Ripening Stage Affects the Chilling Sensitivity of Greenhouse-grown Peppers

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Abstract. **Greenhouse-grown 'Bison' and 'Doria' peppers *(Capsicum annuum* L.) were harvested when mature green (MG) (>95% surface green) or ripe (>95% of surface red or yellow). Both cultivars responded similarly to temperature and neither exhibited chilling injury (CI), as indicated by surface pitting, after storage at 13C for 1 or 2 weeks. Ripe peppers showed no CI when held at 1C for 1 or 2 weeks, while MG peppers exhibited CI after these treatments. Exposing MG peppers to 1C for 3 days caused CI and stimulated C_2H_4 (12.3x) and CO_2 production (2.5x). In contrast, a similar exposure of ripe peppers did not cause CI but stimulated C_2H_4 (6.5x) and CO_2 production (1.4x). It seems that CO_2 and C_2H_4 production was stimulated by exposure to 1C, not necessarily by CI development. Our data question the physiological significance of elevated CO_2 and C_2H_4 production in CI development. The observed tolerance of ripe peppers to 1C suggests that ripe greenhouse-grown peppers can be stored at temperatures lower than those currently recommended for bell peppers.**

Chilling injury (CI) is a physiological disorder of many economically important crops that were indigenous to the tropics and subtropics (Saltveit and Morris, 1990). Exposing these chilling-sensitive crops to nonfreezing temperatures <12C causes a myriad of symptoms that include uneven and abnormal ripening, increased water loss and surface pitting, increased CO_2 and C_2H_4 production upon warming, increased susceptibility to certain diseases, and increased permeability of cellular membranes (e.g., ion leakage). CI becomes progressively more severe during storage for long periods or at low temperatures (Risse et al., 1987). Sweet bell peppers are susceptible to CI at nonfreezing temperatures <7C (Wang, 1977). The visible symptom of pitting occurs after peppers are returned to higher, nonchilling temperatures (e.g., 20C) (Miller and Risse, 1986; Wang and Baker, 1979).

Chilling temperatures stimulate CO_2 production in cucumbers *(Cucumis sativus* L.) (Cabrera and Saltveit, 1990) and peppers (Kozukue and Ogata, 1972) and C_2H_4 production in papayas *(Carica papaya* L.) (Chan et al., 1985), cucumbers (Cabrera and Saltveit, 1990; Wang and Adams, 1982), and peppers (Yao et al., 1986). In higher plants, C_2H_4 is synthesized by the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to C_2H_4 by ACC oxidase (Yang, 1980).

ACC oxidase was previously termed the ethylene-forming enzyme (Abeles et al., 1992). The rate of C_2H_4 synthesis in chilled cucumbers is limited by the availability of ACC and partially limited by ACC oxidase activity (Cabrera and Saltveit, 1990).

Differences in chilling sensitivity have been reported for tomatoes *(Lycopersicon esculentum* Mill.) of different maturities (Autio and Bramlage, 1986; King and Ludford, 1983). Using different methods, however, similar patterns of chilling sensitivity were found in conditioned MG and red-ripe tomatoes (Saltveit, 1991). Most field-grown sweet bell peppers are commercially harvested at the MG stage and, thus, much of the previous research on CI in peppers has been conducted with MG fruit (Miller and Risse, 1986; Phelps and McDonald, 1989; Wang, 1977). Greenhouse-grown peppers, however, are usually harvested at the fully ripe stage (Bakker, 1989). The ripening (coloration) of bell peppers was studied by Saltveit (1977), but the effect of ripening on CI of greenhouse-grown peppers was not investigated.

The objectives of this study were to investigate the chilling sensitivity of two pepper cultivars and of peppers at different stages of maturity and to see if chilling stimulated CO_2 and C_2H_4 production by these greenhouse-grown peppers.

Materials and Methods

Plant materials. Seeds of the commercial sweet bell peppers 'Bison' and 'Doria' (Bruinsma Seeds, Netherlands), red- and yellow-fruited, respectively, were sown on 24 Jan. 1991 on rock-wool cubes and transplanted into 20-liter sawdust bags on 22 Mar. Plants were grown in a greenhouse under natural daylight using standard cultural practices (B.C. Ministry of Agriculture and Fisheries, 1988). The greenhouse was held at 28/19C (maximum/minimum), and relative humidity (RH) was ≈ 70%.

Experimental procedures. MG fruit (>95% of surface green) and ripe fruit (>95% of surface red or yellow) were harvested on 25 June and 15 July and stored at 1 (chilling temperature) or 13C (control) for 1 or 2 weeks. The average RH in the 1 and 13C rooms was 98% [vapor-pressure deficit (VPD) = 0.013 kPa] and 95% (VPD = 0.0075 kPa), respectively. The experiment was a 2^5 factorial, with harvest × cultivar × maturity × temperature × storage time. In addition, freshly harvested fruit were analyzed. There were two greenhouse blocks (north and south). On 25 June, the experimental unit for each treatment consisted of seven fruit. On 15 July, four fruit from each of these two blocks were combined as

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a single experimental unit due to the limited number of fruit. Each experimental unit was assigned randomly to a temperature × storage time combination (Table 1).

To determine CO_2 and C_2H_4 production, an experimental unit of seven (25 June) or eight (15 July) fruit was removed from storage and five to six fruit were sealed in a 6-liter container for 4 h. After 1 h, 0.25-ml gas samples were analyzed for CO_2 production using a gas chromatograph (model GC-9A, Shimadzu Corp., Kyoto, Japan) equipped with a 1.5-m poropak-Q column, a methanizer (model MTN-1, Shimadzu), and a flame ionization detector. Gas samples (2.0 ml) were analyzed after 4 h for C_2H_4 with a gas chromatograph (model 3700; Varian Instrument Corp., Palo Alto, Calif.) equipped with a 2-m activated alumina column and a flame ionization detector. Each experimental unit constituted a replication. There were three replications: two on 25 June and one on 15 July.

On 26 June and 16 July, eight disks (9 mm in diameter) were excised randomly from each of two fruit from each experimental unit. Disks were incubated with 10 µl of 50 µM ACC or distilled water for 5 h in a petri dish, weighed, and sealed in a 10-ml hypovial (serum-type reaction vial 3-3104, Supelco, Oakville, Ontario) for 1 h. The difference in C_2H_4 production with and without ACC was used to calculate ACC oxidase activity (Cabrera and Saltveit, 1990). A sample consisting of 50 g fresh weight from the same fruit was diced and homogenized with 100 ml of cold 2% HCl for 2 min (Lau et al., 1984). The homogenate was centrifuged at 1800 g for 20 min. The supernatant was adjusted to pH 7.0 with 10 M NaOH. A 7.0-ml aliquot was reacted with NaOCl in the presence of Hg to determine ACC by measuring C_2H_4 production (Lizada and Yang, 1979).

Pitting of the fruit surface was rated visually by estimating the percentage of the surface affected at 1, 3, and 7 days after transfer to a room at 20 to 22C and 65% RH (VPD = 0.82 kPa). Only the data obtained after 7 days of transfer to room temperature are reported.

MG fruit of 'Bison' and 'Doria' were harvested from a single block on 6 and 27 Aug. Production of CO_2 and C_2H_4 was measured following the temperature treatments andmethods describedabove. Internal CO_2 and C_2H_4 concentrations were measured from three fruit by withdrawing 0.25 ml and 2.0 ml, respectively, directly from fruit when they reached room temperature.

Statistical analysis. SAS's general linear model procedure (SAS Institute, Cary, N.C.) was used for analysis of variance. To correct for the imbalance in the data, means were estimated by least squares. To provide homogeneous variances, some variables were transformed to logarithms for analysis. When this was done, back-transformed means and relative SES are presented. The SE for a mean is the product of the mean and the relative SE.

Results

CI symptom occurrence in fruit stored at 1C varied with ripening stage. Only MG fruit stored at 1C for 1 or 2 weeks developed surface pitting (Table 1). In MG fruit stored 1 week at 1C, pitting became visible after 1 day at room temperature (20C). Compared to freshly harvested MG fruit, chilled MG fruit showed no change in CO_2 production, elevated (18x) C_2H_4 production, reduced (0.3x) ACC oxidase activity, and an elevated (3x) ACC concentration. In contrast, ripe yellow and red peppers showed no CI after 1 or 2 weeks at 1 C. After 1 week at 1C, ripe peppers showed no change in CO_2 production, elevated (7x) C_2H_4 production, reduced (0.3x) ACC oxidase activity, and an elevated (2x) ACC concentration.

No CI symptoms occurred in MG or ripe fruit stored at 13C for 1 or 2 weeks (Table 1). After 1 week, MG fruit stored at 13C showed reduced (0.4x) CO_2 production, unchanged C_2H_4 production, reduced (0.5x) ACC oxidase activity, and an elevated (3x) ACC concentration. After 1 week of storage at 13C, ripe fruit showed reduced (0.6x) CO_2 production, unchanged C_2H_4 production, reduced (0.4x) ACC oxidase activity, and an elevated (2x) ACC concentration.

MG fruit showed CI after 3 days of storage at 1C (Table 2). These fruit had slightly increased (1.2x) internal CO_2 but decreased (0.7x) CO_2 production. The corresponding internal C_2H_4 concentration increased (48x), as did C_2H_4 production (5x). MG fruit showed no CI at 13C.

CI was associated with high CO_2 ($r = 0.54$, $P = 0.0005$, n = 37) and C_2H_4 ($r = 0.86$, $P = 0.0001$, n = 36) production. However, CI was not associated with ACC oxidase activity ($r = 0.02$, $P = 0.89$, n = 34) or ACC concentration ($r = 0.29$, $P = 0.07$, n = 37).

There were no differences between 'Bison' (red fruit) and 'Doria' (yellow fruit) in surface pitting, ACC oxidase activity, or ACC concentration (Tables 1 and 2). 'Bison' CO_2 production was 3.2 $ml\cdot kg^{-1}\cdot h^{-1}$ (SE = 0.88) lower in ripe red fruit than in MG fruit, but for 'Doria' it was 1.7 $ml\cdot kg^{-1}\cdot h^{-1}$ higher in ripe yellow fruit (significant cultivar × ripeness interaction). The effect of storage temperature on C_2H_4 production, which was measured after 2 h in a sealed container, differed in the two cultivars (significant interaction). For the fruit harvested in June and July, 'Bison' C_2H_4 production was 269 $nl\cdot kg^{-1}\cdot h^{-1}$ (SE = 67) lower after storage at 13C than after storage at 1C when measured at 20C, while for 'Doria', the difference was 558 $nl\cdot kg^{-1}\cdot h^{-1}$. In the fruit harvested in August, the differences were 213 and 79 $nl\cdot kg^{-1}\cdot h^{-1}$ (SE = 30) respectively. At the 6 Aug. harvest, C_2H_4 production was similar in the two cultivars; but, in fruit harvested 27 Aug., C_2H_4 production was 55 $nl\cdot kg^{-1}\cdot h^{-1}$ (SE = 35) higher in 'Bison' and 79 $nl\cdot kg^{-1}\cdot h^{-1}$ lower in 'Doria' than fruit harvested on 6 Aug. (significant cultivar × harvest date interaction).

Discussion

Ripening. When greenhouse-grown bell peppers ripened from MG to yellow or red, there was no change in CO_2 and a decrease in C_2H_4 production. The decrease in C_2H_4 production probably resulted from the reduced ACC oxidase activity, since there was no change in ACC concentration (Table 1). The patterns of CO_2 and C_2H_4 production are in contrast to those of Saltveit (1977), who showed that internal CO_2 and C_2H_4 concentrations increased during ripening of harvested bell peppers. This difference may be due to the fact that the fruit ripened on the plants in this study but ripened after harvest in Saltveit's study. The increase in the internal CO_2 and C_2H_4 concentrations was greater than the increase in CO_2 and C_2H_4 production (Table 2).

Pitting occurred in MG peppers stored at 1C for as little as 3 days and increased in severity during 2 weeks of storage (Tables 1 and 2). Similar levels of chilling sensitivity have been reported for bell peppers (Miller and Risse, 1986; Wang and Baker, 1979). Ripe peppers showed no CI (Table 1). The observed difference in CI between MG and ripe peppers was similar to the decrease in CI of tomatoes with increasing maturity (Autio and Bramlage, 1986). This finding is of practical importance since it seems that ripe greenhouse-grown peppers can be stored for a few weeks at lower temperatures than the 7 to 13C recommended for MG fruit (Hardenburg et al., 1986).

Pitting after chilling is intensified by increased water loss in low vs. high RH (Morris and Platenius, 1939). Elevated water loss was associated with severe pitting in a separate experiment in which the effect of the number of film perforations in storage bags was tested (unpublished data).

Table 1. Effects of ripeness stage[z], storage temperature, and storage time on percentage surface pitting, CO_2 and C_2H_4 production, ACC oxidase activity, and ACC concentration of greenhouse-grown peppers.

Storage temperature (°C)	Storage time (wk)	Surface pitting (%)	CO_2 production ($ml\cdot kg^{-1}\cdot h^{-1}$)	C_2H_4 production ($nl\cdot kg^{-1}\cdot h^{-1}$)	ACC oxidase ($nl\cdot kg^{-1}\cdot h^{-1}$)	ACC ($nmol\cdot g^{-1}$) (fresh equiv.)
			Mature-green fruit			
Fresh harvest	0	0	19.7	60	636	0.0094
13	1	0	8.0	65	298	0.0283
13	2	0	6.5	73	328	0.0156
1	1	57	18.3	1085	201	0.0275
1	2	60	17.7	610	167	0.0572
			Ripe fruit			
Fresh harvest	0	0	18.7	39	279	0.0141
13	1	0	10.6	43	107	0.0324
13	2	0	10.5	43	71	0.0170
1	1	0	15.1	264	88	0.0334
1	2	0	15.2	296	59	0.0509
Relative SE		4.0	0.95[y]	0.256	456	0.194
Significance						
Cultivar		NS	NS	NS	NS	NS
Harvest		**	**	**	***	NS
Ripening (R)		***	NS	*	**	NS
Temperature (T)		***	***	***	NS	***
Storage time (D)		***	NS	NS	NS	NS
R × T		***	***	NS	NS	NS
T × D		NS	NS	NS	NS	***
R × D		***	NS	NS	NS	NS
R × T × D		NS	NS	NS	NS	NS

[z]Mature-green, >95% of surface green; ripe, >95% of surface red or yellow.

[y]SE for CO_2 production

ns,*,**,***Nonsignificant or significant at $P \leq 0.05, 0.01, 0.001$ respectively.

Table 2. Effect of storage temperature and time on percentage surface pitting, CO_2 and C_2H_4 production, and internal CO_2 and C_2H_4 concentrations of mature-green peppers.

Storage temperature (°C)	Storage time (day)	Pitting (%)	CO_2 production ($ml\cdot kg^{-1}\cdot h^{-1}$)	C_2H_4 production ($nl\cdot kg^{-1}\cdot h^{-1}$)	CO_2 internal (%)	C_2H_4 internal (ppb)
Fresh harvest	0	0	22.8	61	3.27	44
13	1	0	13.6	56	2.89	44
	3	0	11.5	146	2.59	145
	7	0	5.7	46	1.09	65
1	1	0	13.0	80	3.22	158
	3	29	16.2	298	3.97	2118
	7	50	12.3	299	4.47	2659
SE		7.7	0.50	0.1[z]	0.183	0.2
Significance						
Cultivar		NS	*	NS	NS	NS
Temperature (T)		**	***	***	***	**
Storage time (D)		*	***	**	NS	**
T × D		NS	**	*	**	**

[z]Relative SE for C_2H_4.

NS,*,**,***Nonsignificant or significant at $P \leq 0.05, 0.01, 0.001$, respectively.

Water loss was negatively associated with pitting and the likely degree of waxiness of the surface of zucchini squash (Mencarelli et al., 1983). The ground spot that likely had lower wax content than the upper part of the zucchini squash developed more severe CI than the top. In contrast, wrapping MG peppers in plastic films (a treatment that should have reduced water loss) did not reduce CI (Miller and Risse, 1986). Our preliminary study with MG peppers showed that pitting occurred at 1 but not 13C, while water loss was similar at the two temperatures; 1.5% and 1.3%, respectively. Ripe and MG fruit had similar water loss during 12 days at 1C (1.5% and 1.3%, respectively), while pitting was absent in ripe fruit and 15% in MG fruit. The ripe and MG greenhouse-grown peppers used in our study may have differed in the quantity and characteristics of cuticular wax (Martin and Juniper, 1970). However, wax content was not examined. The interaction among cuticular wax characteristics, resistance to water loss, degree of water loss, and extent of pitting in peppers warrants further study.

While a sharp increase in CO_2 production has been observed after bell peppers were transferred from 1 to 18C (Kozukue and Ogata, 1972), increased CO_2 production may not be associated with CI (Tables 1 and 2). Peppers subjected to 1C maintained similar CO_2 production regardless of whether CI developed (MG fruit) or not (ripe fruit). Fruit aging during storage was not responsible for the increased CO_2 production, since CO_2 production decreased in MG and ripe fruit stored at 13C. Therefore, the increased CO_2 production from greenhouse-grown peppers exposed to 1C apparently is a physiological response of exposure to 1C rather than a response related to CI development.

The elevated (18x) C_2H_4 production could be used as a sensitive indicator of exposure to chilling temperature in peppers (Table 1). This stimulation of C_2H_4 production is similar to the response observed in other tropical plant species (Tong and Yang, 1987) such as papayas (Chan et al., 1985) and cucumbers (Wang and Adams, 1982). Stimulation of C_2H_4 production is not unique for chilling-injured MG peppers, since 1C storage also stimulated C_2H_4 production (7x) in ripe fruit without CI development (Table 1). The chilling-induced increase in C_2H_4 production without a concomitant increase in pitting indicated that C_2H_4 may not play any role in CI symptom development in peppers. Similar results were observed in other chilling-sensitive crops (Tong and Yang, 1987).

CI in MG peppers was accompanied by elevated ACC concentration after 2 weeks of storage (Table 1). ACC is the only biological substrate for ACC oxidase (Yang and Hoffman, 1984). Most plant tissues are capable of metabolizing ACC to 1-(malonylamino) cyclopropane-1-carboxylic acid (MACC); but, under normal physiological conditions, MACC, the conjugated product, is a biologically inactive end product and is not converted to C_2H_4 (Jiao et al., 1986). The accumulation of ACC upon transfer from chilling to nonchilling temperatures also was observed in cucumbers (Wang and Adams, 1982). Ripe peppers at 1C showed a similar enhancement of ACC concentration without CI development. Therefore, a chilling-induced increase in ACC concentration is another chilling response that does not seem to be involved in pitting.

CI in MG peppers was associated with reduced ACC oxidase activity (Table 1). This reduced ACC oxidase activity is similar to that observed in cucumbers (Cabrera and Saltveit, 1990). MG peppers stored at 13C, however, showed similar low ACC oxidase activity as chilled fruit. Reduced ACC oxidase activity may be a characteristic of MG and ripe peppers, since stored ripe fruit also had reduced (0.3x) ACC oxidase activity.

Production of C_2H_4 did not correlate with ACC concentration (r = 0.32, P = 0.05, n = 36) or ACC oxidase activity [r = (-0.15), P = 0.38, n = 33]. These results are similar to those observed for cucumbers (Cabrera and Saltveit, 1990).

Cultivar. There was no cultivar × temperature interaction in CI development. MG fruit of 'Bison' and 'Doria' developed CI at 1C, while CI did not develop in ripe fruit of either cultivar. On the contrary, there was a cultivar × temperature interaction in C_2H_4 production. Ethylene production by 'Bison' fruit exposed to 1C was 2.5 times that of fruit exposed to 13C, while the corresponding increase for 'Doria' fruit was 13.6x. These differences in cultivar responses to temperature treatment in CI and C_2H_4 production again support the hypothesis that C_2H_4 production plays no direct role in CI of peppers.

Conclusion

The susceptibility of greenhouse-grown peppers to CI depends on their degree of ripeness. Pitting occurred only in MG fruit that were stored at 1C for 3 days or longer. Fully ripe peppers were not susceptible to CI when they were stored at 1C for up to 2 weeks. These ripe peppers showed no pitting after being returned to room temperature for an additional week. These observations suggest that ripe greenhouse-grown peppers could be handled commercially at much lower temperatures than those recommended for MG peppers. However, the minimum temperature at which they could be held and the maximum duration of storage without CI in ripe greenhouse-grown peppers require further investigation.

Previous studies have suggested that there was a connection between the increased CO_2 and C_2H_4 production after exposure to chilling conditions and CI symptom development. By using two ripeness stages of peppers that have different sensitivities to the development of CI symptoms, we have shown that chilling-induced increases in CO_2 and C_2H_4 production are not involved directly in CI symptom development. While our data support the use of enhanced CO_2 and C_2H_4 production to indicate that chilling-sensitive tissue has been exposed to chilling temperatures, it shows that enhanced production of these gases may not be a reliable indicator of CI symptom development.

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