OPTIMAL FERTILIZER CONCENTRATION, WATER-USE EFFICIENCY, AND WHOLE-PLANT GAS EXCHANGE OF SUBIRRIGATED PLANTS UNDER VARYING LIGHT INTENSITY

by

MURTHY NEMALI SAINATH KRISHNA

(Under the guidance of Marc van Iersel)

ABSTRACT

We evaluated the effects of photosynthetic photon flux (*PPF*) on optimal fertilizer concentration, water-use efficiency (WUE), and whole-plant gas exchange of subirrigated plants. Our results indicate that although WUE increased, optimal fertilizer solution concentration [expressed as electrical conductivity (EC)] of subirrigated plants did not vary with increasing *PPF.* The EC of the fertilizer solution in the optimal range was 0.65 to 1.71 $dS \cdot m^{-1}$ in wax begonia (*Begonia semperflorens*-cultorum Hort.) and 1.18 to >2.77 $dS \cdot m^{-1}$ for petunia (*Petunia* x*hybrida* Hort. Vilm-Andr.). When the growing medium contained a starter fertilizer, a low fertilizer EC (0.5 to 0.9 $dS \cdot m^{-1}$) was sufficient for growing wax begonias. Whole-plant gas exchange measurements indicated that growth rate (measured as the amount of carbon accumulated in plants per day) increased linearly with *PPF*, and at lower *PPF* treatments, growth rate of plants decreased due to a smaller fraction of carbohydrates available for growth and growth respiration after meeting the maintenance needs.

INDEX WORDS: *Begonia semperflorens,* Bottom layer, Carbon use efficiency, Dark respiration, Electrical conductivity, Net-photosynthesis, Nutrient uptake, *Petunia* x*hybrida*, Photosynthesis-light response curves, Photosynthetic photon flux density, Quantum yield, Starter fertilizer, Tissue nitrogen concentration, Top layer

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CHAPTER 1

INTRODUCTION

The saying '*a little (saved) each day is much in a year'* appears apt and timely in the context of the present drought situation and increased regulations concerning water ! use in the western and southern United States. There is an urgent need to develop strategies for conserving water ! use in the greenhouse industry. One possible solution is a switch ! over to an irrigation system which allows for recycling water. Although recirculating subirrigation systems, like ebb ! and ! flow and flooded floor, have been popular in Europe since the seventies (Elliot, 1990), it was not until the eighties that these systems started to appear in the United States. In spite of an increase in their use, subirrigation systems are not as popular in the United States as they are in Europe. Subirrigation has many advantages over top ! irrigation. Zero runoff, reduced labor, and nutrient recycling are the most important advantages, which increase the efficiency of fertilizer and water ! use and decrease costs (Elliot, 1990; Yelanich and Biernbaum, 1990; van Iersel, 1996; Morvant et al., 1997; Uva et al., 1998). The other advantages include uniform plant growth [van Iersel (1996), due to uniform uptake of water] and low incidence of foliar diseases [Elliot (1990), because the leaves are not wetted during irrigation].

Compared to overhead or top irrigation, subirrigation involves wetting the growing medium through the holes in the bottom of the container. As water is absorbed against gravity, a force is required to push water up through the growing medium. This force is called 'capillarity or capillary action' which raises water into the tiny pore spaces of the growing medium. Because water is absorbed from the bottom, there is practically no leaching in subirrigation. The advantage is that the fertilizer salts will remain in the growing medium for a longer period and reduce the required fertilizer concentration for plants. On the other hand, when a higher fertilizer concentration, than that required for normal growth, is supplied, excess fertilizer salts will accumulate in the growing medium and can become toxic to plants. However, research has shown that plants thrive within a range of fertilizer concentrations (optimal range) in the growing medium, although very high concentrations can reduce growth (James and van Iersel, 2001; Kang and van Iersel, 2001). To prevent accumulation of excess fertilizer salts in the growing medium, growers should synchronize the demand and supply of nutrients, and maintain the concentration of fertilizer salts in the growing medium within the recommended range.

The concentration of fertilizer salts in the growing medium can be estimated by measuring the electrical conductivity (EC) of the growing medium. Electrical conductivity of the growing medium is proportional to the amount of dissolved fertilizer salts (if the irrigation water does not add a considerable amount of salts). Therefore, the EC of the growing medium indicates the amount of fertilizer available in the root zone of plants, and for this reason

recommendations based on the EC of the growing medium would be better than those based on the actual fertilizer concentration supplied to plants (Kang and van Iersel, 2001). In subirrigation, root growth is more pronounced in the bottom than the top layer of the growing medium due to moisture availability (Morvant et al., 1997; Todd and Reed, 1998), which causes the EC of the bottom layer to be lower (as more fertilizer salts are absorbed in this zone) than that of the top layer (Todd and Reed, 1998; Cox, 2001). Moreover, evaporation from the surface of the growing medium can also increase the nutrient concentration in the top layer (Todd and Reed, 1998), because salts are left behind as the water evaporates. Unless the growing medium is top-watered, accumulated nutrients in the top layer cannot migrate down and thus are unavailable to the plants. Therefore, the EC of the bottom layer is more directly related to crop growth rate than that of the top or both layers put together.

The gradient in the growing medium EC between the top and bottom layers was reported earlier in many scientific papers. Cox (2001) reported that the EC of the sample from the top layer was higher than that of a composite sample (top, medium and bottom layers) and the sample from the overhead irrigated plants. However, in his study, the EC of the bottom layer of subirrigated plants was comparable to that of the overhead irrigated plants. Kent and Reed (1996) indicated that the EC of the top layer remained higher than the recommended range, yet the growth of New Guinea impatiens (*Impatiens* x*hawkeri* Hook. f.) and spathiphyllum (*Spathiphyllum* Schott) was not affected. These results indicate that the EC of the top layer does not greatly affect crop

growth. Kent and Reed (1996) reported that nitrate was undetected in the top layer until the nitrogen concentration in the fertilizer was higher than 8 mM (112 mg $N \cdot L^{-1}$). It requires water of a volume greater than that of the container to push down the accumulated salts from the top to the bottom layer and out of the container (van Iersel, 2000).

Fertilizer requirements of subirrigated plants are well documented in the literature (Kent and Reed, 1996; van Iersel, 1999; Cox, 2001; James and van Iersel, 2001). However, not much work has been done on the effect of greenhouse environment on the optimal fertilizer concentration of subirrigated plants. Kang and van Iersel (2001) concluded that the optimal fertilizer concentration for petunia decreased with increasing temperature. At high relative humidity, dry weight of begonia (*Begonia x hiemalis* Fotsch) was found to be higher at higher fertilizer concentration (Gislerød and Mortensen, 1990). By modifying the shoot environment, the water!use!efficiency (WUE, defined as the ratio of growth to transpiration in plants) of plants is affected (Bugbee, 1995). Plants with a high growth to transpiration ratio or high WUE, absorb a relatively small amount of water while producing a gram of dry matter. A high fertilizer concentration should be supplied to these plants to maintain the desired tissue nutrient levels.

Computer models may be used to determine the required fertilizer concentration by predicting photosynthesis and transpiration rates from environmental data (Kläring and Cierpinski, 1998). The so-called 'quantity concept' (adding the amounts of water and nutrients expected to be taken up by

plants; Kläring, 2001) can be narrowed down to a simple mathematical equation for determining the optimal fertilizer concentration. As crop growth rate determines the nutrient requirement and transpiration rate provides an estimate of the amount of water to be supplied, the optimal nitrogen concentration of the fertilizer ($mg \cdot L^{-1}$) can be calculated as the product of desired tissue nitrogen concentration ($mg \cdot g^{-1}$) and the ratio of growth to transpiration in plants ($g \cdot L^{-1}$; Bugbee, 1995). To illustrate, a crop transpiring 200 mL of water in producing one gram of dry matter (WUE of 5 gAL^{-1}) would require a N-concentration of 45 x 5 = 225 $mgAL^{-1}$ in the fertilizer (assuming a desired N level of 45 $mg \cdot g^{-1}$ in the plant tissue). Since evaporation from the growing medium may be an important factor in subirrigation, the combined value of evaporation from the growing medium and transpiration from the plant [evapotranspiration (ET)] should be used to calculate optimal fertilizer concentrations. In subirrigation, the quantity of fertilizer solution absorbed by the growing medium is related to the amount of moisture lost in ET during the preceding day.

The concept of plant water!use efficiency (WUE) has been used extensively to model crop yields, plan strategies in dry land cropping systems and also, in breeding programs for identification of traits associated with drought tolerance in plants (Caviglia and Sadras, 2001). However, its physiological role in modeling fertilizer requirements of subirrigated plants has not been studied extensively. The information available in the scientific literature points to stomatal conductance as the primary mechanism for controlling or adjusting water!use efficiency in plants. This is perhaps not true in the case of studies

dealing with the effect of photosynthetic photon flux (*PPF*) on WUE. This is because stomatal conductance is only a part of the total CO_2 conductance, others being mesophyll and biochemical (carboxylation) conductance (Farquhar and Sharkey, 1982; Woodrow et al., 1990).

It is known that stomatal aperture increases in response to a decrease in CO_2 concentration in the stomatal cavity, thereby increasing its conductance (Wong et al., 1978; Salisbury, 1985). An increase in *PPF* would increase stomatal conductance by increasing photosynthesis and decreasing the CO_2 concentration in the stomatal cavity. However, the biochemical reactions of photosynthesis are less responsive to changes in stomatal conductance than transpiration rate (Woodrow et al., 1990). Thus, an increase in stomatal conductance with increasing *PPF* could be expected to decrease WUE.

The effect is not same with the internal conductance, which consists of both mesophyll and carboxylation conductance. To the best of our knowledge, effect of increasing *PPF* on mesophyll conductance has not been studied and the potential effects on mesophyll conductance are unknown. The carboxylation efficiency or biochemical conductance would increase with increasing *PPF* due to increased availability of ATP and NADPH. Since an increase in carboxylation conductance increases photosynthesis (and thus growth), but has no effect on transpiration, it would result in an increase in WUE.

Finally, CO_2 diffusion from the air to the carboxylation site is not only affected by the conductance for CO_2, but also by the gradient in CO_2 concentration between air and the carboxylation sites. The CO_2 concentration at

the carboxylation site decreases with increasing *PPF*, because of the increase in CO_2 fixation. This would increase the rate of CO_2 diffusion from the stomatal cavity to the carboxylation site. Since WUE is directly related to the ratio between CO_2 and water vapor diffusion, the increase in the CO_2 gradient from the air to the carboxylation site would be expected to increase WUE.

Overall *PPF* effects on WUE are complicated, because of its effects on stomatal and carboxylation conductance, as well as the CO_2 gradient. An increase in stomatal conductance may decrease WUE, while increases in carboxylation conductance or the CO_2 gradient from the air to the carboxylation sites may increase WUE, by increasing CO_2 diffusion (or photosynthesis). Then the overall effect of *PPF* on WUE depends on whether changes in the stomatal conductance, the carboxylation conductance, or the CO_2 gradient from the air to the carboxylation site are most important. There is compelling evidence in the scientific literature that the rate of carboxylation largely determines WUE with increasing *PPF*. For instance, Israeli et al. (1996) have shown that stomatal conductance in banana (*Musa* sp. L.) grown under different light regimes did not change, but the carbon isotope discrimination ($*^{13}C$) or WUE was positively correlated with *PPF,* implying a role of increased photosynthetic rate in WUE of plants. Caviglia and Sadras (2001) also reported that WUE increased with irradiance. They indicated that 83% of the variation in WUE was accounted for by radiation ! use efficiency (shoot dry weight per unit intercepted light) and evaporation from the soil, whereas WUE and crop conductance (evapotranspiration per unit intercepted light, a measure of conductance in crops

where evaporation from soil is a minor fraction) were unrelated. This is consistent with the idea that the gradient in CO_2 concentration from the air to the carboxylation site is most important in changing the WUE in response to changes in *PPF*. Increasing WUE with increasing *PPF* was also observed in combination with increasing leaf nitrogen concentration (Ponton et al., 2002), implying increased photosynthetic capacity at higher *PPF*. In their study, Ponton et al. (2002) noted that WUE increased with increasing irradiance only due to an increase in photosynthesis as other factors like ambient CO_2 concentration, air temperature, vapor pressure deficit were constant among the different light treatments. They argue that maximizing carbon gain is more important than maximizing WUE under low light conditions, which is consistent with a decrease in WUE at low irradiance. Le Roux et al. (2001) indicated that leaf WUE was lower in the lower, shaded part than in the sun-exposed part of the canopy, but was similar between sun and shade leaves of a walnut (*Juglans regia* L.) tree canopy when they were subjected to same light regime. This would suggest that there was no acclimation or changes in leaf structure (and perhaps in mesophyll conductance) in response to shade in the lower canopy.

Photosynthetic photon flux varies across the country and throughout the year. For this reason, specific fertilizer recommendations may have to be developed, based on the prevailing *PPF* level. When *PPF* is altered, there is an immediate effect on the ratio of growth to transpiration in plants. To accurately determine the optimal fertilizer concentration, measurements of whole plant or crop growth rate and transpiration are needed. Most of the commercially

available equipment for measuring photosynthesis in plants is designed for leaf measurements. Traditional techniques of measuring leaf photosynthesis do not accurately estimate the growth rate of plants (van Iersel and Bugbee, 2000). Continuous measurements of carbon dioxide exchange rates of whole plants can depict the growth rate of plants more accurately than individual leaf measurements, as they directly measure carbon accumulated (a measure of growth rate) in plants (Leonardos et al, 1994; van Iersel and Bugbee, 2000; van Iersel and Kang, 2002). Evapotranspiration in plants can be accurately determined by simple gravimetric measurements.

To understand plant growth thoroughly, it is important to understand its components. Plant growth is the result of excess carbon synthesized in photosynthesis over that lost in respiration. Scientific literature on plant respiration indicates that 30 - 50% of carbon synthesized by plants in photosynthesis is respired during crop growth (Amthor, 1984; Lawlor, 1995; van Iersel and Seymour, 2000). Therefore, the significance of respiration in plant growth should not be underestimated. McCree (1974) related dark ! respiration in plants to gross photosynthesis (P_g) and dry weight and separated it into maintenance and growth components. Maintenance respiration involves release of energy (ATP) only for sub ! cellular maintenance processes, whereas growth respiration involves release of energy for all processes which result in a net increase in biomass (Penning de Vries, 1975). The maintenance component often is considered to have priority over the growth component. Therefore, lower photosynthetic rates could potentially decrease the amount of carbohydrates

available for growth and growth respiration after meeting the maintenance requirements.

High growth rates are a result of increased photosynthetic rate which is strongly correlated to the amount of intercepted *PPF*, which in turn depends on the leaf area of plants (Lawlor, 1995). A decrease in leaf number and increase in specific leaf area [leaf area per unit leaf weight] with decreasing *PPF* have been reported in species with contrasting light requirements like tall fescue [*Festuca arundinacea* Schreb., (Allard et al., 1991)] and dracaena [*Dracaena sanderana* hort. Sander ex Mast, (Vladimirova et al., 1997)]. Other studies have reported modifications in leaf physiology to varying levels of *PPF* (Norcini et al., 1991; Noguchi et al., 2001).

Light requirements are not similar for sun and shade plants. Research has shown that obligate shade plants cannot increase their photosynthesis and growth rate when grown under high *PPF*, because of the absence of high levels of enzymes for carboxylation and electron transport (Björkman, 1981). Indeed, research has indicated a decrease in the quantum yield (moles of carbon fixed per mole of incident *PPF*) of shade plants grown under high *PPF* (Funnell et al., 2002). In contrast, sun-loving species have higher photosynthetic rates and perform better under high than low *PPF* (Björkman, 1981). A large amount of literature is available on the effects of *PPF* on photosynthesis in shade plants (Callan and Kennedy, 1995; Funnell et al., 2002; Greenway and Lieffers, 1997; Norcini et al., 1991). Because of a lower *PPF* requirement, a shade species would grow normally and conversely, a sun species would grow slowly, at low

incident *PPF*. Transpiration rate would be lowered in shade due to decreased stomatal conductance and leaf temperature. It appears that the interactions among *PPF*, optimal fertilizer EC, and water!use efficiency may be complex. The objectives of this research project were to determine:

1. The effects of starter fertilizer and *PPF* on plant water!use!efficiency and optimal fertilizer concentration of subirrigated wax begonia (*Begonia semperflorens!*cultorum Hort.).
2. The effect of *PPF* on the optimal fertilizer concentration and EC of the growing medium in a fast growing, sun!loving species (petunia, *Petunia* x*hybrida* Hort. Vilm!Andr) and slow growing, shade species (wax begonia).
3. The effect of *PPF* on whole!plant photosynthesis, respiration, water!use!efficiency and photosynthetic light response of wax begonia.

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CHAPTER 2

STARTER FERTILIZER AND PLANT WATER ! USE EFFICIENCY CAN AFFECT FERTILIZER REQUIREMENTS OF SUBIRRIGATED WAX BEGONIA [1]

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[1] Sainath Krishna, M.N and M.W. van Iersel. To be submitted to HortScience

Crop Production

Starter Fertilizer and Plant Water-Use Efficiency can Affect Fertilizer Requirements of Subirrigated Wax begonia

Additional index words. *Begonia semperflorens*, electrical conductivity, nutrient uptake, photosynthetic photon flux density, tissue nutrient analysis, water-use efficiency

Abstract. To evaluate the effects of photosynthetic photon flux (*PPF*) and starter fertilizer on the optimum fertilizer concentration 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 growing medium with or without starter fertilizer. Except for shoot dry weight, no significant interactions between *PPF* and fertilizer concentration on any of the growth parameters, including leaf area, plant height, or number of flowers per plant were found. Regardless of *PPF*, there was an interactive effect of fertilizer concentration and starter fertilizer on growth. When the growing medium contained a starter fertilizer, these parameters, except for plant height, did not respond to increasing fertilizer concentration and without a starter fertilizer, all the parameters responded quadratically to increasing fertilizer concentration. Estimated water-use efficiency (WUE) and optimum N concentration (N_{FERT}) at

the end of the experiment were higher for plants grown at 9.9 mol$\cdot m^{-2} \cdot d^{-1}$ than for those grown at 4.4 or 6.2 mol$\cdot m^{-2} \cdot d^{-1}$. However, *PPF* had little or no effect on tissue nutrient composition. These results indicate that fertilizer concentration need not be adjusted based on *PPF* and that without a starter fertilizer, a fertilizer EC of 0.8 to 1.4 dS$\cdot m^{-1}$ is optimal for growing wax begonias. When the growing medium contains a starter fertilizer, a low fertilizer EC (0.5 to 0.9 dS$\cdot m^{-1}$) would be sufficient for growing wax begonias.

Subirrigation systems have become more popular in recent years due to zero runoff and increased efficiency in fertilizer and water&use (Elliiot, 1990; Yelanich and Biernbaum,1990; van Iersel, 1996; Morvant et al., 1997; Uva et al., 1998). Because of the absence of leaching in subirrigation, starter fertilizer can remain in the growing medium for a longer period, especially for slow growing plants with low nutrient removal rates. This could affect the fertilizer requirements as a starter fertilizer would supply a substantial amount of nutrients to plants. Water!use efficiency (defined as the ratio of growth to transpiration in plants) can also affect the fertilizer requirements of plants (Bugbee, 1995). A plant with high growth to transpiration ratio would absorb a relatively small amount of water while producing a gram of dry matter. A dilution of nutrients can occur in a plant with high growth rate unless additional amount of nutrients are supplied to sustain the increased growth (Mills and Jones, 1996). Therefore, a high fertilizer concentration should be supplied to these plants to maintain the desired tissue nutrient level.

Nutrients like N, P, K, and Mn can be removed quickly by plants, whereas most of the other essential nutrients except Ca and B are removed slightly faster than water is removed (Bugbee, 1995). Maintaining a high concentration of the rapidly removed nutrients (N, P, K, and Mn) in the growing medium at all times to make them available to plants might result in excessive uptake and nutrient imbalances. As most of the rapidly removed nutrients are mobile inside plants, they can be stored in roots, stems, or leaves and remobilized as and when needed. Therefore, nutrients can be supplied once a day in the amounts proportional to their optimum growth. By feeding the growing medium daily with the amount of nutrients removed by plants in the preceding day, optimal plant growth can be maintained. However, it is important to remember that the amount of nutrient solution absorbed by the growing medium depends on the dryness of the growing medium or the evapo!transpiration rate (ET) since the last irrigation. In hydroponic studies involving nutrient requirements of plants, photosynthesis and transpiration models are used to predict the optimal EC of the supplied nutrient solution (Kläring and Cierpinski, 1998).

Optimum N concentration of the fertilizer solution ($mg \cdot L^{-1}$) can be obtained as the product of desired tissue N concentration ($mg \cdot g^{-1}$) and WUE ($g \cdot L^{-1}$, Bugbee, 1995). For example, let us assume that 1000 mL of water is lost in ET from a plant in producing 5 g of dry matter during a 24 h period, making its WUE 5 $g \cdot L^{-1}$. To maintain a tissue N concentration of 45 $mg \cdot g^{-1}$ (recommended range for begonia is 20!60 $mg \cdot g^{-1}$; Mills and Jones, 1996), 45 x 5 = 225 mg of N should

be supplied in 1000 mL of water. Therefore, the N concentration to be 'fed' to the growing medium in next cycle would be 225 mgÅL^{-1}.

Photosynthetic photon flux is an important environmental variable affecting WUE and, therefore, possibly optimal fertilizer concentration of subirrigated plants. It is known that stomatal movements caused by changes in *PPF* (Wong et al., 1978; Salisbury, 1985) can alter both the rates of photosynthesis and transpiration. However, biochemical reactions of photosynthesis do not respond in a linear fashion, as does the transpiration rate, to changes in stomatal conductance (Woodrow et al., 1990). This is because, unlike its effect on diffusion rate of H_2O, stomata offer only a part of the total conductance to CO_2 diffusion, others being mesophyll, and carboxylation conductance (Farquhar and Sharky, 1982; Woodrow et al., 1990). Therefore, changes in stomatal conductance can alter the ratio of growth to transpiration in plants.

Photosynthetic photon flux varies considerably across the country and during the year. For this reason, separate fertilizer recommendations may have to be developed, based on the prevailing *PPF* level. Research on optimum fertilizer concentration of plants under different *PPF* levels is limited. Kang and van Iersel (2001) concluded that greenhouse temperature affects the optimal fertilizer concentration of subirrigated petunias (*Petunia* x *hybrida* Hort. Vilm - Andr.), whereas Gislerød and Mortensen (1990) found that tissue nutrient concentration of *Begonia xheimalis* was lower at high (90%) than a low (60%) RH, but increased when the concentration of nutrient solution was increased. The objective of this experiment was to determine the effect of starter fertilizer

and varying *PPF* on optimal N concentration of subirrigated wax begonia. Among the bedding plants, wax begonias are some of the most popular facultative shade plants. We hypothesized that the optimal N concentration would increase with increasing *PPF* and decrease with a starter fertilizer in the growing medium.

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 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 was leached out of half of the pots 3 to 4 times a day and for 3 days using tap water. The EC of the growing medium with and without a starter fertilizer was 2.1 and 0.9 $dS \cdot m^{-1}$, respectively. After transplantation, the seedlings were placed on ebb&and&flow benches (1.2 x 2.4 m^2, Midwest GroMaster, St. Charles, Ill.) and subirrigated with 20N&4.4P&16.6K fertilizer solutions (Peter's 20&10&20 peat&lite special, The Scotts Co. Marysille, Ohio).

Fertilizer solutions were stored in plastic barrels (210 L) and pumped onto watertight trays of the ebb&and&flow system daily, using submersible pumps (NoKorode&2; Little Giant, Oklahoma City, Okla.). The bottom of the pots was immersed in the fertilizer solution for about 13 min (5 min for pumping and 8 min for draining) during which the growing medium absorbed it by capillary action.

The evaporation of water from the plastic barrels and during irrigation increases the concentration of the salts in the fertilizer solution. Therefore, EC of the fertilizer solution was measured using an EC meter (model M90, Corning, Corning, N.Y.) and adjusted when the barrels were refilled weekly. Plants were grown in a greenhouse covered with double&layered polythene. A shade cloth was spread on the roof which transmitted about 63 percent of the incident light. The temperature settings inside the greenhouse were 21/18 °C for day/night, respectively. Photosynthetic photon flux was measured continuously during crop growth using six quantum sensors (QSO!SUN, Apogee Instruments, Logan, Utah) arranged at the plant height in the center of each treatment.

Treatments. Plants were subirrigated with one of the four fertilizer concentrations (0, 50, 130, or 210 mg@L^{-1} N, corresponding to an EC of 0.15, 0.33, 0.86, and 1.4 dS@m^{-1}, respectively). Two groups of 30 plants each (with or without starter fertilizer), were grown under three *PPF* levels (high, medium, and low shade, equivalent to an average daily *PPF* of 4.4, 6.2, and 9.9 mol@m^{-2}@d^{-1}, respectively), provided by shade clothes of different densities. The shade cloth was hung over a partitioned PVC structure positioned on the ebb!and!flow bench.

Measurements. Data on plant height, leaf area, and shoot dry weight were collected once and EC and pH of growing medium were collected twice during the growth period. At the end of the experiment [6 weeks after transplantation (WAT)], data on all parameters including number of flowers per plant were collected. Plant height was measured as the vertical length between

the top of the plant and the surface of the growing medium. 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 a week before measuring their dry weight. Electrical conductivity and pH of the growing medium were estimated by the pour&thru technique (Wright, 1986). Approximately 25 mL of tap water (EC of 0.1-0.2 $dS \cdot m^{-1}$) 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 using EC and pH sensors (model M90, Corning, Corning, N.Y.). Flowers were harvested from six plants in each experimental unit.

Only plants grown without a starter fertilizer in the growing medium were used in the WUE study. A total of 144 plants from different experimental units [4 plants x 3 replications x 12 treatments (4 EC x 3 *PPF* levels)] were shifted to a whole&plant gas exchange system during a period of 5 days (van Iersel and Bugbee, 2000) at the end of the experiment to measure the CO_2 exchange rates. Plants were kept in the gas exchange chamber for a period of 24 h (14 h of light, 10 h of dark period), during which net photosynthesis and dark respiration (P_n and R_d respectively, expressed in $\mu mol \cdot s^{-1}$) rates were measured once every ten minutes. Inside the growth chambers, plants were exposed to the same *PPF* (mix of incandescent and fluorescent bulbs) as in the greenhouse. To determine the amount of water lost in 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:

$GR = [(P_{n,avg} \cdot t_{light} - R_{d,avg} \cdot t_{dark}) \times 0.0036 \times 12 / f_C]$

where $P_{n,avg}$ and $R_{d,avg}$ are the average net photosynthesis and dark respiration rates (: mol s^{-1}), t_{ight} and t_{dark} are the durations of light and dark periods in hours, factors 0.0036 and 12 convert : mol s^{-1} to mol h^{-1}, and moles of carbon to grams of carbon, respectively, and f_C is the carbon content in the plants (converts grams of carbon to grams of dry matter). Water&use&efficiency (g L^{-1}) was calculated as follows:

$WUE = GR / ET.$

Optimal nitrogen concentration of the fertilizer solution (N_{FERT}) was calculated as

N_{FERT} = *WUE x desired tissue nutrient concentration*

Desired nitrogen concentration in the tissue was assumed to be 45 mg·g $^{-1}$ or 4.5%. Entire shoot samples were analyzed to determine the tissue nutrient concentration. Tissue C!, N!, and S! concentrations were measured using a Leco CNS 2000 analyzer (Leco corporation, St. Joseph, Mich.) and the other nutrients were measured using a Jarrel&Ash ICAP 9000 analyzer (Thermo Jarrell Ash corporation, Franklin, Mass.).

Experimental design and data analysis. The treatments were organized in a randomized complete block with a split-split plot design and three replications. Fertilizer concentration 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 sub&split (experimental unit). Data were subjected to ANOVA and regression analysis using statistical analysis software (SAS institute, Cary, N.C.).

To describe the effect of *PPF* and fertilizer EC on the WUE, we fitted the following polynomial regression with an interaction term:

$WUE = \beta_0 + \beta_1 x\ EC + \beta_2 x\ PPF + \beta_3 x\ EC^2 + \beta_4 x\ PPF^2 + \beta_5 x\ EC x\ PPF,$

where β_0.....β_5 are regression coefficients. The fitted polynomial equation was further reduced by backward selection ($P < 0.05$).

Results and Discussion

Plant growth ! light intensity relationship. The three-way interaction among *PPF*, fertilizer concentration, and starter fertilizer on shoot dry weight was non ! significant ($P = 0.07$). However, there was an interactive effect of *PPF* and fertilizer concentration on shoot dry weight. Regardless of the presence of starter fertilizer, shoot dry weight did not respond to increased fertilizer concentration at low *PPF* (4.4 mol m^{-2} d^{-1}) and increased linearly with fertilizer concentration at medium or high *PPF* (6.2 or 9.9 mol m^{-2} d^{-1}, Fig. 2.1). This indicates that *PPF*, and not nutrients, was limiting growth at the lowest *PPF* level in the fertilized treatments. Larouche et al. (1989) also concluded that vegetative growth of greenhouse tomatoes (*Lycopersicon esculentum* Mill. cv. Vedettos) was limited at low *PPF* and there was no response to N increments in the nutrient solution. However, we did not find any significant interaction between *PPF* and fertilizer concentration on leaf area, plant height, or number of flowers per plant. Irrespective of fertilizer concentration and starter fertilizer, these parameters increased linearly with increasing *PPF* (data not shown). An earlier

study on *Begonia xheimalis* (Gislerød and Mortensen, 1990) indicated no interaction between relative humidity and fertilizer EC on number of flowers per plant, whereas Kang and van Iersel (2001) reported an interaction between fertilizer EC and temperature on diameter of flowers in petunia.

Plant growth ! starter fertilizer relationship. There was an interactive effect of fertilizer concentration and starter fertilizer on shoot dry weight, leaf area, plant height, and number of flowers per plant. When the growing medium contained a starter fertilizer, dry weight, leaf area, and number of flowers did not respond to increasing fertilizer concentration, whereas in the absence of a starter fertilizer, they responded quadratically to increasing fertilizer concentration (Fig. 2.2 A, B, D). However, plant height responded quadratically with increasing fertilizer concentration both in the presence and absence of a starter fertilizer, but the response was stronger in the absence of starter fertilizer (Fig. 2.2 C).

When the growing medium did not contain a starter fertilizer, maximum shoot dry weight, leaf area, plant height and number of flowers per plant were obtained when fertilized with an EC of 0.8 to 1.4 dS$\cdot$m^{-1}. Maximum plant height in the presence of a starter fertilizer was obtained when fertilized with an EC of 0.6 to 0.8 dS$\cdot$m^{-1}. These results are similar to those of James and van Iersel (2001), who concluded that a fertilizer EC of 1.7 dS$\cdot$m^{-1} resulted in maximum dry weight of subirrigated wax begonias, and agree with their finding that the flower number of *Begonia semperflorens* did not increase when EC of growing medium increased from 0.85 to 2.3 dS$\cdot$m^{-1}. These results indicate that when the growing medium does not contain a starter fertilizer, a fertilizer EC of 0.8 to 1.4 dS$\cdot$m^{-1} is

optimal and with a starter fertilizer, a low fertilizer EC (0.3 to 0.5 $dS \cdot m^{-1}$) would be sufficient for growing wax begonias.

Light intensity - WUE and N_{FERT} relationship. There was an interactive effect of fertilizer concentration and light intensity on WUE (therefore, on N_{FERT}) of plants. Both WUE and N_{FERT} were higher at 9.9 $mol \cdot m^{-2} \cdot d^{-1}$ than at 6.2 or 4.4 $mol \cdot m^{-2} \cdot d^{-1}$, especially at higher fertilizer concentration (Fig. 2.3). Earlier studies also reported an increase in WUE with increasing *PPF* (Alexander et al., 1995; Vandana, 1999). The optimal nitrogen concentration of the fertilizer was higher or lower than the supplied fertilizer concentration (Table 2.1). Fertilizer concentrations that are higher than the calculated optimal concentration would subsequently result in a higher growing medium EC or higher tissue nitrogen concentration (> 45 $mg \cdot g^{-1}$). The opposite (lower growing medium EC or lower tissue nitrogen concentration than 45 $mg \cdot g^{-1}$) would result in the case where the supplied fertilizer concentration was lower than the optimal concentration. In table 2.1, N_{FERT} increased with increasing *PPF* (i.e., a significant, positive regression coefficient for the EC x *PPF* interaction). However, these results are not supported by the analyses of dry weight and leaf area data. Those analyses indicate that optimal fertilizer concentration did not vary with *PPF* level. One likely reason for this inconsistency is that plants can perform well with a wide range of tissue nitrogen concentrations. Increased leaf nitrogen concentration does not always contribute to photosynthetic nitrogen, but may contribute to substrate nitrogen which can be used at times of nitrogen deficiency (Thornley, 1995). The values of N_{FERT} in our experiment were estimated at a target tissue

nitrogen concentration of 45 mg⇳g^{-1}. However, lower tissue nitrogen concentrations might have been sufficient as well, since the optimal range for begonia is 20 - 60 mg⇳g^{-1} (Mills and Jones, 1996).

The effects of *PPF* and fertilizer concentration on P_n and R_d were similar to those on WUE (Table 2.1). There was an interaction between *PPF* and fertilizer EC on P_n and R_d of the plants. 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 parameters increased linearly with *PPF* in fertilized treatments, and this increase was greater at higher fertilizer EC. 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}. van Iersel and Kang (2002) also reported a quadratic relationship between P_n and R_d and increasing fertilizer EC in pansy (*Viola xwittrockiana* Gams.). There was no interactive effect of *PPF* and fertilizer EC on ET of plants in different treatments. The correlation 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 growing medium. There was an interactive effect of fertilizer EC and starter fertilizer on EC (week 4 and 6, Fig.2.4) and pH (results not shown) of the growing medium. However, on week 2, while there was no interactive effect of fertilizer EC and starter fertilizer on growing medium EC, there was a linear effect of fertilizer EC on growing medium EC, and growing medium EC was higher with than without a starter fertilizer. Electrical conductivity and pH of the growing medium were not affected by *PPF*. Electrical

conductivity of the growing medium increased with increasing fertilizer EC, was always higher with a starter fertilizer than without a starter fertilizer and increased over time (Fig. 2.4).

The EC of growing medium at the end of the experiment (week 6, Fig. 2.4) ranged from 0.64 to 3.65 $dS \cdot m^{-1}$ with a starter fertilizer and 0.32 to 2.4 $dS \cdot m^{-1}$ without a starter fertilizer. The values of EC of the growing medium observed in our experiment were close to those reported by James and van Iersel (2001). When growing medium did not contain a starter fertilizer, optimal fertilizer EC was in the range of 0.86 to 1.4 $dS \cdot m^{-1}$. The EC of the growing medium in this optimal fertilizer range was 1.26 to 2.14 $dS \cdot m^{-1}$. James and van Iersel (2001) found that dry weight of wax begonias was acceptable when the EC of the growing medium remained within a range of 2.1 to 5.4 $dS \cdot m^{-1}$. Pansies were grown successfully with subirrigation when the EC of the growing medium was in the range of 1.5 to 2.4 $dS \cdot m^{-1}$ (van Iersel, 1999). A slow growing species such as wax begonia can perform well with a lower EC in the growing medium as evident from our research. Kang and van Iersel (2001) reported that, for petunias, optimal EC in the growing medium remained similar with increasing temperature, while optimal fertilizer EC varied. Although optimal fertilizer EC could not be estimated from dry weight of plants grown with a starter fertilizer, it can be estimated from the growing medium EC resulting in maximum dry weight of plants. From the equation describing the relation between fertilizer EC and growing medium EC, and the optimal growing medium EC without a starter fertilizer, the optimal fertilizer EC in the presence of a starter fertilizer was

estimated to be in the range of 0.51 to 0.92 $dS \cdot m^{-1}$. As plant growth was not diminished even at the highest growing medium EC observed in our experiment, an upper EC limit for adequate growth could not be established. However, 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 $dS \cdot m^{-1}$.

pH of the growing medium decreased with increasing fertilizer concentration due to the acid!forming nature of the fertilizer. When the growing medium contained a starter fertilizer, the 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). pH of the growing medium did not differ significantly among plants grown with or without a starter fertilizer, when irrigated with tap water (0.15 $dS \cdot m^{-1}$). This suggests that liming effect was not completely lost from the growing medium without a starter fertilizer.

Tissue nutrient composition. Tissue N, Fe, and Zn concentrations responded quadratically to increasing fertilizer concentration, both in the presence and absence of a starter fertilizer. However, tissue!K concentration responded quadratically with increasing fertilizer concentration only in the absence of a starter fertilizer while there was no effect of fertilizer concentration in the presence of starter fertilizer (Table 2.2). There was no response of tissue P, Ca, Mg, S, Cu, Mo, and Al concentrations to increasing fertilizer concentration, 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 in the absence of a starter fertilizer. When the growing medium contained a starter fertilizer, tissue Na, B, and Mn concentrations responded quadratically to increasing *PPF*.

Conclusions

Effect of increasing *PPF* and fertilizer concentration on WUE and N_{fert} suggest that higher fertilizer concentrations should be used for plants grown at high light intensity (9.9 mol·m^{-2}·d^{-1}). However, this was not confirmed by the treatment effects on dry weight or leaf area of the plants. Those data indicated that the optimal fertilizer concentration was the same in all the *PPF* treatments. The absence of an interactive effect of fertilizer concentration and *PPF* on dry weight or leaf area indicates that fertilizer concentration for subirrigated wax begonia need not be adjusted based on *PPF* level. Based on our findings, wax begonias grown without a starter fertilizer should be fertilized with an EC of 0.86 to 1.4 dS·m^{-1}, while low concentrations (about 0.5 to 0.9 dS·m^{-1}) would be sufficient for growing media with a starter fertilizer.

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Table 2.1. Effect of increasing fertilizer electrical conductivity (EC) and photosynthetic photon flux (*PPF*) on dark respiration (R_d), net photosynthesis (P_n), evapotranspiration (ET), growth rate (GR), water!use!efficiency (WUE) and optimum N concentration (N_{FERT}, calculated based on a target tissue concentration of 45 $mg \cdot g^{-1}$ N) of subirrigated wax begonia grown without a starter fertilizer in the growing medium at the end of the experiment.

Fertilizer EC $dS \cdot m^{-1}$ ($mgN \cdot L^{-1}$)	*PPF* $mol \cdot m^{-2} \cdot d^{-1}$	R_d : $mol \cdot s^{-1}$	P_n : $mol \cdot s^{-1}$	ET $mL \cdot d^{-1}$	GR $g \cdot d^{-1}$	WUE $g \cdot L^{-1}$	N_{FERT} $mg \cdot L^{-1}$
0.15 (0)	4.4	0.03	0.05	63	0.04	0.61	27
0.15 (0)	6.2	0.04	0.08	71	0.07	0.94	42
0.15 (0)	9.9	0.05	0.06	123	0.04	0.21	10
0.33 (50)	4.4	0.09	0.31	146	0.35	2.44	110
0.33 (50)	6.2	0.09	0.44	162	0.55	3.43	154
0.33 (50)	9.9	0.13	0.52	190	0.62	3.43	154
0.86 (130)	4.4	0.09	0.41	139	0.53	3.84	173
0.86 (130)	6.2	0.12	0.54	168	0.71	4.18	188
0.86 (130)	9.9	0.21	0.76	179	0.92	5.19	234
1.40 (210)	4.4	0.10	0.30	162	0.34	2.31	104
1.40 (210)	6.2	0.16	0.55	193	0.66	3.48	157
1.40 (210)	9.9	0.21	0.77	200	0.94	4.92	222
Regression	R^2	0.67	0.81	0.37	0.81	0.78	0.78
results	intercept	0.05***	-0.07^{ns}	54.7	-0.13^{z}	0.62	-28.1*
	EC	$-^{ns}$	0.98***	58.16*	1.37***	9.33***	420.5***
	EC^2	-0.032*	-0.707***	-	-0.97***	-6.11***	-275.5***
	PPF	-	-	8.01*	-	-	-
	EC x *PPF*	0.018***	0.063***	-	0.08***	0.32***	14.2***

^{ns}, *, **, *** not significant and significant at $P < 0.05$, 0.005, and 0.005, respectively.

Table 2.2. Regression analysis of effect of fertilizer electrical conductivity (EC) and photosynthetic photon flux (*PPF*) on tissue nutrient concentration of subirrigated wax begonia at the end of the experiment.

	N	P	K	Mg	S	Ca	Na	Cu	Mo	Al	B	Fe	Mn	Zn
with starter	----------			mg·g^{-1}	----------			----------			: g·g^{-1}	----------		
R^2	0.91	0.85	0.91	0.92	0.43	0.61	0.92	0.21	0.38	0.39	0.91	0.83	0.68	0.69
Intercept	50.1^{ns}	7.2*	71.5*	7.3*	3.7^{ns}	11.0^{ns}	5.1***	15.1^{ns}	-0.2^{ns}	414.6^{ns}	63.68**	168.4*	598.2**	22.6^{ns}
EC	59.4*	-	-	-	-	-	-	-	-	-	-	90.2*	-	64.4*
PPF	-^{ns}	-	-	-	-	-	-0.7*	-	-	-	11.1*	-	111.9*	-
EC^2	-31.6*	-	-	-	-	-	-	-	-	-	-	-62*	-	-39*
PPF ^{2}	-	-	-	-	-	-	0.05*	-	-	-	0.69*	-	7.2*	-
EC x *PPF*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Without starter														
R^2	0.89	0.69	0.94	0.82	0.22	0.62	0.81	0.56	0.84	0.21	0.32	0.65	0.65	0.89
Intercept	35.5^{ns}	1.6^{ns}	16.7^{ns}	4.9^{ns}	3.7^{ns}	14.6*	1.9^{ns}	-1.3^{ns}	21.3*	-41.9^{ns}	33.4^{ns}	80.1^{ns}	388.9^{ns}	46.5*
EC	87*	-	58.4**	-	-	-	-	-	-	-	-	-	-	-
PPF	-^{ns}	-	-	-	-	-	-	-	-	-	-	-	-	-
EC^2	-42.7*	-	-33.3*	-	-	-	-	-	-	-	-	-74.1*	-	-18.1*
PPF ^{2}	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EC x *PPF*	-	-	-	-	-	-	-	-	-	-	-	-	-	-

^{ns}, *, **, *** not significant and significant at $P < 0.05$, 0.005, and 0.005, respectively.

Figure 2.1. Effect of fertilizer electrical conductivity (EC) and daily photosynthetic photon flux on shoot dry weight of subirrigated wax begonias at 6 weeks after transplantation. 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 linear effects ($P < 0.05$); *shoot dry weight = 1.05 + 0.45 x EC* ($r^2 = 0.73$) and *1.31 + 0.65 x EC* ($r^2 = 0.69$) for medium (6.2 $mol \cdot m^{-2} \cdot d^{-1}$) and high *PPF* (9.9 $mol \cdot m^{-2} \cdot d^{-1}$), respectively.

Figure 2.1.

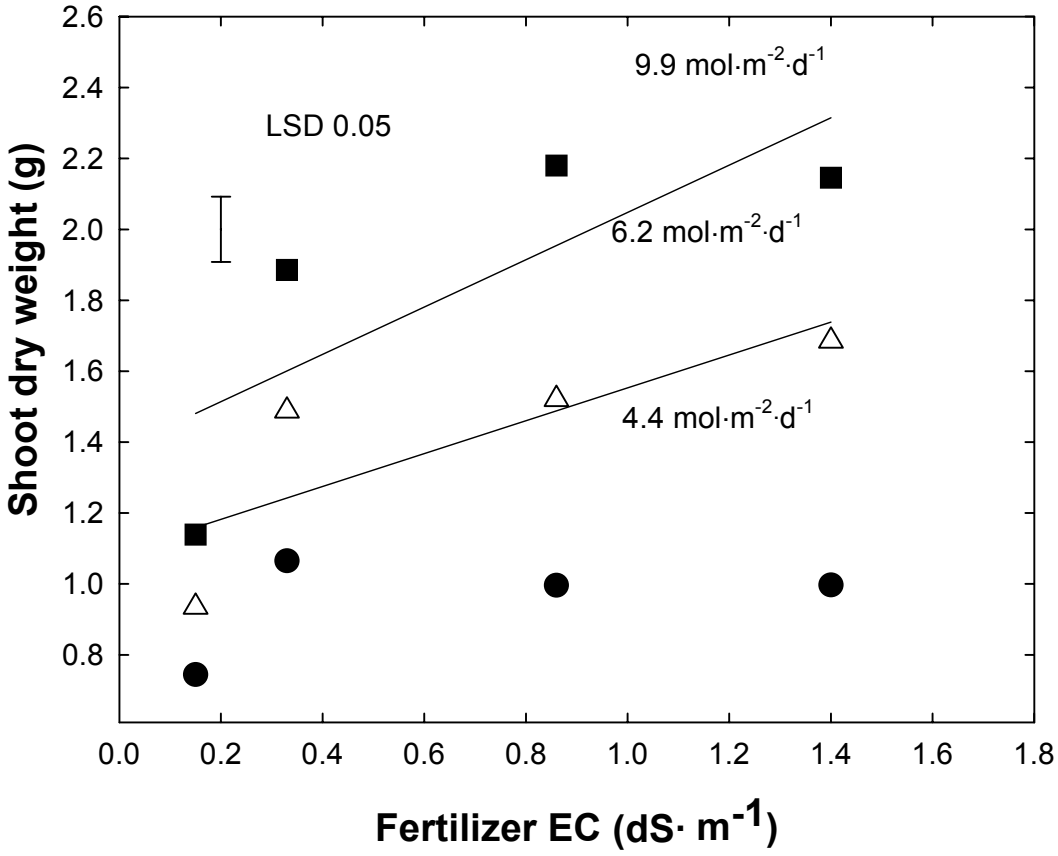

Shoot dry weight (g)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
LSD 0.05
9.9 mol·m-2·d-1
6.2 mol·m-2·d-1
4.4 mol·m-2·d-1
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
Fertilizer EC (dS· m-1)

Figure 2.2. Effect of fertilizer electrical conductivity (EC) and starter fertilizer level on A. shoot dry weight per plant, B. leaf area per plant, C. plant height, and D. flower number per plant in subirrigated wax begonias at 6 weeks after transplantation. The lines indicate significant quadratic effects ($P < 0.05$). The symbol '●' in the graph indicates growing medium without a starter fertilizer, and '□' indicates growing medium with a starter fertilizer. Error bars indicate the interactive least significance difference ($LSD_{0.05}$) between fertilizer ECs within one starter fertilizer level or between starter fertilizer levels within one fertilizer EC. The following equations were fitted to the data: without starter fertilizer: a. *shoot dry weight = 0.09 + 2.62 x EC - 1.07 x EC* ^{2} ($r^2 = 0.97$), b. *leaf area = 0.002 + 0.135 x EC - 0.06 x EC* ^{2} ($r^2 = 0.91$), c. *plant height = -1.9 + 37.96 x EC - 17.34 x EC* ^{2} ($r^2 = 0.98$), d. *flower number = 18.5 + 107 x EC - 53.6 x EC* ^{2} ($r^2 = 0.63$), and with starter fertilizer *plant height = 12.8 + 11.71 x EC - 7.13 x EC* ^{2} ($r^2 = 0.73$).

Figure 2.2.

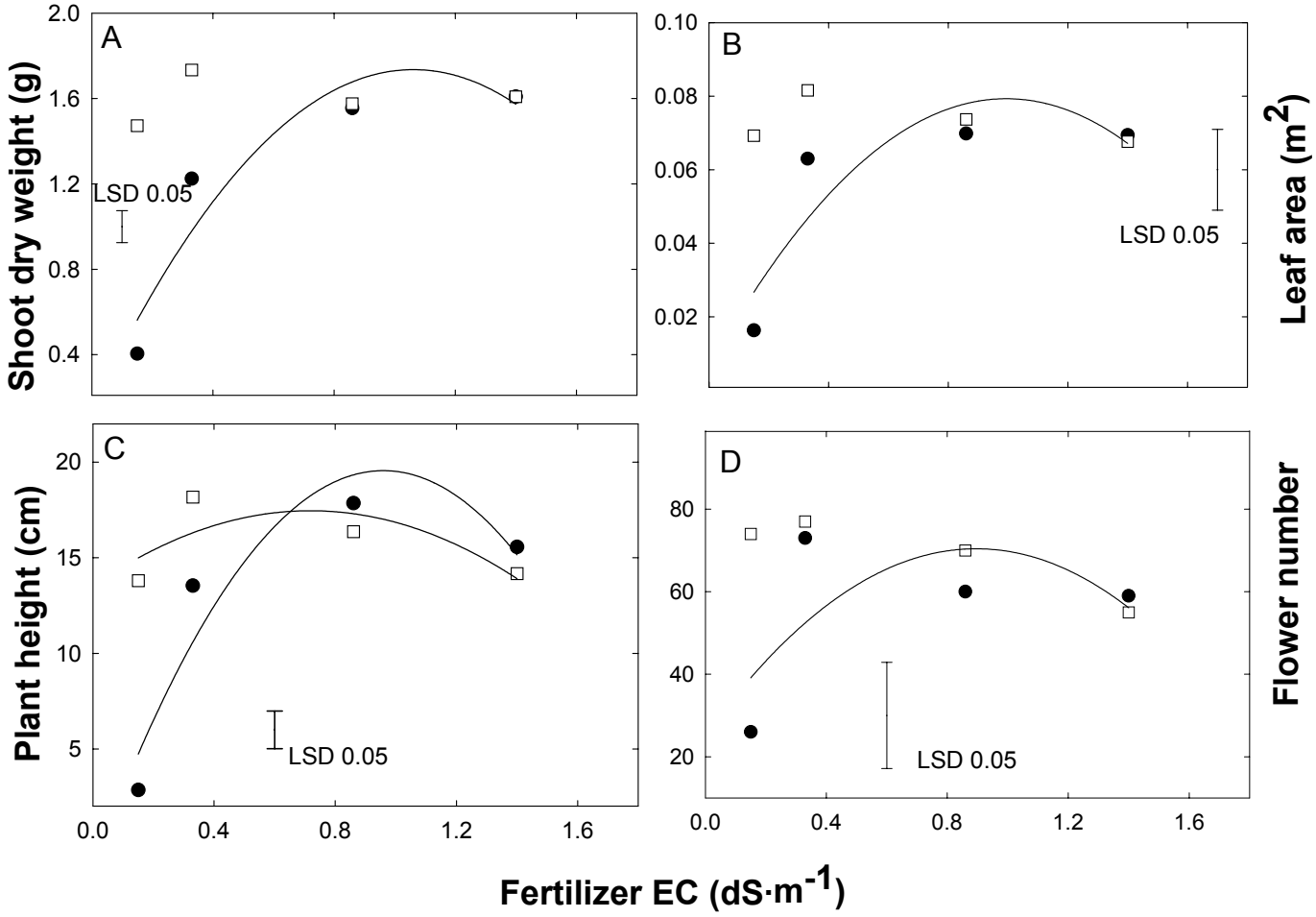

A
B
C
D
Shoot dry weight (g)
Leaf area (m2)
Plant height (cm)
Flower number
LSD 0.05
LSD 0.05
LSD 0.05
LSD 0.05
2.0
1.6
1.2
0.8
0.4
0.10
0.08
0.06
0.04
0.02
20
15
10
5
80
60
40
20
0.0
0.4
0.8
1.2
1.6
Fertilizer EC (dS·m-1)

Figure 2.3. Effect of photosynthetic photon flux and fertilizer concentration (EC) on water ! use efficiency of subirrigated wax begonia at the end of experiment. The lines indicate significant quadratic effects ($P < 0.05$). For regression results, see Table 2.1.

Figure 2.3.

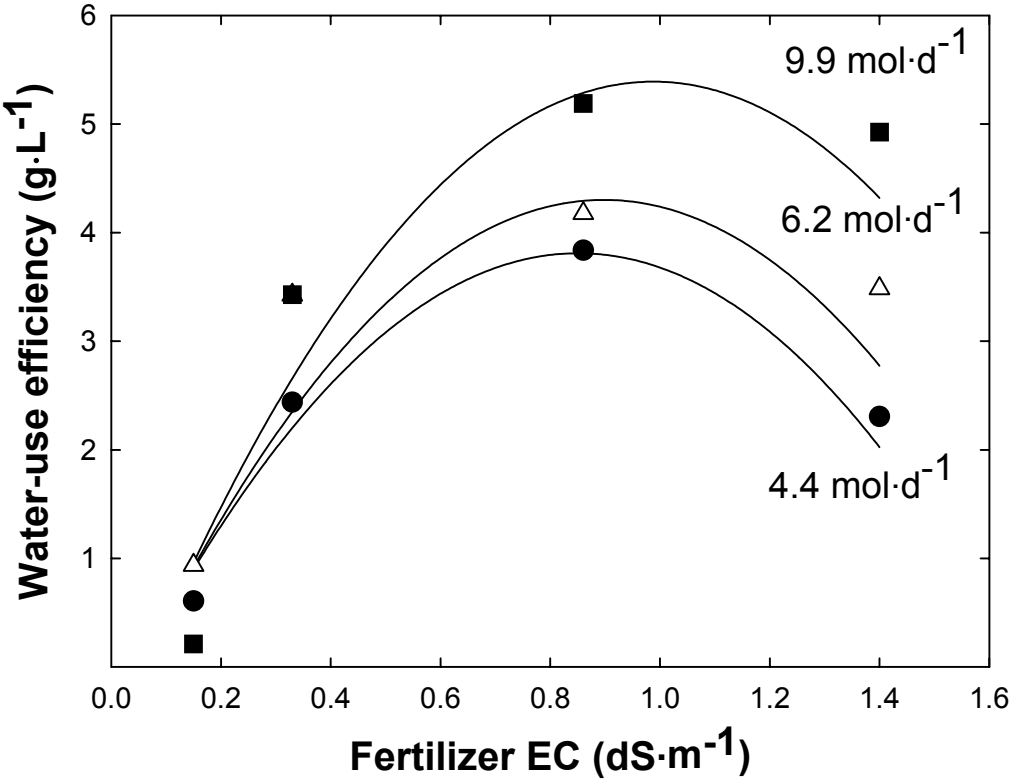
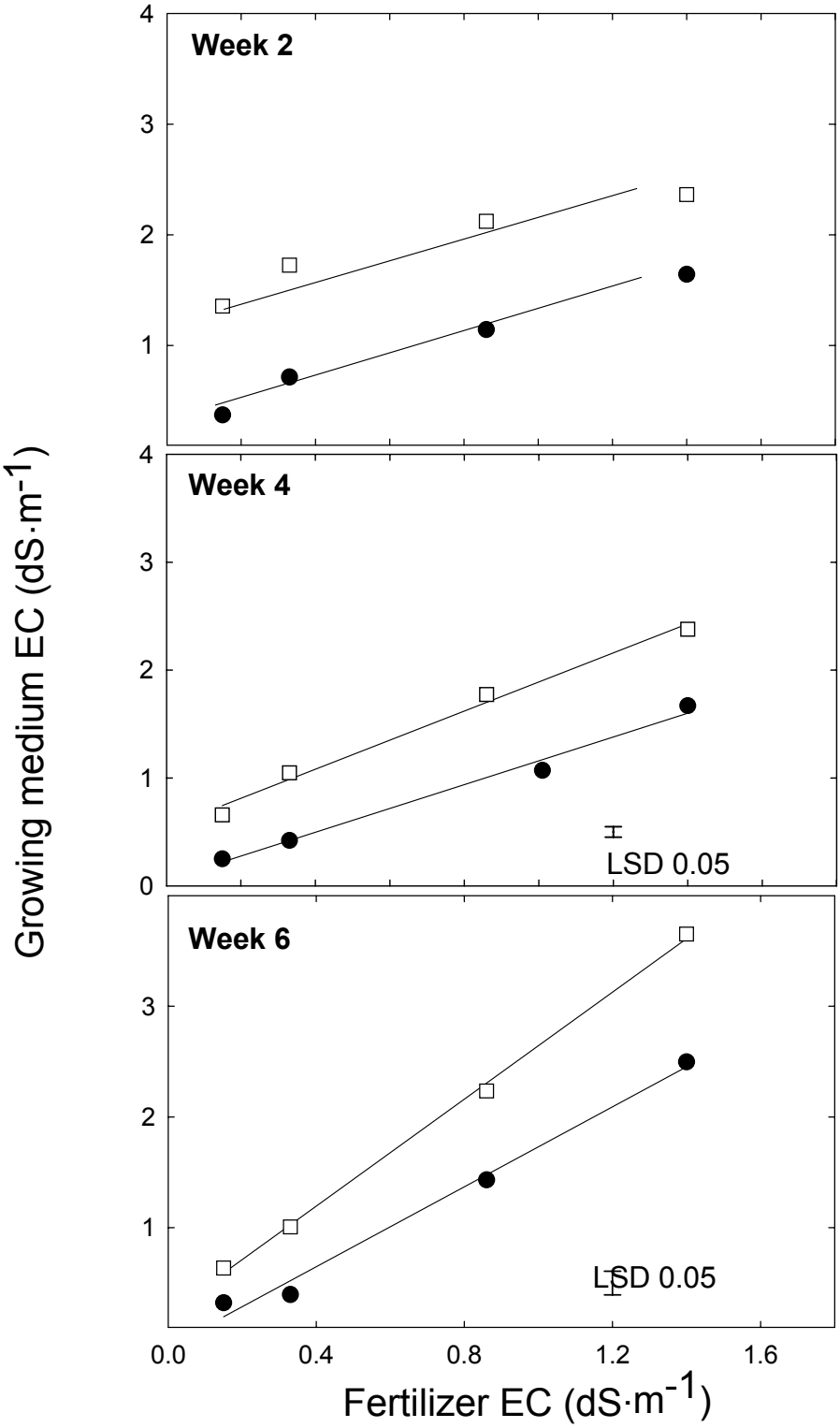

Water-use efficiency (g·L-1)
Fertilizer EC (dS·m-1)
9.9 mol·d-1
6.2 mol·d-1
4.4 mol·d-1
0
1
2
3
4
5
6
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6

Figure 2.4. Effect of fertilizer electrical conductivity (EC) and starter fertilizer on EC of the growing medium at 2, 4, and 6 weeks after transplantation. On week 2, fertilizer EC x Starter fertilizer interaction was not seen, however EC of the growing medium was correlated both with fertilizer EC and starter fertilizer. Error bars represent the interactive least significant differences ($LSD_{0.05}$) between fertilizer concentrations within one starter fertilizer level or between starter fertilizer levels within one fertilizer concentration. The lines indicate significant linear effects ($P < 0.05$). The symbol '●' in the graph indicates growing medium without a starter fertilizer, and '□' indicates growing medium with a starter fertilizer. At week 4, *growing medium EC = 0.47 + 1.24 x EC* ($r^2 = 0.99$, with starter fertilizer) and *0.02 + 1.05 x EC* ($r^2 = 0.99$, without starter fertilizer). At week 6, *growing medium EC = 0.12 + 2.2 x EC* ($r^2 = 0.98$, with starter fertilizer) and *-0.14 + 1.63 x EC* ($r^2 = 0.96$, without starter fertilizer).

Figure 2.4.


Week 2
Week 4
Week 6
LSD 0.05
LSD 0.05
Growing medium EC (dS·m-1)
Fertilizer EC (dS·m-1)
0
1
2
3
4
0.0
0.4
0.8
1.2
1.6

CHAPTER 3

FERTILIZER REQUIREMENTS OF SUBIRRIGATED WAX BEGONIA AND PETUNIA ARE NOT AFFECTED BY LIGHT INTENSITY [1]

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[1] Sainath Krishna, M.N. and M.W. van Iersel. To be submitted to HortScience

Crop Production

Fertilizer Requirements of Subirrigated Wax Begonia and Petunia Are Not Affected by Light Intensity

Additional index words. Bottom layer, electrical conductivity, nutrient uptake, tissue nitrogen concentration, top layer

Abstract. To evaluate the effects of increasing photosynthetic photon flux (*PPF*) on optimal fertilizer concentrations, we grew wax begonia (*Begonia semperflorens* -cultorum Hort.) and petunia (*Petunia* x*hybrida* Hort. Vilm-Andr.) seedlings under three *PPF* treatments (high, medium, and low corresponding to an average *PPF* of 23.2, 15.6, and 9.8 $mol \cdot m^{-2} \cdot d^{-1}$, respectively) and subirrigated with six fertilizer concentrations [electrical conductivity (EC) of 0.12, 0.65, 1.18, 1.71, 2.24, and 2.77 $dS \cdot m^{-1}$]. Compared to low *PPF*, shoot dry weight of wax begonia and petunia seedlings increased two and three ! fold, respectively, at high *PPF.* Fertilizer EC resulting in maximum shoot dry weight remained the same (1.28 and 1.87 $dS \cdot m^{-1}$ for wax begonia and petunia, respectively) in the three *PPF* treatments. Shoot dry weight and leaf area of petunias decreased little at higher than optimal fertilizer EC in the three *PPF* treatments, while growth of begonia was inhibited at high fertilizer EC. The 'optimal fertilizer range', calculated as the lower and upper limits of fertilizer EC within which plant growth did not change more than 10% of that at the optimum EC, remained the same in

the three *PPF* treatments in both the species. The optimal range of fertilizer EC was 0.65 to 1.71 $dS \cdot m^{-1}$ in wax begonia and 1.18 to >2.77 $dS \cdot m^{-1}$ for petunia. Compared to those grown at 1.18 $dS \cdot m^{-1}$, wax begonias grown at 1.71 $dS \cdot m^{-1}$ had similar dry weight, but were shorter in all three *PPF* treatments (average height reduction of 6.5 percent). In general, EC of the top layer was higher than that of the bottom layer of the growing medium in both species. The results of EC analysis of the bottom layer indicated either no effect of *PPF* (wax begonia) or a small increase with increasing *PPF* (petunia).

In recent years, there has been an increase in the use of recirculating subirrigation systems in greenhouse production (Elliiot, 1990; Yelanich and Biernbaum,1990; van Iersel, 1996; Morvant et al., 1997; Uva et al., 1998). Although fertilizer requirements of subirrigated plants are well documented in the literature (Kent and Reed, 1996; van Iersel, 1999; Cox, 2001; James and van Iersel, 2001), not much work has been done on the effect of greenhouse environment on optimal fertilizer concentrations for subirrigated plants. However, there is evidence that the environment affects nutrient uptake in plants. Kang and van Iersel (2001) concluded that the optimal fertilizer concentration for petunia decreased with increasing temperature. Li et al. (2001) reported the modulating effect of transpiration on salinity in tomato (*Lycopersicon esculentum* L.) plants. In their experiment, tomatoes grown at a root zone EC of 9.0 $dS \cdot m^{-1}$ had a higher marketable fresh yield in treatments with lower evapotranspiration (reduced to 65% of reference) than those with high evapotranspiration. At high

relative humidity (RH), dry weight of begonia (*Begonia x hiemalis* Fotsch) was found to be higher at higher fertilizer concentrations (Gislerød and Mortensen, 1990). These studies indicate that factors like temperature and humidity can modify the optimal fertilizer concentration.

In modern greenhouses, computer generated models may be used to determine the required fertilizer concentration by predicting photosynthesis and transpiration rates from environmental data (Kläring and Cierpinski, 1998). The so-called 'quantity concept' (adding the amounts of water and nutrients expected to be taken up by plants; Kläring, 2001) can be reduced to a simple mathematical equation for determining the optimal fertilizer concentration. As crop growth rate determines the nutrient requirement and transpiration rate provides an estimate of the volume of nutrient solution to be supplied, optimal fertilizer concentration ($mg \cdot L^{-1}$ N) can be calculated as the product of desired tissue nitrogen concentration ($mg \cdot g^{-1}$) and water ! use efficiency [WUE, the ratio of growth to transpiration in plants ($g \cdot L^{-1}$), Bugbee, 1995]. Plants with high growth to transpiration ratio or high WUE, would absorb a relatively small amount of water while producing a gram of dry matter. A high fertilizer concentration should be supplied to these plants to maintain the desired tissue nutrient level. Because *PPF* affects both growth and transpiration (Wong et al., 1978; Lawlor, 1995), its possible effect on optimal fertilizer concentration is worthy to investigate.

Electrical conductivity of the growing medium is a good indicator of the amount of fertilizer available to plants in the root zone. Kang and van Iersel (2001) indicated that the optimal growing medium EC remained constant, although optimal fertilizer solution EC decreased, with increasing temperature. In subirrigation, root growth is more pronounced in the bottom layer than the top layer of the growing medium due to higher moisture availability (Morvant et al. 1995; Todd and Reed, 1998). Therefore, the EC of the bottom layer is usually lower than that of the top layer (Todd and Reed, 1998; Cox, 2001). Moreover, evaporation from the surface of the growing medium can also increase the nutrient concentration in the top layer (Todd and Reed, 1998). Unless the growing medium is top-watered occasionally, the accumulated nutrients in the top layer cannot migrate down and are unavailable to the plants. Therefore, the EC of the bottom layer is more directly related to crop growth rate than that of the top or both layers put together.

In this experiment, we planned to quantify the effects of increasing *PPF* on the optimal fertilizer concentration and EC of the growing medium in a fast growing, obligate sun species (petunia) and slow growing, facultative shade species (wax begonia). We hypothesized that the optimal fertilizer concentration would be higher for plants grown at high *PPF* and the optimal EC of the growing medium would not be affected by *PPF* treatments.

Materials and methods

Plant material. Plug seedlings of wax begonia 'cocktail vodka' and petunia 'scarlet purple' were obtained from a commercial grower (Sunbelt greenhouses, Douglas, Ga.) and transplanted into 10 cm (510 mL) pots filled with soilless growing medium (Fafard 2P mix, Fafard, Anderson, S.C.) on 15 Feb. 2002. The growing medium did not contain any starter fertilizer. After transplantation, the pots were shifted to 1.2 x 2.4 m^2 ebb&and&flow benches (Midwest GroMaster, St. Charles, Ill.) and subirrigated 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 daily using submersible pumps (NoKorode&2; Little Giant, Oklahoma City, Okla.). The bottom of the pots were immersed in the fertilizer solution for about 13 min (5 min for pumping and 8 min for draining) every day, during which the growing medium absorbed it by capillary action. The fertilizer EC in the barrels was measured using an EC meter (model M90, Corning, Corning, N.Y.) and adjusted weekly when the barrels were refilled. Plants were grown in a greenhouse covered with double&layered polythene. The temperature control was set at 21/18 °C for day/night, respectively (Wadsworth systems, Arvada, Colo.). At the end of the experiment, quantum sensors (QSO ! SUN, Apogee Instruments Inc., Logan, Utah) connected to a datalogger (CR10X, Campbell Sci., Logan, Utah) were arranged in the center of each experimental unit to measure *PPF* as a percentage of incident *PPF* in each

treatment. Incident *PPF* above the experimental units was measured throughout the experiment with a quantum sensor (LI-190SA, Li-Cor, Lincoln, Nebr.).

Treatments. Plants were subirrigated with one of six fertilizer concentrations [EC of 0.12, 0.65 , 1.18, 1.71, 2.24, or 2.77 $dS \cdot m^{-1}$ (corresponding to fertilizer concentrations of 0, 80, 160, 240, 320, and 400 $mg \cdot L^{-1}$ N, respectively)] and grown under one of the three *PPF* treatments (high, medium, and low corresponding to an average *PPF* of 23.2, 15.6, and 9.8 $mol \cdot m^{-2} \cdot d^{-1}$, respectively). Each ebb&and&flow bench was divided into three zones using shade cloth of varying density (0, 37 or 62 percent shade) to provide different *PPF* levels. In each *PPF* treatment, both wax begonia and petunia seedlings were grown in groups of 30 plants each.

Measurements. At the end of the experiment [4 weeks after transplantation (WAT) for petunia and 6 WAT for wax begonia], data on plant height, leaf area, shoot and root dry weight, EC of the top and bottom layers, and pH of the growing medium were collected for wax begonia and petunia seedlings. Plant height (average of 3 plants) was measured as the vertical length between the top of the plants and the growing medium. Leaf area (average of 3 plants) was measured using an area meter (*LI* 3100, LI-COR, Lincoln, Nebr.). Shoots (from 7 and 15 plants for wax begonia and petunia, respectively) were dried in a forced-air oven maintained at 80°C for a week before measuring the dry weight. Shoot to root ratio was estimated from shoot and root dry weight of a separately measured sample plant. Leaf area ratio (LAR) was determined as the ratio of leaf area to shoot dry weight.

Electrical conductivity and pH of the growing medium were estimated using a pore water conductivity probe (Sigma probe EC1, Delta -T, Burwell, Cambridge, UK) and a pH meter (IQ-150, IQ scientific instruments, San Diego, Calif.) which could directly be inserted into the growing medium, respectively. To measure the EC of the growing medium, the probe was inserted to one ! third (for the top layer) or two ! thirds depth (for the bottom layer). Both measurements were taken from the same pots and the used plants were discarded after measurement. pH of the growing medium was measured by inserting the probe into the bottom layer of the growing medium.

Experimental design and data analysis. Treatments were organized in a split-split-plot design with two replications. Each fertilizer concentration was a whole ! plot, the *PPF* levels were the main split, and species was the sub ! split plots. A group of 30 plants (either wax begonia or petunia) under each *PPF* level constituted an experimental unit. Data were analyzed separately for each species by linear and quadratic regression, using Statistical Analysis Software (SAS institute, Cary, N.C.) and correlations with $P < 0.05$ were considered statistically significant. To obtain acceptable fits of the regression models, a square root transformation of the predictor variable (fertilizer EC) was performed. Because the *PPF* was significantly different under within each shade level, actual *PPF* measured in each treatment was used in regression analysis. In total there were 6 x 3 x 2 = 36 *PPF* levels. However, three constant levels of 37, 62, and 90% of the incident *PPF* were used in plotting curves. The following polynomial

regression model with interaction terms was fitted to describe the effects of treatments on response variables:

$$Y = \$_0 + \$_1 \times PPF_{\%} + \$_2 \times pEC + \$_3 \times PPF_{\%} \times pEC + \$_4 \times PPF_{\%}^2 + \$_5 \times EC + \$_6 \times PPF_{\%} \times EC + \$_7 \times PPF_{\%}^2 \times pEC$$

where 'Y' is any response variable, $PPF_{\%}$ = percentage of incident *PPF*, EC = fertilizer EC, and $\$_0$ ... $\$_7$ are the regression coefficients. This equation was further reduced using backward selection ($P < 0.05$). The optimal fertilizer EC for any response variable was calculated as the EC value at which the first derivative of the function was equal to zero.

Results and Discussion

Environmental conditions. Despite differences among the *PPF* levels in each experimental unit, mean temperature during the growth period did not differ among the three *PPF* treatments. Averaged over the entire growth period, the temperature in the three *PPF* treatments was 21.7 ± 0.2 °C. Average RH was slightly higher (about 6 percent) in the low than medium or high *PPF* treatments. The RH level was similar between medium and high *PPF* treatments (55 and 57 %, respectively). To summarize the results, data are presented by three *PPF* levels, 37, 62 and 90 percent incident light (corresponding to low, medium, and high *PPF* treatments, respectively).

Plant growth. There was an interactive effect ($P < 0.05$) of fertilizer EC and *PPF* on shoot dry weight of petunia and wax begonia. Shoot dry weight increased initially with fertilizer EC (up to 1.28 $dS·m^{-1}$ for wax begonia and 1.87 $dS·m^{-1}$ for petunia) and decreased at high fertilizer EC (Fig. 3.1). In both species, shoot dry weight of fertilized plants was higher (twice and thrice in wax begonia and petunia, respectively) for plants grown at high *PPF* than those grown at low *PPF* treatment (Fig. 3.1). When fertilizer EC was increased from 1.18 to 2.77 $dS·m^{-1}$, shoot dry weight of wax begonia decreased on average by 28% in all the three *PPF* treatments. There was little decrease in the shoot dry weight of petunia at high fertilizer EC (> 1.7 $dS·m^{-1}$). In both species, without fertilizer, shoot dry weight was similar in the three *PPF* treatments, and increased rapidly with increasing fertilizer EC from 0.15 to 0.65 $dS·m^{-1}$. This increase in shoot dry weight was more pronounced at high *PPF*. In both species, optimum fertilizer EC did not change with *PPF.* It was 1.28 and 1.87 $dS·m^{-1}$ in wax begonia and petunia, respectively.

Although optimal fertilizer EC was determined, shoot dry weight in both species was similar over a range of fertilizer concentrations (Fig. 3.1). Therefore, we estimated the range of fertilizer EC in which the change was ± 10% of the estimated dry weight at the optimum fertilizer EC (hereafter, 'optimal range'). In wax begonia and petunia, the optimal range of fertilizer EC for shoot dry weight ranged from 0.65 to 2.0 $dS·m^{-1}$ and 1.18 to > 2.77 $dS·m^{-1}$ among the three *PPF* treatments (shoot dry weight in petunia did not decrease more than 10% even at the highest EC tested), respectively. This clearly shows that both species can be

grown with few problems in a wide range of fertilizer EC, and the range is higher for petunia than wax begonia.

The optimal fertilizer concentration values obtained in our experiment agree with those obtained by James and van Iersel (2001). Their results indicated that dry weight of wax begonias and petunias was acceptable when fertilized with solutions with an EC of 1.0 to 2.4 and 1.4 to 2.9 $dS·m^{-1}$, respectively. Kang and van Iersel (2001) reported that the optimal fertilizer EC for petunias (*Petunia* x*hybrida* Hort. Vilm-Andr.) grown at a constant temperature of 25/ 17 °C was 2.6 $dS·m^{-1}$. However, optimal fertilizer EC for petunias in their experiment depended on the temperature. In their study on begonia (*Begonia x hiemalis* Fotsch), Gislerød and Mortensen (1990) indicated that maximum dry weight was seen at the same fertilizer EC (2.0 $dS·m^{-1}$) for plants grown at 60 and 90 % RH. However, further increase in fertilizer EC in their experiment resulted in greater reduction in dry weight of plants grown at 60 than 90% RH.

Shoot : root ratio in petunia increased with fertilizer EC (Table 3.1). Similar changes were also reported in poinsettia (*Euphorbia pulcherrima*. Willd. ex Klotzsch, Yelanich and Biernbaum, 1993) and salvia (*Salvia splendens* F. Sellow ex Roem. & Schult. 'Scarlet Sage', Kang and van Iersel, in review). Although the general trend in wax begonia also revealed an increase in shoot to root ratio with fertilizer EC, a good correlation could not be established (R^2 = 0.40, Table 3.1).

Treatment effects seen on shoot dry weight were also noted on leaf area in both species (Fig. 3.2). There was no interactive effect of fertilizer EC and

PPF on leaf area of wax begonia. Leaf area of wax begonia increased with increasing *PPF*. Although leaf area of begonia increased as EC increased from 0.15 to 1.18 $dS\,m^{-1}$, it decreased at high fertilizer EC (> 1.18 $dS\,m^{-1}$). The fertilizer EC resulting in maximum leaf area was the same for all the three *PPF* treatments (1.14 $dS\,m^{-1}$, Fig. 3.2) which is close to the optimal fertilizer EC for shoot dry weight in wax begonia (1.28 $dS\,m^{-1}$). Like shoot dry weight, leaf area was also similar over a range of fertilizer concentrations (Fig. 3.2). The optimal range for leaf area was 0.65 to 1.71 $dS\,m^{-1}$ in three *PPF* treatments.

The interaction between fertilizer EC and *PPF* on leaf area of petunia was significant. Because of the interaction, optimal fertilizer EC for leaf area of petunia was different for the three *PPF* treatments [3.2, 1.9 and 1.6 $dS\,m^{-1}$, at high, medium, and low *PPF* treatments, respectively (Fig. 3.2)]. These values are close to the optimal fertilizer EC for shoot dry weight in petunia (1.87 $dS\,m^{-1}$ for the three *PPF* treatments), especially at the medium *PPF* treatment. However, the optimal range of fertilizer EC was close in the three *PPF* treatments. The lower EC limit of the optimal range was close (1.18, 1.30, and 1.50 $dS\,m^{-1}$ for low, medium, and high *PPF*) and the upper EC limit was greater than 2.77 $dS\,m^{-1}$ in the three *PPF* treatments.

Leaf area ratio in wax begonia was affected by both fertilizer EC and *PPF* (Table 3.1). Leaf area ratio decreased at high fertilizer EC (negative coefficient for EC). Although shoot dry weight of wax begonia decreased along with leaf area at high fertilizer EC, the decrease in leaf area was more pronounced than that of shoot dry weight (Figs. 3.1 & 3.2), which resulted in a decrease in LAR at

high fertilizer EC (> 1.18 dS⇳m^{1}). The decrease in LAR indicates that wax begonia does not efficiently produce leaf area at high fertilizer concentrations. Kang and van Iersel (in review) reported that LAR in salvia (*Salvia splendens*) increased up to 1 x full strength and decreased at 2 x full strength of Hoagland nutrient solution. In an other report, van Iersel and Kang (2002) reported that LAR of pansy (*Viola* x *wittrockiana* Gams.) reached a maximum at a fertilizer EC of 2.0 dS⇳m^{-1} and decreased at a fertilizer EC of 3.0 dS⇳m^{-1}. Leaf area ratio in wax begonia decreased with increasing *PPF*. An increase in LAR with increasing shade has been reported in species with contrasting light requirements like tall fescue [*Festuca arundinacea* Schreb., (Allard et al., 1991)] and dracaena [*Dracaena sanderana* hort Sander ex Mast, (Vladimirova et al., 1997)]. Plants grown in low *PPF* increase their LAR to capture more light, thereby increasing their growth rate. Although the trend was similar in petunia *(LAR = 39.2 - 0.198 x* $PPF_{\%}$*)*, the correlation among LAR, fertilizer EC and *PPF* was poor (R^2 = 0.24, Table 3.1).

Effects of fertilizer EC and *PPF* on plant height in both species were similar to those noted on shoot dry weight. The optimal fertilizer EC for plant height in wax begonia was 1.06 dS⇳m^{-1} (Fig. 3.3). Averaged over the three *PPF* treatments, plant height in wax begonia decreased by 38 percent, when fertilizer EC was increased from 1.18 to 2.77 dS⇳m^{-1}. The optimal fertilizer range for begonia height was 0.65 to 1.71 dS⇳m^{-1} in the three *PPF* treatments. Plant height of petunia was less sensitive to increasing fertilizer EC than that of wax begonia (Fig. 3.3). Although optimal fertilizer EC for petunia height was 1.93 dS⇳m^{-1}, the

optimal range was 1.18 to > 2.77 $dS·m^{-1}$ in the three *PPF* treatments. These results agree with those of James and van Iersel (2001), who reported that a fertilizer EC of 1.4 and 1.8 $dS·m^{-1}$ was optimal for plant height in wax begonia and petunia, respectively. A decrease in plant height of wax begonia with increasing fertilizer EC has also been reported in earlier studies (Chase and Poole, 1987; Gislerød and Mortensen, 1990; James and van Iersel, 2001). Decreasing plant height without affecting the overall quality is desirable for bedding plants. Compared to those grown at 1.18 $dS·m^{-1}$, wax begonias grown at 1.71 $dS·m^{-1}$ had similar dry weight, but were shorter in all three *PPF* treatments (average height reduction of 6.5%).

These results indicate that the optimal range of fertilizer EC for plant growth was similar in the three *PPF* treatments for both species (0.65 to 1.71 $dS·m^{-1}$ and 1.18 to >2.77 $dS·m^{-1}$, respectively for wax begonia and petunia). The lack of increase in optimal fertilizer EC with increasing *PPF* does not support our hypothesis that optimal fertilizer concentration for subirrigated plants would increase with increasing *PPF*. Therefore, fertilizer concentrations need not be adjusted based on the *PPF* in the greenhouse. This finding is significant because *PPF* varies across the country and during different parts of the year. Based on our results, separate fertilizer guidelines need not be developed for different regions of the country.

Electrical conductivity of the growing medium. Treatment effects on EC of the growing medium were different between the two species. While there was a direct effect of *PPF* on EC of the growing medium in petunia, it had no effect on

the EC of either the top or bottom layer in wax begonia. In general, growing medium EC was higher in the top than in the bottom layer in both species (Figs. 3.4 and 3.5). Electrical conductivity of the top layer depended on that of the bottom layer in both the species (Fig. 3.6, only data from wax begonia are shown).

In wax begonia, the EC of the bottom and top layers of the growing medium increased with increasing fertilizer EC. Averaged over the three *PPF* treatments, the EC of the bottom layer increased from 0.17 to 3.78 $dS\,m^{-1}$ when the fertilizer EC was increased from 0.12 to 2.77 $dS\,m^{-1}$. The electrical conductivity of the bottom layer in the optimal range of fertilizer EC was 1.43 to 2.8 $dS\,m^{-1}$ and remained the same in the three *PPF* treatments (Fig. 3.4). Changes in dry weight seen with increasing *PPF* were not reflected in the EC of the bottom or top layers of wax begonia. Plants grown at high *PPF* had higher dry weight than those grown at low *PPF*, and therefore should have absorbed more nutrients from the growing medium. This suggests that plants supplied with the same fertilizer EC but grown at a higher *PPF* should have a lower EC in the bottom layer than that of the plants grown at low *PPF*. However, it is likely that the larger plants in the high *PPF* treatment transpired more, which would have resulted in a drier growing medium than in the low *PPF* treatment. A dry growing medium would have absorbed more fertilizer solution, thus replenishing the nutrients taken up by the plants.

In petunia, there was no interaction between fertilizer EC and *PPF* on EC of the bottom layer. Electrical conductivity of bottom layer increased with both

increasing fertilizer EC and increasing *PPF* (Fig. 3.5). However, the increase in EC of the bottom layer of the growing medium with increasing *PPF* was small. The EC of the bottom layer in the optimal fertilizer EC range was 2.18 to >3.46 $dS\,m^{-1}$ at low *PPF*, 2.27 to >3.54 $dS\,m^{-1}$ at medium *PPF*, and 2.36 to >3.64 $dS\,m^{-1}$ at high *PPF*. Kang and van Iersel (2001) reported that a growing medium EC of 3.5 $dS\,m^{-1}$ resulted in maximum shoot dry weight in petunia, which is close to our findings. There was an interactive effect of fertilizer EC and *PPF* on EC of the top layer of the growing medium in petunia. Electrical conductivity of the top layer increased with increasing fertilizer EC and the increase was more at high and medium *PPF* treatments than low *PPF* treatment (Figs. 3.5 & 3.6). Electrical conductivity of the top layer was similar in the high and medium *PPF* treatments.

Higher EC in the top layer than in the bottom layer of the growing medium with subirrigation was reported earlier in the literature. Cox (2001) reported that the EC of the top layer of subirrigated poinsettias was higher than all other treatments, including a composite sample (top, medium and bottom layers), and samples from overhead irrigated plants. However, in his study, the EC of the bottom layer did not differ between treatments. Kent and Reed (1996) indicated that the EC of the top layer remained higher than the recommended range (1.25 $dS\,m^{-1}$), yet the growth of New Guinea impatiens (*Impatiens* x*hawkeri*) and spathiphyllum (*Spathiphyllum* Schott) was not affected. This indicates that the EC of the top layer need not be considered as a factor affecting the growth, as long as the EC of the bottom layer is maintained at a recommended level. In all these experiments, the EC of the top layer was high only at supra!optimal

fertilizer concentrations, indicating that excess soluble salts in the bottom layer migrate to the top layer during the course of crop growth. This is supported by the findings of Kent and Reed (1996) that nitrate was not detected in the top layer until the nitrogen concentration in the fertilizer was higher than 8 mM (112 mg $N \cdot L^{-1}$). Our findings indicate that the EC of the top layer was always higher than that of the bottom layer, but the difference in EC between the top and bottom layers increased with in increasing fertilizer EC in both species. Our results also indicate that EC of the top layer was dependent on the EC of the bottom layer of the growing medium (Fig. 3.6).

The pH of the growing medium was in or near the recommended range (5.5 to 6.5) for most greenhouse crops (Lang, 1996). In petunia, there was an interactive effect of fertilizer EC and *PPF* on pH of the growing medium ($pH = 5.35 + 0.008 \times PPF_{\%} - 0.00051 \times PPF_{\%} \times \%EC$, R^2 = 0.60, data not shown). The pH of the growing medium increased with *PPF*, however the negative sign for the interaction term in the equation indicates that pH decreased with increasing fertilizer EC and the decrease was higher at high *PPF* than at low *PPF* treatment. A good relationship could not be established among fertilizer EC, *PPF* and pH of the growing medium in wax begonia (R^2 = 0.49).

Conclusions

The results of this experiment indicate that the optimal fertilizer concentration for plants was not affected by varying *PPF* treatments. This

implies that growers need not adjust the fertilizer EC based on *PPF*. Crop growth was better under high than low *PPF* treatments. The effect of increasing *PPF* on the EC of the bottom layer was either absent (wax begonia) or small (petunia). Absence of any effect of *PPF* on the EC of the bottom layer in wax begonia indicates that the optimal EC of the bottom layer of growing medium remained same in all three *PPF* treatments. Although the optimal EC of the bottom layer of the growing medium increased with *PPF* in petunia, the difference was small.

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Table 3.1. Regression parameters of the fitted functions among electrical conductivity (EC) of fertilizer, photosynthetic photon flux (*PPF*), shoot to root ratio, and leaf area ratio in wax begonia and petunia. Interaction between fertilizer EC and *PPF* on measured parameters was not significant (*P* 0.05).

Regression	Shoot to root ratio		Leaf area ratio ($m^2 \cdot kg^{-1}$)	
	Wax begonia	Petunia	Wax begonia	Petunia
R^2	0.40	0.64	0.70	0.24
Intercept	-4.26^{NS}	-1.03^{NS}	46.7***	38.92***
/ EC	59.01***	20.44***	27.37**	-
EC	-28.98***	$-^{NS}$	-13.65**	-
PPF	-	-	-0.59**	-0.20**
PPF^2	-	-	0.003*	-

^{NS}, *, **,***, indicate not significant at $P < 0.05$ and significant at $P = 0.05$, 0.005 and 0.0005, respectively

Figure 3.1. Effect of increasing fertilizer EC and photosynthetic photon flux (*PPF*) on shoot dry weight of wax begonia and petunia. Data represent the mean of 2 replications of 7 and 15 plants of wax begonia and petunia, respectively at low (●), medium ([a]), and high (■) *PPF* treatments. Lines pass through the estimated shoot dry weight at 37 (solid line), 62 (dotted line), and 90 (dashed line) percent of incident *PPF* ($PPF_{\%}$). Data are scattered along the fitted curves because of the differences in *PPF* among treatments and not due to error in measurements. Shoot dry weights of wax begonia and petunia were calculated as $1.134 - 0.0325 \times PPF_{\%} + 0.113 \times PPF_{\%} \times \%EC - 0.05 \times PPF_{\%} \times EC$ (R^2 = 0.83), and $0.021 - 0.02 \times PPF_{\%} + 0.082 \times PPF_{\%} \times \%EC - 0.03 \times PPF_{\%} \times EC$ (R^2 = 0.96), respectively.

Figure 3.1

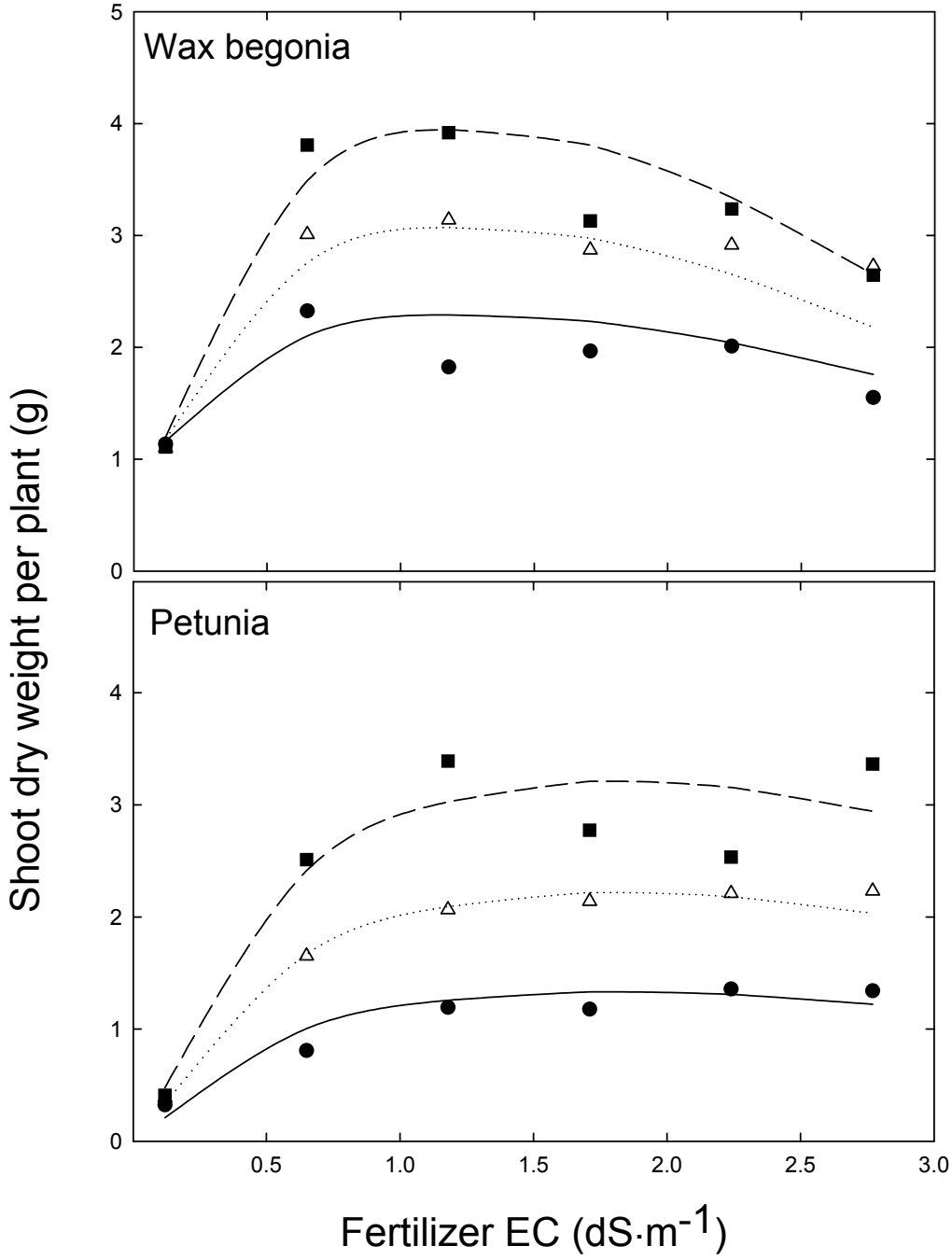

Wax begonia
Petunia
Shoot dry weight per plant (g)
Fertilizer EC (dS·m-1)
0
1
2
3
4
5
0.5
1.0
1.5
2.0
2.5
3.0

Figure 3.2. Effect of increasing fertilizer EC and photosynthetic photon flux (*PPF*) on leaf area of wax begonia and petunia. Data represent the mean of 2 replications of 3 plants each of wax begonia and petunia at low (●), medium ([a]), and high (■) *PPF* treatments. Lines pass through the estimated leaf area at 37 (solid line), 62 (dotted line), and 90 (dashed line) percent of incident *PPF* ($PPF_{\%}$). Data are scattered along the fitted curves because of the differences in *PPF* among treatments and not due to error in measurements. Leaf areas of wax begonia and petunia were calculated as $-0.09 + 0.355 \times \%EC + 0.00042 \times PPF_{\%} - 0.164 \times EC$ (R^2 = 0.81), and $-0.03 + 0.099 \times \%EC + 0.00035 \times PPF_{\%} \times \%EC - 0.044 \times EC$ (R^2 = 0.77), respectively.

Figure 3.2

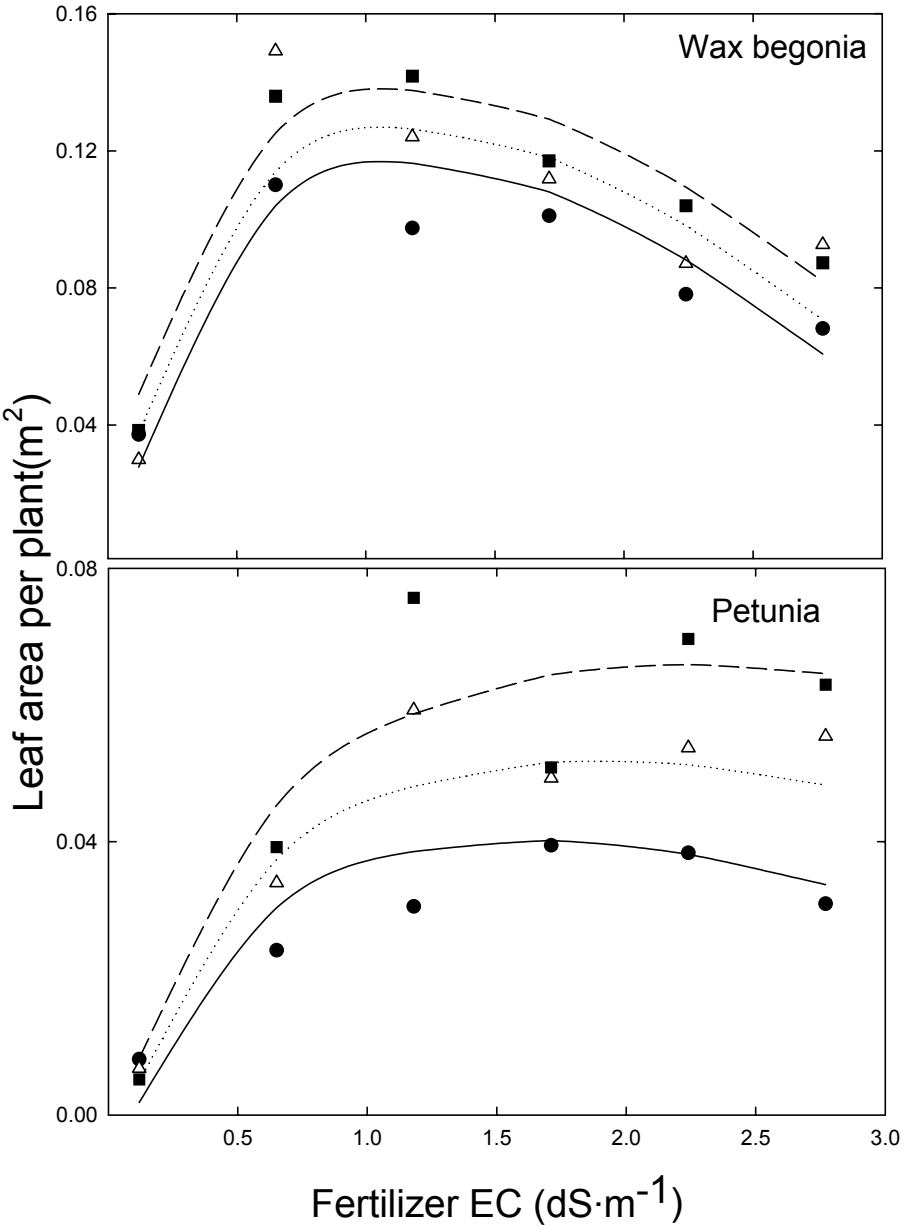

Wax begonia
Petunia
Leaf area per plant(m^2)
Fertilizer EC (dS·m^{-1})
0.16
0.12
0.08
0.04
0.08
0.04
0.00
0.5
1.0
1.5
2.0
2.5
3.0

Figure 3.3. Effect of increasing fertilizer EC and photosynthetic photon flux (*PPF*) on plant height of wax begonia and petunia. Data represent the mean of 2 replications of 3 plants each of wax begonia and petunia at low (●), medium ([a]), and high (■) *PPF* treatments. Lines pass through the estimated plant height at 37 (solid line), 62 (dotted line), and 90 (dashed line) percent of incident *PPF* ($PPF_{\%}$). Data are scattered along the fitted curves because of the differences in *PPF* among treatments and not due to error in measurements. Plant heights of wax begonia and petunia were calculated as $-4.19 + 0.039 \times PPF_{\%} + 44.2 \times \%EC - 21.1 \times EC$ (R^2 = 0.75), and $-3.24 + 0.043 \times PPF_{\%} + 23.9 \times \%EC - 8.6 \times EC$ (R^2 = 0.83), respectively.

Figure. 3.3

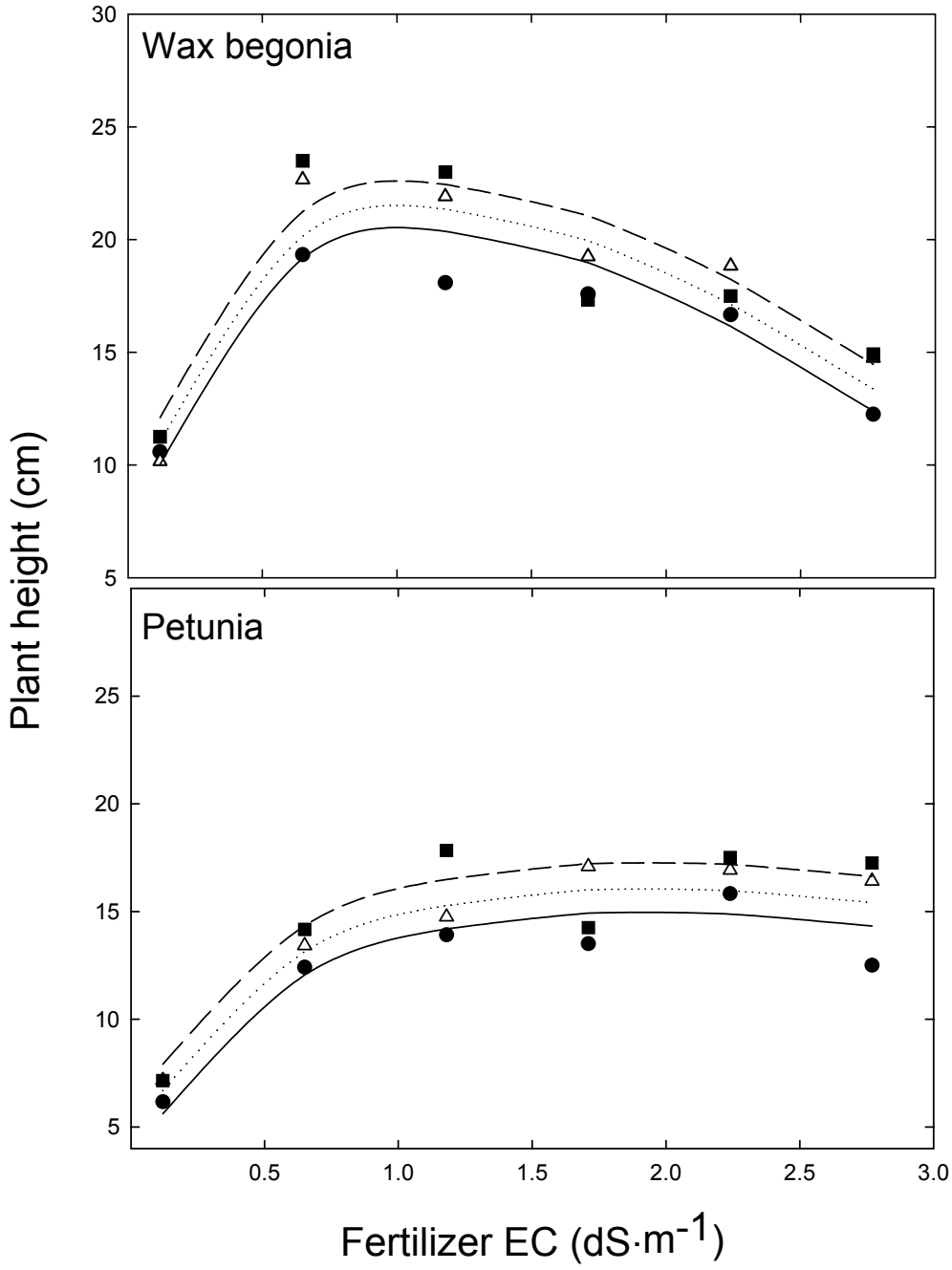

Wax begonia
Petunia
Plant height (cm)
Fertilizer EC (dS·m-1)
30
25
20
15
10
5
0.5
1.0
1.5
2.0
2.5
3.0

Figure 3.4. Effect of increasing electrical conductivity (EC) of fertilizer on EC of the growing medium in the top and bottom layers of wax begonia. Data represent the mean of 2 replications of 3 plants. Lines pass through the estimated growing medium EC at different fertilizer concentrations. The EC of the growing medium in the bottom and top layers was calculated as - $0.78 + 2.74 \times \%EC$ ($R^2 = 0.91$) and, $0.0074 + 2.64 \times \%EC - 0.29 \times EC$ ($R^2 = 0.94$), respectively.

Figure 3.4

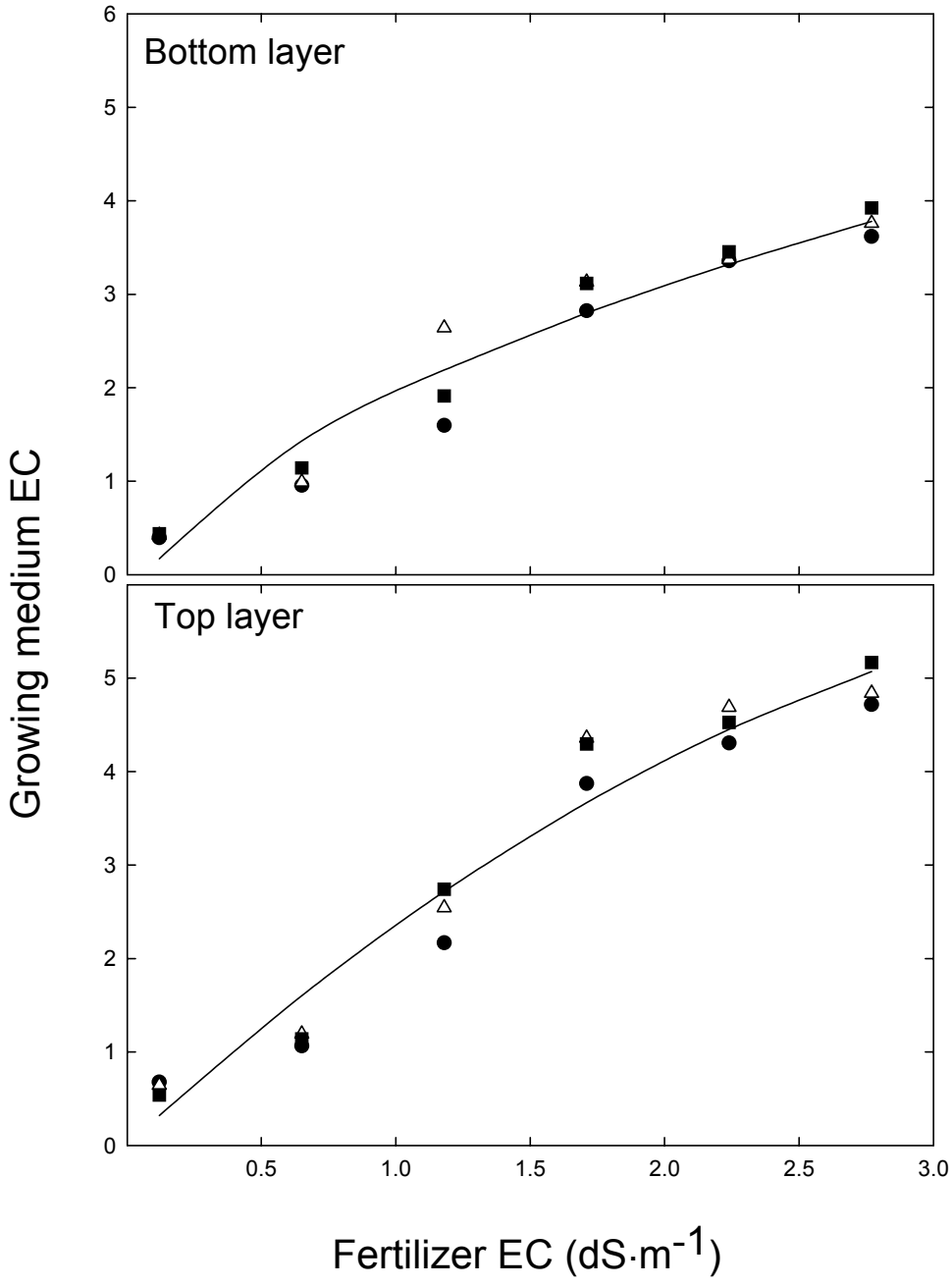

Bottom layer
Top layer
Growing medium EC
Fertilizer EC (dS·m-1)
0
1
2
3
4
5
6
0.5
1.0
1.5
2.0
2.5
3.0

Figure 3.5. Effect of increasing electrical conductivity (EC) of the fertilizer solution and photosynthetic photon flux (*PPF*) on the EC in the top and bottom layers of the growing medium of petunia. Data represent the mean of 2 replications of 3 plants at low (●), medium ([a]), and high (■) *PPF* treatments. Lines pass through the estimated growing medium EC at 37 (solid line), 62 (dotted line), and 90 (dashed line) percent incident $PPF_{\%}$. The EC of the growing medium in the bottom and top layers was calculated as $-0.006 + 1.21 \times \%EC + 0.0034 \times PPF_{\%}$ ($R^2 = 0.97$), and $0.82 + 3.78 \times \%EC + 0.059 \times PPF_{\%} \times \%EC + 2.5 \times EC - 0.0004 \times \%EC \times PPF_{\%}^{2}$ ($R^2 = 0.94$), respectively.

Figure 3.5

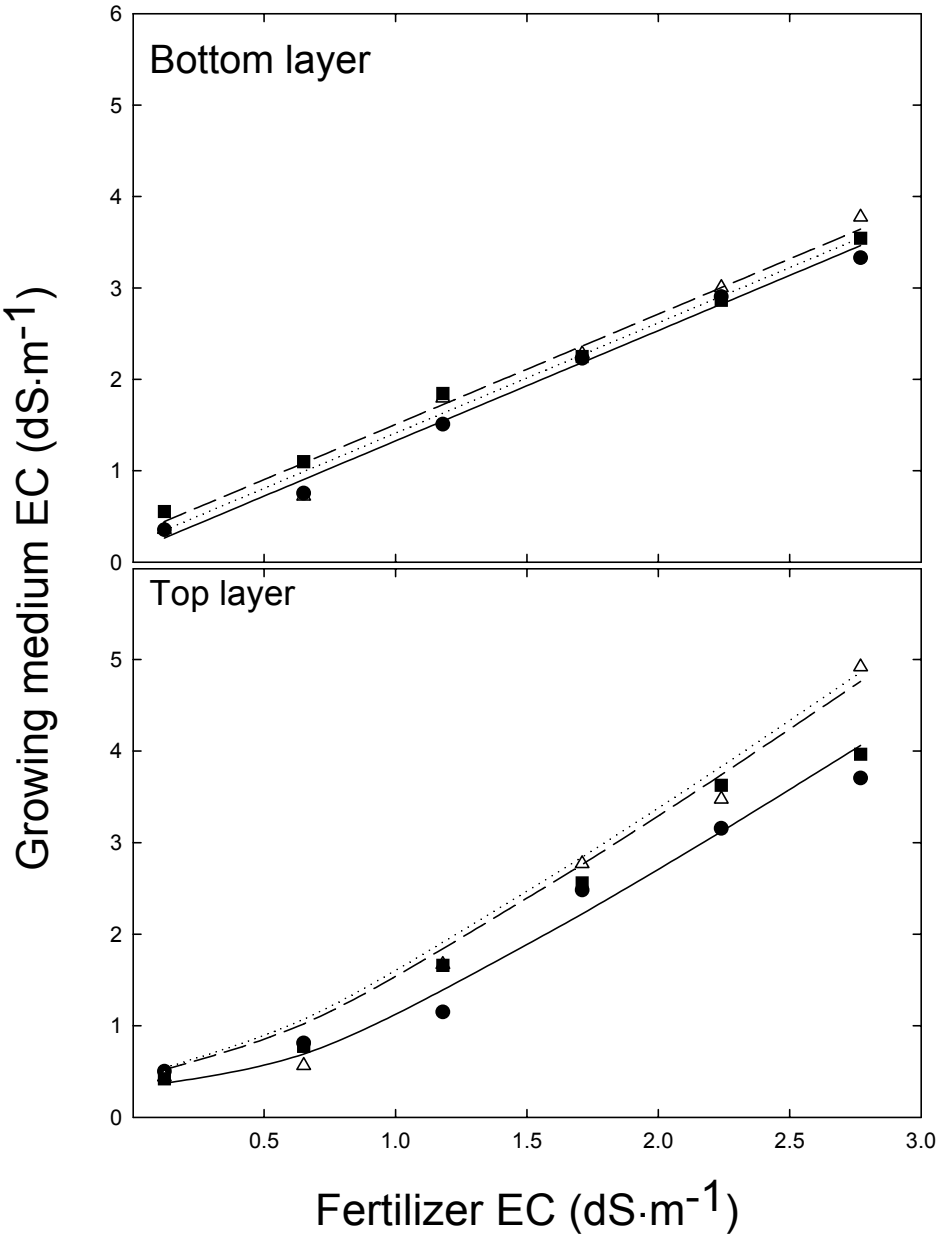
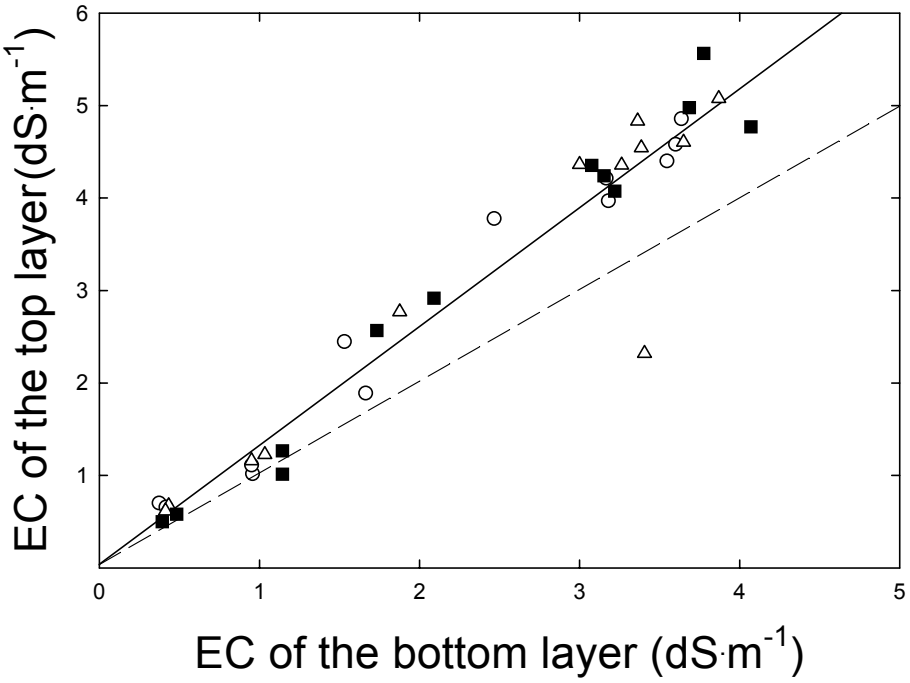

Bottom layer
Top layer
Growing medium EC (dS·m-1)
Fertilizer EC (dS·m-1)
0
1
2
3
4
5
6
0.5
1.0
1.5
2.0
2.5
3.0

Figure 3.6. Correlation between the electrical conductivity of the top (EC_{TL}) and bottom (EC_{BL}) layers of the growing medium in wax begonia. Electrical conductivity of the growing medium in the top and bottom layers did not differ among the three *PPF* treatments. Data represent mean of 3 plants from all experimental units at low (●), medium ([a]), and high (■) *PPF* treatments. The dotted line is drawn to show the increase in EC_{TL} with increasing EC_{BL}. Electrical conductivity of the top layer can be calculated as $EC_{TL} = 0.041 + 1.285 \times EC_{BL}$ (r^2 = 0.93).

Figure 3.6



CHAPTER 4

LIGHT EFFECTS ON WAX BEGONIA: PHOTOSYNTHESIS, GROWTH RESPIRATION, AND MAINTENANCE RESPIRATION [1]

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[1] Sainath Krishna, M.N. and M.W. van Iersel. To be submitted to Journal of the American Society of Horticultural Science

Subject category: Photosynthesis, Source ! Sink Physiology

Light Effects on Wax Begonia: Photosynthesis, Growth respiration, and Maintenance Respiration

ADDITIONAL INDEX WORDS. *Begonia semperflorens,* carbon use efficiency, photosynthesis ! light response curves, quantum yield, water ! use efficiency

Abstract. The effect of increasing photosynthetic photon flux (*PPF*) on photosynthesis and respiration in wax begonia (*Begonia semperflorens&cultorum* Hort.) was examined by measuring CO_2 exchange rates (CER) of plants for a period of 25 d under four *PPF* treatments (5.3, 9.5, 14.4, and 19.4 mol@m^{-2}@d^{-1}) in a whole&plant gas exchange system. Although plant growth rate (GR) increased linearly with increasing *PPF*, plants grown at 5.3 or 9.5 mol@m^{-2}@d^{-1} lost more CO_2 through respiration than was fixed in photosynthesis during the early growth period (13 and 4 d, respectively), resulting in a negative daily carbon gain (DCG). It appears that the cost of acclimation to low *PPF* was high in wax begonia as the percentage of maintenance (R_m) to total respiration (R_T) at harvest was 87 and 83% respectively, for plants grown at 5.3 and 9.5 mol@m^{-2}@d^{-1}. Carbon use efficiency (CUE) of plants was higher at 14.4 or 19.4 mol@m^{-2}@d^{-1} than at 5.3 or 9.5 mol@m^{-2}@d^{-1} due to the lower ratio of R_m to R_T in plants. Canopy quantum yield (") and light-saturated gross photosynthesis (P_{gmax}) of plants increased linearly with

increasing *PPF*. At harvest, crop dry weight (DW_{CROP}) and net assimilation rate (NAR) of plants increased with increasing *PPF*, due to increased photosynthetic capacity and DCG of plants. However, leaf area ratio of neither whole plants (LAR_{PLANT}) nor shoots (LAR_{SHOOT}) differed among treatments. These data indicate that the importance of maintenance respiration in the carbon balance and growth rate of plants increases under low *PPF* conditions. Due to the small carbohydrate pools resulting from lower photosynthetic rates, plants grown at 5.3 and 9.5 $mol·m^{-2}·d^{-1}$ had less carbohydrate available for growth and growth respiration after meeting maintenance requirements than those grown at 14.4 and 19.4 $mol·m^{-2}·d^{-1}$.

Dry matter production and crop growth rate are strongly correlated to the amount of *PPF* intercepted by plants (Lawlor, 1995). To capture the maximum amount of radiation and optimize light use, shade-grown plants may undergo various modifications to their leaf physiology and morphology. For example, a decrease in leaf number and an increase in specific leaf area [leaf area per unit leaf weight] with decreasing *PPF* have been reported in tall fescue [*Festuca arundinacea* Schreb., (Allard et al., 1991)] and dracaena [*Dracaena sanderana* hort Sander ex Mast, (Vladimirova et al., 1997)], while a decrease in leaf number, leaf thickness, and stomatal number have been reported in mangosteen [*Garcinia mangostana* L. (Weibel et al., 1994)]. Other studies have reported modifications in leaf physiology in response to varying levels of *PPF* (Norcini et al., 1991a; Noguchi et al., 2001).

Plant growth is the result of excess carbon synthesized in photosynthesis over that lost in respiration. Experimental evidence indicates that 30 - 50% of carbon synthesized by plants in photosynthesis is lost in respiration during crop growth (Amthor, 1984; Lawlor, 1995; van Iersel and Seymour, 2000). Therefore, the significance of respiration in plant growth should not be underestimated. Research on whole plant respiration has increased since McCree (1974) related respiration to gross photosynthesis (P_g) and dry weight of plants and separated it into maintenance and growth components. According to Penning de Vries (1975), maintenance respiration involves release of energy (ATP) only for sub!cellular maintenance processes, whereas growth respiration involves release of energy for all processes which result in a net increase in biomass. Therefore, to understand the physiological basis of growth, both metabolic processes, photosynthesis and respiration, have to be studied.

Obligate shade plants cannot increase their photosynthesis when grown under high *PPF* because of the absence of high levels of enzymes for carboxylation and the components of electron transport (Björkman, 1981). Research has indicated a decrease in the quantum yield of shade plants grown under high *PPF* (Funnell et al., 2002). While a large amount of literature is available on the effect of *PPF* on photosynthesis in shade plants (Callan and Kennedy, 1995; Funnell et al., 2002; Greenway and Lieffers, 1997; Norcini et al., 1991a, b), limited work has focused on the aspects of respiration in shade plants grown and acclimated to varying *PPF* levels.

Most of the commercially available equipment for measuring photosynthesis and respiration in plants is designed for leaf measurements. Traditional techniques of measuring leaf photosynthesis do not accurately determine the dry matter production and growth rate of plants (van Iersel and Bugbee, 2000). Continuous measurements of CER of whole plants (for weeks) can depict the growth rate of plants more accurately than individual leaf measurements, as they directly measure C accumulated (a measure of growth rate) in plants (van Iersel and Kang, 2002).

Wax begonias are amongst the most popular bedding plants with tolerance to shade. As far as we know, only two studies have been reported on whole!plant photosynthesis in the genus begonia (Giaglaras et al., 1995; Ehler and Hansen, 1998). However, neither study was performed over a prolonged period and data were not used to estimate any growth parameters, as their objective was to develop a model of photosynthesis. In this research, we measured whole!crop CER of wax begonia continuously for a period of 25 d in a 10!chamber, whole!plant gas exchange system. The objective was to quantify the effects of increasing *PPF* on plant growth, photosynthesis, respiration, water!use efficiency (WUE) and photosynthesis*!PPF* !response curves in wax begonia.

Materials and Methods

Plant material. Wax begonia 'Cocktail Vodka' plug seedlings were procured in cell flats (288 cells/flat) from a commercial grower (Speedling Inc., Blairsville, Ga.) on 13 June, 2001. Seedlings were transplanted into 36 ! cell flats (Jumbo 606, TLC polyform, Plymouth, Minn.) filled with a soilless growing medium (Fafard 2P, Fafard Co., Anderson, S.C.). About one gram of a 14N ! 6.1P ! 11.6K slow release fertilizer (14-14-14 Osmocote, The Scotts Co., Marysille, Ohio) was added to the growing medium in each cell prior to transplantation. One cell in each flat was left empty for inserting an irrigation pipe. A double ! layered capillary mat (Vattex F capillary watering system, OS plastics, Norcross, Ga.) placed in a watertight tray was used for subirrigating the seedlings in the cell flats. A portion of the capillary mat was hung over one side of the tray to allow excess water to drain out of the watertight tray. An irrigation pipe was inserted through a hole in the side of the gas exchange chamber, which made it possible to add water to the watertight tray without disturbing the gas exchange measurements. About 2 L of water was added to the trays initially and later at weekly intervals. These assemblies were kept inside whole ! plant gas exchange chambers (0.32 × 0.5 × 0.6 m^3, van Iersel and Bugbee, 2000) arranged inside a growth chamber (model E ! 15, Conviron, Winnipeg, Canada). A total of ten gas exchange chambers and two growth chambers were used in the experiment. Out of the ten gas exchange chambers, two were controls

without plants and the CER data from these empty chambers were used to correct the data for zero drifts of the infra red gas analyzer (IRGA).

Environmental control. The temperature of the growth chambers was set at 18 / 24 °C (day / night) to regulate the temperature inside the gas exchange chambers at 25 °C. A small electric resistance heater (100 W) was used to control the temperature inside the gas exchange chambers. The datalogger controls the heater and maintains the desired temperature. Shielded, aspirated, type T-thermocouples were used to measure the temperature inside all gas exchange chambers. Humidity probes (HTO!45R, Rotronic, Huntington, N.Y.) were arranged in two gas exchange chambers in each growth chamber. To obtain the required *PPF*, gas exchange chambers were covered with shade cloth of varying thickness. The *PPF* was measured simultaneously at the top of the canopy in eight chambers using quantum sensors (QSO!SUN, Apogee Instruments Inc., Logan, Utah) connected to a datalogger (CR10X, Campbell Sci., Logan, Utah). A daily photoperiod of 14 h was maintained inside the growth chambers. Average air temperature and relative humidity during the light/dark period were 25±1 °C and 65-85/80-100%, respectively.

Treatments. The average *PPF* measured at the top of the canopy in different treatments were 5.3, 9.5, 14.4, and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ (corresponding to instantaneous *PPF* of 106, 189, 286, and 385 : $mol \cdot m^{-2} \cdot s^{-1}$, respectively).

Measurements. At harvest (25 d after transplant), chlorophyll content (for 4 leaves from separate plants), leaf area and shoot dry weight of 23 plants were determined in each treatment. Leaf chlorophyll content was assessed using a chlorophyll meter (SPAD-502, Minolta Co., Japan) and leaf areas were measured using a leaf area meter (LI!3100, LI!COR, Lincoln, Neb.). Total leaf area (for 35 plants) was estimated from the leaf area of the measured 23 plants. Root dry weight of the harvested 23 plants was estimated as the product of shoot dry weight of 23 plants and root to shoot ratio measured for the remaining 12 plants, which were used in a subsequent light response study (see below). Total shoot (DW_{SHOOT}) and root dry weights (DW_{ROOT}) (for 35 plants) were estimated and added to determine total crop dry weight (DW_{CROP}). Leaf area ratio of whole plants and shoots were estimated as the ratio of leaf area to DW_{CROP} and DW_{SHOOT}, respectively.

CO_2 exchange rates. The whole!plant gas exchange system (van Iersel and Bugbee, 2000) directly measured net!photosynthesis [P_n, :mol.s^{-1}, which is gross photosynthesis (P_g) minus light!period respiration) and dark respiration (R_d, :mol.s^{-1}) of each crop semi!continuously for 30 s, once every 10 minutes. The CER was measured for 25 d. Approximately 0.4 L·s^{-1} of ambient air was blown into each gas exchange chamber by a rotary vane blower (DT 3.40, Becker, Cuyahoga Falls, Ohio). The mass of air flowing into each gas exchange chamber was measured using mass flow meters (GFM37!32, Aalborg Instruments and Controls, Monsey, N.Y.) and the CO_2 concentration of air from

the blower was measured with an infrared gas analyzer (IRGA, SBA!1, PP!systems, Haverhill, Mass.).

Inside the gas exchange chambers, plants absorb CO_2 from ambient air during the 14!h light period and release CO_2 during the dark period, resulting in a change in the CO_2 concentration of the air exiting the gas exchange chambers. The difference in the CO_2 concentration of the incoming and exiting air from gas exchange chambers was measured with an IRGA in differential mode (LI!6252, LI!COR). Air was drawn by a pump (MAA!P122, Gast, Benton Harbor, Mich.) from one chamber at a time, which was regulated by opening and closing of solenoid valves. The solenoid valves were controlled by a SDM!CD16AC relay module and CR10T datalogger (Campbell Sci.). Before passing through the differential IRGA, air from each chamber was sent through a condenser to remove most of the water vapor. There was a 30 s delay in measuring the data after the solenoids were switched to the next chamber, during which the air from the previous chamber was purged from the tubing and differential IRGA. Hence, every chamber was measured for 30 s, once in 10 minutes, and data were averaged and stored in the datalogger.

The CER (:$mol \cdot s^{-1}$) was calculated automatically by the datalogger as the product of mass flow ($mol \cdot s^{-1}$) and the difference in CO_2 concentration of the air entering and exiting the chambers (:$mol \cdot mol^{-1}$). Errors in measurement due to zero drift of the differential IRGA were corrected by subtracting the average CER of two empty gas exchange chambers from that of chambers containing plants. Since R_d was measured as the CO_2 exchange rate, it is expressed as a negative

value. Hence, daily average gross photosynthesis ($P_{g,avg}$: mol·s^{-1}) was calculated as:

$$P_{g,avg} = P_{n,avg} \; ! \; R_{d.avg} \qquad \text{[Eq. 1]},$$

where $P_{n,avg}$ and $R_{d.avg}$ are the average P_n and R_d during the light and dark period (in : mol·s^{-1}), respectively. This assumes that respiration rates during the light and dark periods were equal (van Iersel and Bugbee, 2000).

Daily carbon gain (: mol d^{-1}, a measure of the total amount of carbon fixed by 35 plants in a gas exchange chamber per day, i. e., growth rate of 35 plants) was calculated as:

$$DCG = (P_{n,avg} \times t_{light}) + (R_{d.avg} \times t_{dark}) \qquad \text{[Eq. 2]}$$

where t_{light} and t_{dark} are the duration of the light and dark periods (s), respectively.

Integrating DCG over time provides an estimate of cumulative carbon gain (CCG, : mol, the total amount of carbon accumulated in plants since the start of experiment) which is a measure of plant size.

$$CCG = \int DCG \, dt \qquad \text{[Eq. 3]}$$

Cumulative carbon gain (mol) at the end of the experiment was plotted against DW_{CROP} (g) in each treatment, and a linear equation was fitted to describe the relationship:

$$DW_{CROP} = DW_0 + 12 \times CCG / f_c \qquad \text{[Eq. 4]},$$

where DW_0 is the estimated initial dry weight of the plants before starting the experiment, and f_c is the carbon content of the plants (g g^{-1}). Dry weight of plants at the end of each day (DW_{day}) in different treatments was estimated from this equation, based on the CCG of the plants.

Growth rate ($g \cdot d^{-1}$) of plants in different treatments can be estimated from DCG ($mol \cdot d^{-1}$) as:

$$GR = 12 \times DCG / f_c \quad \text{[Eq. 5]}$$

where 12 converts moles of carbon to grams of carbon.

Relative growth rate (RGR, defined as growth rate per unit existing biomass, $g \cdot g \cdot d^{-1}$) and NAR at the end of the experiment (growth rate per unit leaf area) of plants were estimated from GR, DW_{day} and leaf area as:

$$RGR = GR/DW_{day} \quad \text{[Eq. 6], and}$$

$$NAR = GR/ \text{leaf area} \quad \text{[Eq. 7]}$$

Carbon use efficiency ($mol \cdot mol^{-1}$, ratio of carbon incorporated into the biomass to that fixed in gross photosynthesis) was calculated as follows:

$$CUE = DCG / (P_{g.avg} \times t_{light}) \quad \text{[Eq. 8]}$$

To determine the relationship between CUE and CCG, we fitted the following asymptotic equation:

$$CUE = CUE_0 + (CUE_{max} - CUE_0) \times (1 - e^{-b \times CCG}) \quad \text{[Eq. 9],}$$

where CUE_0 is the CUE when CCG is zero, CUE_{max} is the maximum CUE of plants, and b is a constant (van Iersel and Kang, 2002).

Growth (r_g) and maintenance (r_m) coefficients were estimated by plotting 1/ CUE ($mol \cdot mol^{-1}$) versus 1/ RGR ($g \cdot g^{-1} \cdot d$) (van Iersel, unpublished results):

$$1/CUE = 1 + r_g + r_m/RGR \quad \text{[Eq. 10].}$$

The Y-intercept can be used to estimate the growth coefficient ($mol \cdot mol^{-1}$), whereas the slope of the line is an estimate of r_m ($mol \cdot mol^{-1} \cdot d^{-1}$). The more traditional units of r_m and r_g are grams of carbohydrate per gram of dry matter per

day ($g \cdot g^{-1} \cdot d^{-1}$) and grams of carbohydrate per gram dry matter ($g \cdot g^{-1}$), respectively. The estimated values of r_m and r_g can be converted to traditional glucose units by multiplying them with $30/(12/f_c)$, where 30 is the multiplier for converting one mole of C to grams of CH_2O and $12/f_c$ converts moles of C to grams of dry weight.

Growth and maintenance respiration rates ($g \cdot d^{-1}$, grams of carbohydrate per day) of plants were estimated as $R_g = r_g \times GR$ (Eq. 11) and $R_m = r_m \times DW_{crop}$ (Eq. 12), where r_g and r_m are expressed as $g \cdot g^{-1}$ and $g \cdot g^{-1} \cdot d^{-1}$, respectively.

Water ! use efficiency. After 25 d of gas exchange measurements, twelve plants from each treatment were used for a WUE study. Plants from different treatments were watered, and the initial weight of the pots with plants was measured. Immediately afterwards, plants were placed back in the gas exchange chambers, and the CER of plants was measured for a 24 h period under the same conditions of the gas exchange study. The pots were weighed again after 24 hours. The amount of water lost in evapo ! transpiration (ET) in the different treatments during the day was measured as the difference in weight of pots before and after the 24 h gas exchange period. The DCG of plants was determined using Eq. 2 and growth rate was estimated from Eq. 5. Water ! use efficiency (grams of dry matter produced per liter of water lost in ET, expressed as $g \cdot L^{-1}$) was calculated as follows:

$$WUE = GR / ET \qquad \text{[Eq. 13]}$$

PPF ! Photosynthesis response curves. The same groups of twelve plants used in the WUE study were used for determining the photosynthesis ! *PPF*

response curves in each experimental unit. Quantum sensors were arranged at the canopy level in each gas exchange chamber to measure the incident *PPF* during this experiment. Plants in different treatments were exposed to a dark period of 10 ! h before starting the study. Subsequently, plants in different treatments were exposed to increasing levels of *PPF* starting from 0 and up to 700 : $mol \cdot m^{-2} \cdot s^{-1}$ in approximate increments of 50 : $mol \cdot m^{-2} \cdot s^{-1}$. Photosynthetic photon flux was increased after P_n had stabilized in all treatments. On average, it took 35 minutes for P_n to stabilize after increasing *PPF*. Steady state P_n per unit ground area (: $mol \cdot m^{-2} \cdot s^{-1}$), leaf area, $DW_{SHOOT,}$ and DW_{ROOT} of the plants were determined as described earlier. The following asymptotic equation was used to calculate dark respiration (R_d) and P_{gmax} per unit ground area (: $mol \cdot m^{-2} \cdot s^{-1}$), and " (mol·$mol^{-1}$, moles of C fixed per mol of incident *PPF*) of plants in different treatments using a non ! linear regression procedure (PROC NLIN) of SAS (SAS Inst., Inc., Cary, N.C.):

$$P_n = R_d + P_{gmax} \; x \; (1\text{-}e^{- "I/Pgmax}) \qquad \text{[Eq. 14]}$$

where *'I'* is the *PPF* incident on top of the plants.

Light compensation and saturation points of plants in different treatments were calculated by substituting $P_g = -R_d$ and *(95%)* P_{gmax}, respectively in the asymptotic regression equations.

To correct for differences in leaf area and dry weight, specific respiration (R_{spec}, : $mol \cdot g^{-1} \cdot s^{-1}$) and maximum gross photosynthesis per unit leaf area ($P_{gmax,LA}$, : $mol \cdot m^{-2} \cdot s^{-1}$) were determined for plants grown in different treatments as follows:

$$R_{spec} = R_d \, / \, (DW_{SHOOT} + DW_{ROOT}) \qquad \text{[Eq. 15]}$$

$P_{gmax,LA}$ = $P_{g,max}$ x ground area / leaf area [Eq. 16]

Experimental design and data analysis. The experimental layout was a randomized complete block with two replications. Each experimental block (growth chamber) consisted of four *PPF* treatments (four gas exchange chambers), and each experimental unit (each gas exchange chamber) consisted of 35 plants. The gas exchange data were analyzed separately for each measurement day. The data were analyzed with both linear and non ! linear (NLIN) regression procedures, with $P < 0.05$ considered to be statistically significant.

Results and discussion

Environmental conditions. The mean temperature and relative humidity (RH) were similar in all treatments. Mean temperature and RH in different treatments were 25.3 ± 0.1 °C (both in the dark and light) and 74.6 ± 2.4%, respectively.

Plant growth ! PPF relationship. Total leaf area of plants increased linearly with increasing *PPF*. However, neither LAR_{SHOOT} nor LAR_{PLANT} were affected by increasing *PPF* (Table 4.1). Leaf area ratio usually increases with decreasing *PPF*. To capture more light, plants grown in shade tend to develop larger and thinner leaves than those grown in full sunlight (Allard et al., 1991; Weibel et al., 1994). Therefore, the increase in total leaf area with increasing *PPF* seems to be the result of increased plant dry matter. Shoot : root ratio did

not differ among the treatments. At harvest, DW_{CROP} increased linearly and leaf chlorophyll content decreased linearly with increasing *PPF* (table 4.1). High levels of total chlorophyll and low chlorophyll *a*: chlorophyll *b* ratios were reported as associated with shading (Adams and Demmig-Adams, 1992, Close et al., 2001). Plants grown in shade require more chlorophyll than those grown in sun to maximize light interception.

PPF ! CO_2 exchange rates. There was a strong correlation between DW_{crop} and CCG (r^2= 0.92), which indicates that gas exchange data were a realistic measure of crop growth (Fig. 4.1). Crop dry weight increased by 21.4 g for every mole of C incorporated by the plants. Carbon content in the plants was estimated from the slope of the equation as 12 $g \cdot mol^{-1}$ / 21.4 $g \cdot mol^{-1}$ = 0.56 $g \cdot g^{-1}$ (a mole of C equals to 12 g). The estimated C content in plants was higher than most other reported values, 0.465 $g \cdot g^{-1}$ for pansy [(*Viola xwittrockiana* Gams., van Iersel and Kang, 2002)], 0.45 $g \cdot g^{-1}$ [pumpkin leaves (*Cucurbita pepo* L., Turgeon and Webb, 1975)], 0.396 $g \cdot g^{-1}$ [white clover (*Trifolium repens* L., McCree and Troughton, 1966)], and 0.421 $g \cdot g^{-1}$ [sugar beet leaves (*Beta vulgaris* L., Terry and Mortimer, 2002)].

Gross and net ! photosynthesis, and dark respiration rates of plants increased linearly with increasing *PPF* throughout the experiment. Dark respiration was higher after watering the plants (watering days indicated by arrows in Fig. 4.2). It seems that water content in the growing medium also affected DCG of plants as quadratic responses in DCG with increasing *PPF* were

seen prior to watering plants during the growth period, while linear effects were seen throughout the rest of the experiment.

Negative DCG values were seen during the initial 13 and 4 d for plants grown at 5.3 and 9.5 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Fig. 4.3). Negative DCG values were also reported after transplanting pansy (van Iersel and Kang, 2002) and vinca *(Catharanthus roseus* L.; van Iersel, 1999). This indicates that plants were respiring more carbohydrates than were synthesized in photosynthesis (possibly from storage forms like starch) soon after transplant. Daily carbon gain also increased after watering plants (Fig. 4.3). As CCG is DCG integrated over time, treatment effects on DCG resulted in differences in CCG as well. Plants grown at 5.3 and 9.5 $mol \cdot m^{-2} \cdot d^{-1}$ had a negative CCG during the initial 20 and 6 d of crop growth, respectively (Fig. 4.3).

As growth rate and DCG are similar, treatments effects on DCG were also seen in growth rate of plants (data not shown). However, from day 9 onwards, quadratic responses to *PPF* were seen with RGR in all treatments. At harvest, the average RGR for plants grown at 5.3, 9.5, 14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ was 0.013, 0.027, 0.036, and 0.035 $g \cdot g^{-1} \cdot d^{-1}$, respectively (data not shown). The estimated RGR values in our experiment were lower than those reported for wax begonia (0.05 - 0.09 $g \cdot g^{-1} \cdot d^{-1}$, Kessler and Armitage, 1992), salvia [*Salvia splendens* F. Sellow ex Roem. & Schult., (0.15 - 0.2 $g \cdot g^{-1} \cdot d^{-1}$), van Iersel, 1997], and impatiens [*Impatiens parviflora,* (0.2 to 0.25 $g \cdot g^{-1} \cdot d^{-1}$), Peace and Grubb, 1982]. However, it is important to note that the growing environment, especially *PPF*, was different between our experiment and the other studies.

Throughout the experiment, CUE of plants responded quadratically to increasing *PPF* (Fig. 4.3). Carbon use efficiency of plants was higher at a *PPF* of 14.4 or 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ than at 5.3 or 9.5 $mol \cdot m^{-2} \cdot d^{-1}$ and did not differ much between 14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$. Carbon use efficiency increased after watering due to increases in DCG. There was a close correlation between CCG and CUE of plants in all treatments (R^2 = 0.85) and CUE_{max} was estimated to be 0.46 (0.18+0.28) $mol \cdot mol^{-1}$ (Fig. 4.4). Carbon use efficiency normally ranges from 0.5 to 0.7 $mol \cdot mol^{-1}$ (Bednarz and van Iersel, 1999; Gifford 1995). The estimated value of CUE_{max} was lower than normal, which may partially explain the slow growth habit of wax begonia.

The value of r_m decreased linearly with increasing *PPF* (Fig. 4.5). The maintenance coefficient was 0.06, 0.056, 0.051, and 0.052 $g \cdot g^{-1} \cdot d^{-1}$, for plants grown at 5.3, 9.5, 14.4, and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. However, there was no effect of increasing *PPF* on r_g of plants (Fig. 4.5). The growth coefficient was 0.70, 0.40, 0.63, and 0.59 $g \cdot g^{-1}$ for plants grown at 5.3, 9.5, 14.4, and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Earlier study on white clover [*Trifolium repens* L. (McCree,1982)] grown initially at high irradiance level (1750 : $mol \cdot m^{-2} \cdot s^{-1}$) and subsequently at low irradiance level (350 : $mol \cdot m^{-2} \cdot s^{-1}$) indicated that r_g remained constant and r_m decreased when plants were shifted from high (0.065 $g \cdot g^{-1} \cdot d^{-1}$) to low irradiance (0.039 $g \cdot g^{-1} \cdot d^{-1}$). In contrast to that experiment, plants in our study were grown in separate, constant *PPF* and better adapted to their environment due to shade tolerance. In their review, Hesketh and Jones (1980), reported r_m values for many species ranging from 0.006 to 0.091 $g \cdot g^{-1} \cdot d^{-1}$. The values of r_m in

our experiment were higher than that of italian ryegrass tops [Lolium multiflorum L. (0.037 $g \cdot g^{-1} \cdot d^{-1}$)], chrysanthemum [*Chrysanthemum morifolium* L. (0.017 $g \cdot g^{-1} \cdot d^{-1}$)], perennial ryegrass [*Lolium perenne* L. (0.014 $g \cdot g^{-1} \cdot d^{-1}$)] and tomato [*Lycopersicon esculentum* L. (0.012 $g \cdot g^{-1} \cdot d^{-1}$)] and lower than roots of italian ryegrass (0.091 $g \cdot g^{-1} \cdot d^{-1}$) as reported in their literature review. Compared to fast growing species, it is possible for a slow growing species like wax begonia to have a higher r_m. The r_g values estimated in our experiment were higher than those of maize [*Zea mays* L. (0.34 $g \cdot g^{-1}$)] and cotton [*Gossypium hirsutum* L. (0.33 - 0.39 $g \cdot g^{-1}$), but close to those of chrysanthemum (0.56 $g \cdot g^{-1}$), and roots of italian ryegrass (0.67 $g \cdot g^{-1}$) (reviewed by Hesketh and Jones, 1980).

Ontogenetic changes in r_m and r_g were reported by Stahl and McCree (1988). Their study on sorghum (*Sorghum bicolor* L.) indicated that r_m and r_g decreased with age. However, a high correlation between 1/CUE and 1/RGR obtained in our experiment (r^2 =0.99 in all treatments) would indicate little or no change in r_m and r_g during the growth period. Both R_m and R_g increased during the growth period within each treatment. Since DCG increased linearly and r_g was not affected by increasing *PPF*, R_g also increased linearly with increasing *PPF*. The values ranged from 0.14 to 0.58 $g \cdot d^{-1}$ at the end of the experiment in the different treatments. On the other hand, R_m at harvest ranged from 0.81 to 1.46 $g \cdot d^{-1}$. Although R_m increased linearly with increasing *PPF* during most of the growth period, quadratic responses were seen in R_m from day 22 onwards. From that stage, there were few differences in R_m of plants grown at 14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$.

The ratio of R_m to R_T in all treatments decreased during the growth period (Fig. 4.6). At the start of the experiment, maintenance respiration accounted for most of the total respiration (105 to 97% R_T). Percentage of R_m to R_T was greater than 100 in the two lowest *PPF* treatments due to negative R_g values resulting from negative DCG during the initial growth stage. However, percentage of R_m to R_T decreased during the growth due to consistent increases in R_g of plants. At harvest, the percentage of R_m to R_T for plants grown at 5.3, 9.5, 14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ were 87, 84, 69, and 71%, respectively. This indicates that the fraction of carbohydrates used in maintenance respiration was high for plants grown at the two lowest *PPF*s in our experiment. Maintenance respiration, according to Penning deVries (1975) includes the processes that maintain cellular structures and intracellular gradients of ions and metabolites, along with cellular acclimation (phenotypic adjustment) to environmental changes. Replacement of one set of enzymes with another during ontogeny may also be considered maintenance (Amthor, 2000). It is possible that the plants grown at the two lowest *PPF* treatments had a higher percentage of maintenance to total respiration to enable them to adapt to the low *PPF*. The decrease in the ratio of R_m/R_T with increasing *PPF* is largely due to the increase in the size of the pool of carbohydrates (due to higher photosynthetic rates), making more carbohydrates available for growth related processes (DCG and R_g). The decrease in r_m and R_m/R_T with increasing *PPF* resulted in an increase in CUE of plants grown at high *PPF*. Usually, growth respiration is large (80% of R_T) during the vegetative stage, and decreases during the reproductive stage (20% of R_T; Lawlor, 1995).

However, wax begonias in our experiment had more maintenance respiration than growth respiration throughout their growth period.

WUE- PPF relationship. Water ! use efficiency of plants responded quadratically with increasing *PPF*. There was a large increase in WUE of plants from 5.3 to 9.5 $mol \cdot m^{-2} \cdot d^{-1}$, a relatively small increase for plants grown at 14.4 $mol \cdot m^{-2} \cdot d^{-1}$, and little further increase for plants grown at 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 4.7). Alexander et al. (1995) reported that WUE of red spruce (*Picea rubens* Sarg.) increased linearly when *PPF* was increased from 100 to 550 : $mol \cdot m^{-2} \cdot s^{-1}$. The initial steep increase in the curve (Fig. 4.7) is due to higher GR and relatively smaller increase in ET (increase of 143 and 18%, respectively) at 9.5 $mol \cdot m^{-2} \cdot d^{-1}$ compared to those grown at 5.3 $mol \cdot m^{-2} \cdot d^{-1}$. Water ! use efficiency of cherry (*Prunus avium* L.) was higher under 39% shade than in natural light conditions due to lower transpiration rates (Centritto et al., 2000). However, compared to plants grown at 9.5 $mol \cdot m^{-2} \cdot d^{-1}$, increase in GR and ET were 71 and 59 % for plants grown at 14.4 $mol \cdot m^{-2} \cdot d^{-1}$. For plants grown at a *PPF* of 19.4 $mol \cdot m^{-2} \cdot d^{-1}$, there was a 17.8 % increase in GR and a slight increase in ET (5.6 %) compared tothose grown at 14.4 $mol \cdot m^{-2} \cdot d^{-1}$.

At the lowest *PPF* level (5.3 $mol \cdot m^{-2} \cdot d^{-1}$), photosynthesis was limited by *PPF,* which resulted in a considerable decrease in WUE of plants. Plants grown at higher *PPF* levels had higher photosynthetic rates due to more available light and also higher transpiration rates due to increased leaf area, and probably higher leaf temperature and stomatal conductance. But WUE of plants increased

with *PPF* because the positive effects of increasing *PPF* on photosynthesis were larger than the negative effects of increasing ET in plants.

Photosynthetic !PPF response curves. There was a close relationship between P_n and increasing *PPF* for plants in different treatments (R^2 ranged from 0.98 to 0.99). In general, P_n was higher for plants grown at 19.1 $mol \cdot m^{-2} \cdot d^{-1}$ than those at 14.4, 9.5, or 5.3 $mol \cdot m^{-2} \cdot d^{-1}$. Dark respiration rate (R_d) of plants was higher (more negative) for plants grown at 19.1 and 14.4 $mol \cdot m^{-2} \cdot d^{-1}$ than those grown at 9.5 and 5.3 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 4.8, Table 4.2).

Although R_d was significantly different, the light compensation point did not differ significantly among different treatments and ranged from 15 to 27 : $mol\,m^{-2}\,s^{-1}$ (Table 4.2). These values are lower than those of angelonia [*Angelonia angustifolia* Benth., (67 to 86 : $mol\,m^{-2}\,s^{-1}$), Miller et al., 2000], and eastern redbud [Cercis canadensis L. (80 : $mol\,m^{-2}\,s^{-1}$), Norcini et al., 1991b], and close to those of *Calamogrostis canadensis* (15.3 to 31.5 : $mol\,m^{-2}\,s^{-1}$, Greenway and Lieffers, 1997) and poinsettia [*Euphorbia pulcherrima* Willd. ex Klotzsch, (31 to 51 : $mol\,m^{-2}\,s^{-1}$), Nell and Barrett, 1986]. The light compensation point of plants grown in shade generally is lower than that of plants grown in full sun due to lower respiration rate (Callan and Kennedy, 1995; Greenway and Lieffers, 1997). However, Norcini et al. (1991) reported that the light compensation point of eastern redbud was not affected by preconditioning plants to either sun or shade.

Quantum yield of plants in different treatments increased linearly with increasing *PPF*. The lowest and highest values observed in our experiment were 0.025 and 0.054 $mol \cdot mol^{-1}$ (Table 4.2). Since " is expressed per unit incident, not

absorbed, *PPF,* the fraction of *PPF* that is absorbed by the plants would be expected to affect ". Indeed, due to increased leaf area, radiation capture was likely higher for plants grown at 19.4 mol m^{-2} d^{-1} than those grown at 14.4, 9.5 or 5.3 mol m^{-2} d^{-1}, resulting in a higher ". Giaglaras et al. (1995) also reported that the measured " (per unit ground area and expressed per unit incident light) value of begonia (*Begonia xheimalis*) as 0.066 mol·mol^{-1}. Miller et al. (2001) reported " values (per unit ground area and expressed per unit incident light) of two cultivars of angelonia as 0.026 and 0.038 mol·mol^{-1}. In general, quantum yield expressed per unit absorbed light, remains insensitive to light environment during the growth period (Thornley, 1998; Close et al., 2001).

We estimated quantum yield per unit leaf area to study the canopy effects and compare with other published values as most of them are based on leaf P_n. Regression analysis indicated no significant increase or decrease in quantum yield per unit leaf area with increasing *PPF* in different treatments. This indicates that increase in " was due to increase in leaf area and not due to any canopy effects like shading of bottom leaves in canopies with large leaf area. The estimated values of quantum yield per unit leaf area for plants grown at 5.3, 9.5, 14.4, and 19.4 mol m^{-2} d^{-1} were 0.019, 0.017, 0.018, and 0.022 mol·mol^{-1}, respectively. Quantum yield expressed on a leaf area basis is likely to be higher than that expressed on ground basis due to high fraction of incident *PPF* usually absorbed by leaves. In contrast to our results, Funnell et al. (2002) reported that the quantum yield measured per unit incident light and expressed per unit leaf area of *Zantedeschia* was lower for plants grown at high *PPF* (694 : mol m^{-2} s^{-1})

than those grown at a low *PPF* (348 : mol m^{-2} s^{-1}). However, the lower *PPF* treatment in their experiment was close to the highest *PPF* treatment in our experiment (394 : mol m^{-2} s^{-1}). Rosati et al. (1999) estimated that " (per unit leaf area and expressed per unit incident light) values differed significantly between inner and outer canopy leaves in nectarine trees [*Prunus persica* L. Batsch (0.031 for inner canopy and 0.061 for outer canopy].

In Fig. 4.8, we can compare the photosynthetic rates of plants grown in different treatments. The curves cross at about 50 : mol m^{-2} s^{-1}. Below this *PPF*, plants grown in low light outperform those grown in high light. Because of lower respiration rates, shade grown plants fix more net CO_2 than sun plants under low light conditions. Above 50 : mol m^{-2} s^{-1}, the effects are reversed. In this region, plants grown in high light had higher P_n than those grown in low light. Generally, photosynthesis becomes limited by RUBISCO levels, with increasing *PPF*. Because sun plants have more RUBISCO and a more efficient photosynthetic apparatus than shade grown plants (Björkman, 1981), they perform better than shade plants under high *PPF*.

Light saturated gross photosynthesis of plants per unit ground area increased linearly with increasing *PPF*, partly due to increased light interception by plants. The values of $P_{g\,max}$ ranged from 4.9 to 9.3 : mol m^{-2} s^{-1} (Table 4.2). When plants are exposed to increased light, their photosynthetic capacity changes gradually and adjusts to the new light intensity. The time constant for this gradual change depends on regeneration of RUBISCO from leaf nitrogen content (Thornley, 1998).

Specific respiration and $P_{g\ max,\ LA}$ increased linearly with increasing *PPF* (Table 4.2). Giaglaras et al. (1994) estimated specific respiration in *Begonia* x *hiemalis* to be 0.01 $\mu mol\ g^{-1}\ s^{-1}$. This value is lower than those obtained in our experiment for wax begonia (0.043 to 0.077 $\mu mol\ g^{-1}\ s^{-1}$). However, the constant temperature under which plants were grown in their experiment was lower (20 °C) than that in our experiment (25 °C). This could possibly explain a higher respiration rate of plants in our experiment than that observed by Giaglaras et al. (1994).

Leonardos et al. (1994) estimated $P_{n\ max,\ LA}$ (Which is $P_{g\ max,\ LA}$ minus R_d) for alstroemeria (*Alstroemeria* 'Jacqueline') as 10.5 $\mu mol\ m^{-2}\ s^{-1}$, which is higher than $P_{g\ max,\ LA}$ estimated for wax begonia in our experiment. Miller et al. (2001) estimated response of leaf photosynthesis to irradiance in angelonia (*Angelonia aungustifolia*). In their experiment, light saturation of whole-plants was not seen at the maximum *PPF* achieved (600 $\mu mol\ m^{-2}\ s^{-1}$). The values of P_n per unit leaf area of angelonia cultivars ranged from 8 to 12 $\mu mol\ m^{-2}\ s^{-1}$. Baille et al. (1996) reported $P_{n\ max,\ LA}$ in rose to be 13.5 $\mu mol\ m^{-2}\ s^{-1}$. This indicates that $P_{g\ max,\ LA}$ in wax begonia is lower than that of other reported crops. This perhaps explains the slow growth rate and higher ratio of R_m / R_T in wax begonias.

Usually, plants grown in full sun have a higher light saturation point than that of shade grown plants (Callan and Kennedy, 1995; Funnell et al., 2002). In our experiment, P_n of plants in all treatments reached 'light-saturation' at around 600 to 700 $\mu mol\ m^{-2}\ s^{-1}$ and the light saturation point did not differ significantly between treatments. Saturation with increasing *PPF* occurs because other

environmental or biochemical factors like the amounts of CO_2, RUBISCO, or its substrate ribulose!*bis*!phosphate become limiting (Lawlor, 1995). However, the light saturation points of soybean (*Glycine max* (L.) Merr.) grown at either high (1000-1500 :mol@m^{-2}@ s^{-1}) or low (250 - 500 :mol@m^{-2}@ s^{-1}) *PPF* also did not differ significantly (Seemann, 1989).

Although light compensation and saturation points did not differ significantly between treatments, the increase in $P_{g\ max,\ LA}$ with increasing *PPF* during the growth period indicate that growth of wax begonias would be better when grown under high *PPF*. It also indicates that wax begonia leaves grown at high *PPF* are more efficient in photosynthesis at high than low *PPF* levels.

Conclusions

Plants grown at 5.3 and 9.5 mol@m^{-2}·d^{-1} had a low growth rate due to inadequate light, insufficient light interception (due to small leaf area), and low photosynthetic rate. Growth rate of plants increased with increasing *PPF* due to consistent increases in the photosynthetic capacity ($P_{gmax,\ LA}$) and radiation capture (due to increased leaf area) resulting in increased quantum yield. Carbon use efficiency and RGR of wax begonia were lower than most reported values for other crops. This study indicates that the importance of maintenance respiration on carbon balance, and thereby, growth rate of plants, increases for plants grown under low *PPF*. Smaller carbohydrate pools result from lower photosynthetic rates compared to those grown at high *PPF*. Therefore, only a

small fraction of the total carbohydrate pool is available for growth and growth respiration after meeting the maintenance requirements. This explains the higher R_m / R_T and lower growth rate of plants grown at 5.3 and 9.5 mol·m^{-2}·d^{-1}. Higher R_m than R_g of plants in all treatments is an interesting result and would partly explain the low CUE and slow GR of wax begonias.

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Table 4.1. Effect of daily photosynthetic photon flux (*PPF*) on growth parameters of subirrigated wax begonia; DW_{CROP}= crop dry weight, DW_{SHOOT} = shoot dry weight, DW_{ROOT} = root dry weight, LAR_{PLANT} = leaf area ratio per plant, LAR_{SHOOT} = leaf area ratio per shoot, shoot to root ratio = DW_{SHOOT} / DW_{ROOT} . Statistical significance was tested using quadratic regression and the quadratic component was found to be not significant (*PPF* = coefficient for linear effect).

PPF	Chlorophyll	Leaf area	DW_{CROP}	DW_{SHOOT}	DW_{ROOT}	LAR_{PLANT}	LAR_{SHOOT}	shoot to root ratio
$mol \cdot m^{-2} \cdot d^{-1}$	spad units	m^2	g	g	g	$m^2 \cdot kg^{-1}$	$m^2 \cdot kg^{-1}$	
5.3	30.3	0.8	23.9	16.4	7.6	31.5	46.2	2.2
9.5	29.3	1.1	30.5	19.8	10.7	36.1	55.8	1.9
14.4	29.2	1.3	36.3	26.3	10.1	35.8	49.6	2.6
19.4	28.5	1.4	38.4	27.2	11.2	37.5	53.1	2.4
R^2	0.71	0.80	0.89	0.89	0.43	0.19	0.03	0.45
significance	L*	L**	L***	L***	NS	NS	NS	NS
intercept	30.6 ***	0.58**	19.4***	12.2 ***	9.9	35.2	51.2	2.3
PPF	-0.11 *	0.05 **	1.07***	0.85***	-^{NS}	-	-	-

^{NS}, *, **, ***, not significant and significant at $P < 0.05$, or 0.005, or 0.0005, respectively

Table 4.2. Effect of photosynthetic photon flux (*PPF*) on photosynthesis - *PPF* response parameters of wax begonia. Measured values per unit ground area include net photosynthesis (P_n), light-saturated maximum gross photosynthesis ($P_{g,max}$), dark respiration rate (R_d), and light saturated maximum net photosynthesis ($P_{n\,max}$). " = quantum yield, R_{spec} = specific respiration, $P_{gmax,LA}$ = maximum gross photosynthesis per unit leaf area, LCP = light compensation point, LSP = light saturation point; Statistical significance was tested using quadratic regression and the quadratic component was found to be not significant (*PPF* = coefficient for linear effect).

PPF $mol \cdot m^{-2} \cdot d^{-1}$	" $mol \cdot mol^{-1}$	P_{gmax} : $mol \cdot m^{-2} \cdot s^{-1}$	R_d : $mol \cdot m^{-2} \cdot s^{-1}$	P_{nmax} : $mol \cdot m^{-2} \cdot s^{-1}$	R_{spec} : $mol \cdot g^{-1} \cdot s^{-1}$	$P_{gmax,LA}$: $mol \cdot m^{-2} \cdot s^{-1}$	LCP : $mol \cdot m^{-2} \cdot s^{-1}$	LSP : $mol \cdot m^{-2} \cdot s^{-1}$
5.3	0.030	4.90	-0.40	4.50	-0.043	3.161	15.0	497
9.5	0.045	6.42	-0.68	5.75	-0.054	3.130	21.0	553
14.4	0.047	9.06	-1.18	7.89	-0.070	3.537	27.0	572
19.4	0.054	9.39	-1.32	8.07	-0.077	3.758	26.0	521
r^2	0.79	0.81	0.89	0.77	0.61	0.61	-^{NS}	-
significance	L*	L*	L*	L*	L*	L*	NS	NS
intercept	0.0197*	3.138*	-0.0385^{NS}	3.102*	-0.0299*	2.843***	22	536
PPF	0.0018*	0.363*	-0.0717*	0.291*	-0.0026*	0.0451*	-	-

^{NS}, *, **, *** not significant and significant at $P < 0.05$, 0.005, or 0.0005, respectively

Figure 4.1. Correlation between crop dry weight and cumulative carbon gain of wax begonia at the end of the experiment. Carbon content in the plants was estimated from the slope of the equation as 12 $g \cdot mol^{-1}$ / 21.4 $g \cdot mol^{-1}$ = 0.56 $g \cdot g^{-1}$ (a mole of C equals to 12 g). Data represents means of 35 plants in each each experimental unit from two replications. Due to loss of data from one experimental unit only seven data points were shown.

Figure 4.1.

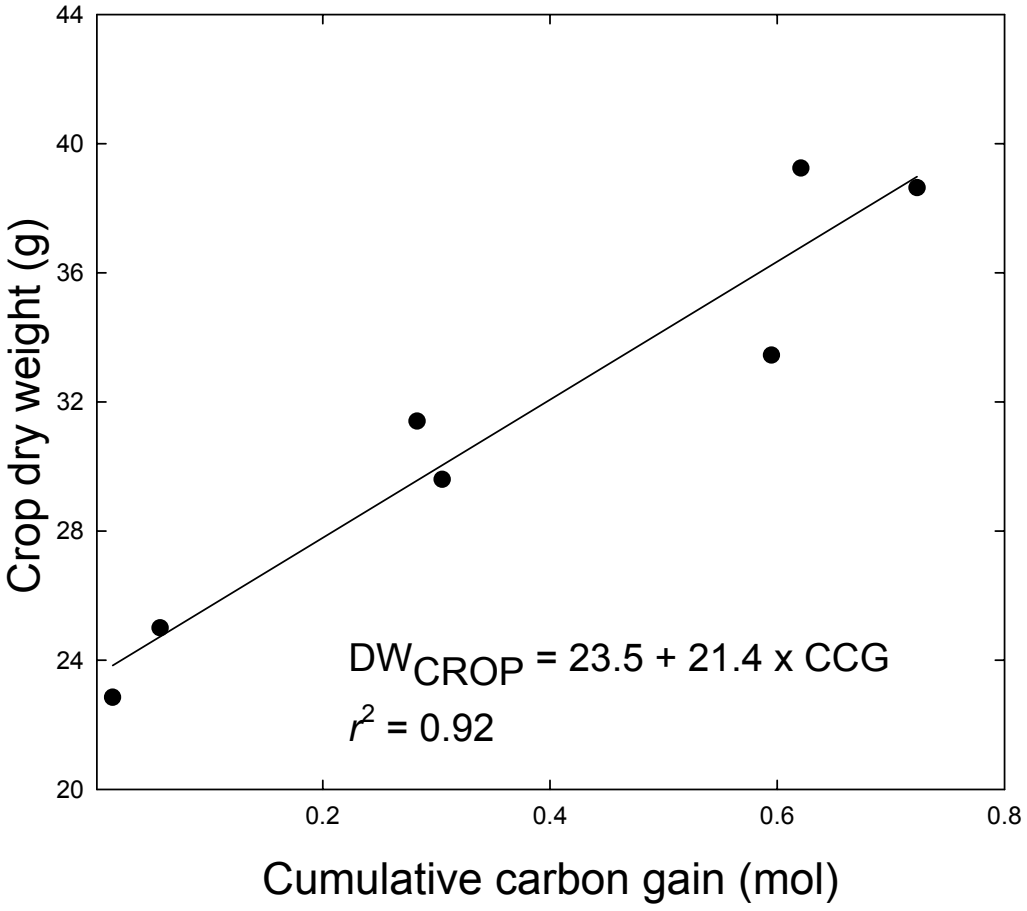

44
40
36
32
28
24
20
Crop dry weight (g)
0.2
0.4
0.6
0.8
Cumulative carbon gain (mol)
DW$_{CROP}$ = 23.5 + 21.4 x CCG
r^2 = 0.92

Figure 4.2. Effect of photosynthetic photon flux on daily average net photosynthesis ($P_{n, avg}$), dark respiration ($R_{d, avg}$), and gross photosynthesis ($P_{g, avg}$) of subirrigated wax begonias during a period of 25 d. Data represent groups of 35 plants, averaged over two replications. Arrows indicate the time that the plants were subirrigated. Data were analyzed daily by regression. Statistical analysis indicated that all the three parameters increased linearly with increasing photosynthetic photon flux throughout the experiment.

Figure 4.2.

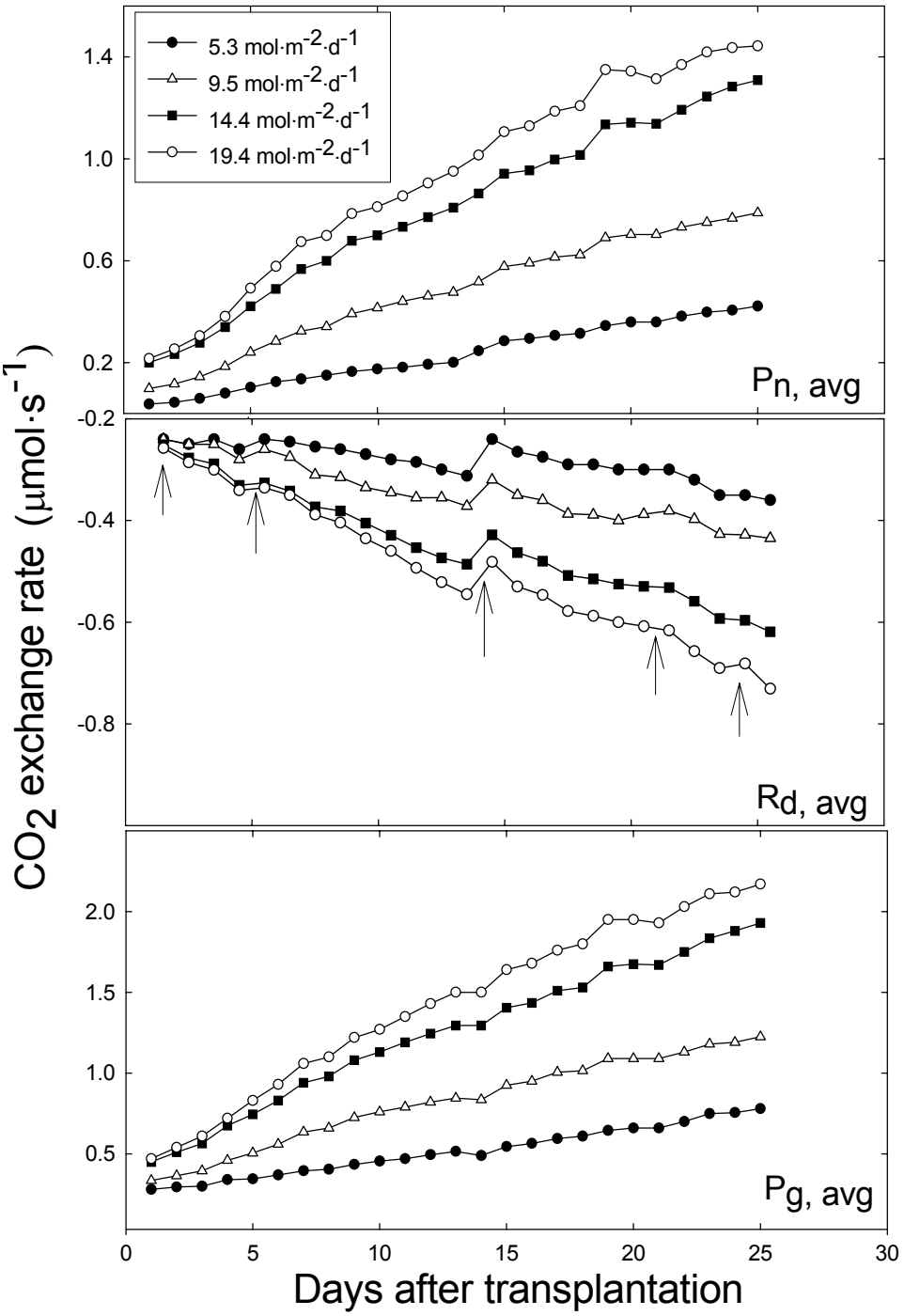

5.3 mol·m-2·d-1
9.5 mol·m-2·d-1
14.4 mol·m-2·d-1
19.4 mol·m-2·d-1
Pn, avg
Rd, avg
Pg, avg
CO2 exchange rate (µmol·s-1)
Days after transplantation
1.4
1.0
0.6
0.2
-0.2
-0.4
-0.6
-0.8
2.0
1.5
1.0
0.5
0
5
10
15
20
25
30

Figure 4.3. Effect of photosynthetic photon flux on daily carbon gain (DCG), cumulative carbon gain (CCG) and carbon use efficiency (CUE) of subirrigated wax begonias during a period of 25 d. Data represent groups of 35 plants, averaged over two replications. Data were analyzed daily by regression. Negative DCG, CCG, and CUE values indicate that respiration rates were higher than gross photosynthesis of plants soon after transplantation. Daily data analysis indicated that DCG and CCG increased linearly and CUE of plants responded quadratically with increasing *PPF* during most of the growth period, however quadratic correlations in DCG and CCG were seen prior to watering plants.

Figure 4.3.

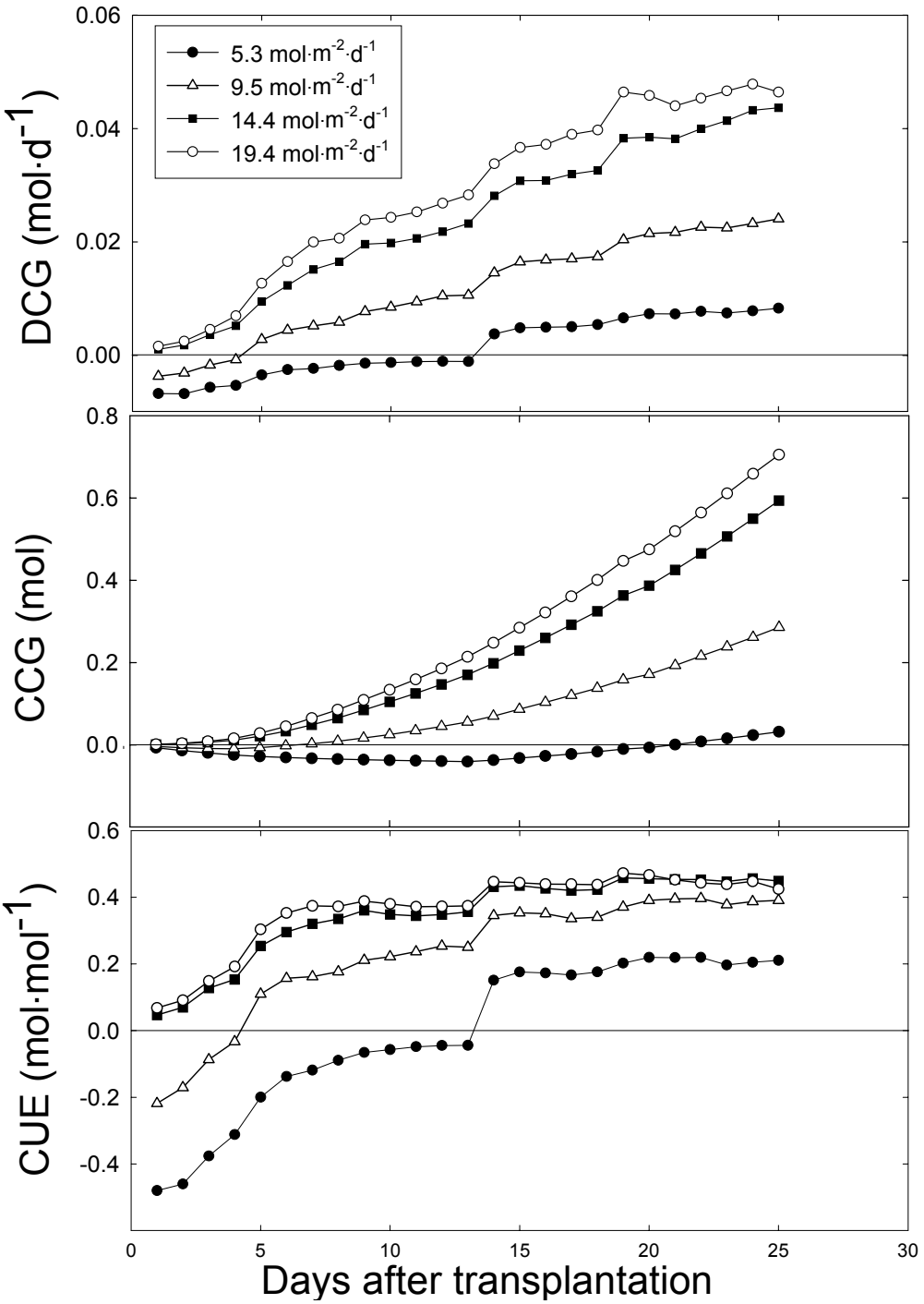

5.3 mol·m-2·d-1
9.5 mol·m-2·d-1
14.4 mol·m-2·d-1
19.4 mol·m-2·d-1
DCG (mol·d-1)
CCG (mol)
CUE (mol·mol-1)
Days after transplantation

Figure 4.4. Carbon use efficiency (CUE) as a function of cumulative carbon gain. An asymptotic equation was fitted to describe the relationships. Data points from all experimental units are shown. Only positive CUE values are shown and were used for the regression.

Figure 4.4.

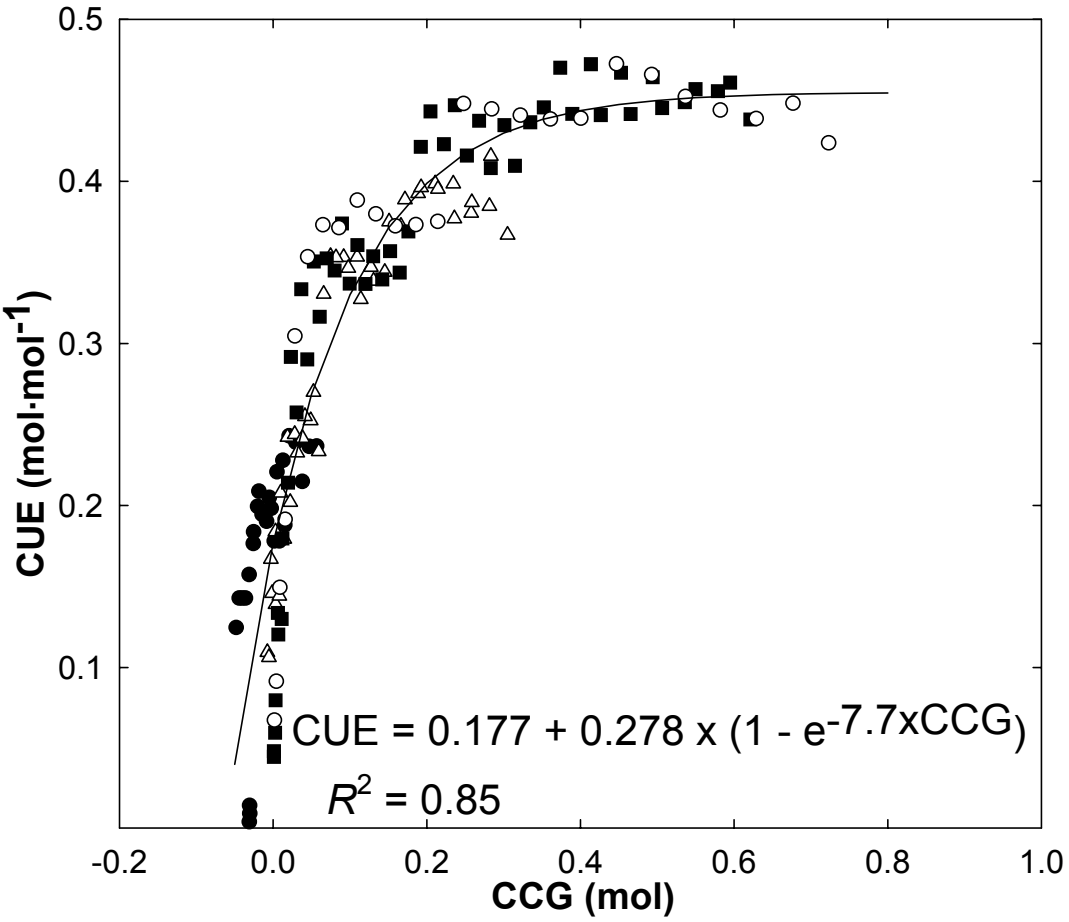

0.5
0.4
0.3
0.2
0.1
CUE (mol·mol-1)
CUE = 0.177 + 0.278 x (1 - e-7.7xCCG)
R2 = 0.85
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
CCG (mol)

Figure 4.5. Correlations between 1/ CUE vs. 1/ RGR in different treatments. Data represent daily measurements from two replications for a period of 25 d on groups of 35 plants in each replication. Linear regression was used to estimate the maintenance (r_m) and growth respiration (r_g) coefficients *(1/CUE = 1+r_g + r_m/RGR)*.

Figure 4.5.

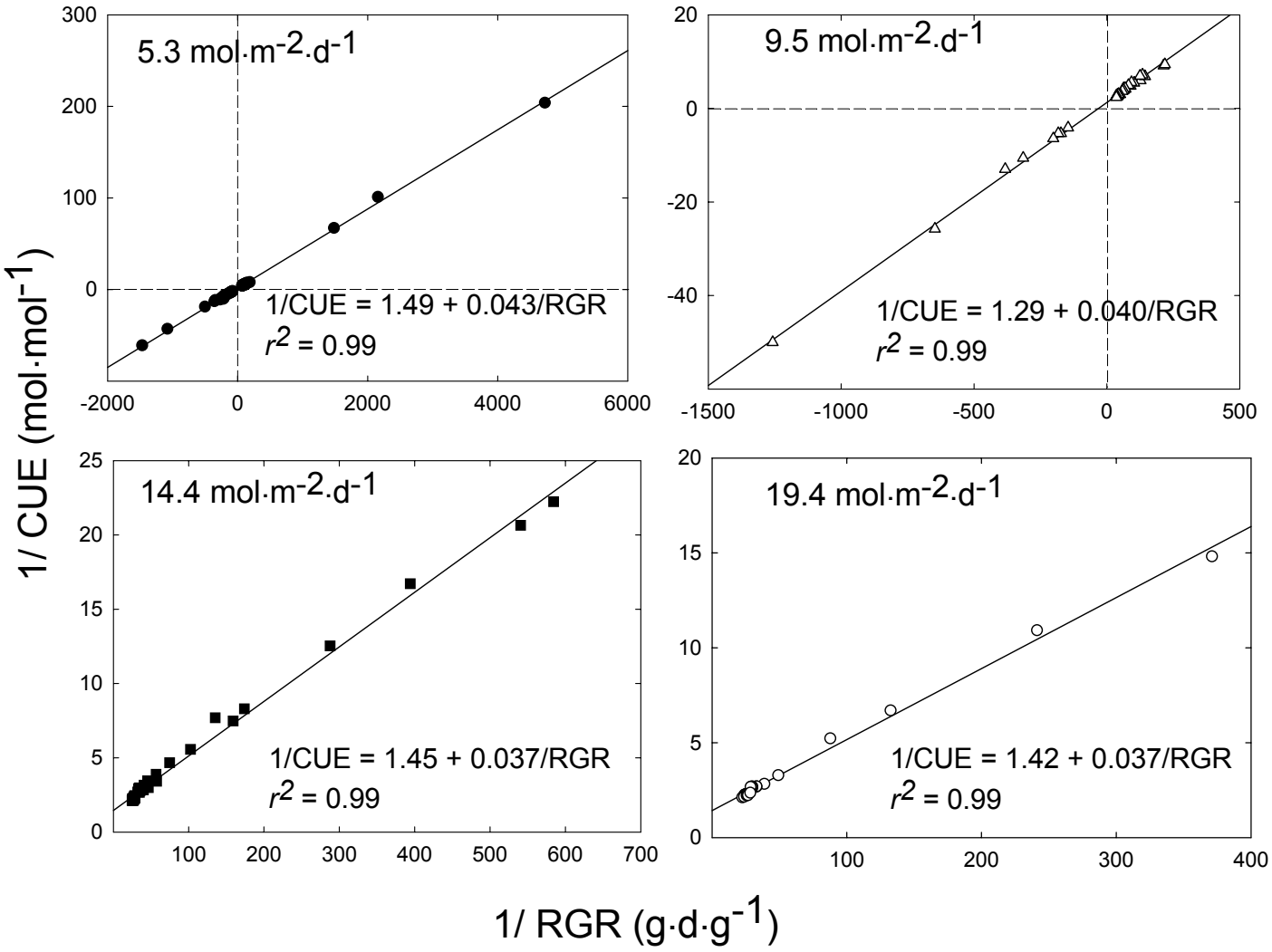

5.3 mol·m-2·d-1
1/CUE = 1.49 + 0.043/RGR
r2 = 0.99
9.5 mol·m-2·d-1
1/CUE = 1.29 + 0.040/RGR
r2 = 0.99
14.4 mol·m-2·d-1
1/CUE = 1.45 + 0.037/RGR
r2 = 0.99
19.4 mol·m-2·d-1
1/CUE = 1.42 + 0.037/RGR
r2 = 0.99
1/ CUE (mol·mol-1)
1/ RGR (g·d·g-1)

Figure 4.6. Estimated maintenance respiration of subirrigated wax begonias shown as percentage of total respiration during 25 d of crop growth. Data represent groups of 35 plants averaged over two replications. Linear correlation between percentage of R_m to R_T and increasing *PPF* was seen from day 5, and from day 12, quadratic responses were noted.

Figure 4.6.

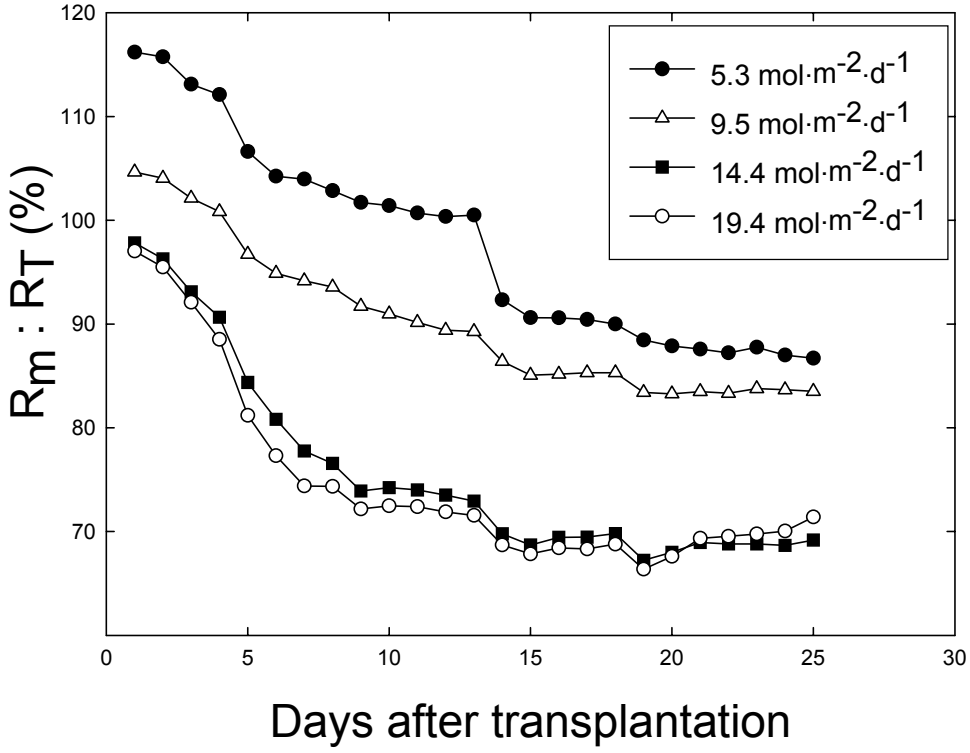

120
110
100
90
80
70
0
5
10
15
20
25
30
$R_m : R_T$ (%)
Days after transplantation
5.3 mol·m-2·d-1
9.5 mol·m-2·d-1
14.4 mol·m-2·d-1
19.4 mol·m-2·d-1

Figure 4.7. Effect of photosynthetic photon flux (*PPF*) on net assimilation rate (NAR) and water use efficiency (WUE) of subirrigated wax begonia at the end of experiment. Data represent groups of 35 and 12 (from all experimental units) plants for NAR and WUE, respectively. Curves in the graphs indicate significant quadratic effects.

Figure 4.7.

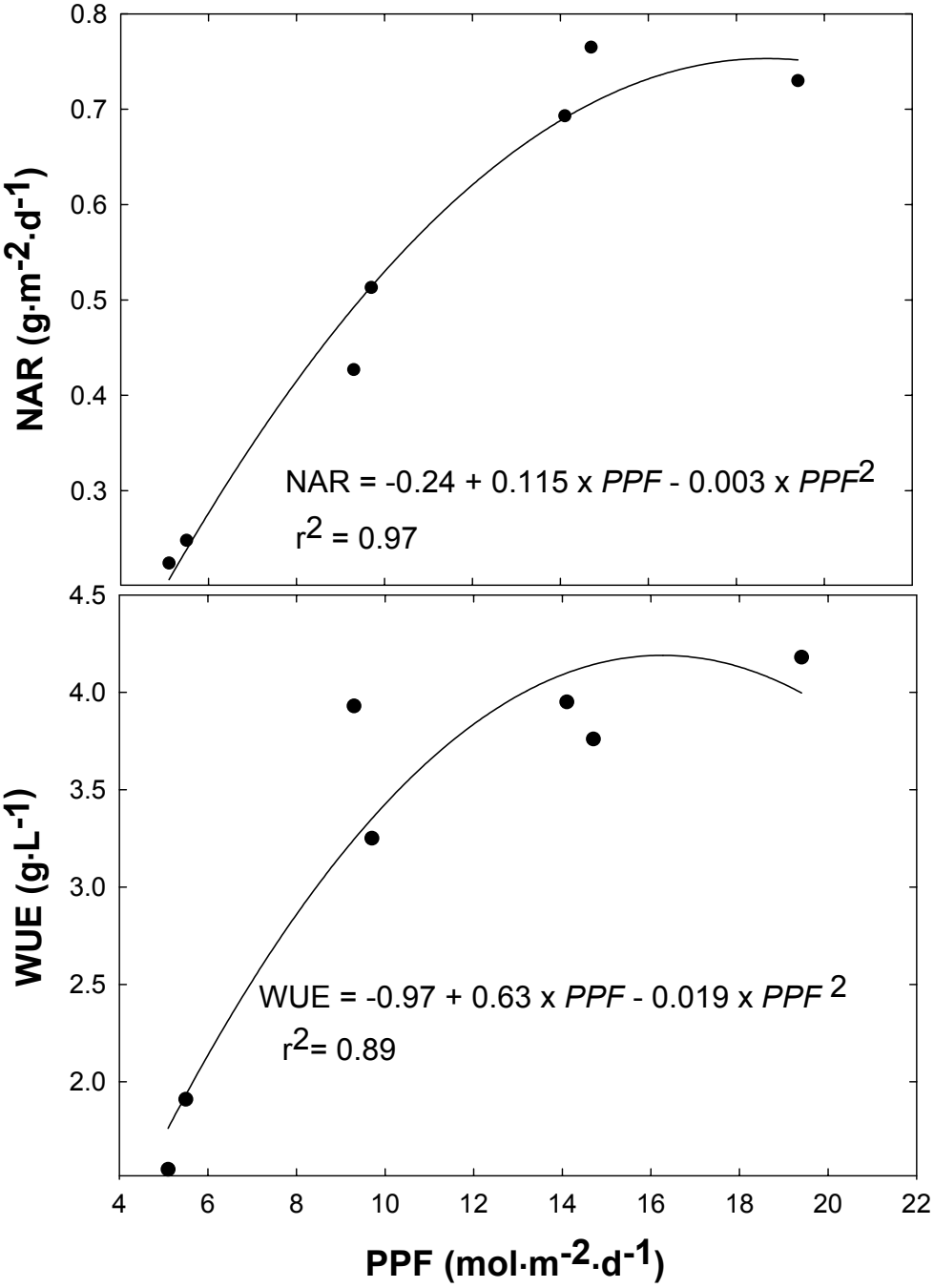
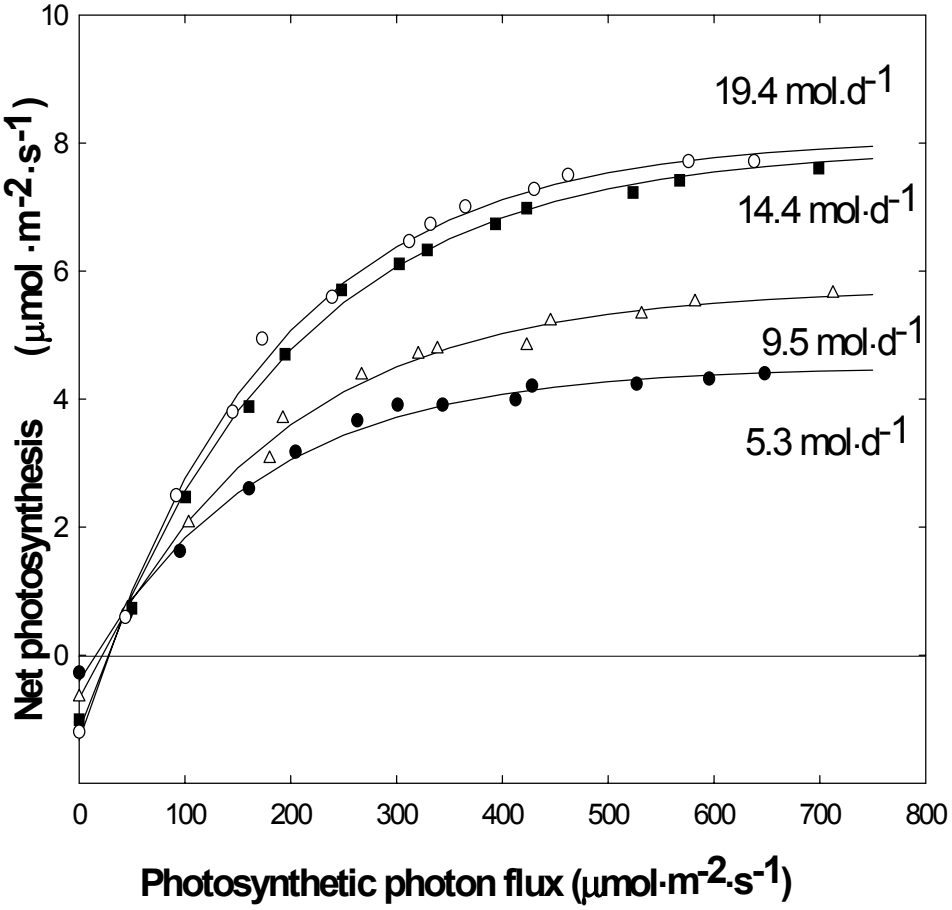

NAR (g·m-2·d-1)
NAR = -0.24 + 0.115 x PPF - 0.003 x PPF2
r2 = 0.97
WUE (g·L-1)
WUE = -0.97 + 0.63 x PPF - 0.019 x PPF 2
r2= 0.89
PPF (mol·m-2·d-1)

Figure 4.8. Effect of increasing photosynthetic photon flux (*PPF*) on net photosynthesis per unit ground area. Data represent groups of 12 plants averaged over two replications. (see Table 2 for regression results). R^2 values ranged from 0.98 to 0.99.

Figure 4.8.


19.4 mol.d-1
14.4 mol·d-1
9.5 mol·d-1
5.3 mol·d-1
Net photosynthesis (µmol ·m-2.s-1)
Photosynthetic photon flux (µmol·m-2.s-1)
10
8
6
4
2
0
0
100
200
300
400
500
600
700
800

CHAPTER 5

CONCLUSIONS

The overall objective of this research project was to see whether fertilizer recommendations should be adjusted based on the prevailing light intensity, and to study the physiological mechanisms by which light affects plant growth and water ! use. In experiments 1 and 2, the effect of increasing photosynthetic photon flux (*PPF*) on water ! use efficiency (WUE) and optimal fertilizer concentration (or electrical conductivity, EC) of subirrigated wax begonia and petunia was studied. Also, in experiment 1, the influence of a starter fertilizer on the optimal fertilizer concentration for subirrigated wax begonia was investigated. In experiment 3, the effect of increasing *PPF* on whole ! plant photosynthesis and respiration, and growth rate of wax begonia was quantified. These three experiments provided valuable information about the effects of *PPF* on plant water ! use efficiency, whole ! plant metabolism, and indirectly, optimal fertilizer concentrations for plants.

In experiment 1, growth of wax begonia at low *PPF* (4.4 mol$\cdot$m$^{-2}\cdot$d^{-1}) was limited by *PPF,* and not nutrients. Shoot dry weight did not respond to increased fertilizer EC at low *PPF* and increased linearly with fertilizer EC (from 0.15 to 1.4 dS$\cdot$m^{-1}) at medium or high *PPF* (6.2 or 9.9 mol$\cdot$m$^{-2}\cdot$d^{-1}) *PPF* treatments. In experiment 2, both the fertilizer EC range (0.12 to 2.77 dS$\cdot$m^{-1}) and incident *PPF*

(9.8, 15.6, and 23.2 mol·m^{-2}·d^{-1}) were higher than those in experiment 1. However, the optimal range of fertilizer EC for wax begonia in experiment 2 was similar in the three *PPF* treatments. The effects of increasing *PPF* and fertilizer EC were similar for the fast growing, sun ! loving species, petunia. The optimal range of fertilizer EC for wax begonia was 0.65 to 1.77 dS·m^{-1} and for petunia, it ranged from 1.18 to > 2.77 dS·m^{-1}. The results from experiments 1 and 2 indicate that the fertilizer concentrations for subirrigated plants need not be adjusted based on the *PPF* level inside a greenhouse, even though the physiological results indicate that WUE and required nitrogen concentration of the fertilizer solution (N_{FERT}, the estimated nitrogen concentration of the fertilizer solution to maintain plant tissue levels at the desired level) for subirrigated wax begonia increased with *PPF*. It is important to note that N_{FERT} was estimated based on a desired tissue N concentration of 45 mg·g^{-1}. The recommended tissue N concentration of wax begonia is between 20 and 60 mg·g^{-1}, which indicates that a lower tissue N concentration than 45 mg·g^{-1} may be sufficient. This possibly explains the inconsistency that the increase seen in N_{FERT} with increasing *PPF* is not supported by data on plant growth in both experiments 1 and 2.

Presence of a starter fertilizer in the growing medium affected the optimal concentration of the fertilizer solution. In the absence of a starter fertilizer, a fertilizer EC of 0.8 to 1.4 dS·m^{-1} was optimal, while a low fertilizer EC (0.3 to 0.5 dS·m^{-1}) was sufficient for growing subirrigated wax begonias in the presence of a starter fertilizer. The electrical conductivity of the growing medium was not

affected by *PPF* in experiments 1 and 2. In experiment 1, when the growing medium did not contain a starter fertilizer, the optimal growing medium EC for wax begonia was in the range of 1.26 to 2.14 $dS \cdot m^{-1}$. In experiment 2, it was in the range of 1.43 to 2.8 $dS \cdot m^{-1}$. However, shoot dry weight in experiment 1 still increased at the highest tested fertilizer EC, so the upper bound of the optimal range determined in that experiment may have been an underestimate. Based on the combined results from experiments 1 and 2, the optimal range of the growing medium EC for wax begonia appears to be from 1.3 to 2.8 $dS \cdot m^{-1}$, which is lower than that seen for petunia (2.2 to > 3.5 $dS \cdot m^{-1}$).

In experiment 3, the effect of *PPF* on the physiology of wax begonia was studied on a whole!plant scale. Gross and net!photosynthesis, and dark respiration rates of plants increased linearly with increasing *PPF* throughout the experiment. Although daily carbon gain (growth rate) increased linearly, relative growth rate of plants increased little at high *PPF*. This indicates that the efficiency of existing biomass to produce new biomass increased little at high *PPF.* This is also seen in carbon use efficiency which was higher at a *PPF* of 14.4 or 19.4 $mol \cdot m^{-2} \cdot d^{-1}$ than at 5.3 or 9.5 $mol \cdot m^{-2} \cdot d^{-1}$ and did not differ much between 14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$. Although maintenance respiration (R_m) increased, the proportion of R_m to total respiration decreased with increasing *PPF*. This is probably due to the larger carbohydrate pool available to plants at the two highest *PPF* treatments (14.4 and 19.4 $mol \cdot m^{-2} \cdot d^{-1}$) than to those at the two lowest *PPF* treatments (5.3 and 9.5 $mol \cdot m^{-2} \cdot d^{-1}$) due to higher gross photosynthesis (P_g). Also, leaf area increased with increasing *PPF* and further

increased P_g in plants. Photosynthetic ! light response curves indicated that increased carbon assimilation with increasing *PPF* was mainly due to increased P_g per unit leaf area.

Overall, the above three experiments indicated significant findings about the effects of *PPF* on optimal fertilizer concentration and growth rate of subirrigated plants. Wax begonias can be grown successfully with low fertilizer concentrations when the growing medium contains a starter fertilizer. Our results indicate that the greenhouse *PPF* level had no effect on the optimal fertilizer concentration of both wax begonia and petunia. Growth rate of wax begonias increased even at the highest *PPF* (19.4 $mol \cdot m^{-2} \cdot d^{-1}$) tested in experiment 3, which indicates that wax begonia is not necessarily an obligate but perhaps a facultative shade species. Plants grown at high *PPF* had higher dry weight than those grown at low *PPF*. Increased growth rate of plants at high *PPF* was due to the larger amount of carbon allotted to growth and growth respiration than in plants at low *PPF*, after meeting the maintenance needs.