

MODELLING FRUIT SET, FRUIT GROWTH AND DRY MATTER PARTITIONING

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Abstract

This paper discusses how fruit set, fruit growth and dry matter partitioning can be simulated by models where sink strength (assimilate demand) and source strength (assimilate supply) are the key variables. Although examples are derived from experiments on fruit vegetables such as tomato, sweet pepper and cucumber, the theoretical basis holds for a wide range of crops including fruit trees. Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. It appears to be primarily regulated by the sink strength of the sinks, with fruits being the major sinks in fruit trees or fruit vegetables. Source strength has only an indirect effect on dry matter partitioning through effects on the number of fruits on a plant. The transport path is only of minor importance for the regulation of dry matter partitioning at the whole plant level. The growth rate of a fruit depends on the source strength and the fraction of the assimilates partitioned into it.

Dry matter partitioning was modelled as a function of the sink strengths of the plant organs, where sink strength of an organ is defined by its potential growth rate (potential capacity to accumulate assimilates). The potential growth rate has been shown to quantitatively reflect the sink strength of an organ. The potential growth of a fruit is a function of both its age and temperature. In several experiments and for different treatments it was shown that dry matter partitioning into a fruit can be simulated as a function of its sink strength relative to that of the other plant organs.

The number of fruits set per plant has a great impact on the dry matter partitioning and fruit growth. Several experiments have shown that fruit set increases with source strength and decreases with sink strength. Consequently fruit set could be reasonably successful modelled as a function of sink and source strength.

Finally it is shown how a photosynthesis-based model combined with submodels for fruit set, fruit growth and dry matter partitioning can be used for predictions of yield and fruit size.

1. Introduction

Although there is considerable information on the operation of individual processes in plants such as photosynthesis, sugar metabolism, translocation, and cell expansion, the controls which actually regulate the partitioning of dry matter at the crop level are still only poorly understood (Wardlaw, 1990). However, there has recently been quite some progress in quantifying and modelling dry matter partitioning in fruits (e.g. Wermelinger

et al., 1991; Grossman and DeJong, 1994) and fruit vegetables (e.g. Dayan *et al.*, 1993; Marcelis, 1994; De Koning, 1994; Heuvelink, 1996).

Besides genotype, developmental stage of the plant, many growth conditions and internal regulation by the plant may all affect dry matter partitioning (e.g. Marcelis, 1996). Only the dry matter partitioned into the harvestable organs contributes to the yield of the crop, indicating the importance of correctly simulating dry matter partitioning. However, for rapid growth of small (young) plants and for early leaf formation in fruit trees dry matter partitioning into the leaves is important, because a large fraction of the light is not yet intercepted by the leaves. Besides, in many fruit crops where harvestable organs are produced over an extended period of the crop's lifetime, an optimum balance between partitioning into the harvestable organs (short-term productivity) and the other plant parts (vegetative parts: future production capacity) should be maintained. Palmer (1986) suggested that for a regular perennial production pattern of apple fruits the fraction of assimilates partitioned into the fruits should not exceed 60-65%. In addition, partitioning relates to product quality, e.g. number versus size of individual fruits.

In this paper the importance of the source, the transport path and the sinks in the regulation of fruit set, fruit growth and dry matter partitioning is discussed. Potential growth rate as a measure of sink strength is evaluated. Models for fruit set, fruit growth and dry matter partitioning are presented in which sink strength (assimilate demand) and source strength (assimilate supply) are the key variables. Finally it is shown how a photosynthesis-based model combined with submodels for fruit set, fruit growth and dry matter partitioning can be used for predictions of yield and fruit size. Although examples are derived from experiments on fruit vegetables such as cucumber, sweet pepper and tomato the theoretical basis holds for a wide range of crops including fruit trees.

2. Regulation of dry matter partitioning

Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. Source organs are defined as organs with a net export and sink organs as organs with a net import of assimilates. In cucumber no noticeable relationship between the fraction of dry matter partitioned into the fruits and solar radiation of the same day or week was observed during a growing season (Liebig, 1978; Marcelis, 1992a). However, a large change in solar radiation seemed to induce a change in dry matter partitioning to the fruits, but the time lag between the change in radiation and the change in partitioning was variable (Marcelis, 1992a). The limited direct effect of irradiance on dry matter partitioning, is substantiated by an experiment where cucumber plants of identical size and with a fixed number of fruits were shaded for 4 days (Marcelis, 1993c). Total plant growth rate decreased by 60%, but the partitioning between generative and vegetative growth was not significantly affected. Heuvelink (1995b) also concluded for tomato that source strength, varied by plant density, had no direct effect on dry matter partitioning between generative and vegetative parts.

Although effects of source strength (radiation) in the short term may be limited, in the long term increased source strength may increase the number of fruits on the plant and hence indirectly effect the dry matter partitioning (Marcelis, 1993c).

Despite the fact that, in some cases, partitioning is related to the relative distance between sinks and sources (Cook and Evans, 1983), distance is generally not an important factor in dry matter partitioning at the whole plant level (e.g. Marcelis, 1996). It has been shown that increasing the distance between source leaves and fruits had no effect on fruit

growth in apple (Hansen, 1977) and cucumber (Schapendonk and Brouwer, 1984). Heuvelink (1995c) showed that in tomato plants with two shoots and a shoot length of more than 2m dry matter partitioning between vegetative and generative parts was not affected whether the fruits were located on only one shoot or whether the same number of fruits were divided over the two shoots.

The fruits appear to be the major sinks in fruit crops and the dry matter partitioning into the fruits positively correlates with the fruit load (number or weight of fruits on a plant) (Marcelis, 1992a; 1993b; Heuvelink and Buiskool, 1995). In tomato, Heuvelink (1995a), observed no direct effect of an increase in temperature on dry matter partitioning in the short term. However, De Koning (1994) and Marcelis (1993b) observed an increased dry matter partitioning into the fruits with increase in temperature in the short term for tomato and cucumber. In the long term this effect diminished, because the fruit load decreased with increasing temperature (De Koning, 1989; Marcelis, 1993b). Bhatt and Srinivasa Rao (1989) also observed that in the long term temperature had no effect on dry matter partitioning in pepper.

As discussed in more detail by Marcelis (1996) it can be concluded that neither the source (assimilate supply) nor the transport path between source and sink organs are dominating factors in regulating dry matter partitioning at the whole plant level and that dry matter partitioning among plant organs is primarily regulated by the sinks.

3. Potential growth rate as a measure of sink strength

As partitioning is primarily regulated by the sinks, for a simulation model it is necessary to find a parameter that quantitatively reflects the sink strength. The term sink strength used here refers to the competitive ability of an organ to attract assimilates and is defined as the potential demand or potential capacity of an organ for assimilate accumulation. This potential capacity can be quantified by the potential growth rate of a sink, i.e. the growth rate under conditions of non-limiting assimilate supply. Conditions for potential growth can be created by growing plants at a high irradiance and/or reducing the number of sinks on a plant. Sometimes problems may arise in measuring the potential growth rate of the vegetative parts (Marcelis, 1994; Heuvelink, 1996), while in sweet pepper potential growth rate of the fruits is hardly measurable as in many fruits blossom-end rot occurs when assimilate supply is high (Marcelis, unpublished). As the potential growth rate of vegetative parts is hardly measurable, Marcelis (1994) and Heuvelink (1996) indirectly estimated the vegetative potential growth from calculated potential fruit growth and from measured dry matter partitioning between fruits and vegetative parts.

Potential growth rate is not a static parameter but may change with e.g. developmental stage or temperature, but not with factors such as light intensity or CO₂ concentration which are assumed to affect only the availability of assimilates. In seeded fruits the potential growth rate may also increase with number of seeds set (Marcelis and Baan Hofman-Eijer, 1997). During development of an organ the potential growth often shows a sigmoid growth pattern (Marcelis, 1992b). Effects of temperature on growth rate are often confounded with effects of the developmental stage. Marcelis and Baan Hofman-Eijer (1993) showed that the development of a cucumber fruit was closely related to the temperature sum and that the effect of temperature on the growth rate of a fruit could be separated from developmental effects by considering growth as a function of the temperature sum. As development is related to temperature sum, the growing period (in days) decreases with increasing temperature. The growth rate of organs usually increases

with increasing temperature (Marcelis and Baan Hofman-Eijer, 1993). However, Heuvelink and Marcelis (1989) and De Koning (1994) did not observe a significant effect of temperature on potential growth rate of tomato fruits. When growth of a cucumber fruit was not limited by assimilate supply, the increase in growth rate with increasing temperature was much higher than at a lower level of assimilate supply (Marcelis and Baan Hofman-Eijer, 1993). As the level of assimilate supply affects the magnitude of the response of the growth rate to temperature, final organ size at a high assimilate supply may increase whereas the final size at a low assimilate supply may decrease with increasing temperature (Marcelis and Baan Hofman-Eijer, 1993).

Cell number has often been proposed to be an important determinant of sink size. However, in cucumber fruits grown at non-limiting assimilate supply, a small number of cells, due to a low assimilate supply during early fruit development, was to a great extent compensated by an increased expansion rate of individual cells (Marcelis, 1993d). Therefore, cell number seems not to be an important determinant of fruit size, although fruit size often correlates positively with cell number (Marcelis, 1993d).

As in many situations the size correlates with the age of an organ, often an apparent relationship between sink size and sink strength is observed. However, the actual growth rate of a cucumber fruit appears to depend on its age rather than its size (Marcelis, 1993d). Different weights of cucumber fruits were achieved by retaining no or 6 competing fruits during 6, 12 or 18 days. Despite strong differences (>300%) in fruit weight, a few days after removal of the competing fruits the small fruits grew almost at the potential rate, i.e. the growth rate of fruits which were grown without competing fruits throughout (Fig. 1). A small size was fully compensated by an increased relative growth rate, indicating the sink strength is reflected by the potential growth rate rather than the potential relative growth rate. Comparable results were observed for tomato fruits (De Koning, 1994). However, in peach generally fruit growth did not fully reach the potential growth rate after removal of competing fruits (Grossman and DeJong, 1995).

4. Simulation of dry matter partitioning

Sink regulation models are most suitable for simulation of dry matter partitioning in fruit crops (Marcelis, 1993a; Marcelis *et al.*, 1998). These type of models have been described in detail for cucumber and tomato by Marcelis (1994) and Heuvelink (1996). In these models the plant is considered to consist of a set of sink organs which receive their assimilates for growth from one common assimilate pool, which is replenished by photosynthesis in the source organs. Part of the assimilates from this pool is used for maintenance respiration and the remaining assimilates are available for growth. Growth respiration of an organ is linearly related to its growth rate. The growth rates of the organs are determined by the amount of assimilates in the assimilate pool and sink strengths of the organs. Differences in growth rates between sink organs and hence dry matter partitioning depend on differences in sink strengths.

The time step of the model is one day. Firstly the number of fruits on the plant is calculated as a function of the rates of fruit appearance, fruit abortion and fruit harvest. The age of each fruit is determined and the sink strengths of the organs are calculated. Then the available assimilates are distributed among the sinks; the fraction of dry matter distributed to a sink i (f_i) equals its sink strength (S_i) relative to the total sink strength of all sinks together (ΣS):

$$f_i = S_i / \Sigma S \text{ (Eqn. 1.)}$$

The sink strength or potential demand for assimilate accumulation is quantified by the potential growth rate of the organ (as described above). The potential growth of an organ is a function of its age and temperature (Heuvelink and Marcelis, 1989; Marcelis and Baan Hofman-Eijer, 1993, 1995; De Koning, 1994). Some authors (e.g. Buwalda, 1991) used the potential relative growth rate as a measure of sink strength instead of the absolute potential growth rate. Moreover, in some models sink strength also depends on the current size of the organ (e.g. Grossman and DeJong, 1994; Goldschmidt et al., 1992).

The potential growth rate of the vegetative parts has been simulated either as a constant or a function of plant developmental stage (Heuvelink, 1996) or a function of the temperature (Marcelis, 1994). For cucumber fruits, the simulation of partitioning among individual fruits was improved when the sink strength of each fruit was not only dependent on its potential demand for assimilates but also on its affinity or priority for assimilates (Marcelis, 1994).

The growth rate of a sink organ (Y_i) is obtained by multiplying the total dry matter production of the plant (*source*) by the fraction of dry matter partitioned into the fruits (f_i) or by multiplying the sink strength of the organ (S_i) by the source/sink ratio (*source*/ ΣS):

$$\begin{aligned} Y_i &= \text{source} \times f_i \\ Y_i &= \text{source} \times S_i / \Sigma S \\ Y_i &= S_i \times (\text{source} / \Sigma S) \end{aligned} \text{ (Eqn. 2.)}$$

When the daily assimilate supply exceeds the daily total potential growth rate, the growth rate of each sink occurs at its potential rate. In that case the assimilate pool is not totally depleted (reserves are formed). For cucumber and tomato, negative feedback on photosynthesis does not need to be included in the model, because in these crops this phenomenon does not seem to occur under normal growing conditions in greenhouses (Marcelis, 1991; Heuvelink and Buiskool, 1995).

The number and timing of fruits on a plant has a strong impact on the total sink strength of a plant and hence on dry matter partitioning. For instance in sweet pepper strong fluctuations in fruit harvest could be ascribed to strong fluctuations in fruit abortion two months prior to harvest (Marcelis, Dogliotti and Heuvelink, unpublished). The formation rate of non-aborting fruits is one of the weakest features of explanatory crop models.

In several reproductive crops like apple (Baumgärtner *et al.*, 1986), citrus (Goldschmidt *et al.*, 1992), cucumber (Marcelis, 1994), grape (Gutiérrez *et al.*, 1985; Wermelinger *et al.*, 1991), kiwifruits (Buwalda, 1991), peach (Grossman and DeJong, 1994), sweet pepper (Marcelis, Dogliotti and Heuvelink, unpublished) and tomato (De Koning, 1994; Heuvelink, 1996) dry matter partitioning has been successfully simulated by models based on sink strengths. For tomato, cucumber and sweet pepper this approach has proven its validity for simulating both the dynamics and average level of dry matter partitioning in a number of experiments covering effects of planting date, plant density, number of fruits per truss (Fig 2), number of trusses and shoots per plant and temperature. Besides partitioning between vegetative and generative plant parts, individual organ growth like tomato trusses (Heuvelink, 1996; Fig. 2) or cucumber fruits (Marcelis, 1994) could be predicted reasonably well. Modelling dry matter partitioning based on sink

strengths of organs is promising, as it is a generic, dynamic and flexible approach, showing good agreement between measurements and simulation for a range of conditions.

5. Simulation of fruit set

Abortion of flowers and fruits may increase with decreasing number of seeds per fruit (Picken, 1984; Marcelis and Baan Hofman-Eijer, 1997), decreasing air humidity (Bakker, 1991) or increasing temperature (Picken, 1984; Marcelis, unpublished). However, the main determinant of fruit abortion appears to be the source/sink ratio during a short period before and after anthesis, as observed in tomato (Kinet, 1977), cucumber (Schapendonk and Brouwer, 1984; Marcelis, 1992a) and sweet pepper (Marcelis, unpublished).

In several experiments with sweet pepper and cucumber it was tested whether fruit set can be modelled as a function of the sink and source strength. Total dry matter production was used as a measure for source strength and potential growth rate of the plant organs as a measure for sink strength. A decrease in plant source strength by decreasing inter-plant distance, light intensity or by leaf removal led to a decrease in fruit set in sweet pepper (Marcelis and Heuvelink, unpublished). In a glasshouse experiment the average fraction of fruits that set was 8, 10 and 16% at a within-row plant distance of 0.27, 0.40 and 0.80 m, respectively. In a glasshouse experiment where 0, 20, 40, 60 or 80% of the leaves were removed in an early stage, fruit set was 78, 69, 67, 50 and 50%, respectively. In a climate room experiment (13 flowers were retained per plant) fruit set was 25, 38, 54 and 92%, at light intensities of 1.1, 1.8, 2.8 and 4.8 MJ PAR m⁻² d⁻¹, respectively. While fruit set increased with increasing source strength, it decreased with increasing plant sink strength. In an experiment with 0, 1, 2 or 4 early formed fruits, fruit set of six later formed fruits was 78, 56, 28 and 6%, respectively (Marcelis and Heuvelink, unpublished).

As can be seen in Eqn. 2 the growth rate of an organ is proportional to the source/sink ratio ($source/\Sigma S$) when its sink strength (S_i) is constant. Assuming sink strength of the vegetative parts to depend only on temperature, at constant temperature conditions the vegetative growth rate is proportional to the source/sink ratio. As it is easier to measure the vegetative growth rate than the source/sink ratio, we experimentally quantified the relationship between vegetative growth rate and fruit set or abortion at constant temperature. In cucumber the fluctuations in fruit set during a growing season correlated with the variations in growth rate of the vegetative plant parts and hence with the source/sink ratio (Marcelis, 1992a). Usually we observed that a decrease in growth of the vegetative parts was accompanied by a decrease in number of young non-aborting fruits, while a time lag often occurred between an increase in vegetative growth and number of young cucumber fruits. In sweet pepper we also observed a positive correlation between fruit set and vegetative growth rate. However, a decrease in vegetative growth rate as a result of more competing fruits had a stronger impact on fruit set than as a result of a decreased number of leaves (source strength). This may indicate that some hormonal control due to dominance of competing fruits might be involved.

Fluctuations in fruit set during a growing season could be reasonably predicted from the source and sink strength in sweet pepper (Fig. 3). Although the average rate of fruit set in cucumber and sweet pepper could be reasonably predicted from the source and sink strength, for individual plants this relationship showed a large variation.

In conclusion, the average rate of fruit set can be reasonably predicted from the source and sink strength. Nevertheless, a better understanding of fruit abortion is necessary to

improve the simulation of fruit set as this has a strong impact on the simulation of dry matter partitioning. Maybe stochastic elements or hormonal control should be incorporated in these models. Developing a truly predictive submodel of fruit set still is a great challenge.

6. Prediction of yield and fruit size

The market as well as modern farm management require prediction of yield and quality of harvested fruits in advance. For cucumber a mechanistic photosynthesis-based dynamic growth model was developed to predict the weekly fresh weight yield and the fresh weight and developmental stage of the individual fruits at harvest (Marcelis and Gijzen, 1998a). The latter two being major criteria of fruit quality. The model consists of modules for greenhouse light transmission, light interception by the crop, leaf and canopy photosynthesis, assimilate partitioning, dry matter production, fruit growth, fruit dry matter content and fruit harvest. Dry matter partitioning was simulated as a function of sink strength and fruit set as a function of the source/sink ratio. The model was validated by comparing simulation results based on actual climate data with production data of 10 commercial growers (Marcelis and Gijzen, 1998a). Input data used for validation were week numbers of planting and removing the crop, weekly data on global radiation outside the glasshouse and glasshouse air temperature and daytime CO₂ concentration. The average error of the weekly prediction of the fresh weight yield averaged over all growers was 12.6%, while the error of the annual yield was only 0.3%. The simulated average fruit size corresponded reasonably well with growers' data, showing an average weekly error of 6.6%.

For predictions of production long-term average weather data were used (Marcelis and Gijzen, 1998b). Only the date of planting of the crop and date scheduled for the last harvest were used as input to the model. To keep the use of the model as simple as possible, average values were assumed for all other factors, e.g. plant density, fruit pruning, frequency of harvesting, cultivar properties. Depending on availability of data and objective of the prediction, the model calculations can be based on more or fewer input data. The average error of the weekly prediction of the fresh weight yield averaged over all growers was 14.9%, while the error of the annual yield was 2.8% in 1996 (Fig. 4A). The predicted average fruit size corresponded reasonably well with growers' data, showing an average weekly error of 6.5% (Fig. 4B).

Marcelis and Gijzen (1998a,b) showed that a mechanistic photosynthesis-based dynamic growth model can be applied for accurate predictions of cucumber yield and fruit size. Such predictions can be used for optimising the price setting, logistic arrangements and marketing of the produce. As growth as well as farm specific conditions are variables of the model, such a model is also a promising tool to control the quantity and quality of the produce such that it better fits to the demand by retailers or consumers. For instance, effects of future cultivation measures and climate set-points on crop growth and harvest can be calculated, so that the most appropriate strategy can be chosen.

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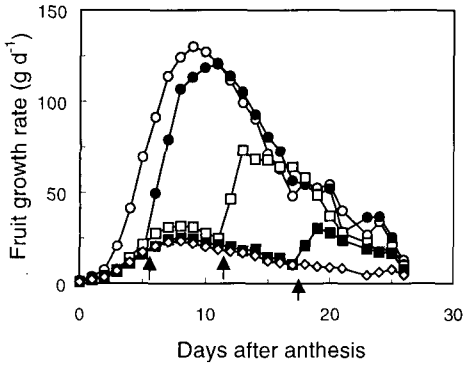


Figure 1 - The fresh weight growth rate of cucumber fruits when growth was constrained by assimilate supply for 0 (○), 6 (●), 12 (□), 18 days (■) or continuously (◇). Assimilate supply was constrained by retaining six competing fruits (from Marcelis, 1993d). Arrows indicate when competing fruits were removed.

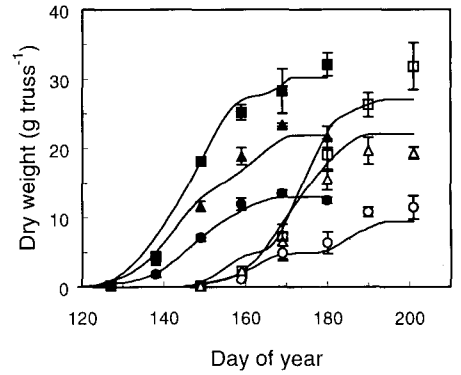


Figure 2 - Measured (●,▲,■: 3rd truss; ○, △, □ : 7th truss) and simulated (—) truss growth curves for tomato plants with 3 (○,●), 5 (△,▲) and 7 (□, ■) fruits per truss. Daily plant biomass increase and greenhouse air temperature were input in the model, partitioning was simulated based on potential growth rates (from Heuvelink, 1996).

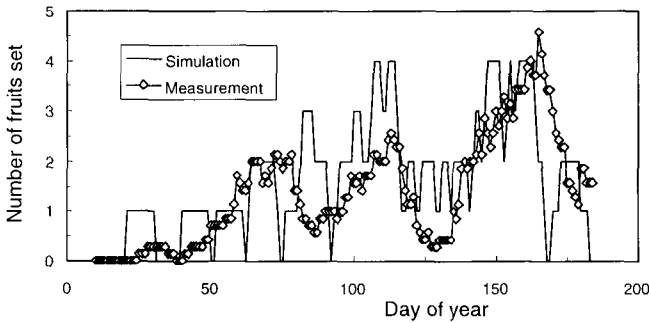


Figure 3 - Measured and simulated fruit set in sweet pepper. Fruit set was simulated as a function of source and sink strength (Marcelis, Dogliotti and Heuvelink, unpublished)

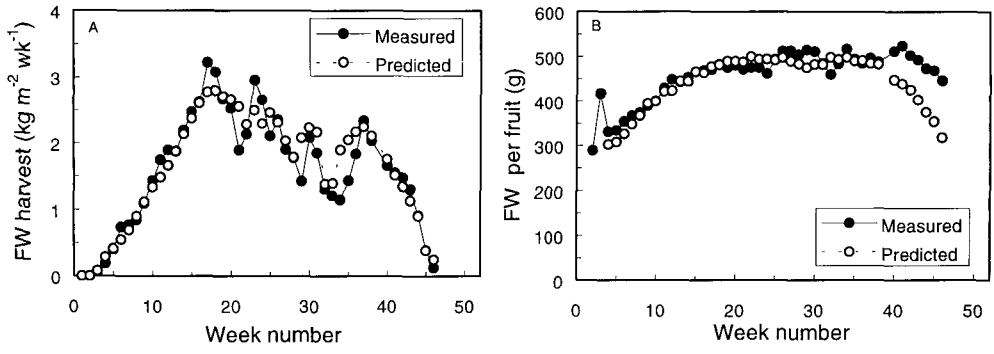


Figure 4 - Predicted and measured weekly fresh weight harvest (A) and average fresh weight per fruit (B). Data are means for 10 commercial growers. Predictions are based on long-term average weather data (from Marcelis and Gijzen, 1998b).