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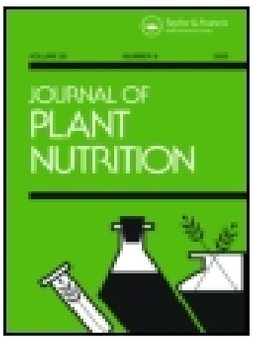

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N, P, K and S uptake response to various levels of CO_2 assimilation and growth rate in lettuce

Francisco Albornoz[a] and J. Heinrich Lieth[b]

[a]Laboratorio de Suelos y Nutrición Vegetal, Instituto de Investigaciones Agropecuarias INIA, Santiago, Chile;
[b]Department of Plant Sciences, University of California, Davis, CA, USA

ABSTRACT

Under conditions of limited nutrient supply, plant nutrient uptake is controlled by the external concentration of the ions. Limited information exists about the whole-plant regulation of nutrient uptake when the supply is adequate. To study the relationship between growth rate and carbon dioxide (CO_2) assimilation with nutrient uptake, growth chamber experiments were conducted with temperatures ranging from 10 to 35°C at medium (600 μmol m^{-2} s^{-1}) and high (1200 μmol m^{-2} s^{-1}) light intensities. Nutrient solution samples were collected every 24 hours and the concentration of ions was analyzed by Inductively coupled plasma -atomic emission spectroscopy (ICP-AES) and nitrate and ammonium (NO_3^-/NH_4^+) conductivity. Leaf photosynthesis was measured using a closed gas exchange system and the total amount of CO_2 assimilated was calculated from dry weight increases. The daily absorption of NO_3^-, Total nitrogen (N), dihydrogen phosphate ($H_2PO_4^-$) and potassium (K^+) responded linearly to plant growth, while ammonium (NH_4^+) and sulfate (SO_4^{2-}) uptake showed a curvilinear response. All the ions studied showed a curvilinear relation with CO_2 assimilation.

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KEYWORDS
Macronutrients; lettuce photosynthesis; relative growth rate; plant nutrient demand

Introduction

Several environmental factors, such as light, temperature, carbon dioxide (CO_2) concentration, water and nutrient availability have a direct effect on plant photosynthetic rates, where it is possible to evidence increases in CO_2 assimilation rates when any of these factors increases within a certain 'safe range' (Sage and Kubien, 2007; Hermans et al., 2006). The enhancement in photosynthetic rates translates into an increment of plant growth rate (Kirschbaum, 2011) followed by a higher demand for nutrients (Ingestad and Agren, 1988) used for the synthesis of new biomass. Nitrogen, phosphorous and sulfur are of special importance in the synthesis of proteins, the storage and distribution of energy within the plant, and in the regulation of growth through the synthesis of nucleic acids (Marschner, 2012); whereas, potassium is highly important for its role in the regulation of the osmotic pressure in growing tissues (Maathuis, 2009). It has been well established that deficiencies of the above-mentioned nutrients impaired primary photosynthesis, sugar metabolism and carbohydrate partitioning between source and sinks (Hermans et al., 2006) but information is lacking on the relationship between the uptake rates of these nutrients and the carbon assimilation and growth rates under well-nutrient supply conditions.

Several studies have established an actual relationship between nutrient absorption with leaf carbon assimilation (Dehlon et al., 1996; Lejay et al., 2003; Lea and Azevedo, 2006). The response of root nutrient uptake to the shoot photosynthetic rates is related to the availability of sugars to be exported

CONTACT Francisco Albornoz fralbornoz@gmail.com Laboratorio de Suelos y Nutrición Vegetal, Instituto de Investigaciones Agropecuarias INIA, CRI La Platina, Santa Rosa 11610, Santiago, Chile.

towards the roots, which determines the energy balance and the availability of adenosine triphosphate (ATP) for the functioning of the root transport systems. The uptake of anions nitrate, phosphate and sulfate (NO_3^-, PO_4^{3-}, SO_4^{2-}) requires energy for the co-transport with protons so as to overcome the negative root cell membrane potential (Reid and Hayes, 2003). The uptake of cations potassium (K^+) requires energy for the maintenance of the concentration gradient that allow the operation of the low-affinity channel-type transport systems, as well as for the functioning of the high-affinity transport systems (Glass, 2002; Gojon et al., 2009; Miller et al., 2009). The availability of carbon skeletons for the assimilation of nutrients in the roots also affects the expression of genes encoding the synthesis of ion transporters, since the concentration of secondary metabolites (such as glutamine, cysteine, proline, glutathione) derived from the assimilation of the absorbed nutrients, exerts a feedback control over this process (Liu et al., 2009).

Ingestad and coworkers (Ingestad and Agren, 1988) have characterized the relationship between nutrient uptake and plant growth rate. These authors developed all their work under the premise of 'steady-state' nutrient concentration, where the concentration of nutrients within the experimental plants was maintained constant over time by adding nutrients at a constant relative addition rate, which was equal to the relative uptake rate (Ingestad and Agren, 1992, 1995). Under these conditions, the authors concluded that there is a linear relation between relative growth rate and the relative uptake (addition) rate of any particular element (Ingestad and Agren, 1995).

Nowadays, in agricultural systems, it is of upmost importance to understand how the uptake rates of nutrients behaves under different environmental conditions and to establish the relation between measurable patterns, such as photosynthesis and growth, in order to minimize fertilizers losses to the environment, reducing the pollution effect (Santos, 2011).

This study was conducted to test the hypothesis that if the uptake rates of nitrogen, phosphorus, potassium, and sulfur (N, P, K, and S) are determined by the shoot photosynthetic rates, then environmental manipulation to enhance CO_2 assimilation will have an instantaneous measurable effect on the uptake rate of the nutrients. The objective was to characterize the relationships between N, P, K, and S uptake with photosynthetic carbon assimilation and growth rate under conditions of well nutrient supply in the rootzone and various environmental conditions of light and air temperature.

Materials and methods

Plant material and growth conditions

Lettuce (*Lactuca sativa* L.) cv. 'Black Seeded Simpson' (Lake Valley Seed, Boulder, CO) plants were grown in a greenhouse during summer 2011, in Davis, California. Seeds were germinated in plastic trays containing peat, sand and redwood compost (1:1:1 v/v). Once the plants had two true leaves they were moved to a greenhouse with natural day/night light conditions and day/night average temperature of 28°C/22°C. In the greenhouse, plants were placed in a hydroponic system, consisting of rectangular 8-liter containers. The containers were interconnected to allow circulation of the solution. The solution was a modified half-strength Hoagland's solution [7.0 mM NO_3^-, 2.0 mM calcium (Ca^{2+}), 1.0 mM magnesium (Mg^{2+}), 3.0 mM K^+, 0.5 mM dihydrogen phosphate $(H_2PO_4)^-$ and 1.0 mM SO_4^{2-}, 46 μM boron (B), 18 μM chloride (Cl), 9 μM manganese (Mn), 0.7 μM zinc (Zn), 0.3 μM copper (Cu), 44 μM iron (Fe) and 0.1 μM molybdenum (Mo); Hoagland and Arnon (1950)], with a pH value of 5.9. The solution was aerated by continuously bubbling air into it, and it was discarded twice per week and replaced with fresh solution. The water level in the container was maintained by supplying fresh solution by gravity from a reservoir connected to the set of containers.

Treatments

Once plants in the greenhouse had grown to a total fresh weight of approximately 200 grams, four plants in independent containers were moved into one of six growth chambers set at one combination of two light intensities (medium: 600 μmol m^{-2} s^{-1}, or high: 1200 μmol m^{-2} s^{-1})

and three air temperatures (10, 25, or 35°C). Specific light intensities were achieved using LED lighting units (model ES330; LumiGrow, Novato, CA) with output control of the photosynthetic photon flux (PPF) projected on the plants. PPF was measured using a quantum sensor (model LI-190; Licor Bioscience, Lincoln, NE). The photoperiod within the chamber was of twelve hours (8:00 am–8:00 pm). The temperature in the nutrient solution was the same as the air temperature.

Plants were preconditioned to the corresponding growth chamber conditions for at least 48 hours prior to the start of the experiments. Each growth chamber experiment had a duration of 48 hours and was repeated twice with different plants. Five liters of the same nutrient solution as in the greenhouse were prepared at the beginning of the sample period and it was completely replaced by fresh solution with the same temperature of the corresponding treatment 24 hours later. Within the hydroponic unit, the solution was agitated continuously through bubbling.

Plant growth and relative growth rate

Fresh weight (FW) was measured at the beginning of the experiment and every 24 hours, using an electronic analytical scale with milligram sensitivity (model XT 400D; Denver Instrument Co., Denver, CO). Plants were removed individually from the hydroponic unit and were weighed in the scale using a container with a known volume of water to avoid water losses from the plant material. For each combination of light and temperature, four plants that were not used in the nutrient depletion experiment were adapted to the environmental conditions of the growth chamber for 48 hours and the dry weight (DW) of these was measured at the end of the sampling period by placing the leaves in an oven at 60°C for 48 hours. Assuming no significant differences existed in DW percentage from day 1 to day 2, the total amount of DW gained was calculated by multiplying the FW by the DW fraction. The relative growth rate (RGR) in g g^{-1} day^{-1} was calculated as the difference of the logarithm of DW in day 1 (t_1) minus the logarithm of DW in day 2, as in Eq. 1

$$RGR = \ln DW_{t1} - \ln DW_{t2} \,/\, (t_1 - t_2) \tag{1}$$

CO_2 assimilation rate

From the DW gain during the experiments, the amount of N, P, K and S absorbed was subtracted to obtain the mass of fixed CO_2, using CH_2O as the primary component from CO_2 assimilation according to the relation CO_2 + water (H_2O) → CH_2O + O_2 (Penning De Vries et al., 1974; Taiz and Zeiger, 2006). The grams of CH_2O were converted into its molecular equivalent by dividing it for the corresponding molecular weight (30 g mol^{-1}). One mol of CH_2O contained one mol of carbon (C)and it was assumed that this C was equal to one mol of CO_2. The absorption of micronutrients was considered negligible for these calculations.

To confirm the net assimilation rate calculations, CO_2 assimilation was measured in single leaves at the end of each 48-hour sampling period, using a portable infrared analyzer (model LI-6400 XT; Licor Bioscience, Lincoln, NE) attached with an LED light source cuvette (model 6400-02B; Licor Bioscience). Within the cuvette, leaves were maintained at constant air temperature accordingly to the growth chamber treatment, and light response curves were built using the following light intensities: 2000, 1600, 1400, 1200, 800, 600, 400, 200, 100 and 0 μmol m^{-2} s^{-1} PPF. The ambient CO_2 concentration within the cuvette was maintained at 380 μmol mol^{-1} and the water mole fraction was kept at 20 mmol mol^{-1}. A minimum of 15 minutes was allowed between light levels for the measurement to be stable before logging the data. The measurement was defined as stable when the rate of change in photosynthesis was lower than 0.1 μmol CO_2 min^{-1}. Six fully expanded leaves on each plant were measured (total number of replicates per light level at each temperature level was 48).

Nutrient uptake rates

Nutrient solution samples were collected on each container at the beginning of the experiment and every 24 hours for 2 consecutive days to determine the depletion of NO_3^-, $H_2PO_4^-$, K^+ and SO_4^{2-}. Changes in the solution volume were tracked by placing the containers on single point load cells (model LCAE-60KG; Omega Scientific, Tarzana, CA). The daily uptake (U) of each nutrient was calculated as the difference in the concentration of the ion every 24 hours corrected for volume changes as in Eq. 2

$$U = (V_{ti}C_{ti} - V_{ti+1}C_{ti+1} / ti + 1 - ti) - V_{Sti}C_{ti} \quad (2)$$

where V is the solution volume, V_S is the sample volume, and C is the concentration at time, t (Mattson and Lieth, 2008). The subscripts i and i+1 refer to the beginning and the end of the time interval (24 hours). Uptake of each nutrient was scaled in terms of total plant dry weight (DW) at the corresponding day of measurement, to determine uptake in units of mmol g^{-1}DW day^{-1}. NO_3^- concentration in the solution samples was determined by diffusion conductivity with a NO_3^-/NH_4^+ analyzer (model TL200; Timberline Instruments, Boulder, CO); while the concentration of $H_2PO_4^-$, K^+ and SO_4^{2-} were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES) instrumentation.

Statistical analysis

Statistical analyses were conducted using the SAS software package (SAS Institute, Cary, NC, USA). Differences in leaf CO_2 assimilation rates across light levels and nutrient uptake rates for each nutrient across the combinations of light and temperature levels were analyzed by analysis of variance (ANOVA) and mean separation was carried out using Tukey's honestly significant difference test. The data for each nutrient uptake from each experiment was pooled into a single data set and a generalized linear model (GLM) approach was used to assess the nature of the relationship between CO_2 assimilation and RGR with the absorption of each single ion. Non-linear regression analyses were used to define the most suitable equation to fit the absorption of the ions to CO_2 assimilation level.

Results

No differences were found in the DW fraction (DW/FW) between treatments, with an average value of 50.7 ± 0.01 g DW kg DW^{-1}. The RGR was significantly different between treatments, with the highest value found at 35°C and 1200 μmol PPF m^{-2} s^{-1} (Figure 1A). The calculated CO_2 assimilation rates were significantly different between treatments, where the highest rates were obtained under high light intensity and 25–35°C (Figure 1B). These results are in agreement with the single leaf net photosynthesis measurements, where increases in temperature enhanced the assimilation rates with PPF values higher than 400 μmol m^{-2} s^{-1} (Table 1). Plant transpiration showed no differences between light treatments, increasing with raising temperatures (Figure 1C).

The daily absorption of NO_3^- doubled when the temperature was increased from 10 to 35°C at 600 μmol PPF m^{-2} s^{-1}. Under high light intensity, the absorption of NO_3^- at 35°C was 3 times higher than at 10°C (Table 2). Temperature had a significant effect on the uptake of $H_2PO_4^-$ (Table 2) under both light intensities, where raising the temperature enhanced the uptake of this ion. This effect was more dramatic at the highest PPF level where the absorption at 35°C was 4-times higher than at 10°C, in comparison to the uptake under medium PPF, where the absorption nearly doubled when the temperature was raised from 10°C to 35°C. The daily absorption of K^+ was significantly affected by light and temperature, as well (Table 2). Under both light intensities, increases in temperature from 10 to 25°C significantly enhanced the uptake of K^+ but further increases in temperature did not affect the uptake of this ion. The uptake of SO_4^{2-} did not show significant differences except at 35°C and 1200 μmol PPF m^{-2} s^{-1} where the rates were 4 - 5 times higher than in the other treatments.

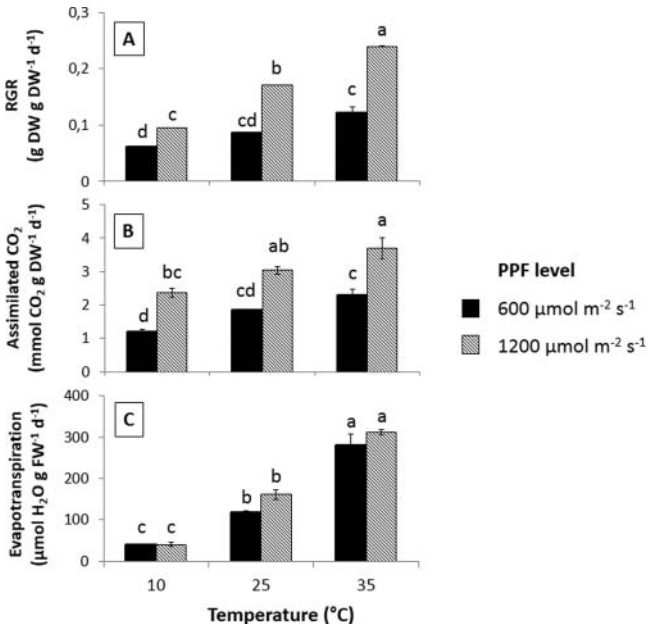

Figure 1. A) Relative growth rate (RGR), B) average assimilated CO_2 and C) evapotranspiration for each temperature at each PPF level. Columns are means ± SE. Different letters on top of each column denote significant differences ($P < 0.05$).

Table 1. CO_2 assimilation rates (μmol m^{-2} s^{-1}) at various light levels in lettuce leaves exposed to air temperatures ranging from 10°C to 35°C. Values are means ± SE. Significance level, ns: not significant; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

	Temperature level (°C)			
Light level (μmol m^{-2} s^{-1})	10	25	35	Significance level
0	−0.67 ± 0.11	−1.87 ± 0.35	−2.31 ± 0.40	ns
100	4.69 ± 0.08	4.01 ± 0.30	3.54 ± 0.16	ns
200	6.14 ± 0.02	7.61 ± 0.25	7.44 ± 0.73	ns
400	7.82 ± 0.10	11.97 ± 0.35	13.55 ± 0.90	*
600	8.77 ± 0.20	14.25 ± 0.90	17.66 ± 0.21	**
800	9.38 ± 0.19	15.57 ± 0.62	20.35 ± 0.80	***
1200	10.12 ± 0.16	17.01 ± 0.86	23.40 ± 0.66	***
1400	10.36 ± 0.23	17.43 ± 1.07	24.30 ± 0.64	***
1600	10.55 ± 0.24	17.76 ± 0.98	24.98 ± 0.75	***
2000	10.83 ± 0.29	18.21 ± 1.06	25.93 ± 0.83	***

Table 2. Daily total uptake of NO_3^-, $H_2PO_4^-$, K^+ and SO_4^{2-} by lettuce roots, in μmol per gram of plant DW. Values are means ± SE. Different letters in the same column denote significant differences ($P < 0.05$).

		Nitrate	Phosphate	Potassium	Sulfate
PPF (μmol m^{-2} s^{-1})	T° (°C)	——— μmol g DW^{-1} day^{-1} ———			
600	10	64.2 ± 9.6 d	20.6 ± 0.1 c	54.1 ± 20.2 c	7.3 ± 2.0 b
	25	104.2 ± 8.7 cd	31.8 ± 0.4 c	228.7 ± 10.2 b	21.7 ±6.4 b
	35	124.2 ± 30.8 c	52.9 ± 1.6 b	197.9 ± 14.8 b	16.6 ± 8.1 b
1200	10	167.6 ± 22.7 c	24.7 ± 3.3 c	81.1 ± 13.3 c	15.6 ± 6.4 b
	25	388.6 ± 24.9 b	53.2 ± 2.7 b	352.7 ± 22.7 a	25.2 ± 6.0 b
	35	581.7 ± 56.2 a	99.7 ± 2.9 a	399.8 ± 29.4 a	88.2 ± 14.7 a

Table 3. Parameters describing the linear response in the uptake of NO_3^-, $H_2PO_4^-$, K^+, and SO_4^{2-} to different levels of RGR and CO_2 assimilation rate. The model corresponds to $y = \beta 0 + \beta 1 \cdot x$.

Nutrient ion	$\beta 0$ (μmol g DW^{-1} d^{-1})	$\beta 1$	X-axis intercept	P-value	R^2
		Independent variable: CO_2 assimilation			
NO_3^-	−341.06	250.8 μmol mmol CO_2^{-1}	1.35 mmol CO_2 g DW^{-1} d^{-1}	0.0055	0.851
$H_2PO_4^-$	−22.994	32.04 μmol mmol CO_2^{-1}	0.71 mmol CO_2 g DW^{-1} d^{-1}	0.0323	0.721
K^+	−157.3	139.4 μmol mmol CO_2^{-1}	1.13 mmol CO_2 g DW^{-1} d^{-1}	0.0434	0.680
SO_4^{2-}	−47.13	32.09 μmol mmol CO_2^{-1}	1.46 mmol CO_2 g DW^{-1} d^{-1}	0.0335	0.716
		Independent variable: RGR			
NO_3^-	−186.4	3482.6 μmol g DW^{-1}	0.05 g DW g DW^{-1} d^{-1}	0.0107	0.947
$H_2PO_4^-$	−6.788	472.46 μmol g DW^{-1}	0.01 g DW g DW^{-1} d^{-1}	0.0061	0.875
K^+	−87.01	2056.9 μmol g DW^{-1}	0.04 g DW g DW^{-1} d^{-1}	0.0121	0.826
SO_4^{2-}	−30.19	467.60 μmol g DW^{-1}	0.06 g DW g DW^{-1} d^{-1}	0.0090	0.849

The relationship between the uptake of nutrients and the assimilation of CO_2 showed a significant linear relation ($y = \beta 0 + \beta 1 \cdot x$) (Table 3). The GLM analysis of this data also showed a significant curvilinear relationship, with a better fit than the linear equation (Figure 2). This curvilinear relationship is characterized by an exponential equation with the form $y = a \cdot e^{b \cdot CO2}$ (Table 4).

The response in the uptake of the studied ions to the RGR was significantly linear (Table 3 and Figure 3) showing a minimum RGR, represented by the 'x-axis' intercept value, required for the uptake to occur.

Discussion

Nutrient uptake response to temperature and light

Temperature affects several aspects of root physiology, including ion uptake, water content, the rate of chemical reactions, and, root growth (Pregitzer and King, 2005). Ion uptake can be characterized as a substrate-enzyme reaction, using Michaelis-Menten relation. Laine et al. (1993) reported that the affinity parameter (K_m) in the absorption of NO_3^- did not differ in Brassica plants exposed to 9°C versus plants exposed to 25°C, but the uptake capacity (V_{max}) showed a Q_{10} value > 2.0. This effect has been related to an increase in root respiration, which would provide more energy for active transport (Atkin et al., 2000). The transport capacity of root cell membranes has also been proven to decrease at low temperatures, due to an increase in water viscosity and a reduced permeability of cell membranes, related to a higher content of unsaturated fatty acids (Pregitzer and King, 2005). This effect drastically limits the mass flow of water towards the root surface. The activity of the enzymes participating in the assimilation of nutrients is influenced by temperature, as well. Atkin and Cummins (1994) reported a reduced activity of nitrate reductase in plants when exposed to temperatures ranging from 3 to 20°C.

The effect of temperature on root growth directly influences the uptake of nutrients, especially those with limited mobility, such as phosphate, as reported by Chapin et al. (1986) who studied the uptake of various species differing in their growth rate growing at various soil temperatures.

Light affects the capacity to assimilate nutrients, therefore, affecting the demand for these. For example, the capacity of the leaves to reduce NO_3^- is enhanced under high light intensities because of the activation of nitrate and nitrite reductase and the higher supply of reducing equivalent from photosystem I and ATP from phosphorylation (De Pinheiro and Marcelis, 2000; Marschner, 2012). Potassium uptake was also expected to increase under high light intensity, since it participates in the activation of several enzymes required in the metabolism and transport of carbohydrates (Maathuis, 2009). It is also important to highlight that K^+ is essential in the maintenance of turgor pressure in growing tissues, therefore at higher growth rates; the demand for this would increase. Sulfur uptake also increased at higher light levels, which we assume is related to the function of S as a component of sulfolipids found in the thylakoid membranes (Maathuis, 2009). At higher light levels, more thylakoid membranes are synthesized per unit area increasing S demand (Kosyk et al., 2009).

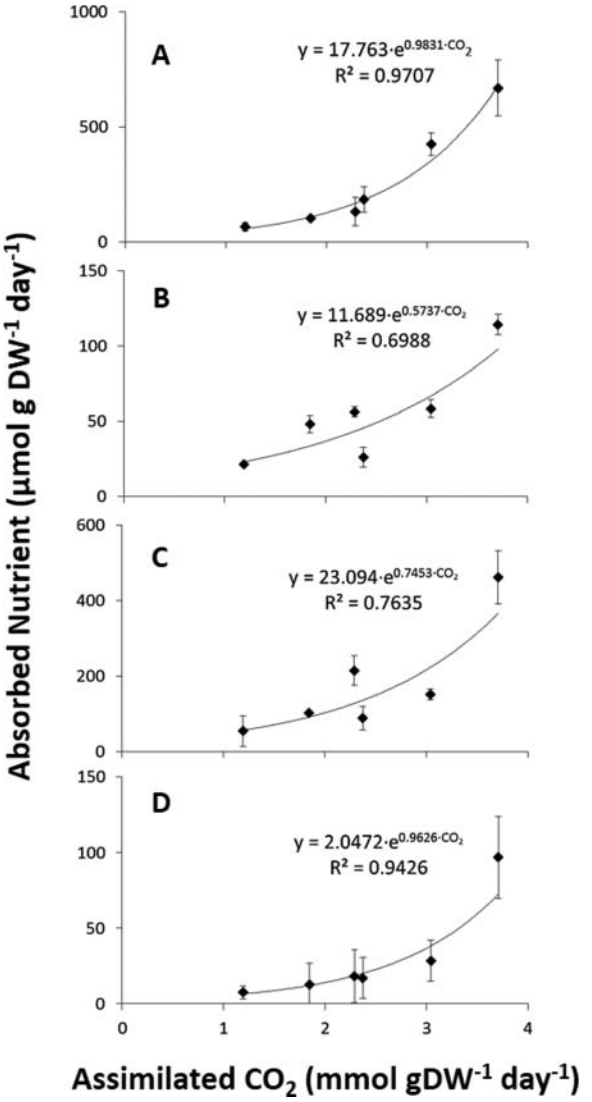

Figure 2. Absorption of A) NO_3^-, B) $H_2PO_4^-$, C) K^+, and D) SO_4^{2-} (in μmol per gram of plant DW per day) at different CO_2 assimilation levels. Symbols are means $\pm$ SE.

Table 4. Parameters describing the exponential response in the uptake of NO_3^-, $H_2PO_4^-$, K^+, and SO_4^{2-} to different levels of CO_2 assimilation rate. The model corresponds to $y = a \cdot e^{b \cdot CO2}$. Significance of the parameters in the model: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Nutrient ion	A	b	P-value	R^2
NO_3^-	17.763 *	0.9831 ***	0.0009	0.970
$H_2PO_4^-$	11.689 *	0.5737 *	< 0.0001	0.698
K^+	23.094 *	0.7453 *	0.0023	0.763
SO_4^{2-}	2.047 *	0.9626 **	0.0131	0.942

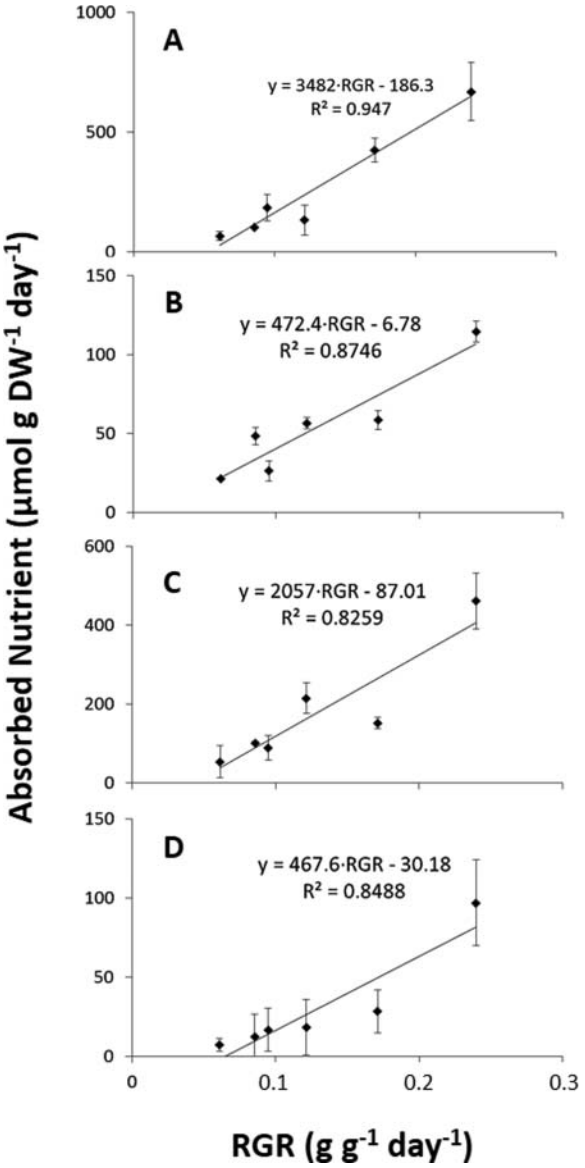

Figure 3. Absorption of A) NO_3^-, B) $H_2PO_4^-$, C) K^+, and D) SO_4^{2-} versus relative growth rate (RGR). Symbols are means ± SE.

Nutrient uptake response to CO_2 assimilation

Higher CO_2 assimilation rates provide higher sugar available within the plant for metabolic processes; therefore, a substantial increase in carbohydrates transported to the roots can be expected. The allocation of carbon to the roots was not investigated in this study, but the response in the absorption of ions can be considered as evidence of higher metabolic activity in the roots. Two control mechanisms have been identified for the concentration of carbohydrates in the roots on the uptake of ions: by coordinating the synthesis of amino acids (Gojon et al., 2009), and by acting on the expression of specific genes encoding for NO_3^-, $H_2PO_4^-$, K^+ and SO_4^{2-} transporters (Lejay et al., 2003). There is also an energy component in the dependence of nutrient uptake to CO_2 assimilation, since the energy required for maintenance respiration, growth respiration, and, ion uptake ultimately depends upon the transport of carbohydrates from the shoots (Poorter et al., 1991). Experimental evidence for this was provided by

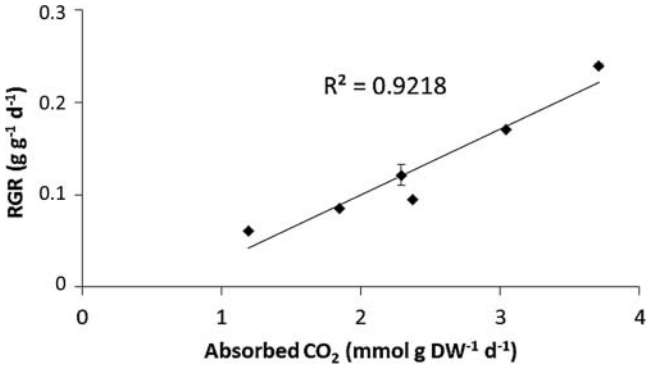

Figure 4. RGR response to CO_2 assimilation rate. Symbols are means ± SE.

Dehlon et al. (1996), who showed how the absorption of NO_3^- in soybean was enhanced during the daytime as a response to the translocation of sugars from the shoot. Also, Van der Werf et al. (1988) reported that the fraction of the respiratory energy invested for ion uptake in the roots increases with RGR.

The exponential response of nutrient uptake to CO_2 assimilation, suggests no clear relation between these two processes at low CO_2 assimilation rates. At low CO_2 assimilation rates, most of the carbohydrates diverted towards the roots are used for maintenance respiration and the sustainment of ion gradients across the membranes (Bouma and De Visser, 1993). On the other hand, at higher assimilation rates, the increase in the uptake of nutrients is almost linear, which is better represented by the relationship between RGR and uptake.

Nutrient uptake response to growth rate

Plant biomass synthesis was enhanced with increasing light and temperature in the applied treatments (Figure 1). The increased growth rates are directly linked to higher leaf CO_2 assimilation rates (Figure 4), as reported previously by several authors (Van Holsteijn, 1981; Knight and Mitchell, 1988; De Pinheiro and Marcelis, 2000) working with lettuce under similar conditions as those imposed in this experiment. The enhancement in biomass production increased the absorption of the studied nutrients, which is in agreement with previously reported findings by Ingestad and Lund (1979), Burns (1994), and Burns et al. (1997).

Mankin and Fynn (1996) derived a general model relating nutrient uptake to plant growth. In their model, the uptake of nutrients (U) is proportional to plant growth rate (G) multiplied by plant nutrient concentration (C), as in $U = G{\cdot}C \pm \beta_0$. The term β_0 refers to luxury consumption when positive, or to remobilization when negative. The slope of the linear equations derived from our data (Table 3) is representative of the nutrient content in plant biomass. For N, the 3.48 mmol g DW^{-1} is equivalent to 48.7 g N kg DW^{-1}; P, 0.47 mmol g DW^{-1} is equivalent to 14.5 g P kg DW^{-1}; K, 2.05 mmol g DW^{-1} is equal to 80.1 g K kg DW^{-1}; and, S, 0.46 mmol g DW^{-1} equals 14.7 g kg DW^{-1}. Hartz et al. (2007) summarizes the sufficiency ranges for lettuce from different sources with N, P, K and S in the range of 20–50, 2.5–8.0, 25–90, and, 2.0–3.5 g kg DW^{-1}, respectively. Our values for N and K lies within these ranges but P and S show a slightly higher value. However, the sufficiency ranges take into account only the leaf nutrient content, and as it has been reported, the content, at least for P, is higher in the roots than in the shoot of lettuce (Almeida et al., 2013).

In the equations derived from our data, the term β_0 is negative, which implies a minimum growth rate required for uptake to occur, below which, remobilization is assumed to supply the required nutrients for new growth. The 'x-axis intercept' value in Table 3 represents this threshold value for RGR. It has been established that chloroplasts are the main source for nutrients remobilization, since Rubisco accounts for 50% of the proteins in leaves (Masclaux-Daubresse et al., 2010). During the

vegetative growth of lettuce, the growth of young leaves reduces the light interception of older leaves (Tei et al., 1996) decreasing the concentration of Rubisco in older leaves and, therefore, inducing remobilization of nutrients towards new leaves. Studies in different plant species have proven that K, P and S are efficiently remobilized to young tissues in parallel with N (Gregersen, 2011).

Poorter et al. (1991) reported how fast-growing species absorb N at a higher rate per unit root weight than slow-growing plants, which was associated to the higher RGR. They concluded that plants with high RGR respired at a higher rate, and those with low RGR invested most of the respiration energy in maintenance respiration of plant biomass.

Conclusions

Manipulation of the environment under which lettuce plants are growing triggers a quick modulation in the uptake of N, P, K and S. The increase in the uptake of the studied ions when subjected to higher growth rates occurs in accordance with the percentage content of each nutrient in the dry matter. The regression analysis show that there is a minimum value of RGR for the uptake of NO_3^-, $H_2PO_4^-$, K^+ and SO_4^{2-} to occur. The exponential relationship between the uptake of the ions and CO_2 assimilation suggests no clear relation between the two processes at low carbon assimilation rates, whereas at medium-high rates, uptake of the ions increases rapidly.

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