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Growth, Partitioning, and Nutrient and Carbohydrate Concentration of *Petunia ×hybrida* Vilm. Are Influenced by Altering Light, CO_2, and Fertility

Jonathan M. Frantz[1]
USDA-ARS, New England Plant, Soil, and Water Laboratory, University of Maine, Orono, ME 04469

Peter Ling
Department of Food, Agriculture and Biological Engineering, The Ohio State University, Wooster, OH 44691

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Abstract. **Fuel prices have fluctuated wildly in the last several years, and faced with unpredictable or rising fuel costs, growers often lower temperature set points to decrease fuel use. However, plant growth and development are influenced by lower temperatures and may actually cause increases in fuel use as a result of longer production times. Alternative strategies to efficient crop production are needed. Fertility, light, and CO_2 are other environmental factors that can be manipulated within a greenhouse but how all three interact together on growth and development are surprisingly not well known. *Petunia ×hybrida* Vilm. were grown in controlled environments in a $2 \times 2 \times 2$ factorial study investigating how light, fertility, and CO_2 influence growth and development, including shoot partitioning, nutrient uptake, and carbohydrate concentration. Generally, light enhanced flowering, both mass and fraction of total biomass, whereas increased fertility was detrimental to the proportion of biomass allocated to flowers. The influence of CO_2 was complex with high CO_2 suppressing flowering and enhancing leaf growth, but only midway through the 7-week experiment. Carbohydrate concentration remained high in elevated CO_2, even when light and fertility were not limiting. This suggests a sink limitation, so even in high light and fertility, crop response to enhanced CO_2 was low. Although CO_2 had no size effect late in growth, CO_2 suppressed nutrient concentrations. Together, these data suggest strategies that growers may have in controlling their crop growth and development and indicate that enhanced growth (leaf and steam mass) may be at the detriment of development (flowering mass and allocation).**

The top 15 states that the USDA tracks for floriculture production had a wholesale value of $4.2 billion with bedding plants representing approximately one-third of this industry (U.S. Dept. Agr., Nat. Agr. Stat. Ser., 2009). Petunia wholesale value in those 15 states, including those sold as bedding plants, flowering potted plants, and hanging baskets, was just over $120 million in 2008. Much of the production of bedding plants occurs in greenhouses, and the plant material marketed for the spring is typically started in the coolest times of the year. For this reason, energy costs are second only to labor costs as the largest or most expensive factor in indirect costs of greenhouse production for many producers in northern or cooler climates.

Although oil and natural gas prices fluctuated by 100% or more in the last 3 years, generally fuel prices have risen by 50% over the last 10 years (U.S. Dept. Energy, 2009). Faced with these costs, growers often lower temperature set points to decrease fuel use. However, growth and development are influenced by lower temperatures, which may delay a crop enough that the cost per crop and the energy consumed per crop actually increase with lower growth temperatures (Runkle et al., 2009). Alternatives to lowering temperatures are needed so that high-quality crops can meet the market demand on time.

Fertility, light, and CO_2 are other environmental factors that can be manipulated within a greenhouse that influence growth and development. For example, Klock-Moore and Broschat (2001) showed a 20% increase in petunia growth when supplied with 50% additional nutrition from overhead irrigation [100 mg·L^{-1} nitrogen (N) increased to 150 mg·L^{-1} N], but generally, additional N can delay or suppress flowering (Díaz-Pérez et al., 2003; Pitchay et al., 2007; Powell et al., 1988; Smith et al., 1998). Kaczperski et al. (1991) modeled petunia growth and development in a combination of light and temperatures and found strong effects of both. The researchers found an optimum temperature environment for minimum time to flower was found to be 25 °C, and a minimum daily light integral for acceptable quality was found to be 13 mol·m^{-2}·d^{-1}. The ability for petunia to accelerate development with light in addition to temperature has recently been reported (Blanchard and Runkle, 2009), so there is an opportunity to optimize development, crop scheduling, and quality with environmental management other than temperature. However, the possible delay of development with high fertility and the influence of CO_2 in an optimized environment have not often been studied extensively.

Only a few multifactor environmental studies have been conducted on a handful of greenhouse crops. Krizek et al. (1974) evaluated cucumber (*Cucumis sativus* L.), tomato (*Solanum lycopersicum* L.), and lettuce (*Latuca sativa* L.) seedling growth in various combinations of light, temperature, and CO_2 concentrations. The influence of each environmental parameter depended largely on the species; leaf area, leaf mass, and stem mass were limited by different parameters depending on the species. Pansy (*Viola wittrockiana* Gams.) growth and quality were strongly influenced by light, temperature, and CO_2, and although light and temperature influenced development rates, CO_2 concentration had no effect (Niu et al., 2000). Miniature roses (*Rosa ×hybrida* L.) were influenced by temperature, light, and CO_2 as well, and development was accelerated by ≈10% when night temperatures were higher than day temperatures in elevated CO_2 but not in ambient CO_2. Additionally, time to flower was accelerated when additional light was given in high CO_2 but not in ambient CO_2 (Niu et al., 2000).

Unfortunately, few other studies have simultaneously investigated the effects of light, CO_2, and fertility on plant productivity, likely as a result of the complex experimental design or need for many different controllable growth areas. It is important to identify the interactive effects these variables have on the crop growth and development for different crops. Higher yield may be most desirable in some crops (i.e., vegetables) and is reflected in size or mass of the plant or plant parts. In floriculture, mass is secondary to a harder-to-define "quality." Expressed simply, flower parts are sold, and it is some combination of flower number, flower longevity, color vibrancy, or flowering characteristics that are preferred by the consumer (Huang, 2007; Huang and Yeh, 2009). It is therefore important to assess partitioning of biomass among leaves, stems, and flowers to determine the impact of any change in environmental management. The "best" performer or recommendations for management for a species may not necessarily be the largest performer. For example, James and van Iersel (2001) found the most growth in petunia at an N supply of 17.8 mM N (250 mg·L^{-1} N), but recommendations for fertility of petunias are much lower at 5.3 to 7.1 mM N (75 to 100 mg·L^{-1} N; Gibson et al., 2007) perhaps as a result of increased flowering associated with this lower rate.

We sought to investigate how biomass is partitioned in petunia among leaves, stems, and flowers in response to significant differences

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[1]To whom reprint requests should be addressed; e-mail jonathan.frantz@ars.usda.gov.

in light, CO_2, and fertility supply. In doing so, trends in the most limiting factor for growth and quality aspects could be determined so that growers could optimize their production environment in a manner that optimizes energy efficiency while producing high-quality crops.

Materials and Methods

Plant material. Petunia ×hybrida seeds (cv. Madness white) were sown in a 288-cell seedling tray (each cell had 14 cm^3 root volume) filled with a commercial sphagnum–peat-based germination mix (Sunshine Mix #3; Sun Gro Horticulture, Canada). Seedlings were maintained in a glass greenhouse at the Plant Science Research Center, the University of Toledo main campus, starting on 22 Feb. 2006. Temperature set points were 23/18 °C day/night temperature. High-pressure sodium (HPS) and metal halide (MH) lamps (1:1 ratio) provided daylength extension to 16-h days by providing 75 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetic photon flux (*PPF*) beginning at 1600 HR. Seedlings were grown for 4 weeks and irrigated with dilute fertilizer solution daily (3.5 mM N based on a 20N–4.4P–16.6K water-soluble fertilizer; Peat Lite Special; The Scotts Company, Marysville, OH). This fertilizer also contained other macro- and micronutrients that, by weight, consisted of magnesium (0.15%), boron (0.02%), copper (0.01%), EDTA-Fe (0.1%), EDTA-Mn (0.05%), molybdenum (0.01%), and EDTA-Zn (0.05%). Additional calcium and magnesium were supplied in the tap water used to mix the fertilizer solutions as well as the limed sphagnum peat mix (see subsequently).

When seedlings were 4 weeks old (15 Mar. 2006), they were transported to Ohio Agricultural Research and Development Wooster Campus, Wooster, OH, and transplanted into 10-cm pots containing a 70:30 ratio of sphagnum peat and perlite amended with 3.0 $g \cdot L^{-1}$ dolomitic lime. Transplanted plants were placed into 12 controlled environment chambers and allowed to acclimate for 1 week. Each chamber accommodated 24 pots.

The chambers were housed in a standalone building that was equipped with an air-handling unit plumbed to provide one air exchange per minute of air to each chamber. The chambers were 1.4 m (height) × 1.0-m diameter cylinders (1100-L volume) constructed of Plexiglas and a metal frame (Fig. 1). A 25-cm paddle fan was mounted at the top of each chamber to mix the air within the chambers. Two type-K thermocouples were used in each chamber to provide air temperature monitoring, and a humidity probe (CS HM 500; Campbell Scientific, Logan, UT) provided humidity monitoring capabilities. CO_2 was added to half the chambers by a CO_2 controller interfaced with a data logger/controller (CR-23X; Campbell Scientific). Initial conditions were 230 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPF* provided by a 1:1 ratio of HPS and MH lamps with a 16-h photoperiod, 23 °C/18 °C day/night temperature, CO_2 concentration of 400 $\mu mol \cdot mol^{-1}$, and a relative humidity maintained between 65% and 80% throughout the day and night period. All plants received irrigation water mixed with fertilizer as needed or approximately every 3 d. Fertilizer was the same commercial-grade water-soluble blend (20N–4.4P–16.6K) diluted to 7.1 mM N.

Fig. 1. Six of the 12 cylindrical chambers in which petunias were grown. The chambers have a 1:1 ratio (low light) or 2:1 ratio (high light) of HPS and MH lamps, a paddle fan mounted inside and at the top of each chamber to mix the air within the chambers, two thermocouples in each chamber to monitor temperature, and a humidity probe. CO_2 was added to half the chambers by a CO_2 controller. HPS = high-pressure sodium; MH = metal halide.

After the acclimation period, half the chambers received supplemental CO_2 to 800 $\mu mol \cdot mol^{-1}$. Within each CO_2 block, three chambers received *PPF* to 420 $\mu mol \cdot m^{-2} \cdot s^{-1}$ by additional HPS lamps (2:1 ratio), and the other half remained at 230 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Half the plants in each chamber received a more concentrated fertilizer blend, diluted to 21.3 mM N, whereas the other half continued to receive 7.1 mM N. Temperatures and relative humidity were maintained at the original set points and varied among chambers by ≈1 °C and 10% relative humidity on any given day.

Every 2 weeks, beginning at Week 3 after transplanting, three plants from each fertilizer rate in each chamber were destructively harvested. In the initial harvest, all plant material was considered to be "leaf" because the stem was small and there were no flowers. In subsequent harvests, plants were divided into leaves, stems, and flowers, rinsed with distilled water for 30 s, and dried in a forced air-drying oven set to 55 °C for at least 48 h. Appearance of a first flower (first fully opened flower) for each plant was recorded.

Elemental analysis. Dried plant material was ground with a mortar and pestle to ≈0.05-mm particle size for tissue analysis. To determine tissue nutrient concentration, 0.15 g of dried tissue was digested in a microwave digester (MARS Express II; CEM Corp., Matthews, NC) using a modified EPA method (EPA method 3051, Nelson, 1988; HNO_3 digestion at 200 °C with an additional peroxide digestion step). Nutrient content, except N, was determined with inductively coupled plasma optical emission spectroscopy (Model IRIS Intrepid II; Thermo Corp., Waltham, MA). A quality control was run every 10 samples and if any element was determined to be more than 10% higher or lower than the standard value, the instrument was recalibrated. Tomato (*Solanum lycopersicum* L.) standards (NIST reference material 1573, National Institute of Standards and Technology, Gaithersburg, MD; Sharpless and Gill, 2000) were compared every 20 samples and tomato and spinach (*Spinacia oleracea* L.) standards (NIST reference material 1570a; Sharpless and Gill, 2000) were compared every 40 samples.

Carbohydrate analysis. Tissue samples (50 mg) were weighed and ground, and 2 mL phosphate buffer (pH = 7.2) was added and thoroughly mixed. After centrifugation at 16,000 × g for 10 min at 4 °C, the supernatant was pipette into a clean tube. A 5% phenol solution (0.5 mL of 5% phenol) was added to the supernatant followed by 2.5 mL concentrated sulfuric acid (18 M). The mixture was allowed to sit for 10 min. Absorbance at 470 nm was measured with a spectrophotometer and compared against a standard curve made with glucose prepared in the same manner.

Statistical analysis. Data were subjected to a protected analysis of variance using Statstix 9.0 (Analytical Software, Tallahassee, FL). The general model was described as leaf, stem, and flower mass or allocation of those components was a function of CO_2, *PPF*, fertility, and all possible two- and three-way interactions. Significant effects from each of these analyses ($P < 0.05$) were subjected to mean comparisons using the Tukey's honestly significant difference. Time or harvest stage was not included in the model, but rather each harvest time point was treated as a discrete event and variables were analyzed at each time point; no trends over time were tested.

Results

Three weeks after transplanting. Plants in all treatments ranged from 5.2 to 5.9 g per plant, so when there were treatment effects, they were small yet statistically significant

(Fig. 2). There was a significant effect of *PPF* and fertility on plant mass, and there was a significant interaction between *PPF* and fertility (Table 1). Plants grown in higher light were ≈0.6 g larger (≈10%) than those in lower light, whereas plants receiving 21.3 mM N fertilizer rates were ≈0.4 g per plant larger than those receiving 7.1 mM N. Plants receiving both higher light and fertility were 0.7 g larger (≈12%) than those receiving low light and fertilizer. There was no effect of CO_2 supply at this stage. No plants had flowered by this time and leaves were not separated from stems.

Elemental concentration of N, potassium (K), and copper (Cu) was influenced significantly by CO_2, but although it was decreased as expected in N and K, Cu concentrations were significantly higher (Table 2). Both *PPF* and fertility influenced the most nutrient concentrations. Increased *PPF* decreased the concentration of all macronutrients other than sulfur (S) and decreased boron (B), manganese (Mn), and zinc. Surprisingly, increased fertility supply decreased the concentrations of calcium (Ca), magnesium (Mg), B, and Mn but increased tissue concentrations in N, phosphorus, and K.

The influence of CO_2 on specific nutrient concentrations depended on both *PPF* and fertility supply. At low *PPF*, increasing CO_2 had no effect on K but caused an increase in Ca, Mg, and Mn. At higher *PPF*, K and Mn decreased with increasing CO_2, and Ca and Mg had no change. When fertility was low, micronutrients B and Mn decreased with increasing CO_2. At high fertility supply, both B and Mn increased significantly with CO_2. The influence of *PPF* also depended on fertility, but only for some of the macronutrients. In low fertility, nutrient concentrations were especially sensitive to increased *PPF* with K, Ca, Mg, and S all decreasing with higher light. Higher fertility supply mitigated the response to *PPF* with no change occurring in the K, Mg, and S concentrations at higher light and a less severe decrease in Ca with increased *PPF* (30% compared with 50% decrease).

The pattern of carbohydrate concentration in the leaf tissue was similar regardless of harvest time, so for brevity, it is reported here once. Carbohydrate concentration was higher in elevated CO_2 and in higher *PPF*, as expected (Tables 3 and 4) with the combination of high *PPF* and high CO_2 resulting in the highest or nearly the highest carbohydrate concentrations at each harvest event. That treatment combination also revealed evidence of sink limitation, because when low and high fertility was supplied, carbohydrate concentration was higher or lower, respectively. That is, when greater fertility could alleviate potential nutrient limitations, carbohydrate could be incorporated into more plant tissue thereby lowering free carbohydrate concentrations.

Five weeks after transplanting. Plants ranged from 15 g per plant to nearly 25 g per plant (total mass; Fig. 3). Leaf mass was significantly influenced by CO_2, *PPF*, and fertility supply, and the interaction between light and fertility remained significant (Table 5). There was ≈0.7 g more leaf mass (≈10% difference) in elevated CO_2 treatments (Fig. 3A). Plants grown in higher light had ≈1.1 g more leaf mass than those in lower light, and plants receiving high fertility had over 3.5 g more leaf mass than those receiving a low fertility supply. Once again, the high light and high fertility had an additive effect on leaf mass with those treatments having ≈5 g more leaf mass than the treatment grown in low light and low fertility.

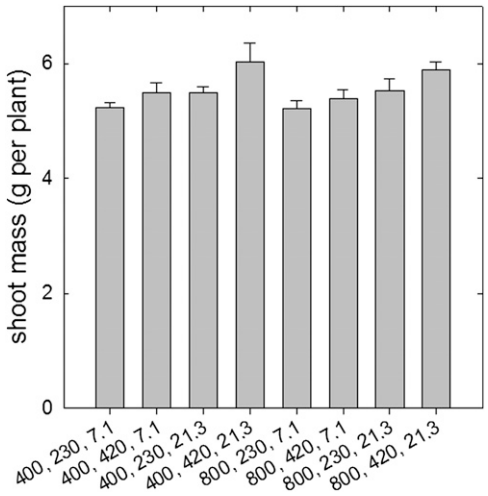

Fig. 2. Week 3 biomass in grams per plant; all harvested biomass was considered to be "shoot" and was not separated further. The treatments are listed by their CO_2 (in μmol·mol^{-1}), photosynthetic photon flux supply (in μmol·m^{-2}·s^{-1}), and fertility supply (mM N), respectively. Error bars represent 1 SD.

Stem mass was only influenced by *PPF* and fertility, and there was a similar interaction between light and fertility as observed in the leaf mass (Fig. 3A–B; Table 5). High light treatments resulted in ≈0.5 g greater stem mass than low light treatments. High fertility increased stem mass by nearly 2 g per plant. Treatments receiving high *PPF* had 0.9 g more stem mass when also receiving high fertility, whereas those in low fertility only had 0.2 g more stem mass in the high light environment.

Flower mass was influenced by CO_2, *PPF*, and fertility. CO_2 interacted with light as well, and there was a three-way interaction among the environmental variables. Flower mass decreased 0.4 g per plant (less than 10% difference) with elevated CO_2; flower number was not recorded, so mass is the only measure of flowering capacity. Higher light stimulated flower mass as did higher fertility. With high and low fertilizer supply, supplemental CO_2 decreased flower mass by 0.5 and 0.3 g, respectively. The three-way interaction was likely a result of a 2-g per plant difference in flower mass between the two extreme treatment combinations of low CO_2, high light and fertility and high CO_2, low light, and fertility (middle two bars of Fig. 3C). All other treatments were within 0.4 g of one another.

Leaf mass made up the largest portion of shoot biomass (Fig. 4A), consisting of between 35% and 47%, depending on the treatment. CO_2 and fertility influenced the proportion of leaf mass, whereas *PPF* by itself was not significant (Table 5). There was, however, an interaction between *PPF* and CO_2 as well as between *PPF* and fertility. Plants receiving elevated CO_2 had more leaf mass than those in "ambient" CO_2 conditions. Plants with 21.3 mM N fertilizer supply also had proportionately more leaf biomass than those with lower fertilizer supply. Plants in elevated CO_2 increased their leaf portion from 41.5% to 42.9% when more light was provided but decreased slightly from 39.7% to 39.2% in lower CO_2 supply. Similarly, plants with a high fertility supply increased leaf allocation from 43.5% to 45% when more light was provided but decreased leaf allocation from 37.7% to 37.2% in low fertility when provided with additional light.

Table 1. *P* values of main effects CO_2, fertility, and photosynthetic photon flux (*PPF*) and all possible interactions for shoot mass at the first harvest (3 weeks after transplanting).[z]

Factor	*P*
CO_2	0.2290
Fertility	<0.0001
PPF	<0.0001
CO_2 × fertility	0.9532
CO_2 × *PPF*	0.1115
Fertility × *PPF*	0.0091
CO_2 × fertility × *PPF*	0.5621

[z]At this harvest, there were no flowers and stem and leaves were combined into total shoot mass.

The proportion of stem mass was only influenced by *PPF* and fertility (Fig. 4B). Plants grown under lower *PPF* supply had slightly more stem, and the proportion of stem decreased when fertilization increased.

The proportion of flower mass was influenced by the same combination of factors as the leaf proportion (Fig. 4C); the gain in leaf biomass came at the expense of flower mass. The proportion of flower mass decreased from 29.4% to 26.6% when grown under elevated CO_2. Increased fertility supply decreased the proportion of flower mass from 31% to 25%. When plants were grown in low fertility, the allocation to flowers decreased

Table 2. Leaf tissue concentration of macro- and micronutrients at harvest 3 weeks after transplanting.[z]

	400 (μmol·m^{-2}·s^{-1})				800 (μmol·m^{-2}·s^{-1})			
	Lo-*PPF*		Hi-*PPF*		Lo-*PPF*		Hi-*PPF*	
	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert
				(g·kg^{-1})				
N	59.10	73.72	48.63	66.20	47.56	70.30	43.66	65.01
P	8.67	8.58	7.08	7.74	8.34	9.12	6.30	7.66
K	82.33	86.14	75.96	88.13	81.14	84.15	55.83	70.97
Ca	15.29	12.34	11.88	10.33	16.08	14.16	10.54	10.58
Mg	9.45	7.08	8.40	7.70	10.24	8.47	7.33	7.47
S	4.29	4.33	3.67	3.87	4.80	4.22	3.58	4.03
				(mg·kg^{-1})				
Fe	158.52	169.18	159.22	159.54	228.10	218.53	210.38	159.08
Mn	183.22	100.57	167.24	80.19	193.43	144.93	136.89	96.74
Zn	92.56	101.26	82.17	93.80	90.16	114.36	74.30	86.05
B	26.54	19.38	25.16	19.31	25.35	22.98	21.26	21.19
Cu	9.43	10.46	10.99	8.30	12.97	13.35	12.26	12.58

[z]Plants were grown in one of two CO_2 concentrations (400 μmol·mol^{-1} or 800 μmol·mol^{-1}), one of two photosynthetic photon flux (Lo-*PPF* = 230 μmol·m^{-2}·s^{-1}; Hi-*PPF* = 420 μmol·m^{-2}·s^{-1}), and one of two fertilizer supplies (Lo-fert = 100 mg·L^{-1} N; Hi-fert = 300 mg·L^{-1} N).
N = nitrogen; P = phosphorus; K = potassium; Ca = calcium; Mg = magnesium; S = sulfur; Fe = iron; Mn = manganese; Zn = zinc; B = boron; Cu = copper.

Table 3. Leaf tissue concentration of carbohydrates at harvest 3, 5, and 7 weeks after transplanting.[z]

	400 (μmol·m^{-2}·s^{-1})				800 (μmol·m^{-2}·s^{-1})			
	Lo-*PPF*		Hi-*PPF*		Lo-*PPF*		Hi-*PPF*	
	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert
Week[y]	(mg carbohydrate/g leaf tissue)							
3	438.7	393.4	906.2	518.1	472.7	359.0	1893.2	1039.4
5	590.4	700.9	877.8	925.2	899.8	812.9	2684.9	1849.6
7	854.1	760.0	1199.4	736.3	1139.4	912.7	1651.3	1001.0

[z]Plants were grown in one of two CO_2 concentrations (400 μmol·mol^{-1} or 800 μmol·mol^{-1}), one of two photosynthetic photon flux (Lo-*PPF* = 230 μmol·m^{-2}·s^{-1}; Hi-*PPF* = 420 μmol·m^{-2}·s^{-1}), and one of two fertilizer supplies (Lo-fert = 100 mg·L^{-1} N; Hi-fert = 300 mg·L^{-1} N).
[y]Harvest week after transplanting into treatment environments.

Table 4. *P* values of main effects CO_2, fertility, and photosynthetic photon flux (*PPF*) and all possible interactions for leaf carbohydrate concentration at 3, 5, and 7 weeks after transplanting.

	Week[z]		
Factor	3	5	7
CO_2	<0.0001	<0.0001	<0.0001
Fertility	<0.0001	0.2392	<0.0001
PPF	0.0001	<0.0001	0.0006
CO_2 × fertility	0.1139	0.0981	0.2143
CO_2 × *PPF*	<0.0001	0.0006	<0.2785
Fertility × *PPF*	0.0018	0.2118	0.0028
CO_2 × fertility × *PPF*	0.2376	0.2909	0.8311

[z]Harvest week after transplanting into treatment environments.

from 32.4% to 29.6% when supplemental CO_2 was used. With high fertility, flower proportion decreased from 26.5% to 23.6% when CO_2 was doubled. Light had an opposite effect on flower allocation in low compared with high fertility environments. In low fertility, increasing *PPF* increased the proportion of flower slightly, but in high fertility, increasing light decreased the proportion of flower biomass.

Elevated CO_2 had a significant main effect on the concentration of all macronutrients except Mg in the leaves with Mg being affected marginally (P = 0.065; Table 6). Similarly, CO_2 influenced the concentration of all micronutrients in the leaves as well, with the exception of B, which was marginally significant (P = 0.0513). The positive or negative influence of CO_2 on nutrient concentration differed, however, depending on the nutrient, the *PPF*, and the fertility supplied. Contrary to the most common observed responses in many CO_2 studies investigating N supply (Taub and Wang, 2008), N concentration increased when CO_2 was high as did all other nutrients with the exception of Cu. The concentration of N was also decreased by an increase in light but, as expected, increased with increased fertility. When additional light was supplied, nutrient concentrations decreased in nearly all cases except the micronutrients B, Cu, and iron. As previously mentioned, it was expected that nutrient concentrations would increase when additional fertility was supplied; however, with the exception of N, nutrient concentration decreased with additional fertility when there was a significant effect. In some cases, especially for micronutrients, the reduction in nutrient concentration was nearly 50% (e.g., Mn in low *PPF*). It is important to note that even with significant decreases in leaf tissue nutrient concentrations, the concentration did not fall below the minimum value observed by Gibson et al. (2007) to cause visible deficiency symptoms. Values of N were frequently below the recommended value for petunia leaf tissue (Mills and Jones, 1996), but no deficiencies were observed and growth remained high.

There were several interactions between variables for different nutrients that are noteworthy. In low light, the concentration of phosphorus (P), Mg, and S remained unchanged with additional CO_2 (Table 6). The concentration of Cu, however, increased with CO_2 in low light only but remained unchanged in high *PPF*. When fertility was changed, only Mg was differentially influenced by CO_2; Mg concentration decreased by ≈10% when additional CO_2 was supplied but remained unchanged at high fertility supply. There was an interaction between *PPF* and fertility supply for P, K, Mg, and Mn. For all of these, there was a significant decrease in nutrient concentration when fertility was low and light was high. However, the decrease was either not significant or much less in high fertility conditions when light increased. This suggests that the plant could better maintain nutrient status in their leaves in a non-limiting light and fertility environment.

Seven weeks after transplanting. Plants ranged from ≈25 g per plant to nearly 50 g per plant (total mass; Fig. 5). The fertility supply had a significant effect on leaf mass with a supply of 21.3 mM N resulting in over a 7-g per plant increase (80% increase) in leaf mass compared with those supplied with 7.1 mM N (Fig. 5A; Table 7). Stem mass was significantly affected by both *PPF* and fertility, and there was a significant interaction between those two parameters (Fig. 5B). High fertility increased stem mass by over 6 g per plant, whereas increased *PPF* from 230 μmol·m^{-2}·s^{-1} to 420 μmol·m^{-2}·s^{-1} increased stem mass by 2.5 g per plant. The increase in stem mass from *PPF* was much greater in elevated fertility than in lower fertility. Flower mass was also increased by *PPF* and fertility, although not to the same extent as leaf and stem mass (Fig. 5C). With higher light, flower mass increased from 9.2 g to 11.4 g, and higher fertility similarly increased flower mass from 9.2 g to 11.4 g. There were no significant interactions among treatment effects for flower mass.

The proportion of leaf mass was influenced by both *PPF* and fertility, and there was an interaction between those two variables as well (Fig. 6A; Table 7). As light increased, leaf biomass allocation decreased from ≈38% to 33.5%, whereas increasing fertility increased the leaf allocation from 33.3% to 38%. At high fertility, increasing light decreased leaf allocation more (≈6%) than at low fertility (≈3%). The proportion of stem mass was also influenced by both *PPF* and fertility (Fig. 6B). Increasing *PPF* increased stem allocation slightly, from 33.3% to 35.3%, and an increased supply of fertility increased stem allocation by approximately the same extent, from 33% to 35.6%. There was a three-way interaction among *PPF*, fertility, and CO_2 indicating that the extent of stem allocation changes in response to *PPF* and fertility depended on the CO_2 supply. In elevated CO_2, stem allocation was high (≈39%) when *PPF* and fertility both were high, but otherwise, CO_2 had no significant effect with stem allocation ranging from 32% to nearly 36%.

Allocation to flower mass was influenced by *PPF* and fertility, and there were interactions between CO_2 and fertility and a three-way

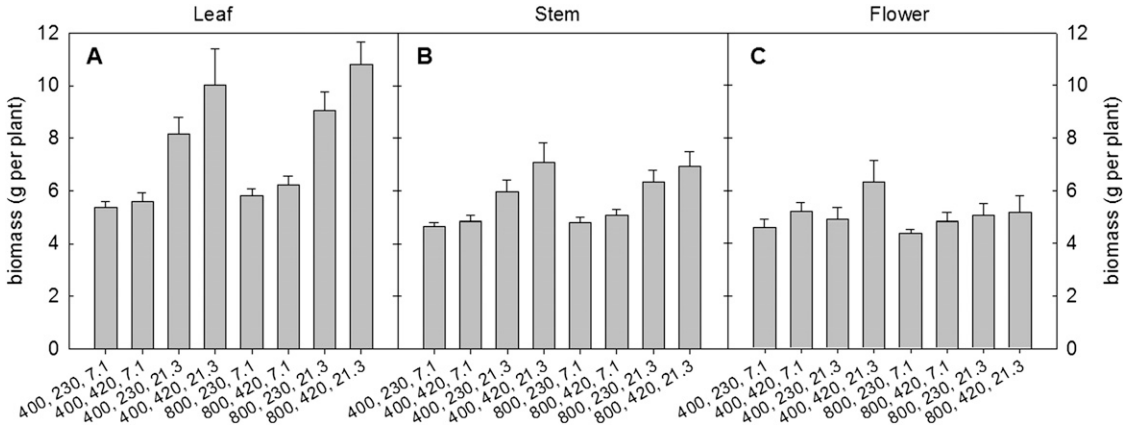

Fig. 3. Week 5 leaf (**A**), stem (**B**), and flower (**C**) weight in grams per plant. The treatments are listed by their CO_2 (in µmol·mol^{-1}), photosynthetic photon flux supply (in µmol·m^{-2}·s^{-1}), and fertility supply (mM N), respectively. Error bars represent 1 SD.

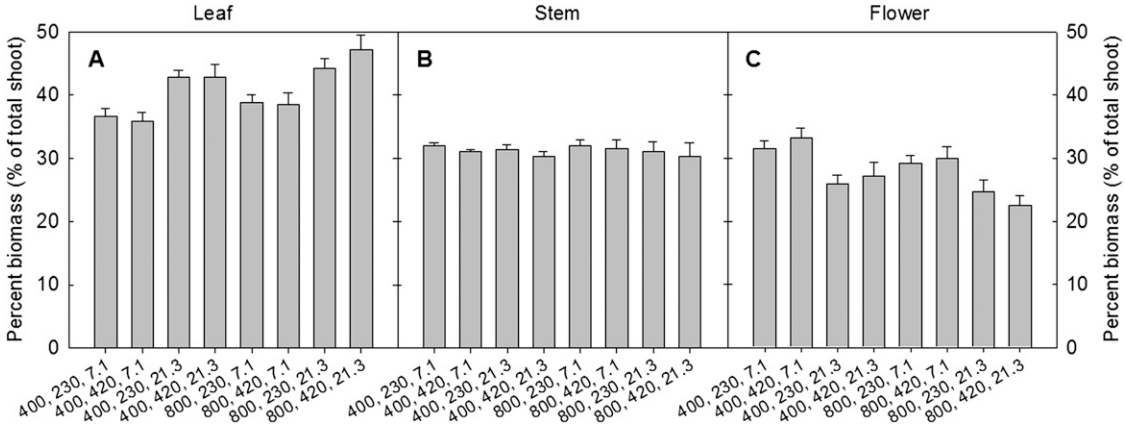

Fig. 4. Week 5 biomass fraction of leaf (**A**), stem (**B**), and flower (**C**) in percent of total shoot mass. The treatments are listed by their CO_2 (in µmol·mol^{-1}), photosynthetic photon flux supply (in µmol·m^{-2}·s^{-1}), and fertility supply (mM N), respectively. Error bars represent 1 SD.

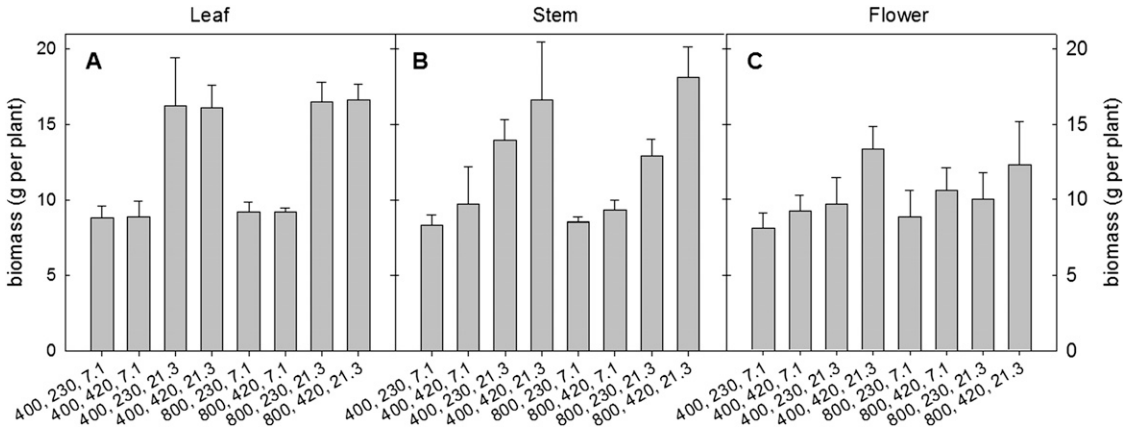

Fig. 5. Week 7 leaf (**A**), stem (**B**), and flower (**C**) weight in grams per plant. The treatments are listed by their CO_2 (in µmol·mol^{-1}), photosynthetic photon flux supply (in µmol·m^{-2}·s^{-1}), and fertility supply (mM N), respectively. Error bars represent 1 SD.

interaction among all three variables (Fig. 6C; Table 7). Generally, as light increased, more biomass was allocated to flowers, but as fertility increased, less was allocated to flowers. Elevated CO_2 enhanced flower mass allocation only when fertility was low. The amount of this enhancement depended on the amount of light that was provided; elevated *PPF* in low-fertility environments resulted in much more flower allocation when elevated CO_2 was provided. When fertility was less limiting (i.e., high fertility treatment), elevated *PPF* and CO_2 had either no effect or a negative effect on flower allocation.

The influence of CO_2 on leaf tissue nutrient concentration was significant for many nutrients at this stage of growth, but overall, the effects were muted compared with that time point. Increased CO_2 decreased N concentration but increased Ca, Mg, S, and Cu concentrations (Table 8). This differs from the time point 2 weeks prior when nearly all nutrients were significantly influenced by differences in CO_2 supply. Higher *PPF* decreased N, K, P, and zinc (Zn) concentrations but increased Ca concentrations. Increased fertility increased only P and K but decreased N, Ca, B, Cu, Mn, and Zn.

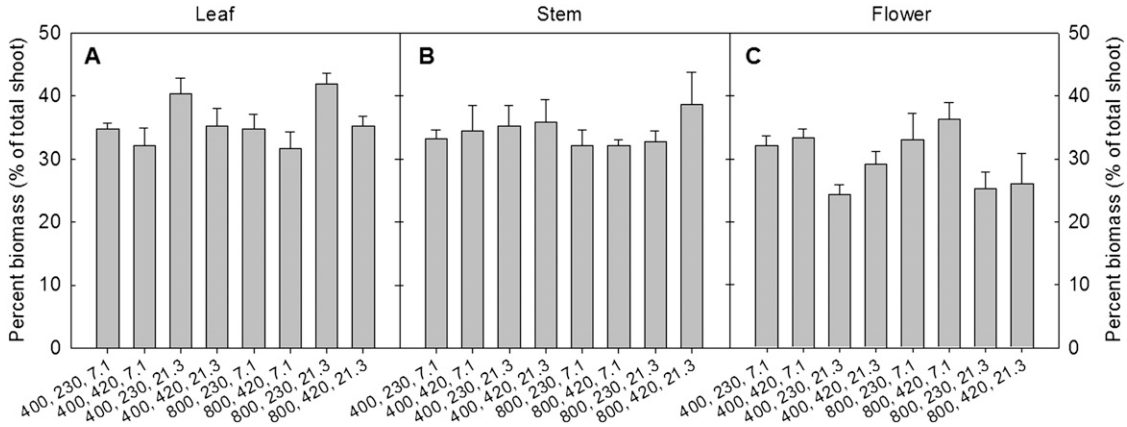

Fig. 6. Week 7 biomass fraction of leaf (**A**), stem (**B**), and flower (**C**) in percent of total shoot mass. The treatments are listed by their CO_2 (in μmol·mol^{-1}), photosynthetic photon flux supply (in μmol·m^{-2}·s^{-1}), and fertility supply (mM N), respectively. Error bars represent 1 SD.

Table 5. *P* values of main effects CO_2, fertility, and photosynthetic photon flux (*PPF*) and all possible interactions for leaf, stem, and flower mass and the proportion of leaf, stem, and flowers at the second harvest (5 weeks after transplanting).

	Mass			Partitioning		
Factor	Leaf *P*	Stem *P*	Flower *P*	Leaf *P*	Stem *P*	Flower *P*
CO_2	<0.0001	0.1294	0.0006	<0.0001	0.7587	<0.0001
Fertility	<0.0001	<0.0001	<0.0001	<0.0001	0.0040	<0.0001
PPF	<0.0001	<0.0001	<0.0001	0.2755	0.0061	0.3129
CO_2 × fertility	0.360	0.7987	0.3118	0.5497	0.5576	0.8628
CO_2 × *PPF*	0.936	0.3392	0.0024	0.0276	0.4591	0.0052
Fertility × *PPF*	<0.0001	0.0025	0.2548	0.0128	0.6581	0.0242
CO_2 × fertility × *PPF*	0.644	0.1363	0.0122	0.1523	0.9626	0.1303

Table 6. Leaf tissue concentration of macro- and micronutrients at harvest 5 weeks after transplanting.[z]

	400 (μmol·m^{-2}·s^{-1})				800 (μmol·m^{-2}·s^{-1})			
	Lo-*PPF*		Hi-*PPF*		Lo-*PPF*		Hi-*PPF*	
	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert
				(g·kg^{-1})				
N	28.13	36.16	24.12	30.16	34.13	38.53	25.31	42.00
P	10.25	10.57	7.90	11.31	9.51	10.30	6.39	9.10
K	58.00	51.92	50.00	44.34	56.70	47.42	38.57	41.71
Ca	17.78	13.40	15.01	13.44	15.69	13.99	12.94	10.96
Mg	12.02	8.95	10.83	10.54	10.93	10.65	8.86	9.63
S	4.22	4.48	4.08	4.30	4.39	4.19	3.63	3.64
				(mg·kg^{-1})				
Fe	215.79	255.43	174.93	243.00	188.54	229.94	216.18	152.01
Mn	225.60	121.55	159.18	101.72	190.73	107.53	122.58	69.10
Zn	72.34	54.70	60.39	41.99	66.89	42.32	42.38	28.85
B	39.45	31.61	34.76	35.57	36.25	33.17	33.11	28.74
Cu	5.20	4.43	5.45	5.57	8.20	8.46	6.77	5.79

[z]Plants were grown in one of two CO_2 concentrations (400 μmol·mol^{-1} or 800 μmol·mol^{-1}), one of two photosynthetic photon flux (Lo-*PPF* = 230 μmol·m^{-2}·s^{-1}; Hi-*PPF* = 420 μmol·m^{-2}·s^{-1}), and one of two fertilizer supplies (Lo-fert = 100 mg·L^{-1} N; Hi-fert = 300 mg·L^{-1} N).
N = nitrogen; P = phosphorus; K = potassium; Ca = calcium; Mg = magnesium; S = sulfur; Fe = iron; Mn = manganese; Zn = zinc; B = boron; Cu = copper.

Table 7. *P* values of main effects CO_2, fertility, and photosynthetic photon flux (*PPF*) and all possible interactions for leaf, stem, and flower mass and the proportion of leaf, stem, and flowers at the third harvest (7 weeks after transplanting).

	Mass			Partitioning		
Factor	Leaf *P*	Stem *P*	Flower *P*	Leaf *P*	Stem *P*	Flower *P*
CO_2	0.2755	0.8824	0.4038	0.5851	0.3113	0.5087
Fertility	<0.0001	<0.0001	<0.0001	<0.0001	0.0005	<0.0001
PPF	0.9684	<0.0001	<0.0001	<0.0001	0.0116	0.0005
CO_2 × fertility	0.9469	0.7088	0.0908	0.2997	0.1917	0.0294
CO_2 × *PPF*	0.9671	0.2833	0.6508	0.4008	0.1803	0.4322
Fertility × *PPF*	0.9823	0.0019	0.0637	0.0048	0.0782	0.7182
CO_2 × fertility × *PPF*	0.7742	0.0872	0.2398	0.6596	0.0194	0.0299

There were numerous interactions among the nutrients. For both Ca and Mg, low *PPF* conditions led to no change in Ca concentrations when CO_2 was increased, but in high *PPF* conditions, Ca concentration increased when CO_2 increased (Table 8). The concentration of Mn decreased in low *PPF* when additional CO_2 was supplied but increased in high *PPF* after CO_2 was supplied. The influence of Cu concentration was opposite that of Ca and Mg with no change occurring in high *PPF* in additional CO_2 but increasing in low *PPF* when CO_2 was supplied. Only P concentrations interacted with CO_2 and fertility. In low fertility supply, P concentrations decreased with additional CO_2 but increased in high fertility supply with additional CO_2.

The concentration of P was influenced by *PPF* only when fertility was low, decreasing when *PPF* increased. Both Mg and B responded to fertility and *PPF* in a similar manner with no change occurring in low fertility but increasing at high fertility when more *PPF* was supplied. The concentration of Zn also was not influenced by *PPF* at low fertility but decreased with *PPF* at high fertility.

Overall observations. Plants achieved ''marketable'' size by Week 5 and remained healthy by the end of the study. There was no difference in the timing for the appearance of the first flower among treatments (data not shown).

Discussion

To achieve rapid growth of high-quality floriculture crops, growers potentially have control overwatering, fertility, CO_2 supply, temperature, and light. Generally, CO_2 supply, temperature, and light are considered more expensive to control because their manipulation depends on features such as structure design (materials, orientation, air infiltration, ventilation, and capacity for supplemental light), fuel cost and supply, and geographic location.

Fertility had the largest influence over crop mass and allocation patterns in this study. Growers would face a choice between faster (to reach a given size), larger growth of their

Table 8. Leaf tissue concentration of macro- and micronutrients at harvest 7 weeks after transplanting.[z]

	400 (μmol·m^{-2}·s^{-1})				800 (μmol·m^{-2}·s^{-1})			
	Lo-*PPF*		Hi-*PPF*		Lo-*PPF*		Hi-*PPF*	
	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert	Lo-fert	Hi-fert
				(g·kg^{-1})				
N	78.80	56.67	78.34	49.67	74.24	49.42	69.44	42.26
P	8.38	11.10	7.00	11.73	8.24	12.54	6.62	12.27
K	37.10	40.57	31.24	35.89	36.13	46.55	27.89	37.42
Ca	17.45	14.05	15.94	13.92	16.22	14.26	19.28	16.56
Mg	10.72	9.99	9.29	10.18	11.20	10.41	11.73	12.63
S	4.69	4.20	4.16	4.36	4.65	4.56	4.94	4.46
				(mg·kg^{-1})				
Fe	93.60	188.78	86.17	184.70	206.16	232.77	141.11	217.37
Mn	175.61	79.34	136.06	70.38	134.45	78.68	164.67	81.03
Zn	50.78	38.62	39.49	26.75	46.41	35.62	46.65	23.02
B	39.21	32.86	34.48	36.97	38.63	31.36	38.84	36.73
Cu	3.76	3.51	5.24	3.49	7.45	6.68	6.13	5.22

[z]Plants were grown in one of two CO_2 concentrations (400 μmol·mol^{-1} or 800 μmol·mol^{-1}), one of two photosynthetic photon flux (Lo-*PPF* = 230 μmol·m^{-2}·s^{-1}; Hi-*PPF* = 420 μmol·m^{-2}·s^{-1}), and one of two fertilizer supplies (Lo-fert = 100 mg·L^{-1} N; Hi-fert = 300 mg·L^{-1} N).
N = nitrogen; P = phosphorus; K = potassium; Ca = calcium; Mg = magnesium; S = sulfur; Fe = iron; Mn = manganese; Zn = zinc; B = boron; Cu = copper.

plants with higher fertility rates and lower quantity of flowers on those plants, thereby potentially decreasing the plant quality. For light, it is recommended to provide at least 10 mol·m^{-2}·d^{-1} for good quality and 17 mol·m^{-2}·d^{-1} for high-quality petunia (Erwin et al., 2004; Verberkt et al., 2004). In the present study, increasing plant quantity (greater flower mass) was achieved by increasing *PPF* from 230 to 420 μmol·m^{-2}·s^{-1} or from 13.2 mol·m^{-2}·d^{-1} to 24.2 mol·m^{-2}·d^{-1}. In practice, growers can boost flower proportion either by boosting light by reducing structural or chemical (spray-on) shading or adding supplemental lighting, but a less expensive alternative would be to decrease fertility. In the production of leaf tissue, there were synergistic effects between *PPF* and fertility, but this came at the expense of flower mass and less proportional growth of flowers. No difference in flower timing or development rate was observed with any variables. In other species, higher N supply has delayed flowering (Díaz-Pérez et al., 2003; Pitchay et al., 2007; Powell et al., 1988; Smith et al., 1998). In our study, all nutrients were increased, not just N, which may have mitigated any influence additional N had on development rates.

Surprisingly, CO_2 was only significant at the second harvest (Week 5 after transplant) for biomass quantity. It has commonly been observed and modeled that an increase in CO_2 concentrations from 400 μmol·mol^{-1} to 800 μmol·mol^{-1} results in an initially large (15% to 50%) increase in growth, photosynthesis, and/or yield in C3 species (Farquhar et al., 1980; Makino and Mae, 1999; Thornley and Johnson, 2000). The extent that this increase persists depends on a myriad of factors. We observed a main treatment effect of CO_2 on leaf and flower mass (but not stem mass) only after 5 weeks of growth (second harvest), but there was no CO_2 effect at the last harvest. Harmens et al. (2000) found a downregulation of single-leaf photosynthesis in elevated CO_2 when N was limiting, but no such change in photosynthesis was observed when N was higher. However, that study investigated N supply up to 6 mM N; in the current study, the low fertility supply was 7.1 mM N. When all other limitations were removed (i.e., light and fertility), CO_2 had little long-term effect on mass in the current study. Still, the allocation to flower mass was influenced by CO_2 when all other conditions favored flower allocation (high light and low fertility). Mortensen and Moe (1995) found development rate accelerated by 4 to 5 d as well as an increase in number of flowering shoots at elevated CO_2 in certain temperature regimes.

The long-term response of plants to CO_2 is, at least partially, related to sink size or a limitation to metabolize fixed carbon (Makino and Mae, 1999; Rogers et al., 1998). That is, when the carbon cannot be fully metabolized, the potential stimulation of plant growth and photosynthesis is dampened. In a thorough review of literature at that time, Arp (1991) found less effect of elevated CO_2 when studies were conducted in root zone-limited containers. In effect, plants grown in small containers, as is common in the greenhouse industry, are sink-limited because of root zone restrictions. This sink limitation hypothesis would help explain some apparent discrepancies in certain crops grown in containers that have strong CO_2 "stimulation" effects. Lewis et al. (2002) observed a decline in photosynthesis during the transition from vegetative growth to flowering followed by an increase in photosynthesis during fruit development. The increase was attributed to increased sink size stimulating photosynthesis above that of flowering stage. Other crops might alter their carbon allocation patterns to effectively increase sink size. In a review of greenhouse crop responses to elevated CO_2, Mortensen (1987) found some crops increased the number of leaves, number of laterals, or, interestingly, the number of flowers. In the current study, increasing the supply of other, potentially limiting factors such as fertility and light was not enough to increase sink size sufficiently to allow for continuous CO_2 growth stimulation. Carbohydrate concentration was increased as a result of elevated CO_2, especially when light was not limiting. When both light and fertility were high, carbohydrate concentration was higher in elevated CO_2 indicating that even when all other environmental sink limitations were absent (other than root zone volume), fixed carbon remained in the leaves as a result of persistent sink limitations.

If there is a sink limitation to consider in floriculture crop production, only certain types of production may benefit from the use of above-ambient CO_2. These include short-term production in young plants where roots have not yet become pot-bound, semiopen root zone environments such as aeroponics, nutrient film technique hydroponics, very large containers such as patio containers for the landscape, and stock plant production where cuttings are collected regularly. In each of these scenarios, sinks either have capacity to expand in the timeframe of production or new sinks are created periodically to reduce permanent limitations.

In addition to mass and biomass allocation patterns, light, fertility, and CO_2 can influence other factors related to growth and quality. In the Krizek et al. (1974) study of cucumber, tomato, and lettuce, precocious flower buds were formed on both tomato and cucumber in elevated CO_2 (2,000 μmol·mol^{-1}). This suggests that, at least in some species, development rates and time to market may be influenced by CO_2. Taub and Wang (2008) report on changes in tissue N concentrations when plants were grown in elevated CO_2, suggesting that minimum recommendations for tissue nutrient concentrations may differ in different environments. Together, manipulation of *PPF*, fertility, and CO_2 have significant and complex effects on plant growth and partitioning and affect many quality indices that plant producers should consider when faced with optimizing production environments. Floriculture crops are especially challenging to determine optimal environments because producers sell tough-to-define "quality" as well as quantity. More multiple-factor interaction studies are needed to understand crop acclimation or responses to the environment.

Literature Cited

Arp, W.J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. Plant Cell Environ. 14:869–875.

Blanchard, M. and E. Runkle. 2009. Energy efficient annuals part 6: Petunias. Greenhouse Grower 27(9):36–41.

Díaz-Pérez, J.C., A.C. Purvis, and J.T. Paulk. 2003. Bolting, yield, and bulb decay of sweet onion as affected by nitrogen fertilization. J. Amer. Soc. Hort. Sci. 128:144–149.

Erwin, J., N. Mattson, and R. Warner. 2004. Light effects on annual bedding plants. In: Fisher, P. and E. Runkle (eds.). Lighting up profits. Meister Media Worldwide, Willoughby, OH.

Farquhar, G.D., S. von Caemmerer, and J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78–90.

Gibson, J.L., D.S. Pitchay, A.L. Williams-Rhodes, B.E. Whipker, P.V. Nelson, and J.M. Dole.

2007. Nutrient deficiencies in bedding plants. Ball Publishing, Batavia, IL.
Harmens, H., C.M. Stirling, C. Marshall, and J.F. Farrar. 2000. Does down-regulation of photosynthetic capacity by elevated CO_2 depend on N supply in *Dactylis glomerata*? Physiol. Plant. 108:43–50.
Huang, L.C. 2007. Behavioral differences in prepurchase processes between purchasers of flowers for self use and for gift use. HortTechnology 17:183–190.
Huang, L.C. and T.F. Yeh. 2009. Floral consumption values for consumer groups with different purchase choices for flowers. HortTechnology 19:563–571.
James, E.C. and M.W. van Iersel. 2001. Fertilizer concentration affects growth and flowering of subirrigated petunias and begonias. HortScience 36:40–44.
Kaczperski, M.P., W.H. Carlson, and M.G. Karlsson. 1991. Growth and development of *Petunia* × *hybrids* as a function of temperature and irradiance. J. Amer. Soc. Hort. Sci. 116:232–237.
Klock-Moore, K.A. and T.K. Broschat. 2001. Irrigation systems and fertilizer affect petunia growth. HortTechnology 11:416–418.
Krizek, D.T., W.A. Bailey, H. Khreter, and R.C. Liu. 1974. Maximizing growth of vegetable seedlings in controlled environments at elevated temperature, light and CO_2. Acta Hort. 39:89–102.
Lewis, J.D., X.Z. Wang, K.L. Griffin, and D.T. Tissue. 2002. Effects of age and ontogeny on photosynthetic responses of a determinate annual plant to elevated CO_2 concentrations. Plant Cell Environ. 25:359–368.
Makino, A. and T. Mae. 1999. Photosynthesis and plant growth at elevated levels of CO_2. Plant Cell Physiol. 40:999–1006.
Mills, H.A. and J.B. Jones, Jr. 1996. Plant analysis handbook II. MicroMacro Publ., Athens, GA.
Mortensen, L. and R. Moe. 1995. Effects of temperature, carbon dioxide concentration, day length and photon flux density on growth, morphogenesis and flowering of miniature roses. Acta Hort. 378:63–70.
Mortensen, L.M. 1987. Review: CO_2 enrichment in greenhouses. Crop responses. Sci. Hort. 33: 1–25.
Nelson, M.R. 1988. Index to EPA methods. EPA Circular 901/3-88-01. U.S. Environmental Protection Agency, Washington, DC.
Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2000. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of pansy (*Viola wittrockiana*). J. Amer. Soc. Hort. Sci. 125: 436–441.
Pitchay, D.S., J. Frantz, J.C. Locke, and C.R. Krause. 2007. Impact of nitrogen supply on uptake, utilization, growth, and development of begonia and New Guinea impatiens, and susceptibility of begonia to *Botrytis cinerea*. J. Amer. Soc. Hort. Sci. 132:193–201.
Powell, C.L., K.I. Caldwell, R.A. Littler, and I. Warrington.1988. Effect of temperature regime and nitrogen fertilizer level on vegetative and reproductive bud development in *Cymbidium* orchids. J. Amer. Soc. Hort. Sci. 113:552–556.
Rogers, A., B.U. Fischer, J. Bryant, M. Frehner, H. Blum, C.A. Raines, and S.P. Long. 1998. Acclimation of photosynthesis to elevated CO_2 under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO_2 enrichment. Plant Physiol. 118:683–689.
Runkle, E., J. Frantz, and M. Blanchard. 2009. Energy efficient annuals: Scheduling bedding plants. Greenhouse Grower 27(4):41–44.
Sharpless, K.E. and L.M. Gill. 2000. Value assignment of nutrient concentrations in 5 standard reference materials and 6 reference materials. J. Assoc. Analyt. Communities Int. 83:413–419.
Smith, M.A., G.C. Elliott, and M.P. Bridgen. 1998. Calcium and nitrogen fertilization of *Alstroemeria* for cut flower production. HortScience 33:55–59.
Taub, D.R. and X. Wang. 2008. Why are nitrogen concentrations in plant tissues lower under elevated CO2? A critical examination of the hypotheses. J. Integr. Plant Biol. 50:1365–1374.
Thornley, J.H.M. and I.R. Johnson. 2000. Plant and crop modeling: A mathematical approach to plant and crop physiology. Blackburn Press, Caldwell, NJ.
U.S. Dept. Agr., Nat. Agr. Stat. Ser. 2009. Floriculture crops 2008 summary. Special Circular 6-1 (09).
U.S. Dept. Energy. 2009. Monthly Energy Review. 27 Nov. 2009. <http://www.eia.doe.gov/emeu/mer/prices.html>.
Verberkt, H., R. Heins, and T. Blom. 2004. Supplemental lighting on potted plants. In: Fisher, P. and E. Runkle (eds.). Lighting up profits. Meister Media Worldwide, Willoughby, OH.