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RESEARCH ARTICLE

ANTIOXIDANT ENZYME ACTIVITY AND INITIAL GROWTH OF WHEAT, RYE AND BEAN UNDER SOIL FLOODING

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ABSTRACT

Adverse environmental conditions have been negatively affecting plant growth and development. The present study aims at evaluating soil flooding effects in the initial growth and enzymatic activity of rye, wheat and bean plants. Plants were cultivated in a growth chamber and subjected to flooding. Afterwards, organ dry matter, leaf area, protein content and antioxidant enzyme activity were determined. Rye plants reduced shoot and root dry matter and increased leaf area and leaf mass ratiobetween two and three days of flooding. In wheat, root dry matter decreased from 3.5 days. In beans, root dry matter decreased and area ratio increased. Regardless of studied species, antioxidant enzyme activity measured in roots was higher in longer flooding periods. Soil flooding adversely affects initial growth and superoxide dismutase, catalase and ascorbate peroxidase enzyme activity. Enzymes are affected differently according to species and soil flooding period.

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INTRODUCTION

Unfavorable environmental conditions have caused yield and quality decrease in agricultural products. Wheat (*Triticumaestivum* L.) and rye (*Secalecereale* L.) belong to the Poaceae family and are the world's most important cereals. In addition, bean (*Phaseolus vulgaris* L.) is one of the main species with economic and social interest in Brazil. Quick plant establishment in the field consists of an important step in species cultivation. Soil flooding is one of the major abiotic stresses in lowland soils, causing restrictions in plant growth and development (Parent *et al.*, 2008). Soil flooding restricts the cultivation of most plant species and may significantly reduce their establishment (Parent *et al.*, 2008). In this environment condition, several changes occur in plant metabolism and growth, such as gas exchange reduction between roots and the pore space in soil (Zabalza *et al.*, 2009). In addition, the energy produced by plants is reduced (Bailey-Serres and Voesenek, 2008; Kumutha *et al.*, 2008; Sairam *et al.*, 2009). Stress caused by soil hypoxia may change several plant metabolism aspects, causinglipid peroxidation (Yordanova and Popova, 2007; Pociecha *et al.*, 2008), hormonal imbalance (Moura *et al.*, 2008) and cellular oxidative stress (Sinha and Saxena, 2006). Increase of stressful conditions leads to reactive oxygen species production and accumulation, which are harmful to plant cells, causing biomolecule, protein and cell membrane damage (Panda and Khan, 2009). An efficient antioxidant enzyme system is necessary to eliminate or reduce this problem, in order to contribute to physiological process maintenance during and after oxidative stress. Superoxide dismutase, catalase and as corbate peroxidase enzymes are part of the antioxidant system (Ahmed *et al.*, 2009), and are responsible for defending cells against stress caused by reactive oxygen species. Given the above, this study aimed at evaluating the effect of soil flooding periods on growth initial performance and antioxidant enzyme activity of wheat, rye and bean plants.

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MATERIALS AND METHODS

The experiment was conducted in Capão do Leão, state of Rio Grande do Sul, Brazil (31º 52’ S; 52º 21’ W, elevation of 13 m), in a growth chamber with temperature and light control. Wheat, rye and bean seeds of Fundacep Bravo, BRS Serrano and IPR Tuiuiúgeno types, respectively, were used. In separate experiments, seeds of different species with germination above 90% were placed in plastic trays, containing substrate of horizon A1 soil of a Albaqualf (Usda, 1999), previously adjusted according to soil analysis and based on the Fertilization Manual (Cqfs, 2004). Flooding was imposed on bean plants when V2 growth stage was reached (Ctsbf, 2012). In rye and wheat plants, flooding was imposed on stage 1 (Large, 1954). A 20 mm water mass was held in the soil surface, in order to avoid gas exchange and soil aeration. Flooding periods ranged between 0(kept at field capacity), 1, 2, 3, and 4 days, when plant collection was conducted to assess antioxidant enzyme activity growth and amount. In each collection, plants were cut close to the soil, separated into organs (leaves, stems and roots) and packed separately in brown paper envelopes. In order to obtain the dry matter, the material was transferred to a forced ventilation oven at 70 °C until reaching constant weight. Leaf area (L_a) was measured with aLicor area meter (LI-3100 Model) and expressed in square meters. Dry matter and leaf area primary data were adjusted through orthogonal polynomials, besides leaf area ratio (F_a) and leaf mass ratio(F_w) instantaneous values, which were estimated by equations; $F_a = L_a/W_t$ and $F_w = W_l/W_t$, where W_l refers to leaves dry matter and W_t indicates total dry matter. Shoot/root ratio (P_w) was estimated by $P_w = W_{pa}/W_r$, where W_{pa} refers to shoot dry matter (leaves and stems) andW_r indicates root dry matter. Total protein contentswere quantified in leaf and root fresh matter samples, as described by Bradford (1976). Superoxide dismutase (EC 1.15.1.1; SOD) enzyme activity was measured by the enzyme capability to inhibit nitrobluetetrazolium (NBT) photoreduction (Giannopolitis and Ries, 1977). Catalase enzyme activity (EC 1.11.1.6; CAT) was estimated according to Havir and McHale (1987). Ascorbate peroxidase activity (EC 1.11.1.11; APX) was estimated according to Nakano and Asada (1981). The experimental design was completely randomized in a three x five factorial (three genotypes; five harvest periods) with 20 repetitions. Total soluble protein and antioxidant enzyme activitycontents were assessed with four repetitions for each genotype in the five collection periods. Data were submitted to analysis of variance. When F values were significant at 5% probability, they were expressed by polynomial regression.

RESULTS

Initial growth and Antioxidant Enzyme Activity in Wheat Plants Wheat initial growth was significantly affected ($P \geq 0.1\%$) by flooding period increase (Figure 1). Shoot dry matter (W_{pa}) was reduced after maximum accumulation at 2.32 days after flooding (DAF). Root dry matter (W_r) had a high determination coefficient ($R^2 \geq 0.93$) and increased until 1.76 DAF. Afterwards, root dry matter decreased until 4 DAF (Figure 1a). Shoot/root ratio reached minimum point at 0.82 DAF. Subsequently, shoot/root ratio significantly increased until4 DAF and was adjusted to the quadratic model, with high $R^2 \geq 0.93$ (Figure 1b). Leaf area ratio (F_a) increased throughout the flooding period until 4 DAF (Figure 1c). Thus, soil flooding increase increased the leaf area useful for photosynthesis. However, leaf mass ratio(F_w) increased from 0.81 DAF, showing that abiotic stress changed leaf dry matter amount (Figure 1d).

Wheat leaf protein content showed no significant differences between flooding periods (Figure 2a). In roots, the minimum point for protein contents was reached at2DAF, increasing until 4 DAF. Superoxide dismutase (SOD) enzyme activity in wheat roots increased until 4 DAF (Figure 2b). In leaves, maximum point for SOD activity occurred at 1.08 DAF, with further decrease until the end of the evaluation period (4 DAF). Root catalase (CAT) enzyme activity reduced as flooding periods increased, until 4 DAF (Figure 2c). In leaves, maximum CAT activity was observed at 2.24 DAF, with subsequent tendency to decrease until the last stress period (4 DAF). Ascorbate peroxidase (APX) enzyme activity increased until 4 DAF in leaves (Figure 2d). However, it was reduced in roots and throughout flooding periods (DAF).

Initial Growth and Antioxidant Enzyme Activity in Rye Plants Rye shoot dry matter (W_{pa}) adjusted to the quadratic trend, with high determination coefficient (Figure 3a). There was W_{pa} increase until maximum point, at 1.25 days after flooding (DAF). Root dry matter (W_r) increased until 1.17 DAF and reduced until 4 DAF afterwards (Figure 3a). Shoot/root ratio adjusted to the quadratic trend, and the highest results were obtained with a high determination coefficient ($R^2 \geq 0.93$), at 4 DAF (Figure 3b). Leaf area ratio (F_a) showed the lowest values before substrate flooding, and stress effect was intensified by flooding period increase (Figure 3c). Similarly, leaf mass ratio (F_w) adjusted to the quadratic model, and flooding effect was higher in plants exposed to the largest flooding periods (Figure 3d). Protein contents obtained in rye leaves increased in plants under the largest flooding periods. Maximum leaf protein content was obtained at 4 DAF (Figure 4a). However, contents quantized in roots reached their maximum at 1.56 DAF. Therefore, there were temporal changes in root protein accumulation compared to leaves. Soil flooding caused significant superoxide dismutase (SOD) enzyme activity reduction in rye leaves, and maximum point was obtained at 2.08 DAF (Figure 4b). However, SOD activity increased until 4 DAF in roots. Therefore, a different response from that observed in leaves was obtained. Catalase (CAT) enzyme activity in rye leaves was higher at 4 DAF compared to leaves before flooding (Figure 4c). However, it is important to note that rye root CAT activity showed no significant differences. Thereby, leaves demonstrated the stress caused by flooding more clearly when measured by CAT activity. In relation to ascorbate peroxidase (APX) enzyme activity, higher activity was observed in roots compared to rye leaves (Figure 4d). Leaf and root minimum points were achieved at 1.72 and 1.83 DAF, respectively, with subsequent increase until 4 DAF. Initial Growth and Antioxidant Enzyme Activity in Bean Plants Soil flooding period increase had no significant effect on bean shoot dry matter (W_{pa}). Root dry matter (W_r) was more drastically affected by flooding compared to shoot. Maximum allocation occurred at 1.73 DAF, with further decrease until the end of the evaluation period (Figure 5a).

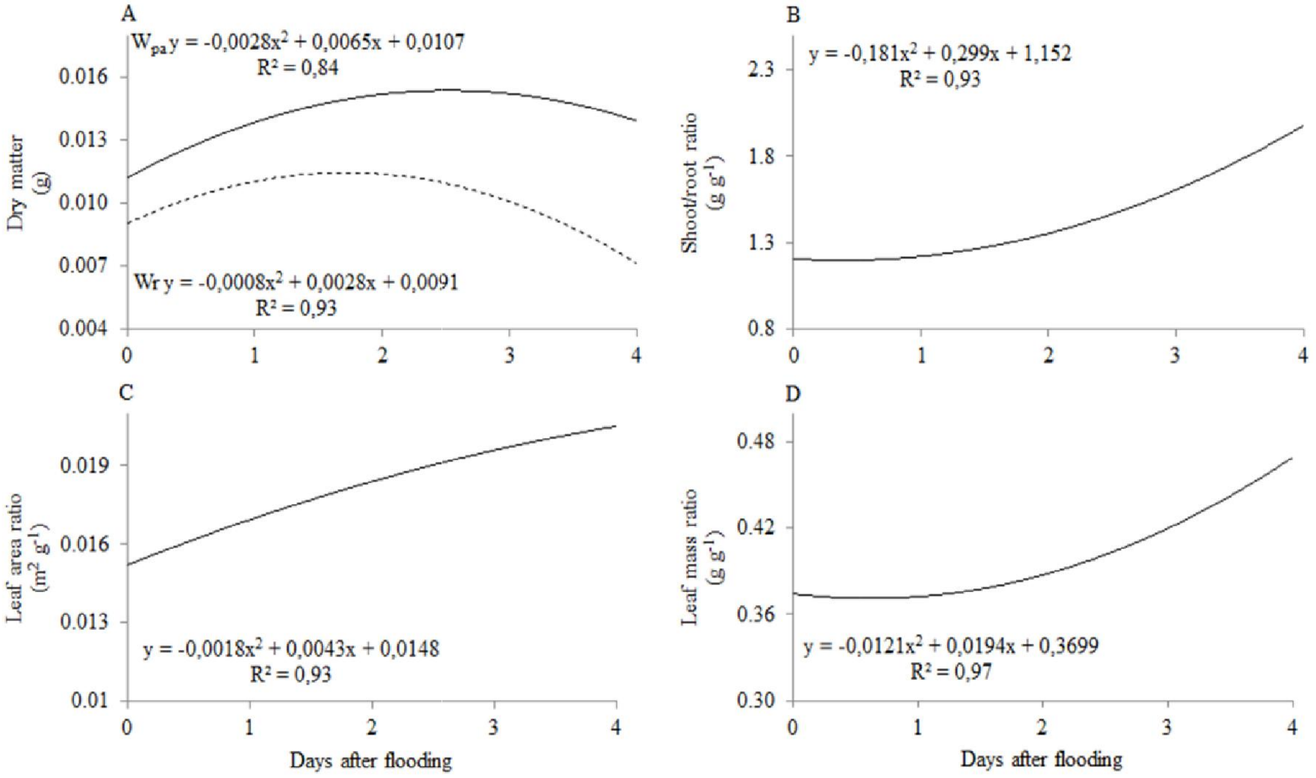

Figure 1. Shoot and root dry matter (a), shoot/root ratio (b), leaf area ratio (c) and leaf mass ratio (d) of wheat plants under influence of flooding periods. Shoot results =W_{pa}. Root results = W_r (1% significance level; ^{NS} non-significant)**

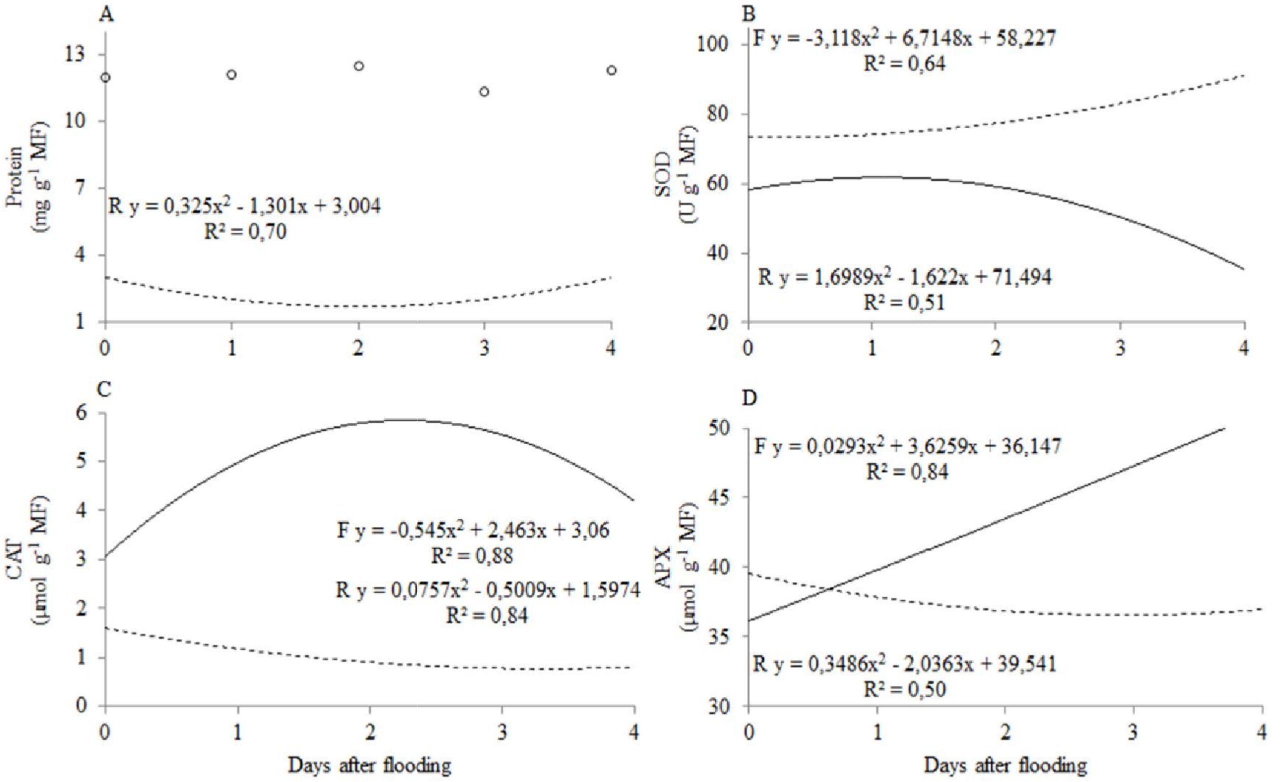

Figure 2. Protein contents (a) and superoxide dismutase (SOD) (b), catalase (CAT) (c) and ascorbate peroxidase (APX) (d) enzyme activity in wheat leaves and roots under different soil flooding periods. Leaves (F); Roots (R). (1% significance level; ^{NS} non-significant)**

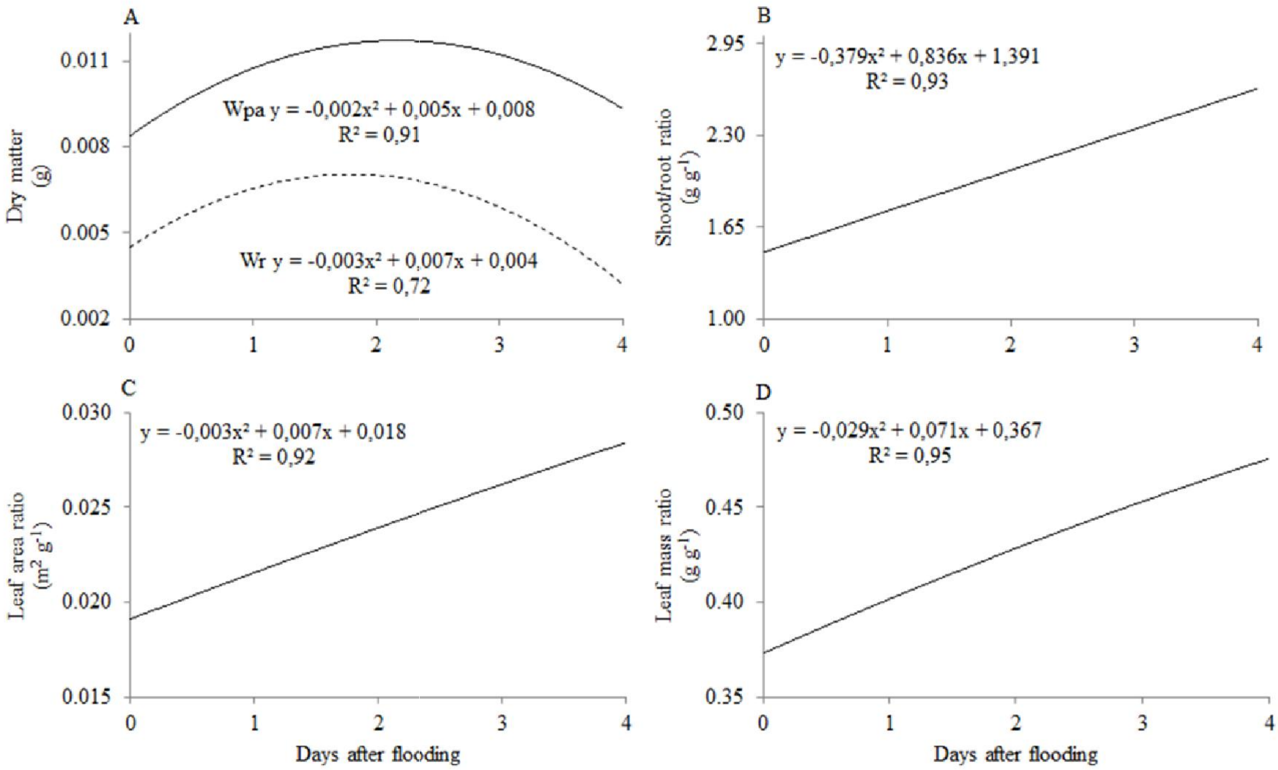

Figure 3. Shoot and root dry matter (a), shoot/root ratio (b), leaf area ratio (c) and leaf mass ratio (d) of rye plants under influence of flooding periods. Shoot (pa); Root (r) (1% significance level; ^{NS} non-significant)**

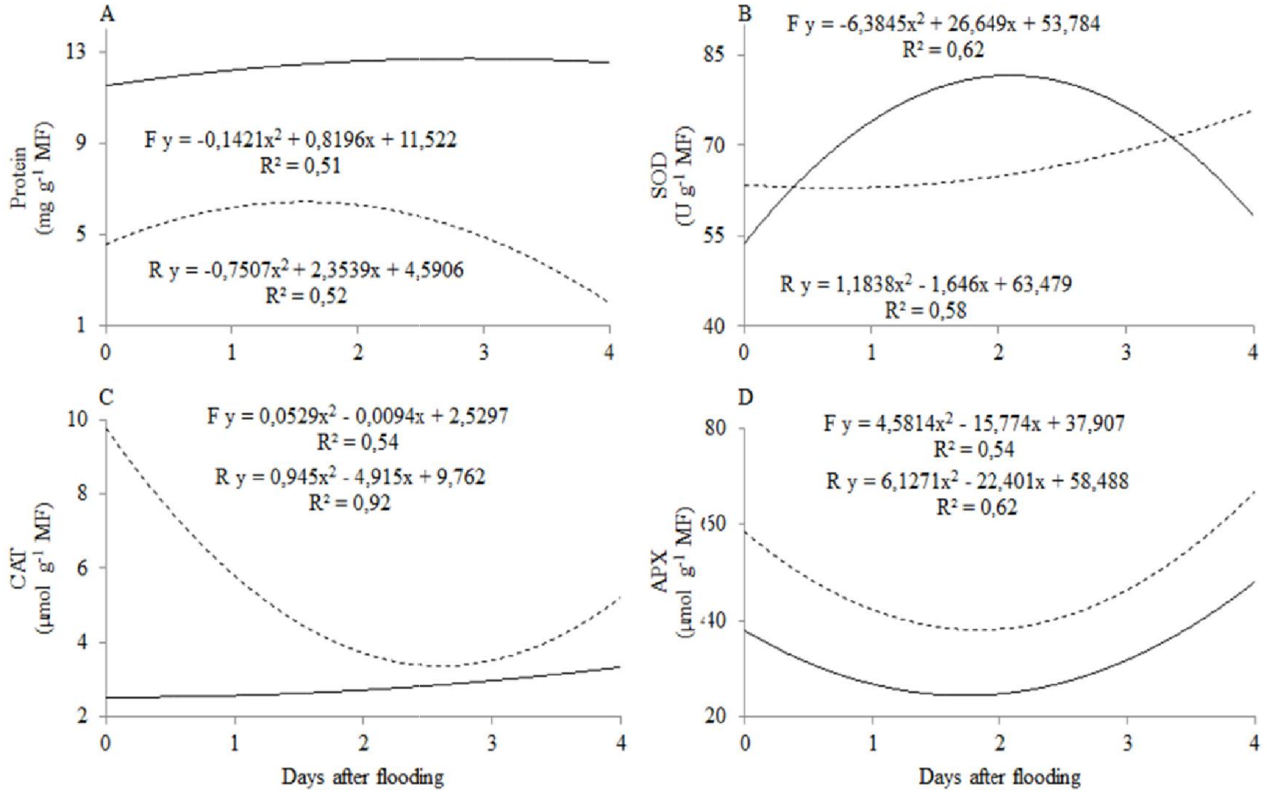

Figure 4. Protein contents (a) and superoxide dismutase (SOD) (b), catalase (CAT) (c) and ascorbate peroxidase (APX) (d) enzyme activity in rye leaves and roots under different soil flooding periods. Leaf results = F. Root results = R (1% significance level; ^{NS} non-significant)**

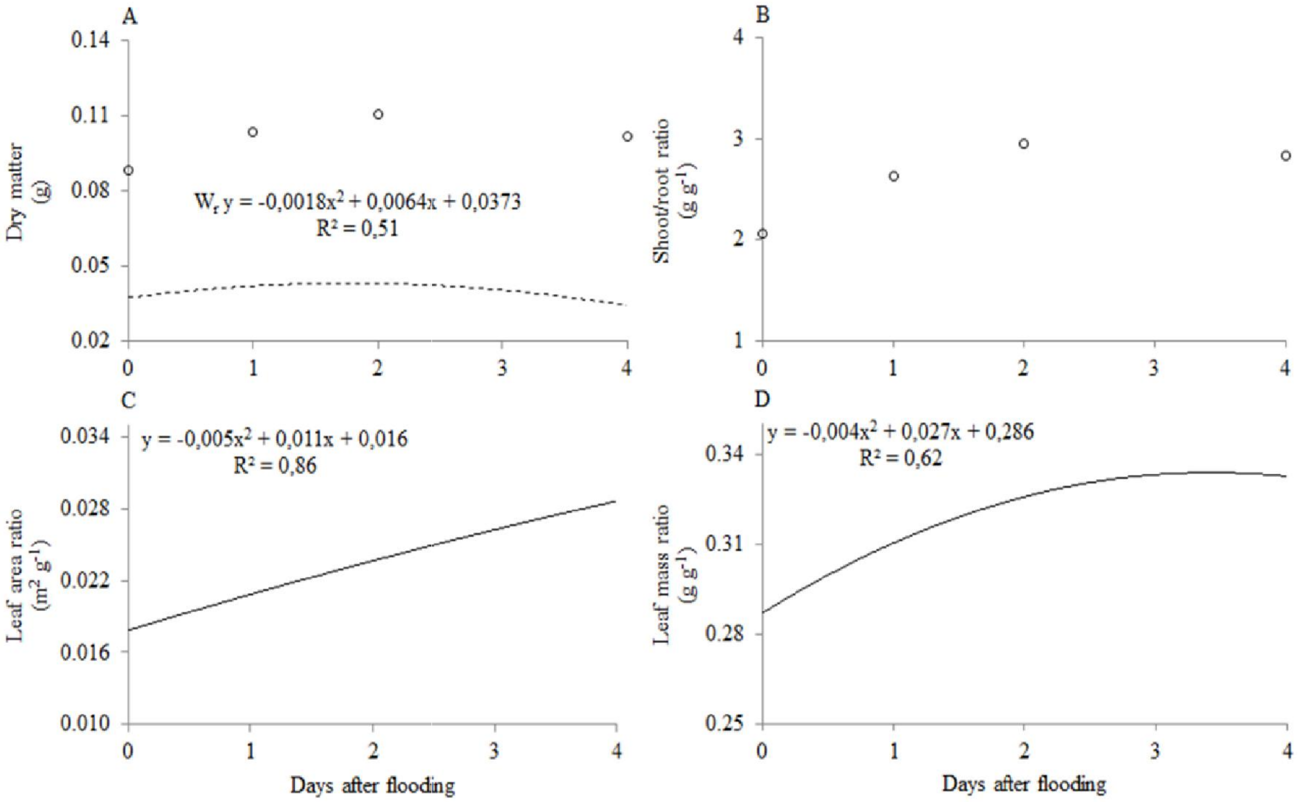

Figure 5. Shoot and root dry matter (a), shoot/root ratio (b), leaf area ratio (c) and leaf mass ratio (d) of bean plants under effect of different flooding periods. Shoot (W_{pa}); Root (W_r) (1% significance level; ^{NS} non-significant)**

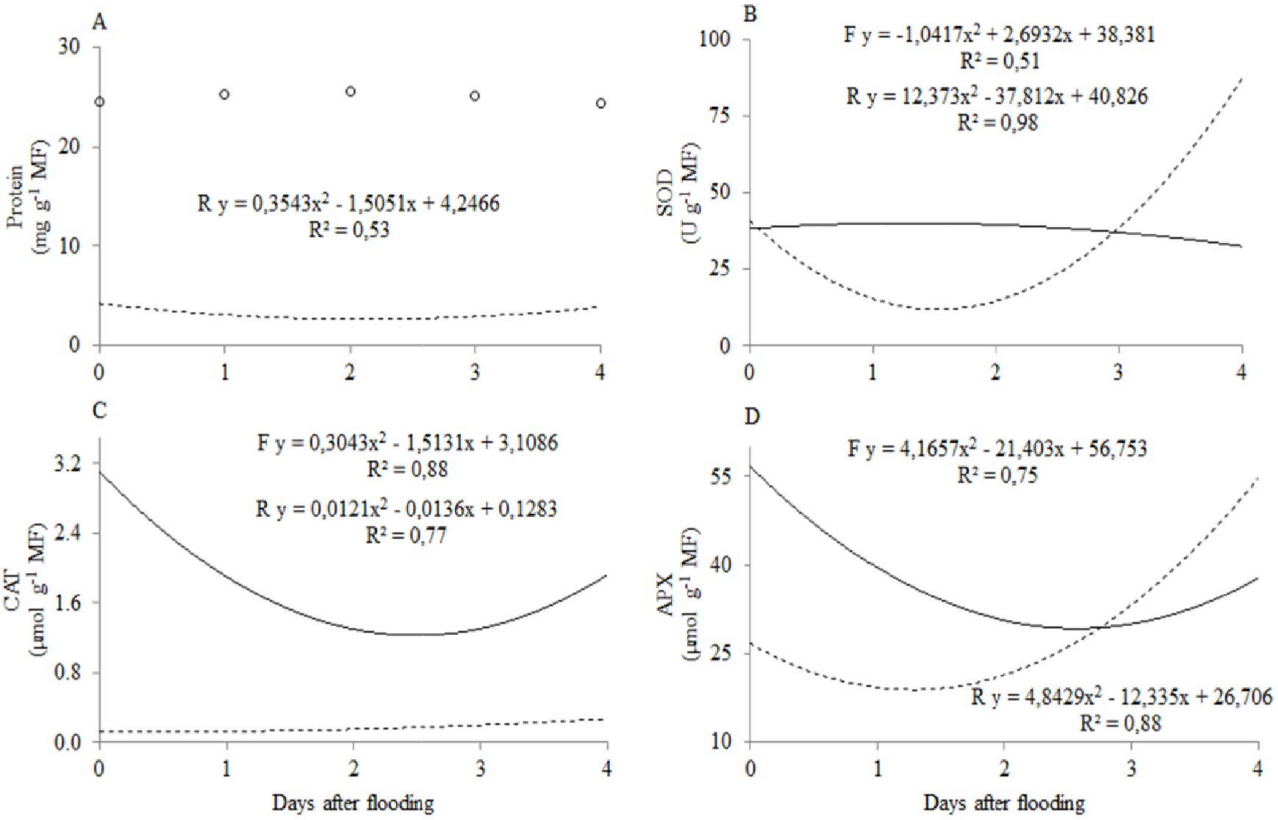

Figure 6. Protein contents (a) and superoxide dismutase (SOD) (b), catalase (CAT) (c) and ascorbate peroxidase (APX) (d) enzyme activity in bean leaves and roots under different soil flooding periods. Leaf = F; Root = R. (1% significance level; ^{NS} non-significant)**

Shoot/root ratio showed no difference at 1% probability (Figure 5b). However, leaf area ratio (F_a) increased until 4 DAF (Figure 5c), and leaf mass ratio (F_w) reached maximum point at 3.38 DAF. There was indication that leaf dry matter allocation was more affected by flooding compared to the leaf useful area to capture light energy in bean plants (Figure 5d).

Protein levels did not have statistical difference when quantified in bean leaves (Figure 6a). Roots reached minimum point at 2.14 DAF, with subsequent increase until 4 DAF. Superoxide dismutase (SOD) enzyme activity in bean leaves was reduced from 1.29 DAF (Figure 6b). On the other hand, SOD activity increased from 1.52 DAF in roots, followed by increases until 4 DAF. Catalase (CAT) enzyme activity in leaves increased from 2.52 to 4 DAF (Figure 6c). In roots, CAT activity, although low, increased during plant flooding until 4 DAF. Ascorbate peroxidase (APX) enzyme activity in leaves decreased until 2.56 DAF, showing subsequent increase until 4 DAF (Figure 6d). Roots had their minimum point from 1.28 DAF, although there was APX activity increase with flooding period advance (4 DAF).

DISCUSSION

Soil flooding triggered different responses in wheat, rye and bean plants in relation to growth and antioxidant enzyme activity. In wheat plants, there was dry matter accumulation decrease in several structures with soil flooding period increase. Dry matter accumulation assessment is an important physiological parameter of acclimatization against stress negative effects (Sena *et al*., 2007), as observed in other species (Silva *et al*., 2009). Higher growth capacity of wheat when subjected to flooding is related to soluble sugar accumulation in the roots (Chen *et al*., 2005) and photo assimilate availability to cells under anaerobic conditions (Parent *et al*., 2008). Such responses may be related to area and leaf mass ratio increases. Similar results were observed in relation to wheat tolerance against soil flooding (Colmer and Greenway, 2011). Thus, plant growth maintenance under soil flooding effect is, in part, due to reduced ATP production by fermentation metabolic pathway (Parent *et al*., 2008), resulting in total dry matter decrease (Silva *et al*., 2009; Wang *et al*., 2012).On the other hand, rye growth decrease may be due to energy content limitation. Furthermore, it is also related to root low capacity of absorbing water and nutrients, thereby affecting biomass allocation (Wang *et al*., 2012). Low dry matter production in bean roots may be due to chlorophyll degradation in relation to soil flooding stress, as noted by Pociecha *et al*. (2008) in *Viciafaba*, reducing photo assimilate production and translocation from leaves to roots. This, combined with leaf mass ratio values obtained in this study, may be related to degenerative changes of physiological processes related to plant performance. Soil flooding may reduce growth in different plant species due to lack of oxygen in roots and mitochondrial respiration inhibition (Wang *et al*., 2012). In addition, it may impair the absorption of nitrogen and other minerals, resulting in low chlorophyll levels (Thomas *et al*., 2005; Pociecha *et al*, 2008) Soil water saturation limits root system growth, causing shoot growth (Alaoui-Sossè *et al*. 2005; Bailey-Serres and Voesenek, 2008). In addition, it also induces leaf chlorosis and photosynthetic capacity reduction (Visser *et al*., 2003). Water excess exposure increase results in photoassimilate translocation reduction in plants (Sachs and Vartapetian, 2007). Photosynthesis decline result may lead to concomitant physiological disorders, such as water transport inhibition and hormonal balance changes (Parent *et al*., 2008) in plant development. In order to properly keep its metabolic activity, the plant uses its carbohydrate reserves. As the initial carbohydrate supply is related to hypoxia or anoxiatolerance level in many species, presumably due to their involvement in providing energy during anaerobic conditions, carbohydrates reserves may be a crucial factor for soil flooding tolerance (Parent *et al*., 2008). Therefore, leaf area ratio increase may be related to soil flooding, asnutrient transport from root to other plant organs is reduced, decreasing leaf expansion and affecting dry matter partitioning between organs. In addition, photosynthesis and photoassimilate production are also negatively affected (Bailey-Serres and Voesenek, 2008). Wheat, rye and bean antioxidant enzyme activity and protein content were modified by increasing flooding periods. Although significant differences were not observed for protein content in wheat leaves in relation to hypoxic stress, there was no shoot growth change until 2.32 DAF (Figure 1a).Yordanova and Popova (2007) have not observed any protein content changes in corn leaves under soil flooding effect. Wheat and bean root protein contents showed their minimal point at 2.0 and 2.14 DAF, respectively, with subsequent increase until 4 DAF. Rye plants showed maximum point at 1.56 DAF. These results indicate that higher protein production until 4 DAF may be related to stress tolerance in soil hypoxia conditions, which occurs due to synthesis of a specific protein group under soil flooding (Shingaki-Wells *et al*., 2011; Perata *et al*., 2011).

Soil flooding increased SOD, CAT and APX enzyme activity in pigeonpea genotypes (Bansal and Srivastava, 2012), confirming the results obtained in this study (Figures 2, 4, 6). At the end of the evaluation period, superoxide dismutase increased its activity in the roots of the three species. Balakhnina *et al*. (2012) found lower SOD activity in roots compared to leaves of *Brassica napus* subjected to soil flooding periods. Superoxide dismutase enzyme is important to the antioxidant system duringsoil flooding stress (Porto *et al*., 2013). In wheat, rye and bean leaves, catalase enzyme activity increased until 4 DAF, probably due to higher hydrogen peroxide accumulation in the leaves (Ahmed *et al*., 2009). However, ascorbate peroxidase enzyme showed higher activity in roots compared to leaves in rye and bean plants, suggesting that it may have a protective role in this organ under hypoxia. However, in corn under soil flooding influence, Chugh *et al*. (2011) found that ascorbate peroxidase reduces activity compared to control plants. Sress caused by prolonged soil flooding is variable between species and may affect enzyme activity (Yordanova and Popova, 2007; Pociecha *et al*., 2008), new leaf production, dry matter production and protein contents (Balakhnina *et al*., 2012). Reactive oxygen species formation is a plant response to hypoxic conditions (Balakhnina *et al*., 2009; Balakhnina *et al*., 2010). It may cause damage to plant cells and lead to oxidative stress. In this regard, reactive oxygen species removal becomes important for stress prevention (Chugh *et al*., 2011). Detoxification is conducted through an efficient enzyme system. Superoxide dismutase removes the superoxide anion (Bowler *et al*., 1992) and catalyzes superoxide radical conversion to H_2O_2. Then, $H_2O_2$is reduced to water and molecular oxygen in reactions catalyzed by catalase and ascorbate peroxidase enzymes (Ahmed *et al*., 2009). Soil flooding reduces organ dry matter accumulation, increasing wheat, rye and bean shoot/root ratio, leaf area ratio and leaf mass ratio. However, superoxide dismutase enzyme activity showed similar behavior among the three species at all flooding periods, increasing root activity and decreasing leaf activity. This fact was also observed for ascorbate peroxidase enzyme in rye and bean plants. Therefore, it was possible to show that wheat plants had satisfactory performance under soil flooding and compared to rye and beans, respectively. There is a close relation between plant height, leaf area and dry matter growth reduction and temporary soil flooding, especially when plants are subjected to stress during the growing period, compared to the reproductive period. Moreover, soil flooding induces leaf damage and chlorophyll content reduction (Pociecha *et al*., 2008) by decreasing energy production and protein synthesis (Parent *et al*., 2008), as observed in this study (Figure 2a; 4a; 6a). Hydrogen peroxide intracellular level varies depending on stress level and antioxidant enzyme activity (Bailey-Serres and Voesenek, 2010). It has been observed in different crops, such as barley, that soil flooding periods promote reactive oxygen species increase and negatively affect cell membrane integrity, causing electrolyte leakage due to lipid peroxidation (Yordanova and Popova, 2007).

However, it should be noted that metabolite production and enzyme activity are related to plant organ, flooding period (Perata *et al*., 2011) and species, as observed in this study for wheat, rye and beans (Figure 2, 4 and 6). Therefore, different tolerance mechanisms against hypoxic stress are needed for each of the three species studied.

Conclusion

For wheat, rye and bean plants, root dry matter was the variable most affected by flooding, in comparison to shoot dry matter. Soil flooding affects the initial growth and superoxide dismutase, catalase and ascorbate peroxidase enzymes are affected differently according to species and soil flooding period. Regardless of the studied species, superoxide dismutase enzyme activity quantified in roots was higher in longer flooding periods during initial growth stages.

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