

Growth and Topological Changes of *Citrus limon* (L.) Burm. f. 'Eureka' in Response to High Temperatures and Elevated Atmospheric Carbon Dioxide

Chris A. Martin and Jean C. Stutz

Department of Botany, Arizona State University, Box 871601, Tempe, AZ 85287-1601

Bruce A. Kimball and Sherwood B. Idso

United States Water Conservation Laboratory, 4331 East Broadway, Phoenix, AZ 85040

David H. Akey

United States Western Cotton Research Laboratory, 4135 East Broadway, Phoenix, AZ 85040

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Abstract. Growth and topological indices of 'Eureka' lemon were measured after 6 months in well-watered and well-fertilized conditions and factorial combinations of moderate (29/21C day/night) or high (42/32C day/night) temperatures and ambient (350 to 380 $\mu\text{mol}\cdot\text{mol}^{-1}$) or elevated (constant 680 $\mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 . In high temperatures, plants were smaller and had higher levels of leaf chlorophyll a than in moderate temperatures. Moreover, plants in high temperatures and elevated CO_2 had about 15 % higher levels of leaf chlorophyll a than those in high temperatures and ambient CO_2 . In high temperatures, plant growth in elevated CO_2 was about 87% more than in ambient CO_2 . Thus, high CO_2 reduced the negative effect of high temperature on shoot growth. In moderate temperatures, plant growth in elevated CO_2 was only about 21% more than in ambient CO_2 . Irrespective of temperature treatments, shoot branch architecture in elevated CO_2 was more hierarchical than those in ambient CO_2 . Specific shoot extension, a topological measure of branch frequency, was not affected by elevated CO_2 in moderate temperatures, but was increased by elevated CO_2 enrichment in high temperatures—an indication of decreased branch frequency and increased apical dominance. In moderate temperatures, plants in elevated CO_2 had fibrous root branch patterns that were less hierarchical than at ambient CO_2 . The lengths of exterior and interior fibrous roots between branch points and the length of second-degree adventitious lateral branches were increased >50% by high temperatures compared with moderate temperatures. Root length between branch points was not affected by CO_2 levels.

High aerial temperatures can reduce plant growth by limiting external and internal carbon acquisition and use (Baker et al., 1988; Bar-Tsur et al., 1985; Levitt, 1980; Murtagh et al., 1987; Ranney and Peet, 1994). High aerial temperatures increase leaf-to-air vapor-pressure gradients, resulting in increased stomatal resistance to gas exchange (Syvertsen and Salyani, 1991) but high temperatures can also affect internal enzyme-catalyzed processes like ribulose-1,5-bisphosphate carboxylation-oxygenation, photosynthetic electron transport, or chloroplast membrane integrity (Berry and Bjorkman, 1980; Syvertsen and Lloyd, 1994). Furthermore, high root-zone temperatures such as those recorded in urban soils and container rooting media in outdoor production nurseries (Graves and Dana, 1987; Martin and Ingram, 1988) reduce plant growth and may decrease carbon assimilation by nonstomatal limitation of photosynthesis (Martin et al., 1989). The optimum temperature range for shoot and root growth of most citrus is 24 to 31C (Girton, 1927; Khairi and Hall, 1976). Shoot growth of 'Eureka' lemon was higher for plants grown at day/night temperature regimens of 25/15C than at 20/10C or 30/20C (Harty and Van Staden, 1988).

Elevated atmospheric CO_2 can increase growth of C_3 horticultural crops like citrus (Andersson, 1991; Eamus and Jarvis, 1989; Idso and Kimball, 1983, 1992; Koch et al., 1986), although the

magnitude of this increase varies considerably with species, growing conditions, and exposure time (Lawlor and Mitchell, 1991). During the last decade, the interactive effects of air temperature and CO_2 on plant growth have been investigated in several studies (Allen et al., 1990; Idso et al., 1987; Imai and Okamoto-Sato, 1991; McKee and Woodward, 1994; Mortensen, 1994). Results from

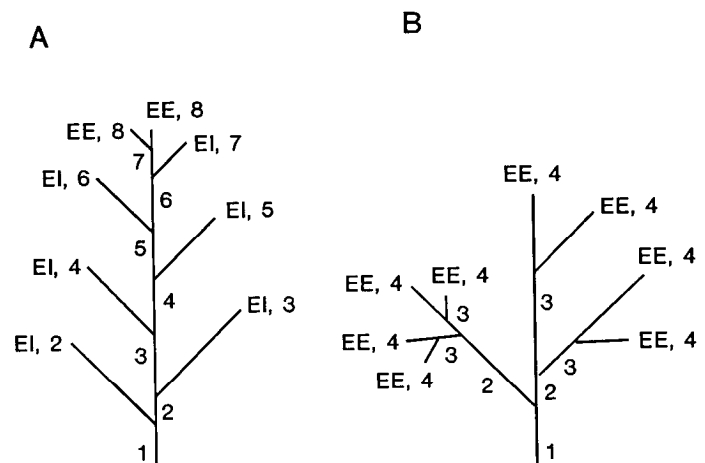


Fig. 1 Diagram showing distinctions between extreme topological patterns [(A) herringbone, (B) dichotomous] and illustration of the branch linkage terms used in this paper. EE = exterior-exterior linkages, EI = exterior-interior linkages, while interior linkages (II) are unlabelled. For each topological pattern, magnitude (μ) = 8 while values for altitude (a) and total pathlength (p) are 8 and 43, respectively, for A, and 4 and 32, respectively, for B.

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these studies suggest that the relative CO₂-enhancement effect of growth caused by elevated CO₂ might increase commensurate with increased temperature to at least 38C (Baker et al., 1994; Rawson, 1992), although we have found no studies about plant growth in response to elevated CO₂ and supraoptimal temperatures >38C.

Architectural branch patterns of shoots and roots play a crucial role in a plant's adaptation to environmental factors by affecting light intensity and quality on leaves via canopy shading patterns and root uptake of water and nutrients via changes in the volume of soil explored and the density of roots within a given volume of soil (Ceulemans and Mousseau, 1994; Fitter, 1987). Architectural patterns of plants, roots in particular, display a degree of geometric plasticity to changes in environmental signals such as drought (Berntson and Woodward, 1992; Fitter, 1987) and low nutrient supply (Fitter and Strickland, 1991) independent of any effects on plant growth. Architectural branch patterns of plants have been quantified topologically (Fitter, 1987; Fitter et al., 1991; Werner and Smart, 1973). Topology is the study of geometric configurations of complex objects and, for plants, is not a function of shoot and root extension growth (Fitter, 1987).

In this paper we use the terminology presented by Fitter (1987) for identifying topological patterns of shoot and root branching (Fig. 1). Using this system, shoots and roots are comprised of a set of links of increasing developmental order. A link is a linear portion of a shoot or root between a meristem and the nearest branch point, two proximal branch points, or a branch point and the crown of the plant. Each link is either exterior, ending in a meristem, or interior, ending at another link. The base link of a shoot or root is the link most distal to an exterior link and has a developmental degree of one. Moving from the base link toward an exterior link, the developmental degree increases by the sum of each proximal link. The altitude (*a_i*) of a root system is the longest path (the highest number of links) between the base link or crown and an exterior link. The total pathlength (*p_i*) of a root system is the sum of all links for each path from the base link to each exterior link. The magnitude (*μ*) is the sum of all exterior links. As Fig. 1 illustrates, when magnitudes are equal, comparisons of values for altitude and total path length can aid in distinguishing differences in the geometric configuration of a root or shoot system. Additional information can be obtained by calculating the specific shoot extension [ratio of total shoot extension to magnitude (*μ*)], which delineates branch frequency and branch link lengths, which indicate elongation. Interior branch links can be further classified into two subgroups, depending on whether adjoining links are exterior or interior (Smart, 1978). As such, each interior link can be categorized as exterior-interior (EI), interior links that adjoin other

exterior links, or interior-interior (II), interior links that adjoin other interior links. Exterior branch links ending in a meristem are referred to as exterior-exterior (EE).

One clear topological study concerning elevated CO₂ showed that elevated CO₂ caused a more branched and elongated root system that foraged through larger volumes of soil (Berntson and Woodward, 1992). The effects of high temperature and the interactive effects of high temperature and elevated CO₂ on woody plant architecture are unknown. The purpose of this study was to investigate the interactive effects of supraoptimal air and root-zone temperatures and elevated atmospheric CO₂ on growth and topology of 'Eureka' lemon.

Materials and Methods

Growing conditions. Uniform rooted cuttings of 'Eureka' lemon (30-cm high) were potted on 2 Apr. 1993 into 27-liter polyethylene containers filled with a mixture of 1 Gilman loam soil : 4 coarse sand (by volume). Plants were then grown for 6 months in either of two, adjacent, identical glasshouses (north-south orientation, 10% light exclusion, similar absolute humidity) that provided moderate (29/21C day maximum/night minimum) or high (42/32C day maximum/night minimum) temperatures. Air temperatures in each glasshouse were computer controlled to oscillate diurnally between maximum and minimum points in a realistic sine wave pattern and deviated by ±1C from the programmed temperatures. Typical leaf-to-air vapor-pressure gradients in the moderate and high temperature glasshouses ranged from 1.6 to 4.3 kPa during the early morning to 4.0 to 6.2 kPa during midday as measured by a portable photosynthesis system [LI-6200; LI-COR, Lincoln, Neb.) with a cuvette chamber humidity sensor calibrated with a dewpoint-controlled water-vapor generator (LI-610). Root-zone temperatures were recorded by copper-constantan thermocouples attached to a micrologger (model 21X; Campbell Scientific, Logan, Utah). Thermocouple junctions were positioned at the center of the container rooting medium. Root-zone temperatures were similar to glasshouse air temperatures with similar sinusoidal patterns and amplitudes (data not shown). Furthermore, both glasshouses were partitioned in half with clear polyethylene plastic to separate an ambient (350 to 380 μmol·mol⁻¹) or enriched (constant 680 μmol·mol⁻¹) CO₂ environment. The CO₂ sampling control system used to monitor and regulate CO₂-in-air mixtures was the same as described by Kimball et al. (1992).

Individual plants were fertilized at the start of the experiment and after 3 months by top dressing with 75 g of 20N-0P-16.6K (slow-release IBDU), 8 g of 0N-19.6P-0K (concentrated super-

Table 1. Canopy leaf, stem, and root dry weights and shoot-to-root ratio (SR) of 'Eureka' lemon plants after 6 months in 27-liter pots and exposure to factorial combinations of either moderate (29/21C day/night) or high (42/32C day/night) air and root-zone temperatures and ambient (350 to 380 μmol·mol⁻¹) or elevated (680 μmol·mol⁻¹) CO₂.

Temp (T)	Atmospheric CO ₂	Dry wt (g/plant)			SR
		Canopy leaf	Stem	Root	
Moderate	Ambient	23.8 ^z	29.8	19.4	2.8
	Elevated	31.1	33.7	23.6	2.8
High	Ambient	12.6	11.3	5.5	4.4
	Elevated +	22.7	21.7	10.7	4.2
Significance					
T		***	***	***	***
CO ₂		***	***	***	NS
T × CO ₂		NS	*	NS	NS

^zValues are treatment means, n = 15.

NS, *, **, ***Nonsignificant or significant at P ≤ 0.05, 0.01, or 0.0001.

Table 2. Total shoot extension, canopy leaf area, leaf number, specific leaf area, specific shoot extension, and leaf chlorophyll density of 'Eureka' lemon plants after 6 months in 27-liter pots and exposure to factorial combinations of either moderate (29/21C day/night) or high (42/32C day/night) air and root-zone temperatures and ambient (350 to 380 $\mu\text{mol}\cdot\text{mol}^{-1}$) or elevated (680 $\mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 .

Temp (T)	Atmospheric CO_2	Shoot extension (m/plant)	Canopy leaf area (m^2/plant)	Leaf no.	Specific leaf area ($\text{m}^2\cdot\text{kg}^{-1}$)	Specific shoot extension (cm/μ^2)	Chlorophyll a ($\text{mg}\cdot\text{m}^{-2}$)
Moderate	Ambient	0.25 ^y	0.24	136	0.08	21.9	114
	Elevated	0.29	0.28	142	0.06	20.2	103
High	Ambient	0.15	0.14	88	0.10	20.6	164
	Elevated	0.20	0.22	104	0.10	28.0	190
Significance							
T		***	***	**	***	*	***
CO_2		**	**	NS	NS	NS	NS
$\text{T} \times \text{CO}_2$		NS	NS	*	NS	**	**

^y μ = Magnitude, the total number of external links.

^zValues are treatment means, n = 15.

^{NS}, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.0001.

phosphate), and 32 g of Micromax micronutrient fertilizer (Grace-Sierra, Milpitas, Calif.). Additionally, each plant was fertilized weekly with 4.4 M H_3PO_4 at 25 $\text{mg}\cdot\text{liter}^{-1}$. Plants were irrigated every second day at 0400 HR with about 1500 ml/pot to prevent water stress.

Data collection. After 6 months of growth, leaf chlorophyll measurements were made with a hand-held chlorophyll meter (SPAD 502; Minolta Corp., Ramsay, N.J.) that measured the differential attenuation by leaves of light in wavebands centered near 650 and 980 nm. Individual measurements were taken on six recently mature leaves per plant; these measurements were then averaged to produce a single mean value of chlorophyll a density per plant. Leaves from all plants were separated from stems and counted, and leaf area was measured with a leaf area meter (LI-3 100). Shoot extension of the remaining stems was measured with a ruler. For shoot canopy topology, a two-dimensional branch drawing of each shoot system was made on paper. On each drawing, the number of branch links was counted and each link was assigned a developmental order. Next, magnitude (μ), altitude (a), total pathlength (p), and specific shoot extension were calculated. Stems were then cut at the rooting medium surface, and root systems were carefully washed free of rooting medium by floating rootballs in a large water bath. The most developed, first-order adventitious root was excised from each root system at 30 consecutive branch links acropetal to the most terminal meristem. For these root samples, μ , a , and p were calculated after also tracing the root samples on paper and counting and ordering all branch links. Additionally, branch links for each root sample were categorized into groups of EE, EI, or II links (Fig. 1), and their lengths were measured. Also, five, second-degree lateral branches per each root sample were randomly selected and their lengths were measured. Finally, all leaves, stems and roots were oven-dried at 65C for 48 h and weighed.

Experiment design and data analysis. The experiment was a split-plot design arranged in a two temperature (main plot) \times two atmospheric CO_2 (subplot) factorial combination with 15 plants in each treatment combination. The general linear models procedure was used to test for significant responses and response interaction of all growth variables to treatments. For topological variables a , and p , a statistical analysis of treatment main effects and interactions for \log_{10} transformed a and p was conducted by analysis of covariance using $\log_{10}\mu$ as the covariate. This was done to compensate for the strong positive correlation of a and p to μ (Bernston, 1994). When magnitude is constant, plants with higher

values of a and p are more hierarchical than plants with lower values of a and p and *visa versa*. Because topology can also be characterized by the slopes of the log-linear relationships of a and p to μ (Fitter, 1987), linear models of $\log_{10}a$, (dependent variable) on $\log_{10}\mu$ (independent variable) and of $\log_{10}p$ on $\log_{10}\mu$ were calculated. If the slope coefficients of these regression equations approach a theoretical maximum ($\log_{10}a = 1.0$ and $\log_{10}p = 1.92$) (Fitter and Strickland, 1991; Werner and Smart, 1973), then branch points of shoot and root systems are mostly limited to a main axis, with lateral branches patterned in two adjacent rows in mostly opposite directions. This topological pattern has been defined as herringbone (Fig. 1) (Fitter, 1987; Fitter and Strickland, 1991). As the slope values decrease to a theoretical minimum ($\log_{10}a = 0.15$ and $\log_{10}p = 1.02$), the branch pattern lacks a main axis and branching consists of a division into two parts. This topological pattern has been defined as dichotomous (Fitter, 1987; Fitter and Strickland, 1991). Intermediate branch patterns between herringbone and dichotomous extremes have been defined as random (Fitter, 1987; Fitter and Strickland, 1991).

Results

High temperatures generally suppressed lemon plant growth as demonstrated by lower leaf, stem, and root dry weights (Table 1); lower total shoot extension, canopy leaf area, and leaf number; and greater specific leaf area (Table 2, Fig. 2). The shoot-to-root ratio and leaf chlorophyll a densities were higher for plants grown in high than moderate temperatures (Tables 1 and 2).

In contrast, elevated CO_2 concentrations generally caused an increase in lemon plant growth demonstrated by greater leaf and roots dry weights (Table 1), total shoot extension, and canopy leaf area (Table 2, Fig. 2). There was no effect of CO_2 enrichment on the shoot-to-root ratio of plants in either thermal environment (Table 1).

There was an interactive effect of CO_2 and temperature on stem dry weight, leaf number, specific shoot extension, and leaf chlorophyll a densities (Tables 1 and 2). Elevated CO_2 had no effect on these variables when temperatures were moderate, but these variables were all increased in response to elevated CO_2 at high temperatures. Elevated CO_2 did not affect specific leaf area in either thermal environment, although, at moderate temperatures, leaves in elevated CO_2 were slightly thicker than for those in ambient CO_2 (Table 2).

The topology of 'Eureka' lemon shoots was predominately

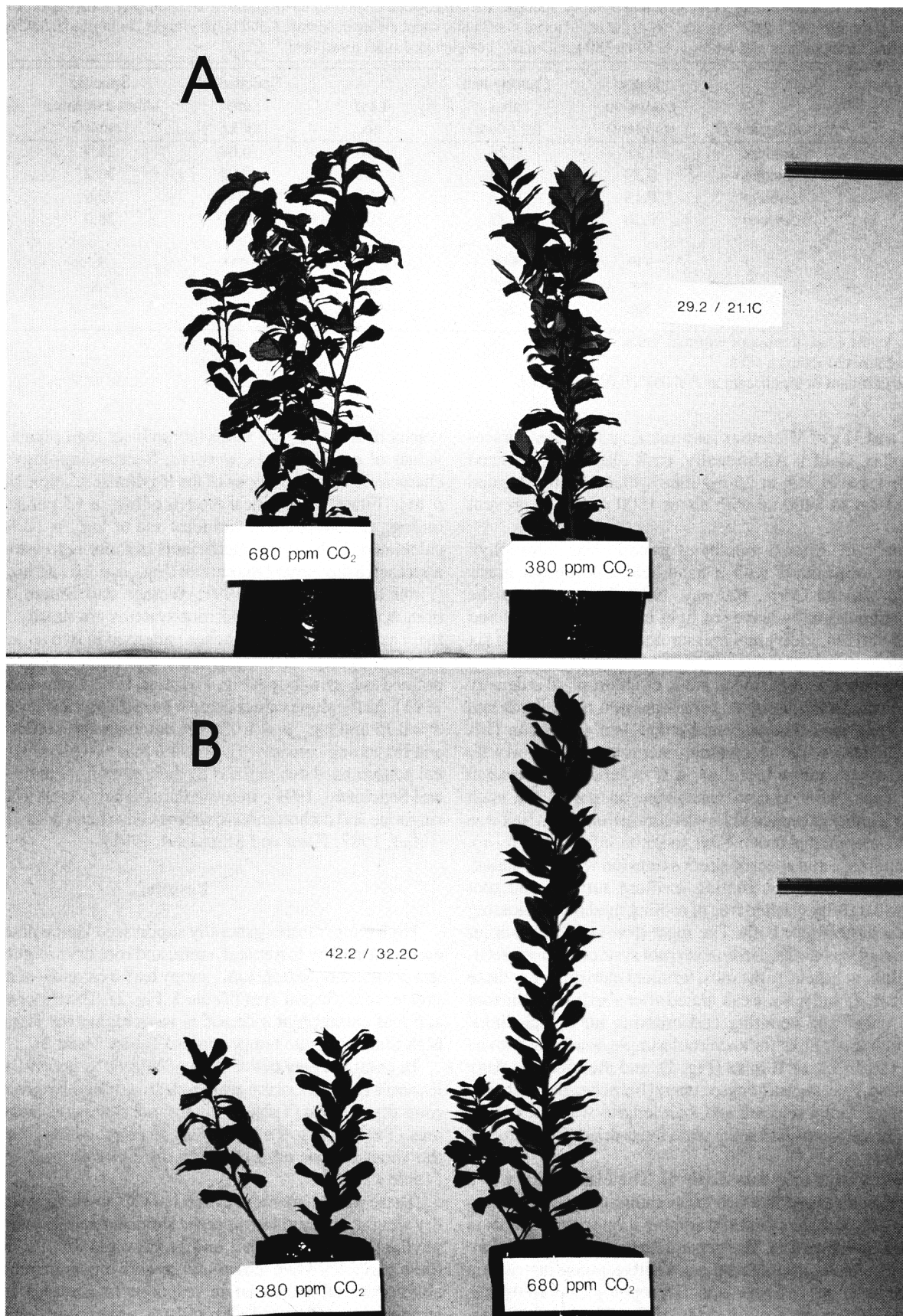


Fig. 2. 'Eureka' lemon plants after 6 months in 27-liter pots and exposure to factorial combinations of either moderate (29/21C day/night) or high (42/32C day/night) air and root-zone temperatures and ambient (350 to 380 $\mu\text{mol}\cdot\text{mol}^{-1}$) or elevated (680 $\mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 . (A). Eureka lemon plants grown in moderate temperatures at elevated (left) or ambient CO_2 (right). (B). Eureka lemon plants grown in high temperatures at ambient (left) or elevated CO_2 (right). Since plants were positioned on the same surface, the horizontal bar is a point of reference depicting relative plant height.

Table 3. Slopes of $\log_{10} a_i$ (altitude) and $\log_{10} p_e$ (total pathlength) on $\log_{10} \mu$ (magnitude) for 'Eureka' lemon shoot canopies and fibrous roots after 6 months in 27-liter pots and exposure to factorial combinations of either moderate (29/21C day/night) or high (42/32C day/night) air and root-zone temperatures and ambient (350 to 380 $\mu\text{mol}\cdot\text{mol}^{-1}$) or elevated (680 $\mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 .

Temp	Atmospheric CO_2	Shoots		Fibrous roots	
		a_i	p_e	a_i	p_e
Moderate	Ambient	0.70 ± 0.17	1.46 ± 0.12	0.37 ± 0.04	1.33 ± 0.05
	Elevated	0.87 ± 0.19	1.59 ± 0.07	0.13 ± 0.07	1.19 ± 0.04
High	Ambient	0.70 ± 0.12	1.46 ± 0.14	0.24 ± 0.10	1.35 ± 0.09
	Elevated	0.98 ± 0.12	1.73 ± 0.11	0.26 ± 0.03	1.35 ± 0.04

Log-transformed topological benchmarks for dichotomous, random, or herringbone branching systems are 0.15, 0.59, or 1.00, respectively, for a_i and 1.02, 1.52, or 1.92, respectively, for p_e (Werner and Smart, 1973). a_i = The highest number of branch links between an external link and the base link or crown; p_e = the sum of the number of branch links in all paths from all external links to the base link; μ = the total number of external links.

herringbone, while the topology of fibrous roots was predominately dichotomous, based on comparisons of the slopes of the log-linear relationships of a_i and p_e to μ with the theoretical minimum and maximum (Table 3). Shoot topology was even more herringbone for plants grown in elevated CO_2 compared to those in ambient CO_2 (Table 3). At moderate temperatures, fibrous root topology of plants grown in elevated CO_2 was even less dichotomous compared to those in ambient CO_2 , while elevated CO_2 did not affect root topology in high temperatures (Table 3). Fibrous root EE and II link lengths were about 1.5 times longer and second-degree adventitious root lateral branches were about 1.6 times longer in high than moderate temperatures (Table 4). Temperature treatments did not affect fibrous root EI linkage lengths. Carbon dioxide treatments had no effect on the length of fibrous root branch links or the length of secondary lateral adventitious roots.

Discussion

High aerial and rhizosphere temperatures of similar amplitude decreased growth of 'Eureka' lemon plants by about 50% and had a more negative effect on root than shoot growth. This negative effect on roots was shown by higher shoot-to-root ratios for plants in high temperatures compared to those in moderate temperatures. Plants in high temperatures had less shoot extension with fewer and thinner leaves that contained higher levels of chlorophyll a than those in moderate temperatures. Even though leaf chlorophyll a densities increased, reduced growth in high temperatures may have been caused in part by alterations in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity favoring oxygenation and the photorespiratory pathway over carboxylation of CO_2 (Jordan and Ogren, 1984). High aerial temperatures also increased leaf to air vapor pressure gradients, which, for citrus leaves, has been positively correlated with stomatal resistance to gas exchange and stomatal limitation of photosynthesis (Syvertsen and Salyani, 1991).

Elevated CO_2 caused about a 21% increase in growth when temperatures were moderate, an amount that was amplified to about 87% when temperatures were high. Leaves in high temperatures and elevated CO_2 also had about 15% more chlorophyll a than those in high temperature and ambient CO_2 , an indication of higher leaf nitrogen content (Evans, 1989). Thus, high CO_2 reduced the negative effects of high-temperature stress on shoot growth. The greater CO_2 -enhancement effect on 'Eureka' lemon plants in high temperatures could be due to increased nitrogen uptake by a larger root system. Other possible explanations for the greater CO_2 -enhancement effect are that Rubisco CO_2/O_2 specificity for oxygenation in high temperatures was changed to carboxylation by increased CO_2 (Jordan and Ogren, 1984) or improved instantane-

ous photosynthetic water-use efficiency caused by high CO_2 suppression of stomatal conductance and enhancement of carbon assimilation (Eamus, 1991). In moderate temperatures, the smaller CO_2 -enhancement effect may have been due to excessive accumulation of chloroplast photoassimilates. Plants in elevated CO_2 and moderate to suboptimal temperatures have been reported to accumulate chloroplast photoassimilates (Farrar and Williams, 1991). This accumulation has recently been implicated in the repression of nuclear gene expression for chloroplast protein synthesis, which would lead to lower CO_2 assimilation capacity (Van Oosten et al., 1994; Webber et al., 1994). Others have suggested that limitations of water or nutrients or restricted rooting volume in containers may reduce CO_2 growth enhancement (Coleman et al., 1993; Long et al., 1992; McConnaughay et al., 1993; Thomas and Strain, 1991). In our study, all plants were well irrigated and well fertilized and visual inspections of all root systems at harvest time showed that no plants had pot-bound root systems.

Carbon dioxide enhancement of 'Eureka' lemon growth was not accompanied by a change in biomass allocation at either temperature treatment, which indicated that the entire plant benefited equally from an increase in carbon substrate. These findings are consistent with those of Sionit et al. (1985) on *Liquidamber styraciflua* and *Pinus taeda* and a recent literature survey of herbaceous and woody plants under nonlimiting conditions for water and nutrients (Stulen and den Hertog, 1993). Our observed increase in 'Eureka' lemon canopy leaf area with CO_2 enrichment agrees with a survey of literature by Ceulemans and Mousseau (1994), who noted that elevated CO_2 promoted an increase in total leaf area, especially under well-fertilized conditions in most woody species. In our study, the increase in canopy leaf area was due to a greater individual leaf area when temperatures were moderate and an increased number of leaves when temperatures were high.

Irrespective of temperature treatments, 'Eureka' lemon plants in elevated CO_2 had a more herringbone shoot branching pattern

Table 4. Exterior-exterior (EE), interior-interior (II), and exterior-interior (EI) link lengths and the length of second-degree lateral branches of 'Eureka' lemon fibrous roots after 6 months in 27-liter pots and exposure to either moderate (29/21C day/night) or high (42/32C day/night) air and root-zone temperatures.

Temp	Link length (mm)			2° lateral length (mm)
	EE	EI	II	
Moderate	18.8	14.4	5.2	54.8
High	28.0	12.5	8.2	90.0
Significance	***	NS	**	***

Values are treatment means, n = 30.

NS, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.0001.

than those in ambient CO₂. This effect was visibly evident in high temperatures (Fig. 2) and was also quantified by lower branch frequency (high specific shoot extension), an indication of increased apical dominance. Few studies have examined the effect of CO₂ on shoot branch patterns, and, to our knowledge, no studies have examined the effect of CO₂ on shoot topology. Elevated CO₂ increased the number of shoot lateral branches of sweet gum (Sionit et al., 1985) and affected canopy shape and height of several tropical trees (Reekie and Bazzaz, 1989); however, it was not clear whether these responses were actual changes in shoot topology or merely a CO₂-enhancement effect on growth because topological analyses were not conducted. On the canopy level, it would seem to us that a herringbone topology may benefit citrus canopies by limiting self-shading.

Fibrous roots of plants in elevated CO₂ were more dichotomous than for those in ambient CO₂ when air and root-zone temperatures were moderate. This response was similar to that reported by Bernston and Woodward (1992), who performed their experiments with *Senecio vulgaris* at 22C day/12C night. Since a dichotomous root system has a higher transport efficiency of water and nutrients than a herringbone system because of a shorter distance between the point of absorption and the shoot (Bernston, 1994), changes to a dichotomous root topology may be a critical response of a plant to meet the demand for increased nutrients in an elevated CO₂ environment. However, we also show that root topology did not respond to elevated CO₂ when temperatures were high and that plants in high temperatures had smaller but more elongate root systems than those in moderate temperatures. In the case of high temperatures, root systems of plants in elevated CO₂ may be responding to the demand for increased nutrients by becoming larger and exploring a greater soil volume rather than acclimating topologically.

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