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Genetic differences in fruit-set patterns are determined by differences in fruit sink strength and a source : sink threshold for fruit set

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- *Background and Aims* Fruit set in indeterminate plant species largely depends on the balance between source and sink strength. Plants of these species show fluctuations in fruit set during the growing season. It was tested whether differences in fruit sink strength among the cultivars explained the differences in fruit-set patterns.
- *Methods Capsicum* was chosen as a model plant. Six cultivars with differences in fruit set, fruit size and plant growth were evaluated in a greenhouse experiment. Fruit-set patterns, generative and vegetative sink strength, source strength and the source : sink ratio at fruit set were determined. Sink strength was quantified as potential growth rate. Fruit set was related to total fruit sink strength and the source : sink ratio. The effect of differences observed in above-mentioned parameters on fruit-set patterns was examined using a simple simulation model.
- *Key Results* Sink strengths of individual fruits differed greatly among cultivars. Week-to-week fruit set in large-fruited cultivars fluctuated due to large fluctuations in total fruit sink strength, but in small-fruited cultivars, total fruit sink strength and fruit set were relatively constant. Large variations in week-to-week fruit set were correlated with a low fruit-set percentage. The source : sink threshold for fruit set was higher in large-fruited cultivars. Simulations showed that within the range of parameter values found in the experiment, fruit sink strength and source : sink threshold for fruit set had the largest impact on fruit set: an increase in these parameters decreased the average percentage fruit set and increased variation in weekly fruit set. Both were needed to explain the fruit-set patterns observed. The differences observed in the other parameters (e.g. source strength) had a lower effect on fruit set.
- *Conclusions* Both individual fruit sink strength and the source : sink threshold for fruit set were needed to explain the differences observed between fruit-set patterns of the six cultivars.

Key words: Fruit-set patterns, fruit sink strength, source : sink ratio, threshold for fruit set, *Capsicum annuum*, cultivars.

INTRODUCTION

Indeterminate crops can show cyclical patterns in fruit set (Schapendonk and Brouwer, 1984; Passam and Khah, 1992; Heuvelink *et al.*, 2004); periods with high fruit set alternate with periods of low fruit set. Different explanations have been proposed for these patterns: hormones exported by growing fruits may inhibit fruit set of new fruits (Bangerth, 1989), and competition for assimilates between rapidly growing fruits and young fruits may cause abortion of young fruits (Bertin, 1995; Marcelis *et al.*, 2004). It has also been suggested that both explanations interact; a decrease in import of assimilates into the fruit might change hormone levels, leading to abscission (Aloni *et al.*, 1997; Marcelis *et al.*, 2004).

In the competition theory, key concepts are source and sink strength, representing the supply and demand for assimilates, respectively. The sink strength of a growing organ can be quantified as its potential growth rate (Marcelis, 1996) and depends on its developmental stage (Schapendonk and Brouwer, 1984; Marcelis and Baan Hofman-Eijer, 1995). The total sink strength of a plant comprises the sink strength of all the organs. The source strength is the supply of assimilates, originating from the photosynthesis. Assimilates are divided over the organs in proportion to their fractional contribution to the total sink strength (Marcelis, 1996). When the total sink strength is high, due to many growing fruits, flowers and young fruits are not able to compete for assimilates with the fast-growing fruits and hence abort. High sink strength, caused by a high fruit load, has resulted in low fruit set in, for instance, sweet pepper (Marcelis *et al.*, 2004), tomato (Bertin, 1995) and cotton (Pettigrew, 1994).

As sink strength plays an important role in fruit set (see above), differences in the sink strength of an individual fruit are expected to result in different fruit-set patterns. Sink strength of an individual fruit often shows a bell-shaped curve skewed to the right as a function of time after anthesis (Marcelis, 1993). Fruit sink strengths of different cultivars may differ in their maximum growth rate, the timing of the maximum growth rate, and fruit-growth duration (time between anthesis until harvest ripe). For example, potential fruit weight of long-life, cherry and beefsteak tomato cultivars

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differed significantly (Bertin *et al.*, 1998) and, in peach, fruit-growth duration and maximum fruit growth rate of two cultivars differed, resulting in different potential fruit weights (Grossman and DeJong, 1995). However, cultivars may also differ in other properties such as source strength (which is affected by leaf area, plant architecture and photosynthetic characteristics), rate of flower formation and the vegetative sink strength. Source strength is also known to influence fruit set (Marcelis *et al.*, 2004). Simulation studies have shown that an increase in vegetative sink strength reduced the number of fruits (Marcelis, 1994).

In this study, an experiment was conducted to elucidate which factors determine differences in fruit-set patterns. Fruit set was followed in detail in six *Capsicum* cultivars with different fruit sizes. The hypothesis that differences in fruit-set patterns between cultivars are due to differences in individual fruit sink strength was tested by combining experimental results with a simple simulation model.

MATERIALS AND METHODS

Experimental set-up

Six *Capsicum* cultivars with different potential fruit weights were used in the experiment. 'Medina' (20 g), 'Fireflame' (20 g) and 'Furila' (45 g) are hot pepper cultivars, 'Gepetto' (135 g) is a cultivar with pointed sweet peppers and 'Nazar' (140 g) and 'Funky' (205 g) produce block-type sweet peppers; values between brackets are the representative fruit fresh weights of each cultivar, as published by the seed company (De Ruiter seeds, The Netherlands). Plants were grown in a Venlo-type greenhouse compartment on rockwool substrate in Wageningen, The Netherlands (lat. 52°N), from April until September at a density of 3·8 plants m^{-2}. Two stems per plant were retained. Average temperature was $21{\cdot}6 \pm 2{\cdot}0\,^{\circ}C$ (mean ± s.d.), recorded using a commercial computer system. Average daily global radiation was $16{\cdot}3 \pm 5{\cdot}6$ MJ $m^{-2}\,d^{-1}$ (mean ± s.d.), and was recorded at an official weather station 300 m away. The experiment was set up as a randomized complete block design, with three blocks and six plots per block, each plot containing one cultivar. A plot consisted of 20 plants in a double row. Eight plants in each plot were used for destructive harvests. Guard plants were placed between plants used for destructive harvest and between the plots in the same row. There was a fourth block, containing additional plants for observations on fruit set, fruit-growth duration and fruit weight. It consisted of a double row with six plots, each plot containing ten plants of one cultivar.

Measurements

Data on plant weight and leaf area were measured at five destructive harvests. Six plants per cultivar (two plants per block) were used in each destructive harvest. Leaf area was measured using the Li-COR measurement system (LI-3100; Lincoln, NB, USA). Observations on flowering and fruit set were made six times a week on 12 plants per cultivar, six plants in the fourth block and the six plants of the last destructive harvest (two per block). Red fruits were harvested twice a week. Results of plant weight, leaf area and yield patterns are given in Wubs *et al.* (2009).

Fruit sink strengths, quantified by the potential fruit growth rates, were obtained by non-destructive measurements on potentially growing fruits, as described by Marcelis and Baan Hofman-Eijer (1995). Potentially growing fruits were fruits growing with very low competition from other fruits, which could attain their potential fruit size. Conditions for potential fruit growth were created by tagging two flowers on a plant from which all fruits were removed. New flowers were removed weekly. Twice a week, length and diameter of the tagged fruits were measured to obtain fruit volume. The number of measured fruits ranged from 29 to 83 fruits per cultivar. To convert fruit volume into fruit dry weight, a relationship between volume and fresh weight, and a relationship between fruit age and dry matter fraction of the fruits had to be obtained. For the first relationship, fruit volume and fruit fresh weight of 178–341 randomly sampled fruits per cultivar were measured. For the second relationship, the ages and dry matter percentages of 114–229 fruits per cultivar were measured.

Data analysis

A fruit was considered to be set if it reached the harvestable stage or if it survived for >10 d in small-fruited cultivars or >20 d in large-fruited cultivars. Percentage fruit set was calculated as the number of fruits set divided by the number of flowers times 100.

On the basis of the lengths and diameters of the potentially growing fruits, their volume was calculated assuming a cylindrical fruit shape. This was subsequently converted into fresh weight, using a linear regression fitted between volume and fresh weight ($R^2 = 0{\cdot}99$). A Gompertz function (eqn 1) was fitted through fresh weight over time (loglikelihood = −4795).

$$w_t = w_m \times \exp\{-\exp[-k(t - t_m)]\} \qquad (1)$$

w_t is the weight at age t (days after anthesis), w_m is upper asymptote of fruit weight (grams), k represents the weighted mean relative growth rate and t_m the age (days) at maximum growth rate.

The Gompertz function was fitted through the data with non-linear mixed modelling. Non-linear mixed models take into account that the measurements on one fruit are grouped. A lower variation is assumed between the measurements of one fruit than between the measurements of different fruits. A mean and standard deviation were estimated for the three model parameters (w_m, k and t_m). The three parameter means were used to describe fruit growth.

As there was variation in final fruit size, the fitted value of w_m was increased to reach the average weight of the largest 10 % of the fruits. This required increasing w_m by 30 % for all cultivars.

A sum of two exponential functions was fitted through the data of fruit age and dry matter fraction (eqn 2; loglikelihood = 2265).

$$f_{dm,t} = a \times \exp(bt) + c \times \exp(dt) \qquad (2)$$

$f_{dm,t}$ is the fraction dry matter (dm) of the fruit at age t (days after anthesis) and a, b, c and d are parameters.

TABLE 1. *Parameter values for the simulations*

	Potential fruit weight (g dm)	Fruit-growth duration (d)	Flower appearance rate (d^{-1})	Source strength (g dm d^{-1})	Vegetative sink strength (d dm d^{-1})	Threshold source : sink ratio for fruit set
Default	8	60	0·5	2·4	1·9	0·5
Sensitivity analysis	4, 18	57, 70	1	2·2, 2·6	1·6, 2·9	1
Small-fruited cultivar	4	57	1	2·2	1·9	0·5
Large-fruited cultivar	18	70	0·5	2·6	1·6	1

The first line gives the default parameter values. The second line gives the parameter values used in the sensitivity analysis. One parameter was changed, while keeping the other parameters at the default value. Small-fruited and large-fruited cultivars represent the parameter combinations for the simulations with realistic parameter combinations.

The sink strength (representing the potential growth rate in grams d. wt) was the derivative of the product of the Gompertz function and the sum of two exponential functions. Potential fruit dry weight was calculated as the upper asymptote of the Gompertz function w_m (grams fresh weight) multiplied by the fraction of dry matter of the fruit at the average harvest time (= average fruit-growth duration).

The correlation of potential fruit dry weight with the percentage fruit set and the variation in weekly fruit set was determined. Weekly fruit set was the number of fruits set per week. The variation in weekly fruit set was defined as the coefficient of variation (CV), which is the standard deviation of weekly fruit set divided by the mean weekly fruit set. The variation in weekly fruit set was calculated using data from weeks 15–28. Correlations were quantified using Spearman *R*, which estimates the correlation between the ranks of two non-normal distributed variables. All analyses were done in *R* version 2.6.0 (R Development Core Team, 2007).

Fruit-growth duration, maximum potential fruit growth rate and the ratio between actual and potential fruit weights were examined. Fruit-growth duration was the time between flowering and harvest. It was calculated from fruits growing on the 12 plants used for observing fruit set as well as potentially growing fruits, because there were no significant differences between these two groups (data not shown). The maximum in the potential fruit growth rate (g d. wt d^{-1}) was the top of the sink strength curve. The ratio of actual to potential fruit weight is a measure for the source : sink ratio – it represents the ratio of actual to potential growth of a fruit.

The sink strength of a set fruit was calculated for each day between flowering and harvest. The total fruit sink strength of a plant was calculated per day by accumulating the sink strength of all fruits which were present that day. The total fruit sink strength per cultivar was averaged over the 12 plants observed. Patterns of total fruit sink strength over time were compared between the cultivars and related to weekly fruit set for each cultivar.

Source strengths of the cultivars were calculated using the crop growth model INTKAM (Marcelis *et al.*, 2006) with measured leaf area index, radiation and temperature as input. Simulated dry matter production was calibrated on the total measured plant weight. Source strengths over time were comparable for all cultivars (see data on total plant growth in Wubs *et al.*, 2009).

Vegetative sink strength was assumed to be constant in time. It was estimated by iteration using simulated source strength, calculated total fruit sink strength and observed dry matter partitioning into the fruits at the five destructive harvests. The total squared deviation between measured and calculated dry matter partitioning into the fruits for the five destructive harvests was minimized. The average deviation between estimated and realised partitioning was between 0·009 and 0·046.

The source : sink ratio was calculated based on total fruit sink strength, vegetative sink strength and source strength. The source : sink ratio was assumed to determine fruit set (Bertin, 1995). The average source : sink ratio at fruit set was calculated.

Simulation studies

A simple deterministic simulation model was developed in Scilab 4.1.2 (www.scilab.org) to study the effect of different parameters on fruit set. Source strength, vegetative sink strength and flower appearance rate were assumed to be constant. Source and sink strength define abortion and assimilate partitioning. Sink strength of a fruit was calculated using the first derivative of the Gompertz function. In the Gompertz function, the maximum growth rate was at one-third of the fruit-growth duration and potential fruit dry weight was the asymptote. Fruit set was regulated by the source : sink ratio: if the source : sink ratio at anthesis was above a certain threshold, the flower would set into a fruit. The realised growth rate of a fruit depended on its share in the total sink

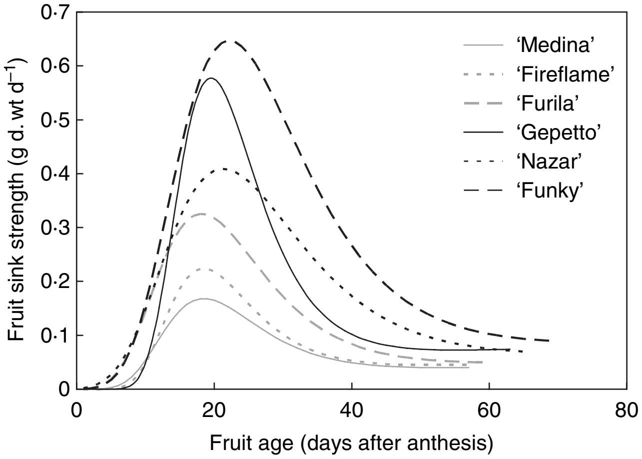

FIG. 1. Fruit sink strength curves for six different sweet pepper cultivars. Curves end at the average growth duration (time from anthesis until harvest ripe) of each cultivar.

strength and on source strength. Model parameters were in the range of values found in the cultivars; the minimum and maximum value and, if applicable, an intermediate value (Table 1).

Simulations were carried out for 200 d. For each simulation, the number of fruits set as well as the percentage fruit set, the variation in fruit set (CV), the average fruit weight of the fruits harvested and the ratio of actual to potential fruit weight were calculated. Variation in fruit set was based on 'weekly' numbers of fruits set, where 'weekly' fruit set was obtained by counting the numbers of fruits set every 7 d.

To investigate the effect of a given parameter on the simulation output (sensitivity analysis), each of the six parameters was changed one-by-one while keeping the default value for the remaining parameters (Table 1). Next, the parameter values were changed simultaneously, taking into account combinations observed in the cultivars (Table 1). These simulations resembled cultivars with small- and large-sized fruits.

TABLE 2. *Fruit-growth duration, maximum potential fruit growth rate, ratio of actual to potential fruit weight, estimated vegetative sink strength and source : sink ratio at fruit set for each of the six cultivars*

	Fruit-growth duration (d)	Maximum fruit growth rate (g dm d^{-1})	Vegetative sink strength (g dm d^{-1})	Ratio actual/potential fruit weight	Source : sink ratio at fruit set
'Medina'	57 ± 0·19	0·18	1·9	0·52 ± 0·01	0·55 ± 0·004
'Fireflame'	58 ± 0·19	0·22	2·2	0·49 ± 0·01	0·53 ± 0·004
'Furila'	59 ± 0·23	0·35	2·9	0·45 ± 0·01	0·46 ± 0·004
'Gepetto'	63 ± 0·51	0·58	2·7	0·70 ± 0·02	0·74 ± 0·013
'Nazar'	66 ± 0·39	0·41	1·5	0·72 ± 0·02	1·06 ± 0·025
'Funky'	69 ± 0·49	0·65	1·6	0·73 ± 0·03	1·03 ± 0·026

Values are means ± s.e. for the measured variables.

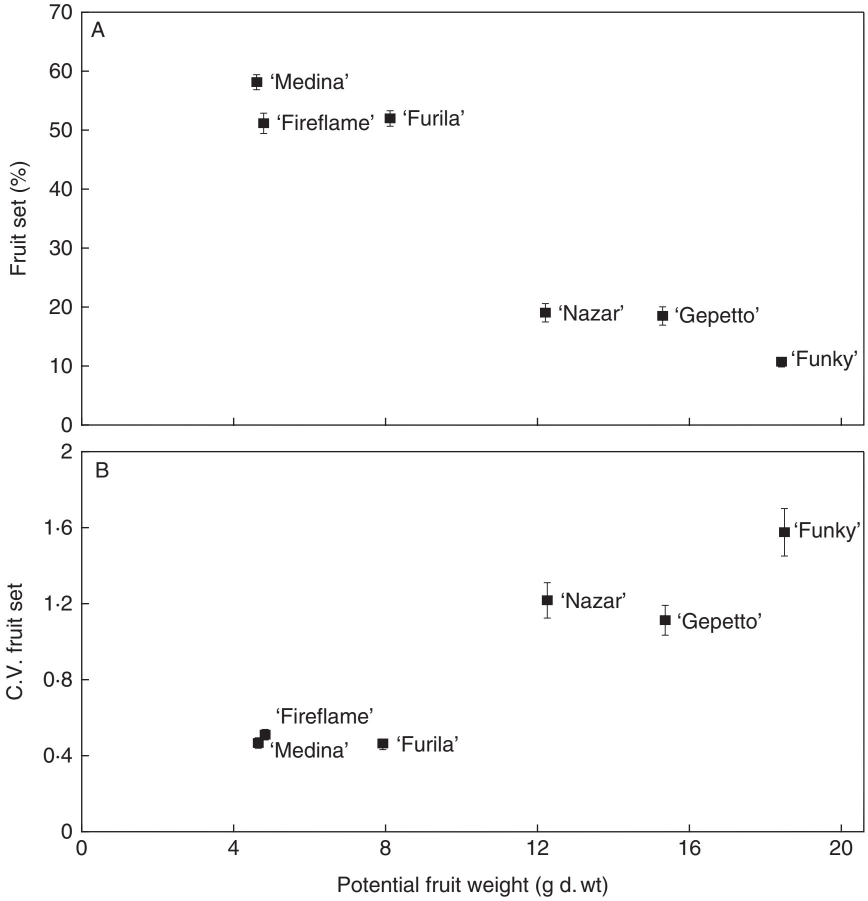

FIG. 2. Relationship between (A) fruit set (%) and potential fruit weight (g dry matter), Spearman $R = -0{\cdot}93$, $P < 0{\cdot}001$, and (B) variations in weekly fruit set and potential fruit weight (g dry matter), Spearman $R = 0{\cdot}80$, $P < 0{\cdot}001$, of six cultivars. Variations in weekly fruit set were defined as the coefficient of variation (CV), calculated as the s.d. of weekly fruit set divided by average weekly fruit set. Error bars represent s.e. ($n = 12$) and are shown when larger than the symbol.

RESULTS

Experiment

Fruit sink strengths differed in maximum growth rate and fruit-growth duration (Fig. 1 and Table 2), although the differences in maximum growth rate were much larger than in fruit-growth duration. Together, the differences in maximum growth rate and fruit-growth duration resulted in different potential dry weights. Timing of the maximum growth rate differed slightly (Fig. 1), but was the same on a normalized scale, namely at one-third of the fruit growth period.

The cultivars showed a different percentage fruit set (Fig. 2A) as well as different fruit-set patterns in time (Fig. 3). The higher the potential fruit weight of a cultivar, the lower the percentage fruit set (Fig. 2A; Spearman $R = -0{\cdot}93$, $P < 0{\cdot}001$). A higher potential fruit weight increased the variation in weekly fruit set (higher CV, Fig. 2B; Spearman $R = 0{\cdot}80$, $P < 0{\cdot}001$). The percentage fruit set and variation in fruit set correlated negatively (Spearman $R = -0{\cdot}85$, $P < 0{\cdot}001$).

Total fruit sink strength per plant differed between the cultivars (Fig. 3); all cultivars had an increasing total fruit sink strength in time, but strikingly the cultivars with the highest total fruit sink strengths were the cultivars with the highest fruit set ('Medina', 'Fireflame' and 'Furila'; Fig. 3A–C). The total fruit sink strength of the large-fruited cultivars 'Gepetto', 'Nazar' and 'Funky' showed a wave-like pattern in time (Fig. 3D–F). For the latter two cultivars, the fruit set was maximal where the fruit sink strength was minimal and vice versa (Fig. 3E, F). The vegetative sink strength differed between the cultivars and was in general lower for the large-fruited cultivars than for the small-fruited cultivars (Table 2).

The wave-like pattern in the source : sink ratio was less clear than in total fruit sink strength due to day-to-day variations in source strength (Fig. 4). Nevertheless, three periods with high source : sink ratios are visible for the large-fruited cultivars 'Nazar' and 'Funky': weeks 15–17, 21–24 and 28–31 (Fig. 4B). The source : sink ratio was higher for these cultivars than for the small-fruited cultivars. This was related to the ratio

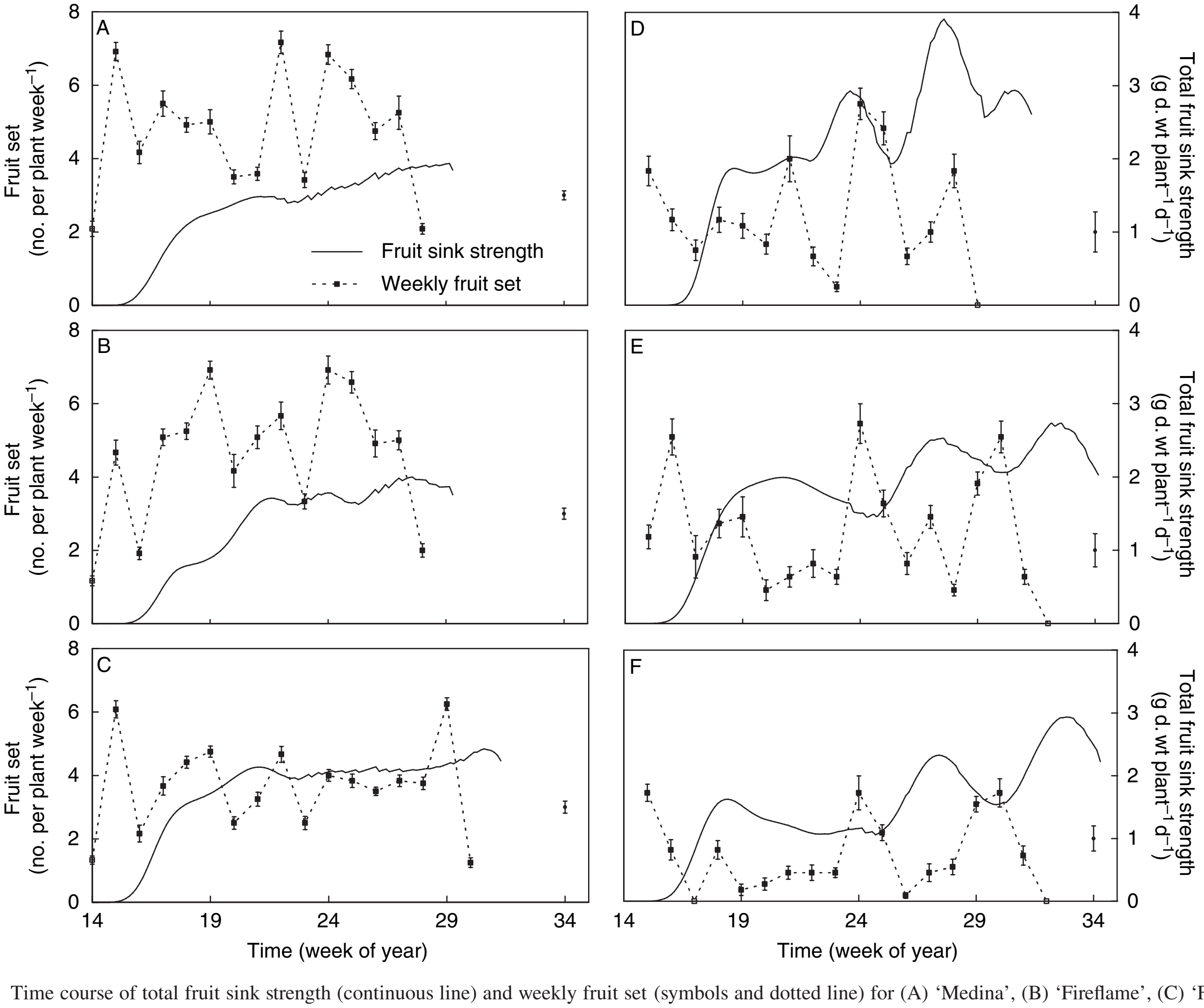

FIG. 3. Time course of total fruit sink strength (continuous line) and weekly fruit set (symbols and dotted line) for (A) 'Medina', (B) 'Fireflame', (C) 'Furila', (D) 'Gepetto', (E) 'Nazar' and (F) 'Funky'. Error bars at fruit set data points represent s.e. ($n = 12$), and the error bar on the right-hand side represents average s.e. of the sink strength.

of actual to potential fruit weight, which was higher for the large-fruited cultivars (Table 2), implying a higher supply of assimilates. The source : sink ratio at fruit set showed a distinctive division into two groups; fruits of small-fruited cultivars set at lower source : sink ratios than the fruits of large-fruited cultivars (Table 2).

Simulations

A higher potential fruit weight resulted in a lower simulated percentage fruit set and a larger variation in fruit set (Table 3). At the same time, average fruit weight increased but the ratio of actual to potential fruit weight was lower. The same happened with fruit set when the source : sink threshold for fruit set was increased, but fruits became heavier, indicating higher source : sink ratios. Different durations in fruit growth hardly affected the simulation results. If the flower appearance rate was reduced, the number of fruits set and the variation in fruit set decreased as well, but the percentage fruit set and the fruit weight increased. Increasing the source strength or decreasing the vegetative sink strength both increased the percentage fruit set and decreased the variation in fruit set, and the fruits became larger as well (Table 3). However, changes in source strength or vegetative sink strength resulted in relatively small changes in the summarized simulation results. None of the changes in parameter values did, at the same time, reduce fruit set, increase variation of fruit set and result in relatively larger fruits. These simultaneous changes were seen in the experimental results. It means that more than one parameter was responsible for the differences in fruit-set patterns.

In the experiment, the parameters were correlated, e.g. a higher potential fruit size was combined with a higher threshold for fruit set. When the simulations were done with parameter combinations observed in the experiment

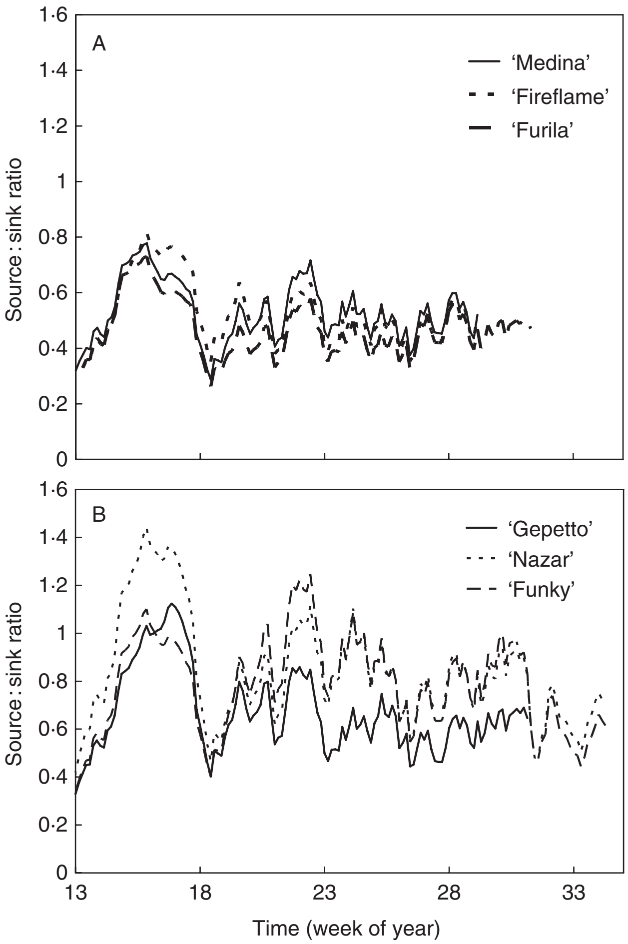

FIG. 4. Time course of the source : sink ratio per plant for the six cultivars ($n = 12$): (A) small-fruited cultivars; (B) large-fruited cultivars. Lines are moving averages over 5 d.

TABLE 3. *Output of the simulation model for default simulation, simulations in which the parameters values were changed one-by-one and simulations with parameter values representing small- and large-fruited cultivars*

Simulation	Changed parameter	Parameter value	Fruit set (no.)	Fruit set (%)	Variation in fruit set (CV)*	Fruit weight (g)†	Ratio actual/potential fruit weight
Default			71	71	0·65	4·21	0·53
Changing parameters one-by-one	Potential fruit weight	4	100	100	0·15	2·51	0·63
		18	41	41	0·99	7·88	0·44
	Source : sink threshold for fruit set	1	26	26	1·46	6·45	0·81
	Fruit-growth duration	57	71	71	0·57	4·19	0·52
		70	70	70	0·64	4·19	0·52
	Flower appearance rate	1	88	44	1·00	3·59	0·45
	Source strength	2·2	64	64	0·69	4·09	0·51
		2·6	79	79	0·50	4·26	0·53
	Vegetative sink strength	1·6	76	76	0·55	4·30	0·54
		2·9	52	52	0·89	3·83	0·48
Small-fruited cultivar‡			123	62	0·69	2·03	0·51
Large-fruited cultivar			21	21	1·84	12·20	0·68

Default simulation had 8 g dm as maximum fruit size, 0·5 as threshold for fruit set, fruit-growth duration of 60 d, flower appearance rate of 0·5 d^{-1}, source strength of 2·4 g dm d^{-1} and vegetative sink strength of 1·9 g dm d^{-1}.

* CV is the coefficient of variation, representing the variation in weekly fruit set calculated as the s.d. of the weekly fruit set divided by the average weekly fruit set

† Of the harvested fruits

‡ For explanation, see Table 1.

(Table 1), fruit-set percentage decreased while variation in fruit set increased when parameters representing small-fruited cultivars were replaced by parameters for large-fruited cultivars (Table 3). At the same time, actual fruit weight and the ratio of actual to potential fruit weight increased. The summarized results of the simulations (e.g. percentage fruit set, CV for fruit set) were close to the experimental results for 'Medina' and 'Funky', although variation in fruit set was overestimated.

DISCUSSION

Several crops show cyclical patterns in fruit set and abortion (Schapendonk and Brouwer, 1984; Passam and Khah, 1992; Heuvelink *et al.*, 2004). In this study, the causes for these fluctuations were analysed with *Capsicum* as a model plant. Marcelis *et al.* (2004) concluded that most of the variation in abortion of sweet pepper flowers/fruits can be related to the source and sink strength of the plant, which is confirmed by the present data for the large-fruited cultivars. Source strength only varied slightly between the cultivars in the current study and therefore, did not contribute to the differences observed in the fruit-set patterns. Fruit set in two of the three large-fruited cultivars was negatively correlated to total fruit sink strength (Fig. 3E, F). In these cultivars, fluctuations in fruit set during the growing season were in anti-phase with fluctuations in plant sink strength. In the other large-fruited cultivar ('Gepetto'; Fig. 3D), fluctuations in total fruit sink strength and fruit set, averaged over 12 plants, were not exactly in anti-phase, due to high interplant variation in the timing of fruit set. Individual plants of this cultivar clearly showed this anti-phase. Cultivars with smaller-sized fruits showed relatively small fluctuations in fruit set and total fruit sink strength. In these cultivars, fruit set also occurred at high values of total fruit sink strength. Hence, the results could not be explained by differences between the cultivars in fruit sink strength alone.

Besides individual fruit sink strength, the source : sink threshold for fruit set played a role in explaining differences in fruit-set patterns of cultivars. The differences in source : sink threshold for fruit set can be interpreted as differences in sensitivity to fruit abortion. Cultivars are known to differ in their sensitivity to abortion, which is often related to high temperature stress (Aloni *et al.*, 1994; Sato *et al.*, 2004; Ledesma *et al.*, 2008) or low light availability (Turner and Wien, 1994; Aloni *et al.*, 1996; Ferree *et al.*, 2001). The temperatures were not so high to cause stress (maximum daily temperature 27 °C) and as the experiment was conducted in spring and summer, light levels were high. Temperature and light stress were therefore not likely in the experiment. Other factors, which have been related to differences in fruit set, were different numbers of seeds (Marcelis and Baan Hofman-Eijer, 1997), differences in sugar and starch content (Lebon *et al.*, 2004) or ovule development stage (Alburquerque *et al.*, 2002). These factors have not been investigated here, but might (partly) explain the different thresholds for fruit set. From an evolutionary point of view, it seems plausible that large-fruited cultivars will need a higher source : sink ratio for fruit set. Their fruits demand more assimilates. The higher threshold will reduce the chance that the plant starts investing in reproduction (fruits with seeds) which can not be successfully completed (source : sink ratio too low during fruit development).

The source : sink ratio is often used in simulation models to simulate fruit set (e.g. Lieth *et al.*, 1986; Bertin and Gary, 1993). Lieth *et al.* (1986) simulated the probability of abortion as a function of the source : sink ratio. Bertin and Gary (1993) used a threshold of the source : sink ratio, below which fruit abortion increased linearly with decreasing source : sink ratio. According to these models, our assumption that fruit set occurs above a certain threshold source : sink ratio is an oversimplification. However, the average source : sink ratio at fruit set is a clear parameter to summarize differences between cultivars.

In a theoretical simulation study, Mathieu *et al.* (2008) showed that alternating patterns in organogenesis (e.g. fruit set) appeared when the demand for assimilates (sink strength) increased too much, causing a decrease in the source : sink ratio. They also used a source : sink threshold to determine whether a fruit could be formed or not. When the threshold for fruit appearance was increased, fewer fruits appeared and the time spans between fruit set flushes increased, as the source : sink ratio was less often above the threshold value and for shorter periods of time. The present experiment demonstrated that the source : sink thresholds for fruit set can indeed differ between cultivars in real-life, but was, in the cultivars used here, correlated to potential fruit size.

Most of the previous research regarding the effect of source and sink strength on fruit set was conducted with just one cultivar (e.g. Pettigrew, 1994; Alkio *et al.*, 2003; Marcelis *et al.*, 2004). Some authors manipulated source and sink strength and observed fruit set in different cultivars (e.g. Egli and Bruening, 2006), but did not explain possible causes of the differences. The present research shows that in comparing fruit-set patterns in relation to source and sink strength, the source : sink threshold for fruit set should be taken into account. It adds a new aspect to the existing knowledge on fruit set in relation to source and sink strength. The results found in the current experiment are also likely to explain differences in fruit set between cultivars with different fruit sizes in other crops such as pumpkin (Stapleton *et al.*, 2000), melon (Valantin-Morison *et al.*, 2006) and cucumber (Jasso-Chaverria *et al.*, 2005). Physiological processes underlying the difference in the source : sink threshold for fruit set should be the subject of further research.

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