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Using leaf economics to find appropriate woody species for rain gardens

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Foreword

This thesis would not have been possible if I had not been given the chance to partake in the research project led by Anna Levinsson at SLU. I would therefore like to thank the project group for giving me this opportunity. I would also like to thank the whole research group for an educational and fun experiment period this summer. Additionally, I especially want to thank my supervisor Björn Wiström and co-supervisor Anna Levinsson for encouragements and excellent guidance during the process of this thesis, and Adam Flöhr for providing wonderful help with my statistical work.

I want to give a special thanks to Elin for keeping me company during the writing of this thesis. Without your coffee and company this fall would have been considerably longer and less fun. I would also like to thank Ida, Leo and Tina for excellent proofreading and for providing good inputs.

Abstract

Urban rainwater management faces great challenges in the future, caused by expected increase in precipitation and frequency of storms associated with climate change. Constructions such as rain gardens may be a mean for adaptation to, as well as mitigation of these effects. However, growing conditions in rain gardens are challenging for most vegetation, and in particular woody vegetation, often leading to failing rain garden constructions. By gaining information on the responses of different woody species during conditions found in rain gardens, the probability for a successful decision of vegetation increases.

This study was made in connection to a research project led by Anna Levinsson at SLU, Alnarp, researching different responses of nine woody species to waterlogging and drought. The species were chosen based on the categorising work by Niinemets and Valladares (2006), and sorted further according to a few additional criteria. This thesis aim to investigate the possible importance of leaf economics when choosing trees for rain gardens, focusing on the conditions during waterlogging.

A literature study explored the current knowledge of waterlogging in urban environments, the effect of waterlogging on trees, and plant strategies centred around Grimes CSR theory and leaf economics. The literature study showed that the most damaging factor to plants during waterlogging is the anoxic conditions created in the soil. Several adaptations exist which may increase the survival-rate for woody species during these conditions, such as the ability for altering root growth, hypertrophied lenticels and a permeable cambium. These adaptations are all associated with the longitudinal transportation of oxygen.

The knowledge gathered in the literature study provided the base for the experimental study. Measurements of midday leaf water potential (ψ_L) and stomatal conductance (g_l) were conducted as well as measurements of leaf morphology focusing on the leaf trait Specific leaf area (SLA). The results of the experimental study indicated that the ability for SLA plasticity might be important for the survival of trees during waterlogging, since the species deemed most flood-tolerant displayed significant, or almost significant, effect when kept in a waterlogged state. Furthermore, it showed that these species had a higher ψ_L and showed no significant effect on g_l, indicating that these species seem to be able to upkeep water levels in the leaves and inhibit stomatal closure during waterlogging. This was somewhat contradictory to what was previously described in the literature.

Further investigations within the responses of ψ_L and g_l towards waterlogging and how plasticity within leaf economics might be related to this are encouraged. This would possibly increase our understanding in what to search for when choosing woody species for rain beds.

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This introductory part provides the base for the rest of the thesis. It includes a background, leading to the focus question and demarcation of the thesis. Materials and methods explain how the different parts of the thesis were conducted.

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Backround

Climate change is one of the greatest challenges of our time and the result of a changing environment can already be seen today (Ipcc 2018). Since 1950, the frequency of heat waves have increased across Europe, as well as the number of heavy precipitation events (Ipcc 2018). The increase in precipitation is joined by the increased risk of flooding, which already is one of the most frequently occurring destructive natural events. With the effects of climate change the frequency is expected to increase more still (Jha et al. 2012). Urban areas are often sensitive to these effects caused by climate change, mainly due to their high concentration of assets and people (Jha et al. 2012). More than half of the world's population currently live in urban areas, a number that is expected to increase to two-thirds by 2050 (Seto et al. 2014). This expansion of urban areas and the associated changes of the landscape, such as increased impermeable surfaces and redirection of waterways, will amplify the effects on flooding caused by climate change (Jha et al. 2012). However, urban growth can potentially catalyse development that aid the adaptation to and the mitigation of effects of future climate change (Bazaz et al. 2018).

There are many ways in which urban areas and its residents can benefit from green structures (Bolund and Hunhammar 1999). Exposure to vegetation has been shown to reduce stress and fatigue of people more efficiently than non-living urban components, such as streets and buildings (Hernández and Hidalgo 2005). Moreover, if planned well it may also favour biodiversity (Nielsen et al. 2014), while simultaneously form structures that save energy and money, by shading buildings and managing stormwater during heavy rains etc. (Bazaz et al. 2018). Ecosystem services such as these can aid in both adaptation to as well as mitigation of climate change. Woody species, and especially trees, are in many cases particularly successful in delivering these ecosystem services, partly due to their size and long lifespan (Forman 2014, Scharenbroch et al. 2015, Livesley et al. 2016). However, a successful delivery of mentioned ecosystem services requires healthy and active individuals (Scharenbroch et al. 2015).

Green-blue infrastructure, in particular rain gardens, have become increasingly popular for mitigating the effects of flooding in urban environments (Siwiec et al. 2018). However, these structures require the use of specific components, such as soil substrate with high infiltration capacity (Riley and Kraus 2016). This together with periodic flooding result in a plant bed with alternating drought and waterlogging, a challenging habitat for most plant species.

In all planning that includes plant material, it is crucial to choose appropriate plant species for each specific site (Deak Sjöman et al. 2015). Today, much of what we know about plant site requirements is based on their natural habitat, and a great variation is often seen between studies when, for example, defining different species' waterlogging tolerance (Niinemets and Valladares 2006). There are many parameters that affect plants in nature. Reproduction possibilities, landscape structure, land use and disturbance regimes such as grazing animals are some of the variables that have a big impact on why plants grow where they do (Wilson 1984). As such, to only study the natural habitat of a plant may sometimes be misleading when trying to pin-point its possible tolerance towards different stressors.

According to certain theories, leaf economics and associated traits may be used to show the level of stress-tolerance of a species (Wright et al. 2004, Pierce et al. 2016). Since a changing climate may require an increase of constructions such as rain beds, the demand for appropriate vegetation for these situations will also increase. If the study of leaf economics can give a clue as to which species are able to survive and grow during waterlogged conditions, this can provide landscape architects with a better basis when selecting plants for these habitats and give us a greater understanding of the plant material often used in cities.

This thesis was written in cooperation with the first phase of a research project at the Swedish University of Agriculture Sciences (SLU) in Alnarp. The project is led by Anna Levinsson and investigates the reaction of nine different woody species during different periods of waterlogging and drought, both short- and long term. This first phase was conducted during one growing season. The period length for waterlogging was decided based on the expected lengths of water retention in rain gardens after a heavy rain event. Most rain gardens are constructed to ensure full infiltration of incoming rain water within two days, and this was consequently set as the shortest length of waterlogging-treatment. The second treatment was subjected to waterlogging for five days and the last treatment was kept waterlogged during the entire experiment period (late June to October). Different responses of all treatments and the control group were measured during the experiment period, in order to investigate both the response towards short periods of flooding and recovery after, and the responses towards longer periods of waterlogging.

Focus question

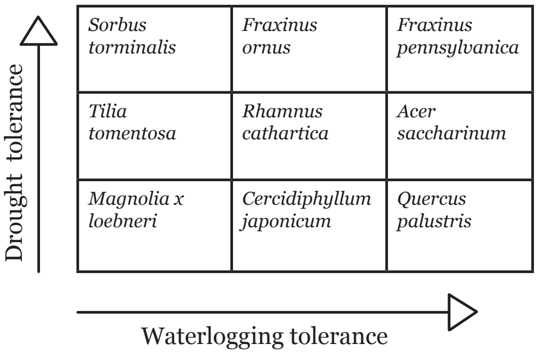
The purpose of this thesis has been to investigate if any connection can be found between trees' leaf investment and their ability to handle waterlogging conditions, thus giving indications of which species that has the potential to function well in locations with frequently occurring floods, such as rain gardens. The thesis further investigates whether the trees show a plasticity in their leaf investment during waterlogging. This may give a better understanding of the species capacity of managing waterlogging.

The focus question of this thesis is:
Can leaf economics indicate trees tolerance towards waterlogging?

Demarcation

The terms waterlogging and flooding are used differently by different authors. Some use them when describing the same condition, and some make a distinction between them. Kreuzweiser and Rennenberg (2014) define them as; flooding - water above soil level and waterlogging - flooding up to, but not exceeding, the soil level. However, in this thesis these words are used interchangeable. It will be noted in any case where the water level is of importance.

Even if conditions in rain gardens include drought, this thesis will solely focus on waterlogging. Further, the literature study has been limited to researching trees. Literature focused on herbaceous species was only included when the information was deemed applicable to trees. When studying the effect of waterlogging and flooding on trees, the focus has been on the effect of stagnant water. Any other aspects of flooding, as inflow of soil or abiotic damages, have not been considered. Further, the research only included literature concerning partial and total submersion in water when this was deemed relevant.



Sorbus torminalis	*Fraxinus ornus*	*Fraxinus pennsylvanica*
Tilia tomentosa	*Rhamnus cathartica*	*Acer saccharinum*
Magnolia x loebneri	*Cercidiphyllum japonicum*	*Quercus palustris*

Fig 1. Table of the nine species included in the study, positioned according to their expected level of waterlogging- and drought-tolerance.

During the experiment, no other species than the nine included in the research project was examined. Additionally, all measurements were conducted within the framework of the ongoing project. This provided the time frame for the measurements as well as possible number of measurements.

Materials and methods

Literature study

The literature study was commenced in September of 2019 and finished in December the same year. Cited references have been found using following databases; Web of Science, Google Scholar and Primo on SLU library's website. Any interesting references cited in read literature was followed-up and used if relevant.

Experimental research

The experimental research was carried out from June to early October 2019 in a greenhouse situated on SLU's grounds in Alnarp. Further explanation of the different parts of the experimental research follows below.

Selection of trees

The tree species studied in the project were *Acer saccharinum*, *Cercidiphyllum japonicum*, *Fraxinus ornus*, *Fraxinus pennsylvanica*, *Magnolia x loebneri*, *Quercus palustris*, *Rhamnus cathartica*, *Sorbus torminalis* and *Tilia tomentosa*. The choice of species for this the research project was based on the values of drought- and waterlogging-tolerance described by Niinemets and Valladares (2006). The species were additionally sorted according to hardiness, minimum size i.e. “smaller tree”, availability in tree nurseries and to ensure no risk of invasiveness. The nine species represented different levels of drought- and waterlogging-tolerance, which can be seen in fig 1.

Planting

The trees were delivered bare-rooted, 60-100cm high. A substrate produced for rain gardens from Bara Mineraler AB was chosen as planting soil and the pots used for planting were 10 l. The trees were all planted before bud burst. *Acer saccharinum* were considerably taller than the other trees when delivered. In order to receive valid results, it was decided that all *A. saccharinum* would be standardized by pruning to be within the same height range as the rest of the species. Both the crown and the root system of *A. saccharinum* were pruned. The trees were put in a greenhouse from the day of arrival and kept there during the experiment period.

Treatments and set-up

The research project included three different treatments and a control group. The treatments differed in the number of days the trees were subjected to waterlogging. The trees in two of the treatments stood in water 2 and 5 days respectively. The trees in the last treatment were left in water during the entire experiment period. The treatments will hereafter be called treatment 2d, treatment 5d and treatment CW (for continued waterlogging).

The trees were placed according to treatment in the greenhouse, as to simplify the measurements. Each treatment consisted of 10 blocks, containing one each of the species. Subsequently, each treatment included 10 individuals of each species. The position of the different species within the blocks were randomized.

The waterlogging treatment started on June 24. The trees were put in plastic containers which were then filled with water until the soil in the pots were covered. Two pots of trees were put in each container. Water was refilled when needed during the experiment period to upkeep the water level at the rim of the soil in the pots. All trees in the control group were kept well-watered.

Prior to the experiment the trees were unforeseeably infested by aphids and later on, spider mites. The trees were treated with Confidor for the aphids and Spical were distributed for the spider mites.

Measurements

The study included measurements of Midday leaf water potential (ψ_L), Stomatal conductance (g_l), leaf area, leaf fresh mass and leaf dry mass. ψ_L and g_l was measured on site in the greenhouse from June to August. The morphological measurements were made in a laboratory outside of the greenhouse and the leaves were collected for this purpose the 2, 7 and 21st day after the start of the waterlogging treatments.

Midday leaf water potential, (ψ_L)

Water potential is a measure of the potential energy in water, and is expressed in megapascals (MPa) (Scholander et al. 1965). For the measurements of ψ_L, a pressure chamber from PMS instruments was used. This method was developed by Scholander et al. (1965). When the leaf is cut, the tension of the water column in the xylem is relieved. This result in a rapid pull of the water to the surrounding living cells by osmosis, leaving the cut surface dry. To perform the measurement of water potential, the leaf is pressurised in the pressure chamber until the distribution of water between the living cells and the xylem is as it was pre-cutting. This is demonstrated visually when water returns to the dry cut surface (Scholander et al. 1965). The amount of pressure needed to re-distribute the water is called the balance pressure, and is an indication of the water status of the tree (Taiz et al. 2015).

Measurements of ψ_L were made on a fully developed leaf growing exposed to sunlight the 2, 7 and 21st day of waterlogging treatment. Measuring ψ_L requires the removal of a leaf, and is thus a destructive measurement. The time-span of the measurements were kept between 10.30-16.00. It is standard procedure when measuring ψ_L to concentrate the time for measurement close to noon. However, since the sun rises around 4:00-5:00 during the summer in Skåne, Sweden, where the project was conducted, the trees can be expected to be fully transpiring already around 10:30. This made it possible to prolong the relevant time for midday determinations. In addition to this, the order of measurements was consistently following the blocking order during the experiment. Thus, any differences in ψ_L caused by the time of measurement will be accounted for in the statistical analyses through inclusion of this blocking factor.

Stomatal conductance, (g_l)

Stomatal conductance (g_l) is a measurement of the level of stomatal opening and is often used as an indication of plant water status. As transpiration reduces when g_l is reduced, this prevent decreases in ψ_L. A reduction in ψ_L may also induce closure of the stomata, resulting in a lower g_l. g_l and ψ_L are thus related to each other (Gimenez et al. 2005). g_l was measured within similar timespan as ψ_L on day 2, 7, 14 and 28 of waterlogging. A porometer from Meter group was used for the measurement. The measurement followed the same blocking order as for ψ_L to account for any differences during the time of measurement.

SLA/LDMC/LA

Specific leaf area (SLA) is given by dividing the one-sided leaf area (LA) by its oven-dry mass (Pérez-Harguindeguy et al. 2013). LA is thus obtained during this measurement process. Leaf dry matter content (LDMC) is the oven-dry mass of a leaf, in milligrams, divided by its water-saturated fresh mass, expressed in grams (Pérez-Harguindeguy et al. 2013). For this study, it was therefore also necessary to measure the fresh leaf mass in addition to leaf area and leaf dry mass.

The trees in the study had a relatively small number of leaves as a cause of their size. It was therefore not possible to collect whole twig sections for the measurements of SLA as Pérez-Harguindeguy et al. (2013) suggests. To limit the number of leaves removed from the trees, the leaves used for measuring ψ_L were put in plastic bags after measurement. The bags were then put in a cooling box to avoid any impact from light or the warm air in the green house. The SLA/LDMC/LA measurements could not be done the same day as collecting the leaves, so to avoid transpirational losses the bags were put in a fridge overnight. This is in line with Pérez-Harguindeguy et al. (2013) recommendations, who emphasises the importance of storing the leaves in a cool and dark location.

There are different opinions as to including the petiole in the measurement of SLA. On one side, some argue that it should be included since it sheds from the tree with the leaf, and supports the leaf structurally as well as with its vascular system. On the other hand, others argue that the petiole should not be included since its role resembles the function of the stem and does not share the main function with the leaf; light interception and carbon fixation (Pérez-Harguindeguy et al. 2013). In this study, it was decided to exclude the petiole since this simplified both the process of collecting the leaves and the ψ_L measurements. The rachis of the compound leaves was included in the measurements of SLA/LDMC/LA as recommended by Pérez-Harguindeguy et al. (2013) and the whole leaves where measured, in contrast to one typical leaflet of the compound leaves.

Measurement of leaf area and fresh leaf weight was conducted within one day of collecting, the 27/6, 2/7 and 16/7. The leaves were kept in the cooling box for as long as possible during the day of measurement. The leaves were not rehydrated before measurement as is recommended by Pérez-Harguindeguy et al. (2013). However, Kleyer et al. (2008) only recommend rehydration of leaves from deciduous woody species when these are stored in dry conditions, which was not the case during this study. Additionally, LDMC was only used for the classification of species to a CSR-strategy, where only the control group was used. Since the control group was grown in well-watered conditions, these could be expected to be sufficiently hydrated when collected. The leaf area was measured using a scanner (LI-3100 AREA METER from LI-COR) with a resolution of 0.001 cm_2. When necessary, the leaf was cut so that no parts of the leaf overlapped or was folded. The scale used for weighing (KERN ADB 200-4) had a resolution of 0.0001 g. Each leaf was after measurement put in envelopes individually. After all leaves had been measured they were dried in 70° celsius for 72 hours. When dried, leaf dry weight was measured.

Statistical analysis

The statistical analysis was made using R software. All the scripts used for the analysis can be found in the appendix. Significate level for the tests were 0.05 and assumptions of the model was validated by plotting the residuals from the models. If not otherwise stated the analyses were made using data from the control and treatment CW.

For several of the analyses, a mixed model ANOVA was used. A mixed model ANOVA is the appropriate method when following terms are realized; the study contains a continuous dependent variable, two or more categorical independent variables, minimum of one independent variable that varies between subjects and minimum of one variable that varies within subjects. Other names for mixed model ANOVA are split-plot ANOVA, mixed factorial ANOVA and mixed design ANOVA. This type of ANOVA is often used in studies with repeated measures. Certain assumptions must be met for the mixed model ANOVA to give unbiased results. The residuals must be normally distributed and the error variance must be the same for the data in groups (Frey 2018), both of which were validated.

Midday leaf water potential, (ψ_L)

The script used for the analysis of ψ_L can be found in the appendix. The analysis was conducted on data from the same three days as collecting the leaves for morphological measurements, day 2, 7 and 21 of waterlogging. Each day was analysed separately. A mixed model ANOVA was used with ψ_L as response, to model the effect of treatment. Treatment and species was set as fixed factors and the block was set as random factor. To analyse seen significance, a tukey post-hoc test was used where the interaction between treatment and species were taken into account.

Stomatal conductance, (g_l)

The analysis of Stomatal conductance was made on the values from day 2, 7, 14 and 28 of waterlogging, using a mixed model ANOVA. Each day was analysed separately, and the script for these analyses can be found in the appendix. g_l was set as the response in the model, species and treatment as fixed factors and the block as random factor. To analyse seen significance, a tukey post-hoc test was used were the interaction between treatment and species were taken into account.

SLA and correlation to ψ_L

The script used for the analyses of SLA and correlation to ψ_L can be found in the appendix. Differences in SLA values between species was explored using a one-way ANOVA using data from the control group. SLA-value was set as the response, species and day as the fixed factors and block as random factor. A plot and tukey post hoc test was done to compare the different species SLA-values.

A mixed model ANOVA was used when analysing the correlation of SLA and ψ_L (see script in the appendix). The species mean was used in the analysis. Here the ψ_L was set as response in the model, day and SLA-value as fixed factors and species as random factor.

CSR and correlation to ψ_L

To calculate each species position in the CSR plot, the excel file found as supplementary information to Pierce et al. (2016)

was used. This calculation required the values of SLA, LA and LDMC. Since this was intended to describe the CSR strategy for the species in general, only the control group was used for the calculation. This meant that 10 different individuals of all species could be included, which is within the standard approach for CSR calculation (Astuti et al. 2018). The script that was used to create a ternary plot correlating to Grime's CSR plot can be found in the appendix.

A mixed model ANOVA was used to analyse eventual correlation between CSR and ψ_L (see script in the appendix). Since the main purpose was to investigate the correlation between ψ_L and stress-tolerance, only the S-value was used in the analysis. To be able to include the treatment effect of ψ_L, the species mean was used in the analysis, as in the analysis of SLA and ψ_L. In this analysis the ψ_L was set as response, day and S-value as fixed factors and species as random factor.

Plasticity of SLA

SLA plasticity was examined in two ways; SLA plasticity of leaves that were developed before the experiment started, and SLA plasticity of leaves developed during the treatment. The script used for the two analyses can be found in the appendix.

To calculate the plasticity of already developed leaves, a mixed model ANOVA was used. Since there was only one data point for *C. japonicum*, treatment CW, day 21, all data of *C. japonicum* was removed for this plasticity analysis. By doing this the result was not affected by missing data. In this analysis the SLA-value was set as response, treatment, species and day as fixed factors and block as well as species as random factors. A tukey post-hoc test was made to further analyse the result of the mixed model ANOVA where treatment, day and species were taken into account.

To analyse the treatment effect day two, data from all treatments (2d, 5d and CW) were included. A mixed model ANOVA was used in the analysis and the script can be found in the appendix. For this analysis the SLA-value was set as the response, treatment and species as fixed factors and the block as random factor.

For the calculation of plasticity of leaves developed during waterlogging, a mixed model ANOVA was used. Since the purpose was to compare the SLA-value before and after the trees were subjected to waterlogging, the analysis was made on the differences of SLA of leaves on the same individual. The difference in SLA-value was set as the response in this model, species as fixed factor and the block as random factor. A sidak post-hoc test was done in order to analyse of the result of the mixed model ANOVA further. *C. japonicum* had not fully developed any new leaves during the treatment and was thus excluded from the analysis. *R. cathartica* had only developed one leaf during the treatment and was therefore also excluded from the analysis.

Introduction

Part 2

Litterature study

Waterlogging in urban environments

Waterlogging

Plant strategies

Given the focus question of this thesis, the following literature study will be examining three subjects; waterlogging in urban environments, the effect of waterlogging on trees, and plant strategies centred around Grimes CSR theory and leaf economics.

Results

Discussion & Conclusion

Waterlogging in urban environments

Urban areas around the world keep expanding. This expansion and the effect it has on the landscape alters the water cycles and the associated ecosystems of those areas (Paul and Meyer 2008). This environmental footprint of urban areas also exceeds their physical boundaries. Changes of the hydrological processes in the urban areas may also have great effect on the water cycles outside of the urban areas (Kim 2018).

Projections of climate change show that we can expect changes in rainfall patterns in the future with an increase of heavy precipitation events (Ipcc 2018). This will in turn result in more frequent and intense flooding events (Jha et al. 2012). Urban areas may themselves have a great effect on local weather, often leading to higher levels of precipitation (Shepherd 2013). These changes will increase the already existing challenges of rainwater management in urban areas.

Even if floods in the rural landscape might affect larger areas, urban flooding are commonly more costly and difficult to manage. This is mainly due to the higher concentration of population and assets in cities (Jha et al. 2012). In addition to this, the water flow normally found in a city differs substantially from how it flows in natural areas. Part of the rainwater falling over urban areas is infiltrated in open soil or hard surfaces and may after this successfully reach the groundwater, and some of the water return to the atmosphere by transpiration from plants or by evaporation from non-living surfaces (Forman 2014). However, a big part of the rainwater falling in cities flows quickly as surface runoff over hard surfaces to pipes and ditches, which in turn transport it effectively out of the city. Wissmar et al. (2004) compared the frequency of floods in different watersheds pre- and post-settlement. A clear increase of floods was shown post-settlement, which was explained by the increase of impervious surfaces and decrease of forest cover (Wissmar et al. 2004). This is to be expected, since the amount of surface runoff is, in general, directly related to the proportion of impervious surfaces in an area (Wessolek 2008, Yeang 2008, Forman 2014).

The stormwater washes the city by carrying dust, pollutants as well as heat away from the streets. Typically, the first flush of the runoff contains the highest amount of pollutants (Forman 2014). Due to rapid stormwater runoff, peak flow (i.e. maximum height of water) occurs earlier in areas with large total-area of impervious surfaces. This results in a higher potential flood level and higher risk of flood damage. The high velocity of run-off in areas with high amount of sealed surfaces may also lead to erosion and damage to structures (Dunnett and Clayden 2007). After storms, urban areas as opposed to forested areas, are often subject to short-duration and a high peak of stormwater discharge (Paul and Meyer 2008, Forman 2014). An effective transportation of stormwater from cities to adjacent rivers puts these rivers at a higher risk of flooding. If the stormwater is high in pollutants this might have an additional negative effect on the rivers and any eventual connected ecosystems (Forman 2014).

The high surface runoff of impervious surfaces also has a negative effect on groundwater recharge. This ultimately leads to a decrease in baseflow discharge to adjacent waterbodies (Paul and Meyer 2008). Opposed to this, water cycles in natural areas include less evaporation and surface runoff and instead more transpiration from plants, subsurface flow and groundwater recharge (Forman 2014).

In a changing climate, we can no longer plan and manage our cities based on the idea of relatively stable climatic conditions. There is an urgent need to change our urban design choices to account for the substantial and complex changes of the climate and ecosystems around us (Kim 2018). This includes the treatment of stormwater.

The different approaches that are frequently used when planning infrastructure for stormwater management are; reduce, slow, infiltrate and filter. Adding more pervious surfaces may reduce runoff in urban areas. Another way is to increase evaporation, which can be done by making smooth surfaces rougher and adding objects to reduce water flow (Forman 2014). Such measures are often not enough in themselves and further action are in many cases needed. However, building out stormwater discharge systems within a city are often both difficult and expensive (Livesley et al. 2016).

Vegetation in different forms can be used as a mean to slow, reduce and purify rain water (Forman 2014, Kim 2018, Siwiec et al. 2018). Soil and plants both increase infiltration and transpiration of water and often contribute to rougher surfaces opposed to the hard surfaces often found in urban areas. This may reduce the speed of the stormwater (Forman 2014). Small catchments situated along the way of water runoff can effectively catch, hold and filter stormwater so that the amount of water reaching the end point of the water way is effectively reduced. These catchments can be represented by wetlands, detention ponds, drainage ditches or rain gardens etc. (Forman 2014).

Urban vegetation can often aid in reducing the effects during high rainfall (Siwiec et al. 2018) and a system based on vegetation normally increases its effectiveness over time as the vegetation matures. The arrangement of the vegetation can also effect stormwater flow considerably (Forman 2014). Systems using vegetation to manage stormwater are often referred to as green-blue infrastructure, and are frequently used as part of climate resilient city planning (Kim 2018). Green-blue infrastructure can be defined further as either terrestrial or aquatic stormwater solutions. Aquatic solutions typically refer to different types of wetlands. Terrestrial solutions include infiltration basins, bioretention, biofilters, and rain gardens, and are often more spatially efficient than aquatic solutions (Zeunert 2017). Woody green spaces have been seen to be especially efficient in reducing runoff of stormwater (Forman 2014). In Scharenbroch et al. (2015), transpiration by trees in studied rain gardens accounted for 46-72% of the total water outputs. However, woody vegetation does not just contribute to more water returning to the atmosphere through transpiration, rain is also to a greater extent intercepted in the crown. This prevents some of the rainwater to even reach the ground, and the water subsequently evaporates back to the atmosphere directly (Livesley et al. 2016). Additionally, by using trees another vegetation layer is added to the structure which often adds multiple ecosystem services to a system (Dunnett and Clayden 2007).

The concept rain gardens originate from Prince George's County, Maryland, USA in the late 1980s (Dunnett and Clayden 2007) and using constructions as rain gardens to meet the challenges of stormwater management in urban areas are becoming increasingly popular worldwide (Siwiec et al. 2018). Rain gardens can work effectively because of their two main components; a filtering substrate with appropriate infiltration rate and suitable vegetation (Riley and Kraus 2016). If constructed properly, they can effectively reduce and delay flood peaks while simultaneously filtering water and recharging groundwater. The rain garden should be positioned to capture as much rain water as possible, preferably where it naturally would end up in the landscape. The sub-soil where the rain garden is located have an impact on the infiltration rate, e.g. high amount of clay reduces the infiltration rate. This should therefore as well be a criterion for positioning (Dunnett and Clayden 2007). Rain gardens are often less expensive in the long run than traditional sewage systems (Ishimatsu et al. 2017). However, this ultimately depends on a proper construction and choice of vegetation. Management of vegetation which are not suited for a site can result in great expenses, while also leading to an unsuccessful water management system. Further, the suitability of any measure towards flooding will inevitably depend on every specific site (Siwiec et al. 2018).

Choice of vegetation for raingardens

There are two main challenges facing vegetation growing in rain gardens; deficient nutrient levels and periodic drought and waterlogged conditions (Riley and Kraus 2016). These conditions are not tolerated by all tree species, and thus not all species can contribute to the function of rain gardens (Scharenbroch et al. 2015).

Vegetation with big root volume are recommended for rain gardens as these may better aid in maintaining the porosity of the soil substrate. An extended root system also has a greater chance of absorbing water in a bigger area, thereupon increasing the amount of water leaving the rain garden through evapotranspiration. However, the root growth should not be so aggressive as to risk drain-clogging (Hunt et al. 2012).

Vegetation with a shadowing canopy can be beneficial as this may effectively cool the water in the rain garden. This is not only beneficial since it reduces possible heat pollution but may also lower any eventual amount of algae in the water, which otherwise risk clogging the drains (Hunt et al. 2012). Preferably they should manage these challenging conditions while maintaining an aesthetic appearance and a continued transpiration (Scharenbroch et al. 2015, Riley and Kraus 2016).

Scharenbroch et al. (2015) identified three factors they deemed critical for trees possible contribution to rain gardens; the stomatal conductance rate, the total leaf area as well as size of the mature tree and, finally, the health and condition of the tree (Scharenbroch et al. 2015). Additionally, older trees are generally found to tolerate flooding or waterlogging better than younger individuals, such as seedlings or saplings, of the same species (Kozlowski 1984b).

Waterlogging

Regardless of a species tolerance-level to flooding, all plants respond to the anoxic[1] conditions in the soil created during waterlogging. This response is connected to both the abiotic factors (e.g. depth, timing and duration of flooding) and the biotic factors (e.g. development stage of the plant) (Glenz et al. 2006). The water by itself is thus not harmful to the plant, but rather the environment created in the soil (Kozlowski 1984b). In the following part of the literature study, the effects of waterlogging, and thereby the effects of O_2[2] depletion, on the soil and any vegetation growing in it will be explored further.

Effects of waterlogging on the soil

A waterlogged soil changes in both physical, chemical and biological ways, which effects its suitability for plant growth. The effect of waterlogging on the soil depends on the physical and chemical properties of the soil in question, as well as the duration of waterlogging (Ponnamperuma 1984).

When water is filling up the previously gas-filled pores in the soil, the level of O_2 lowers or becomes completely depleted (Ponnamperuma 1984, Kozlowski 1997). Any O_2 remaining in the pores is quickly consumed by microorganisms or any living roots present (Kozlowski 1984a, Ponnamperuma 1984). O_2 is however often still present in the upper-most millimetres of the water surface, where gaseous exchange is still possible (Ponnamperuma 1984, Kozlowski 1997).

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[1] Refers to an environment without any dissolved oxygen (Merriam-Webster.Com 2019a). A severe state of hypoxia, which refers to the deficiency of oxygen in an environment (Merriam-Webster.Com 2019b).

[2] It is important to distinguish between the elemental form and the molecular form of oxygen. In this thesis, they will be referred to in following way; oxygen when in elemental form and O_2 when in molecular form.

The composition of gases in a well-drained soil is commonly stable due to rapid gaseous exchange between air and soil. When supply of O_2 to soil is blocked, gases formed by the metabolism of the soil accumulates (Ponnamperuma 1984). Toxic compounds that form in an anoxic waterlogged soil contribute to the damage, growth reduction and mortality of plants growing on the site (Kozlowski 1997).

Effects and responses of woody species

Flooding with stagnant water is more harmful to trees in contrast to moving water, since moving water in general have a continuous influx of O_2. Some flood-tolerant species have even been seen to increase their height growth when flooded by moving water (Kozlowski 1984b). Further, negative effects due to waterlogging is less if it occurs during the dormant period of the tree, and the most sensitive period is in late spring, after the first flush of growth (Glenz et al. 2006). The duration of flooding events is also an important factor (Kozlowski 1984b). Overall the risk of damage increases with the duration of waterlogging. Short but frequent periods of flooding may however result in an accumulation of harmful effects and responses which together can cause serious damage to the tree (Glenz et al. 2006). In this part, the details of trees' responses towards waterlogging will be explored further.

Growth responses

The impeded gas exchange in the soil during waterlogged conditions effect plant performance negatively (Kozlowski 1984b). The lack of O_2 in waterlogged conditions causes decline in energy-consuming processes, and even death, by affecting vital physiological and metabolic pathways (Kozlowski 1984b, Ponnamperuma 1984, Glenz et al. 2006, Kreuzweiser and Rennenberg 2014). This decline of processes includes the growth inhibition of both roots and shoots (Kozlowski 1984a, Kozlowski 1984b, Schmull and Thomas 2000, Smith et al. 2001, Glenz et al. 2006, Kreuzweiser and Rennenberg 2014). However, growth responses is sometimes delayed and therefore not seen until the following growing season (Kozlowski 1984b).

Waterlogged conditions often change the allocation of photosynthate[3] within plants, and often result in a decreased height growth and increased growth of bark tissues (Kozlowski 1997). In Newsome et al. (1982) the dry weight increment of shoots, roots and leaves was reduced in seedlings of *Ulmus americana* after 28 days of flooding. The response of cambial growth varies however, from restriction in some species to acceleration in others (Kozlowski 1984b). An overall increase of stem diameter growth is often seen in flood-tolerant species when subjected to waterlogging. This is explained by Glenz et al. (2006) as the tendency for these species to produce more intercellular spaces and lower density cells, which in turn enables a more effective oxygen transport (Glenz et al. 2006).

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[3] Compounds produced by photosynthesis (Merriam-Webster.Com 2019c).

Leaf formation and expansion have shown to be negatively affected by waterlogging (Newsome et al. 1982, Kozlowski 1984b). The premature abscission of leaves is also commonly promoted in these situations (Kozlowski 1984b). All in all, this reduces the affected trees total leaf area (Kozlowski 1984b).

Roots, among other underground organs, are directly affected by waterlogging since it alters their immediate surroundings (Vartapetian and Jackson 1997). In addition, roots are more sensitive to the level of available O_2 than tissues over ground, and are therefore considerably affected by waterlogging (Kozlowski 1984b). Waterlogging often cause inhibition of root growth and even root dieback (Pereira and Kozlowski 1977). The root dieback caused by waterlogging results in a lower root/shoot ratio (Kozlowski 1997, Schmull and Thomas 2000), and a decrease in root hydraulic conductance (Schmull and Thomas 2000).

In Hallgren (1989), the growth response of 19 different *Populus* clones to different levels of flooding was investigated. The root growth was reduced by flooding and the stem growth increased or was unaffected by the treatment. Flooding caused all clones to develop morphological responses such as hypertrophied lenticels, stem hypertrophy, oxidation of the rhizosphere and increased root porosity. The author found that the capacity to grow roots in flooded soil was associated with the capacity for dry weight production in a flooded soil. The treatments in the study included a control group with well-watered soil as well as pots flooded up to 10 cm below soil surface and 5 cm below soil surface (Hallgren 1989).

Stomatal closure

One of the first responses to waterlogging is, for many species, closure of the stomata (Pereira and Kozlowski 1977, Newsome et al. 1982, Kozlowski and Pallardy 2002). This is likely triggered by a hormonal signal from root to shoot (Kozlowski 1997, Kozlowski and Pallardy 2002), which in its turn is believed by some to be triggered by a decrease in root hydraulic conductance (Reid and Bradford 1984, Schmull and Thomas 2000). However, all does not agree with this explanation of stomatal closure during waterlogging, dismissing the importance of water stress and root hydraulic conductance for the closure of the stomata (Kozlowski 1997).

The rapid reduction of the photosynthesis process that occur early during waterlogged conditions may be associated with the closure of the stomata. The photosynthesis rate is often lowered additionally by further repression of the photosynthesis process, commonly caused by loss of chlorophyll (as a cause of defoliation) and changes in carboxylation enzymes (Kozlowski 1997).

Nutrient uptake

The uptake of macronutrients, especially nitrogen, phosphorus and potassium, decreases during waterlogged conditions (Kozlowski 1997, Glenz et al. 2006). The decreased uptake of macronutrients has been connected to reductions in mycorrhizal content in the soil, transpiration, hydraulic conductivity, root metabolism and root dieback. Mineral absorption is not only reduced by decreased uptake but also by leakage of ions from the roots to the rhizosphere (Kozlowski 1997).

Denitrification processes in a hypoxic soil cause a decrease of nitrogen (Kozlowski 1997). In addition to this, waterlogged conditions, in which O_2 is limited, also cause a decline in nitrogen fixation (Glenz et al. 2006). However, flood-tolerant species often respond to flooding with an increased mineral nutrient uptake, which has been associated with several adaptions such as aerenchyma tissues, hypertrophied lenticels and adventitious roots (Kozlowski 1997).

Survival

Survival during waterlogged conditions can be achieved in two ways; avoidance of anoxia and through "true tolerance of anoxia". True tolerance relies on the use of alcoholic fermentation, among other biochemical changes. These responses can however only be temporarily sustained, and different ways of avoidance is often more important for the survival of the plant (Vartapetian and Jackson 1997). The different strategies and adaptations for surviving waterlogging will now be explored further.

True tolerance

Metabolic adaptations

To enable continued metabolism, anaerobe respiration is usually accelerated during waterlogging at a level which provide the roots with enough energy to continue nutrient uptake (Hook 1984, Armstrong et al. 1994, Kozlowski and Pallardy 2002). And since less tissue often is developed during waterlogging, the need for energy is as well reduced (Hook 1984). This can be regarded as a tolerance to anoxic conditions, and is depended on both the control of metabolism and availability of additional energy resources (Armstrong et al. 1994). Any tolerance of anoxia is however only temporary for vascular plants (Vartapetian and Jackson 1997). Eventually the need for oxygen must be met to enable aerobe respiration, to oxidise nutrients and reduce toxic compounds in the soil (Hook 1984, Armstrong et al. 1994, Vartapetian and Jackson 1997). The length of time during which different plants can survive by anaerobe respiration may however vary from hours to months depending on site-specific conditions and the species affected (Armstrong et al. 1994).

Some species subject to seasonal waterlogging will enter a state called anaerobic dormancy. This refers to a strategy where the shoot tissues survive the anoxic conditions by entering a dormant state with low metabolic activity. Large carbohydrate reserves are necessary for this response (Vartapetian and Jackson 1997).

However, results summarized by Vartapetian and Jackson (1997) indicate that the ability for some species to inhabit waterlogged soils do not seem to be associated with the anoxia-tolerance of the roots. Flood-tolerant species have in fact been shown to be generally more sensitive to anoxia than typical flood-intolerant species. These species must subsequently depend on a continuous supply of oxygen and thus have developed one or several avoidance strategies for the anoxic conditions.

Avoidance

O2-transpiration

In optimal conditions where an oxygen-rich environment cover a large part of the root and shoot surface, there is a lesser need for gases to transport longitudinal between shoot and root. However, in saturated soils, this transport becomes more vital for the survival of the plant (Armstrong 1980). The aerial tissues play an important role in absorbing O_2 in these conditions (Kozlowski 1997, Glenz et al. 2006), which can be transported through the stem and diffuse from the roots to the rhizosphere. For woody species the lenticels on the stem plays an important role in absorbing O_2, in contrast to herbaceous species which are more depended on the leaves for this oxygen-supply (Hook 1984). A permeable cambium, found in some flood-tolerant species, aids further in the supply of O_2 to the plant (Kozlowski 1997). This transportation of O_2 enables in its turn the oxidization of toxic compounds in the soil and the uptake of macronutrients (Glenz et al. 2006). Adaptations such as hypertrophied lenticels, aerenchyma and adventitious roots increase this uptake and promotes the O_2 transport to the root system by forming a continuity of intercellular space from the atmosphere to the rhizosphere (Hook 1984, Vartapetian and Jackson 1997, Glenz et al. 2006).

Roots

Mangrove species have a particular strategy to successfully avoid anoxic conditions during waterlogging. By the formation of stilt roots and pneumatophores, where O_2 is absorbed by lenticels on the surface and transported to submerged roots, a continuous supply of O_2 is achieved (Kozlowski 1984b, Kozlowski and Pallardy 2002). However, few species have these highly specialized adaptations.

Plants experiencing flooding-stress have been seen to produce root forms that are distinctively different from each other. Hook (1984) separate these root forms into three types; adventitious roots, altered soil roots and soil water roots.
Adventitious roots are produced by several different species but are especially associated with flood-tolerant species (Hook 1984, Kozlowski 1984b, Kozlowski 1997, Smith et al. 2001). This type of roots form above the soil and normally beneath the water surface (Hook 1984). They are better adapted to anoxic conditions due to being able to tolerate higher levels of CO_2 and by containing a higher content of aerenchyma (Kozlowski 1984b, Glenz et al. 2006). Adventitious roots aid in oxidizing the rhizosphere and increases the water absorption (Kozlowski 1984b, Kozlowski

1997, Smith et al. 2001). Altered soil roots are roots produced in the soil during waterlogged conditions which are morphologically different from roots produced in a more aerated soil. Soil water roots however, are roots that grow in the submerged soil and does not differ from roots grown in aerated soils. Findings of soil water roots are less reported than the two previously mentioned types (Hook 1984).

In sites with fluctuating flooding, the morphological response to produce new roots during, as well as after, floods are important for the establishment and survival of the affected tree. The ability to grow roots during flooding gives an opportunity to exploit larger soil volumes. This aids in withstanding alternating flooding and drying of a site, since the roots are not restricted to the soil surface, and result in a more stable and extensive root system (Hook 1984, Smith et al. 2001).

Aerenchyma

Many plants form aerenchyma in response to flooding (Kozlowski 1984b, Kozlowski and Pallardy 2002). The formation of aerenchyma is triggered by ethylene and forms generally by the disintegration or separation of the cortical cells. This leaves behind intercellular spaces where gas can flow (Angeles 1992, Glenz et al. 2006). Aerenchyma thus facilitates the transport of O_2 from the aerial tissues to the roots (Kozlowski 1997, Kozlowski and Pallardy 2002, Glenz et al. 2006) but also reduces the number of cells in need for oxygen (Vartapetian and Jackson 1997). Mommer et al. (2006) saw, when studying herbaceous plants completely submerged in water, that the aerenchyma content in the plants directly affected the plants ability for survival.

Hypertrophied lenticels

Hypertrophied lenticels form on the submerged parts of the stem and roots on several different species of gymnosperms and angiosperms during waterlogging (Kozlowski 1984b, Kozlowski 1997). They normally develop in the same location where a stoma earlier occurred (Glenz et al. 2006) and becomes a pathway for the passage of gases (Kozlowski 1984b, Glenz et al. 2006). These aid the exchange of dissolved gasses in the water and, for some species, the release of toxic compounds developed in the soil. Further, they may facilitate the forming of adventitious roots (Kozlowski 1984b). In the study of Newsome et al. (1982) adventitious roots grew through where hypertrophied lenticels previously had been located on all plants subjected to flooding in the study.

Hormones

Many of the morphological responses of trees to flooding has also been shown to be affected in a similar way by application of different plant hormones. The experimental evidence of hormonal responses of trees to flooding is however overall lacking. The most studied hormone is ethylene (Reid and Bradford 1984) which for example have been shown to cause initiation and acceleration of leaf shedding in a similar way as waterlogging (Kozlowski 1997).

Post-flooding

The different alterations caused by flooding affect the productivity and survival of the tree also after the flood has retreated (Kozlowski 1984b). The decreased root/shoot ratio might cause the previously flooded plants to be less drought tolerant because of its lesser root system failing in replenishing transpirational losses (Newsome et al. 1982, Kozlowski 1984b, Kozlowski 1997). Additionally, the capacity for adventitious roots and roots formed in waterlogged soil to oxidize the rhizosphere is lost when the roots harden during dry soil conditions (Hook 1984, Smith et al. 2001). Thus, the production of these root formations does not give the tree an advantage in the event of a returning flood.

Plant strategies

This part of the literature study will explore Grime's CSR-theory of plant strategies and leaf economics. It will then continue by looking at the plant trait Specific leaf area (SLA) and its response towards waterlogging.

The CSR-theory

All life depends on the utilization of carbon and it is therefore interesting to study carbon resource acquisition and the traits involved when trying to understand the adaptive strategies of different plants (Grime and Pierce 2012). The CSR-theory tries to define the primary strategies of all living matter and predicts a trade-off between acquisitive and retentive plant physiology (Grime 2001).

According to Grime (2001) there are two different external factors which limit the quantity of plant material in any habitat; stress and disturbance. Stress is here defined as any factor which restrict photosynthesis. Examples include shortage of light, water or mineral nutrients as well as sub-optimal temperatures. The author further defines disturbance as any factor associated with destruction of plant biomass. This may be caused by e.g. grazing and trampling by herbivores or damage by wind, frost, drought or fire. When the extremes of these two factors are combined, high/low disturbance with high/low stress, four different habitat extremes are apparent. High stress combined with high disturbance are however not a viable habitat for plants, and therefore only three extremes are left.

Stress and disturbance	**Low disturbance**	**High disturbance**
Low stress	Compeditors	Ruderals
High stress	Stress-tolerators	-

Fig 2. Table of habitat extremes. Interpretation based on the table in Grime (2001).

These three extremes give the three different plant strategies first explored by Grime (1979); competitors, stress-tolerants and ruderals (see fig 2). This theory tries to explain the evolutionary trade-off between competing for resources, tolerance towards resource limitation and the handling of biomass damage (Grime and Pierce 2012). A good way to visualize these extremes is to plot high/low disturbance against high/low stress. This results in a triangular space representing the range of conditions viable for plants, and the connected strategies (see fig 3) (Grime 2001).

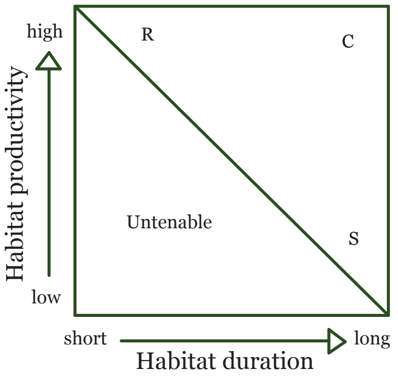

Fig 3. The untenable triangle. Interpretation based on the original in Grime (2001).

In 2003, Mustard et al. (2003) developed a computer model to investigate pattern of strategy variation using model plant populations. The model environment contained varying nitrogen availability and disturbance frequency, representing level of stress and disturbance. When the model was run, the same strategies as described by Grime; competitors, ruderals and stress-tolerants, emerged associating with three extreme combinations of stress and disturbance. The fourth extreme failed to inhabit any plant population long-term, which inhibited the evolution of plant populations. This was the first time that the untenable triangle received theoretical support (Mustard et al. 2003).

Below follows a short explanation of the three main strategies included in the CSR-theory.

Compeditors (C)

Competition is defined by Grime (1979) as “the tendency of neighbouring plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space.” This definition limits the term to include only the capture of resources and how plant supress fitness of neighbouring vegetation by altering the environment (Grime 2001). Competitors are found in productive habitats and survive using traits that maximise acquisition of resources (Grime and Pierce 2012).

Stress-tolerators (S)

In Grime (2001) stress is defined as “the external constraints which limits the rate of dry matter production of all or part of the vegetation.” Vegetation growing in these unproductive habitats have developed strategies to endure the stress at-hand, and are thus categorized as stress-tolerators (Grime 2001). Even if several different types of stresses are possible, these plants survive unproductive and variable habitats by depending on one mechanism; maintenance of metabolic performance. Stress-tolerators generally invest their resources in tough tissues and internal stores. Thicker tissues may however restrict movement of resources within the plant and thus inhibit rapid growth (Grime and Pierce 2012).

Ruderals (R)

Density of vegetation is not only restricted by environmental stress but also by disturbance (Grime 2001). Grime (2001) defines disturbance as “the mechanism which limits the plant biomass by causing its partial or total destruction.” Disturbance is thus distinguished from stress as events causing tissue death, from which the tissue can’t recover (Pierce et al. 2005). Productive habitats affected of low disturbance intensities favours competitive species. However, when disturbance is high and continuously repeated, competitors no longer have an advantage. Vegetation populating these habitats are categorized as ruderals. These plants typically have a short life-span and a high seed production, which enables regeneration in habitats with frequently occurring lethal disturbance (Grime and Pierce 2012). No woody species have been found to be a predominant R-strategist (Grime 2001).

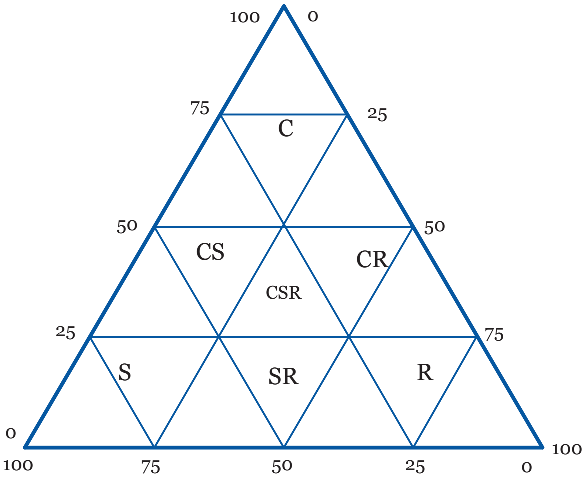

Fig 4. The CSR model is typically demonstrated by a ternary plot, where each axis represents the relative importance of competition, stress and disturbance. Interpretation based on the original in Grime (2001).

However, these are the extremes of Grime's model, and pure C, S or R-strategists are unlikely to be found in nature (Pierce et al. 2005). Different mixtures of these strategies can be found for plants which have evolved in habitats with intermediate levels of stress and disturbance. Thus, four additional possible strategies are apparent; C-R, C-S, S-R and C-S-R (see fig 4) (Grime 2001).

It is important to point out that ecotypic variation may pose a problem when trying to fit a species to a specific strategy. Individuals within species growing in contrasting environments have been shown to exhibit different strategies (Pierce et al. 2013). This is important to take in consideration, especially when trying to find the strategy of a species using data from different biomes.

Traits and leaf economics

Grime showed in 1997 correlations between different plant traits which was said to indicate a "trade-off between attributes conferring an ability for high rates of resource acquisition in productive habitats and those responsible for retention of resource capital in unproductive conditions" (Grime et al. 1997). Trade-offs are caused by the fact that all plants have a limited amount of resources in any habitat, and the difference in how the plants "choose" where to allocate them (Reich 2014). The leaf economic spectrum (LES), published in 2004, used six different plant traits to show that leaf investments of widely different plant forms can be represented on a single axis running from acquisitive to conservative resource economics (Wright et al. 2004). The spectrum ranges from short-lived, easy constructed leaves with a high rate of photosynthesis, to less active, durable leaves that are more expensive to construct (Shipley et al. 2006). This spectrum showed that plants seem to have little room to manoeuvre in regards to how they construct their leaves (Whitfield 2006). Leaf economics have been seen to explain a big part of the variation of CSR-strategies of plants (Pierce et al. 2012) and leaf level variation can be expected to represent variation on the whole-plant level as well (Reich 2014, Díaz et al. 2016, Sartori et al. 2019). However, for woody species the relationship between leaf variation and variation among other tissues might not always be strong, caused by the differing amount of non-photosynthesizing tissues (Sartori et al. 2019).

The LES is linked to the slow-fast continuum (Reich 2014, Sartori et al. 2019). Slow-growing and long-lived species have been shown to generally inhabit cold and/or arid habitats, whilst fast-growing and short-lived species is found in more favourable environments (Sartori et al. 2019). In contrasting environments, different sets of fast-slow strategies evolve along with different leaf traits (Sartori et al. 2019). As with CSR-strategies, leaf economics may vary considerably within a species across its habitat range. This intra-specific variability is important to consider when using species-level mean trait values for regional to continental models (Niinemets 2015).

Since leaf traits can be measured on all plants, variation of leaf economics and leaf size offers potential for a global system of plant ecology comparison (Pierce et al. 2016). Pierce et al. (2016) tried to fit over 3000 plant species growing in different habitats world-wide in the CSR ternary space. They started with using 14 traits on a whole-plant level, and after this using only three leaf traits; leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC). When comparing the resulting multivariate spaces, they saw a relatively small information loss when only using the three leaf traits. Therefore, they concluded that the multivariate space as described only using leaf traits was representative of the functional variation of plants from across the globe. The study resulted in a framework for categorizing the strategies of plants in accordance to the CSR-theory (Pierce et al. 2016).

Specific leaf area, (SLA)

Aside from being used as component in CSR-analysis, SLA is an important plant trait when researching morphology and physiology in different fields as forestry, ecology and agronomy (Poorter et al. 2009). It is often coupled with relative growth rate (RGR) in growth analysis, as they scale positively and linearly to each other (Lambers and Poorter 1992, Poorter et al. 2009).

SLA varies greatly in nature. The variation can be caused by differing number of cells per area, but also because of varying chemical composition, morphology or anatomy (Lambers and Poorter 1992). Some of this variation is seen between functional groups (evergreen, broad leaved, succulents etc.). Biggest part of the variation can however be found within groups and biomes, with slow-growing species possessing overall low SLA (Poorter et al. 2009). For example, evergreen species generally have lower SLA values than deciduous species. But when comparing this variation with variation within the groups, the difference is at least as large (Poorter et al. 2009).

Leaves with high SLA generally have high concentrations of proteins, minerals and organic acids (Poorter 2002). A leaf with higher SLA also have a higher maximum photosynthetic capacity and higher leaf nitrogen. This relationship is seen both within and between functional groups (Reich et al. 1998). In addition to this, species with high SLA generally have a higher nutrient uptake and thus also higher respiration rate. However, when compared to level of carbon fixation, they have a lower respiration rate per carbon fixed than species with low SLA (Lambers and Poorter 1992). In more general terms, one can say that species with high overall SLA are “fast species” (Reich 2014).

Low-SLA leaves generally contain higher amounts of lignin (Poorter 2002). The lignin is found in the cell walls and low-SLA leaves are thus tougher and less attractive to herbivores (Lambers and Poorter 1992, Poorter 2002, Poorter et al. 2009). This investment in protective leaf structure decreases the rate of photosynthesis per leaf, but increases the possibility of a longer leaf lifespan. This further decreases the potential loss of nutrients (Lambers and Poorter 1992). Grown in controlled environments, evergreens with lower SLA also has a longer leaf longevity. This relationship is not as clear for deciduous species. A probable cause is that they are programmed for leaf abscission, and there is therefore little gain in investing in leaf longevity (Poorter et al. 2009). However, Mommer et al. (2006) saw a positive relationship between SLA and leaf longevity during total submersion in water. The authors explained this with a high SLA resulting in an increased gas exchange under water. This contradicts the relationship between SLA and leaf longevity described here and shown in Wright et al. (2004), thus indicating that those general patterns might not hold under stressful conditions.

In addition to what have been said, species with lower SLA tend to have a greater lifespan of their root system. This can aid in the conservation of nutrient and carbon (Poorter et al. 2009), as well as water uptake (Grime 2001). Confirming this, habitats affected by drought and/or limited nutrient availability, e.g. deserts and shrublands, tend to inhabit a large proportion of low-SLA vegetation (Poorter et al. 2009).

SLA of different leaves can vary greatly within the same tree, caused by change in light intensity (Jurik 1986), water availability (Koch et al. 2004), air temperature and wind speed etc. (Baldocchi et al. 2002). SLA of leaves in general change during the development of the leaf. SLA is typically low right after bud-burst, followed by an increase during leaf-expansion and after this the SLA drops (Jurik 1986). This is likely caused by the construction of cell-wall material and chloroplasts during the formation of the leaf (Poorter et al. 2009). After leaf formation SLA may fluctuate but remains over-all stable the rest of the growing season (Jurik 1986, England and Attiwill 2008, Poorter et al. 2009). SLA has been shown to have a diurnal variation as-well, with lowest values at the end of the night and highest at the end of the day (Poorter et al. 2009). In addition to this the height and age of trees affects the SLA of leaves as well (England and Attiwill 2005, Poorter et al. 2009).

Environmental impacts and intraspecific variability

SLA is a highly plastic trait (Poorter et al. 2009, Mitchell and Bakker 2014) and has been shown to vary with a number of different environmental variables (Poorter et al. 2009, Dwyer et al. 2014, Rodríguez et al. 2015, Maracahipes et al. 2018, Rodriguez et al. 2018, Sandel and Low 2019). Although SLA generally varies more between than within species, intraspecific variation is often high when comparing individuals growing in different environments (Jung et al. 2010). Further, species that have a similar mean SLA can differ in their SLA responses towards different environmental conditions (Dwyer et al. 2014).

Intraspecific variability plays a big part in the ability for certain species to grow in different and sometimes widely contrasting habitats. Generalist species depend on a high intraspecific variability to be able to match their habitat strategically (Maracahipes et al. 2018). Maracahipes et al. (2018) showed that this variability was manifested in several different plant traits, including SLA. From this they concluded that these traits probably play a key role for adaptation of the studied species to the habitats included in the study; forest and savannas.

SLA of evergreen species have been shown to vary seasonally correlating with water availability (Liu and Ng 2019). For *Eucalyptus* trees growing in an area prone to seasonal drought, SLA was shown to vary around 20% throughout a year. Lowest values was measured at the end of the 5-month dry season and highest a few month after the beginning of the wet season (Nouvellon et al. 2010).

A study censuring grassland vegetation along a precipitation gradient in California, USA, showed a strong intraspecific SLA variation within different species. Even though higher precipitation areas was populated by species with higher overall SLA, there was a tendency for species to exhibit lower SLA-values as precipitation increased (Sandel and Low 2019). Lajoie and Vellend (2015) showed a similar result along an elevation gradient. While the overall SLA of the vegetation decreased with higher elevation, intraspecific SLA increased. Dwyer et al. (2014) did however see an increase of SLA with higher precipitation, and very little contribution from intraspecific variability to that relationship. Nevertheless, Sandel and Low (2019) suggests that their seemingly paradoxical result might be a cause of covariance of plant traits. They discussed that the decrease in SLA with higher precipitation could be caused by the covariance structure of plant traits shifting with the environmental gradient. In agreement with this Anderegg et al. (2018) saw that few plant traits respond to environmental variables in exactly the same way.

When subjected to shading, leaves have been seen to change morphologically within a number of days. In a study on soybeans the carbon content in leaves (derived from SLA) decreased sharply the first three days of shading, and then stabilized. This was explained by the relocation of mobile carbon compounds from the shaded leaf (Pons and Pearcy 1994). Mature leaves have a less flexible LVA (leaf volume per area) compared to leaves still in expansion phase. The reduction in SLA seen in mature leaves is thus explained as a connection to decreased leaf density (Poorter et al. 2009).

Oguchi et al. (2005) investigated the response towards transferring from low to high irradiance of mature leaves of three different tree species, *Betula ermanii* Cham., *Acer rufinerve* Sieb et. Zucc and *Fagus crenata* Blume. An increase of photosynthesis rate per leaf area could be seen for *B. ermanii* and *A. rufinerve*. However, the cause of this increase was different for the two species. The leaves of *B. ermanii* grown in low light were thick with vacant spaces along the mesophyll cell surface. When transferred to high light these spaces were filled by the enlargement of chloroplasts. *A. rufinerve* however, showed a plasticity of the mesophyll cell surface area and leaf thickness. These increased when in high light, which subsequently increased the number of chloroplasts (Oguchi et al. 2005).

Response to waterlogging

Stress-driven SLA plasticity might play a key-role for plants in managing resources and maintaining a viable productivity when environmental variables such as water levels are variable and unreliable (Liu and Ng 2019). In the study of Rodríguez et al. (2015), changes of post-flooding leaf traits where explored in three different clones of *Populus deltoides*, each with a different degree of flooding sensibility. The authors found that the formerly flooded plants produced leaves with both increased leaf area and leaf thickness compared to the control plants, thus resulting in an unchanged SLA. The plants thus compensated for the reduced growth and leaf abscission during waterlogging by substituting the loss in leaf area rather than increasing the photosynthetic activity (Rodríguez et al. 2015). In another study of two hybrid *Populus* clones a reduction in SLA was seen after the plants were subject to cyclic flooding (Liu and Dickmann 1992). This was also seen in the study of Rodríguez et al. (2015) after longer periods of flooding. Luquez et al. (2012) found that the leaf area of newly expanded leaves for 14 different *Populus* clones decreased after 35 days of flooding. Both Schmull and Thomas (2000) and Colin-Belgrand et al. (1991) saw a reduction of SLA for different species of *Quercus* when subjected to waterlogged conditions, though not all significant. In both studies, *Q. robur* was the only one showing a significant decrease of SLA. Schmull and Thomas (2000) discussed that this response might act as a compensation for the reduction in leaf area during the experiment, and resulting in a better water-use efficiency of the trees. Dale and Causton (1992) saw a significant lower SLA for three different species of *Veronica* when grown in waterlogged soil. This was also seen for three different species of *Brachiaria* growing in waterlogged conditions for two weeks (Dias-Filho and Carvalho 2000).

Waterlogging seems to generally result in smaller leaves and lower SLA, which is

supported in Poorter et al. (2009).
Poorter et al. (2009) suggests that this may be a cause of a hindered water uptake of the roots caused by anaerobic conditions, and the continued evaporation from the leaves still in the air. This is also supported by Luquez et al. (2012), who suggests that a lowered leaf area during waterlogging causes reduced water flow in roots. SLA is often seen to respond similarly to waterlogging as to drought (Poorter et al. 2009, Rodriguez et al. 2018) and as explained by Poorter et al. (2009) the plant subjected to waterlogging suffers from drought stress, which in its turn is causing a lower SLA and leaf area (Poorter et al. 2009). This reduction in leaf area is thought to aid in reducing further water-loss of the plant (Luquez et al. 2012). Reduction of leaf area also reduces the carbon fixing capacity of the plant in question and thus inhibits further plant growth (Luquez et al. 2012, Rodríguez et al. 2015). It is highly probable that the duration of waterlogging influences the level of impact on SLA (Rodríguez et al. 2015).

Introduction

Litterature study

Part 3

Results

- Stomatal conductance
- Midday leaf water potential
- Correlation leaf economics and ψ_L
- Plasticity of specific leaf area

Following part of the thesis will describe the results from the experiment. It will start by describing seen effects on stomatal conductance (g_l), then midday leaf water potential (ψ_L), and after this explore the correlation between ψ_L and leaf economics. Lastly, it will present the results from analyses of SLA plasticity.

Discussion & Conclusion

Stomatal conductance, g_l

A mixed model ANOVA was used to analyse the treatment effect of stomatal conductance (g_l), comparing the control group with treatment CW. Each day was analysed separately and the result of the four analyses can be seen in table 1-4. One asterisk indicates statistically significant differences at $p<0,05$, two asterisk at $p<0,01$ and three at $p<0,001$. An interacting effect of treatment and species can be seen for day 7, 14 and 28. On day 2, only a significant difference of g_l can be found between species.

Fig 5 shows the result of the post-hoc test. Significant treatment effect on stomatal conductance can be seen for approximately half of the measurements, and within most of the species. Only *Tilia tomentosa* show significant effect of waterlogging on stomatal conductance day 2. *Magnolia x loebneri* display one significant treatment effect on day 14. *Acer saccharinum, Fraxinus pennsylvanica, Quercus palustris* stand out by displaying no significant treatment effect for any of the measurements. However, *Q. palustris* day 14 is almost significant with a p-value of 0,0580 and *F. pennsylvanica* day 28 is almost significant with a p-value of 0,0653.

Day 2	F-value	p-value
Species	20,9426	<0,0001 ***
Treatment	2,2344	0,1523
Spec:Treat	1,2591	0,2695

Day 7	F-value	p-value
Species	29,1304	<0,0001 ***
Treatment	10,9674	0,0038 **
Spec:Treat	3,7789	0,0005 ***

Day 14	F-value	p-value
Species	22,3539	<0,0001 ***
Treatment	45,8282	<0,0001 ***
Spec:Treat	3,0556	0,0033 **

Day 28	F-value	p-value
Species	9,8403	<0,0001***
Treatment	25,7605	<0,0001 ***
Spec:Treat	1,2591	0,0286 *

Tables 1-4. ANOVA results of effect on g_l.

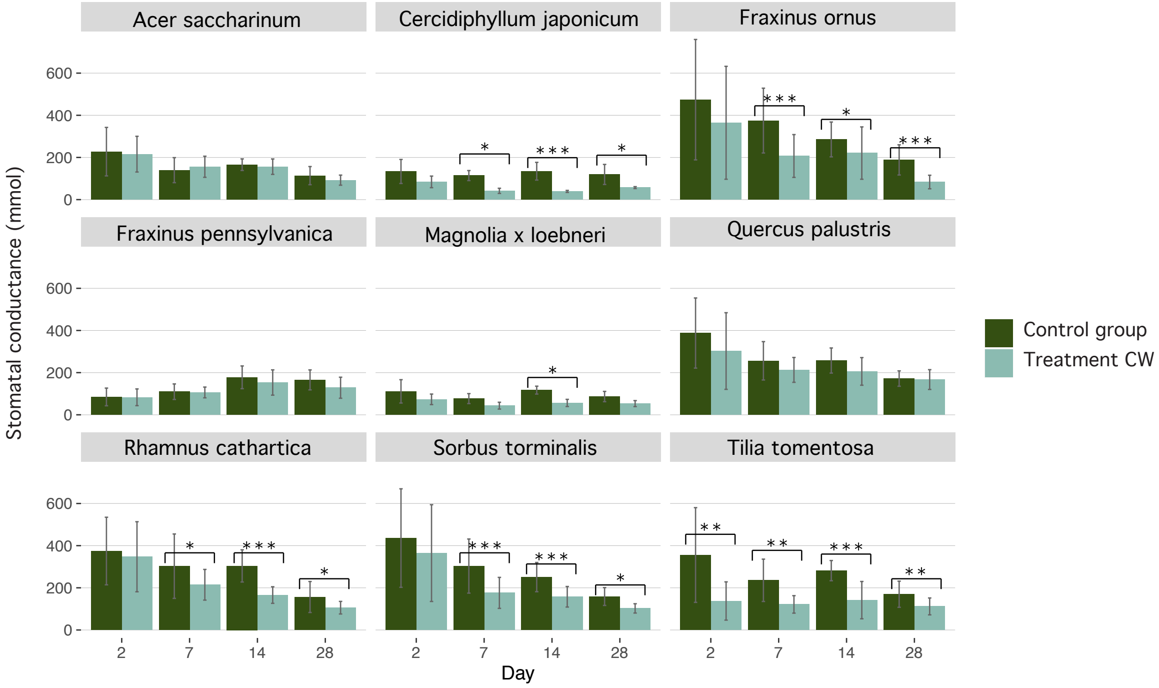

Fig 5. Plot showing treatment-effect on stomatal conductance.

Midday leaf water potential, ψ_L

Mixed model ANOVA was used to explore the differences in ψ_L between the control group and treatment CW. Each day was analysed separately and the result of the analyses can be seen in tables 5-7.

Significant effect can be seen for species on all three days and significance is also seen for treatment on day 21. Interaction effect can be seen between species and treatment day 7. To explore these effects closer a tukey post-hoc test was used. The result can be seen in fig 6.

Only one leaf of *C. japonicum* was left to measure day 21 in treatment CW, which explains its lack of standard error bar. Significant effect of treatment was found for *C. japonicum* day 7, *M. loebneri* day 21, *S. torminalis* day 21. Even if these are the only significant effects that was shown, some trends can be seen in the result.

C. japonicum, *F. ornus*, *M. x loebneri* and *S. torminalis* show a consistently consistently lower (more negative) ψ_L for the treatment. The treatment-effect on *A. saccharinum*, *R. cathartica* and *T. tomentosa* varies, with no clear trend. The treatment of *Q. palustris* and *F. pennsylvanica* show a consistently higher (less negative) ψ_L than the control group for all measurements.

Day 2	F-value	p-value
Species	45,4331	<0,0001 ***
Treatment	1,4432	0,2452
Spec:Treat	1,9043	0,0636

Day 7	F-value	p-value
Species	23,9107	<0,0001 ***
Treatment	0,7671	0,3927
Spec:Treat	2,3514	0,0209 *

Day 21	F-value	p-value
Species	14,9949	<0,0001 ***
Treatment	4.3904	0.0378 *
Spec:Treat	1.8405	0.0736

Tables 5-7. ANOVA results of effect on ψ_L.

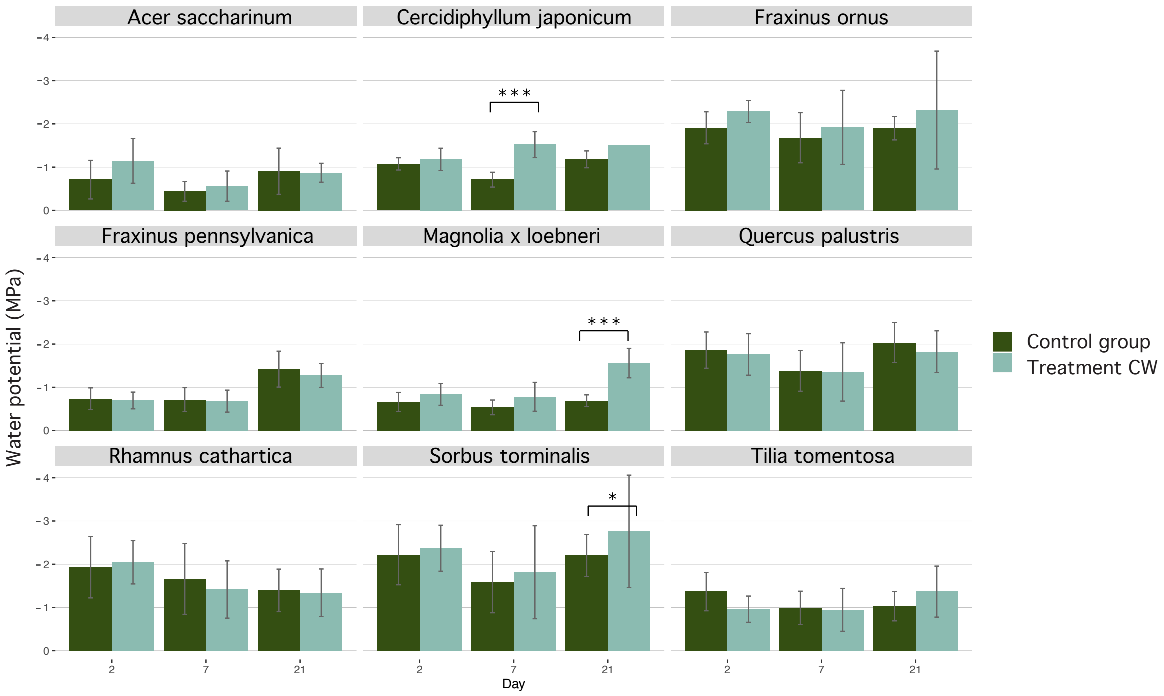

Fig 6. Table showing treatment-effect on midday leaf water potential.

Correlations leaf economics and ψ_L

SLA and ψ_L

By analysing the SLA values of the control groups, which were not subjected to any treatment, it is possible to see if SLA value differs significantly between the species. A one-way ANOVA was used to analyse the different SLA-values of the species.

	F-value	p-value
Species	50.5444	<0,0001 ***
Day	14.4971	<0,0001 ***
Block	0.6916	0.7163
Spec:Day	1.5352	0.0885

Table 8. ANOVA results differences of SLA between species.

	Est. mean	Group
Sorbus torminalis	20.1	a
Quercus palustris	22.6	ab
Fraxinus ornus	23.9	bc
Tilia tomentosa	25.8	cd
Acer saccharinum	26.7	cd
Fraxinus pennsylvanica	26.7	cd
Magnolia x loebneri	26.8	cd
Rhamnus cathartica	28.7	d
Cercidiphyllum japonicum	37.8	e

Table 9. Species grouped by mean SLA values.

The result of the one-way anova shows significant difference in SLA between species and day, and no block effect (see table 8). Tukey post-hoc test was used to explore the differences in SLA between the species. The plot in fig 7 and post-hoc test seen in table 9 illustrates how the species differ from each other.

	F-value	p-value
Day	0.9809	0.4004
SLA	0.7626	0.3980
Day:SLA	1.1107	0.3579

Table 10. ANOVA results of correlation to ψ_L.

To follow this up, a mixed model anova was used to see if any correlations could be found between each species SLA values and the treatment effect of ψ_L. The result seen in table 10 show no significant effect on ψ_L explained by SLA. This lack of significance points towards no correlation between a species SLA and its reaction towards water-logging shown in ψ_L.

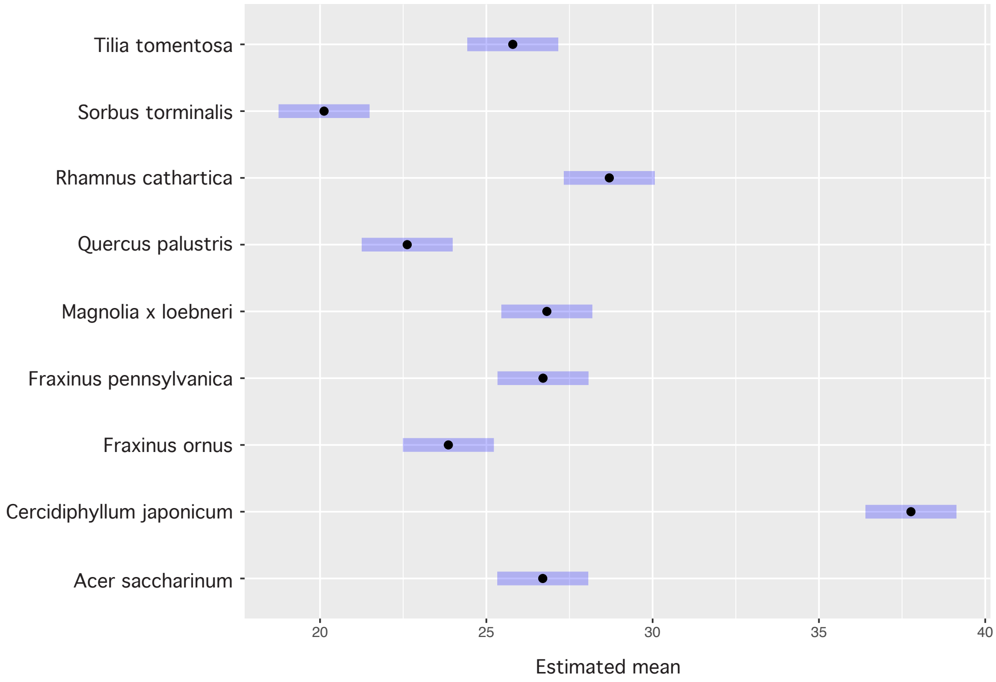

Fig 7. Plot showing estimated mean SLA of the species.

CSR and ψ_L

The spreadsheet from Pierce et al. (2016) was used to categorize the species according to CSR-theory. This was done by using the traits measured during the experiment: SLA, LDMC and LA. The tertiary graph seen in fig 8 shows the calculated position in the CSR ternary plot of the different species, using species mean values. To ensure that the mean values was representable for each species, all individuals within the species was plotted first and the distribution of the data points was analysed. All species clustered sufficiently enough to use the mean for further analysis.

A mixed model anova was used to see if any correlation could be found between each species CSR- strategy and its reaction to waterlogging, described by ψ_L. The analysis was done using the S-value from the calculated CSR-value, since the S-value can be expected indicate a species stress-tolerance.

	F-value	p-value
Day	0.5411	0.5952
Stress-value	0.2542	0.6289
Day:Stress	0.4337	0.6576

Table 11. ANOVA results of correlation to ψ_L.

The result from the ANOVA seen in table 11 showed no significant effect on ψ_L that could be explained by the S-value of each species. This result indicates that the S-value of a species does not correlate with its reaction towards waterlogging as displayed in ψ_L.

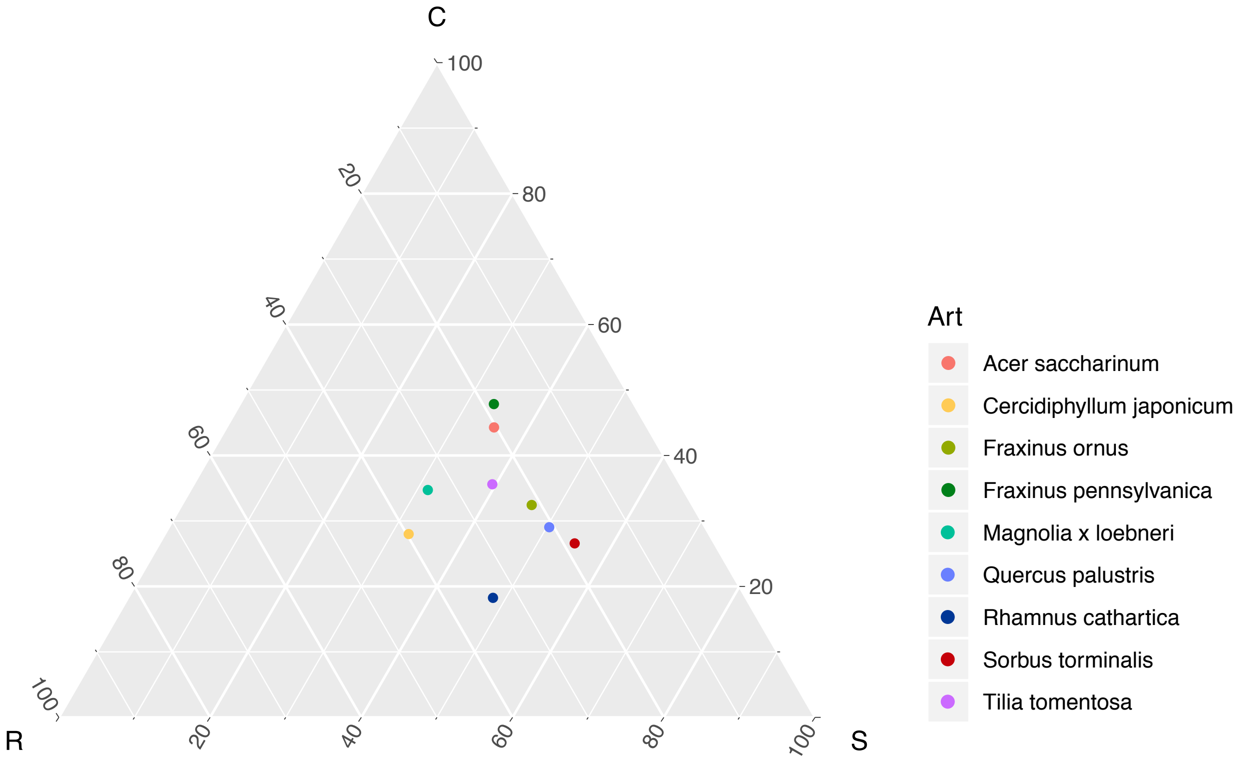

Fig 8. Graph showing calculated CSR-values of the species.

Plasticity of SLA

A few analyses were made to explore any effect on SLA of the different species. This was done to see if the described plasticity of SLA seen in the literature, also could be seen in this study.

Control group vs. treatment

A mixed model ANOVA was used to search for any effects on SLA affected by species, treatment or measurement occasion. Since only one individual of *C. japonicum*, treatment CW had leaves left on the 21st day, the species had to be excluded from this analysis of plasticity.

The results of the mixed model anova seen in table 12 show that the treatment had a significant effect on SLA, and that there is a significant difference between species and day. It further shows that there is an interaction effect of species and day of measurement on SLA. A post-hoc test was conducted to investigate where significant differences could be found (see fig 9). Significant differences between treatment and control group for could be found for; *F. ornus* day 7, *F. ornus* day 21, *R. cathartica* day 2 and *S. torminalis* day 7.

	F-value	p-value
Treatment	16.1475	0.0008 ***
Species	30.9970	<0,0001 ***
Day	28.0877	<0,0001 ***
Treat:Spec	0.8985	0.5100
Treat:Day	0.1269	0.8809
Spec:Day	2.7405	0.0008 ***
Treat:Spec:Day	0.9946	0.4587

Table 12. ANOVA result of treatment-effect on SLA.

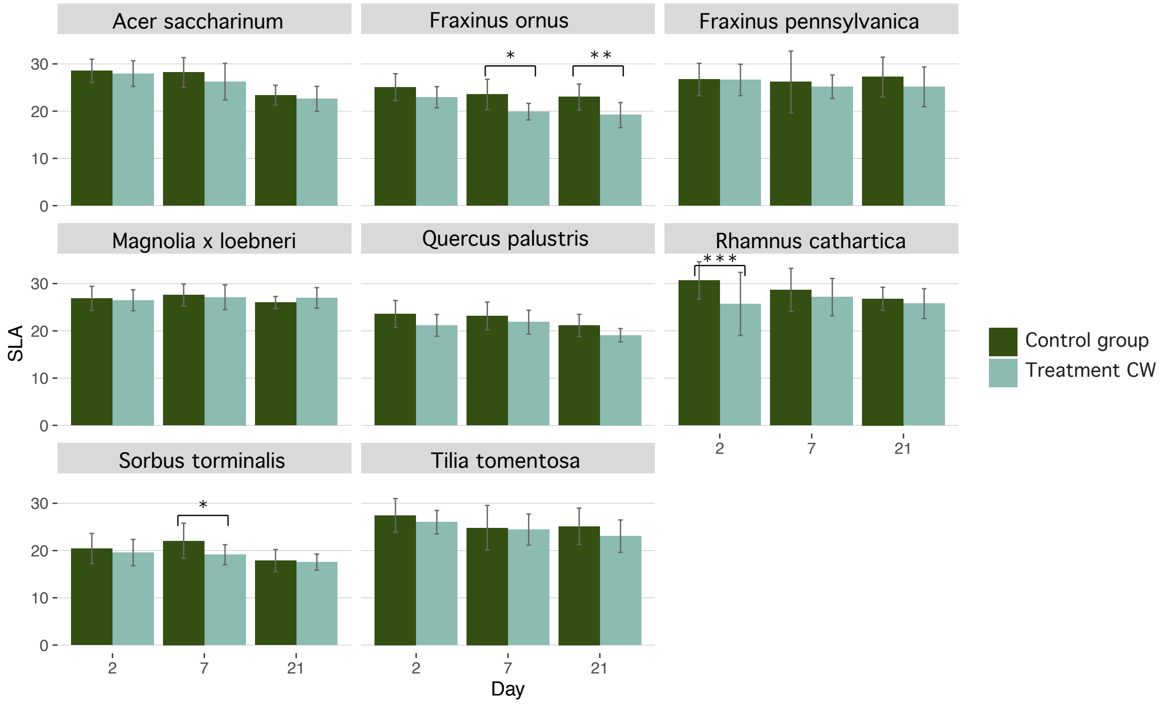

Fig 9. Plot showing treatment-effect on Specific leaf area.

Treatment effect day 2

Since the result from the mixed model ANOVA showed no interaction effect with treatment included, it can be concluded that the treatment effect on SLA of the different species is displayed in the same manner. In fig 9 it seems that this treatment effect can be seen already after 2 days. To explore this further, an analysis of treatment effect day 2 was made. In this analysis, all three treatments (2d, 5d and CW) could be included since all of them was still in water.

	F-value	p-value
Treatment	2.7708	0.0555
Species	147.5339	<0,0001 ***
Treat:Spec	1.2768	0.1777

Table 13. Tables of ANOVA results, treatment effect day 2.

The result from the ANOVA (see table 13) show that an an almost significant effect of waterlogging on SLA can be seen already after 2 days. Further, similar effect is seen among all species, since no interaction effect is shown between treatment and species.

Mature vs. developing leaves

In addition to previously shown analyses of plasticity of SLA, the SLA plasticity of leaves developed during the experiment was also explored. This was done to see if any differences could be seen in how the trees invested in their leaves when in waterlogged, and thus stressful, conditions. On the last day of measurement, day 21, fully developed leaves that had developed during the experiment was collected and measured. The result when analysing the difference between previously developed leaves and leaves developed during the experiment can be seen in table 14 and fig 10.

	Estimated mean	p-value
Acer saccharinum	-3.756	0.0149
Fraxinus ornus	-0.461	0.9997
Fraxinus pennsylvanica	-3.230	0.0517
Magnolia x loebneri	-3.325	0.0635
Quercus palustris	-4.583	0.0017
Sorbus torminalis	-2.654	0.2952
Tilia tomentosa	1.340	0.9275

Table 14. ANOVA results of difference in SLA between mature and developing leaves.

C. japonicum did not develop new leaves during the experiment period and was therefore excluded from this analysis. Only one individual of *R. cathartica* developed new leaves during the experiment, which gives an insufficient number of data points for analysis. *R. cathartica* was therefore also excluded from the analysis. Among the remaining seven species two show a significant difference; *A. saccharinum* and *Q. palustris*. *F. pennsylvanica* has a p-value of 0,0517 which is nearly significant. The plot in fig 10 displays the difference between the SLA of new leaves (e.g. developed during experiment) minus the SLA of old leaves (e.g. developed before experiment). Thus, negative value of a data point mean that the new leaf had a lower SLA than the old leaf on the same tree individual. All species but *T. tomentosa* display a lower mean SLA of their new leaves, however not all are significant. Both *A. saccharinum* and *Q. palustris* is found to display significantly lower SLA of their new leaves, and *F. pennsylvanica* is almost significant.

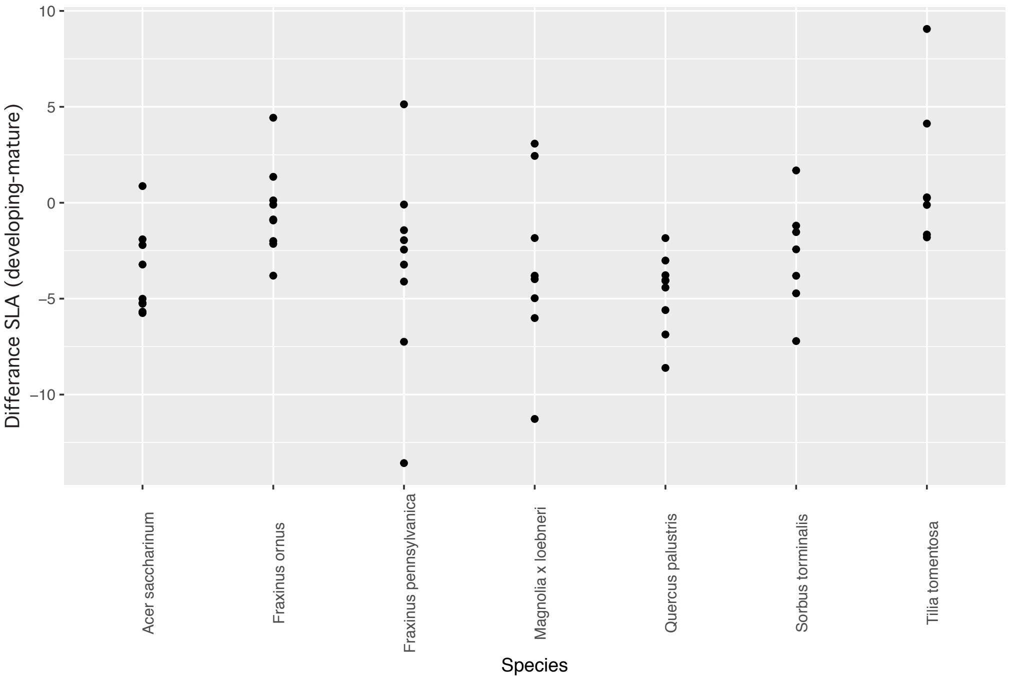

Fig 10. Differance in SLA between mature and developing leaves.

Introduction

Litterature study

Results

Part 4

Discussion and conclusion

Discussion results

Discussion methods

What to consider when chosing trees for rain gardens

Conclusion

This part will discuss the results from the experiment with the foundation created by the literature study. The research question which guided the process of the thesis was; Can leaf economics indicate trees tolerance towards waterlogging?

Discussion

SLA plasticity developing leaves

Two of the studied species, *Acer saccharinum* and *Quercus palustris*, showed a significant lower SLA of the leaves developed while the plants were waterlogged in relation to those developed before the experiment was commenced. *Fraxinus pennsylvanica* showed the same tendency with a nearly significant p-value of 0,0517. These three species seem to react to the conditions caused by waterlogging with altering the morphology of their leaves. Interestingly, these are the three species among the nine studied in this experiment which, according to Niinemets and Valladares (2006), are said to be most tolerant towards waterlogging. This correlation might indicate that a trees' capacity to shifting the design of its leaves to a more retentive structure is somehow connected to its ability to withstand waterlogging.

Several studies (Liu and Dickmann 1992, Schmull and Thomas 2000, Rodríguez et al. 2015) describe the SLA of certain tree species responding to waterlogging in a similar way as seen in the experiments of this thesis. In the study of Schmull and Thomas (2000), *Quercus robur* showed a significant decrease in SLA when subjected to waterlogging. The remaining two species, *Quercus petrea* and *Fagus sylvatica*, showed no significant change in SLA. The authors explained the response of *Q. robur* as a compensation for the loss of leaf area during waterlogging, a response resulting in an enhanced water-use efficiency. In several studies, leaves developed post-flooding among different species of *Populus* displayed a lower SLA than leaves developed prior waterlogging (Liu and Dickmann 1992, Rodríguez et al. 2015). In the study of Luquez et al. (2012) the authors saw a reduction in leaf area for different *Populus* clones after a period of waterlogging. However, SLA was not examined in the study of Luquez et al. (2012).

A change in photosynthate allocation is often seen as a response to waterlogging among plants (Kozlowski 1997). The results from the experiment in this thesis and other studies point towards that such distributional changes can affect the composition of leaves during waterlogging.

SLA plasticity mature leaves

The experiment in this thesis showed an over-all treatment effect on SLA of mature leaves, with significant effect on four different occasions, *Fraxinus ornus* day 7, *Fraxinus ornus* day 21, *Rhamnus cathartica* day 2 and *Sorbus torminalis* day 7. The results suggest that some type of plasticity of mature leaves might be present when trees are subjected to waterlogging. Hence, the leaves developed before the start of the experiment seemingly possess some ability for morphological change when subjected to waterlogging. This plasticity is displayed in all species of the experiment, although in varying levels. Additionally, the results seems to indicate a relatively fast response, seen already after two days of waterlogging, although not significant.

This plasticity of mature leaves has been demonstrated in past studies as well. In the study of Oguchi et al. (2005) two of the three studied tree species showed a plasticity of their mature leaves when transferred from low to high irradiance. One of the species, *Acer rufinerve*, reacted with an increase of its mesophyll cell layer and leaf thickness, and enlargement of its chloroplast volume. This led to an increase in photosynthetic capacity. The morphological changes of the leaves resulted in a lower SLA. In addition to this, chloroplast division was also seen among *A. rufinerve*. *A. rufinerve* thus displayed a morphological plasticity of its mature leaves. Oguchi et al. (2005) explained this plasticity as a strategy for growing in shade, while simultaneously being able to acclimatize when light conditions change. The authors explain that this plasticity however result in a higher vulnerability to disease and physical damage, caused by trading off cell wall crosslinks in the leaves, and thus decreased toughness, for an increased plasticity. One other species in the experiment showed another type of plasticity, and the last species displayed no plasticity at all caused by the change of irradiance. The measurements in the study of Oguchi et al. (2005) were made when the trees was fully acclimatized to the new conditions, which differed among the species. *A. rufinerve* was seen to be fully acclimated after 15 days. The pace of the response is however not displayed in this study, and consequently neither the moment of the first morphological change. In another study, leaves of soybeans showed a decrease in SLA when subjected to shading (Pons and Pearcy 1994). In the study of Pons and Pearcy (1994), a significant difference in SLA could be seen already 3 days after the change of light conditions. This was explained as a result of the relocation of carbon compounds and assimilates within the plants.

However, no studies investigating plasticity of mature leaves during waterlogged conditions have been found. Further explorations into this plasticity of mature leaves during waterlogging would certainly be interesting.

Some fluctuations in SLA of the control group during the experiment period is displayed in fig 9. These fluctuations were however in general not significant and SLA of the control group was thus shown to be overall stable during the experiment period. This slightly fluctuating but essentially stable SLA after leaf formation is also described in the literature (Jurik 1986, England and Attiwill 2008, Poorter et al. 2009).

Stomatal conductance & Midday leaf water potential

The result of the ANOVA analyses of stomatal conductance (g_l) showed no treatment effect day 2. This may be because of more variable values this day, seen by the bigger range of standard error for many of the species (see fig 5). The ANOVAs showed however a significant effect day 7, 14 and 28, all interacting with species. The post-hoc test showed significant treatment effects on these three days for *C. japonicum*, *F. ornus*, *R. cathartica*, *S. torminalis* and

T. tomentosa, indicating that these species respond to waterlogging with a reduced stomata openness. This corresponds with the literature describing the closing of stomata to often be one of the first responses towards waterlogging (Pereira and Kozlowski 1977, Newsome et al. 1982, Kozlowski and Pallardy 2002).

However, *Acer saccharinum*, *Fraxinus pennsylvanica* and *Quercus palustris* stand out by lacking significant effect on stomatal conductance in any of the measurement occasions. This points towards that these three species may successfully maintain the stomata more open during waterlogging. The effect on *Q. palustris* and *F. pennsylvanica* was however almost significant on day 14 and day 28 respectively. This may be explained by the time it takes for certain physiological adaptions to waterlogging to form, e.g. root adaptions. The effect of waterlogging on stomatal conductance on *M. x loebneri* was only significant day 14. This may be explained by the origin of one of the parents to this hybrid, *Magnolia stellata*, which can be found growing in swampy habitats in Japan (Wang et al. 2013). *M. stellata* might subsequently have passed on the ability to maintain the stomata more open during waterlogging to *M. x loebneri*.

The ANOVA analysis of midday leaf water potential (ψ_L) showed a significant treatment effect. The analysis did also show an interacting effect of treatment and species, which indicate that the effect on ψ_L from the treatment is not uniform for all species. A significant effect was also seen from the day of measurement, and an interacting effect of day and species. This indicate that ψ_L was different between the days of measurement, but that this difference did not present itself in the same way among the different species. The post-hoc test showed that the difference of ψ_L between treatment and control group was significant only on three different occasions; *C. japonicum* day 7, *M. loebneri* day 21 and *S. torminalis* day 21. It also showed to be both positive and negative affected of waterlogging, varying between species and day of measurement. Even if few significant effects were seen on ψ_L caused by waterlogging, some over-all trends can be seen. As seen in fig 6, *Q. palustris* and *F. pennsylvanica* display a higher ψ_L for the treatment in all three measurements. Three species, *A. saccharinum*, *T. tomentosa* and *R. cathartica*, show an inconsistent effect on ψ_L. The treatment of *R. cathartica* does however have a higher ψ_L day 7 and day 21 and the treatment of *A. saccharinum* have a higher ψ_L day 21. The four remaining species, *C. japonicum*, *F. ornus*, *M. x loebneri* and *S. torminalis*, consistently have a lower ψ_L during waterlogging.

ψ_L is a relative measurement method since it is affected by the different factors that influence transpiration of the plant (e.g. climatic, plant and soil factors). Air temperature is one of the more important factors influencing ψ_L (Saranga et al. 1991). Further, analysis on ψ_L in the experiment included data from only three measurement occasions. Perhaps three measurements were not sufficient for providing a clear picture of the effect of waterlogging on ψ_L.

However, several studies show an absent effect on ψ_L during waterlogging (Blake and Reid 1981, Bradford and Hsiao 1982, Dreyer et al. 1991, Ahmed et al. 2002). In Blake and Reid (1981) all three species in the study responded to 40 days of waterlogging with closure of their stomata, and no significant decrease in ψ_L was seen for any species. Bradford and Hsiao (1982) explain that by the stomatal closing of the leaves, plants may prevent a decrease in ψ_L (Bradford and Hsiao 1982). Concluded by Blake and Reid (1981) as well as Pereira and Kozlowski (1977), plant water stress does not seem to be an important factor for the different responses of plants towards waterlogging. And in addition to this, several studies reviewed by Kozlowski (1997) have shown that stomatal closure is not induced by leaf water stress or reductions in ψ_L. Bradford and Hsiao (1982) concludes that stomatal closure is not a result of plant water deficit, but rather prevents this water deficit from happening. Stomatal closure might instead be induced by hormonal signals, and thereafter result in the prevention of reduced ψ_L according to Reid and Bradford (1984).

This seems to be the case for the less waterlogging-tolerant trees in this study, which responded to waterlogging with reduced g_l and inconsistent effect on ψ_L. However, two of the trees that have been described by Niinemets and Valladares (2006) to be more tolerant towards waterlogging, *Q. palustris* and *F. pennsylvanica* seem to be able to maintain both leaf water levels and their stomata more open during waterlogging. *A. saccharinum* may also follow the same pattern since it showed a higher ψ_L day 21 and, as well as *Q. palustris* and *F. pennsylvanica,* maintained more open stomata during waterlogging. *M. x loebneri* which displayed similar response concerning g_l, did however have a consistently lower ψ_L during waterlogging, and may thus not follow the same pattern as *Q. palustris*, *F. pennsylvanica* and *A. saccharinum*.

SLA values, Midday leaf water potential & Stomatal conductance

In the study of Schmull and Thomas (2000), in addition to SLA ψ_L was measured as well. *Q. robur*, which showed a significant decrease in SLA of leaves developed during waterlogging, had an insignificant and variable reaction of ψ_L. *Fagus sylvatica*, which did not display an effect of its SLA, had significantly lower ψ_L for the waterlogged plants across the entire experiment period. In that experiment *F. sylvatica* thus seems to experience leaf water stress, contradicting the studies showing an absent effect on ψ_L during waterlogging (Blake and Reid 1981, Bradford and Hsiao 1982, Dreyer et al. 1991, Ahmed et al. 2002).

Poorter et al. (2009) explained responses of SLA to waterlogging with the experienced drought stress caused by continued evaporative demands in the air and inhibition of water uptake of the roots. However, several studies cited earlier dismiss the importance of plant water stress for responses to waterlogging (Pereira and Kozlowski 1977, Blake and Reid 1981, Bradford and Hsiao 1982), and in Schmull and Thomas (2000) the experience of leaf water stress in *F. sylvatica* did not result in reduced, or any alteration of its SLA. Additionally, open stomata are necessary for the continued transpiration of plants and stomatal closure is often seen as one of the first responses to waterlogging (Pereira and Kozlowski 1977, Newsome et al. 1982, Kozlowski and Pallardy 2002). Results from the experiment in this thesis show that the species with a higher ψ_L during waterlogging and the maintenance of open stomata, *A. saccharinum*, F. *pennsylvanica* and *Q. palustris*, responded by developing leaves with lower SLA. *M. x loebneri* did not follow the same pattern as these species concerning ψ_L but had a similar response as these species when looking at g_l. M. x loebneri also displayed an almost significant plasticity of developing leaves with a p-value of 0,0635. Thus, these species' response of altering the construction of their leaves is probably not caused by the experience of drought stress, but rather by some other factor.

Which process that induce seen changes of SLA during waterlogging seems to still be uncertain. According to Luquez et al. (2012), changes in SLA is caused by reduced water flow within the roots of the affected plant, which happens with low O_2-levels and high CO_2-levels. In the study of Liu and Dickmann (1992) they connect the changed patterns of allocation within the plants to oxygen deficiency.

Studies showing reduced SLA of leaves during waterlogging also often see a decrease in stomatal conductance (Schmull and Thomas 2000, Luquez et al. 2012). Luquez et al. (2012) discuss that the reduction of leaf area caused by lower SLA, combined with a lower stomatal conductance probably contributes to maintain water status of the shoot, and thus enable a successful avoidance of water stress. The experimental results of this thesis do however contradict this explanation. The results show that the species described by Niinemets and Valladares (2006) as tolerant towards waterlogging develop leaves with lower SLA during waterlogging, and that these species are also seen to be able to maintain both higher ψ_L and more open stomata during waterlogging. The species in this experiment that followed previously described responses found in the literature; closure of the stomata and inconsistent effect on ψ_L (Blake and Reid 1981, Bradford and Hsiao 1982, Reid and Bradford 1984), displayed no significant plasticity of SLA developed during waterlogging. The reduction of SLA may however result in a more efficient water use of the plant as concluded by several studies (Schmull and Thomas 2000, Luquez et al. 2012, Rodríguez et al. 2015), and thus aiding the plant during conditions which inhibits water uptake. The response of the more waterlogging-tolerant trees in this study to develop leaves with reduced SLA indicate an ability of alteration of leaf economics during flooding. By investing more into leaves which are less active but more durable and also have less surface area from where water can be lost, reduced transpirational losses are achieved which probably aids the tree to survive during waterlogging.

CSR classification

Since the CSR-classification was made using data from the control group it can be assumed that the classification is all-in-all correct. The resulting positions of the nine species in the ternary plot is within the approximate strategic range of trees and shrubs found in Grime (2001) (fig 44 p. 132) which points towards the classification being overall correct. Some of the species included in this thesis could be found in data used in Pierce et al. (2016). The strategy of these species in their study correlated approximately with the result from the classification in this thesis, except S. torminalis which both had a higher C-value and lower S-value in Pierce et al. (2016). It should however be noted that there are other ways than the method of Pierce et al. (2016) to calculate the CSR-strategy of a species. It is possible that calculating the strategy based on other traits than those connected to leaf economics, would give another result.

CSR value & Midday leaf water potential

Stress as defined by Grime (2001); any factor which restrict photosynthesis, is much like the conditions plants experience during waterlogging. However, no correlation was found between the calculated S-value and ψ_L during waterlogging of the different species in this study. The CSR-theory have been tested in previous studies by investigating how population mean CSR-values shift when subjected to stress and disturbance. In these cases stress have often been manifested through low nutrient and/or water supply (Li and Shipley 2017). However, no other studies could be found where the response of tree individuals to a stressor was analysed linked to the CSR-strategy of each species. It is possible that stress-tolerance as described by Grime is too broad to be connected to a distinct stress-factor as waterlogging. The lack of correlation between the S-value and ψ_L value might also be caused by the low appearances of significant effect on ψ_L during waterlogging.

CSR value & Plasticity of SLA

The species that showed a significant plasticity of their leaves developed during the experiment, *A. saccharinum* and *Q. palustris*, was not shown to inhibit a similar S-value in this thesis. Thus, if these species share some way of coping with waterlogging, this does not seem to be able to be described by the CSR-theory. *F. pennsylvanica* and *A. saccharinum* is situated relatively close to each other in the calculated CSR-plot. However, relative to the other species, they have an intermediate S-value. This display no immediate clear correlation between SLA plasticity and the CSR-strategy of a species.

Closing discussion of experimental results

The lack of correlation between CSR-strategies and ψ_L as well as the seen plasticity within SLA, indicates that the use of CSR-classification might not be sufficient when choosing trees for rain gardens, at least when calculated based on leaf economics.

However, the experimental results from this thesis have shown that plasticity within leaf economics might play a role in adapting to the conditions during waterlogging. Two of the trees that according to Niinemets and Valladares (2006) have higher tolerance towards waterlogging developed leaves with significantly lower SLA during waterlogging, and the third species was close to significant. These species were also seen to maintain the stomata more open during waterlogging. Trees which are able to maintain the stomata open during waterlogging and thus maintain active transpiration often have a greater effect in rain gardens and are therefore preferred in those situations (Scharenbroch et al. 2015, Riley and Kraus 2016).

Plasticity within leaf economy of a species might be especially advantageous in rain gardens, where the soil water conditions is particularly variable. This seen plasticity could indicate which species that are able to adapt to such fluctuating soil environments, and would be interesting for further investigations. The result from the experiment in this thesis correlates with other studies of SLA response of flooding (Liu and Dickmann 1992, Schmull and Thomas 2000, Luquez et al. 2012, Rodríguez et al. 2015). This suggests, as noted by Maracahipes et al. (2018), Liu and Ng (2019) and Gotsch et al. (2010), that intraspecific variability and stress-driven plasticity of SLA might play an important role for plants adaption and survival in shifting environments. Further research on the mechanisms behind intra-specific variation of SLA, such as local adaption, genetic variation and plasticity, would contribute to the understanding of species ability to handle environmental stressors such as waterlogging.

SLA holds an advantage over other plant traits since its relatively easy to measure and has good foundation in literature. However, it is possible that it is not necessarily always the best method for predicting performance of plants (Poorter et al. 2009). Further research where other traits is measured as well during waterlogging could further contribute to the understanding of plasticity within leaf economics. Research focusing on these subjects could possibly shine more light on which species that are suitable for rain gardens.

Discussion methods

ψ_L was measured between 10:30 and 16:00. These long measurement sessions can, as noted earlier in this thesis, be supported by long days in Sweden. Since the sun rose as early as between 4:00 and 5:00 during the experiment period, it can be presumed that the trees had reached high transpiration level around 10:30. The measurements of ψ_L can thus be assumed to be overall correct.

The morphological measurements in the experiment were made as far as possible according to Pérez-Harguindeguy et al. (2013). The measurements could unfortunately not be measured the same day as collecting them. They were however done within approximately 24 hours as suggested by Pérez-Harguindeguy et al. (2013), and as they were consistently kept in a cold environment, transpirational losses or decay were likely minimal.

The leaves were not rehydrated as recommended by Pérez-Harguindeguy et al. (2013) before measuring leaf fresh weight for the calculation of LDMC. Such rehydration is however not advised by Kleyer et al. (2008). Furthermore, LDMC was only used to calculate the CSR-strategy of each species by using the values from the control group. Since the control group grew in well-watered soil, it can be expected that the leaves were sufficiently hydrated and that the measurements of LDMC were overall correct.

What to consider when chosing trees for rain gardens

The expansion of urban areas and the expected changes of rainfall patterns (Ipcc 2018) both stress the importance of developments within storm water management in cities. Rain gardens are an effective solution since they can, if properly constructed, reduce and delay floods whilst also filter water and recharge the groundwater. If successful, they are as well often cheaper alternatives to traditional sewer systems (Ishimatsu et al. 2017). However, the conditions for vegetation in rain gardens are commonly challenging, which complicates the selection of vegetation (Riley and Kraus 2016).

Trees are often especially beneficial when it comes to rain water management (Forman 2014). They possess a higher ability for transpiration as well as the capturing of rain water in their canopy (Hunt et al. 2012). An actively transpiring tree have a greater ability for providing ecosystem services (Scharenbroch et al. 2015). Additionally, a big shadowing canopy is often beneficial since it may reduce heat pollution and amount of algae in the water (Hunt et al. 2012). However, the ability of a tree to deliver ecosystem services in urban areas are often complex and highly context-dependent. Thus, a generalized framework or checklist for the choice of trees may not always result in a successful decision (Salmond et al. 2016). By learning more about trees reaction towards waterlogging we increase the possibility for good selection of species when planning rain gardens in a city.

The literature study in this thesis revealed that indication of a species tolerance to waterlogging is unlikely to be associated with its roots tolerance to anoxia (Vartapetian and Jackson 1997). Therefore, it is reasonable to instead study avoidance strategies of a species when searching for species for rain gardens. Particularly interesting avoidance strategies include longitudinal transport of oxygen and associated morphological responses. Such morphological responses may consist of hypertrophied lenticels, increasing permeability of the cambium or altered root formation.

The ability to grow roots, and for existing roots to survive in saturated soils is advantageous for trees growing in rain gardens. A bigger root system result in an increased stability of the tree (Hook 1984, Smith et al. 2001). Survival, and any potential growth, of the root system may also prevent a decrease in root/shoot ratio, hopefully preventing an increased intolerance to drought of the tree in question (Newsome et al. 1982, Kozlowski 1984b, Kozlowski 1997). A decreased root/shoot ratio, and the related increased drought-intolerance, is especially disadvantageous for trees growing in rain gardens as these often are exceedingly dry between flooding events. Species with longer root systems may as well increase water uptake, and thus also evapotranspiration (Hunt et al. 2012). In addition to this, Hallgren (1989) found that the capacity to grow roots in flooded soil was associated with the capacity for dry weight production. And as noted by several authors, a tree with the ability to stay active during waterlogging is beneficial in rain gardens (Scharenbroch et al. 2015, Riley and Kraus 2016). It should however be pointed out that the conditions for roots often are though in constructed plantings in urban areas, with higher risk of packed soil substrate and limited volume for the roots to grow.

The survival and growth of a trees root system is emphasized by many authors to be important both during and after floods. Species with lower SLA have in general been shown to have a greater root lifespan (Grime 2001, Poorter et al. 2009). If this relationship also is true during waterlogging, it would introduce an interesting linkage between leaf economics and suitability for rain gardens. However, as shown by Mommer et al. (2006), the general patterns of the leaf economic spectrum and slow-fast continuum does not always hold when plants are subject to stressful conditions, and this must thus be tested before drawing conclusions.

Literature reviewed by Glenz et al. (2006) show that the response towards flooding may vary with the age of a species. In addition to being shown to vary between flood-tolerant and flooding-intolerant species, this variation was also shown to differ between species tolerant towards flooding. According to Kozlowski (1984b) older tree individuals tend to tolerate waterlogging better than younger ones. Gaining more information on this relationship between age and flooding-tolerance would aid the choice of age and size of plant material when constructing rain gardens. Further, since the risk of damage to vegetation increases with duration of flooding (Glenz et al. 2006), the construction of rain gardens has a substantial impact on the survival of the planted vegetation. Finding a critical waterlogging-period for survival of different species would aid by giving clear goals of the substrate's infiltration-rate when building rain gardens. The infiltration rate is also dependent on the structure and permeability of the sub-soil (Dunnett and Clayden 2007). Therefore, the position of the rain garden also, as well as the construction, influence the duration of waterlogging within the rain garden.

Several different factors are deemed important for the selection of trees for rain gardens, both regarding the survival of the tree but also for its possible contribution to the rain garden construction. As seen in this thesis, knowledge gaps exist when it comes to both trees survival and their possible contribution to rain gardens. Important factors have been formulated but are often not tested enough to reveal specifically which species that may meet presented demands.

The results from the experiment of this thesis have displayed a possible importance of plasticity within leaf economics for the survival during waterlogging. Similar plasticity has also been seen in other studies (Liu and Dickmann 1992, Schmull and Thomas 2000, Luquez et al. 2012, Rodríguez et al. 2015). However, since the cause of this response towards waterlogging have not been fully explained, it is hard to know exactly how much this plasticity may contribute to the survival during waterlogging. Further research within this could clarify the linkages between plasticity of leaf economics and tolerance towards waterlogging, and possibly result in a new criterion when choosing species for rain gardens.

Conclusion

The purpose of this thesis was to investigate if leaf economics may indicate which tree species to choose when constructing rain gardens. The literature study showed that the anoxic conditions created in the soil during waterlogging is the factor that is most harmful to plants. Several adaptations exist which may increase the survival-rate for woody species during waterlogging, such as the ability for altering root growth, hypertrophied lenticels and a permeable cambium. These adaptations are all associated with the longitudinal transportation of oxygen.

The results of the experimental study indicated that the possibility of SLA plasticity might be important for the survival of trees during waterlogging, since the species deemed most flood-tolerant displayed significant, or almost significant, effect in this analysis. Further it showed that these species had a higher ψ_L and showed no significant effect on g_l, indicating that these species seem to be able to upkeep water levels in the leaves and inhibit stomatal closure during waterlogging. Further investigations within the responses of ψ_L and g_l towards waterlogging and how plasticity within leaf economics might be related to this would increase our understanding in what to search for when choosing woody species for rain beds.

References

Ahmed, S., et al. (2002). ”Effects of waterlogging at vegetative and reproductive growth stages on photosynthesis, leaf water potential and yield in mungbean.” Plant Production Science 5(2): 117-123.

Anderegg, L., et al. (2018). ”Within-species patterns challenge our understanding of the leaf economics spectrum.” Ecology Letters 21.

Angeles, G. (1992). ”The periderm of flooded and non flooded ludwigia octovalvis (onagraceae).” IAWA Journal 13(2): 195-200.

Armstrong, W. (1980). Aeration in higher plants. Advances in botanical research. H. W. Woolhouse, Academic Press. 7: 225-332.

Armstrong, W., et al. (1994). ”Mechanisms of flood tolerance in plants.” Acta Botanica Neerlandica 43.

Astuti, G., et al. (2018). ”Narrow endemic species bellevalia webbiana shows significant intraspecific variation in tertiary csr strategy.” Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 153(1): 12-18.

Baldocchi, D., et al. (2002). ”How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest - an assessment with the biophysical model canoak.” Tree Physiology 22: 1065-1077.

Bazaz, A., et al. (2018). ”Summary for urban policymakers: What the ipcc special report on global warming of 1.5° c means for cities.”

Blake, T. J. and Reid, D. M. (1981). ”Ethylene, water relations and tolerance to waterlogging of three eucalyptus species.” Functional Plant Biology 8(6): 497-505.

Bolund, P. and Hunhammar, S. (1999). ”Ecosystem services in urban areas.” Ecological Economics 29(2): 293-301.

Bradford, K. J. and Hsiao, T. C. (1982). ”Stomatal behavior and water relations of waterlogged tomato plants.” Plant Physiology 70(5): 1508.

Colin-Belgrand, M., et al. (1991). ”Sensitivity of seedlings from different oak species to waterlogging: Effects on root growth and mineral nutrition.” Ann. For. Sci. 48(2): 193-204.

Dale, M. P. and Causton, D. R. (1992). ”The ecophysiology of veronica chamaedrys, v. Montana and v. Officinalis. Ii. The interaction of irradiance and water regime.” Journal of Ecology 80(3): 493-504.

Deak Sjöman, J., et al. (2015). Staden som växtplats. Träd i urbana landskap. Lund, Studentlitteratur AB: 231-330.

Dias-Filho, M. and Carvalho, C. (2000). ”Physiological and morphological responses of brachiaria spp. To flooding.” Pesquisa Agropecuária Brasileira.

Díaz, S., et al. (2016). ”The global spectrum of plant form and function.” Nature 529(7585): 167-171.

Dreyer, E., et al. (1991). ”Photosynthesis and shoot water status of seedlings from different oak species submitted to waterlogging.” Ann. For. Sci. 48(2): 205-214.

Dunnett, N. and Clayden, A. (2007). Rain gardens : Managing water sustainably in the garden and designed landscape Portland, Or., Timber Press.

Dwyer, J., et al. (2014). ”Specific leaf area responses to environmental gradients through space and time.” Ecology 95: 399-410.

England, J. and Attiwill, P. (2008). ”Patterns of growth and nutrient accumulation in expanding leaves of eucalyptus regnans (myrtaceae).” Australian Journal of Botany 56.

England, J. R. and Attiwill, P. M. (2005). ”Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, eucalyptus regnans f. Muell.” Trees 20(1): 79-90.

Forman, R. T. T. (2014). Urban ecology: Science of cities Cambridge, Cambridge University Press.

Frey, B. (2018). The sage encyclopedia of educational research, measurement, and evaluation. Thousand Oaks, CA. 4.

Gimenez, C., et al. (2005). Plant–water relations. Encyclopedia of soils in the environment. D. Hillel. Oxford, Elsevier: 231-238.

Glenz, C., et al. (2006). ”Flooding tolerance of central european tree and shrub species.” Forest Ecology and Management 235(1): 1-13.

Gotsch, S. G., et al. (2010). ”Leaf traits and water relations of 12 evergreen species in costa rican wet and dry forests: Patterns of intra-specific variation across forests and seasons.” Plant Ecology 211(1): 133-146.

Grime, J. and Pierce, S. (2012). The evolutionary strategies that shape ecosystems.

Grime, J., et al. (1997). ”Integrated screening validates primary axes of specialisation in plants.” Oikos 79: 259-281.

Grime, J. P. (1979). Plant strategies and vegetation processes Chichester.

Grime, J. P. (2001). Plant strategies, vegetation processes, and ecosystem properties. 2. ed. New York, Wiley.

Hallgren, S. W. (1989). ”Growth response of populus hybrids to flooding.” Annales des sciences forestières 46(4): 361-372.

Hernández, B. and Hidalgo, M. C. (2005). ”Effect of urban vegetation on psychological restorativeness.” Psychological Reports 96(3_suppl): 1025-1028.

Hook, D. D. (1984). Adaptations to flooding with fresh water. Flooding and plant growth. T. T. Kozlowski. San Diego, Academic Press: 265-294.

Hunt, W., et al. (2012). ”Meeting hydrologic and water quality goals through targeted bioretention design.” Journal of Environmental Engineering 138: 698-707.

IPCC (2018). Summary for policymakers. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. V. Masson-Delmotte, P. Zhai, H.-O. Pörtner et al. Geneva, Switzerland, World Meteorological Organization: 32.

Ishimatsu, K., et al. (2017). ”Use of rain gardens for stormwater management in urban design and planning.” Landscape and Ecological Engineering 13(1): 205-212.

Jha, A., et al. (2012). Cities and flooding: A guide to integrated urban flood risk management for the 21st century.

Jung, V., et al. (2010). ”Intraspecific variability and trait-based community assembly.” Journal of Ecology 98(5): 1134-1140.

Jurik, T. W. (1986). ”Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species.” American Journal of Botany 73(8): 1083-1092.

Kim, K.-G. (2018). Low-carbon smart cities: Tools for climate resilience planning Cham, Springer International Publishing.

KLEYER, M., et al. (2008). ”The leda traitbase: A database of life-history traits of northwest european flora.” Journal of Ecology 96: 1266-1274.

Koch, G., et al. (2004). ”The limit to tree height.” Nature 428: 851-854.

Kozlowski, T. T. (1984a). Extent, causes, and impacts of flooding. Flooding and plant growth. T. T. Kozlowski. San Diego, Academic Press: 1-7.

Kozlowski, T. T. (1984b). Responses of woody plants to flooding. Flooding and plant growth. T. T. Kozlowski. San Diego, Academic Press: 129-163.

Kozlowski, T. T. (1997). ”Responses of woody plants to flooding and salinity.” Tree Physiology 17(7): 490-490.

Kozlowski, T. T. and Pallardy, S. G. (2002). ”Acclimation and adaptive responses of woody plants to environmental stresses.” Botanical Review 68(2): 270-334.

Kreuzweiser, J. and Rennenberg, H. (2014). ”Molecular and physiological responses of trees to waterlogging stress.” Plant, Cell & Environment 37(10): 2245-2259.

Lajoie, G. and Vellend, M. (2015). ”Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching.” Ecology 96(11): 2912-2922.

Lambers, H. and Poorter, H. (1992). Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. Advances in ecological research volume 23: 187-261.

Li, Y. and Shipley, B. (2017). ”An experimental test of csr theory using a globally calibrated ordination method.” PLOS ONE 12(4): e0175404.

Liu, S. and Ng, G.-H. C. (2019). ”A data-conditioned stochastic parameterization of temporal plant trait variability in an ecohydrological model and the potential for plasticity.” Agricultural and Forest Meteorology 274: 184-194.

Liu, Z. and Dickmann, D. I. (1992). ”Responses of two hybrid populus clones to flooding, drought, and nitrogen availability. I. Morphology and growth.” Canadian Journal of Botany 70(11): 2265-2270.

Livesley, S. J., et al. (2016). ”The urban forest and ecosystem services: Impacts on urban water, heat, and pollution cycles at the tree, street, and city scale.” 45(1): 119-124.

Luquez, V. M. C., et al. (2012). ”Evaluation of flooding tolerance in cuttings of populus clones used for forestation at the paraná river delta, argentina.” Southern Forests: a Journal of Forest Science 74(1): 61-70.

Maracahipes, L., et al. (2018). ”How to live in contrasting habitats? Acquisitive and conservative strategies emerge at inter- and intraspecific levels in savanna and forest woody plants.” Perspectives in Plant Ecology, Evolution and Systematics 34: 17-25.

Merriam-Webster.com (2019a). ”Anoxic.” Retrieved 15/11-2019, from https://www.merriam-webster.com/dictionary/anoxia.

Merriam-Webster.com (2019b). ”Hypoxia.” Retrieved 15/11-2019, from https://www.merriam-webster.com/dictionary/hypoxia.

Merriam-Webster.com (2019c). ”Photosynthate.” Retrieved 18/11-2019, from https://www.merriam-webster.com/dictionary/photosynthate.

Mitchell, R. M. and Bakker, J. D. (2014). ”Intraspecific trait variation driven by plasticity and ontogeny in hypochaeris radicata.” PLOS ONE 9(10): e109870.

Mommer, L., et al. (2006). ”Ecophysiological determinants of plant performance under flooding: A comparative study of seven plant families.” Journal of Ecology 94(6): 1117-1129.

Mustard, M., et al. (2003). ”The emergence of primary strategies in evolving plant populations.” Evolutionary Ecology Research 5.

Newsome, R., et al. (1982). ”Responses of ulmus americana seedlings to flooding of soil.” Canadian Journal of Botany 60(9): 1688-1695.

Nielsen, A. B., et al. (2014). ”Species richness in urban parks and its drivers: A review of empirical evidence.” 17(1): 305-327.

Niinemets, Ü. (2015). ”Is there a species spectrum within the world wide leaf economics spectrum? Major variations in leaf functional traits in the mediterranean sclerophyll quercus ilex.” 205(1): 79-96.

Niinemets, Ü. and Valladares, F. (2006). ”Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs.” Ecological Monographs 76: 521-547.

Nouvellon, Y., et al. (2010). ”Within-stand and seasonal variations of specific leaf area in a clonal eucalyptus plantation in the republic of congo.” Forest Ecology and Management 259(9): 1796-1807.

Oguchi, R., et al. (2005). ”Leaf anatomy as a constraint for photosynthetic acclimation: Differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees.” Plant, Cell & Environment 28(7): 916-927.

Paul, M. J. and Meyer, J. L. (2008). Streams in the urban landscape. Urban ecology: An international perspective on the interaction between humans and nature. J. M. Marzluff, E. Shulenberger, W. Endlicher et al. Boston, MA, Springer US: 207-231.

Pereira, J. S. and Kozlowski, T. T. (1977). ”Variations among woody angiosperms in response to flooding.” Physiologia Plantarum 41(3): 184-192.

Pérez-Harguindeguy, N., et al. (2013). ”New handbook for standardised measurement of plant functional traits worldwide.” Australian Journal of Botany 61: 167-234.

Pierce, S., et al. (2013). ”Allocating csr plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants.” Functional Ecology 27(4): 1002-1010.

Pierce, S., et al. (2012). ”Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies.” Ann Bot 109(5): 1047-1053.

Pierce, S., et al. (2016). ”A global method for calculating plant csr ecological strategies applied across biomes world-wide.” Functional Ecology 31(2).

Pierce, S., et al. (2005). ”From ancient genes to modern communities: The cellular stress response and the evolution of plant strategies.” Functional Ecology 19: 763–776.

Ponnamperuma, F. N. (1984). Effects of flooding on soils. Flooding and plant growth. T. T. Kozlowski. San Diego, Academic Press: 9-45.

Pons, T. L. and Pearcy, R. W. (1994). ”Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants.” Physiologia Plantarum 92(4): 636-644.

Poorter, H. (2002). Plant growth and carbon economy. Encyclopedia of life sciences. Chichester, John Wiley & Sons Ltd.

Poorter, H., et al. (2009). ”Causes and consequences of variation in leaf mass per area (lma): A meta-analysis.” New Phytologist 182(3): 565-588.

Reich, P. B. (2014). ”The world-wide ‘fast–slow’ plant economics spectrum: A traits manifesto.” Journal of Ecology 102(2): 275-301.

Reich, P. B., et al. (1998). ”Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: Evidence from within and across species and functional groups.” Functional Ecology 12(6): 948-958.

Reid, D. M. and Bradford, K. J. (1984). Effects of flooding on hormone relations. Flooding and plant growth. T. T. Kozlowski. San Diego, Academic Press: 195-219.

Riley, E. D. and Kraus, H. T. (2016). Rain gardens: Understanding their benefits and their beauty©, International Society for Horticultural Science (ISHS), Leuven, Belgium.

Rodríguez, M. E., et al. (2015). ”Leaf traits related to productivity in populus deltoides during the post-flooding period.” Trees 29(3): 953-960.

Rodriguez, M. E., et al. (2018). ”Acclimation of cuttings from different willow genotypes to flooding depth level.” New Forests 49(3): 415-427.

Salmond, J. A., et al. (2016). ”Health and climate related ecosystem services provided by street trees in the urban environment.” Environmental Health 15 Suppl 1: 36.

Sandel, B. and Low, R. (2019). ”Intraspecific trait variation, functional turnover and trait differences among native and exotic grasses along a precipitation gradient.” Journal of Vegetation Science 30.

Saranga, Y., et al. (1991). ”The relations between leaf water potential of cotton plants and environmental and plant factors.” Field Crops Research 28(1): 39-46.

Sartori, K., et al. (2019). ”Leaf economics and slow-fast adaptation across the geographic range of arabidopsis thaliana.” Scientific Reports 9(1): 10758.

Scharenbroch, B., et al. (2015). ”Tree species suitability to bioswales and impact on the urban water budget.” Journal of Environment Quality.

Schmull, M. and Thomas, F. (2000). ”Morphological and physiological reactions of young deciduous trees (quercus robur l., q. Petraea [matt.] liebl., fagus sylvatica l.) to waterlogging.” Plant and soil 225: 227-242.

Scholander, P. F., et al. (1965). ”Sap pressure in vascular plants.” Science 148(3668): 339.

Seto, K. C., et al. (2014). ”Human settlements, infrastructure and spatial planning.”

Shepherd, J. M. (2013). 5.07 - impacts of urbanization on precipitation and storms: Physical insights and vulnerabilities. Climate vulnerability. R. A. Pielke. Oxford, Academic Press: 109-125.

Shipley, B., et al. (2006). ”Fundemental trade-offs generating the worldwide leaf economics spectrum.” Ecology 87(3): 535-541.

Siwiec, E., et al. (2018). ”City greening by rain gardens - costs and benefits.” Environmental Protection and Natural Resources; The Journal of Institute of Environmental Protection-National Research Institute. 29(1): 1-5.

Smith, K. D., et al. (2001). ”The influence of waterlogging on the establishment of four australian landscape trees.” Journal of Arboriculture 27(2): 49-56.

Taiz, L., et al. (2015). Plant physiology and development. 6. ed. Sunderland, Massachusetts, U.S.A, Sinauer Associates.

Vartapetian, B. B. and Jackson, M. B. (1997). ”Plant adaptations to anaerobic stress.” Annals of Botany 79(suppl_1): 3-20.

Wang, Y.-L., et al. (2013). ”Magnolia sinostellata and relatives (magnoliaceae).” Phytotaxa 154: 47.

Wessolek, G. (2008). Sealing of soils. Urban ecology: An international perspective on the interaction between humans and nature. J. M. Marzluff, E. Shulenberger, W. Endlicher et al. Boston, MA, Springer US: 161-179.

Whitfield, J. (2006). ”The cost of leafing.” Nature 444: 539-241.

Wilson, B. F. (1984). The growing tree. Rev. ed., Univ of Massachusetts Press.

Wissmar, R. C., et al. (2004). ”Effects of changing forest and impervious land covers on discharge characteristics of watersheds.” Environmental Management 34(1): 91-98.

Wright, I., et al. (2004). ”The worldwide leaf economics spectrum.” Nature 428(6985): 821-827.

Yeang, K. (2008). Ecodesign, a manual for ecological design Chichester, John Wiley
Sons.

Zeunert, J. (2017). Landscape architecture and environmental sustainability: Creating positive change through design.

Appendix

Stomatal conductance

```
Kond2<- read.csv2(”Konduktans_191219.csv”, header=T)
Kond2 %>% melt(c(”Nr”, ”Art”, ”beh”, ”block”, ”Placering”)) %>%
    rename(dag=variable, Kond=value) %>%
    mutate(beh=as.character (beh), block= as.character (block)) %>%
    filter(beh %in% c(5,8))-> dat_Kond2
dat_Kond2 %>% filter(dag %in% c(”X2”, ”X7”, ”X14”, ”X28”)) -> dat_kond3
```

Day 2

```
dat_kond3 %>% filter(dag %in% c(”X2”), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_kondX2
```

Model

```
mod_kondX2<-lmer(Kond ~ Art * beh + (1|beh:block), dat_kondX2)
anova(mod_kondX2)
emmeans(mod_kondX2, pairwise~ beh|Art)
plot(mod_kondX2)
qqnorm(resid(mod_kondX2))
```

Day 7

```
dat_kond3 %>% filter(dag %in% c(”X7”), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_kondX7
```

Model

```
mod_kondX7<-lmer(Kond ~ Art * beh + (1|beh:block), dat_kondX7)
anova(mod_kondX7)
plot(mod_kondX7)
qqnorm(resid(mod_kondX7))
emmeans(mod_kondX7, pairwise~ beh|Art)
```

Day 14

```
dat_kond3 %>% filter(dag %in% c(”X14”), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_kondX14
```

Model

```
mod_kondX14<-lmer(Kond ~ Art * beh + (1|beh:block), dat_kondX14)
anova(mod_kondX14)
plot(mod_kondX14)
qqnorm(resid(mod_kondX14))
emmeans(mod_kondX14, pairwise~ beh|Art)
```

Day 28

```
dat_kond3 %>% filter(dag %in% c(”X28”), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_kondX28
```

Model

```
mod_kondX28<-lmer(Kond ~ Art * beh + (1|beh:block), dat_kondX28)
anova(mod_kondX28)
plot(mod_kondX28)
qqnorm(resid(mod_kondX28))
emmeans(mod_kondX28, pairwise~ beh|Art)
```

Plot

```
dat_kond3 %>% group_by(Art, beh, dag) %>%
    summarise(mKond=mean(Kond, na.rm = T), s=sd(Kond, na.rm = T),
    l=sum(!is.na(Kond)))  %>%
    filter(beh %in% c(5,8)) %>%
    ggplot(aes(as.factor(dag), mKond, fill=beh)) +
    geom_bar(stat=”identity”, position = position_dodge()) +
    scale_fill_manual(values=c(”#344F12”, ”#8BBBB1”))+
    labs(title=”Stomatal conductance”,
         x= ”Day”,
         y=”SC”)+
    facet_wrap(”Art”) +
    geom_errorbar(aes(ymin = mKond-s, ymax = mKond+s),
    position = position_dodge(0.9), width = 0.1, colour = ”grey40”)+
    theme(panel.background = element_rect(fill=”white”))+
    theme(panel.grid.major.y = element_line(color = ”grey”, size = 0.2),
          panel.grid.major.x = element_line (NA))
```

Midday leaf water potential

```
WP<- read.csv2(”WP.csv”, header=T)
  str_replace_all(WP$X15_07, ”[*]”, ””)->WP$X15_07
  str_replace_all(WP$X15_07, ”[>]”, ””)->WP$X15_07
  str_replace_all(WP$X15_07, ”[,]”, ”.”)->WP$X15_07
  WP$X15_07<-as.numeric (WP$X15_07)

WP %>% melt(c(”Nr”, ”Art”, ”beh”, ”block”, ”Placering”)) %>%
  rename(dag=variable, WP=value) %>%
  mutate(beh=as.character (beh), block= as.character (block),
  dag = recode (dag, X26_06=2, X01_07=7, X15_07=21)) %>%
  filter(beh %in% c(5,8))-> dat_WP
```

Day 2

```
dat_WP %>% filter(dag %in% c(2), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_WP2
```

Model

```
mod_WP2<-lmer(WP ~ Art * beh + (1|beh:block), dat_WP2)
anova(mod_WP2)
emmeans(mod_WP2, pairwise~ beh|Art)
```

Day 7

```
dat_WP %>% filter(dag %in% c(7), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_WP7
```

Model

```
mod_WP7<-lmer(WP ~ Art * beh + (1|beh:block), dat_WP7)
anova(mod_WP7)
emmeans(mod_WP7, pairwise~ beh|Art)
```

Day 21

```
dat_WP %>% filter(dag %in% c(21), block %in% c(1,2,3,4,5,6,7,8,9,10))
-> dat_WP21
```

Model

```
mod_WP21<-lmer(WP ~ Art * beh + (1|beh:block), dat_WP21)
anova(mod_WP21)
emmeans(mod_WP21, pairwise~ beh|Art)
```

Plot

```
dat_WP %>% group_by(Art, beh, dag) %>%
    summarise(mWP=mean(WP, na.rm = T), s=sd(WP, na.rm = T),
    l=sum(!is.na(WP))) %>%
    filter(beh %in% c(5,8)) %>%
    ggplot(aes(as.factor(dag), mWP, fill=beh)) +
    geom_bar(stat=”identity”, position = position_dodge()) +
    scale_fill_manual(values=c(”#344F12”, ”#8BBBB1”))+
    labs(title=”Midday leaf water potential”,
             x= ”Day”,
             y=”WP”)+
    facet_wrap(”Art”) +
    geom_errorbar(aes(ymin=mWP-s, ymax=mWP+s),
    position = position_dodge(0.9),
                  width=0.1, colour=”grey40”)+
    theme(panel.background = element_rect(fill=”white”))+
    theme(panel.grid.major.y = element_line(color = ”grey”, size = 0.2),
          panel.grid.major.x = element_line (NA))
```

SLA-values control group

```
SLA2d <- read.csv2(”SLA2d.csv”, header=F)
SLA7d <- read.csv2(”SLA7d.csv”, header=T)
SLA21d <- read.csv2(”SLA21d.csv”, header=T)
dat <- rbind(SLA2d, SLA7d, SLA21d)

dat$dag <- rep(c(2,7,21),c(363, 180, 180))

dat %>% filter(beh %in% c(5,8))-> dat_SLA
dat_SLA %>% filter(beh %in% c(5)) -> dat_SLAcon
dat_SLAcon$dag <- as.factor (dat_SLAcon$dag)
```

Model

```
modSLA_con <- lm(SLA~Art*dag + block, dat_SLAcon)
anova(modSLA_con)
emmeans(modSLA_con, pairwise~Art)
plot(modSLA)
cld(emmeans(modSLA_con, ~ Art), Letters=letters)
```

Correlation SLA and ψ_L

```
dat_WP %>% group_by(dag, Art, beh) %>% summarise(mWP=mean(WP)) %>%
    dcast(Art+dag ~ beh) %>%
    mutate(diffWP= `5`-`8`) -> WPdiff
WPdiff$dag<-as.factor (WPdiff$dag)

dat_SLA %>% group_by(dag, Art) %>% summarise(mSLA=mean(SLA))-> SLAmeans
  SLAmeans$dag<-as.factor (SLAmeans$dag)
  dat_WP_SLA<-left_join(WPdiff, SLAmeans)
```

Model

```
lmer(diffWP ~ dag * mSLA + (1|Art), dat_WP_SLA) -> modSLA_WP
anova(modSLA_WP)
```

CSR-classification

```
CSR <- read_excel(”CSR.xlsx”, sheet= ”Sannas”, range = ”A4:O274”,
       col_names = T)
names(CSR)[15]<-”R”
CSR %>% melt(c(”Art”, ”dag”, ”block”, ”C”, ”S”, ”R”))-> dat_CSR
```

Plot

```
CSR_plot2<- ggtern(data=CSR_means, mapping= aes(R,C,S, col=Art))+
geom_point()
```

Correlation CSR and ψ_L

```
dat_CSR %>% group_by(dag, Art) %>% summarise(mC=mean(C), mS=mean(S),
            mR mean(R)) -> CSRmeans

CSRmeans$Art <- as.factor (CSRmeans$Art)
CSRmeans$dag <- as.factor (CSRmeans$dag)

dat_WP_CSR <- left_join(WPdiff, CSRmeans)
```

Model

```
lmer(diffWP ~ dag * mS + (1|Art), dat_WP_CSR) -> modCSR_WP
summary(modCSR_WP)
anova(modCSR_WP)
```

Plasticity of SLA

Control group vs treatment

```
dat %>% filter(beh %in% c(5,8), Art != ”Cercidiphyllum japonicum”)->dat2
```

Model

```
lmer(SLA~ beh*Art*dag+(1|behblock) + (1|Art:Nr), dat2)->mod_SLAtid2
summary(mod_SLAtid2)
anova(mod_SLAtid2, type = 2)
emmeans(mod_SLAtid2, pairwise~ beh|dag+Art)
```

Plot

```
dat2 %>% group_by(Art, beh, dag) %>%
         summarise(mSLA=mean(SLA, na.rm = T), s=sd(SLA, na.rm = T),
         l=sum(!is.na(SLA)))  %>%
         filter(beh %in% c(5,8)) %>%
         ggplot(aes(as.factor(dag), mSLA, fill=beh)) +
         geom_bar(stat=”identity”, position = position_dodge()) +
         scale_fill_manual(values=c(”#344F12”, ”#8BBBB1”))+
         labs(title=”Plasticity of already developed leaves”,
                  x= ”Day”,
                  y=”SLA”)+
         facet_wrap(”Art”) +
         geom_errorbar(aes(ymin=mSLA-s, ymax=mSLA+s),
                  position = position_dodge(0.9),
                  width=0.1, colour=”grey40”)+
         theme(panel.background = element_rect(fill=”white”))+
         theme(panel.grid.major.y = element_line(color = ”grey”,size =0.2),
               panel.grid.major.x = element_line (NA))
```

Treatment effect day 2

Model

```
lmer(SLA~ beh*Art+(1|beh:block), SLA2d)->mod_SLA2dNY2
anova(mod_SLA2dNY2)
```

Old vs new leaves

```
SLA21d %>% filter(beh %in% c(8), Art != ”Rhamnus cathartica”,
                                Art !=”Cercidiphyllum japonicum”) %>%
           dplyr::select(”Nr”,”SLA”, ”Art”) -> data3

SLAtopp <- read.csv2(”SLAtopp.csv”,header=T)
merge(SLAtopp, data3, by= c(”Nr”, ”Art”))-> SLA_GoN
```

Model

```
lmer (I(SLA.x-SLA.y) ~ Art+(1|block), SLA_GoN) -> mod_topp
test (emmeans(mod_topp, ~Art ) , adjust=”tukey”)
```

Plot

```
ggplot(SLA_GoN, aes(Art, SLA.x-SLA.y)) + geom_point()+
       labs(title=”Plasticity of developing leaves”,
                x= ”Species”,
                y=”Difference SLA (new-old)”)->plotSLA_GoN
```