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Flower and fruit abortion in sweet pepper in relation to source and sink strength

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Abstract

Source strength (assimilate supply) and sink strength (assimilate demand) of the plant were varied in different ways to investigate to what extent flower/fruit abortion in sweet pepper (*Capsicum annuum* L.) is determined by the availability of assimilates. Source strength was varied by changing the light level, plant density, and leaf pruning. Sink strength was varied by changing the temperature and the number and position of earlier formed fruits. Shading as well as heating for short periods showed that flowers/fruits were the most susceptible to abortion during the first week after anthesis. The different experiments where source strength was varied all showed that when source strength decreased, the rate of abortion increased linearly, whether source strength was decreased by shading, high plant density, or leaf pruning. That flower and fruit abortion not only depends on the source strength but also on the sink strength of competing organs is shown by varying the number or the position of earlier formed fruits. With the same source strength, the rate of abortion showed a close relationship with the growth rate of the earlier formed competing fruits, suggesting that the induction of abortion by earlier formed fruits is due to their sink strength. Most of the variation in abortion could be related to differences in vegetative growth rate, the latter being an indicator of the source–sink ratio. However, with the same vegetative growth rate, the rate of abortion was lower for the leaf pruning treatments where no competing fruits were retained than for the fruit load treatments. This indicates that although most of the variation in abortion can be related to the source and sink strength of the plant, some effects of competing fruits can only be explained by a combination of competition and dominance.

Key words: Abscission, *Capsicum annuum*, competition, dominance, flower abortion, fruit abortion, fruit set, source–sink.

Introduction

Abscission of flower buds, flowers, and fruits is an important yield-limiting factor in many crops including pepper (Wien *et al.*, 1989*a*). However, the simulation of organ abortion is one of the weak features of crop growth models, despite the strong influence on partitioning and yield (Marcelis *et al.*, 1998). In several crop growth models fruit set is simulated as a function of the source–sink ratio (Lieth *et al.*, 1986; Goldschmidt *et al.*, 1992; Bertin and Gary, 1993; Marcelis, 1994). However, the relationships are not very accurate and are based on limited data sets. To improve these models it is essential that the effects of source and sink strength on fruit set are clarified.

Environmental stresses such as heat, drought, and low light conditions or failure of pollination/fertilization (Rylski, 1986; Wien *et al.*, 1989*a*; Aloni *et al.*, 1996; Marcelis and Baan Hofman-Eijer, 1997) are important factors that may induce abscission. Pepper, like some other fruit vegetables, shows a cyclic growth pattern where periods of high fruit set and slow fruit growth alternate with periods of low fruit set and rapid fruit growth (Kato and Tanaka, 1971; Marcelis, 1992).

Many authors claim that abscission of organs is primarily regulated by hormones (Tamas *et al.*, 1979; Van Meeteren and Van Gelder, 1995). The hormonal control of abscission of vegetative and reproductive structures of many species,

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including the reproductive organs of pepper, can primarily be ascribed to the combined action of auxin and ethylene (Wien *et al.*, 1989*a*; Huberman *et al.*, 1997). Several other studies suggest that fruit set is related to the assimilate supply (source strength). For example, shading decreased fruit set in many crops (Guinn, 1974; Kinet, 1977; Wien *et al.*, 1989*b*, Aloni *et al.*, 1996). Differences in susceptibility to abortion of pepper cultivars have been related to assimilate production of the plant and partitioning into reproductive organs (Turner and Wien, 1994*a*, *b*). Effects of heat stress on abscission might also be the result of reduced assimilate availability, but heat stress may specifically reduce the metabolic activity of the flower or the flower bud as well (Aloni *et al.*, 1991). There are some more indications that organ abortion is not solely due to a shortage of assimilate supply but due to other factors which are probably hormonally mediated, such as assimilate utilization and dominance of competing fruits (Schapendonk and Brouwer, 1984; Ruíz and Guardiola, 1994; Aloni *et al.*, 1996).

The presence of a developing fruit can inhibit subsequent set and growth of a young fruit (Stephenson *et al.*, 1988; Bangerth, 1989). This inhibition may be caused by competition for available assimilates, by dominance due to the production of plant growth regulators from the developing fruit, or by a combination of competition and dominance (Tamas *et al.*, 1979; Stephenson *et al.*, 1988; Bangerth, 1989; Marcelis and Baan Hofman-Eijer, 1997; Heuvelink and Körner, 2001). Attempts to quantify the relationship between assimilate demand (sink strength) of older fruits on fruit set of later formed fruits are scarce, and a clear distinction between dominance and competition is usually difficult to make.

The aim of this study was to investigate to what extent flower/fruit abortion in sweet pepper is determined by the availability of assimilates. It was investigated in which stage of flower and fruit development the flower/fruit is susceptible for abscission. The source and sink strengths of the plant were varied in different ways during the susceptible period. Source strength was varied by changing the light level, plant density, and leaf pruning. Sink strength was varied by changing the temperature and the number and position of competing earlier formed fruits.

Materials and methods

Sweet pepper plants (*Capsicum annuum* L. cv. Mazurka) were grown in either aerated nutrient solution in climate chambers (Experiments 2, 3) or on rockwool in glasshouses (Experiments 1, 4, 5) in The Netherlands (Lat 52° N). Plants were pruned to one (Experiments 2–5) or two main branches (Experiment 1) per plant with side shoots stopped at one leaf. Plant density was 3 plants m^{-2}, unless otherwise stated. In Experiments 1, 4, and 5, treatments were arranged in a randomized block design with seven (Experiment 1), six (Experiment 4) or four (Experiment 5) blocks; the total number of replicate plants was 7, 6, or 16, respectively. The data were analysed by analysis of variance. For abortion data of Experiments 4 and 5, the

analysis of variance was carried out by using generalized linear models with binomial distribution. When a plant was destructively harvested before the end of the experiment, it was replaced by a comparable plant in order not to disturb the light distribution in the canopy.

Plant density (Experiment 1)

Seeds were sown on 8 November. No flower or fruit pruning was applied. Plant density was 1.56 plants m^{-2}, 3.12 plants m^{-2}, and 4.63 plants m^{-2}. The number of flowers and fruits were recorded weekly. Fruits were harvested when they turned red. Dry weights of all removed plant parts were determined and on 2 July plants were harvested for determination of plant dry weight (2 d, 105 °C). Average greenhouse temperature was 21 °C, average global radiation outside the greenhouse was 11 MJ m^{-2} d^{-1}.

Susceptible period for shading (Experiment 2)

All flowers were removed except three flowers at nodes 3, 4, and 5 of the main branch. Each flower reached anthesis about 5 d after the previous one.

Plants were grown on an aerated nutrient solution in four containers of five plants each. At different periods plants were shaded for 7 d by cheese cloth which reduced light intensity to 33%. All plants in the same container were shaded at the same time. The experiment was repeated three times. In the first two replicate series, plants were shaded during the first, third, or fifth week after anthesis of the flower at node 3. In the third replicate series, shading was performed the week before anthesis and the second and fourth weeks after anthesis of the flower at node 3. In each replicate series five control plants were not shaded.

Irradiance was provided by high pressure sodium lamps (Philips SON-T 400W) and fluorescent tubular lamps (Metalicht TL 58 W, colour 33; fluorescent lamps:sodium lamps=1:3) for 12 h d^{-1}. Photosynthetically active radiation without shading was 140 µmol m^{-2} s^{-1}. After the main light period, the chambers were illuminated for 15 min by incandescent lamps. The temperature was 20 °C (22/18 °C day/night) and relative air humidity was 85%.

Susceptible period for high temperature (Experiment 3)

All flowers were removed except three flowers at nodes 1, 2, and 3, at nodes 3, 4, and 5 or at nodes 5, 6, and 7 on the main branch. Each flower reached anthesis about 4 d after the previous one. The three treatments were completely randomized among 18 plants. Two weeks after anthesis of the first flowers, temperature was increased to 33 °C (day and night) for four days. One month after anthesis of the first flowers, abortion was determined. After all fruits had been removed, the same plants were used to repeat the experiment by retaining three flowers at nodes 16, 17, and 18, at nodes 18, 19, and 20 or at nodes 20, 21, and 22. Before anthesis all lower leaves were removed, except seven leaves below node 16 in order to have the same number of leaves per plant as in the first experimental series.

Irradiance was provided by high pressure mercury lamps (Philips HPI 400 W) for 12 h d^{-1}. Photosynthetically active radiation was 280 µmol m^{-2} s^{-1} in the first experimental series and 140 µmol m^{-2} s^{-1} in the second one. After the main light period, the chambers were illuminated for 15 min by incandescent lamps. The temperature was 20 °C (22/18 °C day/night) except during the heat treatment (at 33 °C). Relative air humidity was 80% during the whole experiment.

Leaf and fruit removal (Experiment 4)

Seeds were sown on 20 July. At anthesis of the first flower on the main branch (16 September) fruit and leaf removal treatments started. Leaf number was varied by removing 20, 40, 60, and 80% of leaves below the fourth node of the main branch while all flowers below that node were removed (Fig. 1). The number of competing fruits was
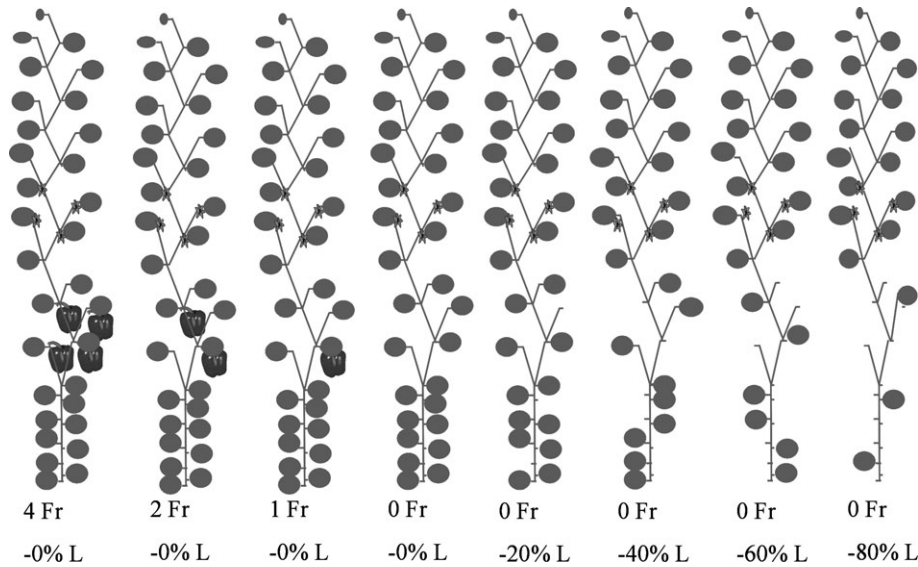
Fig. 1. Schematic drawing of the position of flowers/fruits on the plant to study the effects of fruit and leaf removal on the abortion of four later-formed flowers/fruits in Experiment 4. Zero, 1, 2, or 4 early-formed fruits (Fr) were retained, while 0, 20, 40, 60, or 80% of the full-grown leaves (L) were removed below the later-formed flowers.

varied by retaining 0, 1, 2, or 4 flowers at the first and second nodes of the main branch (anthesis between 16 and 20 September) while no leaves were removed. Abortion of four flowers/fruits at the fourth and fifth node (anthesis between 30 September and 6 October) was studied. Above these flowers all flowers except two flowers at node 6 were removed. Plants subjected to leaf pruning treatments were surrounded by guard plants (no leaves pruned). Rates of dry weight increase of fruits and vegetative parts were determined from destructive harvests on 29 September (at about anthesis of the flowers at node 4) and 12 October (2 weeks after anthesis). Abortion was determined 4 weeks after anthesis of the flowers studied.

From the start until the end of the treatments average greenhouse temperature was 21 °C and global radiation outside the greenhouse was 8 MJ m^{-2} d^{-1}. Supplementary irradiance (35 μmol m^{-2} s^{-1} PAR) was provided by high pressure sodium lamps (Philips SON-T AGRO 400 W) at moments when outside global radiation was lower than 20 W m^{-2} between 07.00 h and 19.00 h.

Position of early-formed fruits (Experiment 5)

Seeds were sown on 20 June. One early-formed fruit was retained at node 1, 3, 5, 7, 8. or 9, while the control contained no early-formed fruit (Fig. 2). The effects of these early-formed fruits on abortion of two flowers/fruits at node 10 were studied. In order to create a wide range of source–sink ratios these treatments were combined, with removal of 50% of the leaves by removing weekly all expanded leaves from the side shoots in half of the plants. On the remaining plants no leaves were removed.

Blocks were replicates in time. In each block the fruits were retained two nodes higher than in the previous block (position of the first retained fruit was always numbered as node 1). For blocks 2–4 one additional fruit per plant was retained in the lower nodes until the start of the treatments (anthesis of the early-formed flower in node 1). Anthesis dates of the first flower which was retained were 21 August and 2, 14, and 25 September in blocks 1, 2, 3, and 4, respectively. Anthesis dates for node 10 were 6 weeks later.

Rates of dry weight increase of the fruits one week after anthesis of the flowers at node 10, were determined from measurements of the length and diameter of all fruits at anthesis at node 10 and one week
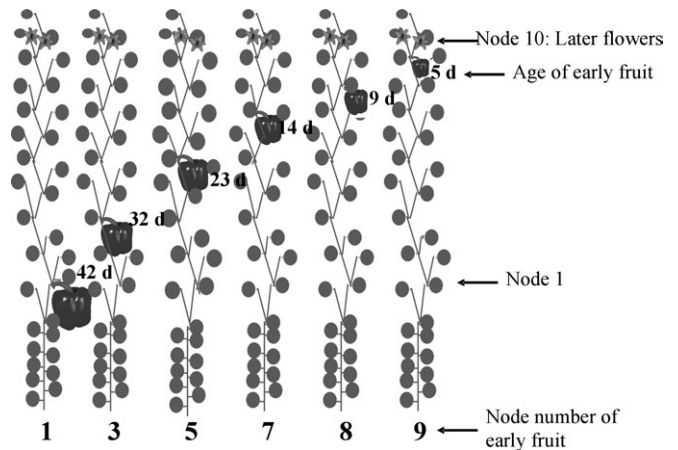

Fig. 2. Schematic drawing of the position of flowers/fruits on the plant to study the effects of different developmental stages of one early-formed fruit on the abortion of the two later-formed flowers/fruits at node 10 in Experiment 5. Age (days from anthesis) of the early-formed fruits at time of anthesis of the later-formed fruits is indicated in the figure. Shown is the treatment with 100% leaves. For the treatment with 50% leaves every other expanded leaf was removed. The control treatment where no early-formed fruit was retained is not shown.

later, as described by Marcelis and Baan Hofman-Eijer (1995). The rate of plant dry weight increase was determined from the destructive harvests of plants at anthesis at node 10 and of (other) plants four weeks later. Assuming a linear relationship between crop growth and radiation (Monteith, 1994), the rate of total plant dry weight increase during the first week after anthesis was estimated from the average growth rate over four weeks and the radiation during the different weeks. The rate of dry weight increase of the vegetative parts during the first week after anthesis was calculated by subtracting the growth rate of all fruits from that of the total plant. At the final harvest (4 weeks after anthesis at node 10), the percentage of aborted fruits was determined.

Average greenhouse temperature was 21 °C. Global radiation outside the greenhouse was 6.7 MJ m^{-2} d^{-1} (4.5 MJ m^{-2} d^{-1} during the fruit set period).

Vegetative growth rate as a measure of source–sink ratio

According to Marcelis (1996) the growth rate of an organ (Y_i) is the product of source strength (source) and fraction of dry matter partitioned into that organ (f_i) (Equation 1). The latter can be calculated by the ratio between sink strength of the organ (S_i) divided by that of the total plant (ΣS) (Equation 2). This means that when the vegetative sink strength is constant, the vegetative growth rate is proportional to the source–sink ratio (source/ΣS) of the plant (Equation 3). At constant temperature the vegetative sink strength of cucumber and tomato was indeed shown to be constant (Marcelis, 1994; Heuvelink, 1996)

$$Y_i = \text{source} \times f_i \quad (1)$$

$$Y_i = \text{source} \times S_i / \Sigma S \quad (2)$$

$$Y_i = S_i \times \text{source} / \Sigma S \quad (3)$$

Results

Under normal growing conditions in a greenhouse sweet pepper plants form a large number of flowers, but only a small fraction sets fruit (Table 1). Increasing plant density decreased dry matter production per plant and increased flower and fruit abortion (Table 1). Shading plants for

Table 1. *The effect of plant density on total plant dry weight, number of flowers produced, and abortion of flowers and fruits of sweet pepper plants grown for 237 d in a greenhouse (Experiment 1)*

Plant density (m^{-2})	Total dry weight (g plant^{-1})[a]	Flower number (plant^{-1})[a]	Abortion (%)[a]
1.6	640 a	136 a	69 a
3.1	448 b	136 a	81 b
4.6	390 b	136 a	86 c
SE mean	25	4	1

[a] Means within a column were not significantly different when followed by the same letter (*P*=0.05).

1 week at different developmental stages showed that flowers and fruits were susceptible to abortion from shortly before anthesis until about 2 weeks after anthesis (Fig. 3A). During the same period abortion could be induced by high temperature (Fig. 3B).

The removal of fully grown leaves reduced dry matter production and increased flower/fruit abortion (Table 2). Increasing the number of early-formed competing fruits increased the abortion of later-formed flowers/fruits, but did not affect total plant growth (Table 2). When comparing the different levels of leaf removal or levels of fruit pruning separately, abortion showed a negative linear relationship to the vegetative growth rate during the period of fruit set; that is, fewer fruits aborted at higher rates of vegetative growth (Fig. 4). However, the slope of the lines for the fruit and leaf pruning treatments were clearly different. With the same vegetative growth rate, abortion was lowest for the leaf-pruning treatments, where no early-formed fruits were present on the plant (Fig. 4). Abortion linearly increased with growth rate of the earlier formed fruits (r^2=0.97, data not shown).

An experiment was conducted (scheme of treatments in Fig. 2), to study the developmental stage in which an early-formed fruit induces the abortion of later-formed flowers and fruits and whether these effects are related to the assimilate demand of the early-formed fruit. Abortion rates of the later-formed fruits were lowest when they were located either close to or far from the early-formed fruits (Fig. 5). The highest abortion rates were observed when the distance was intermediate (3–5 nodes), which means that abortion was most frequent when the early-formed fruits were 2–3 weeks old at anthesis of the later-formed fruits. The negative effect of the early-formed fruits on fruit set was closely related to their growth rates. Similar patterns of competition between fruits were observed whether or not 50% of the leaves were retained (Fig. 5). However, rates of abortion were distinctly increased (on average by 110%), while growth rate of the early-formed fruits was only reduced about 10% by halving the number of leaves. For both leaf-pruning treatments a linear relationship between
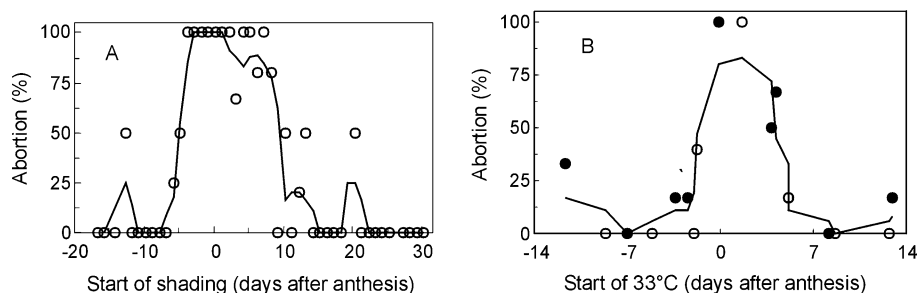

Fig. 3. The effect of different starting dates of a 7 d period of shading (33% light) (A) or a 4 d period of high temperature (33 °C) on flower/fruit abortion (B). Each data point represents 1–6 (A) or 6 (B) replicate buds/flowers/fruits. The lines are moving averages of the previous, the present, and the next day, corrected for a different number of replicates. In the shading experiment photosynthetically active radiation (PAR) at plant level was 140 μmol m^{-2} s^{-1} when unshaded and 47 μmol m^{-2} s^{-1} when shaded; in the high temperature experiment photosynthetically active radiation was 140 (closed circles) or 280 μmol m^{-2} s^{-1} (open circles).

percentage abortion (y) and fruit growth rate (x, gd^{-1}) was observed, but the coefficients of the relationship were different between the leaf-pruning treatments ($y=92-27x$, $r^2=0.80$ for 50% leaves and $y=104-14x$, $r^2=0.90$ for 100% leaves, respectively). Abortion linearly decreased with increasing growth rate of the vegetative parts (Fig. 6). Although the slope of the line seemed to be steeper when 50% of leaves were removed compared with the treatments without leaf removal, one linear relationship adequately described the data for both treatments ($r^2=0.86$).

Discussion

Under temperate climate conditions, without flower or fruit pruning, only a small fraction of sweet pepper flowers sets

Table 2. *The effect of early-formed fruits and full-grown leaves on abortion of later-formed flowers/fruits and the rate of dry matter production of the plant*

The production rate is the average rate during the period from anthesis of later-formed fruits to 2 weeks after anthesis. For schematic drawing of treatments see Fig. 1 (Experiment 4).

Number of early fruits	Removed leaves (%)	Dry matter production (g d^{-1})[a]	Abortion (%)[a]
4	0	1.6 a	100±0 a
2	0	1.5 ab	88±6 b
1	0	1.5 ab	58±8 c
0	0	1.5 ab	8±5 ef
0	20	1.3 bc	13±6 ef
0	40	1.1 cd	17±6 def
0	60	0.8 de	33±8 d
0	80	0.7 e	29±8 de
SE mean		0.1	

[a] Means within a column were not significantly different when followed by the same letter ($P=0.05$).
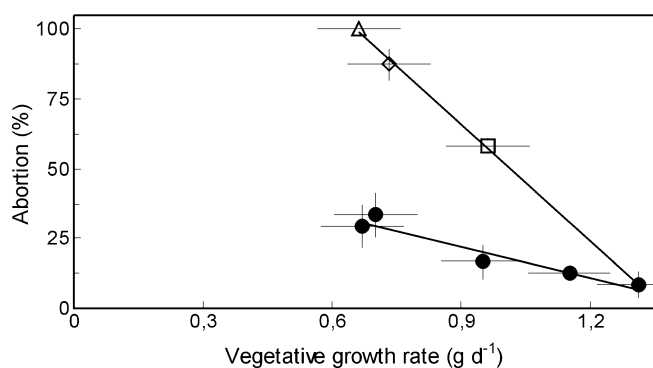

Fig. 4. The relationship between abortion of later-formed fruits and vegetative growth rate when the number of early-formed fruits or leaf number was varied. For the fruit number treatments no leaves were pruned (open symbols), while for the leaf number treatments no early-formed fruits were retained on the plant (closed symbols). The number of early-formed fruits were 0 (circle), 1 (square), 2 (diamond), or 4 (triangle). Growth rate is the average rate during the period from anthesis of later-formed fruits to 2 weeks after anthesis. Horizontal and vertical bars indicate standard errors of means. For schematic drawing of treatments see Fig. 1 (Experiment 4).

fruit, indicating that flower initiation does not limit the number of fruits produced, but that fruit retention is the limiting factor (Table 1). Other authors, have also reported low fractions of flowers setting fruit in pepper (Rylski, 1986; Bakker, 1989).

Susceptible period for abortion

Wien *et al.* (1989*a*) applying shade treatments to pepper plants, concluded that open flowers were the most susceptible to abortion, while Aloni *et al.* (1991), applying heat stress, concluded that flower buds were the most susceptible to abortion. Sato *et al.* (2002) found tomato flowers were most susceptible to elevated temperature stress 8–13 d before anthesis. Applying shade and heat stress at different stages, it was shown that flowers/fruits of sweet pepper were susceptible to abortion from a few days before anthesis until about 2 weeks after anthesis (Fig. 3). Flowers/fruits were probably most susceptible in the middle of this period, i.e. the first week after anthesis. The same susceptible period was found for shade stress and high temperature stress, suggesting that both stresses act on the
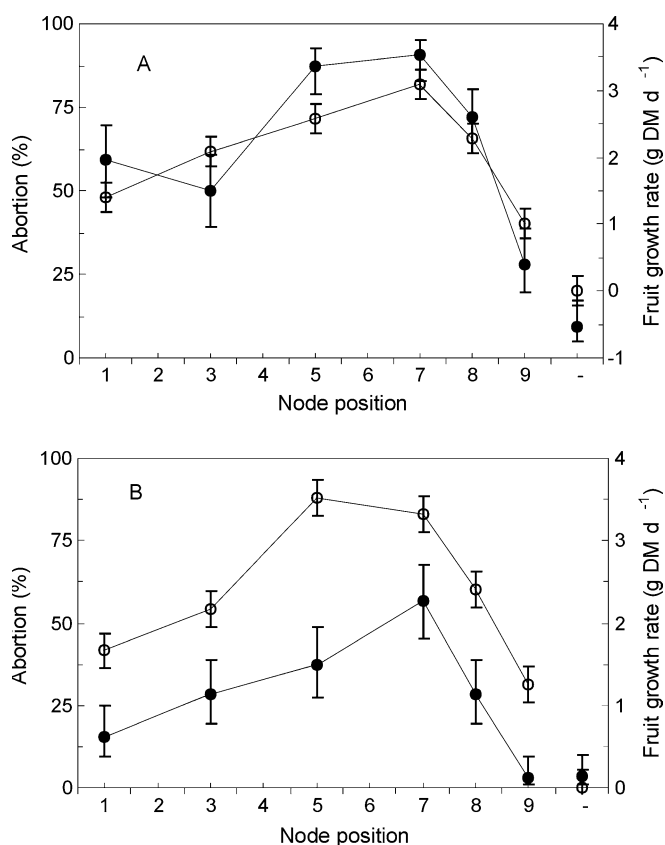

Fig. 5. Abortion of later-formed fruits at node number 10 (closed symbols) and growth rate (open symbols) of competing early-formed fruits when node position of the early-formed fruit was varied in plants with 50% (A) and 100% leaves (B). Growth rate is the average rate during 1 week from anthesis of later-formed fruits. Vertical bars indicate standard errors of means. For schematic drawing of treatments see Fig. 2 (Experiment 5).
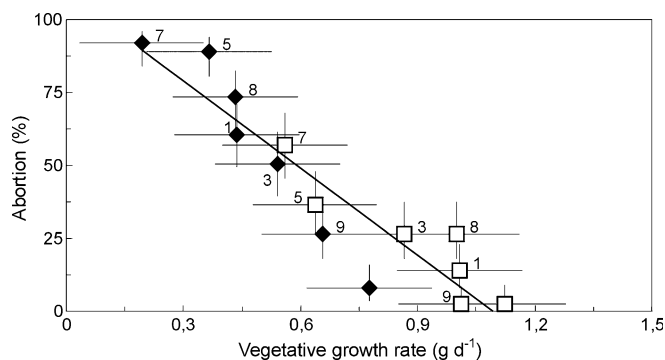
Fig. 6. The relationship between flower/fruit abortion and vegetative growth rate when the position of early-formed fruits was varied in plants with 50% (closed symbols) and 100% leaves (open symbols). Growth rate is the average rate during the period from anthesis of later-formed fruits to 1 week after anthesis. Numbers near the symbols indicate the node position of the early-formed fruits. Horizontal and vertical bars indicate standard errors of means. For schematic drawing of treatments see Fig. 2 (Experiment 5).

same process leading to abscission. Wien *et al.* (1989*a*) also observed that cultivar susceptibility was the same for shade and heat stress. Both stresses may act on assimilates available for flower/fruit development as they both have been reported to reduce sugar concentrations (Wien *et al.*, 1989*b*; Aloni *et al.*, 1991), although effects on capacity to accumulate assimilates cannot be excluded. Less likely, temperature effects could also be confounded with effects of the vapour pressure deficit of the air (*VPD*) on abortion as the *VPD* was not kept constant at the different temperatures (relative humidity was maintained at 80%).

Abortion in relation to the source–sink balance

The different experiments where source strength (assimilate supply) was varied all pointed out that when source strength decreased the rate of flower/fruit abortion increased, whether source strength was decreased by shading, high plant density, or leaf pruning. That these treatments, which all affected light interception per plant, decreased the source strength of the plants was substantiated by the dry weight production of the plants. Using dry matter production as a measure of total source strength of the plant, abortion decreased linearly when source strength of the plant during the critical period increased, as found in the plant density and leaf pruning experiments. The results showed that abortion not only depends on the source strength but also on sink strength (assimilate demand) of competing organs. Varying sink strength by changing the number (Table 2) or position of early-formed fruits (Fig. 5; data about total dry matter production not shown) affected abortion, but not total dry matter production (source strength) during the critical period. With the same source strength, the rate of abortion showed a linear relationship with the growth rate of the earlier formed competing fruits, suggesting that the induction of abortion by earlier formed

fruits is due to their sink strength. In fact, the growth rate of an organ is an indicator of assimilate utilization which is the result of its sink strength as well as the sink strength of other organs and assimilate supply (Marcelis, 1996). As outlined in the Materials and methods, when the vegetative sink strength is constant the vegetative growth rate is proportional to the source–sink ratio of the plant. The observed linear relationships between abortion and vegetative growth rate therefore indicate a linear relationship between abortion and source–sink ratio. In cucumber, a correlation between fruit abortion and vegetative growth rate was also observed (Marcelis, 1992). Bertin (1995) related fruit set in tomato to the ratio between actual and potential fruit growth rate as a measure of the ratio between assimilate supply and demand. She observed a distinct increase in fruit set with an increase in the supply/demand ratio when this ratio was below a threshold value of 0.5.

Most of the observed variation in flower and fruit abortion could be related to differences in vegetative growth rate or source–sink balance of the plant. However, with the same vegetative growth rate the abortion rate was lower for the leaf pruning treatments where no competing fruits were retained than for the fruit load treatments (Fig. 4). This difference could partly be explained by the fact that when full-grown leaves are pruned, probably not only a source but also a sink is removed. Hence, the source–sink ratio was probably relatively less reduced by leaf pruning than the vegetative growth rate (see also Equation 3). The most likely explanation for this difference is that the effects of early-formed fruits on abortion were not completely the result of competition for assimilates, but due to a combination of competition and dominance (Marcelis and Baan Hofman-Eijer, 1997). Similarly, Schapendonk and Brouwer (1984) observed in cucumber some correlation between the growth of older fruits and the abortion of later-formed fruits. However, reducing assimilate supply by removal of all leaves except one did not cause fruit abortion when there were no early-formed fruits, suggesting that abortion was not solely regulated by assimilate availability but also by fruit dominance. Bangerth (1989) hypothesized that fruit dominance can be explained by auxin export of the earlier developed fruits which inhibits the auxin export of later-developed fruits and therefore the development of later-developed fruits.

Hormone versus assimilate theory

Although the hormone theory and assimilate theory may look to be two contrasting theories explaining flower/fruit abscission, it might well be that a change in assimilate availability is the trigger for a change of the hormonal balance which leads to abscission. Shading has been shown to decrease the sugar (fructose, glucose, sucrose) levels in pepper flower buds and in cotton bolls, while ethylene production negatively correlated with sugar content of the buds or bolls (Guinn, 1976; Wien *et al.*, 1989*b*). Several

studies (Farrar, 1992; Koch *et al.*, 1992; Aloni *et al.*, 1997) suggested that sucrose is more than simply an energy source, but may also act as a messenger that operates at the level of gene expression. This indicates that assimilate availability is a key factor in the regulation of organ development.

Establishing the relationship between abortion and assimilate availability is not an easy task as it is difficult to quantify assimilate availability (Brouwer, 1983; Mäkelä and Sievänen, 1987). Measuring sugar contents might help to elucidate this relationship. However, the questions are which sugars should be measured, at which time of the day, and in which tissue. Moreover, an increased concentration can be the result of an increase in supply or a decrease in utilization, while a constant concentration at increasing assimilate supply can be the result of a high utilization rate of sugars. Consequently, many authors did not find a relationship between organ abortion or growth and carbohydrate content (Darnell and Martin, 1988; Erner, 1989; Ruíz and Guardiola, 1994). However, other authors observed a negative correlation between organ abortion and carbohydrate content (Wien *et al.*, 1989*b*; Aloni *et al.*, 1997).

Conclusion

Quantitative information on the relationship between flower/fruit abortion and source and sink strength of the plant is scarce. In this study, total dry matter production of the plant was used as an indicator of source strength and the growth rate of the vegetative parts as an indicator of the source–sink balance. Furthermore, when source strength was constant, growth rate of the fruits was considered an indicator of sink strength. These data show that most of the variation in abortion of sweet pepper flowers/fruits can be related to the source and sink strength of the plant, but some effects of earlier formed fruits can only be explained by a combination of competition and dominance.

References

Aloni B, Karni L, Zaidman Z, Schaffer AA. 1996. Changes of carbohydrates in pepper (*Capsicum annuum* L.) flowers in relation to their abscission under different shading regimes. *Annals of Botany* **78,** 163–168.

Aloni B, Karni L, Zaidman Z, Schaffer AA. 1997. The relationship between sucrose supply, sucrose-cleaving enzymes and flower abortion in pepper. *Annals of Botany* **79,** 601–605.

Aloni B, Pashkar T, Karni L. 1991. Partitioning of [^{14}C]sucrose and acid invertase activity in reproductive organs of pepper plants in relation to their abscission under heat stress. *Annals of Botany* **67,** 371–377.

Bakker JC. 1989. The effects of temperature on flowering, fruit set and fruit development of glasshouse sweet pepper (*Capsicum annuum* L.). *Journal of Horticultural Science* **64,** 313–320.

Bangerth F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiologia Plantarum* **76,** 608–614.

Bertin N. 1995. Competition for assimilates and fruit position affect fruit set in indeterminate greenhouse tomato. *Annals of Botany* **75,** 55–65.

Bertin N, Gary C. 1993. Tomato fruit-set: a case study for validation of the model TOMGRO. *Acta Horticulturae* **328,** 185–193.

Brouwer R. 1983. Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science* **31,** 335–348.

Darnell RL, Martin GC. 1988. Role of assimilate translocation and carbohydrate accumulation in fruit set of strawberry. *Journal of the American Society for Horticultural Science* **113,** 114–118.

Erner Y. 1989. Citrus fruit set: carbohydrate, hormone, and leaf mineral relationships. In: Wright CJ, ed. *Manipulation of fruiting*. London: Butterworths, 233–243.

Farrar JF. 1992. The whole plant: carbon partitioning during development. In: Pollock CJ, Farrar JF, Gordon AJ, eds. *Carbon partitioning within and between organisms*. Oxford: Bios Scientific Publishers, 163–179.

Goldschmidt EE, Harpaz A, Gal S, Rabber D, Gelb E. 1992. Simulation of fruitlet thinning effects in *Citrus* by a dynamic growth model. *Proceedings of International Citriculture* **1,** 515–519.

Guinn G. 1974. Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. *Crop Science* **14,** 291–293.

Guinn G. 1976. Nutritional and ethylene evolution by young cotton bolls. *Crop Science* **16,** 89–91.

Heuvelink E. 1996. Dry matter partitioning in tomato: validation of a dynamic simulation model. *Annals Botany* **77,** 71–80.

Heuvelink E, Körner O. 2001. Parthenocarpic fruit growth reduces yield fluctuation and blossom-end rot in sweet pepper. *Annals of Botany* **88,** 69–74.

Huberman M, Riov J, Aloni B, Goren R. 1997. Role of ethylene biosynthesis and auxin content and transport in high temperature-induced abscission of pepper reproductive organs. *Journal of Plant Growth Regulation* **16,** 129–135.

Kato T, Tanaka M. 1971. Studies on the fruit setting and development of sweet peppers. I. Fruiting behavior. *Journal of the Japanese Society for Horticultural Science* **40,** 359–366.

Kinet JM. 1977. Effect of light conditions on the development of the inflorescence in tomato. *Scientia Horticulturae* **6,** 15–26.

Koch KE, Nolte KD, Duke ER, McCarty DR, Avigne WT. 1992. Sugar levels modulate differential expression of maize sucrose synthase genes. *The Plant Cell* **4,** 59–69.

Lieth JH, Arkin GF, Hearn AB, Jackson BS. 1986. Modeling cotton fruiting from abscission. *Agronomy Journal* **78,** 730–735.

Mäkelä AA, Sievänen RP. 1987. Comparison of two shoot–root partitioning models with respect to substrate utilization and functional balance. *Annals of Botany* **59,** 129–40.

Marcelis LFM. 1992. The dynamics of growth and dry matter distribution in cucumber. *Annals of Botany* **69,** 487–492.

Marcelis LFM. 1994. A simulation model for dry matter partitioning in cucumber. *Annals of Botany* **74,** 43–52.

Marcelis LFM. 1996. Sink strength as a determinant of dry matter partitioning in the whole plant. *Journal of Experimental Botany* **47,** 1281–1291.

Marcelis LFM, Baan Hofman-Eijer LR. 1995. Growth analysis of sweet pepper fruit (*Capsicum annuum* L.). *Acta Horticulturae* **412,** 470–478.

Marcelis LFM, Baan Hofman-Eijer LR. 1997. Effects of seed number on competition and dominance among fruits in *Capsicum annuum* L. *Annals of Botany* **79,** 687–93.

Marcelis LFM, Heuvelink E, Goudriaan J. 1998. Modelling biomass production and yield of horticultural crops: a review. *Scientia Horticulturae* **74,** 83–111.

Monteith JL. 1994. Validity of the correlation between intercepted radiation and biomass. *Agricultural and Forest Meteorology* **68,** 213–220.

Ruíz R, Guardiola JL. 1994. Carbohydrate and mineral nutrition of orange fruitlets in relation to growth and abscission. *Physiologia Plantarum* **90,** 27–36.

Rylski I. 1986. Pepper (*Capsicum*). In: Monselise SP, ed. *Handbook of fruit set and development*. Boca Raton: CRC Press, 341–354.

Sato S, Peet MM, Thomas JF. 2002. Determining critical pre- and post-anthesis periods and physiological processes in *Lycopersicon esculentum* Mill. Exposed to moderately elevated temperatures. *Journal of Experimental Botany* **53,** 1187–1195.

Schapendonk AHCM, Brouwer P. 1984. Fruit growth of cucumber in relation to assimilate supply and sink activity. *Scientia Horticulturae* **23,** 21–33.

Stephenson AG, Devlin B, Horton JB. 1988. The effects of seed number and prior fruit dominance on the pattern of fruit production in *Cucurbita pepo* (Zucchini squash). *Annals of Botany* **62,** 653–661.

Tamas IA, Wallace DH, Ludford PM, Ozbun JL. 1979. Effect of older fruits on abortion and abscisic acid concentration of younger fruits in *Phaseolus vulgaris* L. *Plant Physiology* **64,** 620–622.

Turner AD, Wien HC. 1994*a*. Dry matter assimilation and partitioning in pepper cultivars differing in susceptibility to stress-induced bud and flower abscission. *Annals of Botany* **73,** 617–622.

Turner AD, Wien HC. 1994*b*. Photosynthesis, dark respiration and bud sugar concentrations in pepper cultivars differing in suscep- tibility to stress-induced bud abscission. *Annals of Botany* **73,** 623–628.

Van Meeteren U, Van Gelder H. 1995. Role of flower buds in flower bud abscission in *Hibiscus*. *Acta Horticulturae* **405,** 284–289.

Wien HC, Tripp KE, Hernandez-Armenta R, Turner AD. 1989*a*. Abscission of reproductive structures in pepper: causes, mecha- nisms and control. In: Green SK, ed. *Tomato and pepper pro- duction in the tropics*. Taipei, Taiwan, R.O.C: Asian Vegetable Research and Development Center, 150–165.

Wien HC, Turner AD, Yang SF. 1989*b*. Hormonal basis for low light intensity induced flower bud abscission of pepper. *Journal of the American Society for Horticultural Science* **114,** 981–985.