Available online: www.notulaebotanicae.ro
Print ISSN 0255-965X; Electronic 1842-4309
Not Bot Horti Agrobo, 2016, 44(2):375-381. DOI:10.15835/nbha44210438

AcademicPres

Notulae Botanicae Horti Agrobotanici Cluj-Napoca

Original Article

Effect of Nitrogen Nutritional Statuses and Waterlogging Conditions on Growth Parameters, Nitrogen Use Efficiency and Chlorophyll Fluorescence in Tamarillo Seedlings

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Abstract

Climate change has altered rainfall patterns causing waterlogging periods that often negatively affect the performance of horticultural crops in the Andean region in Colombia. An experiment was carried out under greenhouse conditions using three-month-old tamarillo (*Solanum betaceum* Cav.) seedlings, which were grown under two levels of nitrogen (N) (10 and 150 mg N·L H_2O). At 28 days after transplanting (DAT), waterlogging treatments were established when well-nourished plants (150 mg N L^{-1} H_2O) significantly showed a higher shoot length than poor-nourished plants (10 mg N L^{-1} H_2O) (~20 cm vs. ~10 cm, respectively). Three different periods of waterlogging were performed between 35 and 37, 51 and 55, and 64 and 70 DAT by covering the holes in the plastic pots to ensure a constant water depth. Results showed that well-nourished plants without waterlogging treatments through the experiment's stress showed a greater shoot length (30 cm), total plant dry weight (7.95 g), F_v/F_m ratio (0.62) and leaf chlorophyll content (37.51 SPAD units) than poor-nourished plants without stress condition (15 cm, 5.57 g, 0.5 and 12.69 SPAD units, respectively) at the end of the experiment. Overall, waterlogging reduced leaf area and nitrogen use efficiency (about 75% and 50%, respectively) in both N levels. However, periods of waterlogging enhanced dry matter partitioning to stems (around 30-35%) in both N levels. This study showed that tamarillo plants are susceptible to landscaping situations where periods of waterlogging can be expected regardless of their N nutritional status.

Keywords: allocation of assimilates, F_v/F_M ratio, leaf area ratio, shoot length, stem diameter

Introduction

Tamarillo (*Solanum betaceum* Cav.) is a plant that belongs to Solanaceae family and native from Andean region. This fruit is grown commercially in countries like Brazil, Colombia, Ecuador, USA (California), Australia and New Zealand (Mejía *et al.*, 2009; Correia and Canhoto, 2012). In Colombia, this crop occupied an area of 9000 hectares with a production of 160,000 tons in 2013 (Agronet, 2015).

Horticultural crops have been severely affected due to the increased frequency and intensity of rainfall in Colombia in recent years, as a result of climate change conditions or environmental phenomena such as La Niña, causing prolonged waterlogging periods (Floréz-Velasco *et al.*, 2015). Waterlogging is a situation of excess water that fills soil pores and results in a reduction of available oxygen, causing different physiological responses in plants (Parad *et al.*, 2013). Flooding has some severe consequences on plant growth and its survival strategies (Phukan *et al.*, 2016). In this sense, the following physiological disorders have been reported under waterlogging: a lower plant growth (Aldana *et al.*, 2014), leaf chlorophyll content (Rao and Li, 2003), and total plant dry weight (Florez-Velasco *et al.*, 2015), as well as changes in the plant water status (Striker *et al.*, 2005). Also, waterlogging can alter biomass allocation in plants (Wu *et al.*, 2015)

Plant nutritional status can significantly influence the plant acclimation to stressful environmental conditions. In this respect, the interaction between plant nutritional status and environmental stresses (drought, salinity, temperature, etc.) is important to understand yield losses (Cakmak, 2005). On the other hand, nitrogen (N) is one of the most essential mineral nutrients due to its many effects on plant

Received: 18 June 2016. Received in revised form: 07 Nov 2016. Accepted: 11 Nov 2016. Published online: 14 Dec 2016.

growth and yield (Fageria, 2001). N is involved in fundamental processes such as nutrients uptake, protein metabolism, photosynthesis and carbon partitioning (Maschnner, 2012). Furthermore, it has been documented that the plant N content decreases in plants under waterlogging conditions because O_2 deficiency in the root zone can change the redox state of nutrients, making them unavailable (e.g. nitrogen) or potentially toxic for plants (Rao and Li, 2003: Najeeb *et al.*, 2015).

Plant nutrient deficiency is the leading cause of poor plant growth under waterlogging conditions (Steffens *et al.* 2005). In this sense, it has been reported that an optimum N supply can help to ameliorate the adverse effects of waterlogging in a range of economically important crops (Percival and Keary, 2008). In wheat, a high nitrogen supply improved the plant growth compared to nonfertilized controls under waterlogging stress conditions (Huang *et al.*, 1994). Flórez-Velasco *et al.*, (2015) also observed that lulo plants grown with high N level (110 mg $N{\cdot}L^{-1}$) and subjected to waterlogging conditions showed a major plant height than plants cultivated with low nitrogen (10 mg $N{\cdot}L^{-1}$) under flooded periods. Finally, plant N status is essential for plant recovering after O_2 deficiency in the root zone (Milroy *et al.*, 2009).

The severity of the effects of waterlogging is also associated with the duration and/or frequency of the waterlogging event (Malik *et al.*, 2002; Visser *et al.*, 2003). In tomato, short periods of waterlogging (2-4 days) reduced stem growth and leaf chlorophyll content (Rao and Li, 2003). Malik *et al.* (2002) also reported that even short periods (as short as 3 d) of waterlogging have important long-term effects on the growth of young wheat plants. On the other hand, Ezin *et al.* (2010) and Aldana *et al.* (2014) also observed that leaf growth and plant height varied according to the flooding duration in tomato and cape gooseberry plants, respectively.

In general, studies about physiological responses of some Andean fruit trees species also belonging to Solanaceae family to waterlogging stress conditions have gained importance in recent years in Colombia due to their export potential as fresh fruit (Aldana *et al.*, 2014; Florez-Velasco *et al.*, 2015; Cardona *et al.*, 2016). For that reason, it is important to enlarge the available knowledge on the interaction between nutritional status and waterlogging stress conditions (duration and/or frequency) for the economic and agricultural improvement of tamarillo plants in waterlogging affected areas. Therefore, the objective of this work was to study the interaction between N nutritional status and three short periods of waterlogging stress on the physiological traits of tamarillo seedlings.

Materials and Methods

General growing conditions

The present work was performed under controlled conditions in the greenhouses of the Faculty of Agricultural Sciences at Universidad Nacional de Colombia in Bogotá (2556 m.a.s.l.; 4° 35' 56'' N, 74° 04' 51'' W) for 12 weeks from March to May 2012. Two-month-old 'Amarillo' tamarillo seedlings were transplanted into 1-L plastic pots containing a mix of sand and white peat without nutrients (Base 1 substrate, Klasman-Deilmann GmbH, Geeste, Germany) in a relation 2:1 as substrate. Weather conditions in the greenhouse during the experiment were the following: average temperature 20 ± 4 °C, relative humidity between 60 and 80% and a natural photoperiod of 12 hours (photosynthetically active radiation at noon of 1600 $\mu mol\ m^{-2}\ s^{-1}$).

Nitrogen treatments

At 15 days after transplanting (DAT), a group of 20 plants was chosen to establish each of the nutritional nitrogen statuses. Then, plants were watered during the experiment with ½ Hoagland nutrient solutions with the following composition: 0.25 mM calcium phosphate [$Ca(H_2PO_4)_2$], 2.5 mM potassium chloride (KCl), 1.0 mM magnesium sulphate ($MgSO_4$), 12.5 µM boric acid (H_3BO_3), 1.0 µM manganese sulphate ($MnSO_4$), 1.0 µM zinc sulfate ($ZnSO_4$), 0.25 µM copper sulphate ($CuSO_4$), 0.2 µM ammonium molybdate [$(NH_4)6Mo_7O_{24}$], 10 µM Fe-ethylenediamine-di-o-hydroxy phenylacetic acid and either 10 (low N) or 150 mg N L^{-1} H_2O (high N). The two concentrations of N in the nutrient solutions used in this study were selected because similar ranges were employed in previous studies with the purpose of establishing low and high levels of nitrogen in plants (Belesky *et al.*, 1984; Florez-Velasco *et al.*, 2015). Also, the fertilizer used as a source of N was 46% urea (Monomeros, Barranquilla, Colombia). Furthermore, the concentration of the other macro and micronutrients of this study has also been widely used in studies of mineral nutrition (Garcia-Castro and Restrepo-Díaz, 2013).

Plants were watered twice a week, and the irrigation volume was adjusted throughout the experiment. Tamarillo plants were watered with 150 mL $plant^{-1}$ $week^{-1}$ between 14 and 35 DAT and 200 mL $plant^{-1}$ $week^{-1}$ between 35 and 70 DAT. The water needs of the plants were estimated by the weight of the plants every 24 hours.

Waterlogging treatment

Nitrogen highly influences the growth and development of plants (Maschnner, 2013). For that reason, tamarillo plants were divided into two groups of 10 plants in each nitrogen treatment with the purpose of establishing the waterlogging conditions (with or without waterlogging) when differences on shoot length were observed between the two treatments of nitrogen fertigation (28 DAT). Three different periods of waterlogging with duration of two, four and six days were established. The periods of low availability of oxygen in the soil were developed between 35 and 37 (S1), 51 and 55 (S2), and 64 and 70 (S3) DAT, respectively. Also, plants had a recovery time of 14 days between the first two periods of stress. The conditions of oxygen deficiency in the soil were carried out by covering the holes in the plastic pots to ensure a constant water depth of 1 cm over the substrate during periods of waterlogging. At the end, four groups for different treatments were available: i) well-nourished plants with N, but without waterlogging, ii) well-nourished plants with N and with waterlogging stress, iii) poorly nourished plants with N, but without waterlogging conditions and iv) poorly nourished plants with N and with waterlogging. In general, each treatment consisted of ten plants and the experiment lasted for 70 days.

Determined variables

The shoot length was determined weekly from 14 to 70 DAT. At the end of the trial (70 DAT), the efficiency of photosystem II (F_v/F_m ratio) was determined by using a Fluorescence spectroscopy (Handy PEA, Hansatech Instruments, Kings Lynn, UK). Also, leaf chlorophyll content was obtained by SPAD readings as a non-destructive tool using a chlorophyll meter (SPAD-502; Minolta, Ramsey, NJ). The leaf chlorophyll content and maximum efficiency of PSII were obtained by taking a fully expanded leaf of the outer half portion of the plant. Subsequently, plants were harvested to determine the dry weights of each organ. Leaf area (LA) was also determined at the end of the experiment using a leaf area meter (LI-3100, LI -COR Inc., Lincoln, NE, USA). Likewise, the leaf area was used to calculate the leaf area ratio (LAR) by the relationship between leaf area and total plant dry weight (TPDW). Finally, nitrogen use efficiency (NUE) was also calculated using the methodology described by Florez-Velasco *et al.*, 2015, which consisted in estimating the ratio of the total plant dry weight (TPDW) and the amount of nitrogen applied in each treatment (NUE = TPDW / N applied, g g^{-1}).

Experimental design and statistical data analysis

A factorial design with two factors (nitrogen nutritional status vs. waterlogging conditions) with ten repetitions (plants) per treatment was used. All values in percentages were transformed with the arcsine formula before the analysis. Data were analyzed using the program Statistix v. 8.0 (Analytical Software, Tallahassee, FL, U.S.). Finally, the summary of the analysis of variance of the effect of waterlogging treatments and N nutritional status and their interaction on the physiological response of tamarillo seedlings to waterlogging period is shown in Table 1.

Results and Discussion

Growth parameters

Differences were observed on shoot length due to two nitrogen (N) nutritional statuses (10 vs. 150 mg N L^{-1} H_2O) at 28 DAT. Cultivated plants with a higher N content in the nutrient solution began to show a greater height until the end of the experiment (Fig. 1). Regarding the interaction between nutritional status vs. waterlogging stress, it was observed that shoot growth was lower in tamarillo plants subjected to three waterlogging periods in both N treatments at 70 DAT. On the other hand, stem diameter showed only differences in the N status factor and waterlogging treatments. A higher stem diameter was found when tamarillo seedlings were cultivated with 150 mg N L^{-1} H_2O. Likewise, when plants were subjected to three different periods of waterlogging, the stem diameter was also lower in comparison to plants without stressful conditions (Table 2). Aldana *et al.* (2014) also reported similar observations when a significant reduction in plant height and stem diameter was seen after subjecting cape gooseberry (another Solanaceae species) seedlings to eight-day waterlogging periods. Also, Florez-Velazco *et al.* (2015) also evaluated the effect of the interaction between waterlogging vs. nutritional N status and found that a series of short periods of oxygen deficiency in the soil caused a decrease in the shoot length of lulo plants (another Solanaceae species) cultivated with two levels of N (10 vs. 150 mg N $L^{-1}H_2O$), highlighting that the most significant reduction was observed in plants that were always nitrogen-deficient. A lower plant height under waterlogging conditions can be attributed to low O_2 supply which causes ionic imbalance and/or nutrient stress. Also, waterlogging stress causes a decreased N uptake, affecting the development of the cortical cells (Rao and Li, 2003). For that reason, stem diameter could show a lower diameter in waterlogging plants. In general, several studies on the effects of flooding in crop plants have showed that morphological adjustments (such as plant height, stem diameter, adventitious roots, and hypertrophic lenticels) contribute to flood acclimatization (Liu *et al.*, 2014; Najeeb *et al.*, 2015; Phukan *et al.*, 2016). In the present study, plant height and stem diameter did not increase, indicating that these lacks of changes suggest that *S. betaceum* could not achieve flood tolerance in spite of an optimum N nutritional status.

On the other hand, differences were also obtained in the N nutritional status vs. waterlogging interaction on leaf area and leaf area ratio (LAR) at the end of the experiment (Fig. 2). Plants cultivated with high levels of nitrogen without waterlogging had greater leaf area. Also, this variable was negatively affected by waterlogging conditions since well-nourished plants showed similar leaf area values to those obtained in plants with low nitrogen and without periods of

Table 1. Summary of analysis of variance of the effect of N fertigation status and waterlogging treatments on the physiological behaviour of tamarillo seedlings

Parameter	Abbr.	Source of variation		
		Nitrogen Status (N)	Waterlogging (W)	N × W
Leaves dry weight	LDW	***z	***	*
Stems dry weight	SDW	***	***	**
Roots dry weight	RDW	N.S.	***	N.S.
Plant total dry weight	PTDW	**	***	N.S.
Leaf area	LA	***	***	***
Leaf area ratio	LAR	**	***	**
Stem diameter	SD	***	***	N.S.
Leaf chlorophyll content	SPAD	***	*	**
PS II efficiency	F_v/F_m	*	***	N.S.
Nitrogen use efficiency	NUE	***	***	***
Percentage of allocation toward leaves		***	***	N.S.
Percentage of allocation toward stem		***	***	N.S.
Percentage of allocation toward roots		***	N.S.	*

z*, **, and *** significantly different at the 0.05, 0.01 and 0.001 probability levels, respectively. NS, not significant at α = 0.05.

excess water stress. Finally, tamarillo plants grown with 10 mg N $L^{-1}H_2O$ and waterlogging had the lowest leaf area at the end of the experiment. Similar trends were also obtained in LAR. Waterlogging stress periods also caused a reduction of LAR values in tamarillo seedlings cultivated with either high or low N. The leaf area reduction in tamarillo plants at three periods of waterlogging stress may be due to a reduction in the leaf gas exchange properties (transpiration and stomatal conductance), as observed in other Solanaceae species such as tomato (Rao and Li, 2003) and lulo (Florez-Velasco *et al*., 2015), causing an adverse effect on the photosynthetic capacity of the plant (Alcantara *et al*., 2012). Also, a lower LAR under flooding periods is due to limit nutrients uptake, producing a higher biomass allocation towards stems and/or roots (Rubio *et al*., 1995).

Dry weights and distribution of assimilates

Similar trends to the ones observed in leaf area and LAR were also found in the nutritional status vs. waterlogging interaction on leaves, stems, and total plant dry weight (Table 2). In general, it can be seen that plants under N optimal conditions without waterlogging in soil showed higher dry weights at 70 DAT. Also, waterlogging stress reduced the accumulation of dry matter in both nutritional states (10 and 150 mg N L^{-1} H_2O). Similar results were seen in cotton (Hocking *et al*., 1985) and lulo (Florez-Velasco *et al*., 2015). Regarding roots dry weights, differences were not found between N nutritional status (N) and waterlogging treatments (T). However, when dry weight data were analyzed as dry mass partitioning, it was observed that there were differences in the interaction NxT on root allocation. In general, leaves biomass allocation was negatively conditioned by waterlogging conditions or low nitrogen levels during growing (Fig. 3). In contrast, a greater accumulation of assimilates (about 40%), was found under soil oxygen-deficiency conditions in tamarillo stems in both nutritional states. In this aspect, Trought and Drew (1980) also observed an increase in the dry matter partitioning towards wheat plant stems exposed to a short waterlogging period (8 days) due to a higher accumulation of carbohydrates. Bailey-Serres and Voesenek (2008) has also been reported that a re-allocating biomass (especially starch) to stems and petioles under waterlogging stress because flooding promotes the conversion of starch to glucose as a metabolic acclimation under O_2 deprivation. Finally, a higher dry matter partition towards roots (~70%) was observed when plants were grown in an N deficient medium, despite the waterlogging condition. Plants often respond to nutritional stresses by increasing biomass partitioning towards their roots because more nutrients are absorbed when there is a greater root volume (Mengel and Kirkby, 2001). Poorter *et al.* (2012) also stated that a significant increase in biomass allocation towards roots at the expense of stem and, especially, of the leaf when nutrients are limiting. Data from this study showed that 70% of the biomass was found in roots of tamarillo plants grown in

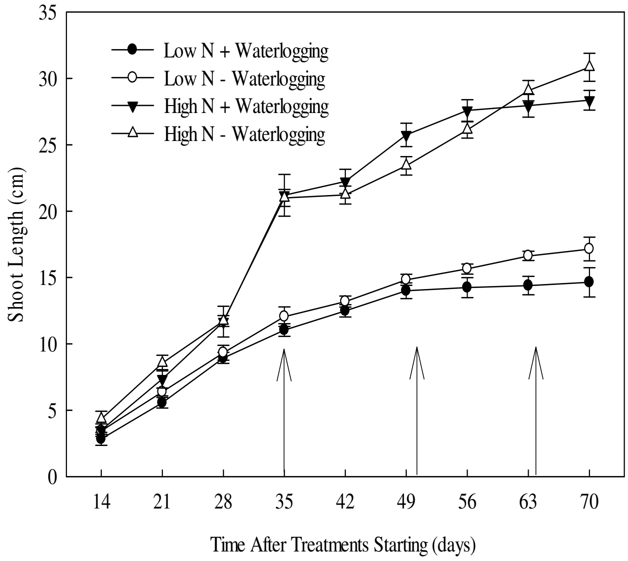

Fig. 1. Effect of the interaction between N nutritional status (10 (Low) and 150 (High) mg N L^{-1} H_2O) and waterlogging conditions (with or without) on shoot length. For each treatment, the values are the mean of 10 plants ± standard error. Arrows indicate when waterlogging stress periods started

Table 2. Effect of the interaction between N nutritional status (10 and 150 mg N L^{-1} H_2O) and waterlogging conditions (with or without) on some growth parameters (Stem Diameter (SD), Leaves Dry Weight (LDW), Stem Dry Weight (SDW), Roots Dry Weight (RDW) and Total Plant Dry Weight (TPDW)) in tamarillo seedlings at 70 days after transplanting

Treatments	SD (mm)	LDW (g)	SDW (g)	RDW (g)	TPDW (g)
			N nutritional status (NS)		
10 mg N L^{-1} H_2O	6.71[z] a[y]	0.49 a	0.73 a	2.66	3.90 b
150 mg N L^{-1} H_2O	8.96 b	1.36 b	1.67 b	2.67	5.70 a
Significance[x]	***	***	***	N.S.	***
			Waterlogging treatments (WT)		
With Waterlogging	7.13 a	0.37 b	0.94 a	1.53 a	2.85 b
Without Waterlogging	8.55 b	1.49 b	1.44 b	3.81 b	6.76 a
Significance	***	***	***	***	***
			NS x WT		
10 mg N L^{-1} H_2O × With Waterlogging	6.08	0.21 b	0.62 c	1.41	2.24 d
10 mg N L^{-1} H_2O × Without Waterlogging	7.35	0.79 b	0.83 c	3.94	5.57 b
150 mg N L^{-1} H_2O × With Waterlogging	8.17	0.53 b	1.26 b	1.66	3.45 c
150 mg N L^{-1} H_2O × Without Waterlogging	9.75	2.19 a	2.08 a	3.67	7.95 a
Significance	N.S.	***	**	NS	*

[z] For all treatments, values are the mean of 10 replicates.
[y] Means with different letters represent statistically significant differences according to Tukey's test ($p \leq 0.05$).
[x] * , ** , and *** significantly different at the 0.05, 0.01 and 0.001 probability levels, respectively. NS, not significant at $\alpha = 0.05$.

an N deficient medium (10 mg N L^{-1} H_2O) in both conditions of waterlogging. Similar observations were found in lulo by Parra-Coronado *et al.* (2015) where they reported that 70% of the dry matter was accumulated in roots under N deficiency.

Chlorophyll content, chlorophyll fluorescence and NUE

Tamarillo plants grown with a high nitrogen concentration and without waterlogging periods showed the highest SPAD readings at the end of the experiment (Table 3). In this context, a low chlorophyll content under waterlogging stress may be because this abiotic stress condition causes a significant decrease in the N uptake due to a reduced root activity (Rao and Li, 2003). On the other hand, plants grown with a low N solution and without low oxygen availability conditions in the soil had the highest nitrogen use efficiency (NUE). NUE was reduced to 50% by waterlogging periods in tamarillo plants in both N levels. In this sense, the effect of the waterlogging vs. N nutritional status interaction has also been reported by Florez-Velasco *et al.* (2015) in lulo seedlings. They found that NUE was also higher when plants were grown under low N. A higher NUE in tamarillo plants cultivated in an N deficient medium can be due to the fact that NUE tends to increase when the N input decreases, since the plant tries to optimize its N absorption through a high-affinity nitrate transport system (Mi *et al.*, 2007). On the other hand, our results also showed that waterlogging caused a lower NUE. Under flooded conditions, the bioavailability of N decreases due to dilution and leaching

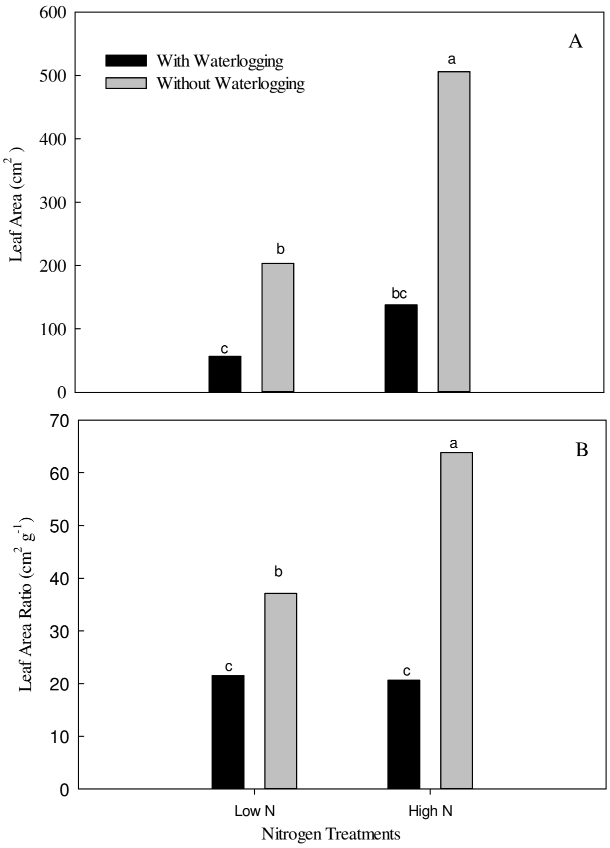

Fig. 2. Influence of the interaction N nutritional status between (10 (Low) and 150 (High) mg N L^{-1} H_2O) and waterlogging conditions (with or without) on leaf area (A) and leaf area ratio (B). Each bar chart represents the mean of 10 plants. Vertical bars represent ± standard error

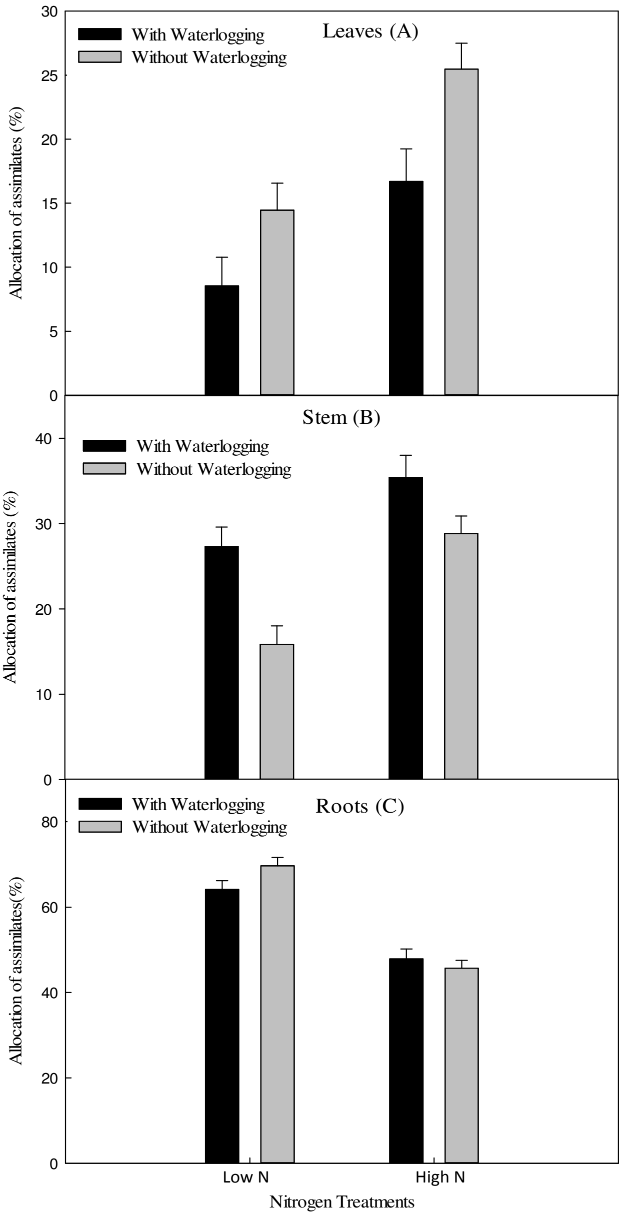

Fig. 3. Influence of the effect of the interaction between (10 (Low) and 150 (High) mg N L^{-1} H_2O) and waterlogging conditions (with or without) on the percentage of dry mass allocation toward leaves (A), stems (B) and roots (C) in tamarillo seedlings. Each bar chart represents the mean of 10 plants. Vertical bars represent ± standard error

(Liu *et al.*, 2013). Also, it is important to consider that under O_2 deficiency in the root zone can change the redox state of nutrients, making them unavailable (e.g. nitrogen) (Najeeb *et al.*, 2015).

Differences were separately observed on F_v/F_m ratio due to N nutritional status, or three short periods of waterlogging. F_v/F_m ratio diminished when plants were subjected to low N or waterlogging conditions (Fig 3). Studies have shown that chlorophyll fluorescence is a good indicator of nutrient stresses (Gorbe and Calatayud, 2012). Parra-Coronado *et al.* (2015) also found that F_v/F_m ratio was lower under nitrogen deficiency in lulo. Furthermore, Lima *et al.* (1999) stated that a drop in

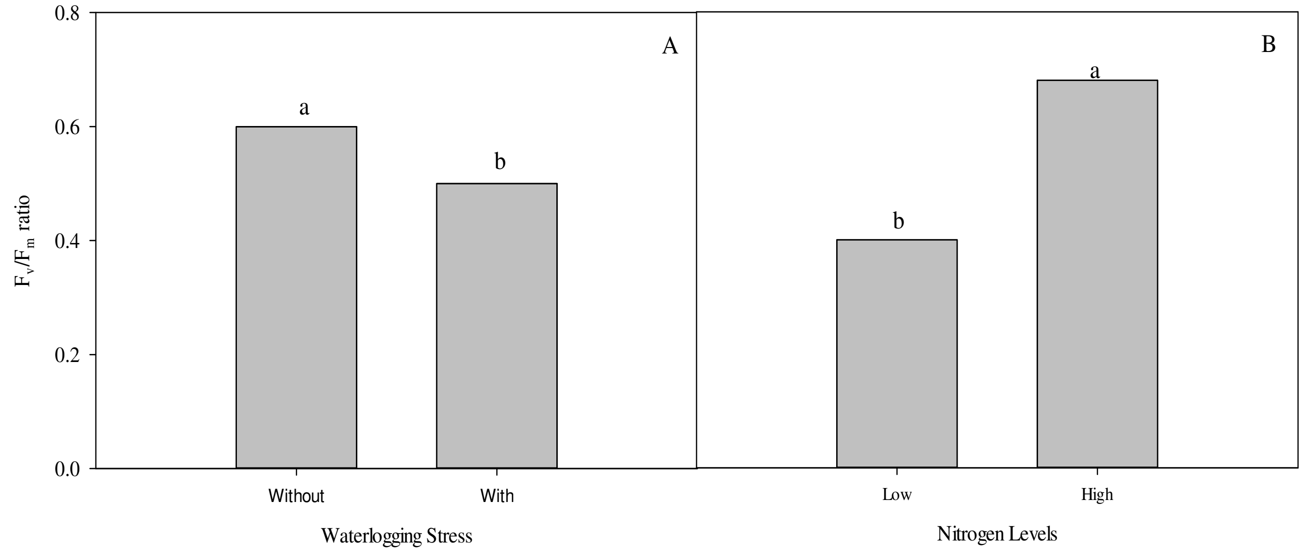

Fig. 4. Influence of the effect of the interaction between waterlogging conditions (with or without) (A) and Nitrogen Levels (10 (Low) and 150 (High) mg N L^{-1} H_2O) (B) on F_v/F_m ratio. Each bar chart represents the mean of 20 leaves replicates. Vertical bars represent ± standard error

Table 3. Effect of the interaction between N nutritional status (10 and 110 mg N L^{-1} H_2O) and waterlogging conditions (with or without) on leaf chlorophyll content (SPAD readings) and Nitrogen Use Efficiency (NUE) in tamarillo seedlings at 70 days after transplanting

Treatments	SPAD Readings	NUE (g DW g N^{-1})
10 mg N L^{-1} H_2O × Without Waterlogging	12.69 c[z]	38.41 a
10 mg N L^{-1} H_2O × With Waterlogging	10.63 c	15.46 b
150 mg N L^{-1} H_2O × Without Waterlogging	37.51 a	4.98 c
150 mg N L^{-1} H_2O × With Waterlogging	23.82 b	2.18 c

[z] Means with different letters represent statistically significant differences according to Tukey's test ($p \leq 0.05$).

the F_v/F_m ratio might be caused by chlorophyll loss and a low nitrogen content created by an imbalance in the allocation of assimilated nutrients. This theory could also be applied to the poor-nourished plants (10 mg N L^{-1} H_2O) in the present trial, which demonstrated a lower F_v/F_m ratio, as these plants had a lower chlorophyll content (Fig. 3) and accumulated less LDW (Table 2). As it was mentioned above, F_v/F_m ratio was conditioned by waterlogging treatments. Malik *et al.* (2015) observed that the PSII efficiency was also negatively affected by waterlogging. Also, Irfa *et al.* (2010) mentioned that a lower F_v/F_m ratio under waterlogging conditions may be due to an increase in the ethylene concentration in leaves because 1-aminocyclopropane-1-carboxilic acid (ACC, a precursor of ethylene) is synthesized and then transported in the xylem to the aerial part where it is rapidly oxidized to ethylene in anaerobic conditions (Ahmed *et al.*, 2006).

Conclusions

In general, this study also showed that a lower shoot length, stem diameter, leaf area, total plant dry weight, NUE, F_v/F_m ratio and chlorophyll content either with a low or high N status. This lack of response in the physiological traits under waterlogging conditions indicates that S. *betaceum* plants could not achieve a flood tolerance mechanism, allowing inferring that this species is susceptible to landscaping situations where periods of waterlogging can be expected in spite of an adequate nitrogen nutrition.

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