

Photosynthetic Responses of Greenhouse Ornamentals to Interaction of Irradiance, Carbon Dioxide Concentration, and Temperature

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ADDITIONAL INDEX WORDS. calibrachoa, carbon dioxide enrichment, environmental control, floriculture, geranium, pepper, petunia, sunflower, verbena

ABSTRACT. Supplemental lighting, temperature control, and CO₂ enrichment can improve the productivity of greenhouse crops, but operating costs for greenhouse control systems to maintain environmental parameters at desired set-points can be expensive. To balance operating costs with productivity, growers need to be able to predict how a crop will perform as a function of photosynthetic photon flux density (*PPFD*), CO₂ concentration, and temperature. The objective of this study was to explore the response of net photosynthetic rate (P_n) to *PPFD* and CO₂ concentration, for plants acclimated to different growth environment temperatures or light intensities. We measured P_n at all combinations of 14 irradiances and four CO₂ concentrations of calibrachoa (*Calibrachoa* × *hybrida* ‘Superbells Lemon Slice’), petunia (*Petunia* × *hybrida* ‘Supertunia Mini Strawberry Pink Veined’), and verbena (*Verbena* × *hybrida* ‘Superbena Royale Whitecap’) grown at three light intensities, and of geranium (*Pelargonium* × *hortorum* ‘Maverick Red’), pepper (*Capsicum annuum* ‘California Wonder’), and sunflower (*Helianthus annuus* ‘Pacino Gold’) grown at three different temperatures. Sunflower, pepper, and geranium were fit to a model representing P_n as a function of *PPFD*, CO₂ concentration, and leaf temperature. Photosynthetic light response curves, at each CO₂ concentration, were fit for each species and growth environment using a nonrectangular hyperbola. These models can be used to identify multiple combinations of *PPFD*, CO₂ concentration, and leaf temperature that would result in equivalent rates of photosynthesis, allowing the most cost-effective combination to be chosen.

Many greenhouse-grown plants are started in late winter or early spring when outdoor light intensity and air temperature are lower than ideal for plant growth (Korczynski et al., 2002). To reduce heating costs, greenhouses are typically sealed as tightly as possible, which can contribute to low CO₂ concentrations inside (Mortensen, 1987). Conversely, greenhouses often require some form of cooling during summer months, typically through use of vents, fans, or evaporative cooling. The timing of CO₂ enrichment should be considered, as the increased air exchange rate during periods of active ventilation, either for temperature or humidity control, minimizes its efficacy. Supplemental lighting, temperature control, and CO₂ enrichment can improve the productivity of greenhouse crops, but capital costs for climate

control systems and operating costs for these systems to control heaters, lights, vents, fans, and/or supplemental CO₂ systems to maintain environmental parameters at desired setpoints can be expensive. To balance operating costs with productivity, growers need to be able to predict how a crop will perform as a function of *PPFD*, CO₂ concentration, and temperature. Determining which combinations can provide similar net photosynthetic rates (P_n) can assist growers in evaluating which combination is most cost-effective for their operation. Net photosynthetic rate is a useful proxy for a plant’s instantaneous productivity and is about proportional to dry matter accumulation (Seginer et al., 1991).

Plant photosynthetic response to *PPFD*, or photosynthetically active radiation (*PAR*) intensity, has been characterized in many studies, both empirically (e.g., Acock, 1991; Johnson and Thornley, 1984; Pachepsky and Acock, 1996) and biochemically (see review by von Caemmerer et al., 2009). Additional studies have examined photosynthetic response to CO₂ concentration and temperature within the context of increasing atmospheric CO₂ concentration and climate change (e.g., Idso et al., 1987), although much of this research has focused on field crops (Bunce and Heichel, 1986). Research focused on measuring photosynthetic responses of greenhouse crops has typically varied only one factor (irradiance, temperature, or CO₂ concentration) at a time. Boldt et al. (2014) measured leaf photosynthetic response, singly, to irradiance, CO₂ concentration, and leaf temperature of 13 herbaceous ornamentals, and the models were incorporated into a decision-support tool for floriculture growers,

Received for publication 28 July 2021. Accepted for publication 15 Nov. 2021. Published online 21 January, 2022.

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This study was supported by the National Science Foundation Graduate Research Fellowship Program (Grant No. DGE-1256259) and an internship provided through the Graduate Research Internship Program. Any findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

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PhotoSim [U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS), 2019]. Erwin and Gesick (2017) measured leaf photosynthetic response of 10 taxa of leafy greens grown in greenhouses to *PPFD* and CO_2 concentration. In both Boldt et al. (2014) and Erwin and Gesick (2017), CO_2 concentration was maintained at $400 \mu\text{mol}\cdot\text{mol}^{-1}$ for the light response curves, and *PPFD* was maintained at $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the CO_2 response curves. Therefore, data gathered in these studies allowed for modeling of P_n along two intersecting lines in a domain of the variables CO_2 concentration and *PPFD*, but not in the rest of the plane. Stanghellini and Bunce (1993) measured leaf P_n of tomato (*Solanum lycopersicum*) at all combinations of CO_2 concentration (100 to $1000 \mu\text{mol}\cdot\text{mol}^{-1}$), *PPFD* (50 to $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and temperature (18, 25, and 32°C), providing insight into the response of P_n over the *PPFD* and CO_2 concentration domain, as well as their interaction with temperature. This allows P_n to be estimated via interpolation at any combination of CO_2 concentration, temperature, and *PPFD* within the domain tested, which encompasses the range of parameters likely to occur for tomato production. Because it is known [e.g., results from Boldt et al. (2014) and Erwin and Gesick (2017)] that photosynthetic responses vary significantly between species, similar data for additional plant species are warranted.

It would be useful to incorporate *PPFD*, CO_2 concentration, temperature, and their interactions into a single equation to estimate how changing multiple greenhouse environmental parameters will affect P_n . Cannell and Thornley (1998) and Körner et al. (2009) have shown clear interactive effects between these parameters. Cannell and Thornley (1998) developed a mathematical model to calculate gross photosynthetic rate as a function of temperature, CO_2 concentration, and *PPFD*. They did so by developing relationships for quantum yield (α) and maximum gross photosynthetic rate (P_{max}) as functions of CO_2 concentration and temperature. These parameters, along with a fitting parameter, θ , characterized the rate of gross photosynthesis in response to *PPFD* using a nonrectangular hyperbolic function. Although the model developed by Cannell and Thornley (1998), which we will refer to as the Cannell and Thornley model, provides great conceptual value, the generic parameter values included in the original publication were not meant to accurately predict photosynthetic rate for any specific plant species.

The growth environment before measurement is another important factor affecting P_n , especially *PPFD* and air temperature. Plants grown at higher *PPFDs* often, but not always, have higher photosynthetic capacities (Bunce and Heichel, 1986). The temperature optimum (T_{opt}) of plants grown at higher temperatures is often higher than plants grown at lower temperatures (Berry and Björkman, 1980).

Therefore, the objectives of our study were to 1) measure the combined effects of light intensity and CO_2 concentration on P_n of plants grown at different *PPFDs*; 2) measure the combined effects of *PPFD*, leaf temperature, and CO_2 concentration on P_n of plants grown at different air temperatures; and 3) fit the data to model P_n as a function of leaf temperature, *PPFD*, and CO_2 concentration.

Materials and Methods

Plant care and treatments

EXPT. 1. Calibrachoa (*Calibrachoa ×hybrida* ‘Superbells Lemon Slice’), petunia (*Petunia ×hybrida* ‘Supertunia Mini

Strawberry Pink Veined’), and verbena (*Verbena ×hybrida* ‘Superbena Royale Whitecap’) cuttings (Pleasant View Gardens, Loudon, NH) in 84-cell count trays were trimmed and transplanted into 11.4-cm-diameter pots filled with soilless substrate (LC1; Sun Gro Horticulture, Bellevue, WA) and grown for 14 d in a growth chamber before the start of treatments. The *PPFD* was ≈ 270 to $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the photoperiod was 14 h, and air temperature was $22/18^\circ\text{C}$ day/night. Plants were watered as needed and fertilized at every irrigation with 20N–4.4P–16.6K (Jack’s 20–10–20; JR Peters, Allentown, PA) at $150 \text{mg}\cdot\text{L}^{-1}$ N.

After 14 d, six plants of each species were moved to growth chambers that provided a *PPFD* of 90, 180, or $270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from cool-white fluorescent lamps. The photoperiod was 16 h, and daily light integrals (DLIs) were 5.2, 10.4, and $15.6 \text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively. Air temperature remained at $22/18^\circ\text{C}$ day/night. Flowers were removed daily to minimize shading of developing leaves. Photosynthetic measurements commenced after 20 d (verbena), 28 d (petunia), and 42 d (calibrachoa) in the lighting treatments. Each crop required a different length of time for leaves initiated after plants were moved into the lighting treatments to expand enough to cover the measuring area of the instrument cuvette (described as follows).

EXPT. 2. Geranium (*Pelargonium ×hortorum* ‘Maverick Red’), pepper (*Capsicum annuum* ‘California Wonder’), and sunflower (*Helianthus annuus* ‘Pacino Gold’) (Ball Seed Co., West Chicago, IL) were sown in 288-cell count trays filled with soilless substrate (LC1). Seedlings were initially watered with reverse-osmosis water until true leaves emerged, at which point they were fertigated at every irrigation with 20N–4.4P–16.6K at $75 \text{mg}\cdot\text{L}^{-1}$ N. Initial *PPFD* in the growth chamber was $\approx 150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the photoperiod was 12 h, and air temperature was $22/18^\circ\text{C}$ day/night. Sunflower and geranium were transplanted 24 d after sowing, and pepper was transplanted 31 d after sowing into 11.4-cm-diameter pots filled with soilless substrate (LC1). After transplant, *PPFD* was increased to $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, photoperiod was increased to 14 h, and the nutrient solution concentration was increased to $150 \text{mg}\cdot\text{L}^{-1}$ N.

Three (pepper) or four (sunflower and geranium) weeks after transplant, seven plants of each species were moved to growth chambers set at constant air temperatures of 14, 21, or 28°C . The *PPFD* remained at $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and the photoperiod was increased to 16 h, resulting in a DLI of $14.4 \text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Photosynthetic measurements commenced after 14 d (sunflower), 21 d (pepper), and 29 d (geranium) in these treatments. As noted previously, each crop required a different length of time for leaves initiated after plants were moved into temperature treatments to expand enough for photosynthetic measurements.

Photosynthetic measurements

In both experiments, P_n was measured once during production for each crop and treatment combination, and all plants in a crop were evaluated before proceeding to the next crop. Five plants per species per treatment (DLI or temperature) were selected in random order for measurement. A single leaf from each plant was used. Recently emerged, fully expanded, unshaded leaves were chosen whenever possible. However, recently emerged leaves on calibrachoa and petunia were often too small to cover the measurement area, and this occurred in all three DLI treatments in Expt 1. In those instances, larger, but not necessarily recently emerged, leaves were selected instead. In Expt. 2, geraniums grown at 28°C exhibited high temperature-induced leaf yellowing and bleaching on leaves that emerged

while at 28 °C. Preliminary tests on the yellowed leaves resulted in negligible P_n , therefore, older (greener) leaves of geranium grown at 28 °C were used instead.

Photosynthetic response curve measurements were collected using a portable photosynthesis system (LI-6400XT; LI-COR Biosciences, Lincoln, NE). Leaf temperature, flow rate, *PPFD*, and reference CO₂ concentration were precisely controlled in a leaf chamber. A cuvette with a 6-cm² area and red and blue light-emitting diodes [LEDs (6400-02B, LI-COR Biosciences)] was used for most species. A cuvette with a 2-cm² measurement area (6400-40, LI-COR Biosciences) was used for calibrachoa and petunia because of their small leaf size. The LI-6400XT reports P_n on a leaf area basis and automatically accounts for a change in measurement area when using cuvettes with different apertures. Both LED sources emitted a red:blue light ratio of 90:10. Leaf temperature was maintained at ambient growth chamber air temperature (22 °C for calibrachoa, petunia, and verbena, and 14, 21, or 28 °C for geranium, pepper, and sunflower).

Measurements were collected using an autoprogram that cycled through a predetermined sequence of conditions, logging P_n at each step once stability parameters were attained. The leaf was placed in the measurement chamber and acclimated to initial conditions of 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ and 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*. Net photosynthesis was then measured at 14 light intensities, ranging from 2000 to 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and four reference CO₂ concentrations (200, 400, 600, and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$). For each leaf, each light response curve was measured at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, then 200, 600, and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Once the leaf was acclimated, measurements were collected in descending *PPFD* (2000, 1500, 1000, 800, 700, 600, 500, 400, 300, 200, 100, 50, 25, and 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). An adjustment period of at least 5 min was programmed at 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* between each light response curve at each CO₂ concentration, and in addition, two consecutive P_n measurements were taken at 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* to verify that P_n had indeed stabilized. Measurements were logged once stability parameters were attained (minimum and maximum wait times of 45 and 90 s, respectively, were defined when using the 6-cm² cuvette, and 60 and 90 s, respectively, when using the 2-cm² cuvette). Stability criteria included the rate of change for P_n , reference CO₂ concentration, reference H₂O concentration, and flow rate.

Data analysis

For each plant, P_n light response curves were fit at each CO₂ concentration using the nonrectangular hyperbola (NRH) function presented in Eq. [1]. It is a common model for fitting photosynthetic response curves to empirical data (e.g., Boldt et al., 2014; Cannell and Thornley, 1998), and the parameter estimates can be related to photosynthetic characteristics of the plant:

$$P_n = 1/2\theta \times \{ \alpha I + P_{\max} - [(\alpha I + P_{\max})^2 - 4\alpha\theta P_{\max} I]^{0.5} \} - R_d \quad [1]$$

where P_n = net photosynthetic rate (micromoles CO₂ per square meter per second), θ = curvature parameter (value constrained between 0 and 1), α = initial quantum efficiency (micromoles CO₂ per micromole photons), P_{\max} = maximum (gross) photosynthetic rate (micromoles CO₂ per square meter per second), R_d = respiration (micromoles CO₂ per square meter per second), and I = irradiance (micromoles per square meter per second).

Parameters in Eq. [1] (P_{\max} , α , R_d , and θ) were fit by minimizing the sum of squares between the data points and the values modeled for measurements taken at each growth environment [GE (DLI for Expt. 1 and temperature for Expt. 2)] and CO₂ concentration combination. Data from each light response curve were fit independently. Regression was performed using the Ipopt solver [version 0.2.6 (Wächter and Biegler, 2006)] in the JuMP modeling language [version 0.17.1 (Dunning et al., 2017)] written in the Julia programming language [version 0.5.2 (Bezanson et al., 2012)].

The light saturation point (LSP) and light compensation point (LCP) were calculated for each light response curve. The LSP was defined as the light intensity at which P_n equaled 90% of the maximum net photosynthetic rate $P_{n,\max}$ ($P_{\max} - R_d$), as previously defined (Jurik et al., 1988; Ronquim et al., 2009). The LCP was the light intensity at which P_n equaled zero.

Analysis of variance was conducted in R (version 3.3.1; R Foundation for Statistical Computing, Vienna, Austria) on the NRH parameter values within each species and GE combination. Where significant ($P < 0.05$), Tukey's honestly significant difference test ($\alpha = 0.05$) was used for mean separation.

Data in Expt. 2 were also fit to a model developed by Cannell and Thornley (1998), which defined α and P_{\max} (as defined in Eq. [1]) as functions of temperature and CO₂ concentration, as shown in Eq. [2] through Eq. [9]. They modeled gross photosynthesis, but by including R_d in Eq. 1, we modeled P_n instead. In addition, we modified the reference CO₂ concentration from 350 to 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ to reflect recent increases in atmospheric CO₂ concentration, and we modified the reference temperature for α ($T_{\text{ref},\alpha}$) from 15 to 14 °C to allow our data to be modeled using a continuous function. At temperatures below T_{ref} , Cannell and Thornley (1998) assumed the value of α was constant in relation to temperature.

The value of α is modeled by Eq. [2] to Eq. [4]:

$$\alpha = \alpha_{\text{ref}} \times f_{C_a,\alpha} \times f_{T,\alpha} \quad [2]$$

where α_{ref} = the value of α at $T_{\text{ref},\alpha}$ and 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, $f_{C_a,\alpha}$ = a factor representing the influence of CO₂ concentration on α , and $f_{T,\alpha}$ = a factor representing the influence of temperature on α .

$$f_{C_a,\alpha} = 1 - \beta/C_a \quad [3]$$

$$f_{T,\alpha} = 1 - c_{T,\alpha} \times (T_{\text{leaf}} - T_{\text{ref},\alpha}) \times 400/C_a \quad [4]$$

where β = a coefficient representing the sensitivity of $f_{C_a,\alpha}$ to CO₂ concentration (micromoles per mole), C_a = CO₂ concentration (micromoles per mole), and $c_{T,\alpha}$ = a coefficient representing the sensitivity of $f_{T,\alpha}$ to temperature (°C⁻¹), T_{leaf} = leaf temperature, and $T_{\text{ref},\alpha}$ = the reference temperature for α . The inclusion of CO₂ concentration in Eq. [4] modifies the sensitivity of α to temperature based on CO₂ concentration.

The value of P_{\max} is modeled by Eq. [5] to Eq. [9]:

$$P_{\max} = P_{\max,\text{ref}} \times f_{C_a,P_{\max}} \times f_{T,P_{\max}} \quad [5]$$

where $P_{\max,\text{ref}}$ = the value of P_{\max} at a reference temperature and CO₂ concentration (assumed to be 20 °C and 400 $\mu\text{mol}\cdot\text{mol}^{-1}$), $f_{C_a,P_{\max}}$ = a factor representing the influence of CO₂ concentration on P_{\max} , and $f_{T,P_{\max}}$ = a factor representing the influence of temperature on P_{\max} .

$$f_{C_a,P_{\max}} = 1/(1 + K_{C_a,P_{\max}}/C_a) \quad [6]$$

$$f_{T,Pmax} = \left[\frac{(T - T_0)}{(T_{ref} - T_0)} \right]^2 \times \left[\frac{(T_{0,Pmax} - T)}{(T_{0,Pmax} - T_{ref})} \right] \quad [7]$$

where $K_{Ca,Pmax}$ = a coefficient representing the sensitivity of $f_{Ca,Pmax}$ to CO_2 concentration (micromoles per mole), T_0 = the lower temperature at which $f_{T,Pmax}$ is 0 ($^{\circ}C$), and $T_{0,Pmax}$ = the upper temperature at which $f_{T,Pmax}$ is 0 ($^{\circ}C$).

$$T_{0,Pmax} = (3 \times T_{max,Pmax} - T_0)/2 \quad [8]$$

$$T_{max,Pmax} = T_{max,Pmax,400} + (T_{max,Pmax,800} - T_{max,Pmax,400}) \times (C_a - 400)/(800 - 400) \quad [9]$$

where $T_{max,Pmax,400}$ = the temperature ($^{\circ}C$) that maximizes P_{max} at $400 \mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 concentration and $T_{max,Pmax,800}$ = the temperature ($^{\circ}C$) that maximizes P_{max} at $800 \mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 concentration.

To fit the general model developed by Cannell and Thornley (1998) with the addition of the parameter R_d , the parameters α_{ref} , β , θ , $c_{T,\alpha}$, $P_{max,ref}$, $K_{Ca,Pmax}$, $T_{max,Pmax,400}$, $T_{max,Pmax,800}$, T_0 , and R_d were determined using least squares regression to minimize differences between data for each species and the Cannell

and Thornley model. Regression was performed as previously described for individual response curves.

Results

EXPT. 1. Verbena and petunia acclimated to higher light intensities (180 and $270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*) had higher rates of P_{max} compared with plants acclimated to $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* (Fig. 1). In verbena, P_{max} ranged from 8.6 to $25.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 for plants grown at $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*, depending on CO_2 concentration, but increased to 11.2 to $33.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 and 12.2 to $33.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 for plants grown at 180 and $270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*, respectively (Table 1). In petunia, P_{max} ranged from 6.9 to $17.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 , 10.3 to $28.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 , and 9.1 to $27.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 for plants grown at 90, 180, and $270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*, respectively (Table 1). Results for calibrachoa were inconsistent between treatments, with the highest values of P_{max} (6.4 to $17.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2) occurring in plants grown at $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* and the lowest values of P_{max}

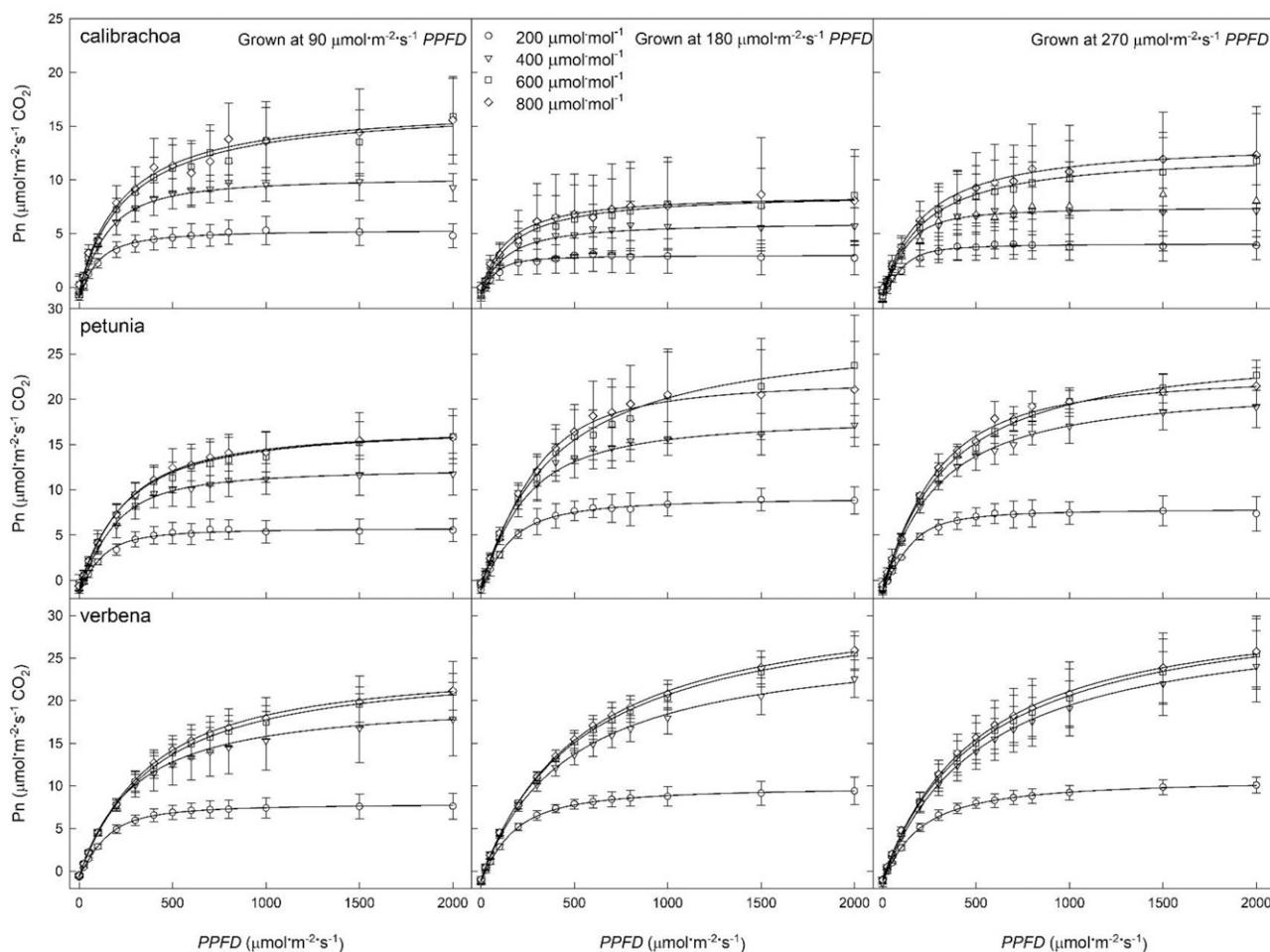


Fig. 1. Net photosynthesis (P_n) of calibrachoa ‘Superbells Lemon Slice’, petunia ‘Supertunia Mini Strawberry Pink Veined’, and verbena ‘Superbena Royale Whitecap’ (top, middle, and bottom rows, respectively) grown at photosynthetic photon flux densities (*PPFDs*) of 90, 180, and $270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (left, center, and right columns, respectively). Plants were measured at 14 *PPFDs* and four CO_2 concentrations. Points plotted are the means (\pm SD) of each treatment ($n = 5$) at each *PPFD*. Lines are the modeled values using the equation $P_n = 1/20 \{ \alpha I + P_{max} - [(\alpha I + P_{max})^2 - 4\alpha\theta P_{max}I]^{0.5} \} - R_d$, with the parameter values listed in Table 1.

Table 1. Nonrectangular hyperbola equation parameters [maximum photosynthetic rate (P_{max}), quantum yield (α), θ , and dark respiration (R_d)] for photosynthetic light response curves of calibrachoa, petunia, and verbena grown at three photosynthetic photon flux densities (90, 180, and 270 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD) and measured at four CO_2 concentrations (200, 400, 600, and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$). The light compensation point {LCP [PPFD at which net photosynthesis (P_n) = 0]} and light saturation point [LSP (PPFD corresponding to 90% net P_{max})] were calculated from the nonrectangular hyperbola, $P_n = 1/2\theta \{ \alpha I + P_{max} - [(\alpha I + P_{max})^2 - 4\theta P_{max} I]^{0.5} \} - R_d$. All fitted parameters and calculated values are mean \pm SD ($n = 5$).

GE/ CO_2^z	P_{max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	α [CO_2 ($\mu\text{mol}\cdot\mu\text{mol}^{-1}$ photons)]	θ	R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	LCP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Pseudo R^2 ($1-\text{SS}_{\text{error}}/\text{SS}_{\text{total}}$) ^y
	(mean \pm SD)						
Calibrachoa ‘Lemon Slice’							
90/200	6.4 \pm 0.9 b ^x	0.0510 \pm 0.0072 c	0.533 \pm 0.045 a	0.98 \pm 0.40	709 \pm 110	20.8 \pm 7.2 a	0.843
90/400	11.0 \pm 1.3 b	0.0550 \pm 0.0031 bc	0.593 \pm 0.347 a	0.64 \pm 0.39	873 \pm 542	11.9 \pm 7.2 ab	0.895
90/600	17.4 \pm 3.8 a	0.0670 \pm 0.0043 ab	0.001 \pm 0.000 b	0.37 \pm 0.34	>2000 ^w	5.5 \pm 5.1 b	0.863
90/800	17.4 \pm 4.9 a	0.0727 \pm 0.0097 a	0.014 \pm 0.028 b	0.37 \pm 0.34	>2000	4.9 \pm 4.6 b	0.800
ANOVA	<0.001	<0.001	<0.001	0.0574	–	0.003	
HSD ^x	5.8	0.0120	0.318	–	–	11.1	
180/200	3.8 \pm 1.9	0.0361 \pm 0.0194	0.733 \pm 0.364 a	0.81 \pm 0.43	359 \pm 193 b	26.8 \pm 11.2 a	0.515
180/400	6.6 \pm 2.3	0.0418 \pm 0.0099	0.329 \pm 0.459 ab	0.47 \pm 0.43	974 \pm 619 ab	11.7 \pm 10.4 ab	0.635
180/600	9.4 \pm 5.0	0.0561 \pm 0.0267	0.054 \pm 0.118 b	0.63 \pm 0.61	1504 \pm 504 a	9.8 \pm 7.0 b	0.505
180/800	9.0 \pm 5.0	0.0567 \pm 0.0123	0.223 \pm 0.333 ab	0.29 \pm 0.29	1047 \pm 506 ab	5.3 \pm 5.1 b	0.452
ANOVA	0.12	0.23	0.038	0.34	0.015	0.008	
HSD	–	–	0.619	–	873	15.9	
270/200	5.0 \pm 1.4 b	0.0307 \pm 0.0077 b	0.833 \pm 0.084 a	0.89 \pm 0.50	436 \pm 153 b	28.9 \pm 11.2 a	0.745
270/400	8.3 \pm 2.5 ab	0.0465 \pm 0.0095 ab	0.757 \pm 0.245 a	0.77 \pm 0.48	553 \pm 382 b	16.9 \pm 9.6 ab	0.737
270/600	13.4 \pm 5.0 a	0.0596 \pm 0.0129 a	0.092 \pm 0.150 b	0.77 \pm 0.45	1915 \pm 522 a	13.0 \pm 6.0 b	0.725
270/800	14.1 \pm 5.5 a	0.0601 \pm 0.0077 a	0.143 \pm 0.203 b	0.50 \pm 0.39	1863 \pm 639 a	8.3 \pm 5.5 b	0.698
ANOVA	0.007	<0.001	<0.001	0.599	<0.001	0.009	
HSD	7.3	0.0176	0.327	–	834	15.3	
Petunia ‘Supertunia Mini Strawberry Pink Veined’							
90/200	6.9 \pm 1.4 b	0.0392 \pm 0.0163	0.747 \pm 0.185	1.12 \pm 0.45	607 \pm 228 b	30.7 \pm 6.0 a	0.872
90/400	13.5 \pm 2.3 a	0.0523 \pm 0.0088	0.670 \pm 0.168	1.05 \pm 0.36	1034 \pm 486 ab	20.4 \pm 5.5 ab	0.903
90/600	17.9 \pm 4.6 a	0.0598 \pm 0.0182	0.421 \pm 0.286	0.65 \pm 0.39	1788 \pm 716 a	11.3 \pm 6.6 b	0.892
90/800	17.9 \pm 3.3 a	0.0578 \pm 0.0177	0.500 \pm 0.334	0.73 \pm 0.53	1592 \pm 714 ab	12.6 \pm 7.5 b	0.929
ANOVA	<0.001	0.197	0.195	0.282	0.019	<.001	
HSD	5.7	–	–	–	1036	11.6	
180/200	10.3 \pm 1.5 b	0.0497 \pm 0.0092	0.618 \pm 0.170 ab	1.09 \pm 0.56	918 \pm 301	22.2 \pm 11.1 a	0.909
180/400	19.1 \pm 3.0 ab	0.0637 \pm 0.0145	0.532 \pm 0.378 ab	0.88 \pm 0.54	1441 \pm 876	13.3 \pm 7.6 ab	0.930
180/600	28.5 \pm 8.1 a	0.0680 \pm 0.0139	0.170 \pm 0.246 b	0.72 \pm 0.47	>2000	10.1 \pm 5.2 ab	0.872
180/800	23.0 \pm 5.9 a	0.0560 \pm 0.0130	0.759 \pm 0.245 a	0.45 \pm 0.45	1443 \pm 702	7.3 \pm 4.7 b	0.874
ANOVA	<0.001	0.155	0.021	0.24	–	0.036	
HSD	9.5	–	0.489	–	–	13.7	
270/200	9.1 \pm 2.1 b	0.0422 \pm 0.0066 b	0.806 \pm 0.105 a	1.15 \pm 0.33	602 \pm 260	27.6 \pm 5.2 a	0.905
270/400	23.1 \pm 2.9 a	0.0707 \pm 0.0093 a	0.280 \pm 0.188 b	1.34 \pm 0.44	>2000	19.5 \pm 4.2 ab	0.971
270/600	27.1 \pm 3.2 a	0.0729 \pm 0.0179 a	0.176 \pm 0.357 b	1.08 \pm 0.57	>2000	14.3 \pm 6.3 b	0.985
270/800	23.9 \pm 3.1 a	0.0632 \pm 0.0155 ab	0.605 \pm 0.260 ab	0.64 \pm 0.61	1554 \pm 694	9.0 \pm 8.5 b	0.973
ANOVA	<0.001	0.008	0.003	0.193	–	0.002	
HSD	5.1	0.0237	0.445	–	–	11.3	
Verbena ‘Superbena Royale Whitecap’							
90/200	8.6 \pm 1.7 b	0.0425 \pm 0.0086 b	0.720 \pm 0.177 a	0.63 \pm 0.14	687 \pm 300	15.1 \pm 1.8 a	0.928
90/400	21.0 \pm 5.8 a	0.0694 \pm 0.0037 a	0.133 \pm 0.218 b	0.68 \pm 0.17	>2000	10.1 \pm 2.4 b	0.874
90/600	25.1 \pm 2.7 a	0.0601 \pm 0.0071 a	0.148 \pm 0.087 b	0.53 \pm 0.22	>2000	8.9 \pm 3.5 b	0.965
90/800	25.1 \pm 4.5 a	0.0592 \pm 0.0053 a	0.289 \pm 0.064 b	0.53 \pm 0.15	>2000	9.0 \pm 2.2 b	0.949

(Continued on next page)

Table 1. (Continued)

	P_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	α [CO_2 ($\mu\text{mol}\cdot\mu\text{mol}^{-1}$ photons)]	θ	R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	LCP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Pseudo R^2 ($1-\text{SS}_{\text{error}}/\text{SS}_{\text{total}}$) ^y
GE/ CO_2^z	(mean \pm sd)						
ANOVA	<0.001	<0.001	<0.001	0.431	–	0.004	
HSD	7.3	0.0116	0.272	–	–	4.6	
180/200	11.2 \pm 1.7 b	0.0507 \pm 0.0071 b	0.548 \pm 0.255 a	1.18 \pm 0.25	1117 \pm 521	25.1 \pm 7.7	0.958
180/400	28.7 \pm 3.3 a	0.0613 \pm 0.0058 a	0.001 \pm 0.000 b	1.10 \pm 0.17	>2000	18.6 \pm 2.3	0.975
180/600	33.3 \pm 3.0 a	0.0623 \pm 0.0027 a	0.001 \pm 0.000 b	1.02 \pm 0.34	>2000	16.8 \pm 5.6	0.986
180/800	33.4 \pm 3.3 a	0.0600 \pm 0.0019 a	0.122 \pm 0.119 b	0.95 \pm 0.37	>2000	16.3 \pm 6.5	0.985
ANOVA	<0.001	0.006	<0.001	0.632	–	0.1	
HSD	5.2	0.0088	0.255	–	–	–	
270/200	12.2 \pm 1.4 b	0.0531 \pm 0.0048	0.375 \pm 0.248 a	1.27 \pm 0.29	1538 \pm 563	25.6 \pm 4.7 a	0.975
270/400	31.5 \pm 6.5 a	0.0598 \pm 0.0068	0.021 \pm 0.044 b	1.28 \pm 0.48	>2000	22.2 \pm 7.9 ab	0.937
270/600	33.0 \pm 5.7 a	0.0612 \pm 0.0087	0.030 \pm 0.065 b	0.98 \pm 0.35	>2000	16.3 \pm 4.0 ab	0.936
270/800	32.5 \pm 5.3 a	0.0600 \pm 0.0086	0.165 \pm 0.225 ab	0.83 \pm 0.38	>2000	13.9 \pm 5.1 b	0.930
ANOVA	<0.001	0.332	0.0164	0.204	–	0.017	
HSD	9.2	–	0.311	–	–	10.2	

^zGE/ CO_2 = growth environment [$PPFD$ (micromoles per square meter per second) in Expt. 1]/ CO_2 concentration at which the photosynthetic light response curve was determined.

^y $\text{SS}_{\text{error}}/\text{SS}_{\text{total}}$ = sum of squares (error)/sum of squares (total).

^xTukey's honestly significant difference (HSD) at $\alpha = 0.05$. A hyphen for HSD indicates test not performed ($P > 0.05$). Within each species and growth environment (GE)/ CO_2 , means followed by similar letters are not statistically different at $\alpha = 0.05$.

^wLSP values exceeding the upper bounds evaluated are noted as $>2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ rather than reporting an extrapolated value; analysis of variance (ANOVA) not performed for the GE.

(3.8 to 9.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$) occurring in plants acclimated to 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ (Fig. 1, Table 1).

In all three species, P_{\max} generally increased with increasing CO_2 concentration, although the magnitude of increase was generally less with higher CO_2 concentrations. For example, P_{\max} of verbena increased 144%, 156%, and 158% from 200 to 400 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$, at 90, 180, and 270 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$, respectively, but increased only 20%, 16%, and 5%, respectively, from 400 to 600 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$, and there was almost no change from 600 to 800 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$. Differences in P_{\max} at different CO_2 concentrations were significant ($P < 0.05$), with the exception of calibrachoa grown at 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ (Table 1). Most common was a lower value of P_{\max} at 200 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ compared with higher CO_2 concentrations.

Across all GE and CO_2 concentrations, α ranged from 0.0425 to 0.0694 $\mu\text{mol} \text{CO}_2$ per micromole photons in verbena, 0.0392 to 0.0729 in petunia, and 0.0361 to 0.0727 in calibrachoa (Table 1). These values fell within the range typically observed for α (0.040 to 0.075) at ambient (350 $\mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 (Cannell and Thornley, 1998), although they were slightly below this general range at sub-ambient CO_2 concentrations. Where significant, α at 200 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ was lower than at 600 and 800 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$, and similar to or lower than at 400 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$.

Dark respiration ranged from 0.53 to 1.28 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$ in verbena, 0.45 to 1.34 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$ in petunia, and 0.29 to 0.98 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$ in calibrachoa (Table 1). In all three species, there was a trend for R_d to generally decrease with increasing CO_2 concentration; however, significant differences were not detected within any of the combinations of species and GEs.

The LCP ranged from 8.9 to 25.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ in verbena, 7.3 to 30.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ in petunia, and 4.9 to 28.9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ in calibrachoa (Table 1). The LCP

generally decreased with increasing CO_2 concentration, and differences were significant within all species and GE combinations, except for verbena grown at 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$.

The calculated LSP, while not compared statistically across light intensities (due to lack of chamber replication), was higher in verbena and petunia acclimated to 180 and 270 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$, compared with those acclimated at 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} PPFD$ (Table 1). The LSP generally increased as CO_2 concentration increased from 200 to 600 $\mu\text{mol}\cdot\text{mol}^{-1}$, then decreased slightly from 600 to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$.

EXPT. 2. Pepper and sunflower showed dramatically increased P_n as growth chamber temperature increased, especially from 14 to 21 °C (Fig. 2). In pepper, P_{\max} at the four CO_2 concentrations evaluated ranged from 1.0 to 4.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$, 7.6 to 19.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$, and 8.3 to 26.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$ at 14, 21, and 28 °C, respectively (Table 2). In sunflower, P_{\max} ranged from 8.2 to 30.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$, 17.7 to 53.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$, and 18.2 to 65.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{CO}_2$ at 14, 21, and 28 °C respectively (Table 2). However, in geranium, higher rates of P_n were attained at 21 °C than at 14 or 28 °C. Lower rates of P_n at 28 °C were likely due to high temperature-induced leaf yellowing and photobleaching (loss of chlorophyll). In all three species, P_{\max} increased with increasing CO_2 concentration, although the magnitude of increase was generally less at higher CO_2 concentrations. For example, in sunflower at 21 °C, P_{\max} increased 150% from 200 to 400 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$, 20% from 400 to 600 $\mu\text{mol}\cdot\text{mol}^{-1}$, and by less than 1% from 600 to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$. In most instances, P_{\max} at 200 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ was significantly lower ($P < 0.05$) than the other three CO_2 concentrations, and P_{\max} at 600 and 800 $\mu\text{mol}\cdot\text{mol}^{-1} \text{CO}_2$ were similar (Table 2).

Values of α ranged from 0.0137 to 0.0765 $\mu\text{mol} \text{CO}_2$ per micromole photons in pepper, 0.0398 to 0.0693 in sunflower, and 0.0213

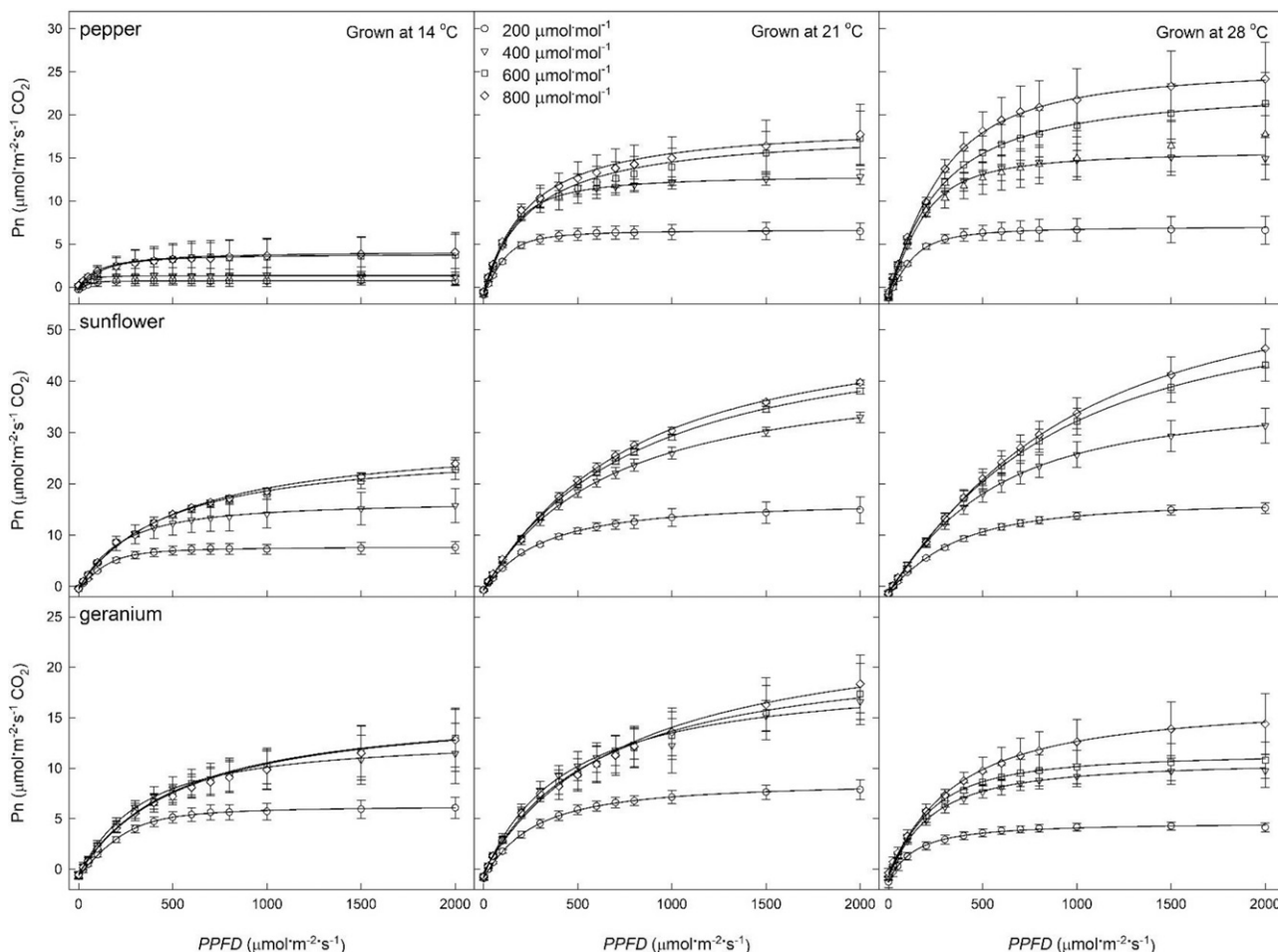


Fig. 2. Net photosynthesis (P_n) of pepper 'California Wonder', sunflower 'Pacino Gold', and geranium 'Maverick Red' (top, middle, and bottom rows, respectively) grown at air temperatures of 14, 21, and 28 °C (left, center, and right columns, respectively). Plants were measured at 14 photosynthetic photon flux densities ($PPFD_s$) and four CO_2 concentrations. Points plotted are the means ($\pm SD$) of each treatment ($n = 5$) at each $PPFD$. Lines are the modeled values using the equation $P_n = 1/2\theta \{ \alpha I + P_{max} - [(\alpha I + P_{max})^2 - 4\alpha\theta P_{max} I]^{0.5} \} - R_d$, with the parameter values listed in Table 2.

to 0.0460 in geranium (Table 2). Significant differences occurred in eight of the nine treatments (species \times GE combinations), but the relationship was inconsistent. In general, α was lowest at 200 $\mu mol \cdot mol^{-1} CO_2$. While not statistically compared across temperatures due to lack of replication of GE, α tended to be lower at 14 °C compared with 21 or 28 °C but only at 200 $\mu mol \cdot mol^{-1} CO_2$.

Dark respiration ranged from 0.01 to 1.17 $\mu mol \cdot m^{-2} \cdot s^{-1} CO_2$ in pepper, 0.18 to 1.36 $\mu mol \cdot m^{-2} \cdot s^{-1} CO_2$ in sunflower, and 0.31 to 1.19 $\mu mol \cdot m^{-2} \cdot s^{-1} CO_2$ in geranium (Table 2). Although statistical differences were detected in only four of the nine treatment combinations, R_d tended to increase with temperature and typically decreased as CO_2 concentration increased.

The LCP ranged from 0.4 to 29.3 $\mu mol \cdot m^{-2} \cdot s^{-1} PPFD$ in pepper, 3.2 to 26.4 $\mu mol \cdot m^{-2} \cdot s^{-1} PPFD$ in sunflower, and 8.7 to 38.8 $\mu mol \cdot m^{-2} \cdot s^{-1} PPFD$ in geranium (Table 2). The LCP generally decreased with increasing CO_2 concentration. For example, in pepper at 28 °C, the LCP was 26.3, 15.5, 12.9, and 9.7 $\mu mol \cdot m^{-2} \cdot s^{-1} PPFD$ at 200, 400, 600, and 800 $\mu mol \cdot mol^{-1} CO_2$, respectively.

The LSP ranged from 143 to $>2000 \mu mol \cdot m^{-2} \cdot s^{-1}$ in pepper, 533 to $>2000 \mu mol \cdot m^{-2} \cdot s^{-1}$ in sunflower, and 803 to $>2000 \mu mol \cdot m^{-2} \cdot s^{-1}$ in geranium (Table 2). These values were calculated as the light intensity corresponding to 90% of net P_{max} . Based on our fitted equation of P_n measured at light

intensities of $\leq 2000 \mu mol \cdot m^{-2} \cdot s^{-1} PPFD$, some of the calculated values exceeded our upper bound. These extrapolated values may not be biologically realistic and, therefore, are reported in Table 2 as $>2000 \mu mol \cdot m^{-2} \cdot s^{-1} PPFD$. In general, the LSP was higher at 21 and 28 °C, compared with 14 °C. The LSP generally increased with increasing CO_2 concentration from 200 to 600, then either increased or decreased from 600 to 800.

FITTING TO THE CANNELL AND THORNLEY MODEL. Values of α_{ref} , β , θ , $c_{T,\alpha}$, $P_{max,ref}$, $K_{Ca,Pmax}$, $T_{max,Pmax,400}$, $T_{max,Pmax,800}$, T_0 , and R_d were determined by the fitting procedure for geranium, pepper, and sunflower (Table 3). Rates of P_{max} increased with CO_2 concentration, although the magnitude of increase was incrementally smaller with increasing CO_2 concentration. This behavior is captured by Eq. [6], in which $f_{Ca,Pmax}$, the factor representing the influence of CO_2 concentration on P_{max} , increased asymptotically due to increasing CO_2 concentration. The measured behavior of P_{max} was also well-represented by Eq. [7], in which P_{max} increased up to a temperature optimum, above which it decreased. The fitted temperature optima fell between 20.9 and 26.5 °C (Table 3).

Cannell and Thornley (1998) predicted α to decrease as temperature increased above 15 °C (Eq. [4], assuming a positive value for c_T), based on a review of multiple studies. However, in

Table 2. Nonrectangular hyperbola equation parameters [maximum photosynthetic rate (P_{max}), quantum yield (α), θ , and dark respiration (R_d)] for photosynthetic light response curves of pepper, sunflower, and geranium grown at three air temperatures (14, 21, and 28 °C) and measured at four CO₂ concentrations (200, 400, 600, and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$). The light compensation point [LCP; photosynthetic photon flux densities ($PPFD$) at which net photosynthesis (P_n) = 0] and light saturation point (LSP; $PPFD$ corresponding to 90% net P_{max}) were calculated from the nonrectangular hyperbola, $P_n = 1/2\theta \{ \alpha I + P_{max} - [(\alpha I + P_{max})^2 - 4\alpha\theta P_{max}I]^{0.5} \} - R_d$. All fitted parameters and calculated values are mean \pm SD ($n = 5$).

GE/CO ₂ ^z	P_{max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO ₂)	α [CO ₂ ($\mu\text{mol}\cdot\mu\text{mol}^{-1}$ photons)]	θ	R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO ₂)	LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	LCP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Pseudo R^2 ($1-SS_{error}/SS_{total}$) ^y
	(mean \pm SD)						
Pepper 'California Wonder'							
14/200	1.0 \pm 0.6	0.0137 \pm 0.0039 b ^x	0.880 \pm 0.068 a	0.31 \pm 0.08 a	214 \pm 140 b	29.3 \pm 19.0 a	0.322
14/400	1.5 \pm 1.0	0.0215 \pm 0.0085 b	0.832 \pm 0.184 a	0.13 \pm 0.11 b	143 \pm 78 b	5.2 \pm 4.9 b	0.270
14/600	3.9 \pm 2.5	0.0239 \pm 0.0109 ab	0.527 \pm 0.358 a	0.04 \pm 0.08 b	700 \pm 374 ab	1.0 \pm 2.3 b	0.401
14/800	4.2 \pm 2.5	0.0361 \pm 0.0066 a	0.001 \pm 0.000 b	0.01 \pm 0.03 b	1064 \pm 594 ab	0.4 \pm 0.8 b	0.418
ANOVA	0.033	0.003	<0.001	<0.001	0.003	<0.001	
HSD ^x	–	0.0143	0.369	0.15	652	17.9	
21/200	7.6 \pm 1.1 c	0.0475 \pm 0.0036 b	0.799 \pm 0.058 a	0.87 \pm 0.21	449 \pm 121	18.9 \pm 4.3 a	0.948
21/400	14.0 \pm 0.9 b	0.0694 \pm 0.0037 a	0.689 \pm 0.087 a	0.88 \pm 0.17	726 \pm 106	13.1 \pm 2.8 ab	0.988
21/600	18.8 \pm 3.6 ab	0.0732 \pm 0.0107 a	0.028 \pm 0.061 b	0.51 \pm 0.42	>2000 ^w	6.8 \pm 5.5 b	0.913
21/800	19.6 \pm 4.4 a	0.0762 \pm 0.0094 a	0.165 \pm 0.225 b	0.54 \pm 0.40	>2000	7.1 \pm 5.3 b	0.914
ANOVA	<0.001	<0.001	<0.001	0.155	–	0.002	
HSD	5.3	0.0137	0.232	–	–	8.3	
28/200	8.3 \pm 2.1 c	0.0459 \pm 0.0081 b	0.752 \pm 0.226 a	1.17 \pm 0.36	610 \pm 440	26.3 \pm 5.1 a	0.909
28/400	17.0 \pm 2.8 b	0.0653 \pm 0.0074 a	0.732 \pm 0.146 a	1.01 \pm 0.37	840 \pm 318	15.5 \pm 4.7 b	0.955
28/600	24.4 \pm 4.6 a	0.0765 \pm 0.0026 a	0.360 \pm 0.145 b	0.96 \pm 0.36	>2000	12.9 \pm 5.0 b	0.938
28/800	26.7 \pm 5.3 a	0.0685 \pm 0.0055 a	0.635 \pm 0.129 ab	0.66 \pm 0.35	1503 \pm 352	9.7 \pm 5.0 b	0.936
ANOVA	<0.001	<0.001	0.006	0.193	–	<0.001	
HSD	7.1	0.0113	0.300	–	–	8.9	
Sunflower 'Pacino Gold'							
14/200	8.2 \pm 1.3 c	0.0398 \pm 0.0024 c	0.807 \pm 0.048 a	0.45 \pm 0.05 ab	533 \pm 125	11.5 \pm 0.9 a	0.936
14/400	17.5 \pm 4.0 b	0.0693 \pm 0.0100 a	0.392 \pm 0.298 b	0.61 \pm 0.11 a	1528 \pm 767	9.2 \pm 1.7 ab	0.884
14/600	27.9 \pm 3.3 a	0.0574 \pm 0.0058 ab	0.040 \pm 0.088 c	0.30 \pm 0.24 b	>2000	5.1 \pm 4.1bc	0.987
14/800	30.0 \pm 2.1 a	0.0544 \pm 0.0065 b	0.001 \pm 0.000 c	0.18 \pm 0.18 b	>2000	3.2 \pm 2.9 c	0.994
ANOVA	<0.001	<0.001	<0.001	0.004	–	<0.001	
HSD	5.2	0.0124	0.284	0.30	–	4.9	
21/200	17.7 \pm 3.7 c	0.0495 \pm 0.0043 b	0.376 \pm 0.297	0.65 \pm 0.06	>2000	13.5 \pm 1.9	0.961
21/400	44.2 \pm 2.2 b	0.0626 \pm 0.0060 a	0.152 \pm 0.109	0.75 \pm 0.22	>2000	12.2 \pm 3.5	0.994
21/600	52.8 \pm 3.1 a	0.0609 \pm 0.0032 a	0.208 \pm 0.149	0.59 \pm 0.16	>2000	9.9 \pm 3.0	0.998
21/800	53.1 \pm 2.2 a	0.0593 \pm 0.0028 a	0.370 \pm 0.076	0.54 \pm 0.24	>2000	9.3 \pm 4.5	0.998
ANOVA	<0.001	<0.001	0.153	0.341	–	0.206	
HSD	5.2	0.0077	–	–	–	–	
28/200	18.2 \pm 1.5 c	0.0402 \pm 0.0034 b	0.598 \pm 0.058	1.04 \pm 0.35	1996 \pm 316	26.4 \pm 7.7	0.990
28/400	38.9 \pm 4.6 b	0.0562 \pm 0.0043 a	0.518 \pm 0.061	1.11 \pm 0.26	>2000	20.3 \pm 5.5	0.976
28/600	59.5 \pm 2.9 a	0.0564 \pm 0.0038 a	0.463 \pm 0.077	1.18 \pm 0.35	>2000	21.2 \pm 6.3	0.987
28/800	65.1 \pm 3.2 a	0.0557 \pm 0.0036 a	0.500 \pm 0.098	1.36 \pm 0.30	>2000	24.8 \pm 6.2	0.984
ANOVA	<0.001	<0.001	0.068	0.468	–	0.421	
HSD	5.9	0.0068	–	–	–	–	
Geranium 'Maverick Red'							
14/200	6.9 \pm 1.3 b	0.0213 \pm 0.0028 b	0.829 \pm 0.049 a	0.63 \pm 0.29	803 \pm 206	29.4 \pm 11.9	0.949
14/400	13.8 \pm 4.0 ab	0.0376 \pm 0.0068 a	0.288 \pm 0.341 b	0.64 \pm 0.22	>2000	18.6 \pm 8.4	0.903
14/600	16.7 \pm 4.9 a	0.0303 \pm 0.0037 a	0.102 \pm 0.226 b	0.46 \pm 0.29	>2000	15.6 \pm 9.4	0.919
14/800	16.8 \pm 5.4 a	0.0302 \pm 0.0031 a	0.051 \pm 0.078 b	0.51 \pm 0.22	>2000	17.6 \pm 8.0	0.908

(Continued on next page)

Table 2. (Continued)

	P_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	α [CO_2 ($\mu\text{mol}\cdot\mu\text{mol}^{-1}$ photons)]	θ	R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2)	LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	LCP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Pseudo R^2 ($1-\text{SS}_{\text{error}}/\text{SS}_{\text{total}}$) ^y
GE/ CO_2^z	(mean \pm sd)						
ANOVA	0.006	<0.001	<0.001	0.618	–	0.139	
HSD	7.6	0.0132	0.379	–	–	–	
21/200	9.7 \pm 1.2 b	0.0319 \pm 0.0029 b	0.384 \pm 0.264 a	0.87 \pm 0.15 a	>2000	28.8 \pm 5.5 a	0.976
21/400	20.3 \pm 2.0 a	0.0460 \pm 0.0074 a	0.049 \pm 0.107 b	0.71 \pm 0.18 ab	>2000	16.1 \pm 3.9 b	0.949
21/600	22.8 \pm 4.9 a	0.0372 \pm 0.0062 ab	0.001 \pm 0.000 b	0.45 \pm 0.32 ab	>2000	11.8 \pm 7.5 b	0.931
21/800	25.4 \pm 5.1 a	0.0330 \pm 0.0065 b	0.001 \pm 0.000 b	0.31 \pm 0.27 b	>2000	8.7 \pm 7.0 b	0.934
ANOVA	<0.001	0.007	0.001	0.009	–	<0.001	
HSD	6.8	0.0108	0.258	0.43	–	11.1	
28/200	5.9 \pm 1.0 c	0.0368 \pm 0.0080	0.340 \pm 0.305	1.19 \pm 0.53 a	1280 \pm 587	38.8 \pm 17.1 a	0.956
28/400	11.7 \pm 2.4 b	0.0448 \pm 0.0075	0.385 \pm 0.297	0.81 \pm 0.27 ab	1780 \pm 921	18.6 \pm 4.7 b	0.961
28/600	12.2 \pm 2.3 b	0.0411 \pm 0.0081	0.592 \pm 0.171	0.55 \pm 0.30 ab	1325 \pm 515	13.5 \pm 6.5 b	0.936
28/800	17.3 \pm 4.2 a	0.0426 \pm 0.0050	0.265 \pm 0.276	0.42 \pm 0.26 b	–	10.0 \pm 6.0 b	0.920
ANOVA	<0.001	0.386	0.288	0.018	–	0.001	
HSD	4.9	–	–	0.65	–	17.9	

^zGE/ CO_2 = growth environment [temperature ($^{\circ}\text{C}$) in Expt. 2]/ CO_2 concentration at which the photosynthetic light response curve was determined.

^y $\text{SS}_{\text{error}}/\text{SS}_{\text{total}}$ = sum of squares (error)/sum of squares (total).

^xTukey's honestly significant difference (HSD). A hyphen for HSD indicates value not reported ($P > 0.05$). Within each species and GE, means followed by different letters are statistically different at $\alpha = 0.05$.

^wLSP values exceeding the upper bounds evaluated are noted as $>2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF_D rather than reporting an extrapolated value; ANOVA not performed for the GE.

the present study, α increased with temperature in pepper and geranium (Table 2). As a result, when fitting our data to the Cannell and Thornley model, the parameter c_T , which represents the impact of temperature on α , was negative in geranium and pepper, instead of positive as expected. The Cannell and Thornley model also assumes α increases with CO_2 concentration (Eq. [3]). Although our measured values of α at 200 $\mu\text{mol}\cdot\text{mol}^{-1}$ were consistently lower than at the higher CO_2 concentrations, α did not consistently increase with CO_2 concentrations above 400 $\mu\text{mol}\cdot\text{mol}^{-1}$. Mean α for a given species and GE was greater (in value, but not necessarily statistically significant) at a CO_2 concentration of 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ than at 600 or 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ for 15 of 36 species and GE combinations.

The root mean square error (RSME) of the fitted model was compared with the average RMSE from the NRH functions fit to each species. Both values are presented in Table 3. The RMSE of the Cannell and Thornley model for sunflower was 1.57 vs. an average of 1.06 when data from each temperature and CO_2 concentration combination were fit individually with an NRH. Likewise, the RMSE of the Cannell and Thornley model for pepper was 1.44 vs. an average of 1.21 when data from each temperature and CO_2 concentration combination were fit individually with an NRH, and 1.29 vs. an average of 1.05, respectively, for geranium.

Discussion

Previous studies have developed photosynthetic response curves for greenhouse ornamentals to light (e.g., Abreu et al., 2014; Ronquim et al., 2009), CO_2 (e.g., Wullschleger, 1993), temperature (e.g., Berry and Björkman, 1980), or some combination (e.g., Boldt et al., 2014; Erwin and Gesick, 2017; Iwakiri

and Inayama, 1975), but typically only along lines in the PPF_D, CO_2 concentration, and temperature variable space; the response to one variable was measured while holding the others constant. For example, data could be used to predict plant responses to a change in light intensity or CO_2 concentration where these lines intersect, but not a simultaneous change in both. Increasing (or decreasing) light intensity and CO_2 simultaneously can result in interactive effects on P_n , especially in combination with changes to leaf temperature as well. Our study is one of the first to report instantaneous P_n measurements at multiple combinations of light intensity, CO_2 concentration, and leaf temperature in greenhouse ornamentals, which can be used to model the interactive effects on P_n . Stanghellini and Bunce (1993) previously evaluated these same environmental variables (light intensity, CO_2 , and temperature) on tomato plants grown at ambient (350 $\mu\text{mol}\cdot\text{mol}^{-1}$). Although general trends were similar between our results and theirs, our results show significant species-to-species variation. This means that additional studies of this type are warranted to model the responses of more species.

All species evaluated displayed the characteristic photosynthetic light response curve shape regardless of the light intensity or temperature to which they were acclimated or the CO_2 concentration during measurement. The NRH parameter values, LCPs, and LSPs (Tables 1 and 2) were generally within expected ranges but also showed substantial differences between results from previous studies measuring the same species. In general, P_{\max} of petunia, verbena, geranium, and sunflower was higher in the present study compared with Boldt et al. (2014), which may be because of the slightly higher growth and measurement temperature (21 to 22 $^{\circ}\text{C}$, as compared with 20 $^{\circ}\text{C}$ for PhotoSim), cultivar, GE, and/or plant age. Photosynthetic responses to

Table 3. Fitted parameters for the Cannell and Thornley model used to model quantum yield (α) and maximum photosynthetic rate (P_{\max}) as functions of temperature and CO₂ concentration, as well as the root mean squared error (RMSE) of the Cannell and Thornley model using these fitted parameters (RMSE_{Cannell-Thornley}) and the average RMSE of each nonrectangular hyperbola, $P_n = 1/2\theta \{ \alpha I + P_{\max} - [(\alpha I + P_{\max})^2 - 4\alpha\theta P_{\max} I]^{0.5} \}$; for each species (Avg. RMSE_{NRH}).

Parameter	Sunflower	Pepper	Geranium
α_{ref} [CO ₂ ($\mu\text{mol}\cdot\mu\text{mol}^{-1}$ photons)] ^z	0.0630	0.0672	0.0460
β ($\mu\text{mol}\cdot\text{mol}^{-1}$)	0.0 ^y	134	127
$c_{T,\alpha}$ ($^{\circ}\text{C}^{-1}$)	0.0104	-0.0615	-0.0356
$P_{\max,\text{ref}}$ ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO ₂)	129.9	28.7	27.7
$K_{\text{Ca},P_{\max}}$ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	1109	498	197
$T_{\max,P_{\max},400}$ ($^{\circ}\text{C}$)	24.4	22.4	22.5
$T_{\max,P_{\max},800}$ ($^{\circ}\text{C}$)	26.5	24.3	20.9
T_0 ($^{\circ}\text{C}$)	4.19	9.73	-0.49
θ	0.355	0.386	0.001
R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO ₂)	0.978	0.79	0.559
RMSE _{Cannell-Thornley}	1.57	1.45	1.29
Avg. RMSE _{NRH}	1.06	1.21	1.05

^z α_{ref} = the value of α at a reference temperature and CO₂ concentration (assumed to be 14 °C and 400 $\mu\text{mol}\cdot\text{mol}^{-1}$), β = a coefficient affecting the sensitivity of α to CO₂ concentration (micromoles per mole), $c_{T,\alpha}$ = a coefficient affecting the sensitivity of α to temperature ($^{\circ}\text{C}^{-1}$), $P_{\max,\text{ref}}$ = the value of P_{\max} at a reference temperature and CO₂ concentration (assumed to be 20 °C and 400 $\mu\text{mol}\cdot\text{mol}^{-1}$), $K_{\text{Ca},P_{\max}}$ = a coefficient affecting the sensitivity of P_{\max} to CO₂ concentration (micromoles per mole), $T_{\max,P_{\max},400}$ = the temperature ($^{\circ}\text{C}$) that maximizes P_{\max} at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, $T_{\max,P_{\max},800}$ = the temperature ($^{\circ}\text{C}$) that maximizes P_{\max} at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, T_0 = the lower temperature ($^{\circ}\text{C}$) at which P_{\max} is 0, θ = a curvature parameter, and R_d = dark respiration (micromoles CO₂ per square meter per second).

^yValue constrained to ≥ 0 to avoid extreme parameter values.

irradiance in field-grown irrigated pepper ‘Quadrato d’Asti’ reached an asymptote at $\approx 25 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO₂ at a leaf temperature of 25 °C (Delfine et al., 2001). This is higher than the P_{\max} of 14.0 and 17.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO₂ observed in our study at ambient CO₂ (400 $\mu\text{mol}\cdot\text{mol}^{-1}$) and temperatures of 21 and 28 °C, respectively, and could be attributed to cultivar, higher irradiance in the field relative to a growth chamber, or differences in production systems. We did not find previous reports of light response curves on calibrachoa.

Previously, LCPs of 24 to 52 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD in herbaceous ornamentals (Boldt et al., 2014) and 13 to 73 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD in leafy greens (Erwin and Gesick, 2017) have been reported at ambient CO₂ (400 $\mu\text{mol}\cdot\text{mol}^{-1}$), which were higher than the calculated LCP values in our study (4.9 to 30.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in Expt. 1 and 0.4 to 38.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in Expt. 2). The lowest LCPs calculated in our study were typically at 600 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, which may explain why some of our LCPs were lower than those reported for other ornamentals. The LCP, the irradiance intensity at which photosynthetic carbon fixation offsets carbon losses from dark respiration and photorespiration, generally decreases as acclimated light intensity decreases or CO₂ concentration increases. This corresponds with what we observed. The reduction in LCP as CO₂ increased indicates that growers may be able to partially offset the impacts of very low ambient irradiance intensities early in the growing season by increasing CO₂; however, this strategy may be more effective at the vegetative stage, when

canopy shading is minimal (low leaf area index) and plant biomass is often a primary quality metric. At the reproductive stage, however, light intensity is an important contributor not just to biomass accumulation but flower initiation and time to flower as well, and may not be able to be offset by CO₂ supplementation.

In general, the LSP increased with increasing CO₂ concentration. At elevated CO₂ concentration (>400 $\mu\text{mol}\cdot\text{mol}^{-1}$), some LSP values were quite high, above 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD, and involved extrapolating outside the tested domain. Therefore, they are only reported as >2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in Tables 1 and 2. In addition, values >2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ are unlikely in greenhouses or other controlled environments. The lower values of LSP calculated likely have more practical meaning to growers. For instance, in pepper at 14 °C and 200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, the measured LSP was only 214 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Such information can be useful for deciding on light, temperature, and CO₂ set points during winter, especially at higher latitudes. At 14 °C and 200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, adding additional light above the LSP would likely be an unnecessary expense and not contribute to increased growth, unless the CO₂ concentration was also concurrently increased or unless the crop canopy was quite dense, in which case the additional light would penetrate deeper into the canopy. Rather, increasing the ambient temperature would be more beneficial. It is worth noting that there are limitations in extrapolating individual leaf responses to whole-plant or canopy measures of P_n (Erwin and Gesick, 2017), e.g., plant age or leaf canopy denseness and depth (and subsequently, the degree of leaf shading). However, modeling these instantaneous measurements, along with knowledge of the crop age, growth stage, and the current environmental conditions they are acclimated to, can provide a starting framework to adjust temperature, irradiance, and CO₂ to optimize growth and yield or maximize biomass production per cost of inputs.

In Expt. 1, we wanted to see if the light intensity of the growth chamber in which plants were grown before measurement impacted photosynthetic response. The increased P_{\max} observed in verbena and petunia acclimated to higher light intensities agreed with previous findings that the higher the light intensity during growth, the higher the photosynthetic capacity of the leaf will be (Bunce and Heichel, 1986). However, this was not the case with calibrachoa. It is possible that the inconsistent results between GE were due to selection bias. As noted in the methods, many of the recently mature calibrachoa leaves of plants grown at 180 and 270 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD were too small to cover even the smaller (2 cm²) cuvette used to measure P_n of calibrachoa and petunia; therefore, larger, older leaves (that unfolded and matured in the lighting environment) and did fully cover the small cuvette were measured in those instances. Studies (e.g., Iwakiri and Inayama, 1975) have shown that older leaves can have lower rates of P_n .

We observed that all three species (calibrachoa, petunia, and verbena) had larger, but fewer leaves at the lowest light intensity and smaller, but more tightly packed leaves at the higher light intensities. These differences can be attributed to morphological responses to light intensity. First, leaves acclimated to lower light intensities tend to be larger and thinner, compared with leaves acclimated to higher light intensities, as a way to maximize light capture (Poorter et al., 2019). Second, internode length often increases as light intensity decreases, leading to a less “tightly packed” appearance (Garcia and Lopez, 2020; Poorter et al., 2019).

In Expt. 2, P_{\max} increased with increasing GE temperature in sunflower and pepper, but not in geranium. At 14 °C, P_n in pepper was especially low. This shows that adding supplemental CO₂ and/or light to pepper (a cold-sensitive plant) would increase P_n somewhat at 14 °C, but not nearly as much as increasing the temperature. In geranium, P_{\max} increased from 14 to 21 °C, then declined at 28 °C. Geraniums grown at 28 °C exhibited photobleaching on leaves that developed after placement in the temperature treatments, a physiological response sometimes observed in geranium in response to high temperature (Owen and Lindberg, 2017). Several measurements on the yellowed leaves resulted in very low rates of P_n . Therefore, older (but greener) leaves were selected for measurement. Also, the lower P_{\max} in geranium at 28 vs. 21 °C could also be attributed to its calculated temperature optimum of 22.5 °C at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ (Table 3), which is close to the 21 °C environment. The temperature optimum for plants in Expt. 2 was determined to be between 20.9 and 26.5 °C, based on regression performed for fitting the Cannell and Thornley model. This fits within the temperature optimum range of 11.1 to 30.8 °C that Boldt et al. (2014) reported for 13 herbaceous ornamentals.

This study may be the first, to our knowledge, that fits NRH parameter values to empirical data to model P_n as a function of light intensity, CO₂ concentration, and leaf temperature, allowing for the estimation of P_n at any combination of these three variables within the domain tested. The Cannell and Thornley model was a good starting point, although we adjusted the

reference values of temperature (14 °C instead of 15 °C) and CO₂ (400 $\mu\text{mol}\cdot\text{mol}^{-1}$ instead of 350 $\mu\text{mol}\cdot\text{mol}^{-1}$) and included R_d to better model our scenario, as described in the materials and methods.

Contour plots for sunflower (Fig. 3) show a comparison of P_n response surfaces interpolated for light intensity and CO₂ by the NRH functions (Fig. 3A) and the fitted Cannell and Thornley model (Fig. 3B). The similarities indicate either one could be used as a decision-support tool. However, the NRH surface plots are limited to the three temperatures evaluated, whereas the fitted Cannell and Thornley model could produce a plot at any temperature between 14 and 28 °C. The quality of fit of the Cannell and Thornley model to our experimental data (RMSE of 1.3 to 1.6, depending on species) may be adequate for a number of applications, including decision support for greenhouse climate control. The Cannell and Thornley model fits all the experimental data with a single model, as compared with fitting separate NRHs for each temperature and CO₂ concentration, hence the greater RMSE compared with individual NRH models (comparison of RMSE in Table 3). However, the small tradeoff in accuracy may be worthwhile for applications that require predicting P_n at conditions that do not fall along one of the NRHs, as it would be experimentally impractical to measure and develop P_n response curves for irradiance and CO₂ at each degree or couple of degrees Celsius for multiple species and cultivars.

Interestingly, we observed an increase in α with increased temperature in pepper and geranium, instead of the expected

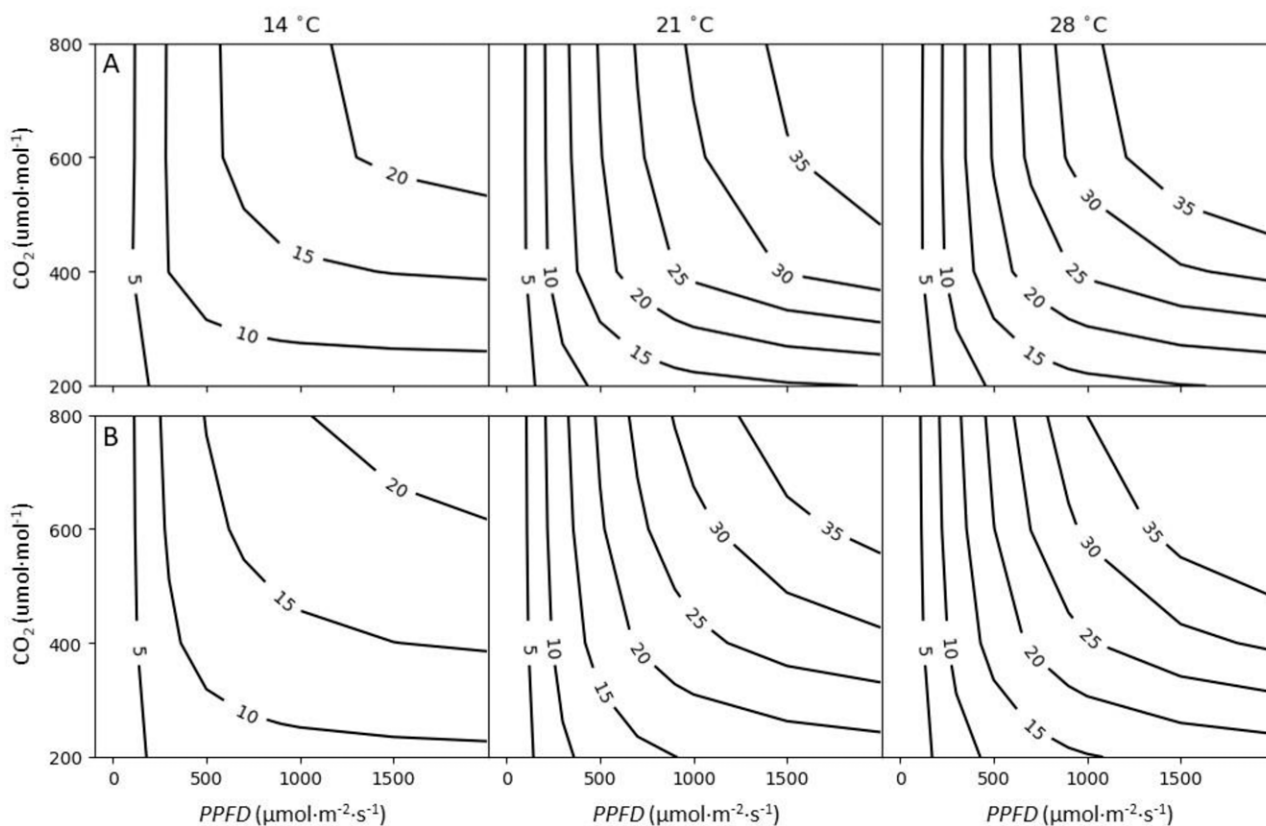


Fig. 3. Comparison of net photosynthesis (P_n) of sunflower ‘Pacino Gold’ modeled by fitting the nonrectangular hyperbola (NRH) equation to data at 14, 21, and 28 °C and each CO₂ concentration (A) and by fitting the Cannell and Thornley model to the same data (B). The NRH equation: $P_n = 1/2\theta \{ \alpha I + P_{\max} - [(\alpha I + P_{\max})^2 - 4\alpha\theta P_{\max} I]^{0.5} \} - R_d$. The Cannell and Thornley model includes equations for α and P_{\max} as functions of temperature and CO₂ concentration.

decrease. It is possible that differences in plant development during growth at different temperatures accounts for this. Peri et al. (2005) found that α decreased by $\approx 40\%$ when leaf nitrogen (N) decreased from 4% to 2%, which corresponded to a decrease in total chlorophyll, from ≈ 0.6 to $0.1 \text{ g}\cdot\text{m}^{-2}$. Although we did not measure N directly, previous research [e.g., review by Sinclair and Horie (1989)] has shown a high correlation between P_n per unit leaf area and leaf N per unit leaf area. As such, it is possible that leaf N may have been lower at 14°C for pepper and geranium, compared with 21 or 28°C , and this relationship may be responsible for the increased values of α at the higher temperatures. Johnson et al. (2010) built on the Cannell and Thornley model using the results from Peri et al. (2005) by incorporating a factor for protein concentration into the expressions for α and P_{max} . If leaf N had been measured, the incorporation of this factor may have improved the fit of the model.

One application of either the NRHs or the fitted Cannell and Thornley model is that they allow growers to assess various combinations of environmental conditions simultaneously, rather than individually. This provides them with the opportunity to see which sets of conditions would result in similar rates of P_n . In Fig. 3, a similar rate of P_n could be achieved at any point located on a contour within the plot. For instance, in sunflower grown at 21°C (Fig. 3), a P_n of $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ CO_2 is achievable at $\approx 600 \mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 and $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD* or at $300 \mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 and $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPFD*. At a temperature of 14°C , much higher levels of light intensity and CO_2 concentration would be needed to attain the same P_n . Based on the species being grown, geographic location, time of year, greenhouse light transmission, electricity and CO_2 costs, and other associated factors, a grower could use these plots, or an associated decision support tool that incorporates them, to assess which combination of light intensity, CO_2 concentration, and temperature is most feasible and economically sound for them to achieve the desired P_n at a minimum cost. In the northern United States, low ambient irradiance is a limiting factor during winter and early spring greenhouse production. Supplemental lighting, historically from high-pressure sodium lamps but now also including LEDs, can be quite expensive to install and operate. If CO_2 supplementation could partially or substantially reduce the need for supplemental lighting, even for a few hours per day when venting is not actively occurring or imminent, without reducing P_n , cost savings may be realized. This is likely to be more advantageous to growers producing leafy crops, ornamental or edible, or during the vegetative stage of crop growth, where the impact of DLI on flower initiation and development is not critical to crop timing.

In lieu of CO_2 supplementation from liquid CO_2 or CO_2 generators, growers could temporally increase the CO_2 concentration of the greenhouse, from sub-ambient to near ambient, by opening vents periodically and using fans to mix the air around the plant canopy to reduce the boundary layer. These strategies would be most feasible when venting is already scheduled for humidity or temperature control; if not, the tradeoff for increasing the CO_2 concentration would be the loss of pre-heated air from the greenhouse and higher heating costs. A cost calculator, based on greenhouse location, time of year, and desired crop growth rates would benefit growers.

In addition, plant acclimation to supplemental CO_2 should be considered. Although most crops exhibit an overall positive response to CO_2 enrichment (Kimball, 1983), they will begin

acclimating after a few weeks (McKinney and Craver, 2021; Yelle et al., 1990). Therefore, CO_2 supplementation may only be early in the cropping cycle when plants are most responsive. For plants with short crop cycles, such as annual bedding plants, CO_2 supplementation may be appropriate throughout production, especially if the greenhouse contains plants at multiple growth stages. Due to acclimation, photosynthetic and growth models developed from instantaneous changes in P_n to CO_2 concentration will likely overestimate plant response as crop duration increases.

In summary, our data are one of the first studies to report instantaneous P_n measurements for ornamental species at multiple combinations of light intensity, CO_2 concentration, leaf temperature, and GE, which can be used to model their interactive effects on P_n . Incorporation of these models into the existing PhotoSim decision-support tool (USDA-ARS, 2019) is planned, to provide growers the opportunity to use these models. The interactive effect of light intensity, CO_2 concentration, and leaf temperature indicates that growers should consider lighting, temperature control, and CO_2 decisions jointly. If ambient CO_2 concentrations in a greenhouse or controlled environment are sub-ambient, and they often are (Erwin and Gesick, 2017; Mortensen, 1987), the expected increase in P_n with supplemental lighting will be tempered by limitations in CO_2 fixation due to lack of available substrate. Similarly, low enzymatic activity at low ambient temperature can result in very low rates of P_n despite high CO_2 concentration and *PPFD*. Therefore, as sole-source or supplemental lighting guidelines are developed for crops, simultaneous consideration of CO_2 concentration and temperature will be critical to achieve the ideal rates of P_n , either based on maximizing photosynthetic rate or optimizing the return on investment of inputs.

Future work measuring and modeling P_n as a function of light intensity, CO_2 concentration, and temperature would benefit from taking data points of these variables in combination, especially in relation to CO_2 and temperature. Algorithm development and/or the use of surface plots could improve this type of modeling, as it would not require collection of data points at all possible combinations of variables and levels. In addition, including a sub-model to represent R_d as a function of temperature and CO_2 concentration might improve the fit of the Cannell and Thornley model.

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