Low-oxygen-induced Poststorage Suppression of Bell Pepper Fruit Respiration and Mitochondrial Oxidative Activity

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Abstract. Bell pepper (*Capsicum annuum* var. *Jupiter*) fruit were exposed to 1.5% O₂ for 1 to 5 days at 20C to examine whether the low-O₂-induced poststorage respiratory suppression (PRS) in whole fruit could be due to limitations in mitochondrial oxidative capacity. Mitochondrial oxidative capacity was not affected after storing bell peppers for 1 day in 1.5 % O₂. Extending the storage period from 1 to 5 days in 1.5 % O₂ resulted in PRS of CO₂ production for about 55 hours after transfer to air, and a marked reduction in the oxidative capacity of isolated mitochondria. Mitochondrial activity was suppressed for 10 hours after transfer to air but, within 24 hours, had recovered to values comparable to those of mitochondria from fruit stored continuously in air. Storing bell peppers in 1.5% O₂ for 5 days resulted in a reduction in the respiratory control (RC), while ADP/O ratios were not affected. The reduction was temporary since the RC attained normal activity after returning bell peppers to air. Cyanide-sensitive cytochrome and CN-insensitive pathways were suppressed after storing fruit in 1.5 % O₂ for 5 days. After returning fruit from a low-O₂ atmosphere to air, the alternative pathway recovered at a greater rate than the cytochrome pathway.

Maintaining low respiration during fruit and vegetable storage is important in delaying senescence and avoiding rapid quality deterioration. Controlled-atmosphere or modified-atmosphere storage with low O₂, elevated CO₂, or both, has successfully reduced respiration and other associated metabolic processes (Kader, 1986).

Our previous studies have shown that whole bell peppers stored in 1.5 % O₂ for 1 day at 20C exhibited suppressed respiration rates that persisted for at least 24 h after transfer from a low-O₂ environment to a normal atmosphere (Rahman et al., 1993). The poststorage respiratory suppression (PRS) was extended to at least 48 h as the storage period under low O₂ was extended from 1 to 3 days. Although whole fruit respiration was continuously suppressed following storage in 1.5% O₂ for 1 day, the inhibition was not reflected in the capacity of isolated mitochondria to oxidize succinate (Rahman et al., 1993).

The central reactions of respiration occur in mitochondria, where several enzymes are involved in transferring electrons from organic molecules to oxygen (Goodwin and Mercer, 1988). Depending on O₂ concentration and exposure duration, enzyme activity could be affected by storage under a low-O₂ environment. The presence of PRS in bell peppers previously exposed to low O₂ could be due to direct or indirect effects on the mitochondrial oxidative capacity. As indicated by Kader (1986), O₂ concentrations below 0.02% restrict the activity of cytochrome oxidase.

Studies have shown that the alternative respiratory pathway (V_{alt}) is induced on exposing plant tissues to adverse environmental conditions. Examples include chill-stressed potato leaves (Ordentlich et al., 1991), postchilled tomatoes (De Virville et al., 1987), and aged and C₂H₄-treated potato slices (Mikitzel and Knowles, 1990). The Objectives of this study were to 1) determine

whether the occurrence of PRS in bell peppers exposed to low O₂ is due to impairment in the mitochondrial oxidative and phosphorylative capacities and 2) examine mitochondrial respiratory components of bell peppers exposed to low O₂.

Materials and Methods

Plant material. Bell peppers were hand-harvested, cleaned, and selected for uniformity of size and shape and freedom from defects. The fruit were wiped with paper towels moistened with 0.25% (v/v) sodium hypochlorite, rinsed with deionized water, and dried. Individual fruit (average weight of 170 g) were placed into 1.7-liter glass jars and kept in a 20C room for 24 h to allow handling-induced respiration to subside. Fruit samples having uniform CO₂ production rates of about 25 ± 2.5 ml·kg⁻¹·h⁻¹ were selected for the experiments.

Gas treatments. Fruit were sealed in 9.5-liter glass jars and exposed to 1.5% O₂ in N₂ or air for 5 days at 20C. The control consisted of fruit exposed to air. The humidified gas mixtures were introduced by means of a continuous flow-through system with a flow rate of 415 ml·min⁻¹ to maintain CO₂ levels below 0.3%.

Gas measurement. Bell pepper CO₂ production, as described by Rahman et al. (1993), was determined at intervals after transferring fruit from low-O₂ atmosphere to air.

Determination of mitochondrial activity. After treatment in 1.5% O₂ or air for 1 or 5 days, fruit were transferred to air and ventilated with humidified air at 20C. Mitochondria were isolated and purified from bell peppers as described in detail in Rahman et al. (1993). Respiratory control (RC) and ADP/O ratios were calculated according to the method of Estabrook (1967).

Oxidative capacity with succinate as the substrate was measured using mitochondria prepared from fruit after transfer from low O₂ to air and again after 24 h in air. In another experiment, mitochondria were prepared from fruit after 10 h in air after storing bell peppers for 5 days in 1.5% O₂.

Determination of mitochondrial respiratory components. Total oxidative activity (V_o) of purified mitochondria was measured using an oxygen electrode (model 53; Yellow Springs Instruments

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Co., Yellow Springs, Ohio) standardized against air-saturated deionized water. The capacity of the alternate pathway (V_{alt}) was determined by measuring the rate of O_2 uptake in the presence of 1 mM KCN and that of the cytochrome pathway (V_{cyt}) in the presence of 10 mM SHAM. Residual respiration (V_{res}) was estimated in the presence of KCN and SHAM. Oxygen consumption rate was expressed as nmol O_2 /mg mitochondrial protein per min. Protein in the mitochondrial preparations was determined using bicinchoninic acid (Smith et al., 1985).

Results

Effect of low O_2 on CO_2 production rate of intact bell peppers. Bell peppers stored for 5 days in 1.5% O_2 had suppressed CO_2 production rate of about 75% 2 h after transferring fruit to air compared to the continuously air-stored fruit (Fig. 1). The CO_2 production rate remained suppressed for 60 h after transfer to air, during which time CO_2 production recovered gradually to values comparable to fruit maintained continuously in air. The CO_2 production rate of fruit stored continuously in air decreased gradually during the experiment (Fig. 1).

Effect of low O_2 on mitochondrial activity. Mitochondria were isolated from fruit stored in 1.5% O_2 for 1 or 5 days to determine whether the low- O_2 induced PRS could be explained by limitations in mitochondrial oxidative capacity. The total O_2 uptake capacity (V_t) of mitochondria isolated from fruit stored in 1.5% O_2 for 1 day was similar to that of mitochondria isolated from fruit stored continu-

ously in air (Fig. 2). Twenty-four hours after transferring fruit from low O_2 to air, mitochondrial O_2 uptake was similar to that of mitochondria obtained from fruit stored in air for 2 days (Fig. 2). These findings confirm our earlier analyses of mitochondrial activity after a short (1 day) exposure to 1.5% O_2 (Rahman et al., 1993).

Bell peppers were stored for 5 days in 1.5% O_2 to determine the effect of extending the storage period on the total oxidative capacity of isolated mitochondria. After removing fruit from 1.5% O_2 storage for 5 days, the oxidative capacity of bell pepper mitochondria, presented here as the maximum rate of state 3 oxidation, was reduced by about 75% compared to that of mitochondria from air-stored fruit (Table 1). Mitochondria prepared from low O_2 -treated fruit 1 day after transfer to air exhibited oxidative capacities similar to those of mitochondria derived from fruit stored continuously in air. In an experiment using fruit from a different harvest, mitochondrial oxidative capacity was reduced by about 65% after storing bell peppers in 1.5% O_2 for 5 days (Table 2). The oxidative capacity of mitochondria exhibited some recovery after transferring fruit to air for 10 h; however, oxidative capacity was still nearly 40% lower than that of mitochondria from air-stored fruit. These experiments indicate that, while the oxidative capacity of mitochondria from low- O_2 stored bell peppers recovers to values comparable to those of air-stored fruit (Tables 1 and 2), the suppression is not rectified immediately upon returning fruit to normal atmosphere but is still apparent 10 h after removing fruit from the low- O_2 environment (Table 2). Although the oxidative competency of mitochondria varied between experi-

Fig. 1. Carbon dioxide production rates of bell peppers in air following storage in 1.5% O_2 for 5 days (●), and air-stored fruit (■). Vertical lines represent SD of the mean.

Fig. 2. Oxygen uptake capacity of mitochondria isolated from bell peppers stored for 1 day in 1.5% O_2 (○), 1 day in air (□), 1 day in 1.5% O_2 plus 1 day in air (●), and 2 days in air (■).

ments (compare Tables 1 and 2), the relative effects of the different storage conditions were quite consistent.

RC values and ADP/O ratios of mitochondria from stored fruit. Respiratory control and ADP/O ratios were examined to determine whether the mitochondrial oxidative and phosphorylative properties were affected by prior storage of bell peppers under low O₂ (Table 3). As shown in Table 3, the RC and ADP/O ratios of mitochondria from fruit stored in 1.5% O₂ for 1 day or 1 day after transfer from 1.5% O₂ to air were not significantly different from those obtained with mitochondria from fruit stored continuously in air. In contrast, the RC values of mitochondria from bell peppers stored for 5 days in 1.5% O₂ were significantly ($P \leq 0.01$) lower than those stored continuously in air (Table 4). There was a significant recovery in RC values noted in mitochondria from fruit stored for 5 days in low O₂ followed by 10 h in air (Table 4); however, values remained significantly ($P \leq 0.01$) lower than those of the air-stored fruit. The recovery trend for RC values parallels that noted for total oxidative capacity. The ADP/O ratios of

Table 1. Maximum sustained state 3 O₂ consumption in mitochondria isolated from bell pepper fruit following storage under low oxygen or in air.

Treatment	nmol O ₂ /mg mitochondrial protein per min ^z
5 Days/air	142.3
5 Days/1.5% O ₂ + 1 Day/air	122.0
6 Days/air	123.7

^zData the means of two separate determinations.

Table 2. Maximum sustained state 3 O₂ consumption in mitochondria isolated from bell pepper fruit following storage under low O₂ or in air.

Treatment	nmol O ₂ /mg mitochondrial protein per min ^z
5 Days/1.5% O ₂	67.4
5 Days/air	188.7
5 Days/1.5% O ₂ + 10 h air	90.3
5.4 Days/air	143.0

^zData the means of two separate determinations

Table 3. Respiratory control (RC) and ADP/O ratios of mitochondria isolated from fruit stored in 1.5% O₂ for 1 day and 1 day after transfer to air, and air-stored fruit.^a

Treatment	RC	ADP/O
1 Day/1.5% O ₂	2.15 a ^z	1.99 a
1 Day/air	2.17 a	2.00 a
1 Day/1.5% O ₂ + 1D/air	2.50a	2.01 a
2 Days/air	2.43 a	2.03 a

^aData are means of three replications. Means followed by the same letter within a column are not significantly different at 0.05 level by DMRT.

Table 4. Respiratory control (RC) and ADP/O ratios of mitochondria isolated from fruit stored in 1.5% O₂ for 5 days and 10 h after transfer to air, and air-stored fruit.^a

Treatment	RC	ADP/O
5 Days/1.5% O ₂	1.42 c ^z	1.81 a
5 Days/air	2.68 a	1.86 a
5 Days/1.5% O ₂ + 10 h/air	2.37 b	1.83 a
5.4 Days/air (130 h)	2.69 a	1.85 a

^aData are the means of three replications. Means followed by the same letter within a column are not significantly different at 0.01 level by DMRT.

mitochondria from fruit stored in 1.5% O₂ or 10 h after transfer to air were not significantly different from those of mitochondria from fruit stored continuously in air (Table 4).

Changes in mitochondrial respiratory components. Experiments were performed to determine the influence of low-O₂ storage on the various oxidative components of mitochondria. Total respiratory activity (V_T) of mitochondria from fruit stored in 1.5% O₂ for 1 day was not significantly different from that of mitochondria isolated from air-stored fruit (Table 5). Twenty four hours after transfer to air, V_T increased slightly but was not significantly different from the V_T of mitochondria isolated from fruit stored in 1.5% O₂ for 1 day, but was higher than VT of mitochondria from air-stored fruit. The capacities of V_{cyt} and V_{alt} were significantly higher ($P \leq 0.01$) after storing fruit for 1 day in 1.5% O₂ compared to those of mitochondria from air-stored fruit (Table 5). One day after transferring fruit from low-O₂ to air, V_{alt} was significantly ($P \leq 0.01$) higher (17%) than the V_{alt} of mitochondria from fruit stored in 1.5% O₂ for 1 day. The V_{cyt} of fruit transferred to air for 1 day following low-O₂ storage was not significantly different from the V_{cyt} of fruit stored in 1.5% O₂ for 1 day. There were no differences in the capacity of V_{cyt} and V_{alt} between fruit stored in air for 1 or 2 days. The ratio of V_{alt}/V_{cyt} of fruit stored in 1.5% O₂ for 1 day was not significantly different from that of fruit stored in air (Table 5). Twenty four hours after transferring fruit from low O₂ to air, the V_{alt}/V_{cyt} ratio recovered by about 15% and was significantly ($P \leq 0.01$) higher from that of the air-stored fruit. The level of residual respiration (V_{res}) in the purified mitochondria was negligible for all treatments (Table 5).

Further experiments were conducted to examine the influence of extended low-O₂ storage on bell pepper mitochondrial oxidative components. The V_T of mitochondria isolated from fruit stored in 1.5% O₂ for 5 days was significantly ($P \leq 0.01$) lower (43%) than that of mitochondrial isolates from air-stored fruit (Table 6). Twenty four hours after transfer of fruit from low O₂ to air, the V_T attained values similar to those of the air-stored fruit. The V_T was not significantly different between fruit stored in air for 5 or 6 days. The capacities of V_{cyt} and V_{alt} were suppressed by about 35% and 60%, respectively, after storage of fruit for 5 days in 1.5% O₂, and were significantly ($P \leq 0.01$) lower than the values for air-stored fruit (Table 6). V_{cyt} and V_{alt} increased, by about 35% and 65%, respectively, 1 day after transferring fruit from low O₂ to air. Although the V_{cyt} recovered after transferring fruit to air, it remained significantly ($P \leq 0.01$) lower than the values obtained for fruit stored continuously in air. The V_{alt}/V_{cyt} ratio was reduced after storing fruit for 5 days in 1.5% O₂, but recovered by about 47% 1 day after transferring fruit from low O₂ to air. The contribution of V_{res} to the total respiratory activity of mitochondria was negligible (Table 6).

In our determinations of the proportional capacities of the two electron-transport components in bell pepper mitochondria, V_{alt} was consistently higher than V_{cyt}. These data represent the V_{alt} and V_{cyt} capacities and do not necessarily reflect the extent of engagement in vivo. It is noteworthy, however, that mitochondria from mature-green tomatoes and cauliflower florets, neither of which exhibited a significant PRS in response to hypoxia, exhibited the more typical pattern of V_{cyt} > V_{alt} (unpublished data).

Discussion

Previous studies (Rahman et al., 1993) demonstrated that bell peppers stored in low-O₂ atmospheres for 1 to 3 days exhibited suppressed total organ O₂ consumption and CO₂ evolution upon transfer to normal atmospheres. This postharvest respiratory sup-

Table 5. Contribution of the alternative (V_{alt}) and cytochrome (V_{cyt}) pathways and residual respiration (V_{res}) to the total respiratory activity (V_T) in mitochondria from fruit stored in 1.5% O_2 for 1 day and 1 day after transfer from low O_2 to air.

Treatment	Oxygen consumption rate ^z (nmol O_2 /mg mitochondrial protein per min)				
	V_T	V_{cyt}	V_{alt}	V_{res}	V_{alt}/V_{cyt}
1 Day/1.5% O_2	194.6 ab ^z	52.3 a	106.1 b	0.13 a	2.03 b
1 Day/air	189.6 bc	44.2 b	87.2 c	0.17 a	1.98 b
1 Day/1.5% O_2 + 1 day/air	198.3 a	54.3 a	127.2 a	0.13 a	2.35 a
2 Days/air	186.5 c	44.1 b	87.3 c	0.00 a	1.98 b

^zData are means of three replications. Means followed by the same letter within a column are not significantly different at 0.01 level by DMRT.

Table 6. Contribution of the alternative (V_{alt}) and cytochrome (V_{cyt}) pathways and residual respiration (V_{res}) to the total respiratory activity (V_T) in mitochondria from fruit stored in 1.5% O_2 for 5 days and 1 day after transfer from low O_2 to air.

Treatment	Oxygen consumption rate ^z (nmol O_2 /mg mitochondrial protein per min)				
	V_T	V_{cyt}	V_{alt}	V_{res}	V_{alt}/V_{cyt}
5 Days/1.5% O_2	62.2 b ^z	23.1 c	22.9 b	1.0 a	0.99 d
5 Days/air	109.2 a	35.8 b	60.2 a	0.6 b	1.68 b
5 Days/1.5% O_2 + 1 day/air	107.2 a	35.7 b	65.0 a	0.7 b	1.82 a
6 Days/air	108.7 a	48.8 a	62.6 a	0.9 a	1.28 c

^zData are means of three replications. Means followed by the same letter within a column are not significantly different at 0.01 level by DMRT.

pression (PRS) was not reflected in the total oxidative capacity of isolated mitochondria (Rahman et al., 1993). This observation provides evidence that the PRS exhibited by intact bell peppers was due to factors such as impairment in general carbon flux or inhibition of nonmitochondrial oxidases. It is also possible that direct effects on mitochondria are rapidly rectified after transferring fruit from low O_2 to air or do not persist after isolating and incubating mitochondria in the substrate-rich environment under which oxidative capacity is determined. In further attempts to determine the influence of low- O_2 storage on mitochondrial reactions, bell peppers were subjected to longer exposures (5 days) to 1.5% O_2 .

The data confirmed our previous observations (Rahman et al., 1993) that exposing bell peppers to 1.5% O_2 for 1 day exerted no apparent effect on the total capacity of mitochondria to use succinate. Additionally evident in the present study is that the RC and ADP/O ratios were not affected by storing fruit for 1 day in 1.5% O_2 .

Storing bell pepper fruit in 1.5% O_2 for 5 days suppressed CO_2 production for at least 55 h following transfer to air. This compares to the 24-h PRS observed for fruit stored for 1 day in 1.5% O_2 (Rahman et al., 1993) and demonstrates that the PRS is prolonged following extended exposure to low O_2 . In contrast to the effect of 1.5% O_2 for 1 day, 5 days storage in 1.5% O_2 resulted in a marked reduction in the total oxidative capacity of isolated mitochondria. The reduction in V_T was temporary and mitochondria attained normal total oxidative capacity within 1 day of transferring fruit from low O_2 to air. The recovery in total oxidative capacity was not immediate, however, as V_T measured 10 h after transferring fruit from low O_2 to air was still lower than that of mitochondria from air-stored fruit. This time period (10 h) is in excess of the period required (about 2 h) for equilibration of internal fruit atmosphere with air (i.e., 21% O_2) on removing fruit from low O_2 and is indicative of a direct effect of low O_2 on mitochondrial function. Anaerobic injury seems unlikely in view of the absence of detectable levels of ethanol in low O_2 -stored peppers (Rahman et al.,

1993). It is possible that the temporary suppression in total mitochondrial oxidative capacity following low O_2 storage reflects an impairment in the capacity of mitochondria to mobilize key substrates. Kays (1991) noted that changes in the internal environment brought about by controlled-atmosphere storage can result in significant metabolic shifts in reactions at which regulatory pathways are controlled. McGlasson and Wills (1972) indicated that low O_2 (3% O_2 , 97% N_2) caused significant increases in pyruvate, oxaloacetate and α -ketoglutarate levels in banana fruit stored for 1 to 4 days at 20°C. These authors suggested that low O_2 limited the operation of the citric acid cycle between pyruvate and citrate, and between α -ketoglutarate and succinate.

A reduction in the total mitochondrial oxidative capacity (V_T) after exposing bell peppers to 1.5% O_2 for 5 days was accompanied by a temporary reduction in the RC values. Unlike total oxidative capacity; however, RC values recovered to control levels within 10 h following transferring fruit to air.

A reduction in V_T after storing bell peppers in 1.5% O_2 for 5 days was accompanied by a suppression in the activity of V_{cyt} and V_{alt} . The activity of both respiratory pathways recovered within 1 day after transferring fruit to air, however, the magnitude of recovery was greater for V_{alt} than V_{cyt} . The increased capacity of V_{alt} 1 day after transferring bell peppers from low O_2 to air may be explained on the basis that energy and ATP are not limiting and V_{cyt} is saturated with electrons (Lambers, 1980; Palmer, 1976). Under these conditions, the ubiquinone pool is highly reduced, causing electron flow to shift from V_{cyt} to V_{alt} (Weger et al., 1990; Lambers, 1980). This shift to the nonphosphorylative V_{alt} allows the citric acid cycle to remain operational with minimal ATP production (Rasmussen et al., 1990) and enables metabolism to continue when cellular energy charge is high (Lambers, 1982). Conditions of high ATP and NADH/NAD⁺ ratios can inhibit the activity of pyruvate dehydrogenase, reducing the conversion of pyruvate to acetyl CoA (Kays, 1991). Kiener and Bramlage (1981) reported that the V_{alt} of cucumber hypocotyls became engaged during the postchilling respiratory burst, and also in postchilled tomatoes (De

Virville et al., 1987). Similarly, Inaba and Chachin (1989) observed an increase in V_{alt} in tomatoes following exposure to 30 or 35°C.

This study indicates that the PRS after exposing bell peppers to low- O_2 atmosphere can be explained, in part, by reduced oxidative capacity of mitochondria. Although the present study addressed suppressed total organ CO_2 exchange and mitochondrial oxidative capacity during the period following exposure to low O_2 , these effects are likely operational during the low- O_2 exposure and may help explain the effectiveness of controlled atmospheres in extending the postharvest longevity of harvested organs. The efficacy of controlled-atmosphere storage is frequently explained on the basis of specific effects of altered O_2 or CO_2 levels on the synthesis and action of ethylene (Kubo et al., 1990). Ethylene has been shown to induce or increase the capacity of V_{alt} in potato tuber tissue (Gude and van der Plas, 1985), pea seedlings (Duncan and Spencer, 1987), and iris bulbs (Marissen et al., 1986). As bell peppers produce minimal quantities of ethylene during postharvest storage and show no change in ethylene production in response to low- O_2 storage (Rahman et al., 1993), peppers may be useful for investigating the biochemistry of controlled atmospheres independent of the influence of ethylene.

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