Competition for Assimilates and Fruit Position Affect Fruit Set in Indeterminate Greenhouse Tomato

N. BERTIN*

Institut National de la Recherche Agronomique, Centre de Recherches d'Avignon, Station de Bioclimatologie, Domaine Saint-Paul, BP91, F84143 Montfavet Cedex, France

Received: 16 November 1993 Accepted: 10 August 1994

Localization and characterization of fruit set in winter tomato crops was investigated to determine the main internal and external controlling factors and to establish a quantitative relationship between fruit set and competition for assimilates. Individual fruit growth and development was assessed on a beef tomato cultivar during the reproductive period (first nine inflorescences). A non-destructive photograph technique was used to measure fruit growth from very early stages of their development and then calliper measurements were made on big fruits. From these measurements we determined the precise developmental stage at which fruit growth stopped. Fruit potential growth, which is defined as the growth achieved in non-limiting conditions for assimilate supply, was also assessed by this method on plants thinned to one flower per inflorescence. The latter was used to calculate the ratio between actual and potential growth, which was found to be a good index of the competition for assimilates.

Time lags of fruit set were observed mainly on distal organs. When more than three flowers were left on each inflorescence, distal organs developed at the same time as proximal organs of the following inflorescence. Consequently they were submitted to a double competition within one inflorescence and among inflorescences. It was shown that, what is commonly named 'fruit set failure', is not an irreversible death of the organ and that a small fruit could resume growth after a delay of several weeks as soon as the first fruits ripened and thus ceased to compete for assimilates. In that case proximal fruits resumed growth before distal ones. The delayed fruits contained only few seeds but a germination test confirmed that fertilization took place before fruit set failed.

Competition for assimilates was calculated during plant development by the ratio between actual and potential fruit growth. Potential growth of proximal fruits was strongly dependent on the position of the inflorescence on the stem, whereas potential growth of distal fruits was lower than or equal to that of proximal fruits of the same inflorescence and it was independent on the inflorescence position. We took into account both inflorescence and fruit positions to establish a quantitative relationship between fruit set of individual inflorescences and the ratio between actual and potential fruit growth.

Key words: Tomato, *Lycopersicon esculentum* Mill., fruit set, competition for assimilates, potential growth, fruit sink strength.

INTRODUCTION

The economic yield of tomato (*Lycopersicon esculentum* Mill.) results from the number of harvested fruits per unit area and their individual size. The latter is an important factor of quality and should be as regular as possible over the whole production period. Number of fruits per inflorescence is determined by fruit set, and it has also an indirect effect on final fruit size, which has been shown to decrease when the number of inflorescences per plant increased (Fisher, 1977). For these reasons, number of fruits per inflorescence is an important component of tomato yield.

Fruit set has been defined as the transition between flower opening and fruit growth inception (Stephenson, 1981) or, by the proportion of flowers which reach anthesis to give fruits of normal size ($\varnothing > 37$ mm) (Picken, 1984). Thus, the term fruit set will be used to design fruit growth inception followed by normal fruit growth and, the term fruit set delay

(the usual term, fruit set failure, will be avoided) will design an interruption of fruit growth at early developmental stage ($\varnothing < 20$ mm). As many external and internal factors may be involved at different stages, it is quite important to define the precise developmental stage that is concerned. Before anthesis, the inflorescence can abort mainly because of the competition for assimilates between the vegetative apex and the last initiated inflorescence (Kinet *et al.*, 1978; Kinet and Leonard, 1983; Leonard *et al.*, 1983). The problems arising before fertilization have been shown to depend on pollen production, viability and transfer (Maisonneuve and Philouze, 1982); they occur under extreme temperature and humidity, but the sensitivity depends on cultivar. Ovule fertilization may also fail at high temperature and low light (Charles and Harris, 1972; Rudich, Zamski and Regev 1977; Picken, 1984). However, under normal commercial conditions in winter, that is for tomato plants grown under controlled climate with assisted mechanical pollination, problems arising before fertilization should be limited except under very low light conditions.

After fertilization, fruit growth can be delayed or stopped immediately (Picken, 1984; De Koning, 1989): that is what

* Present address: Joint Research Centre, Environment Institute, T.P. 050, I-21020 Ispra (VA), Italy.

is usually called 'fruit set failure' in the literature but 'fruit set delay' will be used in this work since fruit set has occurred but fruit growth and development are delayed at an early stage. For many species, hormonal and trophic hypotheses have been used to explain fruit set control and these two approaches seem more complementary than opposed. However, the number of fruit would be limited more by resource availability than by female flower morphology or number and, for most hermaphrodite species, the natural pollination rate exceeds the fruit set rate (Stephenson, 1981; Burge, 1989). According to Stephenson (1981), plant growth regulators may play a role in young fruit differentiation and resource mobilization, but resource availability in the plant is the main limiting factor for fruit set control. In tomato crops, fruit set can be reduced severely in winter under low light conditions and many authors have attributed this growth interruption to the competition for assimilates (Ho, 1984; Picken, 1984; Atherton and Harris, 1986). De Koning (1989) observed that truss growth could be delayed when the competition for assimilates is high and started to grow again when the first trusses reached maturity. Picken (1984) mentioned that CO₂ enrichment could improve fruit set by increasing assimilate supply and that fruit number and fruit size compensated one another. Nevertheless, these hypotheses have never been tested adequately and, until now, the regulation of fruit set and fruit abortion is not clearly understood.

In the south of Europe, tomatoes are harvested earlier and earlier as planting now starts at the end of August and reproduction cycles extend through winter period when light intensity can be very low. Therefore, to achieve uniform fruit set it is necessary to understand how the plant regulates the number of fruits on each inflorescence during its development. The different hypotheses stated in the literature to explain the different types of incidents that can stop flower bud development were mentioned, but very few observations have been made during a long reproductive period. The purpose of this work was to characterize fruit set delays on tomato crop in commercial conditions and to observe the main reproductive events, so as to understand fruit set control on the successive inflorescences. The present work is mainly based on experimental observations of tomato fruit growth and development made, in winter, under greenhouse conditions, on a beef tomato cultivar (Capello) which is very sensitive to fruit set delays. The aims of the observations were to: (1) localize fruit set delays during plant development, (2) characterize the incidents and (3) understand fruit set control and establish a relationship between fruit set and competition for assimilates.

MATERIALS AND METHODS

Three experiments were carried out in 1990, 1991 and 1992, respectively, in southern France (INRA, Avignon) with a beef steak cultivar 'Capello'. The aim of the first experiment was to characterize the chronology of the reproductive events (bud appearance, flowering and fruit set) under different climatic and cultural conditions, and to localize delays of fruit set on the plant during development of the

first nine inflorescences. In the second experiment, individual fruit growth was measured very precisely from corolla abscission until fruit maturity in order to determine the actual stage at which fruit growth stopped and to understand how competition for assimilates might be involved. Then, a quantitative index of the competition for assimilates was attempted by determining the ratio between real growth (growth analysis made in expt 1) and potential growth. The latter was measured in expt 3 on plants thinned to one flower per inflorescence. In all experiments, pruning took place at anthesis of each inflorescence (50% of opened flowers) and flowers were vibrated three times a week to improve pollination. Vegetative branches were removed as soon as they appeared.

Cultural conditions

Expt 1 was carried out in two adjacent polycarbonate greenhouses of 200 m². On 3 Nov. 1989, tomato seedlings of 'Capello' were pricked out in rockwool cubes and were then placed in the two greenhouses on 4 Dec. 1989 at a density of 2.5 plants m⁻². Day/night temperature was 19/16 °C in both greenhouses. From first truss appearance, one greenhouse was enriched to 1000 µl l⁻¹ with pure CO₂ from 0800 to 1200 h. From March (fruit set of the seventh inflorescence), enrichment took place only from 0600 to 1000 h and the actual mean CO₂ level was about 500 µl l⁻¹ because of the frequent ventilations of the greenhouse. Daily average temperature and CO₂ concentration and daily sum of photosynthetically active radiation are shown in Fig. 1. The mean difference of CO₂ concentration between the two greenhouses was about 150 µl l⁻¹, whereas temperature and light were equivalent. Light was measured in one greenhouse only but it was previously controlled that radiation was the same in both greenhouses. CO₂-enrichment stopped early

FIG. 1. Experiment 1. A, Daily average temperature in the CO₂-enriched greenhouse (—) and in the non enriched greenhouse (----) and daily sum of photosynthetically active radiation (○). B, CO₂ concentration in the CO₂-enriched greenhouse (—) and in the non enriched greenhouse (----).

in April (fruit set of the ninth inflorescence). In both greenhouses, plants were pruned to reduce the number of flowers per inflorescence to seven on half of the plants (six on the first inflorescence and seven on the following inflorescences as practiced by the growers in this region with beef steak cultivars) and to three on the other half. In this paper, the four treatments will be referred to by F7C (seven flowers with CO₂ enrichment), F3C (three flowers with CO₂ enrichment), F7 (seven flowers without CO₂ enrichment), and F3 (three flowers without CO₂ enrichment). Plant nutrition and chemical pest and disease control followed commercial practice.

Expts 2 and 3 were carried out in a 6.4 × 30.3 m compartment of a multispan Venlo-type glasshouse. In 1990 and 1991 tomato seedlings were pricked out on 31 Dec. and 22 Nov., respectively in 10 dm³-pots filled with a balanced oxygenated nutrient solution at a density of 2 plants m⁻². The pH and electrical conductivity of the nutrient solution were measured every 2 d and the solution was renewed as often as necessary to keep the pH between 5.5 and 7.0 and the conductivity between 1.5 and 2.5 S m⁻¹. Day/night temperature was 21/19 °C. In expt 2, all inflorescences were pruned to six flowers, whereas only one flower was left on each inflorescence in expt 3.

Development and growth observations

In expts 1 and 2, the number of leaves (length > 2 cm), inflorescences (visual recording), flower buds, opened flowers, set fruits (ovary Ø > 1 cm) and 'aborted' fruits (ovary Ø < 1 cm) were recorded on each plant unit. The first unit was composed of a vegetative part of the plant, under the first inflorescence, and each productive unit was defined by one inflorescence, two leaves below and one leaf above (Atherton and Harris, 1986). Recordings were made three times a week on 26 and 10 plants in expts 1 and 2, respectively, until the ninth inflorescence appeared. In the first experiment, the development of each individual flower bud was recorded on the fifth and sixth trusses of the 26 plants and, every 3 weeks, 10 plants of each treatment were sampled for growth analysis. Dry weight of individual fruit trusses was measured after a period of 5 d in a ventilated oven at 80 °C. The plants used for destructive measurements were replaced by spare plants at the first two samplings.

Individual fruit growth measurement

On three plants of expt 2, growth of the second (proximal) and fifth (distal) fruits of the first six inflorescences was measured non-destructively by using photographs. From corolla abscission, a photograph of the ovary was taken every 2 d in the same position and at the same distance of the lens in order to keep a constant distortion and enlargement of the picture. This was possible by keeping a constant setting of the camera so that the sharpness of the image was obtained only at one constant distance of the fruit. During the first period (fruit Ø < 5 cm), the diameter increase of the fruit was measured on photographs and the actual diameter was calculated according to an experimental relationship (Fig. 2A). When the fruit diameter became

FIG. 2. Experiment 2, each point represents one fruit. A, Relationship between real fruit diameter (cm) and measured diameter on photograph (cm): $y = 0.39x - 0.027$. B, relationship between fruit dry weight (g) and real fruit diameter (cm): $y = 0.014x^{(3.17)}$. Experimental data (○) and fitted curves (—).

greater than 5 cm, it was then measured with a calliper every 3 d. Fruit dry weight was then estimated from fruit diameter, according to an experimental relationship established on detached fruits of plants grown at the same time in similar conditions (Fig. 2B). As tomatoes are not perfectly round, the largest diameter was considered. This method allowed minimization of the stress of the fruit, especially at the initial phase of ovary growth. Experimental growth curves were fitted by a three parameters Gompertz function.

In expt 3, growth of the first (proximal) and fifth (distal) fruit was measured, using the same method, on the first five inflorescences. On four plants only the first flower was left on each inflorescence, and on four other plants only the fifth flower remained. In the first case, the other buds have been removed at anthesis of the first flower. In the second case, the first flowers have been removed just before they were fully opened. Growth of each fruit was measured from petal fall until maturity (red colour).

Seed germination test

At the end of expt 2, some of the fruits (with normal or delayed fruit set) were picked and cut to check the presence of seeds (no parthenocarpic development). A random sample of the seeds was submitted to a germination test in order to verify ovule fertilization. The test was conducted following

FIG. 3. Experiment 1, average of 26 plants. Number of set fruits (A) and number of fruit set delays per plant (B) recorded on the first nine inflorescences: F7 (▨), F7C (■), F3 (□) and F3C (▤).

ISTA (1985): about 50 seeds were put on blotting paper moistened with distilled water (213 % of the paper's weight). They were then placed in a polystyrene box, enclosed in a clear plastic bag and kept in a controlled chamber with an 8 h photoperiod at a photosynthetically active radiation of 3.35 W m^{-2} (halogen lamps) and a day/night temperature of 30/20 °C. Seed germination was observed after 20 d.

RESULTS

Inflorescence development and localization of fruit set delays

Average number of set fruits and delayed fruit set recorded on the first nine inflorescences are shown in Figs 3A and B for the four treatments of expt 1. Less than one fruit per truss failed to set on plants thinned to three flowers per truss (F3C and F3). On plants pruned to seven flowers per truss (F7C and F7), five fruits set on the first two inflorescences and then between three and four fruits set on the following inflorescences. From the fifth inflorescence, the difference in the number of fruit between the two 'thinning' treatments was only one fruit. On the plants thinned to seven flowers, CO_2 enrichment allowed a significantly (Student *t*-test at $P = 10\%$) higher fruit set on the third and fourth inflorescences only. Overall, on the first nine inflorescences, the enrichment had only a small positive effect on fruit set, but this was probably due to the fact that CO_2 supply decreased at the time when fruit load and, thus, competition for assimilates increased.

During observations on development, various kinds of problems were recorded: some flower buds yellowed, dried,

and fell before opening and this was designated by the term 'flower bud abortion'; it was identifiable after pruning took place, and then, in this case, the total number of flowers which reached anthesis was reduced. What we called delay of fruit set happened later, after flower opening and corolla abscission. At this stage, fruit set occurred but fruit growth did not start and one can observe a small ovary ($\varnothing < 1 \text{ cm}$) which does not dry nor abscise. The distribution of these two types of incidents, recorded on the fifth and sixth inflorescences for treatments F7C and F7, is presented in Fig. 4. In Fig. 4, the percentage of aborted flower buds is proportional to the total number of buds after pruning, and the percentage of fruit set 'failures' is proportional to the number of flowers which reached anthesis (total buds minus aborted buds). The first flower bud abortions appeared in the fourth position on the inflorescence and affected 40–60 % of the buds in the most distal position. A very low percentage of fruit set delays was observed in proximal position, whereas 80–100 % of distal fruits did not start growing. Distal organs of the inflorescence aborted first, and when both flower bud abortion and fruit set delays were recorded on a same inflorescence, the first ones were always in the most distal position.

Figure 5 illustrates flowering and fruit set rates on the first five inflorescences recorded on two individual plants for treatments F7 and F3 only, as very few differences were noticed with CO_2 enrichment. When seven flowers were left on each inflorescence, flowering of the last two distal flowers on one inflorescence took place at the same time as flowering of the first two proximal flowers on the following inflorescence. Within one inflorescence, flowering of the

FIG. 4. Experiment 1, average of 26 plants. Percentage of aborted flower buds (A–C) and fruit set delays (B–D) on the fifth (A–B) and sixth (C–D) inflorescences for each flower position within the inflorescence (1 is the proximal flower) for treatment F7 (▨) and F7C (■).

FIG. 5. Experiment 1, individual plant. Numbers of opened flowers (A–B) and set fruits (C–D) on the first five inflorescences (t1 to t5) for treatments F7 (A–C) and F3 (B–D) as a function of the number of days from first truss appearance (A–B) and from first truss anthesis (C–D).

distal flowers coincided with fruit set of the proximal flowers. Therefore, for treatment F7, distal flowers were submitted to a double competition among and within inflorescences. On this individual plant (Fig. 5A–C), selected for its average behaviour, the two distal fruits of the first five inflorescences did not set. For treatment F3, Fig. 5(B–D)

shows that there is no overlap of flowering and fruit set on the successive inflorescences. It can be concluded from these graphs that flowering and fruit set of two inflorescences do not take place at the same time when four flowers, at most, are left on each inflorescence and that proximal fruits always have priority when competition occurs.

FIG. 6. Experiment 2, one plant. Individual fruit growth curves (g dry matter per fruit) over time. Experimental data (●, ○) and fitted curves (—). Each fruit is identified by the inflorescence position (t1 to t5 from stem base) and by fruit position within one inflorescence (f2 for the second fruit: ○, and f5 for the fifth fruit: ●). The dotted line shows an estimation of the fruit cumulative growth rate (g dry matter d^{-1} per plant).

Sensitive developmental stage and qualitative relationship with the competition for assimilates

These observations were made on expt 2. On three plants, a total of 13 delays of fruit set were recorded on the first five inflorescences, only for the two measured fruit positions (2 and 5). Among these 13 fruits, 12 resumed growth after a delay of 10–50 d, when the first fruits of the lower inflorescences ripened. These 'delayed' fruits came to maturity but their final size was smaller than that of the earlier fruits. Figure 6 shows the experimental points and the fitted growth curves for the proximal (position 2) and distal (position 5) fruits of the first five inflorescences on one of the three individual plants. Total life period and actual growth period are given in Table 1. The proximal and distal fruits of the first two inflorescences and the proximal fruit of the third inflorescence grew without any delay. On the other hand, the distal fruit of the third inflorescence and the proximal and distal fruits of the two following inflorescences did not start growing at regular time intervals as expected, but only after a delay of 10–30 d. They matured after a growth period of 50 (third truss) to 35 (fifth truss) d. In Fig. 6, the dotted line represents the cumulative fruit growth rate on the first five inflorescences which was estimated from the fitted growth curves of individual fruits and from numbers of set fruits recorded on each inflorescence. As growth was measured only on two fruit positions (2 and 5), growth of the second fruit was applied to the three proximal fruits and growth of the fifth fruit was applied to the three distal fruits. First the cumulative growth rate increased as there were many growing fruits on the first inflorescences. When these fruits approached maturity the cumulative growth rate started to decrease because of a high number of delayed

fruit sets on the following inflorescences. At about 3 g dry matter per plant d^{-1} , the fruits whose growth had stopped resumed growth until ripeness. For a same fruit position within an inflorescence, fruits of the lower inflorescences started to grow first but the proximal fruits started to grow before the distal fruits, even if the first were located on one or two higher inflorescences on the stem. The total life period of the 'delayed' fruits was longer than that of the 'normal' fruits, but their actual growth period was a little shorter. This leads to the speculation that fruit set delay results from a fruit growth latency which can be lifted by decreasing the competition for assimilates exerted by the other growing fruits. Nevertheless the 'delayed' fruit development could have been associated with parthenocarp or seed abortion, and a seed germination test was performed to verify that ovule fertilization had been successful.

The germination test was performed with seeds from five 'normal' fruits and five 'delayed' fruits. On these fruits (normal or delayed) we never recorded any empty carpel cells, which is typical of parthenocarpic fruits. The 'delayed' fruits contained between 20 and 100 seeds whereas the 'normal' fruits may contain a few hundred seeds. In the fruits picked before ripening, seeds had white teguments and were hardly visible, even in some 'normal' fruits. In all ripened fruits, seeds were bigger and had coloured teguments. About 95% of the seeds extracted from normal fruits germinated, and only 83% of the seeds extracted from delayed fruits germinated, but the difference was not significant (Student's *t*-test $P = 90\%$). In all fruits the number of germinated seeds was higher than 15 which is enough to say that fertilization was not limiting (Philouze, pers. comm.). These results allow the conclusion that delay of fruit set does not involve flower fertilization failures.

TABLE 1. Total life period and actual growth period (d) of the second (F2) and fifth (F5) fruits of the first five trusses (T1 to T5)

Fruit position	T1F2	T1F5	T2F2	T2F5	T3F2	T3F5	T4F2	T4F5	T5F2	T5F5
Life period	58	62	57	57	59	75	74	77	65	45
Growth period	58	62	57	57	59	49	46	46	46	35

FIG. 7. Experiment 1, average of 10 plants. Total fruit growth (g dry matter per plant) measured by growth analysis and fitted growth curves for treatments F7 (●, —) and F7C (○, ----). Vertical bars indicate the 90% confidence interval. Fruit growth curves were fitted by a three parameters Gompertz function and fruit growth rates were estimated from the first derivative of the function.

FIG. 8. Experiment 3, average of 4 plants. Potential growth rates of the first (A) and the fifth fruits (B) on the first (—), second (—), third (·····), fourth (— · —) and fifth (----) inflorescences thinned to only one flower. Experimental data were fitted by a three parameters Gompertz function and these curves represent the first derivatives.

Calculation of a competition index and relationship with fruit set of the successive inflorescences

Potential growth is defined by the growth which would be realized if no factor is limiting, that is, when assimilate supply is higher than or equal to assimilate demand. When competition occurs, the actual growth is lower than the potential growth and it results from the distribution of available assimilates between all the sink organs. The ratio between actual fruit growth (assimilate supply) and potential

fruit growth (assimilate demand) is a good index to express quantitatively the degree of competition for assimilates. This ratio was calculated for treatments F7 and F7C of expt 1, during which real fruit growth was measured by plant sampling. A three parameters Gompertz function was fitted to the experimental data and actual fruit growth rate was deduced from the first derivative of the function (Fig. 7).

Potential fruit growth was measured in expt 3 for proximal and distal fruits on the first five inflorescences (Fig. 8). The potential growth of the first fruit increased on the first five

FIG. 9. Experiment 1. Growth rates of the first nine inflorescences (A, treatment F7C and B, treatment F7) and cumulative inflorescence growth rate (C) estimated from potential growth curves (Fig. 8) and from the real number of set fruits on each inflorescence (Fig. 2). Each curve starts at fruit set of the inflorescence and stops when 50% of the fruits were harvested. Treatments F7C (----) and F7 (—).

FIG. 10. Experiment 1. Ratio between real (Fig. 7) and potential (Fig. 9) fruit growth during crop development. F7C (----) and F7 (—).

inflorescences, whereas the potential growth of the fifth fruit seemed independent of the inflorescence position. To estimate the fruit potential growth on the first nine trusses in expt 1, we took into account both the inflorescence and the fruit position. As potential growth was measured only on five inflorescences, the data of the fifth inflorescence was applied to inflorescences 5–9. Inside each inflorescence, the curve fitted for the proximal fruit was applied to all proximal fruits (positions 1–3), and the curve fitted for the fifth fruit was applied to all distal fruits (positions 4–7). Considering the average fruit set and harvest dates, and the observed number of fruits on the first nine inflorescences, potential truss growth rates and cumulative potential fruit

growth rate were estimated during plant development for treatments F7C and F7 (Fig. 9). The ratio between actual (measured) and potential (calculated) fruit growth rates is shown in Fig. 10. It decreased rapidly from 1 (no competition) to 0.2 (high competition) when the first fruits started growing and then increased again until 0.4 as a large number of fruits didn't set immediately, and as the fruits on the first inflorescences ripened. With CO_2 enrichment, fruit set of the first inflorescences was slightly higher and the ratio between actual and potential growth rates decreased a few days earlier. Afterwards the ratio remained higher in the CO_2 -enriched greenhouse but this was mainly the result of a higher real growth (Fig. 7), whereas potential growth rates

FIG. 11. Experiment 1, average of 26 plants. Numbers of set fruits on the first nine inflorescences as a function of the ratio between real and potential fruit growth (Fig. 10) calculated at fruit set of each inflorescence. Treatments F7 (●) and F7C (○). The line is drawn by hand.

were hardly different between the two treatments. This was due to the fact that the total number of set fruits per plant was not significantly different between F7C and F7, but fruits accumulated more dry matter in the CO₂ enriched greenhouse so that, for F7C, assimilate supply was higher but assimilate demand was equivalent.

Figure 11 shows the relationship between the number of fruits per truss and the ratio between real and potential fruit growth rates calculated at fruit set of each truss. It appears clearly that fruit set was fairly stable when the ratio between real and potential growth was higher than 0.5 and then decreased significantly (Student's *t*-test $P = 10\%$) when the ratio fell under 0.5, until a minimum of less than 3.5 fruits per truss. The two CO₂ treatments did not differ significantly and a similar relationship was observed (Fig. 11).

DISCUSSION

In this work, tomato fruit set 'failure' was defined as fruit growth latency caused by the competition for assimilates among fruits, which agrees with the observations and hypotheses of many authors (Ho, 1984; Picken, 1984; Wolf and Rudich, 1988; De Koning, 1989). As observed by De Koning (1989) fruits can start to grow after a latency period of many weeks, as soon as the previously growing fruits come to maturity and thus cease to compete for assimilates. It was verified here that late fruit development was not due to parthenocarpy. Fruits which started to grow after a delay of many weeks contained fewer seeds than normal fruits, but all the 'delayed' fruits, except one, were on a distal position and, naturally, have less ovules (Bangerth and Ho, 1984). Some of the seeds extracted from these fruits did not germinate, but as there were at least 15 seeds per fruit, one can consider that flower fertilization was non-limiting for fruit development (Philouze, pers. comm.). These results indicate that fruit set delay is quite different from flower fertilization failure.

As mentioned for many herbaceous plants (Stephenson, 1981), the results underlined the higher sensitivity of the

distal organs to fruit set delays and the observations emphasized that, from four flowers per inflorescence, distal flowers of one inflorescence developed at the same time as proximal flowers of the following inflorescence. Consequently young fruits grow under a double competition, i.e. among and within inflorescences, and this could help to explain their high sensitivity to fruit set delay. Many other hypotheses have been proposed in the literature. Assimilates are translocated to the fruits via the phloem pathway and, within one inflorescence, the vascular plexus of the rachis has been observed to be reduced at the inflorescence extremity (André, pers. comm.). This could contribute to the restriction of assimilates to distal fruits.

Distal fruits are also known to have a lower sink strength than proximal fruits (Bangerth and Ho, 1984). It means that their ability to attract assimilates is lower, and that they are disadvantaged in the competition for assimilates. Until now, what determines fruit sink strength is not clearly understood but it is commonly stated that intrinsic fruit sink strength depends on the cell division period (Ho, 1992). Bohner and Bangerth (1988) observed that the difference of cell number at anthesis could be responsible for fruit size at maturity, and they showed that a manual synchronized pollination of proximal and distal flowers eliminated these differences. Many authors stated the hypothesis that at early developmental stages the auxins produced by the developing seeds could play an important role during cell divisions and favour assimilate supply to fruits (Rylski, 1979; Ho, Sjut and Hoad, 1982; Bangerth and Ho, 1984; Bangerth, 1989). Before anthesis, distal fruits contain 18% fewer ovules than proximal fruits (Bangerth and Ho, 1984) and this could explain their lower sink strength. Bohner and Bangerth (1988) didn't observe a role of indole acetic acid in cell division but they suggested a possible effect of the cytokinins produced in the seed tissues. Nevertheless, until now the exact role of auxins and cytokinins in the control of fruit sink activity remains unclear, all the more that cell division seems to take place before the peak of indole acetic acid production (Ho, 1992). So, all these arguments agree, to

justify the higher sensitivity of the distal flowers, but the predominant cause is still unclear. Other factors, implied in the control of the invertase synthesis, could be also directly involved in the control of assimilate partitioning, because the concentration of sucrose in the fruit determines the rate and direction of assimilate translocation (Walker and Ho, 1977).

The last purpose of this work was to establish a quantitative relationship between fruit set and competition for assimilates. The ratio between real and potential growth rates, i.e. between assimilate supply and demand, was assumed to be a good index of the competition for assimilates. The notion of fruit sink strength is now widely used, especially for modelling dry matter distribution, but measuring it remains the biggest difficulty. Potential growth is assumed to be realized when no factor is limiting (Watson, 1971; Warren Wilson, 1972). In our experiment, we assumed that potential growth was nearly realized when only one flower was left on each inflorescence. It is difficult to control that no competition occurred, especially before fruit set, as a large number of cells have been already formed at anthesis. Nevertheless, we can assume that competition was very low and that, in these conditions, fruit growth was relatively close to potential growth. The results clearly show that fruit sink strength depends on the inflorescence position on the stem, on the fruit position within the inflorescence, and probably on the early climatic environment of the young reproductive organ (Bertin, 1993). As the experiment was conducted in winter (planting in December), day length and radiation intensity did increase during plant development. So, it could be that assimilate supply was different for the first and fifth inflorescences but, in practice, it is very difficult to obtain, at the same time, tomato fruits with a same climatic past in different positions on the stem. The effect of the inflorescence position on the stem is very limited for distal fruits and, on all inflorescences except the first, final size of distal fruits is lower than that of proximal fruits. This result disagrees with the observations of Bohner and Bangerth (1988). These authors showed that the different sizes at maturity resulted only from the natural sequence of pollination (7 d between the first and the sixth flowers) and that a synchronized pollination of all the flowers eliminated size differences. It could be that, in our experiment, proximal flowers were removed too late (just before anthesis) when a large number of cells was already formed, or, it could be that the results from Bohner and Bangerth (1988), which were obtained on the third inflorescence only, cannot be extended to the following inflorescences. Very few data are available in the literature for beef tomato cultivars. The maximum growth rate measured on the proximal fruit of the fourth inflorescence was about $1.04 \text{ g dry matter d}^{-1}$, whereas values of 0.20 g d^{-1} (Heuvelink and Marcelis, 1989), 0.27 g d^{-1} (Jones *et al.*, 1991) and 0.37 g d^{-1} (Ho *et al.*, 1983) were mentioned in the literature for round fruited cultivars. In our work, potential growth was measured on the first five inflorescences for proximal and distal fruits and the relationship emphasized in Fig. 11 is quite consistent with the stated hypotheses about fruit set control. When the ratio between actual and potential growth fell under a threshold value (about 0.5 in this case)

fruit set started to fail and then the number of fruit set delays increased as the ratio between real and potential growth decreased. This kind of index has been used in the model Tomgro, a dynamic tomato growth and development model (Jones *et al.*, 1991), which simulates fruit set delays as a negative linear function of the ratio between assimilate supply and demand, with only one potential growth curve for all fruits. The relationship shown in Fig. 11 agrees with the calibrated function of Tomgro, obtained for beef steak cultivar (Bertin and Gary, 1993b) and, a same threshold value of 0.5 was found for the ratio between assimilate supply and demand. To improve the relationship and to be able to anticipate fruit set delays in various cultural and climatic conditions, models would be an appropriate tool to integrate all the variation parameters in calculation of potential fruit growth rate. More generally, sink potential growth is for the moment one of the most effective notion used for dynamic modelling of dry matter partitioning (Heuvelink and Marcelis, 1989; Jones *et al.*, 1991; Bertin and Gary, 1993a; Marcelis, 1993). Therefore, understanding better how potential and actual fruit growth are determined, could help to understand fruit set control, and to elaborate some tools to predict yield and to determine optimal cultural and climatic strategies for greenhouse winter tomato crops.

ACKNOWLEDGEMENTS

I am grateful to the *Institut National de la Recherche Agronomique* (INRA) and the *Association Provençale de Recherches et d'Etudes Légumières* (APREL) for their financial support. Thanks to Drs C. Gary and B. Vaissiere for reading the manuscript and to Mr Sarrouy and Mrs Brunel and Orlando for technical assistance.

LITERATURE CITED

- Atherton JG, Harris GP. 1986. Flowering. In: Atherton JG, Rudich J, eds. *The tomato crop*. London: Chapman and Hall, 167–194.
- Bangerth F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiologia Plantarum* 76: 608–614.
- Bangerth F, Ho LC. 1984. Fruit position and fruit sequence in a truss as factors determining final fruit size of tomato fruits. *Annals of Botany* 53: 315–319.
- Bertin N. 1993. *Environnement climatique, compétition pour les assimilats et modélisation de la nouaison de la tomate en culture sous serre*. Dissertation INA-PG/INRA Bioclimatologie Avignon (France).
- Bertin N, Gary C. 1993a. Tomgro, modèle dynamique de croissance et de développement de la tomate: évaluation dans différentes conditions de force des sources et puits d'assimilats. *Agronomie* 13: 395–405.
- Bertin N, Gary C. 1993b. Tomato fruit-set: a case study for validation of the model TOMGRO. *Acta Horticulturae* 328: 185–193.
- Bohner J, Bangerth F. 1988. Effect of fruit set sequence and defoliation on cell number, cell size and hormone levels of tomato fruits (*Lycopersicon esculentum* Mill.) within a truss. *Plant Growth Regulation* 7: 141–155.
- Burge GK. 1989. Fruit set in the pepino. *Scientia Horticulturae* 41: 63–68.
- Charles WB, Harris RE. 1972. Tomato fruit-set at high and low temperatures. *Journal of Horticultural Science* 52: 497–506.
- De Koning ANM. 1989. The effect of temperature on fruit growth and fruit load of tomato. *Acta Horticulturae* 248: 329–336.
- Fisher KJ. 1977. Competition effects between fruit trusses of the tomato plant. *Scientia Horticulturae* 7: 37–42.

- Heuvelink E, Marcelis LFM. 1989. Dry matter distribution in tomato and cucumber. *Acta Horticulturae* 260: 149–157.
- Ho LC. 1984. Partitioning of assimilates in fruiting tomato plants. *Plant Growth Regulation* 2: 277–285.
- Ho LC. 1992. Fruit growth and sink strength. In: Marshall C, Grace J, eds. *Fruit and seed production. Aspects of development, environmental physiology and ecology*. Cambridge: Cambridge University Press, 101–124.
- Ho LC, Shaw AF, Hammond JBW, Burton KS. 1983. Source-sink relationships and carbon metabolism in tomato leaves. *Annals of Botany* 52: 365–372.
- Ho LC, Sjut V, Hoad GV. 1982. The effect of assimilate supply on fruit growth and hormone levels in tomato plants. *Plant Growth Regulation* 1: 155–171.
- ISTA (International Seed Trade Association). 1985. International rules for seed testing. *Seed Science and Technology* 13(2) 307.
- Jones JW, Dayan E, Allen LH, Van Keulen H, Challa H. 1991. A dynamic tomato growth and yield model (Tomgro). *American Society of Agricultural Engineers* 34: 663–672.
- Kinet JM, Hurdebise D, Parmentier A, Stainer R. 1978. Promotion of inflorescence development by plants grown in insufficient light conditions. *Journal of American Society for Horticultural Science* 103: 724–729.
- Kinet JM, Leonard M. 1983. The role of cytokinins and gibberellins in controlling inflorescence development in tomato. *Acta Horticulturae* 134: 117–124.
- Leonard M, Kinet JM, Bodson M, Bernier G. 1983. Enhanced inflorescence development in tomato by growth substance treatments in relation to ^{14}C -assimilate distribution. *Physiologia Plantarum* 57: 85–89.
- Maisonneuve B, Philouze J. 1982. Action des basses températures nocturnes sur une collection variétale de tomate (*Lycopersicon esculentum* Mill.): I-Etude de la production de fruits et de la valeur fécondante du pollen. *Agronomie* 2: 443–452.
- Marcelis LFM. 1993. Simulation of biomass allocation in greenhouse crops—a review. *Acta Horticulturae* 328: 00–00.
- Picken AJF. 1984. A review of pollination and fruit set in the tomato. *Journal of Horticultural Science* 59: 1–13.
- Rudich J, Zamski E, Regev Y. 1977. Genotypic variation for sensitivity to high temperature in the tomato: pollination and fruit set. *Botanical Gazette* 138: 448–452.
- Rylski I. 1979. Fruit-set and development of seeded and seedless tomato fruits under diverse regimes of temperature and pollination. *Journal of American Society for Horticultural Science* 104: 835–838.
- Stephenson AG. 1981. Flower and fruit abortion: causes and ultimate functions. *Annual Review of Ecological System* 12: 253–279.
- Walker AJ, Ho LC. 1977. Carbon translocation in the tomato: carbon import and fruit growth. *Annals of Botany* 41: 813–823.
- Warren Wilson J. 1972. Control of crop processes. In: Ress AR, Cockshull KE, Hand DW, Hurd RG, eds. *Crop processes in controlled environment*. London: Academic Press, 7–30.
- Watson DJ. 1971. Size, structure and activity of the productive system of crops. In: Wareing PF, Cooper JP, eds. *Potential crop product*. London: Heineman, 76–88.
- Wolf S, Rudich J. 1988. The growth rates of fruits on different parts of the tomato plant and the effect of water stress on dry weight accumulation. *Scientia Horticulturae* 34: 1–11.