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Effects of nitrogen fertilization on the photosynthesis and biomass distribution in a potato crop

Efectos de la fertilización nitrogenada sobre la fotosíntesis y distribución de biomasa en un cultivo de papa

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Abstract

Nitrogen fertilization has positive effects on growth and production of potato crop. The objective of this study was to assess the differences of the photosynthetic response and biomass partitioning patterns during the main phenophases of the potato cultivar Capiro under different nitrogen nutrition fertilization treatments in the tropical Andes of Mérida, Venezuela. Plots of 40 m^2 (2,625 plants m^{-2}) were established under a random block design with three replications by nitrogen fertilization treatment: 0, 100, 200, and 300 kg. N ha^{-1}. Photosynthesis and biomass were measured in the different organs in the main phenological stages of the crop. The results indicate that photosynthesis tends to increase slightly with the nitrogen supply; although the differences were not always significant and, decreases during crop growth. Tubers yield it was markedly influenced by the nitrogen fertilization. The total biomass production, as well as biomass allocation in different organs showed differences between treatments, maintaining the following order: 300-N> 200-N> 100-N> 0-N. When analyzing the biomass accumulation curves, it is estimated that the application of 250 kg N ha^{-1} as mineral fertilizer is enough to reach optimal production yields.

Keywords: *Dry weight accumulation; nitrogen supply, Solanum tuberosum, tuber yield*

Resumen

La fertilización nitrogenada tiene efectos positivos sobre el crecimiento y la producción del cultivo de papa. El objetivo de este estudio fue evaluar las diferencias de la respuesta fotosintética y los patrones de partición de biomasa durante las principales fenofases del cultivo de papa (cultivar Capiro) bajo diferentes tratamientos de fertilización con nitrógeno en los Andes tropicales de Mérida, Venezuela. Se establecieron parcelas de 40 m^2 (2.625 plantas m^{-2}) bajo un diseño de bloques al azar con tres repeticiones por tratamiento de fertilización nitrogenada: 0, 100, 200 y 300 kg N ha^{-1}. La fotosíntesis y la biomasa se midieron en los diferentes órganos en las principales etapas fenológicas del cultivo. Los resultados indican que la fotosíntesis tiende a aumentar ligeramente con el suministro de nitrógeno; aunque las diferencias no siempre fueron significativas y disminuye durante el crecimiento del cultivo. El rendimiento de los tubérculos estuvo marcadamente influenciado por la fertilización nitrogenada. La producción total de biomasa, así como la asignación de biomasa en diferentes órganos mostraron diferencias entre los tratamientos, manteniendo el siguiente orden: 300-N> 200-N> 100-N> 0-N. Al analizar las curvas de acumulación de biomasa, se estima que la aplicación de 250 kg N ha^{-1} como fertilizante mineral es suficiente para alcanzar rendimientos de producción óptimos.

Palabras clave: *acumulación de peso seco; suministro de nitrógeno, Solanum tuberosum, rendimiento*

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Introduction

The response of plants to different types of environmental stress involves structural and functional changes ruled by processes linked to the carbon balance (Lambers, 1998; Lambers *et al.,* 1998; Schurr *et al.,* 2006). Plants may respond to environmental heterogeneity through physiological and morphological plasticity that allows them to optimize resources (Lambers *et al.,* 1998). Additionally, the morphological plasticity may also be a consequence of higher physiological plasticity (Lambers, 1998; Lambers *et al*. 1998; Schurr *et al.,* 2006). Thus, the change in the biomass partitioning patterns throughout the organs may constitute an adaptation or acclimation mechanism in response to the environmental pressures (Osone & Tateno, 2005; Schurr *et al.,* 2006). This ecophysiological approach may serve as a fundamental instrument for addressing crop yields, given its socio-economic and environmental relevance. However, studies with this approach are still lacking for several crops, including superfoods playing a central role in global food security.

Potato is one of the main agricultural products contributing to global food security, given its high-yield production per unit area (Devaux *et al.,* 2014). Potato is originally from the Andes, where it remains one of the main crops for its economic relevance (Villa & Sarmiento, 2009; Machado & Sarmiento, 2012). The Diacol - Capiro cultivar has been farmed due to its high productivity, edaphoclimatic adaptability, and favorable properties for industrial processing (for example, potato chips). This potato cultivar has a vegetative cycle, which ranges from 130 and 150 days, with up to 35 t ha^{-1} crop yields in optimal growth conditions. Nevertheless, there are still not enough ecophysiological data about this cultivar showing the effects of different growing conditions (i.e., nutrients availability) on the biomass and tuber growth, production, and accumulation. Tubers are the organs of main economic interest in the case of potato crop, and they are notable for their high assimilation and nutrient accumulation throughout the crop cycle (e.g., Van Delden, 2001; Machado & Sarmiento, 2012; Qiqige *et al.,* 2017).

Various studies have determined the role of nitrogen as an essential element to attain high productivity levels of potato crop (Biemond & Vos, 1992; Machado & Sarmiento, 2012; Silva *et al*., 2013; Qiqige *et al.,* 2017). Similarly, reduced levels of nitrogen may lead to considerable reductions of production yields and to a reduced biomass distribution (Van Delden, 2001; Alva *et al.,* 2002; Qiqige *et al.,* 2017). This response of the crop has been connected to the influence of leaf nitrogen on photosynthesis (Evans & Poorter, 2001), which varies according to the growth stage and to the nitrogen demand (Lambers *et al.,* 1998; Poorter & Nagel, 2000). One method of analysis of the efficiency of nitrogen fertilization in agricultural crops has been the examination of the photosynthesis dynamics and biomass distribution and accumulation patterns throughout the different organs (Biemond & Vos, 1992; Alva *et al.,* 2002; Qiqige *et al.,* 2017).

The biomass accumulation in potato crop may vary a lot throughout its phenological stages, yet with unchanged fertilization rates and growth conditions (Biemond & Vos, 1992; Van Delden, 2001). On the other hand, nitrogen availability also determines the photosynthetic response within the crops, particularly in the case of leaf nitrogen destined to protein regeneration (Evans & Poorter, 2001). Therefore, the proportion between the nitrogen fertilization and the carbon gains considerably influences the growth and production yields (Lambers *et al.,* 1998; Poorter & Nagel, 2000).

In this context, there is a need to examine nitrogen fertilization alternatives for the potato crop by analyzing the implications for the production. Thus, the objective of this study was to assess the differences of the photosynthetic response and biomass partitioning patterns during the main phenostages of the potato crop cultivar Capiro under different nitrogen nutrition fertilization treatments in the tropical Andes of Mérida, Venezuela.

Material and Methods

Study area and experimental design

The field experiment was carried out in Mucuchíes, in the municipality of Rangel, State of Mérida, Venezuela (8°46'94''N - 70°55'47''W, 3,200 masl) from April through July 2005. The Diacol-Capiro cultivar was selected due to its socio-economic importance in the region and earliness (development cycle of 4 to 4½ months). Mucuchíes has a mean annual temperature of 11.5 °C, and mean annual precipitation of 800 mm. The soil was characterized (0-30 cm) by a loamy-sandy texture, total nitrogen of 0.03%, available phosphorus of 0.8 ppm, 1.0 meq 100 g interchangeable potassium, and pH of 5.5, and bulk density of 0.74 g cm^{-3}.

Twelve plots (each 5 m × 8 m = $40m^2$) were established with a planting density of 2.625 plants per m^{-2} (0.25 m between plants, and 1.5 m between rows), with randomized block design, four different nitrogen fertilization treatment and three replications. Each plot contained five rows 8 m long, with two outer rows acting as barriers, and each row totaled 32 plants. The treatments used were as follows: 0, 100, 200, and 300 kg N ha^{-1}. Ammonium nitrate ($(NH_4)NO_3$) was the source of inorganic nitrogen used. Inorganic fertilization source with ammonium nitrate (33.5% N) was supplied. Potassium sulfate (17% assimilable K_2O) and phosphate rock (25% assimilable P_2O_5) were applied to all plots. A total 20 kg N ha^{-1} were applied in the 100-N treatment, 37.5 kg N ha^{-1} in the 200-N treatment, and 75 kg N ha^{-1} in the 400-N treatment during sowing. During sowing, we also applied 100 kg ha^{-1} P_2O_5 in the form of phosphate rock (400 kg ha^{-1}) and 200 kg ha^{-1} K_2O in the form of potassium sulfate (476 kg ha^{-1}) to all experimental plots.

Data collection

In each plot the growth parameters such as, number of stem, plant height (in cm), and biomass (g. plant) of the different organs was measured along the days after sowing (DAP). The samplings were taken during the main phenological stages of the crop: near the moment of emergence, on the 36th day after sowing (DAP), at the beginning of tuberization (60 DAP), at the time of maximum leaf expansion (105 DAP), and at harvest (127 DAP). Thus, number of stem, plant height and biomass was determined in each phenological stage from six plants selected in each plot, with the exception of the last sampling where ten plants per plot were harvested, given the significance of the crop yield from the agronomic point of view (Villa *et al.*, 2020). Samples of biomass were dried at 70°C until they reached a constant weight; subsequently, these samples were weighted and milled to further obtain composite samples per plot and sampling session.

Gas exchange measurements were conducted in fully expanded leaf blade of three individual in each plot during the emergence (near 36 DAP), tuberization (64 DAP), maximum leaf expansion (105 DAP), and harvest (127 DAP). Three of the fully mature and expanded top leaves were randomly obtained per plot (36 leaves for each treatment). Gas exchange measurements were conducted using portable gas exchange system (LI-COR 6400; LI-COR, Lincoln, Nebraska, USA) measuring leaf photosynthesis for amplitude of photosynthetically active radiation (PAR) from 25 µmol m^{-2} s^{-1} up to 2500 µmol m^{-2} s^{-1}.

Data analysis

All analyses were carried out in R Environment (R Core Team 2018). Variation in the biomass in different organs, number of stem and plant height, were compared between all treatments by one-way analysis of variance (ANOVA; for normally distributed data) followed by a post hoc Tukey's test ($p<0.05$) using the car package (Fox *et al.*, 2017). The different treatments were the factors and the block design effects were key aspects to take into account. This test is suitable for randomized block design and non-normal distribution data (Crawley, 2013).

We adjusted the response curves of assimilation based on gas exchange measurements. The non-rectangular hyperbola equation is commonly used to describe the response of foliar photosynthesis to radiation (Xu *et al.*, 2019). The R software served to estimate the parameters of the non-rectangular hyperbola following the same equation:

$$Pn = 1/2q\,[(mRad + Pmax) - \sqrt{(mRad + Pmax)2 - 4mqPmaxRad}] - Resp \qquad \text{Equation 1}$$

$$Pn = Pb - Resp \qquad \text{Equation 2}$$

Where Pn is the CO_2 exchange rate (net photosynthesis rate), Pb is the gross photosynthesis, and Resp is the leaf respiration in the dark. With respect to the non-rectangular hyperbola, Rad is the radiation incident on the leaves, m is the initial slope of the light response curve, Pmax is the rate of gross photosynthesis when light saturation is reached, q is the Curvature parameter (Table 1).

Table 1. Parameters of the non-rectangular hyperbola during days after planting (DAP) in the different treatments of nitrogen fertilization: 0, 100, 200 and 300 kg N ha^{-1}. The coefficient of determination (R^2) is indicated.

DAP	Treatments	Parameters of the non-rectangular hyperbola				
		Pmax	m	a	Resp	R^2
36	0-N	12.85	0.0034	0.060	2.49	0.92
	100-N	13.06	0.0039	0.080	2.47	0.90
	200-N	14.52	0.023	0.048	0.99	0.96
	300-N	15.22	0.025	0.045	1.55	0.95
64	0-N	11.76	0.010	0.023	1.29	0.91
	100-N	12.05	0.020	0.027	1.03	0.92
	200-N	12.96	0.025	0.037	0.89	0.90
	300-N	13.25	0.027	0.047	0.99	0.93
105	0-N	6.08	0.012	0.020	1.12	0.96
	100-N	7.35	0.019	0.024	1.03	0.94
	200-N	8.12	0.021	0.025	0.90	0.92
	300-N	9.27	0.023	0.027	0.78	0.90
127	0-N	3.90	0.009	0.019	1.05	0.89
	100-N	4.10	0.016	0.020	0.90	0.87
	200-N	5.86	0.025	0.022	0.72	0.86
	300-N	6.09	0.029	0.030	0.60	0.90

Finally, tuber and total accumulated biomass along the DAP were adjusted with Gompertz functions (Y= a*exp-b*exp-c*t), where Y is the biomass, t the time, a, b and c are parameters obtained by adjusting the experimental data.

Results and Discussion

Overall, the results showed that photosynthesis tends to increase with nitrogen supply. This is the case even for non-contrasting differences, mainly at 64 DAP. Photosynthesis tends to drop substantially, from emergence until harvest time (Figure 1). In this study, photosynthesis per unit of leaf area was found to be slightly different (~15 %) between contrasting treatments, but it was consistent in all the samples, following the order: 300-N > 200-N > 100-N > 0-N (Figure 1). In contrast, other studies have shown that nitrogen limitation has a striking effect in the reduction of leaf photosynthesis for different species (Lambers, 1998; De Groot *et al.,* 2003). For instance, De Groot *et al.* (2003), conclude that the limitation of photosynthesis of

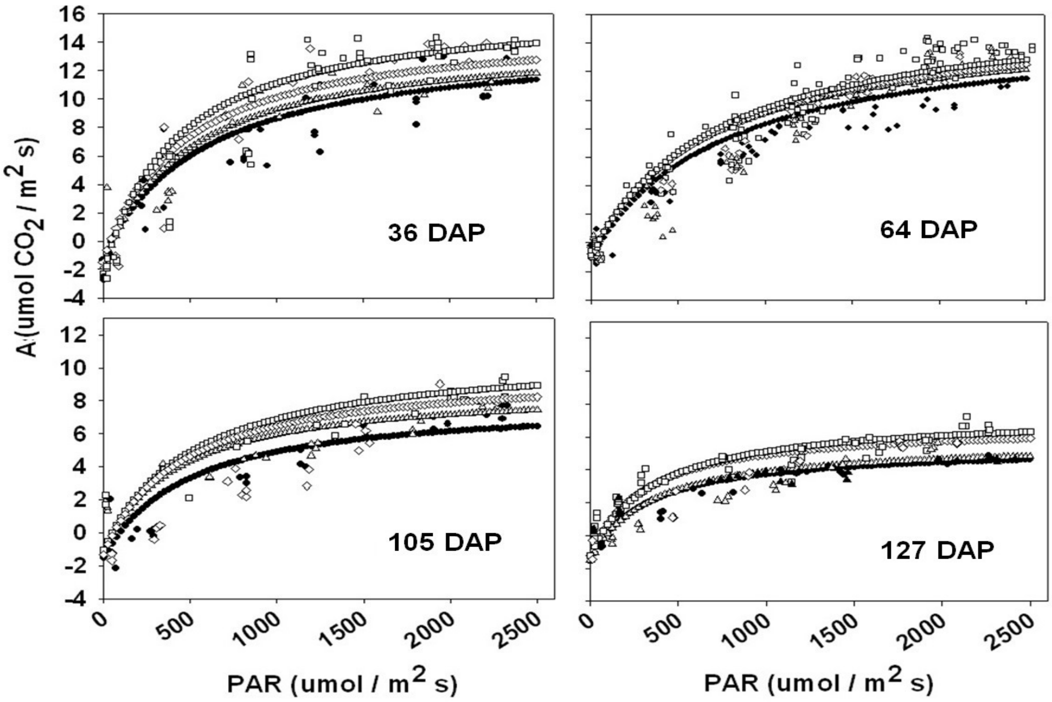

Figure 1. Leaf photosynthesis- photosynthetically active radiation (PAR) response curves. A is the net carbon assimilation rate during days after planting (DAP) in the different treatments of nitrogen fertilization: (●) 0, (Δ) 100, (◊) 200 and (□) 300 kg N ha^{-1}.

Lycopersicon esculentum under nitrogen deficit is due to the excessive production of assimilates that do not have a direct drain or a strong drain, which leads to a significant reduction of photosynthesis, compared to the treatments without nitrogen deficit. In this regard, allegedly, the small differences of photosynthesis between nitrogen deficit conditions and those of fertilization, are due to the tubers' demand of a large proportion of available assimilates, which increases with the time until the final harvest and avoids an accumulation of assimilates in the leaves to take place and, consequently, avoids limited photosynthesis.

Nitrogen fertilization had significant effects on the production of tubers and total biomass, following this order: 300-N > 200-N > 100-N > 0-N (Figure 2), which increased as nitrogen fertilization was higher, 0-N (30.87 ± 4.5 Mg ha^{-1}) <100-N (35.01 ± 2.23 Mg ha^{-1}) <200-N (36.41 ± 1.37 Mg ha^{-1}) <300-N (38.61 ± 3.37 Mg ha^{-1}). However, there was only a 25% difference in tuber production between the 0-N and the 300-N treatments: 36g plant^{-1}, and 49g plant^{-1}, respectively. Furthermore, there was a small difference (4%) between the 200-N and the 300-N treatments, without having significant differences ($p > 0.05$).

These results are consistent with the ones found in other studies, where, as observed, biomass accumulation in potato crop grew with nitrogen supply (Biemond & Vos 1992; Alva *et al.,* 2002; Machado & Sarmiento, 2012; Qiqige *et al.,* 2017). These results suggest that, from an agricultural and ecological point of view, there is no justification for applying measures above 300 kg N ha^{-1}

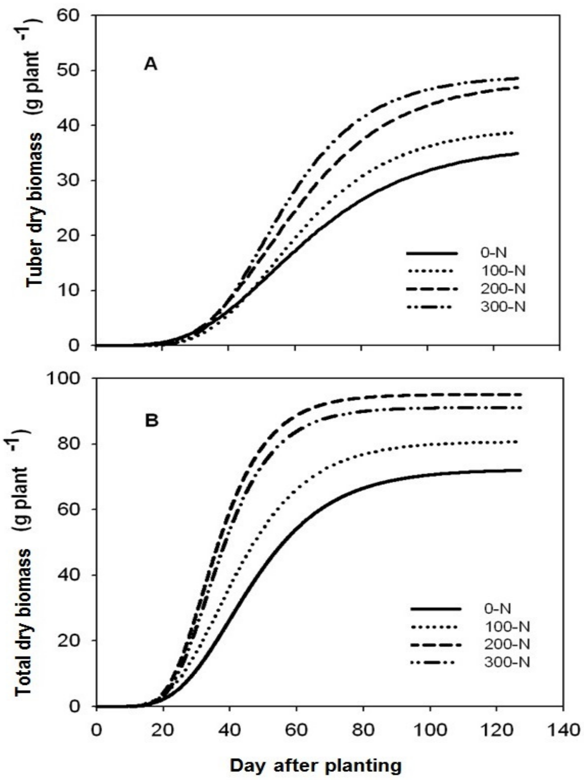

Figure 2. Pattern of total dry biomass accumulation in tubers (A) and total dry biomass (B) during days after planting (DAP) in the different treatments of nitrogen fertilization: 0, 100, 200 and 300 kg N ha^{-1}. The curves correspond to the adjustments Gompertz functions.

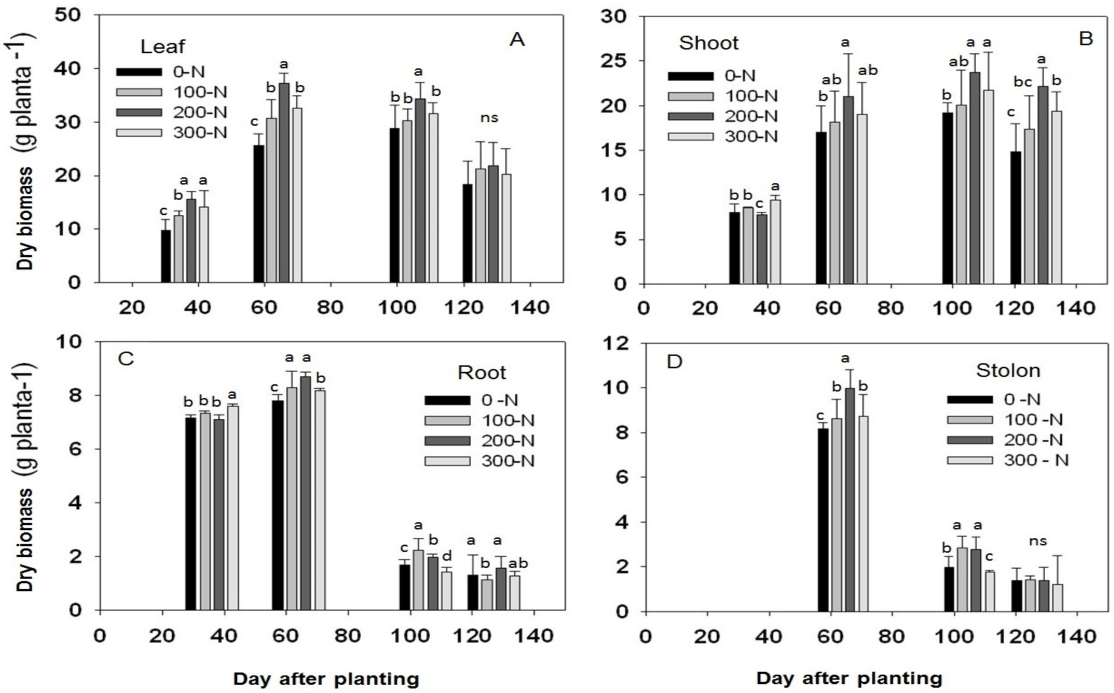

Figure 3. Pattern of dry weight accumulation of different organs during days after planting (DAP) for in the different treatments of nitrogen fertilization: 0, 100, 200 and 300 kg N ha^{-1}. The different letters indicate that there are significant differences between treatments per sampling period ($p < 0.05$).

in the form of mineral fertilizer, and that it would not be financially recommended, as there is no relevant increase of production when plants cannot keep the nitrogen surplus.

The dynamics of biomass accumulation tend to increase up until the 64th DAP and stays stable until its maximum leaf expansion; then, there is a reduction with the onset of senescence, after the 105th DAP (Figure 3). The pattern of biomass partitioning to the roots and stolons was not very different between the treatments (Figure 3). The plants are capable of responding to the heterogeneity of the environment (e.g. availability of nutrients used for growth) through their physiological or morphological plasticity, by which they can optimize the use of resources and the changes in the patterns of biomass partitioning throughout the organs of the plant (Lambers *et al.,* 1998; Schurr *et al.,* 2006; Qiqige *et al.,* 2017). This can be crucial for agricultural production and financial ends. To this day, there are a relevant number of studies on the effects of nitrogen nutrition on the production of potato tubers. Conversely, a reduced number of studies deal with accumulation and partitioning of biomass to the different organs, under contrasting doses of nitrogen fertilization, during the growth of the crop. Even so, a few of them have limited their aim to examine partitioning of biomass to the stem and tubers, though leaving behind additional considerations regarding partitioning to stolon's and roots. Furthermore, these studies have, in a lesser extent, examined the phenomena under nitrogen deficit conditions.

The results suggest that the changes in the patterns of biomass partitioning throughout the plant depend mainly on the strength of the tubers as sinks of assimilated of photosynthesis, despite the nitrogen deficit conditions, maintain a reasonable production capacity from an agroecological perspective.

The result showed significant differences in other growth parameters (i.e. number of stems and height of plants) in the different growth stages before senescence (Table 2). Concerning biomass partitioning, this study found the greatest values of stem biomass during the periods of maximum leaf expansion. In this sense, Alva *et al*. (2002) found that leaf and stem weights were 60g and 30g in each plant, respectively, for Russet Burbank, and between 50 and 20g in each plant for Hilite Russet, respectively. On the other hand, Biemond & Vos (1992) found that, despite the great differences in the total weight of the stems, nitrogen treatments only offered a mild effect (N1= 2.5; N2 = 8 and N3 = 16 g N per plant) on the distribution of the dry weight of the stems throughout the leaves and the stems. The results showed that there is a higher leaves dry weight compared to stems in all treatments. However, near the 44 DAP, leaves dry weight with respect to the stems dry weight was between 60% and 65% for N-100 and N-300, respectively.

The effects of nitrogen nutrition on belowground biomass compartments, like the roots and stem, include more biomass accumulation in these organs under nitrogen deficit conditions, mainly during the first stages of development. It was not the case with the aerial organs. These results lead to conclude that the changes in assimilates distribution patterns of potato crop constitute a plastic response of acclimation to stress due to N deficit (Villa *et al*., 2020). Additionally, these results are very consistent with previous results provided by several review and research works dealing with other vegetal species (Lambers *et al.,* 1998; Forde, 2002). According to other studies, fast-growing species tend to be more plastic than those growing more slowly, in terms of biomass partition as their response to the different levels of nitrogen availability or supply in the soil (Lambers, 1998; Lambers *et al.,* 1998).

Table 2. Number of stem and plant height during days after planting (DAP) in the different treatments of nitrogen fertilization: 0, 100, 200 and 300 kg N ha^{-1}.

DAP	Treatment	Number of stem	Heigth (cm)
36	0-N	2.4 ± 0.50	22.5 ± 2.83
	100-N	3.0 ± 0.69	23.0 ± 2.4
	200-N	3.2 ± 0.50	24.0 ± 2.9
	300-N	3.2 ± 0.69	24.0 ± 2.8
64	0-N	4.5 ± 0.96	50.5 ± 6.85
	100-N	5.2 ± 0.90	50.55 ± 4.2
	200-N	5.2 ± 0.92	52.8 ± 6.8
	300-N	5.3 ± 0.94	54.0 ± 3.5
105	0-N	4.7 ± 0.79	62.4 ± 8.14
	100-N	5.0 ± 0.81	63.0 ± 6.7
	200-N	5.0 ± 0.67	69.2 ± 8.2
	300-N	5.2 ± 0.69	70.0 ± 5.9

Conclusions

This research showed that photosynthesis and growth parameters (i.e. biomass, number of stem, and plant height) tend to increase with the supply of nitrogen. Thus, this result reveals the high potential of the tubers to store assimilated of photosynthesis under conditions of nitrogen deficit. However, results allow us to conclude that the application of 300 kg N ha^{-1} as mineral fertilizer is not justified from a socioeconomic and environmental perspective, considering the little existing differences in tuber production with respect to the 200-N treatment. Thus, we recommend research that demonstrates the efficiency of nitrogen fertilization close to 200 Kg, and even less using combinations with organic fertilizers under different environmental conditions (i.e. topography, climate) and agronomic management (i.e. irrigation). Finally, in this study, the whole harvest did not attain its maximum productive potential. The suggestion is to combine mineral fertilizers with organic sources in order to guarantee and synchronize the nitrogen availability, in accordance with the actual demand of the crop during each phenological stage.

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