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The effect of season on the growth and maturation of bell peppers

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Abstract

Bell peppers grown in greenhouses in the Mediterranean region are frequently subjected to high temperatures in summer and low temperatures in winter. The present experiment was designed to quantify the effect of season on pepper fruit growth, maturation and ripening. Three bell pepper (*Capsicum annuum* L.) cultivars (Yolo Wonder, California Wonder and E84066) were cultivated in an unheated greenhouse during summer and autumn. Fruit size, fresh weight and volume were higher in the autumn due to increased fruit length and pericarp weight. However, colour transition from green to red was significantly delayed in the autumn and the vitamin C concentration was also lower than in the summer. Similarly, the internal C_2H_4 concentration was lower at the mature red stage of the autumn-grown fruit than in the summer, whereas the respiration rate and the internal CO_2 concentration did not differ. Irrespective of season, the internal C_2H_4 and CO_2 concentrations correlated with the number of seeds per fruit, suggesting that seed metabolism significantly influenced the internal atmosphere of the fruit. Additionally, the number of seeds per fruit in the autumn correlated with fresh fruit weight and volume, but not in the summer. In conclusion, bell pepper fruits produced in the autumn were larger in size, but lower in nutritional value (less vitamin C), while the effects of growth season on the pepper fruit morphology and physiology closely related to the number of seeds per fruit in autumn, but to a less extent in summer.

Keywords: *Capsicum annuum*; Fruit ripening; Vitamin C; Respiration; Ethylene; Seeds.

Introduction

The growth and size of bell (sweet) pepper (*Capsicum annuum* L.) fruits are affected by air temperature, daylight and relative humidity (RH) during anthesis, fruit set, development and maturation, as well as by plant growth (Jovicich et al., 2004) and morphology, e.g. leaf shape (Schoch, 1972), plant nutrition (Del Amor, 2007) and agricultural practices (Perez-Lopez et al., 2007) and by competition between fruits that are developing simultaneously on the plant (Ali and Kelly, 1992). Within greenhouse crops cultivated in unheated greenhouses in the Mediterranean region, air temperatures and humidity fluctuate significantly with season. In the summer plants are frequently subjected to high temperatures and low humidity, whereas in the autumn humidity is high but temperatures may be very low (Khah and Passam, 1992; Karapanos et al., 2008).

Fruit size correlates positively with the number of seeds per fruit (Rylski, 1973; Khah and Passam, 1992), but mainly when the number of seeds is relatively small (Bakker, 1989). Plant density and competition between fruits growing simultaneously on the plant are also key factors affecting pepper yield (Marcelis and Baan Hofman-Eijer, 1997; Miccolis et al., 1999; Nasto et al., 2009; Islam et al., 2011). Harvest at the green stage (about 25 days from fruit set) increases the total yield of plants compared with harvest at full maturity.

At temperatures below 10 ^{o}C fruit size decreases due to inefficient pollination and fertilization (Shaked et al., 2004), which causes a reduction in fruit length (Aloni et al., 1999) and possible fruit malformation (Rylski and Aloni, 1994). However, at a day temperature of 24 ^{o}C, pollen viability and fruit set are higher at 15 ^{o}C than at 18-24 ^{o}C during the night (Rylski and Spigelman, 1982).

Under short day length, the provision of light increases plant growth and yield (Deli and Tiessen, 1969), whereas in the case of intense sunlight, shading increases leaf dimensions, plant dry matter content and fruit growth (Rylski and Spigelman, 1986; Schoch, 1972). On the other hand, relative humidity (RH) mainly affects fruit set and not fruit growth (Bakker, 1989).

The aim of the present study was to analyze the influence of growth season (summer or autumn) on the fruit development and maturation of bell pepper with reference to the number of seeds per fruit.

Materials and Methods

Thirty plants each of 3 bell pepper (*Capsicum annuum* L.) cultivars (California Wonder and Yolo Wonder [Agricultural House Spyrou, Greece] and E84066 [Enza-Zaden, Holland]) were grown in an unheated greenhouse during summer and autumn at the experimental field of the Laboratory of Vegetable Production of the Agricultural University of Athens between March and December. Mean day temperatures ranged from 28.5-34.0 ^oC during the summer crop and from 9.9-19.3 ^oC in the autumn. The plants were placed in double rows at a density of 2 plants m^{-2}. To encourage plant growth, the first 3 flowers were removed and 3 branches per plant were allowed to develop. Eight fruits were permitted to set on each plant. Flowers were tagged at anthesis and fruits were harvested every 10 days starting from the 20^{th} day after fruit set. Harvesting took place from 10 July until 12 September (summer crop, SC) and from 27 September until 19 December (autumn crop, AC) and continued until the full-red stage, which occurred 70 and 80 days after fruit set in treatments SC and AC, respectively. After the harvest of each fruit, a new flower was allowed to set fruit in order to maintain a constant number of fruits per plant.

Harvest took place in the early morning. The fruits were harvested together with the pedicel (1-2 cm) and immediately transferred to the laboratory. The following measurements were made on 10 randomly selected fruits for each harvest date: fruit dimensions (length and maximum diameter), fresh weight of the whole fruit and the pericarp, total fruit volume (water displacement method) and the volume of the internal fruit cavity (by measuring of the volume of water required to fill the cavity), the percent dry matter content of the fruit (by weighing before and after drying to constant weight at 70±2 ^oC), fruit colour, the rate of respiration and ethylene (C_2H_4) synthesis by the whole fruit and the concentration of CO_2 and ethylene within the internal fruit cavity.

Fruit colour was measured with a Minolta CR-300 chroma-meter (Minolta Co. Ltd, Osaka, Japan). Colour changes during fruit maturation were assessed by the values L^* (lightness) and a^* (which changed from a negative to positive value as the fruit ripened from green to red).

The respiration rate of fruit was measured by placing fruits individually in a sealed glass container (750 ml) connected via a closed circuit to an IR-chromatograph (Li-6252 CO_2 Analyzer, Li-Cor, Lincoln, Nebraska

USA). The air flow through the analyser was 2 l min^{-1} and the respiration rate was calculated from the volume of CO_2 recorded during incubation for 6-7 minutes at 22 ^oC. The concentrations of CO_2 and C_2H_4 within the internal fruit cavity were measured by withdrawing 1 ml air from the fruit cavity with an air-tight micro-syringe and injecting into a gas analyzer (Perkin-Elmer, model Sigma 8310B) incorporating a flame ionization detector (FID) for the measurement of C_2H_4, a thermal conductivity detector (TCD) for the measurement of CO_2 and an injector (1041 Universal, large bore capillary) for the direct insertion of the sample into the packed column (Porapak R 106-120, 100-120 mesh, length 100 cm) with a detection limit of about 10 nl l^{-1}. The carrier gas was N_2 with a flow rate of 45 ml min^{-1}. The temperature in the injection chamber was 60 ^oC, in the detector 100 ^oC and around the column 50 ^oC.

In order to measure the rate of C_2H_4 synthesis, individual fruits were placed in airtight containers (440 ml) and after incubation at 22 ^oC for 1 h, 1 ml was withdrawn through an airtight seal in the container by a micro-syringe and injected into the chromatograph according to the method described above.

Data were subjected to analysis of variance (ANOVA) and the means were compared using the least significant difference test at P=0.05.

Results

Fruit size and dimensions

The mean fruit weight of Yolo Wonder (which produces smaller fruit than the other two cultivars grown in the present experiment) was unaffected by season (SC and AC), whereas in California Wonder and E84066 the mean fruit weight was higher in the autumn (AC) than in the summer (SC) (Table 1). The relatively higher fruit weights of California Wonder and E84066 during the autumn apparently resulted from an increase in fresh weight of the pericarp, since the percent contribution of the pericarp to the total fruit weight increased, although the percentage of fruit dry matter was lower in this season. In Yolo Wonder no difference in the percent contribution of the pericarp to total fruit weight or in the fruit dry matter content was observed between seasons (Table 1).

The total fruit volume of Yolo Wonder was similar in both seasons, whereas in California Wonder and E84066 total fruit volume in the autumn increased by 31 and 60%, respectively (Table 1). However, irrespective of the total fruit volume, the volume of the internal fruit cavity in relation to the total fruit volume was 40-50% in all cultivars and both seasons.

Measurements of fruit length and diameter showed that the differences in total fruit volume were mainly due to variation in fruit length, whereas fruit diameter was constant for each cultivar, irrespective of cultivar and season (Table 1).

Table 1. Fruit characteristics of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) harvested at the full ripe stage in relation to the cultivation season.

Fruit characteristic	Yolo Wonder		California Wonder		E84066	
	SC	AC	SC	AC	SC	AC
Fresh weight (g)	45.26[a]	49.60[a]	88.41[a]	129.46[b]	78.51[a]	129.87[b]
Fruit weight due to the peri carp (%)	82.10[a]	85.80[a]	81.79[a]	88.68[b]	82.57[a]	86.23[b]
Dry matter (%)	10.00[a]	9.95[a]	9.07[b]	6.22[a]	11.04[b]	8.95[a]
Volume (ml)	83.17[a]	85.67[a]	179.60[a]	235.00[b]	151.40[a]	242.00[b]
Volume of internal cavity in relation to fruit volume (%)	49.10[a]	40.30[a]	47.69[a]	48.08[a]	48.80[a]	46.17[a]
Length (cm)	7.03[a]	7.90[b]	7.88[a]	9.20[b]	6.62[a]	9.46[b]
Diameter (cm)	5.03[a]	4.72[a]	6.72[a]	6.76[a]	6.45[a]	6.60[a]
Number of seeds fruit^{-1} ±S.D.	139.6±56.6	142.8±61.6	198.0±86.9	294.0±80.7	165.9±83.5	256.1±113.4

Notes: Values are the means of 10 fruits. Within each row, the means for each cultivar followed by the same letter do not differ significantly (P=0.05).

Fruit colour and vitamin C content

During maturation and ripening in both seasons, the fruits of California Wonder and E84066 progressively darkened in colour, as indicated by the decrease in L (lightness) value. In contrast, the fruits of Yolo Wonder exhibited a progressive darkening of colour during the summer, but not during the autumn (Table 2). In Yolo Wonder and California Wonder at the green stage (20-30 days after fruit set), the value of L was significantly higher in the summer than in the autumn, whereas at the red ripe stage (60-80 days after fruit set) L was higher in the autumn-grown fruit of all cultivars.

Table 2. The value of L (lightness) of fruits of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) harvested at different days after fruit set and in relation to the cultivation season.

Days after fruit set	Yolo Wonder		California Wonder		E84066	
	SC	AC	SC	AC	SC	AC
20	43.03[c*]	38.93[a*]	44.64[c]	43.07[d]	45.01[d]	43.12[d]
30	42.23[c*]	37.99[a*]	45.26[bc*]	40.77[c*]	43.15[c]	41.89[cd]
40	37.69[b]	37.42[a]	42.33[b]	40.50[c]	40.42[b]	41.61[c]
50	35.33[a*]	38.73[a*]	38.38[a*]	40.31[bc*]	39.05[b]	39.71[b]
60	35.56[a*]	38.73[a*]	36.86[a*]	39.03[ab*]	36.01[a*]	38.63[ab*]
70	35.70[a*]	39.78[a*]	36.51[a*]	38.27[a*]	35.02[a*]	38.21[ab*]
80		38.46[a]		38.27[a]		37.59[a]

Notes: Values are the means of 10 fruits. Within each column, means followed by the same letter do not differ significantly (P=0.05). Statistically significant differences (P=0.05) between treatments SC and AC for each cultivar separately are indicated by an asterisk (*).

The colour transition from green to red is indicated by the change in a^* from a negative (green) to positive (red) value. In the summer, this transition occurred at 38, 41 and 42 days after fruit set in Yolo Wonder, California Wonder and E84066, respectively compared to 62, 70 and 66 days respectively after fruit set in the autumn, i.e. in the autumn the colour change associated with fruit maturation and ripening was delayed by 24-29 days compared to that in the summer (Figure 1). Moreover, by day 80 in the autumn the intensity of red coloration of California Wonder and E84066 was still lower than that of the summer grown fruit on days 50-70.

The vitamin C (L-ascorbic acid) content of the fruits of California Wonder was higher in the summer than those in the autumn, irrespective of the stage of fruit maturation and ripening (Figure 2). In cv. Yolo Wonder and E84066, the vitamin C concentration of fruits was initially the same in both seasons (20 days after fruit set), but as fruits matured and ripened, the vitamin C content was significantly higher in the summer than in the autumn.

Respiration rate, CO_2 and C_2H_4 concentrations within the fruit

The respiration rate of fruit decreased during development and maturation and was lowest at the mature red stage irrespective of cultivar and season. In California Wonder, the respiration rate of the green fruit (20-40 days after fruit set) was higher in the summer than in the autumn, whereas in E84066 respiration was higher in the red fruit during the summer (Figure 3).

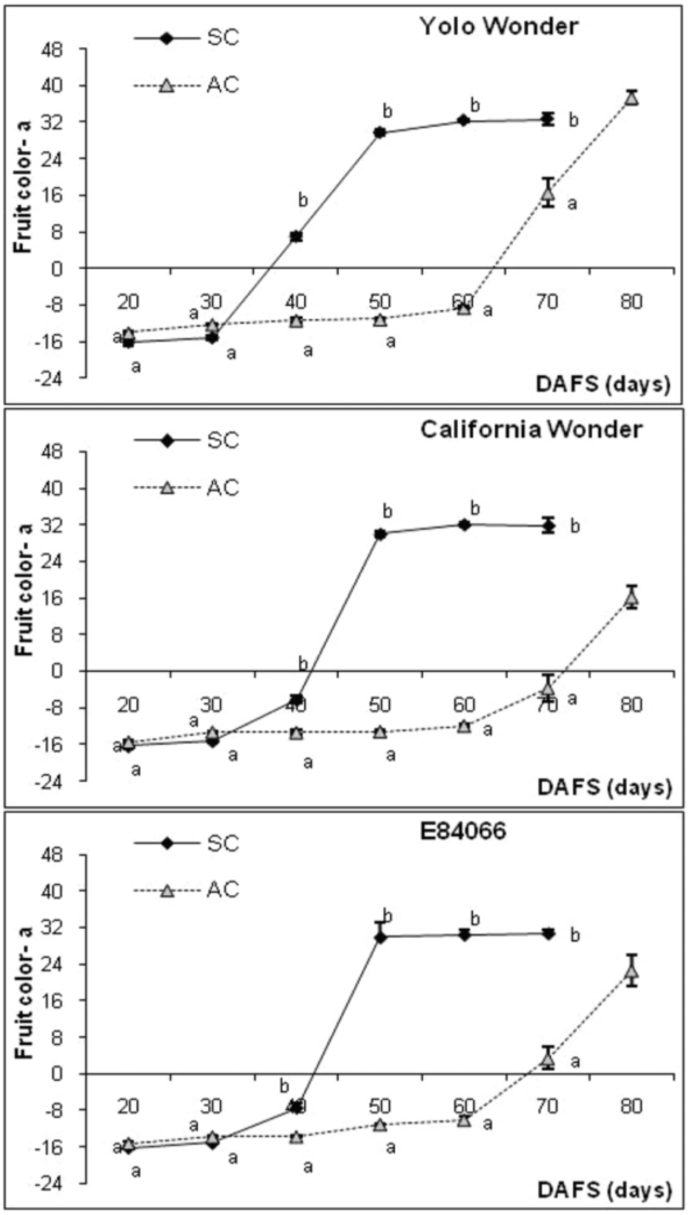

Figure 1. The change in colour (a^*) from green (negative values) to red (positive values) of fruit of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) during maturation and ripening in relation to the season of cultivation. Values are the means of 10 fruits ± s.e. The means for each cultivar accompanied by the same letter do not differ significantly (P=0.05).

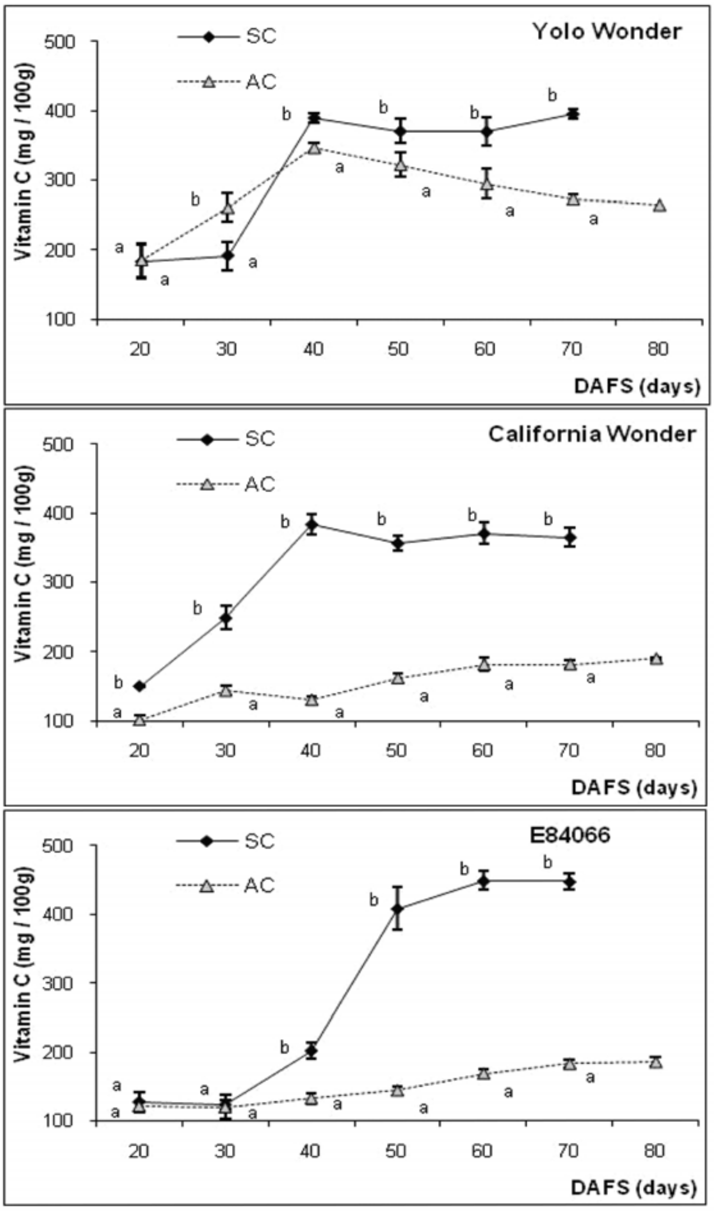

Figure 2. The concentration of vitamin C (L-ascorbic acid) in the fruits of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) during maturation and ripening in relation to the season of cultivation. Values are the means of 10 fruits ± s.e. The means for each cultivar accompanied by the same letter do not differ significantly (P=0.05).

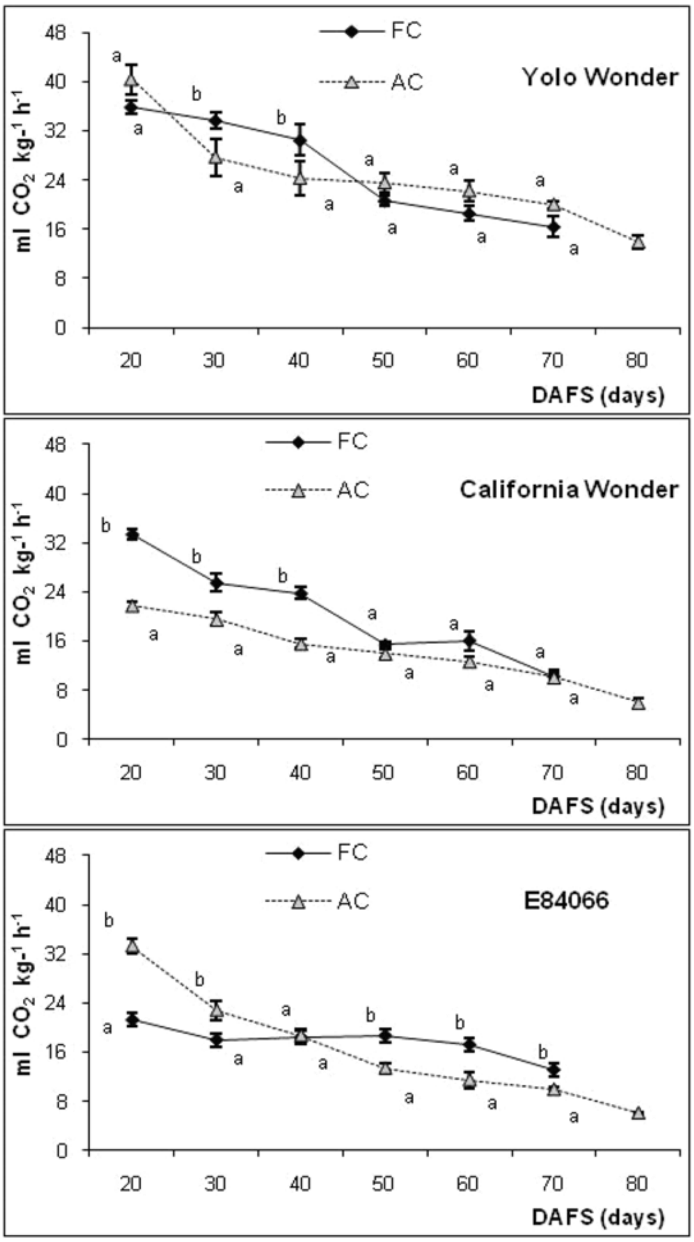

Figure 3. The respiration rate (ml CO_2 kg^{-1} h^{-1}) of the fruits of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) during growth and maturation in relation to the season of cultivation. Values are the means of 10 fruits ± s.e. The means for each cultivar accompanied by the same letter do not differ significantly (P=0.05).

The concentrations of CO_2 within the internal cavity of fruits of Yolo Wonder and E84066 were unaffected by season. In contrast, the CO_2 concentration within the central cavity of the fruits of California Wonder was higher in the autumn than in the summer up to 40 days after fruit set (Figure 4). Overall, at the red ripe stage, the concentration ranged between 12-14 ml CO_2 kg^{-1} for the fruits irrespective of season.

Ethylene synthesis by the whole fruit (measured externally) was lower than the detection level of the method used in the present experiment. However, in all the cultivars, the concentration of C_2H_4 within the internal cavity increased during fruit development and maturation. The highest concentration of C_2H_4 was recorded at the red ripe stage and in all the cultivars was lower in the autumn than in the summer (Figure 5).

The concentrations of CO_2 and C_2H_4 within the internal fruit cavity correlated with the number of seeds per fruit in all the cultivars, irrespective of season. Additionally, in all the cultivars, fruit volume and fresh weight correlated with the number of seeds per fruit in the autumn, but not in the summer (Table 3). This may have been due to the fact that despite large variation, the number of seeds per fruit (especially in California Wonder and E84066) tended to be higher in the autumn than in the summer (Table 1). In contrast, the rate of respiration correlated with the number of seeds per fruit only in the autumn (Yolo Wonder and E84066) or only in the summer (California Wonder) (Table 3).

Table 3. Correlation between the number of seeds and the fresh weight and volume of the fruit, the respiration rate and the CO_2 and C_2H_4 concentrations within the internal fruit cavity of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) harvested at the full ripe stage.

Fruit characteristic in relation to seed number	Yolo Wonder		California Wonder		E84066	
	SC	AC	SC	AC	SC	AC
Fresh weight	ns	*	ns	*	ns	*
Fruit volume	ns	*	ns	*	ns	*
Respiration rate	ns	*	*	ns	ns	*
Concentration of CO_2 in the internal cavity	*	*	*	*	*	*
Concentration of C_2H_4 in the internal cavity	*	*	*	*	*	*

Notes: Values are the means of 10 fruits. A positive correlation is indicated by an asterisk (*) and the lack of correlation by no significance (ns) according to the t-test (P=0.05).

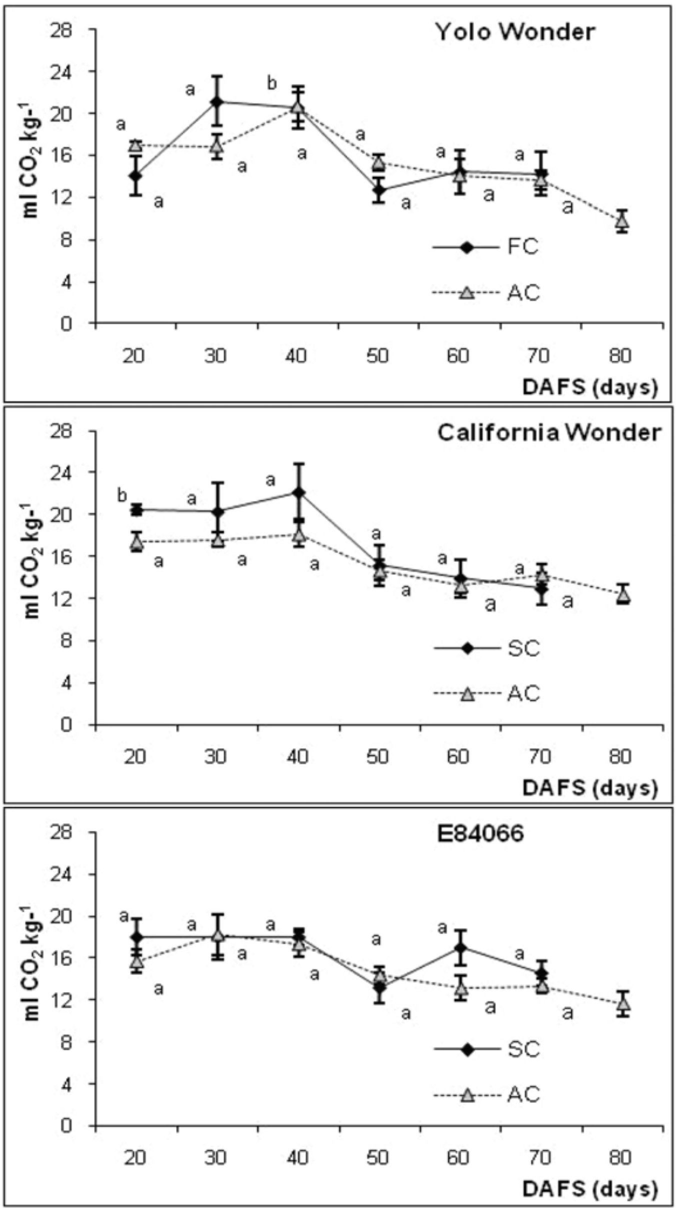

Figure 4. The change in CO_2 concentration (ml CO_2 kg^{-1}) within the central cavity of the fruits of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) during growth and maturation in relation to the season of cultivation. Values are the means of 10 fruits ± s.e. The means for each cultivar accompanied by the same letter do not differ significantly (P=0.05).

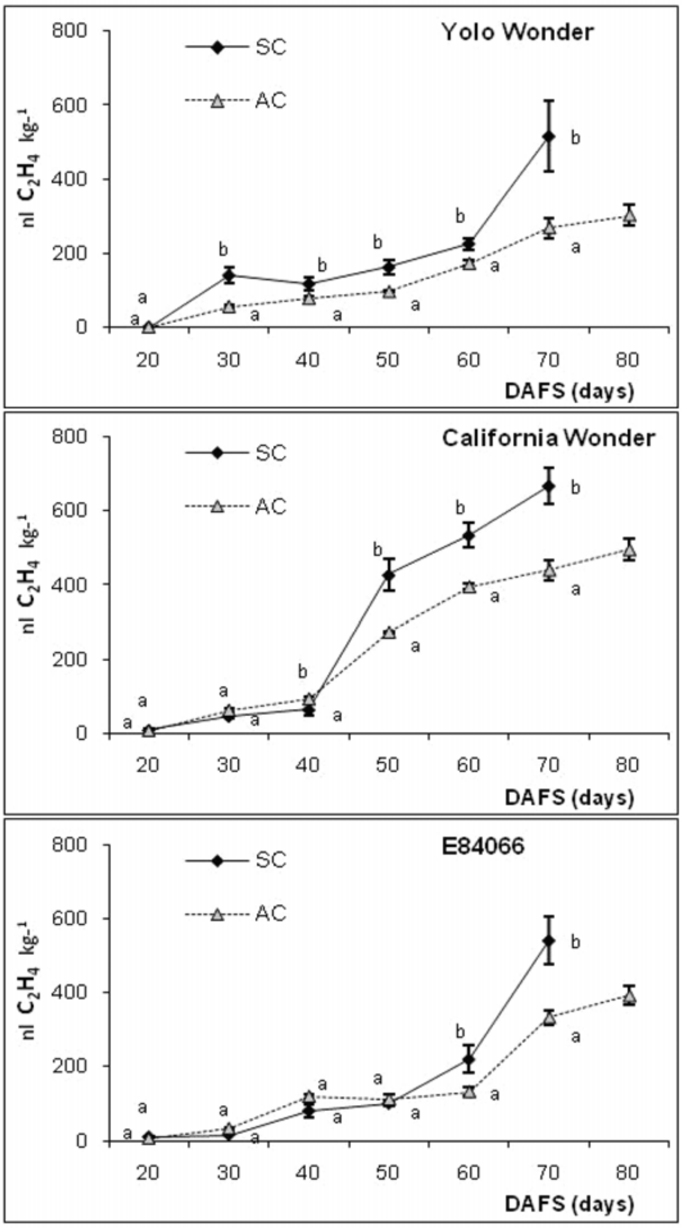

Figure 5. The concentration of ethylene (nl C_2H_4 kg^{-1}) within the central cavity of fruits of 3 bell pepper cultivars (Yolo Wonder, California Wonder and E84066) during growth and maturation in relation to the season of cultivation. Values are the means of 10 fruits ± s.e. The means for each cultivar accompanied by the same letter do not differ significantly (P=0.05).

Discussion

Fruit growth and maturation involves several morphological and physiological attributes, including an increase in fruit volume and fresh weight, changes in pericarp colour, nutrient composition (e.g. vitamin C/L-ascorbic acid), respiration rate and the concentrations of C_2H_4 and CO_2 within the internal cavity of the fruit. According to the present findings, all these parameters were affected to a certain extent by the season of cultivation (summer or autumn).

Differences between growing seasons (summer and autumn) led to an increase in fruit size (fresh weight and volume) in the autumn, which resulted from an increase in fruit length and pericarp weight. However, the colour transition from green to red was significantly delayed in the autumn (AC) and the vitamin C concentration was greatly reduced compared to the corresponding fruit in the summer (SC). Similarly, the internal C_2H_4 concentration at the mature red stage was lower in fruit grown in the autumn (AC) than those grown in the summer (SC), but the respiration rate and internal CO_2 concentrations did not differ. In other crops, e.g. sugar beet, the growing season has been shown to significantly affect yield and composition, largely by its influence on leaf chlorophyll (Tsialtas and Maslaris, 2008a; Tsialtas and Maslaris, 2008b).

Irrespective of growing season, the internal C_2H_4 and CO_2 concentrations correlated with the number of seeds per fruit, suggesting that seed metabolism significantly influences the internal atmosphere of the fruit. Additionally, the number of seeds per fruit in the autumn crop correlated with fresh fruit weight and volume, but no such correlation was observed in the summer crop. These differences in correlation between seasons may reflect the difference in seed number per fruit (Rylski, 1973; Khah and Passam, 1992). Bakker (1989) indicated that seed number correlated with fruit size more when the number of seeds per fruit was relatively low since inter-fruit competition increased in the case of fruits with many seeds. In the present experiment, seed number was relatively higher in the autumn, but since only 8 fruits were allowed to develop on each plant, the effect of inter-fruit competition was reduced; hence the correlation between fruit size and seed number was more apparent. In the summer, fruits have a lower number of seeds per fruit than in the autumn because pollination and fertilization are restricted by the high temperatures and low relative humidity within the greenhouse at that time (Khah and Passam, 1992), whereas the higher humidity of the autumn favours fertilization (Bakker, 1989).

The delay in maturation, especially in the autumn (reflected by the delay in colour transition), meant that fruit had to be retained for a greater length of time on the mother plant if they were to be harvested at the red ripe stage. Under commercial conditions, this means an increase in inter-fruit competition and a possible reduction in yield. It may, therefore, be preferable to harvest fruit during this season at an immature (green) stage. Peppers are non-climacteric (Villavicencio et al., 1999), as indicated also by the low concentrations of C_2H_4 throughout maturation and the lack of a respiratory climacteric in this experiment. As reported for chili peppers by Biles et al. (1993), there is a progressive decrease in respiration with maturation and, because peppers do not ripen after harvest, they must be harvested at the desired stage of ripening. Another disadvantage with the autumn crop is the reduction in vitamin C concentration. Vitamin C is a powerful anti-oxidant and a reduction in the concentration of this compound represents a loss in nutritional value of the fruit. Although the internal concentration of CO_2 correlates with the number of seeds per fruit and tends to be higher at the early stages of fruit development, it seems that the respiration of the whole fruit (assessed by CO_2 evolution into the storage environment) results mainly from the respiratory activity of the pericarp, since it does not correlate with the seed number. There may also be a permeability barrier to the release of CO_2 from the internal cavity to the external environment via the pericarp, since previous work has shown that transpiration is largely mediated through the calyx (Bower et al., 2000; Diaz-Perez et al., 2007). The high initial concentration of CO_2 within the internal cavity of the fruit probably results from the intense metabolic activity of the developing seeds (Blasiak et al., 2006). Subsequently, seeds mature and may enter dormancy, resulting in a concomitant reduction in seed respiration and, therefore, a reduction of CO_2 within the internal fruit cavity.

Although the concentration of C_2H_4 within the internal cavity increased throughout fruit growth and maturation (Lurie et al., 1986; Biles et al., 1993; Villavicencio et al., 1999), the final concentration of C_2H_4 was lower than that required to induce autocatalytic C_2H_4 synthesis in climacteric fruit (Lurie et al., 1986). Villavicencio et al. (2001) reported an increase of C_2H_4 concentration within the fruit cavity of bell and Tabasco peppers until the appearance of fruit colour, followed by a reduction and finally a second increase until full ripeness. The respiration rate of these fruit showed a similar change during fruit growth and maturation, but at full ripeness the respiration rate was reduced. In general, however, as reported here too, pepper fruits of the bell-type are non-climacteric (Howard and Yamaguchi, 1957; Saltveit, 1997).

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