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Cool Orchard Temperatures or Growing Trees in Containers Can Inhibit Leaf Gas Exchange of Avocado and Mango

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Abstract. Leaf gas exchange of avocado (*Persea americana* Mill.) and mango (*Mangifera indica* L.) trees in containers and in an orchard (field-grown trees) was measured over a range of photosynthetic photon fluxes (PPF) and ambient CO_2 concentrations (C_a). Net CO_2 assimilation (A) and intercellular partial pressure of CO_2 (Ci) were determined for all trees in early autumn (noncold-stressed leaves) when minimum daily temperatures were ≥14 °C, and for field-grown trees in winter (cold-stressed leaves) when minimum daily temperatures were ≤10 °C. Cold-stressed trees of both species had lower maximum CO_2 assimilation rates (A_{max}), light saturation points (Q_A), CO_2 saturation points (C_{aSAT}) and quantum yields than leaves of noncold-stressed, field-grown trees. The ratio of variable to maximum fluorescence (F_v/F_m) was ≈50% lower for leaves of cold-stressed, field-grown trees than for leaves of nonstressed, field-grown trees, indicating chill-induced photoinhibition of leaves had occurred in winter. The data indicate that chill-induced photoinhibition of A and/or sink limitations caused by root restriction in container-grown trees can limit carbon assimilation in avocado and mango trees.

Root restriction from growing plants in containers can limit net CO_2 assimilation rates (A) via feedback inhibition (Arp, 1991; Schaffer et al., 1996; Thomas and Strain, 1991). For avocado trees, maximum A (A_{max}) ranged from ≈7 to 23 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with light saturation for A (Q_A) at photosynthetic photon fluxes (PPF) between 400 to 1100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Bower et al., 1978; Scholefield et al., 1980; Schaffer et al., 1987; Whiley, 1994; Whiley and Schaffer, 1994). Mango A_{max} was ≈6 to 18 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with Q_A at PPF between 300 to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Chacko et al., 1995; Pongsomboon et al., 1992; Schaffer and Gaye, 1989; Schaffer et al., 1994; Searle et al., 1995). The range of variation in these data was possibly due to measurement or growth conditions, particularly since the lower values were from trees grown in containers, whereas higher values were from field-grown trees.

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Short-term exposure to temperatures below 10 °C can cause reversible chilling injury resulting in inhibition of A, especially in subtropical and tropical species (Taylor and Rowley, 1971). At high incident PPF, chilling can result in photoinhibitory damage to photosystem 2 (PS II) (Powles, 1984; Smillie et al., 1988) that can be quantified by measuring a decrease in the ratio of variable to maximum chlorophyll fluorescence (F_v/F_m) (Björkman, 1987; Demmig and Björkman, 1987).

Avocado (*Persea americana* Mill.), a polyaxial, terminally flowering, oil-accumulating species (Whiley and Schaffer, 1994) and mango (*Mangifera indica* L.), a polyaxial, terminally flowering, sugar-accumulating species (Schaffer et al., 1994), are gaining commercial importance worldwide and production is expanding into new environments. Whiley (1994) has classified avocado as a "wintergreen" tree, which more closely resembles the physiology of woody deciduous species. There is comparatively little carbon investment into avocado leaves, which grow rapidly but have a longevity of <10 months. In contrast, mango leaves are relatively sclerophyllous with a high investment of carbon during growth. Furthermore, they have drought-resistant mechanisms and are sustained on trees for up to 5 years (Whiley and Schaffer, 1994). Quantifying leaf gas exchange characteristics of these similar evergreen, broad-leaved species may enable the development of models of plant responses to growth conditions (e.g., variation in temperatures and elevated ambient CO_2 concentrations), thereby minimizing deleterious effects from suboptimal environments (Schaffer and Andersen, 1994).

The purpose of this study was to compare photoinhibitory and sink-limitation (root restriction) responses between wintergreen (avocado) and sclerophyllous (mango) leaves of two broad-leaved evergreen trees. To assess potential photoinhibitory damage to leaves, *A* of field-grown trees was determined when minimum daily (overnight) temperatures were below 10 °C. Root restriction responses were assessed by comparing leaf gas exchange responses of field-grown and container-grown trees.

Materials and Methods

Plant material. Four- to six-year-old 'Hass' avocado and 'Kensington' (syn. 'Kensington Pride') mango trees were used in this study. Experiments were conducted with field- and container-grown (55-L black polythene containers) trees at Maroochy Research Station, Centre for Subtropical Fruits, Nambour, Queensland, Australia (lat. = 27° S, elevation = 30 m above sea level). The orchard soil was a well-drained clay loam (≈60% clay fraction) 10 to 16 m deep and showed no obvious physical limitation to root growth (Whiley, 1994). Trees in containers were grown outdoors under ambient conditions in a potting media of course river sand and peat (1:1). For each species, five single-plant replications were used for leaf gas exchange and leaf starch determinations in studies with both field- and container-grown trees. Plants were irrigated and fertilized according to standard commercial practices (Whiley, 1984; Whiley et al., 1988).

Leaf gas exchange. Net CO_2 assimilation of leaves and intercellular partial pressure of CO_2 (*Ci*) were determined for the second or third most recently fully expanded leaf of field- and container-grown plants under a range of PPF and ambient CO_2 concentrations (C_a). Before measurements, plants were grown under full sunlight (maximum PPF of ≈2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and ambient atmospheric CO_2 concentrations (≈350 $\mu mol \cdot mol^{-1}$). Determinations of *A* and *Ci* were made with a CIRAS-1 leaf gas exchange system (PP Systems, Hitchin, Herts., U.K.). Leaf gas exchange was measured when shoot growth on trees was quiescent during early autumn 1994 and minimum daily temperatures were ≥14 °C (noncold-stressed leaves = NCS), and again on field-grown trees in winter 1994 when minimum daily (overnight) temperatures were ≤10 °C (cold-stressed leaves = CS). Cold-stressed leaves were exposed to 24 nights of temperatures of 8 to 10 °C. Measurements in autumn were made between 0800 to 1030 HR when air temperatures were 25 to 28 °C, whereas winter measurements were between 0900 to 1130 HR when air temperatures were 21 to 24 °C. At each time of the year, vapor pressure deficits were 1.0 to 1.2 kPa when measurements were taken.

To investigate leaf gas exchange responses to incident light flux, PPF was varied nonconsecutively by placing 1 m^2 frames covered with polyethylene cloths of different mesh densities, and in different combinations, between the trees and the sun (on a cloudless day) to obtain a range of PPF. The entire canopy was shaded. Frames were placed over the trees for at least 30 min before *A* determinations to allow sufficient time for leaves to equilibrate to the new light environment. Determinations of *A* at zero PPF were obtained by wrapping the leaf cuvette in a black cloth and waiting until CO_2 evolution from the leaf stabilized (8 to 12 min).

Leaf gas exchange responses to C_a were made at saturating PPF (previously determined as >400 $\mu mol \cdot m^{-2} \cdot s^{-1}$). A range of C_a concentrations in the leaf cuvette was achieved using the CIRAS-1 gas exchange system, which allows variable CO_2 concentrations to be delivered to the cuvette from a supplemented CO_2 source. For below ambient concentrations, the air stream was passed through a series of CO_2 scrubbers (cylinders containing soda lime) before entering the cuvette. Determinations of *A* and *Ci* were made when CO_2 flux in the cuvette had equilibrated (≈3 to 5 min after placing the leaf in the cuvette after C_a was changed).

Chlorophyll fluorescence. To quantify chilling injury to PS II, chlorophyll fluorescence of leaves on field-grown trees was measured on four to five leaves per tree at the same time as leaf gas exchange determinations were made using a BioMonitor Stress Meter (BioMonitor SCI, Umeå, Sweden). Cuvettes were attached to each side of the leaf midrib for 30 min between 0900 and 1000 HR. Chlorophyll fluorescence was then determined on the adaxial leaf surface after two seconds of irradiation with 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue light (320 to 550 nm). Variable fluorescence (F_v) was calculated as $F_v = F_m - F_o$, where F_o is the initial constant yield fluorescence and F_m is the maximum fluorescence recorded (Öquist and Wass, 1988). The ratio of F_v/F_m was calculated as an indication of photoinhibitory damage to PS II (Björkman, 1987; Demmig and Björkman, 1987).

Leaf starch. Starch concentrations in avocado and mango trees were determined on the second or third, fully expanded leaf from the most recently matured shoots on each tree. Fifteen leaves were collected from each of five trees from the different treatments between 0800 and 1030 HR and subsequently placed in a convection oven at 60 °C and dried to constant mass. Dried samples were ground at 100 mesh in a cyclone grinder (UDY Corporation, Fort Collins, Colo.) and stored in air-tight containers. Starch was determined by a two-stage enzymatic hydrolysis of starch to glucose and the concentration measured colorimetrically with a coupled glucose oxidase/peroxidase/chromogen system as described by Rasmussen and Henry (1990).

Data analyses. Data were analyzed by regression analysis (Table Curve, SPSS, Inc., Chicago). Light and CO_2 saturation points for *A* were calculated as 90% of A_{max} (Osman and Milthorpe, 1971). Quantum yield (∅) was calculated as the slope of the linear portion of the regression line of *A* vs. incident PPF (Syvertsen, 1984). Significant differences in ∅ between field- and container-grown plants of each species were determined by testing for homogeneity of slopes (SAS Institute, Cary, N.C.).

Results

Leaf gas exchange responses to incident PPF. Net CO_2 assimilation increased and *Ci* decreased asymptotically in response to increasing PPF for both species (Figs. 1 and 2). For both species, A_{max} was greater for field- than for container-grown trees and greater for NCS than for CS leaves (Table 1). For avocado, the light saturation point for *A* (Q_A) was ≈1270 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for NCS, field-grown trees, compared to ≈1040 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for CS, field-grown trees and ≈586 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for container-grown trees (Table 1). The light compensation point (Q_o) for field-grown avocado was lower for NCS (30 $\mu mol \cdot m^{-2} \cdot s^{-1}$) than for CS (50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) trees. For container-grown trees, Q_o was 38 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Cold stress reduced ∅ of field-grown trees from 0.055 μmol CO_2/mol quanta in fall to 0.034 μmol CO_2/mol quanta following exposure to overnight minimums of ≤10.0 °C, whereas the ∅ for container-grown trees was further reduced to 0.021 μmol CO_2/mol quanta. Quantum yield was higher in NCS than in CS leaves ($P \leq 0.01$) and in field- compared with container-grown avocado trees ($P \leq 0.05$).

For container- and field-grown avocado trees, *Ci* initially declined rapidly and then leveled off at PPF above 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 1b). To quantify the effects of PPF on *Ci*, the $Q_{1/2}$, representing the PPF at which *Ci* is reduced by 50%, was calculated from $Q_{1/2} = \ln(0.5)/-k$, where *k* is the third constant in the standard decay curve fitted to the data (adapted from Jones, 1992).

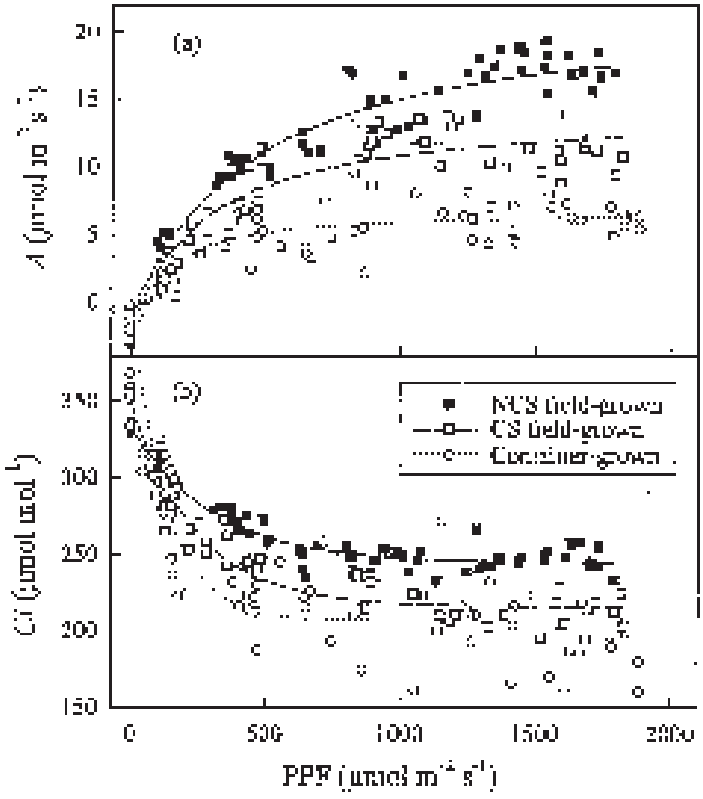

Fig. 1. Net CO_2 assimilation (A) and intercellular partial pressure of CO_2 (Ci) responses of field- and container-grown avocado trees ('Hass') to varying photosynthetic photon fluxes (PPF). The regression line for A (**a**) of noncold-stressed (NCS), field-grown trees is represented by y = 22.08((–30.67 + x)/(427.43 + x)), r^2 = 0.94; cold stressed (CS), field-grown trees is represented by y = 14.17((–46.72 + x)/(250.05 + x)), r^2 = 0.86; and container-grown trees is represented by y = 7.16((–38.366 +x)/(172.12 + x)), r^2 = 0.84. The regression line for Ci (**b**) for NCS, field-grown trees is represented by y = 244.65 + 90.2 exp(–0.0034x), r^2 = 0.94; CS, field-grown trees by y = 215.28 + 135.52 exp(–0.0041x), r^2 = 0.92; and container-grown trees by y = 203.70 + 171.39 exp(–0.0056x), r^2 = 0.87.

The $Q_{1/2}$ for NCS, field-grown avocado trees was 204 μmol·m^{-2}·s^{-1} compared to 169 μmol·m^{-2}·s^{-1} for CS, field-grown trees and 123 μmol·m^{-2}·s^{-1} for container-grown trees, indicating that leaves from CS, field-grown and container-grown trees had a higher light requirement than leaves of NCS, field-grown trees to reduce Ci by one-half.

For NCS, field-grown mango trees, Q_A was ≈1284 μmol·m^{-2}·s^{-1}, compared to ≈1180 μmol·m^{-2}·s^{-1} for CS, field-grown trees and ≈563 μmol·m^{-2}·s^{-1} for container-grown trees (Table 1). The Q_o for field-grown mango was 29 and 66 μmol·m^{-2}·s^{-1} for NCS and CS leaves, respectively. For container-grown trees, Q_o was 47 μmol·m^{-2}·s^{-1}. Lower temperatures reduced ∅ of field-grown trees from 0.042 μmol CO_2/μmol quanta in fall to 0.025 μmol CO_2/μmol quanta for CS leaves in winter, whereas the ∅ for container-grown trees was 0.033 (Table 1). Quantum yield was significantly greater between NCS and CS leaves ($P \leq 0.01$) as well as between NCS, field- and container-grown mango trees ($P \leq 0.05$).

The response of mango Ci to PPF was similar to that of avocado trees: Ci decreased as PPF increased but leveled off as A_{max} was reached (Fig. 2b). The $Q_{1/2}$ for leaves from NCS, field-grown mango trees was 223 μmol·m^{-2}·s^{-1} compared to 74 μmol·m^{-2}·s^{-1} for CS, field- and 161 μmol·m^{-2}·s^{-1} for container-grown trees.

Leaf gas exchange responses to ambient partial pressure of CO_2. For container- and field-grown avocado and mango trees, A increased asymptotically as C_a increased, whereas there was a linear relationship between Ci and C_a (Figs. 3 and 4). The ambient CO_2 concentration at which A_{max} occurred (C_{aSAT}) in avocado was highest for leaves from NCS, field-grown trees (1473 μmol·mol^{-1}) compared with leaves from CS, field- (1357 μmol·mol^{-1}) and container-grown (1261 μmol·mol^{-1}) trees (Table 2). The saturated CO_2 assimilation rate (A_{maxCa}) was also lower for leaves from CS, field- (A_{maxCa} = 34.9 μmol·m^{-2}·s^{-1}) and container-grown (A_{maxCa} = 26.1 μmol·m^{-2}·s^{-1}) avocado trees than for NCS, field-grown avocado trees (A_{maxCa} = 50.6 μmol·m^{-2}·s^{-1}) (Table 2).

For leaves of NCS, field-grown mango, C_{aSAT} was 1113 compared to 871 μmol·mol^{-1} for container-grown and 636 μmol·mol^{-1} for CS, field-grown trees (Table 2). At C_a levels >600 μmol·mol^{-1}, A tended to level off for field- and container-grown trees (Fig. 4a) while A_{maxCa} was higher for NCS, field- (30.3 μmol·m^{-2}·s^{-1}) than for container-grown (21.5 μmol·m^{-2}·s^{-1}) and CS, field-grown (8.3 μmol·m^{-2}·s^{-1}) mango trees (Table 2). For container- and field-grown avocado and mango trees, Ci increased linearly as C_a increased indicating that CO_2 concentration was not limiting A (Figs. 3b and 4b).

Chlorophyll fluorescence. The F_v/F_m ratios for leaves of NCS, field-grown trees were 0.81 ± 0.02 and 0.80 ± 0.03, for avocado and mango, respectively (Table 2). During winter, the F_v/F_m ratio declined to 0.41 ± 0.03 for avocado and 0.45 ± 0.03 for mango.

Leaf starch. Leaf starch concentrations (leaf dry weight basis) measured in NCS, field-grown avocados (17.4 ± 1.4 mg·g^{-1}) were less than those for CS, field- (23.4 ± 4.0 mg·g^{-1}) and container-

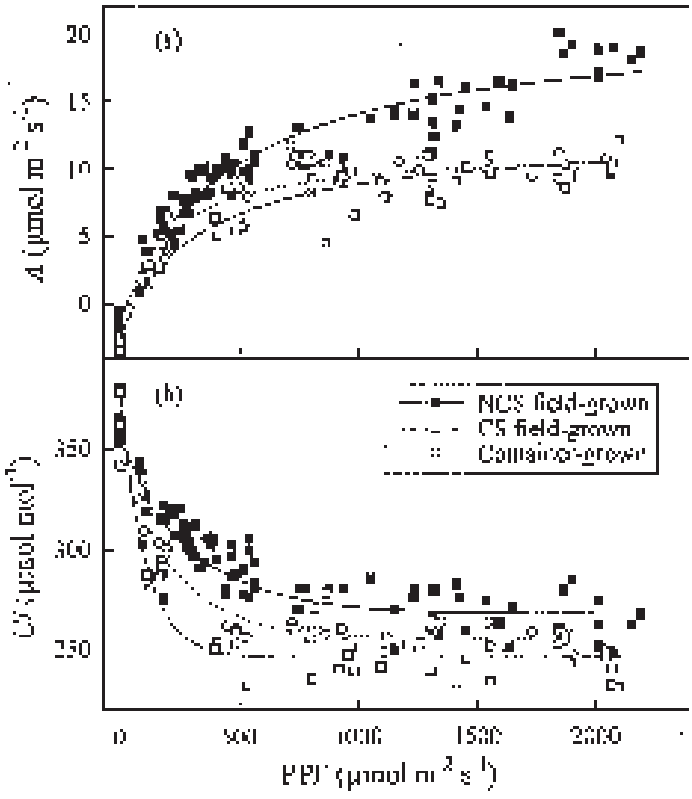

Fig. 2. Net CO_2 assimilation (A) and intercellular partial pressure of CO_2 (Ci) responses of field- and container-grown mango trees ('Kensington') to varying photosynthetic photon fluxes (PPF). The regression line for A (**a**) of noncold-stressed (NCS), field-grown trees is represented by y = 20.94 ((–28.97 + x)/(448.27 + x)), r^2 = 0.94; cold stressed (CS), field-grown trees by y = 12.42((–66.26 + x)/(309.02 +x)), r^2 = 0.91; and container-grown trees by y = 11.40((–45.97 + x)/(152.39 +x)), r^2 = 0.91. The regression line for Ci (**b**) for NCS, field-grown trees is represented by y = 267.27 + 87.38 exp(–0.0031x), r^2 = 0.97; for CS, field-grown trees by y = 245.57 + 133.54 exp(–0.0094x), r^2 = 0.93; and container-grown trees by y = 255.0 + 90.46 exp(–0.0043x), r^2 = 0.95.

Table 1. The effect of growing conditions on light saturation of CO_2 assimilation (Q_A), the compensation point for CO_2 assimilation (Q_o), the maximum rate of CO_2 assimilation (A_{max}) and the quantum efficiency ($\varnothing$) of avocado and mango trees. Values were estimated from the regression models presented in Figs. 1 and 2, which were based on pooled data from one leaf of each of five trees.

Treatment	Q_A ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Q_o ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	$\varnothing$ (μmol CO_2/μmol quanta)
Avocado				
NCS field-grown	1270	30	19.0	0.055a[z]
CS field-grown	1040	50	10.9	0.034b
Container-grown	586	38	5.2	0.021c
Mango				
NCS field-grown	1284	29	15.2	0.042a[z]
CS field-grown	1180	66	8.8	0.025b
Container-grown	563	47	8.1	0.033c

[z]Means followed by different letters for each species indicate significant difference ($P \leq 0.05$) according to a test for homogeneity of slopes.

grown trees (28.0 ± 2.6 mg·g^{-1}) (Table 2). There was also a similar response for leaf starch concentrations in mango with levels in NCS, field-grown trees at 14.0 ± 0.30 mg·g^{-1} dry weight compared with 25.4 ± 1.4 mg·g^{-1} for leaves of CS, field-grown and 32.2 ± 1.8 mg·g^{-1} for container-grown trees.

Discussion

The lower *A* of container-grown than of field-grown plants may have been due to a carbon sink limitation as a result of root restriction in containers. Although the root mass was not determined for container- and field-grown plants in this study, previous experiments have indicated that similar-aged avocado and mango plants maintained in similar-size containers for the time period of this study become pot bound (A.W. Whiley and B. Schaffer, unpublished data). Cold stress (exposing trees to 24 d of 8 to 10 °C temperatures) also limited *A* of avocado and mango in this study. Below saturating PPF, *Ci* decreased linearly as PPF increased, indicating unrestricted CO_2 diffusion through stomata. Thus, the reductions in *A* were apparently due to reduced carboxylation by the plant rather than a reduction in CO_2 diffusion through the mesophyll tissues. However, at Q_A, *Ci* remained relatively constant indicating a point of equilibrium between PPF and the diffusion of CO_2 to fixation sites. Under noncold-stressed conditions, $\varnothing$ for avocado and mango trees approximated the normal range of $\varnothing$ for C_3 species (Ehleringer and Björkman, 1977). The lower $\varnothing$ for CS, field- and container-grown trees than for NCS trees indicated a reduced quantum-use efficiency at low incident PPF as a result of both source and sink limitations to *A*.

The Q_A observed in this study for NCS, field-grown avocado ($Q_A \approx 1270$ $\mu mol \cdot m^{-2} \cdot s^{-1}$) and mango ($Q_A \approx 1284$ $\mu mol \cdot m^{-2} \cdot s^{-1}$) were considerably higher than previously reported rates for these crops (Bower et al., 1978; Scholefield et al., 1980; Schaffer and Gaye, 1989). The higher $Q_{1/2}$ for NCS, field-grown avocado trees than for the CS, field-grown trees and container-grown trees, indicates that leaves of CS, field-grown and container-grown trees had a higher light requirement than leaves of NCS, field-grown trees to reduce *Ci* by one-half. Thus, the Q_A of NCS leaves would be higher than that of leaves from CS, field- and container-grown trees (assuming stomatal conductance is nonlimiting under well-watered conditions), thereby supporting the data presented in Fig. 1. The A_{max} that we observed for NCS, field-grown trees of each species was much greater than data previously published. For field-grown avocado in Florida, A_{max} was reported to be 7 to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Schaffer et al., 1987, 1991) compared to 19.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ observed for field-grown trees in this study. Similarly, A_{max} for field-grown mango in Florida was 6.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Schaffer and Gaye, 1989) compared to 15.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ determined in our study for nonstressed field-grown trees in Australia. In contrast, the A_{max} and Q_A for container-grown avocado (5.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$; 586 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and mango (8.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$; 563 $\mu mol \cdot m^{-2} \cdot s^{-1}$) were similar to those previously reported for trees grown in containers (Bower et al., 1978; Scholefield et al., 1980; Schaffer et al., 1987; Schaffer and Gaye, 1989; Larson et al., 1992; Pongsomboon et al., 1992). For single leaves of container-grown avocado, Bower et al. (1978) and Scholefield et al. (1980) have reported Q_A to be between 400 to 660 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with an A_{max} of $\approx$7.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, while for mango a Q_A of 350 to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with an A_{max} of 6 to 7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ has

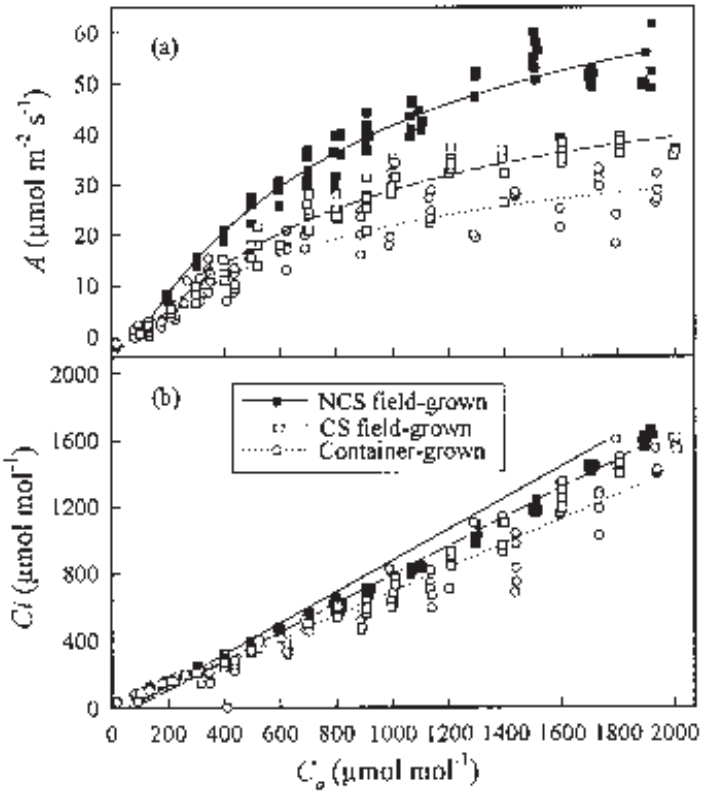

Fig. 3. Net CO_2 assimilation (*A*) and intercellular partial pressure of CO_2 (*Ci*) responses of field- and container-grown avocado ('Hass') trees to varying ambient CO_2 partial pressures (C_a). The regression line for *A* of noncold-stressed (NCS), field-grown trees (**a**) is represented by y = 85.49 ((–96.72 + x)/ (852.75 + x)), r^2 = 0.96; cold-stressed (CS), field-grown trees by y = 58.54 ((–110.10 + x)/(805.77 + x)), r^2 = 0.96; and container-grown trees by y = 42.73((–78.62 + x)/(801.42 + x)), r^2 = 0.92. The regression line for *Ci* (**b**) of NCS, field-grown trees is represented by y = –0.851x – 47.590, r^2 = 0.99; for CS, field-grown trees by y = 0.812x – 60.877, r^2 = 0. 98; and container-grown trees by y = 0.723x – 27.95, r^2 = 0.95.

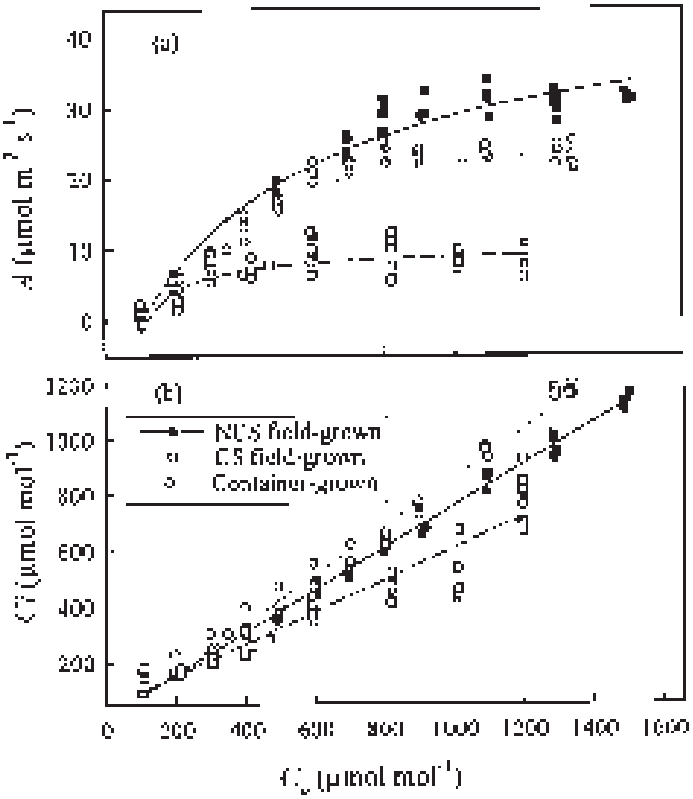

Fig. 4. Net CO_2 assimilation (A) and intercellular partial pressure of CO_2 (Ci) responses of field- and container-grown mango ('Kensington') trees to varying ambient CO_2 partial pressures (C_a). The regression line for A (**a**) for noncold-stressed (NCS), field-grown trees is represented by y = 47.38 ((–105.0 + x)/(462.4 + x)), r^2 = 0.95; cold stressed (CS), field-grown trees by y = 10.24 – 1247.52/x, r^2 = 0.73; and container-grown trees by y = 33.61 – 357.84/$x^{0.5}$, r^2 = 0.91. The regression line for Ci (**b**) for NCS, field-grown trees is represented by y = 9.026 + 0.753x, r^2 = 0.99; CS, field-grown trees by y = 40.67 + 0.568x, r^2 = 0.92; and container-grown trees by y = –10.857 + 0.872x, r^2 = 0.99.

been observed (Schaffer and Gaye, 1989; Larson et al., 1992; Pongsomboon et al., 1992). Hence, for avocado and mango trees grown in containers there is relative consistency between the reported values of Q_A and A_{max}.

The relatively low A_{max} rates that we observed for container-grown compared to field-grown trees may be attributed to containers restricting the root sink, thus causing the photoassimilate supply to exceed the capacity of demand (i.e., end-product inhibition of photosynthesis) (Schaffer et al., 1994). This is supported by the increased concentrations of leaf starch for both crops growing in containers (160% to 230% higher in container-grown compared with NCS, field-grown trees). Increased leaf starch in avocado accompanied by a reduction in A_{max} was reported by Schaffer et al. (1987) who concluded that the latter occurred as a result of feedback inhibition. For other species, reduced A of container-grown plants as a result of root restriction has been attributed to end-product inhibition of photosynthesis caused by root restriction (Arp, 1991; Thomas and Strain, 1991). Although only starch was measured in this study, other nonstructural carbohydrates such as glucose and hexoses may have accumulated in the leaves as a result of sink (root) restriction. It has been recently proposed that accumulation of these end-products, particularly hexoses, in the leaves may repress genes that code for rubisco, resulting in feedback inhibition of A (Drake et al., 1997; Koch, 1996; Stitt, 1991). The hard, oolitic limestone soils of Florida can severely limit root growth, thus restricting the development of this sink (Crane et al., 1994; Schaffer et al., 1994). Thus, the relatively low A_{max} previously observed for field-grown trees in Florida may also be the result of end-product inhibition of photosynthesis.

The lower Q_A and A_{max} of field-grown avocado and mango trees that were determined for CS compared to NCS trees, were most likely due to photoinhibition of A as a result of low temperatures interacting with high incident PPF (Groom et al., 1991). Limited exposure of tropical and subtropical species to below 10 °C can result in reversible inhibition of photosynthesis (Taylor and Rowley, 1971). The F_v/F_m ratios for leaves of NCS, field-grown trees were 0.81 ± 0.02 and 0.80 ± 0.03, for avocado and mango, respectively (Table 2), indicating that the photosynthetic processes were functioning normally in autumn (Öquist and Wass, 1988). The F_v/F_m ratios for avocado and mango trees were lower in winter when minimum daily temperatures decreased below 10 °C compared to early fall when chilling did not occur. Leaves also visibly appeared chlorotic following exposure to winter temperatures suggesting photooxidation of the chlorophyll. The lower F_v/F_m ratios indicated a reduced photochemical conversion efficiency of PS II (Krause, 1988), which can be an effect of photoinhibition at chilling temperatures (Groom et al., 1991). Photoinhibition from chilling injury can reduce ∅ and Q_A (Powles et al., 1983) as we observed for avocado and mango during the winter measurement period. For both species, reduced A in winter may also have been partially a result of feedback inhibition. Since the canopy of avocado and mango trees is relatively quiescent during winter, the resultant reduction in sink strength promotes an increase in starch concentrations in leaves (Whiley, 1994). In our study, leaf starch

Table 2. The effect of growing conditions on CO_2 saturation of CO_2 assimilation (C_{aSAT}), the maximum rate of CO_2 assimilation at saturating partial pressures of CO_2 (A_{maxCa}), chlorophyll fluorescence (F_v/F_m) and leaf starch concentrations on a dry weight basis. Values of C_{aSAT} and A_{maxCa} were estimated from the regression models presented in Figs. 3 and 4 which were based on pooled data from one leaf of each of five trees. F_v/F_m and leaf starch data are mean values ± standard errors (n = 5).

Treatment	C_{aSAT} (μmol·mol^{-1})	A_{maxCa} (μmol·m^{-2}·s^{-1})	F_v/F_m	Leaf starch concn (mg·g^{-1})
Avocado				
NCS field-grown	1473	50.6	0.81 ± 0.02	17.4 ± 0.14
CS field-grown	1357	34.9	0.41 ± 0.03	23.4 ± 0.20
Container-grown	1261	26.1	---	28.0 ± 0.26
Mango				
NCS field-grown	1113	30.3	0.80 ± 0.03	14.0 ± 0.03
CS field-grown	636	8.3	0.45 ± 0.03	25.4 ± 0.14
Container-grown	871	21.5	---	32.2 ± 0.18

concentrations in CS, field-grown avocado and mango trees were higher than in NCS, field-grown trees, thereby creating some doubt about relative importance of photoinhibition to the reduction of *A*. Further investigations to isolate the effect of cold stress from root restriction and elevated carbohydrate concentrations are required to clarify the situation.

The positive linear correlation between *Ci* and C_a implied that CO_2 diffusion through the mesophyll tissue was never limiting *A*. Leaves of NCS, field-grown trees had higher C_{aSAT} than leaves from CS, field-grown and container-grown trees. The carbon source–sink balance is a major factor in determining the response of plants to elevated CO_2 (Arp, 1991). For example, reduced *A* of bean plants in a CO_2-enriched environment has been positively correlated with the carbon source–sink ratio (Peet, 1984). Thus, the lower C_{aSAT} for container-grown than for field-grown avocado and mango presumably was from an increased source–sink ratio due to root restriction. For field-grown trees in winter, either photoinhibition, feedback inhibition of *A* due to the lack of vegetative growth, or their combined effects may have resulted in a downward regulation of *A* and lower C_{aSAT}. However, C_{aSAT} can also be reduced through source-imposed limitations to *A* such as a reduction of incident PPF (Ehret and Joliffe, 1985).

When comparing the relative efficiency and capacity of *A* between the two species in this study, the response of avocado to varying photon and CO_2 fluxes was greater, 25% and 67%, respectively, than for mango. These differences may be attributed to the contrast in leaf longevity between the two species. For many species the photosynthetic rate is negatively correlated to life span of the leaf, with deciduous species in general having higher net photosynthetic rates than evergreen species (Chabot and Hicks, 1982; Larcher, 1969). At the evolutionary level a hypothesis advanced to explain this phenomenon is "longer leaf life spans compensate for environmentally limited photosynthetic activity" (Chabot and Hicks, 1982). Compared to mango trees, the physiology of avocado trees more closely resembles that of woody deciduous species. There is comparatively little carbon investment into avocado leaves that grow rapidly but have a longevity of <10 months. In contrast, mango leaves are very sclerophyllous with a high investment of carbon during growth and are sustained on trees for up to 5 years (Whiley and Schaffer, 1994). While avocado was shown to have a greater capacity to respond to increased C_a, this may not necessarily result in greater yield as there is a higher carbon investment in fruit growth of this oil-rich crop compared with sugar-accumulating species such as mango (Wolstenholme, 1986, 1987).

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