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Mango Tolerance to Reduced Oxygen Levels in Controlled Atmosphere Storage

Renar J. Bender,[1] Jeffrey K. Brecht,[2] Steven A. Sargent, and Donald J. Huber
Horticultural Sciences Department, University of Florida, P.O. Box 110690, Gainesville, FL 32611-0690

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Abstract. 'Haden' and 'Tommy Atkins' mangoes (*Mangifera indica* L.) were stored in air, 2, 3, 4 or 5 kPa O_2 plus N_2, or 25 kPa CO_2 plus air for 14 days at 15 °C or 21 days at 12 °C, respectively, then in air for 5 days at 20 °C to determine their tolerance to reduced O_2 levels for storage times encountered in typical marine shipments. All low O_2 treatments reduced mature green mango respiration (CO_2 production), however, elevated ethanol production occurred in 2 and 3 kPa O_2 storage, with the levels two to three times higher in 'Tommy Atkins' than 'Haden'. In contrast, 'Haden' fruit at the onset of the climacteric also accumulated ethanol in 4 kPa O_2 and produced 10 to 20-fold more ethanol in 2 and 3 kPa O_2 than preclimacteric fruit. While there were no visible injury symptoms, off flavor developed in mature green fruit at 2 kPa O_2 and in ripening initiated fruit at 2 and 3 kPa O_2. Ethanol production was not affected by storage in 25 kPa CO_2. Ethylene production was reduced slightly by low O_2, however, 'Haden' fruit also showed a residual inhibitory effect on ethylene production after 2 or 3 kPa O_2 storage, while 'Tommy Atkins' fruit stored in 2 kPa O_2 produced a burst of ethylene upon transfer to air at 20 °C. Fruit firmness, total sugars, and starch levels did not differ among the treatments, but 2, 3 or 4 kPa O_2 and 25 kPa CO_2 maintained significantly higher acidity than 5 kPa O_2 or air. The epidermal ground color responded differently to low O_2 and high CO_2 in the two mango cultivars. Only 2 kPa O_2 maintained 'Haden' color better than air, while all low O_2 levels maintained 'Tommy Atkins' color equally well and better than air. High CO_2 was more effective than low O_2 in maintaining 'Haden' color, but had about the same effect as low O_2 on 'Tommy Atkins'. Results indicate that preclimacteric 'Haden' and 'Tommy Atkins' mango fruit are able to tolerate 3 kPa O_2 for 2 or 3 weeks at 12 to 15 °C and that tolerance to low O_2 decreases as mangoes ripen. Results also show that low O_2 and high CO_2 affect mango ripening differentially.

Many beneficial effects of controlled atmosphere (CA) storage are attributed to reduction of O_2 concentrations. Some of the positive effects of optimum low O_2 storage atmospheres on fruit crops are reduced ethylene production and respiratory activity, better flavor retention, slower softening rates, slower green color loss, and maintenance of organic acid levels (Thompson, 1998). In contrast to these positive results, undesirable responses can occur when more extreme O_2 atmospheres are used in attempts to extend storage life, alleviate physiological disorders, and for insect disinfestation or control of postharvest pathogens. These undesirable responses consist mainly of discoloration and off flavor development (Thompson, 1998). It is well established that, under hypoxia, the activities of pyruvate decarboxylase and alcohol dehydrogenase (ADH) increase in plants, leading to accumulation of acetaldehyde and ethanol (Kennedy et al., 1992).

The O_2 concentration at which the transition from aerobic to anaerobic respiration occurs has been termed the anaerobic compensation point (ACP) by Boersig et al. (1988). Further studies to determine the lowest O_2 concentration at which anaerobic respiration is absent or avoided has indicated that the ACP, at least in some species, is strongly influenced by the physiological age of the commodity (Boersig et al., 1988) and by the storage temperature (Beaudry et al., 1992). Moreover, tolerance to low O_2 environments is species dependent (Kennedy et al., 1992) and tolerance to various exposure times is characteristic for each commodity (Ke et al., 1993).

A review of the history of modified atmosphere and CA storage of tropical fruits, including mangoes, has recently been published (Yahia, 1998). As with most CA research over the years, the vast majority of CA studies with mango have been conducted with the goal of determining the atmosphere and temperature combination that allows the longest possible storage life to be attained. The general conclusion of these studies has been that there are only modest or no benefits from CA storage for mangoes. This is due mainly to limited disease control by the moderate O_2 (5 kPa) and CO_2 (5 kPa) levels tolerated by mango fruit over extended storage periods at temperatures (12 to 15 °C) required to avoid chilling injury. More recently, Yahia and coworkers (Yahia et al. 1989; Yahia and Tiznado-Hernandez, 1993; Yahia and Vazquez-Moreno 1993) used short exposure times at relatively high temperature to evaluate insecticidal atmospheres for potential disinfestation of mangoes infested with Tephritid fruit flies species. They found that 'Keitt' mangoes tolerated 0.2 to 0.5 kPa O_2 for 5 d at 20 °C with no off-flavors or other signs of injury, and ripened normally after the low-O_2 treatments. Similarly, Bender et al. (1994) found that 'Kent' and 'Tommy Atkins' mangoes tolerated and benefited from a CA of 3 kPa O_2 plus 25 kPa CO_2 if storage time at 12 °C was limited to 3 weeks, however only CO_2 levels were varied in those tests.

In international commerce, most mangoes are picked before the onset of ripening and many are shipped by ocean in refrigerated marine containers with transit times on the order of 2 to 3 weeks. Other than the time spent in transit, there is little or no commercial storage of mangoes longer than a few days. Virtually all mangoes imported into the United States are treated with 46 °C water for 65 to 90 min (depending on variety and fruit weight) for insect disinfestation (U.S. Deprtment of Agriculture, 1998), which has been reported to accelerate some aspects of ripening, especially skin color change, although inhibiting softening and decay (McGuire, 1991; Nyanjage et al., 1998). For mangoes destined for transport over long distances, there is a tendency to

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[1]Current address: Dept. of Horticulture and Silviculture, Univ. Federal Rio Grande do Sul, C.P. 776, 91501-970, Porto Allegre, RS, Brasil.
[2]To whom reprint requests should be addressed.

harvest the fruit before full maturity in an attempt to prolong storage life, which, ironically, increases the likelihood of chilling injury, hot water injury, and poor flavor quality (Johnson et al., 1997; Medlicott et al., 1990). Use of CA during transport could potentially increase storage life sufficiently to allow marine-shipped, fully mature mangoes to be delivered to export markets with consistently acceptable quality. Our objective was thus to determine the tolerance of mangoes to reduced O_2 concentrations for 2 to 3 weeks at normal shipping temperatures, and to evaluate fruit ripening during and after transfer from CA.

Materials and Methods

Plant material. 'Haden' mangoes from Peru and 'Tommy Atkins' mangoes from Brazil were obtained from a commercial importer in Homestead, Florida. The fruit were harvested at normal commercial maturity for refrigerated marine shipment to Florida (i.e., mature green) and handled at the origin under normal commercial conditions, including hot water insect quarantine treatment, coating with a commercial formulation of carnauba wax, and precooling to 15 °C before shipment by airplane in insulated containers to Florida. The experiments with each cultivar were replicated once using fruit from different shipments. Upon arrival in Florida (2 or 3 d after harvest), the mangoes were transported from Homestead to Gainesville by refrigerated truck at 12 °C (7 h in transit). In Gainesville, fruit that were fully mature, uniform in ground color, and free from defects were selected, immediately placed in glass jars, and transferred to the designated storage room. Initial fruit maturity was RS1 (mature green) as described by Miller et al. (1986), except for an additional experiment using 'Haden' mangoes with more advanced ground color development (RS3; Miller et al., 1986) that was conducted to investigate the effect of low O_2 on ripening initiated (tree-ripe) fruit.

Controlled atmospheres. Individual 'Haden' fruit were placed in 1.75-L glass jars, with six replicates per treatment and sampling time, and held in a flow-through system at 15 °C for 14 d. Air, delivered by a compressor, was mixed with nitrogen (N_2) from a cylinder to produce 2, 3, 4, and 5 kPa O_2 treatments. One control treatment was air in the flow-through system, and a 25 kPa CO_2 control was obtained by combining CO_2 with air (resulting in ≈15.6 kPa O_2). We had previously identified 25 kPa CO_2 as the highest concentration tolerated by mangoes during 3 weeks storage (Bender et al., 1994). The same treatments were applied to 'Tommy Atkins' mangoes held in 10-L glass jars for 21 d at 12 °C. In the latter experiments, four fruit per replicate and four replicates per treatment and sampling time were used. Flow rates were selected based on fruit weight such that accumulation of respiratory CO_2 would remain below 0.5 kPa and were adjusted as required. Gas concentrations were confirmed and monitored by gas chromatography. The air and the gas mixtures were humidified by bubbling through water before entering the jars containing the fruit. 'Haden' and 'Tommy Atkins' were stored at different temperatures and for different times based on preliminary work indicating shorter storage life and lower tolerance to low temperature in the former compared to the latter cultivar. Different replicate numbers reflected availability of uniform maturity fruit.

Gas chromatography. Daily during the storage period, 0.5-mL headspace samples were removed from each jar and injected into gas chromatographs (GCs) to measure ethanol, ethylene, and CO_2 production. Ethylene and CO_2 production were not measured during storage in 25 kPa CO_2 due to difficulty in accurately measuring respiratory CO_2 accumulation and previous results showing that ethylene production is undetectable during storage in 25 kPa CO_2. After the storage period, the mangoes were transferred to air at 20 °C for 5 d. During the 5 d of ripening, the fruit were sealed periodically in the jars and, after 1 h, 0.5-mL headspace samples were removed for ethanol and ethylene production and respiration rate determinations in all treatments.

Ethanol was determined on a GC (model 5890; Hewlett-Packard, Avondale, Pa.) equipped with a 1520 × 3.12 mm 80/120 mesh Carbopack B column at 140 °C. The injector and the flame ionization detector temperatures were 200 °C. Ethylene was determined on a GC (model 10A10; Photovac, Thornhill, Ontario, Canada) with a photoionization detector and 760 × 3.12 mm activated alumina column. The temperatures of the injector, detector, and column were not controlled, but both equilibrated at a few degrees above ambient as a consequence of heat from the ultraviolet source. The CO_2 levels were determined on a gas partitioner GC (model 1200; Fisher Scientific, Pittsburgh, Pa.) equipped with a 1966 × 3.12 mm 80/100 mesh Porapak Q column at 60 °C. The injector and the thermal conductivity detector temperatures were 90 °C.

Firmness and composition. Measurements of fruit firmness, titratable acidity, total sugars, and starch content were made initially, at transfer from storage at 12 or 15 °C, and after 5 d in air at 20 °C. 'Haden' firmness was measured using a Cornell firmness device (Hamson, 1952) as modified by Gull (1987). A 1 kg weight was applied to unpeeled fruit and deformation in millimeters was recorded after 5 s. An Instron Universal Testing Machine (model 1132; Canton, Mass.) equipped with a 50-kg load cell and an 11-mm-diameter Magness-Taylor test probe was used to measure 'Tommy Atkins' firmness. The probe was applied to peeled fruit at 10 $cm \cdot min^{-1}$ until the bioyield force was reached. In both cases, two measurements were made on opposing equatorial sides of each fruit. After the firmness measurements, the mesocarp tissue was homogenized and used for determinations of titratable acidity, total sugars, and starch content. Titratable acidity was determined by titrating mango juice to a pH endpoint of 8.2 and was expressed as percent citric acid. Total alcohol-soluble sugars were determined colorimetrically by the phenol-sulfuric method as described by Dubois et al. (1956). Starch content was determined as described in Bergsma and Brecht (1992), entailing overnight enzymic digestion of the alcohol insoluble material at 37 °C with α-amylase and amyloglucosidase (Sigma, St. Louis, Mo.), followed by measurement of the resulting soluble sugars by the phenol-sulfuric method. The fruit were also evaluated for evidence of external and internal injury and evaluated informally for off flavor development at the end of each experiment.

Color measurements. Epidermal color determinations were made initially, at transfer from storage at 12 or 15 °C, and after 5 d in air at 20 °C using a portable chroma meter (CR-200; Minolta Corp., Ramsey, N.J.) calibrated to a white standard plate (CRA43) in the L*c*h* color system (Lightness, chroma, and hue angle, respectively). Measurements were made using diffuse illumination and 0° viewing angle under CIE illuminant C conditions (McGuire, 1992). For each fruit, two random measurements were taken at the distal end and one measurement at the equator on the shaded side (to avoid the red anthocyanin pigment "blush"). Flesh color was determined only with 'Tommy Atkins' mangoes. Two measurements were taken on opposing equatorial sides of each fruit after removing the epidermis.

Experimental design and statistical analysis. The experiments were conducted using a completely randomized design with fruit numbers as described above. Statistical analysis was done using SAS for PC (SAS Institute Inc., Cary, N.C.) with data subjected to analysis of variance (PROC ANOVA) and LSD values calculated for $P = 0.05$.

Results and Discussion

Respiration. Respiration rates in both cultivars were lower in the low-O_2 treatments compared to air control fruit, but the patterns were quite different (Fig. 1A and B). There was a clear distinction among the low-O_2 treatments in 'Haden' fruit and, for the 2, 3, and 4 kPa O_2 treatments, respiration rates were already reduced significantly by the first day of storage. In contrast, the low-O_2 effect was less and there was little difference among the 2, 3, and 4 kPa O_2 treatments for 'Tommy Atkins' fruit; additionally, it took more than 1 week for CO_2 production in the 5 kPa O_2 treatment to fall below that of the air control. After transfer to air at 20 °C, CO_2 production in all the treatments showed similar sharp increases. There was no indication from CO_2 production during storage that the O_2 levels used in this study induced anaerobic respiration.

Ethanol production. Ethanol production rates increased during storage at 15 °C in 'Haden' fruit held in 2 or 3 kPa O_2 (Fig. 1C) with a 5-fold higher level after 2 weeks in 2 kPa O_2 than in 3 kPa O_2, but did not change in fruit held in air or 4 or 5 kPa O_2. In 'Tommy Atkins' (Fig. 1D), ethanol production increased gradually with decreasing O_2 concentrations in the storage atmosphere at 12 °C and did not change in the air control fruit. Ethanol production rates in the 25 kPa CO_2 treatment were similar to the control fruit for both cultivars. After transfer to air at 20 °C, ethanol production continued to increase in 'Haden' fruit from 2 kPa O_2 storage, almost tripling to a peak of ≈1500 $\mu L \cdot kg^{-1} \cdot h^{-1}$, but did not change in fruit from 3 kPa O_2 and increased little (4 and 5 kPa O_2 and air) or not at all (25 kPa CO_2) in the other treatments. Ethanol production increased in 'Tommy Atkins' fruit from all treatments, including the air control, after transfer to air at 20 °C.

'Tommy Atkins' fruit from the 2 kPa O_2 treatment reached a peak of ethanol production more than twice that of 'Haden' fruit from the same treatment and 'Tommy Atkins' fruit from the other low-O_2 treatments all reached peak ethanol production rates at 20 °C that were at least equal to that of 'Haden' fruit from 2 kPa O_2 storage. The 'Tommy Atkins' air control and 25 kPa CO_2-stored fruit also increased ethanol production at 20 °C, to ≈600 to 700 $\mu L \cdot kg^{-1} \cdot h^{-1}$.

It is interesting that the elevated ethanol production rates in 'Haden' and 'Tommy Atkins' mangoes in the low O_2 treatments were not accompanied by corresponding increases in CO_2 production, as is observed typically in tissues undergoing anaerobiosis. Although ADH activity seems clearly to have been induced by the low O_2 treatments, as evidenced by increased ethanol production, it appears that energy demand was low in these mango fruit, limiting carbon flux through the glycolytic pathway. In a separate experiment, 'Haden' mangoes that had initiated climacteric respiration at the beginning of storage (Fig. 2A) had much higher ethanol production rates during low-O_2 storage (Fig. 2B) than the 'Haden' fruit discussed above, which entered storage at a less ripe stage (Fig. 1A and C). The latter fruit remained preclimacteric during the 2-week storage period, while the more advanced fruit went through the climacteric rise in respiration and ripened during storage, but still with no indication of anaerobic CO_2 production (Fig. 2A). Although the climacteric 'Haden' fruit produced much higher ethanol than the preclimacteric 'Haden' fruit, they were still less sensitive to low O_2 concentrations than 'Tommy Atkins' fruit, in that 5 kPa O_2 storage still did not cause any increase in ethanol production compared to the air control (Fig. 2B). Thus, both cultivar and ripeness stage appear to be involved in influencing ethanol production in mangoes.

Ethylene production. The pattern of ethylene production in 'Haden' fruit during storage at 15 °C was similar to the pattern of

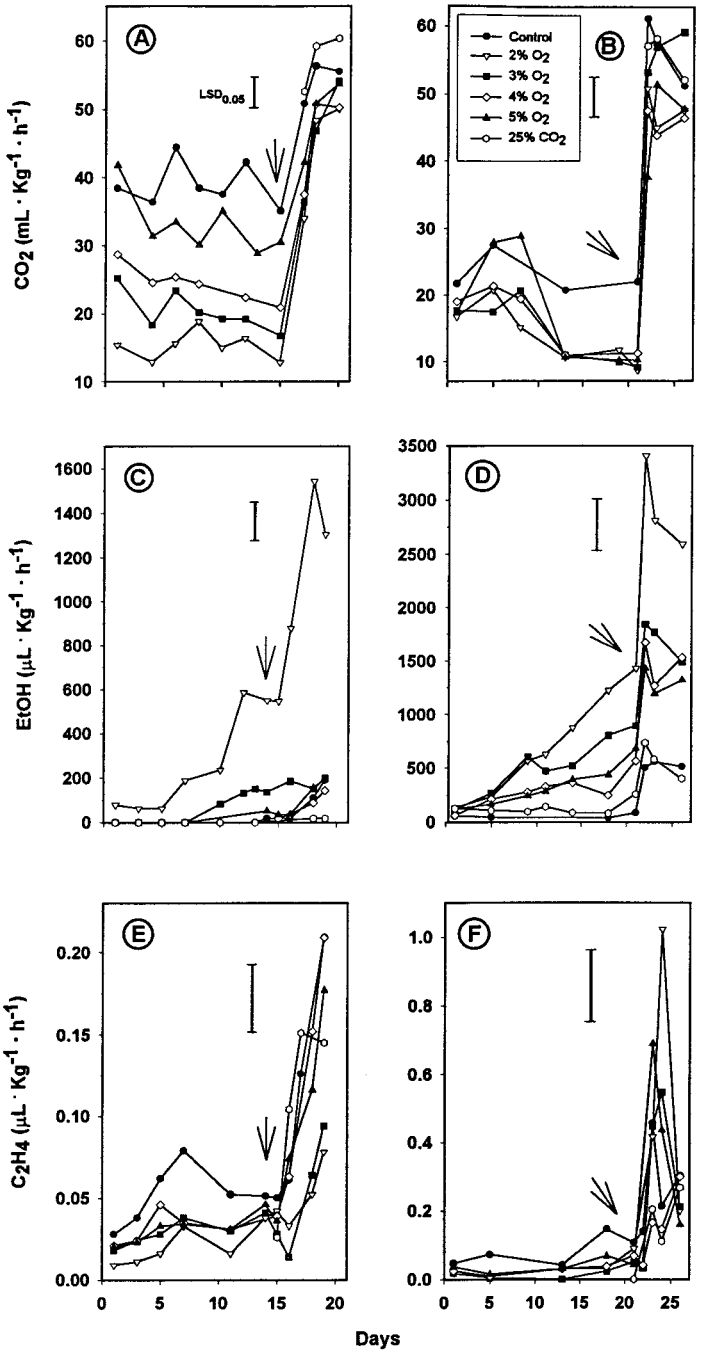

Fig. 1. (**A** and **B**) respiration, (**C** and **D**) ethanol, and (**E** and **F**) ethylene production rates of mature-green (**A**, **C**, and **E**) 'Haden' and (**B**, **D**, and **F**) 'Tommy Atkins' mangoes during 14 d at 15 °C or 21 d at 12 °C, respectively, in air (control) or controlled atmospheres, plus 5 d in air at 20 °C. Arrows indicate transfer to air at 20 °C. Data are means of six ('Haden') or four ('Tommy Atkins') observations.

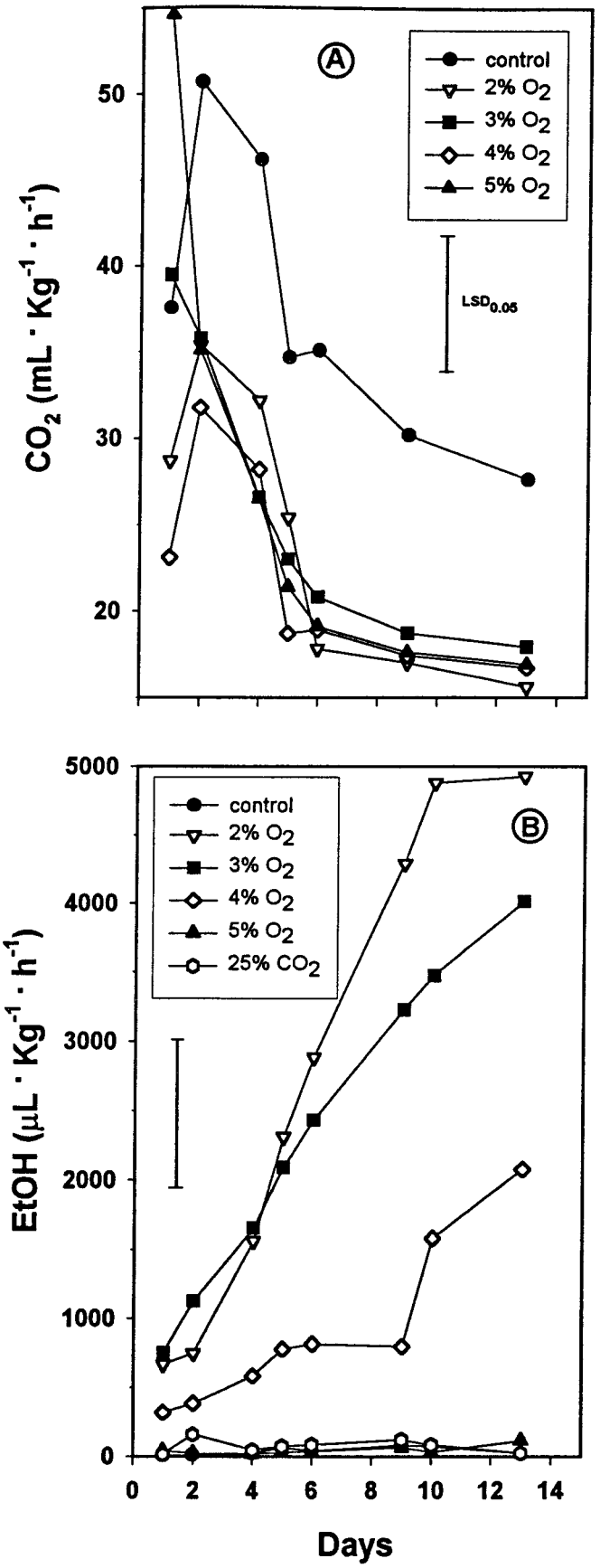

Fig. 2. (**A**) respiration and (**B**) ethanol production rates of ripening-initiated 'Haden' mangoes stored in air (control) or controlled atmospheres for 13 d at 15 °C. Data are means of six ('Haden') or four ('Tommy Akins') observations.

CO_2 production, with air control fruit producing more ethylene than fruit from the low-O_2 treatments, but the rates of ethylene production were extremely low (Fig. 1E). In 'Tommy Atkins' fruit, ethylene production was also low with not much difference among the air and low-O_2 treatments during storage at 12 °C (Fig. 1F). We observed previously that 25 kPa CO_2 almost completely inhibited ethylene production by mature-green 'Tommy Atkins' mangoes during storage for 21 d at 12 °C (Bender et al., 1995). After transfer to air at 20 °C, ethylene production by both cultivars increased significantly in all treatments, however, 'Haden' fruit showed a residual inhibitory effect of the reduced O_2 atmospheres. Ethylene production by 'Haden' fruit from the two lowest O_2 treatments remained lower than that of control fruit after transfer to air at 20 °C. In contrast, ethylene production by 'Tommy Atkins' fruit from the 2 kPa O_2 treatment produced a burst of ethylene at 20 °C that was more than twice that of the air control.

Firmness and composition. Fruit of both cultivars softened during storage, but neither low O_2 nor high CO_2 reduced softening compared to air storage, and further softening after transfer to air at 20 °C was rather limited (data not presented). Similarly, sugar and starch levels were not significantly affected by storage in low O_2 or high CO_2 compared to air in either cultivar; starch breakdown was essentially complete in all treatments at the time of transfer to 20 °C [(0.1% fresh weight (FW)] and, although sugar levels declined by ≈30% to 50% during the 5 d at 20 °C, there was no difference between air and CA-stored fruit (data not presented). In contrast, titratable acidity of both 'Haden' and 'Tommy Atkins' mangoes was significantly affected by the low O_2 and high CO_2 treatments during storage. At transfer from 12 or 15 °C, CA-stored fruit had about twice the acid level of the air-stored fruit; after 5 d in air at 20 °C, the 25 kPa CO_2 treatment and all of the low-O_2 treatments except 5 kPa O_2 maintained significantly higher acidity than the air control (Table 1). These results suggest that higher respiration rates by the air control fruit during storage at 12 or 15 °C were probably due to greater utilization of organic acids as substrates for glycolysis compared to CA-stored fruit. However, sugar consumption was equal in both air and CA-stored fruit, suggesting that glycolysis was running unhindered, perhaps causing an accumulation of pyruvate and subsequently reduced oxidative phosphorylation in the lower O_2 treatments due to less energy demand. Increased amounts of pyruvate could then have stimulated its own reduction to ethanol as indicated by Ke et al.

Table 1. Titratable acidity in mature-green 'Haden' and 'Tommy Atkins' mangoes stored for 14 d at 15 °C or 21 d at 12 °C, respectively, in air or controlled atmospheres, plus 5 d in air at 20 °C.

	Titratable acidity (% FW citric acid)			
Storage	Haden		Tommy Atkins	
atmosphere	At transfer	+5 d in air	At transfer	+5 d in air
Air	0.83[z]	0.61	0.54	0.36
2 kPa O_2 in N_2	2.84	2.03	1.18	1.14
3 kPa O_2 in N_2	ND[y]	1.68	1.48	1.02
4 kPa O_2 in N_2	ND	1.28	0.95	0.81
5 kPa O_2 in N_2	1.93	0.86	1.09	0.60
25 kPa CO_2 in air	1.80	1.38	1.12	0.75
$LSD_{0.05}$	0.31		0.32	

[z]Data are means of six ('Haden') or four ('Tommy Atkins') observations.
[y]No data.

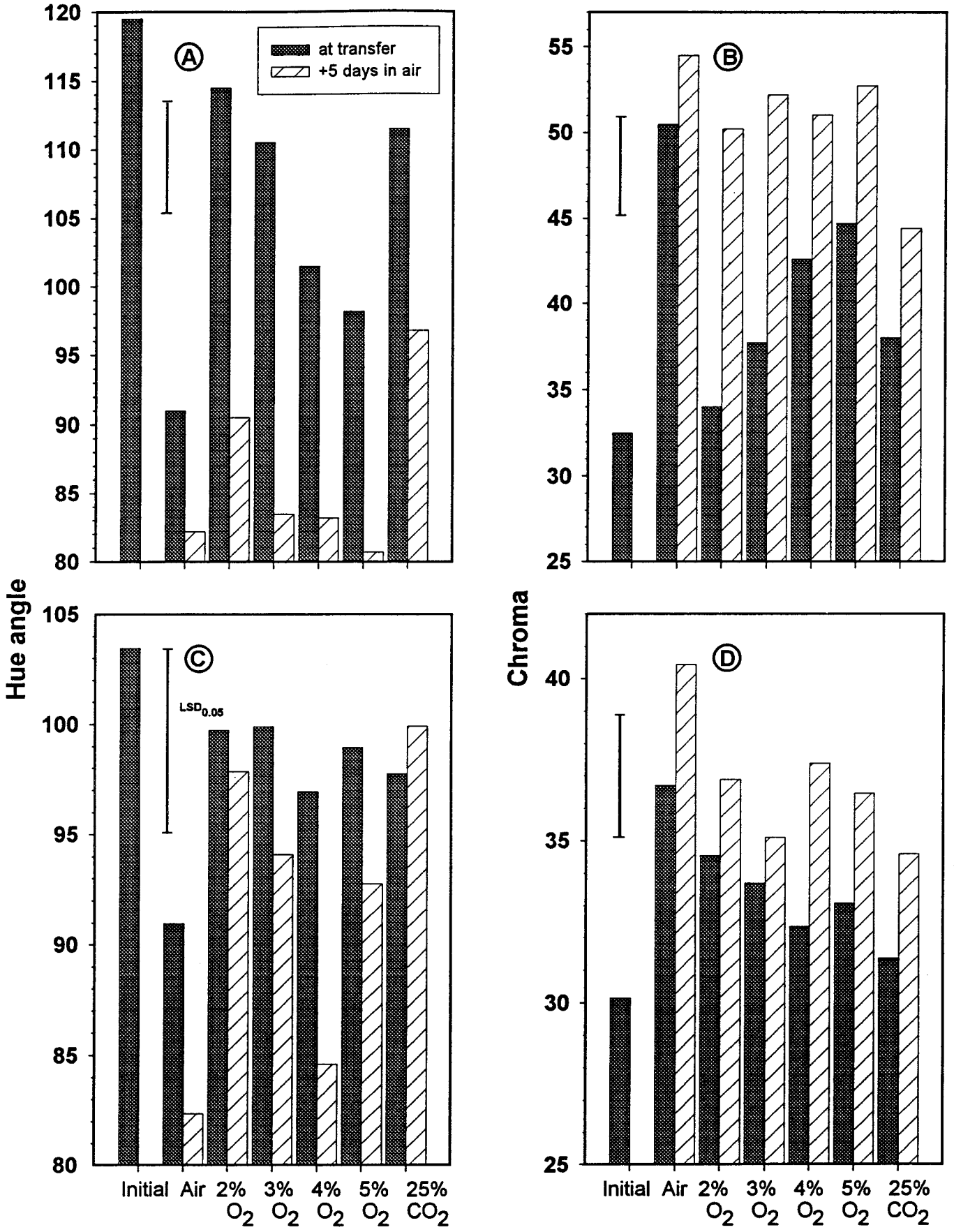

Fig. 3. (**A** and **C**) hue angle and (**B** and **D**) chroma values of mature-green (**A** and **B**) 'Haden' and (**C** and **D**) 'Tommy Atkins' mangoes during 14 d at 15 °C or 21 d at 12 °C, respectively, in air (control) or controlled atmospheres, plus 5 d in air at 20 °C. Data are means of six ('Haden') or four ('Tommy Atkins') observations.

(1993; 1995). This could explain the accumulation of ethanol without the corresponding elevated CO_2 production that would be expected if anaerobiosis was induced.

Color changes. Despite being greener initially than the 'Tommy Atkins' fruit, 'Haden' air control fruit underwent a significant color change during the 2 weeks of storage at 15 °C (Fig. 3A and B). 'Haden' mangoes from the low-O_2 treatments showed an O_2 concentration-dependent response for both epidermal hue and chroma during the CA storage period with all of the low-O_2 treatments maintaining larger hue angles and lower chroma values than the air control. The epidermal hue and chroma of 'Haden' fruit from the 25 kPa CO_2 treatment at transfer were similar to the values of those from the 2 and 3 kPa O_2 treatments. Like 'Haden', 'Tommy Atkins' fruit stored in air at 12 °C also changed hue more than fruit stored in low O_2 or 25 kPa CO_2 (Fig. 3C and D), but unlike 'Haden' there was no difference in hue angle or chroma among the CA treatments at the time of transfer to air at 20 °C. For 'Tommy Atkins', only the fruit in the 25 kPa CO_2 treatment maintained a significantly lower epidermal chroma value than the air control at the time of transfer to 20 °C with the low O_2 treatments having intermediate chroma values (Fig. 3D).

After transfer to air at 20 °C, there was an intense color change in air control fruit of both cultivars (Fig. 3). While the 25 kPa CO_2 treatment strongly inhibited further changes in epidermal hue and chroma in both mango cultivars following transfer to air at 20 °C, the ability of the low-O_2-stored 'Haden' and 'Tommy Atkins' fruit to develop epidermal color after transfer to air at 20 °C was strikingly different. In the case of 'Haden' fruit, only 2 kPa O_2 among the low-O_2 treatments maintained a larger hue angle than the air control after 5 d at 20 °C (Fig. 3A), but epidermal chroma values were the same in the air control and low-O_2-stored fruit (Fig. 3B). In contrast, 'Tommy Atkins' fruit from all the low O_2 treatments maintained both larger epidermal hue angles and lower chroma values than the air control fruit after 5 d at 20 °C (Fig. 3C and D). This residual inhibition of epidermal color development in 'Tommy Atkins' fruit after CA storage occurred despite rates of ethylene production at 20 °C that were at least 2-fold higher than for 'Haden' fruit (Figs. 1E and F). Interestingly, the flesh color of 'Tommy Atkins' mangoes (data not presented) was not affected by the CA treatments. There was also no effect of storage time on flesh color. At transfer from CA to air, the averages for all the CA treatments plus air control fruit were 90.37 ± 0.68 for flesh hue and 57.03 ± 1.65 for chroma. After 5 d in air at 20 °C, the averages were 90.28 ± 1.02 and 56.93 ± 1.84 for flesh hue and chroma, respectively.

Tian et al. (1994) determined that the hue angle of 'Shogun' broccoli florets [*Brassica oleracea* L. (Italica Group)] changed in an ethylene dose-dependent decline. The authors determined that an ethylene concentration as low as 0.01 $mg \cdot L^{-1}$ for 36 h at 20 °C was enough to induce a 20% decrease in hue angle of the florets. Mangoes, in contrast to broccoli, have low levels of ethylene production (Burdon et al., 1996) and, while the fruit from the low-O_2 treatments in the present experiments produced ethylene at rates mostly below 0.1 $\mu L \cdot kg^{-1} \cdot h^{-1}$ for the duration of storage at 15 or 12 °C, i.e., 14 and 21 d, respectively, changes in epidermal hue angles during this period were <10% of the initial value, which could indicate that either ethylene action was suppressed or that mangoes have a higher ethylene threshold level for epidermal color development.

Inhibition of ethylene action was likely involved in the delay of epidermal color development in the CA-stored mangoes based on observations by Burg and Burg (1962), who determined that color development in 'Kent' and 'Haden' mangoes was synchronous with increasing ethylene production during the climacteric rise. The same concurrence was observed by Krishnamurthy and Subrahmanyam (1970) working with 'Pairi' mangoes and by Cua and Lizada (1990) working with 'Carabao' mangoes. The different responses of 'Haden' and 'Tommy Atkins' to CA in terms of color changes could be due to either cultivar or maturity differences in the threshold ethylene levels required for color changes to occur or in the sensitivity of ethylene action to inhibition by low O_2 or high CO_2. The 'Tommy Atkins' fruit may have been at a more advanced maturity stage than the 'Haden' mangoes as discussed below, but ethylene levels were similar during storage for both cultivars. Thus, the greater effect of low O_2 during storage on the epidermal color of 'Tommy Atkins' compared to 'Haden' suggests that the former may require higher concentrations of ethylene to trigger color development. There was also a much greater residual effect of the CA treatments on epidermal color changes in 'Tommy Atkins' after transfer to air at 20 °C, despite the higher ethylene production compared to 'Haden' mentioned above. It is possible that the ethylene signal pathway leading to color change was damaged irreversibly by the low O_2 and 25 kPa CO_2 storage treatments in 'Tommy Atkins'. The 25 kPa CO_2 treatment had a similar effect on the epidermal color development of both cultivars during storage. This may have been due to greater inhibition of ethylene biosynthesis by the high CO_2 compared to low O_2 (Bender et al., 1995) or to direct inhibition of ethylene action by the CO_2 (Abeles et al., 1992) during the CA storage. However, the 25 kPa CO_2 treatment was also generally more effective than low O_2 in maintaining the epidermal color of the mangoes after transfer to air, when no residual effect of the CO_2 treatment on ethylene production was apparent and when any direct effect of the high CO_2 was no longer possible.

Ethanol is normally produced by ripening mango fruit, even in air (Bender et al., 2000). We have measured ethanol production rates as high as 2000 $\mu L \cdot kg^{-1} \cdot h^{-1}$ at 20 °C by 'Tommy Atkins' mangoes held continuously in air for 2 weeks at 12 °C plus 5 d at 20 °C (Bender et al., 1994) without any indication of abnormal flavor development. In the present experiments with mature green 'Haden' and 'Tommy Atkins', there were no external or internal symptoms of injury in CA-stored fruit, and only the fruit held in 2 kPa O_2 developed off flavor (data not presented). Ripening initiated 'Haden' mangoes produced much higher levels of ethanol than mature green 'Haden' fruit and, while the fruit still showed no visible injuries, off flavor developed after 2 weeks in both 2 and 3 kPa O_2. However, it remains possible that the elevated ethanol levels in the mangoes from low-O_2 storage described herein were involved in the residual inhibition of ripening after transfer to air at 20 °C. This possibility is supported by a comparison of the ethanol levels in mature green 'Haden' and 'Tommy Atkins' mangoes from the 2, 3, 4, and 5 kPa O_2 treatments (Fig. 1C and D) with the hue angle values for those fruit (Fig. 3A and C), which show that color maintenance for the different treatments corresponded to the levels of ethanol production measured. The lack of a similar correlation between ethanol levels and color changes in the 25 kPa CO_2-stored mangoes, which produced little ethanol but maintained color as well or better than the low-O_2 treatments, suggests that different mechanisms may be involved in the inhibition of color changes in mangoes by low O_2 and high CO_2.

Different responses of 'Haden' and 'Tommy Atkins' mangoes to low O_2 may be due to inherent cultivar differences. Another

possibility is that maturity differences between the cultivars account for differences in behavior. 'Tommy Atkins' mangoes may have been more advanced physiologically than 'Haden' mangoes when entering CA storage, as indicated by epidermal hue angles of 103.4 ± 2.8 (less green) for 'Tommy Atkins' compared to 119 ± 1.8 (more green) for 'Haden'. In addition, the rates of ethylene production by 'Tommy Atkins' fruit after transfer to air at 20 °C were several times higher than in 'Haden' fruit (Fig. 1E and F), which also suggests that the 'Tommy Atkins' fruit may have been at a more advanced stage of maturity than the 'Haden' fruit. A comparison of the results for preclimacteric and climacteric 'Haden' fruit clearly shows that ripeness stage affected the response to low O_2 in terms of respiration and ethanol production (Fig. 1A and C vs. Fig. 2). Since the two cultivars used in this study came from different production areas, a third possibility is that different preharvest conditions or cultural practices may have influenced the responses to low O_2 storage.

In conclusion, storage of mangoes in 2 to 5 kPa O_2 at 12 or 15 °C induced various levels of ethanol production depending on cultivar and fruit maturity, but did not induce higher CO_2 production typical of anaerobic metabolism. Based on induction of ethanol production, the low O_2 limit for storage of mature green 'Haden' and 'Tommy Atkins' mangoes was only 4 kPa, however, there were no visible injury symptoms and only the fruit held in 2 kPa O_2 developed off flavor within the time frame of these tests. Ripening initiated 'Haden' mangoes produced much higher levels of ethanol than mature green 'Haden' fruit and off flavor developed after 2 weeks in both 2 and 3 kPa O_2. Low O_2 had little effect on ethylene production, firmness or sugar levels in mature green mangoes, but inhibited color changes during storage at 12 or 15 °C, and <5 kPa O_2 maintained higher organic acid levels during ripening in air at 20 °C for both cultivars. Storage in 25 kPa CO_2 did not induce ethanol production, and was more effective than low O_2 in maintaining fruit epidermal color following transfer to air at 20 °C. We conclude that mature green 'Haden' and 'Tommy Atkins' mangoes can tolerate 3 kPa O_2 for 2 or 3 weeks at 12 or 15 °C. Our results indicate a potential for using low O_2 atmospheres to help maintain quality and slow ripening during marine transport of mangoes.

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