

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

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Abstract

The effect of increasing photosynthetic photon flux (PPF) on photosynthesis and respiration in wax begonia (*Begonia semperflorens* –cultorum) was examined by measuring CO₂ exchange rate (CER) of plants continuously for a period of 25 days under four different PPF treatments (5.3, 9.5, 14.4, and 19.4 mol·m⁻²·d⁻¹) in a whole-plant gas exchange system. Net-photosynthesis (P_n) and dark respiration (R_d) in plants increased linearly with increasing PPF. Plants grown at 5.3 or 9.5 mol·m⁻²·d⁻¹ respired more than they photosynthesized during the initial growth period, which resulted in a negative daily carbon gain (DCG). It appears that the cost of acclimation to low PPF for plants grown at 5.3 and 9.5 mol·m⁻²·d⁻¹ was high as the percentage of maintenance (R_m) to total respiration (R_T) at harvest was 87 and 83 %, respectively, while it was only 70% at 14.4 and 19.4 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. At harvest, crop dry weight (DW_{CROP}) increased linearly with increasing PPF. At the end of the experiment, plants grown at high PPF had an increased photosynthetic capacity [because of increased total leaf area (LA) and radiation capture], DCG, and growth respiration. These data indicate that low PPF not only decreases the photosynthetic rate but also increases the importance of maintenance respiration in the carbon balance of the plants, thereby further reducing the growth rate of plants.

INTRODUCTION

Dry matter production and crop growth rate are strongly correlated to the amount of light intercepted by plants (Lawlor, 1995). To capture the maximum amount of radiation and maximize photosynthesis, plants can undergo various modifications to their leaf physiology and morphology in response to light intensity (Allard et al., 1991; Weibel et al., 1994). 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 (Lawlor, 1995; van Iersel and Seymour, 2000). Therefore, to understand the physiological basis of growth, both metabolic processes, photosynthesis and respiration, have to be studied. Although there is a large amount of literature on the effect of light on photosynthesis in shade plants (Callan and Kennedy, 1995; Funnell et al., 2002; Norcini et al., 1991) research on plant respiration is limited. In addition, most of the research on photosynthesis and respiration in plants is based on leaf measurements. Continuous, long-term measurements of carbon exchange rate (CER) of whole plants (for weeks) can determine growth rate and dry matter production more accurately than individual leaf measurements, as they directly indicate the amount of C accumulated (a measure of growth rate) in plants (van Iersel and Kang, 2002). However, not much work has been done on long-term light effects on whole-plant CER.

In this experiment, we measured whole-crop CER of wax begonia continuously for a period of 25 days in a 10-chamber, whole-plant gas exchange system. The objective of this experiment was to quantify the effects of increasing PPF on photosynthesis, respiration, and growth rate of wax begonia.

MATERIALS AND METHODS

Plant Material and Environmental Control

Wax begonia ‘Cocktail Vodka’ plug seedlings were procured in cell flats (288 cells/flat) and transplanted into 36-cell filled with a soilless growing medium. A double-layered capillary mat, placed in a watertight tray, was used for subirrigating the seedlings in cell flats. The whole assembly was kept inside a whole-plant gas exchange chamber ($3.2 \times 5 \times 6 \text{ dm}^3$, van Iersel and Bugbee, 2000) arranged inside a growth chamber. A daily photoperiod of 14-h was maintained inside the growth chambers. Average air temperature and relative humidity during light/dark period were $25 \pm 1/15 \pm 1 \text{ }^\circ\text{C}$ and 65-85/80-100%, respectively.

Treatments, Measurements, and Calculations

To obtain the required PPF, gas exchange chambers were covered with shade cloth of varying density. The PPF was measured at the top of the canopy simultaneously in eight chambers using quantum sensors. The average PPF measured at the top of canopy in different treatments were 5.3, 9.5, 14.4, and $19.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ (corresponding to instantaneous PPF of 106, 189, 286, and $385 \text{ } \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively). At harvest, chlorophyll content (average of 12 leaves in each treatment), whole-crop root (DW_{ROOT}) and shoot dry weight (DW_{SHOOT}) and whole-crop dry weight (DW_{CROP}) of plants were determined in each treatment. Leaf chlorophyll content was measured using a chlorophyll meter (SPAD-502, Minolta Co., Japan) and leaf areas were measured using a leaf area meter (LI-3100, LI-COR, Lincoln, NE, USA). Leaf area ratio of plants ($\text{LAR}_{\text{PLANT}}$) and shoots ($\text{LAR}_{\text{SHOOT}}$) were estimated as the ratio of LA to DW_{CROP} and DW_{SHOOT} , respectively.

The CER of plants was measured using a whole-plant gas exchange system (van Iersel and Bugbee, 2000). The whole-plant gas exchange system directly measures net-photosynthesis and dark respiration (R_d , $\mu\text{mol} \cdot \text{s}^{-1}$; reported here as a negative value) of plants. Hence, daily average gross-photosynthesis ($P_{g,\text{avg}}$ $\mu\text{mol} \cdot \text{s}^{-1}$) was calculated as follows:

$$P_{g,\text{avg}} = P_{n,\text{avg}} - R_{d,\text{avg}} \quad [\text{Eq. 1}],$$

where $P_{n,\text{avg}}$ and $R_{d,\text{avg}}$ are the daily average net-photosynthesis ($\mu\text{mol} \cdot \text{s}^{-1}$) and daily average dark respiration ($\mu\text{mol} \cdot \text{s}^{-1}$), respectively, assuming that dark respiration rates during light and dark periods are equal (van Iersel and Bugbee, 2000). Daily carbon gain ($\mu\text{mol} \cdot \text{d}^{-1}$), i.e., the total amount of carbon fixed by 35 plants per day in each treatment was calculated as follows:

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

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, μmol , the total amount of carbon accumulated in plants since the start of experiment) which is a measure of plant size.

Cumulative carbon gain (in moles) was plotted against DW_{CROP} in each treatment, and a linear equation was fitted to describe the relationship.

$$\text{DW}_{\text{CROP}} = \text{DW}_0 + \text{CCG} \times 12 / f_c \quad [\text{Eq. 3}],$$

where DW_0 is the initial dry weight of the plants (g) and f_c is the carbon content of the plants ($\text{g} \cdot \text{g}^{-1}$). Dry weight of plants in different treatments throughout the experiment (DW_{day}) was estimated using Eq. 3 and calculated CCG values.

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

$$\text{CUE} = \text{DCG} / (P_{g,\text{avg}} \times t_{\text{light}}) \quad [\text{Eq. 4}],$$

To determine the relationship between CUE and plant size (or CCG), we fitted the following equation:

$$\text{CUE} = \text{CUE}_0 + (\text{CUE}_{\text{max}} - \text{CUE}_0) \times (1 - e^{-b \times \text{CCG}}) \quad [\text{Eq. 5}],$$

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 rate (GR, $\text{g} \cdot \text{d}^{-1}$) and relative growth rate (RGR, growth rate per existing

biomass, $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) of plants in different treatments was estimated from DCG ($\text{mol}\cdot\text{d}^{-1}$) as follows:

$$\text{GR} = \text{DCG} / f_c \quad [\text{Eq. 6}], \text{ and}$$

$$\text{RGR} = \text{GR} / \text{DW}_{\text{day}} \quad [\text{Eq. 7}].$$

Growth (r_g) and maintenance (r_m) respiration coefficients were estimated by plotting (Thornley and Johnson, 1990):

$$1/\text{CUE} = 1/Y_g + r_m/\text{RGR} \quad [\text{Eq. 8}],$$

where Y_g = conversion efficiency (moles of dry matter produced per mol CH_2O) and r_g was estimated as $1/Y_g - 1$. The estimated values of r_m ($\text{mol}\cdot\text{mol}^{-1}\cdot\text{d}^{-1}$) and r_g ($\text{mol}\cdot\text{mol}^{-1}$) were converted to more traditional glucose units ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and $\text{g}\cdot\text{g}^{-1}$, respectively) by multiplying them with $30/(12/f_c)$, where 30 is the multiplier for converting one mole of C to grams of glucose and $12/f_c$ converts moles of C to grams of dry weight. Growth and maintenance respiration rates ($\text{g}\cdot\text{d}^{-1}$, grams of carbohydrate per day) of plants can be estimated as follows:

$$R_g = r_g \times \text{GR} \quad [\text{Eq. 9}], \text{ and}$$

$$R_m = r_m \times \text{DW}_{\text{CROP}} \quad [\text{Eq. 10}],$$

where r_g and r_m are expressed as $\text{g}\cdot\text{g}^{-1}$ and $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, respectively. Total respiration (R_T) was estimated as the sum of R_m and R_g .

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 and each experimental unit (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 regression procedures, with $P < 0.05$ considered to be statistically significant. Two empty gas exchange chambers were used to check for measurement errors.

RESULTS AND DISCUSSION

Gas Exchange and Dry Weight

There was a strong correlation between DW_{CROP} and CCG ($\text{DW}_{\text{CROP}} = 23.5 + 21.4 \times \text{CCG}$, $r = 0.96$), which indicates that gas exchange data were a realistic measure of crop growth (data not shown). From the fitted equation, crop dry weight was found to increase by 21.4 g for every mole of C incorporated by the plants. Carbon content in the dry matter of plants was estimated to be $0.56 \text{ g}\cdot\text{g}^{-1}$ ($12 \text{ g}\cdot\text{mol}^{-1} / 21.4 \text{ g}\cdot\text{mol}^{-1}$, 1 mol of C = 12 g). The estimated carbon content of these plants was higher than most other reported values [$0.465 \text{ g}\cdot\text{g}^{-1}$ for pansy (*Viola x wittrockiana*) (van Iersel and Kang, 2002), $0.396 \text{ g}\cdot\text{g}^{-1}$ for white clover (*Trifolium repens*) (McCree and Troughton, 1966), and $0.421 \text{ g}\cdot\text{g}^{-1}$ for sugar beet leaves (*Beta vulgaris*) (Terry and Mortimer, 2002)].

Net Photosynthesis, Dark Respiration, and Daily Carbon Gain

Net-photosynthesis and dark respiration rates of plants increased linearly with increasing PPF throughout the experiment (Fig. 1A, B). During the early part of the growing period, plants grown at 5.3 and $9.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ had a negative DCG, indicating that the plants were losing carbon (for 13 and 4 days at 5.3 and $9.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively). Microbial decomposition of organic material in the growing medium can release CO_2 and cause errors in gas exchange measurements, and could be partly to blame for these negative DCG values. However, negative DCG values were also reported after transplantation of vinca (*Catharanthus roseus*; van Iersel, 1999) into an inert growing medium (diatomaceous earth). Negative DCG values indicate that the plants respired more carbohydrates (possibly from storage forms like starch) than were synthesized in photosynthesis soon after transplanting. Although DCG of plants increased linearly with increasing PPF, quadratic responses of DCG to PPF were seen prior to watering plants, possibly due to mild drought which may have reduced photosynthesis in larger plants.

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·m⁻²·d⁻¹ had a negative CCG during the initial 20 and 6 days of crop growth, respectively (Fig. 1D).

Carbon Use Efficiency

Throughout the experiment, CUE of plants responded quadratically to increasing PPF (Fig. 1F). Carbon use efficiency of plants increased up to a PPF of 14.4 and did not differ much between 14.4 and 19.4 mol·m⁻²·d⁻¹.

Regression analysis, using Eq. 5, showed that there was a close relationship between CCG and CUE of plants (results not shown, $R^2 = 0.85$). From Eq. 5, CUE_{max} was estimated as 0.46 mol·mol⁻¹. Carbon use efficiency normally ranges from 0.5 to 0.7 mol·mol⁻¹ (Bednarz and van Iersel, 1999; Gifford, 1995). The estimated value of CUE_{max} of wax begonia was lower than that of other species, which may partially explain its slow growth habit.

Relative Growth Rate

Relative growth rate of plants responded quadratically with increasing PPF (results not shown). It increased up to a PPF of 14.4 mol·m⁻²·d⁻¹ and a further increase in PPF resulted in little increase in RGR of plants. At harvest, the RGR values for plants grown at 5.3, 9.5, 14.4 and 19.4 mol·m⁻²·d⁻¹ were 0.013, 0.027, 0.036, and 0.035 g·g⁻¹·d⁻¹, respectively. The estimated RGR values in our experiment were lower than those reported in wax begonia (0.05 - 0.09 g·g⁻¹·d⁻¹, Kessler and Armitage, 1992), salvia [*Salvia splendens*, (0.15 - 0.2 g·g⁻¹·d⁻¹) van Iersel, 1997] and impatiens [*Impatiens parviflora*, (0.2 to 0.25 g·g⁻¹·d⁻¹), Peace and Grubb, 1982]. Since RGR depends on plant size, the low RGR at the end of this study may be related to the relatively large size of the plants, as well as the relatively slow growth habit of wax begonias.

Growth and Maintenance Respiration

The value of r_m decreased linearly with increasing PPF and ranged between 0.052 - 0.06 g·g⁻¹·d⁻¹. However, there was no significant effect of increasing PPF on r_g of plants. The growth respiration coefficient ranged from 0.41 - 0.70 g·g⁻¹ in different treatments (data not shown). Earlier study on white clover [*Trifolium repens* (McCree, 1982)] indicated that r_g remained constant, whereas r_m decreased when plants were shifted from high (0.065 g·g⁻¹·d⁻¹) to low irradiance (0.039 g·g⁻¹·d⁻¹). In contrast to that experiment, plants in our study were grown continuously at constant PPF and better adapted to their environment.

The values of r_m in our experiment were higher than those of Italian ryegrass tops [*Lolium multiflorum* (0.037 g·g⁻¹·d⁻¹)], chrysanthemum [*Chrysanthemum morifolium* (0.017 g·g⁻¹·d⁻¹)], perennial ryegrass [*Lolium perenne* (0.014 g·g⁻¹·d⁻¹)] and tomato [*Lycopersicon esculentum* (0.012 g·g⁻¹·d⁻¹)] and lower than roots of Italian ryegrass (0.091 g·g⁻¹·d⁻¹) as reviewed by Hesketh and Jones (1980).

The r_g values estimated in our experiment were higher than those of maize [*Zea mays* (0.34 g·g⁻¹)], cotton [*Gossypium hirsutum* (0.33 - 0.39 g·g⁻¹)], close to that of chrysanthemum (0.56 g·g⁻¹), and roots of Italian ryegrass (0.67 g·g⁻¹) as 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*) indicated that r_m and r_g decreased with age. However, a high correlation between 1/CUE and 1/RGR obtained in our experiment ($r^2 = 0.99$) would indicate little or no change in r_m and r_g during the growth period.

Growth and maintenance respiration in plants increased linearly with increasing PPF (data not shown). At harvest, R_g ranged from 0.14 - 0.58 g·d⁻¹ and R_m ranged from 0.81 - 1.46 g·d⁻¹ in the different treatments. However, R_m did not differ between the two highest PPF treatments during the final growth period. The percentage of R_m to R_T decreased throughout the growth period in all treatments (Fig. 1E). At harvest, the percentage of R_m to R_T for plants grown at 5.3, 9.5, 14.4 and 19.4 mol·m⁻²·d⁻¹ were 87, 84, 70, and 71 %, respectively. Initially, estimated R_m accounted for more than 100% of total respiration at the two lowest PPF levels. This was the result of a negative growth rate (and thus a negative calculated R_g), which suggests that plants were using up stored reserves. Thus, R_m at this

stage includes respiration of carbohydrates from photosynthesis, as well as respiration of stored reserves.

Maintenance respiration, according to Penning de Vries (1975) includes cellular acclimation (phenotypic adjustment) to environmental changes, such as replacement of one set of enzymes with another (Amthor, 2000). It is possible that the plants grown at the two lowest PPFs were burning a higher percentage of carbohydrates in maintenance respiration than those at the two highest PPF treatments to enable themselves adapt to the prevailing low light. The smaller fraction of total respiration allocated to maintenance with increasing PPF resulted in an increase in CUE of plants grown at high PPF.

Leaf Area and Chlorophyll

Total leaf area of plants increased linearly with increasing PPF. However, neither LAR_{SHOOT} nor LAR_{ROOT} were affected by increasing PPF (data not shown). Leaf area ratio often increases with decreasing PPF. To capture more light, plants grown in shade tend to have wider and thinner (less parenchyma tissue) leaves than those grown in full sunlight (Allard et al., 1991; Weibel et al., 1994). Therefore, the increase in total leaf area with increasing light intensity seems to be the result of increased plant size. At harvest, DW_{CROP} was found to have increased and leaf chlorophyll content to have decreased linearly with increasing PPF (data not shown). Plants grown at 5.3 and 9.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ had lower DW_{CROP} due to decreased leaf area resulting in poor light interception and low photosynthetic rates.

CONCLUSIONS

Plants grown at 5.3 and 9.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ had low photosynthetic rates due to inadequate light and poor light interception by plants. Plant growth rate increased with increasing PPF due to consistent increases in the photosynthetic capacity, radiation capture (due to increased LA), and DCG of plants. Although respiration rates increased, the percentage of R_g to R_T also increased with increasing PPF. Carbon use efficiency and RGR of plants were lower than the most other reported values, partly because R_m accounted for a large fraction of total respiration. These data indicate that low PPF not only decreased photosynthetic rates, but also increased the relative importance of maintenance respiration, and thereby reduced the growth rate of plants.

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Figures

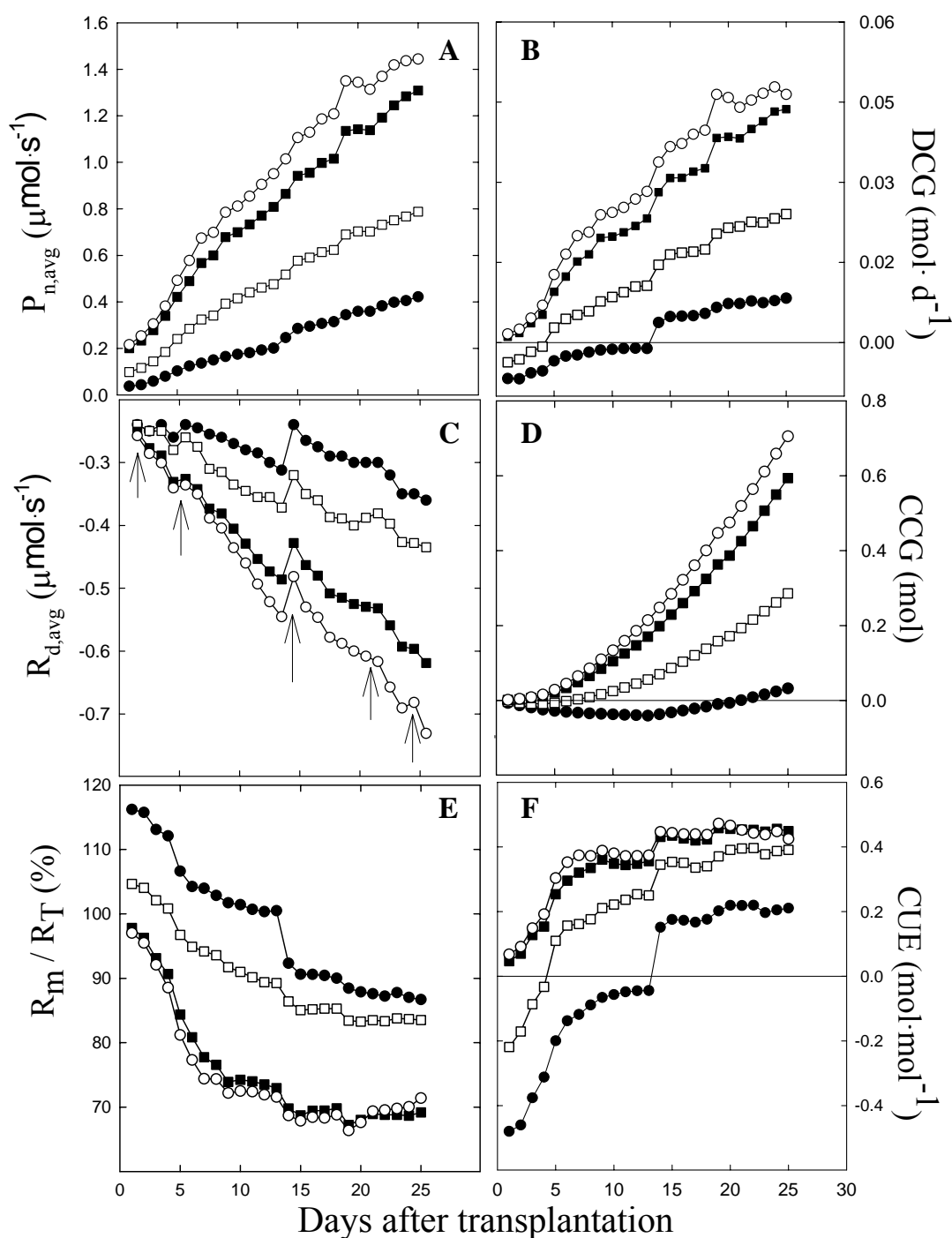


Fig. 1. Effect of photosynthetic photon flux (PPF) on A: average daily net photosynthesis ($P_{n,avg}$); B: daily carbon gain (DCG); C: average daily dark respiration ($R_{d,avg}$); D: cumulative carbon gain (CCG); E: percentage of maintenance respiration (R_m) to total respiration (R_T); and F: carbon use efficiency (CUE) of subirrigated wax begonias for a period of 25 days. Arrows indicate the time that the plants were subirrigated. Data represent groups of 35 plants averaged over two replications. Symbols \bullet , \square , \blacksquare , and \circ indicate a PPF of 5.3, 9.5, 14.4 and 19.4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively.