SCIENTIFIC NOTE

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Effect of different day and night nutrient solution concentrations on growth, photosynthesis, and leaf NO_3^- content of aeroponically grown lettuce

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Nitrate content in leafy green vegetables has raised concerns among consumers and policy makers worldwide. Several cultural practices have been evaluated to manipulate NO_3^- content in fresh leaves with varying degrees of success. The present study was conducted to evaluate different concentrations of the nutrient solution applied during the day (D) and night (N) to aeroponically grown lettuce (*Lactuca sativa* L.) in Davis, California, USA, in the spring of 2012 with the objective of assessing the effect on growth, leaf photosynthesis, and nitrate accumulation in leaves. Two different treatments in the nighttime solution concentration (D25/N75, EC: 1.8 dS m^{-1}; and D25/N50, EC: 1.2 dS m^{-1}), a day nutrient solution of EC 0.6 dS m^{-1}, plus a day and night treatment with constant EC (D50/N50, EC: 1.2 dS m^{-1}) were applied. Plant growth, leaf photosynthesis, and leaf nutrient content were evaluated after 3 wk of growth. Mean shoot weight was 106.3 g with no differences among treatments. Root biomass was lower with D25/N75 (0.14 vs. 0.85 g in the other treatments). The maximum rate of leaf photosynthesis was 66% lower with D25/N75 than in the other treatments. Nitrogen, P, K, Ca, and Mg were lower in leaf tissue in the treatments with different solution concentrations where leaf NO_3^- content was reduced by approximately 75%. Switching nutrient solution concentration between day and night is a viable practice to reduce NO_3^- in lettuce leaves with no detriment to leaf production.

Key words: Aeroponics, *Lactuca sativa*, leaf nitrate concentration, lettuce photosynthesis.

INTRODUCTION

Hydroponic plant production systems allow the manipulation of crop fertilization to modify characteristics such as growth (Oki and Lieth, 2004), mineral nutrient concentration in plant tissue (Gent, 2003), and soluble sugar concentration in fruits (Buck et al., 2008). In leafy green vegetable production, the accumulation of nitrates in leaves can affect human health since methemoglobinemia and gastric cancer have been associated with high levels of NO_3^- in food (Anjana and Iqbal, 2007). This has led the European Union and the World Health Organization to recommend upper limits for NO_3^- concentration in lettuce (*Lactuca sativa* L.) leaves produced under greenhouse conditions; limits were set at 5000 and 4000 mg kg^{-1} fresh weight (FW) for winter and summer crops, respectively (Official Journal of the European Union, 2011). Nitrate content can be reduced in lettuce leaves by dynamically manipulating the nutrient solution. Some strategies reported in the literature include decreasing the supply of NO_3^- in the nutrient solution near harvest (Andersen and Nielsen, 1992), partial replacement of NO_3^- by other N sources such as urea or amino acids (Abu-Rayyan et al., 2004; Pavlou et al., 2007), and supplying NO_3^- in accordance with irradiance levels (Demsar et al., 2004).

The use of different day and night nutrient concentration has been studied mainly in tomatoes as a way to improve fruit quality and save water. Van Ieperen (1996) and Santamaria et al. (2004) concluded that applying a more concentrated nutrient solution on tomatoes during the night rather than during the day increased fruit soluble solid content with no detriment to crop yield; this is contrary to findings by Adams and Ho (1989), who tested higher nutrient concentrations during the day than during the night, resulting in reduced yield and fruit quality. Low nutrient concentrations available to roots can limit plant growth by restricting mineral nutrient availability for adequate growth. On the other hand, high nutrient concentrations can reduce plant growth due to salinity (osmotic) effects, reduce the plant's ability to absorb water, and turgor and plant growth.

We hypothesized that high nutrient concentrations available during the nighttime when stomata are mostly closed would provide enough mineral nutrients for plant photosynthesis and growth during the daytime, while lower nutrient concentrations during the daytime would be beneficial for plant water uptake.

The objective of this research study was to assess the effect on growth and leaf photosynthesis of supplying

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different nutrient concentrations during the day vs. during the night to reduce the nitrate concentration in leaves.

MATERIALS AND METHODS

An experiment was replicated three times between 1 April and 2 June 2012; it was conducted in a greenhouse located in Davis, California, USA. Seeds of a loose leaf type lettuce (*Lactuca sativa* cv. 'Black Seeded Simpson') were germinated in seedling trays containing 1/3 peat, 1/3 sand, and 1/3 redwood compost (v/v). Trays were kept on a mist bench until plants had two true leaves when they were moved to a greenhouse with natural day/night light conditions and an average daytime and nighttime temperature of 28 and 22 °C, respectively (Figure 1). In the greenhouse, plants were placed in aeroponic systems consisting of rectangular 1.2-m long white channels (model AeroFlow6; General Hydroponics, Sebastopol, California, USA). The nutrient solution was sprayed continuously in the channel from a 15-L reservoir with a pump at a flow rate of 3.0 m^3 h^{-1}. This generated enough pressure to create a mist that kept the roots wet at all times. The solution drained back continuously to the reservoir thus maintaining a thin layer of solution in the channel. Six plants were placed in each chamber using 7.6 cm coconut baskets filled with the same substrate used to germinate the seeds. Roots grew freely in the channel.

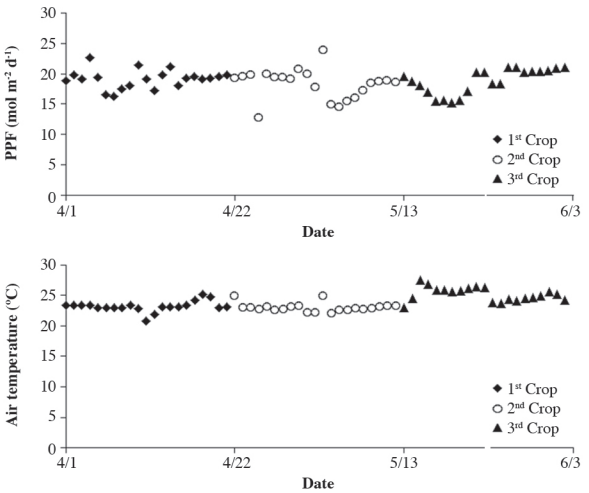


Figure 1. Daily solar radiation expressed as total photosynthetic photon flux (PPF) and average air temperature (°C) throughout the three replicates of the experiment.

Nutrient solution treatments

The three treatments in this study were arranged in a randomized complete block design. The experiment was replicated three times with one experimental unit per treatment (one aeroponic system, six plants). Treatments used different concentrations of the nutrient solution received by plants during the daytime and nighttime. The base nutrient solution was Hoagland's solution (HS) with the following nutrient concentrations: 14.0 NO_3^-, 1.0 NH_4^+, 4.0 Ca^{2+}, 2.0 Mg^{2+}, 6.0 K^+, 1.0 $H_2PO_4^-$ and 2.0 SO_4^{2-}, in mM; 90 B, 36 Cl, 18 Mn, 1.4 Zn, 0.62 Cu, 90 Fe, and 0.20 Mo in μM (Hoagland and Arnon, 1950). The nutrient solution was prepared with deionized water and reagent grade fertilizers. Treatments were applied as D50/N50, D25/N75, and D25/N50 where D refers to the day solution concentration and N to the night solution concentration (Table 1). Plants in treatment D50/N50 were subjected to a constant concentration of 50% diluted HS day and night; D25/75 and D25/N50 were irrigated with a ¼ strength HS during the day but the night solution concentrations were 75% and 50% for D25/N75 and D25/N50, respectively.

Aeroponic systems for treatments D25/N75 and D25/N50 were modified from the original design to include two spray lines, the first sprayed the daytime nutrient solution, while the other sprayed the nighttime solution and each from its respective reservoir (Figure 2). At each end of the channel, drainage holes equipped with solenoid valves allowed the circulation of the solution back to the reservoir. Pumps were controlled by electronic programmable controllers synchronized with the opening and closing of the drains. Drain valves were controlled by a data logger (model 23X; Campbell Scientific, Logan, Utah, USA). The daytime solution was sprayed from 08:01 to 20:00 h and the nighttime solution from 20:01 to 08:00 h. There was a 1 min gap when switching solutions to allow the complete removal of the solution that might remain in the channel in order to reduce the mixing of solutions. The whole solution was completely replaced with a fresh solution twice a week to maintain a constant electrical conductivity (EC) level in each solution. Each time, 15 L were mixed using deionized water and fertilizer grade nutrient salts.

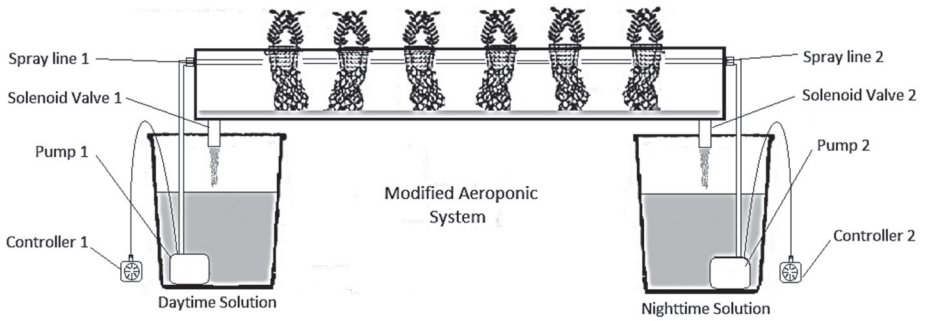
Photosynthesis measurements

Plants grew for 3 wk (21 d) in the aeroponic units. At the third week of growth, single leaf photosynthesis, stomatal conductance, and leaf transpiration were measured on the youngest fully expanded leaf of every

Table 1. Description of treatments used in the experiments.

Treatment	Description	EC day	EC night	Mean EC
		dS m^{-1}		
D50/N50	½ strength HS during the day (D50) ½ strength HS during the night (N50)	1.2 ± 0.1	1.2 ± 0.1	1.2 ± 0.1
D25/N75	¼ strength HS during the day (D25) ¾ strength HS during the night (N75)	0.6 ± 0.1	1.8 ± 0.2	1.2 ± 0.1
D25/N50	¼ strength HS during the day (D25) ½ strength HS during the night (N50)	0.6 ± 0.1	1.2 ± 0.1	0.9 ± 0.1

EC: Electrical conductivity of nutrient solution, HS: Hoagland's solution.



D25/N75: ¼ strength Hoagland's solution (HS) during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

Figure 2. Aeroponic system used in treatments D25/N75 and D25/N50.

plant in each treatment with a closed gas exchange system (model LI-6400XT; LI-COR, Lincoln, Nebraska, USA). Photosynthetic rates were measured at photon flux densities (PPFD) of 0, 400, 800, 1200, 1600, and 2000 μmol m^{-2} s^{-1} with a LED light source (model LI-6400-02B; LI-COR) attached to the cuvette. Conditions within the cuvette were controlled so as to maintain leaf temperature at 25 °C with an ambient CO_2 concentration of 380 μmol mol^{-1} and a constant water mole fraction of 20 mmol mol^{-1}. A minimum of 15 min was allowed between light levels to ensure measurement stability before logging data. The measurement was defined as stable when the rate of change in photosynthesis was lower than 0.1 μmol CO_2 min^{-1}. The fraction of absorbed photons used for photochemistry (Φ_{PSII}) was measured with a leaf chamber fluorometer (model LI 6400-40; LI-COR). The fluorometer settings for the measuring beam were intensity 5, modulation 20 kHz, and a 10 gain factor. The saturating flash was set at an intensity of 8 for a duration of 0.8 s with a modulation of 20 kHz and a mean filter of 50 Hz, and the quantum yield of CO_2 assimilation (Φ_{CO2}, μmol CO_2 μmol^{-1} photons) was measured in the youngest fully expanded leaf of every plant in each treatment.

Plant growth measurements

At the end of the third week of growth, fresh weight of whole plant, leaves, and roots was recorded for each plant with an analytical scale. Plants were harvested after dawn and before 09:00 h. Excess water was removed from the roots with paper towels, plant weight was recorded, and total leaf area was measured with a leaf area meter (model LI-3100C; LI-COR). Once leaf area was measured, leaves and roots were placed individually in paper bags and oven-dried at 70 °C for 72 h, after which plant material was weighed to record plant dry weight.

Calculations of growth components

The relative growth rate (RGR) was calculated on a fresh weight (FW) basis as:

$$RGR = \ln FW_{t1} - \ln FW_{t2} / t_1 - t_2 \quad [1]$$

where FW_{t1} and FW_{t2} are plant dry weights at times 1 and 2. Growth components, specific leaf area (SLA; leaf area/leaf mass), leaf mass ratio (LMR; leaf mass/plant mass), leaf area ratio (LAR; leaf area/plant mass), root mass ratio (RMR; root mass/plant mass), and shoot to root ratio (shoot:root; leaf mass/root mass), were calculated on a fresh weight basis to study morphological traits among treatments (Hunt et al., 2002).

Plant nutrient content analyses

After determining dry weight, dry leaves of each plant from every treatment were ground and passed through a 40 mesh sieve. Three samples of ground material for each treatment and replicate of the experiment (total number of samples per treatment was 9) were collected and sent to a laboratory (University of California Analytical Laboratory, Davis, California, USA) to determine the content of N, P, K, Ca, Mg, S, and extractable NO_3^-. The concentration of N was determined by sample combustion coupled with thermal conductivity/infrared detection. The concentration of the other elements was determined by nitric acid digestion/hydrogen peroxide microwave digestion and by inductively coupled plasma-atomic emission spectrometry (ICP-AES). Extractable NO_3^- was analyzed by flow injection analysis after extraction with 2% acetic acid. To analyze the content of non-structural carbohydrates (NSC), 2-g samples of dry material were enzymatically hydrolyzed at 55 °C with amyloglucosidase for 12 h and analyzed by HPLC with mass selective detection. The analysis was performed with a Phenomenex Luna NH_2 (250 mm × 4.6 mm) HPLC column at a flow rate of 2.75 mL min^{-1} acetonitrile:water (78:22).

Statistical analysis

Data from all replicates of the experiment were pooled and analyzed as a randomized complete block design where each replicate was treated as a block. The block effect was not significant in any of the studied parameters; therefore, the analysis was performed as a completely randomized design. Differences in plant growth, plant weight, and leaf nutrient/NSC concentration were analyzed by ANOVA (PROC ANOVA) and mean separation was performed

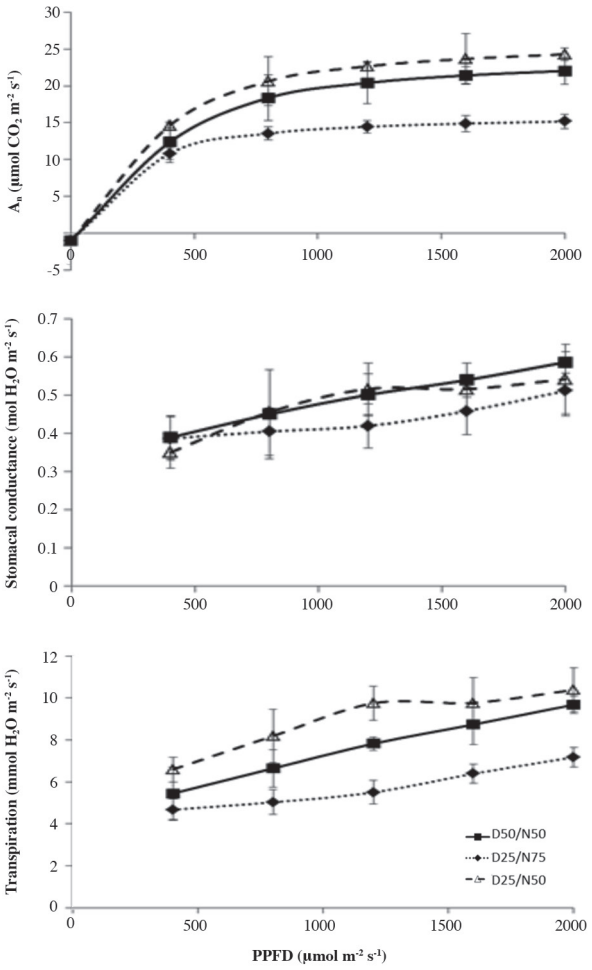
by Tukey's honestly significant difference (HSD) test with the SAS software package (SAS Institute; Cary, North Carolina, USA). Photosynthetic rate, stomatal conductance, leaf transpiration, Φ_{PSII}, and Φ_{CO2} were analyzed at each PPFD level using the same methodology.

RESULTS

Gas exchange measurements showed no differences in net CO_2 assimilation between D50/N50 and D25/N50 treatments with mean values of -0.91, 13.52, 19.43, 21.53, 22.51, and, 23.21 μmol CO_2 m^{-2} s^{-1} at 0, 400, 800, 1200, 1600, and, 2000 μmol PPFD m^{-2} s^{-1}, respectively. For the same PPFD levels, CO_2 assimilation rates of D25/N75 in plants were lower, -1.01, 10.90, 13.44, 14.12, 15.07, and 15.33 μmol CO_2 m^{-2} s^{-1} (Figure 3). Stomatal conductance increased with increasing PPFD values, but no differences were found among treatments. The leaf transpiration rate also increased with increasing PPFD levels showing similar values for the control and D25/N50, but it was reduced by approximately 30% in plants with D25/N75.

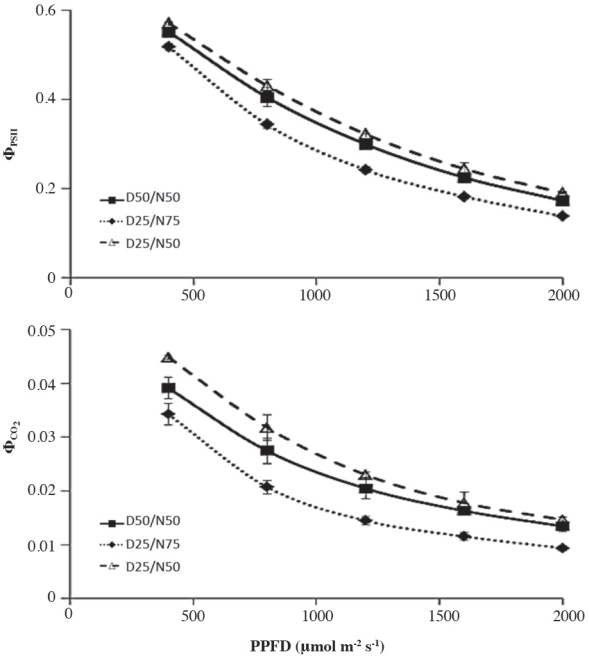
Quantum yield and efficiency in CO_2 assimilation decreased with increasing PPFD values. The quantum yield of plants in D25/N50 was similar to that of the control at every light level; however, Φ_{CO2} was higher in D25/N50 when measured at 400 and 800 μmol PPFD m^{-2} s^{-1} (P-values of 0.0106 and 0.0008, respectively). Values of Φ_{PSII} and Φ_{CO2} in plants with D25/N75 were significantly lower than in the other two treatments at every light level (Figure 4).

No differences were found in plant or leaf fresh weight with a mean plant fresh weight of 123.8 ± 5.4 g after 3 wk growth in the greenhouse (Table 2). Root growth was severely impaired in those plants exposed to the D25/N75treatment where root mass (fresh and dry) was lower than in the other two treatments, but with no symptoms of root damage. Leaf area was significantly higher for D25/N75 than D50/N50. The relative growth rate was similar among treatments with a mean value of 0.228 ± 0.002 g g^{-1} d^{-1}. However, growth components were significantly affected by treatments showing a higher allocation of biomass in leaves of plants exposed to D25/N75 as



Each dot is the mean ± SE.
D50/N50: ½ strength Hoagland's solution (HS) during the day (D50), ½ strength HS during the night (N50); D25/N75: ¼ strength HS during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

Figure 3. Net CO_2 assimilation (A_n), stomatal conductance, and leaf transpiration in lettuce leaves for each treatment at photosynthetic photon flux (PPFD) levels between 0 and 2000 μmol m^{-2} s^{-1}.



Each dot is the mean ± SE.
D50/N50: ½ strength Hoagland's solution (HS) during the day (D50), ½ strength HS during the night (N50); D25/N75: ¼ strength HS during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

Figure 4. Fraction of absorbed photons used in photochemistry (Φ_{PSII}) and quantum yield (Φ_{CO2} in μmol CO_2·μmol photons^{-1}) in lettuce leaves for each treatment at photosynthetic photon flux (PPFD) levels between 0 and 2000 μmol m^{-2} s^{-1}.

Table 2. Fresh and dry weight of plant components and total leaf area after 3-wk experiment.

Parameter	Treatment		
	D50/N50	D25/N75	D25/N50
Total fresh weight, g	123.9 ± 13.4a	118.4 ± 8.7a	129.2 ± 4.7a
Leaf fresh weight, g	101.4 ± 12.5a	114.32 ± 7.9a	103.1 ± 4.3a
Root fresh weight, g	22.4 ± 1.5a	4.09 ± 2.3b	26.0 ± 2.2a
Leaf dry weight, g	5.10 ± 0.56a	6.03 ± 0.54a	5.59 ± 0.21a
Root dry weight, g	0.78 ± 0.05a	0.14 ± 0.08b	0.92 ± 0.08a
Dry plant weight fraction, %	5.07 ± 0.15a	5.24 ± 0.20a	5.43 ± 0.13a
Total leaf area, cm^2	1756.2 ± 190.6b	2382.3 ± 129.4a	1943.6 ± 66.8ab

Values are means ± SE of 18 plants. Different letters in the same row indicate significant differences according to Tukey's test ($P < 0.05$).
D50/N50: ½ strength Hoagland's solution (HS) during the day (D50), ½ strength HS during the night (N50); D25/N75: ¼ strength HS during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

demonstrated by the higher values of SLA, LMR, LAR, and shoot:root (Table 3).

The content of N, P, K, Ca, and Mg in leaves was reduced in treatments D25/N75 and D25/N50 compared with D50/N50 (Table 4). The reduction in total N is the result of a significant decrease in the content of non-metabolized NO_3^-, which was reduced by 4 to 5 times in D25/N75 and D25/N50 with respect to the D50/N50 treatment.

The content of NSC was similar between D50/N50 and D25/N50 with a mean value of 1.63 ± 0.33% DW, but this value was significantly higher ($P < 0.0007$) in leaves with D25/N75 showing a mean value of 7.85 ± 0.15% DW.

Table 3. Plant growth components on a fresh weight basis. Values are means ± SE of 18 plants.

Growth component	Treatment		
	D50/N50	D25/N75	D25/N50
Specific leaf area, $m^2\ kg^{-1}$	1.75 ± 0.05b	2.10 ± 0.06a	1.89 ± 0.06ab
Leaf mass ratio, $g\ g^{-1}$	0.81 ± 0.02b	0.97 ± 0.02a	0.80 ± 0.02b
Leaf area ratio, $m^2\ kg^{-1}$	1.42 ± 0.05b	2.03 ± 0.07a	1.51 ± 0.04b
Root mass ratio, $g\ g^{-1}$	0.19 ± 0.02a	0.03 ± 0.02b	0.20 ± 0.02a
Shoot to root ratio, $g\ g^{-1}$	4.51 ± 0.43b	42.59 ± 10.87a	4.10 ± 0.38b

Different letters in the same row indicate significant differences according to Tukey's test ($P < 0.05$).
D50/N50: ½ strength Hoagland's solution (HS) during the day (D50), ½ strength HS during the night (N50); D25/N75: ¼ strength HS during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

Table 4. Mineral nutrient content in lettuce leaves in the different treatments. Values are means ± SE.

Nutrient (% DW)	Treatment		
	D50/N50	D25/N75	D25/N50
NO_3-N, $mg\ kg^{-1}$	18 890 ± 2 230a	4 220 ± 210b	5 390 ± 50b
N	6.33 ± 0.08a	4.92 ± 0.26b	5.12 ± 0.16b
P	1.18 ± 0.04a	0.78 ± 0.05b	0.79 ± 0.02b
K	11.49 ± 0.76a	7.86 ± 0.50b	8.82 ± 0.11ab
Ca	1.73 ± 0.01a	1.33 ± 0.07b	1.14 ± 0.01b
Mg	0.43 ± 0.01a	0.31 ± 0.01b	0.29 ± 0.01b
S	0.36 ± 0.00a	0.36 ± 0.00a	0.37 ± 0.01a

Different letters in the same row indicate significant differences according to Tukey's test ($P < 0.05$). DW: dry weight. D50/N50: ½ strength Hoagland's solution (HS) during the day (D50), ½ strength HS during the night (N50); D25/N75: ¼ strength HS during the day (D25), ¾ strength HS during the night (N75); D25/N50: ¼ strength HS during the day (D25), ½ strength HS during the night (N50).

DISCUSSION

Lettuce plants are produced for their leaves and this experiment found that there were no differences in leaf fresh weight among the treatments; this implies that dynamic fertilization is technically feasible with no detriment to crop yield. In greenhouse production, nutrients are supplied through irrigation and because there is a higher absorption rate of water rather than nutrients, these accumulate in the solution to levels that might limit plant transpiration. For this reason growers add fresh water (or completely discard the former solution) to keep EC below the threshold for yield reduction (Sonneveld and Voogt, 2009). The advantage of the fertilization schedule studied in this research lies in the fact that using a more diluted solution during the daytime decreases salt accumulation in the solution because of the reduced amount of total fertilizers applied during this time. This, in turn, increases the time that a given mixed solution can be recirculated within the system.

It is important to highlight the significant reduction in leaf NO_3-N content, which was four times lower for D25/N75 and D25/N50 than D50/N50. These results are more significant in D25/N50 because the total amount of NO_3-N applied as fertilizer is also reduced with a 25% reduction compared with a constant solution (D50/N50). Among the fertilization management strategies proposed to reduce NO_3^- in lettuce leaves, varying the ratio of NO_3^- to other nutrients in the solution (Gent, 2003) and replacing NO_3^- by other N forms (Abu-Rayyan et al., 2004) have received most of the attention. However, these strategies do not reduce total N fertilizer applied to the system, which does not reduce N released to the environment. Successful strategies to reduce both NO_3^- and fertilizer use take into account the variation in the demand for NO_3^- according to environmental conditions, such as in the study proposed by Demsar et al. (2004) where NO_3^- applied in the nutrient solution varied according to the light conditions plants were subjected to during cultivation.

Fertilization strategies, similar to the one used in this experiment, have not been studied previously for lettuce but have been tested in tomato where there is no reduction in vegetative growth or fruit yield (Santamaria et al., 2004; Buck et al., 2008).

Despite the reduction in leaf photosynthesis and CO_2 assimilation efficiency, the higher allocation of resources to leaves demonstrated by growth components (SLA, LAR, RMR) was able to maintain plant yield with D25/N75. Van Ieperen (1996) reports similar results working with tomato in a nutrient film technique (NFT) system although the extent of the difference in EC between day and night was much higher (from 1.0 to 9.0 $dS\ m^{-1}$) than the one applied in our study; he found an increase in leaf DM from plants subjected to low/high salinity during the day/night. The concentration of the nighttime nutrient solution in our experiment differed only by 0.6 $dS\ m^{-1}$ (about 340

mg L^{-1} dissolved solids) between D25/N75 and D25/N50; however, the effect on root growth was dramatic. The difference in the osmotic potential, estimated using the solution EC values, from day to night with D25/N75 was twice the value found with D25/N50 (0.04 MPa vs. 0.02 MPa, respectively). Munns (2002) reported that root elongation in maize seedlings was reduced by 0.3 MPa in the osmotic potential of the nutrient solution, a value much higher than the one used in our experiments. Lettuce is a moderately salt-sensitive crop with an EC_e (electrical conductivity of a saturated paste) value of 1.1 dS m^{-1} (equivalent to 0.04 MPa osmotic potential) as the threshold before yield reduction occurs (Ünlükara et al., 2008). Several authors working with different crops have reported decreased root growth with K and Mg deficiencies (Hermans et al., 2006), but no symptoms of such deficiencies were noticed in our study and K and Mg content was similar in plants with D25/N75 and D25/N50.

It is very unlikely that the reduction in leaf photosynthesis with D25/N75 is due to the lower nutrient content in leaves compared with D50/N50 since both D25/N75 and D25/N50 showed similar levels although D25/N50 had higher CO_2 assimilation rates. Furthermore, no deficiency symptoms were observed in any of the plants. Differences in leaf photosynthesis cannot be attributed to differences in stomatal conductance since all the treatments showed similar values. The higher content of NSC in the leaves with D25/N75 might be the response to a lower sink activity in roots. Accumulation of carbohydrates suggests an inhibition of photosynthesis by sugar accumulation through feedback inhibition of RuBisCo activity and low regeneration of RuBP (Roland et al., 2006).

CONCLUSIONS

Applying a more concentrated nutrient solution during the night in lettuce cultivation reduces the accumulation of mineral macroelements in leaves without reducing leaf yield. The most significant reduction is in leaf nitrate, 75% compared with constant nutrition. The plant growth rate is not affected by varying nutrient concentration supplied during the day and night, but the allocation of resources is modified when the differences in electrical conductivity (EC) of nutrient solution used in the day and nighttime is higher than 0.6 dS m^{-1}. Leaf photosynthesis and root growth also decreased with a high difference in EC.

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