Root growth and anatomy of *Typha domingensis* Pers. related to phosphorus availability

Crescimento e anatomia radiculares de *Typha domingensis* Pers. e sua relação com a disponibilidade de fósforo

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Abstract: Aim: The capacity of macrophytes to colonize large areas is often referred to as dependent of the investment in root system and its capacity to uptake nutrients. This work aimed to evaluate the phosphorus (P) effects on the root growth and anatomy as well as its capacity to uptake this nutrient by the aquatic macrophyte *Typha domingensis*. **Methods:** Plants were grown for 60 days in nutrient solution containing 0, 0.2, 0.4, 0.6 or 0.8 mM of phosphorus. At the end of the experiment, the root length and P root content as well as the root anatomy at the maturation and meristematic zones were evaluated. **Results:** Higher P concentrations increased the uptake of this nutrient and plant dry mass. However, the root length was reduced by higher phosphorus levels. In addition, P increased the proportion of the root cap while reduced the proportion of the procambium at the meristematic zone. Higher phosphorus concentrations reduced the xylem vessel diameter and the proportion of the vascular cylinder at the maturation zone, whereas increased phloem proportion was observed under this condition. Furthermore, higher phosphorus levels reduced the endodermis and exodermis thickness as well as the aerenchyma proportion. **Conclusions:** Therefore, the *T. domingensis* P requirement is fulfilled at 0.4 mM of this nutrient and hypertrophic conditions promote the development of unfavorable root anatomical traits and reduction of the root growth.

Keywords: cattail; eutrophication; macrophyte growth; root meristems.

Resumo: Objetivo: A capacidade das macrófitas, para colonizar grandes áreas é frequentemente relatada como dependente do investimento no sistema radicular e a sua capacidade para absorver nutrientes. Este trabalho teve como objetivo avaliar os efeitos do fósforo no crescimento da raiz, na anatomia radicular e na sua capacidade de absorver este nutriente pela macrófita aquática *Typha domingensis*. **Metodologia:** As plantas foram cultivadas por 60 dias em solução nutritiva contendo 0, 0,2, 0,4, 0,6 ou 0,8 mM de fósforo. Ao final do experimento, o comprimento e conteúdo de P da raiz bem como a sua anatomia nas regiões de maturação e meristemática foram avaliados. **Resultados:** Maiores concentrações de P aumentaram a absorção deste nutriente bem como a massa seca das

plantas. Contudo o comprimento da raiz foi reduzido pelas maiores concentrações de fósforo. Além disso, maiores concentrações de P aumentaram a proporção da coifa e reduziram a proporção de procâmbio na zona meristemática. Ademais, maiores concentrações de fósforo reduziram o diâmetro dos vasos de xilema e a proporção do cilindro vascular na zona de maturação apesar de uma maior proporção de floema ter sido observada nestas condições. A espessura da endoderme e a exoderme bem como a proporção de aerênquima foram reduzidas pelas maiores concentrações de fósforo. **Conclusões:** Portanto, a exigência de fósforo de *T. domingensis* é atingida sob 0,4 mM deste nutriente e condições hipertróficas promovem o desenvolvimento de características desfavoráveis na anatomia e um menor crescimento radicular.

Palavras-chave: taboa; eutrofização; crescimento de macrófitas; meristemas radiculares.

1. Introduction

The eutrophication of wetlands is a problem which arises by the uncontrolled deposition of nutrients on the environment (Zamparas & Zacharias, 2014). This process has been enhanced by the agriculture and other human activities (Johnson & Rejmánková, 2005). The inadequate management of agricultural areas accelerates P transfer from these areas to water environments which lead to eutrophication (Tiecher et al., 2017). Anthropic eutrophication process is also achieved by the disposal of untreated urban sewage (Nyenje et al., 2010). According to Carlson (1977) a eutrophic system is that one with high nutrient concentration. Nonetheless, the trophic classification of a specific lake varies depending of the literature used (Silvino & Barbosa, 2015). The eutrophication by phosphorus (P) can be classified from eutrophic with 0.2 mM of P (White et al., 2000) to hypertrophic environments which show 0.999 mM of P (Steinbachová-Vojtíšková et al., 2006). This classification was already used in studies with the P effects in *Typha domingensis* Pers. (cattail) and was efficient to promote plant responses (Santos et al., 2015; Corrêa et al., 2017a).

The uncontrolled population growth of aquatic macrophytes is often promoted by P eutrophication (Zamparas & Zacharias, 2014). In fact, the growth of *T. domingensis* and other aquatic macrophyte species is prompted by excess P in the environment (Miao et al., 2000; Li et al., 2010; Macek et al., 2010). Likewise, these plants cause problems for communities when growing at eutrophic environments by limiting the growth of other native species (Li et al., 2009; Macek et al., 2010). However, the growth of *T. domingensis* under P eutrophication may not change (Escutia-Lara et al., 2009; 2010) adding issues to understand the P effect in these plants. Furthermore, both phosphorus starvation and its excess promoted limitation to *T. domingensis* growth and photosynthesis (Santos et al., 2015). In addition, the growth of

Typha species may be related to endogenous traits found at particular populations (Corrêa et al., 2015). Higher P levels also change the leaf development of *T. domingensis* and its meristem activity (Corrêa et al., 2017a). Nonetheless, very little is known about the phosphorus uptake by *T. domingensis*; although these plants have potential for the removal of phosphorus from hypertrophic environments (Di Luca et al., 2015). Thus, it is necessary more information regarding the P uptake by *T. domingensis* to understand its effect on the plant growth.

Uncontrolled growth resulting from increased phosphorus availability is often reported for *T. domingensis* (Miao et al., 2000; Li et al., 2010; Macek et al., 2010). This response was related to increased photosynthesis and photosynthetic tissues promoted by phosphorus (Webb & Zhang, 2013; Santos et al., 2015). *Typha domingensis* also enhanced the meristem activity under optimal phosphorus levels (Corrêa et al., 2017a). However, the concentration of this nutrient may cause no effect on *T. domingensis* growth (Escutia-Lara et al., 2009, 2010) as both poor-phosphorus or hypertrophic conditions limit its photosynthesis (Santos et al., 2015) and meristem activity (Corrêa et al., 2017a). However, the optimal phosphorus level for *T. domingensis* remains unclear as no information can be found on previous works detailing the real demand for this nutrient.

Roots are the first organs to face nutrient availability and the root anatomy is related to plant capacity to uptake nutrients (Cruz et al., 2020) and in response to population density (Corrêa et al., 2017b). However, no information is available about the phosphorus effects on the root anatomy of this species.

Therefore, the objective of this work was to evaluate root growth and anatomy of *T. domingensis* exposed to different phosphorus levels. We hypothesized that: a) *Typha domingensis* shows root anatomical adaptations which increase its capacity to uptake phosphorus b) the response of

T. domingensis roots can change depending on the phosphorus availability since higher concentrations may reduce root growth and lower concentrations should prompt plant investment in the root system, c) *Typha domingensis* shows limited P demand and excessive concentrations may promote negative effects.

2. Materials and Methods

2.1. Plant material and experimental design

Typha domingensis plants were collected at southeastern region of Brazil in Alfenas, Minas Gerais State, (21°25'44"S and 45°56'49"W), from natural populations. Plants sampled were comprised of rhizomes (23 cm length and 2.5 cm of diameter), roots and about eight leaves. Plants were grown at greenhouse with nutrient solution (Hoagland & Arnon, 1940) at 40% ionic strength for 60 days in order to obtain acclimatized clone plants. The natural populations were located in small ponds without contact with rivers or larger water bodies (reservoirs or lakes). The water pH was measured with a handheld pHmeter and the mean value was 6.9. The location has a humid temperate climate, CWb type according to Köppen-Geiger classification (Mendes-Júnior et al., 2018; Souza et al., 2018), showing annual rainfall between 1000-1500 mm (Souza et al., 2018) and mean annual temperature of 19.9 °C.

The 60 days-old clone plants were standardized according to size (rhizomes showing about 15 cm in length) and number of leaves (about six leaves); all plants showed good phytosanitary condition and were in vegetative stage. Plants were placed in polypropylene pots (38×53×8 cm) containing 4 L of modified nutrient solution at 40% ionic strength with increasing P levels (0, 0.2, 0.4, 0.6 and 0.8 mM) as proposed by Santos et al. (2015) and showed in Table 1. The experiment was kept under these conditions for 60 days and nutrient solution was replenished fortnightly. Nutrient level was monitored weekly with a handheld condutivimeter (Mettler–Toledo, Greifensee, Switzerland). The modified nutrient solution was

prepared according to Hoagland & Arnon (1940) using the following salts and concentrations: $NH_4H_2PO_4$ (Table 1), KNO_3 (Table 1), $Ca(NO_3)_2$ (Table 1), $Mg(NO_3)_2$ (Table 1), K_2SO_4 (0.1 mM), $FeSO_4 \cdot 7H_2O$ (0.003 mM), H_3BO_3 (0.0025 mM), $MnSO_4 \cdot H_2O$ (0.0002 mM), $ZnSO_4 \cdot 7H_2O$ (0.0002 mM), $CuSO_4 \cdot 5H_2O$ (0.00005 mM), $H_2MoO_4 \cdot H_2O$ (0.00005 mM).

The experimental design was completely randomized with five treatments and six replicates. Each replicate comprised of one plant. Plants were kept at experimental conditions for 60 days.

2..2. Growth analysis

At the end of the experiment, the whole plant dry mass was evaluated in an analytical balance AY220 (Shimadzu, Tokyo, Japan). The dry mass was obtained by drying the plant an oven at 60 °C for 48 h.

2..3. Phosphorus measurement

At the end of the experiment, the P content in roots was measured. Roots were dried at 60 °C for 48 h and then the 500 mg of the dry mass was triturated. Further, samples were digested in 10 mL of HNO_3 for 30 min at 150 °C in a digestion block system. Subsequently, 1.0 mL of $HClO_4$ was added, and the temperature was increased to 210 °C for 20 min. The digested material was then diluted to 25 mL with distilled water, and the P concentration was determined with a Perkin-Elmer Elemental Analyzer 2400 (CHNS/O) (Sarruge & Haag, 1974). A standard solution of $NH_4H_2PO_4$ was used for calibration and the quantification was performed at 22 °C using electrodeless discharge lamps (EDL), the precision of the equipment was 1-2% max error.

2..4. Anatomical analysis and root growth

For the anatomical analysis, fragments of roots (20 mm from the root tip) were fixed in a solution of formaldehyde, acetic acid and 70% ethanol (F.A.A. 70) for 72 h and then stored in 70% ethanol until further analysis (Johansen, 1940). Sections were subjected to increasing ethanol concentrations (70%, 90% and 100%) for 2-h

Table 1. Concentrations of P and N sources in the nutrient solution.

Treatment (P mM)	$NH_4H_2PO_4$ (mM)	KNO_3 (mM)	$Ca(NO_3)_2$ (mM)	$Mg(NO_3)_2$ (mM)	Total N (mM)
0	0	0.80	0.30	0.1	1.6
0.2	0.2	0.70	0.25	0.1	1.6
0.4	0.4	0.60	0.20	0.1	1.6
0.6	0.6	0.40	0.20	0.1	1.6
0.8	0.8	0.30	0.15	0.1	1.6

intervals. The samples were embedded in historesin according to the manufacturer's instruction (Leica Microsystems, Wetzlar, Germany). Sections (8 μm thick) were obtained using a semi-automated rotary microtome Yidi YD-335 (JinhuaYidi Medical Appliance CO., LTD, Zhejiang, China) and then stained with toluidine blue O according to O'Brien et al. (1964). The slides were photographed using a trinocular microscope attached to an image capture system CX31 (Olympus, Tokyo, Japan). For each replicate, five sections and five fields were evaluated. The UTHSCSA-Imagetool software was used for image analysis. We measured the following parameters: exodermis thickness, diameter of xylem vessel elements, the proportion of xylem in the vascular cylinder, the proportion of phloem xylem in the vascular cylinder, aerenchyma area and gray level in endodermis cell walls, the proportion of protodermis, the proportion of procambium, the proportion of ground meristem and the proportion of root cap in the root apex.

Roots were randomly sampled and the root length of five roots were measured per replicate using a digital caliper.

2..5. Statistical analysis

Statistical analyses were performed using the SISVAR 5.0 software (Ferreira 2011). Prior to parametric analysis, data were tested for normal distribution using the Shapiro–Wilk test. Further, data were subjected to analysis of variance and means compared by the Scott–Knott test at 5% probability. When regression analyses showed significant adjustment these models were preferred due to the quantitative nature of treatments. Curve adjustment was considered significant when p-values were ≤0.05 for the "x^2" and "x" parameters in the equations: $Y = ax + b$ for linear and $Y = ax^2 + bx + c$ for quadratic model. The R^2 parameter was considered significant when ≥0.6. When both linear and quadratic curves showed significant adjustment, the linear model was preferred. The predictor variable was the P concentration in the growth solution and response variables were: plant dry mass, root length, P content in the root, exodermis thickness, aerenchyma area, shades of gray on endodermis cell walls, diameter of xylem vessels, xylem proportion in the vascular cylinder, phloem proportion in the vascular cylinder, root cap proportion, procambium proportion, protodermis proportion and ground meristem proportion.

3. Results

Higher phosphorus concentrations increased the dry mass production of *T. domingensis* (Figure 1a) but decreased its root length (Figure 1b). In addition, higher P concentrations increased its uptake by *T. domingensis* (Figure 2).

The proportion of tissues and meristems on the root tip were changed by phosphorus. The root cap proportion increased in all P treatments as compared to the one lacking this nutrient (Table 2).
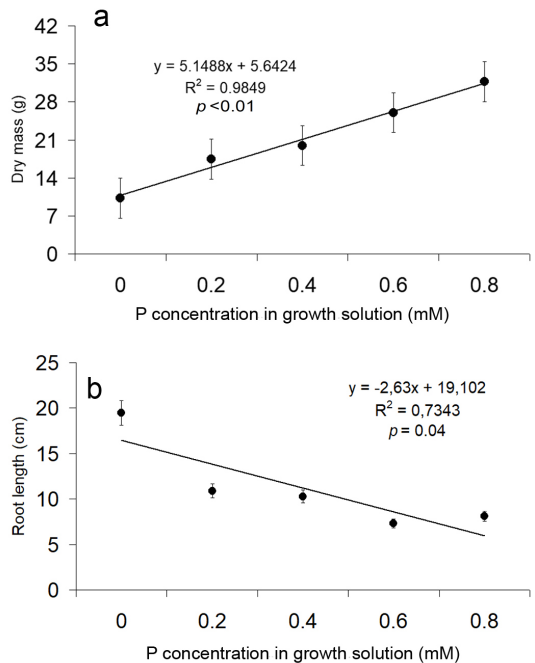
Figure 1. Dry mass and root length of *T. domingensis* plants grown under different phosphorus levels in the nutrient solution. Bars= standard error.
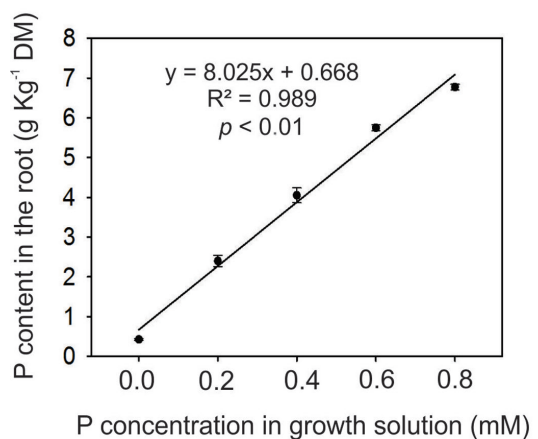
Figure 2. Phosphorus accumulation by *T. domingensis* roots grown under different phosphorus levels in the nutrient solution. Bars= standard error.

Table 2 Anatomical traits of root meristems of *T. domingensis* grown under different phosphorus concentrations. Data is shown as mean ± standard deviation. Means followed by the same letter in rows do not differ by the Scott-Knott test to P<0.05.

| Phosphorus concentration in growth solution (mM)	Root cap (%)	Procambium (%)	Protodermis (%)	Ground meristem (%)
0	6.38 ± 0.6 b	19.64 ± 0.9 a	8.45 ± 2.4 a	66.11± 1.9 b
0.2	8.70 ± 1.3 a	16.21 ± 0.4 b	4.80 ± 2.3 a	71.51 ± 2.4 a
0.4	10.03 ± 2.6 a	17.12 ± 1.1 b	4.85 ± 2.6 a	68.16 ± 3.8 b
0.6	10.19 ± 2.4 a	15.03 ± 1.4 b	6.77 ± 3.4 a	64.72 ± 2.3 b
0.8	9.23 ± 1.6 a	12.51 ± 1.9 b	5.00 ± 2.7 a	72.83 ± 4.9 a

However, the absence of phosphorus increased the procambium proportion whereas no effect was found for the protodermis and the ground meristem showed higher proportion under 0.2 and 0.8 mM of P (Table 2).

The root anatomy of *T. domingensis* shows one layered epidermis containing very thin cuticle and no trichomes. The cortex is comprised of three parts: external cortex with three layers of thick-walled parenchyma cells and no intercellular spaces; the middle cortex shows large aerenchyma chambers and parenchyma cells; the innermost part of the cortex shows two layers of parenchyma with no intercellular spaces and the one-layered endodermis with Casparian strips. The vascular cylinder shows two layers of pericycle and intercalary xylem and phloem vessels, the central part of the vascular cylinder is comprised of parenchymal pith. This overall structure was not changed by any P level but morphometric differences on tissue traits were found (Figure 3, 4 and 5).

The exodermis thickness was reduced by increasing phosphorus levels until 0.6 mM but curve tendency shows increased means for higher concentrations (Figure 4A). The aerenchyma proportion increased under 0.2 and 0.4 mM of P whereas it reduced under 0.6 and 0.8 mM or higher levels of this nutrient (Fig. 3 and 4B). In addition, the endodermis cell wall was also changed by higher P levels as showed by its higher gray levels (Fig. 4C and 5) which indicate a lower density. The diameter of xylem vessel elements was increased under 0.2 and 0.4 mM of P but was reduced at higher concentrations (Fig. 4D). However, the xylem proportion on the vascular cylinder was reduced by phosphorus whereas the proportion of the phloem was increased by higher P concentrations (Figure 3, 4E and 4F and 5).

4. Discussion

The root responses to phosphorus concentrations found in this work are important to give insight on the growth of *T. domingensis* under phosphorus eutrophication. The nutrient solution (Hoagland & Arnon, 1940) provides a eutrophic condition when the recommended P concentration is used (0.4 mM) and, in this work, we reduced this concentration by a half (0.2 mM) and then to zero, keeping plants under these conditions by 60 days. However, according to White et al. (2000) the concentration of 0.2 mM can also be considered as eutrophic. Further investigation is necessary to elucidate the P demand between zero and 0.2 mM of P focusing in lower concentrations. We showed that the phosphorus uptake by *T. domingensis* increases under higher concentrations of this nutrient without a clear limitation for its uptake. The curve equation showed in Figure 2 demonstrated that P accumulation increases proportionally to its concentration in the nutrient solution. This uncontrolled uptake promotes excess P levels to plants, causing limitation to a number of plant metabolic processes. In fact, excess phosphorus was recently reported to mediate ethylene-induced negative responses to plant growth (Shukla et al., 2017). In addition, Corrêa et al. (2017a) showed lower meristem activity in leave of *T. domingensis* grown under P hypertrophic levels. The reduction of the net photosynthesis and development of thinner leaves were also reported by excessive P in *T. domingensis*. The negative responses of excess phosphorus are still barely understood but it raises questions on the eutrophication-stimulated growth. Our results and the consulted literature show a limit to the enhanced growth promoted by phosphorus to *T. domingensis* what may also be truth for other species and should be explored on further works.
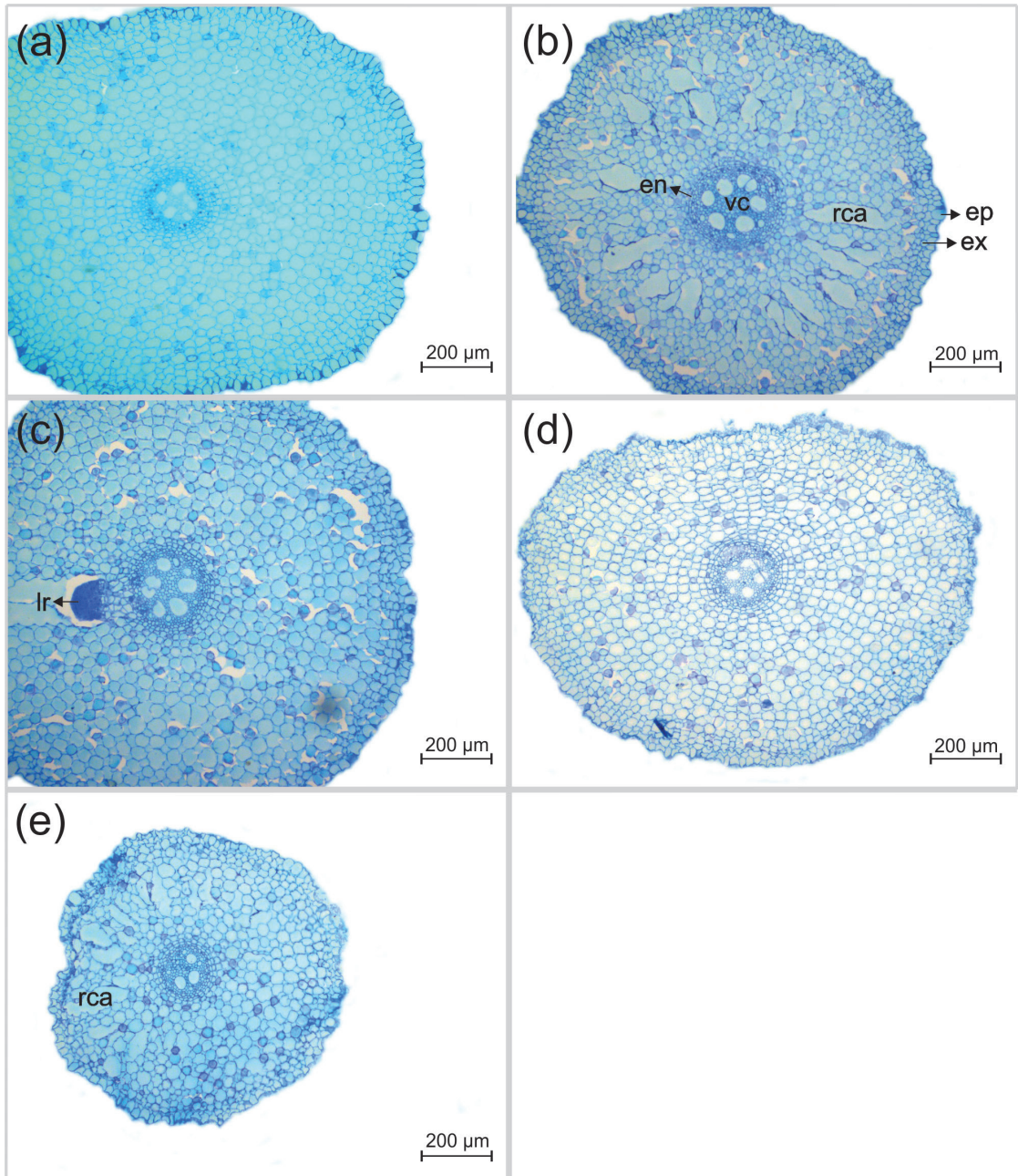
Figure 3. Root anatomical modifications of *T. domingensis* plants grown under different phosphorus levels on the nutrient solution. (a)= 0.0; (b) = 0.2; (c) = 0.4; (d) = 0.6; (e) = 0.8 mM of phosphorus. ep = epidermis, ex = exodermis, en = endodermis, rca = root cortical aerenchyma, vc = vascular cylinder, lr = lateral root.

The changes in the root architecture in response to phosphorus are scarcely investigated (Strieder et al., 2017). There are plants which can enhance the root growth under phosphorus deficiency (Dissanayaka et al., 2017) whereas sensitive plants such as *Arabidopsis thaliana* shows reduced root growth under poor phosphorus condition (Strieder et al., 2017). Phosphorus is required by plants at high concentrations because it is an essential macronutrient as the element is part of key molecules such as DNA and RNA nucleotides and is essential to energy metabolism (Heuer et al., 2017). *Typha domingensis* showed the ability to invest on the root system under poor P levels. The mechanism of phosphorus signaling that stimulates root growth is still unclear whereas lower concentrations of the element increased meristem activity on leaves (Corrêa et al., 2017a)
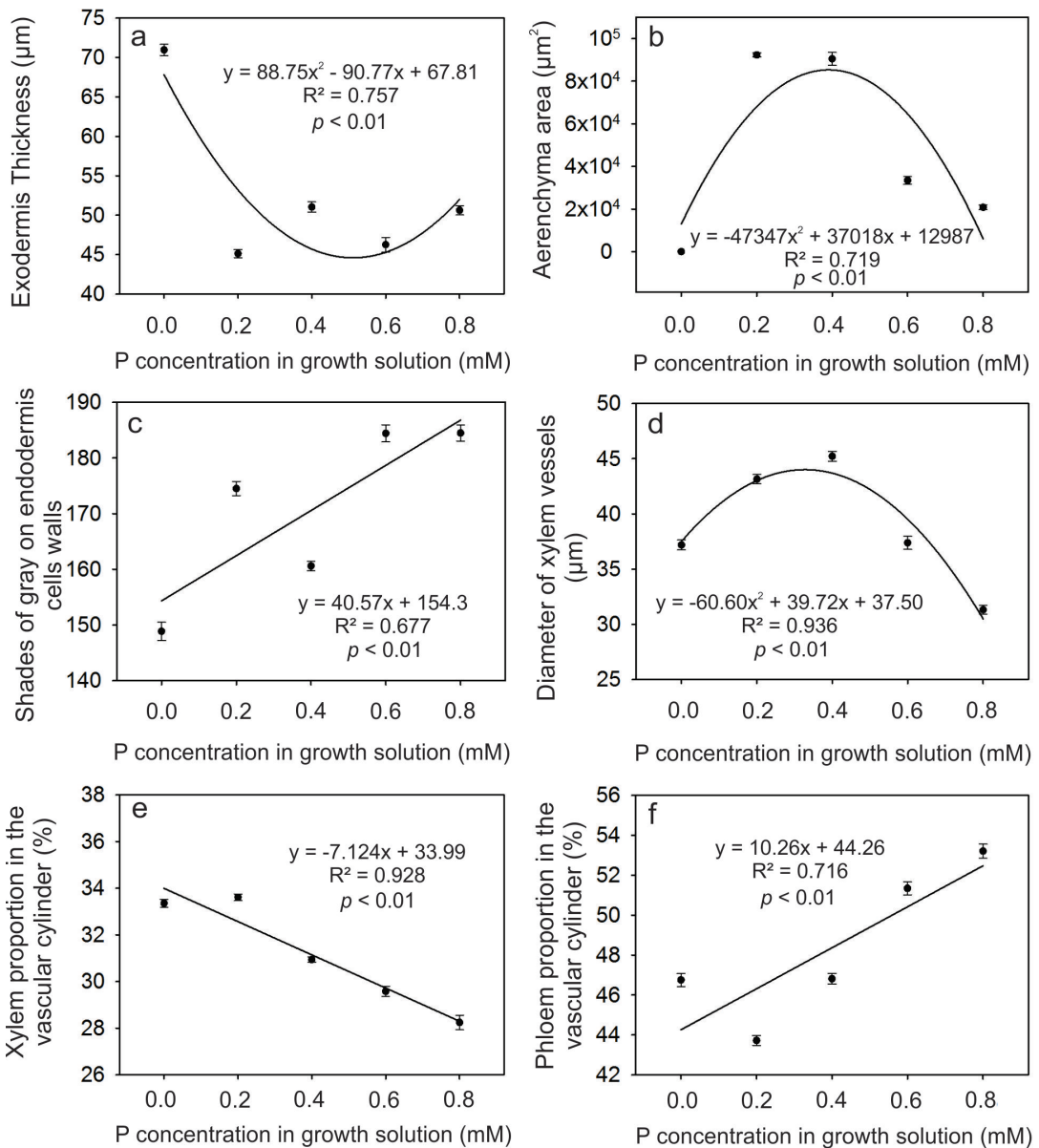
Figure 4. Micromorphometry of root tissues from *T. domingensis* plants grown under different phosphorus levels on the nutrient solution. Bars= standard deviation.

and similar responses may be present on the roots. *Typha domingensis* seems to be tolerant to poor phosphorus condition because it can survive and maintain the photosynthetic activity passed 60 days under P starvation (Santos et al., 2015). These results support the hypothesis that *T. domingensis* demand for phosphorus is not too high. This species showed potential for the phytoremediation of industrial wastewater (Hegazy et al., 2011) and potential toxic elements such as Cd (Oliveira et al., 2018). This plant is referred for the remediation

of sewage disposals because of its high capacity to uptake phosphorus. All *T. domingensis* plants survived under hypertrophic P levels and may thrive in P remediation systems, when its high capacity to uptake P is considered, this species shows high potential for P remediation.

The modifications on the root anatomy of *T. domingensis* supports that meristematic responses modulate root growth in response to phosphorus. The root cap is a protective structure which can produce mucilage to constrain metal uptake
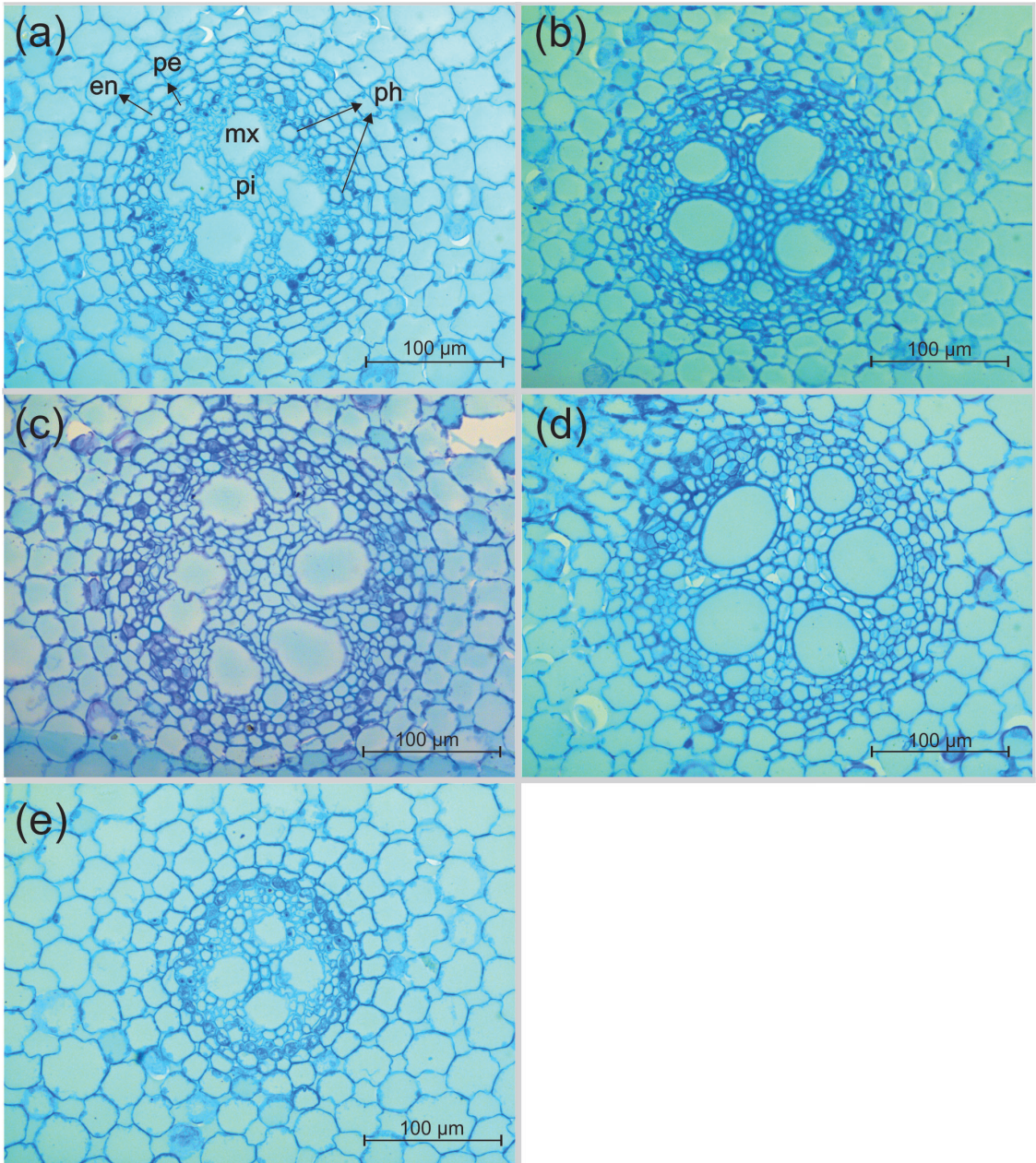
Figure 5. Anatomical modifications of *T. domingensis* vascular cylinder developed under different phosphorus levels on the nutrient solution. (a)= 0.0; (b) = 0.2; (c) = 0.4; (d) = 0.6; (e) = 0.8 mM of phosphorus. en = endodermis, pe = pericycle, pi = pith, mx = metaxylem, ph = phloem.

(Cai et al., 2013). This protective role of the root cap may explain its larger proportion under higher phosphorus levels. Procambium is the meristem related to the development of vascular tissues (Zeng et al., 2016). Therefore, a higher proportion of procambium in plants growing under P starvation may be related to increased investment on xylem which main function is the transport of water and nutrients.

The ground meristem is related to the development of the root cortex and aerenchyma,

which is a key tissue for aquatic macrophytes (Corrêa et al., 2017b). The higher proportion of the ground meristem found under moderate P levels was important for adequate root development. The higher proportion of the ground meristem at 0.2 and 0.8 mM suggests similar responses from both poor and excess phosphorus levels to aerenchyma development. This result is supported by the analysis of leaf meristems from *T. domingensis* grown under low and high phosphorus concentrations (Corrêa et al., 2017a). Thus, modifications of

T. domingensis root anatomy show that phosphorus starvation may prompt plant investment on procambium and ground meristem enhancing P absorption and aerenchyma development.

The larger xylem vessel diameter is related to a higher efficiency on water and nutrient conductances (Sperry et al., 2008). *Typha domingensis* showed larger xylem vessels at lower phosphorus concentrations favoring the transport of this nutrient to shoots. However, excess phosphorus reduced xylem's hydraulic capacity as well as the proportion of this tissue on the vascular cylinder. These results support the hypothesis that excess phosphorus may be negative to this species due to its moderate demand for this nutrient. The minimum P demand by *T. domingensis* must be further investigated using concentrations between zero and 0.2 mM. Both xylem and phloem tissues develop after the procambium (Zeng et al., 2016), as the whole vascular cylinder develops from the same meristem, a lower xylem proportion at higher P levels increases the phloem percentage since the sum of both tissues complements the whole structure.

Root endodermis and exodermis are called apoplastic barriers for pollutants as a consequence of the suberin deposition in cell walls which become hydrophobic (Ribeiro et al., 2015). The higher gray level of endodermis cell wall indicates lower density and may be a consequence of poor suberin deposition favoring phosphorus uptake. In addition, exodermis was strongly reduced by all concentrations of phosphorus which diminished this apoplastic barrier. Therefore, the root of *T. domingensis* is permeable to phosphorus permitting its excessive uptake.

As a consequence of excessive or poor phosphorus concentrations, lower aerenchyma development was found on plants at higher levels of the nutrient. It is well known that aerenchyma development is stimulated at poor phosphorus conditions (Coelho et al., 2006; Vejchasarn et al., 2016; Diaz et al., 2018) and excess phosphorus may limit the development of this tissue on some species. The aerenchyma is a key tissue for *Typha* species in order to diffuse air and oxygen throughout the root (Corrêa et al., 2015). Thus, reduced aerenchyma development under excess or limited phosphorus concentrations may limit *T. domingensis* metabolism and growth. The aerenchyma is required for the oxygenation of root tissues under low O_2 conditions (hypoxia) which are found in aquatic environments (Voesenek and Bailey-Serres, 2015; Duarte et al., 2021). Thus, the reduction of aerenchyma proportion under hypertrophic conditions may have limited internal gas diffusion damaging *T. domingensis* aerobic metabolism. The aerenchyma is also important for the gaseous releases by *T. domingensis* roots since it was showed to be related to radial oxygen loss (Duarte et al., 2021) which is an important process for other aerobic organisms in aquatic environments.

5. Conclusions

Typha domingensis show high capacity for phosphorus uptake due to root anatomical traits such as poor development of apoplastic barriers and large xylem vessel diameter. Poor phosphorus condition promotes root growth in *T. domingensis* which also invest on vascular tissues under this condition. Excess phosphorus constrains the development of aerenchyma and xylem limiting root growth. The growth of *T. domingensis* may be prompted at eutrophic P levels in the environment, however, at hypertrophic conditions lower growth rates may be expected as this species thrives but suffer limitations at excessive P concentrations.

Acknowledgements

References

CAI, M., WANG, N., XING, C., WANG, F., WU, K. and DU, X. Immobilization of aluminum with mucilage secreted by root cap and root border cells is related to aluminum resistance in *Glycine max* L. *Environmental Science and Pollution Research International*, 2013, 20(12), 8924-8933. http://dx.doi.org/10.1007/s11356-013-1815-6. PMid:23749363.

CARLSON, R.E. A trophic state index for lakes. *Limnology and Oceanography*, 1977, 22(2), 361-369. http://dx.doi.org/10.4319/lo.1977.22.2.0361.

CORRÊA, F.F., MADAIL, R.H., BARBOSA, S., PEREIRA, M.P., CASTRO, E.M., SORIANO, A.C.T.G. and PEREIRA, F.J. Anatomy and physiology of cattail as related to different population

densities. *Planta Daninha*, 2015, 33(1), 1-12. http://dx.doi.org/10.1590/S0100-83582015000100001.

CORRÊA, F.F., PEREIRA, M.P., KLOSS, R.B., CASTRO, E.M. and PEREIRA, F.J. Leaf ontogeny and meristem activity of *Typha domingensis* Pers. (Typhaceae) under different phosphate concentrations. *Aquatic Botany*, 2017a, 136, 43-51. http://dx.doi.org/10.1016/j.aquabot.2016.09.007.

CORRÊA, F.F., PEREIRA, M.P., MADAIL, R.H., SANTOS, B.R., BARBOSA, S., CASTRO, E.M. and PEREIRA, F.J. Anatomical traits related to stress in high density populations of *Typha angustifolia* L. (Typhaceae). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2017b, 77(1), 52-59. http://dx.doi.org/10.1590/1519-6984.09715. PMid:27382995.

COELHO, G.T.C., SOUZA, I.R.P., CARNEIRO, N.P., SCHAFFERT, R.E., BRANDÃO, R.A.L., ALVES, V.M.C., PAIVA, L.V. and CARNEIRO, A.A. Formação de aerênquima em raízes de milho sob estresse de fósforo. *Revista Brasileira de Milho e Sorgo*, 2006, 5(3), 443-449. http://dx.doi.org/10.18512/1980-6477/rbms.v5n3p443-449.

CRUZ, Y.C., SCARPA, A.L.M., PEREIRA, M.P., CASTRO, E.M. and PEREIRA, F.J. Root anatomy and nutrient uptake of the cattail *Typha domingensis* Pers. (Typhaceae) grown under drought condition. *Rhizosphere*, 2020, 16, 100253. http://dx.doi.org/10.1016/j.rhisph.2020.100253.

DÍAZ, A.S., AGUIAR, G.M., PEREIRA, M.P., DE CASTRO, E.M., MAGALHÃES, P.C. and PEREIRA, F.J. Aerenchyma development in different root zones of maize genotypes under water limitation and different phosphorus nutrition. *Biologia Plantarum*, 2018, 62(3), 561-568. http://dx.doi.org/10.1007/s10535-018-0773-8.

DI LUCA, G.A., MAINE, M.A., MUFARREGE, M.M., HADAD, H.R. and BONETTO, C.A. Influence of *Typha domingensis* in the removal of high P concentrations from water. *Chemosphere*, 2015, 138, 405-411. http://dx.doi.org/10.1016/j.chemosphere.2015.06.068. PMid:26149856.

DISSANAYAKA, D.M.S.B., MARUYAMA, H., NISHIDA, S., TAWARAYA, K. and WASAKI, J. Landrace of japonica rice, Akamai exhibits enhanced root growth and efficient leaf phosphorus remobilization in response to limited phosphorus availability. *Plant and Soil*, 2017, 414(1-2), 327-338. http://dx.doi.org/10.1007/s11104-016-3129-1.

DUARTE, V.P., PEREIRA, M.P., CORRÊA, F.F., CASTRO, E.M. and PEREIRA, F.J. Aerenchyma, gas diffusion, and catalase activity in *Typha domingensis*: a complementary model for radial oxygen loss. *Protoplasma*, 2021, 258(4), 765-777. http://dx.doi.org/10.1007/s00709-020-01597-8. PMid:33404920.

ESCUTIA-LARA, Y., GÓMEZ-ROMERO, M. and LINDIG-CISNEROS, R. Nitrogen and phosphorus effect on *Typha domingensis* Pers. rhizome growth in a matrix of *Schoenoplectus americanus* (Pers.) Volkart ex Schinz and Keller. *Aquatic Botany*, 2009, 90(1), 74-77. http://dx.doi.org/10.1016/j.aquabot.2008.06.002.

ESCUTIA-LARA, Y., DE LA BARRERA, E., MARTÍNEZ DE LA CRUZ, Y. and LINDIG-CISNEROS, R. Respuesta a la adición de nitrógeno y fósforo en el crecimiento de *Typha domingensis* y *Schoenoplectus americanus*. *Boletín de la Sociedad Botánica de México*, 2010, 87, 83-87. http://dx.doi.org/10.17129/botsci.307.

FERREIRA, D.F. Sisvar: a computer statistical analysis system. *Ciência e Agrotecnologia*, 2011, 35(6), 1039-1042. http://dx.doi.org/10.1590/S1413-70542011000600001.

JOHANSEN, D.A. *Plant microtechinique*. 2nd ed. New York: Mc Graw-Hill, 1940.

JOHNSON, S. and REJMÁNKOVÁ, E. Impacts of land use on nutrient distribution and vegetation composition of freshwater wetlands in Northern Belize. *Wetlands*, 2005, 25(1), 89-100. http://dx.doi.org/10.1672/0277-5212(2005)025[0089:IOLUON]2.0.CO;2.

HEGAZY, A.K., ABDEL-GHANI, N.T. and EL-CHAGHABY, G.A. Phytoremediation of industrial wastewater potentiality by *Typha domingensis*. *International Journal of Environmental Science and Technology*, 2011, 8(3), 639-648. http://dx.doi.org/10.1007/BF03326249.

HEUER, S., GAXIOLA, R., SCHILLING, R., HERRERA-ESTRELLA, L., LÓPEZ-ARREDONDO, D., WISSUWA, M., DELHAIZE, E. and ROUACHED, H. Improving phosphorus use efficiency: a complex trait with emerging opportunities. *The Plant Journal*, 2017, 90(5), 868-885. http://dx.doi.org/10.1111/tpj.13423. PMid:27859875.

HOAGLAND, D.R. and ARNON, D.I. Crop production in artificial culture solutions and in soils with special reference to factors influencing yield absorption of inorganic nutrients. *Soil Science*, 1940, 50, 463-483.

LI, S., MENDELSSOHN, I.A., CHEN, H. and OREM, W.H. Does sulphate enrichment promote the expansion of *Typha domingensis* (cattail) in the Florida Everglades? *Freshwater Biology*, 2009, 54(9), 1909-1923. http://dx.doi.org/10.1111/j.1365-2427.2009.02242.x.

LI, S., LISSNER, J., MENDELSSOHN, I., BRIX, H., LORENZEN, B., MCKEE, K.L. and MIAO, S. Nutrient and growth responses of cattail (*Typha domingensis*) to redox intensity and phosphate availability. *Annals of Botany*, 2010, 105(1), 175-

184. http://dx.doi.org/10.1093/aob/mcp213. PMid:19748907.

MACEK, P., REJMÁNKOVÁ, E. and LEPŠ, J. Dynamics of *Typha domingensis* spread in *Eleocharis* dominated oligotrophic tropical wetlands following nutrient enrichment. *Evolutionary Ecology*, 2010, 24(6), 1505-1519. http://dx.doi.org/10.1007/s10682-010-9397-y.

MENDES JÚNIOR, H., TAVARES, A.S., SANTOS JÚNIOR, W.R. and MINCATO, R.L. Water erosion in oxisols under coffee cultivation. *Revista Brasileira de Ciência do Solo*, 2018, 42, e0170093. http://dx.doi.org/10.1590/18069657rbcs20170093.

MIAO, S., NEWMAN, S. and SKLAR, F.H. Effects of habitat nutrients and seed sources on growth and expansion of *Typha domingensis. Aquatic Botany*, 2000, 68(4), 297-311. http://dx.doi.org/10.1016/S0304-3770(00)00127-3.

NYENJE, P.M., FOPPEN, J.W., UHLENBROOK, S., KULABAKO, R. and MUWANGA, A. Eutrophication and nutrient release in urban areas of sub-Saharan Africa - A review. *The Science of the Total Environment*, 2010, 408(3), 447-455. http://dx.doi.org/10.1016/j.scitotenv.2009.10.020. PMid:19889445.

O'BRIEN, T.P., FEDER, N. and MCCULLY, M.E. Polychromatic staining of plant cell walls by Toluidine Blue. *Protoplasma*, 1964, 59(2), 368-373. http://dx.doi.org/10.1007/BF01248568.

OLIVEIRA, J.P.V., PEREIRA, M.P., DUARTE, V.P., CORRÊA, F.F., CASTRO, E.M. and PEREIRA, F.J. Cadmium tolerance of *Typha domingensis* Pers. (Typhaceae) as related to growth and leaf morphophysiology. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2018, 78(3), 509-516. http://dx.doi.org/10.1590/1519-6984.171961. PMid:29995113.

RIBEIRO, E.S., PEREIRA, M.P., CASTRO, E.M., BARONI, G.R., CORRÊA, F.F. and PEREIRA, F.J. Relações da anatomia radicular na absorção, no acúmulo e na tolerância ao chumbo em *Echinodorus grandiflorus*. *Revista Brasileira de Engenharia Agrícola e Ambiental*, 2015, 19(6), 605-612. http://dx.doi.org/10.1590/1807-1929/agriambi.v19n6p605-612.

SANTOS, K.R., PEREIRA, M.P., FERREIRA, A.C.G., RODRIGUES, L.C.A., CASTRO, E.M., CORRÊA, F.F. and PEREIRA, F.J. *Typha domingensis* Pers. Growth responses to leaf anatomy and photosynthesis as influenced by phosphorus. *Aquatic Botany*, 2015, 122, 47-53. http://dx.doi.org/10.1016/j.aquabot.2015.01.007.

SARRUGE, J.R. and HAAG, H.P. *Análises químicas em plantas*. Piracicaba: ESALQ, 1974.

SHUKLA, D., RINEHART, C.A. and SAHI, S.V. phosphate response reveals ethylene mediated signaling that negatively regulates plant growth and development. *Scientific Reports*, 2017, 7(1), 3074. http://dx.doi.org/10.1038/s41598-017-03061-9. PMid:28596610.

SILVINO, R.F. and BARBOSA, F.A.R. Eutrophication potential of lakes: an integrated analysis of trophic state, morphometry, land occupation, and land use. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2015, 75(3), 607-615. http://dx.doi.org/10.1590/1519-6984.18913. PMid:26292101.

SOUZA, P.H., SANCHES, R.G. and SANTOS, B.C. Índices climáticos e chuvas intensas no município de alfenas/mg no período de 1984-2016. *Edição Especial Dossiê Climatologia de Minas Gerais*, 2018, 14, 320-341.

SPERRY, J.S., MEINZER, F.C. and MCCULLOH, K.A. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant, Cell & Environment*, 2008, 31(5), 632-645. http://dx.doi.org/10.1111/j.1365-3040.2007.01765.x. PMid:18088335.

STEINBACHOVÁ-VOJTÍŠKOVÁ, L., TYLOVÁ, E., SOUKUP, A., NOVICKÁ, H., VOTRUBOVÁ, O., LIPAVSKÁ, H. and ČÍŽKOVÁ, H. Influence of nutrient supply on growth carbohydrate, and nitrogen metabolic relations in *Typha angustifolia. Environmental and Experimental Botany*, 2006, 57(3), 246-257. http://dx.doi.org/10.1016/j.envexpbot.2005.06.003.

STRIEDER, M.L., PINTO, K.G., BERTOLDI, C., DE SCHNEIDER, A.B. and DELATORRE, C.A. Response of *Arabidopsis thaliana* root growth to phosphorus and its relation to media chemical composition. *Biologia Plantarum*, 2017, 61(3), 587-594. http://dx.doi.org/10.1007/s10535-017-0713-z.

TIECHER, T., SCHENATO, R.B., SANTANNA, M.A., CANER, L. and SANTOS, D.R. Phosphorus forms in sediments as indicators of anthropic pressures in an agricultural catchment in southern Brazil. *Revista Brasileira de Ciência do Solo*, 2017, 41(0), e0160569. http://dx.doi.org/10.1590/18069657rbcs20160569.

VEJCHASARN, P., LYNCH, J.P. and BROWN, K.M. Genetic Variability in Phosphorus Responses of rice root Phenotypes. *Rice (New York, N.Y.)*, 2016, 9(1), 1-16. http://dx.doi.org/10.1186/s12284-016-0102-9. PMid:27294384.

VOESENEK, L.A.C.J. and BAILEY-SERRES, J. Flood adaptive traits and processes: an overview. *The New Phytologist*, 2015, 206(1), 57-73. http://dx.doi.org/10.1111/nph.13209. PMid:25580769.

WEBB, J. and ZHANG, X. Organ-disparate allocation of plasticity in phosphorus response as and underlying mechanism for the sawgrass-to-cattail habitat shift in Florida Everglades wetlands. *International Journal of Plant Sciences*, 2013, 174(5), 779-790. http://dx.doi.org/10.1086/670236.

WHITE, J.S., BAYLEY, S.R. and CURTIS, P.J. Sediment storage of phosphorus in a northern prairie wetland receiving municipal and agro-industrial wastewater. *Ecological Engineering*, 2000, 14(1-2), 127-138. http://dx.doi.org/10.1016/S0925-8574(99)00024-5.

ZAMPARAS, M. and ZACHARIAS, I. Restoration of eutrophic freshwater by managing internal nutrient loads. *The Science of the Total Environment*, 2014, 496, 551-562. http://dx.doi.org/10.1016/j.scitotenv.2014.07.076. PMid:25108796.

ZENG, M., HU, B., LI, J., ZHANG, G., RUAN, Y., HUANG, H., WANG, H. and XU, L. Stem cell lineage in body layer specialization and vascular patterning of rice root and leaf. *Science Bulletin*, 2016, 61(11), 847-858. http://dx.doi.org/10.1007/s11434-015-0849-1.

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