table 1**).

***Table 1**: Overview of the tree species used in the larger urban tree study, including scientific names and abbreviations, natural distribution and native or exotic status. Information provided by Rabina Thapa.*

Scientific name, abbreviation	Natural distribution	Status (Native/Exotic)
Acer platanoides, Apl	Europe and western Asia	Native
Acer saccharinum, Asa	Eastern and central North America	Exotic
Betula pendula, Bpe	Europe and Asia	Native
Carpinus betulus, Cbe	Europe and western Asia	Native
Celtis occidentalis, Coc	Central and Eastern North America	Exotic
Koelreuteria paniculata, Kpa	China and Korea	Exotic
Liquidambar styraciflua, Lst	Eastern North America	Exotic
Liriodendron tulipifera, Ltu	Eastern North America	Exotic
Magnolia kobus, Mko	Japan and Korea	Exotic
Nyssa sylvatica, Nsy	Eastern North America	Exotic
Ostrya carpinifolia, Oca	Southern and central Europe	Exotic
Prunus avium, Pav	Europe, western Asia	Native
Sorbus intermedia, Sin	Southern Scandinavia	Native
Sorbus torminalis, Sto	Europe, northwestern Africa, and western Asia	Exotic
Tilia cordata, Tco	Europe and western Asia	Native

All the 15 species from the larger urban study were included in the experimental part (measurements) of this study. While *Sorbus intermedia* was measured, it was excluded from the analyses due to inconsistent data. All the species in this study were broadleaf deciduous angiosperms.

2.2 Sampling, preparation, and measurements of g_{min} and g_{bark}

2.2.1 Sampling and preparation

All sampling was conducted over a two-week period. Although test trees varied in overall size, efforts were made to select branches and leaves of comparable age and developmental stage, prioritizing the most mature branches available in the experiment. For each species, one branch was selected from each of four individual trees. Selected branches included a sufficiently long leafless segment suitable for g_{bark} measurements and healthy, mature leaves appropriate for g_{min} measurements. Branches were chosen to be similar in size and developmental stage across individuals.

Following selection, each branch was labeled with the corresponding species abbreviation and individual tree ID, and subsequently photographed. Branches were then excised near the main stem and immediately placed into sealed dark plastic bags containing a small volume of water and moist paper towels to maintain humidity and minimize light exposure during transport. The bags were transported to the laboratory for temporary storage.

Upon arrival at the lab, branches were transferred to containers filled with water to ensure continued hydration. To facilitate water uptake and minimize the risk of xylem embolism, each branch was recut under water to prevent air entry into the xylem vessels. The containers were then enclosed in dark plastic bags to maintain darkness and reduce potential light-induced physiological changes. Branches were stored under these conditions overnight and used for g_{min} and g_{bark} measurements the following morning.

2.2.2 Measurement methods and calculations

The measurement protocol and the calculations were based on the bench drying method as described by Sack and Scoffoni (n.d.).

To determine g_{min} and g_{bark} selected leaves were detached from the sample branch and smaller leaf-free branch segment were chosen for further analysis. When the leaves and branch segments were cut, the cut ends were covered with nail polish to avoid water losses through them. The size of the leaves were determined by analyzing images of the samples with the Easy Leaf Area app (Easlon & Bloom, 2014) and the size of the branch segments were determined by measuring the diameter in both ends with a vernier caliper and the length with a ruler.

The samples were placed on a metal net for drying. While the samples were drying, a fan was set to a low speed, blowing in the space around the samples to mix the air. The air temperature (T) and relative humidity (RH) in the lab were kept constant during the measurements.

The weight change in leaves and branches was measured by a high precision scale. The weight was recorded every ~ 30 minutes for about 6-8 hours of weighing in total for each sample (and measurement day). The main goal was to get at least 4-6 measurements during which weight loss was linear to get enough data points to make a good approximation.

A routine is provided in **Appendix D**, for a more detailed step-by-step description of the g_{min} and g_{bark} measurements.

To standardize the selection of data points representing the linear phase of the weight loss curve for the calculation of g_{min} and g_{bark}, a routine based on predefined criteria was employed. Any data points that clearly deviated from the expected trend were excluded. Starting from the second measurement, six consecutive data points were initially used to perform a linear regression. If the resulting coefficient of determination (R^2) was ≥ 0.95, the fit was accepted. If R^2 was below this threshold, the starting point was incrementally shifted forward (beginning from the third data point), and the regression was recalculated. This process was repeated until an acceptable R^2 value was achieved. If no acceptable fit could be obtained using six points, the number of points included was reduced, with a minimum of four data points allowed for analysis.

2.3 Measurements of stomatal conductance, g_{sw}

Stomatal conductance to water vapor, g_{sw} as measured as a part of the larger-scale project on the drought response of tree species and conducted by other researchers (for more information, see **2.1.1**). Briefly, the measurements were made with two LI-6800 portable photosynthesis systems (Li-Cor Biosciences, Lincoln, NE, USA) on attached light-exposed mature outer canopy leaves. During the measurements, the chamber conditions were set to saturating light (1200 micromole m^{-2} s^{-1}) and 415 ppm CO_2. Chamber temperature was matched to the environment and relative humidity was not regulated. After a leaf was inserted in the chamber the measurement was made as soon as technical stability was achieved with a maximum waiting time of two minutes. The results from the g_{sw} measurements were received from Rabina Thapa (personal communication, 2025, January 21).

2.4 Statistical methods

2.4.1 Preparation of data for statistical analysis

Before the statistical analysis, the data was quality controlled to identify measurements errors and outliers using Grubb's test within species. After outliers were removed the data was tested for ANOVA assumptions using Levene's test for homogeneity of variance and Shapiro-Wilk's test for normality. In cases where ANOVA assumptions were violated that data was log-transformed before analysis. Negative means of g_{sw} were replaced by 0 as a correction because they were considered due to faulty measurement, e.g., dead leaves.

The statistical analyses were made using R (version 4.5.0) and handled in RStudio (2025.05.0+496 release) (RCoreTeam, 2025). The following R packages were used: dplyr, car, ggplot2, multcompView, outliers, jtools, readxl, openxlsx, ggpubr, xlsx, scales, ggrepel and extrafont.

A one-way ANOVA was performed for species and g_{bark} and g_{min} respectively using the aov () function. Tukey's HSD test was used for post hoc analysis. Simple linear regression was used to test the linear models with mean values of g_{bark}, $g_{sw\ control}$, $g_{sw\ drought}$, LMA and LWC were used to predict significance for each species against g_{min} using the lm () function in R.

3. Results

3.1 Interspecies variation in minimum leaf conductance and bark water vapor conductance

There was a significant among-species difference in g_{min} ($p < 0.001$) and g_{bark} ($p < 0.001$).

Regarding the interspecies variation in g_{min} and g_{bark} for each species, there were 5 groups that were significantly different from each other in mean value of g_{min} ($p < 0.05$) (**Figure 1a**). *A. platanoides* had the lowest (3.7 ± 0.7 SE mmol m^{-2} s^{-1}) and *C. occidentalis* the highest mean value of all species (16.7 ± 0.6 SE mmol m^{-2} s^{-1}).

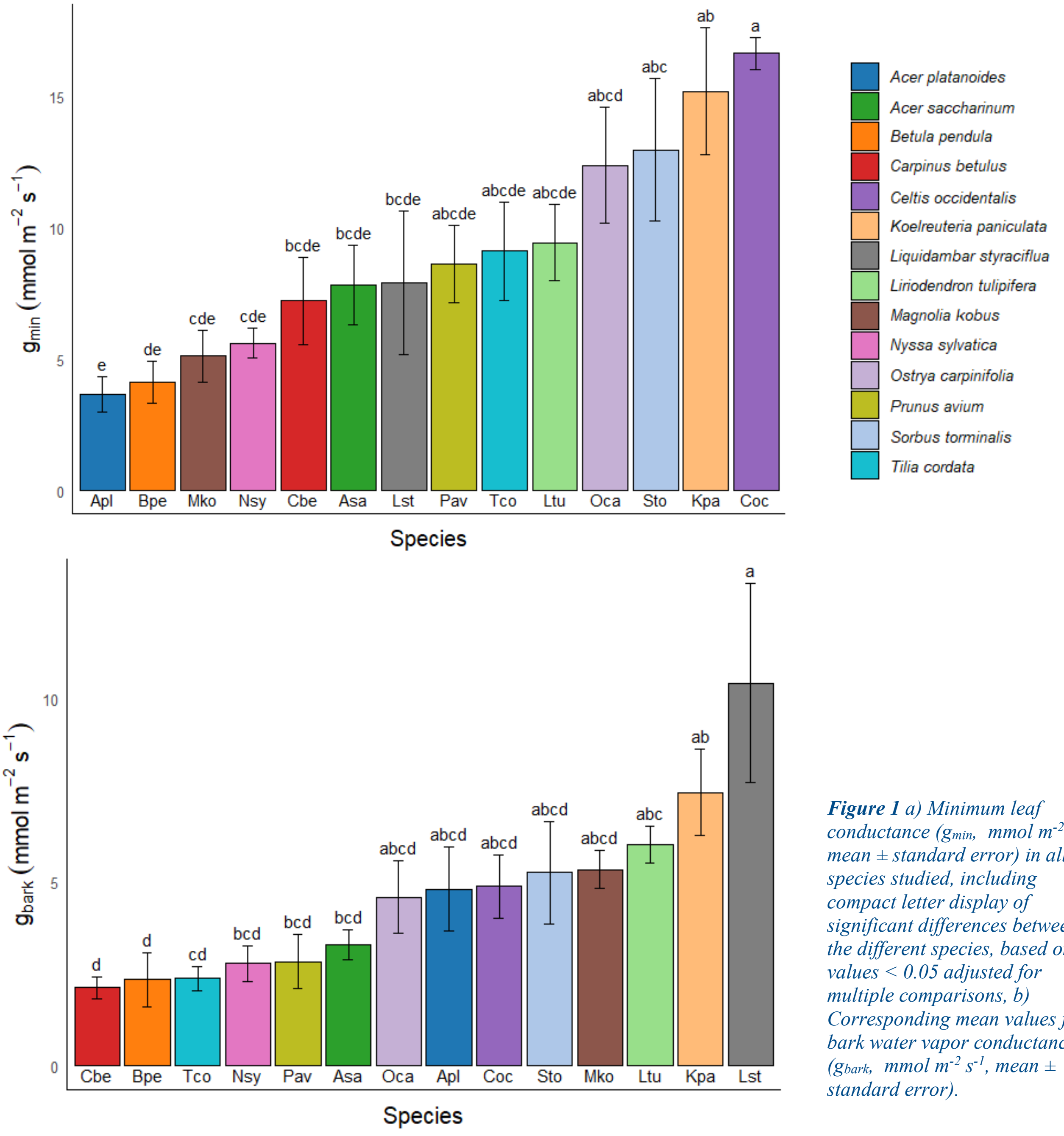

Figure 1 *a) Minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error) in all species studied, including compact letter display of significant differences between the different species, based on p-values < 0.05 adjusted for multiple comparisons, b) Corresponding mean values for bark water vapor conductance (g_{bark}, mmol m^{-2} s^{-1}, mean ± standard error).*

For g_{bark}, 5 significantly different groups of means were identified ($p < 0.05$) (**Figure 1b**). *C. betulus* (2.1 ± 0.3 SE mmol m^{-2} s^{-1}) and *B. pendula* (2.4 ± 0.7 SE mmol m^{-2} s^{-1}) had the lowest mean values, while *L. styraciflua* had the highest mean value of all species (10.4 ± 2.7 SE mmol m^{-2} s^{-1}).

L. styraciflua (group a) were significantly higher than 6 other species (*B. pendula*, *C. betulus*, *A. saccharinum*, *T. cordata*, *P. avium* and *N. sylvatica*). *K. paniculata* (group ab) and *L. tulipifera* were also high, being significantly higher than *B. pendula* and *C. betulus*. *C. betulus* and *B. pendula* were significantly lower than *L. styraciflua*, *K. paniculata* and *L. tulipifera*. *T. cordata* were lower than *L. styraciflua* and *K. paniculata*, positioned in between the mid and low groups.

3.2 Minimum leaf conductance related to other drought-related tree traits

3.2.1 Bark water vapor conductance

When mean g_{min} was related to the mean g_{bark} value for all 14 species, no significant linear relationship was found ($p = 0.30$) (**Figure 2**).

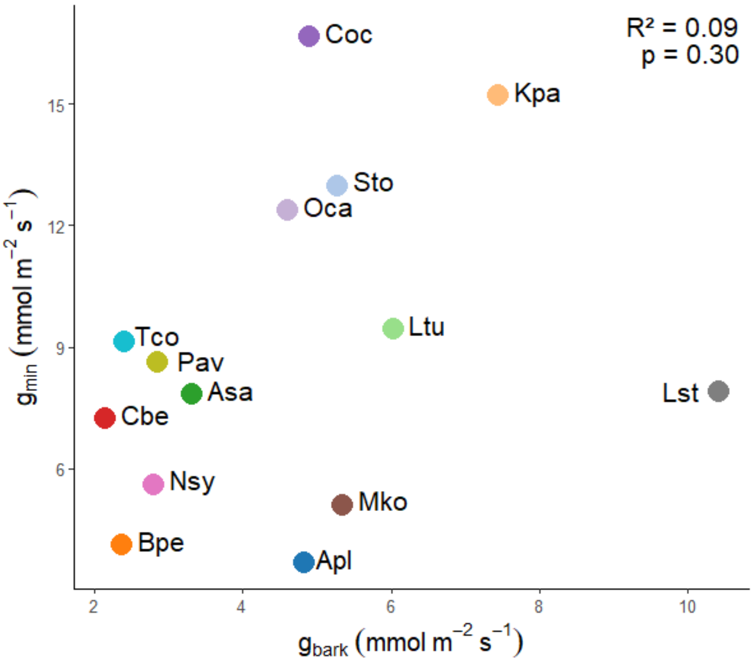

***Figure 2**) Minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error) against bark water vapor conductance (g_{bark}, mmol m^{-2} s^{-1}, mean ± standard error) in all species studied. The abbreviations of species scientific names are summarized in **Table 1**.*

However, some trends could be observed. For example, the mean value of *B. pendula* was in the lower range in both g_{min} (4.1 ± 0.8 SE mmol m^{-2} s^{-1}) and g_{bark} (2.4 ± 0.7 SE mmol m^{-2} s^{-1}) among the studied species, while *K. paniculata* was high in both g_{min} (15.2 ± 2.4 SE mmol m^{-2} s^{-1}) and g_{bark} (7.4 ± 1.2 SE mmol m^{-2} s^{-1}).

3.2.2 Stomatal conductance

Overall, the values in $g_{sw\ drought}$ were lower (3.1 ± 14.1 – 59.5 ± 39.5 SE mmol m^{-2} s^{-1}) than in $g_{sw\ control}$ (91.3 ± 1.3 – 417.3 ± 129.1 SE mmol m^{-2} s^{-1}), but with large variation in $g_{sw\ drought}$. No significant linear relationship could be found between $g_{sw\ control}$ and g_{min} when all species were included ($p = 0.39$, $R^2 = 0.06$). Neither between $g_{sw\ drought}$ and g_{min} ($p = 0.33$, $R^2 = 0.16$) (**Figure 3**).

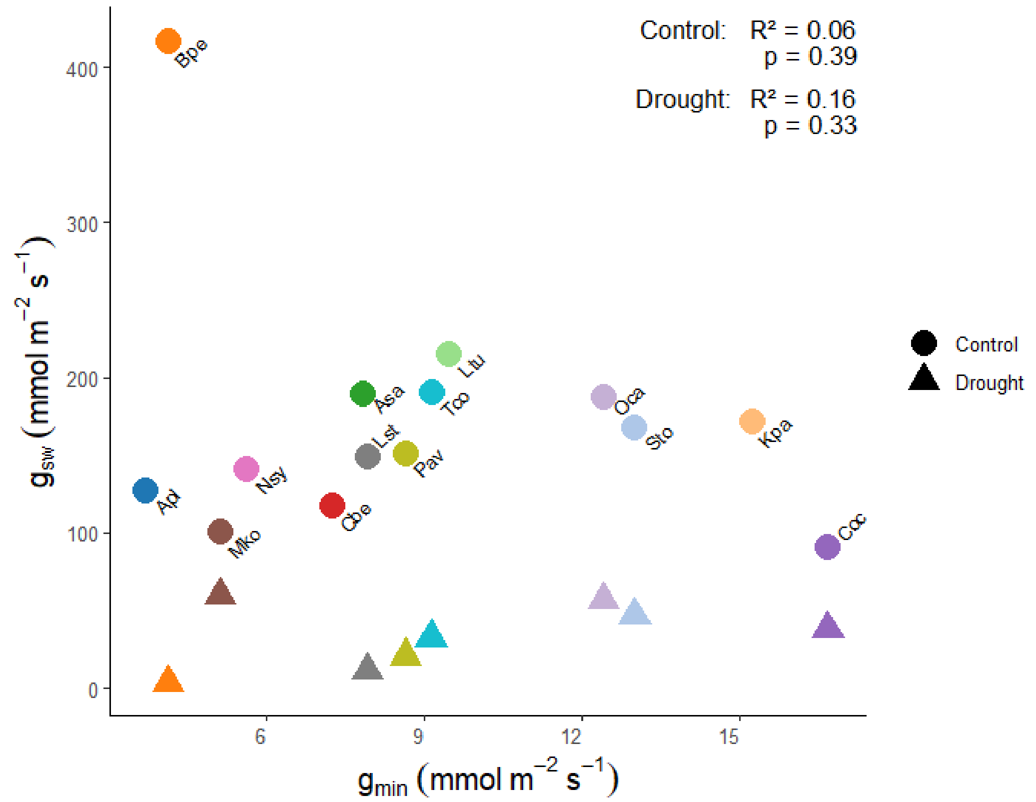

Figure 3*) Stomatal conductance for the control and drought treatment ($g_{sw\ control}$ and $g_{sw\ drought}$, mmol m^{-2} s^{-1}, mean ± standard error) vs minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error) for all 14 species studied, but without species with zero/negative values in $g_{sw\ drought}$ (6 species removed). When B. pendula and C. occidentalis were removed completely, the relationship was significant (p = 0.044). So, 12 out of 14 species followed this trend. The abbreviations of species scientific names are summarized in* ***Table 1****.*

However, if *B. pendula* and *C. occidentalis* were excluded from the analysis, a significant linear relationship was found between $g_{sw\ control}$ and g_{min} (p = 0.044, $R^2 = 0.35$) for the remaining 12 species.

3.2.3 Leaf mass per area and leaf water content

LMA significantly predicted g_{min} (p = 0.048, $R^2 = 0.29$) (**Figure 4a**) while LWC and g_{min} were not significantly related (p = 0.49, $R^2 = 0.039$) (**Figure 4b**).

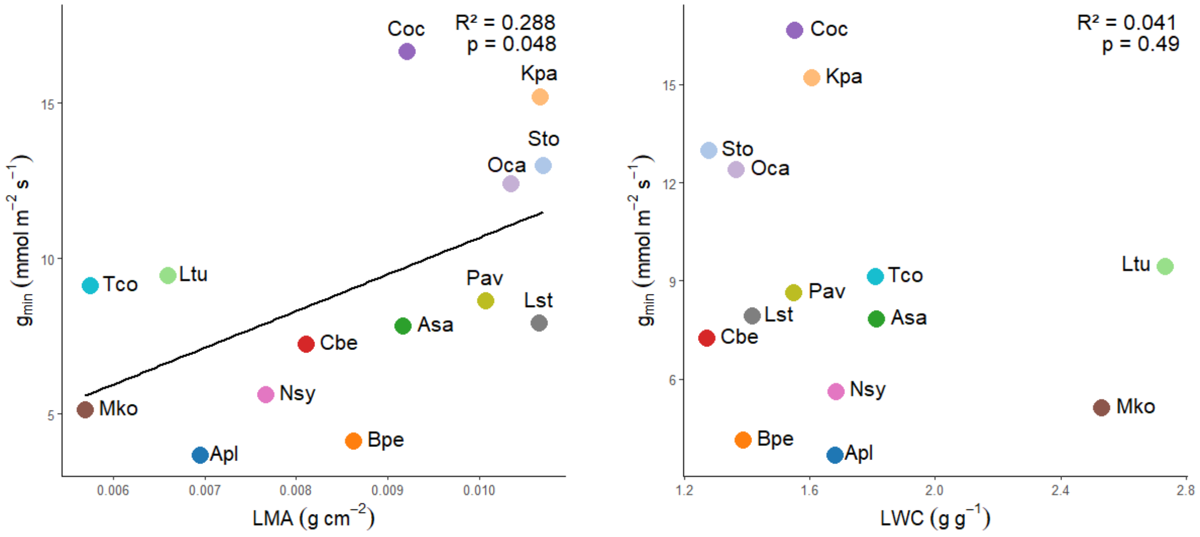

Figure 4 *a) Leaf mass per area (LMA, g cm^{-2}, mean ± standard error) vs minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error), b) Leaf water content (LWC, g g^{-1}, mean ± standard error) vs minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error). All species studied were included in both a) and b). The abbreviations of species scientific names are summarized in* ***Table 1****.*

3.3 Ratio of minimum leaf minimum conductance to stomatal conductance during well-watered conditions

Looking at the proportion of water loss from g_{min} compared to $g_{sw\ control}$, differences between species showed (**Figure 5**). The average ratio of g_{min} to $g_{sw\ control}$ was 6.1%.

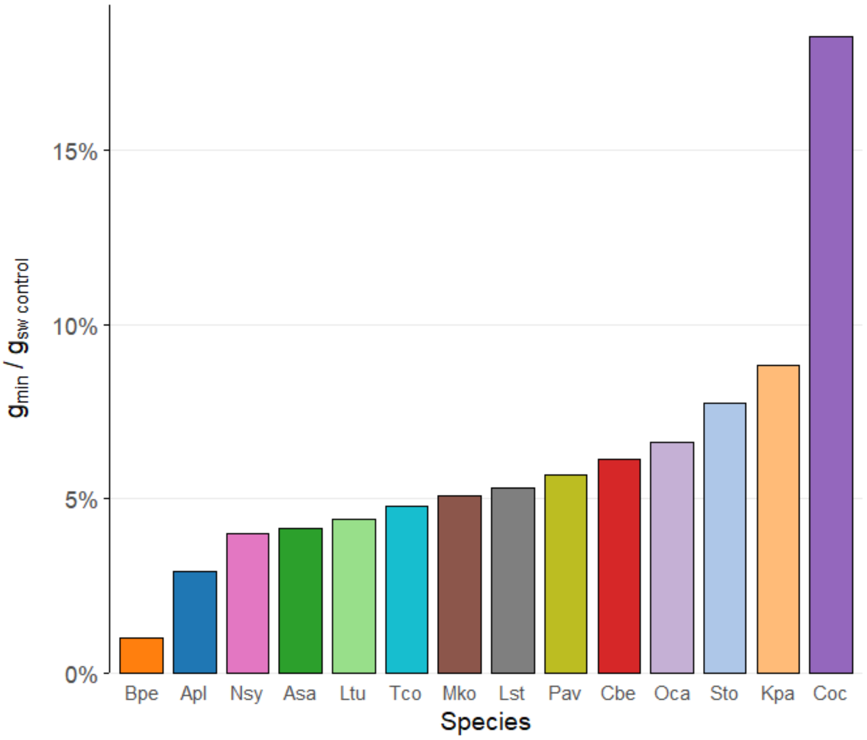

***Figure 5**) Ratio of minimum leaf conductance (g_{min}, mmol m^{-2} s^{-1}, mean ± standard error) to stomatal conductance for the control treatment ($g_{sw\ control}$, mmol m^{-2} s^{-1}, mean ± standard error) for all species tested. Note that for C. occidentalis, the ratio was very much higher compared to the other species' ratios (18.3 % compared to 1.0 - 8.8 %). The abbreviations of species scientific names are summarized in **Table 1**.*

Of all species, it could be seen that *C. occidentalis* had the highest proportion of water loss from g_{min} relative to $g_{sw\ control}$ (18.3 %) compared to the other species (which varied between 1.0 - 8.8 % with *K. paniculata* exhibiting the second highest proportion). The proportion was lowest in *B. pendula*.

4. Discussion

4.1 Interspecies variation in minimum leaf conductance and bark water vapor conductance

4.1.1 Minimum leaf conductance

The mean values of g_{min} varied between 3.7 (± 0.7) – 16.7 (± 0.6) SE mmol m^{-2} s^{-1} (**Figure 1a**), which is in line with previous studies. For example, in the literature compilation in the study by Duursma et al. (2019), where 221 species of plants (among them about two-thirds were woody species) from 10 phylogenetic orders were analyzed, the mean g_{min} value varied between ~ 3-12 mmol m^{-2} s^{-1} and the overall mean was 4.9 ± 2.7 SD mmol m^{-2} s^{-1}.

Furthermore, the fact that an interspecies variation was found (5 different groups) is also interesting, but more complex to understand. There are many possible explanations to this variation that is not investigated in this study but should be further investigated in future studies of g_{min}. However, there are some studies that could link the specific species used in this study to their drought tolerance that are worth mentioning.

A. platanoides and *C. occidentalis* stand out as the low and high extremes that differed significantly from several of the other species studied. *C. occidentalis* had a significantly higher mean value than 7 other species and had the highest mean value of all species. Rissanen et al. (2025) showed that the vessel anatomy of *C. occidentalis* varied to favor safety or efficiency depending on urban site conditions, which implies that *C. occidentalis* may be able to acclimate to dry growing conditions by having other qualities favoring drought tolerance than low g_{min}.

The g_{min} of *A. platanoides* was significantly lower than 4 other species and it had the lowest mean value of all species. Comparing water potential at turgor loss point, π_{tlp} (Ψ_{tlp}), previous studies have found values ranging between −1.89 (± 0.07) and −2.67 (±0.05) MPa for *C. occidentalis* (Sjöman et al., 2018) and between −1.39 and −1.67 MPa for different cultivars of *A. platanoides* (Banks et al., 2019), meaning that *C. occidentalis* can handle a lower leaf water potential than *A. platanoides*. Since *A. platanoides* has a lower g_{min} than *C. occidentalis*, this might mean that *C. occidentalis* has a strategy based on dehydration tolerance rather than avoidance compared to *A. platanoides* (Liang & Ye, 2024).

4.1.2 Bark water vapor conductance

The mean values of g_{bark} varied between 2.1 (± 0.3) – 10.4 (± 2.7) SE mmol m^{-2} s^{-1} across all species (**Figure 1b**). The variation between species was large (about a factor of 4 between the highest and the lowest mean), but they were in a similar range and variation as previous studies. In the study by Wolfe (2020), g_{bark} ranged 10-fold across all studied tree sapling populations, from 0.86 – 12.98 mmol m^{-2} s^{-1}. In other studies of g_{bark}, specifically twigs and small shoots had a broad range of values, from 5.01 – 27.3 mmol m^{-2} s^{-1} in 5 species (~ 5-fold range), which were also temperate and angiosperm (Beikircher & Mayr, 2013; Wittmann & Pfanz, 2008). The findings of this study on saplings may be more comparable to those from studies on twigs and small shoots than to studies on mature trees, as bark structure and thickness vary with tree size (Neumann & Lawes, 2021).

Wolfe (2020) suggested several reasons to why g_{bark} varies between species. Stem succulents as a functional group have shown to have lower g_{bark} and there has also been weak relationships between g_{bark} and traits like bark thickness and stem diameter as well as environmental factors such as temperature and vapor pressure. Also, structural traits of the bark are suggested to be important for g_{bark} variations. However, they also limit their conclusions by explaining that the small number of previous studies makes the underlying mechanisms of the variation hard to understand. A newer study by Ávila-Lovera and Winter (2024) showed that interspecies variation in g_{bark} depended on bark thickness, mean annual precipitation, mean annual temperature and the phylogenetic relatedness of the species.

4.2 The co-variation between minimum leaf conductance and other drought-related tree traits

4.2.1 Bark water vapor conductance

Bark water vapor conductance did not significantly predict g_{min} (**Figure 2**). However, there were species that had low g_{min} and g_{bark} and those that had high g_{min} and g_{bark}. For example, *B. pendula* were in the lower range in both g_{min} and g_{bark} among the species studied. On the other hand, *K. paniculata* was high in both g_{min} and g_{bark}.

This suggests that *B. pendula* may use a more conservative water use strategy compared to *K. paniculata*. However, since there was no significant relationship between the two variables, we cannot say that any general coordination of g_{min} and g_{bark} exists across the studied species. However, this gives us an indication of which of the studied species that tend to save water by minimizing the size of g_{min} and g_{bark} pathways of water loss (Wang et al., 2024; Wolfe, 2020).

4.2.2 Stomatal conductance, during well-watered and drought conditions

No correlation between g_{min} and $g_{sw\ control}$ ($p = 0.39$, $R^2 = 0.06$) or g_{min} and $g_{sw\ drought}$ ($p = 0.33$, $R^2 = 0.16$) could be found for all the 14 species studied (**Figure 3**). However, when *B. pendula* and *C. occidentalis* (which stood out as having a very high g_{sw} (*B. pendula*) or very high g_{min}-to-g_{sw} ratio (*C. occidentalis*) compared to the other species) were removed completely, a significant positive correlation was found ($p = 0.044$, $R^2 = 0.35$), indicating that the remaining 12 species followed this trend. Earlier studies on *B. pendula*, e.g. Konarska et al. (2016), have found g_{sw} values around 90-150 mmol m^{-2} s^{-1} that were nearly three times lower than the measurements used for this study, 417.3 (± 129.1 SE) mmol m^{-2} s^{-1}, suggesting that there may have been problems with the data collection for this species.

Previous studies have shown a positive correlation between stomatal conductance and both g_{min} and carbon assimilation capacity (A) among species (Liao et al., 2025; Machado et al., 2021). Larger carbon assimilation capacity was largely explained by an increase in stomatal conductance, which allowed more diffusion of CO_2 into the leaf. Species with higher stomatal conductance, g_{min} and A were fast growing and had higher water losses from g_{min}. The results from this study align with these findings, as higher stomatal conductance was associated with higher g_{min} for 12 species. The connection to A from previous studies indicates that the benefits of higher growth rate come with the cost of losing more water through g_{min} pathways, which could make these species less drought tolerant.

4.2.3 Leaf mass per area and leaf water content

The results from this study show that high LMA corresponds with higher g_{min} ($p = 0.048$, $R^2 = 0.29$) (**Figure 4a**). This finding differs from the results by Slot et al. (2021) who found a negative correlation between LMA and g_{min}, which was significant for g_{min} at 35°C leaf temperature ($p < 0.05$) but not at 32 or 40°C. In another study by Garen and Michaletz (2025) there was no apparent relationship between LMA and g_{min} at 20°C, but at higher temperatures (40-50°C) LMA explained more of the variance in g_{min}. These contrasting findings suggest that the role of LMA for determining g_{min} at different temperatures is important to consider when studying how g_{min} varies among growing conditions and species.

Because LWC reflects plant water status and is linked to several important plant functions related to water use such as stomatal conductance and photosynthesis (Li et al., 2024), it would not be unreasonable that LWC would co-vary with tree traits linked to drought tolerance such as g_{min}. However, in this study no significant linear relationship could be found between g_{min} and LWC ($p = 0.49$, $R^2 = 0.041$) (**Figure 4b**).

4.3 Linking minimum leaf conductance and bark water vapor conductance to drought tolerance

Low mean values of g_{min} and/or g_{bark} suggest that a species may have a more conservative water use strategy (Liang & Ye, 2024), as this indicates that less water is lost through these "pathways" when stomata are closed (Duursma et al., 2019; Schuster et al., 2017; Wolfe, 2020). This becomes even more important during a drought, when the access to soil water is limited, and the tree risks drying out (Wang et al., 2024; Wolfe, 2020). This means that the species in this study which had low mean g_{min} or g_{bark} values, or a combination of both, might be better at avoiding dehydration during drought than the other studied species and thereby have higher chances of survival. However, the g_{min} and g_{bark} values were measured on trees which were not exposed to drought, so it is possible that the trees may exhibit different strategies or mechanisms for modification of g_{min} and g_{bark} during drought, such as incomplete stomatal closure and changes of the cuticle structure as suggested by Burlett et al. (2025), which found a decline in g_{min} with increasing dehydration.

The overall drought sensitivity of the species studied was evaluated in a parallel study that created a drought-sensitivity index based on several leaf-level physiological indicators related to gas exchange, photosynthesis and leaf water potential in response to moderate drought. According to that index the least drought-sensitive species were *O. carpinifolia*, *M. kobus* and *B. pendula* and the most drought-sensitive species were *C. betulus*, *A. saccharinum* and *N. sylvatica* (R. Thapa, personal communication).

In this study, both *N. sylvatica* and *A. saccharinum* were in the lower range of both g_{min} and g_{bark}. This is contradictory in terms of the assumption that low g_{min} and g_{bark} are associated with a conservative water use strategy and therefore should be more drought tolerant in that manner. *N. sylvatica 'sylvatica'* does best in well-drained soil and survives periods of drought. For example, they are sometimes naturally found in dry mountain environments in eastern US (Sjöman & Slagstedt, 2015a). *A. saccharinum* are known to be fast growing, only thriving in habitats rich in water and nutrients and having a badly developed tolerance for harsher conditions (Sjöman & Slagstedt, 2015b). The contrasting results may indicate that while g_{min} and g_{bark} are important during more extreme drought conditions, for example, g_{min} affects the dehydration rate which determines tree survival time during severe drought (Brodribb et al., 2020; Wang et al., 2024) and higher g_{bark} has been linked to increased stem dehydration and mortality risk during extreme drought (Wolfe, 2020), other factors could be more important during moderate drought conditions.

Improvements and suggestions for future studies

While this study provides new insights into how g_{min} and g_{bark} varies between tree species and what might explain this variation, some limitations should be acknowledged. The sample size was relatively small, which might affect the generalizability of the results, the branches were sampled from young trees, which might be different from stems in older trees with more mature bark and leaves, and g_{min} and g_{bark} were only measured on well-watered trees, not taking drought adaptation nor plasticity into account. Future studies could include larger sample sizes, more mature trees, more different properties linked to g_{min}, e.g. cuticular traits, photosynthetic capacity, light requirement strategy (Burghardt & Riederer, 2003; Liao et al., 2025; Loram-Lourenço et al., 2022; Schuster et al., 2017) and phenotypic plasticity (Wang et al., 2025) and properties linked to g_{bark}, e.g. morphoanatomical properties of the outer bark (Loram-Lourenço et al., 2022), as well as varying environmental conditions such as water availability (Burlett et al., 2025) air temperature and VPD (Esperon-Rodriguez et al., 2020; Garen & Michaletz, 2025; Zailaa et al., 2024).

Conclusions

Both minimum leaf conductance and bark water vapor conductance varied significantly among the studied species. The increase in minimum leaf conductance with increasing leaf mass per area suggests a degree of morphological control. Leaf water content, which relates to plant water status, had no effect on minimum leaf conductance in the well-watered saplings studied. Minimum leaf conductance increased with increasing stomatal conductance in the control treatment for 12 species, suggesting a co-variance between these factors.

It is hard to draw any general conclusions about which trees that is suitable for Swedish cities only based on this study, but it can serve as an important contribution among others to get a deeper understanding of the drought tolerance in deciduous angiosperm tree species suitable for the climate of Swedish cities.

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Appendix A: Popular science summary

URBAN TREE SPECIES: WHO SURVIVES A DROUGHT?

You know how cities are drier and warmer than rural areas and that this will be worse with further global warming? We need to cool them down so that they will be pleasant to live in. Planting trees is a good way to do this. But it requires that the trees survive. In this study we looked at traits important for the survival of urban trees.

DROUGHT & WATER LOSS

A major threat to urban trees is drought. Two tree traits that are important to survive drought are **the residual water loss from the leaves and bark** - minimum leaf conductance, g_{min}, and bark water vapor conductance, g_{bark}. The **residual water loss** is basically how much water the tree loses when already restricting **transpiration** - the largest source of water loss.

Transpiration: the transport of water through the plant – from the absorption of water by the roots to the evaporation of water through stomatal pores in the leaf.

Imagine a tree during normal conditions, transpiring, doing photosynthesis and growing. Then a drought happens – a long period with low precipitation and warmer air temperatures. Less water is available in the soil, so the roots struggle to absorb water. The stomatal pores are still open, losing a lot of water, gradually lowering the water content inside the tree. **To not become lethally dehydrated**, the tree closes the stomatal pores, pausing transpiration. But the tree is still leaking water – from stomatal leakages, the wax layer on leaves and from the bark. For how long will the tree survive living under these conditions? One important factor seems to be how large these other water losses are.

THE STUDY

We wondered if this restriction differs between tree species, and if so, how large the difference is and why it existed. Our results showed that there was a difference in the residual water loss from the leaves and bark between the 14 species we studied and that the loss from the leaves increased with **leaf thickness** - measured as leaf mass per area. In other words:

1. Different species had **varied** ability in restricting water loss from the leaves and bark.
2. Species with **thinner** leaves were **better** at restricting water loss from the leaves.

The 14 species in our study was chosen based on suitability for Swedish cities. Some of them were native and some were exotic to Sweden.

WHAT IT ALL MEANS

This gives us an indication on which tree species that are best at surviving drought, for example maybe **silver birch**, which is useful when deciding on which species to use when planting urban trees, even though more information is needed to make that choice.

Credit: Johnny Dod, retrieved from Public Domain Pictures.

Appendix B: Results from linear regression analyses

***Table B1**: Results from all linear regression analyses in the study. * Marks significant results on a 0.05 significance level.*

Variables	Pr (>|t|) for x	R^2	F (DF)	Standard Errors (SE)
g_{min} vs g_{bark}	0.2974	0.09	F(1,12) = 1.187	0.478
g_{min} vs LMA	0.048 *	0.29	F(1,12) = 4.864	535.939
g_{min} vs LWC	0.488	0.041	F(1,12) = 0.512	2.590
g_{min} vs $g_{sw\ control}$ (excl. outliers Coc 253 & 259)	0.389	0.062	F(1,12) = 0.800	0.014
g_{min} vs $g_{sw\ control}$ excl. Bpe and Coc in g_{sw}	0.044 *	0.348	F(1,10) = 5.331	0.025
g_{min} vs $g_{sw\ drought}$ excl. values = zero/negative	0.332	0.156	F(1,6) = 1.111	0.076

Appendix C: Means, sample sizes and g_{min} / $g_{sw\ control}$ ratios

***Table C2**: Each studied species' means ± standard errors (SE) for minimum leaf conductance, g_{min}, bark water vapor conductance, g_{bark}, leaf mass per area, LMA and leaf water content, LWC.*

Species	g_{min} mmol m^{-2} s^{-1}	± SE	g_{bark} mmol m^{-2} s^{-1}	± SE	LMA g cm^{-2}	± SE	LWC g g^{-1}	± SE
Apl	3.7	0.7	4.8	1.1	0.0070	0.0008	1.7	0.1
Asa	7.8	1.5	3.3	0.4	0.0092	0.0010	1.8	0.1
Bpe	4.1	0.8	2.4	0.7	0.0086	0.0009	1.4	0.1
Cbe	7.2	1.7	2.1	0.3	0.0081	0.0003	1.3	0.0
Coc	16.7	0.6	4.9	0.9	0.0092	0.0006	1.6	0.0
Lst	7.9	2.7	10.4	2.7	0.0106	0.0010	1.4	0.1
Ltu	9.5	1.5	6.0	0.5	0.0066	0.0005	2.7	0.2
Mko	5.1	1.0	5.3	0.5	0.0057	0.0003	2.5	0.1

Species	**g_{min} mmol m^{-2} s^{-1}**	**± SE**	**g_{bark} mmol m^{-2} s^{-1}**	**± SE**	**LMA g cm^{-2}**	**± SE**	**LWC g g^{-1}**	**± SE**
Nsy	5.6	0.6	2.8	0.5	0.0077	0.0003	1.7	0.1
Pav	8.6	1.5	2.8	0.7	0.0101	0.0009	1.5	0.1
Kpa	15.2	2.4	7.4	1.2	0.0107	0.0008	1.6	0.0
Oca	12.4	2.2	4.6	1.0	0.0103	0.0013	1.4	0.1
Sto	13.0	2.7	5.3	1.4	0.0107	0.0010	1.3	0.1
Tco	9.1	1.9	2.4	0.3	0.0058	0.0008	2.1	0.3

Table C3*: Each studied species' means ± SE for stomatal conductance to water vapor, g_{sw} for two treatments – control and drought.*

Species	**g_{sw} control mmol m^{-2} s^{-1}**	**± SE**	**g_{sw} drought mmol m^{-2} s^{-1}**	**± SE**
Apl	127.5	14.1	0.0	-
Asa	189.8	52.2	0.0	-
Bpe	417.3	129.1	3.1	14.1
Cbe	117.8	52.0	0.0	-
Coc	91.3	1.3	37.8	19.8
Lst	149.2	33.0	11.6	11.8
Ltu	215.3	70.8	0.0	-
Mko	100.6	13.6	59.5	39.5
Nsy	141.0	20.4	0.0	-
Pav	151.6	36.7	20.6	27.3
Kpa	172.0	51.7	0.0	-
Oca	187.3	58.5	56.5	13.9
Sto	168.0	39.9	46.7	20.1

Tco	190.8	25.3	32.6	53.7

***Table C4**: Sample sizes (n) for all measured properties in all species studied.*

Species	g_{min}	g_{bark}	**LMA**	**LWC**	g_{sw} **control**	g_{sw} **drought**
Apl	4	4	4	4	6	5
Asa	4	4	4	4	6	6
Bpe	4	4	4	4	5	6
Cbe	4	4	4	4	6	6
Coc	4	4	4	4	4	6
Kpa	4	4	4	4	6	6
Lst	4	4	4	4	6	6
Ltu	4	4	4	4	6	5
Mko	4	4	4	4	5	5
Nsy	4	4	4	4	6	6
Oca	4	4	4	4	6	6
Pav	4	4	4	4	5	6
Sto	4	4	4	4	6	6
Tco	4	4	4	4	6	6
Sum:	**56**	**56**	**79**	**81**	**56**	**56**

***Table C5**: Exact values for ratios between mean g_{min} / mean $g_{sw\ control}$ for all species studied.*

Species	Apl	Asa	Bpe	Lst	Ltu	Nsy	Coc	Mko	Cbe	Pav	Oca	Tco	Kpa	Sto
Ratio	0.029	0.041	0.010	0.053	0.044	0.040	0.183	0.051	0.061	0.057	0.066	0.048	0.088	0.077

Appendix D: Routine for measuring g_{min} and g_{bark}

Note that these measurements should be conducted as soon as possible after collecting the branch samples (with leaves still attached).

Fill a suitable container with water, put the branches under the water surface and cut them a few centimeters at the bottom to give them the best circumstances, restoring water uptake as efficiently as possible. Put a dark plastic bag over the container and let the branches be stored like this in a lab room overnight. The day after, keeping the lab room dark (lights off/low strength) (inform all people using the lab that the room must be dark for the experiment), start with the measurements*:

1. Prepare the setup by cutting off a band for each branch piece, marking them with abbreviation of species name and the tree ID of the sample, e.g. “Apl 258”. Weigh the bands and record the weight in the protocol. Put the bands in order on the table for easy access.
2. Cut branches to pieces with a suitable length (considering availability and so that they fit on the scale). Cut off non-damaged leaves. The branches need to be leaf-free, and the leaves should be cut near the leaf-node, next to the branch.

    a. In this study 4 samples of 2-3 species were measured for one “measurement day”, and the length of the branch pieces varied between 6.1-19.4 cm. The branches with the most mature bark were chosen.
    b. If the leaf-node contains multiple leaves, choose the most mature leaf which is also small enough so that it fits on the scale. Leaves that are too big make it hard to stabilize and risk causing more damage to the leaves during the measurements.

3. Starting with preparing the leaf for weighing** (they dry out faster than the branch pieces):
    a. Apply nail polish so that it covers the petiole of the leaf and both ends of the branch piece. Mark the leaf with species and ID with a marker pen directly at the surface at back of the leaf.
    b. Measure the area in cm^2 with a smartphone using the app “Easy Leaf Area” (**Figure D6**) ***, check that the result is reasonable and then record the value (e.g. by taking a screenshot in the app and record it in the protocol later).
        i. If something went wrong, it is good to also save a raw version of the image (including the red reference square) for correction afterwards.

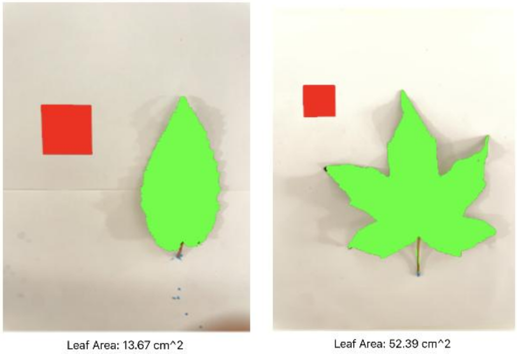

***Figure D6**: Examples of how measurement scans with Easy Leaf App could look like. The leaf is placed on a white paper with a 1 x 1 cm red square as a calibration area to calculate the leaf area. The images were taken during this study.*

    c. Then continue from step (5).

4. Then prepare the branch pieces for weighing*:
    a. Measure the diameter in both ends with a vernier caliper and the length with a ruler. Record in the protocol.
    b. Then continue from step (5).
5. Weigh the leaf/branch piece.
    a. For the branch pieces: tie the prepared marker bands around the corresponding branch piece. Weigh each piece again, with the bands on. Record this weight too.
6. Clip the leaf/branch piece onto the steel net (e.g. with a clothes peg) to dry (with the leaves upside facing upwards).
    a. The first time during the day: start the fan right before you clip the first leaf/branch piece.
    b. Record the time point, e.g. “10:40 am”, the relative humidity (RH) and the air temperature in the room (T).
    c. Set a timer on 30 minutes right after weighing the first leaf/branch piece in a “measurement round”.
7. Repeat step (6a-6c) for each leaf/branch piece. Do at least 8 measurements for all leaves/branch pieces.
    a. If 8 measurements are not enough for any of the leaf/branch pieces, do more measurements and follow the curve to see if the linear phase shows. In some samples/species, you will notice after waiting that this won’t help, then you can finish up anyways, but always after waiting to see first.
8. Make an aluminum bag with an open top (for efficient drying), mark it with the species and ID and put the corresponding leaf/branch piece in the bag. Repeat it for every leaf/branch piece. Then carry them carefully to an oven and dry them at 70ºC. Keep them in the oven at least 24 hours and then measure the dry weight of each leaf/branch piece (remove the marking band from the branch pieces before weighing them).

    a. If this step is not possible: keep them in a refrigerator until they can be oven dried.

9. *Save all leaves and branch pieces for eventual future additional measurements.*

* Handle the samples carefully so they get as little damage as possible during the measurements.

** When weighing the leaf/twig, do as follows: Press “tare” and be sure that the scale zeroes. Put the sample on the scale and wait until the first time “g” shows after the value, meaning that the scale has stabilized. Record the weight with at least 4 decimals.

*** Easy Leaf Area is available to download from an app store (iOS/Android OS) or from this shared GitHub folder. More information about this measurement method can be found in the study by Easlon and Bloom (2014).