

# Plant Traits of *Phalaris Arundinacea* and *Phragmites Australis* – Examining Effects of Water Level, Salinity, and Soil Types in a Mesocosm Experiment

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## Research Article

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# Abstract

Knowledge about the distribution of species along rivers and estuaries is the basis for decisions in nature conservation, but also for nature-based coastal and shore protection. Along rivers and estuaries, abiotic conditions affect plant traits, especially close to the marsh edge, and thus determine the distribution of plant species. *Phragmites australis* and *Phalaris arundinacea* occur along the German Elbe in the inland river and in the estuary, but the distribution of both species is locally and regionally inhomogeneous. We therefore simulated abiotic conditions of respective Elbe sections in a mesocosm experiment and investigated the influence of soil type, salinity, water level, and plant provenance on plant traits of *P. australis* and *P. arundinacea*. We compared growth-related and mechanical plant traits of both species. Productivity of *P. arundinacea* was less affected by sandy soil than that of *P. australis*. *P. australis* was insensitive to salinity and water level fluctuations, while traits of *P. arundinacea* responded to these factors. Furthermore, mechanical properties within a species were mainly dependent on plant growth. *P. arundinacea* was more flexible than *P. australis*, which can be attributed to morphological differences and differences in plant tissue. Plant provenance did not affect the response of plant traits to abiotic conditions. Our study provides clues for understanding the distribution patterns of *P. australis* and *P. arundinacea*.

## 1 Introduction

Along the marshes of rivers and estuaries, the distribution of plants is determined by abiotic and biotic conditions (Carus et al. 2017). The closer to the marsh edge, the stronger is the influence of abiotic conditions, while the influence of competition between species increases with increasing distance to the marsh edge (Bertness and Callaway 1994). These spatial gradients determine the occurrence and zonation patterns of plant species (Pennings and Callaway 1992), whereby the tolerance to abiotic habitat properties as well as the competitive ability of a species depend on plant traits and are related to these (Violle and Jiang 2009). Thus, species exhibit physiological and morphological traits to cope with these abiotic and biotic site conditions (Moor et al. 2017).

In tidal estuaries two dominant abiotic gradients prevail (Engels and Jensen 2009): a horizontal gradient of salinity that decreases from the mouth upstream (Odum 1988; Crain et al. 2004), and a vertical gradient of duration, height, and frequency of flooding that extends between the marsh edge and upland habitats (Hackney et al. 1996; Coops and Van der Velde 1999). In non-tidal inland rivers, the vertical gradient determines the duration and height of flooding (David 1996) and leads to alternating wet-dry cycles with periodic flooding (Crawford 1996; Davis et al. 1996). Furthermore, abiotic site conditions vary locally along the river course and within an estuary, due to differences in hydromechanical conditions, sedimentation processes, and substrate composition (Dietrich and Whiting 1989; Walling and He 1998; Dyer 1995). Exposed and protected shores can be distinguished, with higher and lower mechanical impact due to flow velocities and wave dynamics (Bridge and Jarvis 1982; Hu et al. 2017). Sedimentation and erosion are directly associated with hydromechanical properties (Church 2006), and thus bank sediments vary in grain size and composition along and within the river course (Powels 1998). In the case

of lower hydromechanical energy, more small particles settle, likely leading to sites with higher nutrient supply (Morse et al. 2004; Jones et al. 2012).

A prominent example for these horizontal and vertical vegetation zonation patterns is the Elbe, one of the largest rivers in Germany (Heuner et al. 2019). The Elbe can be separated into a tidal estuary with both freshwater and brackish water influence, and an inland area where the discharge is characterised by flooding in spring and low water levels in summer. In these three sections of the Elbe, hydromechanical stress and thus sediment and soil substrates also vary along the shores. In all Elbe sections, two common species are *Phragmites australis* and *Phalaris arundinacea*, which occur together close to the shore. The distribution patterns of both species as part of the marsh vegetation have been described previously for both the tidal Elbe by, e.g., Wolf (1988), Struyf et al. (2009), and Jensen et al. (2018) as well as the inland Elbe by, e.g., Brandes (1998), and Krumbiegel (2003, 2008), separately. However, distribution patterns vary along the tidal and inland Elbe. Regionally, but also locally, we observe varying patterns in the distribution of both species along prevailing environmental gradients in the marshes. In some places, *P. arundinacea* grows closer to the marsh edge than *P. australis*, in other places it is the other way around. Thus, the zonation patterns of both species do not follow obvious patterns.

Furthermore, the described and observed distribution patterns are in some places in contrast to expected zonation patterns that we derive from existing studies on plant traits in relation to abiotic conditions. For example, *P. arundinacea* is less or not tolerant to salinity (McElgunn and Lawrence 1973) and copes less well with flooding compared to *P. australis* (Coops et al. 1996). Yet, *P. arundinacea* appears closer to the water body even in parts of brackish marshes at the tidal Elbe. Thus, the abiotic factors controlling distribution of both species remain unclear and a deeper understanding of effects of abiotic conditions on the occurrence of both species is needed. To determine the tolerance to abiotic conditions and competitive abilities of a species, various plant traits can be assessed and interpreted (Violle and Jiang 2009). Furthermore, plant traits allow for quantifying the responses of species to local conditions (Violle and Jiang 2009) such as flooding regime, salinity and soil conditions.

Flooding regimes mainly shape distribution and zonation patterns at the tidal and inland Elbe (Engels and Jensen 2010; Leyer 2005). In the tidal Elbe, with increasing distance to the marsh edge, species are flooded twice a day, at least twice a month during neap or spring tides and only during storm surges (Raabe 1986). In contrast, at the inland Elbe, duration, height, and frequency of flooding are related to seasonal discharge with prolonged flooding in spring and prolonged dry phases in summer (Bormann 2010). Flooding leads to physiological stress due to reduced diffusion of oxygen, and reduced availability of light (Blom and Voesenek 1996; Colmer and Voesenek 2009), which can lead to reduced plant growth (McKee and Mendelssohn 1989). Biomass production of *P. arundinacea* often decreases with increasing flooding stress (Miller und Zedler 2003; Kercher and Zedler 2004), while *P. australis* is considered to be highly tolerant to submersion (Brix et al. 1992). Furthermore, soil water salinity is considered to influence species distribution at the tidal Elbe (Engels and Jensen 2010). Increased salinity leads to osmotic stress in the short term and ionic stress in the leaves due to  $\text{Na}^+$  in the long term (Munns 2002; Munns and Tester 2008; Acosta-Motos et al. 2017). Therefore, salt-tolerant species are favoured in areas affected by

brackish water. The biomass production of *P. arundinacea* already decreases at low salt concentrations slightly above 0‰ (McElgunn and Lawrence 1973), while the productivity of *P. australis* is negatively affected by concentrations higher than 5 to 10‰ (Lissner and Schierup 1997). Additionally, hydromechanically induced variation of sediment composition and texture along the river course (Powell 1998) determines the soil-based nutrient supply (Olde Venterink et al. 2006). Areas where fine sediments accrete have higher nutrient supply (Stutter et al. 2007; Jones et al. 2012) and thus a positive influence on plant growth (Jones et al. 2012). Along the Elbe estuary, the occurrence of *P. arundinacea* and *P. australis* has also been described in the context of soil substrate. Wolf (1988) observed an increased occurrence of *P. arundinacea* associated with sandy sites, but we could not find any further evidence for this relation in the existing literature. The productivity of both *P. australis* (Bastlová et al. 2004) and *P. arundinacea* (Figiel et al. 1995) benefits from increasing nutrient supply. However, there is a lack of comparable information for both species as to how the soil substrate affects plant traits. Especially knowledge about how nutrient-poor soil affects plant traits, also in interaction with other abiotic conditions, is missing.

Besides, hydromechanical properties also play a direct role in species distribution and cause zonation and dispersal along water bodies (Zhu et al. 2020), as can also be observed on the Elbe (Carus et al. 2017; Schoutens et al. 2020). Critical hydromechanical stress causes plant stems to fold and break and thus die (Vuik et al. 2018). How a species copes with hydromechanical influences can be determined by its stiffness and flexibility, which can be assessed by Young's modulus and flexural rigidity (Rupprecht et al. 2015; Schulze et al. 2019). *P. australis* is considered a stiff species (Coops and van der Velde 1996) and its mechanical properties are assumed to limit distribution towards mechanically challenging shores (Ostendorp 1995). However, information on the mechanical properties of *P. arundinacea* is lacking, which could be relevant to explain the occurrence and distribution patterns of both species.

Finally, the examination of plant traits must take the provenance of plants into account, as plants can adapt to local conditions. A "suitable environment" for one genotype of a species may be less suitable for another genotype of the same species (Pereira 2016; Reents et al. 2021). Plant morphology and growth traits of *P. australis*, for example, vary depending on latitudinal provenance (Clevering et al. 2001; Hansen et al. 2007), which is attributed to adapted genotypes to local environmental conditions. *P. arundinacea* also shows genetically manifested adaptations to local sites, as individuals exist with an adapted metabolism to cope with local salt stress (Maeda et al. 2006). Thus, the effects of abiotic influences on plant traits have to be examined against the background of different provenances.

The aims of this study are to investigate, how typical abiotic conditions of Elbe sections affect plant traits of *P. australis* and *P. arundinacea* and whether the two species differ in their responses. We therefore apply two types of flooding, salinities and soil types to *P. arundinacea* and *P. australis* within a mesocosm experiment and analyse the response of biomass, the ratio between above- and belowground biomass as well as the number of shoots as growth traits. We further investigate, if and how Young's modulus and flexural rigidity - as mechanical traits of *P. australis* and *P. arundinacea* - differ between abiotic conditions. Lastly, we focus on plant provenance as indicator for different genotypes. We want to

check, if plant provenance has an influence on the expression of plant traits of both species and thus determine whether the response of the traits is due to genotypes or is species dependent.

## 2 Methods And Material

To simulate the environmental conditions of the tidal and inland Elbe, and to investigate their effect on traits of *P. australis* and *P. arundinacea*, we designed an experiment in the free-standing mesocosm facility at Universität Hamburg. The facility consists of four directly adjacent basins that measure 1.5 m×3 m×1.6 m (Height×Length×Width; Figure 1A). Water level in the basins is automatically measured at 15-minute intervals, and water is pumped from external tanks (9000 L) in or out to simulate tides or other water level changes. Our experiment included the treatments: water level (tidal vs. inland water level; Figure 1C and 1D), salinity (brackish water vs. freshwater; Figure 1A), soil type (clay vs. sand), and plant provenance (tidal vs. inland Elbe) of *P. australis* and *P. arundinacea* in the basins (Figure 1B).

The experiment was designed as a full-factorial experiment with both species and four replicates, resulting in 128 individual plants (Figure 1). Each individual was planted in a 25 L bucket (diameter: 30 cm, height: 44 cm). In each bucket, there was a 20 cm high sand layer on a root fleece to allow drainage as the buckets were connected to the water body via holes in the bottom. The positions of the individuals including their treatments were randomly assigned to the basins before transplantation. To avoid competition for light, the individuals were placed at a distance of 30 cm from each other, and to avoid shading by walls, the buckets were installed on a 40 cm high platform.

### *Design of treatment factors and their levels*

In our experiment, half of the test individuals were exposed to brackish water with 10 psu, corresponding to the mean naturally occurring salinity of the tidal Elbe. Dissolved artificial sea salt (Coral Reef Equipment, Sea-Salt) was successively added to a water tank and two experimental basins until the desired salt content was reached. During the experiment, the salt content was controlled weekly and kept constant. The other tank, which regulates the water supply for the other two basins, was filled with fresh water.

Figure 1 Experimental design in the mesocosm facility to simulate abiotic conditions on the Elbe and their influence on *P. australis* and *P. arundinacea*. **(A)** Aerial view of the four basins. Basins I and II contained brackish water, III and IV fresh water. **(B)** In each basin there were 4 replicates of both species on sand and clay, from the tidal and inland Elbe. Plants were arranged randomly. **(C)** The experimental water levels based on mean water levels of inland Elbe at the Scharleuk gauge between 1997 and 2017. The upper and lower edges of the buckets are shown by the grey dashed lines. The water levels of inland Elbe were applied in basins I and III. **(D)** Water levels of tidal Elbe at Krautsand gauge in 2017. The upper and lower edges of the buckets are shown by the grey dashed lines. The tidal water levels were applied in basin II and IV

Furthermore, we simulated two flooding patterns representing the tidal and inland Elbe. In the tidal flooding pattern, individuals were flooded twice a day for 3 hours. The predefined water levels correspond to the values from the Krautsand gauge station (UTM 32N, ETRS 1989: Y: 5.956.254,94; X: 525.817,00) from 2017 (Figure 1D). In the other two basins, a typical water level was simulated as found at the inland Elbe. As a reference for the target values in the basins, the measured water levels of the Scharleuk gauge station (UTM 32N, ETRS 1989: Y: 5.871.264,70; X: 690.579,07) were used as mean values from the period of 1997 to 2017 (Figure 1C). The target values for inland Elbe led to permanently flooding of individuals for 6 weeks, after which the water level slowly dropped. Basins I and III were exposed to the inland water level. Predefined tidal and inland water levels were limited to a maximum, so that water level above the root zone was never higher than 10 cm.

To reproduce two site-specific soil substrates, marine clay (S:20%, U:50%, T:30%, DIN 18123, hereafter only called clay) and pure sand (SS:0-1mm) were used in this experiment. Within the basins, half of the individuals (16 plants) were transplanted into clay, the other individuals (16 plants) into pure sand. In order to reproduce the coherent structure of the clay from the tidal Elbe, it was saturated in water and mechanically homogenized by stirring.

In order to get insight into the impact of plant provenance on plant traits, we planted eight plants per species in each of the two soil types, with four coming from the tidal Elbe and four from the inland Elbe.

#### *Collection, storage, and transplantation of *P. australis* and *P. arundinacea**

Plant sampling took place on March 26th 2019 at the tidal Elbe and on March 29th 2019 at the inland Elbe. *P. australis* and *P. arundinacea* were dug up as rhizome fragments, where a first shoot had already broken through the soil surface. In contrast to *P. australis*, first leaves occurred at *P. arundinacea*. We selected undisturbed sites where both species occurred for plant sampling. Removal always took place at the smallest distance from species occurrences to the Elbe. The removed rhizome fragments were transported to Hamburg, the root balls were completely freed from the original soil material and planted in plastic containers on sand. The plants were watered regularly and stored shaded, to prevent growth before the experiment started. As one fourth of *P. arundinacea* plants of the first sampling had largely died within the first few days due to unknown reasons, a second sampling at one of four sites at the inland Elbe took place on April 17th 2019. On June 3rd 2019, the first day of our experiment, the plants were transplanted into buckets in the basins of the mesocosm facility. Due to a construction problem of the facility, one bucket per basin had to be removed.

#### *Measurement of plant traits*

After 12 weeks, the plant individuals were removed from the basins. All shoots were counted and their diameter (mm) was measured next to the soil surface. One root ball with shoots was dug up and used for mechanical measurements on the same day. All remaining shoots were cut off close to the ground, washed, dried, and weighed, to obtain aboveground biomass (g). The roots were freed from the soil substrate, washed and dried, resulting in belowground biomass (g). Shoots and root material, which were

taken for the mechanical measurements, were subsequently returned and treated in the same way. To determine the flexibility of the plant stem, we carried out three-point bending tests with the bending forces working orthogonally to the plant stem (Schulze et al. 2019). The plant material for the test was taken from the lowest part of the stem near the ground, which was cut out with a scalpel. All test sections examined were cylindrical. To minimise the influence of shear stress in bending tests, the distance between the support bars was always set at a distance corresponding to 10 times the diameter of the stem. The bending tests were conducted with a Zwick/Roell testing machine (type 1120.25, nominal force: max. 1 kN, using a 10 N load cell; preload 0.01 N; Zwick GmbH & Co. KG, Ulm, Germany). For the measurements, a metal-stamp was lowered with a displacement rate of 10 mm min<sup>-1</sup>. Meanwhile, the applied force and the vertical deflection of the tested stem were recorded. The slope of the force-displacement curve was determined from the initial linear part. In addition, the diameter of the stem and the span between the two support bars were used to calculate the second moment of area ( $I$ ) and the flexural rigidity ( $EI$ ) to obtain the Young's modulus ( $E$ ). In this study we analysed Young's modulus as the modulus of elasticity describing the flexibility of the plant tissue without considering the stem morphology, but also flexural rigidity considering stem morphology in addition to solely material properties (Miler et al. 2012; Silinski et al. 2015; Schulze et al. 2019).

### *Statistics*

To analyse the response of plant traits of *P. australis* and *P. arundinacea*, we performed multi-factorial ANOVA explaining the variance in the five response variables: total biomass, root-shoot ratio, number of shoots, Young's modulus, and flexural rigidity. We choose type-III ANOVA, as we do not assume ranked importance of explanatory variables and furthermore take interactions into account (Dormann and Kühn 2012). The analysis included the four treatment variables salinity, water level, soil type, plant provenance as well as their interactions. If necessary, data were log- or square-root transformed to meet the assumptions of ANOVA. In case of count-data (number of shoots), we applied a Generalized linear model assuming a Poisson distribution of errors. In case of over-dispersion, we estimated an additional dispersion parameter. The variance homogeneity of response-variable between the treatments was tested with the Bartlett test and the normal distribution of the model residuals with the Shapiro test. In addition, we checked diagnostic plots for homoscedasticity and leverage. Conspicuous data points were examined in detail. If a conspicuous data point had no relevant influence on the ANOVA results and we found no reason for this data point being conspicuous, this point remained in the analysis, especially since moderate deviations in variance homogeneity are negligible for ANOVA testing in a balanced study design (Box, 1954; McGuinness, 2002). In only one case, total biomass, number of shoots, Young's modulus, and flexural rigidity of one *P. arundinacea* plant under the treatment of fresh water, inland water level, clay, and inland provenance was excluded from analysis. This one plant had the highest final biomass, affecting model results due to high leverages. Already during the experiment, this one plant grew visibly stronger than all others. Yet, root-shoot ratio of this plant wasn't conspicuous and therefore remained in the analysis. In order to represent only the relevant influences on the plant traits, the models are reduced in complexity by excluding non-significant interaction-effects. The main effects were always

part of our models. After fitting a final model, post-hoc comparisons of means were conducted for main effects and significant interactions using the 'emmeans' package (Lenth et al. 2021). If a response variable was transformed, we backtransformed it before comparison of means. All analyses were performed in R version 4.0.1 (R Core Team 2021).

### 3 Results

The plant traits of *P. arundinacea* and *P. australis* responded to the abiotic conditions in a species-specific way. While *P. australis* always produced significantly more biomass on clay than on sand (Figure 2A), its biomass production was not influenced by salinity or water level treatment (Figure 2 and Table 1). In contrast, the biomass of *P. arundinacea* did not significantly differ between the two soil substrates in either of the three simulated Elbe sections tidal brackish, tidal fresh and inland fresh, although ANOVA indicates an influence of soil type on biomass (Table 1).

However, biomass of *P. arundinacea* responded to salinity and varied considerably between the water level treatments (Table 1). Thus, under tidal influence, *P. arundinacea* produced significantly less biomass in brackish water than in fresh water, both on clay (Figure 2A) and on sand (Figure 2A). In addition, *P. arundinacea* produced more biomass on sand and freshwater at tidal water level than at inland water level (Figure 2A), while there was no effect of water levels on the clay soil.

Table 1

Summary statistics of plant traits in the experiment testing for effects of abiotic conditions on *P. australis* and *P. arundinacea*. Variables are analysed by multi-factorial Type III-ANOVA. Significant p-values are shown in bold letters. Interactions between main effects are indicated by "×".  $\chi^2$  statistic was used for count data, while F-statistics were used for continuous data.

Trait	Abiotic conditions	<i>P. australis</i>		<i>P. arundinacea</i>	
		Test statistic	p-value	Test statistic	p-value
Total biomass [g]	Salinity	F = 1.33	.25	F = 28.98	<b>&lt;.001</b>
	Soil type	F = 83.86	<b>&lt;.001</b>	F = 8.86	<b>&lt;.01</b>
	Water level	F = 0.02	.90	F = 0.81	.37
	Provenance	F = 13.82	<b>&lt;.001</b>	F = 0.09	.76
	Soil type × Water level			F = 4.70	<b>&lt;.05</b>
Root-shoot-ratio [*]	Salinity	F = 0.02	.88	F = 0.01	.92
	Soil type	F = 26.18	<b>&lt;.001</b>	F = 33.25	<b>&lt;.001</b>
	Water level	F = 3.75	.06	F = 0.44	.51
	Provenance	F = 3.28	.08	F = 3.75	.06
Shoot number [*]	Salinity	$\chi^2 = 1.98$	.16	$\chi^2 = 0.44$	.51
	Soil type	$\chi^2 = 67.02$	<b>&lt;.001</b>	$\chi^2 = 9.91$	<b>&lt;.01</b>
	Water level	$\chi^2 = 0.012$	.91	$\chi^2 = 7.22$	<b>&lt;.01</b>
	Provenance	$\chi^2 = 0.69$	.41	$\chi^2 = 1.44$	.23
	Salinity × Soil type × Water level			$\chi^2 = 6.70$	<b>&lt;.01</b>
Young's modulus [MPa]	Salinity	F = 0.93	.34	F = 5.87	<b>&lt;.05</b>
	Soil type	F = 0.05	.82	F = 1.45	.24
	Water level	F = 2.03	.16	F = 32.32	<b>&lt;.001</b>
	Provenance	F = 0.48	.49	F = 0.94	.34
Flexural rigidity [Nm <sup>2</sup> ]	Salinity	F = 0.00	.99	F = 11.22	<b>&lt;.01</b>
	Soil type	F = 14.10	<b>&lt;.001</b>	F = 0.04	.85
	Water level	F = 1.04	.31	F = 3.92	.05

	<i>P. australis</i>		<i>P. arundinacea</i>	
Provenance	F = 32.84	<.001	F = 1.74	.19

Besides the species-specific differences in biomass production, the abiotic conditions also influenced root-shoot ratio. Root-shoot ratio followed the same pattern in both species due to the significant effect of soil type on the root-shoot ratio (Table 1). However, *P. australis* generally had higher root-shoot ratios than *P. arundinacea* (Figure 2B). For both species, the sandy soil led to a significantly higher ratio of belowground to aboveground biomass than clay soil. Root-shoot ratio was, however, independent of water levels and salinity (Figure 2B). While *P. arundinacea* had an average ratio of  $0.94 \pm 0.04$  on sand and  $0.65 \pm 0.03$  on clay, the ratio for *P. australis* on sand was  $1.22 \pm 0.06$  and on clay  $0.87 \pm 0.04$ . *P. australis* produced more belowground than aboveground biomass on sand, while *P. arundinacea* had a balanced growth ratio. On clay, both species produced more aboveground than belowground biomass. *P. australis* shoot numbers differed with soil substrate, as observed for the biomass (Table 1). Significantly more shoots were produced on clay than on sandy soil (Figure 2C). Water level and salinity had no effect on the number of shoots of *P. australis* (Table 1 and Figure 2C). For *P. arundinacea*, no difference was found between different water levels and salinities in the number of shoots on sand. On clay, the shoot number was affected by salinity: Brackish water caused significantly fewer *P. arundinacea* shoots to grow on clay than under the influence of fresh water on tidal water levels (Figure 2C).

Figure 2 Total biomass (A), root-shoot-ratio (B), Shoot number (C) of *P. australis* and *P. arundinacea* at the three simulated Elbe sections tidal brackish, tidal fresh and inland fresh, respectively. Presented are boxplots with median, hinges at first and third quantile and whiskers at  $1.5 \times$  Interquartile range. Light boxplots show responses on clay, while dark boxplots show responses on sandy soil. Lower brackets show the difference between soils within one section, upper brackets show the differences between sections on one soil type. Asterisks show significant differences between treatments based on post hoc test

*P. australis* and *P. arundinacea* differed in their mechanical traits: The Young's modulus for *P. australis* was significantly higher than for *P. arundinacea*. While the Young's modulus for *P. australis* did not differ between treatments (Table 1), the Young's modulus of *P. arundinacea* was significantly lower under the inland fresh- compared to the tidal fresh conditions (Figure 3A). Flexural rigidity of *P. australis* was basically higher than of *P. arundinacea* (Figure 3B). Independent of different water levels or salinities, flexural rigidity of *P. australis* was significantly higher on clay than on sandy soil (Figure 3B). In contrast, flexural rigidity of *P. arundinacea* did not react to the soil substrate. However, there were significant differences in stiffness between salinities under tidal water levels. *P. arundinacea* in brackish water had lower flexural rigidity than in fresh water, both on sand and on clay (Fig. 3B).

Figure 3 Young's modulus (A) and flexural rigidity (B) of *P. australis* and *P. arundinacea* at the three simulated Elbe sections tidal brackish, tidal fresh and inland fresh, respectively. Presented are boxplots with median, hinges at first and third quantile and whiskers at  $1.5 \times$  Interquartile range. Light boxplots

show responses on clay, while dark boxplots show responses on sandy soil. In white boxplots, responses are averaged over soil. Lower brackets show the difference between soils within one section, upper brackets show the differences between sections on one soil type. Asterisks show significant differences between treatments based on post hoc test

Regarding the plant provenances, *P. australis* from the inland sections produced more biomass than plants from the tidal sections ( $85.1 \pm 6.1$  g vs.  $58.8 \pm 4.1$  g). Furthermore, the flexural rigidity was significantly higher for *P. australis* from the inland than from tidal sections ( $60.8 \pm 4.9 \text{ Nm}^2 \cdot 10^3$  vs.  $27.7 \pm 3.3 \text{ Nm}^2 \cdot 10^3$ ). Yet, the plant provenance did not interact with other treatments regarding plant traits of *P. australis*. For *P. arundinacea*, we found no effect of plant provenance on plant traits.

## 4 Discussion

To foster our understanding of distribution patterns of *P. australis* and *P. arundinacea* along the Elbe river, we studied the influence of abiotic conditions on plant traits of both species by conducting a mesocosm experiment. We showed that both species respond differently to applied treatments. The growth characteristics of *P. australis* significantly differed between soil types. In contrast, the growth traits of *P. arundinacea* depended on soil type, often in interaction with water level and salinity. We also showed that the mechanical properties of both species differ between treatments. The mechanical properties of both species varied mainly due to morphological differences and less due to effects on the plant tissue.

Regarding the difference in growth traits of *P. australis* due to soil substrate, we observed higher biomass production and stem density in clay compared to sand. This pattern is consistent with a study by Lenssen et al. (1999), in which *P. australis* produces less biomass on purely mineral, nutrient-poor soil substrate, than on nutrient-enriched sediment. It was previously shown that *P. australis* produces more biomass and shoots with a higher nutrient supply (Saltonstall and Stevenson 2007; Rickey and Anderson 2004). Sand has a lower cation exchange capacity (Kennedy 1965; Malcolm and Kennedy 1970) and retains and provides fewer nutrients than clay (Malcolm and Kennedy 1970; Petrovic 2004). We thus assume that the sand in our experiment provides less nutrients than the clay. This is also indicated by the root-shoot ratio, which clearly exceeds one on sand, which we interpret as a reaction to a state of nutrient demand (Shiple and Meziane 2002). An enhanced production of root biomass in the case of low nutrient supply was already demonstrated for *P. australis* by Minchinton and Bertness (2003). In contrast to growth patterns on sand, we observed higher biomass production on clay and a balanced distribution between aboveground and belowground biomass.

In our experiment, neither different flooding treatments nor salinities affected plant traits of *P. australis*, as treatment values were within the previously described tolerance levels. *P. australis* was found to survive salt levels up to 65‰ (Engloner 2009), but its salt tolerance also depends on developmental stage and genotype (Eller et al. 2017; Engloner 2009; Yu et al. 2012). Salt tolerance results from various physiological adaptations (Lissner et al. 1999; Pagter et al. 2005; Eller et al. 2014), but probably also from salt avoidance strategies of the root system (Eller et al. 2017). Negative effects of salt levels of 10‰ on

plant traits of *P. australis* are accordingly unlikely and under certain circumstances, a low salt concentration can even stimulate growth (Lissner and Schierup 1997). The lacking response of *P. australis* to the different flooding treatments in our experiment could be due to its root growth. With a maximum rooting depth of up to 3 m (Mozdzer et al. 2016), *P. australis* was able to penetrate the entire soil space in all buckets. This way, the plants were always connected to the water body under inland water level treatment and regularly flooded by the tidal water level. We can therefore exclude water shortage in both water level treatments. Furthermore, *P. australis* is tolerant to water level fluctuations (White et al. 2007), as well as to flooding, as long as *P. australis* reaches a certain ontogenetic state in which oxygen transport from leaves to roots is possible (Ostendorp 1991). This ontogenetic state was reached at the time of transplantation, so that flooding could probably not have a negative effect on growth.

Concerning the root-shoot ratio, we saw that the sandy soil led to relatively more root biomass than the clay soil, which we attribute to a lower nutrient supply. Plants adjust the allocation of growth resources depending on nutrient availability. While *P. australis* produced more belowground than aboveground biomass in sandy soil, the root-shoot ratio of *P. arundinacea* was one or below in all treatments. We therefore assume an increased nutrient requirement on sand for *P. australis*, but not for *P. arundinacea* (Shipley and Meziane 2002). From this pattern, we conclude that *P. arundinacea* copes better on sand than *P. australis*. Although positive effects on plant growth of *P. arundinacea* due to higher nutrient availability were shown in previous studies (Maurer and Zedler 2002; Martina and von Ende 2008; Chen et al. 2017), these only occurred to a limited extent in our experiment, as we could only demonstrate minor influences of nutrient supply by soil type. Salinity and water level treatment had clear influences on biomass production, which was also demonstrated in other studies, with brackish water having a negative effect on biomass production and shoot number (McElgunn and Lawrence 1973; Prasser and Zedler, 2010) and regular flooding leading to a higher number of shoots and more biomass produced (Miller and Zedler 2003).

The negative effect of salinity on both, biomass production and shoot number of *P. arundinacea*, occurred on clay for both traits, but not on sand for shoot number. This relationship underlines the need to consider the substrate type when evaluating the response of plant traits to salinity (García-Sánchez and Syvertsen 2009). In relation to soil texture, negative influences due to salinity are more likely observed on light textured soils (i.e. with a high content of sand fraction) than on heavily textured soils (i.e. with a high content of clay and silt fraction) (Townsend 1984; Fostad and Pedersen 2000). This relationship occurred in the opposite way in our experiment. We saw a negative influence of salinity on sand for biomass, while salinity on clay negatively influenced biomass and shoot number. Furthermore, salinity led to a stronger decrease in biomass on clay than on sand. We attribute the recurring and stronger negative effect of salt on clay in our experiment to the texture-dependent lower percolation and higher water retention (Li et al. 2014). This leads to a longer contact time of the saline water with the roots on clay, which thus has a more detrimental effect on biomass production than can be expected with sand, with high percolation and low retention (Li et al. 2014). In addition to the substrate-dependent influence of salinity, we also attribute the influence of the water level treatment to soil texture. Although

regular flooding leads to a higher biomass and number of shoots (Miller and Zedler 2003), we observed a negative effect of inland water level on biomass and shoot production compared to the tidal water level only on sand, but not on clay. Due to the lower water retention and higher percolation on sand compared to clay (Li et al. 2014), we assume a lack of water on sand, which can have a negative effect on *P. arundinacea* (Kørup et al. 2018).

Mechanical stem properties differ due to anatomical and morphological differences between plant species, but also within a species by growth stage and adaptation mechanisms (Heuner et al. 2015; Carus et al. 2016; Silinski et al. 2018). For several species occurring on the tidal Elbe, mechanical studies in relation to abiotic environmental conditions exist (Schulte Ostermann 2021; Carus et al. 2016, 2017), although only a few studies have been carried out on *P. australis* (Ostendorp 1995; Coops and Van der Velde 1996; Zhu et al. 2020), and none on *P. arundinacea*. *P. australis* has stiff culms and thus resistance to turbulent water motion, but is considered to be not adaptable to mechanical stress (Coops et al. 1994; Coops and Van der Velde 1996). Coops and Van der Velde (1996) did not find increased strength of wave-exposed *P. australis* stems compared to sheltered stems. However, Coops and Van der Velde (1996) found a positive effect of wave exposure on individual stem length and an increase in critical breaking force and bending stiffness with individual stem length. In the same manner, we also did not find any differences in mechanical properties of plant tissue between treatments in our experiment, looking at Young's modulus of *P. australis*. Yet, we found differences in mechanical properties due to growth traits, looking at flexural rigidity. Besides lignin and cellulose as component of plant tissue, also soil silicates determine the stiffness of a stem (Schoelynck et al. 2012). Nutrient-related differences in physiological stiffness are excluded, at least for *Scirpus maritimus* (Silinski et al. 2018). However, we were also unable to detect any effects of soil type and the associated nutrient supply on plant tissue based stiffness. Thus, although nutrients do not affect the material properties, they affect growth and thus flexural rigidity, i.e. the stiffness, while taking into account the morphological stem properties. The lack of effects of salinity and the water level treatment on plant morphology is reflected in the lack of effects on mechanical plant properties.

The averaged stiffness of the plant tissue of *P. arundinacea* was significantly lower than of *P. australis*. Between the treatments, plant tissue of *P. arundinacea* was nearly similar. However, the inland water level resulted in a significantly lower stiffness than the tidal water level, for which we have no explanation. Potentially, the water level regulates the water supply of the plants and, as Coops and Van der Velde (1996) argue, can influence the relationship between sclerenchyma fibres and their water content, whereby this relationship determines the strength of stems (Vincent 1991; Zebrowski 1992). This relationship, however, should lead to an increase in stiffness in the inland water level. Since mechanical properties also depend on the growth-stage of the plant (Schulze et al. 2019), we cannot exclude that the treatments influence the phenological conditions and thus also the mechanical properties of plant tissue. In contrast to *P. australis*, the stiffness of *P. arundinacea* along the treatments can be attributed to effects on plant tissue, but can also be explained by morphological properties. With regard to flexural rigidity, it is evident that *P. australis* is stiffer than *P. arundinacea*. The different inter-specific mechanical properties

considering morphological plant traits fit into the principle that larger species have stiffer and stronger stems than smaller species, as larger species need stronger shoots for more biomass (Jagels et al. 2018).

For both *P. australis* and *P. arundinacea* different genotypes have been identified (Perdereau et al. 2017; Hansen et al. 2007), which can determine the response to treatments within and between populations (Eller and Brix 2012; White et al. 2004; Collins et al. 2018). Surprisingly, we found an influence of the plant provenance only for *P. australis*. Plants of the inland Elbe had higher biomass production and flexural rigidity compared to plants of the tidal Elbe. The influence of different genotypes on morphological characteristics of *P. australis* is known (Ren et al. 2020; Wani et al. 2020). In contrast to *P. australis*, plant provenance had no effects on plant traits of *P. arundinacea*, although genotypes of *P. arundinacea* may affect their plant traits, like allocation patterns or salt tolerance (Morrison and Molofsky 1998, Maeda et al. 2006). We would like to emphasise that for both species their provenance did not interact with other treatments. Accordingly, the effects of our treatments on plant traits did not result from, or were influenced by, genetically determined adaptation mechanisms. Despite provenance-specific morphological differences, treatments effects are comparable for plants of both provenances. As *P. australis* was not sensitive to low salinity and was not affected by water level, it is possible that no adaptations could be seen, as no morphological or physiological stress occurred.

## 5 Conclusion

We showed that both reed plants *P. australis* and *P. arundinacea* from the inland and tidal Elbe can survive under all simulated abiotic conditions. Nevertheless, we observed species-dependent differences in plant traits in response to abiotic conditions. Growth related traits of *P. australis* depend on soil type and were negatively affected by sand probably due to reduced nutrient supply. In contrast, the growth traits of *P. arundinacea* were mainly affected by salinity, with brackish water leading to reduced growth traits. But growth traits of *P. arundinacea* also depend on water level and soil type, whereby the abiotic conditions affect growth traits often in interaction. We see the reason for the varying response in the interplay between soil physical properties, which can amplify or reduce the effects of salinity and different water levels. The mechanical properties of both species react similar as the growth traits. However, we did not see clear signs of differences of the plant tissue, but rather morphologically determined differences. Therefore, negative influences on growth lead to more flexibility or less stiffness. Finally, we showed that plant provenance does not affect the response of plant traits to abiotic conditions. Our study thus provides first explanations for unclear distribution patterns of *P. australis* and *P. arundinacea* along the river sections, but cannot explain all field observations. *P. arundinacea* should cope better on sandy sites than *P. australis*. Regular flooding favours the growth of *P. arundinacea* compared to prolonged flooding, while *P. australis* can cope with both water levels. Furthermore, brackish water reduces growth of *P. arundinacea*, but not of *P. australis*. Both species have similarly flexible plant tissue, but *P. arundinacea* is more flexible than *P. australis* due to morphological differences and should therefore cope better at mechanically stressful sites. The occurrence of *P. arundinacea* in parts of brackish marshes remains unclear. We identify the need to conduct field surveys in which also dominant

abiotic conditions are quantified repeatedly. That would allow clearer conclusions on the relationships between abiotic site-conditions and plant traits.

## 6 Methodological Considerations

We assume that the presented experimental set-up is suitable to evaluate the influence of various abiotic conditions on plant traits. Nevertheless, we recommend to verify the dependencies between plant traits and abiotic site conditions in field surveys to estimate effects under natural conditions. Especially the interactions between soil substrate and hydrologic conditions are highly complex, so that the simplified representation in the experiment may have influenced the plant traits too weak or too strong.

## Declarations

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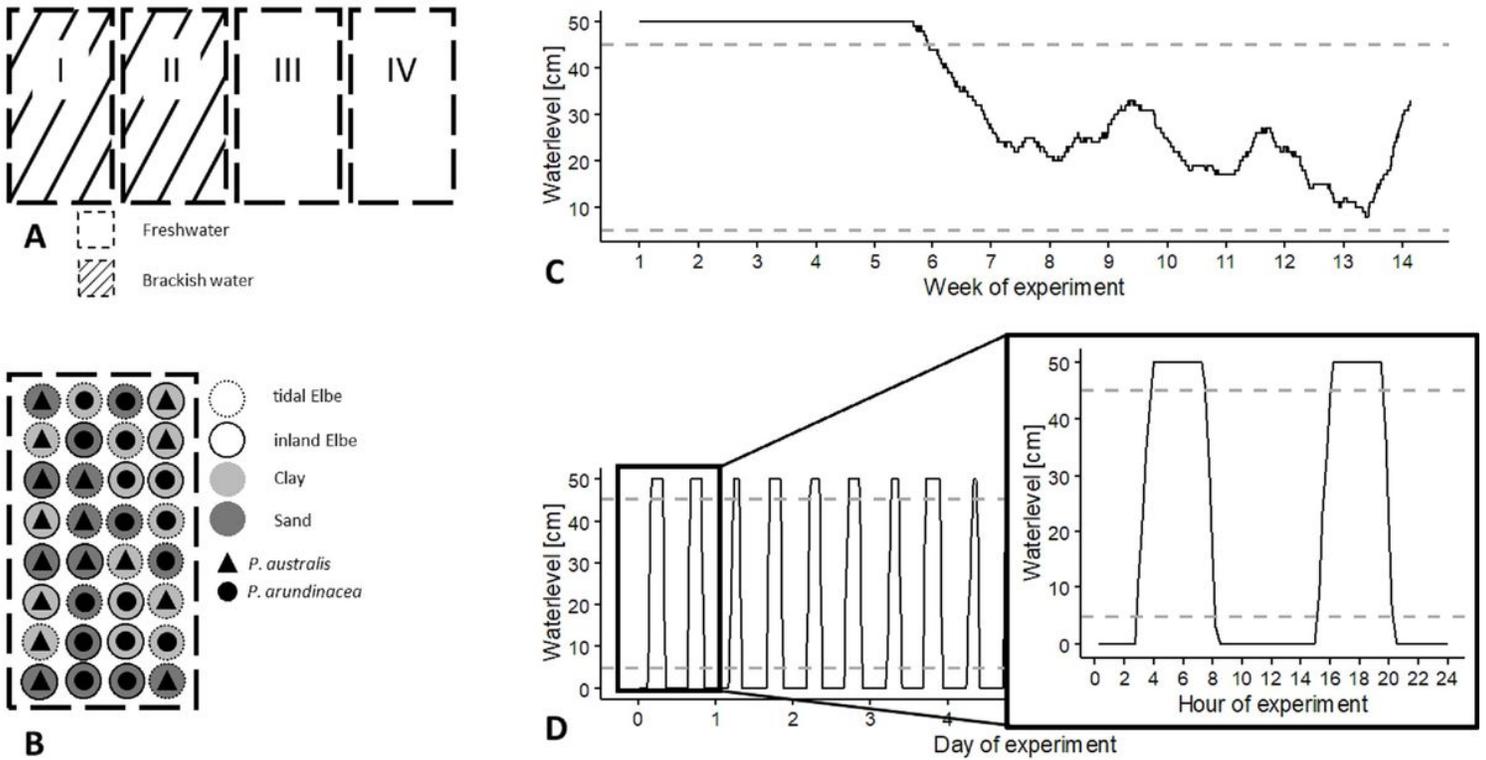
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## Figures

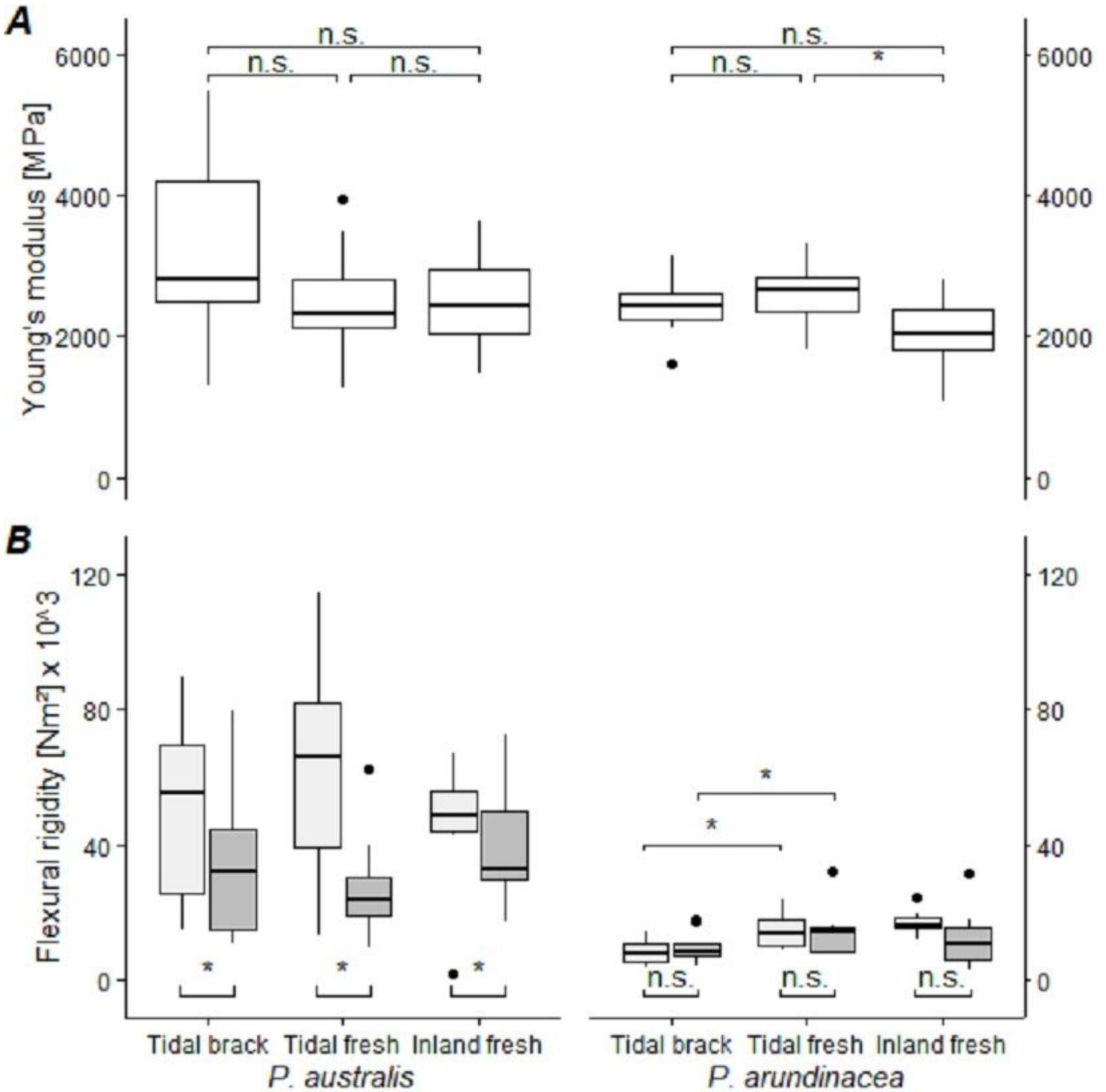


**Figure 1**

Experimental design in the mesocosm facility to simulate abiotic conditions on the Elbe and their influence on *P. australis* and *P. arundinacea*. (A) Aerial view of the four basins. Basins I and II contained brackish water, III and IV fresh water. (B) In each basin there were 4 replicates of both species on sand and clay, from the tidal and inland Elbe. Plants were arranged randomly. (C) The experimental water levels based on mean water levels of inland Elbe at the Scharleuk gauge between 1997 and 2017. The upper and lower edges of the buckets are shown by the grey dashed lines. The water levels of inland Elbe were applied in basins I and III. (D) Water levels of tidal Elbe at Krautsand gauge in 2017. The upper and lower edges of the buckets are shown by the grey dashed lines. The tidal water levels were applied in basin II and IV



difference between soils within one section, upper brackets show the differences between sections on one soil type. Asterisks show significant differences between treatments based on post hoc test



**Figure 3**

Young's modulus (A) and flexural rigidity (B) of *P. australis* and *P. arundinacea* at the three simulated Elbe sections tidal brackish, tidal fresh and inland fresh, respectively. Presented are boxplots with median, hinges at first and third quantile and whiskers at  $1.5 \times$  Interquartile range. Light boxplots show responses on clay, while dark boxplots show responses on sandy soil. In white boxplots, responses are averaged

over soil. Lower brackets show the difference between soils within one section, upper brackets show the differences between sections on one soil type. Asterisks show significant differences between treatments based on post hoc test