UNIVERSIDADE FEDERAL DE LAVRAS

RODRIGO BARBOSA KLOSS

ANATOMICAL AND PHYSIOLOGICAL TRAITS OF MAIZE UNDER CONTRASTING WATER LEVELS AND CATTAIL OCCURRENCE

LAVRAS-MG
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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Botânica Aplicada, área de concentração em Botânica Aplicada, para a obtenção do título de Mestre.

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Orientador.

Prof. Dr. Evaristo Mauro de Castro
Coorientador.

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ABSTRACT

Maize is one of the most important and cultivated crops in the world, with cultivar BRS-4154, known as 'Saracura' maize, a tolerant to flooding genotype. The Southern cattail, *Typha domingensis*, is an aquatic plant with known activity of radial oxygen losses, being widely diffused around the world and highly invasive. The objective of the study was to analyze the interaction of 'saracura' maize with cattail in two distinct environments, under waterlogging and in an in soil at field capacity. The experiment was conducted in a greenhouse at the Federal University of Lavras in the Biology department, where maize seeds were germinated in red latosol at the field capacity with nutrient solution, after 10 days of germination, when the maize plants reached an average height of 12.5 cm and 2 fully expanded leaves per plant, the sources of variation were introduced, the sources being the presence or absence of Southern cattail and waterlogging or field capacity, the experiment was conducted in a 2 x 2 factorial with a completely randomized design and the conditions maintained throughout the experiment by refilling of the water lost by evapotranspiration bidaily. Plant growth data, such as height, number of fully expanded leaves, number of dead leaves were collected fortnightly until the sixty day of the experiment conduction and dry weight was measured at the eightieth day. The analysis of gas exchange and chlorophyll content were made at 30 and 60 days after introduction of sources of variation using an infrared gas exchange analyzer and a SPAD unit meter. At that time, 1 leaf per plant was collected for each date and submitted to usual microtechnique procedures. In the final 5 days of the experiment, the dissolved oxygen content in the substrate of the waterlogged plots was measured consecutively with a dissolved oxygen meter and at the end of the experiment, one root per plant was collected and submitted to usual microtechnique procedures. The waterlogging was detrimental in the growth parameters, gas exchange, foliar and root anatomy of the maize, while southern cattail increased the dissolved oxygen content of the substrate and contributed to maize enhancement in growth, leaf and root anatomy, and gas exchange without presenting effects of competition.

Keywords: Gas exchange. Dissolved oxygen. Typha spp. Zea mays.

RESUMO

O milho é uma das culturas mais importantes e produzidas no mundo, sendo a cultivar BRS-4154, conhecida como milho ‘Saracura’ um genótipo tolerante ao alagamento. A taboa, *Typha domingensis*, é uma planta aquática com conhecida atividade de liberação radicular de oxigênio, sendo amplamente difundida pelo mundo e altamente invasiva. O objetivo do estudo foi analisar a interação do milho ‘Saracura’ com a taboa em 2 ambientes distintos, sob o alagamento e em solo na capacidade de campo. O experimento foi conduzido em casa de vegetação na Universidade Federal de Lavras no departamento de Biologia, onde foram germinadas as sementes de milho em latossolo vermelho com solução nutritiva à capacidade de campo, após 10 dias da germinação, quando as plantas de milho alcançaram uma altura média de 12,5 cm e 2 folhas completamente expandidas por planta, foram introduzidas as fontes de variação, sendo elas, a presença ou ausência de taboa, e o encharcamento ou capacidade de campo, de forma que o experimento foi conduzido em um fatorial 2 x 2 com delineamento totalmente casualizado e as condições hídricas mantidas ao longo do experimento por reposição da água evapotranspirada. Foram feitas coletas de dados de crescimento das plantas, como altura, número de folhas completamente expandidas e número de folhas mortas, quinzenalmente até o sexagésimo dia e o peso seco aferido aos 80 dias. As análises de trocas gasosas e de teor de clorofila foram feitas aos 30 e 60 dias após a inserção das fontes de variação utilizando-se um analisador infravermelho de trocas gasosas e um medidor de unidades SPAD, nessas mesmas datas foi coletado 1 folha por planta para cada data que foi submetida aos processos de microtécnica vegetal. Nos 5 dias finais do experimento foi medido consecutivamente, o teor de oxigênio dissolvido no substrato das parcelas alagadas com um medidor de oxigênio dissolvido e aos 80 dias sendo coletada uma raiz por planta e submetidas aos procedimentos padrões de microtécnica vegetal. O alagamento se mostrou prejudicial nos parâmetros de crescimento, trocas gasosas, anatomia foliar e radicular da planta de milho, enquanto a taboa aumentou o oxigênio dissolvido do substrato e contribuiu beneficiando seu crescimento, trocas gasosas, anatomia foliar e radicular da planta de milho, não apresentando efeitos nocivos de competição.

Palavras-chave: Trocas gasosas. Oxigênio dissolvido. Typha spp. Zea mays.

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1 INTRODUCTION

Cultivation in flooded areas can be damaged by the proliferation of invasive plants of rapid clonal propagation colonizing the area and consuming resources. Crops such as maize (*Zea mays* L.), Soybean (*Glycine max* (L.) Merr.), wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) are among the world's most produced agricultural commodities, but, when cultivated on environments subject to flooding conditions it promotes losses by competition with aquatic macrophytes (DAI et al, 2014).

Considering the high demand for food caused by the ever-increasing human population; the potential use of environments subject to flooding by small and large producers is a viable alternative to meet this demand and should be done sustainably and wise as Willoughby et al show (2000). Wetlands are experiencing changes and losses due to rapid human growth, urbanization and agricultural needs (SUNDAR et al, 2014). Chamers et al (1993) shows that artificial and natural wetlands and its aquatic plants are a great way to control agricultural runoff serving as a biological filter. Thus, knowledge is needed on how plants cope with these environments together with the competition with aquatic macrophytes. Kloss (2016) showed that contrarywise to conventional management practices, the presence of *Typha domingensis* Pers. (Typhaceae) may favour maize physiology. In fact, improving the understanding of low substrate fertility and competition may enable a new green revolution as Lynch (2007) suggests.

One of the characteristics of a given aquatic or flood-tolerant plant is the development of the aerenchyma tissue, which is a specialized parenchyma type that stores and diffuses gas such as CO_2 and O_2 within its intercellular spaces (THOMAS, GUERREIRO, SODEK, 2005). Although aerenchyma helps the survival of plants under flooding-driven hypoxia situations, it generates obstructions to the water and nutrient uptake (Díaz et al. 2018). In addition, some plant species release oxygen in their substrate via their root system; this process is called radial oxygen loss which was reported for *Typha latifolia* L. (Typhaceae) by Jespersen et al (1998) and by Chabbi et al (2000) for *T. domingensis*. This leaching of oxygen may promote a lower demand for gas storage and aerenchyma development, increasing water and nutrient uptake. This effect was showed by Kloss (2016) with *T. domingensis* and maize grown under different phosphorus (P) levels and the presence of *T. domingensis* under higher P concentrations decreased the proportion of aerenchyma in maize roots under waterlogging.

There are few studies on the competition of aquatic macrophytes and crop such as maize, and the conventional agricultural weed management practices are the removal of invasive plants, which can be expensive. However, Kloss (2016) shows that there is not always a need for the removal as competition may not occur, this interaction must be better understood to improve the means for a sustainable agriculture. Thus, a better understanding of the effects of the competition with *T. domingensis* on cultivated areas can contribute to better sustainable use of aquatic ecosystems as well as the lowland agriculture, reducing costs, increasing the productivity and contributing to the preservation of these ecosystems and its diversity.

With this study we aimed to identify how the plants interact and how their interaction is influenced by the water level, with the cv. 'Saracura' maize tolerating intermittent periods of flooding, akin to the seasonality of how wetlands work, it's necessary to know the effects in both conditions.

2 THEORETICAL BACKGROUND

2. 1 AQUATIC MACROPHYTES

Aquatic macrophytes is a group of plants which returned from terrestrial to aquatic environment (SCULTHORPE, 1967). In addition, the photosynthetically active parts of these plants remain partially or totally flooded (COOK, 1996). In this process, morpho-physiological adaptations were required to prevail in this new environment. The most noticeable modifications are shown by submerged plants, which need to absorb all their nutrients from the water, while the floating and rooted ones can fix the atmospheric CO_2 and gather nutrients from the substrate (PIERINI & THOMAZ, 2004).

The study of macrophytes in aquatic systems is important for improving the knowledge about its biodiversity as well as the awareness of local populations about the importance of its preservation (MATIAS et al, 2003).

Macrophytes are important for ecosystems because of their roles as primary producers, by cycling and storing nutrients, controlling pollutant and eutrophication levels (ESTEVES & CAMARGO, 1986; POTT & POTT, 2000); these plants can also be used as shelter and food by animals. In addition, the study of aquatic environments is of essential relevance for its preservation and management (CERVI et al, 2009).

These plants are susceptible to anoxia, which mainly causes a decrease in adenylate energy charge, cytoplasmic acidification, anaerobic fermentation, elevation in cytosolic Ca^{+2} concentration, changes in the redox state and a decrease in the membrane barrier function, besides the deficiency in oxygen is characterized by an increase in reactive oxygen species (ROS) and hydrogen peroxide accumulation (BLOKHINA; VIROLAINEN & FAGERSTEDT, 2003)

Some terrestrial plants under flooding may develop aerenchyma in leaves, stems and roots, allowing the correct functioning of respiratory and photosynthetic metabolisms of these plants (THOMAS; GUERREIRO & SODEK, 2005). Southern Cattail (*Typha domingensis* Pers.) is a cosmopolitan rooted aquatic macrophyte belonging to the family Typhaceae. Its underground parts consist of roots and rhizomes with its aerial parts being formed by leaves and inflorescences (CARVALHO et al, 2014; FOSBERG, 1989).

Compared with the metabolism of aquatic plants, crops when exposed to flooding may develop modifications related to the transportation of water and nutrients (VASELATTI et al, 2001). Maize (*Zea mays* L.) is a crop of great economic importance, although most of its genotypes being generally susceptible to hypoxia, the Brazilian Agricultural Research Corporation (EMBRAPA) – Maize and Sorghum developed a flooding tolerant cultivar called BRS-4154 ‘Saracura’. Maize is a species of high economic interest being one of the five most produced cereals worldwide (MAGALHÃES et al, 2010).

Plant adaptations to flooded environments can vary according to its characteristics leading to different adaptative responses, which can lead to the better development of certain populations due to their physiological and morphological changes. It can be observed on flood-tolerant maize genotypes which exhibit increased root aerenchyma, thickening of the epidermis and endoderm, greater efficiency in the embolism protection in the metaxylem vessels, thickening of the phloem, and thinner cortex (PEREIRA et al, 2008; SOUZA et al, 2009).

Aerenchyma increases root porosity and the storage and diffusion of gases inside the plants (INSAUSTI et al, 2001; VASELLATI et al, 2001). Adaptations may also include modifications in the metabolism of the enzymes of the antioxidant system. Plants with greater activity of the antioxidant system on roots and leaves exhibit better conditions to maintain the cellular metabolism by allowing the preservation of the membrane structures. The excess of water can lead to hypoxia which generates ROS, and the improved antioxidant system can decrease the damage promoted by ROS (DREW, 1997). Differences in antioxidant enzymes activity may occur in plants under flooding; as an example, the activity of catalase and ascorbate peroxidase may increase considerably under these conditions (PEREIRA et al, 2010; PEREIRA et al, 2008).

Knowledge about aquatic flora and the changes that may occur in the composition of these environments over the years is essential for understanding management methods and for preserving the diversity of these environment (RANTA & TOIVONEN, 2008). Brazil is the country with the highest scientific production on macrophytes in Latin America, and the third in the world, behind the US and Germany (PARDIAL et al, 2008). However, the publications with macrophytes focus on descriptive works and most of these works refer to systematics and floristic surveys thus investigation is needed to elucidate the physiological and morphological characteristics of aquatic macrophytes (PARDIAL et al, 2008).

2. 2 INTERSPECIFIC COMPETITION.

Competition between plants cultivated in flooded areas and invasive weeds can cause serious losses on productivity. The geographic region, latitude, proportion of plants in relation to each other, and the genetic diversity are key factors for the competition results and in the decrease on productivity. Weed species are more competitive than the crop ones, producing higher biomass, photosynthetic rate, seed sets among other characteristics and, this higher competitivity damages crop productivity (DAI et al, 2014). However, when grown in flooded environment with nitrogen (N) deficiency crop species show a competitive advantage compared with some weeds (XIONG et al, 2005).

The interspecific competition between different macrophyte species is influenced by habitat structure, zonation of aquatic vegetation, spatial segregation promoted by water levels, probably because of the competitive factor and preferred habitat (CUNHA et al, 2012). Many of these aquatic plants have high primary productivity and intense population growth, characteristics that favours the colonization of large areas by these plants. This excessive growth may be harmful for the use of the aquatic environment as it causes the reduction of biodiversity, problems to nautical practices, and to hydroelectric power plants (THOMAZ, 2002).

The colonization of the environment by aquatic macrophytes is a natural process on ecological succession and it occurs in most lentic ecosystems. The process is faster in these environments due to the more intense sedimentation and anthropic influence, such as deforestation and agricultural activity, promoting the quick development of aquatic macrophytes (FORD, 1990; THOMAZ, 2002).

In order to help prevent potential uncontrolled colonization, information on the biology of aquatic macrophytes as well as the limiting factors for the population increase are essential to the management of these ecosystems, allowing the use of successful actions, reducing expenses and preserving the environment (THOMAZ & BINI, 1999; THOMAZ, 2002).

Limiting environmental factors are studied for the prediction of the colonization potential in aquatic environments (DONABAUM et al, 1999), however, these factors remain unclear and more studies about the plant’s morphology and physiology as related to this high population growth, these studies may give a critical help in biomonitoring of these populations in aquatic environments.

3 EXPERIMENTAL

3. 1 PLANT MATERIAL AND EXPERIMENTAL DESIGN

The maize seeds were acquired from EMBRAPA – Maize and Sorghum located at Sete Lagoas, MG. *Typha domingensis* plants were collected from natural populations in wetlands located at the Federal University of Lavras, Lavras, State of Minas Gerais, Brazil (21°14’43”S, 45°59’59”W).

Maize seeds were germinated in a greenhouse in pots of 15 L capacity containing 11.65 L of soil (red latosol) which was collected and sieved through a 4 mm sieve and irrigated at its field capacity with 2.90 L of Hoagland and Arnon (1950) nutrient solution at 100% of its ionic power. The soil field capacity was calculated to be 24.87% by subtracting the water saturated weight of the sample by its dry weight and dividing it by the water saturated weight and multiplying by 100 [$FC = ((W_{H20} - W_{d})/W_{H20}) * 100$] (LOSS et al, 2014).

After maize plants achieved average 12.5 cm height and two completely expanded leaves, one cattail plants were introduced per pot (cattail plants were 15 cm tall average) and the waterlogging introduced in the designated treatments, with the conditions being maintained throughout the whole experiment by weighing the pots daily. The pots in field capacity had the water lost by evapotranspiration refilled by weighing and refilling it to the weight it had when the nutrient solution were firs applied, the waterlogged parcels were kept by measuring the height of the water above soil level and refilling it to that same height.

The red latosol was evaluated for its nutrient concentration via soil analysis (Table 1), it showed adequate pH and base nutrient levels with the addition of the nutrient solution providing the necessary nutrients to the plants in the same way as Souza et al (2016) used with rice plants grown in soil. The soil analysis was conducted with a sample of soil extracted from each pot and the fractionated sediment was dried in a forced circulation oven at a temperature of 40°C to constant weight. After acid digestion the elements were determined on Perkin Elmer 2400 elemental analyzer (CHNS / O), PerkinElmer Inc., Waltham, USA. Acid digestion (HCl) was carried out in the samples and colorimetric reaction using molybdenum blue and, afterwards, reading at 885 nm in the UV/VIS Spectrophotometer, model DR 200, Hach, Tokyo, Japan (DELGADO et al 1994). To obtain the organic matter and ash content, the samples were calcined in a muffle oven at 550ºC for 4 hours and the organic matter was determined by gravimetry (SFRISO et al, 1999). Soil chemical analysis was carried out at the Soil Science Department (DCS) at the Federal University of Lavras.

Table 1. Soil analysis chart of the red latosol used in the experiment.

*p*H	Macronutrients						Micronutrients				
	N (OM)	P(P-rem)	K	S	Mg	Ca	Zn	Fe	Mn	Cu	B
6.1	1.6	1.3(26.58)	136.6	26.9	0.3	1.9	1.6	67.4	45.5	4.2	0.07

N (OM) = organic matter (dag kg^{-1}); P = Phosphorus (mg dm^{-3}) extracted by Mehlich 1; P-rem = Remaining phosphorus (mg L^{-1}); S = Sulphur (mg dm^{-3}) extracted by monocalcium phosphate in acetic acid; Mg = Magnesium (cmolc dm^{-3}) extracted by KCl 1mol L^{-1}; Ca = Calcium (cmolc dm^{-3}) extracted by KCl 1mol L^{-1}; Zn = Zinc (mg dm^{-3}) extracted by Mehlich 1; Fe = Iron (mg dm^{-3}) extracted by Mehlich 1; Mn = Manganese (mg dm^{-3}) extracted by Mehlich 1; Cu = Copper (mg dm^{-3}) extracted by Mehlich 1; B = Borum (mg dm^{-3}) extracted in hot water.

The experiment was conducted in a 2x2 factorial design with two water levels, being field capacity (24.87% of the soil weight) and waterlogging (layer of water 2 cm above soil level). The total number of parcels were 40 with four treatments and ten replications being each replication constituted of one plant.

3. 2 GROWTH ANALYSIS

The maize plants were fortnightly evaluated for its height, number of fully expanded leaves, dead leaves from the day the sources of variation were introduced until the end of the experiment, 80 days after the introduction of sources of variation. Twenty maize plants (n = 20) were collected at the end of the experiment and oven dried at 60 °C for 48 h and the shoots, roots ant total dry weight was measured using an analytical scale (AY220, Shimadzu, Japan).

The allocation of biomass was calculated by dividing the organ dry mass (ODM), root or shoot, by the total dry mass (TDM) [allocation% = (ODM/TDM) * 100]. The total plant height elongation rate (E%) was calculated by subtracting the final plant height by the initial plant height, dividing it by the final height and multiplying by 100 [E% = $((H_f-H_o)/H_f)$ * 100]. The plant height elongation rate by day (ECM) was calculated by dividing the final height by the number of days passed since the first measurement [ECM = $(H_f/D]$.

3. 3 GAS EXCHANGE AND CHLOROPHYLL ANALYSIS

Gas exchange analysis were performed twice using an infrared gas exchange analyzer (IRGA) model LI-6400XT (Li-COR Biosciences, Lincoln, Nebraska, USA) equipped with a 6 cm^2 cuvette for the measurements. The readings were made on the second fully expanded leaf that could fit the cuvette per plant, eliminating the outliers and considering the means of the two replications in time, making the number of evaluations equals 32 (n = 32). The evaluations occurred passed 30 and 60 days after the beginning of the experiment and started at 08:00 a.m. and did not go beyond 10:00 a.m. The density of photosynthetically active photons was fixed at 1000 $\mu mol\ m^{-2}\ s^{-1}$ in the chamber. The following characteristics were evaluated: stomatal conductance (g_s), transpiratory rate (E) and photosynthetic rate (Pn). The photosynthetic water-use efficiency (WUE) was calculated by the ratio Pn/E. The concentration of chlorophyll in the leaves was evaluated with the portable chlorophyll meter SPAD-502 (Konica Minolta, Tokyo, Japan). The second fully expanded leaf per plant in three positions per leaf (base, medium and apex) were evaluated in two times with the data evaluated excluding the outliers and being averaged to one plant (n=32).

3. 4 DISSOLVED OXYGEN ANALYSIS

The evaluations were conducted 80 days after beginning of the experiment for five consecutive days in the morning from 8:00 a.m to 10:00 a.m. using the portable dissolved oxygen (DO) meter Oakton DO600 (Cole Parmer, Illinois, USA). These measurements were performed by introducing the probe 2 cm away from the maize plants only on waterlogged parcels (with and without *T. domingensis*). A total of 100 measurements were made with the data submitted to analysis of variance excluding outliers (n=86). The substrate from field capacity treatments were not evaluated due to its natural oxygenated condition provided by the soil pores. The device was calibrated before every evaluation according to the company instructions, with the mean substrate temperature of the five consecutive days measured by the device being 27.3, 22.5, 27.2, 21.7 and 23.1 °C respectively from the first day to the fiftieth day of evaluation.

3. 5 ANATOMICAL ANALYSIS

Leaves were collected twice for the anatomical analysis, at 30 and 60 days of the experiment beginning, with the data from the two samples being averaged as one, and were fixed in FAA70% solution (formaldehyde, acetic acid and ethanol 70% in a ratio of 1: 1: 18), for 48 hours and then transferred to a solution of ethanol 70% (JOHANSEN, 1940). The sections were performed in the median region of the leaves.

For the analysis of adaxial and abaxial epidermis, paradermic impressions were made on the surface of the leaves with cyanoacrylate ester resin (Superbonder®, Loctite, Dusseldorf, Germany). After the resin's drying, four prints per replication (n = 160) were removed and mounted in slides using 50% glycerol (m v^{-1}).

Five cross sections per replication (n = 200) were obtained by hand with the use of steel blades and clarified with 50% sodium hypochlorite and washed in distilled water for 10 minutes and then stained with safrablau solution (safranin 1% and astra blue 0.1% in a ratio of 7: 3) and mounted in slides with 50% glycerol (m v^{-1}).

Root samples were collected at the end of the experiment at 80 days after introduction of sources of variation. Cross sections were obtained approximately 2 cm away from the root tip by hand using steel blades and stained with 1% aqueous safranin (m v^{-1}). Two roots per replication (n = 40) with one section per root were mounted in slides with 50% glycerol (m v^{-1}). The sections were clarified with 50% sodium hypochlorite and washed in distilled water for 10 min, stained and mounted on slides with 50% glycerol (JOHANSEN, 1940).

The slides were photographed using an Olympus microscope model CX31 (Olympus, Tokyo, Japan). These images were analysed using the ImageJ software, calibrated with microscopic rulers photographed in the same configuration of the images obtained from the material where the quantitative parameters of the tissues of leaves and roots were evaluated according to the methodologies described by Pereira et al. (2008) and Souza et al (2010).

3. 6 STATISTICAL ANALYSIS

Data were submitted to ANOVA and the means compared by the Scott-Knott test, with 5% probability with the aid of the statistical program SISVAR, version 5.0 (FERREIRA, 2011).

4 RESULTS

Any of the growth parameters showed no significant interaction between the presence of *T. domingensis* and waterlogging ($p>0.05$) The number of fully expanded leaves was affected only by the presence of *T. domingensis* which increased this parameter (Table 2). However, the number of dead leaves was not affected by *T. domingensis* but increased under waterlogging (Table 2). In addition, waterlogging decreased the average plant height but the presence of *T. domingenis* increased this parameter (Table 2). Furthermore, the elongation rates were also increased in the presence of *T. domingensis* but decreased under waterlogging (Table 2).

Table 2 - Growth parameters of maize plants grown under different water levels and interaction with *T. domingensis*.

Water level	FEL	DL	Height	E%	ECM
Field capacity	5.02 a	2.07 b	92.93 a	198.24 a	1.02 a
Waterlogged	4.94 a	2.90 a	43.71 b	59.69 b	0.27 b
Interaction	**FEL**	**DL**	**Height**	**E%**	**ECM**
Maize+Typha	5.12 a	2.54 a	74.64 a	151.71 a	0.75 a
Maize	4.84 b	2.53 a	62.00 b	106.22 b	0.54 b

Means followed by the same letter in the columns does not differ by the Scott-Knott test for $p < 0.05$. FEL = Fully expanded leaves (number plant^{-1}); DL = dead leaves (number plant $^{-1}$); Height = average plant height at 60 d from the beginning of the experiment (cm); E% = elongation rate percentage (%); ECM = elongation rate in cm day^{-1}.

The dry weight was decreased by waterlogging while *T. domingensis* did not affected maize weight (Table 3). However, the biomass allocation showed interaction between the factors (p < 0.04) and the presence of *T. domingensis* promoted plants, under waterlogging condition only, allocated more biomass to its shoots (Table 4).

Table 3 - Dry weight of maize plants grown under different water levels and interaction with *T. domingensis*.

Water level	Shoot (g)	Root (g)	Total (g)
Field capacity	22.67 a	28.19 a	50.85 a
Waterlogged	11.16 b	09.06 b	20.22 b
Interaction	**Shoot (g)**	**Root (g)**	**Total (g)**
Maize+Typha	15.86 a	21.77 a	37.63 a
Maize	17.96 a	15.47 a	33.43 a

Means followed by the same letter in the columns does not differ by the Scott-Knott test for $p < 0.05$

Table 4 - Biomass allocation of maize plants grown under different water levels and interaction with *T. domingensis*.

	Shoot (%)	
Water level	Maize+Typha	Maize
Field capacity	39.25 bA	54.01 aA
Waterlogged	58.42 aA	51.04 aA
	Roots (%)	
Water level	Maize+Typha	Maize
Field capacity	60.75 aA	45.99 aA
Waterlogged	41.58 bA	48.96 aA

Means followed by the lowercase letter in the columns and uppercase letter in the rows doesn’t differ by the Scott-Knott test for $p < 0.05$

Gas exchange parameters showed no interaction between the water availability and the presence of *T. domingensis* ($p > 0.09$) except for photosynthetic water-use efficiency that showed significant interaction ($p = 0.008$). Waterlogging reduced the net photosynthesis, transpiration rate and stomatal conductance of maize (Table 5), in addition, these parameters were also increased by the presence of *T. domingensis* (Table 5). The chlorophyll content was decreased by waterlogging however, no significant effect was found for *T. domingensis* presence (Table 5). The water-use efficiency was higher in plants under field capacity condition (Table 6), however, this parameter was reduced by the presence of *T. domingensis* in field capacity treatment but not for waterlogged plants (Table 6).

Table 5 - Gas exchange parameters of maize plants grown under different water levels and interaction with *T. domingensis*.

Water level	Pn	E	g_s	SPAD
Field capacity	12.65 a	1.21 a	0.041 a	30.11 a
Waterlogged	7.23 b	0.88 b	0.027 b	26.19 b
Interaction	**Pn**	**E**	**g_s**	**SPAD**
Maize+Typha	10.77 a	1.25 a	0.040 a	27.17 a
Maize	9.11 b	0.84 b	0.028 b	29.14 a

Means followed by the same lowercase letter in the columns does not differ by the Scott-Knott test for $p < 0.05$. Pn = net photosynthesis (μmol_{CO2} m^{-2} s^{-1}); E = transpiration rate (mmol $_{H2O}$ m^{-2} s^{-1}); g_s = stomatal conductance (μmol_{CO2} m^{-2} s^{-1}); SPAD = chlorophyll content in SPAD units.

Significant interaction between the factors were found for stomatal traits ($p > 0.064$). The stomatal size was not affected by waterlogging when maize was grown alone; however, when these plants were cultivated together with *T. domingensis* and under waterlogging, the stomatal size was reduced on both adaxial and abaxial leaf sides as shown by the stomatal width and length (Table 7). In addition, smaller stomata reflected on higher stomatal density on both leaf sides when maize plants were grown together with *T. domingensis* under waterlogging whereas no significant differences were found to plants under field capacity (Table 7). Furthermore, stomatal density in both leaf sides was smaller to maize plants grown together with *T. domingensis* but, under waterlogging, the stomatal density was higher on maize plants grown together with *T. domingensis* (Table 7).

Table 7 – Stomatal parameters of maize plants grown under different water levels and interaction with *T. domingensis*.

Abaxial stomatal width (μm)		
Soil	Maize+Typha	Maize
Field capacity	36.05 aA	31.41 aB
Waterlogged	30.08 bA	31.89 aA
Abaxial stomatal lenght (μm)		
Soil	Maize+Typha	Maize
Field capacity	43.20 aA	41.56 aA
Waterlogged	39.34 bA	39.81 aA
Abaxial stomatal density (stomata mm^{-2})		
Soil	Maize+Typha	Maize
Field capacity	59.17 bB	68.85 aA
Waterlogged	88.85 aA	73.33 aB
Adaxial stomatal width (μm)		
Soil	Maize+Typha	Maize
Field capacity	31.01 aA	29.16 aB
Waterlogged	27.92 bB	30.24 aA
Adaxial stomatal lenght (μm)		
Soil	Maize+Typha	Maize
Field capacity	42.56 aA	42.75 aA
Waterlogged	39.68 bB	43.98 aA
Adaxial stomatal density (stomata mm^{-2})		
Soil	Maize+Typha	Maize
Field capacity	41.87 bB	53.85 aA
Waterlogged	49.58 aA	41.04 bB

Means followed by the same lowercase letter in the columns and uppercase letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

The maize leaf anatomy was significantly modified by waterlogging condition as all tissues became thinner as compared to field capacity substrate as seen in fig. 1A, 1B, 1C and 1D (Table 8). In addition, the proportion of the mesophyll in the leaf and the vascular bundle in the mesophyll were reduced by waterlogging seen in fig. 1C and 1D whereas no significant effect was found to the proportions of vascular bundle sheath, instead the field capacity reduced the bundle sheath proportion in maize mesophyll (Table 8). No significant effect was found for most of the leaf anatomical traits under interaction with *T. domingensis*, except for the adaxial epidermis thickness and mesophyll proportion which were reduced in these conditions as seen in Fig. 1C and 1D (Table 9).

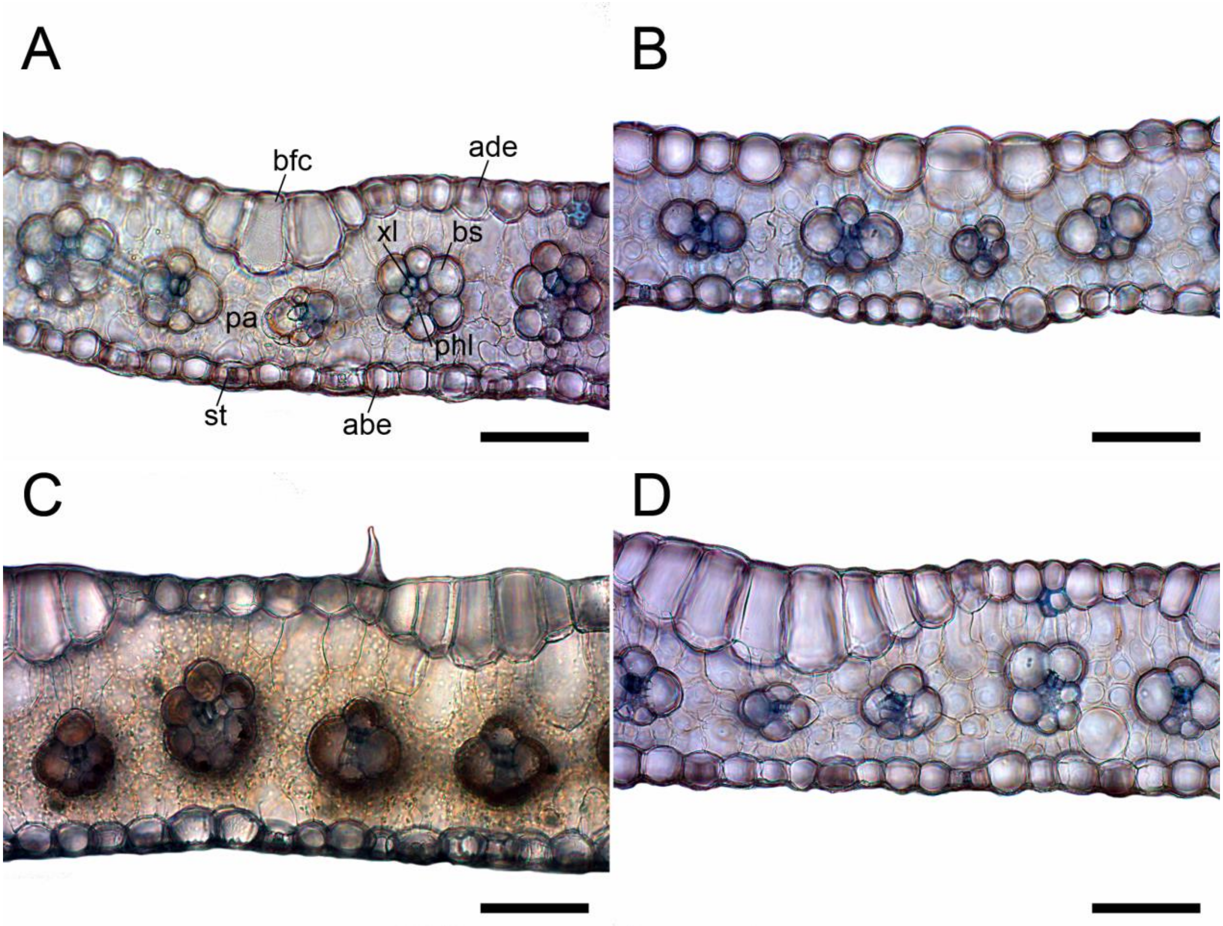

Figure 1. Transversal sections of maize leaves grown under different water levels and interaction with *Typha domingensis*. A, C = Field Capacity; B, D = Waterlogged; A, B = maize grown alone; C, D = maize grown under interaction with *T. domingensis*. Ade = adaxial epidermis, abe = abaxial epidermis, bfc = bulliform cells, st = stomata, xl = xylem, phl = phloem, bs = bundle sheath, pa = chlorophyll parenchyma. Bars = 100 µm.

Table 8– Leaf anatomical parameters of maize plants grown under different water levels.

Parameter	Field capacity	Waterlogged
Adaxial epidermis thickness (µm)	46.17 a	43.39 b
Mesophyll thickness (µm)	119.73 a	105.18 b
Mesophyll proportion (%)	62.01 a	60.69 b
Vascular bundle proportion (%)	5.30 a	4.73 b
Bundle sheath proportion in the vascular bundle (%)	82.87 a	81.99 a
Bundle sheath proportion in the mesophyll (%)	27.21 b	28.74 a

Means followed by the same letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

Table 9 – Leaf anatomical parameters of maize plants grown under interaction with *T. domingensis*.

Parameter	Maize+Typha	Maize
Adaxial epidermis thickness (µm)	43.95 b	45.62 a
Mesophyll thickness (µm)	113.23 a	111.68 a
Mesophyll proportion (%)	60.77 b	61.94 a
Vascular bundle proportion (%)	5.05 a	4.98 a
Bundle sheath proportion in the vascular bundle (%)	82.37 a	82.49 a
Bundle sheath proportion in the mesophyll (%)	27.91 a	28.05 a

Means followed by the same letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

Only the leaf vascular bundle diameter and abaxial epidermis thickness showed interaction between the sources of variation ($p < 0.0001$; $p < 0.0004$), Vascular bundle diameter was increased by the presence of *T. dominguensis* under waterlogging as shown in fig. 1D (Table 10) and while the same was true for the abaxial epidermis thickness, the aquatic plant increased the abaxial epidermis thickness in field capacity as seen in fig. 1C and D (Table 10).

Table 10 – Leaf vascular bundle diameter and abaxial epidermis thickness of maize plants grown under different water levels and interaction with *T. domingensis*.

Vascular bundle diameter (µm)		
Soil	Maize+Typha	Maize
Field capacity	70.14 aA	67.74 aA
Waterlogged	62.27 bB	68.16 aA
Abaxial epidermis thickness (µm)		
Soil	Maize+Typha	Maize
Field capacity	29.47 aA	27.11 aB
Waterlogged	24.18 bB	27.18 aA

Means followed by the same lowercase letter in the columns and uppercase letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

Under waterlogging conditions, the presence of *T. domingensis* significantly increased the average DO concentration in the substrate by 1.45 mg L^{-1} (Figure 2).

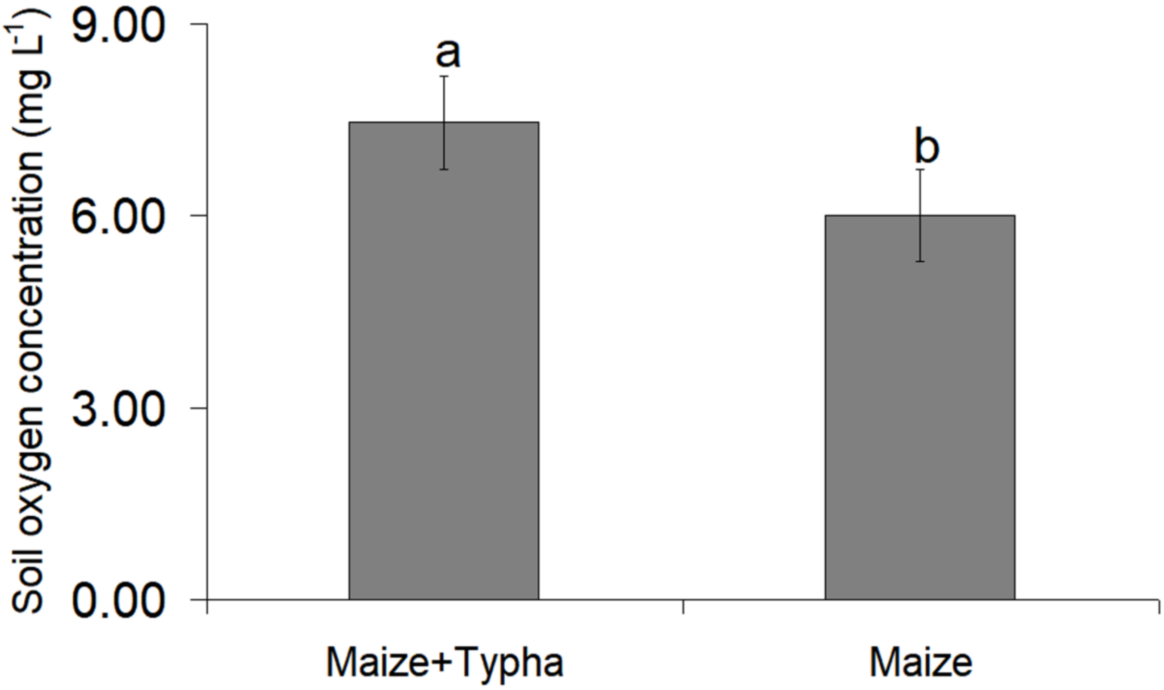

Figure 2. Oxygen concentration in waterlogged soils containing maize plants alone or maize and *T. domingensis* individuals under interaction. Bars = standard error. Different letters in the columns show significantly different means according to Scott-Knott test to $p < 0.05$.

Maize root tissues were not changed by waterlogging, except for the vascular cylinder proportion, xylem vessels area which were reduced and cortex proportion which was increased by waterlogging shown in fig. 3B and D (Table 11). In addition, most of root tissues remained unaffected by the presence of *T. domingensis* which is seen in fig. 3A and C of maize roots under interaction with *T. domingensis* whereas the exodermis and endodermis thicknesses were reduced by the interaction with *T. domingensis* (Table 12).

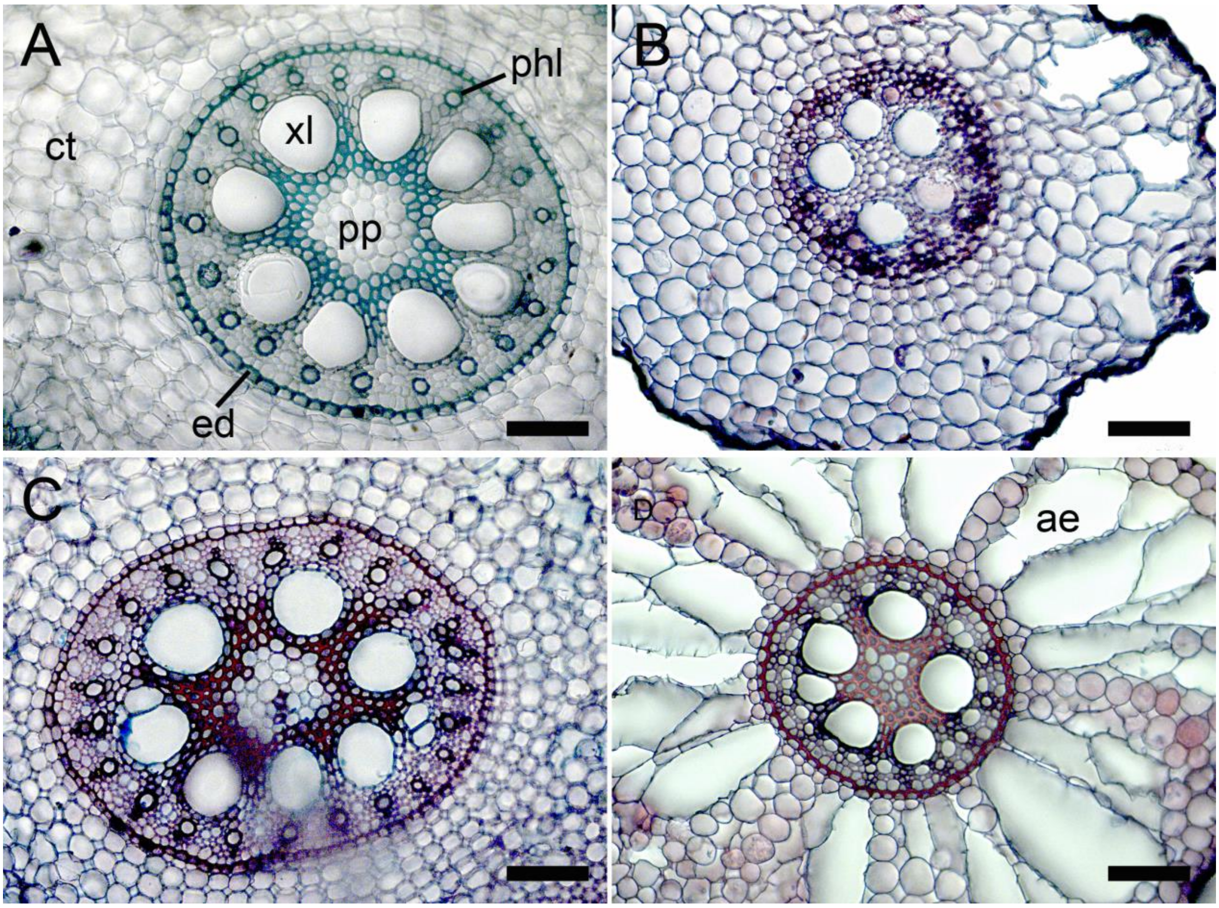

Figure 3. Transversal sections of maize roots grown under different water levels and interaction with *Typha domingensis*. A, C = Field Capacity; B, D = Waterlogged; A, B = maize grown alone; C, D = maize grown under interaction with *T. domingensis*. ed = endodermis, ct = cortex, ae = aerenchyma, xl = xylem vessel, phl = phloem, pp = pith parenchyma. Bars = 50 µm.

Table 11 – Root anatomical parameters of maize plants grown under different water levels.

Parameter	Field capacity	Waterlogged
Root cross section area (µm^2)	9455.33 a	7374.23 a
Exodermis thickness (µm)	19.62 a	18.81 a
Endodermis thickness (µm)	12.24 a	11.97 a
Cortex thickness (µm)	291.88 a	299.65 a
Xylem vessel diameter (µm)	65.82 a	60.67 a
Xylem vessel area (µm^2)	360.05 a	185.83 b
Vascular cylinder area (µm^2)	1880.62 a	896.74 b
Vascular cylinder proportion (%)	19.89 a	12.08 b
Cortex proportion (%)	80.39 b	87.92 a
Xylem proportion in the vascular cylinder (%)	18.26 a	20.11 a

Means followed by the same letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

Table 12 – Root anatomical parameters of maize plants grown under interaction with *Typha domingensis*.

Parameter	Maize+Typha	Maize
Root cross section area (μm^2)	8235.11 a	8594.44 a
Exodermis thickness (μm)	17.55 b	20.87 a
Endodermis thickness (μm)	11.29 b	12.91 a
Cortex thickness (μm)	303.97 a	287.53 a
Xylem vessel diameter (μm)	58.92 a	67.56 a
Xylem vessel area (μm^2)	263.55 a	282.34 a
Vascular cylinder area (μm^2)	1351.16 a	1426.20 a
Vascular cylinder proportion (%)	16.46 a	15.51 a
Cortex proportion (%)	83.54 a	84.77 a
Xylem proportion in the vascular cylinder (%)	18.82 a	19.55 a

Means followed by the same letter in the rows does not differ by the Scott-Knott test for $p < 0.05$

5 DISCUSSION

The higher rate of dead leaves, lower height and weight on plants under waterlogging is a common effect under hypoxia (BAILEY-SERRES; LEE & BRINTON, 2012; HERZOG et al, 2016) those parameters are all related with the decrease in photosynthesis caused by waterlogging, as the plant has decreased resources to allocate for growing. While *T. domingensis* show no effects of competition with maize for its growth parameters instead benefitting it, the biomass allocation differed when grown with *T. domingensis* in waterlogging increasing allocation of biomass on aerial parts in detriment of the roots which is in line with studies that show a decrease in the proportion of root to shoot in waterlogged plants compared to well-watered ones (BELONI et al, 2017; PROKHAMBUT et al, 2010).

Berendse and Möller (2008) shows that in soils without nutrient deficiency plants tend to compete for light more than for soil resources which explains why the interaction caused a higher shoot to root ratio under waterlogging as some of the nutrients become more available under waterlogging along with some of the nutrients being more available under waterlogging and the higher DO contributing to the mineralization of the organic matter as well as decreasing the concentration of phytotoxic compounds such as reduced forms of Fe, Mn, ethanol, etc (ELZENGA & VAN VEEN, 2010; BORNETTE & PUIJALON, 2011). *T. domingensis* combined with waterlogging decreased the apoplastic barriers of maize roots decreasing the need of a lower shoot to root ratio as the roots have higher hydraulic conductance and nutrient uptake.

The net photosynthesis, transpiration rate and stomatal conductance as well as the SPAD values were decreased by waterlogging in the same way as described by Else et al

(1995) work, probably because of anoxia damages such as the increase in ROS and the reduction of the mitochondrial electron transport chain, Conaty et al (2008) found the same behaviour in cotton (Gossypium spp. – Malvaceae). Interestingly no effect from competition was shown, instead *T. domingensis* plants increased all gas exchange parameters while maintaining SPAD unit values.

Waterlogging didn’t change stomatal size for maize grown alone but decreased the stomatal density on the adaxial epidermis and decreased the stomatal density compared to maize grown with *T. domingensis*, stomata size of both epidermis when grown with *T. domingensis* decreased which according to Hubbard et al. (2001) and Berry et al. (2010) would cause a decrease in photosynthesis, transpiration rate and stomatal conductance as bigger stomata stays open for longer, increasing transpiration rate, gas uptake and photosynthesis. As a compensation for smaller stomata the maize plants increased stomatal density demonstrated by Pereira et al (2016) that it increases CO_2 uptake and photosynthesis.

The vascular bundle diameter smaller values in maize leaves subjected to waterlogging and interaction is probably a measure to protect the plant against embolism as related by Souza et al (2010) a decrease in vascular tissues diameter is related to tolerance to waterlogging, since the aquatic plant reduced it compared to maize alone it shows an advantageous interaction when waterlogged. The decrease in mesophyll thickness under waterlogging show that the plant had its metabolism damaged as Santos et al (2015) and Pereira et al (2016) show that thicker mesophyll is often related to increased photosynthesis.

Bai et al (2013) shows that hydroponically grown *Mallus sieversii* (Ledeb.) M. Roem. - Rosaceae and *Mallus hupehensis* (Pamp.) Rehder – Rosaceae showed decreases in photosynthesis and stomatal conductance by low DO levels, which explains why the maize plant grown with *T. domingensis* increased gas exchange parameters as it had higher DO in the substrate. The increase in DO may have contributed to the anatomical changes as the radial oxygen loss increases apoplastic barriers tend to get more lignified and thicker decreasing hydraulic conductance and gas exchange such as transpiration rate, thus the increase in gas exchange parameters and decrease in apoplastic barriers in interaction with *T. domingensis*.

The decrease in vascular cylinder area, vascular cylinder proportion root cross section, and reduced xylem vessel area under waterlogging shown in maize plants under waterlogging is a mechanism of protection against embolism as seen in Souza et al (2010) work. The cortex proportion increase in waterlogged plants is a mechanism to increase the apoplastic barriers decreasing the water intake and radial oxygen loss from the roots, but this decrease in hydraulic conductance is at the cost of a decrease in transpiration rate, photosynthesis and stomatal conductance which was true for waterlogged maize.

The decrease in apoplastic barriers thickness in roots of maize grown with *T. domingensis* is a mechanism which favours the plant by increasing nutrient and water uptake, thus increasing photosynthesis, stomatal conductance and transpiration rate as shown by the description of the endodermis and exodermis functions in roots by Enstone et al (2002), this may be directly related with the increase in height, elongation rate and number of fully expanded leaves shown in maize plants.

Normally plants under waterlogging stress develop thicker apoplastic barriers to minimize damage caused by radial oxygen loss and toxins as shown by Cheng et al (2012) while a decrease in radial oxygen loss is related to anatomical changes caused by the environment. The overall management of maize root anatomy in presence of *T. domingensis* may be related to the oxygenation of the substrate which is in line with Calaway and King (1996) study that shows *T. latifolia* as a facilitator in *Myosotis laxa* Lehm (Boraginaceae) survival in anaerobic soils by oxygenating it.

One of the greatest benefits of the increase of DO is that it minimizes the oxidative damage caused by ROS with the maize plant better allocating resources instead of spending it in the biochemical machinery to reduce it. As well as increasing respiration efficiency, providing the necessary means for the mitochondrial electron transport chain to work. Maintenance of cell membrane structure by the increased DO can enhance hydraulic conductance efficiency via symplast and apoplast increasing the plant Pn as well as evapotranspiration (BLOKHINA, VIROLAINEN & FAGERSTEDT, 2003).

Goto et al (1996) shows that the use of pressurization systems and injection of pure O_2 in the hydroponic systems can be expensive whereas could be made cheaper by using plants such as *T. domingensis* which increases DO in the substrate. While the increased DO concentration was more than what is considered necessary for lettuce, the demands for oxygen is plant specific with plants such as maize demanding a much higher DO.

The intercropping with aquatic plant such as T. domingensis could be an efficient way of conducting riparian zone management, as these zones have a great biodiversity housing many small animals and plants which increases its biological oxygen demand (BOD), being benefitted by the increase in DO provided by the aquatic plant, increasing the water quality and quality of life for the inhabitants of those ecosystems (GYAWALI et al, 2013).

The interaction of cattail and maize plants in artificial wetlands for treatment of agricultural runoffs could be beneficial in both waste management and as a biomass source for bioenergy plants as Nkemka et al (2015) shows the viability of the use of cattail and maize biomass for lignocellulosic energy, meaning that the plants could be cleaning the area as a biological filter while decreasing the carbon footprint emissions.

Aquaculture is one of the new alternatives for a sustainable agriculture, with approximately 70% of the whole world production concentrated in China. While a viable form of sustainable agriculture it can increase pollution of water systems because of its high BOD, whereas new management systems such as using *T. domingensis* plants which increases DO, decreasing BOD is necessary, whereas the use of a system consisting of Maize and *T. domingensis* could still be used for biomass production creating a viable sustainable system (FANG et al, 2017; LI et al, 2011; NKEMKA et al, 2015).

6 CONCLUSION

The study shows that maize suffers no effect from competition with *T. domingensis* plants and is instead favoured by its presence which increased DO concentration in the substrate and photosynthetic rates promoted by a higher stomatal density and decreased root apoplastic barriers, which may increase nutrient uptake and hydraulic conductance.

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