

Stochastic Dynamic Simulation of Fruit Abortion: a Case Study of Sweet Pepper

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Abstract

Abortion of reproductive organs diminishes yields in many crops. In indeterminate greenhouse crops, alternating periods of fruit abortion and fruit set exist, resulting in fluctuations in fruit yield. Factors affecting the level of abortion are e.g., the supply and demand for assimilates (source and sink strength, respectively), temperature and cultivar. However, simulation of fruit abortion is still a weak part of crop simulation models. Variation in fruit abortion exists between plants, which results in differences in the timing and the number of set fruits. Therefore, simulating fruit abortion with variation could give more realistic simulation results. The probability of a fruit to abort should be related to factors like source strength and sink strength. The more favourable the circumstances are for fruit abortion, e.g., low source strength or high sink strength, the more likely it is that the fruit aborts. Survival analysis estimates parameters quantifying the influence of explanatory variables on the abortion rate. Time-varying explanatory variables can be used in the analysis. In a case study, we used survival analysis to analyse a data set with observations on flowering, fruit abortion and fruit harvest for sweet pepper. Source and sink strength were used as explanatory variables. The resulting equation determining the probability of abortion per day was implemented in a simple simulation model to simulate fruit set. The model output, as an average of 100 plants, showed similar timing in the fluctuations in fruit set as the observations, although the amplitude of the fluctuations was in some cases underestimated. The percentage fruit set was simulated correctly.

INTRODUCTION

In many crops, yield is limited due to the abortion of flowers and young reproductive organs, e.g., pods abort in peas (Doré et al., 1998), fruits in citrus trees (Goldschmidt, 1999) and kernels in grains like maize (Cárcova et al., 2000). In indeterminate vegetable greenhouse crops, a periodic pattern with alternating periods of fruit set and fruit abortion leads to fluctuations in fruit yield (e.g., Marcelis, 1992; Bertin, 1995; Heuvelink et al., 2004). Yield loss reduces profits, and irregular yield causes difficulties in the logistics of harvesting, processing and marketing.

Simulation models might help to provide insight in how to reduce yield loss or diminish fluctuations in fruit yield. This requires adequate simulation of abortion. Marcelis and Heuvelink (1999) concluded that abortion of organs was a weak part of crop simulation models, and it still is. Hence, there is a need to improve this aspect in crop simulation models, using knowledge of factors that are responsible for reproductive organ abortion.

Crop growth models are predominantly deterministic of nature. Applying a

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specific input (climate, cultivation measures), one single output value without confidence limits is obtained for e.g., the final yield. Models typically simulate average plants neglecting the existing variation among plants. Regarding the growth of individual organs, it is assumed that each organ obeys in exactly the same way to internal or external factors. In reality, inter-plant and inter-organ variation is observed under apparently identical conditions.

Improving the simulation of reproductive organ abortion and incorporating stochastic elements in dynamic crop growth models are a challenge in crop modelling. In this study, we give a short overview of the factors playing a role in reproductive organ abortion. We describe if and how these factors are used to simulate abortion in current crop simulation models. In the second part, we focus on stochasticity. An overview of existing models with a stochastic component is given. In the last part we show an example of our current work on introducing stochasticity in the simulation of fruit set in sweet pepper.

FACTORS AFFECTING ORGAN ABORTION

Abortion of organs can be induced by low supply of assimilates (source strength), high competition from other organs (sink strength), high temperatures (Marcelis et al., 2004), shortage of water and nutrients (Guilioni et al., 2003) and a low number of seeds (Marcelis and Baan Hofman-Eijer, 1997). Additionally, hormonal dominance of one organ over the other plays a role (Bangerth, 1989). Between cultivars, high differences exist in the level of fruit abortion (Wubs et al., 2009).

DETERMINISTIC MODELLING OF FRUIT ABORTION

Source and sink strength can be combined into the source-sink ratio. This ratio is often used in models simulating abortion. In the tomato growth model TOMGRO (Bertin and Gary, 1993; Heuvelink and Bertin, 1994), fruit abortion increased linearly with decreasing source-sink ratio from 0% at a source-sink ratio of 0.42 till 70% abortion at source-sink ratio of zero (Bertin and Gary, 1993). Marcelis (1994) used the source-sink ratio and temperature to determine the number of young non-aborting fruits in cucumber. Schepers et al. (2006) made the abortion of pepper fruits dependent on their fruit weight and assimilate supply: above a threshold of these two factors, a fruit would not abort any more. Buwalda et al. (2006) simulated fruit set based on an empirical function where the difference between source and sink strength determined the amount of newly set fruits. In all these models, abortion of individual organs was simulated, assuming that each organ obeyed the same deterministic rule in relation to the factors determining abortion.

Recently, grain simulation models have been adapted to simulate grain number, or grain set. In the model Ceres-maize, the number of kernels (sinks) depends on ratio of male to female flowers and their difference in timing and duration of flowering (Lizaso et al., 2007). Final simulated number of kernels is the minimum of the source- and sink-limited kernel set. In the model Ceres-wheat, kernel set depends on accumulated stem biomass between flag leaf sheath opening and 50% anthesis. Additionally, temperature reduces the number of kernels when the average temperature shortly after anthesis is above 25°C (Moreno-Sotomayor and Weiss, 2004). A similar method is used for sorghum in the model SORKAM: the number of seeds depends on the accumulation of plant dry weight between panicle branch and spikelet appearance or panicle elongation and anthesis. An empirical factor accounts for water stress (Gerik et al., 2004).

VARIATION AMONG PLANTS AND ORGANS

Observations

Variation exists in all biological processes. Despite growing under the same circumstances, plants have different numbers of fruits and/or a different pattern in fruit set. In sweet pepper, variation in timing of fruit set exists between individual indeterminate plants, although over many plants an average pattern of nodes with fruits and nodes

without fruits can be observed (Fig. 1). In pea, the position of the first reproductive node could vary two or three nodes (Guilioni et al., 1997). This led to different numbers of reproductive organs. Pearson et al. (1996) reported the number of trusses in tomato plants varying between 25 and 35. In deterministic crops with an ear or composed flower, not all florets set. In sunflower, florets in the outer radius were more likely to set than florets in the centre of the flower (Alkio et al., 2003). In maize, there was a considerable variation in the number of kernels per plant, related to dominating and dominated plants (Pagano et al., 2007).

Modelling

A few examples of simulation with variation in crop growth models exist. Pearson et al. (1996) developed a stochastic model for truss appearance in tomato. Truss appearance rate was assumed to be normally distributed, where the mean rate depended on temperature and the standard deviation was constant. The number of degree-days between the appearance of two trusses varied from truss to truss and from plant to plant. This led to plant-to-plant variation in the set of trusses. In the beginning, truss set was more or less synchronized over all plants, but this synchronization diminished as crop growth proceeded. Agostini et al. (1999) stochastically simulated the number of flowers and timing of flowering in kiwi. The number of buds per cane was determined by an estimated probability distribution, depending on vine length. The probability and timing of bud break were determined by position and orientation. Ganeshiah and Uma Shaanker (1992, 1994) proposed a model with self regulating sinks, in which the difference in growth rate from sinks, which had initially the same growth rate, originated from random drift of the assimilates to the sinks. Lieth et al. (1986) combined source-sink ratio and hormonal status (related to the age of the boll) to simulate the abscission of cotton bolls. First, the probability of abortion was calculated based on the boll age, after which the probability was corrected for the assimilate balance.

An alternative to obtain variation in simulation output is to add variability to the outcome of deterministic models after the simulation. Benjamin et al. (1999) established relations between mean weight and the variation in mean weight of different size classes, which could be used to calculate the variation in weight when only the mean weight is simulated. Alternatively, variation in model outcome can be simulated by conducting large numbers of simulation runs with random input from an n-dimensional hypercube with pre-defined limits (Monte Carlo simulations; e.g., Bouman and Jansen, 1993) or with parameter values drawn from a theoretical distribution (e.g., Scholten and Van der Tol, 1994). In these cases, variation is not an intrinsic part of the model.

INTRODUCING STOCHASTICITY IN MODELLING FRUIT ABORTION

Method

The idea of stochastically simulating fruit abortion is to let the circumstances, e.g., source and sink strength, determine the probability of fruit abortion. For example, a low source strength combined with a high sink strength gives a probability of 0.8 for the fruit to abort, while a high source strength and low sink strength decreases this probability to 0.2. If the probability of abortion is high, the fruit aborts in most of the cases, but there are also some cases in which the fruit sets. If a fruit sets, it contributes to the total fruit sink strength. Consequently, it affects the probability of abortion of the next fruit.

In such a stochastic model, each simulation run would represent a plant. Therefore, a large number of simulations needs to be done to simulate a crop. A fruit at the same position in different plants can abort or set, depending on what happened to the earlier formed flowers. From the batch of simulations, the average fruit set pattern as well as its confidence limits can be calculated.

With survival analysis, a relation between the rate of abortion and factors affecting this rate is quantified. Survival analysis estimates the effects of explanatory variables using survival or time-to-event times (Kleinbaum, 1996; Kalbfleisch and Prentice, 2002).

In the present case, it is the time from flowering until abortion of a certain flower or fruit. When the event does not occur, because the fruit is harvested or the experiment is ended before abortion or harvest occurred, the observation is called censored. Survival analysis is developed to properly deal with this kind of data. The purpose of the analysis is to find out whether certain explanatory variables affect the event rate. The method has been applied to a variety of biological cases such as types of behavioural data (Vos et al., 1998), abscission of blueberry leaves (Ojiambo and Scherm, 2005) and hibiscus flowers (Van Meeteren and Van Gelder, 2000) and the development of malaria mosquitoes (Koenraadt et al., 2004).

Stochastic Modelling of Fruit Abortion in Sweet Pepper

Below, an example is given of stochastic modelling of fruit abortion in sweet pepper. An experiment is described in which data on flower and fruit abortion in sweet pepper were collected. These data on flower and fruit abortion were analysed with survival analysis, using source and sink strength as explanatory variables. The resulting formula was used in a simple simulation model and observations and simulation results on fruit set were compared.

1. Experiment. Sweet pepper (*Capsicum annuum* L.) cultivar ‘Red Spirit’ (Enza seeds, Enkhuizen, The Netherlands) was grown on rockwool slabs at a density of 2.5 plants m⁻² in a compartment of a multispan Venlo-type glasshouse at Wageningen, The Netherlands (52°N). Water and nutrient supply were ample. The twin branch system was applied resulting in two stems per plant, with side shoots restricted to one leaf and flower. The experiment lasted from mid-December to the beginning of September. Temperature was controlled by heating and ventilation. The average daily outside global radiation was 11.6±7.7 MJ m⁻² d⁻¹ (mean±sd), 24-h temperature was 22±2.0°C (mean±sd) and the average day-time CO₂ concentration was 430±25 (mean±sd) μmol mol⁻¹.

Every 3 to 4 days, each node on 7 plants was checked for new flowers, abortion of flowers and fruit harvest. Fruit set was defined as flowers resulting in a harvested fruit. The survival time of each fruit, defined as the time between flowering and abortion, the time between flowering and harvest or the time between flowering and the end of the experiment, was calculated. In total, data of 843 flowers were collected. Red fruits were harvested every three to four days and their weights determined. Seven destructive harvests, 34-42 days apart, were conducted in which dry mass of stems, leaves and fruits and leaf area of six plants were measured.

2. Deriving Source and Sink Strength. Source strength was calculated using the crop model INTKAM (Marcelis et al., 2006). Measured leaf area index, daily global outside radiation, average 24-h inside temperature and average daily CO₂ were used to simulate plant growth. Simulation output was calibrated on the measured data. Growth rate per day minus the maintenance respiration was taken as the source strength. For each fruit, sink strength on every day of its survival time was calculated. Sink strength was described by the first derivative of a Richards function, based on the data of Marcelis and Baan Hofman-Eijer (1995). From these data, the total sink strength per plant was calculated.

3. Survival Analysis. The survival time of each flower was related to source strength and total sink strength with Cox proportional hazards model. A time-dependent survival analysis was done, implying that the values of the explanatory variables changed from day to day. Cox proportional hazards model quantifies the effect of the n explanatory variables $X(t)$ ($X_1(t)$, $X_2(t)$, ..., $X_n(t)$) on the baseline hazard rate $h_0(t)$. The abortion rate ($h(t, X(t))$) on day t given the explanatory variables $X_i(t)$ is calculated as

$$h(t, X(t)) = h_0(t) * \exp\left[\sum_{i=1}^n \beta_i X_i(t)\right] \quad (1)$$

Coefficient β_i indicates the influence of the explanatory variable $X_i(t)$ on the hazard rate, a negative β_i implies that the hazard rate is decreased (abortion rate is lower),

while a positive β_i increases the abortion rate. Moving averages of source and total sink strength over periods of 1 to 10 days were calculated and used as explanatory variables. All combinations of averages of source and sink strength and their interaction were tried (100 combinations in total) to obtain the best fit. The moving average of eight days for source strength and 10 days for total sink strength gave the best fit. Analysis was done in R 2.8.0 (R Development Core Team, 2007).

During the critical period for abortion, the baseline hazard $h_0(t)$ was assumed to be constant. It was quantified by dividing the total number of aborted fruits by the total survival time of all fruits. The cumulative baseline hazard indicated that no more fruits aborted after 30 days after flowering. However, as most flowers abort within 10 days after flowering (Marcelis et al., 2004), the baseline hazard was multiplied by three and the time in which flowers could abort was divided by three, resulting in a critical period of 10 days after flowering and a baseline hazard of 0.1.

4. Model Description. A simple simulation model was constructed in which fruit set and abortion were simulated. The model had the source strength from the experiment as input. Flowers appeared every day. For fruits aged 1 to 10 days, the probability of abortion per day was calculated every day, based on the source strength and total fruit sink strength. If this probability per day was less than a random number, drawn from a uniform distribution between 0 and 1, the fruit aborted. Fruits surviving the first 10 days were harvested after 65 days. Simulated time was 217 days (31 weeks). In total 100 simulations were performed. Weekly fruit set was calculated as the number of set fruits in 7 days, calculated every 7 days.

5. Simulation Results. The average simulated pattern of fruit set showed peaks in fruit set which were nearly correctly timed, although the amplitude in the second and third peaks was not as extreme as in the observations (Fig. 2). The standard error of simulated weekly fruit set was rather small compared to the observations, due to a high number of simulations (100) compared to the observed plants (7). The overall percentage fruit set in the simulation was 28%, which was comparable to the observed fruit set (30%).

6. Conclusion. We demonstrated that stochastic dynamic simulation of fruit set results in accurate simulation results. Next step is to incorporate the abortion function in a model which also simulates plant and fruit growth. Further improvements regarding the abortion function are to incorporate the effect of temperature and cultivar on the abortion rate.

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Figures

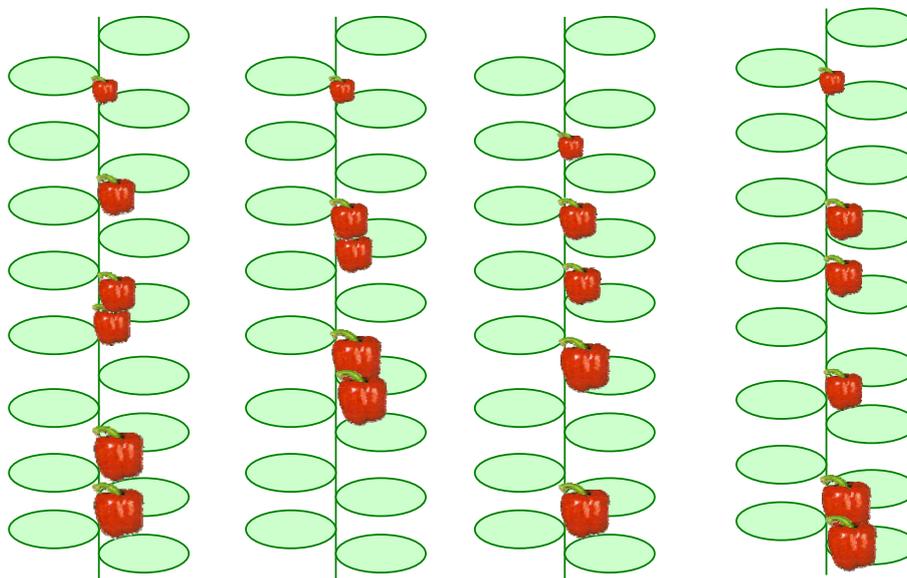


Fig. 1. Observed differences in fruit set patterns on sweet pepper plants grown under the same conditions.

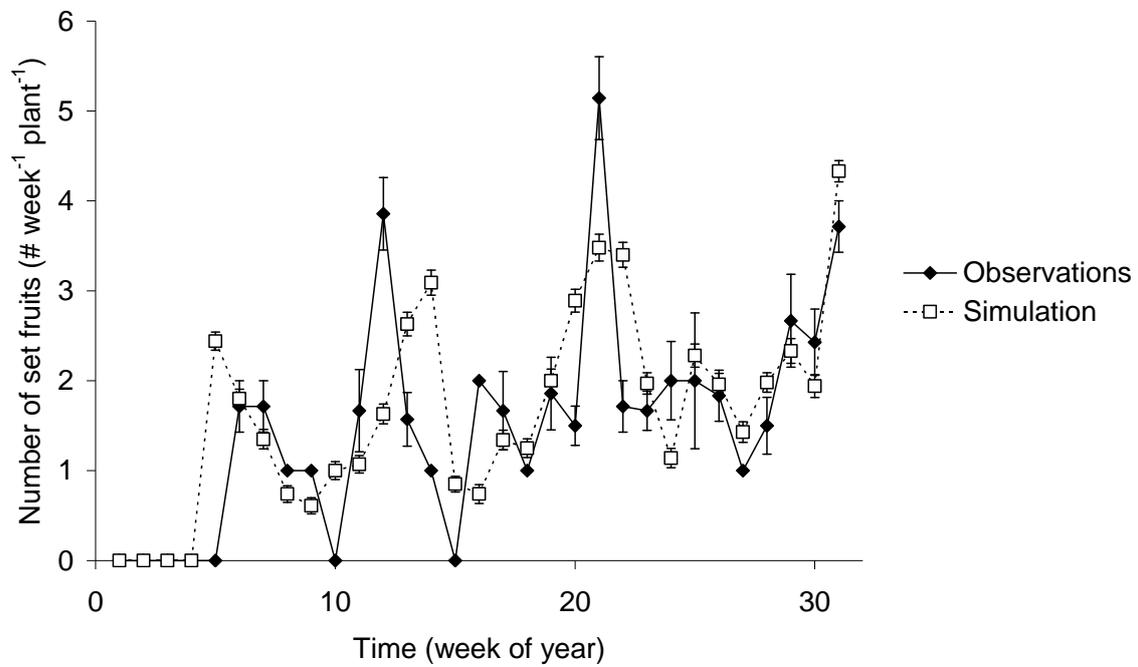


Fig. 2. Observed ($n=7$) and simulated ($n=100$) weekly pattern of fruit set. Points represent the averages, error bars the standard error.