Anatomical traits related to stress in high density populations of *Typha angustifolia* L. (Typhaceae)

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Abstract

Some macrophytes species show a high growth potential, colonizing large areas on aquatic environments. Cattail (*Typha angustifolia* L.) uncontrolled growth causes several problems to human activities and local biodiversity, but this also may lead to competition and further problems for this species itself. Thus, the objective of this study was to investigate anatomical modifications on *T. angustifolia* plants from different population densities, once it can help to understand its biology. Roots and leaves were collected from natural populations growing under high and low densities. These plant materials were fixed and submitted to usual plant microtechnique procedures. Slides were observed and photographed under light microscopy and images were analyzed in the UTHSCSA-Imagetool software. The experimental design was completely randomized with two treatments and ten replicates, data were submitted to one-way ANOVA and Scott-Knott test at p<0.05. Leaves from low density populations showed higher stomatal density and index. These modifications on stomatal characteristics were more evident on the leaf abaxial surface. Plants from low density populations showed thicker mesophyll and higher proportion of aerenchymal area. Roots from low density populations showed a higher proportion of the vascular cylinder. Whereas, plants from higher density populations showed greater thickness of the endodermis, exodermis, phloem and root cortex. Higher density populations showed a higher proportion of aerenchymal gaps in the root cortex. Therefore, cattail plants from populations growing under high density population show anatomical traits typical of plants under stress, which promotes the development of less functional anatomical modifications to aquatic environments.

Keywords: anatomical plasticity, cattail, macrophytes, plant handling, eutrophication, stress.

Características anatômicas relacionadas ao estresse em altas densidades populacionais de *Typha angustifolia* L. (Typhaceae)

Resumo

Algumas espécies de macrófitas podem apresentar um elevado potencial de crescimento, colonizando extensas áreas de ambientes aquáticos. O crescimento descontrolado da taboa (*Typha angustifolia* L.) causa problemas para a biodiversidade local e para atividades antrópicas, isso também pode levar à competição e problemas para a própria espécie. Dessa forma, o objetivo desse trabalho foi verificar se ocorrem modificações anatômicas em plantas de *Typha angustifolia* L. de diferentes densidades populacionais, uma vez que essas podem auxiliar na compreensão da biologia dessa espécie. Raízes e folhas de *T. angustifolia* foram coletadas de populações naturais com alto e baixo adensamento populacional. Esse material vegetal foi fixado e submetido a procedimentos usuais de microtécnica vegetal. As lâminas foram observadas e fotografadas em microscopia de luz e as imagens analisadas no software UTHSCSA-Imagetool. O delineamento experimental foi inteiramente casualizado com dois tratamentos e dez repetições, os dados foram submetidos à análise de variância e ao teste de Scott-Knott para p<0,05. As folhas das populações com baixa densidade demonstraram maior densidade e índice estomáticos. Essas características foram mais evidentes na superfície abaxial em comparação com a superfície adaxial. As plantas de populações com baixo adensamento demonstraram maior espessura do mesofilo e área de aerênquima foliar. As raízes das populações com baixo adensamento demonstraram maior proporção do cilindro vascular. Por outro lado, as plantas de populações com alto adensamento demonstraram maior

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espessura da endoderme, exoderme, floema e do córtex nas raízes. Populações de alto adensamento demonstraram maior proporção de aerênquima no córtex radicular. Portanto, plantas de taboa sob alto adensamento populacional estão sob estresse o qual promove o desenvolvimento de modificações anatômicas menos funcionais para os ambientes aquáticos.

Palavras-chave: plasticidade anatômica, taboa, macrófitas, manejo, eutrofização, estresse.

1. Introduction

Macrophytes are a plant group that colonizes water environments. These plants play an important role in water ecosystems, participating in nutrient cycling, organic matter production, eutrophication and pollutant control. Furthermore, they may colonize extensive areas of water bodies and provide shelter and food to animals (Cervi et al., 2009; Pereira et al., 2011).

Macrophytes can have elevated reproductive capacities, being able to achieve intense population growth, which favors the colonization of vast water body areas. This population behavior may damage hydroelectric energy production, river traffic, agricultural irrigation and nautical sports practice (Thomaz, 2002). Cattail population growth, in special, may decrease the size of other macrophyte population, as reported to *Cladium jamaicense* by Li et al. (2009) and *Eleocharis* spp. by Macek et al. (2010). The elevated proliferation capacity of macrophytes may be related to plant genotype, which induce anatomical and external morphology modifications (Pereira et al., 2008; Souza et al., 2009). More competitive macrophytes, for example, exhibit higher leaf production and increased root porosity. These modifications are related to a better use of atmospheric resources and gas diffusion throughout the plant (Insausti et al., 2001; Pierini and Thomaz, 2004).

Anatomical modifications that provide higher competitive capacity may be related to stomata characteristics (Ribeiro et al., 2012), photosynthetic tissue thickness (Boeger et al., 2008; Pengelly et al., 2010), aerenchyma formation (Pereira et al., 2010), root apoplastic barriers (Armstrong et al., 2000; Hameed et al., 2009; Pereira et al., 2011) and vascular tissue characteristics (Vasellati et al., 2001). These characteristics may be related to macrophyte survival in stress conditions or higher photosynthetic capacity and nutrient absorption, which enable higher growth capacities in some plants or populations.

Despite the ecologic importance of macrophytes, most of the studies addressing these species are related to plant systematics and flower surveys. This raises the need for works that better elucidate macrophyte biology (Padial et al., 2008). In these species, for example, the population density may influence intraspecific competition, reducing growth rates (Demirezen et al., 2007). A more complete knowledge of macrophyte biology might assist with macrophytes management, contributing to government decisions, expense reduction and environmental preservation (Thomaz, 2002). Cattail (*Typha angustifolia* L.) is an important macrophyte found throughout Brazilian territory. Cattail is known to exhibit an elevated growth potential, causing problems for management. However, Cattail populations can show different growth capacities, colonizing extensive or reduced areas of environmental water. These growth potentials may be related to anatomical modifications in different *T. angustifolia* populations.

Therefore, the aim of this work was to evaluate anatomical modifications between *T. angustifolia* plants from populations which exhibit different population densities. This knowledge may help to understand the Cattail biology in natural wetlands and how to cope with the problems related to high density species, harmful to local biodiversity and human activities.

2. Material and Methods

Fragments of *T. angustifolia* L. roots and leaves were collected at the Brazilian southeast region of Alfenas, Minas Gerais State, 21° 25' 44" S, 45° 56' 49" W, from populations growing at natural water bodies. These materials were obtained from populations showing high density (which colonize over 50% of the water body), as well as low density populations (which colonize less than 50% of the water body). Root and leaf fragments were collected in healthy condition, showing no necrosis, chlorosis or fungi evidences. Ten samples were obtained from five plants of two populations from high or low densities, totaling ten samples per density type. Root and leaf fragments were fixed immediately after sampling in a solution comprising formaldehyde, acetic acid and ethanol 70% (F.A.A.$_{70\%}$ at 1:1:18 ratio) for 72 h and stored in 70% ethanol solution until further analysis.

Leaf paradermic sections were obtained using steel blades on both abaxial and adaxial sides. These sections were clarified in sodium hypochlorite solution containing 1% chlorine, washed in distilled water twice for 10 min, stained with 1% safranin solution and mounted on microscope slides with 50% glycerol (Kraus and Arduin, 1997). Transverse sections were performed at the middle region of leaves, as well as in the root maturation zone using a LPC model microtome. These sections were clarified in sodium hypochlorite solution containing 1% active chlorine, rinsed in distilled water twice for 10 min, stained with aqueous safrablau solution (1% safranin and 0.1% astra blue at 7:3 ratio) and mounted on microscope slides with 50% glycerol (Kraus and Arduin, 1997).

The mounted sections were imaged under a Zeiss Microimaging GmbH Scope A1 microscope (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) coupled to a digital camera. The obtained images were analyzed in UTHSCSA-Imagetool and quantitative tissue characteristics were measured in one slide per replicate. Five sections and four fields were considered per slide. Furthermore, stomatal density (number per mm^2) and stomatal index [(stomatal number/epidermal cells number)*100] were calculated.

The experiment was carried out in completely randomized design with two treatments (high and low population densities) and 10 replicates. Data were submitted to one-way ANOVA and means compared of by Scott-Knott test at p<0.05 using Sisvar statistical software (Ferreira, 2011). Data was shown as means ± standard deviation.

3. Results

The stomata of *T. angustifolia* are tetracytic and little or no sinuosity is observed at the anticlinal cell walls of both leaf sides. Furthermore, parallel rolls of epidermal cells are found over the bundle sheath sclerenchymal extensions and show no stomata (Figure 1). In the leaf adaxial side, only stomatal index exhibit significant differences between populations (Table 1). Stomatal index was 3.7% higher in low density populations (Table 1). On the leaf abaxial side the stomatal density was 5.7% higher in low density populations (Table 1). In low density populations, stomatal index was 4.1% higher than in high density populations (Table 1).

T. angustifolia leaves have a one-seriated epidermis in both the abaxial and adaxial sides, followed by three layered palisade parenchyma. Collateral vascular bundles are arranged in parallel rolls in both adaxial and abaxial sides, these bundles show bundle sheath extensions comprising of sclerenchymal fibers, which bind the vascular bundles to the epidermis. Spongy parenchyma is placed between palisade parenchyma of both leaf sides, forming trabeculae,

Table 1. Leaf stomatal characteristics of *Typha angustifolia* from different natural conditions of population densities.

Condition	Adaxial Side	
	SD	SI (%)
High density	438.78 ± 95.46 a	10.01 ± 1.26 b
Low density	450.42 ± 68.37 a	10.38 ± 0.84 a

Condition	Abaxial Side	
	SD	SI (%)
High density	433.41 ± 84.52 b	9.71 ± 1.08 b
Low density	458.16 ± 79.75 a	10.11 ± 0.94 a

(SD) – stomatal density; (SI) – stomatal index. Means followed by the same letter do not differ (Scott-Knott, 5%). Data was shown as means ± standard deviation.
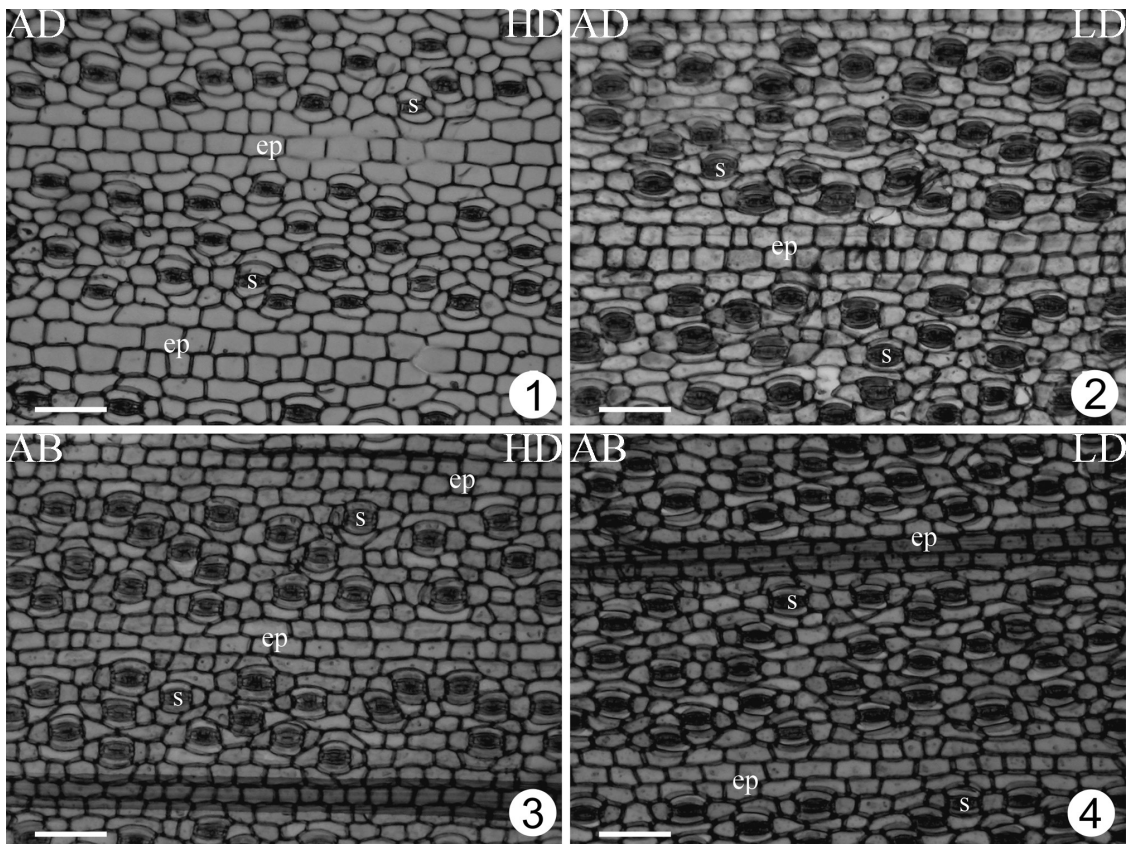

Figure 1. Leaf paradermic sections of *Typha angustifolia* L. from different natural conditions of population densities. 1 and 2 = Adaxial side; 3 and 4 = Abaxial side; 1 and 3 = high density population; 2 and 4 = low density population. Bars= 50 µm. (s) – stomata; (ep) – epidermal cells; (AD) – adaxial side; (AB) – abaxial side; (HD) – high density population; (LD) – low density population.

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which delimit large aerenchymal chambers (Figure 2). The mesophyll thickness was 10.3% higher in low density than high density populations (Table 2), with similar results being observed for aerenchymal gaps percentage that was 10.9% higher in low density populations. However, the adaxial epidermis was 4.3% thicker in plants from high density populations (Table 2).

The roots of *Typha angustifolia* show one-seriated epidermis with few trichomes. Root cortex is separated into three regions: external cortex (parenchyma cells with few intercellular spaces), middle cortex (large aerenchymal chambers and parenchymal trabeculae) and inner cortex (few layered parenchyma with smaller cells). One-seriated endodermis is visible around the vascular cylinder, followed by one or two layers of pericycle cells (Figure 3). All evaluated characteristics of *T. angustifolia* root anatomy showed statistical differences between populations (Table 3). Exodermis was 5.2% thicker in plants from high density populations compared to low density populations. Similar results were observed for endodermis and cortex thickness, which exhibit 4.1% and 13.4% larger values in high density populations (Table 3). Regarding the vascular tissues, phloem was 13.9% thicker in high density population plants, however, the proportion of the vascular cylinder in roots was higher in low density populations. The aerenchyma proportion in root cortex was 23.8% higher in plants from high density populations.

Table 2. Leaf cross-section anatomical characteristics of *Typha angustifolia* from different natural conditions of population densities.

Condition	MT (µm)	ATA (mm^2)	EAD (µm)	EAB (µm)
High density	2062.87 ± 672.30 b	4.46 ± 2.02 b	17.24 ± 2.61 a	17.88 ± 3.26 a
Low density	2274.83 ± 459.11 a	4.94 ± 1.31 a	16.54 ± 2.34 b	17.72 ± 2.85 a

(MT) – mesophyll thickness; (ATA) – aerenchyma total area; (EAD) – epidermis thickness from adaxial side; (EAB) – epidermis thickness from abaxial side. Means followed by the same letter do not differ (Scott-Knott, 5%). Data was shown as means ± standard deviation.
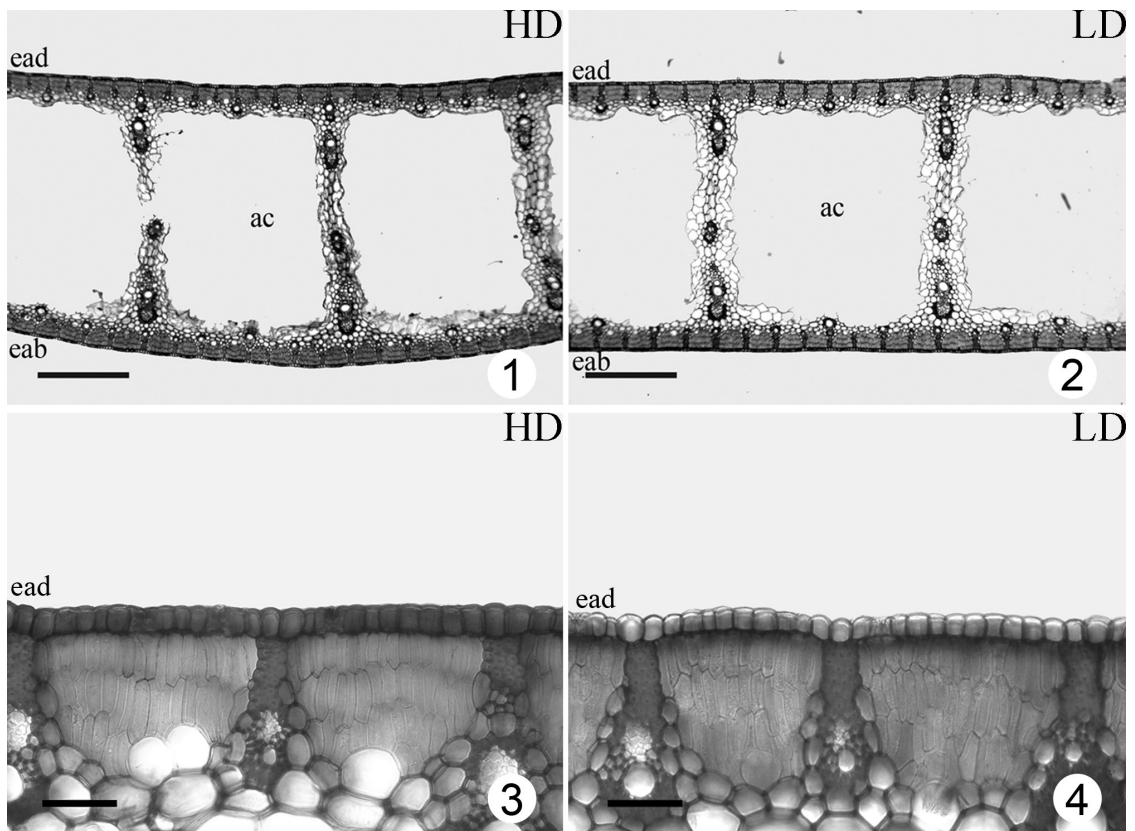

Figure 2. Leaf cross-sections of *Typha angustifolia* L. from different natural conditions of population densities. 1 = Leaf cross-section of high density population; 2 = Leaf cross-section of low density population; 3 = Adaxial epidermis details of high density population; 4 = Adaxial epidermis details of low density population. Bars= 500 µm (1 and 2); Bars= 50 µm (3 and 4). (ac) – aerenchymal chamber; (ead) – adaxial epidermis; (eab) – abaxial epidermis; (HD) – high density population; (LD) – low density population.
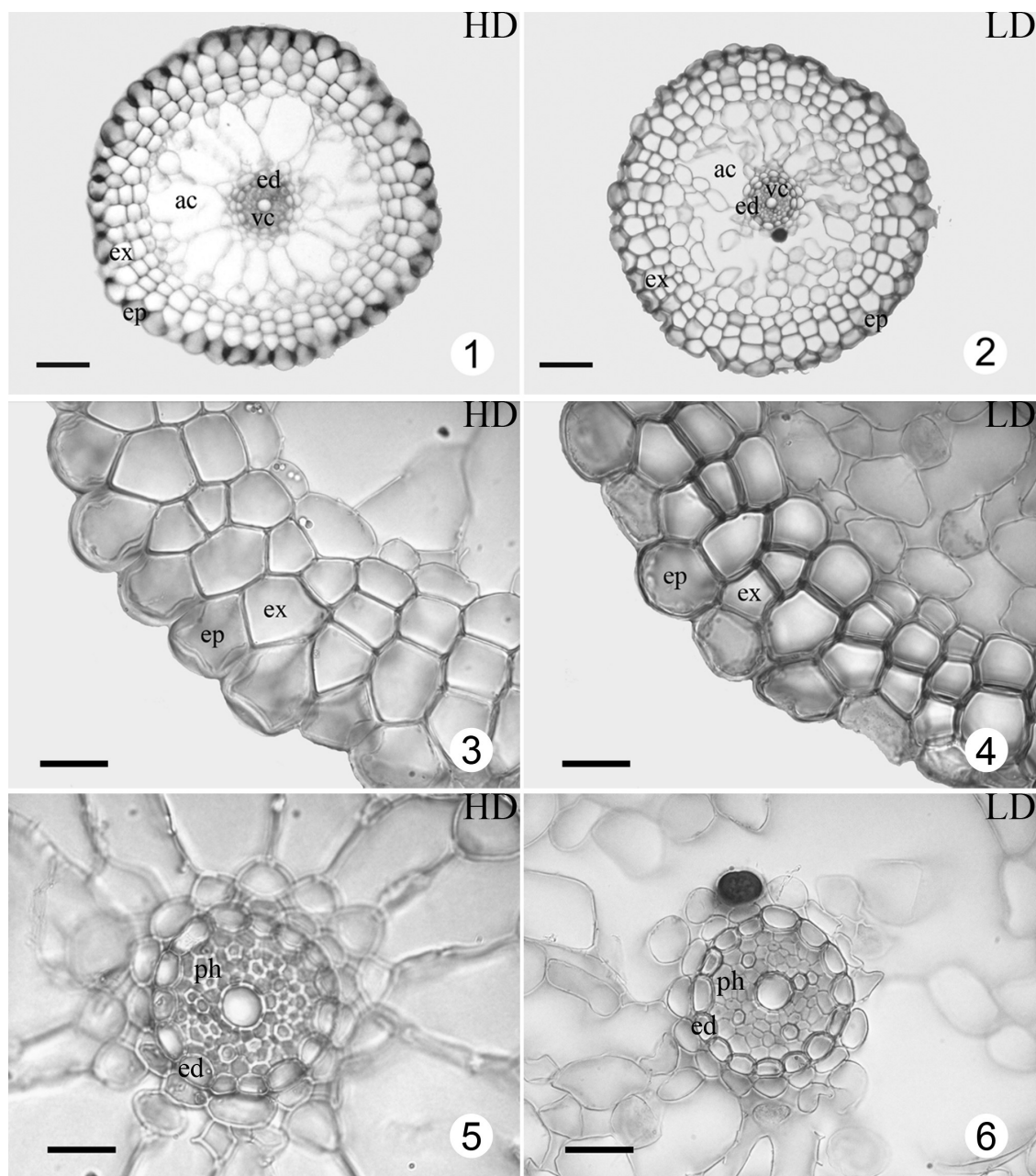
Figure 3. Root cross-sections of *Typha angustifolia* L. from different natural conditions of population densities. 1 = Root cross-section of high density population; 2 = Root cross-section of low density population; 3 = Epidermis and exodermis details of high density population; 4 = Epidermis and exodermis details of low density population; 5 = Endodermis and vascular cylinder details of high density population; 6 = Endodermis and vascular cylinder details of low density population. Bars= 50 μm (1 and 2); Bars= 20 μm (3, 4, 5 and 6). (ac) – aerenchymal chamber; (ep) – epidermis; (ex) – exodermis; (ed) – endodermis; (vc) – vascular cylinder; (ph) – phloem; (HD) – high density population; (LD) – low density population.

4. Discussion

Stomata are modified plant cells related to CO_2 uptake and water and O_2 release (transpiration). As stomata cells are related to photosynthesis, a higher stomatal density may lead to a higher potential for CO_2 uptake and photosynthetic efficiency (Pereira et al., 2011). Genetic variations may lead to different stomatal density, however, species might show differences in stomatal traits due to many environmental factors (Batista et al., 2010; Ribeiro et al., 2012). Therefore, plants growing in high density condition may are under stress, once cattail plants of low density populations show

Table 3. Root cross-section anatomical characteristics of *Typha angustifolia* from different natural conditions of population densities.

Condition	REX (μm)	RED (μm)	RCT (μm)	PT (μm)	VCP (%)	APC (%)
High density	20.94 ± 3.04 a	6.05 ± 1.23 a	120.80 ± 21.42 a	13.14 ± 2.40 a	2.40 ± 0.38 b	26.06 ± 6.37 a
Low density	19.90 ± 3.99 b	5.81 ± 1.13 b	106.56 ± 20.95 b	11.53 ± 1.97 b	2.58 ± 0.47 a	21.18 ± 9.54 b

(REX) – root exodermis thickness; (RED) – root endodermis thickness; (RCT) – root cortex thickness; (PT) – phloem thickness; (VCP) – vascular cylinder proportion; (APC) – aerenchyma proportion in root cortex. Means followed by the same letter do not differ (Scott-Knott, 5%). Data was shown as means ± standard deviation.

enhanced stomatal characteristics, potentially increasing its photosynthesis.

According Ellison (1987), macrophytes growing under high population density might result in a shading effect, reducing radiation for lower plant parts. Likewise, leaves exposed to lower radiation intensity tend to exhibit lower stomatal density (Pompelli et al., 2010). Therefore, high population density promotes shading stress on plant leaves, reducing stomatal efficiency via structural changes. As a consequence, this may reduce the potential for CO_2 uptake and photosynthesis.

Palisade parenchyma is another plant tissue strongly related to photosynthesis. According Boeger et al. (2008), shading reduces the thickness of leaf mesophyll and palisade parenchyma. Pengelly et al. (2010) reported thicker leaves in *Flaveria bidentis* exposed to higher radiation intensity. However, very little is known about the effects of light intensity on the internal structures of macrophytes. Higher radiation intensity may lead to increased growth and morphological modifications on macrophytes, such as the higher development of fluctuating leaves (Cronin and Lodge, 2003). Thus, the thicker palisade parenchyma of *T. angustifolia* growing under lower population density may be related to a more efficient radiation use. This also supports the fact that the higher population density lead to a shading condition, which may damage the overall photosynthetic capacity through the development of less functional leaves.

The epidermis is one of the most important tissues for plants and is related to plant tolerance for many environmental conditions, such as excessive radiation, pathogens and herbicides (Tuffi Santos et al., 2009; Parent et al., 2008). According to Braccini et al. (2008) and Casa et al. (2007), high density population of plants may lead to a higher incidence of pathogens. Therefore, a thicker epidermis in the leaves of *T. angustifolia* from high density populations could be related to the need for greater protection against an increased pathogen incidence. This would be in-line with the view that high density populations of *T. angustifolia* may be related to stress conditions.

Aerenchyma is a modified parenchymal tissue related to gas storage and is critical for plant survival in aquatic or flooding environments (Insausti et al., 2001; Vasellati et al., 2001; Pereira et al., 2010). As a consequence, plant genotypes more tolerant to flooding conditions often develop higher aerenchyma proportion (Pereira et al., 2008; Souza et al., 2009). Therefore, as low density population showed greater

aerenchyma development, it is possible that the harsh condition caused by high density also affects negatively aerenchyma development, promoting a less functional internal structure to cope aquatic environments.

The endodermis and exodermis are important as root apoplastic barriers protecting roots to shoots from soil pollutants and pathogen flux (Hameed et al., 2009; Pereira et al., 2011). According to Armstrong et al. (2000) and Meyer et al. (2011) these structures might also lower water and nutrient uptake from the soil. As high density populations may show increased pathogen development, thicker apoplastic barriers may reduce pathogens flux from roots to shoots of *T. angustifolia*. Therefore, it could be a tolerance mechanism.

The cortex is related to the root hydraulic conductance because a thinner cortex equates to a shorter distances for water to travel from soil to vascular cylinder (Souza et al., 2009). The thickness of the root cortex can be influenced by both environment and genetic characteristics and a thicker root cortex leads to lower water transport efficiency (Pereira et al., 2008; Hameed et al., 2009; Souza et al., 2009). However, the thicker root cortex observed under high population density might act as a defense mechanism against pathogens but consequently reduce water and nutrient flux, therefore becoming less functional for high density population plants.

Phloem is the principle transport tissue for photosynthesis products and this transport is important for growth capacity and competition (Heo et al., 2014). Therefore, the greater phloem thickness observed in high population density *T. angustifolia* may have been induced by competition between individuals, promoting root growth to achieve higher nutrient uptake capacity. Aerenchyma proportion in root cortex also may be related to intraspecific competition, since this characteristic has been seen to increase under environmental stress (Vasellati et al., 2001; Coelho et al., 2006; Pereira et al., 2010). Moreover, a higher proportion of root aerenchyma allows greater gas diffusion, mainly oxygen, promoting higher ATP production and growth.

According Souza et al. (2009), the lower proportion of vascular cylinder may also be related to lower hydraulic conductance, supporting the hypothesis that there is a restriction for water and nutrient transport in high density population plants. Thus, we propose that high population density promotes a stress condition in *T. angustifolia* plants. As preventive evaluation of macrophytes populations is a key point for the proper management of cattail plants

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(Thomaz, 2002), the anatomical differences observed here might assist with the understanding of the different behaviors of cattail populations.

In conclusion, cattail populations from different density conditions show anatomical differences in leaves and roots. Moreover, the data indicates that the *T. angustifolia* plants of high density population present a less favorable internal structure to aquatic environment, indicating a stressful condition for those populations.

Acknowledgements

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