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Response of *Eragrostis plana* and *Eragrostis pilosa* (L.) P. Beauv. submitted on flooded soil

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ABSTRACT. The development of *Eragrostis plana* and *Eragrostis pilosa* was evaluated in a greenhouse when submitted to different soil moisture conditions. The design was completely randomized, consisting of a factorial 2x3, with the following factors: *Eragrostis* accessions and soil moisture levels (50% of water retention capacity (WRC), 100% of WRC and soil with water depth of 10 cm). The morphological-anatomical parameters of the plants were evaluated and the aerenchyma and adventitious roots were quantified. In addition, the photosynthetic pigments and the electron transport capacity of the photosynthetic chain were quantified, with the intention of verifying if the amount of water in the soil interferes with these parameters. Similar responses were observed between the two species when submitted to a water table environment, where there were larger aerenchymal formations in the roots and stems, as well as adventitious roots at the soil surface, inferring adaptations for survival to anaerobic stress. Negative effects on the transport of electrons and the formation of chlorophyll pigments were observed for both species when submitted to the hypoxic environment and, consequently, there was reduction of dry mass of shoot and roots, as well as reduction in the emission of tiller. It is concluded that the irrigation water management and the water blade in the rice crop are important, together with the control of invasive plants, considering the negative effects caused to the growth and development of these plants.

Keywords: hypoxi; morphology; photosynthesis; flooding.

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Introduction

Grasses are the main weeds that affect the cultivation of irrigated rice (*Oryza sativa* L.), due to the fact that they present morphology, nutritional requirements and similar growth habit, making it even more difficult to control (Nagargade, Singh, & Tyagi, 2019). Among the grasses that affect rice crops, the species *E. plana* and *E. pilosa* stand out due to the recent introduction to rice crops environment and competition with the crop.

Capim-annoni-2, popularly known as *E. plana*, has high prolificity, rusticity and the ability to acclimatize in distinct environments with rapid naturalization, due to its allopathic action, characteristics that confer invasiveness and strong competition (Favaretto, Basso, Felini, Zoch, & Carneiro, 2011). According to Basso, Favaretto, Felini, and Cecchin (2012) Capim-annoni-2 is the most aggressive invader and difficult to control in the fields of Rio Grande do Sul.

Popularly known as Indian lovegrass, *E. pilosa* is commonly found competing with rice cultivation. This species has a high seed production, its inflorescence is characteristic and distinguishes it from other species of the genus, through the position of the spikelets with an angle of 90º in relation to the main raceme and gray color (Kissmann, 1997).

The irrigated rice production areas are in constant flooding. The lack of oxygen (hypoxic environment) for long periods, reflects on morphological, anatomical and physiological responses, such as the formation of diageotropic roots, adventitious roots, aerenchymas and the formation of cortical or epidermal WRCcks in stems resulting from hypertrophy (Ezin, De La Pena, & Ahanchede, 2010; Dias, Lemke, & Oliveira, 2011;

Kato & Okami, 2011; Parlanti et al., 2011). In addition to the reduction of biomass, formation of adventitious roots, aerenchyma and pneumatophores, leaf expansion, induction of leaf abscission and senescence (Zanandrea et al., 2009; Oliveira & Joly, 2010).

The research aims to describe the mechanisms and anatomical changes developed by accessions of *E. plana* and *E. pilosa* to survive in environments of rice fields through the simulation of this flooded environment in a greenhouse. The knowledge of the adaptive strategies of these plants is important so that control strategies can be designed within an integrated management of rice cultivation.

Material and methods

A hundred grams of seeds of *E. plana* and *E. pilosa*, previously identified in the field, were collected as one access to each collected plant. In the laboratory, the seeds were cleaned and dried for better storage.

The analysis of the anatomical plasticity of the accessions took place in a greenhouse. Sowing of caryopses was carried out in pots divided into three conditions of soil water retention capacity (WRC). The soil used came from an irrigated rice cultivation area, which was sieved with a 5 mm sieve and subsequently placed in pots with a capacity of 7.5 liters, packed with a 0.2 mm plastic mesh splint, filled with 6,0 kg of soil.

The experiment consisted of 60 pots divided between the two species (30 pots for each species). Each pot received 5 seeds of the same species. After seedling emergence, thinning was carried out, leaving one plant per pot. Sowing took place on December 30, 2014 and seedlings emerged between January 06 and 09, 2015.

Pots containing seeds of the same species were divided into three groups of 10. The three groups are described as follows: the first group presents 50% of the WRC with the intention of simulating a dry environment (coxilha), the second group received 100% of the WRC in order to simulate waterlogged environments (floodplains) and the third group presented a 10 cm water depth simulating an irrigated rice crop environment (flooded frame). The experimental design used was completely randomized with a 3 x 2 factorial, where factor A presents the three humidity conditions (50% of the WRC; 100% of the WRC and 10 cm water depth) and Factor D the two species (*E. pilosa* and *E. plana*) and 10 repetitions per treatment.

The WRC was obtained using the following equation:

$$WRC = P2 - P1$$

WRC is the water holding capacity; P1 is the weight of the pot with dry soil; P2 is the weight of the pot with soil in field capacity.

To obtain the treatment humidity (50% and 100% of the WRC), formulas were used to determine:

$$PV100\% = (PVCRA - PVdry).1 + PVdry$$

$$PV50\% = (PVCRA - PVdry).0.5 + PVdry$$

PVn% is the weight of the pot for each treatment; PVWRC is the water holding capacity of the soil; PVdry is the weight of the pot filled with dry soil.

The treatments of 50%, 100% of the WRC and water depth were introduced when the plants were in the stage of 3 to 4 leaves. Until that moment, the plants received constant irrigation of 75% of the WRC. For the determination of 75% of the WRC it was based on the formula:

$$PV75\% = (PVCRA - PVdry).0.75 + PVdry$$

PVn% is the weight of the vessel for each treatment; PVWRC is the water holding capacity of the soil; PVdry is the weight of the pot filled with dry soil.

On January 21, 2015, fifteen days after seedling emergence, treatments started. The maintenance of the treatments was performed through daily irrigations with the weighing of the pots on an ACS System scale with a precision of 5 g, and the replenishment of water in the pot to reach the WRC of each predetermined treatment (pot weight + dry soil weight + body of water to reach the required WRC). The fertilization of the experimental units was based on soil analysis based on the recommendations for the cultivation of irrigated rice. Homogeneous fertilization was carried out in all experimental units.

The collection of material for anatomical analysis of the accessions was performed when the plants were in the flowering stage. With the aid of a scalpel, cuts were taken from the middle third of the root and stem of each plant in each experimental unit. In a test tube containing 1% glutaraldehyde fixative and 4% formaldehyde, in 0.1 M phosphoric buffer, the sections were placed in order to maintain cell integrity. The

storage of the tubes containing the collected material occurred in wire racks in an upright position at 5ºC and were fixed in a vacuum chamber and later stored in a refrigerator until the blades were made.

The technique used for making the slides followed the protocol modified by Mariath and Santos (1996), the Historesin-Jung technique. The material was packaged in hydroxyethyl methacrylate, with the aid of a rotating microtome, anatomical cross-sections of 4 micrometers thick were obtained and subsequently processed and fixed on a glass slide stained with 0.05% toluidine blue (Feder & O'brien, 1968).

Anatomical cuts of root and stem of both species were evaluated. For observation and photographic recording of the anatomical sections and their detailed structures, a Zeiss optical microscope (Axio Scope.A1) was used with a high resolution camera attached and integrated with a microcomputer carrying the Zen 2012 image analysis software. The photographic record, the images underwent an evaluation in order to determine the relative area of the root and stem section that effectively presented formation of air or aerenchyma spaces. For this, the Zen 2012 software was used, which has an analysis and image editing tool, in which the total area of the cut section and the area occupied by the aerenchyma structures were measured, thus allowing by means of a simple equation to determine the relative area in percentage (%). The results were analyzed using the SISVAR® 5.3 software (Ferreira, 2011), where they were subjected to analysis of variance via bootstrap with 2000 simulations and the treatment averages for each species, and were separately compared using the Tukey test at the level of 5 % of significance.

The concentrations of chlorophyll a (Chl a), chlorophyll b (Chl b) and total chlorophyll (Chl total), as well as the carotenoid content, were determined following the methodology described by Hendry and Price (1993), using four samples per treatment.

From the middle third of the flag leaf of plants for each treatment, tissue samples were collected, immediately frozen in liquid N2. The samples were macerated in a crucible. Afterwards, 50 mg of each sample was homogenized in 5.0 mL of 80% acetone, being transferred to Falcon tubes with the aim of centrifuging at 4,000 rotations for 3 minutes at a temperature of 25° C as recommended in the methodology.

The absorbances of the supernatant at 480, 645 and 663 nm were determined in a spectrophotometer model SF325NM (Bel Engineering, Italy) and the concentrations of chlorophyll a, b, total, as well as the carotenoids were calculated using the equations:

$$Chl\ a\ (mg\ g-1\ MF): \frac{(((11.75\ x\ A663)\ -\ (2.35\ x\ A645))\ x\ V)}{MF}$$

$$Chl\ b\ (mg\ g-1\ MF): \frac{(((18.61\ x\ A645)\ -\ (3.96\ x\ A663))\ x\ V)}{MF}$$

$$Chl\ total\ (mg\ g-1\ MF): Chl\ a\ +\ Chl\ b$$

$$Carotenoids\ (mg\ g-1\ MF): \frac{((1000\ x\ A480)\ -\ (2.27\ x\ Chl\ a)\ -\ (81.4\ x\ Chl\ b))\ /227)\ x\ V}{MF}$$

Chl a = Chlorophyll a, Chl b = Chlorophyll b, A480 = Supernatant absorbance at 480nm, A645 = Supernatant absorbance at 654nm, A663 = Supernatant absorption at 663nm, V = leaf extract volume (mL) and MF = fresh mass sample (mg).

The chlorophyll fluorescence parameters a: initial fluorescence (Fo), maximum fluorescence (Fm), variable fluorescence/maximum fluorescence ratio (maximum photochemical efficiency of PSII) (Fv Fm^{-1}), the variable fluorescence/initial fluorescence ratio (Fv Fo-1), the effective quantum yield of PSII (YII125) and the electron transport rate (ETR1500) were measured with the JUNIOR-PAM modulated pulse fluorometer (Walz, Germany) between 3:00 am and 8:00 am. For the measurements, the flag leaf of the mother plant of each evaluated plant was used. Before the measurements, the leaves to be analyzed were pre-adapted in the dark for a period of 30 minutes to determine the initial fluorescence (Fo) and, subsequently subjected to a pulse of saturating light (10,000 µmol m-2 s) for 0, 6 s, thus determining the maximum fluorescence (Fm). The maximum photochemical efficiency of PSII (Fv Fm-1) was calculated using the variable fluorescence ratio (Fm-Fo) and the maximum fluorescence and the Fv Fo-1 ratio using the variable fluorescence ratio (Fm-Fo) and the initial fluorescence. The electron transport rate (ETR1500) was determined using light curves (electron transport rate versus light intensity - PAR), which were constructed by subjecting each sample to nine levels of radiation (0, 125, 190, 285, 420, 625, 820, 1150 and 1500 µmol

electrons m^{-2} s^{-1}) every 10 s. The curves and graph generation were obtained using the SIGMAPLOT version 2011 program. The data were subjected to analysis of variance after verifying the assumptions regarding normality and homogeneity. Being significant, they were submitted to the Tukey means test at 5% probability of error.

The measurements were adjusted using the equation ETR = ETRmax [1 – e ^ _kQ], where k is a fitting constant, and Q represents the light intensity (PAR), according to the methodology described by Rascher, Liebig and Lüttge (2000).

The number of tillers was counted at the stage of full flowering. For dry mass analysis, four plants were removed from the pots and the aerial part (including mother plant and tillers) was separated from their roots. After that, the root system was cleaned with running water in a closed container, recovering the loose roots. The clean materials were placed in porous paper bags, and placed in an oven with forced air drying at a temperature of 65° C until it reached constant weight.

Results and discussion

The results obtained for the root anatomy (Table 1) allow us to observe that both *E. pilosa* and *E. plana* species presented a similar response regarding the formation of aerenchyms in this organ. With 50% of the WRC, no aerenchymatic tissues were observed in the cortex and in the central root cylinder of the cuts analyzed (Figures 1 and 2). As the amount of water in the soil increased, from 100% of the WRC there was a greater formation and occupation of relative areas of the cortex with aerenchymas, and with a water depth, a statistically greater relative area was obtained with these air reserve tissues and O2 diffusion in response to flooding.

Table 1. Tukey test with a significance level of 5% for the variable relative area (%) of the root section with formation of air spaces (aerenchyma).

Soil moisture condition	Relative area (%) of root section	
	E. plana	*E. pilosa*
1. 50% of the WRC	0.0000 c	0.0000 c
2. 100% of the WRC	26.7744 b	35.9471 b
3. Water depth	57.6090 a	55.6949 a
DMS	7.9181	16.1524
CV (%)	14.0848	26.8110
Pr>F	0.0003	0.0000

*Averages followed by the same letter in the column do not differ statistically under different water conditions, using the Tukey test at 5% probability of error.

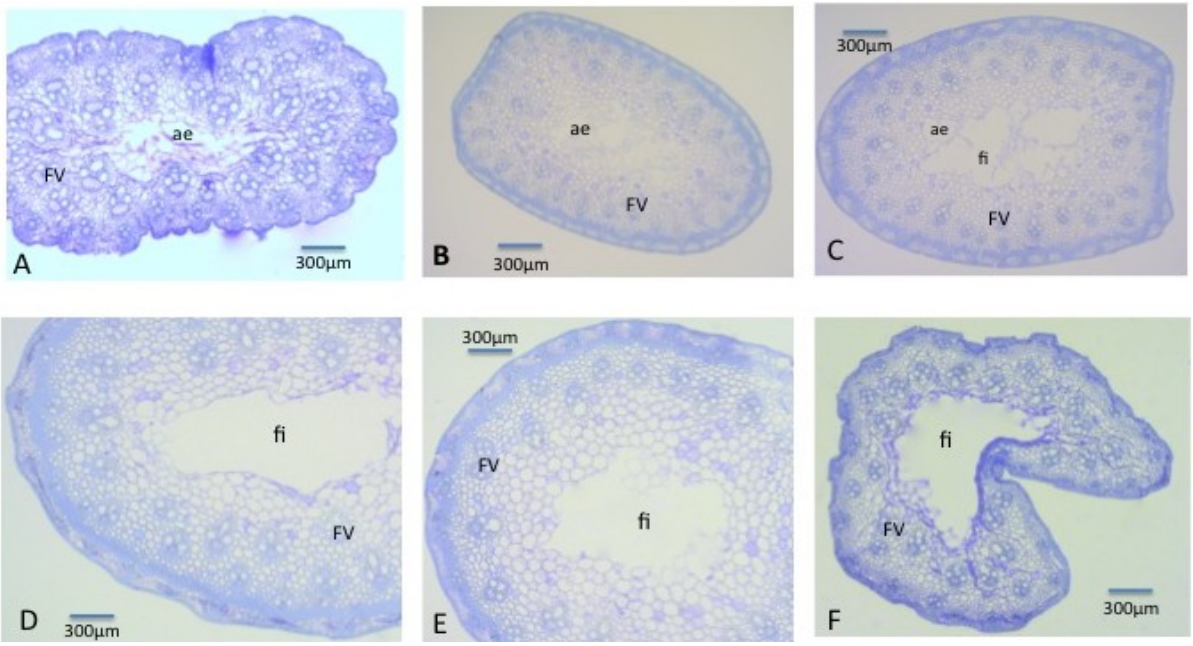

Figure 1. Cross sections of stems of *E. plana* (A- 50% WRC; B- 100% WRC; C- Water depth) and *E. pilosa* (D- 50% WRC; E- 100% WRC; F- Water depth. Ae = aerenchyma; fi = fistula marrow; fv = vascular bundles.

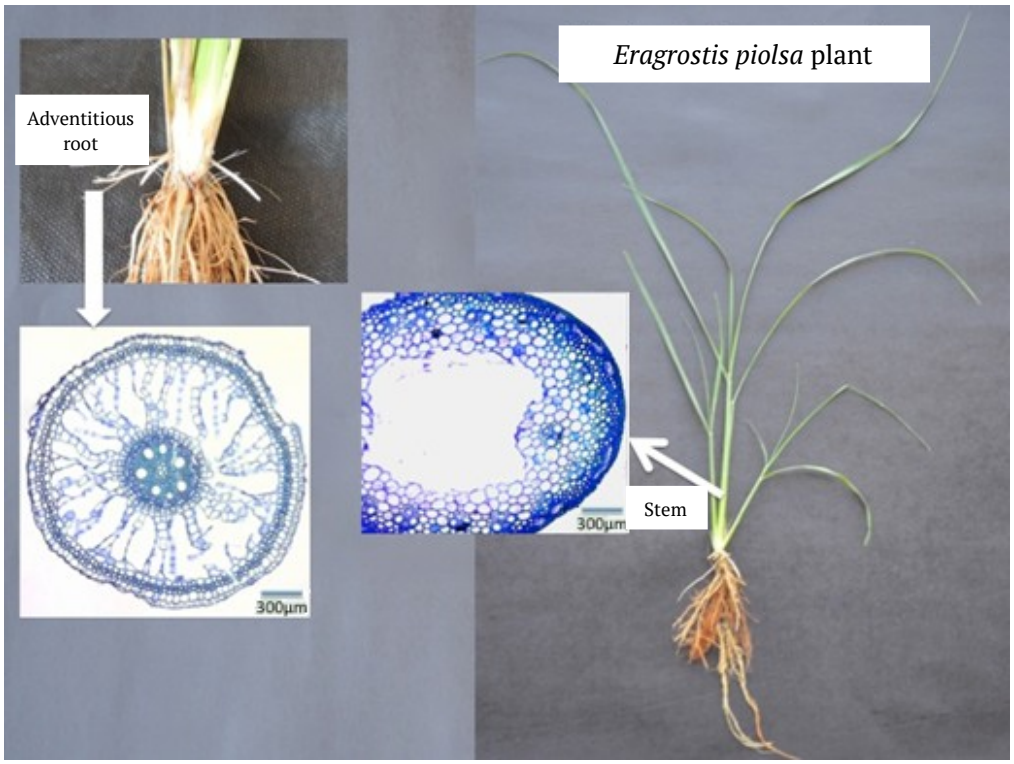

Figure 2. Cross sections of stems and roots of *E. pilosa* under water depth. Detail of the formation of adventitious roots on the soil surface.

In *Zea mays*, Pires, Castro, Magalhães, Silva Neta, and Monteiro (2015) also found greater aerenchyma formation in plant roots subjected to flooding with maintenance of water depth on the soil surface when compared to 50% WRC water. Results that corroborate those obtained in the present study with species of the genus *Eragrostis*.

The analysis of the data related to the relative area (%) of the stem occupied by aerenchyma (Table 2), allows to verify that for *E. pilosa* there was no statistically significant difference (p-value > 0.05) between the treatments with different amounts of water in the soil (50% of the WRC, 100% of the WRC and 10 cm water depth). These results are due to the greater adaptation of this species to the flooded environment, since it is a common species in lowland rice production environments, as stated by Kissmann (1997). It is assumed that this characteristic is already incorporated into the genotype of the species for the longest period of adaptation to the flooded environment, and the plant forms more aerenchyms in the root cortex than in the stem cortex, in addition to adventitious roots on the soil surface, morphological changes that allow these plants to survive in this hypoxic environment.

Table 2. Relative area (%) of the stem section with formation of air spaces (aerenchyma) in *E. plana* and *E. pilosa* plants. Santa Maria-RS, 2015.

Soil moisture condition	Relative area (%) of stem section	
	E. plana	*E. pilosa*
1. 50% da WRC	7.1594 b	1.85 ^{ns}
2. 100% da WRC	5.0836 b	1.70
3. Water depth	10.1956 a	1.56
DMS	5.8896	3.8857
CV (%)	44.2944	27.4883
Pr>F	0.0300	0.7013 ^{ns}

*Averages followed by the same letter in the column do not differ statistically under different water conditions, using the Tukey test at 5% probability of error. ** ns = not significant (p > 0.05).

Evaluating the *E. plana* species, which is a species that originally grows in high and well-drained land (Kissmann, 1997), it appears that the relative area occupied by aerenchyms in the stem is significantly larger (p-value < 0.05) in the condition where the plants were submitted to water depth, possibly an adaptive response to the hypoxia found in this environment.

In grasses, the immediate reaction to flooding is the formation of aerenchyms due to the presence of ethylene which promotes an ethylene-H_2O_2 signaling process (Pires et al., 2015), accumulating substances

such as ethanol, acetaldehyde and lactate in the cells that acidify the cytoplasm causing disruption of the cell wall (damage to elastins, cellulose, hemicellulose and wall lignins), effects on the tonoplast membrane and the nuclear membrane, causing an increase in areas in the tissues for oxygen storage and diffusion, which are commonly called aerenchymas.

In Table 3, it is possible to observe that as the amount of water in the soil increased from 100% of the field capacity, adventitious roots were formed in the stem-root transition zone in the two species evaluated (*E. pilosa* and *E. plana*). The greater formation of adventitious roots on the soil surface was observed in the condition of water depth in response to the anaerobic condition and probably due to the use of this oxygen diffused from the aerenchyma system formed in the stem and roots for this oxidized soil zone, just below the flooded surface. In soybean plants grown in flooded lowlands, Pereira, Castro, Souza, and Magalhães (2008) found that the adaptability mechanism of this grass to anaerobiosis is not only the formation of aerenchyma, but mainly the formation of adventitious roots.

Table 3. Average amount of adventitious roots formed, number of tillers and aerial dry mass, and roots depending on different soil moisture conditions. Santa Maria-RS, 2015.

Soil moisture	Number of tillers per plant		Dry mass (g)				Average amount of adventitious roots formed on the soil surface	
			Aerial part		Root			
	E. plana	*E. pilosa*	*E. plana*	*E. pilosa*	*E. plana*	*E. pilosa*	*E. plana*	*E. pilosa*
1. 50% WRC	99.45a	52.23a	75.46a	46.79a	91.35 ^{ns}	52.42a*	0.00c	0.00c
2. 100% WRC	81.62a	47.99a	66.66a	42.04a	92.36	47.50a	6.25b	10.20b
3. Water depth	79.33b	8.93b	35.49b	10.23b	89.27	11.98b	24.25a	27.75a
CV (%)	12.84	10.03	15.61	19.72	-	14.95	25.87	19.79

*Averages followed by the same letter in the column do not differ statistically from each other under different water conditions by the Tukey test at 5% probability of error. ** ns = not significant (p > 0.05). WRC = Water Retention Capacity in the soil.

The plant under hypoxia, to form superficial and aerenchymal adventitious roots, diverts carbohydrates to the new structures. Normally, these carbohydrates would be carried to expand the leaf area (Costa et al., 2018). In grasses they also divert energy for the emission of tillers. However, to ensure the adaptability and survivability of the plant, these photoassimilates are translocated preferentially for the formation of superficial adventitious roots compared to primary roots due to their high porosity (Yamauchi, Colmer, Pedersen, & Nakazono, 2018).

In the case of the *Poaceas* evaluated in this research, there was no damage caused by fissures to the primary and secondary root system, and both aerenchyma and adventitious roots showed fundamental anatomical-morphological changes in their adaptation to the hypoxic environment promoted by the 10 cm water depth.

Tables 4 and 5 show that the hypoxia condition caused by the water depth influenced the electron transfer rate measured by the chlorophyll fluorescence in both species of *Eragrostis*. The maximum luminosity measurement (ETR1500) demonstrated that the increase in the amount of water in the soil negatively affected photosynthesis in the evaluated *Eragrostis* species. Other important responses to the anaerobic condition to which plants are subjected to flooding conditions are related to the lower growth of the aerial part (Farooq, Kobayashi, Ito, Wahid, & Serraj, 2010) with reduction of the photosynthetically active leaf area index (Kozlowski, 1984).

Table 4. Electron transport rate (ETR) of *E. pilosa*, submitted to different water conditions. Santa Maria-RS, 2015.

Treatment	PAR (light intensity)								
	0	125	190	285	420	625	820	1150	1500
A	0^{ns}	26.6a	32.2^{ns}	38.8a*	47.6a	50.2a	57.0a	64.1a	69.4a
B	0	22.5a	28.5	37.1a	45.1a	49.2a	54.9a	63.5a	70.5a
C	0	18.9b	25.0	30.7b	36.9b	41.2b	45.5b	53.6b	64.8b

*Averages followed by the same letter in the column do not differ statistically from each other by the Tukey test at 5% probability of error. ** ns = not significant (p > 0.05). Treatments: A (50% of WRC), B (100% of WRC) and C (Water depth). WRC = Water holding capacity in the soil.

Table 5. Electron transport rate (ETR) of *E. plana*, submitted to different water conditions. Santa Maria-RS, 2015

Treatment	PAR (light intensity)								
	0	125	190	285	420	625	820	1150	1500
A	0^{ns}	25.6^{ns}	32.2^{ns}	40.7^{ns}	48.8^{ns}	52.7a*	59.6a	68.0a	74.3a
B	0	23.5	29.4	36.7	43.9	46.8a	52.6a	61.0a	63.9a
C	0	21.3	25.7	31.0	36.6	38.4b	45.5b	53.5b	57.8b

*Averages followed by the same letter in the column do not differ statistically from each other by the Tukey test at 5% probability of error. ** ns = not significant (p > 0.05). Treatments: A (50% of WRC), B (100% of WRC) and C (Water depth). WRC = Water holding capacity in the soil.

The extreme condition of hypoxia called anoxia (total absence of oxygenation) that occurs in the deepest areas of the flooded soil, limits plant development (Morard & Silvestre, 1996) since they promote physiological disturbances in the most sensitive plants due to the difficulty of root absorption of soil nutrients, especially nitrogen (Gutiérrez-Gamboa et al., 2018) and phosphorus. Nitrogen is important for pigment formation and phosphorus deficiency negatively influences on chlorophyll production and fluorescence (Gutiérrez-Gamboa et al., 2018).

This stress is one of the factors that must have influenced the lower dry matter production of the aerial part of the plants, as well as the lower tillering under water depth (Table 3). According to Maxwell and Johnson (2000), as fluorescence is one of the ways of dissipating the absorbed light energy and the variations that occur in it, they can be measured to demonstrate changes in other ways of dissipation such as heat or photosynthesis, the values measured allow to demonstrate responses to stresses that these plants go through. In the case of hypoxia, this result may also be related to less nitrogen absorption, as well as by the accumulation of iron or manganese (toxicity) and gases such as carbon dioxide and ethylene.

Under hypoxia/anoxia, there is a change in the gaseous phase of the soil, forming undesirable gases such as CH_4, H_2S, N_2O, C_2H_4, H_2 occurring O_2 deficiency and carbon dioxide accumulation (Batista, Medri, Bianchini, Medri, & Pimenta, 2008) which causes a reduction in phosphorylation oxidative and ATP production with protein denaturation (Steffens, Hütsch, Eschholz, Losak, & Schubert, 2005) and effect on the formation of important pigments. This way, it is possible verify the effects of stress on photosynthesis, such as that caused by the effects of hypoxia, by measuring the amount of photosynthetic pigments (Hendry & Price, 1993). Photosynthetic pigments such as chlorophyll a and b and carotenoids are chemical structures responsible for the absorption and capture of light energy in the initial stages of photosynthesis, so negative effects on the formation of these compounds can be measured.

There was a significant increasing reduction ($p < 0.05$) in the concentration of chlorophyll a and total chlorophyll pigments (Table 6) when the *E. pilosa* and *E. plana* plants were subjected to increasing amounts of water in the soil, especially in the condition of 10 cm water depth. This measure reinforces the values found for the electron transport rate (ETR) whose response was similar, which allows us to infer that the lower amount of chlorophyll a pigments and the lower electron transfer by PSII, affected photosynthesis in the plants studied (Figure 3) explaining their lower growth and development.

Table 6. Effect of three soil moisture conditions (50% of the WRC; 100% of the WRC and 10 cm water depth) on the concentration of chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl total), in the chlorophyll a to chlorophyll b ratio (Chl a / b), the carotenoid concentration and the carotenoid to total chlorophyll ratio (carotenoids / total Chl). Santa Maria-RS, 2015.

Soil moisture	Evaluated parameters					
	Chl a (mg g^{-1} MF)	Chl b (mg g^{-1} MF)	Chl total	Carotenoids (mg g^{-1} MF)	Chl a/b	Carot/Chl total
			E. plana			
1. 50% WRC	1.125a	0.236^{ns}	1.160ab	0.270^{ns}	3.69^{ns}	0.252a
2. 100% WRC	1.206a	0.244	1.301a	0.281	3.91	0.240ab
3. Water depth	1.016b	0.231	1.011b	0.263	4.42	0.210b
CV%	7.90	20.38	11.55	6.64	17.03	6.56
			E. pilosa			
1. 50% WRC	1.387a	0.267^{ns}	1.669a	0.334^{ns}	4.90^{ns}	0.237a
2. 100% WRC	1.348a	0.260	1.607a	0.359	4.94	0.232a
3. Water depth	1.025b	0.282	1.288b	0.310	3.93	0.199b
CV%	7.23	14.54	7.24	10.35	11.13	5.90

*Averages followed by the same letter in the column do not differ statistically from each other by the Tukey test at 5% probability of error. ** ns = not significant ($p > 0.05$). Treatments: A (50% of WRC), B (100% of WRC) and C (Water depth). WRC = Water holding capacity in the soil.

The results found for the chlorophyll a fluorescence variables, such as initial fluorescence (Fo), maximum fluorescence (Fm) and effective quantum yield of PSII (YII) $_{125}$ were not affected by the increase in the amount of water in the soil (not significant $p > 0.05$).

In physiologically balanced plants, the $Fv\ Fm^{-1}$ values normally reach approximately 0.85 in low radiation conditions, which may vary between species (Nordenkampf et al., 1989), and values lower than this may indicate that the plants were exposed to some type of biotic or abiotic stress that reduced the photochemical capacity of photosystem II (Dias & Marenco, 2007).

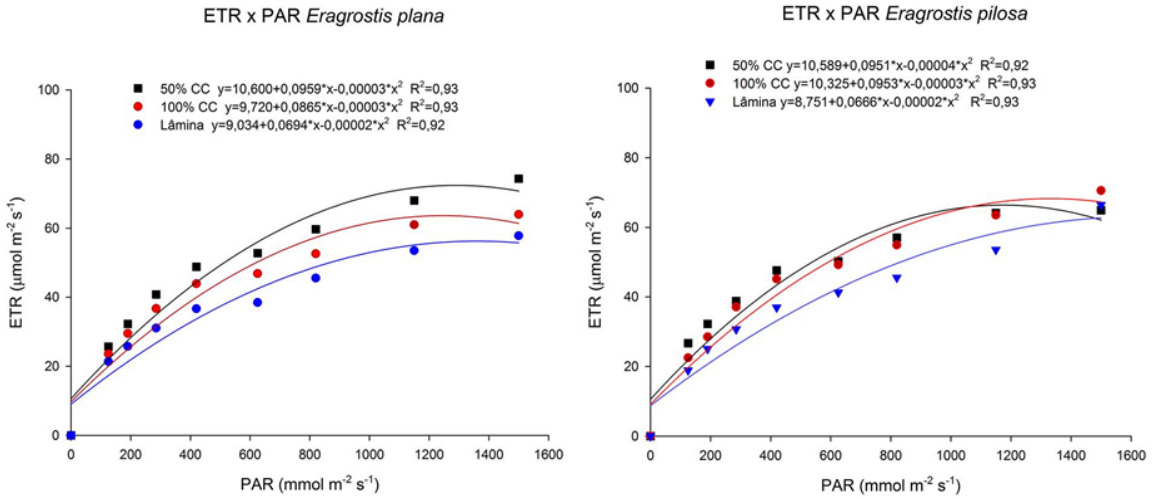

Figure 3. Electron Transfer Rate (ETR) versus light intensity (PAR) measured by chlorophyll fluorescence in three soil moisture conditions and two plant species A. *E. plana* and B. *E. pilosa*.)

In this context, it can be seen from Tables 7 and 8 that, although there was no statistically significant difference ($p > 0.05$) between treatments with different amounts of water in the soil in the parameter quantum efficiency of photosystem II (PSII - Fv Fm^{-1}), the values found below what is considered to be normal (<0.85) reveal that there may be some stress on the plants even with 50% of the WRC. In the case of water depth, when the electron transport rate is verified at maximum brightness (ETR1500), it can be inferred that the generated energy that should be used to fix CO_2, as the quantum efficiency of PSII is not statistically different between treatments, must have been carried to produce adventitious and aerenchymal roots, hindering the growth and development of the aerial part of the plants.

Table 7. Basal fluorescence (Fo), and maximum fluorescence (Fm) of chlorophyll *a*; Potential quantum efficiency of FSII (Fv Fm^{-1}), of *E. pilosa* submitted to different soil water conditions. Santa Maria-RS, 2015

Treatment	Fo	Fm	Fv/Fm
50% of the WRC	152.250^{ns}	675.750^{ns}	0.774^{ns}
100% of the WRC	152.500	660.500	0.769
Water depth 10 cm	138.000	594.250	0.767

Averages followed by a different lowercase letter in the column differ statistically under different soil water conditions, using the Tukey test at 5% probability of error. ** ns = not significant ($p < 0.05$). WRC = soil water holding capacity

Table 8. Basal fluorescence (Fo), and maximum fluorescence (Fm) of chlorophyll *a*; Potential quantum efficiency of FSII (Fv Fm^{-1}), of *E. plana* submitted to different soil water conditions. Santa Maria-RS, 2015

Treatment	Fo	Fm	Fv/Fm
50% of the WRC	162.000^{ns}	730.250^{ns}	0.777
100% of the WRC	155.25	698	0.777
Water depth 10 cm	157.33	684.67	0.77

*Averages followed by a different lowercase letter in the column differ statistically under different soil water conditions, by Tukey's test at 5% error probability. ** ns = not significant ($p < 0.05$). WRC = soil water holding capacity

These responses vary between species. Plants more sensitive to anaerobiosis by flooding produce less ATP (Pereira et al., 2008), form ethylene and close stomata reducing CO2 assimilation with damage to their growth and development (Medri et al., 2010). More tolerant plants, react to anaerobic stress by forming aerenchymatic tissues (in the cortex of roots and stems) that are specialized in the diffusion of oxygen from the aerial part to the root system (Leite, França, & Scatena, 2012), or they can form adventitious roots where the produced carbohydrates are carried, especially if these roots are important for adaptability to this environment as in *Z. mays* (Pereira et al., 2008). However, by diverting this energy to produce adventitious roots, it has affected its physiology due to the lower rate of liquid photosynthesis and thus, it may show less growth and development of the aerial part, however they promote a higher survival rate to the hypoxic environment (Pisicchio et al., 2010).

Conclusion

Flooding causes the plants of *E. pilosa* and *E. plana* to acclimatize in hypoxia conditions, emit adventitious roots on the soil surface, form root and stem aerenchyma with impaired growth of the aerial part due to negative effects verified in photosynthesis, measured by the lowest amount of chlorophilic pigments produced and the lowest electron transfer rate.

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