

Atmospheric CO₂ Enrichment, Root Restriction, Photosynthesis, and Dry-matter Partitioning in Subtropical and Tropical Fruit Crops

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The mean atmospheric CO₂ concentration of the Earth is currently $\approx 350 \mu\text{mol}\cdot\text{mol}^{-1}$ but could reach $\approx 600 \mu\text{mol}\cdot\text{mol}^{-1}$ by the year 2050 as a result of the burning of fossil fuels (Coleman et al., 1991; Ehleringer and Cerling, 1995; Houghton and Skole, 1990). The projected increase in ambient CO₂ concentration is expected to increase mean global temperatures by 3 to 4 °C, with a 1 to 2 °C increase predicted for tropical latitudes (Cambridge Univ. Press, 1990).

Increasing global CO₂ concentrations will undoubtedly affect agriculture, since CO₂ enrichment almost always increases biomass production in C₃ plant species (Idso and Idso, 1994) because of enhanced photoassimilation (Allen et al., 1988; Downton et al., 1987, 1990; Idso et al., 1991a; Reekie and Bazzaz, 1989; Schaffer et al., 1996; von Caemmerer and Farquhar, 1981). Plant responses to atmospheric CO₂ enrichment will probably be affected by temperature and nutrient supply (Baker, 1989; Conroy et al., 1990; Hocking and Meyer, 1991a, 1991b). The net result of increased carbon assimilation will be an increase in total nonstructural carbohydrate accumulation (Allen et al., 1988; Poorter et al., 1997). In several species, atmospheric CO₂ enrichment alters the partitioning of biomass from leaves to roots (Pearson and Brooks, 1995; Stulen and Den Hertog, 1993). This increase in the root : shoot ratio may be advantageous by improving the plant's ability to extract water and nutrients for growth but may reduce the harvest index, resulting in a lower economic yield (Wolfe, 1994). In addition to increasing carbohydrate accumulation, atmospheric CO₂ enrichment can reduce critical concentrations of mineral elements (Conroy, 1992; Hocking and Meyer, 1991a, 1991b; Peñuelas et al., 1997; Poorter et al., 1997; Schaffer et al., 1997) and organic nitrogen compounds (Poorter et al., 1997), thereby increasing the carbon : nitrogen ratio (Curtis et al., 1989; Poorter et al., 1997), and affecting biomass partitioning between vegetative and reproductive organs of C₃ plants. Increased atmospheric concentrations of CO₂ could favor biomass partitioning in fruit crops to reproductive organs, thereby increasing the harvest index.

Managing yields of fruit trees is achieved primarily by manipulating resource (assimilate) allocation between the reproductive and vegetative structures. However, this source-sink balance is a major factor in determining the response of plants to elevated CO₂ (Arp, 1991). Potential yields of subtropical and tropical fruit species are related to plant architecture and ecological succession in their native habitat (Verheij, 1986; Verheij and Coronel, 1991; Whiley and Searle, 1996). Single-stem species such as banana (*Musa* sp.) and papaya (*Carica papaya* L.) grow continuously and maintain a constant root :

shoot ratio. These are pioneer species, and rapid growth is directly coupled to the development of reproductive structures, providing an adaptive advantage for reproduction in their indigenous habitat during a relatively short period of opportunity (Whiley and Searle, 1996). For single-stem, subtropical, and tropical species, atmospheric CO₂ enrichment should increase allocation of carbohydrates equally to vegetative and reproductive structures. In contrast, for branched, woody, subtropical, and tropical fruit species, the direct source : sink competition (spatial separation) is usually a less important consideration for tree management than is tree phenology, which represents a temporal separation of potentially competing sinks (vegetative vs. reproductive) (Whiley, 1994; Whiley and Searle, 1996). Polyaxial, terminally fruiting subtropical and tropical species, such as avocado (*Persea americana* Mill.) and mango (*Mangifera indica* L.) and polyaxial, cauliflorous-fruiting species, such as macadamia [*Macadamia integrifolia* (L.) Maiden and Betche] (Hallé et al., 1978), have a vegetative bias resulting in a greater allocation of dry matter to vegetative than to reproductive organs (Whiley et al., 1988, 1989). Phenological patterns in branched, woody, subtropical, and tropical fruit crops can be manipulated so that potentially competing sinks can be temporally separated, resulting in complementary resource allocation (Wolstenholme, 1990). An understanding of whole-tree phenological responses is essential for optimizing the beneficial effects of increased atmospheric CO₂ concentrations on productivity of subtropical and tropical fruit crops.

LEAF GAS EXCHANGE RESPONSES

Carbon dioxide enrichment

Elevated ambient CO₂ can increase net CO₂ assimilation (*A*) due to increased intercellular partial pressure of CO₂ (*C_i*) (von Caemmerer and Farquhar, 1981). However, inhibition of *A* following long-term exposure at high ambient partial pressures of CO₂ (*C_a*) has been reported for several plant species (Arp, 1991; Ehret and Joliffe, 1985; Thomas and Strain, 1991). In several studies with *Citrus* sp., increasing the atmospheric CO₂ concentration markedly increased *A* (Downton et al., 1987; Idso and Idso, 1994; Idso et al., 1991b, 1993). However, there have been few reports of the effects of elevated ambient CO₂ concentrations on leaf gas exchange of other subtropical and tropical fruit crops. Recently, increased *A* has been reported for banana (Schaffer et al., 1996), avocado, mango (Schaffer et al., 1997; A.W. Whiley, C. Searle, and B. Schaffer, unpublished data), and mangosteen (*Garcinia mangostana* L.) (Downton et al., 1990) as a result of atmospheric CO₂ enrichment.

Short-term exposure (2–5 min) of avocado and mango leaves to increasing CO₂ concentrations resulted in a linear increase in *A* until maximum carboxylation was reached at CO₂ concentrations of 1000 to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ (Whiley and Schaffer, 1997). No additional in-

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crease in A was observed above $1200 \mu\text{mol}\cdot\text{mol}^{-1}$, as leaves reached their maximum biochemical capacity to fix carbon.

After exposing mangosteen trees for 1 year to an atmospheric CO_2 concentration of $800 \mu\text{mol}\cdot\text{mol}^{-1}$, A rates (measured at $800 \mu\text{mol}\cdot\text{mol}^{-1}$) were 40% to 60% higher than those (measured at $400 \mu\text{mol}\cdot\text{mol}^{-1}$) of trees grown in ambient CO_2 concentrations (Downton et al., 1990). Long-term (6–12 months) exposure of banana and mango to ambient CO_2 concentrations of 700 or $1000 \mu\text{mol}\cdot\text{mol}^{-1}$ increased A rates relative to those of plants grown in $350 \mu\text{mol}\cdot\text{mol}^{-1}$ when A was measured at the same atmospheric CO_2 concentration as that of the growth environment (Fig. 1) (Schaffer et al., 1996, 1997). However, carboxylation efficiency (the amount of carbon fixed per mole of ambient CO_2) was lower in the CO_2 -enriched environment (Schaffer et al., 1996, 1997). Carbon dioxide response curves for banana and mango grown at both elevated and ambient CO_2 concentrations showed that C_i increased linearly, even when maximum carboxylation was reached (Fig. 1). This indicates that A was not limited by a restriction of CO_2 uptake and diffusion through the mesophyll, even at elevated CO_2 concentrations (Schaffer et al. 1996). The reduction of A at high ambient CO_2 concentrations was presumably due to decreased carboxylation efficiency, since atmospheric CO_2 enrichment reduced the concentrations of ribulose biphosphate carboxylase concentrations in several plant species (Bowes, 1991; von Caemmerer and Farquhar, 1984; Vu et al., 1983; Wong, 1979).

Root restriction

In several studies, inhibition of photosynthesis due to root restriction (sink limitation) was observed as a result of growing plants in containers (Fig. 2) (Arp, 1991; Clough et al., 1981; Ismail and Noor, 1996; Schaffer et al., 1996, 1997; Thomas and Strain, 1991). A lower maximum net CO_2 assimilation rate (A_{max}) for field-grown mango trees in south Florida compared with other parts of the world may be caused by the hard rock soils, which limit root penetration (Schaffer et al., 1994; Whiley and Schaffer, 1997). This reduction of A due to root restriction for other species has been attributed to an accumulation of carbohydrates in leaves as a result of reduced sink strength of the root (Arp, 1991; Ehret and Joliffe, 1985; Thomas and Strain, 1991). Increased sugar concentration in the leaves as a result of root restric-

tion may also inhibit expression of genes transcribing for rubisco (Drake et al., 1997; Koch, 1996; Sheen, 1994; Stitt, 1991), thus resulting in inhibition of A . Also, an increase in starch concentration in the leaves may reduce A , as has been observed in avocado (Schaffer et al., 1987). Starch can accumulate in leaves of woody, subtropical, and tropical fruit species such as avocado and mango (Table 1) as a result of sink limitation (root restriction). However, root-restricted banana plants accumulated less starch in the leaves than did non-root restricted plants (Table 1). This was attributed to the fact that banana plants possess a rhizome that serves as an alternate sink for starch accumulation; therefore, the effect of root restriction on A could not be attributed to a feedback inhibition due to starch accumulation in the leaves (Schaffer et al., 1996).

Interactions between CO_2 enrichment and root restriction

In several studies of plants in containers, inhibition of photosynthesis in an enriched ambient CO_2 environment has been related to root restriction (sink limitation) (Arp, 1991; Schaffer et al., 1996, 1997; Thomas and Strain, 1991). Therefore, Arp (1991) suggested that root restriction may confound the effects of atmospheric CO_2 enrichment on carbon assimilation and dry-matter gain. The reduction of A at elevated ambient CO_2 concentrations has been attributed to a feedback inhibition from the source (leaves), which occurs when the ability of the source to supply assimilates exceeds sink capacity. Growing plants in containers in an elevated CO_2 environment often results in accumulation of starch in the leaves, which may interfere with photosynthesis (Barrett and Gifford, 1995; Ehret and Joliffe, 1985). The repression of the expression of genes that code for rubisco has recently been postulated as the most likely mechanism for carbohydrate-mediated feedback inhibition of A (Drake et al., 1997; Koch, 1996; Sheen, 1994; Stitt, 1991). Although root restriction inhibited A in mango (Schaffer et al., 1997) and banana (Schaffer et al., 1996), there were no interactions between CO_2 enrichment and root restriction, i.e., the inhibitory effects of root restriction on A were independent of atmospheric CO_2 concentration. Thus, decreased carboxylation in mango and banana as a result of CO_2 enrichment were not artifacts due to confounding effects of root restriction (Schaffer et al., 1996) as was suggested for other crops (Arp 1991; Thomas and Strain, 1991).

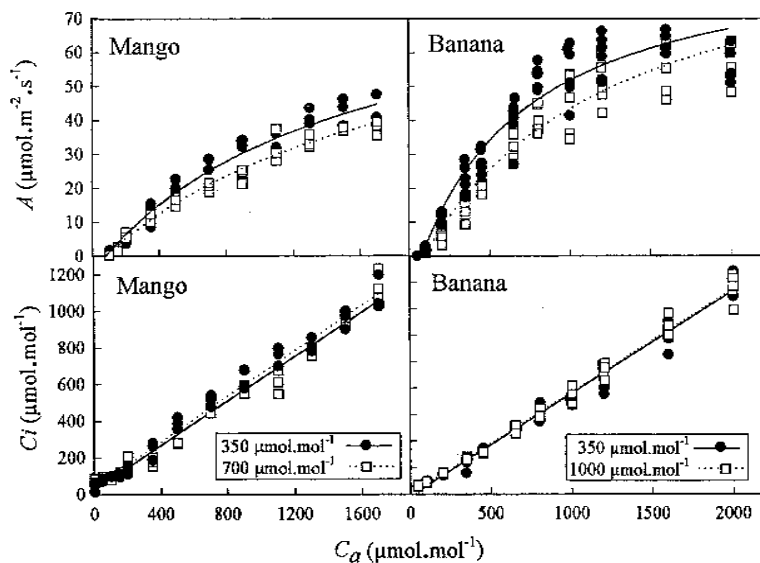


Fig. 1. Response of net CO_2 assimilation (A) and intercellular partial pressure of CO_2 (C_i) of mango (cv. Kensington) and banana (cv. Gros Michel) to varying CO_2 concentrations in the leaf cuvette (C_a) for non-root restricted plants. (Adapted from Schaffer et al., 1996, 1997).

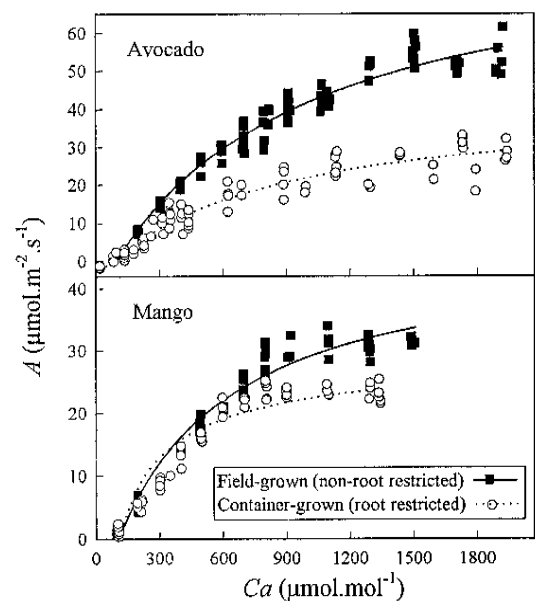


Fig. 2. Response of net CO_2 assimilation (A) of container-grown (root-restricted) and field-grown (non-root restricted) avocado (cv. Hass) and mango (cv. Kensington) trees to varying partial pressures of CO_2 in the leaf cuvette (C_a). (Whiley et al., 1999).

Table 1. Effect of root restriction² on the maximum net CO₂ assimilation rates (A_{\max}) of avocado (cv. Hass), mango (cv. Kensington) and banana (cv. Gros Michel) for plants grown in ambient atmospheric CO₂ (350 $\mu\text{mol}\cdot\text{mol}^{-1}$).³

	A_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf starch concn (%)
<i>Avocado</i>		
Non-root restricted	19.0	1.74
Root restricted	5.2	2.80
Significance	---	**
<i>Mango</i>		
Non-root restricted	15.2	1.40
Root restricted	8.1	3.22
Significance	---	**
<i>Banana</i>		
Non-root restricted	20.8	22.1
Root restricted	15.6	16.8
Significance	---	**

²Root restriction of avocado, mango, and banana was the result of growing plants in containers. Non-root restricted avocado and mango plants were in an orchard; non-root restricted banana plants were grown aeroponically in large root chambers.

³From Schaffer et al., 1996, 1997; Whiley et al., 1999.

**Significant at $P \leq 0.01$. Significance was not determined for A_{\max} as it was calculated from regression models.

Table 2. Effects of 6 months of atmospheric CO₂ enrichment on organ dry weights and dry-matter partitioning in banana plants (cv. Gros Michel).²

Plant organ	Atmospheric CO ₂ concn ($\mu\text{mol}\cdot\text{mol}^{-1}$)			
	350		1000	
	Dry wt (kg)	Partitioning (%)	Dry wt (kg)	Partitioning (%)
Leaf (+ petiole)	0.216 b ^y	19.0	0.500 b	18.3
Pseudostem	0.656 a	57.4	1.460 a	53.5
Root	0.219 b	19.2	0.638 b	23.4
Rhizome	0.051 c	4.5	0.133 c	4.8
Total	1.142		2.731 ^a	

²From Schaffer et al., 1996.

^yMean separation within columns by Duncan's multiple range test ($P \leq 0.05$).

^aDifference in total dry weight between plants grown at 350 or 1000 $\mu\text{mol}\cdot\text{mol}^{-1}$; significant at $P \leq 0.05$.

DRY-MATTER ACCUMULATION AND PARTITIONING

Atmospheric CO₂ enrichment increased biomass accumulation in several woody, subtropical, and tropical fruit species, including citrus (Downton et al., 1987; Idso et al., 1991a, 1991b; Koch et al., 1986, 1987), mangosteen (Downton et al., 1990), and mango (Schaffer et al., 1997). For several C₃ species, the effects on A from growing plants in high atmospheric CO₂ concentrations is seldom maintained for long periods of time (Wolfe, 1994). However, sour orange (*Citrus aurantium* L.) trees grown in the field at elevated atmospheric CO₂ concentrations for >2.5 years continued to accumulate dry matter at a greater rate than did trees grown at ambient CO₂ concentration (Idso et al., 1991a, 1991b). In most orchards, root restriction seldom occurs and water and nutrients are generally not limiting. Therefore, the "leveling off" of dry-matter accumulation observed for many crops grown at elevated CO₂ concentrations was probably the result of eventual sink and/or resource limitations. Thus, we suggest that in most orchard situations, dry-matter accumulation in subtropical and tropical fruit crops is likely to be source rather than sink limited.

In a recent study, avocado, mango, and macadamia trees were grown for 6 months in a CO₂-enriched environment. The increased dry matter was primarily partitioned to the roots (Whiley and Searle, unpublished data) (Fig. 3). Presumably, when conditions are not sink-limited, such as in an orchard, increased water and nutrient uptake resulting from the increased root mass would eventually increase assimilate partitioning to the aboveground organs, as observed for citrus (Idso et al., 1991a, 1991b).

Atmospheric CO₂ enrichment increased total dry-matter accumulation in banana plants but, in contrast with observations with branched,

woody, tropical fruit species, did not affect the partitioning of dry matter among the leaves, pseudostems, rhizomes, or roots (Table 2) (Schaffer et al., 1997). When the total source : sink ratio was expressed as total dry matter accumulated per leaf area, banana plants grown in an enriched CO₂ environment (1000 $\mu\text{mol}\cdot\text{mol}^{-1}$), conditions that were not sink-limiting, had almost twice the source : sink ratio of plants grown in ambient CO₂ (350 $\mu\text{mol}\cdot\text{mol}^{-1}$) (Schaffer et al., 1997). Again, the presence of a rhizome, with a greater proportion of nonstructural to structural carbohydrates than in woody species, which lack a specific carbohydrate storage organ, may be responsible. Further studies should be conducted with fruiting, single-stem tropical fruit plants to determine the effects of atmospheric CO₂ enrichment on assimilate partitioning and accumulation.

Atmospheric CO₂ enrichment increased fruit set in citrus (Downton et al., 1987) and improved fruit retention of avocado, mango, and macadamia fruit during early fruit ontogeny (Whiley and Searle, unpublished data). In mango and macadamia, increasing atmospheric CO₂ concentrations increased total fruit weight at harvest. On an individual nut/fruit basis, an increased CO₂ environment increased partitioning of dry matter to the husk and kernel of macadamia fruit tissues and to the flesh of the mango fruit (Fig. 4). There were no significant effects of atmospheric CO₂ concentration on dry-matter accumulation in the shell of macadamia nuts or the skin, testa, and seed of mango (Fig. 4). Increased partitioning of assimilates to the "edible" portion of the nut or fruit as a result of atmospheric CO₂ enrichment would undoubtedly increase fruit quality, thus raising economic yields.

FUTURE EFFECTS OF ATMOSPHERIC CO₂ ENRICHMENT ON CARBON ASSIMILATION IN SUBTROPICAL AND TROPICAL FRUIT CROPS

Based on the species studied to date, increased atmospheric CO₂ concentrations (up to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$, which far exceeds the anticipated rate of increase for the next 50 years) appear to enhance carbon assimilation of subtropical and tropical fruit crops, provided there are no sink restrictions. Therefore, these species should benefit from predicted increases in atmospheric CO₂ concentrations. However, elevated atmospheric CO₂ concentrations may result in global warming (Houghton and Skole, 1990; Watson et al., 1990), although the increase in mean temperature at tropical latitudes is expected to be minimal (1 to 2 °C). Nevertheless, this may be sufficient to increase respiratory losses from tree fruit crops, thereby negating some of the benefits from increased atmospheric CO₂ concentrations.

Productivity of subtropical and tropical fruit crops should increase as a result of increased global CO₂ concentrations. For banana, a herbaceous, single-stem tropical species, atmospheric CO₂ enrichment increased dry-matter accumulation, but did not affect biomass partitioning (Schaffer et al. 1997). The effects of CO₂ enrichment on biomass accumulation have not been reported for other single-stem tropical species such as papaya. However, since these species grow continuously and maintain a relatively constant root : shoot ratio, atmospheric CO₂ enrichment should increase the allocation of assimilates equally to vegetative and reproductive structures, resulting in increased productivity. As in other C₃ species (Stulen and Den Hertog, 1993; Wolfe, 1994), branched, woody, subtropical, or tropical species such as avocado, mango, and macadamia allocated more assimilates to the roots as a result of CO₂ enrichment. In addition, atmospheric CO₂ enrichment of citrus (Downton et al., 1987), mango, and macadamia (Whiley and Searle, unpublished data) increased yield and/or fruit size. Thus, a global increase in atmospheric CO₂ concentrations should increase productivity of branched, woody, subtropical, and tropical species. However, given the slow rate at which the global CO₂ concentration is increasing, plants may adapt to elevated CO₂ levels over an extended time period. For example, initial reductions in nutrient uptake by sour orange trees as a result of atmospheric CO₂ enrichment disappeared after trees had been exposed to elevated CO₂ for several years (Peñuelas et al., 1997). Before definitive predictions can be made about the effects of global CO₂ changes on subtropical and tropical fruit crops, further studies need to be

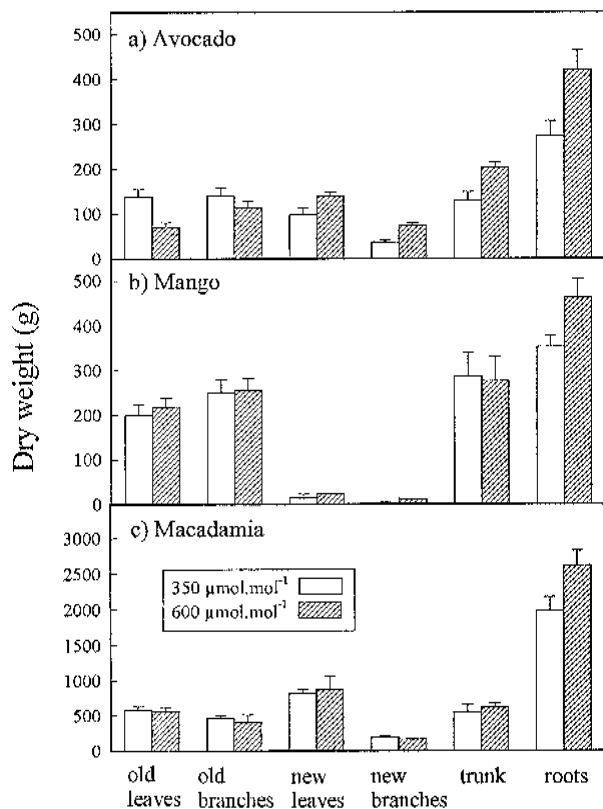


Fig. 3. Partitioning of dry matter in (a) avocado (cv. Hass), (b) mango (cv. Kensington) and (c) macadamia (cv. 246) trees grown for 6 months in atmospheric CO₂ concentrations of 350 or 600 µmol.mol⁻¹. Bars represent means (n = 6) ±SE (Whiley and Searle, unpublished data).

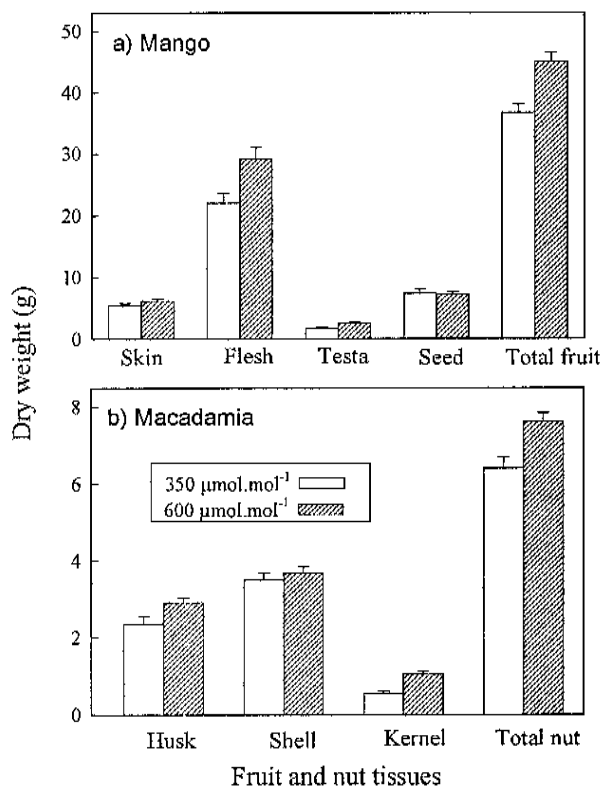


Fig. 4. Partitioning of dry matter in (a) mango (cv. Kensington) fruit and (b) macadamia (cv. 246) nuts grown for 6 months in atmospheric CO₂ concentrations of 350 or 600 µmol.mol⁻¹. Bars represent means (n = 33–49 for mango; n = 9–15 for macadamia) ±SE (Whiley and Searle, unpublished data).

conducted in which mature trees are exposed to several years of atmospheric CO₂ enrichment at a range of temperatures.

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