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Effects of soil flooding on photosynthesis and growth of *Zea mays* L. seedlings under different light intensities

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Soil flooding is one of the major abiotic stresses that repress maize (*Zea mays* L.) growth and yield, and other environmental factors often influence soil flooding stress. This paper reports an experimental test of the hypothesis that light intensity can influence the responses of maize seedlings to soil flooding. In this experiment, maize seedlings were subjected to soil flooding at the two-leaf stage under control light (600 μmol m^{-2} s^{-1}) or low light (150 μmol m^{-2} s^{-1}) conditions. Under control light growth conditions, the average photosynthetic rate (P_N), transpiration rate (E) and water use efficiency (WUE) were 70, 26 and 59%, respectively, higher in non-flooded than in flooded seedlings; and the average chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and Chl *a+b* were 31, 42 and 34%, respectively, higher in non-flooded than in flooded seedlings; and the average belowground biomass and total biomass were 52 and 34%, respectively, higher in non-flooded than in flooded seedlings. There was a slight decrease of seedling biomass in six days flooded seedlings under low light growth conditions. The effects of flooding on photosynthetic, seedling growth and shoot/root ratio were more pronounced under control light growth conditions than under low light growth conditions, which indicate that even for maize which is a C$_4$ plant, relatively high light intensity still aggravated soil flooding stress, while low light growth condition mitigated soil flooding stress, and suggests that light effects should be considered when we study maize responses to soil flooding.

Key words: Biomass accumulation, gas exchange, light limitation, maize, stress.

INTRODUCTION

Flooding is one of the remarkable abiotic stresses and yield-limiting factor following water shortage, salinity and extreme temperatures in most arable farmland for many crops (Rosenzweig et al., 2002; Huang and Rozelle,1995; Visser et al., 2003). Soil flooding rapidly depletes soil oxygen and lowers soil redox pote-ntial; thereby, the roots suffer a shortage of oxygen and roots aerobic respiration is dramatically decreased. This will result in a sharp decline in ATP level (Vartapetian and Jackson, 1997). Insufficient energy reduces mineral elements, water absorption and transportation, thereby, altering diverse aspects of plant metabolism such as accelerating lipid peroxidation and leaf senescence and inhibiting growth (Kozlowski, 1984; Pezeshki, 2001; Boru et al., 2003; Yan et al., 1996; Vartapetian and Jackson, 1997). The reduction of net photosynthetic rate (P_N) is one of the most important responses of plants to soil flooding which could be caused by stomata and non-stomata limitations to photosynthesis and lead to severe yield reduction (Yordanova and Popova, 2007; Rosenzweig et al., 2002).The stomata limitation occurs in the first few hours after soil flooding and leads to a rapid decrease in photosynthesis and transpiration by monitoring stomata morphometric, intercellular CO_2 (C_i) and stomata

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Abbreviations: C$_4$, C$_4$ Plants; **Chl,** chlorophyll; **Ci,** intercellular CO_2 concentration; **E,** transpiration rate; **Fv/Fm,** maximum photochemical efficiency of PSII; **g$_s$,** stomata conductance; **NF,** non-flooded; **P$_N$,** net photosynthetic rate; **PPFD,** photosynthetic photon flux density; **PSII,** photosystem 2; **RuBPCO,** ribulose-1,5-bisphosphate carboxylase/oxygenase; **WUE,** water use efficiency.

conductance (g_s) (Yordanova et al., 2005; Jackson, 2002).

With prolonged flooding stress, non-stomata limitation also plays an important role in photosynthesis reduction. The non-stomata limitation is mainly caused by the damage of photosynthetic apparatus and lower biochemical reactions efficiency of the photosynthesis. This includes lipid peroxidation caused by chloroplast membrane structure destruction, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity and maximum photochemical efficiency of PSII (Fv/Fm reduction) (Yordanova and Popova, 2007; Pociecha et al., 2008; Yordanova and Popova, 2001; Mielke and Schaffer, 2010a).

Leaf chlorophyll destruction of flooded plants was also confirmed by a great deal of studies (Yan et al., 1996; Yordanova and Popova, 2001; Mielke and Schaffer, 2011; Jing et al., 2009). Responses to soil flooding could also be influenced by other environmental factors such as temperature and light (Ojeda et al., 2004; Mielke and Schaffer, 2011; Mielke and Schaffer, 2010a, b, 2011; Lavinsky et al., 2007).

The interaction effects between soil flooding and light intensity on photosynthesis have been discovered on C_3 species (Mielke and Schaffer, 2010a, b, 2011; Lavinsky et al., 2007). However, little attention was paid to C_4 species because the C_4 species have a higher light saturation point and light use efficiency. During the crop growth period, flooding stress was often caused by heavy precipitation or prolonged rainfall accompanied by dense clouds and low irradiance for photosynthesis. Since most of the cereal crops are fond of light, lots of agronomists did a lot of studies on the effects of low irradiance on crops photosynthesis physiology (Li et al., 2005; Zhang et al., 2007; Drozak and Romanowska, 2006) and yield (Lazaro et al., 2010; Earley et al., 1966; Gerakis and Papakostatasopoulou, 1980; Kiniry and Ritchie, 1985; Reed et al., 1988; Jia et al., 2011).

The authors are aware of few published work on the effects of both flooding and different irradiance on photosynthesis physiology of mesophyte C_4 species. To test the hypothesis that different light intensities can alter the response of mesophyte C_4 species to soil flooding on photosynthesis, we conducted an experiment aiming at investigating the effects of soil flooding under control light (600 µmol m^{-2} s^{-1}) and low light (150 µmol m^{-2} s^{-1}) conditions on chlorophyll fluorescence, leaf chlorophyll content and leaf gas exchange of *Zea mays* L., which is an important high light demanding crop and most sensitive to soil flooding at two-leaf stage (Liu et al., 2010).

MATERIALS AND METHODS

Plants cultivation and treatments

Maize elite hybrid ZhengDan958 (ZD958) was used in this experiment. Seeds were sown in plastic pots (6 L) with Eutric Cambisol sandy loam soil (USDA), which was taken from the Experimental Farm of the Henan Agricultural University, China, amended with 1.0 g $(NH_4)_2SO_4$, 0.8 g P_2O_5 and 0.6 g K_2O per kg soil and cultivated at light intensity of 600 µmol m^{-2} s^{-1} at canopy height, 14/10 h day/night, 28/22°C day/night and about 60% relative humidity in a growth chamber until the second leaf fully expanded. The low light treatment was grown at light intensity of 150 µmol m^{-2} s^{-1} at canopy height with other environmental factors kept the same with the high light treatment. Flooding stress was initiated at the two-leaf stage by filling with water to 20 to 30 mm above the soil surface. The controls were irrigated as needed to avoid drought stress or flooding stress.

Gas exchange measurements

Leaf gas exchange was measured on the second leaf at six days after flooding treatment. P_N, g_s, C_i and E were simultaneously recorded with a portable photosynthesis measurement system (CIRAS-1, PP-System, Hitchin, UK) under uniform conditions [28°C, 450 ± 10 µmol (CO_2) mol^{-1}, 60% RH]. The photosynthetic photon flux density (PPFD) was maintained at 600 µmol m^{-2} s^{-1}.

Chlorophyll content analysis and maximum quantum efficiency of PSII determination

Leaf pigments were extracted in 20 ml 95% ethanol in the dark by using 0.1 g leaf samples at 25 Leaf pigments were extracted in 20 ml 95% ethanol in the dark by using 0.1 g leaf samples at 25°C till fully blanched. The concentrations of leaf chlorophyll content were determined according to Lichtenthaler (1987), where absorbance was measured at 470, 649 and 664 nm using spectrometer (TU-1810SPC, Purkinje General, China). At various flooding intervals (0, 2, 4 and 6 days), chlorophyll fluorescence was measured with a pulse modulated fluorometer (FMS-2, Hansatech Instruments, Norfolk, UK) in the same leaves previously used for gas-exchange measurements. Minimal fluorescence of dark-adapted state (F_0) was measured under the low modulating light over a 1.6-s period on leaves adapted to dark for 20 min, and maximal fluorescence of dark-adapted state (F_m) was induced by a single saturating pulse of light (8,000 µmol m^{-2} s^{-1}) applied over 0.8 s. The F_v/F_m was determined as $(F_m - F_0)/F_m$.

Biomass allocation

Plant biomass was measured using five seedlings per pot. After separating plants into shoots and roots, biomass accumulation was determined after drying to a constant weight at 70°C, and the shoot/root ratio was calculated as the ratio of shoot to root biomass.

Statistical analysis

General linear model univariate analysis was used to assess the relationships between flood and light intensity treatments simultaneously. When interactive effects between flooding and light intensity were observed, independent-samples T-test was used for comparisons of flooding effects within light environments and light intensity effects within flood treatments. When interactive effects were not observed, only comparisons between flood treatments within light environments were analyzed by independent-samples T-test. Data were expressed as mean ± standard deviations (SD) of four replications within each factor. All analyses were performed using SPSS 16.0 for Windows (SPSS, Inc., Chicago, IL).

Table 1. Responses of net photosynthetic rate (P_N), intercellular CO_2 concentration (Ci), stomata conductance (g_s), transpiration rate (E) and water use efficiency (WUE) to soil flooding under control light (CL, 600 µmol m^{-2} s^{-1}) and low light (LL, 100 µmol m^{-2} s^{-1}) conditions.

Variable	CL		LL		ANOVA		
	NF	FL	NF	FL	L	F	L*F
P_N (µmol m^{-2} s^{-1})	18.9±1.5[a]	5.1±2.5[b]	17.1±0.3[a]	14.2±3.0[a]	*	*	*
Ci (µmol mol^{-1})	127.2±27.5[b]	210.4±31.8[a]	121.4±38.4[a]	111.7±11.2[a]	*	*	*
g_s (mmol m^{-2} s^{-1})	126.8±23.8[a]	110.8±22.3[a]	97.5±26.3[a]	75.0±13.5[a]	*	ns	ns
E (mmol m^{-2} s^{-1})	3.3±0.3[a]	2.43±0.2[b]	2.8±0.6[a]	2.3±0.3[a]	*	*	*
WUE [mmol (CO_2) mol (H_2O)]	5.9±1.0[a]	2.1±1.2[b]	6.4±1.3[a]	6.2±0.5[a]	*	*	*

Different letters show significant differences among means at $p<0.05$. Means ± SD (n = 4). NF, non-flooded; FL, flooded; ns, $p>0.05$; *, $p<0.05$.

RESULTS

Gas exchange

Six days after flooding treatment, there were significant differences between control light and low light grown seedlings for P_N, Ci, g_s, E and WUE ($p<0.05$) and significant differences between non-flooded and flooded seedlings for P_N, Ci, E and WUE ($p<0.05$) (Table 1). There were significant interactions between flood and light treatments for P_N, Ci, E and WUE ($p<0.05$). The average values of P_N, E and WUE were significantly higher ($p<0.05$), and Ci was significantly lower ($p<0.05$) in non-flooded than in flooded seedlings under control light growth conditions. However, all the parameters related to photosynthesis were similar in both non-flooded and flooded seedlings under low light growth conditions. The average P_N, E and WUE were 70, 26 and 59%, respectively, higher, whereas Ci was 57% lower in non-flooded than in flooded seedlings under control light growth conditions.

Chlorophyll content and chlorophyll fluoresce

Six days after flooding treatment, chlorophyll contents in low light growth seedlings were similar to that of the control light growth seedlings, while there were significant differences between non-flooded and flooded seedlings for Chl *a*, Chl *b* and Chl *a+b* ($p<0.05$) (Figure 1). There were significant interactions between flood and light treatments for Chl *a*, Chl *b*, Chl *a+b* and Chl *a/b* ($p<0.05$) (Figure 1). The average values of Chl *a*, Chl *b*, and Chl *a+b* were significantly higher ($p<0.05$) in non-flooded than in flooded seedlings under control light growth conditions. However, chlorophyll contents were similar in both non-flooded and flooded seedlings under low light growth condition. The average Chl *a*, Chl *b* and Chl *a+b* were 31, 42 and 34%, respectively, higher in non-flooded than in flooded seedlings under control light growth conditions.

There was no significant variation in Fv/Fm among the treatments two days after flooding treatment. The average values of Fv/Fm in flooded seedlings were significantly lower at four ($p<0.05$) and six ($p<0.001$) days after flood treatment than the control under control light grown conditions (Figure 2). There was a slight decrease of Fv/Fm in the seedlings of six days flooding period under low light growth conditions.

Seedling biomass and allocation

Six days after flood treatment, there were significant differences between control light and low light grown seedlings for shoot biomass, belowground biomass and total biomass ($p<0.05$) and significant differences between non-flooded and flooded seedlings for below-ground biomass, total biomass and shoot/root ratio ($p<0.05$) (Figure 3). There were significant interactions between flood and light treatments for belowground biomass, total biomass and shoot/root ratio ($p<0.05$). The average values of belowground biomass and total biomass were significantly higher ($p<0.05$) and shoot/root ratio was significantly lower in non-flooded than in flooded seedlings under control light growth conditions (Figure 3). However, seedling biomass and shoot/root ratio were similar in both non-flooded and flooded seedlings under low light growth conditions. The average belowground biomass and total biomass were 52 and 34%, respectively, higher in non-flooded than in flooded seedlings under control light growth condition. There was a slight decrease of seedling biomass in six days flooded seedlings under low light growth conditions.

DISCUSSION

Results of this experiment show that control light grown seedlings were more sensitive to soil flooding, which is in agreement with previous studies on *Eugenia uniflora* L. (Mielke and Schaffer 2010a, b, 2011), even for the plant used here which is a C_4 pathway. There was an interactive effect of soil flooding and light intensities on maize seedling photosynthesis and growth (Table 1   and
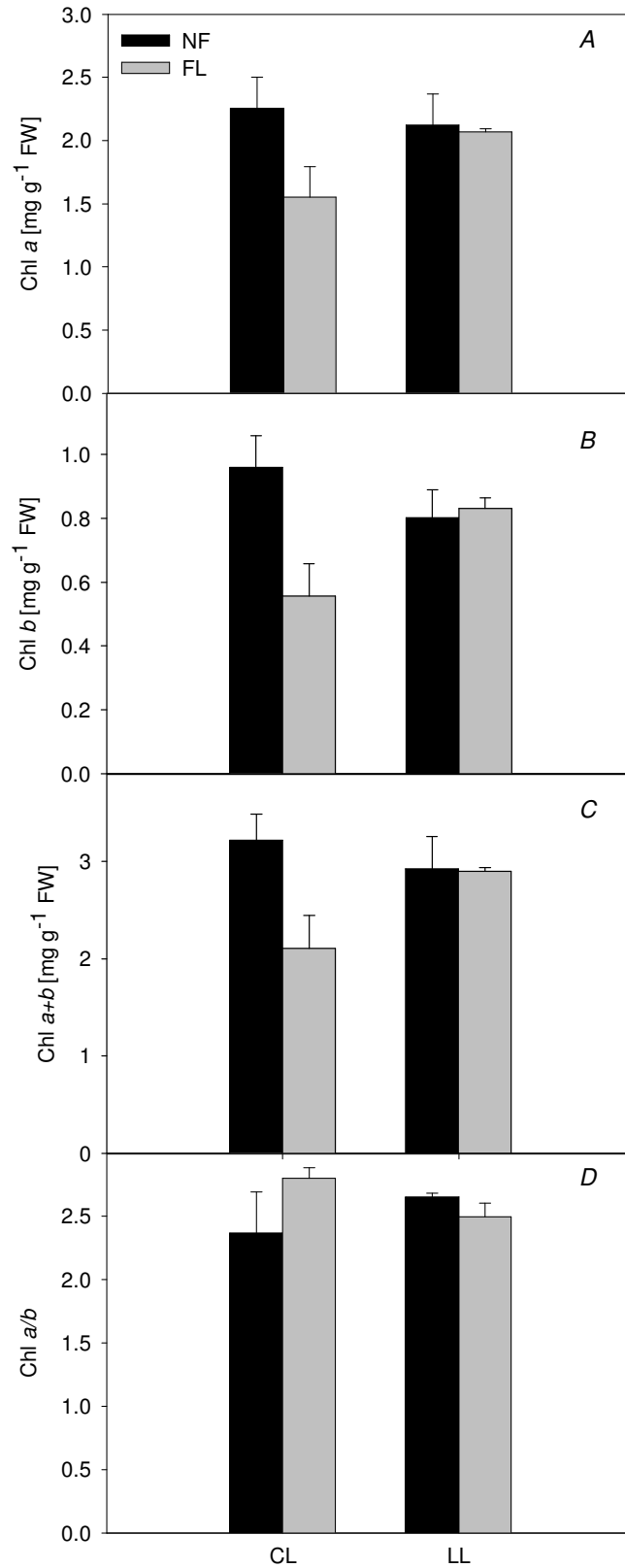
Figure 1. Responses of Chl *a* (A), Chl b (B), Chl a+b (C) and, Chl a/b (D) to soil flooding under control light (CL, 600 µmol m^{-2} s^{-1}) and low light (LL, 100 µmol m^{-2} s^{-1}) conditions. Means ± SD (n = 4). NF, non-flooded; FL, flooded.
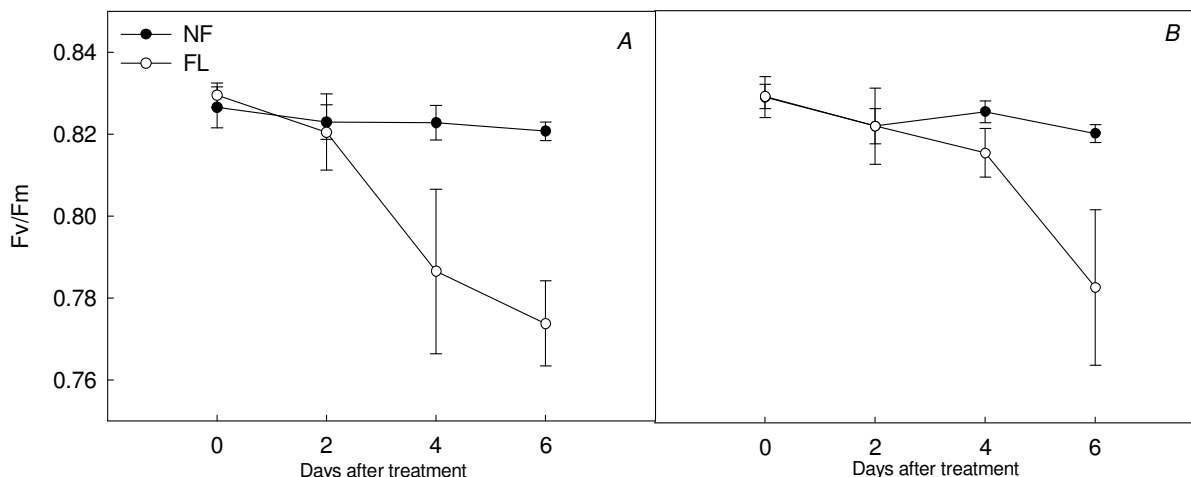
Figure 2. Responses of maximum photochemical efficiency of PSII, and Fv/Fm of maize seedlings after zero, two, four and six days exposure to soil flooding under control light (600 µmol m^{-2} s^{-1}, A) and low light (100 µmol m^{-2} s^{-1}, B) conditions. Means ± SD (n = 4). NF, non-flooded; FL, flooded.

Figure 3), which is similar to the previous study on *Genipa americana* L. (Lavinsky et al., 2007).

Effects of soil flooding on photosynthesis of *Z. mays* L. seedlings under different light intensities

The markedly decrease of P_N was observed in flooded seedlings with non-significant changes in the E and g_s under low light growth conditions. These results are in agreement with that of Yordanova and Popova (2007) for maize seedlings subjected to flooding under 160 µmol m^{-2} s^{-1} PAR. Ci value was higher in flooded seedlings than non-flooded seedlings under control light growth conditions and similar in both flooded and non-flooded seedlings under low light growth conditions. This indicates that stomata closure was not the primary limitation for the reduction of P_N. A non-stomatal effect on the photosynthetic process can play a more important role in the P_N decrease. We also found a significant interaction effect of light irradiance level and flood treatment of photosynthesis of maize seedlings as there are several reports on tree species (Wagner and Dreyer, 1997; Lavinsky et al., 2007; Mielke and Schaffer, 2010a, b). Despite the fact that maize is a C$_4$ pathway plant, a relatively higher light irradiance still aggravating flooding stress induced photosynthesis capacity decrease.

P_N is positively correlated with leaf chlorophyll content (Hidema et al., 1991; Kura-Hotta et al., 1987). Six days after flooding treatment, chlorophyll content in the leaves of control light grown seedlings decreased significantly. This is possibly because flooding stress resulted in a significant increase in chlorophyll breakdown (Yan et al., 1996; Yordanova and Popova, 2001; Pociecha et al., 2008). However, contrary to the result of Yordanova and Popova (2007), chlorophyll contents in the leaves of low

light grown seedlings were similar both for flooded and non-flooded treatments. This might be because the samples in their experiment were all leaf tissues, but we only sampled the second leaf. In fact, we did observe that the first leaf was senescence and turned yellow. According to Ashraf and Arfan (2005), Chl *a/b* in flooded seedlings was higher than non-flooded seedlings under high light grown conditions because the declining extent of chl *b* was more than chl *a*. So, here in our experiment, the reduction of P_N was accompanied by chlorophyll content decrease, showing another evidence for their correlation.

Fv/Fm values for non-stressed leaves are remarkably consistent (about 0.83) (Björkman and Demmig, 1987). A decline of Fv/Fm provides very useful information to reflect the effects of biotic and abiotic stresses in light on photosynthesis (Lavinsky et al., 2007; Baker, 2008; Balachandran and Osmond, 1994). The significant decrease of Fv/Fm at four (p<0.05) and six (p<0.001) days in flooded than non-flooded seedlings under control light growth conditions (Figure 2) indicate that an important portion of photosynthetic electron transport system was destroyed whereas, the average value of Fv/Fm was similar between flooded and non-flooded seedlings under low light growth conditions indicating that leaves of flooded seedlings grown under high light were more susceptible to the photoinhibition of photosynthesis (Mielke and Schaffer, 2011; Baker, 2008).

Effects of soil flooding on growth of *Z. mays* L. seedlings under different light intensities

Flood significantly repressed root growth under both control light and low light growth conditions, and increased shoot/root ratio under control light growth
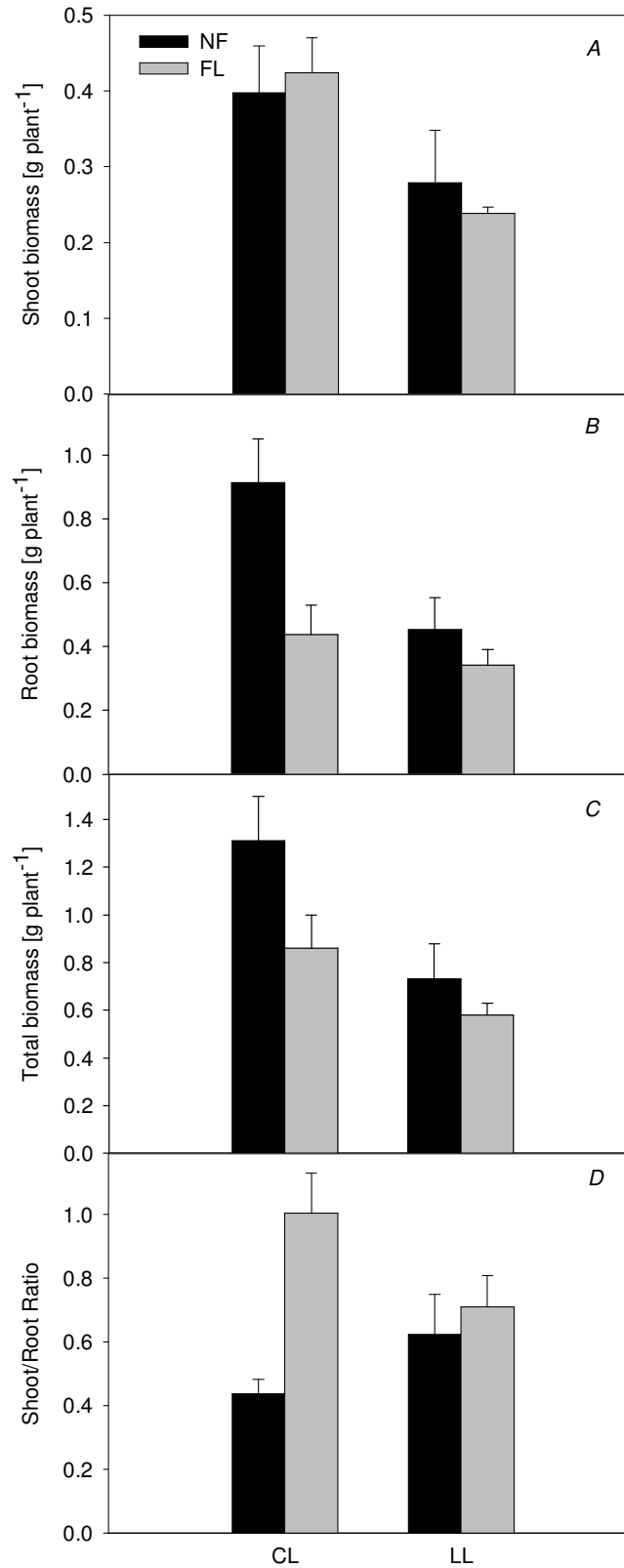
Figure 3. Responses of shoot biomass (A), root biomass (B), total biomass (C) and shoot/root ratio (D) to soil flooding under control light (CL, 600 µmol m^{-2} s^{-1}) and low light (LL, 100 µmol m^{-2} s^{-1}) conditions. Means ± SD (n = 5). NF– non-flooded; FL– flooded. Means ± SD (n = 5). NF– non-flooded; FL– flooded.

conditions but shoot/root ratio was similar between flooded and non-flooded low light grown seedlings (Figure 3). Repressed root growth is a common response to flood stress for many plants (Mielke and Schaffer, 2010b; Chen et al., 2002; Wagner and Dreyer, 1997). As flooding leads to lack of oxygen around the roots, insufficient oxygen inhibits mitochondrial respiration and ATP synthesis, and enhances a less efficient metabolism pathway-glycolysis. In turn, energy limitation decreases the ability of roots to absorb water and nutrients, then decrease root growth rate and dry matter accumulation under hypoxic conditions (Mielke and Schaffer, 2010b; Kozlowski, 2002) whereas, decreased biomass allocation to root is an adaptive mechanism to soil flooding of the plant by diminishing the metabolic requirement of roots for oxygen (Naidoo and Naidoo, 1992).

In summary, an interactive effect of flood and light intensity was found in maize in laboratory conditions, although the control light we used was 600 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR), which is much lower than maize light saturation point. Plant undergoing flood stress was more sensitive when grown under relative high light conditions than low light conditions, demonstrating that the responses of the C_4 plant to flooding stress may be also dependent on light availability during the growth period. Interactions between flooding stress and light intensity on photosynthesis and growth of the plant should be considered in studies aimed at predicting changes in the plant production as a function of changes in rainfall associated with global climate change.

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