

Nutrient Solution Concentration Affects Whole-plant CO₂ Exchange and Growth of Subirrigated Pansy

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ABSTRACT. To determine the effect of fertilizer concentration on plant growth and physiology, whole-plant C exchange rates of pansies (*Viola ×wittrockiana* Gams.) subirrigated with one of four fertilizer concentrations were measured over 30 days. Plants were watered with fertilizer solutions with an electrical conductivity (EC) of 0.15, 1.0, 2.0, or 3.0 dS·m⁻¹ (N at 0, 135, 290, or 440 mg·L⁻¹, respectively). Plants watered with a fertilizer solution with an EC of 2 dS·m⁻¹ had the highest shoot dry weight (DW), shoot to root ratio, leaf area, leaf area ratio (LAR), and cumulative C gain at the end of the experiment compared to those watered with a solution with a higher or lower EC. Shoot tissue concentrations of N, P, K, S, Ca, Fe, Na, and Zn increased linearly with increasing fertilizer concentration. A close correlation between final DW of the plants and the measured cumulative C gain (CCG) ($r^2 = 0.98$) indicated that the C exchange rates were good indicators of plant growth. There were quadratic relationships between fertilizer EC and gross photosynthesis, net photosynthesis, and dark respiration, starting at 13, 12, and 6 days after transplanting, respectively. Although plants fertilized with a fertilizer solution with an EC of 2 dS·m⁻¹ had the highest C exchange rates, the final differences in shoot DW and CCG among ECs of 1.0, 2.0, and 3.0 dS·m⁻¹ were small and it appears that pansies can be grown successfully with a wide range of fertilizer concentrations. Plants with a high LAR also had higher DW, suggesting that increased growth was caused largely by increased light interception. A detrimental effect of high fertilizer concentrations was that it resulted in a decrease in root DW and a large increase in shoot to root ratio.

Recirculating subirrigation systems have become increasingly popular in the greenhouse industry. Growers have reported labor, water, and fertilizer savings, more uniform crops, and better productivity with subirrigation systems, as compared to more traditional irrigation systems (Uva et al., 1998). An additional advantage is that recirculating subirrigation systems decrease water and fertilizer use, while minimizing the potential for runoff from greenhouses.

Fertility guidelines that have been developed for overhead-irrigated plants are not applicable to subirrigated plants because excess fertilizer is not leached from the bottom of the pots, as is the case with overhead irrigation (Birnbaum, 1992). Instead, fertilizer salts accumulate in the top portion of subirrigated containers as water evaporates from the surface of the growing medium (Argo and Birnbaum, 1996; van Iersel, 2000). Because most of the root growth of subirrigated plants occurs in the bottom of the pot (Kent and Reed, 1996), the salt accumulation near the top of the growing medium normally is not detrimental to the plants. However, salts can also accumulate in the middle and bottom levels of the growing medium if the fertilizer concentration is high (Kent and Reed, 1996). Ideally, the nutrient concentration of the middle and bottom layers of the growing medium should be high enough to provide plants with the needed mineral nutrients but not so high that it causes salt damage to the plants. Therefore, it is crucial to apply the appropriate fertilizer concentration to subirrigated plants. Previous research

(van Iersel, 1999a) demonstrated that greenhouse-grown, subirrigated pansies had a higher dry weight (DW) when they were subirrigated with N at 160 to 250 mg·L⁻¹, than with other concentrations in the range from 70 to 530 mg·L⁻¹. However, this study did not evaluate the physiological processes underlying growth and dry matter accumulation of the plants.

One method to study growth processes in plants is by carbon (C) exchange rate (CER) measurements, since C assimilation is the primary process responsible for dry matter increase in plants (Lawlor, 1995). Whole-plant CER measurements are particularly useful to determine effects on growth rate, since they provide a direct measure of C accumulation by plants (Bugbee, 1992; van Iersel and Bugbee, 2000) and provide a nondestructive measurement of growth. Continuous CER measurements over a prolonged period (weeks) also make it possible to determine when treatment effects occur. This type of information is difficult to determine with more traditional techniques such as DW or leaf photosynthesis measurements.

The hypothesis of the following research was that both lower and higher than optimal fertilizer concentrations reduce whole-plant photosynthesis and therefore growth. Thus, the objectives of this study were to 1) quantify the effects of fertilizer concentration on whole-plant photosynthesis, respiration, and C accumulation, 2) determine the effect of fertilizer concentration on the growth of subirrigated pansies, and 3) determine the effect of fertilizer concentration on tissue mineral nutrient levels.

Materials and Methods

PLANT MATERIAL AND ENVIRONMENTAL CONDITIONS. Plug seedlings (288 seedlings/flat) of 'Golden Crown' pansy were received

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from a commercial grower (Speedling, Blairsville, Ga.) on 16 Nov. 1999. Thirty five cells (cell volume 150 mL) in each cell flat (36 cells/flat, Jumbo 606; TLC polyform, Plymouth, Minn.) were filled with a peat-based, soilless growing medium (Metro-Mix 300; The Scotts Co., Marysville, Ohio) and seedlings were transplanted into these 35 cells on 17 Nov. One cell in each flat was left empty to facilitate subirrigation.

The growing medium contained starter fertilizer (NO_3^- at 64 $\text{mg}\cdot\text{L}^{-1}$, NH_4^+ at 5.8 $\text{mg}\cdot\text{L}^{-1}$, P at 3.4 $\text{mg}\cdot\text{L}^{-1}$, K at 190 $\text{mg}\cdot\text{L}^{-1}$, Ca at 190 $\text{mg}\cdot\text{L}^{-1}$, Mg at 128 $\text{mg}\cdot\text{L}^{-1}$, and all essential micronutrients), had an initial pH of 5.1 and electrical conductivity (EC) of 2.1 $\text{dS}\cdot\text{m}^{-1}$, as determined with the saturated medium extract method (Warncke, 1986). The flats were placed in watertight carrying trays with a double layer of capillary mat (Vattex F capillary watering system, OS plastics, Norcross, Ga.) in the bottom. The capillary mat was used to prevent the roots from being submerged in water. The trays were put inside acrylic gas exchange chambers ($0.32 \times 0.5 \times 0.6 \text{ m}^3$; van Iersel and Bugbee, 2000), which were then placed inside two growth chambers (model E-15; Conviron, Winnipeg, Canada), so that each growth chamber contained four gas exchange chambers.

Temperature inside the gas exchange chambers was not controlled directly, but regulated by setting the temperature of the growth chambers to appropriate set points. Temperature in each gas exchange chamber was measured with a shielded, aspirated, type T thermocouple connected to a thermocouple multiplexer (model AM25T; Campbell Sci., Logan, Utah) and relative humidity (RH) was measured with humidity probes (HTO-45R; Rotronic, Huntington, N.Y.). Air temperature and RH were $25 \pm 1/15 \pm 1 \text{ }^\circ\text{C}$ and 65% to 85%/80% to 100% during the light and dark periods, respectively. Light was provided by fluorescent lamps, with a photoperiod of 14-h and a photosynthetic photon flux (PPF) of $400 \pm 5 \text{ } \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the top of the canopy, resulting in a total daily PPF of 20.2 $\text{mol}\cdot\text{m}^{-2}$. Irradiances were measured with a line quantum sensor (LQS50-6-ELEC; Apogee instruments, Logan, Utah) in each gas exchange chamber at the start of the study and adjusted by placing neutral density shade cloth on top of the chambers as needed.

TREATMENTS. Plants were subirrigated as needed with different treatment nutrient solutions. The ECs of the nutrient solutions were 0.15 (no added fertilizer), 1.0, 2.0, or 3.0 $\text{dS}\cdot\text{m}^{-1}$ and contained N at 0, 135, 290, or 440 $\text{mg}\cdot\text{L}^{-1}$, respectively. The fertilizers solutions were prepared using tap water and a commercially available, water-soluble fertilizer (20N-4.4P-16.6K; 20-10-20 Peat-Lite Special; The Scotts Co.), formulated especially for soilless growing media. This fertilizer contained all essential macro- and micronutrients, except for Ca which was provided by the lime in the growing medium. The tap water used to mix the fertilizer solutions was low in Ca^{2+} (10 $\text{mg}\cdot\text{L}^{-1}$) and Mg^{2+} (1.7 $\text{mg}\cdot\text{L}^{-1}$), had a low EC (0.15 $\text{dS}\cdot\text{m}^{-1}$) and total alkalinity (CaCO_3 at 50 $\text{mg}\cdot\text{L}^{-1}$), and a pH of 6.4 and therefore was of excellent quality for irrigation, according to guidelines by Bunt (1988).

Plants were watered by pouring 1 L of nutrient solution through a polyvinyl chloride (PVC) pipe (2.5 cm diameter), which entered the gas exchange chambers through a hole in the side and was inserted into the empty cell in each flat. By watering this way, the fertilizer solution accumulated in the bottom of the watertight tray, and the growing medium in the other cells absorbed the nutrient solution through the holes in the bottom of the cells. The PVC pipe was closed off with a stopper between irrigations. This allowed for subirrigation without disturbing the plants or opening the gas exchange chambers. Plants in the 1.0,

2.0, or 3.0 $\text{dS}\cdot\text{m}^{-1}$ treatments were watered eight times and the plants in the 0.15 $\text{dS}\cdot\text{m}^{-1}$ treatment were watered seven times during the experiment.

MEASUREMENTS. The CO_2 exchange rate of whole flats of plants was measured every 10 min for 30 d (16 Nov. to 16 Dec.), using a multichamber, semicontinuous CO_2 exchange system (van Iersel and Bugbee, 2000). About 0.5 $\text{L}\cdot\text{s}^{-1}$ of ambient air was blown into the acrylic gas exchange chambers and airflow into the chambers was measured with mass flow meters (GFM37-32; Aalborg Instruments and Controls, Monsey, N.Y.). The CO_2 concentration of the incoming air was measured with an infrared gas analyzer (IRGA) (SBA-1; PP-systems, Haverhill, Mass.). The difference in the CO_2 concentration of the air entering and exiting the chamber was measured with an IRGA in differential mode (LI-6251; LI-COR, Lincoln, Nebr.). Air flow to the differential IRGA was controlled by opening and closing solenoid valves so that air from each gas exchange chamber could be sampled separately. The solenoid valves were controlled by a SDM-CD16AC relay module and CR10T data logger (Campbell Sci., Logan, Utah). Whole chamber CO_2 exchange ($\mu\text{mol}\cdot\text{s}^{-1}$) was calculated as the product of mass flow ($\text{mol}\cdot\text{s}^{-1}$) and the difference in CO_2 concentration of the air entering and exiting the chamber ($\mu\text{mol}\cdot\text{mol}^{-1}$). Every chamber was measured for 30 s, once every 10 min. There was a 30 s delay in data collection after solenoids were switched to measure the next chamber to assure that all air from the previous gas exchange chamber was purged from the tubing and differential IRGA. The data from the 30 s measuring period was automatically collected, averaged, and stored by the datalogger. Errors in the measurements due to zero drift of the differential IRGA were corrected by subtracting the CO_2 exchange rates of empty gas exchange chambers (placed outside of the growth chambers) from the measured CO_2 exchange rate of the plants.

Gross photosynthesis (P_{gross} , $\mu\text{mol}\cdot\text{s}^{-1}$) was calculated as

$$P_{\text{gross}} = P_{\text{net}} + R_{\text{dark}} \quad [\text{Eq. 1}]$$

where P_{net} = average net photosynthesis during the light period ($\mu\text{mol}\cdot\text{s}^{-1}$) and R_{dark} = average respiration rate during the dark period ($\mu\text{mol}\cdot\text{s}^{-1}$). This equation assumes that the respiration rates in the light and dark are equal (see van Iersel and Bugbee, 2000). Estimates of P_{gross} are not corrected for photorespiration, because R_{dark} measurements do not include photorespiration, while P_{net} measurements do. Daily C gain (DCG, the net amount of carbon fixed by a group of plants in a 24-h period) was calculated as

$$\text{DCG} = (P_{\text{net}} \times t_{\text{light}}) - (R_{\text{dark}} \times t_{\text{dark}}) \quad [\text{Eq. 2}]$$

where t_{light} and t_{dark} are the durations of the light and dark periods (s), respectively. Cumulative C gain (CCG) was calculated as the sum of the DCG values. DCG is a measure of crop growth rate (in mol C per day), while CCG is a measure of the weight of the plants (i.e., the total amount of C accumulated by the plants since the start of the experiment). Carbon use efficiency (CUE, the fraction of the total amount of C fixed in photosynthesis that is actually incorporated into the plant) was calculated as

$$\text{CUE} = \text{DCG} / (P_{\text{gross}} \times t_{\text{light}}) \quad [\text{Eq. 3}]$$

where $P_{\text{gross}} \times t_{\text{light}}$ is the estimated amount of C fixed in gross photosynthesis during a 24-h period.

At the end of the experiment, 30 d after transplanting, all flats were watered with 1 L of nutrient solution. One hour later, the plants were removed from the gas exchange chambers and the pH and EC of the growing medium in three cell packs (containing six

plants each) from each tray were determined with the pour-through method (Wright, 1986). About 50 mL of tap water was poured on top of the growing medium and the leachate was collected and measured with an EC/pH meter (model M90, Corning, Corning, N.Y.).

Leaf area of the plants was measured with a leaf area meter (LI-3100; LI-COR). Shoot DW of 29 plants from each flat was determined. Roots of the remaining six plants were washed carefully to remove the growing medium and root and shoot DWs of these plants were determined. The shoot to root ratio of these six plants was used to estimate total plant DW of all 35 plants in each experimental unit. All DWs were determined after drying the plants at 80 °C for 3 d. Leaf area ratio (LAR) was estimated as the ratio of leaf area to both total plant DW (LAR_{plant}) and shoot DW (LAR_{shoot}).

The entire dried shoots (leaves, stems, and flowers) were then used for mineral nutrient analysis. Total N was determined using the Dumas method (Mills and Jones, 1996) using a CNS analyzer (model 2000; LECO Corp., St. Joseph, Mich.), while P and K were determined by dry ashing and inductively coupled plasma spectrometry (ICAP 9000; Thermo Jarrell Ash Corp., Franklin, Mass.) (Jones and Case, 1990).

EXPERIMENTAL DESIGN AND DATA ANALYSIS. The treatments were arranged in a randomized complete block design with two replications (each of the two growth chambers contained four gas exchange chambers, and all four treatments were present in each growth chamber). Thus, a growth chamber was the experimental block with a group of 35 plants as the experimental unit. Data were subjected to linear and quadratic regression analysis, with $P < 0.05$ considered to be statistically significant. The gas exchange data were analyzed separately for each measurement day. In case of significant quadratic correlations, the regression curve was used to calculate the EC at which a particular variable would be expected to have its maximum value. To test the correlation between CUE and CCG, we used a modified rectangular hyperbola:

$$CUE = CUE_{\max} \times (CCG - CCG_0) / (CCG - CCG_0 + a) \quad [\text{Eq. 4}]$$

where CUE_{\max} = the estimated maximum CUE, CCG_0 = the CCG at which $CUE = 0$, and a = constant. In this equation, $CCG_0 + a$ is the CCG at which CUE is $0.5 \times CUE_{\max}$. Only data from the period that the plants had a positive CUE were used in this regression. To determine the effect of fertilizer EC and plants size (or CCG) on P_{gross} , we used a quadratic regression with an interactive term:

$$P_{\text{gross}} = x_0 + x_1 \times CCG + x_2 \times EC + x_3 \times EC(CCG + x_4 \times EC^2 + x_5 \times CCG^2) \quad [\text{Eq. 5}]$$

where x_0, \dots, x_5 are constants. Only data from the period that CCG was positive were used for this analysis. By analyzing P_{gross} as a function of EC and CCG, it was possible to determine the effects of EC on P_{gross} , while correcting for differences in plant size. The fertilizer EC resulting in maximal P_{gross} (EC_{\max}) was estimated from the derivative of Eq. 5, using the following equation:

$$EC_{\max} = (x_2 + x_3 \times CCG) / (-2 \times x_4) \quad [\text{Eq. 6}]$$

Results and Discussion

PLANT GROWTH. Shoot to root ratio, leaf area, shoot DW, total DW, CCG, and LAR reached a maximum at a fertilizer EC of 2.0 to 2.5 $\text{dS}\cdot\text{m}^{-1}$ (Table 1). All these parameters increased most rapidly as fertilizer EC was increased from 0.15 to 1 $\text{dS}\cdot\text{m}^{-1}$, with a smaller increase with an increase in fertilizer EC from 1 to 2 $\text{dS}\cdot\text{m}^{-1}$. This indicates that the starter fertilizer in this growing medium was insufficient to sustain plant growth throughout the 30 d growing period. In contrast to shoot growth, root growth decreased with increasing fertilizer concentration, which resulted in large treatment effects on the shoot to root ratio of the plants, ranging from 2.0 at a fertilizer EC of 0.15 $\text{dS}\cdot\text{m}^{-1}$ to 10.8 at a fertilizer EC of 2.0 $\text{dS}\cdot\text{m}^{-1}$ (Table 1).

The fertilizer concentration resulting in maximum shoot growth was higher in this experiment (2.1 $\text{dS}\cdot\text{m}^{-1}$, N at 300 $\text{mg}\cdot\text{L}^{-1}$), than reported in the previous greenhouse experiment [1.2 to 1.8 $\text{dS}\cdot\text{m}^{-1}$ (N at 160 to 250 $\text{mg}\cdot\text{L}^{-1}$); van Iersel, 1999a], although the same water-soluble fertilizer was used in both experiments. This difference may be due to differences in environmental conditions between these two experiments. Environmental conditions affect water use efficiency of plants, which in turn affects the optimal fertilizer concentration (Bugbee, 1995). When water use efficiency is high, high concentrations of fertilizer should be provided, because the total volume of fertilizer solution applied to the plants is relatively low. RH in the current experiment was higher than what is typical for greenhouse conditions. High RH reduces the air-to-leaf vapor pressure deficit, and thus the transpiration rate, increasing water use efficiency (Dewar, 1997).

TISSUE AND MEDIUM MINERAL NUTRIENT CONCENTRATIONS. Because optimal fertilizer concentrations depend on the environmental conditions (Kang and van Iersel, 2001), it has been argued that maintaining growing medium EC may be a better approach

Table 1. Effect of fertilizer electrical conductivity (EC) on shoot and root growth of subirrigated pansies. The results of the quadratic regressions ($Y = x_0 + x_1 \times EC + x_2 \times EC^2$) were used to estimate the EC ($\text{dS}\cdot\text{m}^{-1}$) at which the different parameters would be expected to have their maximum or minimum value; LAR = leaf area ratio.

EC ($\text{dS}\cdot\text{m}^{-1}$)	Shoot to root ratio	Leaf area (m^2)	Shoot dry wt (g)	Root dry wt (g)	Total dry wt (g)	Cumulative C gain (mol)	LAR _{plant} ($\text{m}^2\cdot\text{kg}^{-1}$)	LAR _{shoot} ($\text{m}^2\cdot\text{kg}^{-1}$)
0.15	2.0	0.16	12.8	6.39	19.2	0.55	8.0	12.2
1.0	6.3	0.45	29.9	4.75	34.6	1.09	13.0	15.0
2.0	10.8	0.57	34.6	3.21	37.8	1.25	15.0	16.4
3.0	9.9	0.47	31.2	3.17	34.4	1.13	13.8	15.2
r^2	0.95	0.91	0.94	0.93	0.85	0.77	0.91	0.77
x_0	0.5 ^{NS}	0.09 ^{NS}	9.6*	6.85***	16.5**	0.45*	7.0**	11.5***
x_1	8.1***	0.47**	25.0**	-2.76*	22.2**	0.80*	7.7**	4.7*
x_2	-1.6**	-0.11**	-6.0**	0.51*	-5.5*	-0.19*	-1.8**	1.2*
Estimated max or min EC	2.5	2.0	2.1	2.7	2.0	2.1	2.1	2.0

^{NS}, **, ***, Nonsignificant, or significant at $P < 0.05$, 0.005, or 0.0005, respectively; $n = 2$.

Table 2. Effect of fertilizer electrical conductivity (EC) on leachate EC and pH of pansies after a 30 d growing period. EC and pH were measured with the pour-through method (Wright, 1986).

Fertilizer EC (dS·m ⁻¹)	Leachate EC (dS·m ⁻¹)	Leachate pH
0.15	0.31	6.3
1.0	0.72	6.0
2.0	2.00	5.8
3.0	3.14	5.9
Correlation with fertilizer EC (<i>r</i> ²)	0.97	0.43
Intercept	-0.04 ^{NS}	6.2*
Slope	1.03*	-0.13 ^{NS}

^{NS,*}Nonsignificant or significant at *P* < 0.0001, respectively; *n* = 2.

to fertility management than controlling the concentration of the fertilizer solution (van Iersel, 1999a). As expected, leachate EC at the end of this experiment increased with increasing fertilizer EC (Table 2) and was within the previously recommended range of 1.5 to 4.0 dS·m⁻¹ (as determined by the pour-through method; van Iersel, 1999a) in the 2.0 and 3.0 dS·m⁻¹ treatments. However, the EC of the leachate was only 0.72 dS·m⁻¹ when plants were fertilized with a fertilizer solution of 1.0 dS·m⁻¹. This leachate EC is lower than recommended, but it appeared to have little or no detrimental effects on the plants. Shoot growth was reduced (14%), while root growth was increased (48%) in the 1.0 dS·m⁻¹ treatment, as compared to the 2.0 dS·m⁻¹ treatment (Table 1). Leachate pH was similar in all treatments (Table 2), and within the recommended range for most floricultural crops (5.4 to 6.3; Bailey and Bilderback, 1997).

Shoot tissue concentrations of N, P, K, S, Ca, Fe, Na, and Zn increased linearly with increasing fertilizer concentrations (Table 3), while other nutrients were not affected (data not presented). These results differ greatly from those of the greenhouse experiment by van Iersel (1999a), who reported that only shoot concentrations of P and Mn increased, and those of Mg and Na decreased with increasing fertilizer concentration. The differences between this and the previous experiment may be related in part to the different fertilizer concentrations used in these experiments. The lowest concentration used by van Iersel (1999a) had an EC of 0.6 dS·m⁻¹, while in the current experiment we included a treatment without any fertilizer in the irrigation solution. Tissue concentrations of N, P, and K in particular increased rapidly as the fertilizer EC was raised from 0.15 to 1.0 dS·m⁻¹.

Since there was a linear relationship between fertilizer EC and tissue concentrations of N, P, K, S, Ca, Fe, Na, and Zn, but a quadratic correlation between fertilizer EC and DW (Table 1), it seems unlikely that the effects of fertilizer EC on DW can be explained by direct effects of tissue nutrient status on photosyn-

thesis or respiration. In particular the decrease in DW at higher than optimal fertilizer ECs does not appear to be related to mineral nutrient concentrations in the plants.

CARBON EXCHANGE RATES. There was a strong linear correlation ($DW = 5.55 + 25.8 \times CCG$, $r^2 = 0.98$) between CCG and total DW of the plants (Fig. 1), which indicates that the CER measurements were an accurate measure of plant growth rate. The intercept in the regression equation (5.6 ± 1.2 g, intercept \pm SE) is an estimate of seedling DW at the start of the experiment (total of 35 seedlings), while the regression line slope (25.8 ± 1.5 g·mol⁻¹, slope \pm SE) is an estimate of the increase in DW for each mol of CO₂ fixed by the plants. Assuming that the C content of the plants in all treatments was similar, this value can be used to estimate the C content of the plants as $12 \text{ g} \cdot \text{mol}^{-1} / 25.8 \pm 1.5 \text{ g} \cdot \text{mol}^{-1} = 0.465 \pm 0.027 \text{ g} \cdot \text{g}^{-1}$ (estimate \pm SE). The estimated C content is higher than most previously reported values [0.396 g·g⁻¹ for white clover (*Trifolium repens* L.) (McCree and Troughton, 1966), 0.421 g·g⁻¹ for sugar beet leaves (*Beta vulgaris* L.) (Terry and Mortimer, 1972), and 0.45 g·g⁻¹ for pumpkin leaves (*Cucurbita pepo* L.) (Turgeon and Webb, 1975)]. Hadley and Causton (1984) showed that the organic C content in plants changes during development and differs among plant parts. They reported that C content in barley (*Hordeum vulgare* L.) and brussels sprouts [*Brassica oleracea* L. Gemmifera Group)] organs ranged from 0.30 g·g⁻¹ to 0.52 g·g⁻¹, with the vast majority of measurements between 0.35 and 0.50 g·g⁻¹. Thus, our estimate of 0.47 g·g⁻¹ appears to be reasonable.

The first differences in gas exchange rate were seen at 6 d after transplanting, when there was a quadratic correlation between fertilizer EC and R_{dark} (Fig. 2). At this stage, plants watered without fertilizer (EC = 0.15 dS·m⁻¹) had a lower R_{dark} than plants in the other three treatments. However, consistent treatment effects were not observed until 11 d after transplanting. Throughout the latter part of the experiment, there was a quadratic relationship between fertilizer concentration and R_{dark} . Plants fertilized with a solution of 2.0 dS·m⁻¹ had the highest R_{dark} , while those that did not receive fertilizer consistently had the lowest R_{dark} . Interestingly, R_{dark} of the plants increased after watering, especially during the last 15 d of the experimental period. The reason for this increase is not clear, but perhaps plants were subjected to mild water deficits during this period. However, watering had little or no effect on the photosynthetic rate of the plants.

Similar effects regarding the above mentioned were seen in P_{net} and P_{gross} (Fig. 2). Plants watered with a fertilizer solution with an EC of 2.0 dS·m⁻¹ consistently had the highest P_{net} and P_{gross} , while plants watered without any fertilizer had the lowest photosynthetic rate. These differences became statistically significant at 12 and 13 d after transplanting for P_{gross} and P_{net} , respectively,

Table 3. Effect of fertilizer electrical conductivity (EC) on mineral nutrient concentrations in the shoots of subirrigated pansies.

EC (dS·m ⁻¹)	N	P	K	S	Ca	Fe	Na	Zn
			(mg·g ⁻¹)				(μg·g ⁻¹)	
0.15	36.8	3.1	37.1	1.9	5.3	67	490	69
1.0	52.8	6.4	51.6	2.3	6.7	91	561	79
2.0	61.5	9.6	62.2	2.4	8.0	132	660	100
3.0	61.2	12.0	60.1	3.1	8.7	124	842	104
<i>r</i> ²	0.64	0.96	0.60	0.81	0.75	0.54	0.62	0.71
Intercept	40.1***	3.1***	40.1***	1.8***	5.3***	69**	450***	68***
Slope	8.4*	3.0***	8.2*	0.4**	1.2**	22*	121*	13*

***Significant at *P* < 0.05, 0.005, or 0.0005, respectively; *n* = 2.

and these differences continued throughout the remainder of the experiment. The measured P_{net} was negative in all treatments during the first 5 d after transplanting. This indicated that, even when exposed to light, the plants respired more carbohydrates than were produced in P_{gross} . However, P_{net} may have been

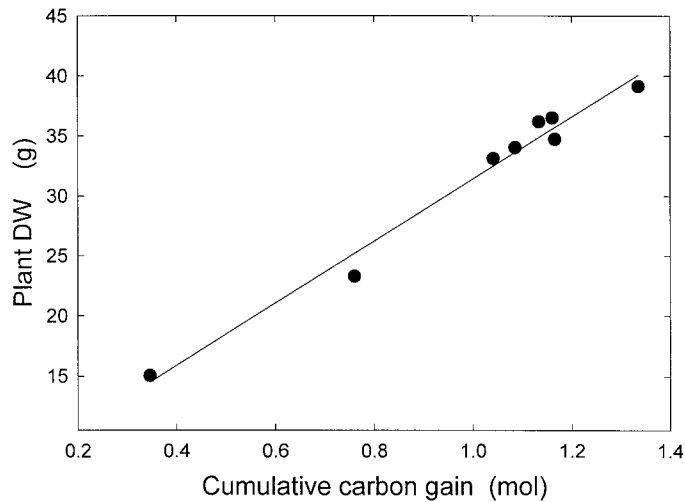


Fig. 1. Correlation between the total amount of C incorporated into pansies during a period of 30 d (cumulative C gain, CCG) and the whole plant DW of the plants at the end of that period. The line indicates the regression results ($DW = 5.55 + 25.8 \times CCG$, $r^2 = 0.98$).

underestimated in this experiment, since the CER measurements include respiration caused by microbial breakdown of the organic materials in the growing medium. Although this source of CO_2 is negligible when plants are growing rapidly, it may induce significant errors when small, slow-growing plants are measured (van Iersel and Bugbee, 2000). However, negative P_{net} values have been reported previously when bare-rooted annual vinca [*Catharanthus roseus* (L.) G. Don] seedlings were transplanted into diatomaceous earth, an inert growing medium (van Iersel, 1999b). Since respiration from the microbial breakdown of the growing medium was not a factor in that experiment, it would appear to be possible for plants to have a negative P_{net} following transplanting.

The negative or low P_{net} early in the experimental period, in combination with the respiratory C loss during the dark period, resulted in a negative DCG during the first 7 to 8 d after transplanting (Fig. 3). However, the importance of these negative DCG values should not be overestimated, since the total estimated C loss during this entire period was in the same order of magnitude as the increase in the C content of the plants during one single day at the end of the experiment (Fig. 3). There was a steady increase in DCG throughout most of the experiment, starting at 5 d after transplanting. There was a quadratic relationship between DCG and fertilizer EC starting at 13 d after transplanting. DCG was lowest consistently in the $0.15 \text{ dS}\cdot\text{m}^{-1}$ treatment and highest

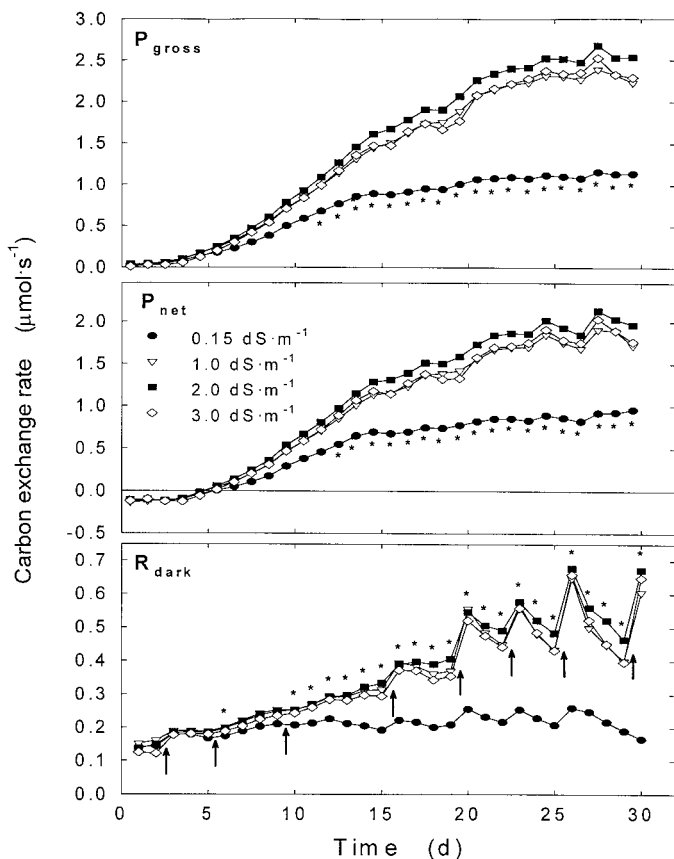


Fig. 2. Gross photosynthesis (P_{gross}), net photosynthesis (P_{net}), and dark respiration (R_{dark}) of subirrigated pansies, as affected by the electrical conductivity (EC) of the fertilizer solution. Data represent the total CO_2 exchange rate of groups of 35 plants, averaged over two replications. Arrows indicate the time that the plants were fertiligated. *Significant quadratic relationship between fertilizer EC and the measured variable.

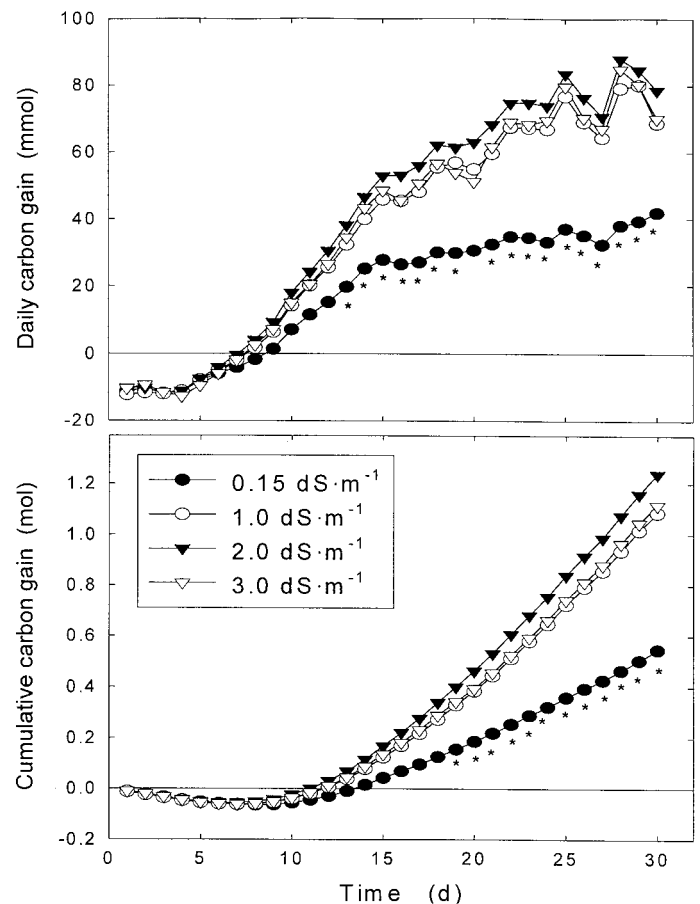


Fig. 3. Daily (DCG) and cumulative carbon gain (CCG) of pansy during a 30-d growing period, as affected by the EC of the fertilizer solution. A negative DCG indicates there was a net loss of C from the plants during that 24 h period, while a negative CCG indicates that the plants contain less C than at the time of transplanting. *Significant quadratic correlation between fertilizer EC and the calculated variable ($n = 2$).

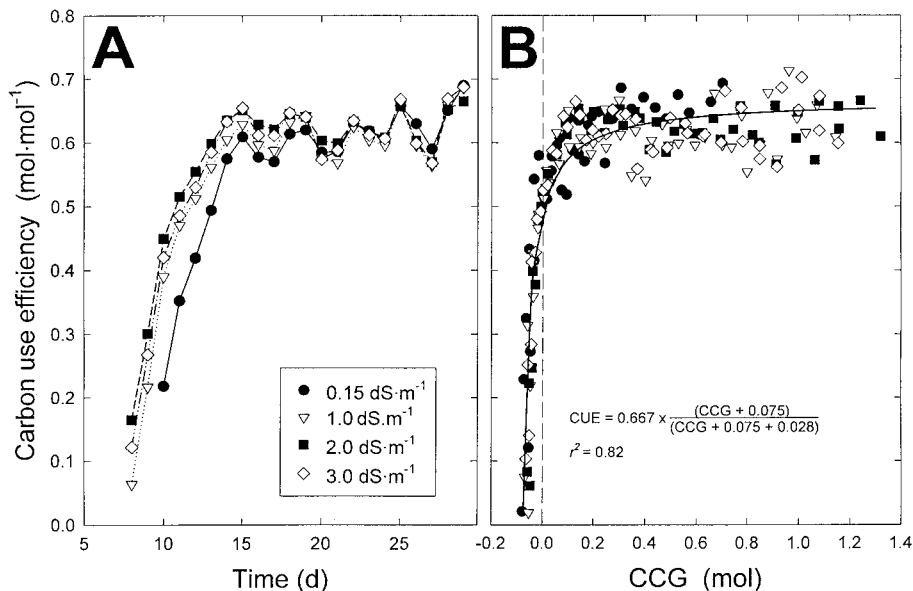


Fig. 4. Carbon use efficiency (CUE) of pansy as affected by the EC of the fertilizer solution. Data are shown as (A) a function of the time after transplanting and (B) cumulative C gain (CCG), a measure of plant size. A modified rectangular hyperbola was used to determine the relationship between CUE and CCG (Eq. 4). Data points in A represent the treatment means ($n=2$), while in B data points from all experimental units are shown.

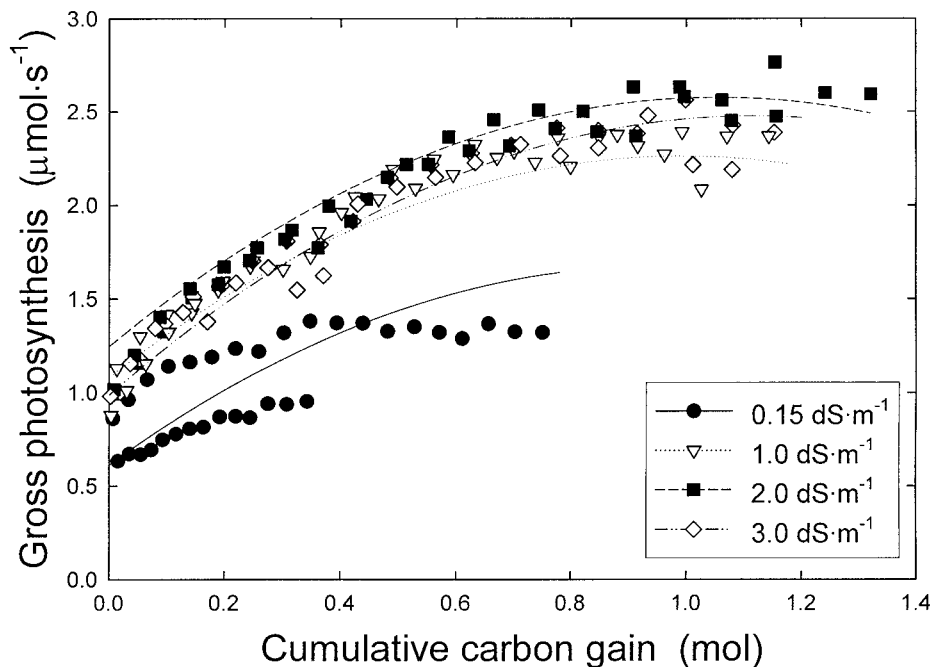


Fig. 5. Effect of the EC of the fertilizer solution on the relationship between gross photosynthesis (P_{gross}) and cumulative C gain (CCG). $P_{\text{gross}} = 0.50 + 0.80 \times \text{EC} + 2.23 \times \text{CCG} + 0.147 \times \text{EC} \times \text{CCG} - 0.212 \times \text{EC}^2 - 1.2 \times \text{CCG}^2$, $r^2 = 0.94$. All regression parameters are significant at $P < 0.0005$. The lines represent the estimated P_{gross} at fertilizer ECs of 0.15, 1.0, 2.0, or 3.0 $\text{dS}\cdot\text{m}^{-1}$. Data from all experimental units are shown.

in the 2.0 $\text{dS}\cdot\text{m}^{-1}$ treatment. DCG in the 1.0 and 3.0 $\text{dS}\cdot\text{m}^{-1}$ treatments were similar throughout the experiment. Treatment effects on DCG closely reflected effects on P_{net} and P_{gross} .

Since CCG is the integrated value of DCG, treatment differences in DCG are reflected in CCG as well. However, treatment differences in CCG were not significant until 19 d after trans-

planting. As would be expected from the differences in DCG, the 2.0 $\text{dS}\cdot\text{m}^{-1}$ treatment had the highest CCG, while that in the 0.15 $\text{dS}\cdot\text{m}^{-1}$ treatment was the lowest (Table 1).

CUE of the plants increased throughout the experiment, but there were no significant differences among the treatments (Fig. 4A). There was a close correlation between CCG and CUE (Fig. 4B). Based on results of regression analysis, the maximum CUE of these plants was estimated to be $0.667 \pm 0.007 \text{ mol}\cdot\text{mol}^{-1}$ (estimate \pm SE). If microbial breakdown of the growing medium was a significant factor early in the experiment, this could explain the low CUE during the first 2 weeks of the experiment, because it would have resulted in an underestimation of DCG, the numerator in CUE calculations. Estimates of P_{gross} would not be affected by microbial respiration, unless this respiration

was different during the light and dark periods. However, the finding of an increase in CUE is consistent with a previous report showing a similar increase in CUE with increasing CCG (van Iersel, 1999b). The increase in CUE reported in that study was not due to microbial breakdown of the growing medium, since the plants were grown in diatomaceous earth, an inert, inorganic substrate.

CUE of most plants normally ranges from 0.5 to 0.7 (Amthor, 1989; Bednarz and van Iersel, 1999; Gifford, 1995; McCree et al, 1990; van Iersel and Bugbee, 1996), although it depends on growing conditions (van Iersel and Lindstrom, 1999), such as temperature, irradiance, and photoperiod. During the last 2 weeks of this experiment, CUE was within the normal range, while it was lower during the first 2 weeks after transplanting, perhaps because the plants suffered from transplant shock.

To determine whether plants of equal size (i.e., equal CCG), but watered with fertilizer solutions with different EC had similar P_{gross} , P_{gross} was plotted as a function of CCG (Fig. 5) and P_{gross} was estimated as a function of EC and CCG (Eq. 5). Irrespective of CCG, a fertilizer EC of 2.0 $\text{dS}\cdot\text{m}^{-1}$ resulted in a higher P_{gross} than the other fertilizer treatments, while an EC of 0.15

$\text{dS}\cdot\text{m}^{-1}$ resulted in the lowest P_{gross} . Since there was an interactive effect of EC and CCG on P_{gross} , the EC value at which P_{gross} was estimated to be maximal varied with CCG, and increased from 1.89 $\text{dS}\cdot\text{m}^{-1}$ at a CCG of 0 mol to 2.34 $\text{dS}\cdot\text{m}^{-1}$ at a CCG of 1.3 mol.

Since P_{gross} of plants with equal CCG differed among fertilizer treatments, the treatments affected the photosynthetic capacity of the plants, even when plants of equal size are compared. The effect of fertilizer EC on P_{gross} may have been related to differences in LAR among the treatments. Plants with a high LAR produce a relatively large leaf area per unit biomass. Since a larger leaf area generally results in interception of more light, and light interception by a canopy is closely related to growth of the plants

(Lawlor, 1995), a high LAR would be expected to increase growth. Our finding that plants with a high LAR_{plant} also had a high DW (Table 1) is consistent with the report by Veneklaas et al. (2002) that differences in growth rate among several woody species were due mainly to differences in LAR.

Differences in LAR_{plant} were due in part to differences in shoot to root ratio; plants with a high shoot to root ratio also had a high LAR_{plant} . This is not surprising, since plants with a high shoot to root ratio invest relatively little energy in the production of roots, and therefore can grow larger shoots. However, shoot to root ratio did not account entirely for differences in LAR_{plant} , since there were also treatment differences in LAR_{shoot} (Table 1) and LAR_{plant} could be described accurately as a function of both shoot to root ratio and LAR_{shoot} ($LAR_{plant} = -5.1 + 1.06 \times LAR_{shoot} + 0.29 \times \text{shoot to root ratio}$, $r^2 = 0.98$). It is not clear why LAR_{shoot} was affected by the fertilizer treatments.

Conclusions

The 2.0 $dS \cdot m^{-1}$ treatment resulted in the best plant growth and highest whole-plant photosynthesis. However, differences in growth among the 1, 2, and 3 $dS \cdot m^{-1}$ treatments were small, and pansies can be grown successfully with a wide range of fertilizer concentrations. This is consistent with previous results (van Iersel, 1999a). One potential drawback of using high fertilizer concentrations is that it results in a high shoot to root ratio, which could potentially affect establishment and performance of the plants in the landscape.

Differences in LAR_{plant} appear to be the most likely explanation for the differences in photosynthetic rate among treatments. Since there was a strong correlation between LAR_{plant} and plant DW, plants with a high LAR_{plant} apparently grew faster than those with a low LAR_{plant} . This likely was due to increased light interception by plants with a high LAR_{plant} . The correlation of LAR_{plant} with both LAR_{shoot} and the shoot to root ratio raises the question of whether it is possible to increase LAR_{plant} without an increase in the shoot to root ratio. An increase in LAR_{shoot} , without a concurrent effect on shoot to root ratio, may result in faster growing plants without the disadvantage of producing plants with small root systems. Whether this increase in LAR_{plant} can be achieved using cultural or breeding approaches warrants further attention.

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