



Comparison of water depth tolerance in two major wetland macrophytes, *Phragmites australis* and *Typha angustifolia*

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Abstract

Two major emergent macrophytes, *Phragmites australis* and *Typha angustifolia*, show a clear zonation with respect to water depth, i.e., *P. australis* occupies shallower water than *T. angustifolia*. However, the reasons for this interspecific difference is unclear. Therefore, this study focused on the features that enable *T. angustifolia* to survive at greater water depths than *P. australis*. In both outdoor and greenhouse experiments, *P. australis* did not survive at the deepest water depth and showed significantly lower biomass, nitrogen content, and photosynthesis in most deep and/or aerated water than *T. angustifolia*. Differences in tolerances to changes in the water depth and responses to root aeration may underlie the clear zonation of the two species. As *T. angustifolia* and *P. australis* are both very common in wetlands around the world, understanding the causal factors determining their depth distributions, such as differences in photosynthetic rate at different depths, will be of great importance for managing or controlling these species.

Keywords: antioxidant enzyme activity; cattail; ecophysiology; photosynthesis; reed; wetland.

Introduction

Wetlands are important ecosystems for biodiversity conservation, nutrient retention, and water supply (Tiner 1984), and provide many ecosystem services of benefit to humans (Carlsson *et al.* 2003). Wetlands are also believed to play an important role in mitigating future global climate change (Erwin 2009, Song *et al.* 2013). Wetland macrophytes have several intrinsic properties that make them important ecosystem components. Macrophytes stabilize the sediment surface and provide a habitat for attached microbial growth (Brix 1994). Their remediation ability helps improve water quality (Song *et al.* 2018), and they provide shelter for many other species (Gregg and Rose 1982).

Reeds (*Phragmites* spp.) and cattails (*Typha* spp.) are representative emergent macrophytes in freshwater (Maddison *et al.* 2009, Rejmankova 2011). They show

a clear zonation with respect to water depth, with the common reed, *Phragmites australis* (Cav.) Trin. ex Steud., occupying shallower and slower-flowing water than the narrow-leaf cattail, *Typha angustifolia* L. (Asaeda *et al.* 2005). Song *et al.* (2018) found that *T. angustifolia* occurred at a much greater maximum water depth than *P. australis*. However, the reasons behind these interspecific differences are not clear. Differences in germination under submerged conditions (Coops and van der Velde 1995), oxygen demand/aeration (Yamasaki 1984), niche competition (Findlay *et al.* 2002), morphological plasticity (Bellavance and Brisson 2010), ability to elongate shoots rapidly above the water surface (de Assis Murillo *et al.* 2019), formation of adventitious roots (Pedersen *et al.* 2017), and molecular signaling pathways involved in germination under submergence (Pedersen *et al.* 2017) may allow *T. angustifolia* to outcompete *P. australis* in deep water conditions. Also, the fundamental niche of

Highlights

- Reed and cattail show a clear zonation with respect to water depth
- Cattail showed higher resilience of photosynthesis to water depth and better use of root aeration
- Causal factors determining reed and cattail depth distributions were discovered

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P. australis for water depth would be much lower than that of *T. angustifolia*. However, while important features of submerged plants, such as photosynthesis (Spence and Chrystal 1970), antioxidant enzyme activity (Li *et al.* 2011), and nutrient availability (Yuan *et al.* 2016), have been studied, there is little information on emergent macrophytes, in particular, there have been no studies relating plant features to a water depth. Consequently, this study of zonation in *P. australis* and *T. angustifolia* focuses on the features that enable cattails to survive at greater water depths. It was tested whether the difference in (1) photosynthetic rate change by water depth and (2) ability to utilize dissolved oxygen could be a factor affecting survival water depth of two species (*T. angustifolia* has bigger maximum water depth than *P. australis*).

Materials and methods

Plant depth limits in the study area: The study area, Sudokwon landfill in Incheon, South Korea (37°34'52"N, 126°37'29"E), has one of the world's largest leachate processing facilities (Song *et al.* 2018). The landfill has buffering wetlands, which were constructed during landfill construction to minimize the environmental impact of the emitted leachate. However, these 15-years (at the time of study) old wetlands did not consider ecological features of remediation plant during construction that only edge of the wetlands is covered with macrophytes at the time of this research (Song *et al.* 2018). Three vegetated buffer wetlands (termed A, B, and C) were used as study sites. The maximum depth limits of *P. australis* and *T. angustifolia* were measured in June 2007.

Outdoor tank experiment: In April 2007, rhizome clusters (400 g) of *P. australis* and *T. angustifolia* harvested from buffering wetlands were planted in pots (diameter of 36 cm, height of 45 cm) with sand and placed in a tank (2 × 5 × 1.2 m) with running water at depths of 10, 40, or 70 cm (10 replicates per treatment). The experiment was designed to reenact the situation where the shoot from the rhizome penetrates the water layer to rise to the surface of the water in spring. The 70-cm maximum experimental depth was set to exceed the observed natural depth limit for *P. australis* (~ 60 cm). There was also a negative depth treatment with water level approximately 5 cm below the sand surface. Ten replicates were used for each treatment and species combination. The mass per unit area of rhizomes in each pot was set at the value recorded in wetland A (400 g 0.1 m⁻²). Pot depths were modified by standing them on blocks. Nutrients were supplied to each pot in the form of 15 g *Osmocote Plus* [13% N + 13% P + 13% K + 2% MgO], *Scotts International B.V.*, Geldermalsen, Netherlands). The photosynthetic rates and chlorophyll (Chl) content of the experimental plants were measured in August. Plants were harvested for biomass and nutrient measurement in late October.)

Greenhouse experiment: The greenhouse experiment used both plants grown from rhizomes and from seeds. In the first category, 35 g of rhizomes were planted in

each pot (diameter of 108 mm, height of 120 mm, six replicates per treatment) with the same mass per unit area as the tank experiment. For seed-grown treatments, plants were transferred to pots 45 d after germination. To test the physiological responses of plants to water depth and level of aeration, plants were grown at three experimental depths: negative (−5 cm), shallow (5 cm), and deep (35 cm). Treatments involved either aeration (air flow of 7 L min⁻¹ m⁻²) at the bottom of the pots or no aeration to determine whether root aerobic respiration capacity affects growth (Matsui and Tsuchiya 2006). Plants were grown in coarse sand and perlite to maximize air flow to the roots. Photosynthetic rates and total antioxidant activity (TAA) were measured in July 2010, one month after planting. Dissolved oxygen (DO) was measured using a portable DO meter (*YSI Model 30*, *YSI*, Yellow Springs, USA). Plants were harvested for biomass and nutrient measurement after the 3-month growing period.

Analytical methods: Photosynthesis of aerial leaves was measured at 30°C and 400 ppm CO₂ using a portable photosynthesis measurement system (*LI-6400*, *LI-COR Biosciences*, Lincoln, USA). Leaf chlorophyll (Chl) content was measured by extraction with dimethyl sulfoxide (Hiscox and Israelstam 1979) using a spectrophotometer (*SpectraMax*, *Molecular Devices*, San Jose, USA). Carbon and nitrogen contents were measured with an elemental analyzer (*Flash EA 1112*; *Thermo Electron*, San Jose, USA).

For antioxidant enzyme activities, plant leaves (0.1 g) were frozen in liquid nitrogen, and 50 mM phosphate buffer (pH 7.2) was used for extraction. TAA was measured by determining antioxidant activity of organic liquid using bathocuproine (Song and Lee 2010). TAA values were determined by examining induced changes of spectrophotometric measurements (*SpectraMax*, *Molecular Devices*, San Jose, USA) at 490 nm by copper sulfate solution addition. Plant leaves for analysis were collected from the second highest branch from the top.

Statistical analysis: Differences between two treatments (or species) were analyzed using the *Mann-Whitney's U* test. One-way analysis of variance (*ANOVA*) was used to test differences between treatments. When a significant difference (*P* < 0.05) was detected, a *post hoc* *Duncan's* multiple range test was performed using the *ANOVA* procedure in *SAS 9.1* (*SAS Institute*, Cary, USA). Correlation matrix results among biotic parameters were analyzed using *R 3.1.2* (open-source software, *R Developmental Core Team*).

Results

Plant depth limits in the study area: The two species showed a clear difference in maximum recorded depth of occurrence in the landfill study area (Table 1). *T. angustifolia* was found at greater depths in all three wetlands of the landfill. There was a clear zonation between the two species in the wetlands; *T. angustifolia* inhabited deeper areas than that of *P. australis*.

Outdoor tank experiment for comparison of maximum depth tolerance: The Chl content of *T. angustifolia* increased with the water depth. By contrast, *P. australis* did not survive at 70-cm depth and showed a significant decrease in the Chl content as the depth increased from –5 to 10 and 40 cm (Table 2). For *P. australis*, the rate of photosynthesis was significantly lower in the 40-cm depth treatment than that in the negative depth treatment (–5 cm, Fig. 1A). *T. angustifolia* showed the opposite pattern (Fig. 1A), consistent with the differences in Chl content.

The biomass of *P. australis* declined significantly with the water depth (Fig. 2A), with 100% mortality in the 70-cm depth treatment. The aboveground biomass in the 40-cm water depth was only ~ 20% of that in the negative depth treatment (–5 cm). The rhizome biomass did not increase over the course of the experiment. The aboveground biomass of *T. angustifolia* also decreased with the water depth, but values at 40 and 70-cm depth were still 85 and 72% of the negative depth biomass, respectively (Fig. 2A). The nitrogen content decreased significantly with the water depth in both species (Fig. 2A).

Greenhouse experiment for testing species response to water depth and aeration: The biomass of *T. angustifolia* increased significantly with aeration, especially in the deep treatment (Fig. 2B). Seed-grown *T. angustifolia* survived in a deep water only when aerated. *P. australis* grown from rhizomes also showed a positive effect of aeration but no differences were found in seed-grown plants (Fig. 2B). The nitrogen content of *T. angustifolia* was significantly higher in aerated treatments (Fig. 3) but there were no differences in TAA (Fig. 3). Results indicate that the plants

were under severe stress in deep water and that stress (one of the factors believed to define the maximum depth at which a plant can survive) was not reduced by aeration. Aeration significantly increased the rate of photosynthesis in *T. angustifolia* but not in *P. australis* (Fig. 1B,C). In both species, photosynthesis declined with the increasing water depth. Correlation matrix results among biotic parameters showed a clear positive relationship among photosynthetic rate, biomass, and N contents while TAA results showed the negative relationship (Table 3).

Discussion

All three wetlands studied showed a clear zonation of *P. australis* and *T. angustifolia*, with the latter species consistently extending to much greater water depths (Table 1). This pattern is consistent with published results (Squires and van der Valk 1992, Asaeda *et al.* 2005). The mean depth of occurrence for *P. australis* has been reported as ~ 45 cm in some areas (Coops *et al.* 1996), whereas the stand biomass of *Typha* species has been found to decrease only at depths below 85 cm (Waters and Shay 1992). In wetland areas of land reclamation sites (similar to the present study sites), *P. australis* occurs only at depths of ~ 30 cm whereas *T. angustifolia* extends down to 1 m (Kang and Joo 1999). The results consistently showed *T. angustifolia* dominated the deeper areas and *P. australis* dominated the shallower areas of wetlands. This zonation pattern could be a reflection of niche differentiation. However, it could also be interpreted as an intermediate stage of succession, where the lower-marsh species *T. angustifolia* (Squires and van der Valk 1992) will eventually be replaced by the upper-marsh species *P. australis*. Wetland C has low values of plant water depth because leachate emission causes water depth to fluctuate over a wide range (Song 2010).

In the outdoor tank experiment, *P. australis* showed a pattern consistent with the field data by failing to survive at a depth of 70 cm. Chl content also decreased significantly with the water depth (Table 2). By contrast, the Chl content of *T. angustifolia* was significantly higher at depths of 40 cm and 70 cm, and it was the lowest at a depth of 10 cm. The results indicate that *T. angustifolia* is well-adapted to deep water, while *P. australis* prefers

Table 1. Maximum water depths recorded for *Typha angustifolia* and *Phragmites australis* in three Korean wetlands. Values represent means \pm SE ($n = 30$). P value – Mann-Whitney's U test.

	Maximum water depth [cm]		
	Wetland A	Wetland B	Wetland C
<i>Typha angustifolia</i>	73.3 \pm 6.0	94.6 \pm 7.5	79.6 \pm 6.1
<i>Phragmites australis</i>	56.7 \pm 3.9	58.4 \pm 5.4	49.5 \pm 6.3
P value	< 0.001	< 0.001	< 0.001

Table 2. Chlorophyll content of *Typha angustifolia* and *Phragmites australis* at different water depths (outdoor tank experiment). Values represent means \pm SE ($n = 5$). Means within a column followed by the same superscript letter are not significantly different at $P=0.05$.

Species	Water depth [cm]	Chl a [mg L ⁻¹]	Chl b [mg L ⁻¹]	Total Chl [mg L ⁻¹]
<i>Typha angustifolia</i>	–5	11.2 \pm 0.6 ^{ab}	5.2 \pm 0.3 ^{ab}	16.4 \pm 0.9 ^{ab}
	10	7.7 \pm 1.7 ^b	3.6 \pm 0.8 ^b	11.4 \pm 2.5 ^b
	40	13.2 \pm 1.7 ^a	5.7 \pm 0.7 ^{ab}	18.9 \pm 2.4 ^a
	70	13.4 \pm 1.6 ^a	5.9 \pm 0.7 ^a	19.3 \pm 2.3 ^a
<i>Phragmites australis</i>	–5	13.6 \pm 1.7 ^b	5.9 \pm 0.6 ^b	19.4 \pm 2.3 ^b
	10	17.0 \pm 0.7 ^a	7.3 \pm 0.2 ^a	24.3 \pm 0.8 ^a
	40	8.2 \pm 0.5 ^c	4.3 \pm 0.2 ^c	12.5 \pm 0.7 ^c
	70	Dead	Dead	Dead

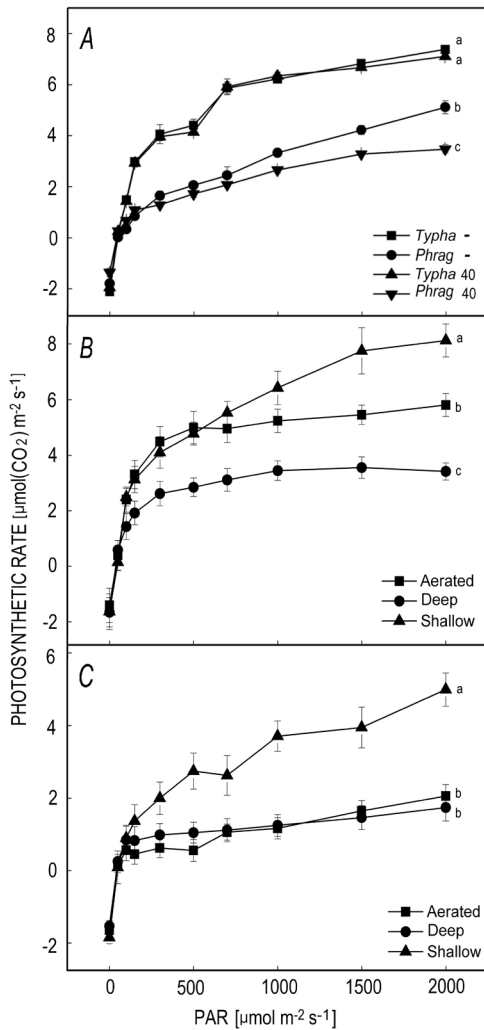


Fig. 1. Photosynthetic performance of (A) *Typha angustifolia* (*Typha*) and *Phragmites australis* (*Phrag*) (outdoor tank experiment); (B) *Typha angustifolia* and (C) *Phragmites australis* at different water depths and aeration (greenhouse experiment). Values represent mean \pm SE of four replicates. Values having the same letter are not significantly different at $P=0.05$. ‘-’ and 40 in (A) mean negative (-) and 40 cm water depth.

shallow water. This pattern is also reflected in rates of photosynthesis (Fig. 1A), which in *T. angustifolia* were not affected by water depth, whereas *P. australis* showed lower rates in deeper water. The physiological activities of *T. angustifolia* appeared to be unaffected by the water depth (down to 40 cm) but those of *P. australis* showed a consistent depth-related decrease. *T. angustifolia* showed a higher photosynthetic performance in both 10 and 40-cm water depths. The physiological activities of *P. australis* showed a depth inhibition, while in *T. angustifolia*, the rates were unaffected down to 40 cm, at which point performance was still higher than that in the negative (-5 cm) depth treatment.

The aboveground biomass of *P. australis* in 40-cm water depth was less than 21% of the value recorded in

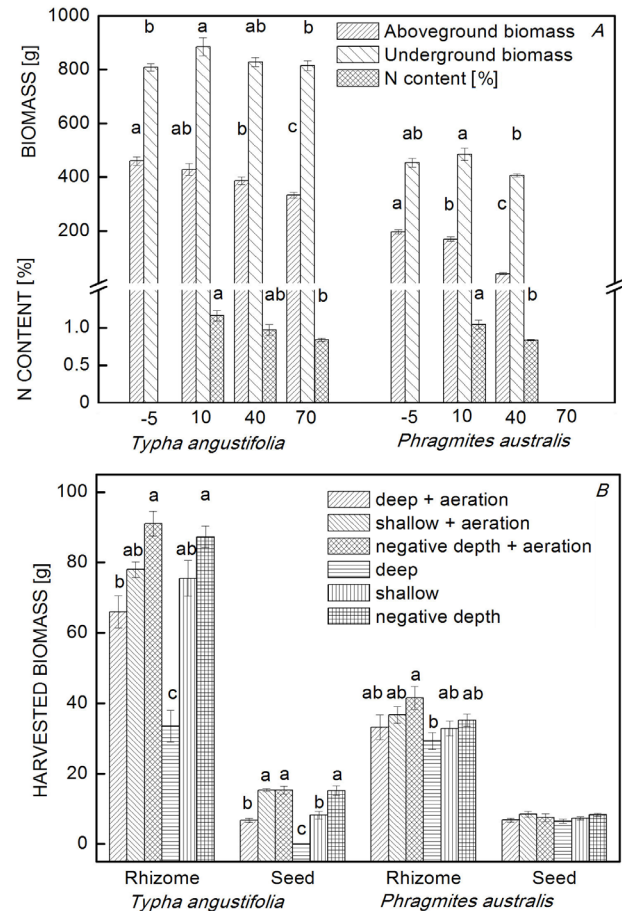


Fig. 2. (A) Harvested biomass (fresh mass) and nitrogen contents of plants (outdoor tank experiment) by water depth [cm] and (B) harvested biomass (dry mass) of plants (greenhouse experiment) by treatments. Values represent mean \pm SE of ten replicates (A) or six replicates (B). N contents of -5-cm water depth were not measured (A). Values with the same superscript letter are not significantly different at $P=0.05$.

the negative depth treatment. *T. angustifolia* biomass also decreased with the water depth but the rate of decline was much lower than that in *P. australis*. *T. angustifolia* in 70-cm water still showed 72% of the aboveground biomass seen in the negative depth treatment, indicating that the species is able to grow in deep water. The underground biomass of *T. angustifolia* more than doubled over the course of the experiment and showed little difference between treatments. By contrast, *P. australis* showed a maximum 20% biomass increase at a depth of 10 cm, no increase at 40 cm, and 100% mortality at 70 cm, indicating that the plant did not grow well in deep water. Previous studies have found that water depth does not suppress growth of *Typha* species (Tulbure *et al.* 2007) while water depth is the major factor that affects growth of *P. australis* (Engloner 2009). Plant nitrogen content decreased significantly with the water depth in both species (Fig. 2A). This indicates that although the plants may be adapted to tolerate deep water (*T. angustifolia*), they may still experience stress (Song 2017).

Ecophysiological parameters, such as Chl content, photosynthesis, and biomass, show clearly that *T. angustifolia* grows better in deep water than *P. australis* and is better suited to a range of static water depths (White *et al.* 2007). These differences explain the clear zonation of *P. australis* and *T. angustifolia* observed in the field.

The greenhouse experiment was designed to test the responses of plants in more tightly controlled conditions and also to test whether root aerobic respiration capacity affects plant growth (Matsui and Tsuchiya 2006). With aeration, the biomass of *T. angustifolia* increased significantly, particularly in the deep treatment (Fig. 2B). Seed-grown *T. angustifolia* survived in deep water only

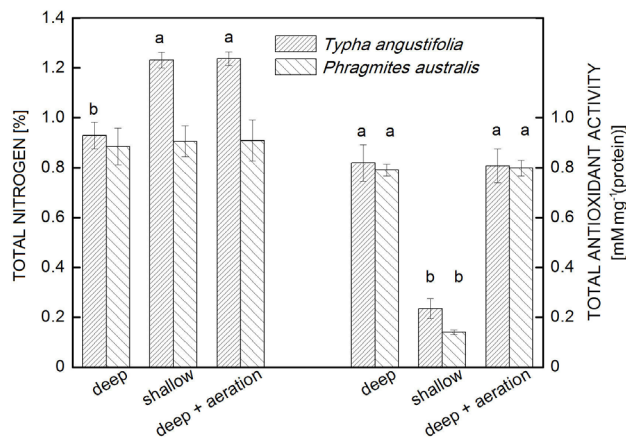


Fig. 3. Nitrogen contents and total antioxidant activity by water depth. Values represent means \pm SE ($n = 3$). Values followed by the same superscript letter are not significantly different at $P=0.05$.

when aerated. *P. australis* grown from rhizomes also showed a positive aeration effect but there was no difference in plants grown from seeds (Fig. 2B). Wetlands with high concentrations of dissolved oxygen, or where conditions permit root aeration (Matsui and Tsuchiya 2006) may allow *T. angustifolia* to grow better in deep water than *P. australis*. For *P. australis*, aeration did not significantly affect performance in the shallow treatments. In treatments without aeration, there were no differences between water depths. The lack of an aeration effect suggests that *P. australis* has a very limited ability to use dissolved oxygen. The ability to take advantage of aerobic conditions in the rooting environment may allow *T. angustifolia* to have a higher water depth tolerance than *P. australis*, which lacks this ability.

P. australis performed better than *T. angustifolia* in the greenhouse experiment for both rhizome- and seed-grown plants. This unexpected result may provide insight into a question why *P. australis* is the most dominant species in the study area (Incheon, Korea) and in many other countries. Results suggest that when grown from seeds, *P. australis* is more adaptable than *Typha* species. It appears to be a generalist able to inhabit wetlands across a wide geographic range (Ailstock *et al.* 2001, NHDES 2018).

Total root biomass and fine root biomass are both important factors to consider when testing the effects of root aeration. In this experiment, fine roots were all attached to perlite and were difficult to isolate from the sands. Root biomass values are therefore not presented. Dissolved oxygen (DO) was measured during the experiment and showed a $\sim 50\%$ difference between aerated and control treatments. However, the later discovery of a fault with the DO meter meant that the values recorded were unreliable,

Table 3. Correlation matrix results among biotic parameters. of *Typha angustifolia* and *Phragmites australis*. TAA – total antioxidant activity.

<i>Typha angustifolia</i> correlation				
	Photosynthetic rate	Biomass	N content	TAA
Photosynthetic rate	1.000	0.855	0.803	−0.790
Biomass	0.855	1.000	0.830	−0.711
N content	0.803	0.830	1.000	−0.443
TAA	−0.790	−0.711	−0.443	1.000
<i>Phragmites australis</i> correlation				
	Photosynthetic rate	Biomass	N content	TAA
Photosynthetic rate	1.000	0.657	0.086	−0.870
Biomass	0.657	1.000	−0.196	−0.748
N content	0.086	−0.196	1.000	−0.052
TAA	−0.870	−0.748	−0.051	1.000
Correlation using both <i>Typha angustifolia</i> and <i>Phragmites australis</i>				
	Photosynthetic rate	Biomass	N content	TAA
Photosynthetic rate	1.000	0.882	0.771	−0.555
Biomass	0.882	1.000	0.806	−0.406
N content	0.771	0.806	1.000	−0.155
TAA	−0.555	−0.406	−0.155	1.000

and they were not presented here.

Aeration significantly increased the nitrogen content of *T. angustifolia* (Fig. 3) but had no effect on *P. australis*. The N content of plants is an indicator of plant health (Song and Lee 2010) that shows higher values when plants are in good conditions. TAA values are also a good indicator of plant stress; when plants are under stress, the values would rise (Song and Lee 2010). TAA showed no significant aeration effects (Fig. 3). Results indicate that the plants in deep water experienced severe stress, and that this stress was not reduced by aeration. Aeration significantly increased photosynthesis in *T. angustifolia* but not in *P. australis* (Fig. 1B,C). Rates of photosynthesis in both species declined with the increasing water depth, but the extent to which this decrease can be mitigated by other factors determine their respective water depth limits. Correlation matrix shows a clear positive relationship among photosynthetic rate, biomass, and N contents, while TAA results shows negative relationship to other parameters (Table 3). As increased TAA indicates elevated stress of plants (Sairam *et al.* 2000), the results mean that photosynthetic rate, biomass, N contents, and less stressed conditions are positively related. Also *P. australis* shows negative correlation between N content and biomass as N contents of *P. australis* did not change by treatment while biomass significantly decreased by water depth but was not affected by aeration.

In both outdoor and indoor experiments, *T. angustifolia* and *P. australis* showed decreased performance with respect to biomass, nitrogen content, photosynthesis, and TAA with increasing water depth. *P. australis* did not survive in the deepest treatment (70 cm) and showed lower resilience of biomass, nitrogen content, and photosynthesis in most deep and/or aerated treatments compared to *T. angustifolia*. Differential tolerances to changes in water depth and responses to root aeration may underlie the clear zonation of the two species. As *T. angustifolia* and *P. australis* are both very common in wetlands around the world, understanding the causal factors determining their depth distributions will be of great importance for managing or controlling these species.

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