



Hydraulic constraints to stomatal conductance in flooded trees

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Abstract

Stomatal closure is a pervasive response among trees exposed to flooded soil. We tested whether this response is caused by reduced hydraulic conductance in the soil-to-leaf hydraulic continuum (k_{total}), and particularly by reduced root hydraulic conductance (k_{root}), which has been widely hypothesized. We tracked stomatal conductance at the leaf level (g_s) and canopy scale (G_s) along with physiological conditions in two temperate tree species, *Magnolia grandiflora* and *Quercus virginiana*, that were subjected to flood and control conditions in a greenhouse experiment. Flooding reduced g_s , G_s , k_{root} and k_{total} . Path analysis showed strong support for direct effects of k_{total} on g_s and for flood duration on k_{total} , but not k_{root} on k_{total} . A process-based model that accounted for the k_{total} reduction predicted the timeseries of G_s in flood and control treatment trees reasonably well (predicted versus observed G_s $R^2 = 0.80$ and 0.51 for *M. grandiflora* and *Q. virginiana*, respectively). However, accounting only for k_{root} reduction in flooded trees was insufficient for predicting observed G_s reduction. Together, these results suggest that hydraulic constraints were not limited to roots and highlight the need to account for flooding effects on k_{total} when projecting forest ecosystem function using process-based models.

Keywords Plant stress · Process-based modeling · Root hydraulic conductance · Temperate forest · Soil–plant–atmosphere continuum · Waterlogging

Introduction

Terrestrial water is distributed heterogeneously both spatially and temporally at scales from microhabitats to biomes. Plants are generally adapted to a narrow range of water conditions outside of which their performance is impaired (Silvertown et al. 1999; Araya et al. 2011). When terrestrial

plants incur drought or flood conditions, they commonly reduce their stomatal conductance (g_s), which reduces both transpiration and photosynthesis (Rogers et al. 2017; McDowell et al. 2022). During droughts, reduced transpiration slows the decline of water potential within plant tissues, including leaves (Ψ_{leaf}), and soil (Ψ_{soil}) in the rooting zone. Water potential decline causes the total hydraulic conductance in the soil-to-leaf continuum (k_{total}) to decline as air spaces form, blocking water flow (Venturas et al. 2017). Drought mortality is associated with reduced k_{total} , particularly reduced stem hydraulic conductance (k_{stem}) (Adams et al. 2017). As such, in dry conditions, plants must control g_s to balance the loss of k_{total} and the uptake of CO_2 for photosynthesis. These relationships have been incorporated into process-based models of the soil–plant–atmosphere (SPA) hydraulic continuum that predict g_s with plant traits and environmental conditions (Mencuccini et al. 2019). However, SPA models have rarely been used to predict g_s under flood conditions, in part because the processes that drive g_s are less well understood than under water deficit (Liu et al. 2022).

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Soil waterlogging (i.e., surface flooding) reduces oxygen availability in the rooting zone, which limits root mitochondrial respiration (Zhou et al. 2020). The effects on plant physiological function vary among species depending on traits that enable increased oxygenation of the rooting zone, such as the development of aerenchyma, adventitious roots, and hypertrophied lenticles (Fukao et al. 2019). Waterlogged plants commonly experience reduced k_{total} , particularly root hydraulic conductance (k_{root}) (Aroca et al. 2012). The radial pathway of k_{root} (i.e., between the root surface and xylem) is reduced by the regulation of aquaporins and the formation of suberin layers; responses that promote oxygen retention within the root (Aroca et al. 2012; Domec et al. 2021). Longer term waterlogging can also cause k_{root} decline through root dieback and reduced root growth (Pezeshki et al. 1996).

In principle, the benefit that plants derive from controlling g_s to balance CO_2 uptake and k_{total} protection should apply to waterlogged scenarios as well as water deficit scenarios. If so, the reduction in k_{root} associated with waterlogging can be incorporated into SPA models to predict g_s responses to flooding (Liu et al. 2022). Alternatively, g_s responses to flooding could be mediated by factors independent of hydraulic constraints, in which case SPA models would be ineffective for predicting g_s in flood scenarios. In many parts of the world, the frequency of flooding is likely to increase this century (Hirabayashi et al. 2013). Ecosystem models that project responses to climatic conditions have recently been improved by incorporating SPA hydraulic processes (McDowell et al. 2013; Christoffersen et al. 2016; Anderegg and Venturas 2020). However, these models do not generally include responses to soil waterlogging.

Incorporating greater mechanistic realism, such as stomatal responses, into ecosystem models is a major goal towards improving projections (Fisher et al. 2018). If SPA models can be enabled with waterlogging responses, then incorporating them into ecosystems models would be a promising approach for projecting the effects of flooding on ecosystem dynamics. Recently, this approach was tested with the FATES-Hydro ecosystem demography model, where soil salinity and hypoxia effects were incorporated to reduce k_{root} and thus g_s through a SPA submodel (Ding et al. 2023). The model predicted the effects of saltwater intrusion on transpiration in coastal forests well; however, predictions under freshwater flooded conditions remain untested (Ding et al. 2023).

We tracked g_s in seedlings of two flood-sensitive tree species that were exposed to waterlogged conditions in a greenhouse experiment. We monitored physiological conditions (i.e., Ψ_{leaf} , k_{root} , k_{stem} , and k_{total}) and structural conditions (i.e., leaf area, root biomass, basal area) with two main objectives. First, we tested for associations between g_s regulation and tree physiological and structural conditions

and used path analysis to elucidate the processes that drive stomatal responses in waterlogged conditions. Secondly, we tested the feasibility of using a SPA model to predict stomatal responses in waterlogged trees. We incorporated our measurements of physiological conditions into a SPA model that assumes plants regulate g_s to avoid the excessive loss of k_{total} (Sperry et al. 2016). We compared predicted and measured stomatal regulation to test the hypothesis that stomatal responses associated with waterlogging are driven by k_{total} reduction, and particularly k_{root} reduction.

Materials and methods

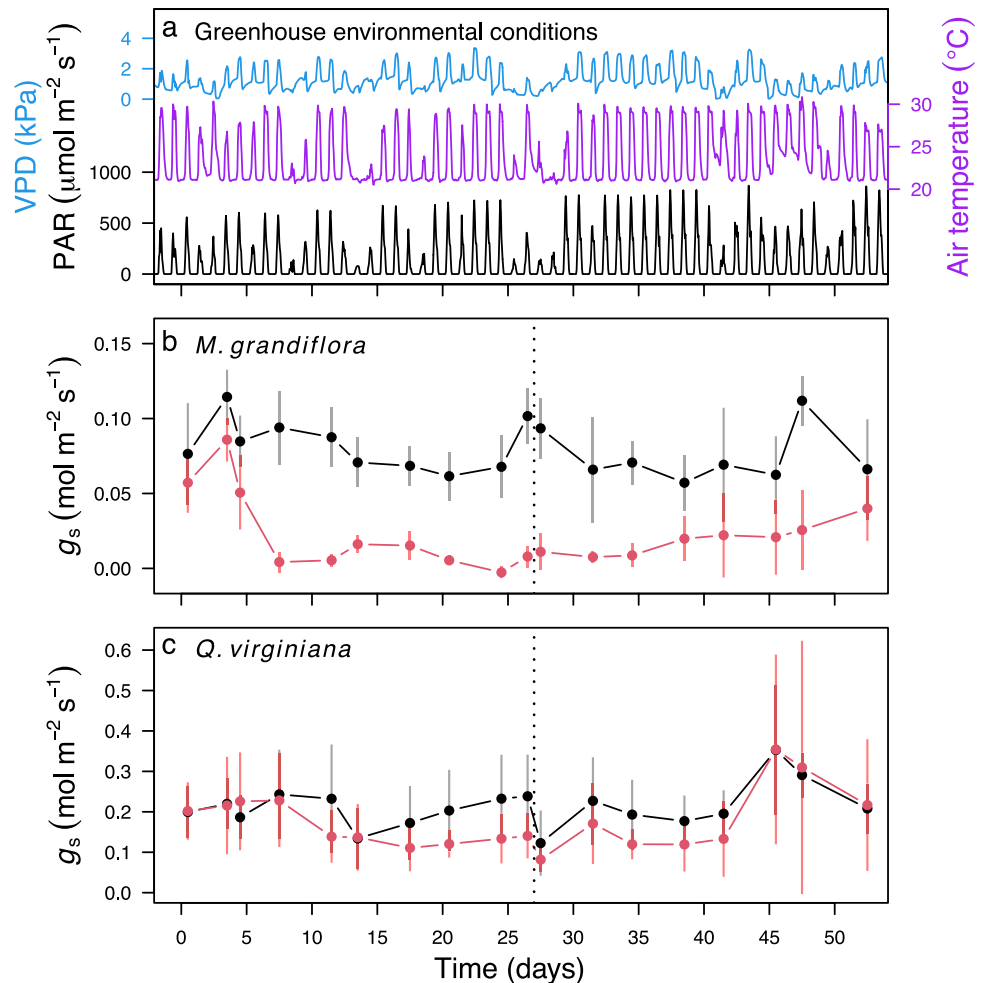
Plant material and greenhouse environmental conditions

We studied two tree species: *Magnolia grandiflora* L. (southern magnolia) and *Quercus virginiana* Mill. (live oak). Both are common within temperate deciduous forests of the southeastern United States and have been categorized as weakly tolerant to intolerant to flooding (McKnight et al. 1980). Seedlings were approximately six months old when purchased from Rennerwood, Inc. (Tennessee Colony, TX, USA) in December 2021 and transported to a greenhouse at the Louisiana State University Agricultural Center Plant Material Center in Baton Rouge, LA. Upon arrival, the seedlings were transplanted into 2.37 L containers filled with a 50–50 mixture of sand and loamy sand topsoil sourced from Clinton Township, LA, USA. At the initiation of the experiment in January 2022, seedlings of *M. grandiflora* and *Q. virginiana* were 34 ± 5 cm and 32 ± 10 cm (mean $\pm$ SD) in height and 5.9 ± 0.7 mm and 3.7 ± 0.8 mm in basal diameter, respectively. During the experiment, midday (10:00–14:00 h) greenhouse air temperature was 27.4 ± 2.8 °C, vapor pressure deficit (VPD) was 1.95 ± 0.85 kPa, and midday photosynthetically active radiation (PAR) was 423 ± 209 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1a).

Experimental design

The experiment consisted of two measurement components: (1) a timeseries of midday g_s measurements on trees that were repeatedly measured while being subjected to experimental treatments, and (2) measurements of physiological and structural conditions on trees that were subjected to experimental treatments for varying durations and then destructively harvested. Plants were randomly assigned to be either repeatedly measured or to be destructively harvested. The timeseries of midday g_s measurements consisted of ten plants of each species that were measured for midday g_s over 51 days. At intervals of 1–5 days (Fig. 1), each plant was measured for g_s at midday (10:00–14:00 h) on

Fig. 1 Greenhouse environmental conditions **a** and timeseries of stomatal conductance (g_s) in seedlings of *Magnolia grandiflora* **b** and *Quercus virginiana* **c**. In **a** lines represent hourly averages of vapor pressure deficit (VPD; blue), air temperature (purple), and photosynthetically active radiation (PAR; black). In **b** and **c**, red and black circles represent the mean g_s among 5 plants in the flood and control treatments, respectively. Error bars extend to 1 SD and are drawn either above or below the mean to avoid overlap. The dotted line after day 26 represents the end of the flood treatment, after which flooded plants were treated the same as controls



three randomly selected leaves with a porometer/fluorometer (LI600, LiCor Inc., Lincoln, NE, USA). During the initial 26 days, five randomly selected plants of each species were subjected to flood conditions by placing their pots in tanks filled with tap water to 2 cm above the soil surface. Two tanks were used for the repeatedly measured plants, each with 2–3 plants per species. Dissolved oxygen was measured in one of the tanks hourly with a dissolved oxygen meter and datalogger (SDL150, Extech Nashua, NH). Dissolved oxygen content during the experiment was $4.7 \pm 0.9 \text{ mg L}^{-1}$ (mean $\pm$ SD), which is mildly hypoxic (Sasidharan et al. 2017). The remaining five plants of each species were controls that were watered to field capacity every 1–3 days throughout the experiment. After 26 days, the flooded plants were removed from the tanks and watered along with the control plants to assess post-flood recovery of g_s .

Destructively harvested plants were subjected to the same flood and control treatments described above for various durations to measure physiological and structural conditions. Durations were 1, 3, 7, 10, 13, 16, 21, and 25 days. For each duration, we measured four flooded plants and two control plants of each species ($N=96$ destructively harvested plants

total). This unbalanced design was chosen to improve our ability to detect changes in conditions in the flood treatment, whereas we expected the conditions to remain unchanged with duration in the control treatment. Start and end dates of the treatments were staggered to enable replication of treatment durations, such that plants were harvested between 11-Jan-2022 and 28-Feb-2022. Eight tanks were used for the harvested plants in the flood treatment. Each tank held up to six plants at a time. Species were mixed within tanks. Flood duration was randomly assigned within and among tanks (Fig. S1). In summary, the measurements on harvested plants approximated a completely randomized design, which was used for statistical analyses.

Physiological and structural measurements

Harvested plants were measured for the following physiological conditions: g_s , light-adapted quantum efficiency (ΦPSII ; i.e., the estimated proportion of absorbed light used in Photosystem II photochemistry, Krall and Edwards 1992), Ψ_{leaf} , k_{root} , k_{stem} , k_{total} , and presence of hypertrophied lenticels. On three leaves per plant, we used a porometer/fluorometer

(LI600, LiCor Inc.) to measure g_s and Φ_{PSII} . Following the porometer/fluorometer measurements, Ψ_{leaf} was measured on three leaves with a pressure chamber (1505D-EXP; PMS Instrument Co., Albany, OR, USA). All leaves were removed from each plant with razors at the petiole base and total leaf area was measured with an area meter (LI3100, LiCor Inc.). Basal diameter was measured with calipers and used to calculate basal area assuming that stem cross sections were circular. We visually inspected the base of each harvested plant for the presence or absence of hypertrophied lenticles.

We used the vacuum chamber technique described by Kolb et al. (1996) to measure.

k_{root} and k_{stem} (Fig. S2). This technique is well-suited for measuring responses to stress in both k_{root} and k_{stem} (Kursar et al. 2009; Torres-Ruiz et al. 2015; Venturas et al. 2018). Stems were excised approximately 5 cm above the root collar with pruning shears while the plants were submerged in tap water to avoid xylem air entry. For k_{root} , the pot, including soil and intact root system, was placed in a vacuum chamber with the stump protruding out of the chamber through a hole that was sealed with rubber gaskets and parafilm to achieve vacuum pressure within the chamber. The cut end of the stump was recut with a fresh razor and connected via tubing to a reservoir and graduated pipette filled with 10 mM KCl solution that was filtered to 0.2 μ m and degassed. Vacuum pressure was applied in a sequence of 0, 20, 40, and 0 kPa for at least five minutes at each pressure. The volume of solution in the pipette was tracked to obtain flow rate at each pressure. Hydraulic conductance was calculated with linear regression as the slope of the relationship between flow rate and pressure. Hydraulic conductance was standardized by basal area to obtain k_{root} . Although the soil could confound our assessment of k_{root} , this effect was likely negligible because hydraulic conductivity is orders of magnitude higher in saturated soil than in roots (Sperry et al. 1998). To measure k_{stem} , we used the same methods as for k_{root} by placing the stem (with leaves removed) in the vacuum chamber with the cut end protruding. Note that k_{stem} and k_{root} are not scaled by pathlength (to obtain conductivity) because the pressure gradient was applied to the entire surface of stem and root.

For each harvested plant, we calculated k_{total} by combining leaf-level measurements of transpiration (E) and Ψ_{leaf} , where $k_{total} = E / (\Psi_{leaf} - \Psi_{soil})$ (e.g., Limousin et al. 2013). Because soils were maintained near saturation and at saturation in the control and flood treatments, respectively, we used $\Psi_{soil} = 0$ for all samples. E was output from the LI600 porometer, which was measured on three leaves per plant and averaged. The E value assumes negligible leaf boundary layer resistance, which was valid in our experiment because ceiling fans in the greenhouse continually moved air and the seedlings had minimal canopy development that would impede air movement. To scale k_{total} by basal area

for comparison with k_{stem} and k_{root} we multiplied E (which is scaled by leaf area) by total leaf area and divided by stem basal area.

After measuring k_{root} , we carefully rinsed the soil from the roots, using a 2-mm mesh screen to collect disconnected roots. Dead roots were distinguished by their color and friability (Powers and Pérez-Aviles 2013) and excluded from analyses. Fine roots (< 2 mm diameter) and coarse roots were separated and dried at 65 °C to obtain dry mass. Root dry mass was scaled by basal area to obtain fine root dry mass per basal area (DM_{fine_root}) and coarse root dry mass per basal area (DM_{coarse_root}). Similarly, total leaf area was divided by basal area to obtain leaf area per basal area (LA:BA).

Statistical analyses

All statistical analyses were completed in R 4.3.0 (R Core Team 2023). To test for an effect of flooding (days 0–26 in Fig. 1) on the repeatedly measured plants, we used linear mixed effect models in the package lme4 (Bates et al. 2015). Treatment, duration, and their interaction were fixed effects. Individual plant was a random effect. We used a likelihood-ratio test between the full model and a model with the treatment effects removed to test for the significance of a flood effect on g_s . Separately, we used the same model structure to test for an effect of treatment during the post-flood period (days 27–52 in Fig. 1).

In the harvested plants, we tested whether the rate of change in physiological conditions (i.e., g_s , Φ_{PSII} , and Ψ_{leaf} , k_{total} , k_{stem} , k_{root}) and structural conditions (i.e., DM_{fine_root} , DM_{coarse_root} , LA:BA, and basal area) differed between flood and control treatments with linear models of the interaction between treatment and duration. For g_s , Φ_{PSII} , and Ψ_{leaf} , which had three measurements per plant, values were averaged within plant prior to analysis. For these tests, we used a shared intercept term because at the model intercept (i.e., duration of zero) the flood treatment had not yet been applied, so physiological conditions were assumed to be equal. To account for the unbalanced design, we used Type II ANOVA tests in the car package (Fox and Weisberg 2019) to test for the significance of the treatment by duration interaction. We used logistic regression to analyze the relationship between flood duration and the presence/absence of hypertrophied lenticels. None of the control-treatment plants formed hypertrophied lenticels, so they were excluded from this analysis. Pairwise Spearman correlations were used to evaluate the bivariate relationships between physiological and structural conditions within plants. For each species, we tested each correlation with plants from both treatments (i.e., control and flood) combined and in isolation.

We used path analysis to assess the causal relationships between g_s , physiological conditions, and environmental

conditions. A set of four candidate models was tested with data from the harvested plants of each species. Each model included direct effects of conditions known to affect g_s (i.e., PAR, VPD, and k_{total}) and the cascading effects of flood duration on k_{root} and k_{root} on k_{total} . The models varied in their inclusion of paths from flood duration to k_{total} , representing a hydraulic constraint separate from k_{root} , and path from flood duration to g_s , representing a constraint on g_s separate from hydraulics. Model selection followed the protocol suggested by Garrido et al. (2022). The models were ranked by Akaike weights calculated from the Akaike information criterion index corrected for the sample size (AICc). The AICc balances goodness of fit with model complexity and is adjusted for finite samples to ensure accurate comparisons across different datasets or study sizes. The Akaike weights represent the relative probability that each model is the best one given the data. In the final model, the path coefficients (β ; i.e., an indicator of relationship strength and direction between two variables) were calculated with weighted averages from the highest-ranking models that accounted for $\geq 55\%$ Akaike weight. For path analysis, variables were transformed to improve multivariate normality, including g_s , k_{total} , and flood duration. All variables were zero centered and scaled by SD. Path coefficients were estimated with maximum likelihood in the R package lavaan (Rossee 2012).

Soil–plant–atmosphere hydraulic modeling

We used the hydraulic model developed by Sperry et al. (2016) to test whether the stomatal responses that we observed in flooded plants could be predicted by observed reductions in k_{root} and k_{total} . The model has accurately predicted stomatal behavior in a wide variety of trees and environmental conditions, but to our knowledge it has not been applied to flood scenarios (Sperry et al. 2016; Wolfe et al. 2016). The model assumes that plants control g_s to balance the supply of water available for transpiration with the atmospheric demand for water (i.e., VPD). Water supply is a function of Ψ_{soil} and hydraulic conductance in the rhizosphere, roots, stems, and leaves. Hydraulic conductance in each of these components is defined by a vulnerability curve that responds to water potential and by the component's proportional contribution to the maximum total hydraulic conductance ($k_{\text{total,max}}$, i.e., k_{total} when Ψ_{soil} is high and VPD is low). The model predicts steady-state canopy vapor conductance (G) given a timeseries of VPD and Ψ_{soil} . G is standardized by tree basal area and includes boundary layer resistance. For our purposes, since boundary layer resistance was negligible, we assumed that G was equal to canopy-scale stomatal conductance (G_s). We converted measurements of g_s to G_s by multiplying g_s by total leaf area and dividing by basal area.

Details of our modeling approach are in described in Methods S1. Briefly, our approach had three steps. First, we fit the model to the timeseries of repeatedly measured control-treatment plants (i.e., the plants represented by black circles in Fig. 1). This included inputting environmental conditions, including soil texture, Ψ_{soil} , and VPD; and plant traits including vulnerability-curve coefficients, and the partitioning of $k_{\text{total,max}}$ among roots, stems, and leaves (Table S1). We adjusted two unknown parameters, $k_{\text{total,max}}$ and maximum G , to find the best fit between predicted and measured G_s , following the approach of Sperry et al. (2016). We performed a sensitivity analysis by varying inputted vulnerability-curve coefficients to test how assumptions of vulnerability segmentation affected model outputs.

Next, we predicted G_s in the timeseries of repeatedly measured flood-treatment plants (i.e., the plants represented by red circles in days 0–26 in Fig. 1) by incorporating the effects of flooding on hydraulic traits that were observed in the harvested plants (Table 1). We compared two parameterizations; both used the same parameter values as in the control treatment plants and had an additional parameter that adjusted $k_{\text{total,max}}$ as a function of flood duration. One parameterization reduced $k_{\text{total,max}}$ by the amount predicted by measurements of k_{root} and one reduced $k_{\text{total,max}}$ by the amount predicted by measurements of k_{total} . Lastly, we tested the model's performance in predicting G_s across flood and control treatments by fitting least squares linear regressions through observed versus model-predicted values. We used R^2 as an indicator of goodness of fit and the slope and intercept as indicators of bias.

Results

Among the repeatedly measured plants, *M. grandiflora* g_s was stable in the control treatment throughout the experiment; however, in the flood treatment g_s declined during the first six days and remained low (Fig. 1b). Between days 6 and 26, g_s was reduced on average by 91% in the flood treatment compared to the controls. Overall, the effect of flooding on g_s was highly significant ($P < 0.001$; Fig. 1b). When the flood treatment was stopped (i.e., day 27 onward in Fig. 1b), g_s remained on average 74% lower in the flooded plants compared to the controls ($P < 0.001$). Flooding had less of an effect on *Q. virginiana* g_s . Between days 6 and 26, g_s was reduced on average by 31% in the flood treatment compared to the controls ($P < 0.001$; Fig. 1c). When the flood treatment was stopped, g_s in *Q. virginiana* mostly recovered. On average, it was only 15% lower than the controls, which was not a significant difference ($P = 0.29$; Fig. 1c).

Among the harvested plants, there were no significant differences in Ψ_{leaf} or k_{stem} between control and flood treatments in either species, or for g_s in *Q. virginiana* (Fig. 2,

Table 1 Results from linear models for the effects treatment (flood versus control) on the change in physiological conditions over time

Condition	Intercept	Control treatment slope	Flood treatment slope	<i>P</i>	<i>R</i> ²
<i>M. grandiflora</i>					
g_s (mmol m ⁻² s ⁻¹)	0.065 ± 0.010	0.0019 ± 0.0009	- 0.0030 ± 0.0007	1.8e- 6	0.44
Φ_{PSII} (unitless)	0.614 ± 0.035	0.0011 ± 0.0032	- 0.0129 ± 0.0026	4.8e- 6	0.42
Ψ_{leaf} (MPa)	- 0.738 ± 0.037	0.0006 ± 0.0034	- 0.0004 ± 0.0028	0.95	0.002
k_{total} (mol m ⁻² s ⁻¹ MPa)	3.96 ± 0.49	0.103 ± 0.045	- 0.178 ± 0.037	4.1e- 8	0.51
k_{stem} (mol m ⁻² s ⁻¹ MPa)	28.36 ± 5.45	0.457 ± 0.499	0.2667 ± 0.418	0.64	0.02
k_{root} (mol m ⁻² s ⁻¹ MPa)	5.87 ± 0.43	0.005 ± 0.039	- 0.091 ± 0.033	9.4e- 3	0.18
DM _{fine_root} (kg m ⁻²)	100.6 ± 9.2	0.79 ± 0.83	- 1.46 ± 0.70	0.013	0.14
DM _{coarse_root} (kg m ⁻²)	58.5 ± 6.0	0.64 ± 7.67	7.74 ± 6.47	0.11	0.05
LA:BA (m ² m ⁻²)	1839 ± 97	- 5.7 ± 8.9	- 3.0 ± 7.5	0.81	0.00
Basal area (mm ⁻²)	21.8 ± 1.2	0.16 ± 0.11	0.03 ± 0.10	0.37	0.00
<i>Q. virginiana</i>					
g_s (mmol m ⁻² s ⁻¹)	0.232 ± 0.034	0.0021 ± 0.0030	0.0022 ± 0.0025	0.66	0.02
Φ_{PSII} (unitless)	0.708 ± 0.017	- 0.0007 ± 0.0016	- 0.0035 ± 0.0013	0.025	0.11
Ψ_{leaf} (MPa)	- 1.565 ± 0.124	0.010 ± 0.0113	0.0084 ± 0.0094	0.58	0.02
k_{total} (mol m ⁻² s ⁻¹ MPa)	1.49 ± 0.52	0.221 ± 0.051	0.043 ± 0.040	2.6e- 4	0.31
k_{stem} (mol m ⁻² s ⁻¹ MPa)	26.31 ± 3.50	- 0.212 ± 0.315	0.114 ± 0.265	0.55	0.03
k_{root} (mol m ⁻² s ⁻¹ MPa)	3.32 ± 0.84	0.251 ± 0.084	0.143 ± 0.065	0.012	0.17
DM _{fine_root} (kg m ⁻²)	159.9 ± 23.2	4.69 ± 2.10	1.94 ± 1.78	0.093	0.06
DM _{coarse_root} (kg m ⁻²)	609.3 ± 84.7	1.05 ± 0.54	7.74 ± 6.47	0.43	0.00
LA:BA (m ² m ⁻²)	599 ± 77	- 1.7 ± 7.0	- 5.8 ± 5.9	0.59	0.00
Basal area (mm ⁻²)	10.3 ± 1.1	- 0.02 ± 0.10	- 0.11 ± 0.08	0.42	0.00

Values are estimates ± 1SE. Slopes are units per day. *P* refers to Type II test for treatment by time interaction. Those in bold are < 0.05. *R*² is the coefficient of determination for the model

Table 1). All other physiological conditions measured (i.e., Φ_{PSII} , k_{total} , k_{root}) were affected by the flood treatment in both species. In general, the effects of flooding were stronger in *M. grandiflora* than in *Q. virginiana* (Fig. 2; Table 1). In *Q. virginiana*, most physiological conditions did not decrease with duration in the flood treatment; rather, they had lower rates of increase than in the control treatment. In contrast, *M. grandiflora* had a reduction (i.e., negative slope with duration) in most physiological conditions in the flood treatment, but not in the controls (Fig. 2; Table 1).

Structural conditions, including LA:BA, DM_{coarse_root}, and basal area did not change with duration or vary between the flood and control treatments (Table 1, Fig. S4). However, DM_{fine_root} in *M. grandiflora* decreased with duration in the flood treatment and did not change with duration in the control treatment (Fig. 2; Table 1). Flooded plants of both *M. grandiflora* and *Q. virginiana* developed hypertrophied lenticels (Fig. S5). Logistic regression estimates for the flood duration at which 50% of plants produced hypertrophied lenticels were 15.3 and 23.5 days in *M. grandiflora* and *Q. virginiana*, respectively (Fig. S5, Table S2).

Among the pairwise correlations between physiological and structural conditions, in the flood treatment *M. grandiflora* g_s was positively correlated with k_{root} , Φ_{PSII} , and k_{total}

(Fig. 3a, Table S3). Furthermore, Φ_{PSII} was positively correlated with k_{root} and k_{total} ; Ψ_{leaf} was positively correlated with k_{stem} ; k_{total} was positively correlated with k_{root} ; and k_{root} root was positively associated with DM_{fine_root}. In contrast, in the control treatment, *M. grandiflora* g_s was associated only with Φ_{PSII} ; however, Φ_{PSII} was negatively correlated with k_{root} , Ψ_{leaf} was positively correlated with k_{root} , and k_{stem} was positively correlated with DM_{fine_root}. In flooded *Q. virginiana*, g_s was positively correlated only with k_{total} and Φ_{PSII} was positively correlated with Ψ_{leaf} (Fig. 3b, Table S3). In the control treatment, *Q. virginiana* k_{total} was positively correlated with Ψ_{leaf} , and DM_{fine_root} was positively associated with k_{root} .

The best-fitting path model (i.e., accounting for ≥ 55% Akaike weight) for *M. grandiflora* was the model with a direct path from flood duration to k_{total} but not from flood duration to g_s (Table S4). The model showed strong support (i.e., β and β/SE far from zero) for direct effects of flood duration on k_{root} ($\beta = -0.37$, $\beta/SE = -3$) and k_{total} ($\beta = -0.78$, $\beta/SE = -9$), but only weak support for an effect of k_{root} on k_{total} ($\beta = 0.11$, $\beta/SE = 1$) (Fig. 4a). For *Q. virginiana*, the best fitting model included the model with a direct effect of flood duration on k_{total} and the model with only the direct effect of flood duration on k_{root} (Table S4). The model

Fig. 2 Responses of physiological conditions to flood and control treatments in *Magnolia grandiflora* (a,c,e,g,i,k,m) and *Quercus virginiana* (b,d,f,h,j,l,n). Red and black symbols represent the flood and control treatments, respectively. Each circle represents the mean of 2–4 plants. Lines represent outputs from linear models with the treatment by duration interaction as the independent variable and the physiological condition as the dependent variable. Shaded regions are the 95% confidence intervals. Solid lines indicate that the flood and control treatments had significantly different slopes ($P < 0.05$), otherwise the lines are dashed

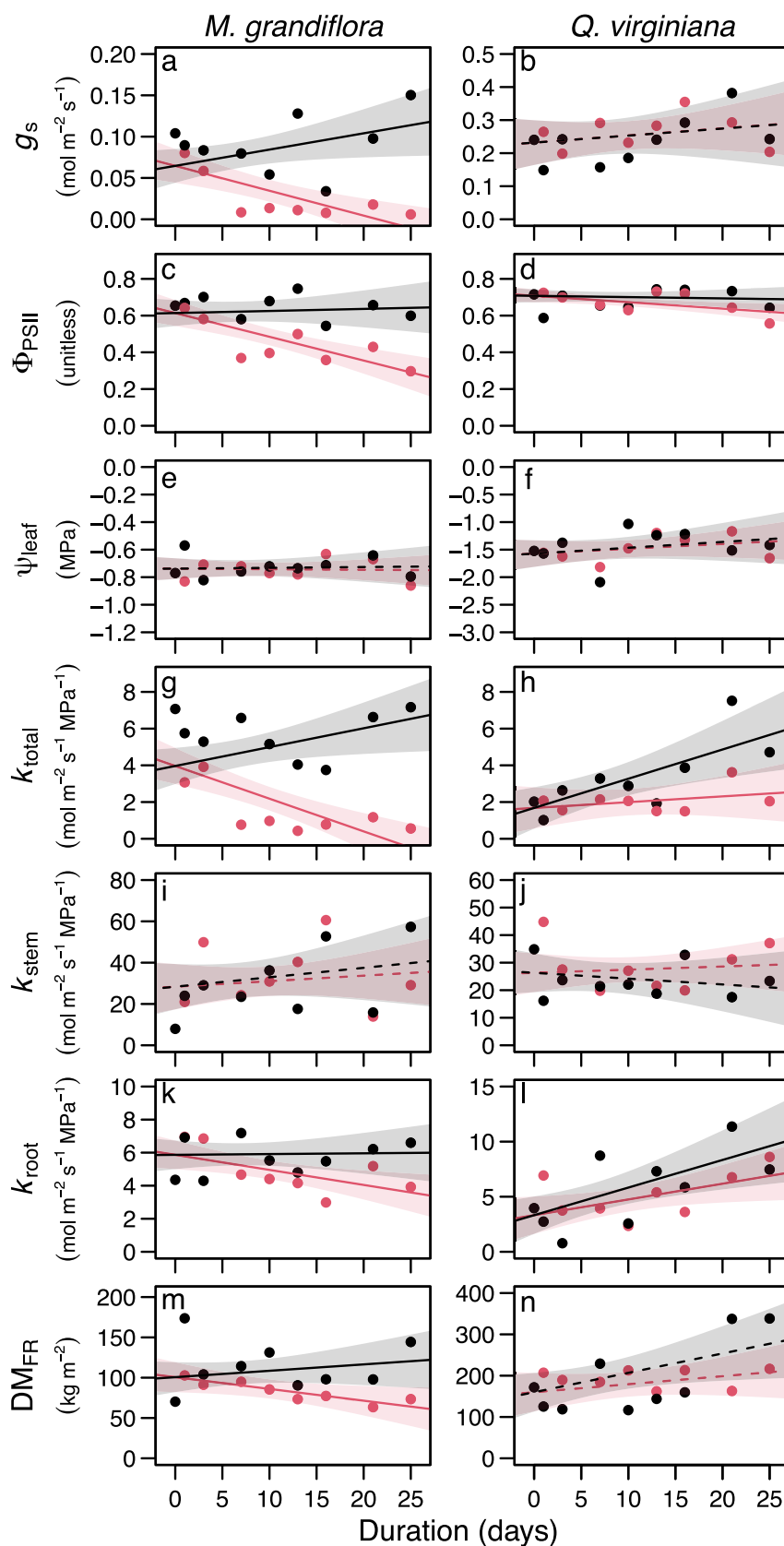
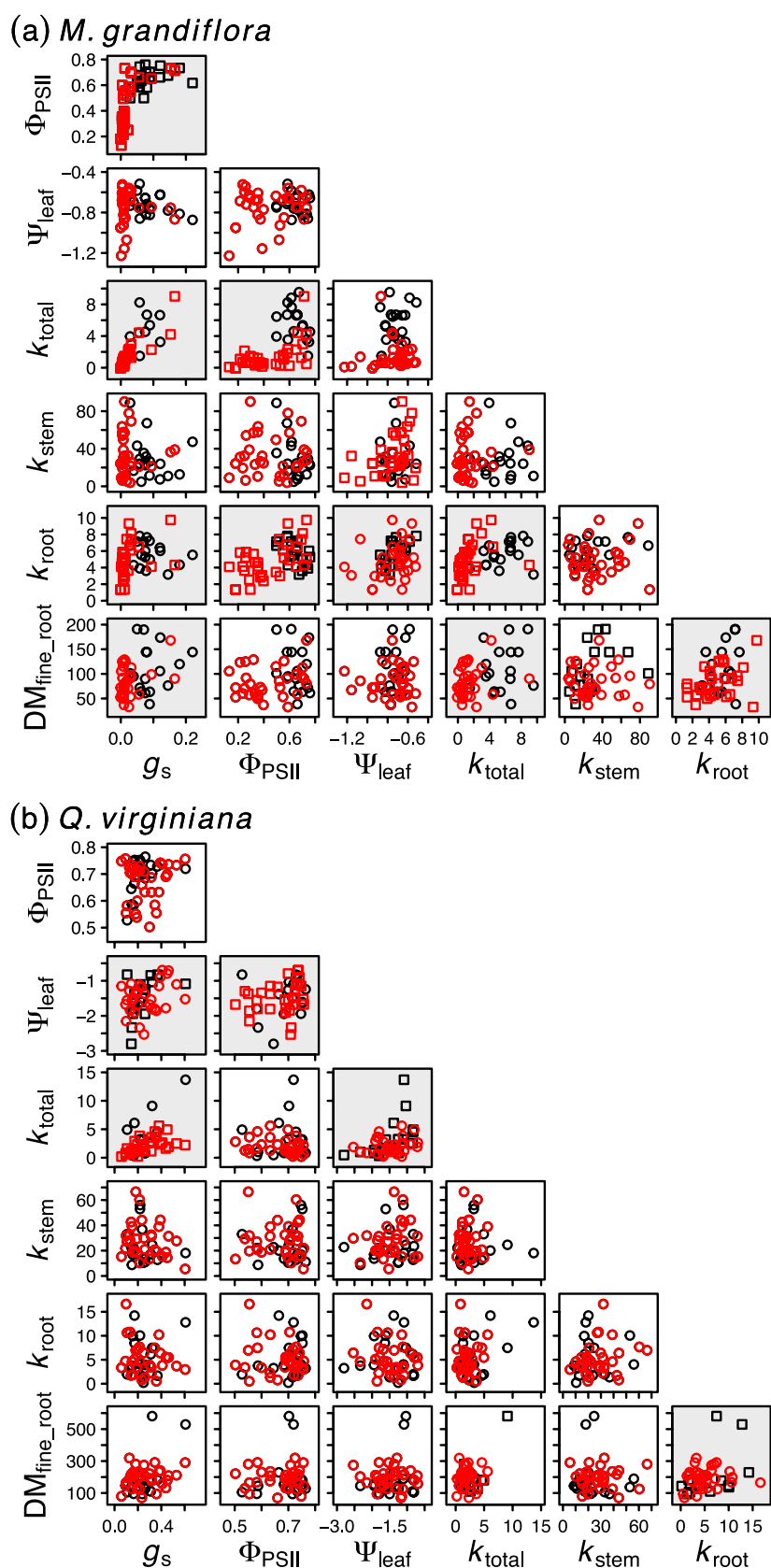


Fig. 3 Bivariate relationships between physiological conditions in harvested plants of *Magnolia grandiflora* **a** and *Quercus virginiana* **b**. Red and black symbols represent individual plants in the flood and control treatments, respectively. Plants are represented as squares when the Spearman correlation coefficient within treatment differed from zero ($P < 0.05$) and otherwise as circles. Shaded panels indicate that the Spearman correlation coefficient for treatments combined differed from zero. Correlation coefficients are given in Table S3. Units of measurement are given in Table 1



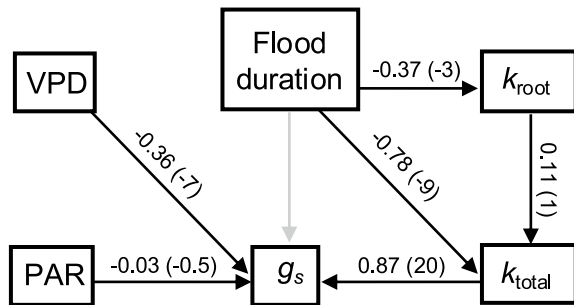
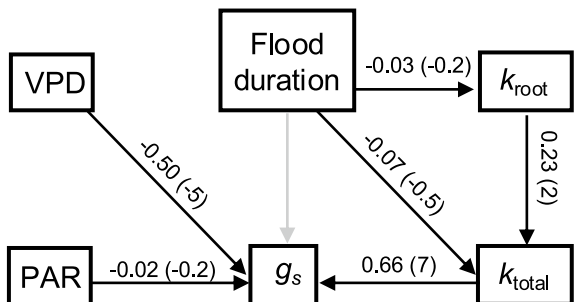
(a) *M. grandiflora*(b) *Q. virginiana*

Fig. 4 Path analysis models for the effects of environmental conditions and their physiological mediators on stomatal conductance (g_s) for *Magnolia grandiflora* **a** and *Quercus virginiana* **b**. Boxes and arrows represent variables and hypothesized causality, respectively. Variables include flood duration, root hydraulic conductance (k_{root}), total soil-to-leaf hydraulic conductance (k_{total}), photosynthetically active radiation (PAR), and vapor pressure deficit (VPD). Numbers indicate weighted means of path coefficients (β) and β/SE in parentheses. Gray arrows represent relationships that were not included in the final model (Table S4)

showed strong support for an effect of k_{root} on k_{total} ($\beta=0.23$, $\beta/SE=2$), but weak support for effects on flood duration on k_{root} ($\beta=-0.03$, $\beta/SE=-0.2$) and k_{total} ($\beta=-0.07$, $\beta/SE=-0.5$) (Fig. 4b). For both species, k_{total} and VPD were the main drivers of g_s variation. PAR was relatively low throughout the experiment because of the seasonally low solar zenith angle (Fig. 1), and it had no effect on g_s variation (Fig. 4).

The SPA hydraulic model predicted G_s reasonably well when fit to the control plants, with mean absolute errors between predicted and observed G_s of 14 and 21% for *M. grandiflora* and *Q. virginiana*, respectively (Figs. 5, 6). With these reasonable model fits in the control plants, we were able to predict the effects of flood-induced reductions in k_{root} and k_{total} on G_s . In both *M. grandiflora* and *Q. virginiana*, measured reductions in k_{root} were not sufficient to predict the observed reduction in G_s (red circles are below the 1:1 line in Fig. 6a, c). In contrast, measured reductions in k_{total} predicted G_s in the flooded plants well (red circles

are near the 1:1 line in Fig. 6b, d). The models that incorporated the effects of flooding on k_{total} had better fit than those that incorporated k_{root} in isolation ($R^2=0.80$ vs. 0.69 for *M. grandiflora* and $R^2=0.51$ vs. 0.28 for *Q. virginiana*; Fig. 6; Table S5). Results were insensitive to the hydraulic vulnerability assumptions, including varying vulnerability by 20% and introducing hydraulic segmentation (Table S6).

Discussion

Compared to control conditions, flooding reduced g_s , G_s , Φ_{PSII} , k_{total} and k_{root} , but not Ψ_{leaf} or k_{stem} in seedlings of *M. grandiflora* and *Q. virginiana* (Figs. 1, 2). Path models indicated that the g_s response to flooding was likely mediated by hydraulic constraints (Fig. 4). When we parameterized a SPA hydraulic model with the k_{total} reduction caused by flood conditions, it predicted the timeseries of G_s in flooded seedlings reasonably well (Figs. 5, 6). However, accounting for k_{root} reduction alone was insufficient for predicting measured G_s reduction in flooded trees, suggesting that hydraulic constraints are not limited to roots and may also occur in leaves. Our results demonstrate the utility of SPA hydraulic models for projecting the effects of flooding on forest ecosystem function and the need to consider k_{total} reduction during flooding.

Physiological responses to waterlogging

Reduced g_s is commonly observed in trees subjected to flood conditions, with the timing and extent of g_s reduction varying widely among species (Kozlowski 1984; Pezeshki and Anderson 1997; Lopez and Kursar 2003; Aroca et al. 2012). These leaf-level effects are likely mediated by hydraulic and chemical signals that originate at the site of waterlogging in the roots, but this communication pathway is poorly understood (Vartapetian and Jackson 1997; Jackson 2002). Reduced g_s in waterlogged trees is often correlated with reduced k_{root} (Andersen et al. 1984; Schmutt and Thomas 2000; Islam and Macdonald 2004; Aroca et al. 2012; Karlova et al. 2021), supporting the hypothesis that g_s reduction is a response to hydraulic constraints. Consistent with these results, we found concurrent reductions in g_s and k_{root} among *M. grandiflora* seedlings after 6 days of flooding (Figs. 2, 3; Table 1). In *M. grandiflora*, k_{root} reduction may have, at least partially, been caused by fine root dieback, as evidenced by the reduction in DM_{fine_root} and the correlation between DM_{fine_root} and k_{root} (Figs. 2, 3; Table 1). However, this result does not exclude the possibility that k_{root} was affected by aquaporin activity (Domec et al. 2021) or embolisms (Li et al. 2015).

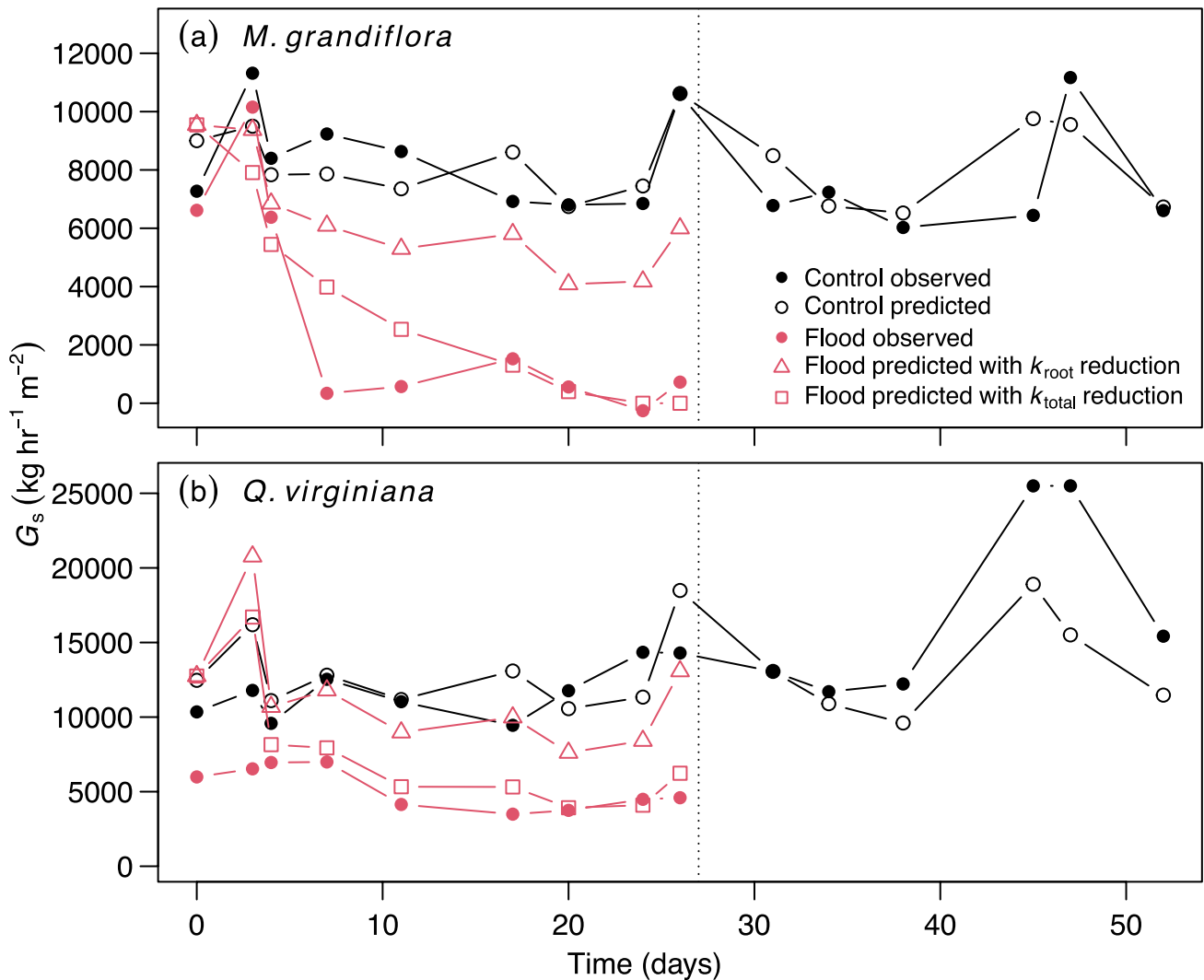


Fig. 5 Timeseries of observed and soil–plant–atmosphere model-predicted canopy-scale stomatal conductance (G_s , $\text{kg water hr}^{-1} \text{m}^{-2}$ basal area) for *Magnolia grandiflora* **a** and *Quercus virginiana* **b**. The legend in **a** also applies to **b**. The dotted line after day 26 represents

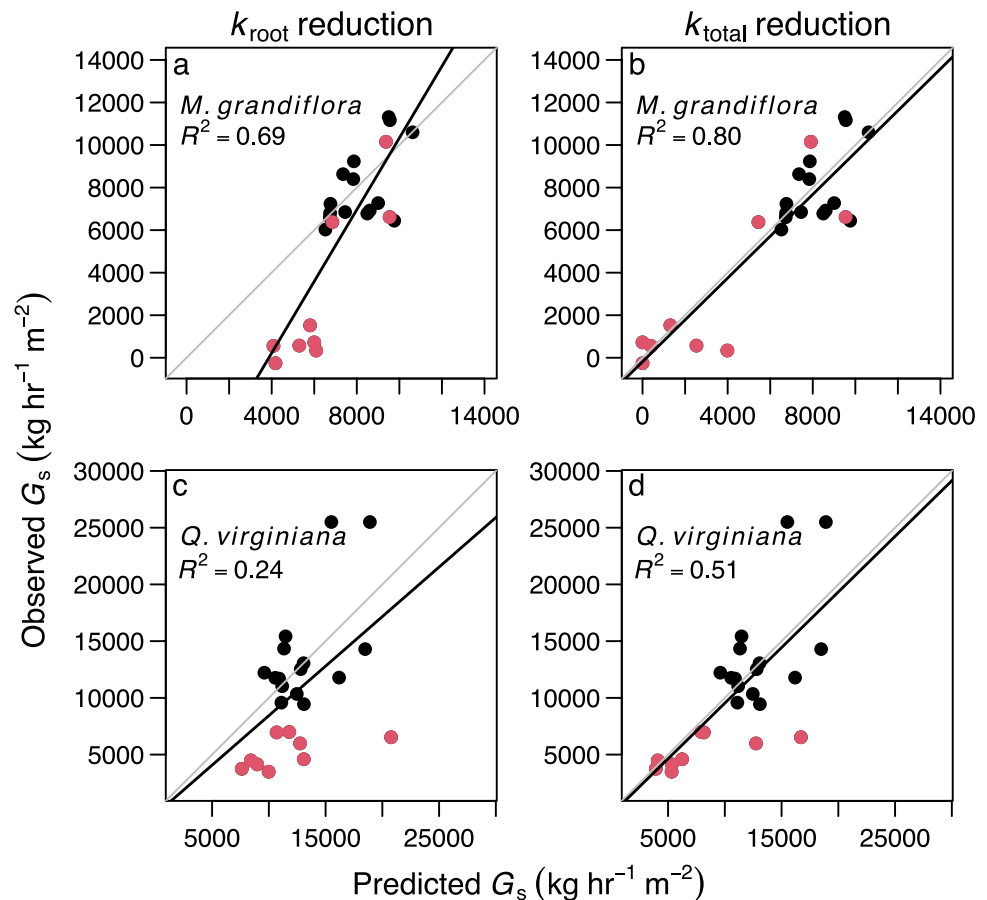
the end of the flood treatment. In the flooded plants, reductions of hydraulic conductance in roots (k_{root}) and whole plants (k_{total}) were simulated using the linear models obtained from harvested plants (Table 1)

In both species, k_{total} increased with duration in the control treatment, while in the flood treatment it decreased (*M. grandiflora*) or remained the same (*Q. virginiana*) (Fig. 2, Table 1). Since k_{root} followed the same pattern (Fig. 2, Table 1) and since k_{total} and k_{root} were positively correlated (Fig. 3, Table S3), it is possible that k_{root} limited k_{total} in flooded plants compared to control plants. Unless k_{root} reduction was compensated by higher k_{stem} or leaf hydraulic conductance (k_{leaf}), it would cause k_{total} reduction. However, for both species, the divergence in k_{root} between flood and control treatments was less than that of k_{total} (Fig. 2, Table 1). Since k_{stem} was unaffected by flooding in either species, the remaining impact on k_{total} likely occurred in the leaves. We did not measure k_{leaf} , however k_{leaf} is known to be highly dynamic in response to environmental conditions such as

PAR, VPD, and Ψ_{soil} (Prado and Maurel 2013). In loblolly pine (*Pinus taeda*), 35 days of flooding reduced aquaporin activity in leaves, contributing to a 47% reduction in k_{total} (Domec et al. 2021). Together, these results suggest that k_{leaf} reduction may be a common response to flooding. Furthermore, our path analysis showed that g_s was highly responsive to k_{total} , but k_{root} did not mediate k_{total} (Fig. 4). Instead, when flooding affected k_{total} it was through a direct link (Fig. 4a), which is likely explained by a reduction in k_{leaf} .

Midday Ψ_{leaf} was unaffected by flooding in either species (Fig. 2, Table 1), indicating that stomatal control compensated for k_{total} reduction, resulting in Ψ_{leaf} homeostasis. Flooding also had no effect on Ψ_{leaf} in similar experiments on tomato plants (*Lycopersicon esculentum*) (Bradford and Hsiao 1982; Else et al. 2009), pea plants (*Pisum sativum*)

Fig. 6 Observed canopy-scale stomatal conductance (G_s , kg water $\text{hr}^{-1} \text{m}^{-2}$ basal area) versus soil–plant–atmosphere model-predicted G_s . Black and red circles represent the means of five plants repeatedly measured in the control and flood treatments, respectively. In the flooded plants, reductions of hydraulic conductance in roots (k_{root} , panels **a** and **c**) and whole plants (k_{total} , panels **b** and **d**) were simulated using the linear models obtained from harvested plants (Table 1). Gray lines are 1:1. Black lines and R^2 values represent least squares regressions fit through all points. Regression fits are summarized in Table S5



(Zhang and Davies 1986), sweetgum seedlings (*Liquidambar styraciflua*) (Pezeshki and Chambers 1985), and oak seedlings (*Quercus robur* and *Quercus petraea*) (Schmull and Thomas 2000). In contrast, flooding reduced midday Ψ_{leaf} compared to well-watered controls in beech seedlings (*Fagus sylvatica*) by 16% across three months (Schmull and Thomas 2000), in apricot saplings (*Prunus armeniaca*) by 67% after 50 h (Nicolás et al. 2005), and in almond seedlings (*Amygdalus communis*) by 125% after 7 days (Sanchez-Blanco et al. 1994). Flooding also increased midday Ψ_{leaf} in elm seedlings, by 18% across 60 days in *Ulmus laevis* and by 12% across 45 days in *U. minor* (Li et al. 2015). Ψ_{leaf} regulation in response to soil drying varies among plant species across a spectrum of isohydry to anisohydry (Klein 2014; Meinzer et al. 2016). Although Ψ_{leaf} regulation under waterlogging has been studied far less than under soil drying, our results combined with those in the literature suggest that a similar spectrum of Ψ_{leaf} regulation exists in response to soil waterlogging. Whether or not species' positions on a spectrum of Ψ_{leaf} regulation in response to drought and waterlogging are associated is unclear. Both of our focal species can be described as partially isohydric in response to drought (Cooper et al. 2018; Vastag et al. 2020). Considering that they also maintained Ψ_{leaf} in response to waterlogging

(Fig. 2), this limited sample suggests an association between degrees of drought and waterlogging isohydricity.

In *M. grandiflora*, flooding reduced Φ_{PSII} by 54% compared to controls, while in *Q. virginiana*, flooding reduced Φ_{PSII} by only 9% (Fig. 2, Table 1). For *M. grandiflora*, Φ_{PSII} and g_s reduction occurred concurrently (Fig. 2a,c) and the two physiological conditions were highly correlated among plants (Fig. 3, Table S3). It is possible that stomatal closure was a response to Φ_{PSII} reduction, since stomata close in response to reduced carbon assimilation (Wang et al. 2020). However, it is more likely that the reduction in Φ_{PSII} was a result of stomatal closure. Reduced g_s would lead to reduced internal CO_2 concentration (c_i). Reducing c_i either by flooding or by experimentally reducing ambient CO_2 concentration has been shown to affect Φ_{PSII} similarly, likely because NADP^+ (nicotinamide adenine dinucleotide phosphate) regeneration slows when c_i is low (Else et al. 2009). Although we did not measure other photosynthetic parameters, flooding has also been shown to affect maximum quantum yield and ribulose biphosphate activity in *L. esculentum* (Else et al. 2009) and *P. taeda* (Domec et al. 2021).

Predicting the effects of waterlogging on stomatal control with SPA hydraulic models

SPA hydraulic models are useful for predicting G_s or g_s with sets of plant traits and environmental conditions. They parametrize k_{total} with vulnerability curves that reduce rhizosphere conductance, k_{root} , k_{stem} , and k_{leaf} as a function of their respective water potentials under scenarios of Ψ_{soil} and VPD (Mencuccini et al. 2019). Because they generally do not account for other factors that influence k_{total} , such as soil waterlogging, their utility is limited to water deficit scenarios (Liu et al. 2022). To predict responses to flooding, we incorporated into an existing SPA hydraulic model a parameter that reduced k_{total} as a function of time in waterlogged soil. This arrangement was able to predict the contrasting patterns in G_s that we observed in timeseries of flooded seedlings of *M. grandiflora* and *Q. virginiana* (Figs. 4bd, 5bd). A recent SPA hydraulic model developed for predicting the effects of soil waterlogging on stomatal behavior incorporated only the effect of waterlogging on k_{root} to parameterize a k_{total} response (Liu et al. 2022). Similarly, the recent inclusion of waterlogging into the SPA hydraulic submodel of the FATES-Hydro ecosystem demography model incorporated only effects on k_{root} (Ding et al. 2023). These approaches follow the common assumption that the effects of waterlogging on plant hydraulics are limited to roots. However, our SPA model runs that accounted for the reduction in k_{root} alone did not generate the G_s response that we observed in flooded plants (Figs. 5, 6). These results suggest that SPA model development aimed at projecting G_s in flooded plants should account for the effects of waterlogging on hydraulics in leaves as well as roots.

Species-specific coefficients for the response of k_{total} to flood duration (Eq. 3) were required for the SPA model to predict the contrasting patterns in G_s for flooded *M. grandiflora* and *Q. virginiana* (Fig. 5). Similarly, coefficients for the response of k_{stem} to water potential (i.e., vulnerability curves) vary greatly among sympatric tree species (McCulloh et al. 2019). Accounting for variation in hydraulic vulnerability underpins SPA modeling. Our results suggest that accounting for variation in the k_{total} response to flooding will enable SPA models to capture variation in flood performance among species and plant functional types. We used linear response curves for simplicity and because they fit well over our relatively short flood duration, but nonlinear responses, including recovery of k_{total} over time are likely to fit better for other species and flood scenarios.

We used a pragmatic SPA model that incorporates only the balance between water supply and demand to predict G_s (Sperry et al. 2016). Optimality-based G_s or g_s models that incorporate SPA dynamics along with parameters for carbon gain and storage perform better when light and CO_2 levels vary (Wang et al. 2020; Potkay et al. 2025). Parameters for

flood responses could be incorporated into such models. They would need to account for the effects of flooding on photosynthetic capacity along with k_{total} effects. The reduced Φ_{PSII} that we observed (Fig. 2) suggests that flooding caused photosynthetic decline and highlights the importance of incorporating the multiple impacts of flooding on plant physiological processes when projecting stomatal behavior under varying light and CO_2 levels.

Conclusions

Much of the progress made towards predicting tree stomatal responses has focused on water deficit conditions, however flood conditions also induce stomatal responses that are pervasive yet variable among tree species. Flooding and associated soil waterlogging are projected to increase in frequency and severity this century (Hirabayashi et al. 2013). The impacts of flooding on forests depend on the timing, duration, depth of floodwater, as well as forest composition and structure (Kozlowski 1997). Developing process-based models that project these impacts will help to predict forest dynamics and, if incorporated into land and Earth system models, global carbon and water cycling. Our results point towards accounting for flooding effects on k_{total} in SPA hydraulic modeling as a promising approach to project the stomatal responses that govern transpiration and influence plant growth and mortality during flood events.

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Author Contribution statement BTW, YF and NM originally formulated the idea. BTW designed the experiment. MJB, KSC, JAO, BTW conducted the experiment, performed statistical analyses, and wrote the manuscript. Other authors provided editorial advice.

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Data availability The experimental data and analyses are publicly available on Zenodo at <https://doi.org/10.5281/zenodo.17080340>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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