



Experimental evaluation of waterlogging and drought tolerance of essential *Prunus* species in central Europe

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ABSTRACT

Fruit-bearing and flowering minority tree species, such as many species from the *Prunus* genus, are essential for multiple ecosystem services in the landscape. Although common, but never dominating, these minority species are often overlooked compared to commercial timber trees in relation to climate change. Induced stress on trees through climate change in central Europe will not only be caused by drought but also by extreme precipitation and pluvial flooding. This study experimentally address this by testing both waterlogging and drought tolerance in three key species of *Prunus* for central Europe that naturally span a wide variation of habitat conditions. The selected species *Prunus mahaleb*, *Prunus avium* and *Prunus padus* were subjected to both drought and waterlogging in a greenhouse experiment. Plant functionality in the form of midday leaf water potential, stomatal conductance and turgor loss point together with different aspects of biomass allocation and growth was tested. All included species lost their stomatal conductance and leaf water potential within a few days in the waterlogging treatment. Only *P. padus* had the capacity to recover with new leaves after the waterlogging ended, suggesting that avoidance strategies through leaf shedding can be a complementary mechanism to withstand waterlogging. *P. padus* kept its stomatal conductance and water potential for the longest time in the drought treatment followed by *P. mahaleb* and *P. avium*. This longevity in the drought treatment for *P. padus* could be explained by both tolerance strategies through lower turgor loss point, but also avoidance strategies with fast changes in growth and higher allocation of biomass to the roots. There is a clear risk that ecosystem service from *Prunus* species in the landscape can be negatively affected not only by drought but also by increased events of waterlogging. This highlights the need for including minority species and also other climate stressors in addition to drought in the planning and management of multifunctional landscapes.

1. Introduction

Central European forests are essential for soil and water conservation, landscape connectivity, habitat for wild life, recreation, carbon sequestration, and wood production. However, many of these increasingly important functions risk being negatively affected by a changing climate (e.g., Thuiller et al., 2011; Hanewinkel et al., 2013). Predicted increase in the frequency, duration, and severity of drought and heat stress associated with climate change will fundamentally alter the composition, structure, and biogeography of many forest systems globally (Allen et al., 2010; IPCC, 2021). Besides a warmer and periodically dryer climate, annual increase in precipitation is also predicted in central and northern Europe, together with more extreme precipitation

events, with pluvial flooding as a consequence (Ozolinčius et al., 2014; IPCC, 2021). In comparison with other continents in the northern hemisphere, Europe has fewer tree species than North America and Asia (e.g., Eiserhardt et al., 2015; Beech et al., 2017). Even though intra-specific variability with locally adapted populations and high phenotypic plasticity can counter balance a lower number of tree species, there is a risk that European forests might be less resilient towards tree species decline due to changing climate. Such losses will have extensive consequences for organisms linked to threatened species where complementary species are few or lacking (Schulze et al., 2016). Additionally even without species losses, climate induced stress can lower the capacity of species to deliver valuable ecosystem services. So far, most experimental studies of woody species in relation to climate change have

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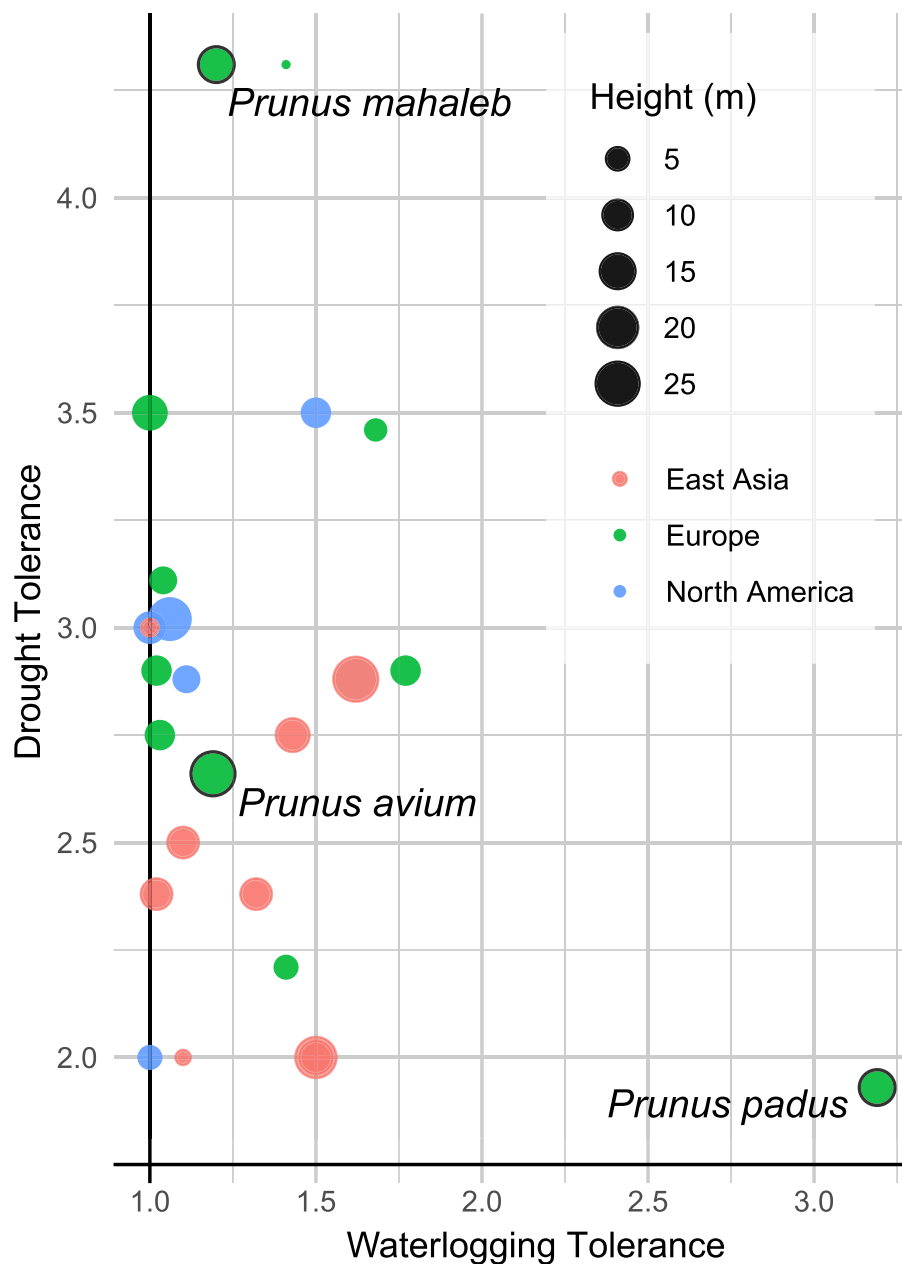


Fig.1. Bubble chart of drought and waterlogging tolerance on a scale from one to five, for all *Prunus* species included in Niinemets and Valladares (2006) dataset of temperate woody species from Europe, East Asia and North America. Bubble size shows maximum average heights derived from local floras. Selected species for this study are highlighted with a black circle and named in the graph showcasing that the species selection covers a large variation of main realised niches in relation to drought and waterlogging.

studied effects of drought or waterlogging separately on commercially important and dominating trees species (e.g., Hemery et al., 2010; Hanewinkel et al., 2013).

For ecosystem services connected to biodiversity, recreational and cultural aspects, flowering and fruit-bearing species are of great value and importance (e.g., Goodness et al., 2016; Wawrzyniak et al., 2020). As an example taken from the European atlas of forest species by San-Miguel-Ayanz et al. (2016), approximately only one fifth of the included European species have berries or other fleshy fruits, and roughly, one third of those species are cherry (*Prunus*) species. Thus, *Prunus* is a key genus, often overlooked for many ecosystem services in temperate Europe (e.g. Spiecker, 2006; San-Miguel-Ayanz et al., 2016; Nestby, 2020). The genus *Prunus* consists of almost 340 species (POWO, 2022), and has its main distribution in the temperate northern hemisphere. Cherry species can be found in many habitats – from dry and poor rock outcrops for *Prunus davidiana* Franch. in northeastern China, to rich and wet woodland habitats for *Prunus padus* L. in Europe.

To gain insight about responses to drought and waterlogging stress

on *Prunus*, this study investigated three *Prunus* species with wide distribution and importance in central Europe (Caudullo et al., 2019; San-Miguel-Ayanz et al., 2016). The species were chosen to reflect a gradient in habitat occurrence concerning drought and waterlogging (Fig. 1), where *Prunus padus* L. is typically found in wet environments, *Prunus avium* (L.) L. on mesic sites and *Prunus mahaleb* L. on xeric sites. All of the species are common, but nearly never the dominating species in the landscape and therefore, easily overlooked as important components for multiple ecosystem services (Table 1).

Based on their respective occurrence in different environments, Niinemets and Valladares (2006) rank the drought tolerance for *P. padus* as low, *P. avium* as intermediate and *P. mahaleb* as high. Data from Choat et al. (2012) using resistance to stem embolism to determine drought tolerance, gives the same rank order. Opposite, in a compilation of flooding tolerance in central European woody species, both *P. avium* and *P. mahaleb* were ranked low, whereas *P. padus* was ranked high (Glenz et al., 2006) which corresponds to Niinemets and Valladares (2006) data for waterlogging tolerance.

Table 1Overview of habitat conditions and some main ecosystem services related to *Prunus padus*, *Prunus avium* and *Prunus mahaleb* according to the literature.

	<i>Prunus padus</i> L.	<i>Prunus avium</i> (L.) L.	<i>Prunus mahaleb</i> L.
Stem Cavitation ψ_{50} (1)	-3.54 MPa	-4.76 MPa	-5.55 MPa
Drought tolerance (2)	1.93	2.66	4.31
Waterlogging tolerance (2)	3.19	1.19	1.2
Supporting ecosystem services			
Habitat occurrence	Edges and verges, wooded pastures, floodplain forests (3,5).	Open deciduous woodlands, scrubland, edges, glades and clearings (5).	Open woodlands, edges, rocky slopes, scrubland (5).
Hostplant for other organism	Macro fungi, Beetles, Lepidoterans, Hymenopterans, Hemipterans, Arachnids (4).	Macro fungi, Beetles, Lepidoterans, Hemipterans (4).	Macro fungi (6), Beetles (7), Lepidoterans (8), Hymenopterans (9), Hemipterans (10).
Food source for other organism	Food source for birds, pollen and nectar source for insects (4,5).	Food source for birds, pollen and nectar source for insects (4,5).	Food source for birds, pollen source and nectar source for insects (5).
Provisioning ecosystem services			
Wood	Traditionally used as firewood, smaller household tools and as detergent against rodents (3).	Important hardwood for paneling, cabinet-making, veneer production, parquet floors and musical instruments (5,11).	Heavy wood with pleasant smell used for carving small objects like tobacco pipes and canes (5).
Food	Fruits used for jams and liquer (3).	Common and popular fruit trees, consumed fresh but also widely used in a wide range of foods and drinks (13).	Fruits are edible, seeds have long tradition as a spice and can be used to produce seed oil (5,12).
Medical uses	Traditional medicinal plant (3).	Traditional use as medical plant. Extraction of anthocyanins and polyphenolics might have medical uses (14).	Seeds contains α -eleostearic acid and coumarin which might have medical uses. Large use as part of cosmetic products (12).
Regulating ecosystem services			
Ecological engineering	Slope stabilization and erosion control (15, 16).	Increase the stability of slopes and mitigate erosion (15,16).	Erosion control, wasteland reclamation, green roofs (5,17).
Afforestation	Edge plantings and understory to ash and oak (18).	Main crop tree, admixing species and edges (18).	Edge plantings and as nurse plant (5).
Horticultural use	Shelter plantings and parktree including several cultivars especially in Northern Europe (5,19).	Park and street tree plantings. Orchards. Rootstock for different ornamental cherries (5,19).	Hedges and shelter plantings. Used as rootstock for cherry fruit trees (5,19).
Cultural ecosystem services			
Use in Literature, Religion and Folklore	Mainly as part of poetry describing the spring. Traditionally sometimes used to protect from evil (3).	Numerous examples of symbolic values and uses in relation to the spring and as a fruit tree.	Important in the Mediterranean region e.g. as part of sacred places and as symbolic uses related to fruit trees and medical uses (20, 21).

(1) Choat et al., 2012; (2) Niinemets and Valladares, 2006; (3) Gunnarsson, 1988; (4) Sundberg et al., 2019; (5) San-Miguel-Ayanz et al., 2016; (6) Antonín and Dvořák, 2010; (7) Mifsud and Bily, 2002; (8) Alonso, 1999; (9) Heibo et al., 2014; (10) Bennewicz and Barczak, 2016; (11) Savill, 2019; (12) Ercisli and Orhan, 2008; (13) Chockhaisawasdee et al., 2016; (14) Švarc-Gajić et al., 2018; (15) Florineth et al., 2002; (16) Norris et al., 2008; (17) Savi et al., 2015; (18) Gustavsson and Ingelög, 1994; (19) Sjöman and Slagstedt, 2015; (20) Bermejo and Sánchez, 1998; (21) Stara et al., 2015.

Stomata closure is a first response to drought, preventing low leaf water potential (Ψ_L) and reducing the risk of leaf wilting (Kozłowski and Pallardy, 2002). Meanwhile, stomata closure reduce gas exchange; on a short-term resulting in reduced transpiration and photosynthesis, and on a long-term in reduced vitality and growth (McDowell et al., 2008). Severe drought leads to hydraulic failure due to xylem embolism (Urli et al., 2013) causing tree crown desiccation. However, the level of water deficit inducing plant drought stress is species, and even ecotype dependent (Abrams et al., 1992) as there are several functional and morphological traits connected to drought tolerance. For example, the above relations have been described as a gradient between so-called isohydry and anisohydry (McDowell et al., 2008; Klein, 2014; Ratzmann et al., 2019). Isohydric species have a more strict stomatal regulation to upkeep Ψ_L and thus, lower risk of hydraulic failure at the cost of reduced photosynthesis capacity. Anisohydric species have a less strict regulation of stomata and related Ψ_L , thus prioritizing carbon accumulation at the cost of higher risk of hydrolic failure. Another trait is the species-specific capacity to develop deep root systems (Delzon, 2015; Nardini et al., 2016), allowing a maintained leaf water potential. Yet another central aspect of drought tolerance in trees is the ability to make use of low leaf water potential. Preservation of a low osmotic potential at turgor loss point (Ψ_{p0}), as mechanism to endure lower leaf water potentials and maintaining the turgor, is central for this (Bartlett et al., 2012a; 2012b). Additionally many deciduous species are believed to avoid xylem embolism by shedding their leaves as a kind of hydraulic fuse (Wolfe et al., 2016). These different adaptations to drought stress, have been conceptualized, as two main overall drought strategies,

avoidance and tolerance (Delzon, 2015; Hiron and Thomas, 2018). Strong stomatal regulation (more isohydric), leaf shedding and reduced growth are seen as avoidance strategies by reduction of water use, whereas deep roots prevent water deficits by maximizing the water acculation (Hiron and Thomas, 2018). Accordingly, low Ψ_{p0} and high resistance to xylem embolism could be seen as tolerance of water deficit (Delzon, 2015; Hiron and Thomas, 2018).

Waterlogging creates anaerobic conditions in the root zone, and reduced oxygen availability hinders root metabolism, and thereby water uptake (Kozłowski and Pallardy, 2002; Leksungnoen et al., 2017). As for drought, an early plant response to waterlogging is stomata closure (Du et al., 2012; Kreuzwieser and Rennenberg, 2014). However, for many species, stomatal closure induced by waterlogging is not correlated with a decrease in leaf water potential (Dreyer et al., 1991; Kozłowski, 1997; Nielsen et al., 2010), with Kozłowski (1997) suggesting that waterlogging per se does not cause leaf water deficits. However, prolonged disturbances in both root metabolism and gas exchange lead to reduced vitality and visually detectable stress indications, such as reduced overall growth, small leaf formation and leaf shedding similar to drought induced stress symptoms (Newsome et al., 1982). Waterlogging-tolerance is highly species dependent and some species are known to even increase growth during flooding, by producing low-density wood with intercellular spaces, facilitating oxygen transport within the plant (Glenz et al., 2006). Other common adaptations to waterlogging conditions are the development of lenticels and adventitious roots (Kozłowski, 1997).

The main aim of this study was to experimentally evaluate drought

and waterlogging tolerance and related plant adaptations for three European cherry species (*P. avium*, *P. mahaleb* and *P. padus*) under controlled conditions to quantify and analyse the extent of their tolerance, and hence their capacity to deliver ecosystem services in different climate scenarios.

2. Method and material

The experiment was conducted during 2018 in a greenhouse situated at the Swedish University of Agricultural Sciences at Alnarp, located outside Malmö in Southern Sweden. For each species, 24 field grown bare-rooted seedlings were potted in the greenhouse during two days in late April. All plants had been cool-stored before planting and were dormant at the time of planting. The plant material was from a German nursery, representing typical central European provenances. The plants were two years old and of the nursery quality 50–80 cm high, transplanted once. All plants were planted in plastic 20 L pots in the homogenous Bara Mineral Hekla® raingarden substrate, which is mix of pumice, sand and compost. The commercial substrate used has a total pore volume of 60% and a bulk density of 900 kg/m³ at field capacity. It is designed to provide suitable growth conditions for both dry and wet conditions. The pots were filled with 15 L of substrate of known moisture content and total weight recorded. Length of plants (roots excluded), total weight and root volume using Archimedes' principle was recorded at time of planting. Given the different growth rhythm of the species there was a significant difference in these measurements in the following order *P. avium* > *P. mahaleb* > *P. padus*. In prioritizing same age or equality in size, we choose age. After potting, all plants were kept in the greenhouse until the end of the experiment. The plants were regularly watered until the start of the experimental treatments.

The experiment started on 29th of May, when all plants had developed mature leaves for the measurements. Each pot was watered to field capacity to obtain a starting reference value for each individual plant, reflecting no initial water stress and to determine water use during the course of the experiment.

Treatments were randomized to contain eight replicates of each species in three different treatments; control, waterlogging and drought. The waterlogging was created by placing the pots into plastic bowls filled with water level with the top of the soil of the planting containers. The plants in the control were kept well irrigated throughout the experiment and the plants subjected to the drought treatment received no irrigation after the 29th of May.

On the 11th of June, the waterlogging treatment was ended, since all individuals had defoliated and none showed signs of producing new shoots or leaves. After the extraction from being submerged, the pots were regularly weighed but were otherwise left undisturbed until the 2nd of July when it was noted that some plants were starting to set new buds. The amount of new green buds was counted directly and afterwards the plants were cut down and set for biomass extraction.

On the 15th of July the experimental measures (see below) for the drought and control treatments were terminated. Trees were removed from the pots, soil was cleaned off and the biomass was divided between aboveground and belowground compartments with a division at the root collar. The collected material was dried in a drying cabinet (Heratherm OGS400) to a constant weight at 85 °C (Pettersson and Ståhl, 2006; Jagodziński et al., 2020) and then weighed using a scale (KERN ADB 200-4) with a resolution of 0.0001 g. Two below ground samples were intermixed in the drying process and therefore, treated as missing data in the analysis.

2.1. Shoot length

For a non-destructive capture of the growth during treatment, the shoot length of the three longest shoots on each plant were measured at the start of the experiment. The measurements of shoot length were repeated using the same shoots for every measurement at weekly

intervals until shoot length had stagnated.

2.2. Water status in the plant

Water status was measured daily at midday on the initial days, and then at intervals of two to four days for the rest of the experiment. Water status was measured with determinations of both midday leaf water potential (Ψ_L) and stomatal conductance (g_s). For Ψ_L , the lowest situated light-exposed mature leaf from each seedling was collected and directly installed in a pressure chamber (Model 1000, PMS Instrument Company, OR, USA). Due to unexpectedly small petioles on the *P. mahaleb* leaves it was not possible to insert them safely in the pressure chamber and thus, they could not be included in the Ψ_L measures. In parallel, g_s was determined on two different light-exposed leaves using a porometer (METER Group AG, Munich, Germany). The mean of the two measurements was calculated for each plant. Measuring order of the plants for Ψ_L and g_s shifted regularly between the treatments in order to counteract biases of time effect during the measurements taking place between 11:00–13:00.

2.3. Water status in the soil

Gravimetric water content at field capacity at the start of the experiment was determined on small 20 g soil samples. Samples were weighed before and after placement in a drying oven at 105 °C until no further weight loss could be recorded (ISO, 2014). Gravimetric water content was converted to volumetric water content through multiplication with substrate bulk density. Water status of the pots was measured through weighing every day at the start of the experiment and every 2nd day during the final part of the experiment to determine volumetric water content.

2.4. Turgor loss point

To obtain values of the turgor loss point (Ψ_{p0}) we used the approach described by Bartlett et al. (2012a) in the following way: when a species showed signs of leaf wilting in the drought treatment, one branch per plant for both the drought treatment and the control of that species was harvested for Ψ_{p0} estimation. The dates for collecting Ψ_{p0} data were 2nd, 9th and 13th of July, depending on the wilting of the species. The harvested branch was directly recut under water, at least two nodes from the original cut, and placed in a water tube without exposing the cut surface to the air (Bartlett et al., 2012a). These samples were then stored in a dark chamber with >75% relative humidity overnight to rehydrate. Following the rehydration, one 8 mm leaf disc per plant from the mid-lamina region was extracted using a cork borer. The discs were wrapped in foil and placed in liquid nitrogen for 2 min and then punctured 10–15 times with sharp tipped forceps to aid evaporation through the cuticle and reduce equilibration time, before shutting the leaf disc in the vapour pressure osmometer (Vapro 5600, Westcor, Logan, UT, USA) using a standard 10 μ l chamber. After 10 min equilibration time the Initial solute concentration (c_s (in mmol kg⁻¹)) reading was recorded. c_s was then recorded in repeated readings at ~2 min intervals where 5 mmol kg⁻¹. Solute concentration was converted to osmotic potential (Ψ_π) using Van't Hoff's relation (Eq. (1)):

$$\Psi_\pi = -RTc_s \quad (1)$$

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

Using the equation (Eq (2)) from Sjöman et al. (2015) Ψ_{p0} was predicted from the osmotic potential at full turgor ($\Psi_{\pi100}$). This equation is an adjustment of Bartlett et al. (2012a, 2012b) original global equation and dataset so that it only includes temperate trees.

$$\Psi_{p0} = -0.2554 + 1.1243 \times \Psi_{\pi100} \quad (2)$$

2.5. Statistical analysis

All statistical testing was performed in R (R Core team, 2019) with a significance level of <0.05. Validation of model assumptions was made by plotting the residuals from the models (Zuur et al., 2009). Graphical data representations were performed using the *ggplot2* package (Wickham, 2016).

2.5.1. Biomass

We tested the effect of treatment and species on biomass using linear models with ANOVA type II sum of squares (Langsrud, 2003; Fox and Weisberg, 2019) using the *lm* function and *car* package (R Core team, 2019; Fox and Weisberg, 2019). Response for each model was separately: *biomass above ground*, *biomass below ground*, *total biomass* and the ratio between below and above biomass (*root/shoot ratio*). Explanatory variables were *species* (factor with 3 levels) and *treatment* (factor with 3 levels), including their interaction. *Starting weight* at planting was included as a covariate in all models as it gave higher adjusted R² values for all models compared to the root volume at planting. To fulfill the assumptions of the models the response was square-root transformed. Post hoc testing was performed for significant variables using pairwise comparison of back transformed ls-means (a.k.a. estimated marginal means) with Tukey-adjustment for multiple testing in the *emmeans* package (Lenth, 2021). Due to interactions, these comparisons focused on both main treatment effect across species and within species treatment effects.

2.5.2. New buds after waterlogging

To test for differences between species concerning observed *new buds* after the waterlogging treatment had ended we used permutation tests in the *coin* package (Hothorn et al., 2008). First we tested for overall difference using a General Independence Test, and then performed pairwise post hoc tests with the same function together with a Bonferroni correction for the multiple testing.

2.5.3. Shoot length

The mean value for the three shoots measured for each plant was calculated for each week, and used as the response in the analysis. Already after one week shoot growth had stagnated in the waterlogging treatment, therefore the analysis focused on the drought treatment in relation to the control. Due to the longitudinal and repeated structure of the data we used generalised least squares (GLS) with appropriate variance-covariance structure to incorporate the repeated structure of the data. This modelling was done using *gls* function in the *nlme* package (Pinheiro et al., 2020). The best fitting variance-covariance structure was based on Akaike information criterion (AIC) together with log-likelihood test and inspection of residual plots. Structures tested were Compound Symmetry, Unstructured, Autoregressive and Autoregressive Heterogeneous Variances. First, a full model with *species*, *treatment* (drought and control) and *weeks* of treatment including their two-way interactions were tested. Post-hoc test of *treatment* effect across *species* effects was performed using pairwise comparison of ls-means with Tukey adjustment in the *emmeans* package (Lenth, 2021). Since both *treatment*, *species* and *week* was significant with large interactions between *week* and *treatment* as well as *species*, we built individual models for each species within the drought treatment to further explore these relations. Explanatory fixed variables included in these models was the *treatment* and *week* including their interaction.

2.5.4. Water status

Missing values due to technical malfunctions were imputed using the average values calculated from the individual time points closest to the missing data point. These values were cross-calibrated to the other water status measurements and treatment to avoid larger than average changes in the imputed measurement compared to the other parts

Table 2
ANOVA tables for the models of biomass variables using Type II tests.

Explanatory variables	Above-ground Biomass			Below-ground Biomass			Total Biomass			Ratio of Below/Above		
	SSq	Df	F-val	P-val	SSq	Df	F-val	P-val	SSq	Df	F-val	P-val
Species	1.06	2	4.62	0.013	25.12	2	16.90	<0.001	19.79	2	17.51	<0.001
Treatment	7.03	2	30.51	<0.001	69.38	2	46.68	<0.001	56.48	2	49.97	<0.001
Start Weight	10.39	1	90.10	<0.001	6.47	1	8.70	0.005	14.93	1	26.42	<0.001
Species:Treatment	1.54	4	3.33	0.016	20.39	4	6.86	<0.001	15.04	4	6.65	<0.001
Residuals	7.15	62			44.59	60			33.90	60		

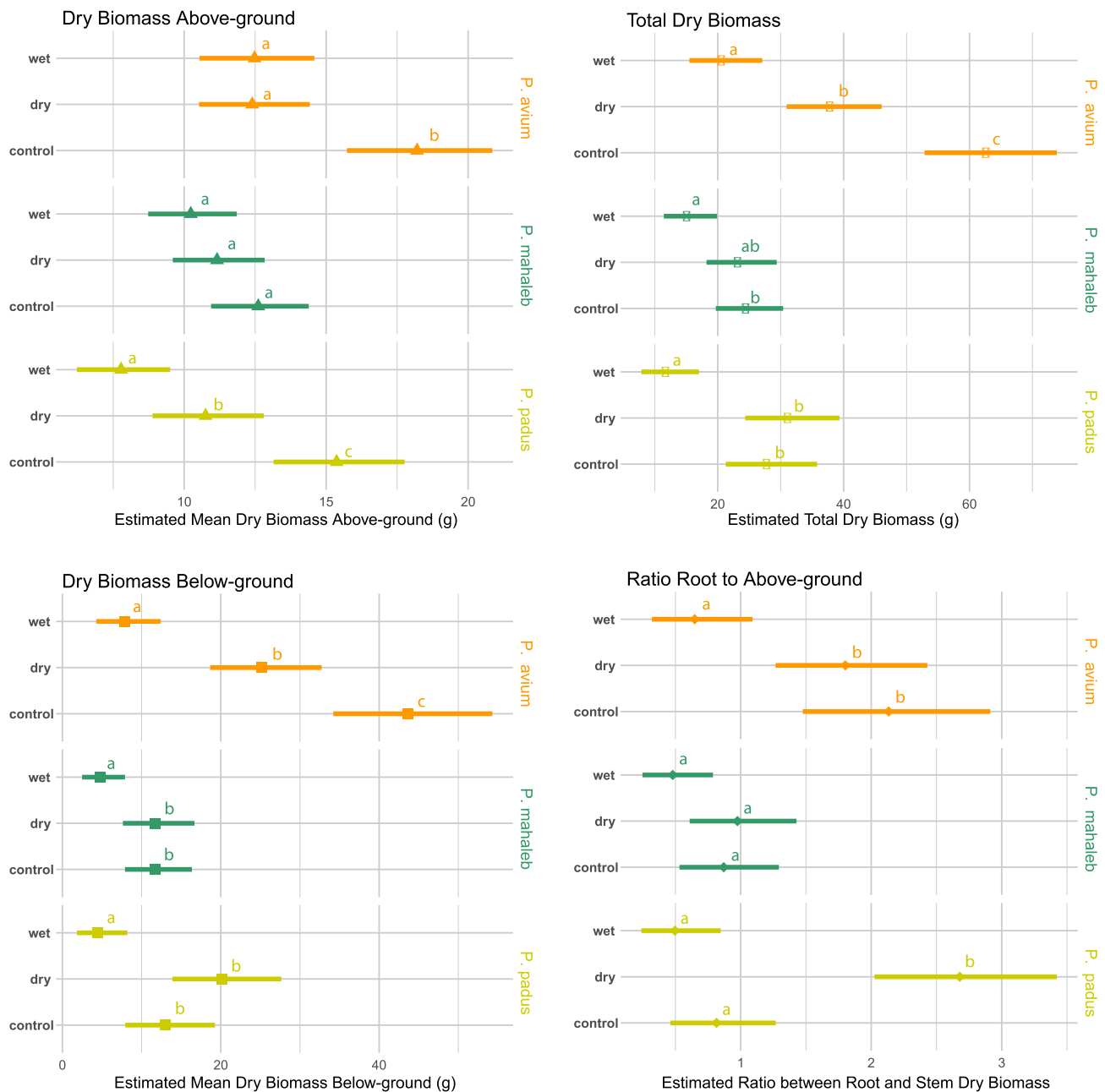


Fig. 2. Figure of least square means and their 95% confidence intervals for each species and treatment derived from linear models of above-ground biomass, below-ground biomass, total biomass and the ratio between below-ground and above-ground biomass. Pairwise comparison made within each species and significant differences are denoted by different letters.

included in evaluating the water status. For Ψ_L values, ~2% was imputed and ~5% of g_s values. When plotting Ψ_L and g_s against *days* and *treatment* it was evident that the waterlogging treatment diverged strongly from the other treatments and only gave meaningful measurements for the first eight days, whereas the water status was measurable for almost the whole experimental period in the drought treatment. Due to this high skewness, we modeled waterlogging against the control and drought against the control as separate models for water status. This modelling was done using *gls* function in the *nlme* package (Pinheiro et al., 2020), with an autoregressive heterogeneous variances structure to incorporate the repeated structure of the data. Response variables were Ψ_L and g_s . Explanatory variables included were the *treatment* (drought or waterlogging vs control) and *species*. *Days* of measurement including interaction as covariate was tested as first, second and third degree polynomials, with the final number of

polynomials to include based on Akaike information criterion (AIC) together with log-likelihood test and inspection of residual plots.

2.5.5. Turgor loss point

We tested the effect of treatment and species on Ψ_{p0} with linear models ANOVA type II sum of squares (Langsrud, 2003; Fox and Weisberg, 2019) using the *lm* function and *car* package (R Core team, 2019; Fox and Weisberg, 2019). Explanatory variables were *species* (factor with 3 levels) and *treatment* (factor with 2 levels), including their interaction. Post hoc testing was performed for significant variables using pairwise comparison of ls-means with Tukey-adjustment for multiple testing in the *emmeans* package (Lenth, 2021).

Table 3

Estimated coefficient with standard error (SE) and t-value based p-values from repeated measure models of shoot length for the control and drought treatment for each individual species. Reference levels in the table are the control treatment and first baseline measure of shoot length when treatments started (Week 0).

Est. Parameters	<i>Prunus avium</i>			<i>Prunus mahaleb</i>			<i>Prunus padus</i>		
	Coefficient	SE	p-value	Coefficient	SE	p-value	Coefficient	SE	p-value
(Intercept)	25.06	2.74	<0.001	7.08	1.80	<0.001	14.43	1.70	<0.001
Drought	-6.46	3.87	0.010	-1.31	2.55	0.607	2.09	2.40	0.387
Week 1	5.83	0.76	<0.000	1.67	0.54	0.003	2.92	0.52	<0.001
Week 2	10.98	1.07	<0.001	3.50	1.08	0.002	6.21	0.75	<0.001
Week 3	15.04	1.29	<0.001	4.52	1.20	<0.001	7.74	0.81	<0.001
Week 4	16.38	1.48	<0.001	4.96	1.29	<0.001	8.09	0.93	<0.001
Drought: Week 1	0.52	1.08	0.631	0.46	0.77	0.552	-0.26	0.74	0.731
Drought: Week 2	-1.13	1.52	0.460	-0.61	1.53	0.695	-2.79	1.05	0.010
Drought: Week 3	-4.63	1.84	0.014	-1.48	1.71	0.389	-4.09	1.16	<0.001
Drought: Week 4	-5.81	2.10	0.007	-1.85	1.82	0.314	-4.30	1.37	0.002

3. Results

3.1. Biomass

The model for *above-ground biomass* was significant ($F = 66.39, p < 0.001$) with *treatment* as well as *species* effects and a small interaction effect (Table 2). Biomass of *P. avium* was clearly affected by drought and waterlogging compared to biomass of the control plants, whereas *P. padus* differed with higher biomass in the drought and control compared to the waterlogging (Fig. 2). A similar, non-significant, trend could be seen for *P. mahaleb*. The model for *below-ground biomass* was significant ($F = 29.46, p < 0.001$), with *treatment*, *species* effects and interaction being significant (Table 2). For all species, *root biomass* was the lowest in the waterlogging treatment and for *P. avium* there was also a difference between drought and control. *P. padus* had tendencies to higher below-ground allocation in the drought treatment than in both the waterlogging treatment and the control (Fig. 2). These below-ground patterns were similar for the *total biomass* model ($F = 45.48, p < 0.001$). This means that the *root/shoot* ratio model ($F = 11.23, p < 0.001$) gave lowest values for waterlogging in all cases, but also a significantly higher ratio in the drought treatment for *P. padus*, which was not found for the other species (Fig. 2). Post-hoc test of total biomass between the species within each treatment showed that *P. avium* had significantly larger values in the control than *P. padus* and *P. mahaleb*, however in the drought treatment there was no significant difference compared to *P. padus* and only marginal towards *P. mahaleb*. This means that biomass difference at start of the experiment between species have evened out in the drought treatment and especially between *P. padus* and *P. avium*.

3.2. New buds after waterlogging

All *P. padus* plants started to set *new buds* after the waterlogging had ended. None of the plants of the two other species did this. The permutation testing supported that this difference was significant at the level of $p < 0.05$.

3.3. Shoot length

For all species, *shoot length* stagnated within the first week in the waterlogging treatment. For the full model with drought and control there were both a significant *species* effect ($F = 16.57, p < 0.001$), *treatment* effect ($F = 4.98, p = 0.027$) and *week* effect ($F = 76.87, p < 0.001$) including large interaction effects with time (*week*) for both *species* ($F = 11.41, p < 0.001$) and *treatment* ($F = 7.30 < 0.001$). Post-hoc test of the *treatment* effect across *species* in the control gave the following significant order between species $P. avium > P. padus > P. mahaleb$. However for the *drought treatment* only *P. mahaleb* differed significantly from the two other species with the following order $P. avium \sim P. padus > P. mahaleb$. The strong time effect, with increasing total *shoot length* over time compared to the control can be seen in (Table 3). The interaction effect between the *drought treatment* and *weeks* is illustrated in Fig. 3. *P. mahaleb* showed no significant treatment or interaction effects, whereas *P. padus* already at week two showed a stagnation in *shoot length* for the drought stressed plants compared to the control plants. This effect was delayed one more week for *P. avium*.

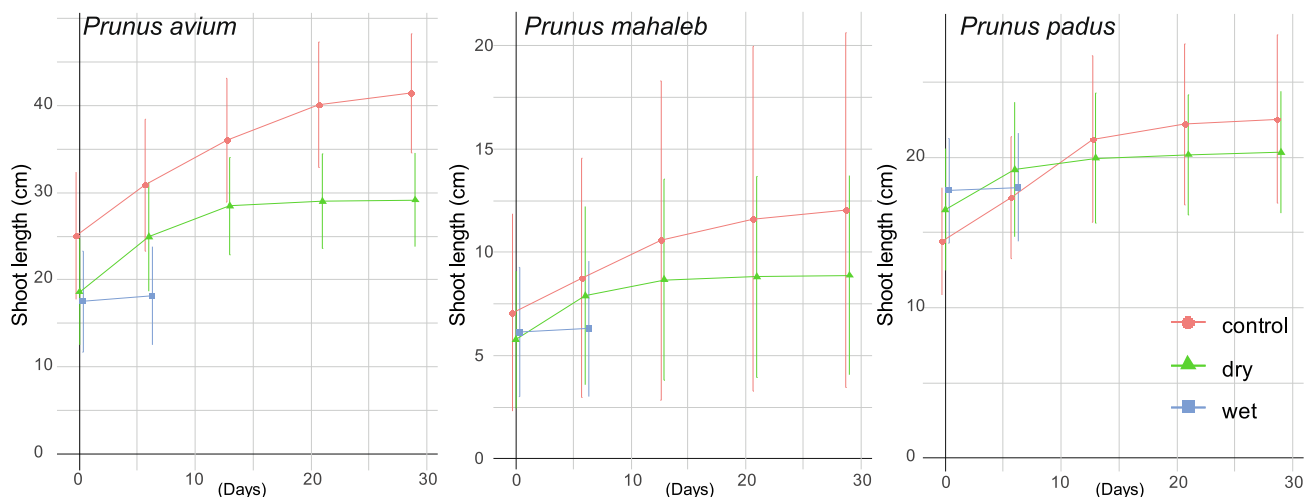


Fig. 3. Shoot length development over time (weekly) with 95% confidence intervals for the different species and the treatments control, drought (dry) and waterlogging (wet).

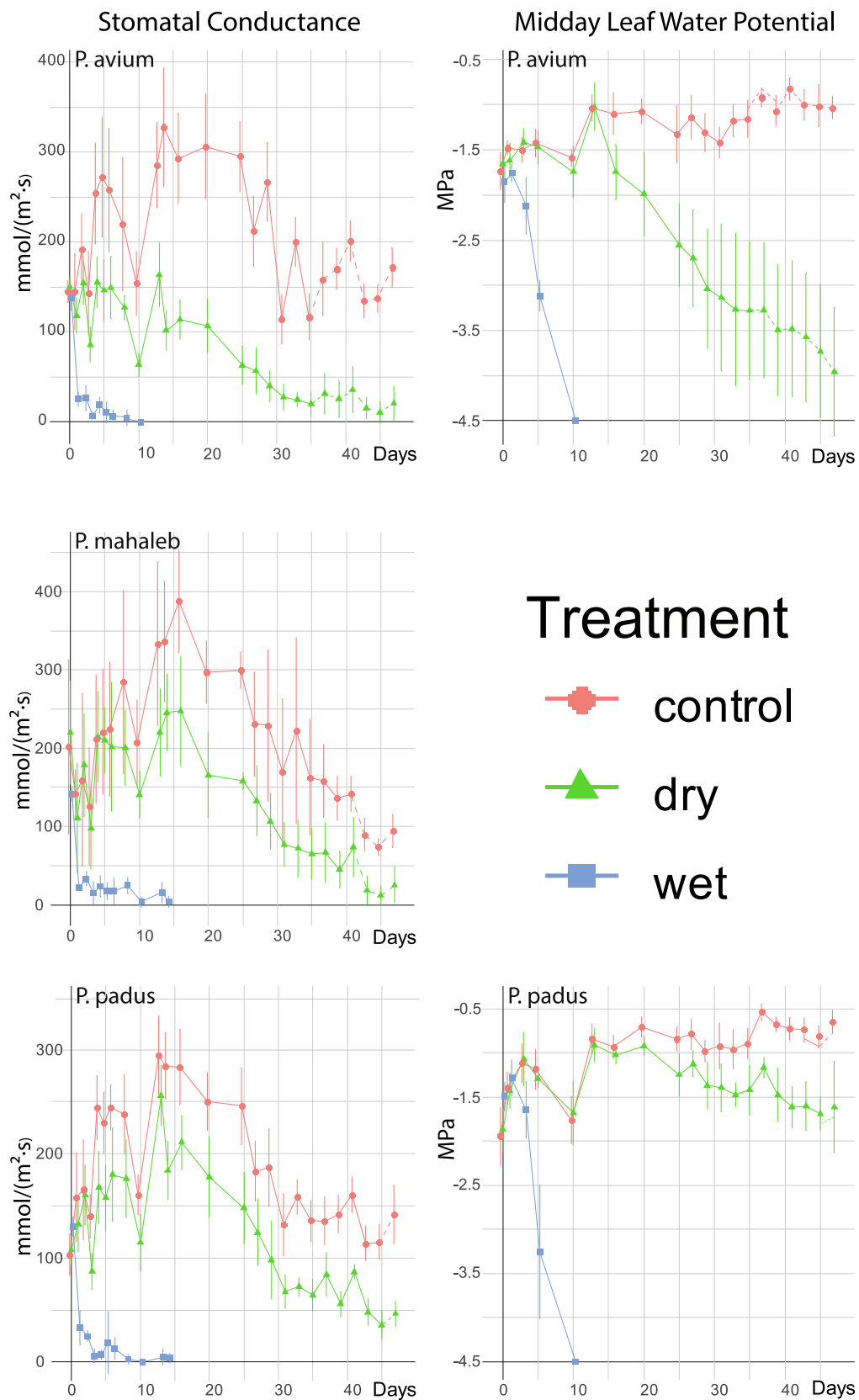


Fig. 4. Development of stomatal conductance and water potential over time for the different treatments and species. Each day of measurement is represented by mean values and related 95% confidence intervals. Left panels show stomatal conductance and right panels show water potential. Dotted lines indicate measurements made after cuttings were taken for turgor loss point estimation. Note the large deviation of the waterlogging treatment (wet) compared to the control and drought treatment.

Table 4

ANOVA table for the repeated measures model of stomatal conductance and water potential in relation to the drought and waterlogging treatment.

Explanatory variables	g_s Dry vs Control			Ψ_L Dry vs Control			g_s Waterlog. vs Control			Ψ_L Waterlog. vs Control		
	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value
(Intercept)	1	1965.1	<0.0001	1	3846.5	<0.0001	1	2342.6	<0.0001	1	773.0	<0.0001
species	2	11.1	<0.0001	1	30.2	<0.0001	2	0.7	0.5079	1	0.6	0.4312
treatment	1	358.1	<0.0001	1	419.1	<0.0001	1	524.9	<0.0001	1	206.0	<0.0001
poly(Days ³)	3	85.8	<0.0001	3	5.4	0.0011	3	12.4	<0.0001	3	1.7	0.1718
species: treatment	2	27.3	<0.0001	1	73.6	<0.0001	2	2.0	0.1356	1	2.4	0.1254
species: poly(Days ³)	6	8.8	<0.0001	3	1.5	0.2212	6	4.1	0.0006	3	4.6	0.0044
treatment: poly(Days ³)	3	21.9	<0.0001	3	69.4	<0.0001	3	65.6	<0.0001	3	155.0	<0.0001
spec: treat: poly(Days ³)	6	3.7	0.0013	3	10.7	<0.0001	6	2.8	0.0113	3	2.1	0.1046
Denominator df	1066			618			305			144		

3.4. Midday water potential and stomatal conductance

As seen in Fig. 4, g_s for all three species deviated from the control plants directly on the first treatment day in the waterlogging treatment. The Ψ_L followed the same pattern shortly afterwards, on the third day of measurements. There were no differences between the species in relation to g_s or Ψ_L in the waterlogging treatment, although the treatment effect was strong (Table 4). In the drought treatment, there were differences in species behavior, including interactions with time and treatment (Table 4). To visualize the main patterns of interest, we calculated the percentage differences of each species in relation to its control over time, which can be seen in Fig. 5. From this it is evident that *P. padus* retained functionality through g_s and Ψ_L for the longest time and *P. avium* for the shortest time, whereas *P. mahaleb* had an intermediate position between the other two species. However, for the 10 initial days, there was a trend with higher g_s for *P. mahaleb* than *P. padus*. Nonetheless, over time *P. padus* managed to change to a less negative slope compared to the two others.

3.5. Water status in the soil

There was a continued decrease in the volumetric moisture content (VWC) over time (Fig. 6). The water loss from un-vegetated reference pots and pots containing *P. mahaleb* showed similar patterns over the first eight days of drought treatment. The overall pattern of change over time was similar for all species, but differed partly in magnitude with the largest water consumption in *P. avium*, followed by *P. padus* and then *P. mahaleb*. All planted pots showed lower VWC compared to un-vegetated reference pots.

3.6. Turgor loss point

There was a treatment effect ($F = 17.91$; $p < 0.001$) and species effect ($F = 66.77$; $p < 0.001$) on the Ψ_{p0} and no interaction effect. Irrespective of species, the drought treatment gave a more negative Ψ_{p0} with an estimated overall difference of -0.35 MPa between control and drought treatment. Individual differences between treatments for the species was -0.40 MPa for *P. padus*, -0.35 MPa for *P. avium* and -0.24 MPa for *P. mahaleb*. All species differed significantly from each other in Ψ_{p0} with *P. padus* having the most negative values and *P. avium* the least negative (Fig. 7).

4. Discussion

4.1. Drought

Stomata closure is central in trees' response to drought. In this study, *P. padus* was able to upkeep its g_s relative to the control for a longer time compared to especially *P. avium* but also to *P. mahaleb*. For *P. avium*, the Ψ_L dropped markedly from the control in conjunction with the relative g_s decreasing to around 50% after 10 to 15 days of drought. This change was slower and less direct for *P. padus*, taking place around 35 to 40

days. This indicates more of an anisohydric behavior for *P. padus* and an isohydric for *P. avium*, as isohydric species adjust stomata opening more to stabilize Ψ_L . This relates to the range of water potentials over which stomata is effective in controlling Ψ_L (the so-called hydroscape), were species with larger ranges are expected to be more anisohydric (Meinzer et al., 2016). Following this reasoning, Fu and Meinzer (2018) and Ratzmann et al. (2019), state that Ψ_{p0} provides a proxy for the degree of iso/anisohydry across species if growing in comparable environments. *P. padus* given its lower Ψ_{p0} could therefore, be seen as more anisohydric than *P. avium* and *P. mahaleb*. This is supported by that *P. padus* could utilize a lower Ψ_L compared to *P. mahaleb* and *P. avium* by relatively increasing more in biomass compared to these two species in the drought treatment. Interestingly this was done by increasing the root biomass while reducing height growth faster than *P. avium*.

Departing from Delzon (2015) and Hirons and Thomas (2018) conceptualization of drought avoidance and tolerance strategies, implies that *P. padus* is combining both avoidance of water loss by decreased shoot growth, avoidance of water deficit by increasing water uptake by roots but also tolerance through a low Ψ_{p0} . This points towards the argumentation of Nardini et al. (2016) that drought tolerance involves multiple interacting traits as well as the notion of Ratzmann et al. (2019) that iso/anisohydry and similar relative concepts such as tolerance and avoidance are not binary but continuums where species can show large plasticity in their behaviors.

The only species of the three tested that we found published reference values of Ψ_{p0} for was *P. mahaleb* with -2.62 MPa from field grown trees (Kikuta et al., 1997), and -2.59 MPa on a green roof installation (Savi et al., 2015), both in northeast Italy. These values are well in line with the mean value of -2.65 found in this study in the control treatment. Given the high resistance against stem embolism (Choat et al., 2012) and deep rooting (Nardini et al., 2016) of *P. mahaleb*, the reason for it being described as very drought tolerant, probably is related more to stem and root adaptations than leaf aspects. However, since stem cavitation was not measured in this study this needs further confirmation as well investigation of rooting patterns between different life stages of the species. The overall treatment difference on Ψ_{p0} of -0.35 MPa is in well in line with the global meta-analysis of Bartlett et al. (2014) who reported a mean difference of -0.44 MPa between pre- and post-drought. Despite this overall treatment effect on Ψ_{p0} , the rank order was the same for the species in the treatments and correlated well with the species performance over time in the drought treatment. This provides further experimental support for using Ψ_{p0} from osmometer predictions as performance indices for the drought tolerance of trees (Bartlett et al., 2012a; Sjöman et al., 2015), but also the need for including the growing context for the Ψ_{p0} measurements.

That *P. padus* maintained its relative Ψ_L and g_s longer than the other two species and had the lowest Ψ_{p0} , seems contradictory to its frequent occurrence in wet sites. Lawesson and Oksanen (2002) found that *P. padus* had one of the narrowest niches of Danish woody species, with clear correlation to wet soil, and discussed that this might be related to lack of developing to a larger tree in dense and shady forests with high competition from other species. However, Wiström and Nielsen (2017),

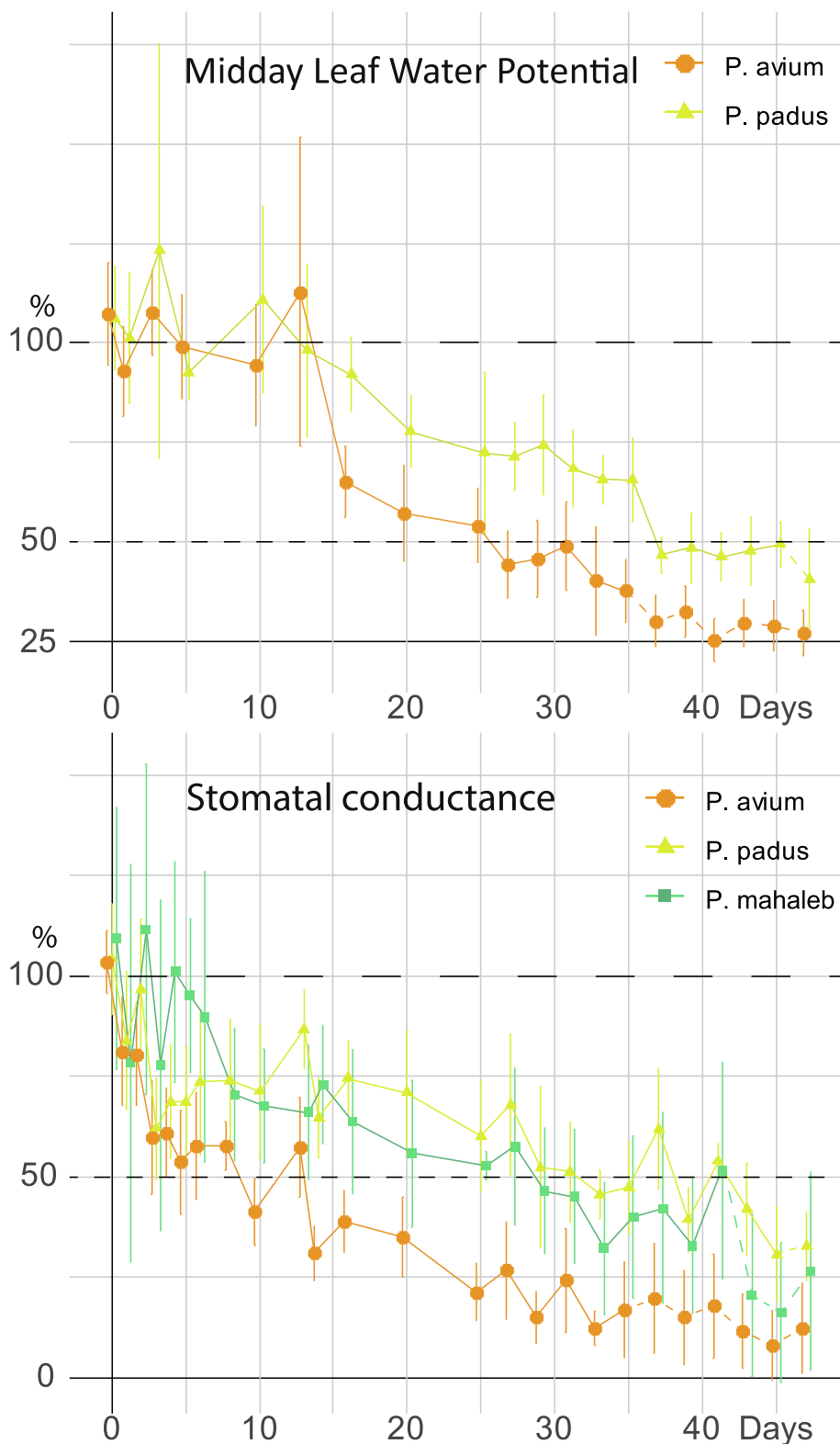


Fig. 5. Percentage difference of water potential (upper panel) and stomatal conductance (lower panel) for the drought treatment compared to the control for each species. Dotted lines for time trend indicate measurements made after cuttings were taken for turgor loss point estimation and thus, when individuals of the species were starting to wilt.

studying edge habitats in southern Sweden, where such light driven competition would be less, also saw a correlation to wetter sites for *P. padus*. One possible explanation for its ability to handle drought could be the fast decline in height growth and its change to larger investments in its roots. Such conservative approach to height growth might be less

competitive over time in less wet sites. Leather (1996), departing from Jarvis (1960), concluded that *P. padus* has a very large plasticity in its shoot growth due to site conditions and can also survive longer drought periods when old, but is more sensitive when young. Another explanation for the difference between general occurrence data and the results

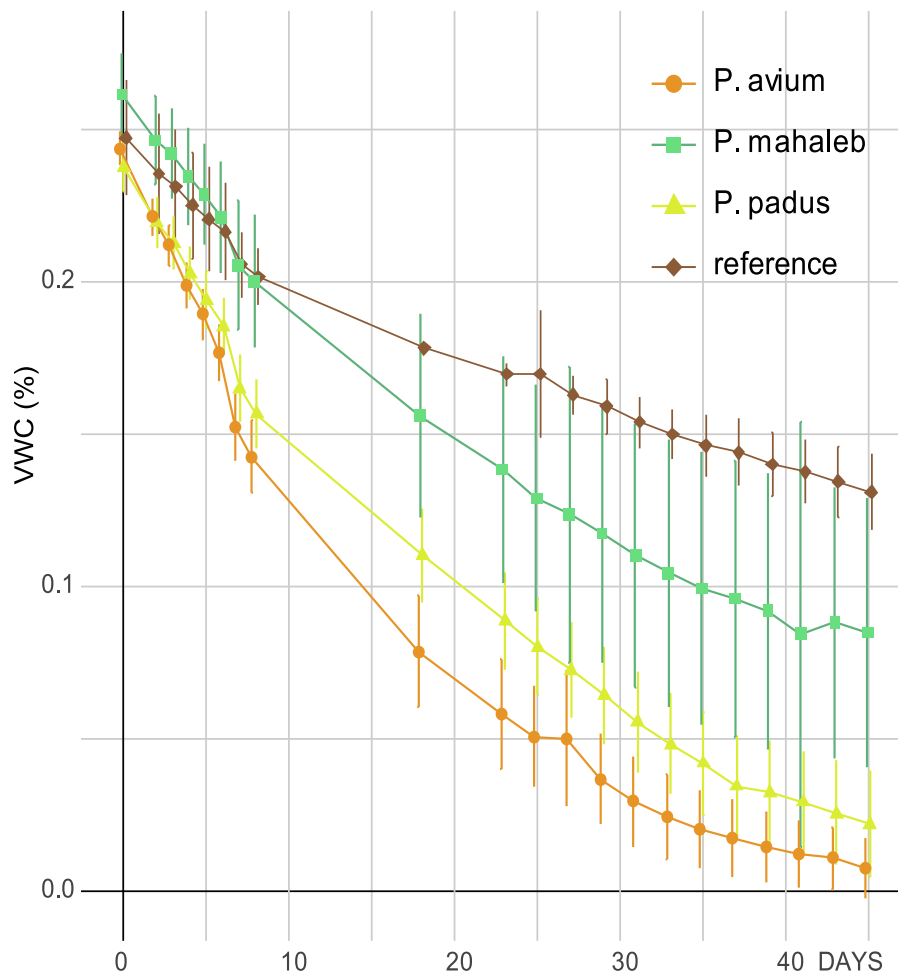


Fig. 6. Development of volumetric moisture content (VWC) over time in the drought treatment for the different species. Reference is unvegetated pots. Each day of measurement is represented by mean values and related 95% confidence intervals.

presented here could be the large distribution of the species used in this study, as there might be intraspecific differences depending on the specific genotype or ecotype of the species (Abrams et al., 1992; Baliuckas et al., 2000, 2005; Hannus et al., 2021). However, there are other examples of wetland species showing high drought tolerance in controlled experiments, e.g., *Alnus maritima* (Marshall) Muhl. ex Nutt., (Schrader et al., 2005), *Taxodium distichum* (L.) Rich., and *Magnolia virginiana* L (Nash and Graves, 1993).

4.2. Waterlogging

Similar to other waterlogging studies of *Prunus* (Pimentel et al., 2014; Iacona et al., 2019; Lee et al., 2022) there was an overall decline in g_s within one week. These studies of waterlogging of *Prunus* have used weekly intervals, with declining g_s after one week for most of the species or rootstock hybrids included. In the current study, we could see that the waterlogging effect on *Prunus* can be evident also within days as reported earlier for *Prunus armeniaca* L. (Nicolás et al., 2005). Sharp decline of Ψ_L followed shortly after the decline of g_s , similar to the response of *P. armeniaca* (Nicolás et al., 2005) but opposite to the review of several non-*Prunus* tree species by Kozłowski (1997). Stomatal closure in flooding is suggested to be more related to hormonal signals than actual water deficits and hydraulic conductivity (Nicolás et al., 2005). However, for *P. armeniaca* Nicolás et al. (2005) propose that there might be partial water deficit effects concerning g_s and its Ψ_L relations, which could explain the clear drop in Ψ_L in the current study, although further

research is needed to conform this.

All of the species tested showed what perhaps could be conceptualized as an avoidance strategy in the waterlogging treatment through leaf shedding. However, *P. padus* was the only species that showed signs of recovery from the waterlogging treatment induced in this study, and thus, a functional avoidance strategy. *P. avium* and *P. mahaleb* could probably be seen as lacking strategies for coping with longer durations of waterlogging. Similarly, Pimentel et al. (2014) also found a total mortality of pure *P. avium* rootstocks after 14 days of waterlogging, and low performance for related crossings, among others with *P. mahaleb*. Performance was best for the non-*P. avium* rootstocks, including *Prunus cerasus* L. and *Prunus cerasifera* Ehrh., which was linked to development of hypertrophied lenticels on the stem, indicating some type of tolerance within the genus. This higher waterlogging tolerance of *P. cerasifera* crossings or specific rootstock cultivars of it, have also been reported by (Ranney, 1994; Iacona et al., 2019). The difference in rootstock cultivars (Iacona et al., 2019) of this shrub-tree species implies that ecotypic difference could be of importance also concerning waterlogging of *Prunus*. Comparing waterlogging studies has inherent problems due to methodological differences. Nevertheless when comparing the performance of waterlogging with several other genera, showing good performance of species for several weeks (Ferreira et al., 2009; Du et al., 2012; Glenz et al., 2006; Domisch et al., 2020), it is evident that the performance of *Prunus* species in this study indicate low tolerance to waterlogging.

Given that *P. padus* is perceived as one of the most waterlogging

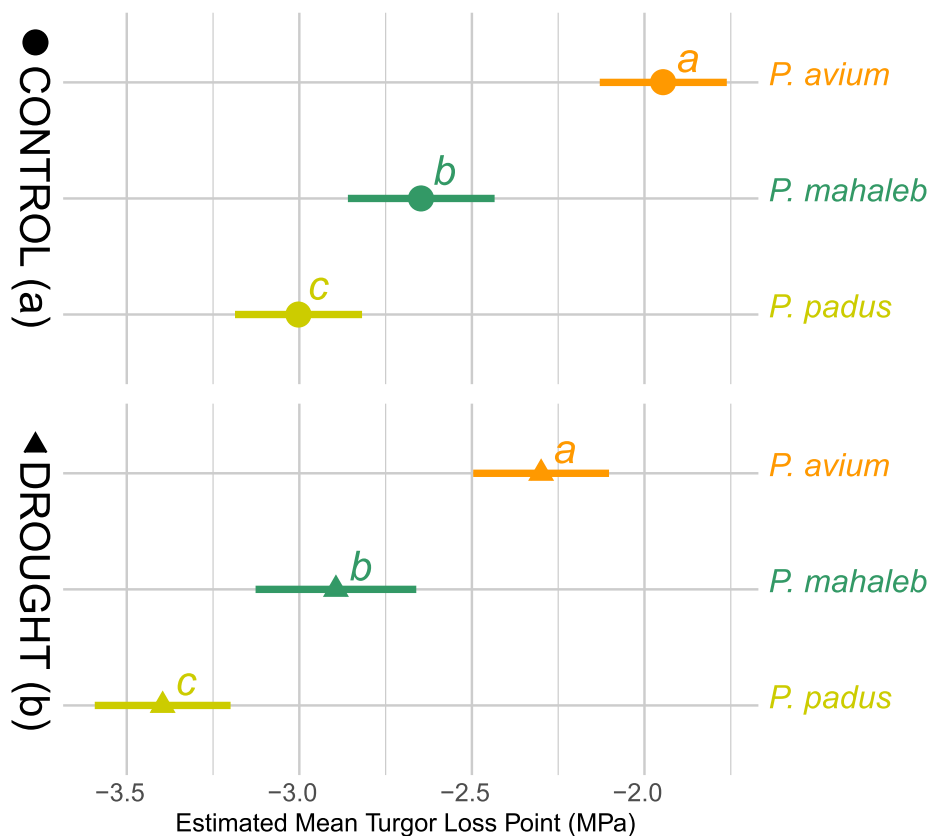


Fig. 7. Illustration showing least square means and 95% confidence intervals for each species and treatment derived from linear models of Turgor Loss Point. Pairwise comparison made between each species (in color and *italics*) and overall between treatment (in black). Significant differences are denoted by different letters.

tolerant *Prunus* species correlated to wet sites in its general natural occurrence (Glenz et al., 2006), it is surprising that it did not maintain its functionality in the waterlogging treatment much longer than the other species tested. *P. padus* is known for its strong recuperation capacity from insect defoliation by the bird cherry ermine moth (*Yponomeuta evonymellus*), where it can produce new foliage after full defoliation within one to two weeks (Leather, 1986). As such, an avoidance strategy of shedding leaves, paired with high foliage recuperation capacity, might be a viable strategy for handling waterlogging. Additionally, the high plasticity in growth regulation in *P. padus* is also reflected in its capacity to set root suckers, which is believed to be central for its capacity to hold its ground in riparian forest with high disturbance levels (Deiller et al., 2003; Leuschner and Ellenberg 2017).

4.3. Practical landscape implications

An important caveat in interpreting the results in a wider landscape context is that mature trees might cope with stresses differently than young seedlings (Kreuzwieser and Rennenberg, 2014) and therefore, the results should be seen as indications for the species performance in a landscape context.

The results indicate that all the studied species are sensitive to increased flooding and drought occurrences that are expected results of climate change. All three species reacted strongly to waterlogging, and *P. avium* quickly showed clear signs of drought stress when irrigation was withheld. Longer periods of drought, and events of heavy rains with flooding, might negatively affect these minority species with high importance for multiple ecosystem services.

The abundances of bird spread species such as *Prunus* have been shown to be affected, both by the vegetation structure of edges and woodland itself, as well as by the surrounding landscape structure and

herbivory (e.g., Sarlöv-Herlin and Fry, 2000; Wiström and Nielsen, 2016). Future decline of *Prunus* species induced by climate change can thus, be affected by the spreading possibilities from the surrounding landscape as well as the management of existing woodland edges and browsing wildlife. Supporting existing minority species such as *Prunus* through selective clearing and thinning in landscape and forest management, as well as inclusion in afforestation and edge restoration in the landscape, is therefore worth further consideration to increase the overall landscape resilience (Larsen and Nielsen, 2012; Messier et al., 2015).

There is some evidence for common and dominating forest species, that species mixing can reduce drought stress (Pardos et al., 2021). How such mixing effects work for minority species such as those studied here needs further exploration. Parallel studies of positive mixing effects for waterlogging is lacking, but it is well known that reduction of trees due to stress or disturbance (i.e., clear-cuts) increases soil wetness. Waterlogging might thus, be induced not only by cloudbursts but also by other disturbances from climate change or human land uses that leads to tree mortality. Additionally, in many afforestation projects former man-made drainage is reduced and more natural wetness regimes are created (Larsen and Nielsen, 2012). If not taken into account in the afforestation planning, such changes could be disadvantageous for *Prunus* species and their related ecosystem services.

4.4. Conclusion

There is a clear risk that the ecosystem services from *Prunus* species in the landscape can be negatively affected not only by drought but even more so by increased events of waterlogging due to climate change. Establishment and management efforts of *Prunus* species in different landscape types need to address this risk, so that further provision of the

wide range of ecosystem services that this species group provides in European landscapes is upheld. All three *Prunus* species tested showed low ability to maintain leaf functionality (relative g_s and Ψ_L) during waterlogging as seedlings. *P. padus* waterlogging tolerance seemed to be connected to an avoidance-like strategy though leaf shedding and not direct tolerance. The drought tolerance and related strategies however differed between all three species.

CRedit authorship contribution statement

Björn Wiström: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Tobias Emilsson:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – review & editing, Funding acquisition. **Henrik Sjöman:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. **Anna Levinsson:** Conceptualization, Methodology, Investigation, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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