

Parthenocarpic Fruit Growth Reduces Yield Fluctuation and Blossom-end Rot in Sweet Pepper

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The aim of this work was to investigate whether parthenocarpic fruit growth could avoid flushing, i.e. an irregular yield pattern, in sweet pepper. Plants were grown in a greenhouse compartment from April until August. Half of the plants were grown without a fruit set treatment (control), whereas parthenocarpic fruits were allowed to develop on the other plants by preventing self-pollination and applying auxin to the stigma. For node positions 3 to 17, fruit set per node varied between 21 and 55 % for control plants [coefficient of variation (CV) = 11 %], whereas auxin-treated plants showed much less variation in fruit set (41–57 %; CV = 5 %) and average fruit set was higher. In agreement with fruit set, fruit yield was also much more regular in the auxin-treated plants. Fruit fresh yield varied between 0.2 and 1.0 kg m⁻² for control plants (CV = 20 %), and between 0.4 and 0.8 kg m⁻² for auxin-treated plants (CV = 9 %). Results showed that developing seeds in sweet pepper fruits are the main cause of the abortion of new flowers, and irregular fruit set and yield. Parthenocarpic fruit growth resulted in flatter, 30 % smaller fruits, because of a reduction in fruit growth rate; the duration of fruit growth was 1 week longer than for fruits from control plants. Parthenocarpic fruits were hardly affected by blossom-end rot (BER) with only 1 % of fruits being affected compared to 31 % in the control. Total dry mass production was the same for treated and control plants; however, in auxin-treated plants, 50 % of the total dry mass was allocated to the fruits, compared to 58 % in control plants. © 2001 Annals of Botany Company

Key words: Abortion, auxin, BER, blossom-end rot, *Capsicum annum* L., flushing, fruit set, irregular yield pattern, parthenocarpic, sweet pepper.

INTRODUCTION

Peppers are grown in most countries of the world, with The Netherlands being the world leader in intensive greenhouse sweet pepper production (Bosland and Votava, 1999). Sweet peppers are planted in greenhouses in December, fruit production starts in March and the same crop continues to produce fruit until November, yielding about 10 kg of fruit per plant. An important problem in sweet pepper production is 'flushing': weeks with high yields are alternated by weeks with low yield. This irregular harvest pattern makes it difficult for growers to meet regular weekly demands. As this cyclic production pattern is more or less the same for all growers, it results in weeks with a high market supply and low prices alternating with weeks with a low market supply and high prices. Flushing also results in strong fluctuations in labour demand in the greenhouses. Hence, avoiding an irregular pattern of sweet pepper production is of great economic importance.

Marcelis and Baan Hofman-Eijer (1997) suggested that cyclic fluctuations in sweet pepper fruit production during a growing season can, to a large extent, be explained by cyclic fluctuations in fruit set. Several fruits set at more or less the same time. The presence of these developing fruits inhibits subsequent set and growth of new fruits both by

competition for limited assimilates as well as by dominance due to the production of plant growth regulators (Marcelis and Baan Hofman-Eijer, 1997). Flowers initiated on the plant in this phase will generally abort. Only when the early-formed fruits are almost full-grown and their sink strength (competitive ability to attract assimilates) is low can new fruit set occur. Hence, on a sweet pepper stem, a group of nodes with fruits is followed by a group of nodes without fruits, explaining the periods of high and low yields. In cucumber (Marcelis, 1994) and tomato (Bertin and Gary, 1993), fruit set also shows a negative correlation with the source : sink ratio. In addition to a high source : sink ratio, climatic stress, e.g. low irradiance (Wien *et al.*, 1989; Jaafar *et al.*, 1994), severe water stress and high irradiance (Jaafar *et al.*, 1994) or high temperatures (Rylski and Spigelman, 1982) can induce flower abortion in peppers.

Blossom-end rot (BER) is a physiological disorder, caused by local calcium deficiency during the initial stage of fruit development (Bangerth, 1979; Morley *et al.*, 1993). BER may result from a high seed number per fruit or a high initial fruit growth rate (Marcelis and Ho, 1999); it causes high economic losses in sweet pepper production, as affected fruits have little value.

Marcelis and Baan Hofman-Eijer (1997) concluded that an increase in seed number in sweet pepper increased the inhibitory effect of a fruit on set and growth of

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later-developing fruits. Therefore, we propose that parthenocarpic cultivars, which show fruit growth without seeds, could be a partial solution to the flushing problem. The aim of this work was to investigate whether parthenocarpic fruit growth can prevent irregular fruit set and hence irregular harvest in sweet pepper, as well as reduce the occurrence of blossom-end rot. Parthenocarpic sweet pepper cultivars are not yet available; therefore, chemical manipulation was used to induce parthenocarpy. Auxins, gibberellins and cytokinins (Sjut and Bangerth, 1982/83; Kim *et al.*, 1992), as well as auxin transport inhibitors (Beyer and Quebedeaux, 1974; Kim *et al.*, 1992), have all been successfully applied to several fruit vegetable crops. In the present experiment, parthenocarpic pepper fruits were produced by preventing self-pollination combined with application of auxin to the stigma.

MATERIALS AND METHODS

Plant material and greenhouse conditions

Sweet pepper (*Capsicum annuum* L.) plants of the yellow-fruited cultivar 'Fiësta' (Enza seeds, Enkhuizen, The Netherlands), obtained from a commercial propagator and grown on Rockwool[®] cubes, were planted on Rockwool[®] slabs on 7 Apr. 1998 at a density of 2.5 plants m⁻² in a compartment of a multispan Venlo-type glasshouse at Unifarm, Wageningen, The Netherlands (52 °N). Nutrient solution was prepared according to Voogt and Bloemhard (1993) and was supplied by trickle irrigation. The terminal flower was removed from all plants at anthesis to support vegetative growth. The twin-branch system was applied, resulting in two stems per plant, with all side shoots restricted to one leaf and flower. The experiment ended on 5 Aug. 1998.

Inside dry and wet-bulb air temperature and CO₂ concentration in the compartment were recorded at 5 min intervals by a commercial Vitaco computer system (Hoogendoorn, Vlaardingen, The Netherlands) and temperature was controlled by heating and ventilation. The average daily temperature was 23 °C and varied between 20 and 28 °C, the average CO₂ concentration during the day was 440 μmol mol⁻¹ and the average relative air humidity was about 80 %.

Treatments

Two treatments were conducted. In the control, plants were grown according to commercial practice (no fruit set treatment). In the other treatment, fruits were grown parthenocarpically. To obtain parthenocarpic fruit growth, flowers of eight plants per plot were examined every day between 0900 and 1000 h. Flowers close to anthesis (balloon stage) were slightly opened using the tip of a syringe. The stigmas were covered with a lanolin paste from the syringe, mixed with water (1 : 1) and enriched with 0.05 % 1-naphthalene acetic acid (NAA) (Wien and Zhang, 1991) [NAA dissolved in water was mixed with heated lanolin (100 °C), stirred to a homogeneous paste and cooled to room temperature]. The day of anthesis, fruit set

and fruit abortion were recorded twice a week for each node on two plants per plot for both treatments. Fruits were considered mature for harvest if they were completely yellow. Harvests were made every 4 d starting on June 8 (week 24 of the year) on eight auxin-treated plants and on three control plants per plot. Fruits were classified in one of three groups according to the incidence of blossom-end rot: fruits without BER; fruits with less than 5 % BER; and fruits with more than 5 % of their surface affected by BER.

Fresh and dry masses (ventilated oven, 105 °C for two cycles of 10 h) of all fruits were measured separately for each plant. Length and diameter as well as harvest day, were recorded for individual fruits of two plants per plot for both treatments. Fruit weight of 14 individual fruits growing on these plants between 26 April and 11 June was estimated seven times between anthesis and the harvest date using fruit length and diameter measurements (Marcelis and Baan Hofman-Eijer, 1995). Fruit growth was fitted with a Gompertz growth function. Differences in fruit shape and size as well as the average day of harvest and average fruit growth period for different node positions were calculated from these data.

Statistical design and analysis

Treatments were arranged in a randomised complete block design consisting of seven blocks and 12 plants per plot in two rows of six plants. Only the eight plants in the centre of a plot were used in the measurements. Analysis of variance was conducted and treatment effects were tested by an *F*-test at the 5 % probability level. Differences in variance were tested according to Brown and Forsythe (1974). The statistical software package SAS (version 6.12, SAS, 1994) was used.

RESULTS

In the auxin-treated plants, 86 % of the fruits were seedless (parthenocarpic) and 95 % contained less than 30 seeds per fruit. For the control plants, 62 % of the fruits were well-pollinated and contained more than 100 seeds, while none contained less than 60 seeds.

Anthesis and fruit set

No difference in the date of anthesis of the first flower was found between control and auxin treated plants. Later flowers of auxin-treated plants reached anthesis earlier than flowers on the control plants in the same node position; this difference increased over time. At the final harvest, the highest node position with a flower at anthesis was 16.8 for control plants and 18.5 for auxin-treated plants; this difference was statistically significant ($P < 0.05$). Fruit set was high in the lowest node of the control (90 %) and auxin-treated plants (74 %; Fig. 1). In the second node, fruit set was equal to that in the first node for auxin-treated plants, whereas for the control plants it was slightly lower (83 %). Thereafter, fruit set in both treatments decreased rapidly to levels below 50 %. Fruit set in control plants varied between 21 and 55 % [coefficient of variation

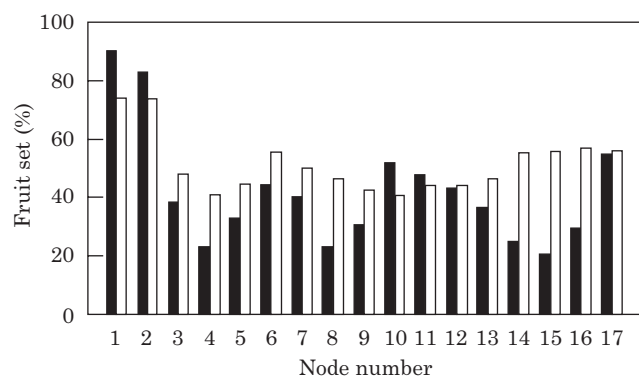


FIG. 1. Fruit set (%) as a function of the node number for control (■) and auxin-treated (□) plants. Data are means for 14 plants and every node number refers to four positions in the plant (twin-branched with side shoots pruned above first leaf).

(CV) = 11 %], whereas auxin-treated plants showed significantly ($P < 0.01$) more regular fruit set, fluctuating between 41 and 57% (CV = 5%). With a mean fruit set of 50%, auxin-treated plants showed significantly ($P < 0.001$) higher fruit set than control plants (37%).

Harvest time courses and final yield

Control plants showed a cyclical pattern for weekly harvested fruit yield, with two high peaks and a 3-week period of low yields in between; the yield pattern of auxin-treated plants was more stable than that of control plants (Fig. 2A). This difference is also shown by the cumulative yield curves (Fig. 2B) and by the coefficients of variation (Table 1). Harvested fruit numbers (Fig. 3) showed almost the same time course as fruit fresh mass, but relative levels were different. The cumulative number of harvested fruits was lower for auxin-treated plants than for control plants during weeks 25–27, but the situation was reversed later on (Fig. 3B). The harvested fruit fresh mass was always lower in auxin-treated plants compared to control plants (Fig. 2B).

The final number of harvested fruits was significantly ($P < 0.001$) higher (20%) in auxin-treated plants compared to control plants (Fig. 3B). There was no significant difference ($P = 0.50$) in the final fruit fresh yield between either treatment (Fig. 2B). However, if non-BER affected fruits are considered alone, final fruit fresh yield was significantly higher ($P < 0.001$) for the auxin-treated plants at 4.7 kg m^{-2} compared to 3.7 kg m^{-2} for control plants.

BER

The incidence of BER was very high in control fruits harvested in the first week (week 24) but decreased gradually so almost no BER-affected fruits were harvested in the last weeks (Fig. 4). Over the whole period, 31% of the fruits harvested from the control plants were affected by BER. In more than half of these fruits, over 5% of surface area was affected by BER. In contrast, auxin treatment resulted in very low numbers of BER-affected fruits. The highest incidence of BER was observed in week 24, when

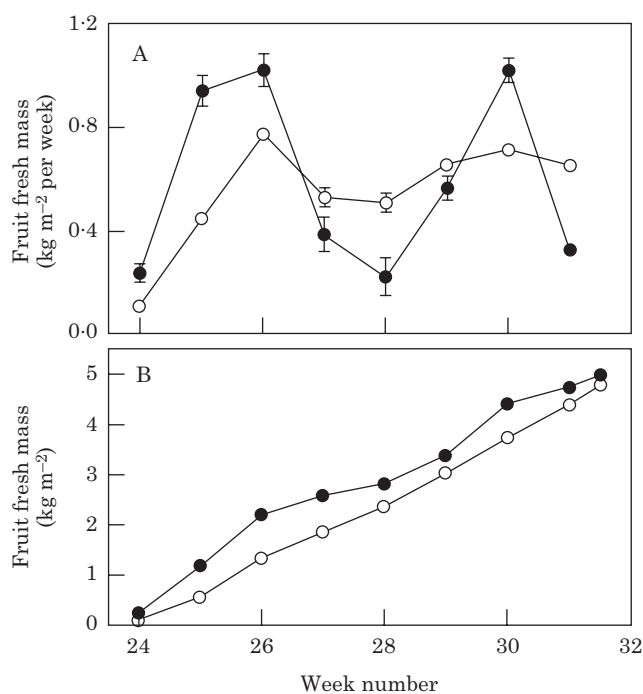


FIG. 2. Weekly (A) and cumulative (B) harvested fruit fresh mass as a function of week of the year for control (●; $n = 21$) and auxin-treated (○; $n = 56$) plants. Vertical bars indicate s.e.m. when larger than symbols.

TABLE 1. Coefficients of variation and probability values of Brown-Forsythe's (1974) test on equality of overall variances for weekly (weeks 25 to 31) numbers and fresh mass of harvested fruit for control ($n = 56$) and auxin-treated plants ($n = 21$) both for all fruits and for 'non-BER' fruits only

	Coefficient of variation		
	Control	Auxin	Probability
Number of fruits			
All fruits	22.4	8.2	0.13
Non-BER fruits only	19.5	7.3	0.54
Fresh mass of fruit			
All fruits	20.4	8.6	0.01
Non-BER fruits only	20.0	7.8	0.17

11% of the harvested fruits were affected. From week 26 onwards, almost no BER fruits were harvested from the auxin-treated plants, and averaged over the whole harvest period only 1% of the fruits were affected by this disorder, which was significantly ($P < 0.001$) lower than for control plants.

Dry mass production and partitioning

Final dry mass production was almost 1 kg m^{-2} , and did not differ between control and auxin-treated plants (Table 2). However, dry mass partitioning was significantly influenced by the treatment. In control plants, 58% of total

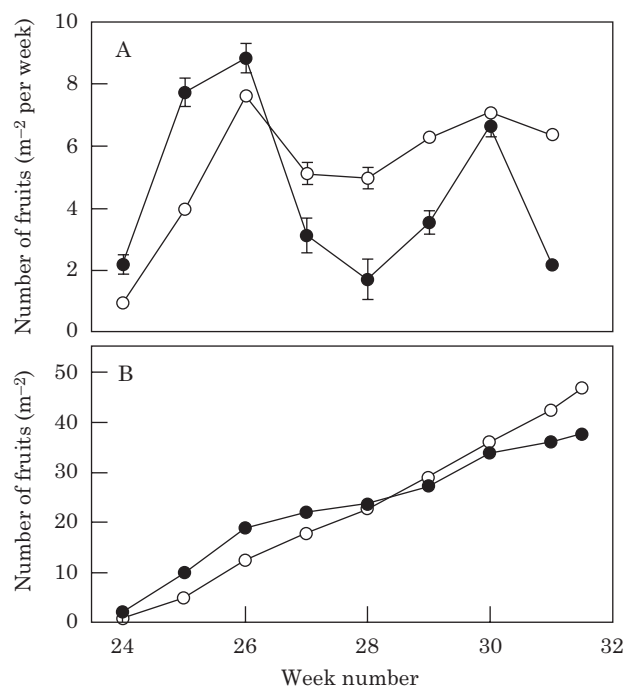


FIG. 3. Weekly (A) and cumulative (B) harvested numbers of fruit as a function of week of the year for control (●; $n = 21$) and auxin-treated (○; $n = 56$) plants. Vertical bars indicate s.e.m. when larger than symbols.

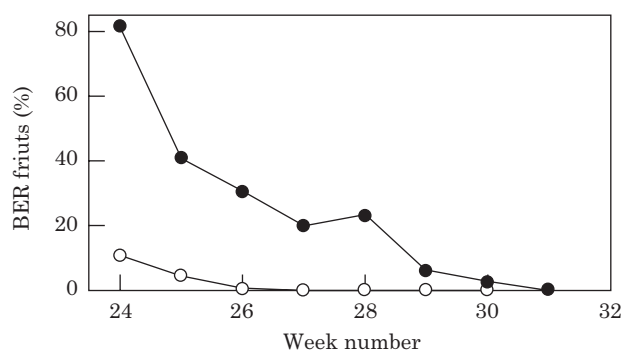


FIG. 4. Time course for relative numbers of BER fruits for control (●) and auxin-treated (○) plants. Data are averages of 14 plants.

dry mass was partitioned to the fruits, whereas in auxin-treated plants this value was significantly lower at only 50% (Table 2).

Fruit growth, mass and shape

Growth of individual fruits showed a sigmoidal pattern. The start of growth of auxin-treated fruits was delayed by an average of 3 d compared to that of control fruits. For auxin-treated fruits, the average time from anthesis to harvest was 60 d, which was significantly ($P < 0.001$) longer than that for control fruits (53 d). The average fruit growth rate was higher for control fruits and the final mean fruit mass was also significantly higher compared to auxin-treated fruits (Table 2).

TABLE 2. Total dry mass by the end of the experiment (9 August), dry mass of unripe fruits, dry mass fraction partitioned into the fruits (unripe and harvested) and mean fruit fresh mass for all ripe fruits and 'non-BER' ripe fruits for control ($n = 14$) and auxin-treated plants ($n = 14$)

	Control	Auxin
Total dry mass (g m^{-2})	988 ^a	969 ^a
Unripe fruit dry mass (g m^{-2})	184 ^a	108 ^b
Fraction to the fruits	0.58 ^a	0.50 ^b
Mean fruit fresh mass (g per fruit)		
All fruits	134 ^a	105 ^b
Non-BER fruits only	146 ^a	105 ^b

Means followed by different letters indicate significant differences at the 5% level (F -test).

TABLE 3. Partitioning of fresh mass within ripe fruits (%) for control and auxin-treated plants

	Control	Auxin
Stalk	1.6 ^a	1.8 ^b
Pericarp	88.9 ^a	93.7 ^b
Placenta	8.1 ^a	4.5 ^b
Seeds	1.4 ^a	0 ^b

Data are means for 30 'non-BER' fruits, randomly selected on 2 d (24 Jun. and 18 Jul. 1998). Means followed by different letters indicate significant differences at 5% level (F -test).

Significant ($P < 0.001$) differences in diameter : length ratio were observed between control and auxin-treated fruits, due to the flatter fruit shape of auxin-treated plants. The diameter : length ratio was 1.0 and 1.1 for control and auxin-treated plants, respectively. On average, auxin-treated fruits were less attractive and had a less regular shape than fruits from control plants.

Seeded and seedless fruits were found to differ structurally. All fruit portions (stalk, pericarp and placenta) showed significant ($P < 0.001$) differences between control and auxin-treated plants (Table 3). Although the mass of auxin-treated fruits was significantly lower (Table 2), their pericarp was significantly ($P < 0.001$) thicker. Despite the fact that in control fruits seeds represented only 1.4% of the fresh mass, they represented 13.4% of fruit dry mass due to their high dry matter content.

Dry matter content of fruits was evaluated throughout the whole harvest period. It was significantly ($P < 0.001$) higher for auxin-treated fruits (7.8%), compared to control fruits (7.4%).

DISCUSSION

Parthenocarpy, fruit set and yield pattern

The application of lanolin paste enriched with 0.05% NAA was successful in effecting fruit set, without pollination and fertilization, and resulted in growth of parthenocarpic fruit. Except for some early fruits, where experience in paste

application had still to be gained, and some other fruits where, due to high temperatures, the lanolin paste dropped from the stigma, all treated fruits were seedless. This is in agreement with Wien and Zhang (1991), who also obtained parthenocarpic pepper fruit growth by application of NAA to the ovary of emasculated flowers, and with Kim *et al.* (1992) and Sjut and Bangerth (1982/83) who obtained parthenocarpic fruit growth by application of auxin in cucumber and tomato, respectively.

Fruit set was more regular in auxin-treated plants (Fig. 1). In control plants, flowers in certain nodes (e.g. nodes 4, 8 and 15) showed much higher abortion rates than flowers in other nodes (e.g. nodes 6, 10 and 17), whereas in auxin-treated plants abortion rates were almost identical for all nodes and were lower than in the control plants. This supports the suggestion of Marcelis and Baan Hofman-Eijer (1997) that breeding strategies to reduce seed numbers in fruits with acceptable mass might offer a method of producing more consistent or stable yields. Since total plant dry mass at the end of the experiment did not differ between either treatment (Table 2), one may conclude that total assimilate availability over the whole experimental period was the same. As only 50% of the total dry mass was distributed to the fruits in auxin-treated plants compared to 58% for the control plants (Table 2), the total amount of assimilates used in fruit growth was less in the auxin-treated plants. Yet, total fruit set was higher in these plants compared to the control. Our results suggest that besides competition for assimilates, dominance, due probably to hormone production by seeds in developing fruits, plays an important role in sweet pepper fruit set and growth.

A more regular fruit set (Fig. 1) resulted in a more regular yield (Figs 2 and 3). This supports the suggestion of Marcelis and Baan Hofman-Eijer (1997) that irregular yield in sweet pepper results from irregular fruit set. Yield patterns do not follow fruit set patterns exactly, as the growth period from anthesis to maturity differs between fruits. We observed yield patterns for a period of 7 weeks only (Fig. 2); however, yield is expected to be more regular in treated plants than control plants for at least 8 more weeks, as fruit set was more regular up to at least node number 17 (Fig. 1).

BER, fruit size and fruit shape

BER was hardly observed in parthenocarpic fruits, whereas seeded fruits from control plants in the same greenhouse showed a high incidence of blossom-end rot. This agrees with the observation of Marcelis and Ho (1999), that the number of seeds in sweet pepper fruits was positively correlated with the incidence of BER. Parthenocarpic fruits were 30% smaller (Table 2) and time from anthesis to harvest was 1 week longer than for fruits from control plants. Hence, average fruit growth rate was much lower for parthenocarpic fruits, significantly reducing the chances of BER (Marcelis and Ho, 1999).

The observed difference in fruit shape, with parthenocarpic fruits having a reduced height, was also reported by Rylski (1986) and Wien and Zhang (1991). The greater deformation in shape of parthenocarpic fruits compared to

seeded fruits is also well-known (Bosland and Votava, 1999). Many authors have reported a positive correlation between fruit size and number of seeds (Rylski, 1973; Varga and Bruinsma, 1976; Shipp *et al.*, 1994). Similarly, and in agreement with Wien and Zhang (1991), our results showed that parthenocarpic pepper fruits (no seeds) were significantly smaller than seeded fruits (Table 2). However, seed number is only one of many factors determining fruit size. Other factors reported for tomato and cucumber include the number of competing fruits (Heuvelink, 1997), temperature (Marcelis and Baan Hofman-Eijer, 1993) and radiation (Marcelis, 1993).

Parthenocarpic fruits were 30% smaller than control fruits (Table 2), which could be the result of reduced cell number and/or reduced cell size. However, we did not measure these fruit characteristics. Studying indole-3-acetic acid (IAA)-induced parthenocarpic tomato fruits, Büngler-Kibler and Bangerth (1982/83) observed a higher rate of cell division, a reduced cell division period and a similar number of cells as in control fruits. Hence, IAA-induced parthenocarpic tomato fruits were 28% smaller than control fruits because of reduced cell enlargement. We speculate that the reduced size of parthenocarpic sweet pepper fruits is also the result of reduced cell enlargement, rather than reduced cell number. The higher dry matter content in the pericarp of parthenocarpic fruits supports the assumption of smaller cells in parthenocarpic fruits.

Total biomass production, partitioning and yield

Total biomass production was the same for control and auxin-treated plants (Table 2). Since the leaf area index was the same for both control and auxin-treated plants (not shown), this means that the larger number of growing fruits on auxin-treated plants did not result in a positive feedback on photosynthetic rate. Similarly, Nielsen and Veierskov (1988) observed no difference in plant dry matter increase in sweet pepper when branching was unrestricted and fruit number was restricted to zero, one or three fruits per plant. In cucumber (Marcelis, 1991) and tomato (Heuvelink and Buiskool, 1995), the number of fruits did not influence biomass production, except in extreme cases e.g. only one cucumber fruit per plant or only one tomato fruit per truss.

Since seeds are most responsible for the sink strength of a fruit (Varga and Bruinsma, 1976; Marcelis and Baan Hofman-Eijer, 1997), the sink strength of parthenocarpic fruits is expected to be lower than the sink strength of seeded fruits, resulting in a reduced mean fruit mass. The higher number of fruits growing on the auxin-treated plants only partly compensated for the loss of sink strength per fruit, resulting in a less favourable partitioning of dry matter between fruits and vegetative parts in the auxin-treated plants (Table 2).

Seeds represented 13.4% of the total dry mass and only 1.4% of the total fresh mass in control fruits. Parthenocarpic fruits have no seeds, hence they might be expected to have a higher fruit fresh mass. This was not the case here, since the absence of seeds resulted in the fruits having less competitive strength for assimilates relative to vegetative plant parts (Table 2) and the dry matter content of the

parthenocarpic fruits (7.8%) was higher than that of seeded fruits (7.4%).

Parthenocarpic fruit growth seems to reduce total yield slightly (Fig. 2B). This does not necessarily mean a reduction in financial returns for producers, as a more regular yield results in a more regular labour demand and a higher average price, because more peppers are produced at times of low supply (Fig. 2A).

CONCLUSIONS

Our results clearly demonstrate that parthenocarpic fruit growth in sweet pepper results in a more regular fruit set and yield and hence reduces the problem of flushing. Therefore, breeding strategies should focus on the development of parthenocarpic sweet pepper cultivars, which are also much less susceptible to blossom-end rot.

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