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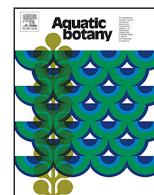

Leaf ontogeny and meristem activity of *Typha domingensis* Pers. (Typhaceae) under different phosphate concentrations

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ABSTRACT

Phosphorus eutrophication may promote increased growth, photosynthesis, and shoot investment in cattail (*Typha domingensis*). However, its influence in early leaf development and meristem traits remains unclear. Therefore, this work aimed to evaluate the effects of phosphate levels on meristem structure and activity as well as tissue differentiation during the leaf development of *T. domingensis*. Plants were subjected to modified nutrient solutions containing three phosphate concentrations. The leaves were collected daily for 7 days, and were used to evaluate growth, meristem characteristics and tissue differentiation. In addition, phosphorus content was measured in roots and rhizomes exposed to phosphate treatments. The leaf primordia cultured in 0.4 and 0.8 mM phosphate levels showed a larger proportion of ground meristem than those grown in 0.1 mM. The procambium proportion was higher under 0.8 mM phosphate when compared to other concentrations. However, the proportion of protodermis was greater in 0.1 mM phosphate when compared to 0.4 and 0.8 mM. In addition, leaf primordia submitted to 0.4 and 0.8 mM phosphate increased meristem cell production. These primordia also showed fewer dividing cells and shorter cell cycle as compared to 0.1 mM phosphate. The development of aerenchyma and palisade parenchyma was promoted by greater phosphate concentrations. Higher aerenchyma proportion was found in plants from 0.8 mM phosphate treatment. Phosphorus content was higher in root than rhizomes for plants grown at 0.4 and 0.8 mM of phosphate. Likewise, the higher phosphate concentrations increased P levels in both roots and rhizomes. Therefore, optimal phosphorus levels promote the development of leaves with a higher photosynthetic potential, which may contribute to the uncontrolled growth of cattail under phosphorus eutrophication.

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1. Introduction

Typha species colonize wetlands all over the world (Svengsouk and Mitsch, 2001), showing high growth potential and creating environmental and biodiversity problems (Santos-Neves et al., 2011). The increased population growth of *Typha domingensis* may reduce the abundance of other macrophytes, such as *Cladium jamaicense* (Li et al., 2009), *Eleocharis* spp. (Macek et al., 2010) and *Schoenoplectus americanus* (Escutia-Lara et al., 2009).

This intense colonization capacity of *T. domingensis* is related to increased nutrient levels in wetlands, mainly phosphorus (P) (Miao et al., 2000; Li et al., 2010; Macek et al., 2010). This process, beginning with the nutrient deposition and further consequences to environmental chemistry and macrophyte colonization, is called "eutrophication" (Zamparas and Zacharias, 2014). Eutrophication may be a natural step in wetlands, but anthropic activities, such as agriculture, enhance its occurrence (Johnson and Rejmánková, 2005).

Phosphorus is often related to eutrophic environments; however, different concentrations are reported in these situations. White et al. (2000), classified environments with 0.2 mM as eutrophic. Likewise, Steinbachová-Vojtíšková et al. (2006) considered environments with 0.999 mM to be hypertrophic. However, concentrations of 25 mg L^{-1} have also been reported to be hypertrophic (Wang et al., 2013). Despite different classification criteria for P eutrophic wetlands, most works show that increased P can change macrophyte physiology and morphology (Al-Hamdani and Sirna, 2008; Wang et al., 2013). Likewise, changes in the leaf biomass allocation, photosynthesis, respiration, protein and RNA content, and palisade parenchyma of *T. domingensis* have been reported when the plant is cultured in different P levels (Webb and Zhang, 2013; Santos et al., 2015).

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As demonstrated by Koteyeva et al. (2014), studying leaf ontogeny is essential to understand the photosynthetic metabolism. There can be variations in leaves with the same type of photosynthetic system. All of these modifications are related to leaf function and may lead to a difference in the plant growth capacity. However, the effect of P on leaf ontogeny is still unclear. Some studies have reported that crop plants grown under P-deficient conditions during early development have smaller and less efficient leaves (Chiera et al., 2002; Kavanová et al., 2006). Furthermore, no information is available regarding the effect of excess P on leaf development. According to Thomaz (2002), studies on macrophyte physiology and anatomy provide key information related to macrophyte control and management. Therefore, understanding the effects of P on leaf ontogeny is essential to determining how this nutrient affects the final leaf structure, ultimately determining plant photosynthesis and growth.

Therefore, the objective of this work was to evaluate the effects of phosphate levels on meristem structure and activity as well as tissue differentiation during the leaf development of *T. domingensis*.

2. Experimental

2.1. Plant propagation and experimental design

Cattail plants (*Typha domingensis* Pers. – Typhaceae) were collected from the natural populations in wetlands located at Alfenas – MG (21° 25′ 44″ S, 45° 56′ 49″ O) in the southeast region of Brazil. The collected plants were comprised of rhizomes (about 25 cm in length and 3 cm in diameter) and approximately ten leaves (1.5 m in length). These plants were subjected to hypochlorite 50% [commercial sodium hypochlorite solution and distilled water (v^{-1}) as the final NaClO concentration was 3% (w v^{-1})] for 10 min and then washed with tap water before further cultivation in the greenhouse. The plants were grown in 60-L plastic pots containing 10 L of a nutrient solution (Hoagland and Arnon, 1940) at 40% ionic strength for 60 d to obtain acclimatized clone plants.

All of the leaves were removed from the clone plants, resulting in rhizomes (10 cm in length, 1.8 cm in diameter and 110 g), which were then grown in modified Hoagland and Arnon (1940) nutrient solution at 40% ionic strength for further leaf primordia sampling. Hoagland and Arnon (1940) nutritive solution contains the following salts: $NH_4H_2PO_4$, $Ca(NO_3)_2$, $Mg(NO_3)_2$, KNO_3, K_2SO_4, $FeSO_4{\cdot}7H_2O$, H_2BO_3, $MnSO_4{\cdot}H_2O$, $ZnSO_4{\cdot}7H_2O$, $CuSO_4{\cdot}5H_2O$, and $H_2MoO_4.H_2O$. The composition of the nutrient solution was modified by changing the $NH_4H_2PO_4$ levels. The following three phosphate levels were used in the experiments: normal (0.4 mM) as proposed by Hoagland and Arnon (1940), P-poor solution (0.1 mM) and P-rich solution (0.8 mM). The P-rich solution was considered excessive because it can be classified as hypertrophic (Steinbachová-Vojtíšková et al., 2006; Santos et al., 2015).

Experimental design was completely randomized with three treatments (0.1, 0.4 and 0.8 mM of phosphate) and 14 replicates for the leaf anatomical and growth data. For the P uptake experiment, the design was completely randomized in a factorial 4×2 scheme using four P availabilities (untreated, 0.1, 0.4 and 0.8 mM of phosphate) and the P allocation in two organs (rhizomes and roots). In this last experiment six replicates were performed.

2.2. Shoot sampling

Rhizome fragments containing shoots in development were used for leaf sampling. In *Typha* plants, the shoots are comprised only of leaves that grow imbricate, supporting each other (Kaul, 1974). The samples were collected on a daily basis for the first to seventh day of development. Shoot sampling was controlled by age, checking arising new shoots twice per day and labeling the new ones. Two shoots containing many leaves were collected per day. The sampling was stopped after the seventh day because large, mature-like green leaves containing palisade parenchyma were visible.

2.3. Shoot growth evaluation

The mass of the collected shoots was evaluated immediately after sampling using an analytical precision scale (AY 220, Shimadzu, Japan). The leaf length was evaluated using images captured with a stereomicroscope (SMZ745T, Nikon Imaging, Tokyo, Japan). The analysis was performed using calibrated UTHSCSA-Imagetool software version 3.00 (The University of Texas Health Science Center, San Antonio, Texas, USA). The tallest leaf of the shoot was used for the length measurements. Using the leaf length, the elongation rate was calculated [(length of the seventh-day leaf – length of the first-day leaf)/number of days] as described by Kavanová et al. (2006).

2.4. Anatomical analysis

The collected shoots were fixed in a solution of F.A.A. 70% [formaldehyde, acetic acid and 70% ethanol (ethanol and distilled water v v^{-1}) 1:1:18] for 72 h and then stored in 70% ethanol until further analysis (Johansen, 1940). For the longitudinal sections, the shoots were subjected to increasing ethanol concentrations (70%, 90% and 100%) for 2-h 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 (Jinhua Yidi Medical Appliance CO., LTD, Zhejiang, China). The sections were stained with toluidine blue 1% (m v^{-1}) and mounted on slides with Canada balsam (O'Brien et al., 1964).

The slides were photographed using a trinocular microscope attached to an image capture system (CX31, Olympus, Tokyo, Japan). The images were evaluated using UTHSCSA-Imagetool software. All of the quantitative analyses were performed in the first two leaves found closest to the shoot apical meristem. On the first and second day of development (when the leaves are comprised only of meristems), the proportions of the primary meristems were calculated by measuring the area of the whole leaf, ground meristem, procambium and protodermis. The individual data from each meristem were used to calculate the ground meristem proportion (GMP), protodermis proportion (PDP), and procambium proportion (PCP) by dividing each individual area by the area of the whole leaf. For each phosphate concentration, 30 sections and two microscope fields were evaluated. These data were averaged to each replicate.

On the seventh day of development, the mean mature cell diameter was measured in ground parenchyma, epidermis and vascular bundles (which were already differentiated). In addition, the number of cells in the ground meristem undergoing division (NCD) was evaluated. The mature cell diameter, leaf elongation rate, and number of cells under division were used to calculate the cell production (cell division) rate in the ground meristem (CPGM), protodermis (CPPD) and procambium (CPPC). The length of the cell cycle in ground meristem (CCGM) was also calculated. All the above calculations were performed using the equations proposed by Ivanov and Dubrovsky (1997).

On the seventh day of development, the aerenchyma chamber proportion (ACP) was calculated as a percentage by dividing the total aerenchyma chamber area (ACA) by the whole leaf area (WLA) and multiplying by 100. In addition, the mean of the individual aerenchyma chamber areas (MAC) was measured. For all the variables measured on the seventh day, 20 sections and five microscope

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