J. Amer. Soc. Hort. Sci. 122(6):849–855. 1997.

Leaf Gas Exchange, Dry Matter Partitioning, and Mineral Element Concentrations in Mango as Influenced by Elevated Atmospheric Carbon Dioxide and Root Restriction

Bruce Schaffer
Tropical Research and Education Center, IFAS, University of Florida, Homestead, FL 32611

Anthony W. Whiley, Christopher Searle, and Robert J. Nissen
Maroochy Horticultural Research Station, Department of Primary Industries, Nambour 4560, Queensland, Australia

Additional index words. *Mangifera indica*, CO_2 enrichment, photosynthesis, CO_2 internal partial pressure

Abstract. The effects of atmospheric CO_2 enrichment and root restriction on net CO_2 assimilation (A), dry mass partitioning, and leaf mineral element concentrations in 'Kensington' and 'Tommy Atkins' mango (*Mangifera indica* L.) were investigated. Trees were grown in controlled-environment glasshouse rooms at ambient CO_2 concentrations of 350 or 700 μmol·mol^{-1}. At each CO_2 concentration, trees were grown in 8-L containers, which restricted root growth, or grown aeroponically in 200-L root mist chambers, which did not restrict root growth. Trees grown in 350 μmol·mol^{-1} CO_2 were more efficient at assimilating CO_2 than trees grown in 700 μmol·mol^{-1} CO_2. However, total plant and organ dry mass was generally higher for plants grown at 700 μmol·mol^{-1} CO_2 due to increased A as a result of a greater internal partial pressure of CO_2 (Ci) in leaves of plants in the CO_2 enriched environment. Root restriction reduced A resulting in decreased organ and plant dry mass. In root-restricted plants, reduced A and dry matter accumulation offset the increases in these variables resulting from atmospheric CO_2 enrichment. Atmospheric CO_2 enrichment and root restriction did not affect dry mass partitioning. Leaf mineral element concentrations were generally lower for trees grown at the higher ambient CO_2 concentration, presumably due to a dilution effect from an increased growth rate.

Within the last 30 years, the CO_2 concentration in the earth's atmosphere has increased by ≈25% and is expected to continue to rise at an increasing rate (Ehleringer and Cerling, 1995; Houghton and Skole, 1990). The expected rise in atmospheric CO_2 concentration will undoubtedly affect agriculture, since CO_2 enrichment often increases productivity of C_3 crops (Idso and Idso, 1994). The magnitude of atmospheric CO_2 effects on crop yields is modified by other environmental factors, CO_2 effects on weed competition, and genotypic variation in carbon metabolism and growth capacity (Wolfe, 1994).

Little is known about the effects of elevated ambient CO_2 levels on leaf gas exchange, mineral nutrition, growth, and dry matter partitioning in tropical fruit trees, including mango. When field- and container-grown mango trees ('Kensington') were exposed to short durations (2 to 5 min) of elevated CO_2, the net CO_2 assimilation rate (A) increased as ambient CO_2 concentration increased up to 1200 μmol·mol^{-1} (A.W. Whiley and B. Schaffer, unpublished data). Short-term exposure to CO_2 concentrations >1200 μmol·mol^{-1} did not result in an additional increase in A, probably because leaves had reached their maximum biochemical capacity to fix carbon. For some species, long-term (weeks or months) exposure to elevated CO_2 results in decreased photosynthetic efficiency (Wolfe, 1994).

Elevated ambient CO_2 can result in increased A due to an increase in internal partial pressure of CO_2 (Ci) in the leaves (von Caemmerer and Farquhar, 1981). However, a reduction in this increase in A at high ambient partial pressures of CO_2 has been reported for several plant species (Arp, 1991; Ehret and Joliffe, 1985; Thomas and Strain, 1991), and increases in the ambient CO_2 concentration may result in increased nonstructural carbohydrate concentrations in the leaves (Ehret and Joliffe, 1985), which can suppress expression of genes transcribing for rubisco (Drake et al., 1997; Sheen, 1994; Stitt, 1991). Thus, CO_2 enrichment can decrease photosynthetic capacity when photoassimilate supply exceeds sink demand (Drake et al., 1997; Ehret and Joliffe, 1985). This downward regulation of A at high ambient CO_2 concentrations has been attributed to sink limitations caused by feedback inhibition due to restricted sink capacity (Thomas and Strain, 1991). Additionally, Arp (1991) has suggested that, as a result of growing plants in containers, root restriction may limit A due to carbohydrate-mediated feedback inhibition.

There is little information in the literature on the effects of atmospheric CO_2 enrichment on mineral element concentrations in tissues of tropical C_3 plants (Hocking and Meyer, 1991a, 1991b). Conroy (1992) observed that atmospheric CO_2 enrichment alters foliar nutrient concentrations required to maintain maximum productivity (critical concentrations). Critical concentrations in leaves are routinely used to evaluate nutrient status of crops and manage fertilizer programs (Conroy, 1992). Since atmospheric CO_2 is expected to increase steadily (Ehleringer and Cerling, 1995; Houghton and Skole, 1990), knowledge of changes in foliar nutrient concentrations in response to CO_2 enrichment is important for diagnosing nutrient deficiencies that are based on critical concentrations (Conroy, 1992; Hocking and Meyer, 1991b).

The purpose of this study was to determine the effects of long-term (12 months) exposure to elevated atmospheric CO_2 and root restriction on leaf gas exchange, dry matter partitioning, and leaf mineral element concentration and mango trees.

Received for publication 24 Jan. 1997. Accepted for publication 31 July 1997. Bruce Schaffer thanks the Queensland Department of Primary Industries and the Rural Industries Research and Development Corporation for financial support while on study leave at the Maroochy Horticultural Research Station, Nambour, Queensland, Australia. This article is Florida Agricultural Experiment Station journal series no. R-05461. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Materials and Methods

Plant materials and growth conditions. Mango trees ['Kensington' (syn. 'Kensington Pride'), and 'Tommy Atkins'] were propagated by air-layering as described by Nuñez-Elisea et al. (1992) to obtain genetically uniform and physiologically mature trees. Air layers were planted in a 1 sand : 1 peat (v/v) medium in 8-L polyethylene containers and maintained in a glasshouse for 6 months. To provide a nonrestricting root environment, six trees of each cultivar were removed from the polyethylene containers after 6 months and placed in root mist chambers described by Schaffer et al. (1996). Root chambers were made from 200-L, black cylindrical polyethylene containers, which were painted silver to reflect infrared radiation. Trees were supported in wire-mesh baskets inserted through a hole cut in the top of each root chamber so that the root system occupied the air space below the lid. Silver-colored polyethylene was placed around the lid to reflect heat and prevent light from reaching the roots. The trees in containers and root mist chambers were then moved into one of two controlled-environment (CE) glasshouse rooms described by Whiley et al. (1988). Three trees of each cultivar in containers and three trees of each cultivar in root mist chambers were placed in each of the two CE glasshouse rooms. In one glasshouse room, the atmospheric CO_2 concentration was maintained at 350 ± 10 μmol·mol^{-1} (which is about the mean global atmospheric CO_2 concentration) and at 700 ± 10 μmol·mol^{-1} in the other CE glasshouse room.

Trees in containers were fertilized at 14-d intervals with a soluble complete fertilizer (Peters Professional). For trees in the root chambers, roots were misted with a commercial nutrient solution (Duet Blue and Duet Red Hydroponics Formula; Duet Scientific Co., Bundaberg, Queensland, Australia). The nutrient solution was delivered from storage tanks through black polyethylene irrigation tubing to the root chambers. Roots inside each chamber were misted from two microjet nozzles, at 2 L·min^{-1} for 30 s at 20 min intervals. Delivery of the nutrient solution to the chambers was controlled by electronic timers and solenoid valves. Each root chamber had a drainage hole 3 cm from the bottom to allow drainage of the nutrient solution from the chamber after the roots were misted.

Temperatures in both glasshouse rooms were maintained at 28/20 ± 1 °C (day/night) and relative humidity was maintained at 60% ± 5%. Throughout the experiment, temperatures inside the root chambers stayed within 1 °C of the room air temperature. In each CE glasshouse room, the ambient CO_2 concentration was adjusted by injecting CO_2 from a compressed gas cylinder into the glasshouse. Atmospheric CO_2 concentrations were controlled with an infrared gas analyzer–controller (WMA-2; PP Systems, Hitchin, Herts., U.K.).

After 12 months, A, Ci, leaf mass per unit area (W_a), and leaf starch concentration were determined on the second or third fully expanded leaf from the most recently matured flush of each tree. Responses of A to increasing Ci were also determined for trees in each root and atmospheric CO_2 treatment. Trees were then harvested and total leaf area was determined with a leaf area meter (LI-1000; LI-COR Inc., Lincoln, Nebr.). Dry mass of leaves, stems, and roots was determined after drying tissues at 70 °C to a constant mass.

Leaf gas exchange. A and Ci were determined with a leaf gas exchange system (CIRAS-1; PP Systems) as described by Schaffer et al. (1996). Leaf gas exchange was determined at a photosynthetic photon flux (PPF) of 1500 μmol·m^{-2}·s^{-1} using a high intensity lamp. The response of A to CO_2 concentrations was determined over a range of CO_2 concentrations in the leaf cuvette (C_a) from 0 to 1100 μmol·mol^{-1}. For A response curves, C_a was varied nonconsecutively. Net CO_2 assimilation was determined for three single-tree replicates (blocked over time) per treatment. Determinations of A and Ci were made when CO_2 flux in the cuvette had stabilized (3 to 5 min after placing the leaf in the cuvette).

Starch and mineral element concentrations and leaf mass per unit area. Ten leaves from the youngest mature flush on three to five terminals were collected from each tree for starch and nutrient analyses. Leaf samples were washed in a mild detergent (sodium lauryl sulfate, 1 g·L^{-1}), rinsed in triple deionized water, washed in acetic acid (0.5 mL·L^{-1}), rinsed twice more in triple deionized water and dried for 72 h at 70 °C. Leaf samples were then ground in a cyclone grinder (UDY Corp., Fort Collins, Colo.). Ground leaf samples from each plant were divided in halves: one half was used for starch analysis and the other half was used for nutrient analysis.

Starch in the ground samples was hydrolyzed to glucose by a two-stage enzymatic hydrolysis and starch content was quantified colorimetrically using a coupled glucose–peroxidase–chromogen system as described by Rasmussen and Henry (1990).

Nitrogen concentration was determined from finely ground tissue samples using a semimicro Kjeldahl digestion technique (Searle, 1974). Phosphorous was analyzed colorimetrically using

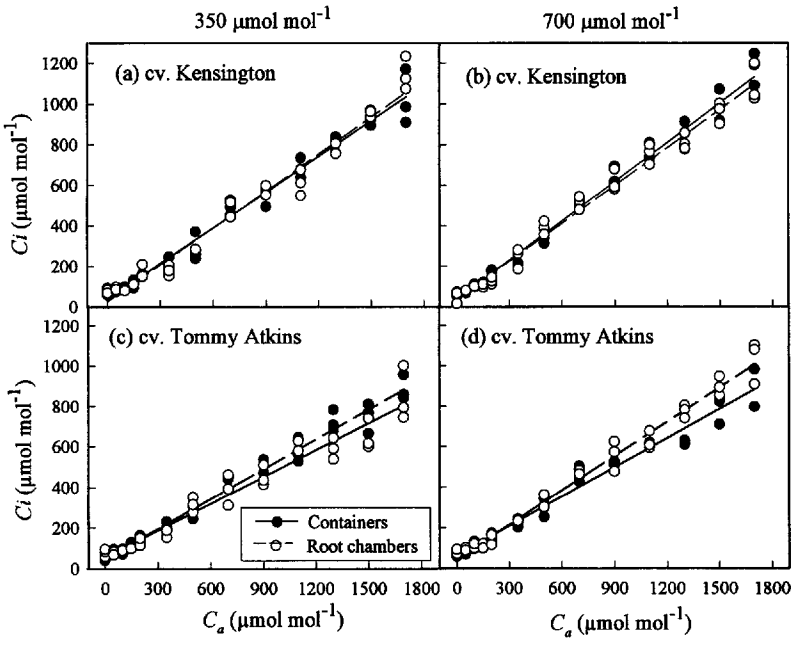

Fig. 1. Relationship between intercellular CO_2 concentration (Ci) and CO_2 concentrations in the leaf cuvette (C_a) of container-grown (root-restricted) and root chamber-grown (nonroot-restricted) 'Kensington' and 'Tommy Atkins' mangoes grown in an atmospheric CO_2 concentration of 350 or 700 μmol·mol^{-1}. Symbols represent data for individual plants. The regression line for (**a**) 'Kensington' trees grown in 350 μmol·mol^{-1} for container grown trees is represented by $Ci = 0.59C_a + 38.67$, $r^2 = 0.98$, and for root chamber-grown trees by $Ci = 0.61C_a + 25.53$, $r^2 = 0.98$. The regression line for (**b**) 'Kensington' trees grown at 700 μmol·mol^{-1} (d) for container-grown trees is represented by $Ci = 0.64C_a + 37.53$, $r^2 = 0.99$, and for root chamber-grown trees by $Ci = 0.44C_a + 54.56$, $r^2 = 0.95$. The regression line for (**c**) 'Tommy Atkins' trees grown in 350 μmol·mol^{-1} for container-grown trees is represented by $Ci = 0.49C_a + 48.64$, $r^2 = 0.98$, and for root chamber-grown trees by $Ci = 0.44C_a + 54.56$, $r^2 = 0.95$. The regression line for (**d**) 'Tommy Atkins' trees grown at 700 μmol·mol^{-1} for container-grown trees is represented by $Ci = 0.48C_a + 64.56$, $r^2 = 0.97$, and for root chamber-grown trees by $Ci = 0.56C_a + 45.38$, $r^2 = 0.98$.

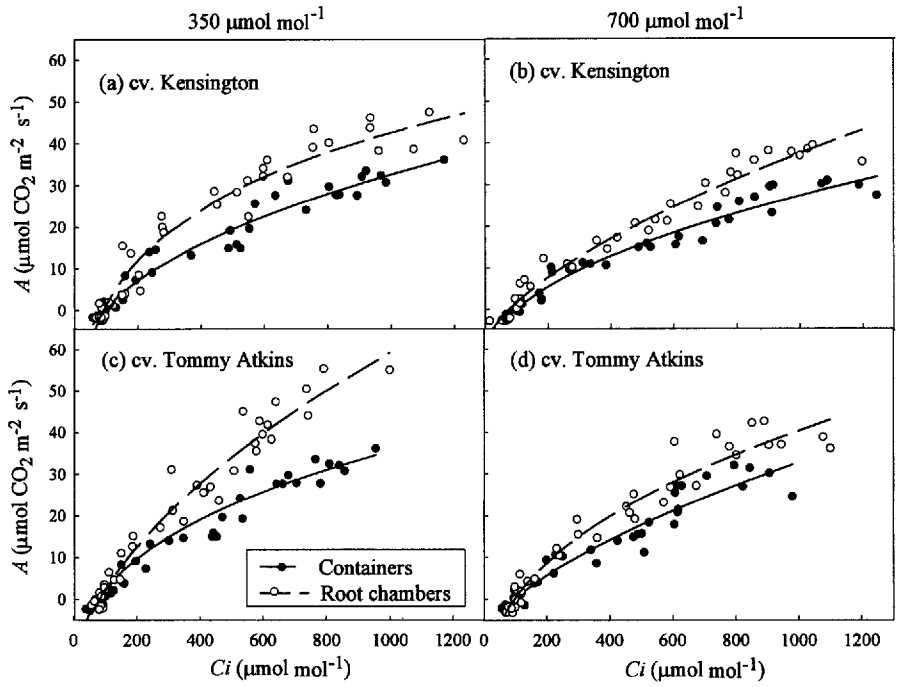

Fig. 2. Relationship between net CO_2 assimilation (A) and intercellular CO_2 concentration (Ci) response of 'Kensington' and 'Tommy Atkins' mangoes grown in an atmospheric CO_2 concentration of 350 or 700 μmol·mol^{-1} in containers (root restricted) or root chambers (not root restricted). Symbols represent data for individual plants. The regression line for (**a**) 'Kensington' trees grown in 350 μmol·mol^{-1} in containers is represented by $A = -17.92 + 2.5Ci^{0.44}$, $r^2 = 0.96$ and for trees grown in root chambers by $A = -31.67 + 1.56(\ln Ci)^2$, $r^2 = 0.95$. The regression line for (**b**) 'Kensington' trees grown in 700 μmol mol^{-1} in containers is represented by $A = -12.92 + 1.4Ci^{0.49}$, $r^2 = 0.97$ and for trees grown in root chambers by $A = -7.74 + 0.21Ci^{0.5}\ln Ci$, $r^2 = 0.97$. The regression line for (**c**) 'Tommy Atkins' trees grown in 350 μmol·mol^{-1} in containers is represented by $A = -24.8 + 5.46Ci^{0.35}$, $r^2 = 0.94$ and for trees in root chambers by $A = -19.51 + 1.67Ci^{0.56}$, $r^2 = 0.96$; The regression line for (**d**) 'Tommy Atkins' trees grown in 700 μmol·mol^{-1} in containers is represented by $A = -8.52 + 0.19Ci^{0.5}\ln Ci$, $r^2 = 0.93$ and for trees in root chambers by $A = -25.17 + 3.85Ci^{0.41}$, $r^2 = 0.96$.

the procedure described by Murphy and Riley (1962). For B analysis, samples were dry ashed and, after acid dissolution, B concentrations were determined by inductively coupled argon plasma spectrometry (Lyons et al., 1984). To determine K, Ca, Mg, Cl, Mn, Fe, Zn, and Cu concentrations, tissue samples were ground to <1 μm in a pulverizing mill and analyzed in a simultaneous–sequential x-ray fluorescence spectrometer (ARL 8480; GBC Co., Melbourne, Australia).

To determine W_a (dry leaf mass divided by leaf area for each tree), 20 leaves were collected from each tree and the petioles were removed. Leaf area was measured with a leaf area meter (LI-1000; LI-COR). Leaves were then oven dried at 70 °C to a constant mass.

Data analysis. Data were analyzed by one-way analysis of variance to determine if statistical interactions existed between cultivar, ambient CO_2 concentration, and size of the root chamber for each of the variables measured. Linear regressions and differences among slopes were determined using a general linear models (GLM) procedure and mean differences between treatments were determined with a standard t test (SAS Institute, Cary, N.C.). The response curves of A to varying CO_2 concentrations in the leaf cuvette were determined by nonlinear regression analysis using TableCurve (SPSS Inc., Chicago).

Results

Before this study, in the same glasshouse, no leaf gas exchange, growth, or developmental differences were observed between trees of the same cultivars grown in different CE rooms exposed simultaneously to the same ambient CO_2 concentration (i.e., there were no CE room effects). Therefore, it was assumed in the present study that differences between trees in different ambient CO_2 concentrations were not confounded by CE room effects in the glasshouse during the experiment.

After trees were harvested, it was observed that container-grown trees had compressed root masses, which filled the entire container, indicative of root restriction. Roots of trees in the root chambers were not compressed or matted, i.e., root restriction was assumed not to have occurred.

Leaf gas exchange. There was no significant effect of ambient CO_2 concentration or root restriction on Ci, regardless of the C_a (Fig. 1). As C_a increased, there was a linear increase in Ci for trees of both cultivars in containers and in root chambers grown in ambient CO_2 levels of 350 and 700 μmol·mol^{-1}. For each cultivar, slopes of the linear regression lines were not significantly different ($P > 0.05$) among or between atmospheric CO_2 treatments and root restriction treatments.

For both cultivars, A (at Ci greater than 150 μmol·mol^{-1}) was lower for container-grown trees than for trees grown in root mist chambers at both ambient CO_2 concentrations (Fig. 2). For trees grown at a CO_2 concentration of 700 μmol·mol^{-1}, preventing root restriction by growing trees aeroponically in mist chambers offset the decrease in A (on a leaf area basis) that resulted from growing trees in the higher ambient CO_2 concentration (Fig. 2 b and d). However, for plants grown in a CO_2 concentration of 700 μmol·mol^{-1}, increases in A of trees grown in the root mist chambers was considerably less for 'Kensington' trees (A_{max} at Ci of 1000 μmol·mol^{-1}, ≈ 48 μmol·m^{-2}·s^{-1}; Fig. 2) than for 'Tommy Atkins' trees (A_{max} at cuvette Ci of 1000 μmol·mol^{-1}, >55 μmol·m^{-2}·s^{-1}; Fig. 2).

Plant dry matter partitioning and leaf area. For both cultivars, plant and individual organ dry mass tended to be higher for trees grown at 700 μmol·mol^{-1} than for trees grown at 350 μmol·mol^{-1} (Fig. 3). For both cultivars, plant and individual organ dry mass tended to be greater for trees in root chambers than trees in containers at both ambient CO_2 concentrations (Fig. 3). For 'Tommy Atkins', dry mass differences between the two root treatments were generally greater in an atmospheric CO_2 concentration of 700 than in 350 μmol·mol^{-1} (Fig. 3 b, d, f, and h). In contrast, 'Kensington' trees grown in an atmospheric CO_2 concentration of 350 μmol·mol^{-1} exhibited greater plant, leaf, and root dry mass differences between root treatments than trees of the same cultivar grown in an atmospheric CO_2 concentration of 700 μmol·mol^{-1} (Fig. 3 a, c, e, and g).

The root/shoot ratio for both cultivars tended to be higher for trees grown in an atmospheric CO_2 concentration of 350 than in 700 μmol·mol^{-1} (Fig. 4 a and b). There were no significant effects ($P > 0.05$) of atmospheric CO_2 concentration on W_a for trees of either cultivar grown in containers (Fig. 4 e and f).

For both cultivars, trees in root chambers grown in an atmospheric CO_2 concentration of 350 μmol·mol^{-1} tended to have higher root/shoot ratios and leaf areas than trees grown in contain-

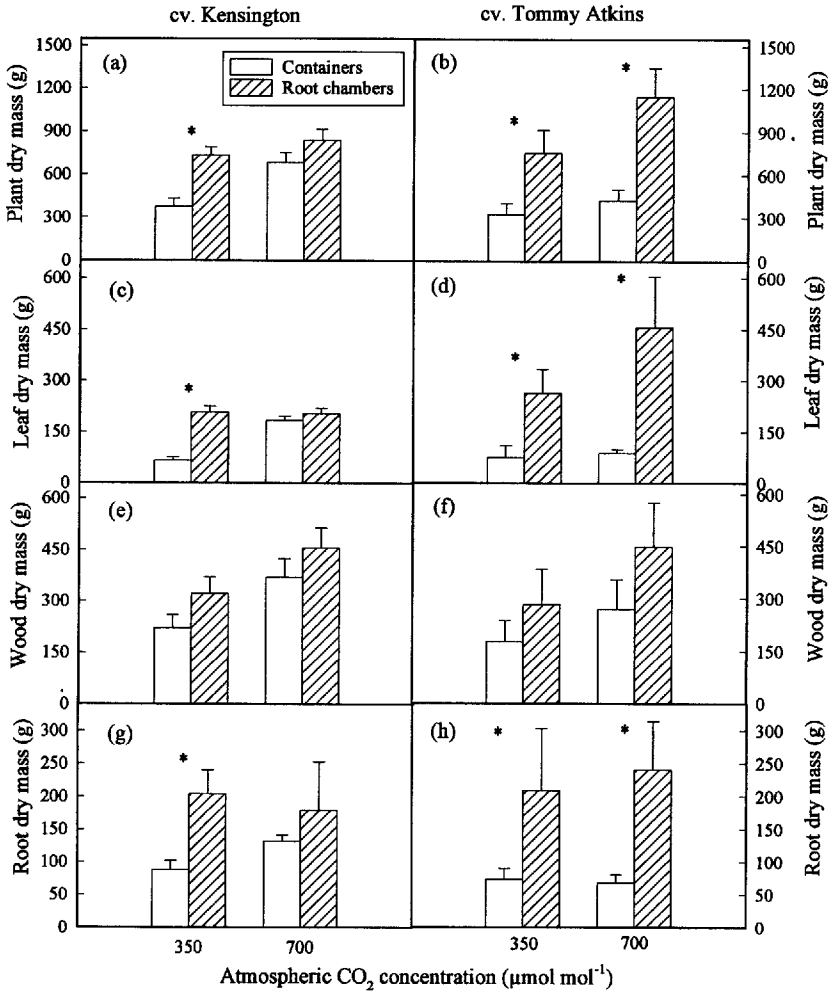

Fig. 3. Plant and organ dry mass of 'Kensington' and 'Tommy Atkins' mangoes grown for 12 months in containers (root restricted) or root mist chambers (non-root restricted) in an atmospheric CO_2 concentration of 350 or 700 μmol·mol^{-1}. Bars represent means ± 1 SD. Asterisks indicate a significant difference between root treatment means ($P \leq 0.05$) within each atmospheric CO_2 concentration.

ers (Fig. 4 a–d). For 'Kensington' grown in an atmospheric CO_2 concentration of 700 μmol·mol^{-1}, W_a was lower for trees in containers than those in root chambers, whereas there was no effect of root treatment on W_a of trees grown in a CO_2 concentration of 350 μmol·mol^{-1} (Fig. 4f). There was no significant effect of root treatment on W_a of 'Tommy Atkins' trees grown in atmospheric CO_2 concentrations of 300 or 700 μmol·mol^{-1}. For 'Tommy Atkins' trees grown in 350 μmol·mol^{-1}, leaf starch concentration was higher in container-grown trees than in trees grown in root chambers, whereas there were no significant differences due to root treatment at 700 μmol·mol^{-1} (Fig. 4g). In contrast, for 'Kensington' trees, there was no significant difference in starch concentration between root treatments at an atmospheric CO_2 concentration of 350 μmol·mol^{-1}, but, at 700 μmol·mol^{-1}, trees in root chambers had significantly higher leaf starch concentrations than trees in containers (Fig. 4h)

Leaf mineral element concentrations. Differences in fertilizer application methods (soluble granular fertilizer versus nutrient solutions) between container-grown trees and those grown in root mist chambers prevented comparisons of leaf mineral element concentrations between the two groups of trees. Also, there were no significant interactions ($P > 0.05$) between container type (container versus root chamber) and ambient CO_2 concentration with regard to leaf mineral element concentrations. Therefore, foliar mineral element concentrations are reported only for trees in root chambers (Table 1). Due to a significant interaction ($P \leq 0.05$) between cultivar and ambient CO_2 concentration for leaf concentrations of some elements, ambient CO_2 effects on leaf mineral element concentrations were compared separately for each cultivar.

In both cultivars, concentrations of all mineral elements investigated were higher in trees grown in an atmospheric CO_2 concentration of 350 μmol·mol^{-1} than in trees grown in 700 μmol·mol^{-1}, although for some elements the differences were not statistically significant (Table 1). In 'Tommy Atkins', foliar concentrations of P, S, Cl, Cu, and B were significantly higher in trees grown in a CO_2 concentration of 350 μmol·mol^{-1} than in trees grown in 700 μmol·mol^{-1} (Table 1). In 'Kensington', foliar concentrations of P, K, S, Fe, Zn, Mn, and Cu were significantly higher in trees grown in an atmospheric CO_2 concentration of 350 μmol·mol^{-1} than in trees grown in 700 μmol·mol^{-1} (Table 1).

Discussion

Responses to CO_2 enrichment and root restriction were generally similar between cultivars. Mango cultivars can be classified into two ecotypes based on embryony. Cultivars with nucellar embryony (polyembryonic types) such as 'Kensington' evolved in warm, humid tropical climates of Indo-China. Cultivars with a single zygotic seed (monoembryonic types) such as 'Tommy Atkins' evolved in the cool, dry subtropical regions of the Indian subcontinent (Mukherjee, 1972; Schaffer et al., 1994; Sukonthasing et al., 1991; Whiley and Schaffer, 1997). There were no obvious differences among ecotypes in response to CO_2 enrichment or root restriction. In a parallel study with mango cultivars Nam Dok Mai (polyembryonic) and Sensation (monoembryonic), embryony was not related to plant responses to atmospheric CO_2 enhancement or root restriction (B. Schaffer, A.W. Whiley, and C. Searle, unpublished data).

Photosynthetic efficiency decreased when trees were grown in an enriched CO_2 environment, as evidenced by the lower *A* rates in trees grown in an atmospheric CO_2 concentration of 700 μmol·mol^{-1} compared to trees grown in 350 μmol·mol^{-1}, when *Ci* was >150 μmol·mol^{-1} (Fig. 2). The decreased photosynthetic efficiency for trees grown in an enriched CO_2 environment was not sufficient to offset increased *A* associated with a constant elevated *Ci* in the CO_2-enriched environment.

For plants in both CO_2 environments, *A* increased curvilinearly as *Ci* increased and approached an asymptote at the maximum carboxylation rate. However, *Ci* increased linearly throughout the range of CO_2 concentrations in the leaf cuvette (Fig. 1), indicating that *A* was not limited by restriction of CO_2 uptake and diffusion through the mesophyll at any ambient CO_2 concentration. For banana (*Musa acuminata* Colla 'Gros Michel'), the limitation of *A* at high CO_2 concentrations in the cuvette was attributed to decreased ribulose-1,5 bisphosphate (RuBp) regeneration when CO_2 levels in the cuvette were high (Schaffer et al., 1996). A similar response may occur in mango. The lower initial slope of the *A*/*Ci* curves for mango trees grown in an atmospheric CO_2 concentration of 700 μmol·mol^{-1} than for trees grown in 300 μmol·mol^{-1} indicates that there was a RuBp-carboxylase limitation to photosynthesis at the higher ambient CO_2 concentration (Wolfe, 1994).

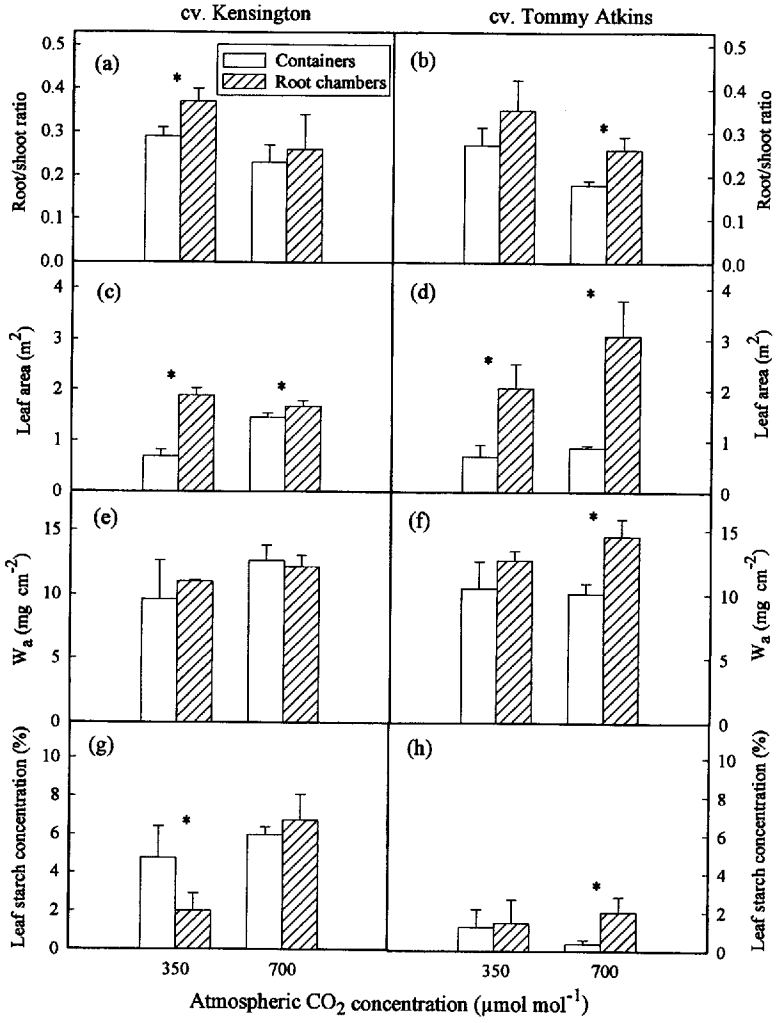

Fig. 4. Leaf starch concentrations, root/shoot ratio (dry mass basis), leaf starch concentration, total leaf area, and leaf mass per unit area (W_a) of 'Kensington' and 'Tommy Atkins' mangoes grown for 12 months in containers (root restricted) or root mist chambers (not root restricted) in an atmospheric CO_2 concentration of 350 or 700 μmol·mol^{-1}. Bars represent means ± 1 SD. Asterisks indicate a significant difference between root treatment means ($P \leq 0.05$) within each atmospheric CO_2 concentration.

Mango trees grown in an atmospheric CO_2 concentration of 700 μmol·mol^{-1} had more dry matter and leaf area than plants grown in 300 μmol·mol^{-1}. Similar observations were made with other species exposed to enriched CO_2 environments for long periods of time (Downton et al., 1990; Downton and Grant, 1994; Idso and Idso, 1994; Idso and Kimball, 1991; Nobel and Israel, 1994). Dry matter partitioning was not affected by CO_2 enrichment under nonroot-restricting conditions. The root system of mango trees produced by air layering is morphologically different from those of seedling trees in that air-layered trees lack a tap root. However, many observations have indicated that growth and development characteristics are similar between mature seedling trees or trees on seedling rootstocks and air-layered trees (R. Nuñez-Elisea, personal communication). Therefore, it is unlikely that the effects atmospheric CO_2 or root restriction on dry matter partitioning were specific to air-layered trees. For trees in containers, there was a difference between cultivars in the effect of CO_2 enrichment on dry matter partitioning and the root/shoot ratios. Differences in effects of atmospheric CO_2 enrichment among cultivars may have been related to the relative growth rate of each cultivar or differences in synchronicity between root and shoot growth flushes, which may differ among cultivars (Schaffer et al., 1994).

The lower *A* rates for container-grown trees compared to trees in root chambers may have been due to the downward regulation of photosynthesis as a result of root restriction. A downward regulation of *A* due to root restriction was observed for several other species and has been attributed to carbohydrate buildup in the leaves as a result of limiting the strength of the root sink (Arp, 1991; Ehret and Joliffe, 1985; Thomas and Strain, 1991). There were no consistent differences in leaf starch concentrations between container-grown and root chamber-grown trees in this study. In a previous study, leaf starch concentration was higher in mango and avocado trees grown in containers than in trees grown in an orchard (A.W. Whiley, B. Schaffer, C. Searle, and D. Simpson, unpublished data). The reduced *A* rates of container-grown trees compared to those of orchard-grown trees was attributed to feedback inhibition of *A* due to starch accumulation in the leaves. However, the data from the present study does not support a feedback inhibition of *A* due to of starch accumulation in mango leaves as a result of root restriction. A more likely mechanism for the observed downward regulation of *A* is a repression of the expression of genes transcribing for rubisco, caused by accumulation of specific sugars, such as glucose or hexose, in the leaves (Drake et al., 1997; Sheen, 1994; Stitt, 1991).

Atmospheric CO_2 enrichment tended to decrease mineral element concentrations in mango leaves. These reduced leaf mineral element concentrations were presumably due to a dilution effect since the increased atmospheric CO_2 concentration resulted in increased leaf area and dry mass. Similarly, early senescence and decreased chlorophyll content in *Castanea sativa* Mill. were associated with a nutrient dilution resulting from rapid growth of trees in an atmospheric CO_2 concentration of 700 μmol·mol^{-1} compared to trees grown at 350 μmol·mol^{-1} (Mousseau and Enoch, 1989). Wong (1979) attributed decreased nitrogen concentrations in cotton and maize leaves developed in elevated atmospheric CO_2 concentrations, to a dilution effect brought about by increased total leaf area. Also, reductions in N for plants grown in enriched atmospheric CO_2 has been attributed to a reduced synthesis of RuBp-carboxylase at higher ambient CO_2 concentrations (Drake et al., 1997). For, *Liriodendron tulipifera* L. grown in a forest, N, B, and S concentrations in leaf tissue were reduced by atmospheric CO_2 enrichment, whereas uptake of other elements either was unaffected by CO_2 enrichment or proportional to plant growth rates in the different CO_2 environments (O'Neill et al., 1987). Apparently for this species, the dilution effect resulting from increased growth at greater atmospheric CO_2 concentrations was offset by increased soil exploration due to a larger root mass. In the present study with mango, root growth in containers was restricted, minimizing any effects of increased nutrient uptake on root growth. Critical nutrient concentrations used for assessing crop nutrient status may have to be reassessed as the atmospheric CO_2 concentrations rise (Conroy, 1992). This may be particularly true for tropical fruit crops such as mango, in which tissue dilution of nutrients at high atmospheric CO_2 concentrations may be exacerbated because of their high growth rate relative to temperate tree species. In addition, micronutrient concentrations in soils of subtropical and tropical regions are often deficient for normal plant growth (Aitken et al., 1987). Boron is one micronutrient already

Table 1. Mineral element concentrations in leaves of 'Tommy Atkins' and 'Kensington' mango grown for 12 months in root chambers in atmospheric CO_2 concentrations of 350 or 700 $\mu mol \cdot mol^{-1}$.

Ambient CO_2 concn	N	P	K	Ca	Mg	S	Cl	Fe	Zn	Mn	Cu	B
($\mu mol \cdot mol^{-1}$)	(%)							($mg \cdot kg^{-1}$)				
Tommy Atkins												
350	2.62	0.43	1.48	1.35	0.15	0.20	0.15	65.66	30.33	566.67	20.33	52.00
750	2.05	0.26	1.29	1.28	0.14	0.16	0.08	61.00	20.67	450.0	7.20	33.67
Significance[z]	*	**	NS	NS	NS	**	**	NS	NS	NS	**	**
Kensington												
350	2.19	1.49	2.09	2.88	0.30	0.21	0.10	25.67	70.33	1003.33	25.66	74.00
750	2.12	0.71	1.40	2.15	0.24	0.19	0.07	10.40	37.33	576.66	10.40	65.67
Significance	NS	**	**	NS	NS	*	NS	**	**	**	**	NS

[z]Mean separation between ambient CO_2 concentration treatments by standard t test.
NS,**,*Nonsignificant or significant at $P \leq 0.05$ or 0.10, respectively.

limiting crop production in some subtropical and tropical regions (Whiley et al., 1996), requiring careful management to achieve normal growth of fruit tree crops. Increasing atmospheric CO_2 concentrations is likely to enhance the potential for deficiencies of boron and other micronutrients. Thus, sustainable practices will need to be developed if the production benefits from climate change projections are to be realized. However, the impacts of atmospheric CO_2 enrichment on plant mineral element concentrations can decrease over time. For example, in sour orange (*Citrus aurantium* L.) trees exposed to elevated atmospheric CO_2 concentrations (≈700 $\mu mol \cdot mol^{-1}$) for 85 months, initial reductions in leaf N, Mg, Ca, and Mn concentrations gradually disappeared over time (Peñuelas et al., 1997). Thus, given the slow rate at which the global atmospheric CO_2 concentration is increasing, it is possible that plants will adapt to elevated ambient CO_2 concentrations over time with respect to mineral nutrition.

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