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Light Intensity and Fertilizer Concentration: I. Estimating Optimal Fertilizer Concentrations from Water-use Efficiency of Wax Begonia

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Abstract. **Environmental conditions and incorporation of nutrients into the growing medium can affect the fertilizer needs of bedding plants. To evaluate the effects of photosynthetic photon flux (*PPF*) and starter fertilizer on the fertilizer requirements of subirrigated plants, we grew wax begonias (*Begonia semperflorens-cultorum* Hort.) under three *PPF* levels (averaging 4.4, 6.2, and 9.9 mol·m^{-2}·d^{-1}) and four fertilizer concentrations [electrical conductivity (EC) of 0.15, 0.33, 0.86, and 1.4 dS·m^{-1}] in a normal (with starter fertilizer, EC = 2.1 dS·m^{-1}) and heavily leached (with little starter fertilizer, EC = 0.9 dS·m^{-1}) growing medium. Except for shoot dry mass, we did not find any significant interactions between *PPF* and fertilizer concentration on any of the growth parameters. There was an interactive effect of fertilizer concentration and starter fertilizer on all growth parameters (shoot dry mass, leaf area, plant height, and number of flowers). When the growing medium contained a starter fertilizer, fertilizer concentration had little effect on growth. When the growing medium was leached before transplanting, growth was best with a fertilizer EC of 0.86 or 1.4 dS·m^{-1}. Water-use efficiency (WUE) was calculated from 24-hour carbon exchange and evapotranspiration measurements, and used to estimate the required [N] in the fertilizer solution to achieve a target tissue N concentration of 45 mg·g^{-1}. Increasing *PPF* increased WUE and the required [N] (from 157 to 203 mg·L^{-1} at *PPF* levels of 4.4 and 9.9 mol·m^{-2}·d^{-1}, respectively). The *PPF* effect on the required [N] appeared to be too small to be of practical significance, since dry mass data did not confirm that plants grown at high light needed higher fertilizer concentrations. Thus, fertilizer concentrations need not be adjusted based on *PPF.***

Subirrigation systems have become more popular in recent years due to zero runoff, and increased efficiency in fertilizer and water use (Elliot, 1990; Morvant et al., 1997; Uva et al., 1998; van Iersel, 1996; Yelanich and Biernbaum,1990). Because of the absence of leaching in subirrigation, starter fertilizer can remain in the growing medium for a longer period, and reduce the fertilizer requirements by supplying a substantial amount of nutrients to plants. Water-use efficiency (WUE, the ratio of growth to transpiration in plants) can also affect the fertilizer requirements of plants (Bugbee, 1995). A plant with a high growth to transpiration ratio takes up a relatively small amount of water while producing a gram of dry matter. Therefore, a higher fertilizer concentration should be supplied to these plants to supply adequate nutrients.

The product of tissue nutrient concentration and the mass of newly formed tissue determines the amount of nutrients taken up by the plant (nutrient demand), while the product of the volume of the applied fertilizer solution and the nutrient concentration of the solution equals the amount of nutrients supplied to the plants (nutrient supply). To prevent nutrient deficiencies or toxicities, nutrient supply and demand should be balanced. The volume of the applied fertilizer solution absorbed by the growing medium equals evapotranspiration, if there is no leaching and the medium is rewatered to the same moisture level at each irrigation. Thus, to maintain the balance between supply and demand for N nutrition specifically

$$[N_{tissue}] \times GR = [N_{fert}] \times ET \qquad \text{[Eq. 1]}$$

where $[N_{tissue}]$ is the desired tissue N concentration (mg·g^{-1}), GR is the growth rate (g·d^{-1}), $[N_{fert}]$ is the required N concentration of the fertilizer solution to maintain the balance between N supply and demand (mg·L^{-1}), and ET is evapotranspiration (L·d^{-1}). Since GR/ET is the WUE:

$$[N_{fert}] = [N_{tissue}] \times WUE \qquad \text{[Eq. 2].}$$

This concept has been used in hydroponic studies, where photosynthesis and transpiration models can be used to predict the optimal electrical conductivity (EC) of the supplied nutrient solution (Kläring and Cierpinski, 1998). In bedding plant production, evaporation from the growing medium may be an important factor in determining the total water-use, and the combined value of evaporation from the growing medium and transpiration from the plants should be used to calculate optimal fertilizer concentrations.

Photosynthetic photon flux is an important environmental variable affecting WUE, and therefore possibly optimal fertilizer concentration of subirrigated plants. Water-use efficiency normally increases with increasing light intensity (Alexander and Donnelly, 1995; Caviglia and Sadras, 2001; Israeli et al., 1996; Le Roux et al., 2001; Ponton et al., 2002; Vandana, 1999). Photosynthetic photon flux varies considerably across the country and throughout the year. Thus, fertilizer recommendations may have to be adjusted based on the prevailing *PPF* level. Surprisingly, research on optimum fertilizer concentrations of plants grown under different *PPF* levels is scant, although there is some research that looked at the effect of other environmental factors on nutrient uptake. Kang and van Iersel (2001) concluded that temperature affects the optimal fertilizer concentration of subirrigated petunias (*Petunia* ×*hybrida* Hort. Vilm-Andr.), whereas Gislerrd and Mortensen (1990) found that tissue nutrient concentration of *Begonia* ×*heimalis* was lower at high (90%) than a low (60%) relative humidity, but increased when the concentration of nutrient solution was increased.

The objective of this experiment was to study the effect of starter fertilizer and varying light intensities on optimal N concentration of the fertilizer solution for the production of subirrigated begonias. We hypothesized that the optimal N concentration would increase with increasing *PPF* (because of the increase in WUE) and decrease with a starter fertilizer in the growing medium. Wax begonia was used as a model crop, because it can be grown under a variety of light intensities, and it is one of the most popular shade-tolerant plants in floriculture.

Materials and Methods

Plant material. Plug seedlings of wax begonia ‘Cocktail Vodka’ were obtained from a commercial grower (Speedling Inc., Blairsville, Ga.) and transplanted into square, 10-cm (510-mL) containers filled with a soilless growing medium (Fafard 2P mix; Fafard, Anderson, S.C.) on 13 June 2001. The starter fertilizer in the growing medium contained 89, 37, and 32 g·m^{-3} of N, P, and K, respectively. The starter fertilizer was leached out of half of the pots by watering heavily for about ten times over a three day period. The EC of the normal (hereafter, with starter fertilizer) and leached (hereafter, without starter fertilizer) growing medium were determined with the pour-through technique (Wright, 1986) to be 2.1 and 0.9 dS·m^{-1}, respectively. After transplanting, the seedlings were placed on 1.2 × 2.4-m^2 ebb-and-flow benches (Midwest GroMaster, St. Charles, Ill.) and subirrigated daily with 20N–4.4P–16.6K fertilizer solutions (Peter’s 20–10–20 peat-lite special, The Scotts Co., Marysville, Ohio). Fertilizer solutions were stored in plastic barrels (210 L) and pumped into the watertight trays of the ebb-and-flow system using submersible pumps (NoKorode-2; Little Giant, Oklahoma City, Okla.). The bottoms of the pots were immersed in fertilizer solution for about 13 min

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(5 min for pumping and 8 min for draining) during which the growing medium absorbed it by capillary action. The EC of the fertilizer solution was measured using an EC meter (model M90, Corning, Corning, N.Y.) and adjusted weekly by adding fertilizer when the barrels were refilled. Plants were grown in a greenhouse covered with double-layered polyethylene and a shade cloth which transmitted ≈63% of the incident light. The average day and nighttime temperatures were 32.2 and 23.7 °C, respectively (with an average of 27.1 °C over the course of the experiment).

Treatments. Plants were placed on one of 12 ebb-and-flow benches, and each bench was subirrigated with one of four fertilizer concentrations (0, 30, 110, or 190 $mg \cdot L^{-1}$ N, corresponding ECs of 0.15, 0.33 , 0.86, and 1.4 $dS \cdot m^{-1}$, respectively). Each bench was divided into three sections with different *PPF* levels, by placing different shade cloths over PVC frames, which were placed on each bench. This resulted in 63%, 35%, or 0% shade (in addition to the shade due to the shade cloth covering the greenhouse), equivalent to an average daily *PPF* of 4.4, 6.2, and 9.9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Two groups of 30 plants each (with or without starter fertilizer), were grown in each bench section with different *PPF* levels. Six quantum sensors (QSO-SUN; Apogee Instruments, Logan, Utah) were arranged in different experimental units to measure daily *PPF*.

By watering daily, plants were provided with enough water to prevent drought stress in any of the treatments. Although all plants were subirrigated daily, this does not imply that all plants received equal amounts of water. With subirrigation, the growing medium absorbs water to near saturation, and the actual amount of water, and thus fertilizer, absorbed by the growing medium depends on the ET since the last irrigation. Thus, the growing medium of plants with high ET rates (i.e., larger plants grown under higher *PPF*) absorbed more water and fertilizer than plants with low ET rates.

Measurements. Data on plant height, leaf area, shoot dry mass, and number of flowers were collected at the end of the growing period (6 weeks after transplanting). Plant height was measured from the surface of the growing medium to the top of the plant. Leaf area was measured using an area meter (LI-3100; LI-COR, Lincoln, Nebr.). Shoots from sample plants were dried in a forced-air oven maintained at 80 °C for 1 week before measuring their dry mass. Flowers from six plants in each experimental unit were counted. Electrical conductivity and pH of growing medium were collected three times during the growing period (after 2, 4, and 6 weeks), using the pour-through technique (Wright, 1986). About 25 mL of tap water (EC of 0.1 to 0.2 $dS \cdot m^{-1}$) was poured evenly on top of the growing medium an hour after subirrigating the plants, and the collected leachate was used to measure EC and pH of the growing medium with EC and pH sensors (model M90; Corning, Corning, N.Y.). Plants used for determining EC of the growing medium were not used in any subsequent analyses, because the pour-through method may change salt gradients within the growing medium, which in turn may affect the subsequent growth of the plants.

Only plants grown without a starter fertilizer in the growing medium were used in the WUE study. Four plants from each experimental unit were placed in an eight-chamber, whole-plant gas exchange system (van Iersel and Bugbee, 2000) at the end of the experiment to measure the CO_2 exchange rates. Since there were 36 experimental units [3 replications × 12 treatments (4EC × 3 *PPF* levels)], and eight groups of plants could be measured simultaneously, these data were collected during a 5-d period. Plants were kept in the gas exchange chambers for a period of 24 h (14 h of light, 10 h of dark), during which whole-plant net photosynthesis and dark respiration (P_n and R_d respectively, expressed in $\mu mol \cdot s^{-1}$) rates were measured once every 10 min. Inside the growth chambers, plants were exposed to the same *PPF* as in the greenhouse. To determine ET, pots were weighed before and after the gas exchange measurements. Growth rate (GR, $g \cdot d^{-1}$; amount of dry matter produced by a group of four plants in a day) was calculated as follows:

$GR = [(P_{n,avg} \times t_{light} - R_{d,avg} \times t_{dark}) \times 12/f_C\ ]$ [Eq. 3]

where $P_{n,avg}$ and $R_{d,avg}$ are the average net photosynthesis and dark respiration rates ($mol \cdot s^{-1}$), t_{ight} and t_{dark} are the durations of light and dark periods in seconds, 12 converts moles of carbon to grams of carbon, and f_C is the carbon content ($1/f_c$ converts grams of carbon to grams of dry matter) determined from total shoot tissue analysis of plants in different treatments (f_c ranged from 0.39 to 0.43). Water-use efficiency ($g \cdot L^{-1}$) was calculated as

WUE = GR/ET [Eq. 4]

Optimal nitrogen concentrations of the fertilizer solutions were calculated as described in Eq. 2, assuming a desired $[N_{tissue}]$ of 45 $mg \cdot g^{-1}$, based on the recommended range of 20 to 60 $mg \cdot g^{-1}$ (Mills and Jones, 1996). Note that the assumed value for $[N_{tissue}]$ will affect the calculated $[N_{fert}]$, but not the relative differences among treatments. Those differences are solely dependent on WUE instead.

The entire shoot samples were analyzed to determine the tissue nutrient concentration. Tissue C, N, and S concentrations were measured using a C–N–S analyzer (model 2000; Leco corporation, St. Joseph, Mich.) and the other nutrients were measured using a ICAP analyzer (model 9000; Thermo Jarrell Ash corporation, Franklin, Mass.).

From the collected data, $[N_{fert}]$ was calculated as follows: if $P_{n,avg}$ (during the 14-h light period) and $R_{d,avg}$ (during the 10-h dark period) rates of plants were 1.0 and 0.5 $\mu mol \cdot s^{-1}$, respectively, and f_c of the plants was 0.40, then GR of plants can be calculated as $GR = \{[(1.0 \times 14 \times 3600) - (0.5 \times 10 \times 3600)]/1{,}000{,}000\} \times 12/0.4 = 0.972\ g \cdot d^{-1}$. The denominator 1,000,000 converts the photosynthetic or respiration rate from $\mu mol \cdot s^{-1}$ to $mol \cdot s^{-1}$. Let us assume that 200 mL of water is lost in evapotranspiration in producing 0.972 g of dry matter during the 24-h period. Therefore, WUE = 0.972/0.2 = 4.86 $g \cdot L^{-1}$, and $[N_{fert}] = 4.86 \times 45 = 219\ mg \cdot L^{-1}$.

Experimental design and analysis. The treatments were organized in a randomized complete block with a split-split-plot design and three replications. Fertilizer EC was the main blocking factor, with three light intensities as main splits, and a group of 30 plants either with or without starter fertilizer was a subsplit (experimental unit). Data collected on physical growth parameters, including dry mass, leaf area, plant height, and number of flowers per plants, and EC and pH of the growing medium were subjected to ANOVA and regression analysis using statistical analysis software (SAS institute, Cary, N.C.). Since the absence or presence of starter fertilizer is a noncontinuous variable (i.e., a class variable), it could not be included in regression models. Plant growth was modeled as a function of EC according to:

$Y = \beta_0 + \beta_1 \times \ln(EC) - \beta_2 \times EC$ [Eq. 5]

where $\beta_0 ... \beta_2$ are regression coefficients. The log transformation of EC was included, because it resulted in a good empirical fit, while simple linear or quadratic regression did not describe the data adequately. Since there was a significant two-way interactive effect of fertilizer EC and *PPF* on shoot dry mass, regression were done separately for each *PPF* level. Since the interaction between *PPF* and the presence of starter fertilizer was not significant for any of the growth parameters, data were averaged over all three *PPF* levels to describe the effect of fertilizer EC on plant growth in the presence and absence of starter fertilizer. A log transformation was not required in the analysis of the EC of the growing medium, since the trends could be adequately described by simple linear regression.

The analysis of physiological parameters (net photosynthesis, dark respiration, evapotranspiration, growth rate, WUE, and $[N_{fert}]$) was done using multiple regression, with an interaction term:

$Y = Y_0 + Y_1 \times EC + Y_2 \times PPF + Y_3 \times EC^2 + Y_4 \times PPF^2 + Y_5 \times EC \times PPF$ [Eq. 6]

where $Y_0 .... Y_5$ are regression coefficients. Nonsignificant terms were removed by backward selection ($P < 0.05$).

A similar regression was done with $[N_{fert}]$ as the dependent variable, except that the actual N concentration of the fertilizer solution ($[N]_a$) was used as the independent variable, instead of EC. If $[N]_a$ is lower than $[N_{fert}]$, either the actual N concentration in the plant will be lower than $[N_{tissue}]$, or the [N] in the growing medium will decrease. Vice versa, if $[N]_a$ is higher than $[N_{fert}]$, this will result in a tissue [N] higher than 45 $mg \cdot g^{-1}$, or an increase in the [N] of the growing medium. The [N] in the fertilizer solution to maintain the balance between supply and demand (assuming 45 $mg \cdot g^{-1}$ N in the tissue) can be determined as the concentration at which $[N]_a$ and $[N]_{fert}$ are equal (or $[N]_a - [N]_{fert} = 0$).

Results and Discussion

Plant growth–light intensity relationship. The three-way interaction among *PPF*, fertilizer EC, and starter fertilizer on shoot dry mass was nonsignificant ($P = 0.07$), but there was an interactive effect of *PPF* and fertilizer EC on shoot dry mass, indicating that the growth

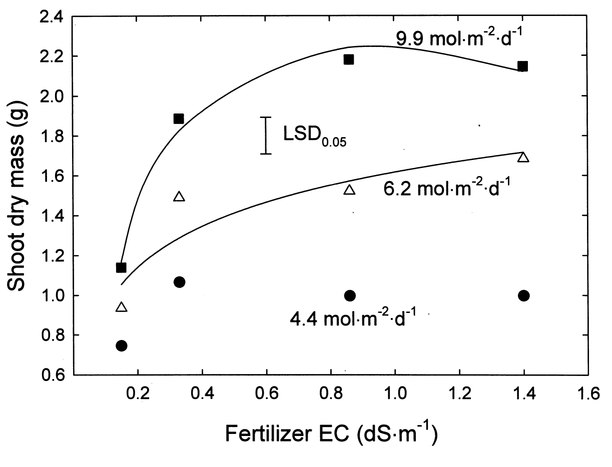

Fig. 1. Effect of fertilizer electrical conductivity (EC$_{fert}$) and daily photosynthetic photon flux on shoot dry mass of subirrigated wax begonias at 6 weeks after transplanting. The error bar indicates the interactive least significant difference among fertilizer ECs within one light intensity and among light intensities within one fertilizer EC. The lines indicate significant effects ($P < 0.05$); DW$_{shoot}$ = 1.62 + 0.30 × ln(EC$_{fert}$)) ($r^2 = 0.70$) and 3.47 + 1.12 × ln(EC$_{fert}$) + 1.23 × EC ($R^2 = 0.83$), for medium (6.2 mol·m^{-2}·d^{-1}) and high *PPF* (9.9 mol·m^{-2}·d^{-1}), respectively.

response to fertilizer EC depended on the *PPF* level. Irrespective of fertilizer EC, shoot dry mass increased with increasing *PPF* (Fig. 1). At all three *PPF* levels, dry mass increased as the fertilizer EC was increased from 0.15 to 0.33 dS·m^{-1}. This increase in dry mass with increasing EC was more pronounced at medium or high (6.2 or 9.6 mol·m^{-2}·d^{-1}) than at low (4.4 mol·m^{-2}·d^{-1}) *PPF*, presumably because *PPF*, not nutrition, was the main limiting factor for growth at low *PPF.* Similarly, Larouche et al. (1989) concluded that vegetative growth of greenhouse tomatoes (*Lycopersicon esculentum* Mill. 'Vedettos') was limited by light at low *PPF*, and therefore did not respond to increased N in the nutrient solution. However, we did not find any significant interaction between *PPF* and fertilizer EC on leaf area, plant height, or number of flowers per plant. Irrespective of fertilizer EC and starter fertilizer, these variables increased linearly with increasing *PPF* (data not shown).

Plant growth–starter fertilizer relationship. There were interactive effects of fertilizer EC and starter fertilizer on shoot dry mass, leaf area, plant height, and number of flowers per plant (Fig. 2). These interactions indicate that, irrespective of *PPF* level, plant growth response to fertilizer EC depended on the presence or absence of starter fertilizer. When the growing medium contained starter fertilizer, shoot dry mass and number of flowers did not respond to increasing fertilizer EC, while leaf area and plant height increased slightly with an increase in fertilizer EC from 0.15 to 0.33 dS·m^{-1} and decreased with a further increase in fertilizer EC. There was a strong increase in shoot dry mass, leaf area, and plant height in response to increasing fertilizer EC in the absence of a starter fertilizer. Starter fertilizer in the growing medium greatly increased shoot dry mass (360%), leaf area (425%), plant height (480%), and flower number (280%) when the irrigation solution did not contain fertilizer (EC = 0.15 dS·m^{-1}), but had little effect on plant growth if the irrigation solution did contain fertilizer (Fig. 2). Since even the highest fertilizer EC did not result in a clear reduction in plant growth, optimal fertilizer concentrations cannot reliably be estimated from these data. Nemali and van Iersel (2004) found that a fertilizer EC of 1.3 dS·m^{-1} resulted in maximum growth of wax begonias in a growing medium without any starter fertilizer, irrespective of *PPF*.

Light intensity – WUE and [N$_{fert}$] relationships. The fitted polynomial equation (Eq. 6) indicated that there was an interactive effect of fertilizer EC (or [N]) and light intensity on WUE and [N$_{fert}$] of plants. These models indicate that both WUE and [N$_{fert}$] increased with increasing *PPF*, especially at higher fertilizer concentrations (Fig. 3, Table 1). Earlier studies also reported an increase in WUE of various species with increasing *PPF* (Alexander et al., 1995; Caviglia and Sadras, 2001; Israeli et al., 1996; Le Roux et al., 2001; Ponton et al., 2002; Vandana, 1999). Increasing fertilizer EC from 0.15 to 0.86 dS·m^{-1} also increased WUE and thus [N$_{fert}$], while a further increase in fertilizer EC resulted in a small decrease (Fig. 3).

There generally was a difference between [N]$_a$ and [N$_{fert}$] (Fig. 4), indicating that N supply and demand were not balanced in such a way to maintain N in the plants. When [N]$_a$ – [N$_{fert}$] < 0, not enough N is applied to maintain tissue [N] at 45 mg·g^{-1} unless the [N] in the growing medium decreases, and when [N]$_a$ – [N$_{fert}$] > 0, excess N will accumulate either in the plant or the growing medium. Supply and demand for N are balanced when [N]$_a$ – [N$_{fert}$] = 0. Photosynthetic photon flux affected at which [N]$_a$ this occurred. At *PPF* levels of 4.4, 6.2, and 9.9 mol·m^{-2}·d^{-1}, supply and demand were equal at [N]$_a$ of 157, 172, and 203 mg·L^{-1} N, respectively.

This suggests that fertilizer concentrations should be increased with increasing *PPF*. However, this conclusion was not confirmed by the dry mass data, since even the highest fertilizer EC did not result in a decrease in dry mass. This made it impossible to estimate the optimal fertilizer EC from the dry mass data (Fig. 1). There was no interactive effect of fertilizer EC and *PPF* on leaf area, indicating that fertilizer EC effects on leaf area were similar at different *PPF* levels. In a subsequent, similar experiment with higher fertilizer concentrations, including superoptimal ones, we did not find an effect of *PPF* on the [N] of the fertilizer solution resulting in maximal growth (Nemali and van Iersel, 2004). Apparently, the effect of *PPF* on the optimal [N] of the fertilizer is too small to have a practical impact. One possible reason for the lack of a practical effect of *PPF* on the optimal [N] is that plants can perform well over a wide range of tissue [N]. Increased leaf [N] does not always contribute to photosynthetic N, but may contribute to stored N, which can be used at times of a N deficiency (Thornley, 1995). It is possible that tissue [N] < 45 mg·g^{-1} would have been sufficient as well, since the optimal range for begonia reportedly is 20 to 60 mg·g^{-1} (Mills and Jones, 1996). In addition, the growing medium can act as a buffer for nutrients,

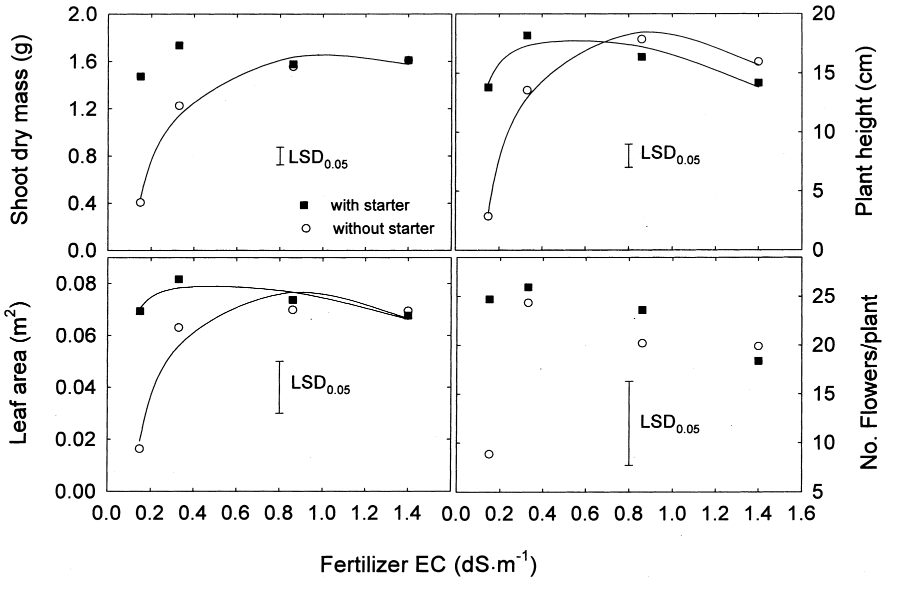

Fig. 2. Effect of fertilizer electrical conductivity (EC) and starter fertilizer level on shoot dry mass, leaf area (LA), plant height (PlHt), and flower number of subirrigated wax begonias at 6 weeks after transplanting. Error bars indicate the interactive least significance difference (LSD$_{0.05}$) between fertilizer ECs within one starter fertilizer level and between starter fertilizer levels within one fertilizer EC. The lines indicate significant effects ($P < 0.05$). Without a starter fertilizer, DW$_{shoot}$ = 2.802 + 1.153 × ln(EC) – 1.153 × EC, ($R^2 = 0.88$), LA= 0.15 + 0.064 × ln(EC) – 0.076 × EC, ($R^2 = 0.83$), Pl Ht = 38.69 + 17.12 × ln(EC) – 20.55 × EC, ($R^2 = 0.97$) and with a starter fertilizer, LA = 0.11 + 0.018 × ln(EC) – 0.036 × EC, ($R^2 = 0.58$) and PlHt = 28.93 + 6.75 × ln(EC) – 12.44 × EC, ($R^2 = 0.52$).

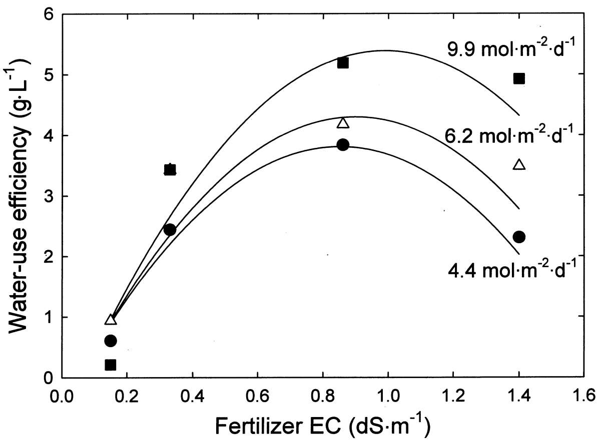

Fig. 3. Effect of photosynthetic photon flux and fertilizer concentration (EC) on water-use efficiency (WUE) of subirrigated wax begonia at 6 weeks after transplanting. WUE = 0.62 + 9.33 × EC – 6.11 × EC^2 + 0.32 × EC × *PPF*, R^2 = 0.78.

and changes in the nutrient concentrations in the growing medium do not necessarily affect tissue nutrient concentrations. For example, if N supply is less than demand, it is possible that tissue [N] is relatively stable while [N] in the growing medium decreases.

Gas exchange parameters. There was an interactive effect of *PPF* and fertilizer EC on P_n and R_d of the plants (Table 1). There was little or no effect of *PPF* on P_n and R_d in unfertilized treatments (EC = 0.15 dS·m^{-1}), but both P_n and R_d increased linearly with *PPF* in fertilized treatments, and this increase was greater at higher fertilizer EC (*i.e.* a positive fertilizer EC × *PPF* interaction term). Both P_n and R_d increased as fertilizer EC increased from 0.15 to 0.86 dS·m^{-1}, with little or no further increase as fertilizer EC increased from 0.86 to 1.40 dS·m^{-1}. Similarly, van Iersel and Kang (2002) reported a quadratic relationship between P_n and R_d and increasing fertilizer EC in pansy (*Viola ×wittrockiana* Gams.). There was no interactive effect of *PPF* and fertilizer EC on ET of plants in different treatments and the relationship among ET, *PPF*, and fertilizer EC was poor (R^2 = 0.37). In general, ET increased with increasing *PPF* and also with increasing fertilizer EC.

EC and pH of the growing medium. There was an interactive effect of fertilizer EC and starter fertilizer on growing medium EC at 4 and 6 weeks after transplanting, but not at 2 weeks after transplanting (Fig. 5). Electrical conductivity of the growing medium increased with increasing fertilizer EC, and was always higher with than without a starter fertilizer. At 4 and 6 weeks after transplanting, the increase in growing medium EC with increasing fertilizer EC was higher for growing medium with than without a starter fertilizer. Electrical conductivity of the growing medium was not affected by *PPF*. This supports our finding that the fertilizer concentration for subirrigated wax begonia need not be changed with changing light intensities. It is important to realize that the lack of *PPF* effects on growing medium EC does not imply that *PPF* did not affect nutrient uptake. Plants grown at higher *PPF* had more evapotranspiration (Table 1), and the growing medium of these plants thus absorbed more water and fertilizer during each subirrigation event.

The EC of growing medium at the end of the experiment (week 6, Fig. 5) ranged from 0.64 to 3.65 dS·m^{-1} with starter fertilizer and 0.32 to 2.4 dS·m^{-1} without a starter fertilizer. James and van Iersel (2001) found that growth of wax begonias was acceptable when the EC of the growing medium remained within a range of 2.1 to 5.4 dS·m^{-1}. Thus, wax begonias can tolerate higher growing medium ECs than occurred in this experiment, which explains the lack of a decrease in growth at the highest fertilizer EC (Figs. 1 and 2). Since we did not see large effects of fertilizer EC on growth when the growing medium contained a starter fertilizer, this suggests that even a growing medium EC of 0.64 dS·m^{-1} may be sufficient for begonia. However, when the growing medium contained a starter fertilizer and the fertilizer EC was 0.15 dS·m^{-1} (i.e., no fertilizer in the solution, Fig. 5), the EC of the growing medium decreased during the experiment. Since the pour-through method measures the EC in the bottom part of the growing medium, this decrease in EC indicates that either the plants removed nutrients from the growing medium during the experiment or that nutrients moved to top layer of the growing medium, as can happen with subirrigation (Nemali and van Iersel, 2004).

In the presence of a starter fertilizer in the growing medium, plants grew best with a fertilizer EC of 0.33 dS·m^{-1}, while the optimal fertilizer EC was 0.86 to 1.40 dS·m^{-1} in the absence of starter fertilizer. This corresponds to a final growing medium EC of 1 to 2.5 dS·m^{-1}. However, since there was no clear reduction in growth at the highest EC, a reliable upper EC limit for adequate growth could not be established. However, in subsequent research we found that a growing medium EC of 1.4 to 2.8 dS·m^{-1} results in optimal growth (Nemali and van Iersel, 2004). In contrast, James and van Iersel (2001), reported that plant growth of wax begonias was not reduced by more than 10 percent when the growing medium EC was increased from 2.1 to 6.3 dS·m^{-1}.

Growing medium pH was not affected by light intensity, but decreased with increasing fertilizer EC due to the acid-forming nature of the fertilizer. When the growing medium contained a starter fertilizer, the pH values ranged from 5.2 to 6.2 and without a starter fertilizer from 5.3 to 6.8 (data not shown). These values are in or near the recommended range (5.5 to 6.5) for most greenhouse crops (Lang, 1996). When irrigated with tap water (0.15 dS·m^{-1}), pH of the growing medium did not differ significantly among plants grown with and without a starter fertilizer. This suggests that lime was not completely lost in leaching the starter fertilizer from the growing medium.

Table 1. Effect of fertilizer electrical conductivity (EC) and photosynthetic photon flux (*PPF*) on dark respiration (R_d), net photosynthesis (P_n), evapotranspiration (ET), and growth rate (GR) of subirrigated wax begonia. Data were collected at 6 weeks after transplanting. Regression coefficients are based on $Y = Y_0 + Y_1 \times EC + Y_2 \times PPF + Y_3 \times EC^2 + Y_4 \times PPF^2 + Y_5 \times EC \times PPF$.

Fertilizer EC (dS·m^{-1})	*PPF* (mol·m^{-2}·d^{-1})	R_d (µmol·s^{-1})	P_n (µmol·s^{-1})	ET (mL·d^{-1})	GR (g·d^{-1})
0.15	4.4	0.03	0.05	63	0.04
	6.2	0.04	0.08	71	0.07
	9.9	0.05	0.06	123	0.04
0.33	4.4	0.09	0.31	146	0.35
	6.2	0.09	0.44	162	0.55
	9.9	0.13	0.52	190	0.62
0.86	4.4	0.09	0.41	139	0.53
	6.2	0.12	0.54	168	0.71
	9.9	0.21	0.76	179	0.92
1.40	4.4	0.10	0.30	162	0.34
	6.2	0.16	0.55	193	0.66
	9.9	0.21	0.77	200	0.94
Regression coefficients					
R^2		0.67	0.81	0.37	0.81
Intercept		0.05***	–0.07^{NS}	54.7	–0.13
EC		^{NS}	0.98***	58.16*	1.37***
EC^2		–0.032*	–0.707***	---	–0.97***
PPF		---	---	8.01*	---
EC × *PPF*		0.018***	0.063***	---	0.08***

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

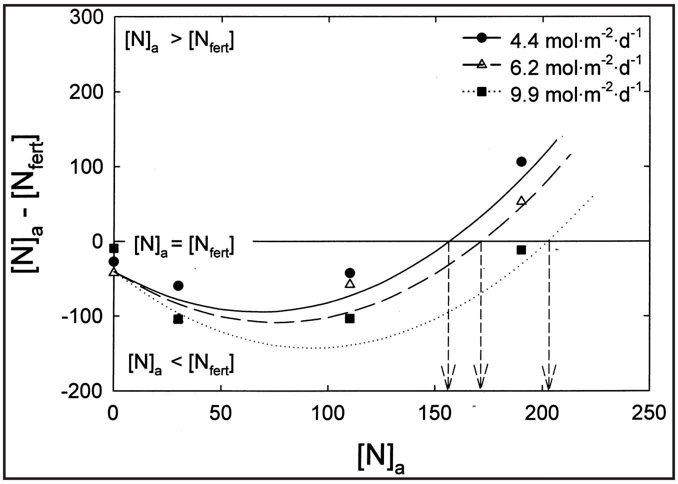

Fig. 4. The effect of photosynthetic photon flux (*PPF*) and fertilizer concentration of the fertilizer ($[N]_a$) on the difference between $[N]_a$ and the fertilizer concentration needed to maintain tissue [N] at 45 $mg·g^{-1}$ ($[N_{fert}]$). When $[N]_a - [N_{fert}] < 0$, N supply is less than demand, when $[N]_a - [N_{fert}] > 0$, supply exceeds demand, and when $[N]_a - [N_{fert}] = 0$ supply equals demand. Arrows indicate the $[N]_a$ at which N supply and demand are balanced at different *PPF* levels. Curves were calculated from the regression of $[N_{fert}]$ versus $[N]_a$: $[N_{fert}] = -40.65 - 1.12 \times [N]_a + 0.0119 \times [N]_a^2 + 0.1096 \times [N]_a \times PPF$, $R^2 = 0.75$. Data points are the mean of three replications.

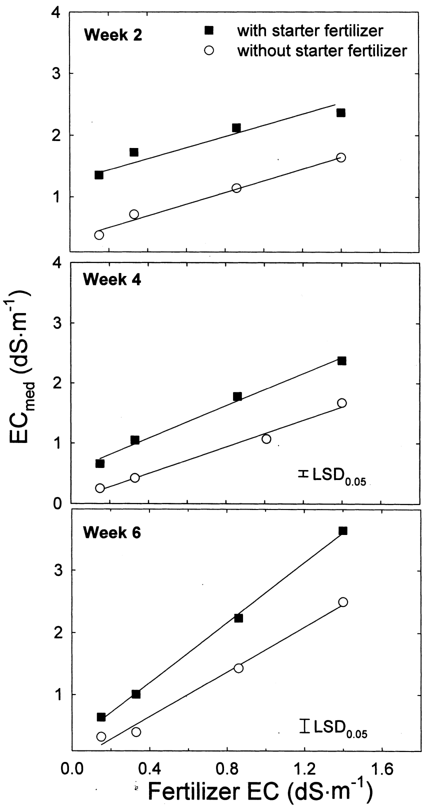

Fig. 5. Effect of fertilizer electrical conductivity (EC_{fert}) and starter fertilizer on the EC of the growing medium (EC_{med}) at 2, 4, and 6 weeks after transplanting. Error bars represent the interactive least significant difference ($LSD_{0.05}$) between fertilizer concentrations within one starter fertilizer level, and between starter fertilizer levels within one fertilizer concentration. The lines indicate significant correlations ($P < 0.05$). Week 2: $EC_{med} = 1.29 + 0.86 \times EC_{fert}$, $r^2 = 0.89$ (with starter) and $EC_{med} = 0.38 + 0.86 \times EC_{fert}$, $r^2 = 0.89$ (without starter). Week 4: $EC_{med} = 0.54 + 1.35 \times EC_{fert}$, $r^2 = 0.90$, (with starter fertilizer) and $0.07 + 1.15 \times EC_{fert,}$ $r^2 = 0.98$, (without starter fertilizer). Week 6: $EC_{med} = 0.23 + 2.42 \times EC_{fert}$, $r^2 = 0.89$, (with starter fertilizer) and $-0.01 + 1.62 \times EC_{fert}$, $r^2 = 0.79$ (without starter fertilizer).

Tissue nutrient composition. Tissue N, Fe, and Zn concentrations responded quadratically to increasing fertilizer EC, both in the presence and absence of a starter fertilizer. However, tissue K concentration responded quadratically with increasing fertilizer EC only in the absence of a starter fertilizer, while there was no effect of fertilizer EC on K in the presence of starter fertilizer (Table 2). There was no response of tissue P, Ca, Mg, S, Cu, Mo, and Al concentrations to increasing fertilizer EC, either in the presence and absence of a starter fertilizer. Overall, *PPF* had no effect on tissue nutrient composition, except for tissue Na, B, and Mn concentrations, which responded quadratically to increasing *PPF* in the presence of a starter fertilizer.

Conclusions

The effect of increasing *PPF* and fertilizer EC on WUE and $[N_{fert}]$ suggest that plants at high light intensity should be grown with higher fertilizer concentrations. However this effect may be too small to be of practical significance, because this finding could not be confirmed based on dry mass or leaf area data. Based on our findings, wax begonias grown without a starter fertilizer should be fertilized with a fertilizer solution with an EC of 0.86 to 1.4 $dS·m^{-1}$, while lower concentrations ($EC < 0.86\ dS·m^{-1}$) would be sufficient for growing media with a starter fertilizer.

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Table 2. Regression analysis of effect of starter fertilizer, fertilizer electrical conductivity (EC), and photosynthetic photon flux (*PPF*) on tissue nutrient concentration of subirrigated wax begonia at the end of the experiment. Regression coefficients are based on $Y = Y_0 + Y_1 \times EC + Y_2 \times PPF + Y_3 \times EC^2 + Y_4 \times PPF^2$. There were no significant interactive effects between EC and *PPF* on any of the nutrients. In the absence of EC or *PPF* effects, the intercept represents the average concentration from all treatments combined.

	N	P	K	Mg	S	Ca	Na	Cu	Mo	Al	B	Fe	Mn	Zn
Parameter				($mg·g^{-1}$)							($µg·g^{-1}$)			
With starter														
R^2	0.91	---	---	---	---	---	0.92	---	---	---	0.91	0.83	0.68	0.69
Intercept	50^{NS}	5.4	44.8	7.7	3.0	8.8	5.1^{***}	8.3	4.4	108	64^{**}	168^{*}	598^{**}	23^{NS}
EC	59^{*}	---	---	---	---	---	---	---	---	---	---	90^{*}	---	64^{*}
PPF	NS	---	---	---	---	---	-0.7^{*}	---	---	---	11^{*}	---	112^{*}	---
EC^2	-32^{*}	---	---	---	---	---	---	---	---	---	---	-62^{*}	---	-39^{*}
PPF^2	---	---	---	---	---	---	0.05^{*}	---	---	---	0.69^{*}	---	7.2^{*}	---
Without starter														
R^2	0.89	---	0.94	---	---	---	---	---	---	---	---	0.65	---	0.89
Intercept	36^{NS}	5.0	17^{NS}	8.6	2.9	10.0	2.2	8.5	7.4	116	31	80^{NS}	244	46^{*}
EC	87^{*}	---	58^{**}	---	---	---	---	---	---	---	---	---	---	---
PPF	NS	---	---	---	---	---	---	---	---	---	---	---	---	---
EC^2	-43^{*}	---	-33^{*}	---	---	---	---	---	---	---	---	-74.1^{*}	---	-18^{*}
PPF^2	---	---	---	---	---	---	---	---	---	---	---	---	---	---

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

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