Development and dry matter distribution in glasshouse tomato: a quantitative approach

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Abstract

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In the glasshouse cultivation of a long-season tomato crop, maximum fruit production is obtained when there is a proper balance between the demand and the supply of assimilate, and an optimum proportion of vegetative growth throughout the season in order to sustain the crop photosynthetic capacity. These aspects of crop growth are mainly affected by the fruit load, defined as the assimilate demand of all fruits together. In practice fruit load is controlled by plant density, fruit thinning and temperature. These measures for crop control can be more precise and effective if their effects are known in quantitative terms. An explanatory dynamic growth model was developed that simulates assimilate demand and dry matter distribution in an indeterminate tomato crop. Number of growing organs was evaluated through prediction of initiation, abortion and harvest of individual organs. Assimilate demand was based on potential organ growth rates (growth at nonlimiting assimilate supply). Dry matter distribution in the model was in proportion to the potential growth rates of the organs.

In total 11 glasshouse experiments were conducted, six of which included temperature treatments. Truss formation rate increased with temperature (17-27°C) and declined with plant age. Truss formation rate was found to depend on the genotype, while fruit load, plant density, season and electrical conductivity of the root environment (EC: 0.3-0.9 S m^{-1}) had no effect. The number of fruit that develop per truss was positively correlated with the vegetative growth of the top of the plants. The duration of the fruit growth period (time between anthesis and start of colouring) was shortened with increasing temperature, young and old fruits being the most sensitive. At the same air temperature the fruit growth period in summer was shorter than in spring. Fruits of old plants had slightly longer growth period than fruits of young plants. Potential weight of the fruits at harvest was negatively correlated with temperature, mainly due to the shorter fruit growth period. Further, the potential size increased with ontogeny, which effect was more pronounced in early than in late spring. The course of potential weight in time was described by a Gompertz growth curve exhibiting the maximum growth rate at about 40% of the fruit growth period. When during fruit development a fruit changed from limiting to nonlimiting assimilate supply, it did not immediately reach the same growth rate as fruits grown constantly at nonlimiting assimilate supply. A mechanism is proposed that explains this phenomenon. The fraction of dry matter distributed to vegetative growth declined substantially with temperature. The (apparent) potential growth rate of a vegetative unit at 24°C was estimated to be as much as 50% lower than at 19°C. The dry matter content of fruits was negatively correlated with temperature and EC of the root environment and was higher in summer than in spring and autumn.

The model was tested with data from five commercial crops. Truss formation rate, fruit growth period and dry matter distribution were predicted reasonably well. The modelling of the number of fruits per truss requires more investigation. Simulated assimilate demand of a mature tomato crop reached values of 10 and 60g CH_2O m^{-2} d^{-1} for maintenance respiration and growth respectively. The potential growth rate (as defined by the sinks) appeared to be about twice the actual growth rate.

A simulation study indicated that maximum fruit production of tomato is probably obtained at a fairly low leaf area index (2-3 m^2m^{-2}). At supra-optimum leaf area index additional leaf area for extra light interception requires more assimilate than it would produce. Computations showed that in spring and early summer the optimum plant density is determined by the required number of fruits (sink capacity) whereas in summer a combination of high plant density and fruit thinning seems required for sufficient leaf area. The results are discussed with respect to the crop sink-source system and temperature control in the glasshouse. Prospects for practical applications of the model are presented.

Key words: tomato, *Lycopersicon esculentum* Mill., glasshouse cultivation, temperature, electrical conductivity, fruit thinning, plant density, plant development, abortion, fruit development, sink, fruit growth, dry matter distribution, simulation model, temperature control.

Contents

1

GENERAL INTRODUCTION

1.1 Tomato production in the Netherlands

The tomato is one of the major glasshouse crops in the Netherlands. At present the crop covers circa 1400 ha or 14% of the Dutch glasshouse area and 30% of all glasshouse vegetables. The total annual yield of about 600,000 tonnes represents a value of one thousand million NLG. Round tomatoes occupy about half of the total area, beefsteak and intermediate types one quarter each, while cherry tomatoes cover about 40 ha (Anonymous, 1993; 1994).

Usually, the crop is grown in multi-span Venlo-type glasshouses which are heated by a distribution system of heating pipes just above ground level fed by a central boiler. Modern glasshouses are equipped with an independently controlled second heating system consisting of small pipes amidst the canopy which can be raised vertically. Heating, ventilation and CO_2-supply are computer controlled. Almost the total area is provided with artificial substrates, mainly rockwool with trickle irrigation for water and nutrient supply. Most of the crops are sown in November, commence flowering in January and produce fruits from March until November. The plants grow indeterminately, producing a truss after each three leaves (Shishido and Hori, 1977), and are usually trained according to the high wire system (van de Vooren *et al.*, 1986). Commonly the distance between rows is 0.8 m and the distance between plants within the row is circa 0.5 m, resulting in about 2.5 plants per m^2. At the end of the cropping season each plant reaches a stem length of nearly 10 m and has then produced about 100 leaves, 35 trusses, 300 fruits (round tomato) and 20 kg fruit fresh weight (de Koning, 1993).

1.2 Control of crop growth

In the Netherlands, temperature requirements of tomatoes and other fruit vegetables can be satisfied all the year round in heated glasshouses, but in winter light conditions are too poor for any substantial fruit growth (Huijs, 1989). Therefore, these crops are usually sown in November, planted in December in the glasshouse and grown until October or November the following year. After an initial vegetative phase, the crops enter the generative phase in January when fruit growth is allowed. Because production has to continue for almost a year, vegetative growth has to be maintained also in the generative phase. Thus the assimilate produced by photosynthesis has to be balanced over generative and vegetative growth. In the short term, fruit yield will be high when a large portion of the assimilate is partitioned to the fruits, but vegetative growth may then become too low to sustain the crop's photosynthetic capacity and consequently

future yield is affected adversely. Therefore, long-term maximum yield is only obtained through a proper balance between vegetative and reproductive growth.

It is generally accepted that assimilate distribution is primarily regulated by the sinks (Gifford and Evans, 1981). The (competitive) power of a sink to attract assimilate is commonly called *sink strength* (e.g. Wareing and Patrick, 1975; Wolswinkel, 1985). Unfortunately, this general description allows for different interpretations and consequently in the literature the use of the term sink strength is not unambiguous (Farrar, 1993*a*; Minchin and Thorpe, 1993). Here the sink's power to attract assimilate is assumed to be defined by its maximum ability to process carbohydrates (including respiratory losses) and called *assimilate demand* to avoid the different interpretations of sink strength.

In a full-grown tomato crop the fruits are the main sinks as they receive about 70% of the total dry matter available for growth (Hurd *et al.*, 1979; de Koning, 1993). The total assimilate (sink) demand of all fruits on a plant is generally denoted as fruit load, but again this term is not precisely defined. In this study *fruit load* is considered to be the assimilate demand of all fruits together. Note that, according to this definition, the number of fruits on the plant is an important, but not the only, determinant of fruit load.

Besides causing low vegetative growth, high fruit load also reduces fruit size (Hurd *et al.* 1979; van Noort, 1991) due to mutual competition between fruits. Abortion of flowers and young fruits is enhanced by shortage of assimilate (Atherton and Harris, 1986) and consequently acts as negative feedback to fruit load. Alternation of high fruit load with much abortion and low fruit load accompanied by less abortion induces a cyclic pattern of dry matter distribution between fruit and vegetative organs (de Koning, 1989*a*; Marcelis, 1992*b*) and results in an irregular pattern of fruit production (Bakker, 1989). Large fluctuations in fruit load, and consequently in the growth rate of individual fruits, enhance the risk of cuticle cracking (Bakker, 1988; Ehret *et al.*, 1993), large fruit cracks (Wright, 1989) and blossom-end-rot (Ho *et al.*, 1993). Under favourable light conditions low fruit load may cause thick deformed leaves with small leaf area (Nagaoka *et al.*, 1979; Nederhoff *et al.*, 1992) while extremely low fruit load may even inhibit photosynthesis (Gucci and Flore, 1989). The importance of fruit load in commercial tomato cultivation is reflected by the fact that it is one of the crop characteristics most frequently recorded by growers (Peerlings, 1988; Kip, 1989). At present, recording is limited to the number of fruits, because of insufficient quantitative knowledge about factors that affect the fruit's assimilate demand.

The optimum fruit load depends principally on the amount of dry matter available for growth. Daily radiation integral, and consequently photosynthesis and the amount of dry matter available, vary significantly during the year (de Koning, 1993). Ideally, fruit load should vary accordingly. The main measures to adapt fruit load to seasonal variation are initial plant density, retaining side shoots and fruit pruning. These measures all affect the number of fruits per unit cropping area and, therefore, are primarily appropriate for long-term control. They are part of the (tactical) cultivation plan based on expected average climate conditions for the whole cropping season.

Additional to seasonal variation, radiation integral may vary widely from day to day and even weekly averages may deviate significantly from the long-term average. The assimilate production will vary accordingly. Though, through storage of assimilate in the crop, temporary imbalance between supply and demand may be compensated for such that dry matter distribution is not affected in the long term (de Koning, 1990), frequent adjustment of the demand for assimilate to assimilate production reduces the risk of prolonged imbalance. Hence, a grower needs a tool for short-term control of fruit load. Temperature appears most suitable, as changing this factor affects the fruit's assimilate demand immediately (Walker and Ho, 1977) without changing photosynthesis rate (15-25°C, Nilsen *et al.*, 1983; Acock, 1991). The use of temperature for short-term control of the crop's assimilate demand, however, may have consequences for fruit load in the long term because temperature affects fruit initiation and fruit development (Klapwijk, 1987). Moreover, temperature has a dual effect on assimilate required for maintenance, as temperature increases maintenance respiration per unit biomass (Walker and Thornley, 1977) but decreases crop weight (de Koning, 1989*a*).

Thus, besides high instantaneous photosynthesis rate, maximum production in the long term require that the assimilate demand is in accordance with the supply, that vegetative and reproductive growth are in optimum balance and that respiratory losses are low. As discussed above, a grower tries to achieve these sub-goals, summarized as '*control of crop growth*', through crop measures and climate control. In current practice decisions at the tactical level, e.g. concerning sowing date and plant density, are based on experience and general rules. Daily crop control (operational level) anticipates on the expected crop response to the actual conditions. In addition to the direct control, measures may be taken afterwards on the basis of visual judgement of the crop. The tool applied depends mainly on the experience of how different measures quantitatively affect different aspects of crop growth.

1.3 Objectives of the study

With a better understanding of the effects of different measures, and especially if crop response can be predicted quantitatively, crop control can become more precise and more effective. The general objective of this study is to contribute to the understanding of crop growth for the use of crop control. Two aspects discussed above will be investigated in particular, *viz.* (1) control of assimilate demand as the counterpart of assimilate production and (2) control of dry matter distribution between vegetative and generative plant parts.

Each control tool, especially temperature, affects several plant processes which may all contribute to the ultimate crop response. Moreover, in the plant many interactions occur between different processes. Interactions may also play a role in feedback mechanisms, so that long-term effects of crop measures may differ from the short-term effects. Therefore, predicting the result of crop measures and climate factors is rather complex and for reliable long-term predictions not only the direct effects but also the indirect after-effects should be taken into account.

The problem can be approached by mathematical modelling. Simulation models appear successful tools in prediction and explanation of the behaviour of a complex, dynamic system as a growing crop (de Wit and Arnold, 1976; Loomis *et al.*, 1979). In such a model the crop, at any moment, is quantitatively characterized by state variables. Each state variable is associated with rate variables that define their change with each time-step. Rate variables may be identified with specific plant processes and are formulated as mathematical expressions of external variables (such as temperature) and internal variables (such as plant weight). Generally a model should describe the system at least at one hierarchical level lower than the level it explains (Loomis *et al.*, 1979). Hence, to understand assimilate demand and dry matter distribution at the whole-plant level, a model that considers growth and development of separate organs seems appropriate.

Several models predict the assimilate production of a crop with reasonable accuracy (for tomato e.g. Acock *et al.*, 1978; Gijzen *et al.*, 1990; Acock, 1991; Bertin and Heuvelink, 1993; Nederhoff and Vegter, 1994) but understanding and modelling of dry matter distribution is still in its infancy (Challa, 1985; Marcelis, 1993*a*). The first sub-goal of this thesis is to quantify the crop's demand for assimilate. This should support the grower in adjusting the demand to the supply of assimilate. As a first practical application, it may result in a better parameter

for fruit load than just the number of fruits. The other aspect of crop control investigated in this thesis concerns the balance between fruit growth determining short-term yield and vegetative growth required for long-term production capacity. The second sub-goal, therefore, is to investigate and model dry matter distribution among fruits and vegetative organs.

For long-term predictions of assimilate demand and dry matter distribution, the number of growing organs has to be evaluated through prediction of initiation, abortion, ageing and harvest of individual organs. So, besides the modelling of growth of individual organs, part of this study concerns the developmental aspects of a tomato crop.

A model should be validated with data that are independent from those used to develop the model (van Keulen, 1976; Loomis *et al.*, 1979). In view of the proposed application of the model in commercial practice, data for validation are collected in commercial crops.

Primarily this study will attempt to obtain quantitative descriptions of responses at the organ level and to understand and model assimilate demand and dry matter distribution from the relationships obtained. It is not intended to explain the physiological mechanisms underlying the responses at the organ level. Nevertheless, at the crop level the model will help to increase insight into crop growth as an integrated phenomenon. The results of this study, especially concerning the understanding of crop functioning, have relevance to other fruit vegetables than tomato, as growth and control of growth of these crops show many similarities. Although parameter values and possibly some sub-models will be crop specific (Challa, 1989), the general principles underlying the model may be identical for many indeterminate vegetable crops.

1.4 Modelling dry matter distribution

With respect to modelling of dry matter distribution some different principles can be distinguished (reviewed by Marcelis, 1993*a*). Descriptive allometry, proposing predetermined ratios that may change with the developmental stage of the crop, is frequently used because it provides a simple description of dry matter distribution. For indeterminate crops this empirical approach may be valid for long-term averages (Challa and Heuvelink, 1993) when cyclic distribution patterns are levelled out, but it accounts neither for instantaneous deviations nor for effects of crop measures and climate control intended to manipulate the distribution between fruits and vegetative parts.

Secondly, dry matter distribution may be modelled by a functional equilibrium, assuming that the plant tends to approach an optimum balance between the activities of different organs. This approach appeared successful to simulate changes of shoot:root ratio (Marcelis, 1993*a*), but as fruits have no distinct function in the growth process, the principle seems difficult to apply when reproductive organs are involved.

A third type of partitioning models assumes that dry matter distribution is regulated primarily through competition between individual sinks. This approach seems to have the best prospects to explain dry matter distribution in indeterminate crops (Marcelis, 1993*a*). Here, the competition for assimilate is determined by demand functions of separate sinks that may be described by their potential growth rates obtained under conditions of non-limiting assimilate supply (Marcelis *et al.*, 1989). Modelling dry matter partitioning proportionally to potential growth rates showed fairly good results for cucumber (Schapendonk and Brouwer, 1985; Marcelis, 1994*b*) and rose (Lieth and Pasian, 1991). Also for tomato this approach appeared promising (Kano and van Bavel, 1988; Heuvelink and Marcelis, 1989; Jones *et al.*, 1991; Dayan *et al.*, 1993*a*, 1993*b*; Heuvelink and Bertin, 1994). Some models that use demand functions to simulate dry matter partitioning in tomato are briefly discussed below.

In TOMATOSIMULATOR (Hoogenboom, 1980) dry matter distribution between leaves, stem, roots and fruits is a forcing function of plant age, but dry matter distribution among fruits is regulated by mutual competition. The fruit's demand function is described by a normalised growth rate and defined by its age and position on the plant. TOMATOSIMULATOR is based on the general crop model BACROS (de Wit *et al.*, 1978) with crop specific parameters gained from the literature. TOMATOSIMULATOR is not suitable to use for control of dry matter distribution as it assumes a fixed ratio between vegetative and total fruit growth. Moreover, it ignores any possible effect of temperature on fruit development rate, fruit growth rate and crop biomass.

Kano and van Bavel (1988) briefly described a simulation model that is based on leaf photosynthesis and respiration. The main purpose of their model is to predict effects of environmental factors on fruit growth and yield of glasshouse tomato for optimizing glasshouse climate control (Kano and Shimaji, 1988). Partitioning of dry matter is described by the demand (sink capacity) for assimilate of individual trusses and the vegetative part of the plant as a whole. Unfortunately, it is not clear how the demand for assimilate is defined and how plant and fruit

development are incorporated. The assimilate demand of all vegetative plant parts together is a fixed value, independent of the plant ontogeny.

Jones *et al.* (1989, 1991) and Dayan *et al.* (1993*a*, 1993*b*) also developed a dynamic tomato growth model, TOMGRO, for optimizing temperature and CO_2 control in glasshouse tomato production. In this comprehensive growth model, canopy photosynthesis is computed with the model of Acock *et al.* (1978). Leaf and truss initiation rates are functions of temperature and CO_2-concentration. Number of leaves, stem segments and fruits move through successive age classes according to development rate of each component depending on temperature and CO_2-concentration. Dry matter is distributed proportionally to the potential growth rates for each class and each plant component. The potential growth rate of leaves in TOMGRO is computed from a potential leaf area expansion rate, determined by physiological age of the leaf, temperature and CO_2-concentration, and the specific leaf area (SLA) which depends on light, CO_2 and temperature. Fruit abortion in TOMGRO is a function of the ratio of carbohydrate supply to demand (Bertin and Gary, 1993; Dayan *et al.*, 1993*a*).

All three models were principally applied in short-term control of the glasshouse climate. The descriptions of plant development and organ development, required for reliable long-term prediction, and sink demand functions (potential growth rates) generally lack a solid basis and many assumptions and simplifications had to be made to construct a complete model. Moreover, none of the models mentioned is extensively validated, while sometimes the data-sets used for validation were not independent from those used for model development. Hence, there is a definite need for systematic research to develop solid descriptions of development rates and growth functions and the results should be tested with independent data.

So far one model has been left indiscussed, *viz.* TOMSIM, a tomato simulation model recently developed by Heuvelink (Bertin and Heuvelink, 1993; Heuvelink and Bertin, 1994). The reason for this omission is that descriptions of plant and fruit development in TOMSIM originate from this thesis. TOMSIM simulates dry matter production according to the model of Gijzen (1992) and dry matter distribution on the basis of potential growth rate of the vegetative plant as a whole and that of separate trusses (Heuvelink and Marcelis, 1989). TOMSIM predicted dry matter distribution reasonably well but some parameters had to be adjusted for cultivar dependent properties (Heuvelink and Bertin, 1994).

1.5 Conceptual model

Following the objectives, the proposed model should predict the instantaneous as well as the long-term assimilate demand and dry matter distribution in a tomato crop. Dry matter available for growth is here input to the model. To model the relatively slow growth responses at the whole-plant level, a time step of one day is most appropriate (Loomis *et al.*, 1979). Previous research, showing that development and dry matter distribution in tomato are not affected by the diurnal temperature regime (de Koning, 1988*b*), confirms that there is no need for a shorter time-interval. The model covers only the generative phase of the cropping period and simulation therefore starts at the flowering of the first truss.

The assimilate demand of a sink organ is defined as the maximum ability to process carbohydrates (section 1.2). In the sink, assimilates are used for growth and maintenance. The component for growth is assumed to be determined by the potential growth rate of the sink. The sink's maintenance respiration is proportional to its biomass (Penning de Vries, 1975).

The distribution of dry matter available for growth is assumed to be proportional to potential growth rates, as in TOMGRO and TOMSIM. Since a fruit is the smallest unit in cultivation measures (e.g. fruit pruning and harvest) each fruit is considered separately. This approach agrees also with common crop recording of numbers of fruit set and number of fruits on the plant. In the first two months of the generative phase the number of leaves per plant increases from about 10 to 25. Therefore, one sink for the whole vegetative plant (as in the model of Kano and van Bavel and TOMSIM) is considered too coarse. Instead, a stem segment and (three) leaves between two successive trusses is regarded as one functional sink, here called a *vegetative unit*. Changes in numbers of fruits and vegetative units occur through plant development, abortion, ageing and harvest.

Root growth comprises 13 to about 6 percent of the cumulative dry weight growth of a young (Heuvelink, 1989) or mature tomato crop (Hurd *et al.*, 1979; Yoshioka and Takahashi, 1979), respectively, which implies that even large changes in the root's assimilate demand have a rather limited effect on total crop assimilate demand and dry matter allocated to leaves and fruits. This and the considerable effort required to measure root growth, were decisive in confining the model to above ground organs only.

The conceptual model is presented as a relational diagram (fig 1.5.1). Note that descriptions of maintenance and growth respiration are used only for predicting the crop's assimilate demand and not for predicting dry matter distribution.

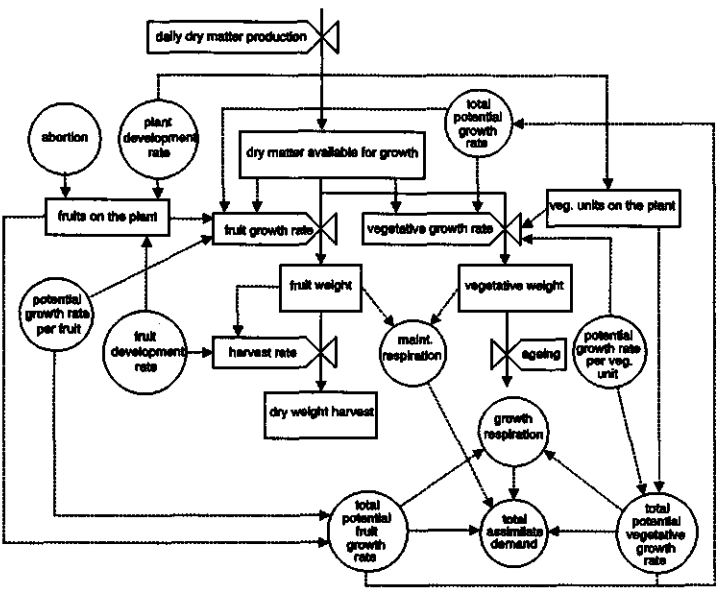

Figure 1.5.1
Relational diagram of a conceptual model predicting the assimilate demand and the dry matter distribution in an indeterminate tomato crop (symbols according to Forrester, 1961).

The hypotheses underlying the model and the structure of the model are largely similar to those of TOMGRO, except for two differences. First, TOMGRO considers several age classes of plant components while in our model each fruit and each vegetative unit is described separately. Use of age classes may decrease required computing time but as application of the model in fast responding on-line climate control is not intended yet, computing time is not regarded as a serious problem. Secondly, the potential dry weight increase of leaves in TOMGRO is determined by potential leaf area expansion and specific leaf area (SLA). Our model does not consider leaf area and (as with fruits) uses a direct description of potential dry weight increase per vegetative unit.

1.6 Outline of the thesis

Chapter 3 describes the experimental results and modelling concerning plant development and the formation and development of fruits. As these processes are predominantly dependent on temperature (Klapwijk, 1987), experiments are mainly aimed at quantifying temperature responses. In addition, truss formation rate was measured in some cultivar trials conducted at commercial nurseries.

Chapter 4 deals with assimilate demand of vegetative units and individual fruits. Because fruits are the main sinks for assimilate, considerable attention has been given to quantifying the potential fruit growth rate. Fruit growth rate varies with age (e.g. Varga and Bruinsma, 1976), the position of the fruit on the plant (Bangerth, 1989) and temperature (Walker and Thornley, 1977; de Koning, 1989*a*). The effects of these factors are investigated and modelled. Growth and maintenance respiration rates are quantified according to the literature (Penning de Vries, 1975; Walker and Thornley, 1977; Spitters *et al.*, 1989; Gijzen, 1994). Although modelling dry matter content of fruits was not an objective of this study, a preliminary description is obtained from some readily available data.

Because many of the glasshouse experiments conducted in this study included measurements of development and potential growth, the 'Materials and Methods'-sections of all experiments are presented in a separate chapter (Chapter 2) to avoid repetition.

In Chapter 5 the sub-models obtained are integrated in the ultimate growth model. For testing the model, data were collected at commercial nurseries. The data cover the entire cropping season and include recordings of crop development, growth and environmental factors. Comparisons of model predictions with these data are presented in Chapter 6, together with a brief sensitivity analysis on the model.

Chapter 7 includes predictions of the crop assimilate demand, some case-studies and an example of how to model can be used to advise about optimum shoot density and number of fruit per truss. Finally, Chapter 8 includes a discussion of the sink-source system with regard to the subjects investigated, a reflection on the model and an outlook of possible applications of the model in practice.

2

MATERIALS AND METHODS

2.1 Experiments at GCRS

2.1.1 equipment and climate control

From 1987 until 1992 11 experiments were conducted in several glasshouses at the Glasshouse Crops Research Station. The code used to denote the different experiments consists of the number of the glasshouse and the year.

The Venlo-type glasshouses were heated with warm water filled heating pipes between the plant rows at approximately 0.5 m above ground level. Ventilation took place by windows in both sides of the roof. A distributed computer system was used for climate control and data acquisition (Bakker *et al.*, 1988). The environmental conditions were recorded every minute, averaged as hourly values, and filed. Temperature and humidity were measured centrally in the compartments 1.5 m above-ground level with screened and aspirated PT-100 sensors (dry and wet bulb). The CO_2 concentration was measured with Siemens infra-red gas analyzers. In all experiments pure CO_2 was supplied to a level of 350 μmol^{-1} during daytime. In general excessively high (> 90% RH) humidity was prevented by minimum pipe temperature settings and set-points for ventilation that were 0.2 to 0.5°C above the setpoints for heating by day as well as at night. In all temperature experiments, in order to achieve the desired 24-h mean temperature, the temperature setpoints were adjusted every minute according to the achieved temperature from sunrise onwards (de Koning, 1988*a*). In general the adjustment of night temperature required, was less than 2°C, and desired 24-h mean temperatures were achieved within 0.1°C. Night started at sunset and ended at sunrise. In all temperature experiments, day as well as night temperature settings were equal to the desired 24-h mean temperature, except in some treatments of experiment 210/90 where the day/night regime was an experimental factor. In general, for the low temperature treatments, the setpoints for heating and ventilation were decreased with increasing solar radiation (above a threshold value) in order to compensate for the temperature rise from solar radiation. Thermal screens were not used by day. For experiments 211/87 and 307/90a, closing of thermal screens at night depended on the outside weather conditions (temperature and windspeed) and the desired temperature inside. Consequently, screening was used most frequently for high temperature treatments. Thermal screens were not used in experiments 402/88, 307/88, 402/89, 210/89, 307/90b, 210/90, 111/91, 103/92 and 307/92.

2.1.2 general information

Several round tomato cultivars were used for the different experiments (table 2.1.1). Selection depended mainly on the cultivar commonly used by commercial growers. In the 307/90a experiment also the beefsteak cultivar 'Dombito' was included. Generally, experiments started at flowering of the first truss. All crops were grown on rockwool slabs and irrigated with a standard nutrient solution (Sonneveld and de Kreij, 1988) by means of a trickle irrigation system. Excess solution was collected and re-used without sterilization. For experiments 211/87, 307/90a and 210/90, the rockwool was held in troughs (Libra-trough) in order to be able to move plants (two plants per trough) between compartments. In this way, plants could be exposed to different temperatures for longer (expt 211/87) or shorter periods (expts 307/90a and 210/90).

Table 2.1.1
Cultivar and flowering date of the first truss for all experiments at GCRS.

experiment	cultivar	flowering of first truss
211/87	'Counter'	14 January
402/88	'Counter'	19 January
307/88	'Counter'	5 April
210/89	'Counter'	21 January
402/89	'Blizzard'	3 February
307/90a	'Calypso'	11 January
307/90a	'Dombito'	18 January[1)]
307/90b	'Calypso'	27 August[2)]
210/90	'Calypso'	27 August
111/91	'Liberto'	23 January
103/92	'Pronto'	20 January
307/92	'Astrid'	24 January

1) flowering of second truss, first truss was removed
2) young plants, old plants as in experiment 307/90a

The standard plant density was 2.1 plants m^{-2} (0.8 × 0.6 m) in all experiments. Because of the limited height available in the glasshouses used in experiments 211/87 and 111/91 the plants were not layered but were trained up to the wire

and then down again. In other experiments (307/90a, 307/90b, 103/92, 307/92), the crop was trained to a high wire and layered weekly. For some short-term experiments (402/88, 307/88, 402/89, 210/89 and 210/90), the experiment was ended when the top of the plants reached the wire. Twisting and removing of side-shoots and old leaves (up to the harvestable truss) was done each week, as normal in commercial growing. Flowers were pollinated with the aid of an 'electric bee' three times a week and by bumble bees in experiments 103/92 and 307/92. Generally, harvestable fruits were picked on Mondays, Wednesdays and Fridays each week.

2.1.3 experiment 211/87

In this experiment, plants were grown in four compartments at 17, 19, 21 and 23°C, respectively, from 14 January (first truss flowering) until 11 March. On 28 January and again on 11 and 25 February, plants were removed from each compartment and transferred to the other compartments, where they remained until the end of the experiment. In this way, 40 different treatments were obtained. There were 24 plants in each treatment, divided between three plots. The date of flowering and harvestable truss numbers were recorded three times a week on each plant. Averages per plot were used to estimate correlations between flowering rate and achieved temperature and for calculations of the fruit growth period (time between anthesis and start of colouring).

2.1.4 experiment 402/88

To investigate the effect of truss position and the number of fruits per truss on fruit weight, the first fruit was retained on each truss of three plants while, on another three plants, the first and second fruits were retained. Pruning was done at anthesis or just after fruit set. Fruits of trusses 1 to 8 were weighed at harvest.

2.1.5 experiment 307/88

In this experiment the effect of fruit position within a truss on potential weight was investigated. All trusses were pruned to leave only one fruit per truss. In one treatment, the fruit was retained at position 1 (proximal fruit), while in four other

treatments the single fruit was retained at positions 2, 4, 6, or 8. Each treatment consisted of three plants. After some weeks many young fruits were affected by blossom-end rot and only fruits of trusses 2, 3 and 4 were completely unaffected.

2.1.6 experiment 402/89

This experiment consisted of some small sub-experiments, mainly concerning potential fruit weight. Fruit weights of plants grown with only the first positioned fruit per truss were compared with those where the first and second fruit remained. Pruning was done for all trusses but, due to the incidence of blossom-end-rot, only trusses 1 to 8 were used for comparisons. Both treatments were carried out on eight plants.

In four further treatments, one fruit was retained at either position 1, 2, 4 or 6 on each of trusses 1 to 4 and at truss 5 and above two fruits were retained at either positions 1+2, 2+4, 4+6 or 6+8. Each treatment consisted of four plants. The effects of fruit position and of ranking (first or second fruit) were calculated over truss 1 to 7 and 5 to 7, respectively.

To investigate fruit growth after a dramatic increase of assimilate supply (change from source to sink limitation), normally grown plants were pruned to one or two fruits per truss for all existing trusses. This was done on 5 March, when fruits of the first truss had started to colour. From this date newly flowering trusses were pruned at anthesis. Both pruning treatments and two control treatments, grown with one or two fruits from the start (continuous potential growth) respectively, were applied to eight plants each. Diameters of the remaining fruits were measured on 5 March and at harvest. From the control treatments, the diameters of fruits from truss 2 to 9 were determined twice a week.

In order to determine the change in dry matter content during the development of a fruit, fruits (from all within truss positions) of different trusses, and therefore different development stages, were picked when the fruits of the first truss started to colour. Fruits were cut in half and dried for four days in a forced air oven at 80°C. Samples consisted of 10 to 30 fruits, depending on their size. Three samples from each truss number were dried, except for the very young fruits where, because of the large number of fruits required per sample, there were only enough fruits for one or two samples.

2.1.7 experiment 210/89

The aim of this experiment was to investigate the limits on temperature and time within which a tomato crop is able to integrate temperature (de Koning, 1990). Therefore, periods of several days at low temperature were alternated with equal periods at high temperature. The 24-h mean temperature varied from 15 to 22°C. As 24 compartments were available, six treatments were carried out in four replicates. Each experimental plot consisted of 32 plants and was surrounded by guard rows. Treatments lasted from 28 January until 10 April; before and after this period, temperatures were equal for all treatments. Within the compartments plants of two different ages were planted on 22 December 1988. At the start of treatment, the older plants were flowering on the first truss and the younger plants started to flower ten days later. Results have been previously published (de Koning, 1990).

In this study the experiment was used to obtain data about the short-term temperature response of plant development rate. Flowering truss and position of the latest open flower on this truss were recorded twice a week. Data were averaged per plot before being processed further.

2.1.8 experiment 307/90a

This experiment was conducted in eight compartments. On 11 January the first truss was in full bloom and temperatures of either 17, 19, 21 or 23°C were applied in two compartments for each temperature. These 24-h mean temperatures were maintained until 1 May, thereafter temperatures were set equal. The desired temperature was usually achieved but became too high in the 17°C compartments on some warm and sunny days (data not shown). The experiment ended on 6 August for four compartments, while the crops in the other four (one of each previous temperature treatment), were used for a following experiment (expt 307/90b).

Flowering and harvestable truss numbers were recorded from experimental plots of 16 plants once a week. Data were averaged per plot before being related to recorded temperatures. Once per fortnight, a sample of ten fruits per plot was dried for at least four days at 80°C in order to obtain their dry matter content.

Number of flowers that reached anthesis and fruit-set were also investigated at the same four temperatures (each in duplicate) in combination with three different plant densities and different fruit loads as shown in table 2.1.2. Plant

densities of 3.1, 2.1 and 1.6 plants m^{-2} were obtained by increasing the distance between plants within a row from 0.4 to 0.6 or 0.8 m, respectively. Experimental plants were guarded on all sides by plants at equal density. Fruit load differences were established by pruning the distal fruits of a truss just after fruit set. Each of the six 'plant density × fruit' load treatments consisted of four plants per compartment. The numbers of flowers and fruits that had set were recorded three times a week and trusses were pruned afterwards. Old leaves and harvested fruits were weighed as they were removed. On 13 March, all plants were harvested and the fresh weights of leaves, stem and fruits were measured separately. One plant per plot, was used to determine leaf area and dry weight. Leaf area and dry weights of the remaining three plants of each plot were estimated from their fresh weights and the ratio obtained between leaf area and leaf fresh weight and the dry matter contents of leaves, stem and fruits.

Table 2.1.2
Number of fruits left on the plants used for investigating flower abortion and fruit-set in experiment 307/90a.

	plant density (plants m^{-2})					
truss number	3.1	3.1	3.1	2.1	2.1	1.6
1	1	2	3	2	3	3
2	3	4	7	5	7	7
3 and above	4	5	8	6	8	8

To investigate the interaction between temperature and development stage of the fruit on fruit development rate, round tomato plants were transferred for a fortnight to another temperature. For different plants this was done each week from 11 January until 15 March. All temperature combinations were included. For the 17°C ↔ 23°C and 19°C ↔ 21°C exchanges, four plants were transferred each week. For all the other temperature combinations, two plants per week were available. Flowering date, day of reaching 5 mm fruit diameter and harvest date of the second flower and fruit, respectively, of the first three trusses were recorded.

To determine the effect of temperature on potential fruit weight, nine plants (round tomato) in each compartment were pruned to leave one fruit (first position) on the first and second truss and two fruits (first and second position)

on all the following trusses. For four plants per compartment, the diameter of each fruit was measured twice a week in order to quantify the potential growth. The flowering rate and the fruit growth period were also calculated for these plants. At harvest, fruit of all plants were weighed. On 17 April and 1 May samples of ten fruits per compartment were dried (four days at 80°C) to determine dry matter content of potentially grown fruits.

By the time temperatures were set equal (1 May), the tops of the plants were very different. Those grown at high temperature had a thin appearance, while those at low temperature were very heavy. This provided an opportunity to investigate the influence of top size on the potential growth of fruits. On the day that temperatures were set equal, six normally loaded plants from each former temperature treatment were pruned to leave two fruits per truss (first and second position) for all trusses, and the flowering truss was labelled. Pruning was continued until harvest of the last experimental fruit. The fruits of the labelled truss plus the following two trusses were weighed at harvest.

2.1.9 experiment 307/90b

In experiment 307/90b, the flowering rate and fruit growth period of young and old plants were compared. Four compartments with the crop from the 307/90a experiment were used. Two compartments (17 and 21°C in expt 307/90a) were maintained at 19°C 24-h mean temperature, and the set-points for the other two compartments (former 19°C and 23°C) were changed to 23°C. In August, some old plants were replaced by young ones flowering at the first truss on 27 August. On this date, all fruits and nearly all leaves were removed from some of the remaining old plants so that they resembled young plants in so far as they had the same number of leaves and just one truss in flower. A number of these plants were kept with their tops near the wire, like the un-treated old plants, while the rest were layered in order to get their top at the same height as the young plants. In this way four 'plant' treatments were obtained; 'Normal' old, young, stripped old high and stripped old low. There were 12 plants of each treatment in each compartment. The number of flowering and harvestable trusses were recorded twice a week until 5 November and averaged per plot before statistical evaluation.

2.1.10 experiment 210/90

In this experiment, the effects of high temperature and a large difference between day and night temperature on flowering rate and fruit development were investigated. On 15 August, young plants were planted in 12 compartments. From 27 August until 5 November, temperature settings for day temperature and 24-h mean temperature (treatments in duplicate) were: 19/19, 23/23, 27/27, 27/23 and 19/23. For the latter two treatments, the calculated night temperature was about 19 and 27°C, respectively. Day to night and night to day switches were made at 06.00 and 18.00 h, respectively. Flowering and harvestable truss numbers of 32 plants per compartment were recorded twice a week.

In order to examine the temperature effect on assimilate distribution in a mature crop, in a sixth treatment (also in duplicate) temperature settings were 19/19 (day/24-h) from 27 August until 1 October (flowering of the sixth truss) and 23/23 until the end of the experiment. In this treatment and in the reference with 19°C continuously, six plants in each compartment were harvested on 1 and 15 October. Branched trusses were pruned back to one branch before flowering. Numbers of flowers, fruits and flowers that failed to set were determined for each truss, as well as fresh weights of leaves, stem and fruits. From half the number of plants also dry weights and leaf area was measured. No leaves or fruits were picked before 15 October.

To investigate interaction between the development stage of the fruit and temperature on fruit development rate, four plants were exchanged between all possible temperature combinations (restricted to equal day/night temperature regimes) each week. After two weeks at the new temperature the plants were transferred back to the original temperature. Dates of flowering, reaching 5 mm fruit diameter (set fruit) and harvest of the second flower/fruit of the first and second trusses were recorded.

2.1.11 experiment 111/91

The main goal of this experiment was to investigate the effects of temperature and salinity (EC) of the nutrient solution on taste and quality of tomato fruits. Therefore, three temperatures; 19, 21, and 23°C, were combined with three conductivity levels; 0.3, 0.6 and 0.9 S m^{-1}, measured in the rockwool slab. Differences in EC were achieved by raising the concentration of all nutrients,

without changing the composition. Measurements were made of flowering rate, fruit growth period, fresh weight production and dry matter content of fruits and leaves. As it was expected that early yield from plants grown at high temperature would consist mainly of small fruits, an attempt was made to overcome this by planting at a wider spacing. Therefore the 23°C treatment was applied at two densities, *viz.* 2.1 and 1.6 plants m^{-2}. In the latter treatment, a second stem was kept on each plant just after the fifth truss. All four temperature treatments were conducted in two replicates (two separate compartments). Experimental plots consisted of twelve or eight plants for the normal and wide spacing, respectively. There was one plot per compartment per EC level, giving a total of 24 plots. Young plants were planted on 27 December and temperature treatments started on 4 February when the second truss was flowering. From early February, different nutrient solutions were applied and the desired EC levels were achieved midway through this month. Flowering and harvestable trusses were recorded weekly. Fruit dry matter content was determined every fortnight from samples of ten harvest ripe fruits per plot.

2.1.12 experiment 103/92

This experiment was conducted primarily to determine the effect of salinity on fruit quality. The opportunity was taken to obtain some extra measurements of salinity effects on development and fruit dry matter content. Plants were raised at an EC of 0.5 S m^{-1} in the root medium. The first truss reached anthesis on 20 January. After 3 February different nutrient solutions were supplied and three weeks later (anthesis of the fifth truss) the desired EC levels were obtained in the root medium. The following six treatments were maintained: standard nutrient composition at 0.3 S m^{-1}, standard composition at 0.6 S m^{-1}, standard composition at 0.3 S m^{-1} plus extra sodium to 0.6 S m^{-1}, standard composition at 0.3 S m^{-1} plus extra NaCl to 0.6 S m^{-1}, standard composition at 0.9 S m^{-1} and standard composition at 0.3 S m^{-1} plus extra sodium to 0.9 S m^{-1}. For the treatments with extra sodium, the relative composition of the anions was equal to the standard. Each treatment consisted of four experimental plots of 10 plants. Flowering and harvestable trusses were recorded every week until truss 14. From harvests of 15 May and 22 June fruit dry matter content was determined from samples of 10 fruits per experimental plot.

2.1.13 experiment 307/92

This short experiment was aimed at investigating growth of fruits after a sudden increase in assimilates available. On 9 March, at flowering of the seventh truss, 42 plants were selected for equal development stage. In order to obtain unlimited assimilate, during seven weeks each week six plants were pruned to leave two fruits per truss on all trusses. The diameters of the first and second fruits of trusses 8 and 9 of all 42 treated plants were measured weekly. At harvest of these fruits diameter and fresh and dry weights were determined. On 20 May, just after picking the last fruits of truss 9, leaf area and stem and leaf fresh and dry weights were determined of the vegetative units belonging to the trusses 8 and 9 from the six first pruned plants.

2.2 Flowering rates in cultivar trials at commercial nurseries

In order to determine possible differences in flowering rate between cultivars, measurements were carried out in 1989 and 1991 during some cultivar trials conducted at commercial nurseries (table 2.2.1). In the first year, only the number of trusses achieved at the end of the growing season (September) was counted. In the second year recordings were also made at the start (January) and halfway (May) through the season. All crops were grown on rockwool and in a high wire system.

Table 2.2.1
Number of cultivars, nurseries, plots per nursery and plants per plot used for determining flowering rate of different cultivars.

year	type	crop	cultivars	nurseries	plots	plants
1989	round	early	5	1	2	14
1989	round	late	8	2	2	13
1989	beefsteak	early	16	2	2	12
1991	round	early	8	4	2	14
1991	beefsteak	early	5	2	2	14

3

ORGANOGENESIS AND DEVELOPMENT

3.1 Introduction

A tomato plant is constructed of sympodial shoots, each consisting of a stem section with three leaves and a terminal inflorescence (truss) (Shishido and Hori, 1977; Russell and Morris, 1983). In glasshouse-grown indeterminate tomatoes only the main sympodium is allowed to develop and other lateral shoots are removed. In this way an apparent single main stem bearing trusses separated by three leaves is obtained. The development stage of an indeterminate tomato can be defined by the number (position on the main stem) of the truss that has reached anthesis; the rate of formation of trusses, therefore, is a measure of plant development rate. The rate of leaf initiation is three times the rate of truss formation. It is most practical to measure the development rate by the rate at which successive trusses reach the flowering stage; in accordance with common use this rate is called the flowering rate, expressed in trusses per unit of time. Like many developmental processes, flowering rate of tomato is strongly affected by temperature (Klapwijk and Wubben, 1977; Klapwijk and Buitelaar, 1977; Klapwijk, 1987).

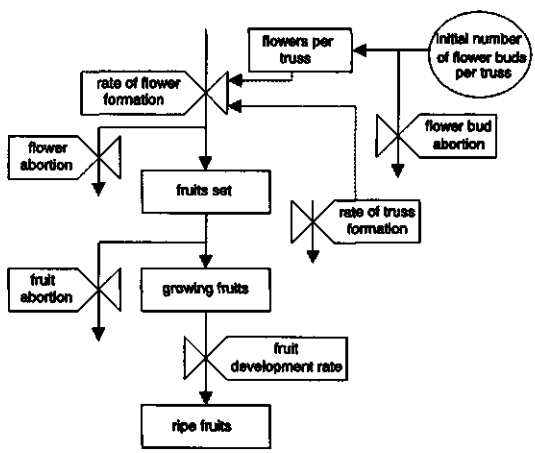

Figure 3.1.1
A relational diagram of the number of growing fruits on an indeterminate tomato plant (symbols according to Forrester, 1961).

In figure 3.1.1 the most important processes determining fruit number are presented in a diagram. The formation rate of new flowers results from the flowering rate and the number of flowers per truss. Flower buds may abort

before flowering and fruit may not set. Consequently, the number of developing fruits is the overall result of the flowering rate, the number of flowers initiated per truss and the incidence of abortion of flower buds, flowers and fruits.

In general, flower bud abortion is enhanced by low assimilate supply during development (Atherton and Harris, 1986), while the number of flowers that become young fruits (fruits set) depends strongly on the flower and pollen quality and prevailing environmental conditions (Picken, 1984). In contrast to many other fruit vegetables, abortion of fruits is very rare for tomato.

In this study, fruit-set of an individual truss is regarded as the number of fruits that develop as a percentage of the number of flowers of the same truss that reached anthesis. Flower abortion, therefore, is included in the percentage fruit-set. In consequence, description of the number of fruits that develop is reduced to quantifying the rate of truss formation and the number of fruits per truss, where the latter is determined by the number of flowers that reach anthesis and the percentage fruit-set (fig 3.1.2).

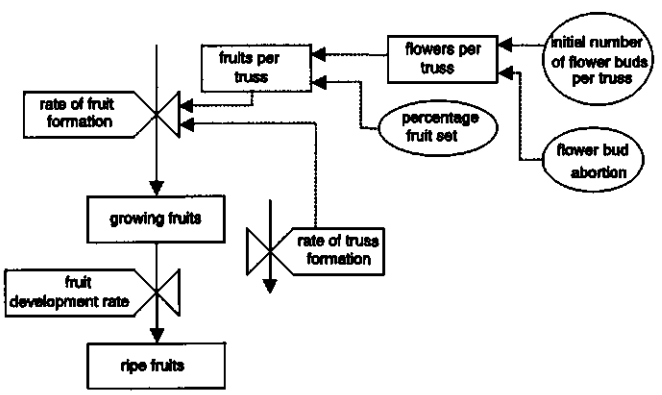

Figure 3.1.2
A relational diagram of the model describing the number of growing fruits on an indeterminate tomato plant (symbols according to Forrester, 1961).

After a growth period of about two months a tomato fruit is ripe to harvest. The duration of the fruit growth period decreases with increasing temperature (Klapwijk, 1987). Moreover, the temperature effect on the fruit development rate seems to be affected by the fruit's development stage (Klapwijk, 1987). In the present study the fruit growth period is defined as the time from anthesis until the moment the fruit is ripe for harvest, i.e. changing colour from green to

orange. It might be better to start at the moment of fruit-set instead of flowering but the precise moment of fruit-set is difficult to determine.

Since temperature seems the major factor affecting the rate of fruit formation and the fruit development rate, some experiments were conducted to quantify the temperature responses. Those experiments indicated that flowering rate differs significantly between cultivars and, therefore, recordings were carried out in some of the annual cultivar trials at commercial nurseries. In addition to temperature responses, effects of fruit load, plant age and salinity on flowering rate (section 3.2) and fruit development (section 3.4) were investigated. The number of fruits per truss (section 3.3) has been investigated in only one experiment (307/90a), that included temperature, plant density and fruit load as variables.

3.2 Flowering rate

3.2.1 results

calculation of flowering rate

In general, the air temperatures achieved were very close to the desired 24-h mean temperatures (data not shown). For the constant temperature treatments the flowering rate was estimated by fitting a linear relationship between the number (position) of the flowering truss and time. The estimated slope of the fitted lines represents the flowering rate. For temperature experiments with several similar experimental plots within a compartment the data were pooled per compartment before regression. In general, flowering truss number and day number were very highly correlated (r^2>0.99) with low standard errors (<2%) for the estimated rates. Table 3.2.1 gives the time period, range of truss numbers and number of records used in the regressions for the different temperature experiments.

For some experiments at GCRS and the cultivar trials at commercial nurseries temperatures were not constant. In those cases the flowering rates were gained from the total number of trusses flowered during the experimental period divided by the duration of the experimental period. Unless otherwise specified, differences in flowering rate were tested by ANOVA.

Table 3.2.1
Time interval, initial and final truss number and number of records (per regression) of the regressions between flowering truss number and day number for all temperature experiments.

experiment	time (days)	truss	records
211/87	50	1 - 8	24
307/90a	105	1 - 14	16
307/90a [1)]	70	5 - 14	11
307/90a	35	32 - 37	6
307/90b	63	32 - 39/1 - 9	19
210/90	42	2 - 8	13
111/91	63	2 - 11	10 [2)]/30 [3)]

1) cv. 'Dombito'
2) EC treatments
3) temperature treatments

effect of cultivar

In experiment 307/90a, two cultivars were used, *viz.* 'Calypso' (round tomato) and 'Dombito' (beefsteak tomato). In spring, both were grown in eight compartments. The first trusses of 'Dombito' were of poor quality. Hence, for comparisons between cultivars, the flowering rate was estimated over trusses 5 to 14. Flowering rate of 'Calypso' was slightly higher than that of 'Dombito' (table 3.2.2). There was a very significant (P=0.002) promoting effect of temperature, but no interaction was found between temperature and cultivar, which indicates that the effect of temperature was similar for both cultivars.
In autumn, on the same crop, a second period of constant temperature was applied, but only in four compartments. Flowering rates were lower than for the young crop in spring. As in spring, high temperature increased flowering rate (P=0.016) but, here the difference between the two cultivars was not statistically significant (table 3.2.3).

Table 3.2.2
Flowering rate (trusses d^{-1}) of two tomato cultivars at four temperatures (expt 307/90a, young crop in spring).

temperature (°C)	flowering rate 'Calypso'	'Dombito'	
17	0.1190	0.1124	
19	0.1365	0.1309	
21	0.1454	0.1422	
23	0.1546	0.1560	
mean	0.1388	0.1354	LSD 5% = 0.0031

Table 3.2.3
Flowering rate (trusses d^{-1}) of two tomato cultivars at two temperatures (expt 307/90a, old crop in autumn). Means were not significantly different (Student's *t*-test, P=0.05).

temperature (°C)	flowering rate 'Calypso'	'Dombito'
19	0.0869	0.0760
23	0.1104	0.1084
mean	0.0986	0.0922

Also in the cultivar trials at commercial nurseries, flowering rate (table 3.2.5) and the number of trusses achieved after a whole cropping season (1989, table 3.2.4; 1991, table 3.2.5) differed significantly between cultivars and between times of the year. Despite a higher temperature in summer, generally the flowering rate was lower than in spring (table 3.2.5). The extent of this decrease was cultivar dependent and seemed to be larger for weakly growing cultivars (data not presented). The standard deviation within a cultivar was about 3% on average (tables 3.2.4. and 3.2.5). For some trials the variance of number of trusses, and hence homogeneity in flowering rate, tended to be significantly different between cultivars (statistical analysis not shown).

Table 3.2.4
Number of trusses achieved and its standard deviation in three cultivar trials of tomato in 1989.

cultivar	number of trusses	standard deviation
a. *early crop round tomato*		
Liberto	34.6	1.05
84065	34.3	1.42
Blizzard	32.4	1.27
Calypso	30.6	0.83
72-29	30.5	1.29
LSD 5%	2.4	
b. *late crop round tomato*		
Liberto	17.6	0.71
B6110	17.4	0.62
Rapide	17.1	0.84
Blizzard	17.0	1.04
W1260	16.8	0.87
Criterium	16.8	0.78
Spectra	16.7	0.99
72-51	16.7	0.78
LSD 5%	0.3	
c. *early crop beefsteak tomato*		
Colombo	29.0	1.20
E18462	28.2	0.96
E19006	28.0	1.61
E19565	27.9	0.90
Dombito	27.9	1.52
88-03	27.9	1.37
87-27	27.7	1.35
E18436	27.5	1.06
72-52	27.4	0.81
W1392	27.2	0.92
88-04	27.2	1.31
Furon	27.2	1.29
Farao	26.5	0.98
72-53	26.4	0.91
W1603	25.7	0.82
W1219	25.5	1.14
LSD 5%	0.8	

Table 3.2.5
Flowering rate of tomato in spring (January until May) and summer (May until September), their difference (summer-spring) and the total number of trusses achieved with its standard deviation in two cultivar trials in 1991.

cultivar	flowering rate (trusses d^{-1})			number of trusses	standard deviation
	spring	summer	difference		
a. *round tomato*					
Pronto	0.145	0.139	-0.006	34.3	0.96
Liberto	0.144	0.136	-0.007	34.1	1.06
E22042	0.142	0.128	-0.014	32.6	1.18
Frondito	0.142	0.134	-0.007	33.0	1.04
E17908	0.141	0.127	-0.013	32.6	0.88
Calypso	0.137	0.131	-0.007	32.3	0.98
Pannovy	0.136	0.138	0.002	33.5	1.26
72-08	0.136	0.122	-0.014	31.3	1.00
LSD 5%	0.003	0.003	0.005	0.5	
b. *beefsteak tomato*					
Furon	0.124	0.112	-0.012	29.2	0.88
Dombito	0.122	0.114	-0.008	29.6	0.92
Belmondo	0.121	0.111	-0.011	29.0	0.81
LM218	0.121	0.108	-0.014	28.2	1.01
W1741	0.116	0.109	-0.007	27.9	0.90
LSD 5%	0.005	0.003	n.s.	0.6	

effect of fruit load

In spring 1990 (expt 307/90a), four plants were pruned to leave up to two fruits per truss at each temperature in order to obtain maximum fruit size (Chapter 5). At 23°C, pruning accelerated flowering slightly, but in the other three treatments pruning had a small, but statistically significant, retarding effect on flowering rate. Hence there was a significant (P=0.019) 'temperature × pruning' interaction.

Table 3.2.6
Flowering rates (trusses d^{-1}) of normally loaded and extremely pruned (2 fruits per truss) tomato plants (cv. 'Calypso') at four temperatures (expt 307/90a).

temperatures	normal	pruned	LSD 5%
17	0.1096	0.1022	0.0054
19	0.1245	0.1182	0.0054
21	0.1407	0.1353	0.0054
23	0.1519	0.1585	0.0054

effect of plant age

In the 307/90b experiment, young and old plants were compared in four compartments at two temperatures. Leaves and fruits were stripped from some old plants so that their top was similar to the complete young plants. The top of the stripped plants was left either near the wire or put at the same height as for the young plants. Again, temperature had a significant (P=0.002) enhancing effect on the flowering rate. Flowering rates of the stripped and normal old plants did not differ (table 3.2.7), but a very significant (P<0.001) effect of plant age on flowering rate was found. No interactions between temperature and plant age occurred, thus flowering rates of both, old and young plants, responded similarly to temperature.

Table 3.2.7
Flowering rate (trusses d^{-1}) of young, old and stripped old tomato plants at two temperatures (expt 307/90b). For the stripped plants the top was positioned either high or low.

temperature (°C)	young	old			LSD 5%
		normal	stripped low top	stripped high top	
19	0.1287	0.0913	0.0963	0.0967	
23	0.1462	0.1179	0.1130	0.1185	
mean		0.1046	0.1047	0.1076	n.s.
mean	0.1374		0.1056		0.0069

effect of salinity and plant spacing

In experiment 111/91, the flowering rate was not influenced by plant spacing nor by electrical conductivity of the root medium (table 3.2.8). As in preceding experiments, high temperature had a very significant promoting ($P<0.001$) effect on flowering rate. No interactions were present.

Table 3.2.8
Flowering rate (trusses d^{-1}) at three temperatures, two plant densities (only at 23°C) and three electrical conductivity levels in the root medium (expt 111/91). Means were not statistically different (Student's *t*-test, P=0.05).

temperature (°C)	plant density (plants m^{-2})	flowering rate EC (S m^{-1})			
		0.3	0.6	0.8	mean
19	2.1	0.1491	0.1464	0.1496	
21	2.1	0.1566	0.1611	0.1599	
23	2.1	0.1682	0.1715	0.1703	0.1700
23	1.6	0.1714	0.1677	0.1660	0.1683
mean		0.1613	0.1617	0.1614	

In contrast to the absence of a salinity effect in experiment 111/91, high salinity decreased plant development slightly (-4% from 0.3 to 0.9 S m^{-1}) in experiment 103/92. The composition of the nutrient solution had no influence (table 3.2.9).

Table 3.2.9
Flowering rate of tomato at different salinities (EC) and compositions of the nutrient solution in the root medium (expt 103/92).

EC (S m^{-1})	nutrient composition	flowering rate (trusses d^{-1})
0.3	standard	0.154
0.6	standard	0.154
0.6	standard + Na	0.150
0.6	standard + NaCl	0.151
0.9	standard	0.148
0.9	standard + Na	0.149
		LSD 5% = 0.0033

effect of constant temperature

Temperature had a very significant promoting effect on flowering rate in all experiments (e.g. tables 3.2.2, 3.2.3, 3.2.6, 3.2.7 and 3.2.8). In order to quantify the relation between flowering rate (FR) and temperature (T), all available flowering rate - temperature pairs, restricted to young round tomato and constant temperature treatments, were analyzed together. Daily 24-h mean temperatures were averaged over the same period as taken for the estimations of flowering rates. In total 30 pairs divided over five experiments were available. Except for experiment number, pairs were independent. Models were fitted to weighted flowering rates according to the reciprocal of their standard error. A linear relationship,

$$FR = a + b \times T, \qquad \text{[eqn 3.2.1]}$$

fitted moderately, but incorporation of different intercepts (a_i) for the different experiments significantly increased the percentage variation accounted for from about 65 to 97%. This relationship, however, overestimated flowering rates at low and high temperatures. Also in other species curvilinear responses to temperature are observed (section 3.2.2). Adding a quadratic term $c \times T^2$ gave a statistically better fit. A similar result was obtained by a model with the (natural) log-transformed temperature,

$$FR = a_i + b \times \ln(T), \qquad \text{[eqn 3.2.2]}$$

Because this model has only one regressor it is preferred to the quadratic one and will be used in further computations. Results for the tested models are given in table 3.2.10. Estimated intercepts were significantly (P=0.05) different. Incorporation of separate slopes for different experiments did not significantly increase the percentage variance accounted for (results not shown), hence the effect of temperature on flowering rate is regarded to be the same in all experiments (fig 3.2.1). For the temperature range from 17 to 27°C predicted values and their standard errors were calculated for all five experiments. In general the standard errors were less than 1% and never exceeded 2% of the predicted value.

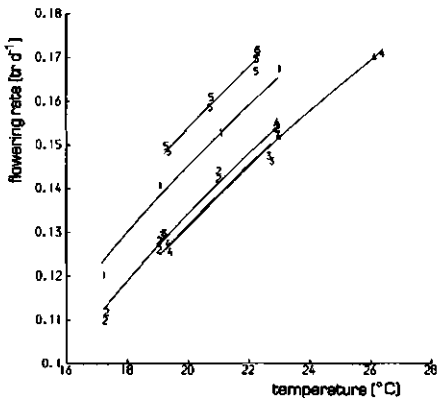

Figure 3.2.1
Relationship between flowering rate and temperature for five experiments. 1, expt 211/87 cv.'Counter'; 2, expt 307/90a cv.'Calypso'; 3, expt 307/90b cv.'Calypso'; 4, expt 210/90 cv.'Calypso'; 5, expt 111/91 cv.'Liberto'.

Table 3.2.10
Parameters a_i (i=experiment number), b and c for different relationships between flowering rate (FR; trusses d^{-1}) and temperature (T; °C).

parameter	model FR=a_i+b×T	FR=a_i+b×T+c×T^2	FR=a_i+b×ln(T)
a_1 (expt 211/87)	0.0041	-0.1419	-0.2903 a[1)]
a_2 (expt 307/90a)	-0.0067	-0.1531	-0.3013 b
a_3 (expt 307/90b)	-0.0090	-0.1557	-0.3038 b
a_4 (expt 210/90)	-0.0101	-0.1550	-0.3041 b
a_5 (expt 111/91)	0.0135	-0.1337	-0.2816 c
b	0.00702	0.02123	0.1454
c	-	-0.0003419	-
R^2	0.974	0.984	0.982

1) differences significant at P=0.05

effect of varying temperature

In experiment 211/87, plants were transferred to another temperature between flowering of the first and eighth truss. The average flowering rate was calculated from the time it took from the first to the eighth truss in flower. Also per experimental plot, the number of flowering trusses was simulated using the daily temperature and the model estimated from the constant temperature treatments of the same experiment: $FR=-0.2903+0.14541\times\ln(T)$ (table 3.2.10). The simulated and the measured average flowering rates, as calculated over the period of flowering of the first truss until the eighth truss, were plotted against each other (fig 3.2.2). The flowering rate was predicted correctly for constant temperature but, where temperature was varied, the model underestimated high flowering rates and overestimated low rates. Thus on varying temperature, the temperature response was stronger than at constant temperature.

In experiment 210/89, low and high 24-h mean temperatures were alternated with a frequency of 3 to 12 days. Growth and development were compared with a control treatment with constant temperature (de Koning, 1990). Flowering truss was recorded twice a week, and flowering rates were calculated over the 3 or 4 day periods. To quantify the (short-term) temperature effect, the difference in flowering rate from the control was fitted against the temperature difference from the control over the same 3 or 4 day periods. The correlation was highly significant ($r=0.825$, $n=163$, $P<0.001$) and the regression parameter (fitted without intercept) was estimated on 0.0125 (SE = 0.0007) trusses $d^{-1}\ {}^{o}C^{-1}$.

effects of large differences between day and night temperature

In experiment 210/90 treatments with extremely large differences between day and night temperature, *viz.* 27/19 and 19/27, were compared with constant temperatures of 19, 23 and 27°C. Unfortunately, the 24-h mean temperature of the day/night temperature treatments was not exactly equal to that of the constant temperature treatments. In order to decide whether possible differences result from different day/night regime or different 24-h temperature, the data were analyzed by linear regression (instead of ANOVA). The flowering rate at 27°C day 19°C night temperature was ($P=0.01$) lower (-0.0044 trusses d^{-1}) than expected from the achieved 24-h mean temperature. Flowering rate at the 19/27°C day/night temperature treatment did not differ from that at constant temperature. Flowering rates in all treatments are graphically presented in figure 3.2.3.

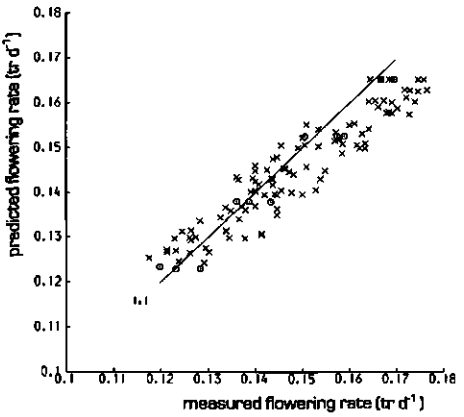

Figure 3.2.2
Simulated flowering rate for constant (O) and changing (X) temperature treatments versus measured flowering rate averaged from flowering of the first truss until flowering of the eighth truss in experiment 211/87.

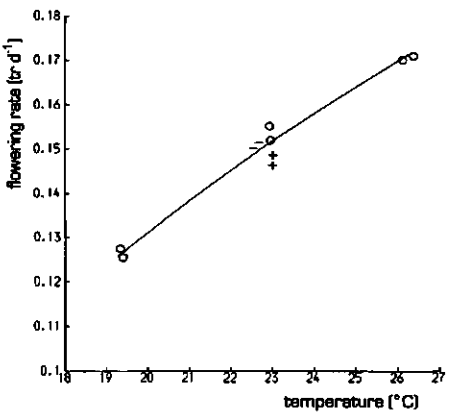

Figure 3.2.3
Flowering rate at equal day/night (O), high day/low night (+) and low day/high night (−) temperature regimes (expt 210/90). The regression line is based on constant temperature regimes only.

3.2.2 discussion

In general, plant development is sensitive to temperature. Rate of leaf appearance of several species is frequently found to be linearly related to temperature e.g. Milford *et al.* (1985) for sugar beet, Rawson and Hindmarsh (1982) for sunflower, Karlsson *et al.* (1988) for easter lily and Karlsson *et al.* (1991) for Hibiscus. Consequently, development stage can be related to the heat sum elapsed, i.e. integrated daily temperature above a base temperature below which no development occurs (e.g. Gallagher (1979) for wheat and barley; Ottosson and Hakansson (1989) for peas, lettuce and chinese cabbage).

In the present experiments, the highly significant positive effect of temperature on flowering rate could also be described well by a linear relationship. However, the temperature response tended to be curvilinear and a slightly better fit was obtained with a quadratic relationship ($FR=a+b\times T+c\times T^2$) or after a log-transformation of temperature ($FR=a+b\times \ln(T)$). A curvilinear relationship has been reported for maize (Tollenaar *et al.*, 1979). With the same

crop, Warrington and Kanemasu (1983) and Cutforth and Shaykewich (1990) reported a non-linear response with a maximum rate of leaf appearance at 30°C and a sharp decline at higher temperatures. Similar asymmetric curves with optima round 30°C are reported for several development rates of dahlia (Brøndum and Heins, 1993). Leaf initiation rate of chrysanthemum shows an optimum response over the range 10 to 28°C with a maximum at about 22°C (Cockshull, 1979) and Karlsson (1992) could adequately model the leaf unfolding rate of begonia in the range of 13 to 28°C by a second order polynomial with a maximum around 21°C. Obviously, the distinction between linear, curvilinear and optimum responses and the general applicability of a linear relationship depend strongly on the temperature range concerned. Flowering rate of tomato appears rather heat tolerant as it increased considerably in the range from 23 to 27°C.

Development rate is equally related to day and to night temperature and therefore, to the 24-h mean temperature, as observed for tomato (de Koning, 1988*a*), cucumber (van Uffelen, 1989), chrysanthemum (Cockshull *et al.*, 1981) and easter lily (Karlsson *et al.*, 1988). Due to the slightly curved response pattern, large differences between day and night temperature may cause lower flowering rates than would be expected from the 24-h mean temperature. This was found in experiment 210/90 for the high day / low night temperature treatment. The practical significance of this difference is only small. On the basis of the equation $FR=-0.3041+0.14541\times\ln(T)$ (table 3.2.10; constant temperature treatments of expt 210/90), flowering rate was 0.1518 trusses d^{-1} at a constant temperature of 23°C, while with 12 hour at 27°C plus 12 hour at 19°C (average also 23°C), flowering rate was 0.1496 trusses d^{-1}, a difference of only 1.5%.

The immediate response of flowering rate to current temperature may be different from the long-term response, as indicated by the results of expt 210/89, where the effect of short-term (several days) temperature variation was estimated to be 0.0125 trusses d^{-1} $°C^{-1}$ (section 3.2.1). This response is considerably greater than the rate of 0.0078 trusses d^{-1} $°C^{-1}$ (first derivative of $FR=a+0.14541\times\ln(T)$ in T=18.7°C) estimated in the long-term temperature experiments. This discrepancy can be explained by the effect of temperature on the time between initiation of the flower bud and anthesis. Similarly, it has been reported already by Schwabe (1957) that the rate of unfolding of leaves is affected more by temperature than is the rate of leaf initiation. It was noted by Calvert (1964), Lake (1967) and Hurd and Cooper (1967, 1970) that the time interval between bud initiation and anthesis in tomato is shortened by increase of temperature;

a Q_{10} of 1.5 at 20°C was calculated from Lake's data. Due to the effects of temperature on the rates of bud initiation and of flower bud development, if temperature is changed, the apparent effect on flowering rate may be distorted in the short-term. In the long-term, however, these different effects reach a steady state at which flowering rate reflects the underlying rate of bud initiation. When alternating high and low temperatures for several days, the long-term flowering rates were similar to those in treatments at constant temperature, provided that the mean temperature was the same (de Koning, 1990). Furthermore, the observed rates of flowering were similar to those predicted from the equation $FR=-0.2903+0.1451\times\ln(T)$ (table 3.2.10; cv. 'Counter'). Extra retarding when changing from high to low temperature is probably compensated by extra acceleration when changing back to high temperature. The small differences between the predicted and observed rates following the short-term temperature changes of experiment 211/87 (fig 3.2.2) may be caused by differences in the short- and long-term responses. As the temperature response curves in the experiments with 'Calypso' in spring (307/90a) and summer (307/90b and 210/90) did not differ, it may be concluded that there is neither a direct effect of season (light intensity and day length) nor an interaction of season with temperature on flowering rate.

Development rate is affected by genotype e.g. with tomato (Paul, 1984; Papadopoulos and Ormrod, 1991; Cockshull *et al.*, 1992), pigeonpea (McPherson *et al.*, 1985) and bean (Yourstone and Wallace, 1990). Flowering rate of tomato cultivars may differ by as much as 10% (tables 3.2.4 and 3.2.5). The differences in intercept (a_i) for the different temperature experiments (table 3.2.10) can be fully explained by the different cultivars used, as there is a perfect coincidence of the mutual differences found and the cultivars used, *viz.* 'Counter' in experiment 211/87, 'Calypso' in the experiments 307/90a, 307/90b and 210/90 and 'Liberto' in experiment 111/91. Flowering rate of 'Liberto' is higher than that of 'Calypso'(tables 3.2.4a and 3.2.5a), and the relative difference is of the same magnitude as observed among the temperature experiments. The third cultivar used, 'Counter', was not included in the cultivar trials, but Cockshull *et al.* (1992) noticed that 'Counter' flowers faster than 'Calypso'. This agrees with the difference found between experiment 211/87 ('Counter') and experiment 307/90a ('Calypso').

In the present experiments, extremely low fruit load hardly affected flowering rate (table 3.2.6) and no effect at all was found after stripping off nearly all leaves and fruits (table 3.2.7). Equal flowering rates for several fruit pruning

treatments were noticed earlier by Buitelaar (1985). On the contrary, Hurd *et al.* (1979) reported a 10% increase in the number of trusses after removal of two-thirds of the flowers. Moreover, in an experiment with leaf removal, Slack (1986) observed that very severe de-leafing (continuous removal of all leaves up to the third truss counted from the flowering truss) delayed flowering. In less severe leaf pruning treatments he observed no difference. Therefore, it can be concluded that flowering rate is affected by sink-source ratio only in very extreme cases.

This is consistent with the observation that flowering rate was equal for two plant spacings (table 3.2.8) and the results of Papadopoulos and Ormrod (1991), who observed that only combinations of very high plant densities (>4 plants m^{-2}) and low light conditions (spring) reduced the number of trusses. They reported a decrease of up to 16% for the very high density of 11 plants m^{-2}. The unimportance of light intensity (or light sum) is confirmed by the fact that the temperature response was equal for experiments with cv. 'Calypso' conducted in spring and in summer. Also light reduction by shading up to 32 and 23% did not affect flowering rate, as described by Buitelaar and Janse (1983) and Cockshull *et al.* (1992), respectively, in spring-time experiments.

Additional support to the proposition that sink-source ratio has a very limited effect on flowering rate was gained in an experiment with low (340 μmol mol^{-1}) and high (520 μmol^{-1}) CO_2-concentration treatments (Nederhoff *et al.*, 1992), showing the same flowering rate (data not presented). This confirms results of Calvert (1972) who observed that, although CO_2 enrichment shortens the time from sowing until flowering of the first truss, it caused no cumulative increase in earliness for the successive trusses.

Soil temperature (Hurd and Graves, 1985; de Koning, 1986) and air humidity (Bakker, 1990; Holder and Cockshull, 1990) do not affect flowering rate of tomato.

3.2.3 model

Flowering rate appeared to be affected by temperature, cultivar, and plant age. The other factors investigated (*viz.* fruit load, plant spacing and electrical conductivity of the root medium) had no or only very little effect on flowering rate. As no interactions were found, either between temperature and experiment number or between temperature and cultivar (expt 307/90a), it seems plausible to assume that the influence of temperature on flowering rate is similar for all cultivars. Consequently, flowering rate can be described by a cultivar dependent

parameter (a_{FR}) plus the effect of temperature; f(T). For f(T) a linear relationship may be applicable in many cases, but $a_{FR}+b\times\ln(T)$ is preferred as the temperature response clearly tends to be curvilinear. This relationship describes the change in flowering rate linearly related to the reciprocal of the temperature; $\delta FR/\delta T=b/T$. For b=0.1454 (table 3.2.10), the flowering rate increases by $0.1454/T_{mean}$ when the temperature increases by 1°C. At 18°C this increase is 0.0081 trusses d^{-1} $°C^{-1}$ above a basic rate of about 0.12 trusses d^{-1}, which is similar to a Q_{10} of 1.7 as found by Hurd and Graves (1985). At higher temperatures the Q_{10} is less, e.g. 1.4 at 23°C.

After cultivar and temperature, plant age is the third factor that has to be taken into account for modelling flowering rate. Unfortunately, no literature was found on this factor and therefore experiment 307/90b is the single useful observation available to quantify the aging effect. It is assumed that flowering rate is linearly related to plant age, and that plant age can be expressed as the number of the flowering truss. Flowering rate was calculated over trusses 1 to 9 and 32 to 39 for the young and old plants respectively (table 3.2.1). So, on average the difference in age between old and young plants was 31 trusses. The observed difference in flowering rate was 0.0318 trusses d^{-1} (table 3.2.7), consequently, the effect of plant age was estimated to be 0.0010 trusses d^{-1} $truss^{-1}$. This value corresponds well with the magnitude of the difference in flowering rate observed between spring and summer in the cultivar trials (table 3.2.5), although differences between cultivars also exist. As no interaction between temperature and plant age was observed (section 3.2.1) the ultimate equation for flowering rate becomes:

$$FR_t = a_{FR} + 0.1454 \times \ln(T_t) - 0.0010 \times A_{t-1},$$
$$\text{with } A_t = A_{t-1} + FR_t, \text{ and } A_0 = 1, \qquad \text{[eqn 3.2.3]}$$

where FR_t is the flowering rate (trusses d^{-1}) at t days after anthesis of the first truss, a_{FR} is a cultivar dependent parameter, T_t is the 24-h mean temperature (17-27°C) and A_t is the plant's physiological age expressed as the number of the flowering truss.

In this equation the cultivar effect on the decrease of flowering rate with plant age is neglected. This interaction has only a minor effect on the flowering rate and including it would make the model complicated and very hard to adapt for other cultivars. The different effect of aging for different cultivars (table 3.2.5) may be due to differences in crop vigour. Consequently, the decrease of

flowering rate with age may be regarded as a parameter for crop vigour. The physiological cause of decreasing vigour and its relation to cultivars requires more research. If the model including plant age is used, the constant a_{FR} from table 3.2.10 should be corrected for the average truss number (table 3.2.1). After correction and averaging over experiments 307/90a, 307/90b and 210/90 (all 'Calypso') a_{FR} equals -0.296 for 'Calypso', -0.286 for 'Counter' and -0.276 for 'Liberto'. 'Dombito' flowers slightly more slowly than 'Calypso' (table 3.2.3) and from this difference, a_{FR} can be estimated to be -0.302 trusses d^{-1} for 'Dombito'. In case of new cultivars it is only necessary to adjust parameter a_{FR}. This can be done by measuring the flowering rate and average temperature and then calculating a_{FR} from the general model or by growing a known cultivar together with the new one and adjusting a_{FR} to the difference in recorded flowering rates.

The model may fail to predict flowering rates accurately at extreme sink-source ratios. Also, when averaging temperature over large temperature differences, flowering rate will be slightly overestimated, and so it is better to apply the model to the original temperature data without averaging.

3.3 Number of fruits per truss

3.3.1 results

The number of fruits that develop per truss was investigated in experiment 307/90a. Different temperatures were combined with different plant densities and fruit pruning treatments. Only the trusses 4 and 5 are considered as these trusses were initiated and developed (until fruit-set) during the period with temperature treatments. Number of flowers that reached anthesis and percentage fruit-set (number of fruits set as a percentage of number of flowers formed at the same truss) were averaged over both trusses. Dry weights of leaves, stem and fruits after 61 days' treatment period (11 January until 13 March) were averaged per experimental plot of four plants. Number of flowers per truss and percentage fruit-set were tested for correlations with the treatment variables and total vegetative and fruit growth until the end of the experiment. Variation in the number of flowers per truss may be due to variation in the number initiated or in the number aborted (section 3.1), but the present observations do not allow us to distinguish between them.

The greater part of the variation in number of flowers per truss can be attributed to the temperature treatments, whereas plant density and fruit pruning, the other treatment variables, did not correlate significantly with the number of flowers on trusses 4 and 5 (table 3.3.1). Regression analysis showed that plant density and fruit pruning, added to the temperature effect, did not increase the percentage variance accounted for (analysis not shown). A high positive correlation was observed between the number of flowers and the total weight of the vegetative parts (table 3.3.1). Since the vegetative weight was correlated with temperature (table 3.3.1), *viz.* low temperature caused high vegetative weight, the relationship with vegetative weight was analyzed for each temperature treatment separately. A significant correlation between the number of flowers and the vegetative weight remained at 17 and 23°C (fig 3.3.1). Because the variation in vegetative weight within temperature treatments could not always be attributed to differences in plant density and fruit pruning (analysis not shown), other factors, for example location in the greenhouse, may have caused the differences.

Table 3.3.1
Correlation matrix of the number of flowers per truss (FLPT), the percentage fruit-set (PFS), the vegetative weight at the end of the experiment (VW), temperature (T), plant density (PD) and fruit pruning (FP) (expt 307/90a). n=48 and $P(-0.36<\underline{r}<0.36\ \rho=0)=0.99$, except for correlations with PD and FP where n=24 and $P(-0.52<\underline{r}<0.52\ \rho=0)=0.99$.

	FLPT	PFS	VW
PFS	0.390		
VW	0.844	0.415	
T	-0.825	-0.480	-0.839
PD[1)]	-0.175	-0.279	-0.535
FP[2)]	0.066	0.134	0.170

1) only treatments without fruit pruning
2) only treatments with PD=3.1 plants m^{-2}

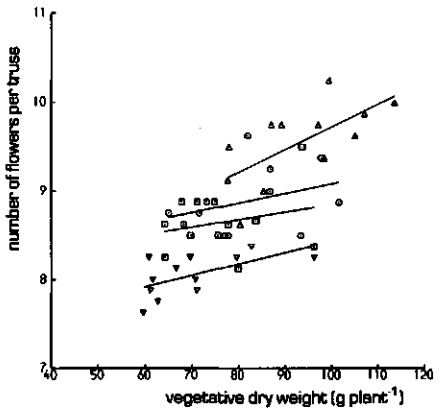

Figure 3.3.1
Number of flower buds per truss that reached anthesis (FLPT) plotted against the total vegetative plant dry weight for plants grown at different temperatures during 61 days after anthesis of the first truss (expt 307/90a). Δ, 17°C; ○, 19°C; □, 21°C; ▽, 23°C.

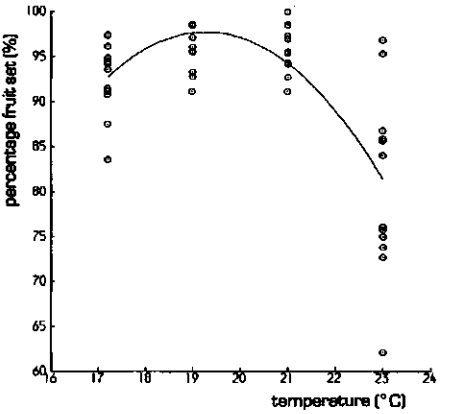

Figure 3.3.2
Percentage fruit-set (PFS) for tomato plants grown at different constant temperatures (expt 307/90a).

The percentage fruit-set of trusses 4 and 5 showed the highest correlation with temperature (table 3.3.1). The relationship could best be described by a second order polynomial (fig 3.3.2), but due to variance in fruit-set at each temperature, it accounts for only 52% of the variance. Including the variables plant density and fruit pruning did not improve the percentage variance accounted for. Furthermore, the residuals showed no correlation with parameters of vegetative growth. Hence, the percentage fruit-set is described as a function of temperature only:

$$PFS = 97.2\text{-}1.70\times(T\text{-}20) - 1.174\times(T\text{-}20)^2, \quad (SE_{y.x}=5.8;\ r^2=0.52;\ n=48) \qquad \text{[eqn 3.3.1]}$$

where PFS is the percentage fruit-set (percentage of flowers that develop into fruits) and T is the 24-h mean temperature (17-23°C).

In experiment 210/90, the percentage fruit-set at the fifth truss was 99 and 85% for the 19 and 23°C treatments, respectively. Those data correspond fairly well with the relation between fruit-set and temperature found in experiment 307/90a.

3.3.2 discussion

In the introduction to this chapter three factors were distinguished determining the number of fruits that develop per truss: (1) the number of flower buds initiated per truss, (2) the incidence of flower bud abortion and (3) the percentage fruit-set (fig 3.1.2). Obviously, the potential number of flower buds initiated per truss differs among tomato types. It is assumed that this number is genetically determined and that it is not affected by physiological or environmental variables. An exception should be made for the incidence of branching of trusses, which is promoted by low temperature during truss initiation, especially at high light level (Atherton and Harris, 1986).

Assuming that the number of flowers initiated on a single branched truss is not affected by temperature, the results (fig 3.3.1) demonstrate an increase of flower bud abortion with increasing temperature. Similar results have been observed by Calvert (1957, 1969), Saito *et al.* (1963), Aung (1976), Levy *et al.* (1978), Rylski (1979) and El Ahmadi and Stevens (1979). Generally, conditions increasing the availability of assimilates, e.g. high light intensity (Calvert, 1959, 1969; Saito *et al.* 1963; Kinet, 1977; Atherton and Othman, 1983; Baevre, 1990; Cockshull *et al.*, 1992) and CO_2 enrichment (Cooper and Hurd, 1968; Hand and Postlethwaite, 1971; Calvert and Slack, 1975) or decreasing the assimilate demand e.g. fruit pruning (Murneek, 1926) reduce flower bud abortion.

Since in experiment 307/90a the number of leaves and trusses formed increased with temperature (section 3.2), at high temperature the amount of assimilates available for the young flower buds of trusses 4 and 5 was presumably less and as a consequence flower bud abortion was higher and less flowers reached anthesis than at low temperature. Analogously, high assimilate demand by the fruits at high temperature may be the cause of the low vegetative weight at the end of the experiment (table 3.3.1, fig 3.3.1) and explains the correlation between number of flowers and vegetative growth. Since within two temperature treatments the number of flowers per truss was correlated with the vegetative weight, the latter is probably a better parameter than temperature to describe the number of flowers per truss.

Contrary to expectation, fruit pruning and plant density had no clear effect on the number of flowers. Possibly, for the young plant at development of the flower buds of the fourth and fifth truss total fruit load was too low to cause any significant effect of pruning on the total plant's assimilate demand. The limited effect of plant density may be explained by the fact that the young plants did hardly shade each other. In agreement with our results, Marcelis (1992*b*)

observed a positive correlation between number of fruits that is formed and vegetative growth of cucumber.

In experiment 307/90a the percentage fruit-set appeared to be mainly affected by temperature, the best fruit-set being obtained at 19 to 20°C. Those results are consistent with the literature as reviewed by Picken (1984). Any direct influence of other environmental or physiological factors cannot be excluded due to correlation among variables. However, van Ravestijn (1970) observed no significant effect of humidity and solar radiation on pollen germination and fertilization and Bakker (1991) observed no humidity effect on the total number of harvested fruits. Limited importance of light intensity and day length is indicated by the fact that data from the summer experiment (expt 210/90) fitted the model estimated from data collected in spring reasonably well. However, Rodriguez and Lambeth (1975) observed better fruit-set with supplementary lighting and wider plant spacing. The temperature effect on fruit-set differs between cultivars (Rudich *et al.*, 1977; Levy *et al.*, 1978), so that the estimated relationship may be rather specific for 'Calypso'.

3.3.3 model

The relation observed between number of flowers per truss and vegetative growth is presumably not causal. It is more likely that both depend on assimilate availability. An approach that is based on the competitive abilities of flower buds to attract assimilates and the ratio of supply to demand for assimilates would probably better reflect the internal mechanisms determining flower formation. Since, however, such an approach would require a great deal of extra knowledge that is not available at present, the observed correlation with vegetative growth will be used. It should, however, not be interpreted as a causal relation.

In order to obtain a general relationship that can be used in the growth model, it is assumed that the total number of flowers of an individual truss is related to the growth of the corresponding vegetative unit (stem part and three leaves preceding the truss) during the period when flower bud abortion may occur. The critical period for flower bud abortion is the time from macroscopic bud visibility to anthesis (Calvert, 1969; Kinet, 1977). The length of this period may vary with the environmental conditions (Kinet, 1977). Differences in truss development rate may be accounted for by taking the weight of the corresponding vegetative unit at a certain development stage of the truss. The formation rate of flowers within a truss is likely proportional to the formation

rate of trusses such that for round tomato the sixth flower and first flower of the next truss reach anthesis simultaneously (Cockshull, pers. comm.). So, it seems plausible to relate the number of flowers that reach anthesis on a particular truss to the weight of the vegetative unit achieved when the next truss starts to flower.

Unfortunately, the weights of the vegetative units 4 and 5 at anthesis of trusses 5 and 6, respectively, were not determined. Therefore, they were estimated from the measured total vegetative weights at the end of the experiment. According to the assumption that dry matter is distributed proportionally to the potential growth rates (Chapter 1), for each temperature treatment the ratio between the growth of vegetative units 4 and 5 until anthesis of the trusses 5 and 6, respectively, and the total vegetative growth until the end of the experiment could be predicted on the basis of potential growth rates calculated by the model (Chapter 5). The (predicted) ratio between the potential weight of vegetative units 4 and 5 until anthesis of the next trusses and the total potential vegetative weight at the end of the experiment decreased with increasing temperature because high temperature enhanced the formation of new vegetative units and their development stage. The vegetative weight of units 4 and 5 achieved at anthesis of the next trusses was obtained by multiplying the measured total vegetative weight by the predicted distribution ratio.

Plotting the number of flowers per truss that reached anthesis against the estimated weight of the vegetative unit at anthesis of the next truss (averaged over trusses and units 4 and 5) showed that all temperature treatments fitted reasonably the same linear relationship (fig 3.3.3),

$$FLPT = 7.1+0.37\times VW_{FLPT},\ (SE_{y.x}=0.34;\ r^2=0.72;\ n=48) \qquad \text{[eqn 3.3.2]}$$

where FLPT is the number of flowers of an individual truss that reached anthesis and VW_{FLPT} is the dry weight of the corresponding vegetative unit at anthesis of the next truss (2-8 g).

The residuals of this relationship were not correlated with any of the treatment variables.

Similar calculations for data from experiment 210/90 yielded over trusses 4 and 5 an average of 9.6 flowers and 7.3 g for the weights of corresponding vegetative units. Those data are in good agreement with equation 3.3.2 that predicts 9.8 flowers for a weight of 7.3 g.

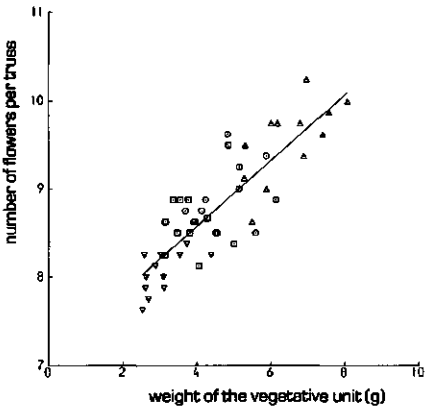

Figure 3.3.3
Number of flower buds per truss that reach anthesis (FLPT) plotted against the dry weight of the corresponding vegetative unit at anthesis of the next truss (VW_{FLPT}) for plants grown at different temperatures (expt 307/90a). ▵, 17°C; ○, 19°C; □, 21°C; ▽, 23°C.

According to equation 3.3.2, the minimum number of flowers per truss that reach anthesis is circa 7. This does not agree with the fact that under very adverse conditions a truss may abort completely (Cooper and Hurd, 1968; Calvert, 1969; Kinet, 1977). Therefore, some caution should be exercised when extrapolating the model beyond the range tested. On the other hand, confidence for a certain general validity of the model is gained from the good agreement with the results of experiment 210/90, that was conducted in late summer while the model is based on an early spring experiment.

In the introduction to this chapter, it was proposed to describe the number of flowers per truss as a (cultivar determined) number of flower buds initiated and the flower bud abortion (fig 3.1.1). According to equation 3.3.2 all initiated flower buds reach anthesis at a maximum attainable weight and flower bud abortion might be described by the ratio between the actual VW_{FLPT} and the maximum VW_{FLPT}. However, neither the number of flowers initiated nor the maximum attainable weight of the vegetative unit can be obtained from the present observations. Genotypic differences in potential number of flowers can probably best incorporated as a multiplicative factor to equation 3.3.2.

The relationship between the percentage fruit-set and temperature (eqn 3.3.1) is based on constant temperature treatments. When temperature varies during flowering of the truss (as is normally the case) averaging temperature over the whole flowering period easily causes an overestimation of the percentage fruit set, due to the shape of the response curve (fig 3.3.2). A better prediction will be obtained when daily values of PFS (eqn 3.3.1) are averaged over the period between anthesis of its first to anthesis of its last flower.

Hence, the total model defining the number of fruits (FPT) that develop on a truss, is formed by the equations:

$$FLPT = CFFLPT \times (7.1 + 0.37 \times VW_{FLPT}), \quad \text{[eqn 3.3.3]}$$

$$PFS = \{\sum_{t=1}^{t=k}[97.2 - 1.70 \times (T_t - 20) - 1.174 \times (T_t - 20)^2]\}/k, \quad \text{[eqn 3.3.4]}$$

$$FPT = FLPT \times PFS/100, \quad \text{[eqn 3.3.5]}$$

where FLPT is the number of flower buds reaching anthesis for a particular truss, CFFLPT is the number of flower buds initiated relative to 'Calypso', VW_{FLPT} is the dry weight of the corresponding vegetative unit at anthesis of the next truss (2-8 g), PFS is the percentage fruit-set (%) of the truss, index t represents the number of days after anthesis of the first flower, k is the value of t at anthesis of the last flower, T_t is the 24-h mean air temperature (17-23°C) and FPT is the number of fruits that develop on the truss.

In the model it is assumed that the distal flower buds and flowers are more susceptible to flower bud abortion and fruit-set failure than those at the proximal positions and, therefore, decrease of truss size starts from the distal end.

The present set of equations should be regarded as a preliminary model to describe the number of fruits that develop. In further research it might be better to relate flower bud abortion directly to sink-source relationships. Whether this results in a better prediction than the present approach is not certain for, when sink-source ratios were used to describe fruit-set in tomato, Bertin and Gary (1993) found the relationships varied between experiments while with cucumber (Marcelis, 1994*b*), the parameters of such a relationship depended on temperature. The modelling of fruit-set also requires more research, as the present relationship only accounted for about half the variance in the data.

3.4 Fruit development

3.4.1 results

calculation of fruit growth period and fruit development rate

Flowering and harvestable trusses were recorded on two or three occasions each week for each plant and averaged per experimental plot. By interpolation in the averaged recordings of flowering and harvestable truss, the moment a particular truss started to flower and the time the first fruit of this truss could be harvested were estimated. Then, for each truss, the growth period and average temperature over this period were calculated. The number of trusses grown at constant temperature from flowering until harvest was limited by the duration of the treatment period. Moreover, because the fruit growth period is shorter at high temperature, more trusses were available for high temperature treatments than for low temperatures. Since fruit growth period was not affected by truss number (data not presented), fruit growth period and average temperature were calculated per experimental plot by averaging the data of the appropriate trusses. Table 3.4.1 gives the number of trusses used, with the lower value corresponding with the lowest temperature. With the two lower temperatures (17 and 19°C) in experiment 211/87 no trusses could be harvested before the end of the temperature treatment.

Table 3.4.1
Number of trusses per plant from which the fruit growth period was calculated.

experiment	number of trusses
211/87	0 - 2
307/90a	4 - 9
307/90b	1 - 3
210/90	32-34/2 - 5
111/91	4 - 8
103/92	7

As in dynamic models it is more convenient to use rates instead of durations, for constant temperature treatments fruit development rate (FDR) is calculated as the reciprocal of fruit growth period (FGP). The moment of anthesis and harvest ripe are defined as 0 and 1, respectively. In some cases the moment of harvest is regarded as 100% and then fruit development rate is expressed in percent per unit of time (*viz.* % d^{-1}).

effect of cultivar

In experiment 307/90a, no difference was observed between 'Calypso' (round tomato) and 'Dombito' (beefsteak tomato) (table 3.4.2). High temperature decreased the fruit growth period very significantly ($P<0.001$) and both cultivars responded similarly to temperature.

Table 3.4.2
Duration of the fruit growth period (d) of two tomato cultivars at four temperatures (expt 307/90a). Means were not significantly different (Student's *t*-test, P=0.05).

temperature (°C)	fruit growth period 'Calypso'	'Dombito'
17	71.9	73.8
19	62.0	61.8
21	56.2	55.1
23	48.6	47.9
mean	59.7	59.7

effect of fruit load

At 17 and 19°C (expt 307/90a) the fruit growth period of fruits grown with only two fruits per truss was slightly longer than that of fruits grown on normally loaded plants (table 3.4.3). Temperature had a very significant ($P<0.001$) effect and the response seemed to be slightly stronger at low fruit load as indicated by a significant (P=0.013) 'fruit load × temperature' interaction.

Table 3.4.3
Duration of the fruit growth period (d) of normally loaded and extremely pruned (two fruits per truss) tomato plants (cv. 'Calypso') at four temperatures (expt 307/90a).

temperature	normal	pruned	LSD 5%
17	71.9	74.9	2.1
19	62.0	64.9	2.1
21	56.2	54.3	n.s.
23	48.6	46.8	n.s.

effect of plant age

In experiment 307/90b, young and old plants were grown together in four compartments, at one of two temperatures (19 or 23°C). Fruits and leaves were stripped from some of the old plants. The top of those plants was left either near the wire or put at the same height as for the young plants. At both temperatures, the growth period of fruits from the young plants was a few days shorter ($P<0.001$) than those of the old plants (table 3.4.4). The duration of the fruit growth period was, again, very significantly ($P=0.003$) shortened by increasing temperature. The response to temperature was equal for both plant ages and no differences were found between stripped and normal old plants or between old plants with their tops at either the level of the wire or at the level of the young plants.

Table 3.4.4
Duration of the fruit growth period (d) of young, old and stripped old tomato plants at two temperatures (expt 307/90b). For the stripped plants the top was positioned either high or low.

temperature (°C)	young	old			LSD 5%
		normal	stripped low top	stripped high top	
19	53.8	60.0	56.5	58.5	
23	44.5	47.9	48.3	48.3	
mean		54.0	52.4	53.4	n.s.
mean	49.1		53.2		1.2

effect of plant spacing and salinity

Decreasing plant spacing (expt 111/91) tended to shorten the fruit growth period slightly. The electrical conductivity in the root medium, investigated in the same experiment, did not affect fruit development rate (table 3.4.5). As in all other experiments, temperature had a very significant (P=0.002) accelerating effect and there were no interactions with other factors. Salinity did not affect the fruit growth period in experiment 103/92 either (table 3.4.6).

Table 3.4.5
Duration of the fruit growth period (d) of tomato grown at three temperatures, two plant densities (only at 23°C) and three electrical conductivity levels in the root medium (expt 111/91). Means were not statistically different (Student's *t*-test, P=0.05).

temperature (°C)	plant density (plants m^{-2})	fruit growth period EC (S m^{-1})			
		0.3	0.6	0.8	mean
19	2.1	58.2	57.6	57.3	
21	2.1	53.1	52.8	52.4	
23	2.1	49.3	49.5	49.8	49.5
23	1.6	47.1	48.4	48.7	48.1
mean		51.9	52.1	52.1	

Table 3.4.6
Duration of the fruit growth period (d) of tomato grown at different salinities (EC) and compositions of the nutrient solution in the root medium (expt 103/92). Differences were not significant (Student's *t*-test, P=0.05).

EC (S m^{-1})	nutrient composition	fruit growth period
0.3	standard	53.4
0.6	standard	53.4
0.6	standard + Na	53.2
0.6	standard + NaCl	53.3
0.9	standard	53.1
0.9	standard + Na	52.8

effect of constant temperature

As with flowering rate (section 3.2.1), all available 'fruit growth period - temperature pairs', restricted to young round tomato and constant temperature treatments, were analyzed together. In total 28 pairs obtained from five experiments were available. A linear and a quadratic function of temperature were fitted to the data. Adding different intercepts for different experiments increased the percentage variance accounted for from about 85% to 95%. Results for the models tested are given in table 3.4.7. The quadratic model fitted the data significantly better and is graphically presented in figure 3.4.1.

Table 3.4.7
Parameters a_i (i=experiment number), b and c for different relationships between fruit growth period (FGP; d) of tomato and temperature (T; °C).

parameter	FGP=a_i+b×T	FGP=a_i+b×T+c×T^2
a_1 (expt 211/87)	114.1	259.8 ab[1)]
a_2 (expt 307/90a)	115.8	259.8 a
a_3 (expt 307/90b)	108.7	254.0 d
a_4 (expt 210/90)	111.0	254.0 cd
a_5 (expt 111/91)	112.4	257.7 bc
b	-2.81	-16.46
c	-	0.3191
R^2	0.913	0.977

1) differences significant at P=0.05

Fruit development rate (FDR=100/FGP) was fitted with a linear and a quadratic function of temperature and also with a linear function of the log-transformed temperature. All relationships fitted the data well (table 3.4.8). For the same reason as with flowering rate, the log-transformed temperature function is preferred to the quadratic function for describing FDR. Differences in the estimated intercept coincide with the time of year the experiment was conducted, *viz.* expts 211/87, 307/90a and 111/91 in early spring versus expts 307/90b and 210/90 in late summer. Fruit development rate seems higher in summer. Expanding the model with different slopes (i.e. parameter b) in each experiment did not significantly decrease the residual variance. Hence, the response to temperature did not differ between experiments. Experimental data and predicted curves for FDR are presented in figure 3.4.2. Generally, standard errors of

predicted values for fruit growth development rate between 17 and 27°C were within 2% of the predicted value.

Table 3.4.8
Parameters a_i (i=experiment number), *b* and *c* for different relationships between fruit development rate (FDR; % d^{-1}) of tomato and temperature (T; °C).

parameter	FDR=a_i+*b*×T	FDR=a_i+*b*×T+*c*×T^2	FDR=a_i+*b*×ln(T)
a_1 (expt 211/87)	-0.283	-2.655	-4.668 ab[1)]
a_2 (expt 307/90a)	-0.300	-2.644	-4.672 a
a_3 (expt 307/90b)	-0.066	-2.432	-4.449 c
a_4 (expt 210/90)	-0.118	-2.447	-4.485 c
a_5 (expt 111/91)	-0.216	-2.581	-4.598 b
b	0.1000	0.3223	2.1310
c	-	-0.00519	-
R^2	0.958	0.971	0.967

1) differences significant at P=0.05

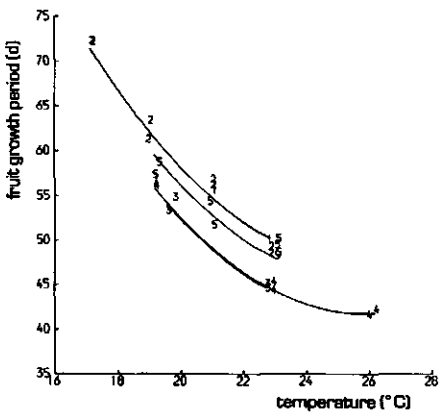

Figure 3.4.1
Relationship between fruit growth period of tomato and temperature for five experiments. 1, expt 211/87;
2, expt 307/90a; 3, expt 307/90b;
4, expt 210/90; 5, expt 111/91.

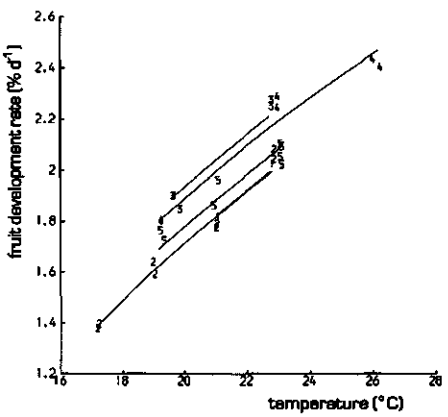

Figure 3.4.2
Relationship between fruit development rate of tomato and temperature for five experiments. 1, expt 211/87;
2, expt 307/90a; 3, expt 307/90b;
4, expt 210/90; 5, expt 111/91.

The date when each fruit reached 5 mm diameter (fruit-set) was also recorded on plants used to investigate differences in temperature response of FDR during fruit development in expts 307/90a and 210/90 (section 3.4.1). For fruits grown at a constant temperature (i.e. not transferred during their growth period) the FGP and time between fruit-set and harvest were fitted by a second order polynomial of temperature, assuming the same temperature response for both experiments. Table 3.4.9 gives the predictions for T=20°C and figure 3.4.3 shows the relationships graphically. The fact that the fruit growth period for the spring experiment 307/90a was 6.3 days longer than that for the summer experiment 210/90, appeared to have been caused by a difference of 2.7 days in the period from anthesis to fruit-set and a difference of 3.6 days after fruit-set.

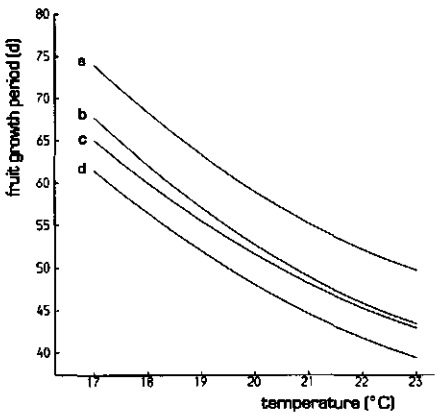

Figure 3.4.3
The temperature effect on fruit growth period (FGP in days) of tomato fruit expressed as time from anthesis until harvest (a and b) and time from fruit-set until harvest (c and d) for experiment 307/90a (a and c) and experiment 210/90 (b and d) conducted in spring and summer, respectively.
a: $FGP=269.4-16.99\times T+0.3233\times T^2$, b: $FGP=263.1-16.99\times T+0.3233\times T^2$,
c: $FGP=231.9-14.35\times T+0.2667\times T^2$, d: $FGP=228.4-14.35\times T+0.2667\times T^2$

Table 3.4.9
Predicted fruit growth period (d) from anthesis until harvest and from fruit-set until harvest, at 20°C in spring (expt 307/90a) and summer (expt 210/90). Standard errors of the differences between both experiments are given between brackets.

	307/90a	210/90	difference
anthesis - harvest	59.0	52.7	6.3 (0.38)
fruit-set - harvest	51.6	48.0	3.6 (0.42)
anthesis - fruit-set	7.4	4.7	2.7

interaction between temperature and development stage

In experiments 307/90a and 210/90 the interaction between temperature and fruit development stage on the duration of the fruit growth period was investigated by transferring plants for a fortnight to a compartment with another temperature. It should be possible to describe the effect of fruit development stage (FDS) on the temperature response of fruit development rate (FDR) as a (recursive) function of temperature (T) and development stage; $FDR_t=f(T_t,FDS_t)$ where $FDS_t=\Sigma_1^t FDR_t$. Since it is impossible to measure the fruit development stage between anthesis and the start of fruit colouring no indication could be obtained on the function type. To solve this problem, the fruit growth period was divided into a number of equal time periods, and then the average temperature for every period was calculated for each individual fruit. These average temperatures were used as explanatory variables for the duration of the fruit growth period; $FGP=f(T_1, T_2...T_n)$. In theory the accuracy of such a model will increase with increasing number of periods. However, since in the available data-set plants were moved for 14 days to another temperature, for a large number of short periods the average temperatures in successive periods are highly correlated, and consequently estimated parameters have low statistical significance. It was found by trial and error that dividing the total fruit growth period into five sub-periods gave a reasonable balance between accuracy and statistically significant parameters. As when describing fruit growth period for fruits grown at constant temperature, a relationship between the reciprocal of FGP, i.e. fruit development rate (FDR), with the natural logarithm of temperature was most successful.

$$FGP = 100/\{a_i+b_1\times\ln(T_1)+b_2\times\ln(T_2)+b_3\times\ln(T_3)+b_4\times\ln(T_4)+b_5\times\ln(T_5)\},$$ [eqn 3.4.1]

where FGP is the fruit growth period (d), a_i is an experiment dependent parameter, $b_{1\text{-}5}$ are parameters representing the temperature sensitivity and T_1, T_2, T_3, T_4 and T_5 are average temperatures (°C) of five successive parts of the total fruit growth period.

Table 3.4.10 comprises the results of the fittings of data-sets from experiment 307/90a and experiment 210/90 separately and of a fitting of the combined data-set.

Table 3.4.10
Parameters (standard errors within brackets) for the relationship:
$FGP = 100/\{a_i+b_1\times\ln(T_1)+b_2\times\ln(T_2)+b_3\times\ln(T_3)+b_4\times\ln(T_4)+b_5\times\ln(T_5)\}$, where FGP is the fruit growth period (d), a_i is an experiment dependent parameter, $b_{1\text{-}5}$ are parameters and T_1, T_2, T_3, T_4 and T_5 are the average temperatures (°C) of five successive equal parts of the total fruit growth period.

parameter	expt 307/90a		expt 210/90		both experiments	
a_1	-5.775	(0.148)			-5.854	(0.129)
a_2			-6.096	(0.284)	-5.646	(0.139)
b_1	0.326	(0.053)	0.703	(0.109)	0.394	(0.047)
b_2	0.357	(0.060)	0.149	(0.108)	0.320	(0.052)
b_3	0.039	(0.057)	0.071	(0.092)	0.050	(0.048)
b_4	0.760	(0.058)	0.958	(0.103)	0.817	(0.050)
b_5	1.006	(0.056)	0.785	(0.083)	0.940	(0.046)
n	419		114		533	
R^2	0.863		0.902		0.934	

In both experiments FGP is shortened by high temperature in the young development stage (first and second period), then the fruit becomes insensitive to temperature (third period) and close to the mature stage temperature has a very large impact, as represented by the values for $b_{1\text{-}5}$. Parameter a differed significantly ($P<0.001$) between both experiments, as found already in the constant temperature treatments (table 3.4.8).

On the basis of the values fitted for $b_{1\text{-}5}$ of the 'five periods model' (eqn 3.4.1) a third order polynomial of fruit development stage (FDS) seems a suitable function to describe the response of fruit development rate (FDR) to temperature during fruit development. As FDS can not be measured between anthesis and fruit colouring, FDR is defined to be constant at a reference temperature of 20°C. Consequently, at constant 20°C the fruit's development stage is proportional to its age. The fitted model is given by:

$$FDS_0 = 0, \qquad \text{[eqn 3.4.2]}$$

$$FDR_t = a_{FDR}+\ln(T_t/20)\times(b+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3), \qquad \text{[eqn 3.4.3]}$$

$$FDS_t = FDS_{t-1}+FDR_t, \qquad \text{[eqn 3.4.4]}$$

where FDS_t is the fruit development stage at t days after anthesis (anthesis = day number 0), FDR_t is the fruit development rate (d^{-1}), T_t is the 24-h mean temperature (°C), a_{FDR} is a parameter representing FDR at constant 20°C and *b*, *c*, *d* and *e* are parameters of the temperature response curve.

The predicted fruit growth period is determined by the day number when FDS passes 1. In the fitting procedure (GENSTAT, Payne and Lane, 1987) the difference between estimated and measured FGP was minimized (least square difference). The initial value for parameter a_{FDR} was calculated from the equation based on constant temperature (table 3.4.8), while the initial values for *b*, *c*, *d* and *e* were obtained from fitting a third order polynomial to the values of parameters $b_{1\text{-}5}$ of the 'five periods model' (table 3.4.10). Regressions were made for experiment 307/90a and 210/90 separately, and also for data of fruits from the first truss of experiment 211/87. For the latter experiment only averages per experimental plot (8 plants) were available, instead of data of each individual fruit.

The third order polynomial gave a good fit to the data of all three experiments (table 3.4.11). Except for near-mature fruits, the sensitivity of FDR to temperature during fruit development was similar in all experiments (fig 3.4.4). At a fruit development stage of about 0.3, the fruit development rate appears relatively insensitive to temperature, in contrast to young and near-mature fruits which are very temperature sensitive. This corroborates the results obtained by the 'five periods model'.

Table 3.4.11
Parameters (standard errors within brackets) for the relationship:
$FDR_t = a_{FDR,\,i} + \ln(T_t/20) \times (b+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3)$, where FDR_t is the fruit development rate (d^{-1}) at t days after anthesis, T_t is the 24-h mean temperature (°C), FDS_t is the fruit development stage, $a_{FDR,\,i}$ is an experiment dependent parameter and *b*, *c*, *d* and *e* are parameters representing the temperature response.

parameter	expt 307/90a		expt 210/90		expt 211/87		all experiments	
a_1	0.01702	(.000047)					0.01712	(.000004)
a_2			0.01905	(.000017)			0.01931	(.00002)
a_3					0.01779	(.000051)	0.01814	(.00002)
b	0.04471	(.00378)	0.05413	(.00039)	0.02107	(.00729)	0.03923	(.00009)
c	-0.2675	(.0368)	-0.3139	(.0019)	-0.1202	(.0659)	-0.2127	(.0005)
d	0.5831	(.0907)	0.6249	(.0037)	0.316	(.152)	0.4505	(.0008)
e	-0.3286	(.0633)	-0.3058	(.0028)	-0.195	(.101)	-0.2400	(.0009)
n	419		114		120		653	
R^2	0.856		0.882		0.882		0.913	

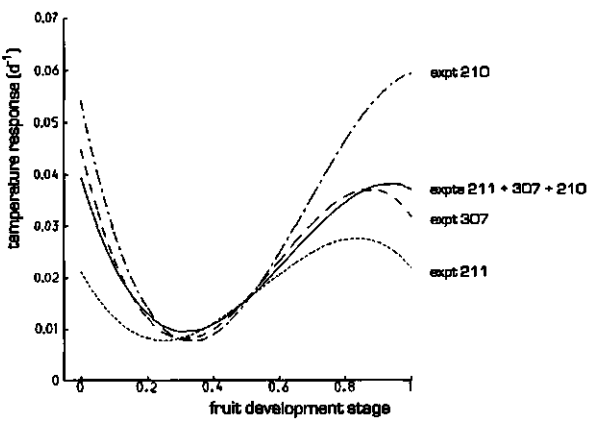

Figure 3.4.4
Temperature sensitivity of fruit development rate of tomato during fruit development as estimated in three experiments. The corresponding equations are presented in table 3.4.11.

The third order polynomial was also fitted to the full data-set including all three experiments, with different intercepts (parameter a_{FDR}) for separate experiments and an 'experiment × temperature' interaction according to:

$$FDR_t = a_{FDR,\,i} + f_i \times \ln(T_t/20) \times (1+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3), \quad \text{[eqn 3.4.5]}$$

where FDR_t is the fruit development rate (d^{-1}) at t days after anthesis, index i represents the experiment number, FDS_t is the fruit development stage, T_t is the 24-h mean temperature (°C), a_{FDR} is a parameter representing FDR at 20°C and *f, c, d* and *e* are parameters of the temperature response curve.

Although the parameter values *f* differed significantly between experiments, an equally high R^2 (i.e. 0.915 and 0.913, respectively) was obtained by the model without interaction,

$$FDR_t = a_{FDR,\,i}+\ln(T_t/20)\times(b+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3) \quad \text{[eqn 3.4.6]}$$

Since the latter model is easier to apply it is preferred for further computations. The parameter values for this model are given in table 3.4.11.

Temperature response of fruit development rate at 0.1, 0.3, 0.6 and 0.9 development stage is graphically presented in figure 3.4.5. The crossing of all response curves at 20°C in this figure is a consequence of the definition of the fruit development rate, which is then constant at this temperature. The Q_{10}-value for development rate varies from nearly 1 at 0.3 FDS to about 3 for young and near-mature fruits at low temperature (fig 3.4.6).

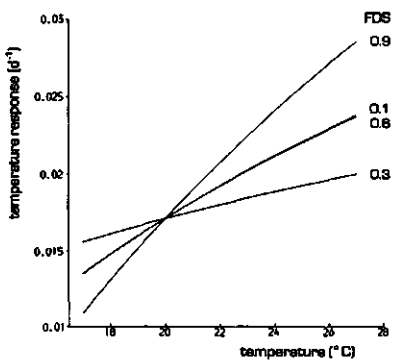

Figure 3.4.5
Temperature sensitivity of fruit development rate of tomato at 0.1, 0.3, 0.6 and 0.9 development stage (FDS).

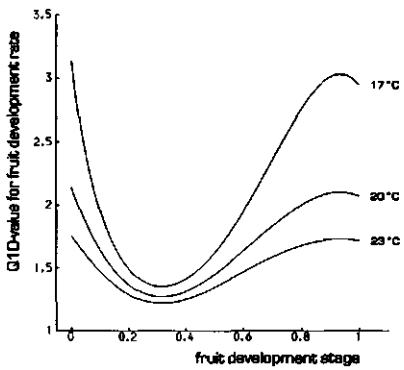

Figure 3.4.6
The effect of fruit development stage on the Q_{10}-value for fruit development rate at three temperatures (relationship as given in the last column of table 3.4.11 with a_{FDR} = 0.01712).

effects of large differences between day and night temperature

The fruit growth period in the treatments with large day-night temperature amplitudes (expt 210/90) was compared by regression with the fruit growth period measured in treatments with equal day and night temperature. Fruit growth period of all treatments (in duplicate) are plotted in figure 3.4.7. In both large amplitude treatments, day/night 27/19 and 19/27, respectively, fruit growth period was 2.1 ($P<0.001$) and 1.2 ($P=0.01$) days longer than at similar 24-h mean temperatures achieved by equal day and night temperatures.

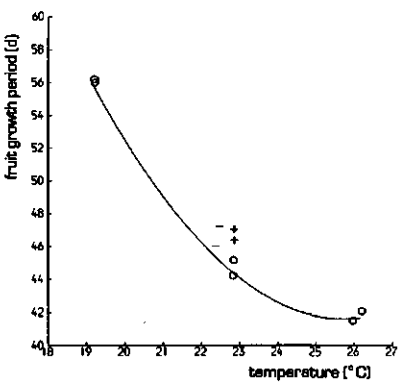

Figure 3.4.7
Fruit growth period of tomato at equal (○), positive (+) and negative (−) day-night temperature amplitude (expt 210/90).

3.4.2 discussion

Of all the variables investigated, temperature appears the principal factor determining the duration of the fruit growth period (FGP). In the present experiments FGP varied from about 73 days at 17°C to only 42 days at 26°C. Those data agree very well with observations by Rylski (1979). A reduction in the growth period of reproductive organs with increasing temperature has frequently been observed with several species, e.g. the fruit growth period of sweet pepper (Bakker, 1989), the grain filling period of wheat (Spiertz, 1977) and the boll maturation period of cotton (Mutsaers, 1976). The fruit growth period can be well described by linearly relating its reciprocal (i.e. fruit development rate) to temperature. Using the same approach, good results were also obtained by Vos (1981), Auld *et al.* (1978) and Milford *et al.* (1985) when

describing the duration of the grain filling period of wheat and the duration of leaf expansion for field bean and sugar beet, respectively. In the present study, little improvement was gained by relating fruit development rate (FDR) to the natural logarithm of temperature (table 3.4.8), which represents a slight decrease of the temperature effect at increasing temperature. From the fitted relationship, the Q_{10} for fruit development rate was calculated to be 1.8 at constant 18°C and 1.4 at 23°C. Earlier, Hurd and Graves (1985) estimated the Q_{10} for fruit development at 1.7.

Because of the non-linearity of the temperature response, fruit development rate (FDR) may be overestimated (underestimation of fruit growth period) if temperature is averaged over a wide temperature range before calculating FDR. Indeed, a temperature regime with a large day-night amplitude caused a slightly longer fruit growth period (FGP) than a zero-amplitude regime with the same 24-h mean temperature (fig 3.4.2). According to the equation $FGP=100/\{-4.485+2.131\times\ln(T)\}$ (table 3.4.8, expt 210/90), the FGP in a regime with 12 hour at 27°C plus 12 hour at 19°C is about 1 day longer than at constant 23°C. So, in general it is better to use the actual temperatures in the model although, provided the temperature amplitude is not too large, temperature averaging causes only small errors.

The accelerating effect of temperature is not equal during fruit development. In fact, the pattern of sensitivity to temperature appears to be the opposite to that of fruit growth rate, which is at its greatest half-way between anthesis and harvest ripe (section 4.3). The course of the temperature response reflects the sensitivity to temperature of successive physiological processes determining the fruit growth period. Just after anthesis, the affected processes may be cell division and seed growth, while near maturity the onset of processes involved in colouring will be accelerated by temperature. It is beyond the scope of this thesis to go into further detail about these physiological processes themselves.

For different experiments statistically significant differences were found for the parameter a in the model $FDR=a+b\times\ln(T)$ (table 3.4.8). In contrast with the model for flowering rate (section 3.2), where differences between experiments seem to be associated with differences between cultivars, the differences in fruit development rate correspond to the season, i.e. early spring versus late summer. Fruit growth period in late summer is about 6 days less than in spring, and about half this difference was achieved in the period from flowering until reaching 5 mm fruit diameter (table 3.4.9). It is plausible to suppose that the duration of the early period is affected by the assimilates available for the very young fruit,

as it has frequently been observed that, under competitive conditions, young fruits develop slowly from pollination until the 5 mm stage. Within trusses this is manifested as a longer fruit growth period for distal fruits (Cooper, 1959; Schilstra-van Veelen and Bakker, 1985; Bertin and Gary, 1992), especially under low light conditions (Cockshull *et al.*, 1992). Under conditions of severe competition as at high temperature (de Koning, 1989*a*) or with a heavy fruit load (Hurd *et al.*, 1979), development and growth of complete trusses may even be postponed. At high temperature in experiment 307/90a, FGP was shortened by decreasing fruit load (table 3.4.2). When competition declines, the fruits that were delayed develop and grow normally (Cooper, 1959; de Koning, 1989*a*). However, moderate alterations of sink-source ratio, e.g. fruit pruning up to four fruits per truss (Buitelaar, 1985) and light reduction of 32% (Buitelaar and Janse, 1983) and 23% (Cockshull *et al*, 1992) did not affect FGP.

Severe fruit pruning at low temperature increased FGP as compared with FGP of normally loaded plants. This agrees with Stenvers and Staden (1976) who observed delay of colouring of the locular tissue relative to colouring of the pericarp at low fruit load and low temperature. Since they also measured high ascorbic acid content in those fruits, the delaying effect of severe fruit pruning at low temperature may possibly be attributed to a disturbed hormone balance.

At low irradiance, fruit temperature is equal to air temperature, but at high irradiance current temperature of exposed fruits may be up to 9°C higher (van Holsteijn, 1989). Therefore the observed season effect on FGP may be due to differences between (measured) air temperature and fruit temperature. A 6 days difference in FGP corresponds to a continuous temperature difference of 1.5 to 2°C. Since such a large difference is not likely to occur between average fruit and air temperature, it is probably not the only factor explaining the effect of season. For the period from 5 mm stage until harvest ripe the observed difference of 3 to 4 days between FGP in spring and summer corresponds to a temperature difference of 0.5 to 1°C between air and fruit temperature, which is plausible in summer. Also for the period until 5 mm fruit diameter the effect of the temperature difference between fruit and air may be substantial as at this stage fruits are very sensitive to temperature and moreover they may be less shaded by leaves.

In summary, the effect of season on duration from anthesis until the 5 mm stage can probably be ascribed to differences between fruit and air temperature as well as assimilate availability, while after the 5 mm stage, an irradiance-induced difference between air and fruit temperature seems the main determinant. A direct promoting effect of irradiance in the latter stage cannot be excluded as darkness inhibits pigment formation of immature tomato fruit (Raymundo *et al.*, 1976).

The fruit growth periods of 'Calypso' and 'Dombito' were found to be equal (table 3.4.2). This result seems to be fortuitous as generally FGP differs between cultivars (e.g. Mizrahi, 1982; Sharaf and Hobson, 1986; Cockshull *et al*, 1992). Cockshull *et al.* (1992) observed differences between four round tomato cultivars, but the largest difference was only 2.4 days on an average of 70 days. Therefore, with related cultivars differences probably are very limited.

In our experiments, absence of any effect of EC in the rooting medium on FGP as presented in table 3.4.5 and table 3.4.6 is convincing. However, several authors reported a few days decrease of FGP if salinity was raised by NaCl (Mizrahi, 1982; Mizrahi *et al*, 1982; Sharaf and Hobson, 1986). The difference in response to salinity when raised with major nutrients as compared with NaCl only, may be explained by sodium antagonism on the uptake of potassium (Adams, 1991), which at low concentration reduces FGP (Besford and Maw, 1975). However, high sodium concentration in experiment 103/92 (table 3.4.6) did not affect FGP.

In previous research it was found that increased root temperature has no (de Koning, 1986) or only a very limited (Hurd and Graves, 1985) retarding effect on the fruit growth period. Air humidity does not affect FGP of tomato (Bakker, 1991). Severe water stress shortens the duration of the fruit growth period (Wolf and Rudich, 1988).

Removing leaves, a routine crop management measure, causes a slight increase in the number of harvestable fruits produced some days later (Buitelaar, pers.comm.). This growers' opinion is supported by an experiment of Slack (1986) where severe de-leafing around near-mature fruits accelerated fruit development, possibly due to a reduction in the ripening inhibitory substance produced by the leaves (Sawamura *et al*, 1978).

3.4.3 model

For dynamic modelling of the duration of fruit growth period (FGP), a model of daily fruit development rate (FDR) is preferred to a direct description of the duration of FGP. FDR is described on the basis of constant (table 3.4.8) and varying (eqn 3.4.6) temperature during fruit development. Rewriting the model for constant temperature to a reference temperature of 20°C changes parameter a_{FDR} to 0.01712 and 0.01899 d^{-1} for experiments 307/90a and 210/90,

respectively. These values are almost equal to parameter a estimated on the basis of the varying temperature treatments (table 3.4.11). Both FDR models predict identical FGP at constant temperature except at low temperature (table 3.4.12). Although this difference may be artificial, it is conceivable that the stronger temperature response at changing temperature is caused by extra delay and acceleration when changed to lower and higher temperature, respectively. Therefore, the model based on constant temperature may be preferred when temperature during fruit development is not very variable.

Table 3.4.12
Predicted duration of the fruit growth period by two models, one based on constant temperature and one based on varying temperature during fruit development. Predictions are made for conditions (constant temperature) and estimated parameters (model for FDR; d^{-1}) in experiments 307/90a (spring) and 210/90 (late summer).

experiment	307/90a		210/90	
model [1]	constant	varying	constant	varying
a_{FDR}	0.01712	0.01712	0.01899	0.01931
temperature (°C)				
17	74	77	-	-
19	63	63	56	56
21	56	55	50	49
23	50	50	46	45
27	-	-	40	39

1) constant temperature model: $FDR_{f(T)}=a_{FDR}+0.02131\times\ln(T/20)$
varying temperature model :
$FDR_{f(T\times FDS)}=a_{FDR}+\ln(T/20)\times(0.0392^{-}0.2127\times FDS+0.4505\times FDS^{2-}0.2400\times FDS^{3})$,
where FDR is the fruit development rate (d^{-1}), T is the 24-h mean temperature (°C) and FDS is the fruit development stage.

Differences in FGP among experiments, as expressed by parameter a_{FDR}, were correlated to season and it has been argued (section 3.4.2) that solar irradiance is the most probable determinant. A considerable part of the season effect was caused in the period just after anthesis, and, therefore, it is assumed that the

effect of season can be quantified using a relationship between parameter a_{FDR} and the average daily solar irradiance incident on the crop in the three weeks after anthesis. Additionally, it is assumed that at low irradiance, the effect of extra light is stronger than at high irradiance and therefore the natural logarithm of the irradiance is preferred. For experiments 307/90a and 210/90, - both conducted with cv 'Calypso' -, parameter a_{FDR} was estimated to be 1.712 and 1.899 while the average irradiance incident on the crop (RAD_{FDR}) was 2.0 and 9.6 MJ m^{-2} d^{-1}, respectively. Hence, the effect of season on parameter a_{FDR} in the equation for FDR was assessed to be $0.0012 \times \ln RAD_{FDR}$ d^{-1}. Plant age affected the fruit growth period and since the temperature response for young and old plants was equal (table 3.4.4), this factor can also be included by adjusting parameter a_{FDR} in the model for FDR. Age is expressed as the number of the relevant truss. The observed decrease of FGP from 49.1 to 53.2 days (table 3.4.4) at a difference 31 trusses (expt 307/90b, table 3.4.1) corresponds to a decrease in parameter a_{FDR} of 0.00005 d^{-1} $truss^{-1}$. Among trusses of individual experiments no difference in FGP was observed, which seems to argue against including an aging effect in the model. In the experiments, however, the range of trusses was too small to detect any significant effect, e.g. a difference of five trusses corresponds to less than 1 day difference in FGP.

In summary, the models for FDR including temperature, plant age and effects of season are for constant temperature during fruit development:

$$FDR_{f(T),t} = 0.0165 + 0.0012 \times \ln RAD_{FDR} - 0.00005 \times TRUSS + 0.02131 \times \ln(T_t/20),$$

and for varying temperature during fruit development:

[eqn 3.4.7]

$$FDR_{f(T \times FDS),t} = 0.0165 + 0.0012 \times \ln RAD_{FDR} - 0.00005 \times TRUSS + \ln(T_t/20) \times (0.03923 - 0.2127 \times FDS_{t-1} + 0.4505 \times FDS_{t-1}^{2} - 0.2400 \times FDS_{t-1}^{3})$$

[eqn 3.4.8]

where $FDR_{f(T)}$ and $FDR_{f(T \times FDS)}$ are the fruit development rates (d^{-1}) calculated without and with 'temperature × FDS' interaction respectively, index t represents the number of days after anthesis, RAD_{FDR} is the average solar irradiance received by the crop (MJ m^{-2} d^{-1}) averaged over three weeks after anthesis of the fruit considered, TRUSS is the truss position (truss number), T_t is the 24-h mean temperature (17-27°C) and FDS_t is the fruit development stage ($0 \leq FDS_t \leq 1$) with $FDS_t = FDS_{t-1} + FDR_t$.

The models are based on experiments with 'Calypso', but as differences between cultivars seem relatively small they are probably also valid for other cultivars. Adaptation of the models to other cultivars can probably best be done by adjustment of parameter a_{FDR}, assuming that the response on temperature, plant age and season are cultivar independent. It should be noted that the available data on which modelling of season and plant age are based are too few and that more research is needed to describe these effects more accurately. Not included in the models presented are possible effects of salinity, de-foliation, assimilate availability and water stress.

4

FRUIT GROWTH ASSIMILATE DEMAND AND DRY MATTER DISTRIBUTION

4.1 Introduction

4.1.1 sink strength

Source organs export assimilates produced by photosynthesis or mobilized from storage, while sink organs (sinks) import assimilates and utilize them in respiration, growth and storage. For a glasshouse tomato crop as grown in the Netherlands, growth and yield seems generally limited by the amount of assimilates produced (source-limited), as continuous shading with 6% (Cockshull *et al.*, 1992) and temporary shading with 40% at high irradiance in summer (de Koning, 1988*c*) reduced fruit yield. Additionally, concerning a whole year, highest growth rates coincide with weeks with highest irradiance (de Koning, 1993).

Source limited growth implies that the sink organs grow less than their potential ability and that there is mutual competition for assimilates. The competitive power of an organ to attract assimilates is called sink strength (Wareing and Patrick, 1975; Wolswinkel, 1985) and this is defined as the ability of an organ to import assimilates (Warren Wilson, 1972). It can be estimated by the maximum rate of assimilate accumulation (Ho, 1988*a*). For better conception of sink strength, it is proposed by Warren Wilson (1972) that:

$$\text{SINK STRENGTH} = \text{SINK SIZE} \times \text{SINK ACTIVITY},$$

where sink size can be regarded as the physical constraint and sink activity as the physiological constraint of sink strength (Ho, 1988*a*; 1992). In this view, the sink size of an organ accounts for the physical factors such as cell number and storage capacity within, while sink activity represents the physiological processes concerning the uptake and processing of imported assimilates.

In a tomato fruit, cell division is finished within two weeks after anthesis (Ashira *et al.*, 1968; Davies and Cocking, 1965). Once cell number is finalized, the evolution of sink strength during development is determined by the genetically programmed sequence of metabolic activities in each cell. In addition to ontogenetic variation, sink strength will be affected by environmental conditions. For example, temperature affects the metabolic activity and probably also the rate and duration of cell division. In general, the sink strength of an organ at any moment depends on (1) its actual intrinsic abilities determined by genetical properties as well as previous conditions and (2) the prevailing environmental conditions.

SINK STRENGTH	=	**SINK SIZE**	×	**SINK ACTIVITY**
maximum rate of assimilate accumulation		**number of cells**		**apoplastic unloading** or **hydrolysis of sucrose** or **uptake of sugars by the protoplast or vacuole**
		physical constraint		physiological constraint

Sink strength of an organ as determined by sink size and sink activity (after Ho, 1992).

The maximum ability to attract assimilates is fully expressed at nonlimiting assimilate supply and is defined as the *potential sink strength* (Ho, 1988*a*). Under such conditions each cell reaches its maximum (potential) size, resulting in the potential size for the whole organ at maturity. When the plant's cumulative assimilate demand exceeds the supply, also the sink's position in the whole sink-source system, such as distance to the sources, position with respect to competing sinks, vascular connections etc. is important for the sink's competitiveness (Wardlaw, 1990). Those factors will gain significance with decreasing assimilate availability. The ultimate competitiveness of a sink, that results from its intrinsic properties (potential sink strength) and the properties of the whole sink-source system, is regarded as the *actual sink strength* (Ho, 1988*a*). The dependence of actual sink strength (ASS) on potential sink strength (PSS) and availability of assimilates (substrate, S) may be described by Michaelis-Menten kinetics (Thornley, 1977):

$$ASS = PSS \times S / (K_m + S), \qquad \text{[eqn 4.1.1]}$$

where the Michaelis-Menten constant K_m is determined by the sink's position in the whole sink-source system. With this relationship it is possible to model differences between sinks in affinity or priority for assimilates (Marcelis, 1993*a*; Minchin *et al.*, 1993). In terms of assimilate flow, PSS can be regarded as the maximum unloading rate of a sink.

As a first approximation, in this study, it is assumed that assimilate partitioning is regulated only through the potential sink strength, which implies that differences in affinity, priority and other competitive properties, that are expressed at limiting assimilate supply, are neglected. This simplification is supported by evidence that within the plant assimilates can freely move (one single assimilate pool) and the carrying capacity of the phloem is not a regulating factor in dry matter distribution (Milthorpe and Moorby, 1969; Wareing and Patrick, 1975; Gifford and Evans, 1981; Wardlaw, 1990).

The assimilate demand (maximum ability to process carbohydrates; Chapter 1) of an individual organ is defined to be equal to its potential sink strength. It comprises growth (dry matter accumulation) and respiration (growth and maintenance respiration). The growth component can be estimated by the organ's potential growth rate and is regarded as the *apparent sink strength* (Ho, 1988*a*). Generally the apparent sink strength will be the major determinant of assimilate demand.

PSS	=	**APPARENT SINK STRENGTH**	+	**RESPIRATION**
potential assimilate demand		**potential growth rate** (maximum dry matter accumulation)		**maintenance** + **growth respiration**

Components of potential sink strength (PSS).

This study concentrates on quantifying the potential growth rate during fruit development, including the effects of fruit position and responses to temperature. Maintenance and growth respiration are assumed to be proportional to dry weight (Penning de Vries, 1975) and growth rate (Penning de Vries *et al.*, 1974; Vertregt and Penning de Vries, 1987), respectively. Respiration is not investigated in this study but the required coefficients are obtained from the literature.

4.1.2 outline of the chapter

Exploratory experiments demonstrated that when the fruit number is restricted to two fruits per truss, potential growth for the remaining fruits is obtained

(section 4.3). The fruit's daily growth rate can be assessed by repeated non-destructive diameter measurements during fruit development and subsequent curve fitting with a sigmoid growth function (Hunt, 1982). One of the most flexible and frequently used growth functions is the generalized logistic or the Richards function (Richards, 1959).

Since temperature affects the fruit growth period (Klapwijk, 1987) as well as sink strength (Farrar, 1988; Verkleij and Challa, 1988) and the actual fruit growth rate (Walker and Ho, 1977; de Koning, 1989*a*), potential fruit growth rate is assessed at different temperatures. In experiments where temperature was not constant only the potential size of a fruit at harvest is determined because, due to the influence of temperature, a 'smooth' curve is not expected (Wickens and Cheeseman, 1988). For tomato fruit the growth rate at maturity approximates zero (Monselise *et al.*, 1978) and consequently the potential fruit size at harvest will be close to the parameter of the Richards function that represents the upper asymptote of the sigmoid growth curve. It is assumed that the shape of the curve is not affected by the final size, which allows us to consider the asymptote independently of the other parameters of the sigmoid growth function. Effects of fruit position and temperature on potential fruit size are described in section 4.3, while section 4.4 deals with the time course of potential growth rate between anthesis and fruit maturity.

The course of fruit dry matter content during fruit development is tentatively modelled to be able to convert fruit fresh weight estimated from diameter readings into dry weight (section 4.2). In addition, fruit dry matter content at harvest is described on the basis of some available data concerning the influences of season, temperature and salinity.

Whether the fruit's assimilate demand is affected by the previous availability of assimilates is investigated by subjecting sub-potentially growing fruits to a sudden change from limiting to nonlimiting assimilate supply, and comparing growth of those fruits with that of potentially growing fruits from anthesis onwards. Results are presented in section 4.5.

Section 4.6 deals with the assimilate demand of vegetative plant parts. A tomato leaf becomes net exporting for assimilates at about 15 to 25% leaf expansion (Ho and Shaw, 1977). Thus, strictly speaking, a leaf is a sink organ for only a short time. However, even though assimilates for growth and respiration are supplied by the leaf itself, for the purpose of modelling assimilate demand and dry matter distribution it is assumed that the leaf has to compete for those assimilates in the

same way as other sinks. Export of assimilates will occur even when a leaf grows less than potential. The possible benefit a leaf may have from being sink and source in the case when the total plant's assimilate demand exceeds the supply will be neglected in this study. In future modelling this specific feature of leaves may be expressed in a high priority for assimilates.

Analogous to the assimilate demand of fruits, in theory, the demand of vegetative organs can be quantified by their potential growth rate achieved at nonlimiting assimilate supply. Due to storage of assimilates in leaves and stem (Starck *et al.*, 1979), this method may overestimate the real vegetative sink strength in terms of structural dry weight. Moreover, prolonged exposure to low sink-source ratio can even reduce vegetative growth (Nederhoff *et al.*, 1992). Therefore it is probably better to estimate the assimilate demand of vegetative plant parts from dry matter distribution in source-limited plants. According to the hypothesis that the share of organs in total growth of source-limited plants is proportional to the potential growth rates, the potential growth rates of the vegetative plant parts relative to those of the fruits can be deduced from the ratio between vegetative and fruit growth in source-limited plants. Both, assessment of the potential weight of a (full grown) vegetative unit (leaves and stem in-between two successive trusses) at nonlimiting assimilate availability, and determination of the vegetative potential growth rate relative to the potential growth rate of a fruit in source-limited plants, are made.

4.2 Fruit dry matter content

4.2.1 results

effect of development stage

In experiment 402/89 the evolution of fruit dry matter content (FDMC in g dw g^{-1} fw $\times$ 100%) during fruit development was assessed. When fruits at the first truss started to colour, fruits from all trusses were picked. Fruit development stage (FDS) is defined as 0 at anthesis (truss 9) and 1 at the start of colouring (truss 1). Assuming rates of truss initiation and fruit development have been constant, the development stages of the fruits of truss 2 to 8 were calculated proportionally to truss number, i.e. 0.125 development stage units to each truss.

FDMC declined from about 9% for very young fruits to 5.4% for harvest ripe fruits. It is assumed here that the observed differences can be fully ascribed

to development stage only. The relationship is described perfectly by a second order polynomial (R^2=0.98) of development stage. A second order polynomial with its minimum exactly at FDS=1 fits as well as the general form and is preferred as the coefficients can be related directly to FDMC0 at FDS=0 and FDMC1 at FDS=1. The relationship with the coefficients expressed in FDMC0 and FDMC1 is:

$$FDMC_t = FDMC0 + (FDMC1 - FDMC0) \times 2 \times FDS_t + (FDMC0 - FDMC1) \times FDS_t^2, \quad \text{[eqn 4.2.1]}$$

where $FDMC_t$ is the fruit dry matter content ($g^{-1} \times 100\%$), FDM0 is the fruit dry matter content at FDS=0 , FDM1 is the fruit dry matter content at FDS=1 and FDS_t is the fruit development stage ($0 \leq FDS \leq 1$) at t days after anthesis.

For the resulting relationship (fig 4.2.1) the parameters are: FDMC0=10.2% and FDMC1=5.3% (R^2=0.98; n=14).

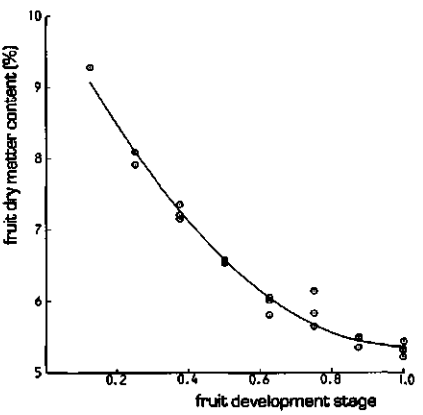

Figure 4.2.1
Fruit dry matter content ($g^{-1} \times 100\%$) during development of a tomato fruit from anthesis (fruit development stage = 0) to harvest ripe (fruit development stage = 1). Each data point represents a sample of 10 to 30 fruits (expt 402/89).

effect of fruit load and environment

Effects of fruit load (expts 402/89 and 307/90a), temperature (expts 307/90a and 111/91) and salinity (expts 111/91 and 103/92) on fruit dry matter content at harvest were analyzed with ANOVA. Fruits grown in experiment 402/89 at nonlimiting assimilate supply had a significantly (P=0.004) higher dry matter content than fruits grown on normally loaded plants, *viz.* 5.6% and 5.2%, respectively. A similar difference was found in experiment 307/90a for fruits grown at 19°C (table 4.2.1). At low temperature the difference was even larger whilst at high temperature (23°C) FDMC of potentially grown fruits and fruits grown under restricted assimilate supply was equal. This 'fruit load × temperature' interaction is statistically significant (P=0.025). Fruits grown in experiment 307/92 had only slightly higher (0.001-0.004 g^{-1}) dry matter content when grown under ample assimilate supply than fruits grown with limiting assimilate supply (section 4.5, table 4.5.2).

Table 4.2.1
Fruit dry matter content (g^{-1} × 100%) of harvest ripe tomato fruit grown at limiting and nonlimiting assimilate supply and at four temperatures (expt 307/90a). Means are based on two replicates and harvests on 20 April and 2 May. Means (within the same column as well as between colums) that are followed by the same letter do not differ significantly (Student's *t*-test, P≤0.05).

temperature (°C)	assimilate supply	
	nonlimiting	limiting
17	6.11 a	5.32 de
19	5.68 b	5.17 e
21	5.64 bc	5.37 cde
23	5.61 bcd	5.65 bc

At nonlimiting assimilate supply in experiment 307/90a fruits grown at 17°C had a higher FDMC than fruits grown at the higher temperatures, while at limiting assimilate supply fruits grown at 23°C had the highest dry matter content (table 4.2.1). After the temperature treatments were stopped measurements of FDMC from source-limited plants were continued. It appeared that the effect of temperature was still present 30 days after temperatures were set equal (1 May, day 120). Only after 60 days, a full fruit growth period, the effect of previous

temperature exposure disappeared (fig 4.2.2). Also in experiment 111/91 high temperature caused slightly higher fruit dry matter content (table 4.2.2).

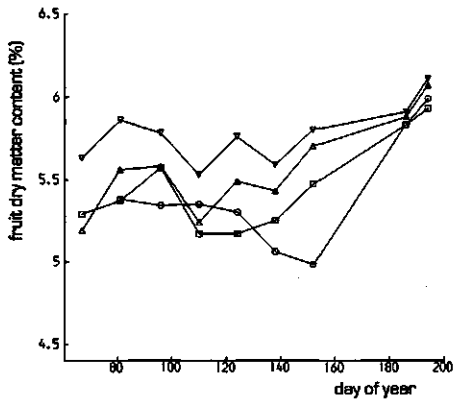

Figure 4.2.2
Fruit dry matter content (g^{-1} × 100%) at harvest of tomato grown at four different temperatures until day number 120 and equal temperatures after (expt 307/90a).
Δ, 17°C; ○, 19°C; □, 21°C; ▽, 23°C.

Table 4.2.2
Fruit dry matter content (g^{-1} × 100%) of harvest ripe tomato fruit grown at three temperatures and three salinities (EC) of the root environment (expt 111/91). The data are based on two replicates and four harvests between 3 April and 15 May.

temperature (°C)	EC in the root environment (S m^{-1})			
	0.3	0.6	0.8	mean
19	5.16	5.65	6.14	5.65
21	5.38	5.86	6.29	5.85
23	5.42	5.96	6.21	5.86
LSD 5%				0.11
				LSD 5%
mean	5.32	5.82	6.21	0.21

Big differences in FDMC were found between fruits grown at different salinity. Increasing the EC from 0.3 to 0.8 S m^{-1} in experiment 111/91 increased FDMC from 5.3 to 6.2% (table 4.2.2). Apparently the effects of temperature and salinity are additive as no interaction between those variables was present.

The salinity effect in experiment 103/92 (table 4.2.3) was similar to that in experiment 111/91. Increasing salinity by Na or NaCl increased FDMC slightly more than when salinity was raised with the standard composition of nutrients.

Table 4.2.3
Fruit dry matter content (g^{-1} × 100%) of harvest ripe tomato fruit grown at different salinities (EC) and compositions of the nutrient solution in the root environment (expt 103/92).

EC (S m^{-1})	nutrient composition	fruit dry matter content
0.3	standard	5.33
0.6	standard	5.76
0.6	standard + Na	5.92
0.6	standard + NaCl	5.88
0.9	standard	6.28
0.9	standard + Na	6.53
LSD 5%		0.07

4.2.2 discussion

Decrease of fruit dry matter content (FDMC) during fruit growth, with a fast decrease in early development as shown in figure 4.2.1, is also reported by Ward and Miller (1970) and Ehret and Ho (1986*a*) for tomato and Marcelis (1992*a*) for cucumber. Results of Ehret and Ho (1986*a*) demonstrate that FDMC of young fruits is hardly affected by the conductivity level of the nutrient solution (EC) while FDMC of harvest ripe fruits increased significantly with increasing salinity. Therefore, by assuming FDMC0 is not affected by environmental conditions and equal to 10%, an adequate estimate of FDMC at any development stage can be made if only the fruit dry matter content at harvest is known.

About half the dry matter of mature fruits consists of reducing sugars (fructose and glucose), about 15% consists of organic acids and 10% of minerals. The remaining quarter, separable as alcohol insoluble solids (AIS), consists of proteins, pectic substances, cellulose and hemicellulose (Davies and Hobson, 1981). Minerals, sugars and organic acids are the osmotic elements which account for the osmotic potential of fruit cells (Rudich and Luchinsky, 1986) while the fraction AIS corresponds with the cell wall material (Davies and Hobson, 1981).

Nonlimiting assimilate supply slightly increased the fruit dry matter content at maturity (table 4.2.1) probably due to extra storage of carbohydrates. Increase of FDMC at nonlimiting assimilate supply is also reported for cucumber (Marcelis, 1992*a*). The observed influence of sink-source ratio on FDMC is consistent with the decrease of dry matter (Davies *et al.*, 1958) and sugar (Janse, 1992) content at partial defoliation. A seasonal trend of FDMC, i.e. low FDMC in spring and autumn and high FDMC in summer (Adams and Winsor, 1977; de Koning, 1993), has also been ascribed to varying sink-source ratio (Winsor and Adams, 1976). However, light reduction by shading (Buitelaar and Janse, 1983) or increased CO_2-concentration (Davies and Winsor, 1967; Madsen, 1976) did affect fresh weight production but not the fruit dry matter content. FDMC is determined not by assimilate supply alone but also by the fruit's water accumulation (Ho, 1988*b*). Since along with the course of solar radiation also temperature and humidity and subsequently the water relations in the plant vary, the season effect may be based on a number of variables.

Possibly the increase of FDMC with increasing temperature as observed for tomato grown with limiting assimilate supply (tables 4.2.1 and 4.2.2) may also be attributed to differences in the plant's water relations, as together with temperature air vapour pressure deficit (VPD) usually also increases in glasshouses. For example, in experiment 307/90a the mean VPD over the growth period of the fruits concerned was 0.66, 0.70, 0.71 and 0.83 kPa in the 17, 19, 21 and 23°C treatments, respectively. However, Bakker (1991) observed no clear effects on FDMC in tomato and cucumber of VPD varying from 0.3 to 0.9 Kpa. Also Janse and Schols (1993) measured in a phytotron no effect of air humidity (0.2-0.7 Kpa, 20°C) on FDMC while, at 0.6 Kpa VPD, a 6 degree temperature difference resulted in a similar effect to that observed in our greenhouse experiments. Although those results give evidence for a specific temperature effect without involvement of transpiration rate, the physiological background of

increase of FDMC with increasing temperature is not certain. Its likely that increasing temperature reduces cell size (discussed in section 4.3) and consequently, assuming no reduction in cell wall thickness, increases the total weight of cell walls relative to the fruit's volume. Apart from cell size, temperature may also increase the dry matter content of the cytoplasm and vacuole. The interaction between temperature and fruit load (table 4.2.1) remains unexplained but indicates the complexity of processes and mutual relationships determining FDMC.

Many authors report an increase of FDMC when the salinity in the root environment is raised (Mizrahi, 1982; Mizrahi *et al.*, 1982; Massey *et al.*, 1984; Adams and El-Gizawy, 1986; Sharaf and Hobson, 1986; Ehret and Ho, 1986; Hobson and Adams, 1988; Sonneveld and Welles, 1988; Adams and Ho, 1989; Gough and Hobson, 1990; Sonneveld and Voogt, 1990; Mitchell *et al.*, 1991; Ohta *et al.*, 1991; Adams, 1991) or water supply is restricted (Amable and Sinnadurai, 1977; Rudich *et al.* 1977; Adams and El-Gizawy, 1986; Adams, 1990; Mitchell *et al.*, 1991). Inhibited water uptake by root temperature as low as 14°C also increased FDMC while between treatments with 18, 22 and 26°C root temperature no differences were observed (Adams, 1988). Generally, measures that affect the water relations, only change the fresh weight but not the dry weight of the fruits (e.g. Ho *et al.*, 1987) and, therefore, only alter the water import to the fruit (Mitchell *et al.*, 1991). When exposed to higher salinity or increased transpiration a plant reduces its osmotic potential in order to maintain turgor. Because this osmotic adjustment is achieved by increase of the concentration of osmotic solutes dry matter content probably also increases. Decrease of cell size with increasing salinity may also contribute to higher FDMC. Presumably both osmotic adjustment and cell size are involved but unfortunately neither our own experiments nor reports in the literature give a decisive answer. Increase of FDMC due to increase of salinity with standard nutrients does not change the content of mineral nutrients on dry weight base (Sonneveld and Welles, 1988; Sonneveld and Voogt, 1990). Since also total dry weight accumulation does not change with salinity (Ho *et al.* 1987), the sink strength of the fruit for assimilate does not seem readily affected by the water relations in the plant (Ehret and Ho, 1986*a*; Ho, 1988*b*).

4.2.3 model

In an explanatory model for FDMC it is inevitable to deal with the plant's water relations. But, as investigation of the water relations is beyond the scope of this study, modelling here will be only descriptive. On the basis of the presented results, the model should at least include the factors air temperature and EC in the root environment. Possibly also a season effect should be included as FDMC varies significantly during a year (Winsor and Adams, 1976; Adams and Winsor, 1977; de Koning, 1993).

Since in experiments 307/90a and 307/90b FDMC was measured during the whole cropping period, any influence of season, apart from temperature and EC effects, could be approximated. The 23°C treatment was most suitable as temperature outside the treatment periods, i.e. 1 May until 27 August, was closest to this temperature. Data from early spring (up to day 100) were omitted as those fruits were grown with a high conductivity level in the root environment (> 0.35 S m^{-1}), as a standard cultivation practice in spring. Describing the season effect by the mean daily solar irradiance sum 2, 4 or 6 weeks prior to harvest failed because of very poor correlations ($r^2<0.3$) with FDMC. Therefore a rather non-physiological approach was chosen by relating FDMC simply to the Julian day number (DAYNO). A sine function was fitted as it will behave properly in the periods in which experimental data are lacking, since data on FDMC at passably constant temperature (circa 23°C) and EC level (circa 0.3 S m^{-1}) were only available from 20 April to 27 September. Despite substantial scatter the data show a seasonal trend (fig 4.2.3) and 56% (n=11) of the variance was accounted for by the sine function:

$$FDMC = 5.39 - 0.743\times(\cos\{2\times Pi\times[DAYNO-16]/365]\}), \qquad \text{[eqn 4.2.2]}$$

where FDMC is the fruit dry matter content ($g^{-1} \times 100\%$) at harvest, Pi=3.14159 and DAYNO is the day number with 1 = 1 January.

The standard errors of the estimated coefficients 5.39, -0.743 and -16 are 0.14, 0.203 and 6.9, respectively. Although fitted on a very limited data-set, the estimated relationship looks plausible with a yearly average of 5.4%, and an annual variation from 4.7 in January to 6.1 in July. The highest FDMC occurring in late summer is consistent with results of Winsor and Adams (1976) and Adams and Winsor (1977). Since this model is based on data from a single crop grown from December until October possible effects of ontogeny on FDMC are

included implicitly and strictly speeking the model is specific for the cropping system and other conditions as in experiments 307/90a and 307/90b.

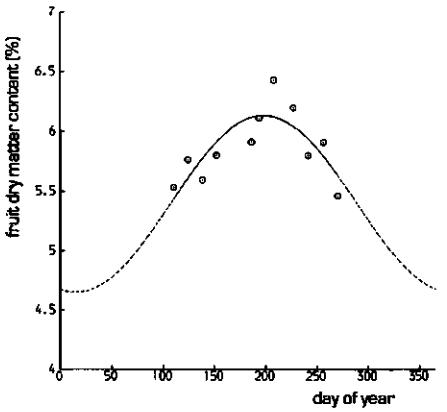

Figure 4.2.3
Annual course of fruit dry matter content (g^{-1} × 100%) at harvest of tomato grown at circa 23°C and an electrical conductivity in the root environment of circa 0.3 S m^{-1} (expts 307/90a and 307/90b).

The temperature effect on FDMC was quantified from four harvest times between 22 March and 2 May for experiment 307/90a and six harvests between 20 March and 15 May for experiment 111/91. Despite a small difference in average FDMC, the response of FDMC to temperature was equal for both experiments (307/90a and 111/91) *viz.* 0.07 (SE=0.010) percent per degree Celsius. Those effects are based on constant temperature but the question rises over which period temperature determines FDMC if during the fruit growth period temperature varies. Concerning the after-effect as shown in figure 4.2.2, averaging the temperature from anthesis to harvest seems plausible.

For experiment 111/91 the effect of salinity with standard nutrients was estimated at 0.18 (SE=0.011) percent per unit EC (0.1 S m^{-1}), while in experiment 103/92 0.16 (SE=0.008) percent per unit EC was calculated. The average for both experiments was 0.17 (SE=0.008). Several authors referred to previously observed similar salinity response, despite differences in the general average level of FDMC which are apparently due to differences in other experimental conditions. At very high salinity FDMC increases more than proportionally with the EC-level as indicated by results of Adams and El-Gizawy (1986) and Adams

(1991). As water relations appear to have a significant after effect (Adams, 1990), the prediction of FDMC is based on the average EC-level from anthesis until harvest.

Tomato types (Ho, 1988*b*; de Koning and de Ruiter, 1991) and varieties (Davies and Winsor, 1969; Davies and Hobson, 1981) may differ significantly in FDMC. Although no physiological explanation is available yet, this effect may be modelled as a multiplicative parameter since throughout the year the FDMC of cherry tomato appeared always 1.5 times that of round tomato (de Koning and de Ruiter, 1991).

In order to compose a model including the parameters season, salinity and temperature, the two latter parameters were added to the season effect. Together with a multiplicative parameter for cultivar differences, FDMC of harvest ripe fruits is given by:

$$\text{FDMC}=r_{\text{FDMC}}\times(5.39-0.743\times\cos\{2\times\text{Pi}\times[\text{DAYNO}-16]/365\}+ 1.7\times[\text{EC}-0.3]+0.07\times[\text{TF}-23]), \qquad \text{[eqn 4.2.3]}$$

where FDMC is the fruit dry matter content ($g^{-1} \times 100\%$) at harvest, r_{FDMC} is a cultivar determined constant (r_{FDMC}=1 for cv. 'Calypso'), Pi=3.14159, DAYNO is the day number with 1 = 1 January, EC is the average electrical conductivity in the root environment (0.3-0.9 S m^{-1}) and TF is the average temperature (17-23°C) during the fruit growth period.

This model is based on fruits grown with limiting assimilate supply. Sink-limited conditions increased dry matter content but the increase varied for different temperatures the fruits were grown at (table 4.2.1). Furthermore, whether dry matter content increases with increasing assimilate availability or only at a surplus of assimilates (nonlimiting assimilate supply) is not known. In the present model, therefore, the effect of assimilate availability on dry matter content is ignored.

The model should be regarded as a first attempt to describe FDMC. A more accurate and mechanistic model must be based primarily on the water relations in the plant, and probably contain a specific temperature effect and an effect of assimilate supply.

4.3 Potential fruit weight

4.3.1 results

number of fruits per truss to obtain potential growth

In order to verify whether with only two fruit per truss potential fruit growth is obtained, in the experiments 402/88 and 402/89 plants were grown with either one or two fruits per truss. Per plant the average final fruit fresh weight of the first position within a truss was calculated over trusses 1 to 8. Difference in final fruit weight for fruits grown with one or two fruits per truss was tested with ANOVA.

When growing two fruits per truss fruits reached 100 to 130 g fresh weight (table 4.3.1). Since normally loaded (not pruned) plants in those experiments produced trusses with a final weight of more than 500 gram (data not shown), it seems plausible that with two fruit per truss, the weight per truss was limited by the number of fruits and the supply of assimilates has been sufficient to obtain potential growth for the remaining fruits. However, even at only two fruits per truss there seems to be some competition as small differences in fruit weight were found for one versus two fruits per truss in experiment 402/88 (table 4.3.1). Obviously competition between fruits of one truss increases when assimilate availability decreases. The better light conditions during experiment 402/89 compared to experiment 402/88 (table 4.3.8), therefore, may account for the fact that no difference was observed in experiment 402/89, while in experiment 402/88 one fruit per truss resulted in slightly bigger fruits than when two fruits per truss were grown (table 4.3.1). In experiments examining potential fruit growth, therefore, one fruit per truss was kept on young plants and at low light conditions while at better light conditions two fruits per truss were kept.

Table 4.3.1
Final fresh weight (g) for fruits grown with one or two fruits per truss. Means of fruits of the first fruit position over trusses 1 to 8.

number of fruits	expt 402/88	expt 402/89
1	114	136
2	100	132
difference significant at:	P = 0.047	P = 0.26

effect of fruit position within a truss

In two experiments (307/88 and 402/89) the effect of fruit position within a truss on potential weight was investigated. In experiment 307/88 only one fruit per truss (trusses 2 to 4) was present, but in experiment 402/89 from truss 5 onwards two fruits per truss were retained. Therefore, data from the latter experiment were divided into three sub-sets; fruit from trusses 1 to 4 (one fruit per truss), first ranked fruits from trusses 5 to 7 and second ranked fruits from trusses 5 to 7. ANOVA was applied to averages per plant over those trusses.

Retaining one fruit at different positions within a truss resulted in differences in final fruit weight. Generally, potential fruit weight at the first, sixth or eighth position tended to be lower than that of fruits grown at position 2 or 4 (table 4.3.2). Fruits at the second truss position of plants with only the first and second positioned fruits in experiments 402/88 and 402/89 were 101 and 139 g, respectively, which was not significantly larger than the first positioned fruits (100 and 132 g, respectively, table 4.3.1).

When only two fruits per truss are grown, as in experiment 402/89, ranking order (i.e. first or second ranked) had no effect on fruit weight (comparison of the last two colums of table 4.3.2, statistical analysis not presented).

Table 4.3.2
Potential final fresh weight (g) of fruits at different positions within a truss.

fruit position	expt 307/88	expt 402/89[1)]	expt 402/89[2)]	expt 402/89[3)]
1	110.4	122.1	161.7	-
2	120.0	133.5	165.9	161.4
4	115.2	124.8	163.2	158.4
6	111.9	120.4	138.7	161.1
8	107.2	-	-	129.8
LSD 5%	8.2	15.0	19.1	26.4

1) trusses 1 to 4
2) trusses 5 to 7, first ranked fruits
3) trusses 5 to 7, second ranked fruits

effect of truss position

Influence of truss position on potential fruit weight was investigated in several experiments, mostly in combination with other treatments. Because different trusses were measured on the same plants, observations were not independent. Therefore, instead of ANOVA on the whole data-set, each combination of means of two different trusses was separately tested for differences (Student's *t*-test). For experiments 402/88 and 402/89 truss means of fruits on the first position within a truss were calculated, while for experiment 307/88 fruit weight was averaged over fruit position 1, 2, 4, 6 and 8 (different plants for different positions).

Influence of truss position in the temperature experiment 307/90a was calculated for the four temperature treatments separately. At low temperatures fewer trusses were available than at high temperatures due to differences in development. The first truss was omitted because the temperature treatments started a few days later than flowering of this truss. Only the first fruit of a truss was taken into account. In experiment 307/90a the potential fruit weight of a beefsteak tomato was also investigated at different temperatures and for several trusses, by growing only one fruit per truss. Since fruit-set at trusses 1, 2 and 3 was poor only data of the upper trusses were used, in as far as fruits developed within the period of temperature treatments. Furthermore, at 17°C fruit-set was poor for all trusses, causing small fruits. Therefore, this temperature treatment was excluded from further calculations. For beefsteak tomato the within treatment variation was far larger than for round tomato and consequently differences in fruit weight were not readily significant.

In all experiments, fruit weight increased significantly with truss number (tables 4.3.3, 4.3.4 and 4.3.5). The maximum fruit size was achieved at about truss 7 or even later.

Table 4.3.3
Potential final fresh weight (g) of fruits at different truss positions. Means within an experiment followed by a common letter are not significantly different (Student's *t*-test, P=0.05).

truss number	expt 402/88[1)]	expt 307/88[2)]	expt 402/89[1)]
1	70.9 a	-	86.6 a
2	79.4 a	105.7 a	105.7 b
3	86.9 ab	112.1 b	118.6 c
4	104.6 bc	119.6 c	143.8 d
5	117.2 cd		157.7 e
6	121.3 de		152.3 e
7	132.2 ef		160.1 e
8	135.4 f		

1) first fruit position only
2) mean of fruit position 1, 2, 4, 6 and 8

Table 4.3.4
Potential final fresh weight (g) of round tomato fruits, at different truss number and at four temperatures (expt 307/90a). Means within a column followed by a common letter are not significantly different (Student's *t*-test, P=0.05).

truss number	temperature (°C)			
	17	19	21	23
2	77.8 a	74.7 a	56.3 a	48.8 a
3	78.9 a	71.2 a	62.3 b	47.2 a
4	75.6 a	85.2 b	76.4 c	59.1 b
5	97.4 b	102.4 c	88.5 d	67.2 c
6		116.0 d	105.1 e	75.2 d
7		129.8 e	117.5 f	93.6 e
8			121.0 f	100.7 f
9			133.5 g	106.6 hf
10			143.5 g	115.4 h
11				111.3 gh
12				120.5 h

Table 4.3.5
Potential final fresh weight (g) of beefsteak tomato fruits at different truss number and at three temperatures (expt 307/90a). Means within a column followed by a common letter are not significantly different (Student's *t*-test, P=0.05).

truss number	temperature (°C)		
	19	21	23
4	198 a	215 a	-
5	241 b	203 a	177 a
6	281 bc	235 ab	203 a
7	310 c	285 b	241 b
8		252 ab	241 b
9		261 b	234 b
10			254 b
11			263 b
12			245 b

effect of temperature

The effect of temperature on potential final fruit weight was investigated in experiment 307/90a. Data on fruit fresh weight are presented in tables 4.3.4 and 4.3.5. Fruit dry weights were estimated from fruit fresh weight and fruit dry matter content for each temperature (table 4.2.1). Differences in fruit dry weight were analyzed with ANOVA for each truss (2 to 5) separately (table 4.3.6).

Temperature had a significant effect on potential fruit weight. In experiment 307/90a fresh (tables 4.3.4 and 4.3.5, statistical analysis not presented) and dry weight (table 4.3.6) increased with decreasing temperature, except for fruits grown at 17°C which were about as large as those grown at 19°C.

Table 4.3.6.
Potential final dry weight (g) of round tomato fruits at four temperatures (expt 307/90a) for trusses 2 to 5.

temperature (°C)	truss number			
	2	3	4	5
17	4.77	4.82	4.90	6.28
19	4.27	4.26	5.02	6.18
21	3.19	3.58	4.54	5.21
23	2.72	2.65	3.42	3.94
LSD 5%	1.60	0.44	1.01	0.96

effect of state of the top at fruit initiation

Different temperatures resulted in plant tops of very different size (visual observation only) at the end of the temperature treatments in experiment 307/90a. At that moment, 1 May, plants were pruned to two fruits per truss for all trusses. Remaining fruits from the flowering truss on 1 May plus the next two trusses were weighed at harvest. Possible effect of the top size during fruit initiation on final potential fruit fresh weight was analyzed on averages per temperature pre-treatment (Student's *t*-test).

Surprisingly little variation was observed between fruits initiated at thin or heavy plant tops grown at high and low temperature, respectively. Only fruits initiated at the tops grown before at 23°C grew slightly smaller than fruits initiated at tops grown before at 17, 19, or 21°C (table 4.3.7).

Table 4.3.7
Potential final fresh weight (g) of fruits grown at similar temperature but initiated at tops grown previously at different temperatures (expt 307/90a). Means followed by a common letter are not significantly different (Student's *t*-test, P=0.05).

pre-treatment temperature (°C)	potential weight (g)
17	139.6 a
19	142.0 a
21	139.0 a
23	123.1 b

4.3.2 discussion

All the presented experiments investigating the effect of truss number on potential fruit weight were conducted in spring, implying a parallel between increasing truss number and increasing light. Consequently from those results it is hard to separate these factors and to prove an independent effect of truss position. In phytotron experiments and also in a greenhouse experiment conducted in autumn, Heuvelink (pers.comm.) observed between-truss effects that were of the same size as in the present study. Thus it seems justified to ascribe the observed effects principally to truss position.

Potential fruit weight (PFW) at maturity is determined by sink size developed at fruit initiation and sink activity during fruit growth. The main factor of sink size is the fruit's cell number (Ho, 1992). The final cell number is reached within two weeks after anthesis (Ashira *et al.*, 1968; Davies and Cocking, 1965; Geelen *et al.*, 1987) and depends on the initial cell number in the ovary before anthesis and the rate of cell division thereafter (Coombe, 1976; Bohner, 1986). Mature leaf size of poplar and sunflower increases with plant development (Rawson and Hindmarsh, 1982) due to apex enlargement accompanied by a larger number of cells initiating a primordium (Pieters, 1974; Pieters, 1985). Rate of leaf elongation in tall fescue (Volenec and Nelson, 1984) and leaf size of rice (Yamazaki, 1964) are positively correlated with the size of the meristem or shoot apex, respectively. Ontogenetic increase of leaf size is also observed in broad bean (Dennett *et al.*, 1979). Similarly, in tomato the increase of final potential fruit weight with higher truss position, may be explained by enlargement of the apex and subsequent increase of the fruit's cell number during ontogeny. Cell counts, however, are needed for a decisive answer.

In contrast with the supposed effect of apex size, in experiment 307/90a the state (size) of the top had surprisingly little effect on PFW (table 4.3.7). Probably, in this experiment, even at the thinner tops grown at high temperature the maximum potential fruit weight is nearly achieved due to progressed ontogeny. A similar experiment with younger plants, therefore, may show differences.

Differences in fruit weight as affected by fruit position within a truss are well known for unthinned trusses (Beadle, 1937; Hobson and Adams, 1988; Bangerth, 1989), and these differences increase with limited assimilate supply (Ho, 1980; Ho and Sjut, 1983; Bohner and Bangerth, 1988). They originate, at least in part, from differences in cell number before anthesis, as it was found by Bohner and Bangerth (1988) that at anthesis proximal ovaries have more cells than distal ovaries and that cell division activity in both positions was similar in the first 10 days of fruit development. However, when pollination within a truss is synchronized, differences in fruit weight become significantly smaller (Bohner and Bangerth, 1988; Bangerth, 1989) and therefore the relative moment of pollination appears to be the main factor causing fruit size differences within a truss. The relatively small effects of fruit position in our experiments will be due to limited competition as only one or two fruits per truss were left. Ho (1980) reported substantially smaller differences in fruit weight within a truss after fruit pruning, compared to intact trusses. In addition to pollination sequence, proximal fruits may benefit from being closer to the source. Hence, pollination sequence

and proximity to the source are significant factors determining the actual sink strength and subsequently assimilate partitioning within a truss. Since these factors are not determined by intrinsic characteristics of fruits (i.e. potential sink strength) and they do not express at nonlimiting assimilate supply, potential fruit growth fails to assess the contribution of those factors in competition for assimilates. Assessment of their influence should be done in source-limited plants, but would not be easy due to increasing significance of the actual sink strength with increasing competition for assimilates. In the present experiments for round tomato the second to fourth positioned fruits became the largest, which agrees with results of Stenvers and Staden (1976).

High temperature decreased PFW (table 4.3.6). The fruit growth period is shortened by temperature (Chapter 3), but whether this affects the cell number by restricted duration of cell division or decreases final cell size cannot be concluded from the present results nor from the literature. The response of potential fruit growth rate to temperature is described and discussed in section 4.4.

Weight of individual fruits appears highly correlated with number of seeds (Imanishi and Hiura, 1975). Poor pollination reduces seed number and actual fruit weight (Verkerk, 1957; Varga and Bruinsma, 1976). The relationship between seed number and the size of fruits from intact plants varies with truss position (Bakker, 1991) and environmental conditions (Rylski, 1979). Decrease of competition for assimilates by fruit pruning increases fruit size, but has no effect on seed number (van Ravestijn and Molhoek, 1978). Moreover, Stenvers and Staden (1976) observed small fruits with many seeds at high fruit-leaf ratio (the number of fruits relative to the number of leaves), while at low fruit-leaf ratio fruits grew larger but contained less seeds. At the same fruit-leaf ratio they found a positive correlation between fruit size and seed number. So, in competition for assimilates seed number is apparently an important factor determining the fruit's relative sink strength, while average fruit weight depends mainly on the availability of assimilates. Parallel to the increase in potential fruit weight at increasing truss number the number of seeds per fruit also increases (Bakker, 1991). Most likely, this is no causal relationship but seed number as well as potential fruit weight increase with ontogeny. Assuming that pollination has been adequate, possible influence of seed number on potential fruit weight in the present experiments is implied in the effects of truss position and temperature.

4.3.3 model

round tomato

A model for potential fruit weight should at least include the factors: fruit position within a truss, truss number and temperature. Moreover, as it is likely that potential fruit weight is genetically determined, the model should also contain a factor that accounts for differences between cultivars. Experiments 402/88 and 307/88 were similar in the mentioned factors but the observed potential fruit weight differed considerably (table 4.3.3). The most probable cause of this difference seems to be the moment of starting the crop, *viz.* January and April, respectively. Thus, including a kind of 'season effect' seems inevitable.

Only in experiment 307/90 temperature was kept constant at desired 24-h temperatures (17, 19, 21, and 23°C, respectively). For the other experiments temperature varied slightly with outside conditions making those experiments strictly speaking unsuitable for quantifying the temperature effect on PFW. Therefore, the effects of temperature and truss number for round tomato will be assessed from experiment 307/90a first while, fixing the temperature effect, the variables season and cultivar are quantified including data from the other experiments. The effect of fruit position within a truss will be modelled separately and added to the model based on fruit from the first fruit position only. Potential fruit weight of beefsteak tomato (expt 307/90a) is modelled apart from round tomato.

Regressions are carried out on fruit dry weight. For round tomato of experiment 307/90a potential fruit dry weights were calculated from fresh weights and fruit dry matter content given in table 4.2.1. Dry weights from experiments 402/88, 307/88, 402/89 and 307/92 were obtained from fresh weights and 5.7% (estimated) dry matter content. In experiment 307/92 fruit dry weight of potentially grown fruits of trusses 8 and 9 was directly measured.

Data from experiment 307/90a suggest that potential fruit weight (PFW) is highest at 17 to 19°C (table 4.3.6). Furthermore, at increasing truss number the gain in fruit weight decreases (tables 4.3.3, 4.3.4 and 4.3.5). For describing PFW, a quadratic function of temperature (T) combined with an asymptotic relationship of truss number (TRUSS) seems reasonable. A negative exponential of truss

number multiplicative to a quadratic temperature effect:

$$PFW = (a + b\times T + c\times T^2) \times [1 - d\times\exp(-k\times TRUSS)], \qquad \text{[eqn 4.3.1]}$$

fitted as well to the data (R^2 of 0.938) as the additive alternative (R^2=0.931):

$$PFW = a + b\times T + c\times T^2 - d\times\exp(-k\times TRUSS). \qquad \text{[eqn 4.3.2]}$$

For the multiplicative form the absolute effects of temperature and truss number depend on the scale of PFW, while the relative effects are constant. This model suits better to the physiological concept of relative effects (section 4.1) and, when extrapolated it will probably behave better than the additive combination of T and TRUSS. The multiplicative form, therefore, is chosen for further modelling. Several other asymptotic functions of TRUSS (multiplicatively combined with T), fitted as well to the data as the negative exponential. All tested asymptotic functions, however, estimated improbably high asymptotes, e.g. 22.8 g at 21°C for the negative exponential, compared to circa 8.2 g dry weight (140 g fw) observed for truss 14 in the same experiment (table 4.3.7). This overestimation is due to the fact that for the available truss numbers the asymptote was not approximated yet (table 4.3.4), which obviously causes wrong predictions when the model is extrapolated to higher truss numbers. In order to get the asymptote down, the model was forced through 8.2 g for T=21°C and TRUSS=14. Fitting the model:

$$PFW=8.2\times[1+b\times(T-21)+c\times(T-21)^2]\times\{1-d\times(\exp[-k\times(TRUSS-14)]-1)\}, \qquad \text{[eqn 4.3.3]}$$

to the data estimated an asymptote for 21°C at 9.2 g. This model accounts for 90.7% of the variance, which is almost as much as the model with the freely estimated asymptote (table 4.3.9). Measured data and fitted model are plotted in figure 4.3.1. Extrapolating the estimated model for PFW to higher temperatures results in a zero fruit weight at about 29°C (fig 4.3.2). Since it is unlikely that no fruit growth at all is possible at such high temperatures, extrapolating the model by more than a few degrees beyond the range tested, *viz.* 17 to 23°C 24-h mean temperature, probably caused significant error.

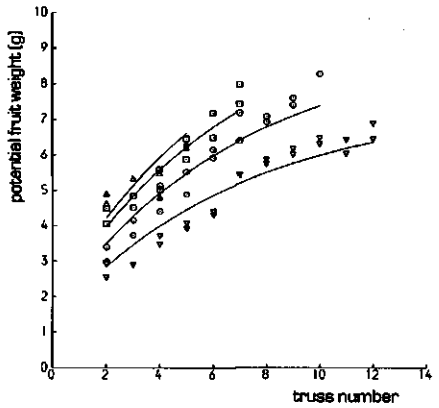

Figure 4.3.1
Measured data and fitted model for potential fruit weight of round tomato (cv. 'Calypso') at four temperatures as affected by truss position (expt 307/90a). Δ, 17°C; ○, 19°C; □, 21°C; ▽, 23°C.

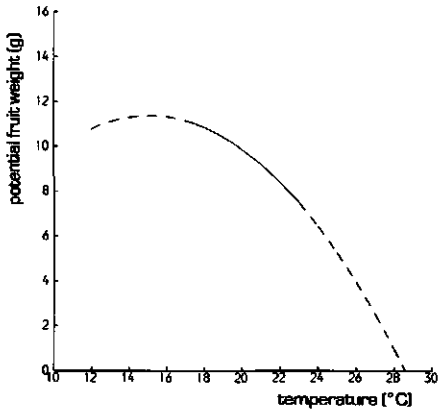

Figure 4.3.2
Predicted effect of temperature on maximum potential fruit weight for the first fruit position within a truss of cv. 'Calypso' (broken line represents the model beyond the tested temperature range).

Solar irradiance is regarded to be the main determinant of season, and therefore used as representative variable for the season effect. To smooth daily variation the daily radiation integral (RAD_{PFW}, MJ m^{-2} d^{-1}) received by the crop is averaged over 3 weeks after flowering of the first truss. A summary of relevant characteristics of the experiments investigating the effects of cultivar and season is presented in table 4.3.8.

Table 4.3.8
Cultivars used, temperature (T) and solar radiation integral received by the crop, averaged over the first 3 weeks after first flowering (RAD_{PFW}) for the experiments used to model potential fruit weight.

experiment	cultivar	T (°C)	RAD_{PFW} (MJ m^{-2} d^{-1})
402/88	'Counter'	19	1.76
307/88	'Counter'	20	9.59
402/89	'Blizzard'	19	3.06
307/90a	'Calypso'	17,19,21,23	1.38
307/92	'Astrid'	21	1.75

While including cultivar and season effect the temperature effect and asymptote as established in experiment 307/90a were fixed. This implies that the (relative) temperature effect is supposed to be independent of cultivar and season. Since the difference in potential fruit weight between different cultivars is largely determined by differences in fruit cell number (Ho, 1992) the effect of cultivar is regarded as a multiplicative factor to the model describing the effect of other variables on PFW. The most successful modelling was gained by combining the effects of TRUSS and RAD_{PFW} in the same negative exponential:

$$PFW = r_i \times 9.2 \times [1 - 0.0803 \times (T-21) - 0.0068 \times (T-21)^2] \times \{1 - d \times \exp(-k \times TRUSS - l \times RAD_{PFW})\}, \qquad \text{[eqn 4.3.4]}$$

where r_i, d, k and l are parameters, T is the temperature (17-23°C), TRUSS is the truss number and RAD_{PFW} is the average daily solar irradiance over 3 weeks after first flowering (1.8-9.6 MJ m^{-2} d^{-1}).

According to this model TRUSS and RAD_{PFW} are substitutional, which indicates that both factors may affect the same physiological process. For sunflower Pieters (1985) demonstrated that high irradiance stimulates the expansion of the apex and produce bigger primordia and consequently larger leaves. Increase in cucumber leaf size with increasing radiation could be fully ascribed to greater cell number (Horie *et al.*, 1979). In tomato Hussey (1963) observed that high light conditions promote enlargement of the shoot apex. Therefore it seems plausible that the interaction between ontogeny (truss position) and season can be ascribed to increased cell number, due to faster ontogenetic enlargement of the apex at better light conditions. Effects of ontogeny and season as predicted by the model are visualized in figure 4.3.3. Possibly PFW decreases when the plant ages and loses vigour, but this should be experimentally verified.

Measured values and fitted model for experiments 402/88, 307/88, 402/89 and 307/92 are plotted in figure 4.3.4. The model fits well for all experiments. Table 4.3.9 summarizes the results of the regressions. The fitted parameter r for 'Blizzard' is 1.3, which indicates that potential weight of 'Blizzard' is 30% higher than for 'Calypso'. 'Counter' appears to have a similar potential weight as 'Calypso', *viz.* the estimated r does not differ significantly from 1, while the potential size of 'Astrid' may be slightly larger than that of 'Calypso'. It should be noted that the accuracy of those possible differences between cultivars is limited as the cultivar parameters are estimated from different experiments. Moreover, the season effect is actually based on the difference between only two experiments (402/88 and 307/88) and is, therefore, not very reliable either.

Table 4.3.9
Fitted parameters (standard error between brackets) for models predicting potential fruit weight (PFW; g) from cultivar, temperature, (T; °C), truss number (TRUSS) and average daily solar irradiance received by the crop over three weeks after first flowering (RAD_{PFW}; MJ m^{-2} d^{-1}).

model	1		2		3	
experiment	307/90a		307/90a		307/90a, 402/88, 307/88, 402/89, 307/92	
n	59		59		79	
parameter						
a	22.8	(12.3)	8.2	(fixed)	9.2	(fixed)
b	-0.0956	(0.0052)	-0.0803	(0.0054)	-0.0803	(fixed)
c	-0.0110	(0.0024)	-0.0068	(0.0029)	-0.0068	(fixed)
d	0.906	(0.042)	0.117	(0.028)	0.878	(0.027)
k	0.034	(0.0024)	0.150	(0.017)	0.143	(0.006)
l					0.0465	(0.0097)
r_0					1	(fixed)
r_1					1.03	(0.028)
r_2					1.30	(0.033)
r_3					1.07	(0.044)
R^2	93.8		90.7		92.4	

model 1; $PFW = a\times[1+b\times(T-21)+c\times(T-21)^2]\times[1-d\times\exp(-k\times TRUSS)]$
model 2; $PFW = a\times[1+b\times(T-21)+c\times(T-21)^2]\times\{1-d\times(\exp[-k\times(TRUSS-14)]-1)\}$
model 3; $PFW = r_i\times a\times[1+b\times(T-21)+c\times(T-21)^2]\times[1-d\times\exp(-k\times TRUSS-l\times RAD_{PFW})]$

r_0: 'Calypso', r_1: 'Counter', r_2: 'Blizzard', r_3: 'Astrid'

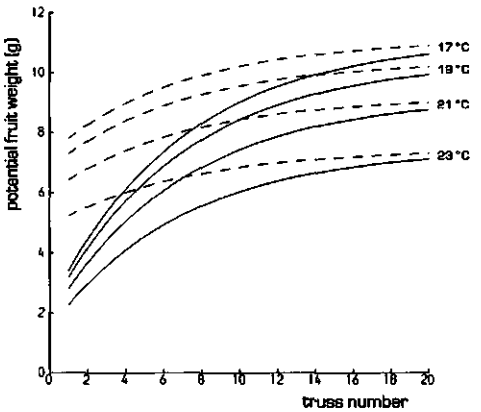

Figure 4.3.3
Predicted effect of ontogeny (truss number), season and temperature on potential fruit weight for the first fruit position within a truss of cv. 'Calypso'.
—— RAD_{PFW} = 2 MJ m^{-2} d^{-1},
------ RAD_{PFW} = 20 MJ m^{-2} d^{-1},
representing winter and summer season in North-West Europe respectively.

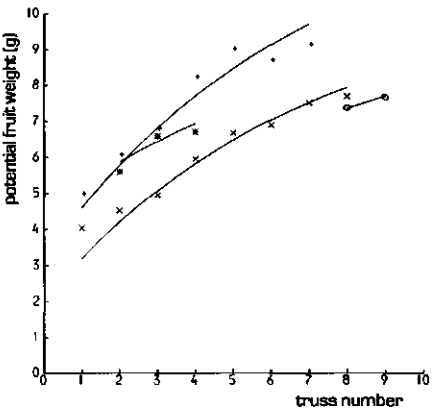

Figure 4.3.4
Measured data and fitted model for potential fruit weight in different experiments. ×, 402/88 (cv. 'Counter', winter); *, 307/88 (cv. 'Counter', spring); +, 402/89 (cv. 'Blizzard', early spring); ○, 307/92 (cv. 'Astrid', early spring).

The effect of fruit position within a truss was incorporated as a multiplicative factor (FP) joined to equation 4.3.4. For quantifying this factor data presented in table 4.3.2 were divided by the measured potential fruit weight for the first position within a truss. Assuming no effect of rank order, fruit weights of the secondly ranked fruits of experiment 402/89 were divided by the fruit weight of the first positioned fruits (and consequently first ranked) of the same experiment. Then, a quadratic function of fruit position (FPOS) was fitted through the obtained ratios. This function was forced through FP=1 for FPOS=1 in order not to alter the model for fruits of the first position. This resulted in:

$$FP=0.966+0.040\times FPOS-0.006\times FPOS^2 \quad (n=16,\ R^2=0.35,\ P<0.05) \text{ [eqn 4.3.5]}$$

Measured data and fitted curve are presented in figure 4.3.5.

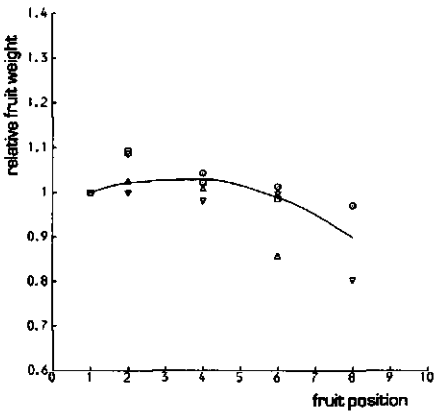

Figure 4.3.5
Effect of fruit position within a truss on potential fruit weight relative to the first fruit position. ○, experiment 307/88; □, experiment 402/89 trusses 1 to 4; △, experiment 402/89 trusses 5 to 7 first ranked fruits; ▽, experiment 402/89 trusses 5 to 7 second ranked fruits.

The final model for potential fruit dry weight for round tomato including the effects of cultivar, temperature, truss position, season, and fruit position within a truss then becomes:

$$\begin{aligned} PFW = r_i \times (0.966 + 0.040 \times FPOS - 0.006 \times FPOS^2) \times \\ 9.2 \times [1 - 0.0803 \times (T - 21) - 0.0068 \times (T - 21)^2] \times \\ [1 - 0.878 \times \exp(-0.143 \times TRUSS - 0.0465 \times RAD_{PFW})], \end{aligned} \qquad \text{[eqn 4.3.6]}$$

where r_i is a parameter determined by the cultivar, FPOS is the fruit position within a truss, T is the temperature (17-23 °C), TRUSS is the truss number and RAD_{PFW} is the average daily radiation integral received by the crop over three weeks after first flowering (1.8-9.6 MJ m^{-2} d^{-1}).

It is recognized that cultivars may differ in the effect of fruit position but insufficient data were available to validate, let alone to quantify this. Therefore some care should be exercised when the given model is applied to cultivars that were not tested.

Since sink strength is effected by the quality of fruit-set (Rylski, 1979) which is assumed optimal in the model, at unfavourable conditions for fruit-set the model may overestimate potential fruit weight. CO_2-concentration and air humidity are not included in the model but it is assumed that they have no significant effect on potential fruit weight.

beefsteak tomato

For potentially grown beefsteak tomato fruit (expt 307/90a) dry matter content was not determined. Therefore fruit dry weights of this tomato type were obtained with fruit dry matter content of round tomato (table 4.2.1). The variation in fruit weight was relatively large compared to the treatment (temperature and truss position) effects. Moreover, the number of data available was limited due to excluding the 17°C treatment and the fruits from the lower trusses. Hence, the procedure of modelling as followed with round tomato fruits of the same experiment failed. More successful was treating the data like another cultivar of round tomato, i.e. assuming the effects of temperature, truss position and season on potential weight of beefsteak tomato to be the same as for round tomato. So, the model for round tomato was adapted for beefsteak tomato by estimating only parameter r that expresses the relative size of the cultivar to 'Calypso'. This model accounted for 60% of the variation. The remaining variance was largely due to experimental error as indicated by large differences between the replicates (fig 4.3.6). Parameter r was estimated at 2.26 (SE=0.04, n=37), implying the potential weight of 'Dombito' to be about 2.3 times that of 'Calypso'.

The effect of fruit position on PFW was not investigated for beefsteak tomato, but as beefsteak fruits are larger and bear less fruits per truss decline of sink strength with fruit position is expected to be sharper than for round tomato.

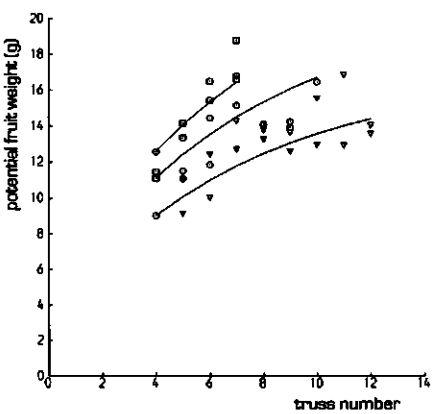

Figure 4.3.6
Measured data and fitted model for potential fruit weight (PFW) of beefsteak tomato (cv. 'Dombito') at three temperatures as affected by truss number. ○ ,19°C; □, 21°C; ▽, 23°C.

4.4 Potential fruit growth rate

4.4.1 methods

estimating fruit dry weight

In experiment 307/90a, the diameters of round and beefsteak tomato fruits growing at 17, 19, 21 and 23°C were determined twice a week. Fruits of the first truss (flowering before the temperature treatments started) and fruits harvested after 1 May (end of the temperature treatments) were excluded from the analysis. Fruit fresh weights (FFW, g) of round tomato were estimated from fruit diameters (D, mm) by:

$$FFW = 0.001055 \times D^{2.801}, \qquad \text{[eqn 4.4.1]}$$

This relationship was established from fruits of all stages grown in experiment 402/88 by linear regression of ln(FFW) against ln(D) (r^2=0.996, n=365).

For beefsteak tomato a similarly obtained relationship was used:

$$FFW = 0.001158 \times D^{2.754}, \qquad \text{(expt 307/88, cv. 'Dombito', } r^2\text{=0.990, n=621)} \qquad \text{[eqn 4.4.2]}$$

Because potential growth was defined on the basis of dry weight, fruit fresh weight was multiplied by the estimated fruit dry matter content (FDMC). Decrease of FDMC with fruit development was described by a quadratic relationship, with the fruit harvest ripe as its minimum (section 4.2). The dry matter content of fruits at harvest is determined by temperature (section 4.2). The influence of both factors, fruit development stage (FDS) and temperature on FDMC, are given by:

$$FDMC_t = FDMC0 + (FDMC1 - FDMC0) \times 2 \times FDS_t + (FDMC0 - FDMC1) \times FDS_t^2, \qquad \text{[eqn 4.2.1]}$$

where $FDMC_t$ is the fruit dry matter content (g^{-1} × 100%) at t days after anthesis, FDMC0 is the fruit dry matter content at FDS=0 with the value of 10.2 (section 4.2), FDMC1 is the fruit dry matter content at harvest (FDS=1) with a value of 6.1, 5.7, 5.6, and 5.6% at 17, 19, 21 and 23°C, respectively, (table 4.2.1) and FDS_t is the fruit development stage ($0 \leq FDS_t \leq 1$).

FDS was assumed to be proportionally related with time between anthesis (FDS=0) and harvest ripe (FDS=1). Because of the lack of data on fruit dry matter content of potentially grown beefsteak tomato, equation 4.2.1 obtained with round tomato was used also for beefsteak tomato.

fitting growth curves

For each fruit a sigmoidal growth curve as a function of time (t) after anthesis was fitted to the calculated fruit dry weights (FDW). Fitting the Richards function with GENSTAT (Payne and Lane, 1987),

$$FDW_t = C/\{1 + r\times\exp[-B\times(t\text{-}M)]\}^{1/r}, \qquad \text{[eqn 4.4.3]}$$

with C, r, B and M being parameters, failed as for the majority of the fruits r could not be estimated. The Gompertz curve, a special case of the Richards function, fitted more successfully. The formula for the Gompertz growth function as used (GENSTAT) is:

$$FDW_t = C\times\exp\{-\exp[-B\times(t-M)]\}, \qquad \text{[eqn 4.4.4]}$$

where FDW is fruit dry weight (g), t is time after anthesis (days) and C, B and M are parameters.

This sigmoidal curve is asymmetrical around the inflexion point: t = M, and it has an upper asymptote C (fig 4.4.1), while parameter B represents the steepness of the curve.

Next, in order to derive one description of the growth curve that accounts for all experimental variables, an attempt was made to describe the fitted parameters C, M and B each as a function of the mean temperature during the fruit growth period and the fruit characteristics: fruit weight at harvest, truss position, fruit position within a truss (first or second) and fruit growth period. In these regressions, the reciprocal of the standard error of the fitted Gompertz curves for the individual fruits was used as a weighting factor. Data of round tomato and beefsteak tomato were treated separately.

Finally, the daily potential fruit growth rate (PFGR, g d^{-1}) at constant temperature during fruit development is given by the first derivative of the Gompertz equation:

$$PFGR_t = C \times \exp\{-\exp[-B \times (t-M)]\} \times B \times \exp[-B \times (t-M)], \qquad \text{[eqn 4.4.5]}$$

where t is the time after anthesis and C, M and B are parameters, each described as a function of temperature and fruit characteristics.

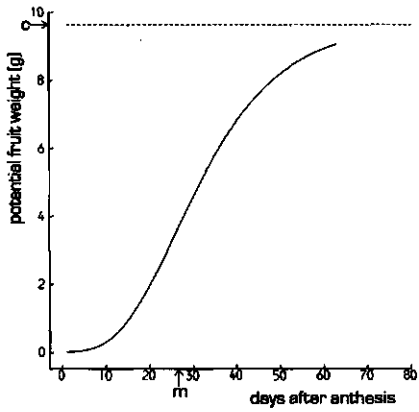

Figure 4.4.1
Growth of a tomato fruit represented by a Gompertz growth function. C = upper asymptote, M = inflexion point (moment of maximum growth rate).

description as function of fruit development stage

The description of potential growth rate would be more generally applicable if it were to be expressed as a function of the fruit's development stage (FDS) instead of time. Such a relationship can be obtained by transformation of the time after anthesis for each fruit into the fruit development stage according to $FDR_{f(T)}$ (eqn 3.4.7) or $FDR_{f(T \times FDS)}$ (eqn 3.4.8) before fitting the growth curves. For two reasons it was decided not to follow this approach. Firstly, the original time data had to be replaced by predicted FDS before curve fitting, which makes the fitted curve specific for the description of FDR applied. Secondly, in order to account for possible differences between observed and predicted fruit growth period, the predicted FDS should be adjusted such that at the date of harvest predicted FDS=1. When applying $FDR_{f(T \times FDS)}$ such a 'normalisation' is rather difficult due to the 'temperature × FDS' interaction. Instead, the description of fruit growth rate as a function of FDS is deduced from fitted time-based curves as described below.

According to equation 3.4.7 (section 3.4) at constant temperature FDS is proportional to time. Then for the fruit development stage at t days after anthesis (FDS_t) holds:

$$FDS_t = t/FGP \qquad \text{[eqn 4.4.6]}$$

The Gompertz equation (4.4.4) can be written as:

$$FDW_t = C\times\exp\{-\exp[-B\times FGP\times(t/FGP - M/FGP)]\}, \qquad \text{[eqn 4.4.7]}$$

and according to equation 4.4.6 as:

$$FDW_t = C\times\exp\{-\exp[-B'\times(FDS_t - M')]\}, \qquad \text{[eqn 4.4.8]}$$

where $B' = B\times FGP$ and $M' = M/FGP$ and FDW_t is the fruit dry weight at t days after anthesis and FGP is the fruit growth period (days).

The first derivative of equation 4.4.8, dFDW/dFDS, represents the fruit growth per unit FDS (PFGR').

$$PFGR'_t = C\times\exp\{-\exp[-B'\times(FDS_t - M')]\} \times B'\times\exp[-B'\times(FDS_t - M')],$$

$$\text{with } FDS_t = FDS_{t-1} + FDR_{f(T),t} \quad (FDS_0 = 0,\ 0 \le FDS_t \le 1) \qquad \text{[eqn 4.4.9]}$$

Daily fruit growth is obtained after multiplication with the fruit development rate (FDR):

$$PFGR_t = PFGR'_t \times FDR_{f(T),t} \qquad \text{[eqn 4.4.10]}$$

In Chapter 3 it was demonstrated that under non-constant temperature (as is normally the case in glasshouses), a better prediction of the fruit growth period is obtained with a model that accounts for an interaction between temperature and development stage ($FDR_{f(T\times FDS)}$, eqn 3.4.8). $FDR_{f(T\times FDS)}$ may not be simply used in equations 4.4.9 and 4.4.10 as these are derived for constant FDR (i.e. FDS is proportional to the time from anthesis until harvest). The consequences of applying different descriptions of FDR on predicted potential fruit growth rate were analyzed for constant 17 and constant 23°C.

4.4.2 results

description as function of time, round tomato

For round tomato data of 366 fruits were available. The Gompertz growth curve, fitted for each fruit to the dry weights derived from the diameter measurements, accounted generally for more than 99 percent of the variance. The correlations between the fitted parameters C, M and B from the individual Gompertz curves and fruit weight at harvest, truss number, fruit position, fruit growth period and temperature are given in table 4.4.1.

Table 4.4.1
Correlation matrix of the fitted parameters C, M and B of the Gompertz growth curve and fruit dry weight at harvest (PFW), truss number (TRUSS), fruit position within a truss (FPOS), fruit growth period (FGP) and temperature (T) for potentially grown fruits at different temperatures (n=366) (expt 307/90a). $P(-0.15<\underline{r}<0.15\ \rho=0) = 0.99$

	C	M	B	PFW	TRUSS	FPOS	FGP
M	0.011	1.000					
B	-0.282	-0.793	1.000				
PFW	0.978	-0.088	-0.155	1.000			
TRUSS	0.580	-0.605	0.348	0.625	1.000		
FPOS	0.178	-0.155	0.112	0.195	0.147	1.000	
FGP	0.129	0.916	-0.721	0.086	-0.493	-0.122	1.000
T	-0.225	-0.869	0.710	-0.186	0.429	0.044	-0.956

As was expected (section 4.1), parameter C (asymptotic maximum) is highly correlated with fruit weight at harvest (PFW). PFW increases with truss number and temperature (section 4.3). The poor correlation between C (or PFW) and temperature in the present data-set (table 4.4.1) results from the fact that at high temperature more trusses were harvested before the end of the experiment. Hence the effect of larger fruits at low temperature (section 4.3) is masked by the larger fruits from the higher trusses at high temperature. Restricting the data to the trusses harvested at low temperature (trusses 2 to 5) increased the correlation between C and temperature to -0.66 (n=201). Fitting a proportional relationship of C against PFW resulted in:

$$C = 1.082\ (SE=0.003) \times PFW, \quad (r^2=0.968, n=366) \qquad \text{[eqn 4.4.11]}$$

By including either an intercept, truss number, temperature or any combination of these this did not increase the percentage of variance accounted for. Hence, the (relative) difference between C and PFW seems independent of TRUSS or T.

The inflexion point M is highly correlated with the length of the fruit growth period (FGP) and, as FGP depends on temperature (section 3.4), also with temperature (table 4.4.1). It is most convenient not to relate M directly to temperature but to FGP in order to make the model easier to adapt to other factors affecting FGP (e.g. genotype). A linear relationship, $M = a + b \times FGP$, fitted well (table 4.4.2). In general the residuals of this relationship were relatively large at low truss position (fig 4.4.2). The decreasing difference with higher truss position was accounted for by including a negative exponential relationship of TRUSS:

$$M = (a + b \times FGP) \times [1 + c \times \exp(-k \times TRUSS]), \qquad \text{[eqn 4.4.12]}$$

where FGP is the fruit growth period (days), TRUSS is the truss number and a, b, c and k are parameters. Fitting this model significantly increased the percentage of variance accounted for (table 4.4.2). Residuals of this model were not correlated with any of the other variables. Although statistically significant, the model without intercept a is easier to adapt to conditions or cultivars that differ considerably from FGP in this experiment. The same model but without intercept fitted nearly as well as the one with intercept (table 4.4.2).

Table 4.4.2
Parameters (standard errors between brackets) for models predicting the parameter M of the Gompertz growth curve for potentially grown fruits (n=366) from the fruit growth period (FGP; days) and truss number (TRUSS).

	model					
model parameter	1		2		3	
a	-4.93	(0.70)	-1.78	(0.61)	-	
b	0.548	(0.013)	0.442	(0.020)	0.396	(0.016)
c	-		0.408	(0.036)	0.446	(0.036)
k	-		0.270	(0.071)	0.219	(0.058)
R^2	0.841		0.891		0.888	
$SE_{y.x}$	3.29		2.72		2.75	

model 1; $M = a + b \times FGP$
model 2; $M = (a + b \times FGP) \times [1 + c \times \exp(-k \times TRUSS)]$
model 3; $M = (b \times FGP) \times [1 + c \times \exp(-k \times TRUSS)]$

Parameter B of the Gompertz growth curve was correlated most with parameter M, and because of interrelation, also to the fruit growth period (FGP) and temperature (T) (table 4.4.1). Plotting B against M suggested a hyperbolic relationship (fig 4.4.3). From various hyperbolic functions the model:

$$1/B = a + b \times M, \qquad \text{[eqn 4.4.13]}$$

where a and b are parameters, fitted best. The estimated coefficients are: a=2.44 and b=0.403 (n=366, r^2=0.74, $SE_{y.x}$=1.97). Concerning the residuals a cluster of deviant observations was present for small fruit grown at the lower trusses. However, extending the model with truss number did not improve the predictive value. Excluding fruits smaller than 4 g dry weight gave a slightly better fit (r^2=0.79, n=308) but did not really change the coefficients. The residuals of the first mentioned model were not correlated with temperature or any other variable.

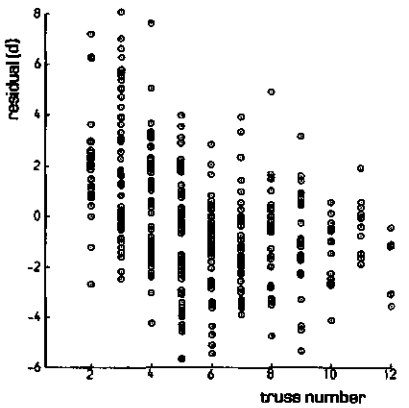

Figure 4.4.2
Residuals of the linear relationship between parameter M of the Gompertz curve and the fruit growth period (FGP), plotted against truss number.

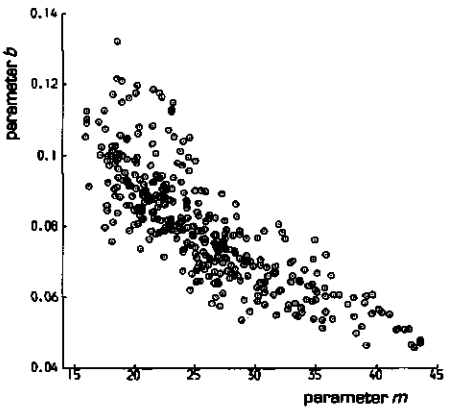

Figure 4.4.3
Parameter B plotted against parameter M, both are parameters of the Gompertz growth curve.

In the full data-set temperature and truss number were significantly correlated (table 4.4.1), because fruits from the higher truss number were only available at high temperatures. As mentioned before, this correlation can be avoided by restricting the data-set to truss numbers 2 to 5. However, repeating the fittings with this restriction gave no noticeably different relationships. Therefore the

definitive relationships, based on the full data-set (n=366), predicting the parameters of the Gompertz growth function of potentially grown fruits as function of time (t, days after anthesis), are:

$$C = 1.082 \times PFW, \quad \text{[eqn 4.4.11]}$$

$$M = (-1.78+0.442 \times FGP) \times [1+0.408 \times \exp(-0.270 \times TRUSS)], \quad \text{[eqn 4.4.14]}$$

or without intercept

$$M = 0.396 \times FGP \times [1+0.446 \times \exp(-0.219 \times TRUSS)], \quad \text{[eqn 4.4.15]}$$

$$B = 1/(2.44+0.403 \times M), \quad \text{[eqn 4.4.16]}$$

where C, M and B are parameters of the Gompertz curve:

$$FDW_t = C \times \exp\{-\exp[-B \times (t-M)]\}, \quad \text{[eqn 4.4.4]}$$

and PFW is the potential fruit dry weight (g) at harvest, FGP is the fruit growth period (days), TRUSS is the truss number and FDW_t is the fruit dry weight (g) at t days after anthesis.

In order to check the compound model, daily fruit growth rate of each fruit (n=366) was simulated (using the equation for M without intercept, eqn 4.4.15). In the simulation the parameters C, M and B varied slightly during fruit development since the determinants PFW (section 4.3) and FGP (1/FDS) (section 3.4) vary with temperature. In addition to daily 24-h mean temperature, required input variables were: truss number (TRUSS), fruit position (FPOS) and the solar irradiance integral averaged over three weeks after anthesis of the first truss (RAD_{PFW}).

For each fruit the cumulative simulated growth was compared with the fruit dry weights estimated from measured fruit diameter. The mean difference per fruit between simulated and fruit weight estimated from measured diameters was not correlated with either average temperature, truss number or fruit position, neither was the corresponding variance of the differences. Thus the model did not under- or overpredict consistently for any of the experimental variables and the model also suited the course of growth in time equally well for all experimental variables.

The average difference over all fruits was 0 with a standard deviation of 0.40 g. Simulated and observed (estimated from fresh weight) final fruit dry weights at harvest were compared as well. Differences per fruit were not correlated with any of the experimental variables. On average the model overestimated final weight by 0.035 g, which is less than 1% of the average

weight (5.4 g). The standard deviation of the difference between simulated and observed final weight was 0.75 g. It could not be determined from the data which part of the differences between predicted and observed fruit weight was due to model errors and which part was caused by experimental error. From this comparison it was concluded that the compound model predicted the growth rate during fruit development and the final fruit weight accurately, irrespective of the experimental variables; temperature, truss position and fruit position.

description as function of time, beefsteak tomato

For beefsteak tomato considerably less data were available as only one fruit per truss was retained and all fruits grown at 17°C and fruits of trusses 2 and 3 had to be excluded because of poor fruit set. Correlations between the fitted parameters C, M and B of the Gompertz growth curve and fruit dry weight at harvest, truss number, fruit growth period and temperature (table 4.4.3) were very similar to those for round tomato (table 4.4.1). Fruit position within a truss was no experimental variable as only the first fruit of each truss was retained.

Table 4.4.3
Correlation matrix of the parameters C, M and B of the Gompertz growth curve and fruit dry weight at harvest (PFW), truss number (TRUSS), fruit growth period (FGP) and temperature (T) for potentially grown beefsteak tomato fruits at different temperatures (n=99) (expt 307/90a). $P(-0.26<\underline{r}<0.26\ \rho=0) = 0.99$

	C	M	B	PFW	TRUSS	FGP
M	-0.035	1.000				
B	0.069	-0.806	1.000			
PFW	0.992	-0.089	0.135	1.000		
TRUSS	0.276	-0.548	0.575	0.296	1.000	
FGP	0.013	0.922	-0.806	-0.023	-0.624	1.000
T	-0.076	-0.772	0.798	-0.036	0.444	-0.851

Parameter C was correlated most with PFW at harvest and linear regression resulted in:

$$C = 1.040\ (SE=0.003) \times PFW, \quad (r^2=0.98, n=99) \qquad \text{[eqn 4.4.17]}$$

As for round tomato, an intercept or extra variables did not improve the percentage accounted for.

Also for beefsteak tomato, M is most highly correlated with the fruit growth period (FGP). Results of linear regression with and without an intercept are given in table 4.4.4. Although the intercept was statistically significant, its importance is low as differences between M predicted by both relationships are less than 2 days. No extra explanation was gained by including truss number, probably due to the absence of fruits from the lower trusses.

Table 4.4.4
Parameters (standard errors between brackets) for linear relationships predicting the parameter M of the Gompertz growth curve for potentially grown fruits (n=99) from the fruit growth period (FGP; days) (expt 307/90a).

model parameter	M=*a*+*b*×FGP		M=*b*×FGP	
a	-7.09	(1.20)	-	
b	0.570	(0.024)	0.428	(0.006)
R^2	0.848		0.796	
$SE_{y.x}$	1.52		1.76	

The inverse of parameter B of the Gompertz function was fitted against parameter M for the same reason as for round tomato. The estimated relationship is given by:

$$1/B = 0.87 + 0.410 \times M, \quad (r^2=0.70, n=99, SE_{y.x}=1.04) \qquad \text{[eqn 4.4.18]}$$

As the residuals were not correlated with any of the remaining variables.

In summary, the model describing potential growth of beefsteak tomato fruits as a function of time after anthesis is:

$$C = 1.040 \times PFW, \qquad \text{[eqn 4.4.17]}$$
$$M = -7.09 + 0.570 \times FGP, \qquad \text{[eqn 4.4.19]}$$

or without intercept

$$M = 0.428 \times FGP, \qquad \text{[eqn 4.4.20]}$$
$$B = 1/(0.87+0.410 \times M), \qquad \text{[eqn 4.4.18]}$$

where C, M and B are parameters of the Gompertz curve:

$$FDW_t = C \times \exp\{-\exp[-B \times (t-M)]\}, \qquad \text{[eqn 4.4.4]}$$

and PFW is the potential fruit dry weight (g) at harvest, FGP is the fruit growth period (days) and FDW_t is the fruit dry weight (g) at t days after anthesis.

description as function of fruit development stage, round tomato

According to equation 4.4.8, B' and M' were calculated from fitted B and M and the observed FGP for each fruit (n=366). Parameter C and its description remained unaltered.

In the equations 4.4.14 and 4.4.15, M was described by FGP and truss number (TRUSS), but after dividing by FGP, M' appeared mainly correlated with the truss number (table 4.4.5). Analogous to equation 4.4.15 the M' is described by:

$$M' = 0.397 \times [1+0.401 \times \exp(-0.202 \times TRUSS)], \quad (r^2=0.35,\ n=366,\ SE_{y.x}=0.049) \qquad \text{[eqn 4.4.21].}$$

M' remained slightly correlated with FGP and temperature, which agrees with the significant intercept in equation 4.4.14. The effect of one degree lower temperature was only 0.007 (units FDS) higher M', while the relationship accounts only for 11 percent of the variance. Therefore the effect is neglected.

B' was not correlated with any of the variables except M' (table 4.4.5). In contrast to the relationship between B and M when fruit growth is described as a function of time, the correlation of B' with parameter M', therefore, can be fully attributed to experimental error. Hence, B' is given by the average value:

$$B' = 4.38 \quad (SE=0.62) \qquad \text{[eqn 4.4.22]}$$

Table 4.4.5
Correlations of M' and B' with the parameters C of the Gompertz growth curve and fruit dry weight at harvest (PFW), truss number (TRUSS), fruit position within a truss (FPOS), fruit growth period (FGP) and temperature (T) for potentially grown fruits at different temperatures (n=366) (expt 307/90a). $P(-0.15<\underline{r}<0.15\ \rho=0) = 0.99$

	M'	B'
C	-0.216	-0.220
M'	1.000	-0.481
B'	-0.481	1.000
PFW	-0.365	-0.073
TRUSS	-0.563	-0.041
FPOS	-0.142	0.030
FGP	0.358	0.090
T	-0.329	-0.059

For constant temperature and FDS calculated from $FDR_{f(T)}$, fruit growth rate predicted by this model is the same as predicted by the model on the basis of time (simulation results not shown). It was argued (section 4.4.1) that a model on the basis of $FDR_{f(T\times FDS)}$ is preferred. In the model FDR is applied to calculate the fruit development stage required in equation 4.4.9 as well as to convert growth per unit FDS into growth per day (eqn 4.4.10). When for both $FDR_{f(T\times FDS)}$ was used, predicted fruit growth differed considerably from that predicted by the description as a function of time (fig 4.4.4). However, when $FDR_{f(T\times FDS)}$ was used only to calculate FDS and in equation 4.4.10 $FDR_{(T)}$ was used, predicted growth rate did not differ essentially from that predicted by the original time based model (fig 4.4.4). As a consequence, FDS in the growth model may be confined to one state variable calculated from $FDR_{f(T\times FDS)}$. In summary, the potential fruit growth rate of round tomato as a function of fruit development stage is given by:

$$C = 1.082 \times PFW, \qquad \text{[eqn 4.4.11]}$$

$$M' = 0.397 \times [1+0.401 \times \exp(-0.202 \times TRUSS)], \qquad \text{[eqn 4.4.21]}$$

$$B' = 4.38, \qquad \text{[eqn 4.4.22]}$$

$$PFGR'_t = C \times \exp\{-\exp[-B' \times (FDS_t - M')]\} \times B' \times \exp[-B' \times (FDS_t - M')], \qquad \text{[eqn 4.4.9]}$$

$$\text{with } FDS_t = FDS_{t-1} + FDR_{f(T \times FDS),t} \quad (FDS_0 = 0,\ 0 \leq FDS_t \leq 1)$$

$$PFGR_t = PFGR'_t \times FDR_{f(T),t} \qquad \text{[eqn 4.4.10]}$$

where PFW is the potential fruit dry weight (g) at harvest, TRUSS is the truss number, $PFGR'_t$ is the potential fruit growth rate per unit FDS (g) at t days after anthesis, FDS_t is the fruit development stage, $PFGR_t$ is the daily potential fruit growth rate (g d^{-1}) and $FDR_{f(T \times FDS),t}$ is the fruit development rate (d^{-1}) described by equation 3.4.8 and $FDR_{f(T),t}$ is the fruit development rate (d^{-1}) described by equation 3.4.7.

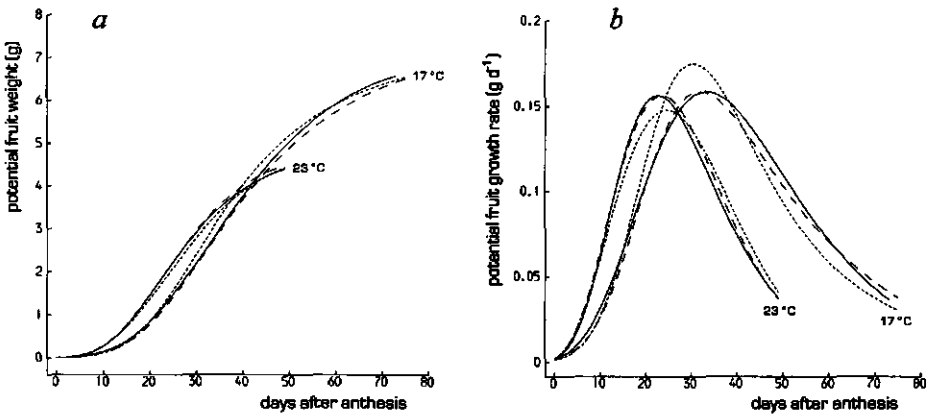

Figure 4.4.4
Predicted potential cumulative fruit growth (*a*) and daily fruit growth rate (*b*) at 17 or 23°C according to the description as a function of time (——) and according to the description as a function of fruit development stage with the conversion from growth rate per unit FDS to daily growth rate either with $FDR_{f(T \times FDS)}$ (-----) or with $FDR_{f(T)}$ (— —).

As with the description as a function of time, predictions with the model on the basis of FDS were compared with the observed data. Also with the latter model the average difference between predicted and observed fruit weight during fruit development was 0 with a standard deviation of 0.40 g. Final fruit weight was on average overestimated by 0.098 g which is more than for the time-based model (0.035 g), but still small compared to the average final weight (5.4 g). The

standard deviation of the difference between predicted and observed fruit weight at harvest remained unchanged at 0.74 g. Hence, the model for potential fruit growth rate on the basis of FDS satisfactorily suits the measurements.

description as function of fruit development stage, beefsteak tomato

As with round tomato, M' increases with decreasing temperature but the effect was only $-0.009^{\circ}C^{-1}$ and statistically not very significant. Despite some other correlations (table 4.4.6), neither M' nor B' could be described successfully as a function of other variables. The means, therefore, are the best estimations of M' and B', i.e. 0.425 (SE=0.033) and 5.23 (SE=0.59), respectively. This makes the description of potential growth for beefsteak tomato:

$$C = 1.040 \times PFW, \qquad \text{[eqn 4.4.17]}$$

$$M' = 0.425, \qquad \text{[eqn 4.4.23]}$$

$$B' = 5.23, \qquad \text{[eqn 4.4.24]}$$

$$PFGR'_t = C \times \exp\{-\exp[-B' \times (FDS_t - M')] \times B' \times \exp[-B' \times (FDS_t - M')], \qquad \text{[eqn 4.4.9]}$$

$$\text{with } FDS_t = FDS_{t-1} + FDR_{f(T \times FDS),t} \quad (FDS_0 = 0,\ 0 \le FDS_t \le 1)$$

$$PFGR_t = PFGR'_t \times FDR_{f(T),t} \qquad \text{[eqn 4.4.10]}$$

where PFW is the potential fruit dry weight (g) at harvest, $PFGR'_t$ is the potential fruit growth rate per unit FDS (g) at t days after anthesis, FDS_t is the fruit development stage, $PFGR_t$ is the daily potential fruit growth rate (g d^{-1}) and $FDR_{f(T \times FDS),t}$ is the fruit development rate (d^{-1}) described by equation 3.4.8 and $FDR_{f(T),t}$ is the fruit development rate (d^{-1}) described by equation 3.4.7.

Table 4.4.6
Correlations of M' and B' with the parameter C of the Gompertz growth curve and fruit dry weight at harvest (PFW), truss number (TRUSS), fruit growth period (FGP) and temperature (T) for potentially grown fruits at different temperatures (n=99) (expt 307/90a). $P(-0.26 < r < 0.26\ \rho = 0) = 0.99$

	M'	B'
C	-0.066	0.098
M'	1.000	-0.428
B'	-0.428	1.000
PFW	-0.140	0.186
TRUSS	-0.246	0.291
FGP	0.481	-0.355
T	-0.368	0.488

4.4.3 discussion

Thornley *et al.* (1981) used the Gompertz curve successfully to describe the potential growth of tomato leaves. The present work shows that the growth of individual fruits can also be described well by a Gompertz equation. The parameters of logistic growth functions are highly correlated (Causton and Venus, 1981). For the fitted curves as a function of time, parameter B could even be described best by a function of parameter M. For the description of the fruit growth curve this interdependence of parameters had no negative consequences.

Parameter C, representing the upper asymptote of the sigmoidal growth curve is proportional to the final potential fruit weight (PFW) that is described and modelled in section 4.3. By relating C to PFW, effects of temperature, truss position, fruit position and cultivar on potential fruit weight and hence on potential fruit growth rate are included implicitly. When the fruit is ripe to harvest (start of colouring) its weight reaches 92 and 96% of the upper asymptote of the sigmoidal curve for round and beefsteak tomato, respectively. The fact that C and PFW are not correlated with the other parameters of the Gompertz curve (tables 4.4.1, 4.4.3, 4.4.5 and 4.4.6) justifies the supposition that the shape of the growth curve is independent of the attainable fruit weight.

Except for the attainable fruit size, the shape of the growth curves for round and beefsteak tomato are very similar (fig 4.4.5), as reflected by the similar values for M' and B'. The inflexion point of the growth curve, i.e. the moment of maximum fruit growth rate, appears to be fairly constant at 40% of the fruit growth period irrespective of temperature, truss position fruit position and tomato type. Fruits growing under limiting assimilate supply show growth curves of similar shape, with the maximum growth rate just before half-way through the fruit growth period (Varga and Bruinsma, 1976; Monselise *et al.*, 1978; Yoshioka and Takahashi, 1979; El-Gizawy *et al.*, 1986; Ho *et al.*, 1987). Salinity does not substantially affect the shape of the curve (Ho *et al.*, 1987; Verkerke, pers. comm.). The small delay in the moment of maximum growth rate for fruits of the lower trusses remains unexplained.

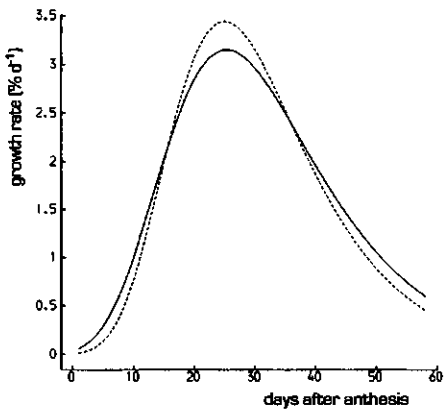

Figure 4.4.5
Predicted potential fruit growth rate of tomato fruits of round tomato cv 'Calypso' (——) and beefsteak tomato cv 'Dombito' (-----) relative to their final fruit weight (=100%) at 20°C.

Time-courses of predicted potential growth rates for the investigated temperatures (fig 4.4.6*b*, table 4.4.7) show that potential fruit growth rate is not much affected by temperature which corroborates results of Heuvelink and Marcelis (1989). Consequently, the final potential fruit weight is mainly determined by the duration of fruit growth (fig 4.4.6*a*, table 4.4.7). Surprisingly, in the range of 19 to 23°C fruit growth rate decreased with increasing temperature. This was not expected on the basis of studies on carbon-import by tomato fruits (Walker and Ho, 1977; Dinar and Stevens, 1982; Yoshioka *et al.*, 1986) and translocation speed of photosynthates in the petiole (Moorby *et al.*, 1974; Yoshioka *et al.*, 1986), which are processes promoted by temperature. In addition, Walker and Thornley (1977) observed an increase of the specific growth rate from 0.026 to 0.050 g^{-1} d^{-1} with temperature increase from 17.5 to 25°C during 48 hours. The different results may be explained by the fact that in this study fruits were subjected to various temperatures during their entire development while for the short-term experiments described in the literature fruits were grown at equal temperature and only subjected to different temperatures during an experimental period of 48-hours at most. In the last section (4.7) to this chapter a possible mechanism is proposed that explains the differences between short- and long-term responses of fruit growth rate.

Table 4.4.7
Predicted fruit growth period (FGP), maximum growth rate, average growth rate and final fruit weight of potentially grown round tomato fruits at four temperatures (TRUSS=5, RAD_{PFW}=1.38 MJ m^{-2} d^{-1}). Values relative to 19°C are presented between brackets.

temperature (°C)	FGP (d)		average growth rate (g d^{-1})		maximum growth rate (g d^{-1})		final weight (g)	
17	73	(117)	0.091	(91)	0.165	(93)	6.6	(107)
19	62	(100)	0.100	(100)	0.178	(100)	6.2	(100)
21	55	(88)	0.099	(99)	0.175	(98)	5.5	(88)
23	50	(80)	0.090	(90)	0.155	(87)	4.5	(72)

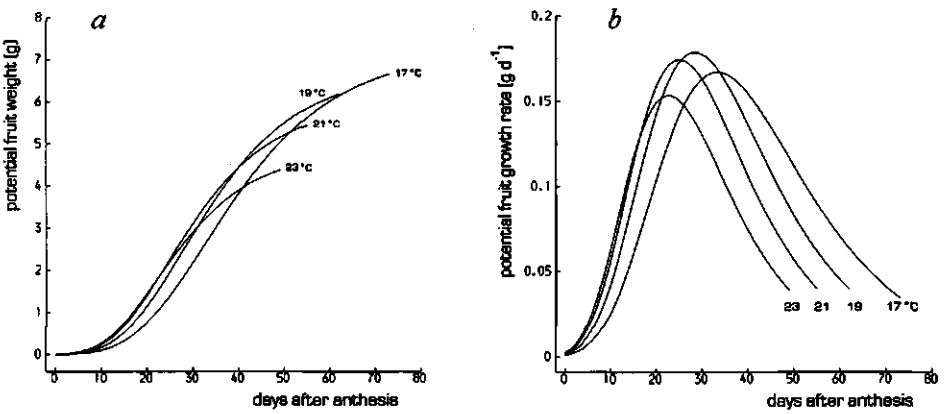

Figure 4.4.6
Predicted potential cumulative growth (*a*) and daily fruit growth rate (*b*) for round tomato at four temperatures (TRUSS=5, RAD_{PFW}=1.38 MJ m^{-2} d^{-1}, cv.'Calypso').

4.5 Potential fruit growth after limiting assimilate supply

4.5.1 results

In order to investigate whether potential fruit growth rate is affected by previous assimilate supply, in experiment 402/89 normally grown (source-limited) plants were pruned to one and two fruits per truss when the fruits of the first truss started to colour (5 April, day of the year 94). Growth of the remaining fruits from 5 April until harvest was compared to growth of potentially grown fruits of the same age from plants which were pruned to one and two fruits per truss from anthesis of the first truss. Measured fruit diameter (D) was transformed into fruit fresh weight (FFW) by: $FFW = 0.001055 \times D^{2.801}$ (eqn 4.4.1).

Generally, the fresh weight increase of fruits previously grown at limiting assimilate supply was less than that of the control fruits grown at ample assimilate supply from anthesis (table 4.5.1). For the older fruits (truss 2 and 3) differences were not significant, probably because growth from pruning until harvest was small compared to variance within the treatments. After subjection to ample assimilate supply, fruits from trusses 4 to 7 reached only about 80% of the growth of control fruits. Very young fruits (truss 8) achieved 90% of the control, while fruits from truss 9, completely grown after pruning, approximated the size of the control fruits (table 4.5.1).

In a second experiment (expt 307/92) to investigate potential fruit growth after limiting assimilate supply, only fruits of two trusses, i.e. 8 and 9, were examined, but pruning was done at different times for different treatments starting one week before anthesis of the eighth truss. Weekly records of diameter (D, mm) of the first and second fruit per truss were converted to fresh weight (FFW, g) by:

$$FFW=0.001356 \times D^{2.753}, (r^2=0.97, n=166), \qquad \text{[eqn 4.5.1]}$$

obtained from removed fruits in this experiment. Additional to fresh and dry weight at harvest of fruits from the pruned plants, normally grown fruits from neighbouring plants were also weighed. This was done on five fruits each day that treatment fruits were harvested (n=7).

Table 4.5.1
Day number of anthesis (FD) and harvest (HD) and fruit growth (fresh weight) from day 94 until harvest of fruits potentially grown since anthesis (control) and fruits subjected to ample assimilate supply since day 94 (time of pruning). Plants were pruned to one (first position) or two (first and second position) remaining fruits per truss (expt 402/89). When pruned differed significantly from the control (Student's *t*-test, P=0.05) the ratio of growth (pruned/control) is given.

truss	FD	HD	control (g)	pruned (g)	pruned/ control
first within truss position					
3	49	111	26	26	-
4	56	121	58	49	0.84
5	64	127	91	72	0.79
6	72	132	119	95	0.80
7	80	137	144	116	0.81
8	86	142	144	128	0.89
9	93	145	132	132	-
second within truss position					
2	43	103	16	11	-
3	50	112	35	26	-
4	58	120	49	48	-
5	65	127	99	68	0.68
6	73	131	121	92	0.76
7	80	136	141	117	0.83
8	87	142	129	119	0.92
9	93	145	123	116	0.95

Early subjection to ample assimilate supply during fruit development, increased fruit dry weight at harvest (table 4.5.2). As in experiment 402/89, after changing to ample assimilate supply, growth of the remaining fruits achieved circa 80% of that of fruits grown potentially from anthesis (table 4.5.3). After transition from source- to sink-limited conditions it took two to three weeks before fruit growth rate (fresh weight) was as fast as that from fruits grown potentially from anthesis (table 4.5.3). Thus the observed differences in growth from the moment of pruning until harvest were due to the time needed for fruits to adapt to increased assimilate supply.

Generally fruit dry matter content was not much affected by decreased fruit load, but in fruits changed to ample assimilate supply two weeks after anthesis it seemed slightly higher than that in fruits grown on normal loaded plants (table 4.5.2). For all parameters there was no difference between fruits from the first and second position in a truss (analysis not shown). The fruit growth period (anthesis - harvest) was circa 8 weeks for all treatments.

Table 4.5.2
Dry weight and dry matter content at harvest for fruits subjected to nonlimiting assimilate supply at different times during fruit development (expt 307/92).

time of pruning (wks after anthesis)	fruit dry weight (g)		dry matter content (%)	
	truss 8	truss 9	truss 8	truss 9
-1	7.3	7.5	5.6	5.6
0	7.3	7.3	5.7	5.4
1	6.8	6.9	5.7	5.7
2	6.2	6.6	5.9	5.8
3	5.2	5.8	5.6	5.7
4	4.7	4.7	5.6	5.6
5	4.4	-	5.7	-
LSD 5%	0.5	0.6	0.1	0.2
normal loaded plants[1)]	3.9 (0.2)		5.5 (0.1)	

1) standard error between brackets

Table 4.5.3
Weekly growth (fresh weight) of fruits subjected to nonlimiting assimilate supply at different times during fruit development (expt 307/92). Growth at nonlimiting assimilate supply is underlined. The last column gives the ratio between growth since subjecting to nonlimiting assimilate supply and growth of fruits from plants pruned one week before anthesis of the eighth truss.

growth period (wks after anthesis)	growth rate (g wk^{-1}) 1	2	3	4	5	6	7	8	relative growth
fruit age at pruning (wks after anthesis)									
eighth truss									
-1	3	15	23	25	21	26	11	8	1
0	1	11	23	22	23	23	17	9	0.97
1	1	10	19	22	21	20	17	10	0.92
2	1	7	15	19	19	20	15	10	0.86
3	1	8	12	14	17	16	16	10	0.80
4	1	6	13	10	13	15	15	11	0.82
5	2	8	13	10	10	13	14	10	0.82
LSD 5%	1	4	3	3	3	4	ns	ns	
ninth truss									
-1	3	14	25	25	26	22	22	9	1
0	2	13	23	23	26	21	24	9	0.96
1	1	9	18	23	23	21	26	15	0.90
2	1	8	16	19	23	19	26	10	0.86
3	1	7	12	17	18	20	31	17	0.91
4	1	7	13	11	12	14	27	14	0.76
LSD 5%	ns	5	2	4	4	5	ns	7	

4.5.2 discussion

After a change from limiting to nonlimiting assimilate supply during fruit development, fresh weight growth until maturity is less than for fruits grown potentially from anthesis. Apparently, the fruit could not adapt its growth rate immediately to a surplus of assimilates and it needed about two weeks for full

acclimation. This observation was confirmed by Farré (1993). A similar but faster response to a sudden surplus of assimilates was observed with cucumber fruits (Marcelis, 1993*e*).

The fact that the dry matter content of fruits subjected to assimilate surplus during fruit development is higher than that of fruits grown potentially from anthesis, however, may indicate that dry weight increase adapts immediately and only fresh weight increase is delayed. However, even the largest difference in dry matter content, *viz.* 0.004 g^{-1} (table 4.5.2), accounts for only 6 gram fresh weight at most. As this is considerably less than the observed differences in fresh weight growth after subjection to ample assimilate supply (4.5.1), is seems plausible that dry weight increase does not reach the level of potentially grown fruits from anthesis immediately after availability of ample assimilates. Ultimately the fruit can match the maximum potential growth rate, indicating that, in terms of sink strength, sink activity rather than sink size is affected by previous assimilate supply.

A physiological explanation of the delay is that the fruit's capacity to process assimilates may be adapted to its previous assimilate availability and that time is needed to adjust it to a significant increase of assimilate supply. Control of sink activity, e.g. the enzymatic capacity for synthetic metabolism, by sink-source relationships has been suggested earlier by Farrar (1988) and Farrar and Williams (1991).

Generally, the positive effect of increased assimilate availability on fruit dry matter content at harvest was not large, but significant for fruits subjected to ample assimilates two weeks after anthesis (table 4.5.2). The largest increase was observed when pruning was done just before half way through the fruits growth period, *viz.* the period of rapid growth rate (section 4.4). At that time a fruit stores a lot of starch (Ehret and Ho, 1986*a*) and possibly not all extra stored carbohydrates can be remobilised and subsequently employed for fresh weight growth.

The experiments demonstrated that when a fruit has grown less than potentially due to restricted assimilate supply it doesn't grow faster after subjection to assimilate surplus than fruits grown potentially from anthesis. Consequently, sub-potential fruit growth due to assimilate shortage seems irreversible and in modelling potential growth rate no account has to be taken of such former 'growth losses'.

4.5.3 model

As a first approximation the effect of a gradual adaptation to a sudden increase in availability of assimilates may be described by restricting the daily increase of potential fruit growth rate relative to the growth rate of fruits grown potentially from anthesis:

$$(PFGR_t/PFGRM_t) - (PFGR_{t-1}/PFGRM_{t-1}) \leq af, \qquad \text{[eqn 4.5.2]}$$

that can be rearranged into:

$$PFGR_t \leq (PFGR_{t-1} + af \times PFGRM_{t-1}) \times PFGRM_t/PFGRM_{t-1}\,, \qquad \text{[eqn 4.5.3]}$$

where $PFGR_t$ is the potential fruit growth rate at t days after anthesis, $PFGRM_t$ is maximum potential fruit growth rate, i.e potential growth rate for fruits grown potentially from anthesis and *af* is the maximum relative change (adaptation factor).

The ratio $PFGRM_t/PFGRM_{t-1}$ in equation 4.5.3 describes the change in potential growth rate with fruit development.

Fruits growing about half the maximum potential growth rate (PFGRM) reached the potential level in circa 17 days (2-3 weeks) after subjection to ample assimilate supply (table 4.5.3). Hence, parameter *af* can be estimated at $(1-0.5)/17 = 0.03\ d^{-1}$. Comparison of model predictions with measured data (table 4.5.4) shows that growth after subjection to ample assimilate supply is predicted reasonably well. Only change to nonlimiting assimilate supply for the oldest fruits (5 wks after anthesis) resulted in a considerable underestimation of real growth, which may indicate a more rapid adaptation when, - due to fruit development -, the fruit's growth rate decreases.

Decline of the potential growth rate in case of decreasing assimilate availability is likely but has not been examined. It is assumed that the maximum daily decrease of potential fruit growth is as large as the maximum increase.

Table 4.5.4
Measured and predicted ratio between fruit growth (fresh weight) after changing from limiting to nonlimiting assimilate supply and growth of control fruits grown potentially from initiation for two experiments.

time of changing (wks from anthesis)	expt 402/89[1)]	expt 307/92[2)]	model
0	-	0.97	0.97
1	0.90	0.91	0.93
2	0.81	0.86	0.88
3	0.79	0.86	0.88
4	0.75	0.79	0.79
5	0.83	0.82	0.75

1) mean of first and second within truss position
2) mean of eighth and ninth truss

The daily adjustment is assumed to be proportional to the difference in the plant's amount of dry matter available for growth (DMA) and the amount of dry matter demanded by growth. The latter can be quantified by the cumulative potential growth rates of individual organs, i.e. ΣPGR. Since the adaptation factor *af* is expressed as a fraction of the maximum potential demand (ΣPGRM) it is described by:

$$af = (\mathrm{DMA} - \Sigma\mathrm{PGR})/\Sigma\mathrm{PGRM}, \text{ with: } -0.03 \leq af \leq 0.03 , \qquad \text{[eqn 4.5.4]}$$

where a is the relative adaptation of the actual potential growth rate to the availability of dry matter, DMA is the plant's dry matter available for growth (g d^{-1}) and ΣPGR and ΣPGRM are the plant's cumulative actual and cumulative maximum potential growth rates (g d^{-1}), respectively.

Subsequently, the potential growth rate of an individual fruit is given by:

$$PFGR_t = (PFGR_{t-1} + af_{t-1} \times PFGRM_{t-1}) \times PFGRM_t/PFGRM_{t-1}, \quad \text{[eqn 4.5.5]}$$
with $0 \leq PFGR_t \leq PFGRM_t$,

where $PFGR_t$ is the potential fruit growth rate at t days after anthesis, $PFGRM_t$ is maximum potential fruit growth rate, i.e potential growth rate for fruits grown potentially from anthesis and af_t is the maximum relative change.

Note that in this model parameter *af* is independent of the fruit's development stage. It is recognized that this exploratory model, especially with respect to the decrease of potential fruit growth rate, is supported by too few experimental data, and that more experimental work is needed.

4.6 Potential vegetative growth

4.6.1 results

Similar to the assessment of potential fruit weight, a direct estimate of the potential weight of a vegetative unit (stem and leaves in-between two successive trusses) may be obtained by growing plants at nonlimiting assimilate supply. In experiment 307/92 characteristics of potentially grown vegetative units corresponding to trusses 8 and 9 were measured. Total dry weight was 24 g; 16 and 8 g for leaves and stem section, respectively (table 4.6.1).

Table 4.6.1
Characteristics of a vegetative unit (stem section with three leaves) grown under nonlimiting assimilate supply. Data are averaged over units corresponding to truss 8 and 9 (expt 307/92). Standard errors are given between brackets.

leaf area (m^2)	0.230	(0.021)
leaf dry weight (g)	16.3	(2.6)
stem dry weight (g)	8.0	(1.4)
total dry weight (g)	24.3	(3.4)
leaf dry matter content (%)	12.3	(0.6)
stem dry matter content (%)	14.8	(0.7)
Specific Leaf Area ($cm^2\ g^{-1}$)	144	(20)

As argued before (section 4.1) it is probably better to estimate the potential vegetative growth rate from dry matter distribution in source-limited plants. Since temperature affects the ratio between vegetative and reproductive growth (de Koning, 1989*a*), in experiment 210/90 dry matter distribution was measured at 19 and 23°C. Indirect effects of temperature on dry matter distribution, due to different development rates and numbers of fruits set, were limited by exposing similar mature plants (anthesis of the sixth truss, grown at 19°C) to 19 and 23°C for two weeks. Although even after two weeks plants may differ slightly in ontogenetic stage, this period was considered as the minimum for accurate growth measurement. Weight increase is presented for each compartment separately because the experimental scale, i.e. two treatments in duplicate, was too small for proper statistical analysis. An experimental plot within a compartment consisted of six plants.

The variation within treatments was considerable, but two weeks exposure to 23°C apparently decreased the growth of the vegetative plant parts compared to the plants staying at 19°C, while total growth was similar for both treatments (table 4.6.2); the dry matter partitioned to the fruits was circa 68% and 80% at 19 and 23°C, respectively. According to the hypothesis that dry matter partitioning is proportional to the potential growth rates, the ratio between fruit growth and vegetative growth is equal to the ratio between total potential growth rate of all fruits and that of the vegetative plant parts. During the two weeks' treatment period the plants consisted on average of circa seven vegetative units and 60 fruits. The average growth of a vegetative unit relative to that of a single fruit was about 3.6 and 1.8 for 19 and 23°C respectively (table 4.6.2).

Table 4.6.2
Above ground dry weight increase of mature tomato plants raised at 19°C during two weeks exposure to 19 and 23°C (expt 210/90).

	19°C		23°C	
replicate	1	2	1	2
fruits (g plant^{-1})	33	39	38	44
stem and leaves (g plant^{-1})	17	18	12	8
total (g plant^{-1})	49	57	50	52
fruits/total (%)	66	69	76	84
fruits (g plant^{-1})	0.55	0.65	0.66	0.73
stem and leaves (g vegetative unit^{-1})	2.4	2.5	1.7	1.2
vegetative unit/fruit	3.8	3.4	2.3	1.4

4.6.2 discussion

Since in experiment 307/92 the potential weights of a vegetative unit and that of fruits of the corresponding trusses were circa 24 (table 4.6.1) and circa 8 g (section 4.5, table 4.5.2), respectively, the ratio between potential weights of a vegetative unit and a single fruit was approximately 3. Considering the average temperature of 21°C, this ratio is well in line with 3.6 and 1.8 for 19 and 23°C, respectively, estimated from the source-limited plants of experiment 210/90 (table 4.6.2).

In mature tomato plants about 70% of the above ground dry matter production is distributed to the fruits (Ward, 1964; Hurd *et al.* 1979; Ehret and Ho, 1986*a*; de Koning; 1993), but as instantaneous partitioning may vary considerably (de Koning; 1989*a*), fruit growth of 68 and 80% of the total during two weeks 19 and 23°C, respectively (table 4.6.2), seems reasonable. The actual growth rate, and so potential growth rate, of a vegetative unit relative to that of a single fruit halved with only a 4°C temperature increase. Since potential fruit growth rate at 23°C is about 10% lower than at 19°C (section 4.4), the potential growth rate of the vegetative plant parts decreases more than 50% with a 4 degrees temperature increase. For cucumber leaves grown on plants without fruit load Marcelis (1993*c*) also observed a considerable reduction of dry weight with increasing temperature. In the present experiment the effect of temperature may be overestimated. Possibly during the two weeks high temperature, the sink strength of fruits has been significantly greater than predicted on the basis of potential growth rate at constant 23°C as the fruits had grown before at low (19°C) temperature. Furthermore, temperature-promoted remobilization of stored carbohydrates from the vegetative parts to the fruits might have caused an underestimation of the temperature effect on the increase in structural dry matter of the vegetative parts. For decisive conclusions concerning the temperature effect on vegetative sink strength much more experimentation is needed.

4.6.3 model

It is recognized beforehand that the available data are too few and too inaccurate for proper modelling. However, the effect of temperature on the vegetative sink strength cannot be neglected and therefore a preliminary attempt is made to describe the vegetative potential growth relative to the more extensively investigated potential growth of fruits. It is assumed that the development rate of

a vegetative unit is equal to that of a fruit and that at any moment during development the potential growth rate of a vegetative unit is proportional to that of a fruit. As discussed before, the ratio between potential fruit growth rate and potential vegetative growth rate, varies with temperature from about 3.6 at 19°C to about 1.8 at 23°C (table 4.6.2). To describe this proportional factor as a function of temperature a hyperbolic relationship seems most plausible.

Several hyperbolic functions fitted well to the (few) data of experiment 210/90 but an exponential decay function behaved most reasonable beyond the temperatures in the experiment (fig 4.6.1). The estimated relationship is:

$$PVGR/PFGR = 3.59 \times \exp[-0.168 \times (T-19)], \quad (r^2=0.80,\ n=4) \qquad \text{[eqn 4.6.1]}$$

which after rearranging gives:

$$PVGR = \{3.59 \times \exp[-0.168 \times (T-19)]\} \times PFGR, \qquad \text{[eqn 4.6.2]}$$

where PVGR is the potential growth rate of a vegetative unit (g d^{-1}), PFGR is the potential growth rate of a single fruit (g d^{-1}) and T is the temperature (19-23°C).

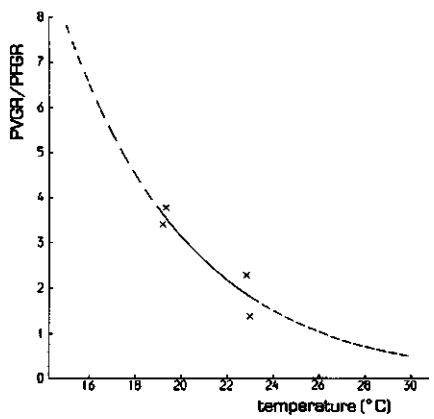

Figure 4.6.1
The ratio between potential growth of the vegetative unit (stem section with three leaves) and that of a single fruit as a function of temperature (expt 210/90).

It should be noted the relationship between PVGR and PFGR may be very specific for the experimental conditions, e.g. for the cultivar 'Calypso'.

4.7 Discussion

To round off this chapter a conceptual mechanism for the control of sink activity with respect to assimilate availability and temperature is presented. Also a mathematical description for the short-term temperature response of potential growth rate is proposed. Furthermore, the obtained models for dry matter distribution and assimilate demand are discussed.

Potential growth rate of a sink organ is determined, as discussed in section 4.1, by cell number (sink size) and the rate of metabolic processes (sink activity). Increase of potential growth with ontogeny (truss position) and favourable light conditions (season effect) could both be explained by enlargement of the apex and subsequently the fruit's cell number (discussed in section 4.3.2). Also differences in fruit size between cultivars appear mainly due to differences in the fruit's cell number (Ho, 1992). Whether temperature affects the cell number is not known. Since the final cell number in tomato fruit is reached within two weeks after anthesis, the potential growth rate during fruit development reflects mainly the evolution of sink activity.

Potential growth rate of a fruit and therefore its sink activity, appears to adapt to the previous supply of assimilate. The acclimation to increased assimilate availability seems limited to about 3% of the maximum rate per day. It has been discussed in section 4.5 that probably the amount of enzymatic machinery for uptake and processing of assimilates is adapted to the amount of assimilates available and time is needed for acclimation when assimilate supply changes. Possibly the difference between short and long-term temperature response of fruit growth may be explained by this acclimation.

Generally, low temperature reduces the rate of biochemical and biophysical processes. For photosynthesis it has been proven that at decreasing temperature the photosynthetic apparatus enlarges and in this way compensates for the slower reaction rates (Berry and Björkman, 1980). Full acclimation of the photosynthetic apparatus of mature leaves to altered temperature requires at least several days (Berry and Björkman, 1980). There is some evidence for a similar mechanism in the processing of assimilates. Farrar (1988) demonstrated that temperature during a 48-h pre-treatment affects carbon import and competitive power to attract assimilates in barley roots. Hunter and Rose (1972) reported a large increase in the amount of ribosomal RNA in yeast cells cultured at low temperature, and they suggest that this increase may tend to compensate for the decline of protein synthesis rate per unit rRNA as temperature is reduced. Possibly, expression of

key genes coding for proteins involved in the rate control of growth is directly affected by sucrose (Farrar, 1992). Thus, concerning the carbohydrate uptake and processing activity of a sink at low temperature, the slow reaction rates may be compensated for by an increase of in the amount of machinery. The feedback that controls the amount of machinery through the difference between sink activity and assimilate availability, and involvement of temperature is schematically presented in figure 4.7.1.

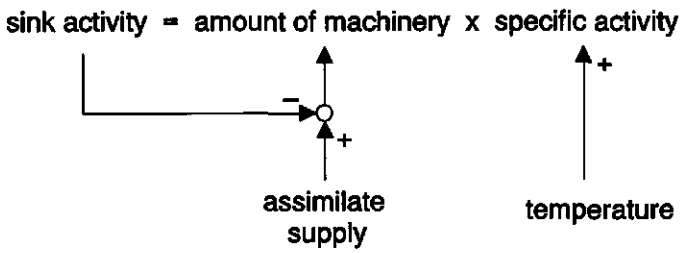

Figure 4.7.1
Feedback control of sink activity.

The specific activity, i.e. the activity per unit machinery, responds immediately to temperature, while changes in the amount of machinery will require some time. The consequence is that when a low temperature adapted fruit is suddenly subjected to high temperature it expresses an extra large sink strength due to the combination of a large machinery and high specific activity. On the other hand, fruits at high temperatures develop a limited machinery and exhibit very low sink activity when subjected to low temperature. The overshoot reaction at changing temperature due to temperature acclimation is probably an important cause of the discrepancy between short- and long-term temperature response of sinks mentioned in section 4.4.

To describe the short-term temperature response, the potential fruit growth rate (PFGR) may be multiplied by a factor:

$$Q_{10,g}^{0.1(T-TF)}, \qquad \text{[eqn 4.7.1]}$$

where, $Q_{10,g}$ is the Q_{10} value of the short-term temperature response of potential fruit growth, T is the 24-h mean air temperature (°C) and TF is the average temperature since anthesis (°C), i.e. the temperature the fruit is acclimated to.

It should be noted that if the temperature during the fruit growth period does not change, this factor has no effect on the potential fruit growth rate. For reference temperature the average temperature since anthesis is chosen, which implies that the rate of adaptation to temperature decreases with increasing fruit age. It is recognised that probably a period with a fixed length is more realistic, but this should be investigated in future experiments. From a short-term temperature experiment of Walker and Ho (1977) 2.4 seems a reasonable estimate for $Q_{10,g}$ between 17 and 25°C.

Adaptation of the processing machinery of vegetative sinks may be different from that of fruits. The strong response of the ratio between vegetative and fruit growth after temperature increase in experiment 210/90 (section 4.6) may be explained by a faster adaptation of the vegetative parts than fruits. However, since any information about adaptation rates of vegetative organs is lacking, in the present model acclimation of vegetative sinks and acclimation of fruits are regarded to be similar.

As the result of acclimation, the actual plant's cumulative demand for assimilate is close to the previous assimilate supply. Consequently, as adaptive changes in sink strength are relatively slow, at fast improving light conditions net-photosynthesis may easily exceed the demand for assimilates. The surplus of carbohydrates is then probably stored. It has been demonstrated that the storage of surplus of assimilates is mainly located in the plant's stem tissue (Ho *et al.*, 1983; Hammond *et al.*, 1984). For proper modelling, therefore, an assimilate buffer should be included to accommodate temporary storage of assimilates. Also due to acclimation of the plant's assimilate demand, sink and source are in balance which makes it difficult to decide if growth is source or sink limited (Farrar, 1993*b*). An absolute maximum assimilate demand (sink potential) is realised when all organs grow at their maximum potential rate, which is achieved only after a nonlimiting assimilate supply is provided for a longer time. Therefore, it is useful to distinguish between short-term sink limitation, for instance, caused by a sudden increase of source activity and long-term sink limitation due to low number of sinks.

Tomato fruits are supplied with assimilates mainly by the surrounding leaves (Shishido and Hori, 1977; 1991), and therefore a truss with three leaves immediately below can be regarded as a source-sink unit (Tanaka and Fujita, 1974). This relation, however, is not absolute as removing a truss results in yield increase of the remaining trusses above and below the one removed (Slack and Calvert, 1977). Additional evidence of less rigid sink-source relationships after

fruit or leaf removal is reported by Tanaka and Fujita (1974), Fisher (1977) and Yoshioka and Takahashi (1979, 1984), but their results also clearly demonstrate that sinks gain competitive benefit from being close to the source leaves. Within a truss this is expressed by high susceptibility to abortion of the distal flowers (section 3.3). In addition, vascular connections may also cause discrimination between sinks (Shishido and Hori, 1977, 1991; Cook and Evans, 1983; Shishido *et al.*, 1988). However, if the disturbance is not too severe, the distribution of assimilates seems flexible enough to assume available assimilates as present in one pool from which they are distributed. As discussed in section 4.1 in this study all benefits a sink may have from its position in the sink-source system at limiting assimilate supply are neglected.

In growth models with a photosynthesis routine, the assimilates available for growth can be calculated from gross photosynthesis and maintenance respiration (Gijzen, 1992; Dayan *et al.*, 1993*a*). In the present model, however, dry weight increase will be one of the input variables of the model. Respiration is included only to calculate total assimilate demand.

As discussed in the introduction to this chapter, the organ's assimilate demand can be quantified by the sum of potential growth rate, growth respiration and maintenance respiration. Maintenance respiration (Rm) includes three components: maintenance of concentration gradients across membranes, turnover of proteins and a component related to the intensity of metabolism (Penning de Vries, 1975).

Reasonable estimates for the maintenance respiration coefficient (MAINT) at 25°C are 0.03, 0.015, 0.015 and 0.01 g CH_2O g^{-1} dw d^{-1} for leaves, stem, roots and fruits, respectively (Spitters *et al.*, 1989, Gijzen, 1992). On the basis of a leaf-stem ratio of 7:3 (Heuvelink, 1995*a*), MAINT for vegetative units is equal to 0.025 g CH_2O g^{-1} dw d^{-1}. Temperature immediately affects maintenance respiration and a Q_{10} of 2.0 appears to be a reasonable estimate (Walker and Thornley, 1977; Penning de Vries *et al.* 1989). The maintenance respiration of an organ, therefore, is described by:

$$Rm = MAINT \times W \times Q_{10,m}^{0.1(T-Tr)}, \qquad \text{[eqn 4.7.2]}$$

where Rm is the maintenance respiration rate (g CH_2O d^{-1}), MAINT is the maintenance respiration coefficient (g CH_2O g^{-1} dw d^{-1}) at a reference temperature Tr, W is the organ's dry weight (g), $Q_{10,m}$ is the Q_{10}-value for the temperature effect on maintenance respiration rate at Tr and T is the actual temperature (°C).

Growth respiration can be defined as the CO_2 evolution resulting from conversion of glucose into structural dry weight, including translocation of the glucose from the source to the growth site and the energy required for uptake of inorganic constituents from the root medium (Penning de Vries *et al.*, 1989). The ratio between the carbohydrate requirement and the biomass produced is called the assimilate requirement quotient (ASRQ) or growth conversion efficiency, and its value depends mainly on the composition of the biomass. Gijzen (1994) estimated the ASRQ for leaves, stem and fruits, from characteristics of the biochemical components according to the method of Vertregt and Penning de Vries (1987), to be 1.25, 1.20 and 1.20 g CH_2O g^{-1} dw, respectively. ASRQ is independent of temperature (Walker and Thornley, 1977). Because the assimilate requirement quotient includes a respiratory as well as a conversion component, instead of describing growth and respiration separately, the total growth component of an organ's assimilate demand is given by the potential growth rate multiplied by the assimilate requirement quotient. Hence, the organ's assimilate demand is described by:

$$AD = MAINT \times W \times Q_{10,m}^{0.1(T-Tr)} + PGR \times ASRQ, \qquad \text{[eqn 4.7.3]}$$

where AD is the assimilate demand (g CH_2O d^{-1}), MAINT is the maintenance respiration coefficient (g CH_2O g^{-1} dw d^{-1}) at a reference temperature Tr, W is the organ's dry weight (g), $Q_{10,m}$ is the Q_{10}-value for the temperature effect on maintenance respiration rate at reference temperature Tr, T is the actual temperature (°C), PGR is the organ's potential growth rate (g d^{-1}) and ASRQ is the assimilate requirement quotient (g CH_2O g^{-1} dw).

The maximum assimilate demand, expressed at prolonged nonlimiting assimilate supply, is obtained by substitution of PGR by the maximum potential growth rate (PGRM).

The assimilate requirement of an organ that grows at its potential rate is equal to its assimilate demand as given by equation 4.7.3. For an organ that grows at less than its potential, the assimilate requirement can be calculated by replacing the potential growth rate (PGR) in equation 4.7.3 by the actual growth rate. For example, predicted daily and cumulative assimilate requirements for fruits that achieve a final weight of 5 g (90 g fw) at 17 and 23°C are shown in figure 4.7.2. Maintenance respiration has a substantial contribution to the total assimilate requirement only for near-mature fruits. Because growth respiration is not directly affected by temperature, at both temperatures an equal amount of

assimilates is lost by growth respiration, *viz.* 1.0 g, to achieve a final weight of 5 g. The instantaneous maintenance respiration increases with temperature, but since the growth period is longer at high temperature, cumulative assimilate requirement for maintenance respiration, estimated over the whole fruit growth period, appeared to be 1.0 g for both temperatures. The equality is due to the fact that maintenance respiration and fruit development rate both have a Q_{10}-value of about 2. Therefore, it can be concluded that for growing a certain amount of fruit weight assimilate losses due to maintenance respiration can hardly be manipulated by temperature.

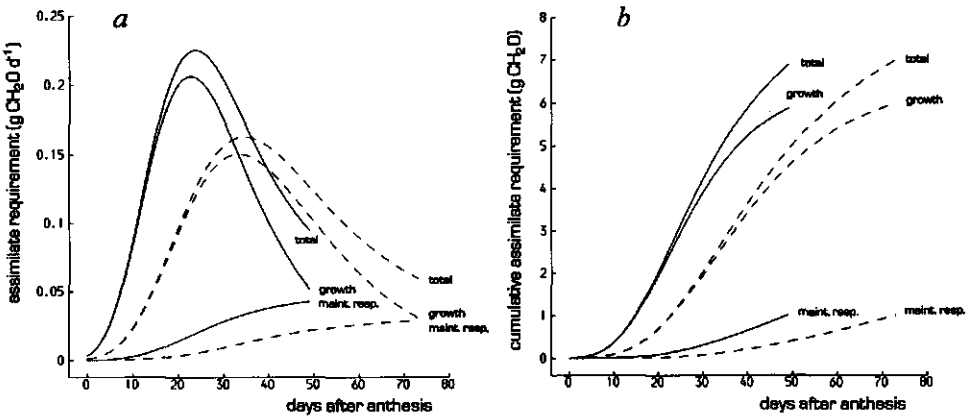

Figure 4.7.2
Daily (*a*) and cumulative (*b*) assimilate requirement of a round tomato fruits achieving a final weight of 5 g (≈90 g fresh weight) at 17 (- - - - -) or 23°C (——).

5

DESCRIPTION OF THE MODEL

5.1 Outline of the model

The primary objective of this study (Chapter 1) is to develop a model that can predict the crop assimilate demand and dry matter distribution between vegetative and generative plant parts. The demand for assimilate consists of the requirements for maintenance and (potential) growth. The demand for growth is defined by the potential growth rate, i.e. the growth rate at nonlimiting assimilate supply.

Dry matter for growth is assumed to be available as one common pool from which sink organs obtain their share through mutual competition. The competitive strength of an organ is quantified by its potential growth rate. In the model, the fruits are considered individually. Vegetative parts are clustered in vegetative units consisting of a stem segment with three leaves preceding a truss. In the present model the roots are not included.

The time step of the model is one day. Formation of new trusses and vegetative units is mainly a function of temperature. The number of fruits that develop on a truss is dependent on the number of flowers that reach anthesis and on fruit set. In the model the amount of flowers that reach anthesis is related to the growth of the corresponding vegetative unit during the period that flower bud abortion may occur, reflecting the effect of common determinants rather than representing a causal relation between both variables. Fruit set is a function of temperature. The increase of physiological age or development stage of each organ is determined principally by temperature. Fruits are harvested when their development stage exceeds a reference value. Leaves are removed when the first fruit of the corresponding truss starts to colour.

Potential growth rate of fruits is described as a function of development stage, position on the plant and temperature. In the model the potential growth rate of a vegetative unit is expressed pragmatically as the potential growth rate of a fruit times a temperature dependent factor. The actual potential growth rates adapt to the amount of assimilate available, but an absolute maximum rate exists for prolonged nonlimiting assimilate availability.

Maintenance and growth respiration are proportional to the crop's biomass and crop growth rate, respectively, and described according to the literature. Dry matter production is input to the model. When the daily amount of dry matter available for growth exceeds the actual potential growth rate of all organs together, each organ grows at its potential rate and the surplus of dry matter is stored for the next day.

Fresh weight of harvested fruits is derived from dry weight by an empirical relationship of the fruit dry matter content with season, air temperature and salinity (EC) in the root environment.

5.2 Structure of the model

In the model the state of the plant is largely described by two (vector) sets of state variables (fig 5.2.1). One set represents the properties of the fruits, with an element for each individual fruit. The state variables are: truss position (TRUSS), fruit position within a truss (FPOS), fruit development stage (FDS) and fruit dry weight (FW). From these variables relevant cumulative state variables can be derived, e.g. number of fruits and fruit weight per plant. The other vector set characterizes the vegetative plant parts. In these vectors an element represents a vegetative unit. The modelled properties of the vegetative units are: position on the plant (VPOS) which is defined as the number of the corresponding truss, development stage (VDS) and dry weight (VW).

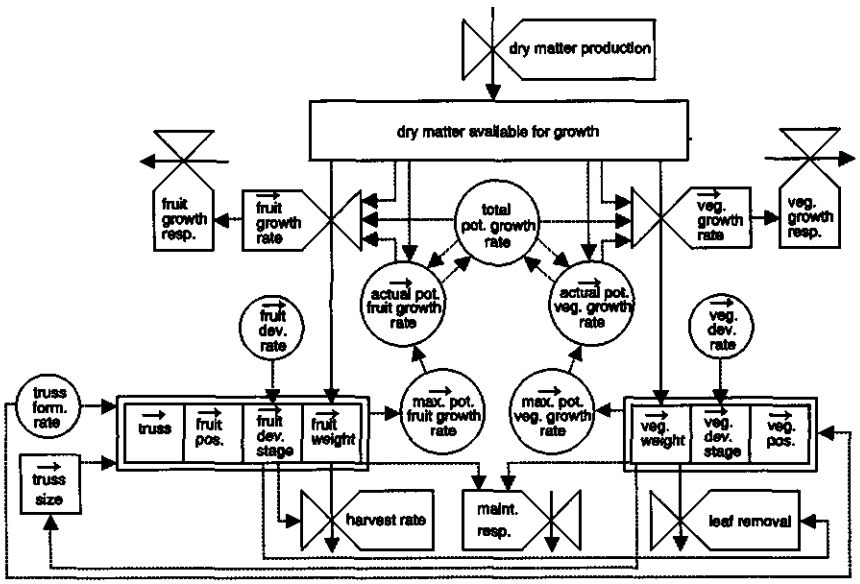

Figure 5.2.1
Diagram of the structure of the model describing development, dry matter distribution and assimilate demand of indeterminate tomato (symbols according to Forrester, 1961). Vector type variables are superscribed by an arrow.

Additionally, for fruits as well as vegetative plant parts an extra state variable, FSTATE and VSTATE, respectively, is introduced to describe the state of organs, *viz.* not existing, existing on the plant or harvested.

As the increase in number of fruits is based on the truss formation rate and number of fruits per truss, a third vector set is augmented that describes the state of each truss (not existing, flowering, after flowering) and the number of fruits per truss. Furthermore, the model contains some scalar type state variables that represent whole plant properties, e.g. the physiological age of the plant (A), expressed as the highest flowering truss number, and the amount of dry matter available for growth (DMA). The change of state variables with every time step (one day) is determined by the value of rate variables of which descriptions are given in the next sections.

5.3 Organogenesis and development

5.3.1 formation of new fruits

The rate of fruit formation was described by a set of equations representing: the rate of truss formation (flowering rate, FR), the number of flowers per truss (FLPT) and the percentage fruit set (PFS) (Chapter 3). FR is given by:

$$FR_t = a_{FR} + 0.1454 \times \ln(T_t) - 0.0010 \times A_{t-1}, \quad \text{[eqn 3.2.3]}$$
$$\text{with } A_t = A_{t-1} + FR_t, \text{ and } A_0 = 1,$$

where FR_t is the flowering rate (trusses d^{-1}) at t days after the start of anthesis of the first truss, a_{FR} is a cultivar dependent parameter; -0.296 for 'Calypso', T_t is the 24-h mean air temperature (17-27°C) and A_t is the plant's physiological age expressed as the number of the flowering truss.

As each fruit is considered separately, the formation rate of flowers within a truss (FRT) also has to be known. According to Cockshull (pers.comm.) this rate approximates 5 times the formation rate of trusses:

$$FRT = 5 \times FR, \quad \text{[eqn 5.3.1]}$$

where FRT is the flowering rate within a truss (flowers d^{-1}) and FR is the flowering rate of a plant (trusses d^{-1}).

The final number of flower buds per truss that reach anthesis is related to the weight of the corresponding vegetative unit:

$$FLPT = CFFLPT \times (7.1 + 0.37 \times VW_{FLPT}), \quad \text{[eqn 3.3.3]}$$

where FLPT is the final number of flower buds per truss reaching anthesis, CFFLPT is a cultivar dependent factor defining the number of flowers initiated relative to 'Calypso' and VW_{FLPT} is the dry weight of the corresponding vegetative unit (2-8 g) when the next truss starts to flower.

Due to failure of fruit-set, not all flowers of a truss become fruits. In the model, the percentage fruit-set of a truss (PFS) is solely described by temperature. PFS is calculated as the average of daily percentage fruit-set from anthesis of the first flower until anthesis of the last flower of the truss:

$$PFS = \{\sum_{t=1}^{t=k}[97.2 - 1.70 \times (T_t - 20) - 1.174 \times (T_t - 20)^2]\}/k, \quad \text{[eqn 3.3.4]}$$

where PFS is the percentage fruit-set of a truss (%), index t represents the day number after anthesis of the first flower of the truss, k is the value of t at anthesis of the last flower and T_t is the 24-h mean air temperature (17-23°C) at day t.

The final number of fruits that develop on a truss (FPT) is given by:

$$FPT = FLPT \times PFS/100, \quad \text{[eqn 3.3.5]}$$

5.3.2 fruit development

In the model fruits are harvest ripe when their development stage exceeds 1 (100%). The rate of fruit development is given by:

$$FDR_{f(T\times FDS),t} = a_{FDR} + 0.0012 \times \ln(RAD_{FDR}) - 0.00005 \times TRUSS + \ln(T_t/20) \times (0.03923 - 0.2127 \times FDS_{t-1} + 0.4505 \times FDS_{t-1}^2 - 0.2400 \times FDS_{t-1}^3), \quad \text{[eqn 3.4.8]}$$

where $FDR_{f(T\times FDS),t}$ is the fruit development rate (d^{-1}), index t represents the number of days after anthesis of the fruit considered, a_{FDR} is a cultivar dependent parameter; 0.0165 for 'Calypso', RAD_{FDR} is the solar irradiance received by the crop (MJ m^{-2} d^{-1}) averaged over three weeks after anthesis of the fruit considered, TRUSS is the truss number, T_t is the 24-h mean air temperature (17-27°C) and FDS_t is the fruit development stage ($FDS_t = FDS_{t-1} + FDR_t$, $FDS_0 = 0$, $0 \le FDS_t \le 1$)

For fruits younger than three weeks, RAD_{FDR} is calculated from anthesis until the current day. Figure 5.3.1 summarizes in a diagram the processes and factors involved in fruit formation and fruit development.

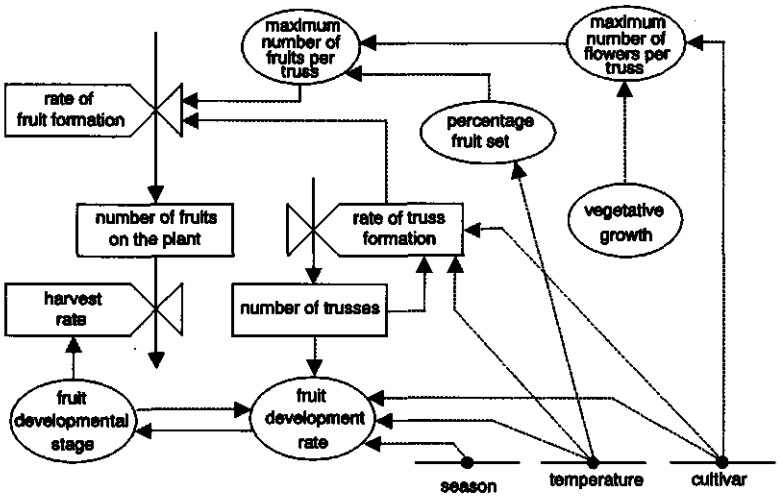

Figure 5.3.1
Diagram of the processes and factors involved in fruit formation and fruit development (symbols according to Forrester, 1961).

5.3.3 vegetative plant parts

The formation rate of vegetative units is equal to the formation rate of trusses (FR). In the model the n^{th} vegetative unit starts to grow (development stage = 0) at anthesis of truss n−3. This implies that a vegetative unit starts to grow about 3 weeks prior to anthesis of the corresponding truss. As the development rate of a vegetative unit (VDR) is defined to be equal to that of a fruit (FDR), the vegetative development rate is calculated by equation 3.4.8 but with TRUSS being the corresponding truss number and FDS replaced by the vegetative development stage (VDS). Leaves are removed at harvest of the first fruit of the corresponding truss.

5.4 Potential growth rate

5.4.1 potential growth rate of fruits

Dry matter distribution and assimilate demand are determined by the potential growth rates of the individual organs. The maximum potential growth rate of a round tomato fruit, i.e. the growth rate at nonlimiting assimilate supply is described by the first derivative of a Gompertz growth curve and given by the equations:

$$C = 1.082 \times PFW, \qquad \text{[eqn 4.4.4]}$$

$$M' = 0.397 \times [1+0.401 \times \exp(-0.202 \times TRUSS)], \qquad \text{[eqn 4.4.21]}$$

$$B' = 4.38 \qquad \text{[eqn 4.4.22]}$$

$$PFGRM_t' = C \times \exp\{-\exp[-B' \times (FDS_t - M')]\} \times B' \times \exp[-B' \times (FDS_t - M')], \qquad \text{[eqn 4.4.9]}$$

$$\text{with } FDS_t = FDS_{t-1} + FDR_{f(T \times FDS),t} \quad (FDS_0 = 0,\ 0 \le FDS_t \le 1)$$

$$PFGRM_t = PFGRM'_t \times FDR_{f(T),t} \qquad \text{[eqn 4.4.10]}$$

where PFW is the potential fruit dry weight (g) at harvest, TRUSS is the truss number, $PFGRM'_t$ is the maximum potential fruit growth rate per unit FDS (g) at t days after anthesis, FDS_t is the fruit development stage, $PFGRM_t$ is the maximum potential fruit growth rate per day (g d^{-1}) and $FDR_{f(T \times FDS),t}$ and $FDR_{f(T),t}$ is the fruit development rate (d^{-1}) with (eqn 3.4.8) and without (eqn 3.4.7) an interaction between temperature and FDS, respectively.

$FDR_{f(T),t}$ is given by:

$$FDR_{f(T),t} = a_{FDR} + 0.0012 \times \ln(RAD_{FDR}) - 0.00005 \times TRUSS + 0.02131 \times \ln(T_t/20), \qquad \text{[eq.3.4.7]}$$

where a_{FDR} is a cultivar dependent parameter; 0.0165 for 'Calypso', RAD_{FDR} is the solar radiation received by the crop (MJ m^{-2} d^{-1}) averaged over the three weeks after anthesis, TRUSS is the truss number and T_t is the 24-h mean air temperature (17-27°C).

The potential fruit dry weight at harvest (PFW, g) is described by:

$$\begin{aligned} PFW = {} & r_{PFW} \times (0.966+0.040\times FPOS-0.006\times FPOS^2)\times \\ & 9.2\times[1-0.0803\times(TF-21)-0.0068\times(TF-21)^2]\times \\ & [1-0.878\times\exp(-0.143\times TRUSS-0.0465\times RAD_{PFW})], \end{aligned} \quad \text{[eqn 4.3.6]}$$

where r_{PFW} is a cultivar dependent parameter representing the potential fruit weight relative to 'Calypso', FPOS is the fruit position within the truss, TF is the average temperature (17-23°C) since anthesis, TRUSS is the truss number and RAD_{PFW} is the average solar radiation (MJ m^{-2} d^{-1}) received by the crop over the three weeks after anthesis of the first flower of the first truss.

Note that it is assumed here that the long-term potential fruit growth rate is determined by the average temperature (TF) since anthesis.

On top of the long-term effect of temperature it is supposed that when the current temperature (T) deviates from the average temperature (TF) to which the fruit is adapted, a short-term temperature effect on PFGRM exists that can be represented by the factor:

$$Q_{10,g}{}^{0.1(T-TF)}, \quad \text{[eqn 4.7.1]}$$

where $Q_{10,g}$ is the Q_{10}-value for short term temperature response of potential fruit growth and equals 2.4, T is the 24-hour mean air temperature (°C) and TF is the average temperature since anthesis (°C).

Furthermore, the potential growth rate of a fruit adapts to the plant's amount of dry matter available for growth (DMA) according to:

$$\begin{aligned} & af_t = (DMA_t-\Sigma PGR_t)/\Sigma PGRM_t, \\ & \text{with } -0.03 \le af_t \le 0.03, \end{aligned} \quad \text{[eqn 4.5.4]}$$

where af_t is the relative adaptation factor of the actual potential growth rate to the availability of dry matter at day t, DMA_t is the plant's dry matter available for growth (g d^{-1}) and ΣPGR_t and $\Sigma PGRM_t$ are the actual and maximum potential growth rates cumulated over the above-ground plant (g d^{-1}), respectively.

The actual potential fruit growth rate is given by:

$$PFGR_t = (PFGR_{t-1} + af_{t-1} \times PFGRM_{t-1}) \times PFGRM_t/PFGRM_{t-1},$$
$$\text{with } 0 \leq PFGR_t \leq PFGRM_t, \qquad \text{[eqn 4.5.5]}$$

where $PFGR_t$ is the potential fruit growth rate at day t from anthesis, $PFGRM_t$ is the maximum potential fruit growth rate, i.e the potential growth rate for fruits grown with nonlimiting assimilated supply from anthesis and af_t is the relative adaptation to the dry matter available.

The adaptation factor *af* is assumed to be equal for all organs and, moreover, *af* is not affected by the organ's development stage. Hence, in the model the amount of calculations are reduced when introducing a single scalar type variable that represents the cumulative (over time)-adaptation (CAF).

$$CAF_t = CAF_{t-1} + af_t,$$
$$\text{with } 0 < CAF_t \leq 1 \text{ and } CAF_0 = 1, \qquad \text{[eqn 5.4.1]}$$

$PFGR_t$ then is simply related to $PFGRM_t$ as:

$$PFGR_t = CAF_{t-1} \times PFGRM_t, \qquad \text{[eqn 5.4.2]}$$

Implicitly, it is assumed that for each new fruit the initial potential growth rate ($PFGR_0$) is already adapted to the previous assimilate availability. The determinants of the fruit's potential growth rate are schematically presented in figure 5.4.1.

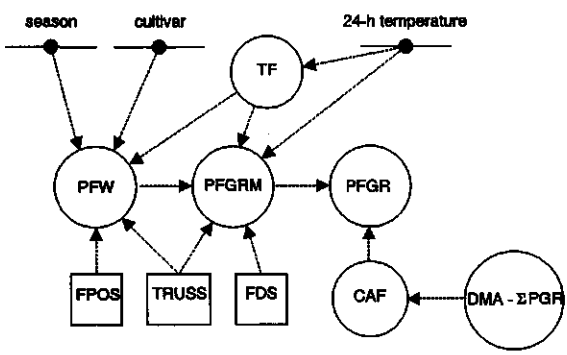

Figure 5.4.1.
Determinants of the potential fruit growth rate (PFGR). PFW is the potential fruit weight, PFGRM is the maximum potential fruit growth rate, TF is the average temperature since anthesis, FPOS is the position of the fruit in the truss, TRUSS is the truss number, FDS is the fruit's development stage, CAF is a factor representing the cumulative adaptation to assimilate availability, DMA is the dry matter available for growth and ΣPGR is the actual potential growth rate cumulated over the above-ground plant.

5.4.2 potential growth rate of vegetative plant parts

The shape of the growth curve of a vegetative unit is assumed to be equal to that for fruit growth (section 4.6). The potential growth rate of a vegetative unit is related to the potential growth rate of a single (first positioned) fruit of the corresponding truss by:

$$PVGR_t = \{3.59 \times \exp[-0.168 \times (T_t - 19)]\} \times PFGR_t, \qquad \text{[eqn 4.6.2]}$$

where $PVGR_t$ is the potential growth rate (g d^{-1}) of a vegetative unit t days after start of growth, T_t is the 24-h mean temperature (^oC), and $PFGR_t$ is the potential growth rate (g d^{-1}) of a single fruit (first fruit position in the truss) of the corresponding truss.

PFGR required for equation 4.6.2 is calculated with the vegetative development stage (VDS=0 at start of growing) and average temperature (TV) determined analogously to FDS and TF in the description of PFGR. According to the assumption that the growth period of a vegetative unit is equal to that of a fruit, a vegetative unit stops growing when the value of VDS exceeds 1. Note that since leaves start to grow about three weeks before fruits of the corresponding truss but are removed at harvest of the fruits (section 5.3.3), the period the leaves are on the plant is longer than the duration of the fruit growth period.

Usually, the first truss is initiated after about 9 to 12 leaves (Dieleman and Heuvelink, 1992), which, in the model, are all considered to belong to the first vegetative unit. In order to account for the higher number of leaves and longer stem, the potential growth rate of the first vegetative unit is set at 2.5 times that of a unit with three leaves. This ratio is less than expected on the basis of the number of leaves because the first leaves are small compared to those just preceding the truss. Furthermore, as the model starts at anthesis of the first truss, the initial values for the development stages of the first three vegetative units is set at 0.40, 0.24 and 0.12, respectively.

5.5 Dry matter distribution

When growth is limited by assimilate supply (source-limited), the dry matter available for growth (DMA) is equal to the plant's increase in dry weight. In the present model, daily increase in dry weight is one of the input variables but, in combination with a model for crop photosynthesis, DMA may be calculated from gross photosynthesis and respiratory losses. In the model DMA is distributed proportionally to the potential growth rates of the individual organs. So, the growth rate of each organ is given by:

$$GR_j = PGR_j/\Sigma PGR \times DMA, \text{ for } DMA \leq \Sigma PGR,$$
and
$$GR_j = PGR_j, \text{ for } DMA > \Sigma PGR, \qquad \text{[eqn 5.5.1]}$$

where GR_j is the growth rate of organ j (g d^{-1}), PGR_j is the potential growth rate of organ j (g d^{-1}), ΣPGR is the potential growth rate (g d^{-1}) cumulated over the above-ground plant ($\Sigma PGR=\Sigma PVGR+\Sigma PFGR$) and DMA is the amount of dry matter available for growth (g d^{-1}).

When the plant's cumulative potential growth rate (ΣPGR) is less than the dry weight available for growth, i.e. the growth is sink-limited, all organs grow at their potential rate and the surplus of DMA ($DMA-\Sigma PGR$) remains available for the next day. It should be noted that because the factor CAF is common to all organs, as long as there is no significant storage, simulated dry matter distribution is not affected by adaptation of potential growth rates to assimilate availability.

5.6 Assimilate demand

The assimilate demand of an organ is determined by the requirements for maintenance respiration and growth (section 4.1) and is described by:

$$AD = MAINT \times W \times Q_{10,m}^{0.1(T-Tr)} + PGR \times ASRQ, \qquad \text{[eqn 4.7.3]}$$

where AD is the assimilate demand (g CH_2O d^{-1}), MAINT is the maintenance respiration coefficient; equal to 0.025 and 0.01 g CH_2O g^{-1}dw d^{-1} at 25°C for vegetative parts and fruits, respectively (Spitters *et al.*, 1989), W is the organ's dry weight (g), T is the 24-h mean temperature (°C), Tr is the reference temperature (here 25°C) and $Q_{10,m}$ is the Q_{10}-value for the temperature effect on maintenance respiration and equals 2.0 (Walker and Thornley, 1977), PGR_t is the organ's potential growth rate (g d^{-1}) and ASRQ is the assimilate requirement quotient; equal to 1.23 and 1.20 g CH_2O g^{-1}dw for vegetative plant parts and fruits, respectively (Gijzen, 1994).

Maintenance respiration of the stem part of the vegetative unit after the leaves are removed is ignored. The plant's total assimilate demand equals the sum of the demand by the individual organs. It has been discussed in section 4.7 that it may be useful to distinguish between the actual assimilate demand, - which is based on the actual potential growth rates that account for acclimation to previous assimilate availability -, and the potential assimilate demand calculated from the maximum potential growth rates. In the model the plant's actual as well as the potential assimilate demand are calculated. In both the short-term temperature effect on potential growth rates ($Q_{10,g}$) is included.

5.7 Fruit dry matter content

Dry matter content of harvestable fruits depends on the day of year, air temperature and the electrical conductivity in the root zone as described by:

$$FDMC = r_{FDMC} \times [5.39 - 0.743 \times \cos\{2 \times Pi \times (DAYNO - 16)/365\} + 1.7 \times (EC - 0.3) + 0.07 \times (TF - 23)], \quad \text{[eqn 4.2.3]}$$

where FDMC is the fruit dry matter content ($g^{-1} \times 100\%$) at harvest, r_{FDMC} is a cultivar dependent parameter representing the dry matter content relative to 'Calypso', Pi is a constant equal to 3.14159, DAYNO is the day of the year, EC is the electrical conductivity (0.3-0.9 S m^{-1}) in the root environment averaged over the fruit growth period and TF is the average air temperature (17-23°C) during the fruit growth period.

5.8 Modelling per unit ground area

To simulate the effect of retaining extra shoots, -for example retained in a ratio of one to every four plants-, calculations are made per unit ground area instead of per plant. Conversion from plant to ground area is done by multiplying state and rate variables that are expressed per plant, by the shoot density (number of shoots per ground area). Two extra vector type state variables are added, representing the number of fruits (FN) and vegetative units (VN) per ground area with similar position on the plant, respectively. FN and VN are integers with a value less or equal to the number of shoots in the area considered. In the present model for numerical reasons the area is 1000 m^2.

5.9 Input required

The model requires daily values of 24-h mean temperature (°C), global radiation outside the glasshouse (MJ m^{-2} d^{-1}), electrical conductivity in the root environment (S m^{-1}) and dry weight increase (g m^{-2} d^{-1}). Further, initial plant density (plants m^{-2}), day of flowering of the first truss, number of extra shoots relative to the initial number of plants (e.g. 1:4), date of first flowering of the extra side shoots, day of removing the tops and the glasshouse's light transmission are needed. In case of truss pruning the (maximum) number of fruits left on each truss is also required.

When another cultivar than 'Calypso' is used, some cultivar dependent parameters have to be set, *viz.* the constants in the equations for flowering and fruit development rate, the number of flower buds initiated per truss relative to 'Calypso', the maximum fruit weight relative to 'Calypso' and a factor that represents the fruit dry matter content relative to 'Calypso'.

5.10 Constraints

The sub-models on organogenesis and development are mainly obtained from experiments with the round tomato cultivar 'Calypso', a temperature range of 17 to 27°C, an electrical conductivity in the root environment between 0.3 and 0.9 S m^{-1}, North-West European light conditions and adequate watering and nutrition. Concerning the factors air humidity and CO_2-concentration, it seems reasonable to assume that these do not affect development processes (Chapter 3).

Fruit growth and dry matter distribution were studied in experiments in which temperatures were between 17 and 23°C for at least several weeks (long-term response). Short-term response, however, may be different. It is assumed that electrical conductivity in the root environment, air humidity and CO_2-concentration do not affect potential growth rates (Chapter 4) and subsequent dry matter distribution.

Fruit dry matter content was investigated in a temperature range from 17 to 23°C and at EC-values from 0.3 to 0.9 S m^{-1}. The seasonal trend in fruit dry matter content is probably rather specific for glasshouse cultivation in North-West Europe.

6

EVALUATION OF THE MODEL

6.1 Introduction

A simulation model has to be evaluated on the validity of its predictions. Evaluation is generally done by comparing model predictions with data obtained from the real system. These data should be independent of experiments used to develop the model (van Keulen, 1976; Loomis *et al.*, 1979). Discrepancies between simulation results and the real system may have different causes, e.g. incorrect hypotheses the model is based on, wrongly chosen mathematical equations or erroneous parameter values.

The hypotheses underlying the model can be tested best with results from rather extreme treatments. For example, whether assimilates are partitioned from one imaginary pool was checked by growing tomato plants consisting of two shoots and comparing fruit growth of shoots bearing very different numbers of fruits (Heuvelink, 1995*c*). In addition to testing the hypotheses, for proper validation each mathematical equation in the model, corresponding to distinct plant processes, has to be verified separately (van Keulen, 1976). This puts specific demands on the data to compare the model predictions with.

Data for validation were collected in commercial crops. It is accepted beforehand that these data can not satisfy all of the above mentioned requirements (e.g. extreme treatments) for a thorough evaluation. In data the variation of environmental factors corresponds mainly with the time of year. Solar radiation is low in spring and autumn and high in summer. Temperature (e.g. fig 6.3.1*a*) and crop growth rate (e.g. fig 6.3.7) show a similar seasonal pattern. In addition, crop age is related to the day of year. The main input variables required by the model, therefore, are highly correlated, which makes the data less suitable for model validation. Comparison with model predictions, however, will demonstrate whether the model can predict development and dry matter distribution in a normally grown crop, an essential condition for using the model in practice. Additional to the value for testing the model, the results from measurements in practice provide insight in climatic conditions and development and growth of a commercially grown crop throughout a whole cropping season.

Predictions of crop assimilate demand cannot be validated because assimilate demand cannot be measured directly. Therefore simulation results concerning assimilate demand are discussed in the next chapter.

A more extensive validation of the model requires additional independent experiments in which environmental conditions or crop measures differ considerably from normal practice. Such experiments and subsequent model

validations have recently been conducted by Heuvelink for the principle of dry matter distribution (Heuvelink, 1995*c*) and the descriptions of truss flowering rate and fruit development (Heuvelink, 1995*d*).

For further development or applications of the model it is useful to know which variables should be known or predicted with high accuracy and which may be less precise. To this purpose, effects of changes in input and crop variables on relevant outputs of the model are investigated. Because the model does not describe the whole sink-source system, -for example feedback on changes in vegetative growth on assimilate production is absent-, it should be emphasized beforehand that the results of this analysis reflect the sensitivity of the model rather than predict the real crop behaviour.

The interaction between fruit development stage and temperature on fruit development rate makes the model rather difficult to apply. Furthermore, the decrease of flowering rate with crop age and the adaptation of the actual potential growth rate to the supply of assimilate increase the complexity of the model while quantifying is based on limited experimental data. Therefore, the consequences of ignoring these influences on the model output are investigated.

6.2 Measurements at commercial nurseries

Data were collected from four crops grown in 1988, 1989, 1990 and 1992 in the same nursery (nursery I). A fifth data-set was obtained in 1989 at another nursery (nursery II). In all cases it concerned the round tomato cv. 'Calypso', except for 1992 when the cultivar was 'Pronto'. The crops were grown in Venlo-type glasshouses and trained according to the high-wire system. Generally, the first truss started to flower in January, the plants were stopped in September and fruits were harvested from March until November. In nursery I, the initial plant density was 2.27 plants m^{-2} for all years, but in March 1992 on each fourth plant one extra side shoot was retained, resulting in 2.84 shoots m^{-2}. In nursery II the plant density was 2.50 plants m^{-2}. All crops were grown on rockwool, watered with a standard mineral nutrient solution (Sonneveld and de Kreij, 1988). The glasshouses were heated with a pipe-rail heating system and an additional pipe amidst the canopy for nursery II and nursery I in 1990 and 1992. CO_2 was applied from the central boiler and supplemented with liquid CO_2 at nursery I. The set-point was reduced with increasing ventilation rate of the glasshouse. CO_2-concentrations achieved between 10 and 16 h were circa 800,

400 and 500 μmol^{-1}, respectively for spring, summer and autumn period. Environmental control and data acquisition (sample time of one minute) was accomplished with a Priva (De Lier, the Netherlands) process computer at both nurseries.

Temperature was measured by a shaded and ventilated NTC-element in the centre of the glasshouse, just below the top of the plants and recordings were averaged per day before stored. The recordings were occasionally verified with readings from a calibrated sensor. CO_2-concentration in the glasshouse was recorded as hourly averages. A few times a year the sample tubes were checked for leakage and the analyzers (Siemens) were calibrated. Outside solar radiation was measured by a Kipp CM11 solarimeter at GCRS, which is at a distance of circa 3 and 4 km from nursery I and nursery II, respectively. The light transmission of the glasshouses for diffuse radiation was measured to be 0.70 at nursery I and 0.75 at nursery II. Weekly recordings of the electrical conductivity in the rockwool slab were available from nursery I.

Non-destructive measurements were done on a stand of six tomato plants in the centre of the glasshouse. In 1992 eight plants with a total of 10 shoots were measured. The highest flowering and harvestable trusses and also the highest number of flower and harvest ripe fruit within these trusses were recorded weekly. For each truss the number of fruits was recorded at completion. Picked fruits and removed leaves (totals for the whole stand) were counted and weighed. Recordings at different harvests were add up to make weekly values. In 1990, once a week the cumulative weight of each of the six plants was measured non-destructively with a weigh-clock (10 kg $\pm$ 10 g) and, after a correction for crop layering (+37 g fw per event, estimated from the number of events and the stem weight at the end of the season). From this weekly increase in above-ground fresh weight for the whole stand was calculated. Stem and remaining leaves and fruits of each of the six plants were weighed at the end of the cropping season. In 1992, eight plants were weighed continuously by two electronic force gauges (Aikho 9020) and 5-minute readings were recorded by the process computer. From these data daily fresh weight increase was calculated (de Koning and Bakker, 1991). Every fortnight in 1989 and 1990 dry matter content was determined of a sample of ten harvest-ripe fruits (drying 5 days at 80°C), whereas in 1992 every four weeks 15 fruits were dried.

In addition to the non-destructive measurements of plant fresh weight, destructive measurements were made every four weeks in 1990 and 1992. On each sampling occasion, three and four plants in 1990 and 1992, respectively, were selected from the centre of the glasshouse but at sufficient distance from

the plants used for non-destructive measurements. In 1992 one plant per sample had an extra shoot. Leaf, fruit and stem fresh and dry weights and leaf area were measured. Dry matter content of total crop growth since the last harvest was calculated for each 4-week period and used to calculate dry weight growth from non-destructive (weekly and daily for 1990 and 1992, respectively) measurements of fresh weight increase.

To obtain a data-set that is also suitable for evaluation of more comprehensive models (e.g. including a photosynthesis routine), measurements not required for testing the present model were included (e.g. leaf area and CO_2-concentration). Some of the results have been published previously (de Koning, 1989*b*; 1993).

6.3 Comparing model predictions with measurements

6.3.1 procedure

Sub-models of truss formation rate, fruit growth period, dry matter distribution, number of fruits that develop per truss and fruit dry matter content at harvest were tested separately as much as possible. As in the model flowering rate (truss formation rate) and fruit growth period are independent of growth rate and dry matter distribution, their descriptions could be verified for all five crops measured. Fruit growth period was simulated for the first positioned fruit of each truss and compared with the fruit growth period estimated from interpolation of weekly recordings of flowering and harvestable truss.

Dry matter distribution and number of fruits that develop per truss could only be predicted where dry matter increase was determined (nursery I, 1990 and 1992). For the prediction of dry matter distribution, truss formation rate and numbers of fruits per truss were input to the model. Although fruit growth period was measured, it could not be used as an input because the model simulates fruit development rate where fruit growth period is a result. The measurements allowed for calculating vegetative and generative growth rate for 4-week periods. The output of the simulations was averaged over the same periods to facilitate the comparison.

In the model the number of fruits per truss is related to the weight of the corresponding vegetative unit at anthesis of the next truss (section 3.3) but this characteristic was not measured. Therefore the number of fruits per truss was predicted from vegetative weight as simulated with measured number of fruits as input. Information about the different simulations performed is summarized in table 6.3.1.

Table 6.3.1
Output of the (sub-)model, number of crops available, interval at which predictions were compared with observed data and input (daily values) to the model.

output	number of crops	interval	input measured	input predicted
number of flowering truss	5	1 week	temperature	
fruit growth period	5	1 truss	temperature, radiation	
dry matter distribution between fruits and vegetative plant parts, fruit dry weight at harvest	2	4 weeks[1)]	temperature, radiation, crop growth rate, truss formation rate, number of fruits per truss	fruit growth period
number of fruits per truss	2	1 truss	temperature	weight of each vegetative unit at anthesis of the next truss
fruit dry matter content at harvest	3	2 weeks[2)]	temperature, EC, fruit growth period	

1) fruit weight per week
2) 4 weeks in 1992

The model is mainly based on experiments with cv. 'Calypso'. In 1992, however, 'Pronto' was grown and some cultivar dependent parameters may differ from those determined for 'Calypso'. Cultivar trials at commercial nurseries showed that the flowering rate of 'Pronto' is 0.008 trusses d^{-1} higher than that of 'Calypso' (table 3.2.5) from which it follows that the constant a_{FR} in the equation for flowering rate (eqn 3.2.3) is -0.288 trusses d^{-1} for 'Pronto' (-0.296 for 'Calypso'). The cultivar dependent parameter in the equation for fruit development rate was assumed to be equal to that of 'Calypso', which seems plausible as Cockshull *et al.* (1992) observed only small differences between the fruit growth period of four round tomato cultivars. Additionally, the cultivar dependent parameters in the descriptions for number of fruits per truss, potential fruit weight and dry matter content of 'Pronto' were assumed to be equal to those for 'Calypso'.

6.3.2 results

flowering rate and fruit growth period

Flowering rate and fruit development are mainly determined by temperature (Chapter 3). For all years the 24-h average temperature was circa 19°C in spring and late autumn and some degrees higher, with extremes up to 26°C, in summer (figs 6.3.1*a*, 6.3.2*a*, 6.3.3*a*, 6.3.4*a* and 6.3.5*a*). The summer of 1988 was relatively cool, while late summer of 1990 was fairly warm.

Until topping, the tomato plants produced 30 to 35 trusses. Up to about truss number 10 predicted and observed truss numbers agreed well but, except for the crops of 1989 (figs 6.3.2*b*, 6.3.3*b*), the predicted flowering truss number at the end of the cropping season was lower than the actually observed number (figs 6.3.1*b*, 6.3.4*b*, 6.3.5*b*). To account for the different flowering rate observed for a young and an old crop (section 3.2) a linear decrease with plant age was assumed (eqn 3.2.3). However, the present crop recordings indicate that the decline appears rather suddenly, as demonstrated for the crop of 1992 (fig 6.3.5*c*). Therefore, simulation runs were also made ignoring the effect of age ($FR=-0.303+0.1454\times\ln(T)$, table 3.2.10; mean of expts 307/90a, 307/90b and 210/90). In most cases, this gave a better prediction in the first half year but for three crops the flowering rate at the end of the cropping season was overestimated (figs 6.3.1*b*, 6.3.2*b*, 6.3.3*b*, 6.3.4*b*, 6.3.5*b*), indicating that the influence of plant age cannot be ignored completely. At the end of the season the decrease in flowering rate may be even larger than the effect predicted by the model with the effect of plant age included (fig 6.3.5*c*).

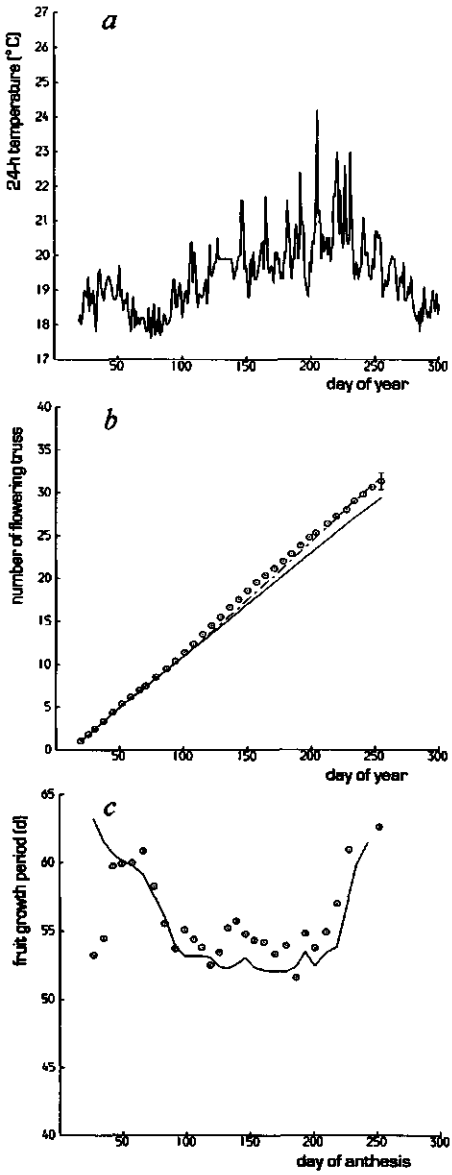

Figure 6.3.1
Nursery I, 1988. *a*: time course of the 24-h mean temperature, *b*: measured (O) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering truss number, *c*: measured (O) and predicted (——) fruit growth period.

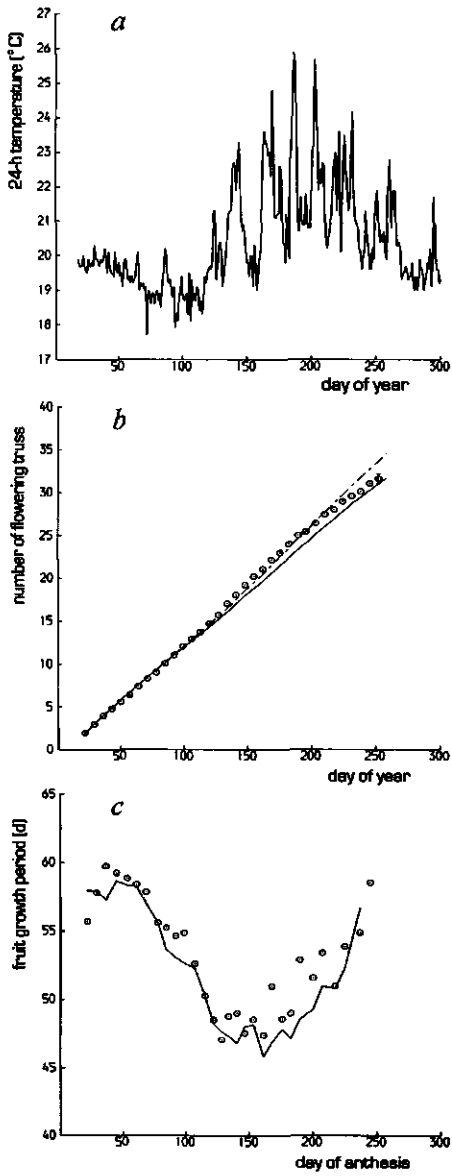

Figure 6.3.2
Nursery I, 1989. *a*: time course of the 24-h mean temperature, *b*: measured (O) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering truss number, *c*: measured (O) and predicted (——) fruit growth period.

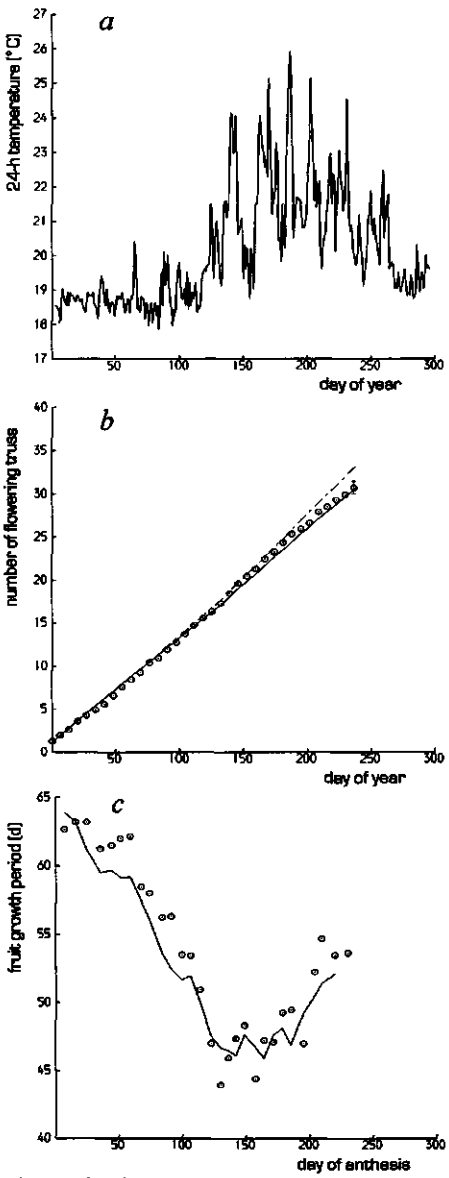

Figure 6.3.3
Nursery II, 1989. *a*: time course of the 24-h mean temperature, *b*: measured (O) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering truss number, *c*: measured (O) and predicted (——) fruit growth period.

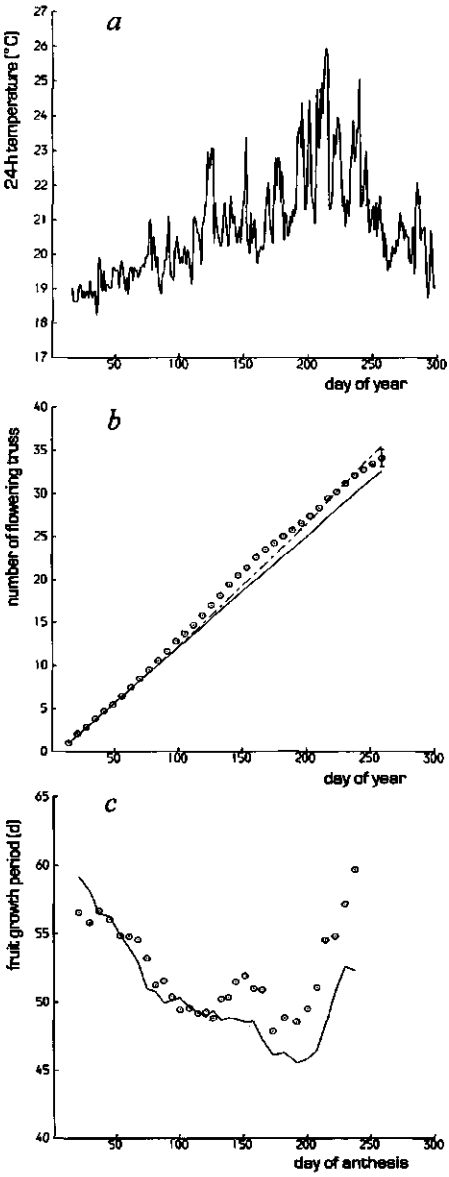

Figure 6.3.4
Nursery I, 1990. *a*: time course of the 24-h mean temperature, *b*: measured (O) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering truss number, *c*: measured (O) and predicted (——) fruit growth period.

In figures 6.3.1*c*, 6.3.2*c*, 6.3.3*c*, 6.3.4*c* and 6.3.5*d* observed and simulated fruit growth period of each truss (first positioned fruit) are plotted against the date of anthesis. Generally, in early spring and in autumn it took about 60 days from anthesis until harvest, while in summer the fruit growth period approximated 45 days, except in the cool summer of 1988. For the two crops of 1989 (figs 6.3.2*c* and 6.3.3*c*) and the crop of 1992 (fig 6.3.5*d*) the model predicted the fruit growth period accurately. In 1988 the growth period of the first two trusses was much shorter than predicted (fig 6.3.1*c*). For the same crop and especially for the crop of 1990 (fig 6.3.4*c*), the fruit growth period in the second semester was consistently underestimated by a few days.

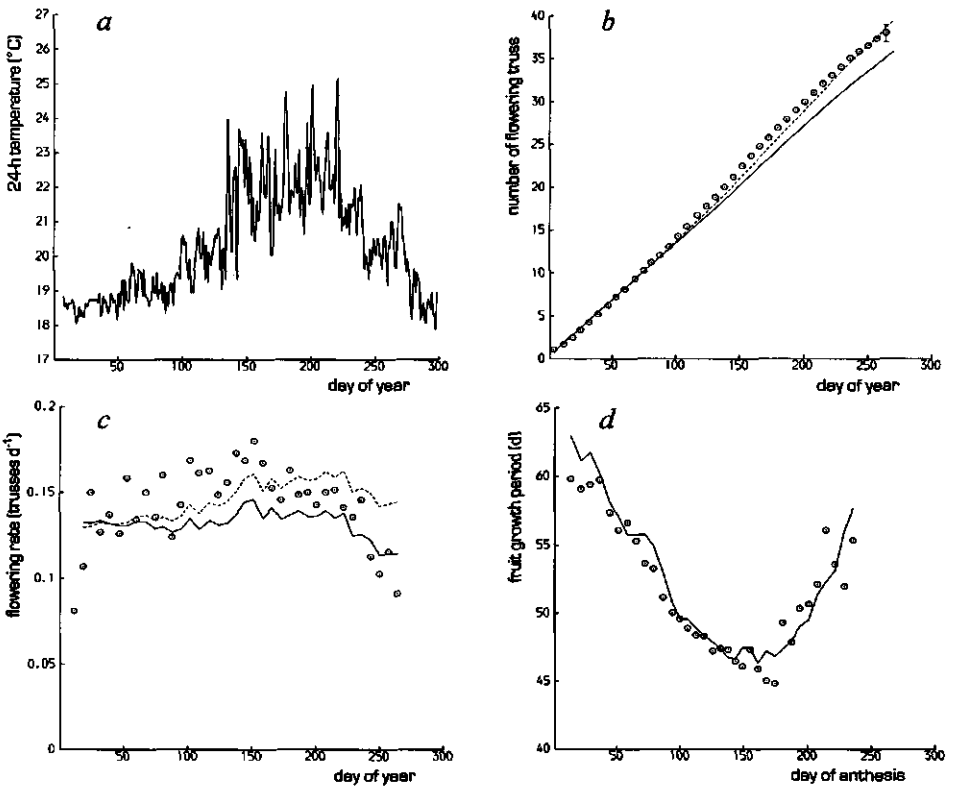

Figure 6.3.5

Nursery I, 1992. *a*: time course of the 24-h mean temperature, *b*: measured (○) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering truss number *c*: measured (○) and predicted (—— with effect of ageing; ----- without effect of ageing) flowering rate, *d*: measured (○) and predicted (——) fruit growth period.

dry matter distribution and fruit weight

In both years cumulative dry matter production was about 4 kg m^{-2} (fig 6.3.6) with daily rates up to 28 g m^{-2} day^{-1} (section 7.2). The cumulative fraction of dry matter distributed to the fruits was 0.72 for both crops. Predicted values were 0.75 and 0.72 for 1990 and 1992, respectively. The difference in 1990 resulted from an underestimation of vegetative growth in late summer (fig 6.3.7*a*).

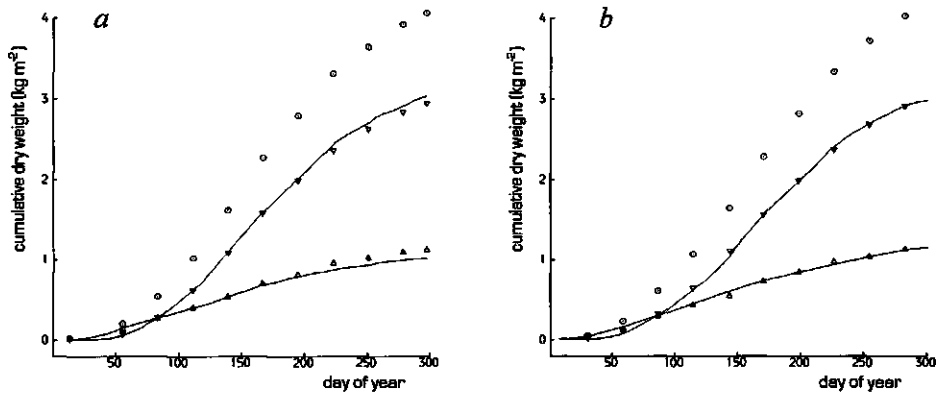

Figure 6.3.6

Nursery I, measured (○, total above ground; △, stem and leaves; ▽, fruit) and predicted (——) cumulative dry weights. *a*: 1990, *b*: 1992.

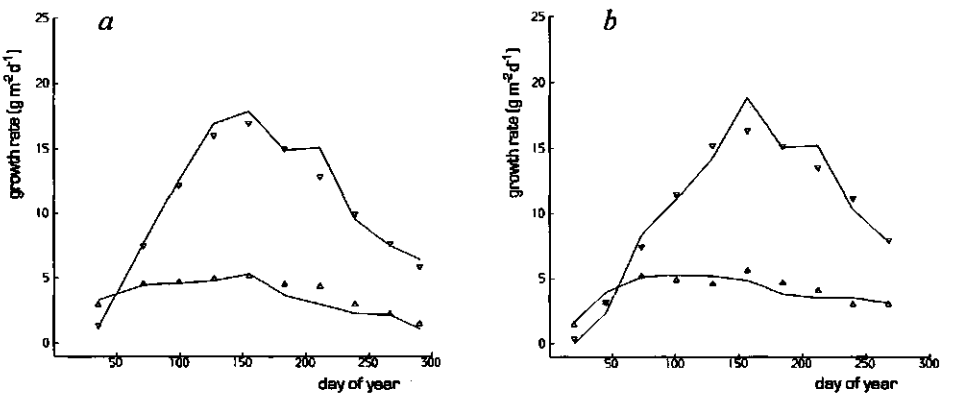

Figure 6.3.7

Nursery I, measured (△, stem and leaves; ▽, fruit) and the predicted (——) growth rates. *a*: 1990, *b*: 1992.

In 1990 the seasonal variation in fruit weight (fig 6.3.8) was larger (2.7-5.4 g fruit^{-1}) than in 1992 (2.6-4.2 g fruit^{-1}). Fruit weight was predicted accurately except for considerable overestimation in late summer of 1990 (fig 6.3.8*a*) and underestimation in the first harvests of 1992 (fig 6.3.8*b*).

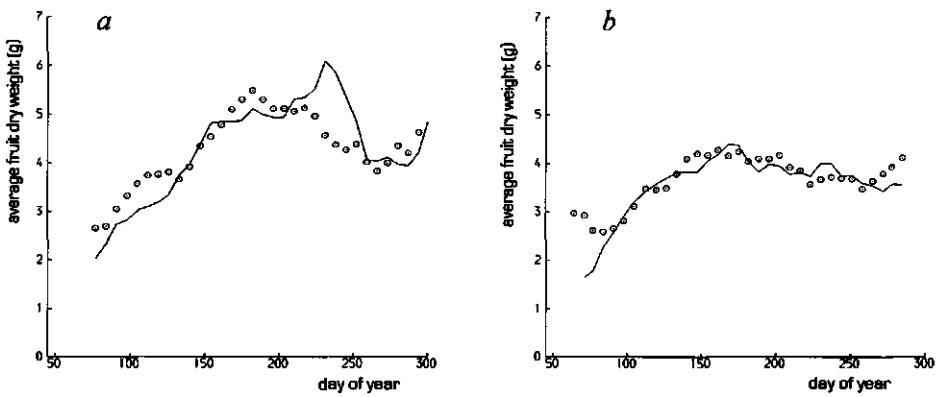

Figure 6.3.8

Nursery I, time course of weekly averages of fruit weight at harvest, measured (○), predicted (——). *a*: 1990, *b*: 1992.

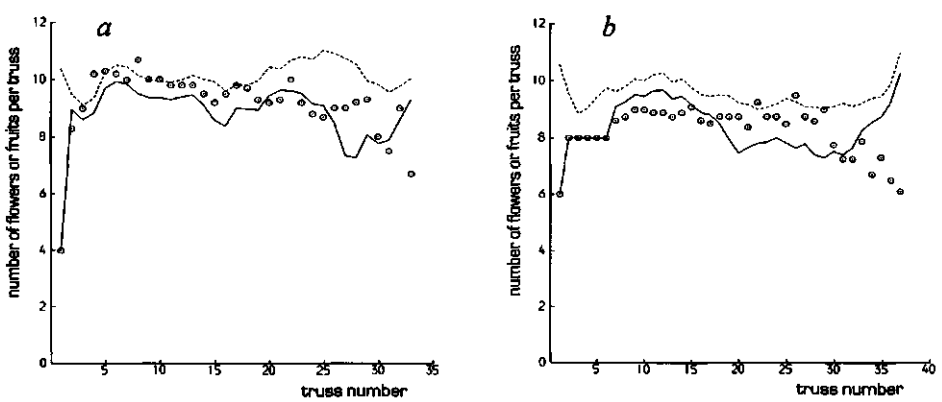

Figure 6.3.9

Nursery I, observed numbers of fruits per truss (○) and predicted number of flowers (-----) and fruits (——) per truss. *a*: 1990, *b*: 1992. In 1990 the trusses 1 and 2, and in 1992 the trusses 1 to 6 were pruned.

number of fruits per truss

In both crops the number of fruits that develop per truss were remarkably constant during the cropping season, while predicted numbers, especially in 1992, showed considerably more variation (fig 6.3.9). Thus, though the general level was predicted reasonably, the number of fruits formed per truss was not predicted satisfactorily.

fruit dry matter content

In all three years where the sub-model of fruit dry matter content (FDMC) was tested, the electrical conductivity in the root zone varied between 0.7 S m^{-1} in spring and 0.3 S m^{-1} in summer. FDMC exhibited significant seasonal variation but also large differences between successive sampling dates (fig 6.3.10). Increase of FDMC in early summer was simulated well, but the model slightly overestimated the dry matter content of fruits harvested in late summer. In all three years FDMC of fruits harvested in the last few weeks was underestimated.

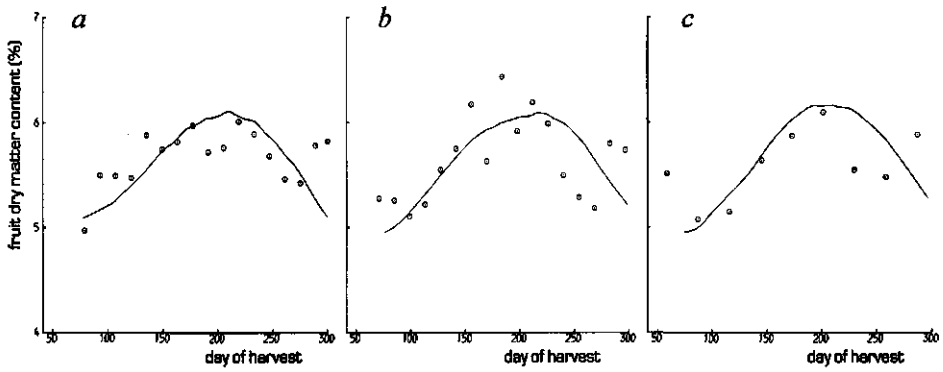

Figure 6.3.10

Nursery I, measured (○) and predicted (——) fruit dry matter content at harvest.
a: 1989, *b*: 1990, *c*: 1992.

6.4 Sensitivity analysis

6.4.1 procedure and assumptions

A sensitivity analysis was conducted on the basis of the simulation of the 1992 crop of nursery I. Input to the model consisted of daily crop growth rate, 24-h mean air temperature, daily solar radiation integral and EC in the root environment. The crop response to changes in flowering rate, numbers of fruits per truss, fruit development rate, potential fruit growth rate, potential vegetative growth rate, daily solar radiation integral and temperature were investigated. The responses to 5 percent higher value of the investigated variable are expressed as the partial sensitivity of the model output: (Dy/Y)/(Dv/V), where Dy/Y is the relative change in model output and Dv/V is the relative change in the value of the variable (here 0.05). Concerning temperature the relative effects are given for an increase of 1°C.

Using again the simulation of the 1992 crop as reference, the consequences of the following simplifications in the model were investigated: (1) ignoring the effect of plant age on flowering rate (omitting the last term of eqn 3.2.3), (2) ignoring the effect of fruit development stage on fruit development rate (using eqn 3.4.7 instead of eqn 3.4.8) and (3) ignoring adaptation to assimilate availability and short-term temperature effects on potential growth rates (i.e. CAF=1 and $Q_{10,g}$=1).

Because the model did not predict the fruit number per truss satisfactorily, in the sensitivity analysis numbers of fruits per truss were set at 6 fruits on the first truss, 8 fruits on trusses 2-6 and 9 fruits on all following trusses (based on observed numbers in the 1992 crop). As a consequence, fruit number formed is determined by truss formation rate only and any influence of assimilate availability on number of fruits formed is ignored. Predicted fruit number and variables depending on fruit number, therefore, may differ from the real crop behaviour.

For both tests the model output consisted of: number of fruits formed, vegetative growth rate, generative growth rate, maximum potential growth rate of the whole crop, and dry and fresh weight per fruit at harvest. As preliminary calculations demonstrated that the young and mature crops may respond differently, output is considered over two periods, *viz.* the time from first flowering (start of simulation) until 60 days (≈ fruit growth period in spring) later, representing the transition from a vegetative crop to a mature reproductive crop, and a subsequent period of 190 days covering the time till topping. The output of the reference is expressed per day to facilitate comparison of both periods.

6.4.2 results

effect of input and model variables

The maximum potential crop growth rate, and hence maximum assimilate demand (potential sink activity), increases with increasing number of organs formed (increasing FR and FPT) and increasing potential growth rates of individual organs (increasing PFGR and PVGR) (table 6.4.1). Since in the model the potential growth rate of a vegetative unit (PVGR) is proportionally related to the potential growth rate of a fruit (PFGR), an increase in PFGR resulted in an equally high increase of potential crop growth rate (table 6.4.1). A higher rate of fruit development (FDR) had no influence on the predicted potential growth rate of a mature crop but it substantially increased the potential growth rate of a young crop (table 6.4.1). Since temperature affects FDR, the influence of temperature on potential crop growth also differs between young and mature crops (table 6.4.1). In spite of the higher organ formation rate, potential crop growth rate declines with increasing temperature (table 6.4.1), which results from decreasing potential fruit weight (eqn 4.3.6) and decreasing PVGR (eqn 4.6.2).

Most important model variables affecting the ratio between vegetative and generative growth are potential growth rate per vegetative unit (PVGR), number of fruits per truss (FPT), and (only for a young crop) fruit development rate (FDR) (table 6.4.1). Since in the model PVGR is in proportion to PFGR (eqn 4.6.2), a change in PFGR does not affect the ratio between PVGR and PFGR and consequently dry matter distribution. Likewise, truss formation rate affects potential crop growth rate but since the ratio between number of fruits and number of vegetative units is not altered, it has no influence on the predicted ratio between generative and vegetative growth of mature crops (table 6.4.1). Higher temperature reduced the predicted amount of dry weight distributed to vegetative organs considerably (table 6.4.1) as in the model the ratio between PVGR and PFGR declines with temperature (eqn 4.6.2).

Solar radiation (RAD) is included in descriptions of fruit development rate (eqn 3.4.8) and potential fruit weight (eqn 4.3.6), but since the influences are the same for vegetative organs and fruits, the ultimate result of a change in RAD on predicted dry matter distribution is negligible (table 6.4.1).

weight per fruit decreases with greater number of fruits formed (increasing FR and FPT) and less total generative growth (table 6.4.1). The slightly different response of fruit dry and fresh weight to temperature (table 6.4.1) results from the influence of temperature on fruit dry matter content (eqn 4.2.3).

Table 6.4.1
Sensitivity of model output to a change in flowering rate (FR), number of fruits per truss (FPT), fruit development rate (FDR), potential growth rate of an individual fruit (PFGR), potential growth rate of a vegetative unit (PVGR), solar radiation integral (RAD) and temperature (T). Crop growth rate was input to the model. Simulation of the 1992 crop of nursery I was used for reference. Model output was averaged over 60 days after start of flowering, representing the transition from a vegetative to a mature crop, and between 61 and 250 days after start of flowering, representing a mature non-topped crop. Sensitivity of model output is expressed as the relative change to a relative increase of the investigated model variable (Dy/Y)/(Dv/V), except for temperature were the relative change is given per change of 1°C ((Dy/Y)/degree × 100%).

model output	reference	FR	FPT	FDR	PFGR	PVGR	RAD	T
no. of fruits formed	(m^{-2} d^{-1})							
1-60	2.49	1.1	0.8	0.0	0.0	0.0	0.0	5
61-250	3.27	0.8	1.0	0.0	0.0	0.0	0.0	4
pot. crop growth rate	(g m^{-2} d^{-1})							
1-60	10.68	1.0	0.2	1.0	1.0	0.6	0.2	-1
61-250	34.63	0.9	0.5	0.0	1.0	0.2	0.0	-7
vegetative growth rate	(g m^{-2} d^{-1})							
1-60	3.04	-0.2	-0.1	-0.4	0.0	0.3	-0.1	-11
61-250	4.36	-0.1	-0.5	-0.1	0.0	0.7	-0.0	-13
generative growth rate	(g m^{-2} d^{-1})							
1-60	2.05	0.4	0.2	0.6	0.0	-0.5	0.1	16
61-250	13.68	0.0	0.2	0.0	0.0	-0.2	0.0	4
fruit weight at harvest	(g $fruit^{-1}$)							
dry weight	4.09	-0.8	-0.7	-0.1	0.0	-0.3	0.0	0
fresh weight	70.4	-0.8	-0.7	-0.1	0.0	-0.3	0.0	-1

simplifications of the model

Ignoring the effect of plant age on truss formation rate which increased the number of fruits formed, especially for older plants, and consequently the potential crop growth rate (table 6.4.2). Dry matter distribution is not markedly affected because the ratio between number of fruits and number of vegetative units does not change. Average fruit weight decreased because the predicted number of organs formed increased (table 6.4.2).

Using the more simple description of fruit development rate (eqn 3.4.7) had no effect on dry matter distribution between vegetative and generative growth in the present example (table 6.4.2). Potential crop growth rate and fruit weight were also unaltered as fruit development rate has no effect on the number of organs formed. The same holds for ignoring the sinks' adaption to assimilate availability and the short-term effect of temperature on their potential growth rates (table 6.4.2).

Table 6.4.2
Relative change in model output (Dy/Y×100%) to (1) ignoring the effect of plant age on flowering rate, (2) using the description for fruit development rate without an influence of fruit development stage and (3) ignoring adaptation to assimilate availability (CAF=1) and short-term effects of temperature ($Q_{10,g}$=1) on potential growth rates. Simulation of the 1992 crop of nursery I was used for reference. Model output was averaged over 60 days after start of flowering, representing the transition from a vegetative to a mature crop, and between 61 and 250 days after start of flowering, representing a mature non-topped crop.

model output	original model	no effect of age on FR	no effect of FDS on FDR	CAF=1 and $Q_{10,g}$=1
no. of fruits formed	(m^{-2} d^{-1})			
1-60	2.49	4	0	0
61-250	3.27	16	0	0
pot. crop growth rate	(g m^{-2} d^{-1})			
1-60	10.68	3	0	-2
61-250	34.63	14	-1	-2
vegetative growth rate	(g m^{-2} d^{-1})			
1-60	3.04	-1	0	1
61-250	4.36	-1	0	0
generative growth rate	(g m^{-2} d^{-1})			
1-60	2.05	1	1	1
61-250	13.68	0	0	0
fruit weight at harvest	(g $fruit^{-1}$)			
dry weight	4.09	-10	0	0
fresh weight	70.4	-10	0	0

6.5 Discussion

By means of crop control, a grower aims at low (flower bud) abortion and a proper balance between vegetative and generative growth. This probably explains why numbers of fruit that developed per truss (fig 6.3.9) and vegetative growth rate (fig 6.3.7) exhibit little variation. As a consequence, these data are inappropriate to demonstrate the operation of feedback mechanisms in the crop, let alone to test a model on this aspect.

The development stage of a young crop, i.e. the number of highest flowering truss, was predicted reasonably well when the effect of plant age was ignored. Heuvelink (1995*d*) demonstrated that the same description of flowering rate is also valid at low fruit load, different plant densities and air temperatures from 17 to 23°C. With crops younger than circa six months the effect of age may be ignored, but with old crops the decrease of flowering rate has considerable influence on the number of organs formed and consequently the crop's sink capacity (table 6.4.2). Quantifying this phenomenon, however, is complicated by the fact that it does not occur very consistently, as also observed by Heuvelink (1995*a*). The decline of flowering rate seems to be related to loss of plant vigour (section 3.2). May and June of 1989 were relatively warm which may have caused early loss of vigour and explains the good predictions by the model accounting for a proportional decline of flowering rate with plant age (figs 6.3.2*b* and 6.3.3*b*). It is not exactly known what factors cause loss of plant vigour. In addition to low flowering rate, possibly the number of fruits per truss (fig 6.3.9) and the crop photosynthetic capacity (Dayan *et al.*, 1993*b*) are adversely affected. The understanding of crop vigour, therefore, deserves more attention in future research.

The considerable week-to-week differences of observed flowering rate (fig 6.3.5*c*) may (in addition to experimental error) be explained by the relatively strong response to short-term temperature variation (section 3.2). The predictions do not show any effect of these short-term fluctuations as the model simulates only the long-term temperature response.

Generally the fruit growth period was simulated accurately, giving confidence in the description of fruit development rate. The few discrepancies, e.g. the consistent underestimation in 1990 (fig 6.3.4*c*), remain unexplained. Additional support for the validity is reported by Heuvelink (1995*d*). In many cases, for

example at relatively constant temperature or when only dry matter distribution is simulated (table 6.4.2), adopting a constant temperature effect on fruit development rate (i.e. ignoring the interaction with fruit development stage) has no consequences for the predictions, while it simplifies the model considerably.

Numbers of fruit per truss was not predicted satisfactorily. Unfortunately, it cannot be ascertained whether the description of flower number (eqn 3.3.3) or the description of fruit-set (eqn 3.3.4) is wrong, because the numbers of flowers per truss were not recorded. At high temperature the prediction of the percentage fruit-set is not very reliable due to considerable variation in the experiment underlying its description (section 4.6). The underestimation of final truss size in summer (fig 6.3.9), therefore, is probably the result of the predicted percentage of flowers failing to set being too high. Observed fruit numbers on the final trusses were generally lower than predicted, which may be caused by a less vigorous crop at the end of the season. An accurate prediction is important because the number of fruits per truss is a major determinant of maximum potential crop growth, dry matter distribution between vegetative and generative growth and fruit size (table 6.4.1) and has a key position in feedback on high sink-source ratio (Chapter 1).

The distribution of dry matter between vegetative and generative growth is determined by the number of vegetative units relative to the number of fruits present and the competitive strength of the vegetative and generative sinks to attract assimilates for growth. The predictions of dry matter distribution (figs 6.3.6 and 6.3.7) and fruit weight (fig 6.3.8) support the assumption underlying the model that the (relative) competitive strength of individual organs can be quantified by potential growth rate. In the model the potential growth rate of a vegetative unit relative to that of a fruit is negatively correlated to temperature (eqn 4.6.2) but the experimental basis is weak (section 4.6). Heuvelink (1995*b*) observed no direct effect of temperature on dry matter distribution and satisfactorily simulated dry matter distribution at different temperatures assuming that potential growth rates are independent of temperature. Underestimated vegetative growth rate in summer 1990 (fig 6.3.7*a*) when temperature was high (fig 6.3.4*a*) puts extra doubts on the validity of equation 4.6.2. Therefore, simulation runs were also made ignoring the temperature effect, i.e. assuming a fixed ratio between the potential growth rate of a vegetative unit and that of a single fruit equal to 3.59. This ratio was obtained from plants grown at 19°C continuously (section 4.6). Except in spring (when temperature

was circa 19°C and consequently the distribution hardly changed) this resulted in a consistent overestimation of the dry matter distributed to the vegetative organs (results not shown). Hence, the fraction of dry matter distributed to the fruits at the end of the year was underestimated, *viz.* 0.68 and 0.67 for 1990 and 1992, respectively, compared to 0.72 measured in both years. These results are an extra indication of the existence of a direct influence of temperature on competition for assimilate between vegetative and generative sinks. However, considering the difference with the results of Heuvelink and the fact that growers regard temperature as a major tool in control of the balance between vegetative and generative growth (Chapter 1), more experimental work is needed for a better understanding and a more solid description of this aspect.

Potential crop growth rate and dry matter distribution of young and mature crops may respond differently to changes in model variables or temperature (table 6.4.1). The different response is mainly due to the fact that the organs present on a young plant are (on average) relatively young, in contrast to a mature crop where all development stages are present in more or less equal numbers. Higher organ development rate (at the same temperature), for example, increases the potential growth rate of a young plant because (1) potential growth rates of individual organs increase directly (fruit growth period decreases while the potential size is not affected) and (2) for a very young crop the (relatively low) average development stage becomes closer to the stage at which highest potential growth rate is obtained. The first effect also holds for a mature crop but is compensated by a proportional decrease in number of organs present on the plant (Chapter 8).

The ratio between number of vegetative units and fruits is high at first fruit set, and decreases to a more or less stable value when the crop reaches maturity. High plant development rate (FR) enhances this decrease and therefore promotes generative growth in a young crop (table 6.4.1). In addition, initially the average development stage of fruits, and consequently their potential growth rate and competitive strength to attract assimilates, is low compared to the vegetative plant parts. This difference decreases faster with increasing FDR which explains the positive effect of FDR on fruit growth in a young crop (table 6.4.1). The effect of number of fruits per truss (FPT) and potential vegetative growth rate (PVGR) on dry matter distribution depends on the distribution ratio itself and therefore differs between young and mature plants (table 6.4.1).

FR, FDR, potential fruit weight and the ratio between PVGR and PFGR are all influenced by temperature. Predicting the final temperature effect on assimilate demand and dry matter distribution to temperature is a major feature of the present model. Without trying to explain the overall response from changes in distinct variables, it is concluded from the simulations that increase of temperature (1) significantly reduces vegetative growth in young as well as mature crops, (2) promotes generative growth relatively most in a young crop and (3) reduces the maximum potential growth rate of a mature crop (table 6.4.1).

Adaptation of potential growth rates to assimilate availability (*af* in eqn 4.5.4) as well as the short-term effect of temperature on potential growth rates ($Q_{10,g}$) were assumed similar for all organs (Chapter 5). Hence these factors did not affect the relative competitive strength of individual sinks which explains why the effect could be ignored without changing predicted dry matter distribution (table 6.4.2). In fact, then dry matter distribution is in proportion to the maximum potential growth rates, as in the models TOMGRO (Dayan *et al.*, 1993*a*) and TOMSIM (Heuvelink and Bertin, 1994). In the present example the growth of individual organs was not affected (results not shown) but differences can be expected when supply of assimilate exceeds the actual demand for longer time or adaptation rates differ for different organs.

The general level and seasonal trend of fruit dry matter content at harvest was predicted well. Underestimation at the end of the cropping season (fig 6.3.10) may be explained by decrease of water availability due to less frequent watering in this period in order to dry the rockwool slabs. In addition, a relatively high assimilate availability for the last fruits (Chapter 7; figs 7.2.1*a* and 7.2.2*a*), as confirmed by the relatively high weight of the final fruits (fig 6.3.8), may contribute (section 4.2). The model did not account for considerable differences in FDMC of successive samples. In experiments similar differences were found for different sample data but not between replicates (data not shown), which indicates that the observed variation is real. Possibly the short-term fluctuations are related to changes of the crop water status.

6.6 Conclusions

In summary, it is concluded that the formation rate of trusses (flowering rate) and consequently that of vegetative plant parts is predicted well, though the influence of plant age has to be quantified better to improve predictions for old crops. The accurate prediction of the fruit growth period puts confidence in the description of fruit development rate. In several cases, e.g. for prediction of the ratio between vegetative and generative growth, the varying sensitivity to temperature during fruit development may be ignored. Yearly courses of vegetative and generative crop growth rate and weight of fruits at harvest were successfully predicted which support the hypothesis underlying the model that dry matter distribution can be quantified by the potential growth rates of individual organs. It made no difference whether dry matter distribution was modelled on the basis of maximum or actual (adapted to assimilate supply and including a short-term response to temperature) potential growth rates. More research, however, is needed for better understanding and modelling (potential) growth rate of vegetative plant parts, especially with respect to the influence of temperature. Number of fruits that develop per truss was not predicted satisfactorily. When improving the model more attention should be given to the different processes determining truss size.

7

THE MODEL AS THEORETICAL BASIS FOR CROP CONTROL

7.1 Introduction

The objective of this study was to develop a growth model that can advise the grower in the use of crop measures (i.e. shoot density and fruit pruning) and temperature for control of crop growth, in particular with respect to assimilate demand and dry matter distribution (Chapter 1). This chapter presents three ways the model can support crop control. The first example concerns predicting the crop's assimilate demand. Yearly course of assimilate demand is simulated on the basis of measurements on commercially grown crops as presented in Chapter 6. Secondly, the model may be used to predict the effect of crop measures and temperature on assimilate demand, assimilate distribution and fruit production. Results of some case studies are discussed. Thirdly, this chapter demonstrates how model predictions may be a basis for a tactical plan (covering a whole cropping season) concerning shoot density and fruit pruning.

7.2 Yearly course of assimilate demand

7.2.1 introduction

Assimilate demand, defined as the maximum ability of a plant to process carbohydrates (Chapter 1), consists of a requirement for maintenance and a demand for growth (section 4.1). The latter seems to adapt to the previous assimilate availability (section 4.5). Therefore, a potential and an actual assimilate demand can be distinguished (section 4.7). The potential demand is fully expressed after a prolonged surplus of assimilate (sink-limited growth) and is determined by the number and maximum potential growth rates of the sinks present. The actual demand also depends on the extent to which potential growth rate (i.e. the amount of processing machinery, section 4.7) is decreased through adaptation to limited assimilate supply. It should be remembered that assimilate demand, as the counterpart of assimilate production, is an abstract variable that cannot be measured directly. The crop's assimilate demand, therefore, can only be estimated by simulation.

Yearly courses of potential and actual assimilate demand were simulated for the two crops of which growth rate was measured (nursery I, 1990 and 1992; Chapter 6). As the model ignores roots and the part of the stem from which leaves are removed, predictions do not account for growth and maintenance of these plant parts. It would be interesting to compare the assimilate demand with

the assimilate production. Unfortunately, data about assimilate production were not available. Instead, the potential crop growth rate (potential growth rate of all sinks together) is compared with the observed crop growth rate. Input to the model was the same as for the simulation of dry matter distribution presented in Chapter 6 (table 6.3.1).

7.2.2 results and discussion

Maximum values for the potential assimilate demand (based on maximum potential growth rates) were predicted to be about 10 and 60 g CH_2O m^{-2} d^{-1} for the maintenance and growth component, respectively (fig 7.2.1). In 1992 the potential demand was higher than in 1990 mainly due to larger numbers of fruits and vegetative plant parts per unit ground area resulting from there being an extra shoot on each fourth plant in 1992. Temperature fluctuations caused relatively large day-to-day differences due to short-term temperature effects on potential growth rate (section 4.7). The predicted seasonal trend in maintenance respiration (fig 7.2.1) can mainly be ascribed to the changes in above-ground crop dry weight that reached a maximum of 800 g m^{-2} in summer, and to a lesser extent to seasonal variation in temperature. Estimated over the whole cropping season the maintenance respiration appeared to be about 22% of the actual assimilate demand (based on actual potential growth rates). Because the average actual assimilate demand approximates the average supply (section 4.5), the same percentage (22%) of the amount of assimilate produced over the whole cropping season is predicted to be lost by maintenance respiration.

Generally, the maximum potential crop growth rate was larger than the observed growth rate (fig 7.2.2), which means that the growth in the long term was limited by assimilate supply. The actual assimilate demand is commonly lower than the potential demand (fig 7.2.1) due to adaptation to supply of assimilate. As in the model acclimation to higher assimilate supply takes several days, growth was limited by sink demand and some assimilate was temporarily stored (simulation results not shown) after sudden increase of the supply. In practice, a low sink-source ratio may occur temporarily with sudden decrease of temperature (decline of the sink demand) or fast improving light conditions (increase of the supply). During a short period in summer 1990 the observed growth rate approximated the maximum potential crop growth rate (fig 7.2.1*a*), which indicates that the long-term growth was limited by sink capacity in this period. In the summer of 1992 high assimilate demand resulting from extra shoots caused a potential crop growth rate that was consistently about twice as high as the observed growth rate (fig 7.2.2*b*). The more constant fruit weight in 1992

compared to 1990 (fig 6.3.8) agrees with the more constant ratio between potential and actual growth rate in 1992 than in 1990 (fig 7.2.2.). The maximum potential growth rate of cucumber is on average three times higher than the actual growth rate (Marcelis, 1994*b*). The relatively greater sink potential may be related to the greater flexibility of cucumber to increase the number of fruits (Marcelis, 1992*b*) as compared with tomato.

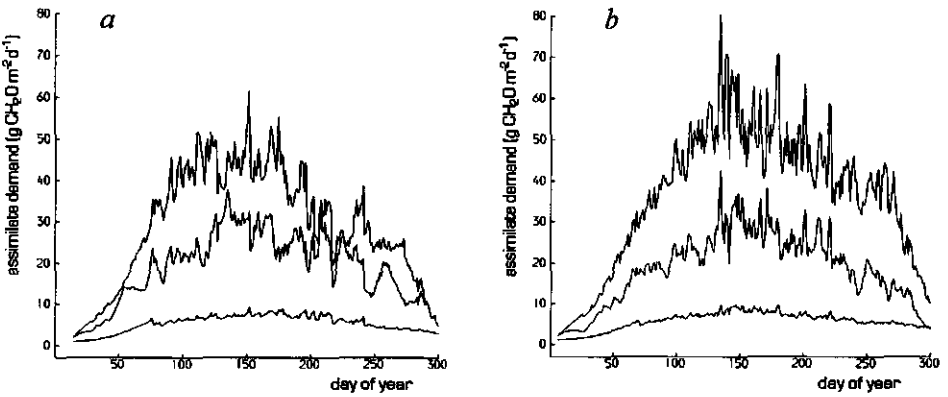

Figure 7.2.1
Nursery I. Simulated assimilate demand by maintenance respiration (lower line), by growth based on actual potential growth rate (middle line) and by growth based on maximum potential growth rate (upper line). *a*: 1990, *b*: 1992.

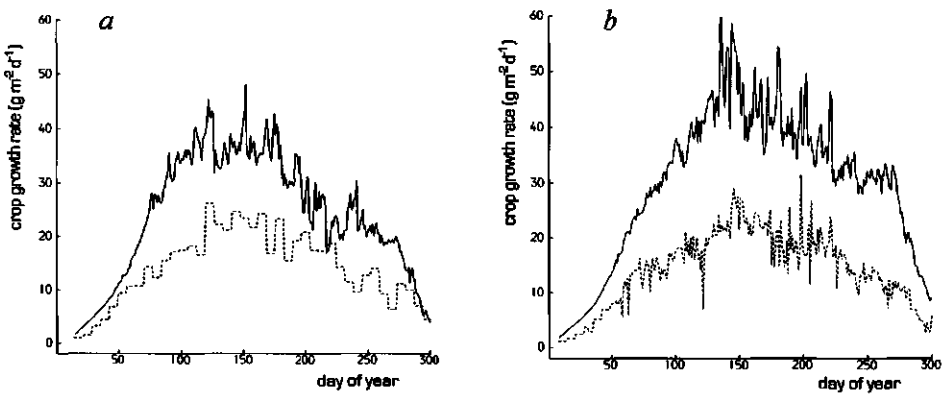

Figure 7.2.2
Nursery I. Maximum potential crop growth rate (——) and measured crop growth rate (-----). *a*: 1990, *b*: 1992.

7.3 Case studies

7.3.1 introduction

The output of the sensitivity analysis presented in Chapter 6 does not always reflect the behaviour of a real crop because the model does not account for some essential parts of the sink-source system. In fact, dry matter production is input to the model and therefore any influence of dry matter distribution on future assimilate production and this effect and the effect of respiratory losses on assimilate available for growth are absent. Some adjustments were made that take into account these effects when predicting the crop response to changes in crop measures and temperature.

First, daily assimilate production was made input. Respiration (already simulated in the original model) was used to compute dry matter available for growth from assimilate production. Furthermore, a routine was supplemented which accounts for the feedback of dry matter distributed to leaves on assimilate production. Unfortunately, number of fruits per truss was not satisfactorily simulated (Chapter 6) and had to be input to the model, in spite of the fact that this adversely affects the validity of the predictions.

The adjusted model was used to predict the crop response to the following changes: (1) 10 percent higher flowering (truss formation) rate, (2) 10 percent higher fruit development rate, (3) fruit pruning to 6 fruits per truss, (4) harvesting at fruit development stage 1.1, (5) 1 degree higher temperature, (6) 10% higher plant density and (7) retaining double the amount of extra shoots without changing the number of fruits formed per unit ground area. The first two changes may be obtained through breeding. The third and fourth cases represent changes when growing truss tomatoes (harvest of trusses with a fixed number of fruits) and harvesting red (instead of orange-green), respectively. When harvesting red, fruits are longer on the plant but, in line with common practice, in the simulations the moment when a particular leaf is removed was not changed. The last case represents an attempt to increase the crop leaf area in summer. Simulations covered a whole cropping season with the 1992 crop of nursery I (Chapter 6) as reference.

7.3.2 procedure and assumptions

In the new model the amount of assimilate available for growth was computed as daily assimilate production (input to the model) minus simulated maintenance respiration. Subsequently, assimilate for growth was converted into available dry matter according to the conversion efficiency of assimilate to dry matter (C in g dw g^{-1} CH_2O). C is equal to the reciprocal of the average assimilate requirement quotient for crop growth as calculated from assimilate requirement quotients of generative and vegetative growth weighted to the simulated distribution fractions:

$$ASRQ_{crop} = \{\Sigma PFGR/(\Sigma PFGR+\Sigma PVGR)\}\times ASRQ_{fruit} + \{\Sigma PVGR/(\Sigma PFGR+\Sigma PVGR)\}\times ASRQ_{veg}, \quad \text{[eqn 7.3.1]}$$

where $ASRQ_{crop}$, $ASRQ_{fruit}$ and $ASRQ_{veg}$ are the assimilate requirement quotients of crop, fruit and vegetative growth, respectively ($ASRQ_{fruit}$=1.20 and $ASRQ_{veg}$=1.23 g CH_2O g^{-1} dw (Gijzen, 1994)), ΣPFGR is the potential growth rate of all fruits together (g m^{-2} d^{-1}), ΣPVGR is the potential growth rate of all vegetative plant parts together (g m^{-2} d^{-1}).

The positive feedback of extra vegetative growth on the crop's assimilate production was accounted for by a daily value of the relative change of assimilate production (ASP) to a relative change of the crop's vegetative weight (VW). Some assumptions were made to assess this variable. First, the specific leaf area and the leaf-stem ratio were assumed to be constant with changing ASP. Under this condition a relative change in total vegetative weight results in an equal relative change of leaf area index (δLAI/LAI = δVW/VW). In addition it was assumed that a relative change of intercepted light (photosynthetically active radiation, PAR), resulting from a change of leaf area, changes assimilate production proportionally (δASS/ASS = δPAR/PAR). On the basis of an exponential light extinction with increasing LAI (Goudriaan, 1988) the relative change of PAR to a relative change of LAI is given as:

$$(\delta PAR/PAR)/(\delta LAI/LAI) = LAI\times k\times e^{-k\times LAI}/(1-e^{-k\times LAI}) \quad \text{[eqn 7.3.2]}$$

where δPAR/PAR is the relative change of intercepted light, δLAI/LAI is the relative change of LAI and k is the canopy light extinction coefficient.

Note that (δPAR/PAR)/(δLAI/LAI) is independent of the amount of light incident on the crop. With k = 0.6 and the LAI as measured in the 1992 crop at nursery I, the relative change of intercepted light with a relative change of LAI varied from 0.4 at high LAI in early summer to about 0.8 at low LAI in spring and autumn (fig 7.3.1). Since it was assumed that δASP/ASP = δPAR/PAR and δLAI/LAI = δVW/VW, the relative change of assimilate production to a relative change of vegetative weight is given by:

$$(\delta ASP/ASP)/(\delta VW/VW) = LAI \times k \times e^{-k \times LAI}/(1-e^{-k \times LAI}) \qquad \text{[eqn 7.3.3]}$$

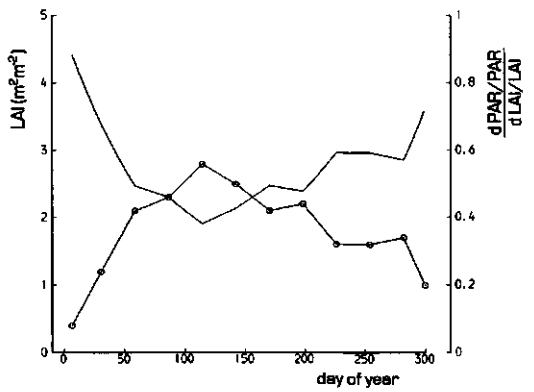

Figure 7.3.1
Leaf area index (LAI, m^2m^{-2}) at nursery I, 1992 (—o—) and the relative change of light interception to a relative change of LAI as calculated by eq. 7.3.2 (——).

Daily assimilate production, as required input to the new model, was estimated by the original model from observed daily dry matter production and predicted maintenance and growth respiration for the reference (nursery I, 1992). Other were inputs to the simulations: daily values of temperature, solar radiation integral, EC in the root environment (all as measured in 1992), relative change of assimilate production to a change of vegetative weight relative to the reference (fig 7.3.1) and vegetative crop weight of the reference. With respect to the last variable it should be noted that the model ignores weight, growth and maintenance respiration of the roots and the stem part from which the leaves are

removed. Numbers of fruit per truss were set at 6 fruits on the first truss, 8 fruits on trusses 2-6 and 9 fruits on all following trusses.

Model output included daily values of: number of fruits formed, potential crop growth rate, vegetative weight, generative weight (weight of all fruits on the plant), maintenance respiration, crop growth rate, vegetative growth rate, generative growth rate and dry and fresh weight per fruit at harvest. As the response of young and old crops may differ (Chapter 6), output was averaged over two periods, *viz.* 60 days following first anthesis and a subsequent period of 190 days, representing young and mature plants, respectively.

7.3.3 results and discussion

Increase of flowering rate (without changing temperature), increases the number of fruits formed and the potential crop growth rate (sink capacity). As explained in Chapter 6, dry matter distribution of a mature crop is not affected and consequently also crop growth rate remained the same (table 7.3.1). As a result the average fruit weight decreases. For practice this means that when growing cultivars with high flowering rate, less plants per unit ground area are required to obtain a certain fruit load.

Effects of fruit development rate on potential crop growth rate and dry matter distribution have been discussed in the sensitivity analysis of the model (Chapter 6). Increase of fruit development rate reduces the fruit growth period and consequently the number (not shown) and weight of fruits present on the plant (table 7.3.1), except for young plants where generative weight increases for reasons mentioned in section 6.4. Since leaf picking is related to the harvestable truss, a shorter fruit growth period also reduces the time a leaf is present on the plant, successively resulting in less vegetative weight, less intercepted light and, in spite of lower crop maintenance respiration, slightly lower crop growth rate (table 7.3.1). Breeding for shorter fruit growth period, therefore, would only be advantageous when the aging of leaves does not change and the grower accepts leaves below the harvestable truss.

Table 7.3.1
Predicted relative change in crop response (dY/Y×100%) to (1) 10 percent higher flowering (truss formation) rate, (2) 10 percent higher fruit development rate, (3) fruit thinning to 6 fruits per truss, (4) harvesting at fruit development stage 1.1, (5) 1°C higher temperature, (6) 10% higher plant density and (7) retaining double the amount of extra shoots without changing the number of fruits formed per unit ground area. Simulation of the 1992 crop of nursery I was used for reference. Predicted crop response was averaged over 60 days after start of flowering, representing the transition from a vegetative to a mature crop, and between 61 and 250 days after start of flowering, representing a mature non-topped crop. Units of weight represent dry weights, except for fruit fresh weight.

	reference	FR × 1.1	FDR × 1.1	FPT = 6	harvest red	T + 1	plant density × 1.1	extra shoots × 2
no. of fruits formed	(m^{-2} d^{-1})							
1-60	2.49	12	0	-22	0	5	10	0
61-250	3.27	8	0	-33	0	4	10	0
pot. crop growth rate	(g m^{-2} d^{-1})							
1-60	10.68	10	10	-6	0	-1	10	0
61-250	34.63	10	0	-22	2	-7	10	6
vegetative weight	(g m^{-2})							
1-60	127.3	-1	-2	1	0	-7	7	0
61-250	221.5	-4	-9	41	-4	-26	1	13
generative weight	(g m^{-2})							
1-60	25.6	5	7	-6	0	14	3	0
61-250	350.8	2	-10	7	12	-12	0	3
maint. resp.	(g CH_2O m^{-2} d^{-1})							
1-60	2.2	0	-1	1	0	2	7	0
61-250	6.7	-2	-10	30	2	-15	1	10
crop growth rate	(g m^{-2} d^{-1})							
1-60	5.08	1	-1	-1	0	-6	3	0
61-250	18.04	1	-2	20	-4	-12	0	7
veg. growth rate	(g m^{-2} d^{-1})							
1-60	3.04	-2	-5	5	0	-15	4	0
61-250	4.36	-1	-3	52	-5	-23	0	17
gen. growth rate	(g m^{-2} d^{-1})							
1-60	2.05	4	4	-8	0	9	3	0
61-250	13.68	1	-2	10	-3	-8	0	4
fruit weight at harvest	(g $fruit^{-1}$)							
dry weight	4.09	-7	-2	52	-2	-11	-9	2
fresh weight	70.4	-7	-2	52	-2	-12	-9	2

Fruit pruning decreases the ratio between number of fruits and number of vegetative organs and consequently the fraction of dry matter partitioned to the fruits (table 7.3.1). Hence, generative growth in the short term decreases, but as vegetative weight and leaf area increase, total crop growth increases to such an extent that, in spite of the lower fraction of dry matter distributed to fruits and the considerably higher maintenance respiration (+30%), in the long term the predicted quantity of dry matter available for fruit growth increases considerably. However, since the crop's sink capacity (potential crop growth rate) declines significantly and the supply of assimilate increases, sink-source ratio declines and thicker leaves may be formed (Nederhoff *et al.*, 1992). In the simulation specific leaf area (SLA) was assumed to be equal to the reference. Lower SLA would reduce the positive effects of higher vegetative crop weight after fruit pruning. Furthermore, a consequence of very low sink-source ratio is that fruits approximate the potential size (table 7.3.1) which may affect fruit quality adversely (Chapter 1). When pruning fruits, therefore, sink-source ratio should not become too low which may be accomplished by increasing shoot density.

When fruits are harvested red instead of orange-green, they stay on the plant longer and as a result the fruit weight on the plant increases by about 12% (table 7.3.1), causing higher assimilate loss by maintenance respiration. Potential crop growth rate hardly increases because the potential growth rate of orange-green fruits is low (Chapter 4). The fraction of dry matter distributed to vegetative organs decreases slightly causing diminished leaf area which, together with higher maintenance respiration, reduces final crop growth. Total generative growth is predicted to be slightly lower (-3%) when harvesting red instead of orange-green fruits (table 7.3.1).

One degree higher temperature affected all output variables (table 7.3.1). Due to a lower fraction of dry matter distributed to vegetative growth and a shorter leaf residence time (time a leaf is on the plant) vegetative plant weight and crop growth rate decline considerably. The decrease of growth rate is amplified by the feedback of leaf area on assimilate production. Hence, although the fraction of dry matter distributed to the fruits increases, in the long term dry matter for fruit growth decreases. In combination with the larger number of fruits formed, lower generative growth results in considerably smaller fruits at harvest (-11%). The crop's maintenance respiration decreases with temperature, which implies that in the present example the influence of lower crop weight is more important than the effect of higher maintenance respiration per unit biomass.

More plants per unit ground area increases the number of fruits, the number of vegetative organs and the crop's sink capacity in proportion (table 7.3.1). Early growth is enhanced by better light interception as the crop starts with more leaf area. Growth of a mature crop is unaffected as in the simulation the higher sink-source ratio had neither influence on the number of fruits formed per truss nor on the crop's leaf area. The higher number of fruits formed per unit ground area results in proportionally smaller fruits at harvest. The same would have been true for retaining more shoots. Therefore, in the case with double the amount of extra shoots it was decided to reduce truss size so that the number of fruits formed per unit ground area was equal to the reference. Hence, the ratio between number of fruits and of vegetative organs decreased, causing relatively more vegetative growth and subsequent higher light interception and finally even more generative growth (table 7.3.1).

It should be noted that the predictions for treatments that considerably change the sink-source ratio (mainly through affecting the number of fruits formed or affecting vegetative weight per unit ground area) are less reliable because of the absence of any effect of sink-source ratio on (flower bud) abortion or SLA. In general these effects act as negative feedback and, therefore, real crop response will be less pronounced than predicted here.

In most investigated cases the ultimate effect on fruit yield (generative growth rate) appeared to be dominated by the positive feedback of vegetative weight on total growth rate. This indicates that vegetative growth and LAI (fig 7.3.1) of the reference crop was suboptimal at least for part of the cropping season.

These case studies indicate the importance of a proper balance between vegetative and generative growth. Furthermore, they show how the model may advise in quantitative terms about the effects of crop measures and temperature on assimilate demand, dry matter distribution and fruit production. For breeding, case studies as presented may indicate which changes of crop characteristics have high potential to improve crop production.

7.4 Optimum shoot density and number of fruits

7.4.1 the principle

Varying shoot density and number of fruits per truss are the most appropriate measures to adapt assimilate demand to the seasonal course of assimilate supply (Chapter 1). A grower aims at a certain size of the individual vegetative tops, which is approximated by a more or less constant demand-supply ratio. Thus, when applying the model to advise about these measures it has to be known which is a proper ratio between demand and supply for optimum crop performance.

With a normal crop the actual growth rate appeared to be half the maximum potential crop growth rate (section 7.2). As a first approximation, therefore, it seems plausible to aim at this ratio in crop control. Although this ratio probably may vary between certain margins around 0.5 without adversely affecting total crop performance, a relatively low or high ratio would leave insufficient room to meet deviations when the actual conditions differ from the averages the cultivation plan is based on. At a ratio of 0.5 between actual and potential growth rate all organs grow at half their potential maximum rate and reach half their maximum potential weight at maturity. For round tomato this means that fruits are about 80 g (fresh weight) at harvest.

Besides a proper demand-supply ratio, the crop's leaf area (LAI) should be adequate for high light interception and related level of assimilate production. Hence, with a certain size (i.e. half the potential weight) of the vegetative plant parts, for this a minimum number of shoots per unit ground area is necessary. With a certain growth rate for each vegetative top, higher shoot density increases the total amount of assimilate required for vegetative growth. It depends on the extra amount of assimilate produced and dry matter required for vegetative growth whether higher LAI and related shoot density result in more assimilate for fruit growth.

According to the desired ratio between assimilate demand and supply, fruit load has to be in proportion with the amount of dry matter available for fruit growth. At a certain shoot density this has to be accomplished by manipulating the number of fruits per truss. As a matter of course the cultivation plan has to take into account that the number of fruits per truss cannot be more than the genetically determined maximum, for example circa 10 fruits for round tomato.

Rather than trying to present an optimum cultivation plan, predictions were made on the required shoot density, the dry matter available for fruit growth and the related number of fruits per truss for different constant levels of LAI throughout the cropping season. Figure 7.4.1 presents a brief outline of the procedure. First the yearly course of vegetative weight of a shoot growing at half the maximum potential rate was predicted. In combination with stem-leaf ratio and the 'whole-crop' specific leaf area, the course of shoot density required for different leaf area index (LAI) was determined (fig 7.4.1, left). In addition to the weight of the vegetative plant parts (and under the same conditions) the vegetative growth rate per shoot was predicted, which after multiplying with the estimated shoot density yielded the yearly course of vegetative growth rate per unit ground area needed for a certain LAI (fig 7.4.1, centre).

Due to increasing light interception, dry matter production generally increases with increasing LAI. Adopting a description of the daily dry matter production as a function of LAI, daily amounts of dry matter available for fruit growth per unit ground area and per shoot was predicted (fig 7.4.1, bottom-right). In the end, the (average) numbers of fruits per truss that correspond with the amounts of dry matter available for fruit growth were determined by using the predicted yearly course of generative growth rate of a shoot with on each truss one fruit growing at half the maximum potential rate (fig 7.4.1, top-right).

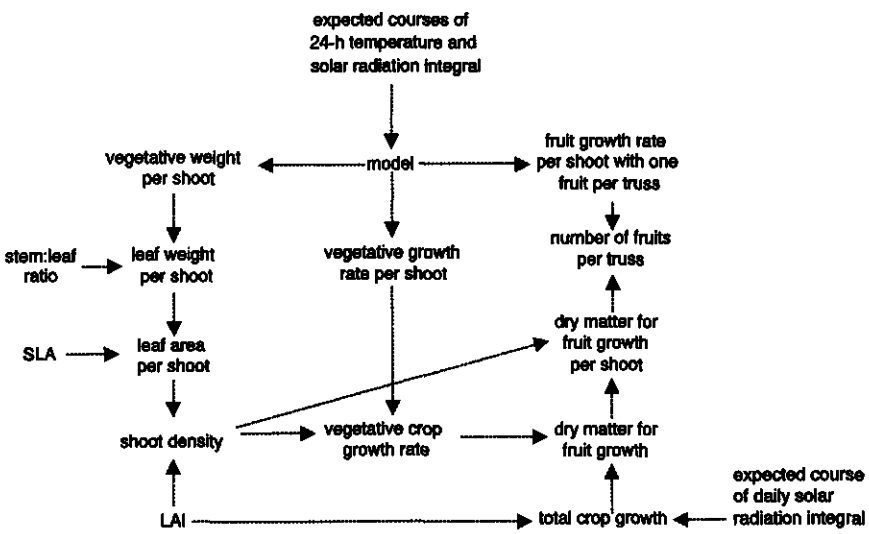

Figure 7.4.1
Scheme of the procedure used to predict the shoot density for maximum fruit growth and required number of fruits per truss. SLA is the specific leaf area, LAI is the leaf area index.

7.4.2 additional relationships and computations

number of shoots

Usually old leaves are removed up to the oldest harvestable truss and even when old leaves are not removed they do not seem to contribute to the amount of assimilate available for growth (Longuenesse and Tchamitchian, 1990). Therefore the predictions of leaf weight and leaf area per shoot only accounted for the leaves above the oldest harvestable truss. The leaves (petioles inclusive) constitute 70% of the total vegetative weight, independent of season and fruit load (Heuvelink, 1995*a*). This factor was used to deduce leaf weight from predicted total vegetative weight (without the stem part from which the leaves are removed). Predicted leaf weight was converted into leaf area using an empirical description of the seasonal course of the whole-plant specific leaf area (SLA) as fitted to observed SLA in the 1990 and 1992 crops of nursery I (fig 7.4.2):

$$SLA = 385.4 - 2.433 \times DAYNO + 0.00562 \times DAYNO^2 \quad (n=20,\ r^2=0.95) \qquad \text{[eqn 7.4.1]}$$

where SLA is the specific leaf area ($cm^2\ g^{-1}$) of leaves (petioles inclusive) and DAYNO is the day of the year.

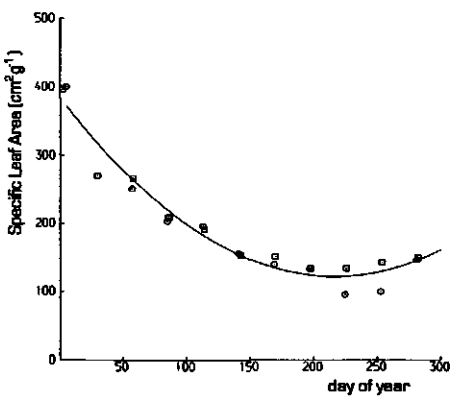

Figure 7.4.2
Course of the specific leaf area (SLA, $cm^2\ g^{-1}$) throughout the year.
○, observed in 1990; □, observed in 1992;
——, fitted curve: $SLA=385.4-2.433\times DAYNO+0.00562\times DAYNO^2$

The number of shoots is obtained by dividing LAI by the leaf area per shoot.

vegetative growth rate

The prediction of the vegetative growth rate per shoot followed the same procedure and assumptions as for vegetative weight. Multiplying the growth rate per shoot with the shoot density required for different LAI resulted in the vegetative growth rate per unit ground area.

dry matter available for fruit growth

A coarse relationship between daily crop growth rate and intercepted radiation integral (photosynthetically active radiation, PAR) was previously estimated for data of the 1990 crop at nursery I (de Koning, 1993).

$$\text{growth} = 47.3\times(\text{PAR}+0.29)/(\text{PAR}+7.96), \qquad \text{[eqn 7.4.2]}$$

where growth is the daily dry matter increase (g m^{-2} d^{-1}) and PAR is the intercepted daily radiation integral (400-700 nm, MJ m^{-2} d^{-1}).

PAR intercepted by the crop was calculated from the daily outside solar radiation integral, assuming a constant light transmission of the glasshouse (0.7), on average 50% PAR in the global radiation and an exponential light extinction with increasing LAI (de Koning, 1993):

$$\text{PAR} = (\text{outside global radiation})\times 0.7\times 0.5\times(1-e^{-0.6\times LAI}), \qquad \text{[eqn 7.4.3]}$$

The amount of dry matter available for fruit growth equals the difference between the daily growth rate and the dry matter required for vegetative growth at certain LAI.

number of fruits per truss

The optimum number of fruits per truss is proportionally related to the amount of dry matter available for fruit growth and negatively correlated to shoot density, truss formation rate and final fruit size (i.e. half the potential size). Predicted generative growth rate of a shoot with one fruit at each truss takes into account the effects of the last two variables. The number of fruits per truss was calculated by dividing the available dry matter per shoot by the predicted generative growth rate of a shoot with one fruit per truss (fig 7.4.1). It should be noted that differences in (potential) size between fruits of the same truss were ignored, i.e. all fruits of a particular truss became as large as the proximal fruit.

predictions

Predictions were made for a 'standard' round tomato crop that commences flowering at 5 January and is topped 255 days later. Input data were the average daily solar radiation integral (Naaldwijk, 1971-1990) and an adopted course of 24-h average air temperature in the glasshouse, *viz.* 19°C for the first 100 days, followed by successive periods of 50 days of 20, 21 and 20°C, and 19°C for the rest of the year. LAI for which calculations were made ranged from 1 to 4 m^2 m^{-2} (mature crop). For a young crop the LAI increased linearly from 0.15 m^2 m^{-2} at flowering of the first truss to the final value 75 days later. After topping LAI decreased linearly to zero after a further 80 days. Finally, the daily values of predicted shoot density and number of fruits per truss for different LAI were averaged over four successive periods of 50 days, *viz.* days of the year 51-100 (March), 101-150 (April-May), 151-200 (June-July) and 201-250 (August).

It should be stressed that this exercise is merely a demonstration of how the model may advise in determining the long-term strategy concerning shoot density and fruit pruning. The presented results have limited validity due to uncertainty about the description of potential growth of a vegetative unit in the model, the fairly straightforward prediction of dry matter production, the specificity of the description of the SLA and arbitrariness of the chosen temperatures.

7.4.3 results

Predicted leaf weight of a shoot was highest in April and May (fig 7.4.3) because at that time the small early leaves (ontogenetic effect on leaf weight) have been removed, potential leaf weight is relatively high due to low temperature and the shoot has a maximum number of leaves resulting from the relatively long fruit growth period. In contrast, in summer at high temperature, the fruit growth period is short and potential leaf weight is low, resulting in relatively low leaf weight per shoot (fig 7.4.3).

Mainly due to the large variation of SLA (fig 7.4.2) and to a minor extent to the course of vegetative weight, leaf area per shoot varied from 1.4 m^2 in April to as low as 0.8 m^2 in August (fig 7.4.3). As a consequence, to obtain (for example) a LAI of 2.5 the shoot density varied from less than 2 in spring to more than 3 shoots m^{-2} in late summer (fig 7.4.4). The predicted vegetative growth rate per

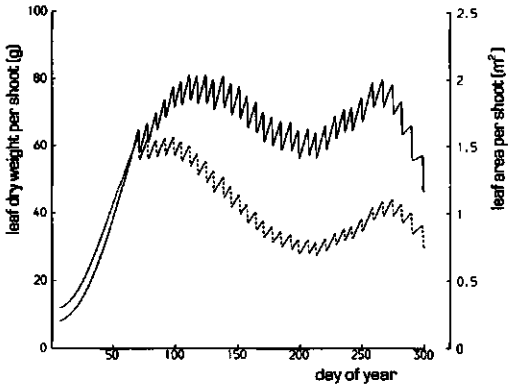

Figure 7.4.3
Predicted seasonal course of leaf weight (——) and leaf area (----) per shoot growing at half the maximum potential growth rate. The sawtooth shape is caused by periodic leaf picking.

shoot (mature crop) was fairly constant at about 2 g d^{-1} (not shown). So, for a given LAI, the daily quantity of dry matter left for fruit growth was mainly determined by the shoot density and the daily crop growth rate. The predicted number of fruits required per truss was highest in April and May due to a combination of high crop growth rate and low shoot density, whereas in August at relatively low crop growth rate and high shoot density the number of fruits was low (e.g. fig 7.4.4 for LAI=2.5).

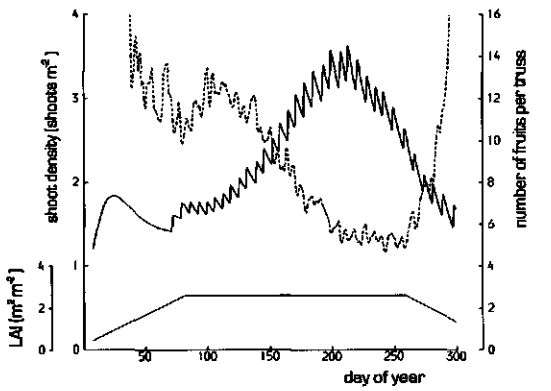

Figure 7.4.4
Predicted shoot density (——) to obtain a LAI as shown (2.5 m^2 m^{-2} for a mature crop) and corresponding number of fruits per truss (-----) for a tomato crop growing at half the maximum potential growth rate.

Since dry matter required for vegetative growth is linearly related to LAI and total dry matter production follows a saturation response with increasing LAI, the dry matter left for fruit growth as function of LAI shows an optimum response. Considering different LAI maintained during a whole cropping season, the response curve appeared rather flat with the optimum between 2 and 3 m^2 m^{-2} (fig 7.4.5).

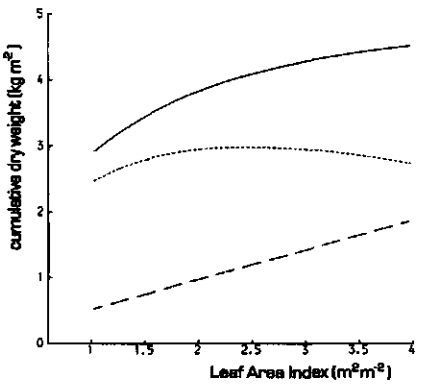

Figure 7.4.5
Predicted cumulative above ground (——), vegetative (— —), generative (-----) growth for different LAI.

In spring and early summer the optimum shoot density seems to be determined by the maximum truss size rather than by LAI, *viz.* if adopting a maximum truss size of 10 fruits, the minimum shoot density corresponds to a LAI of about 3 (fig 7.4.6*a* and *b*), which is higher than the LAI that yields the largest quantity of dry matter for fruit growth (fig 7.4.5). In contrast, in late summer a combination of high shoot density and truss pruning is required to realize the LAI corresponding to the maximum fruit production (figs 7.4.5 and 7.4.6*d*).

7.4.4 discussion

High fruit growth was predicted for a wide range of LAI (fig 7.4.5). This agrees with the observation in practice that very different canopies can produce similar high yields. Surprisingly, the maximum amount of dry matter available for fruit growth is obtained at fairly low LAI and light interception (circa 80%). The

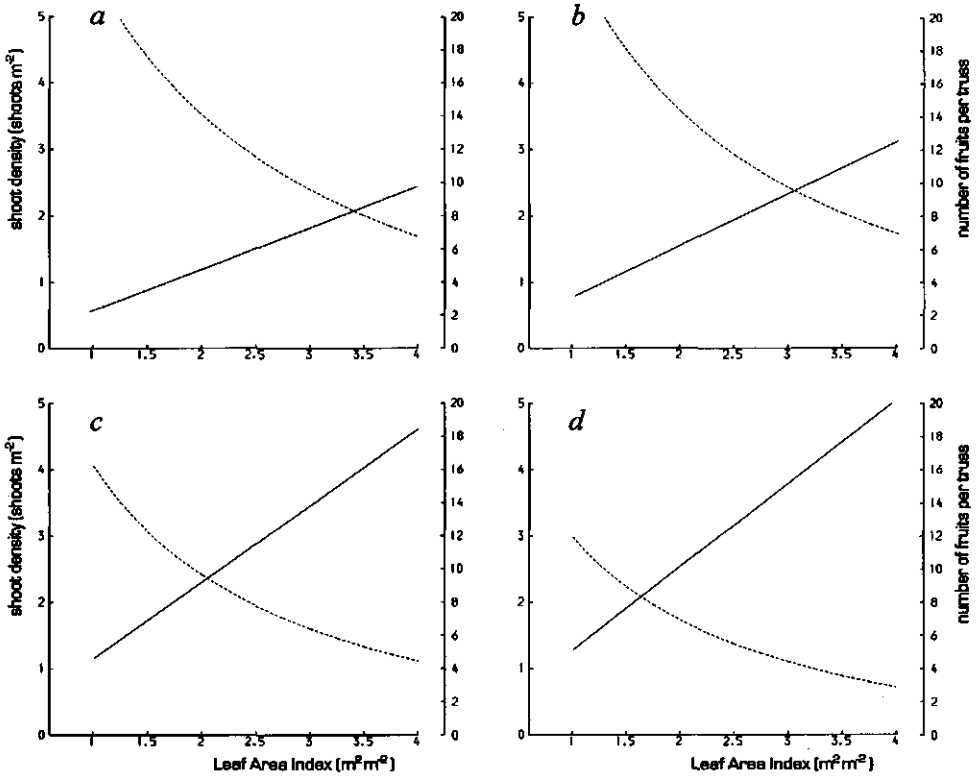

Figure 7.4.6
Predicted shoot density to obtain different LAI (——) and corresponding number of fruits per truss (-----) at different times of year. *a*: days 51-100 (March), *b*: days 101-150 (April-May), *c*: days 151-200 (June-July), *d*: days 201-250 (August).

costs of supra-optimum LAI exceed the future benefits. The extra amount of dry matter needed (whole-season average) for sustaining extra LAI is represented by the slope of the line showing the cumulative vegetative growth in fig 7.4.5. As the costs of extra LAI are inversely proportional to SLA, increasing the SLA (e.g. through breeding) would be very effective in increasing fruit production. Namely, when slope decreases (higher SLA and lower costs) the amount of assimilate available for fruit growth (above ground minus vegetative growth) as well as the optimum LAI and consequently light interception and dry matter production, will increase. Especially low SLA in summer seems unfavourable as this requires high shoot density and a considerable investment in vegetative growth to achieve reasonable light interception, where at the same time trusses

have to be pruned to a low number of fruits. High plant density without pruning would result in too high sink-source ratio causing poor vegetative growth per shoot, high (flower bud) abortion and small fruits.

In the present example, different alternatives with constant LAI for a whole year were considered. The optimum LAI for dry matter available for fruit growth, however, is likely to vary throughout the cropping season due to varying SLA and light conditions. In general, the optimum LAI would be high when SLA is large (low costs) and expected future solar radiation is high (high benefits).

Besides a maximum amount of dry matter for fruit growth, the optimum shoot density should take into account some other aspects. First, at high amount of assimilate available for fruit growth, as likely in spring and early summer, a higher shoot density than related to optimum LAI is required to ascertain sufficient sink capacity (fruit load). Furthermore a minimum amount of leaf area may be needed to shade fruits from high irradiances that harm fruit quality (Adegoroye and Jolliffe, 1987; Janse, 1988; van Holsteijn and Glas, 1989). Moreover, for a maximum financial result the plant costs related to the initial plant density, the extra labour costs of increasing shoot density and the costs of fruit pruning should be considered. Furthermore, the variation in price of the fruits may be taken into account, as retaining extra shoots (and therefore investing extra dry matter in vegetative growth) implies a loss of fruit yield in the short term in favour of higher yield in future.

8

GENERAL DISCUSSION

8.1 Introduction

In addition to optimizing the glasshouse climate for instantaneous assimilate production, a grower manipulates the utilization of assimilate (summarized as crop control) by means of crop measures and temperature control (Chapter 1) for maximum crop production in the long term. At present, these measures are mainly based on the knowledge of qualitative effects on crop growth. When effects are known in quantitative terms the application of control tools can be more effective. This study concentrated on quantifying two aspects of crop control in glasshouse tomato, *viz.* (1) the assimilate demand (sink) as counterpart of the assimilate production (source) and (2) the distribution of dry matter between vegetative and generative plant parts. A certain measure may effect several processes in the whole crop system which makes the final result difficult to predict. Moreover, through the operation of feedback controls short- and long-term effects may differ. To handle the complexity of the crop system an explanatory model was developed that simulates assimilate demand and dry matter distribution.

In the next section (8.2) of this chapter the operation of the sink-source system and the practical consequences of feedback controls are discussed. Special attention is given to the role of temperature. The same section presents some mathematical relationships between relevant rate and state variables, which facilitate insight into the long-term consequences of the temperature level on crop growth. Subsequently, shortcomings, limitations and possible extensions of the model are discussed in section 8.3, while section 8.4 deals with some complementary simulation models. Furthermore, as temperature is a major tool for crop control in glasshouse cultivation, implications for temperature control are considered (section 8.5). This general discussion ends with an outlook on possible practical applications of models simulating assimilate demand and dry matter distribution (section 8.6).

8.2 The crop sink-source system

The production of assimilate, the basic process for crop growth, is principally determined by the amount of light intercepted by the canopy, and can be increased by increasing the CO_2-concentration of the glasshouse air. Part of the assimilate formed is respired for maintenance. Furthermore, crop production is affected by the distribution of assimilate (fig 8.2.1). Control mechanisms in the

plant ensure that these factors are not independent of each other. The most obvious internal controls are (1) the positive feedback of assimilate allocated to vegetative growth on the future assimilate production and (2) the negative feedback of relatively high assimilate demand (high sink-source ratio) on the future demand through increased flower and fruit abortion (fig 8.2.1). As the results of feedback mechanisms become manifest only in the long term (e.g. Marcelis, 1993*b*), short- and long-term crop responses to crop measures and climate may differ.

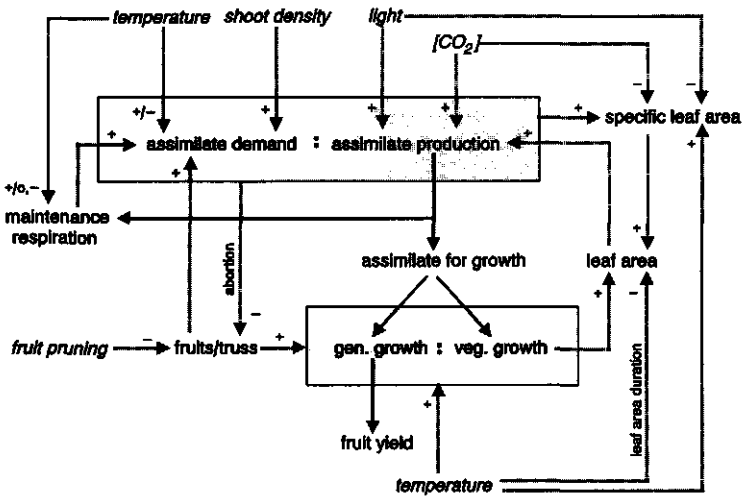

Figure 8.2.1
Schematic representation of the main factors determining assimilate production, assimilate demand and dry matter distribution in an indeterminate tomato crop. Ratio's are graphically represented by boxes. Where possible the influence of a variable on a ratio is given by the specific effect on one of the components, otherwise the arrow stops at the edge of the box. Similarly, lines may start from one component of the ratio or from the edge of the box. External control variables are in italics. The signs indicate positive (+), neutral (o) or negative (−) influences. In case of two signs (separated by a slash) the short- (first sign) and the long-term (second sign) responses differ.

optimum proportion vegetative growth

Indeterminate crops require the continuous formation and growth of leaves to sustain a certain amount of photosynthetically active leaf area. In terms of crop control, dry matter allocated to vegetative growth can be regarded as an investment in future growth potential. Investment in extra leaf area is profitable if it results in extra assimilate production that exceeds the extra costs made. For

this reason maximum assimilate production obtained at saturating light interception does not automatically result in the highest amount of assimilate available for fruit production and explains why tomato crops with low leaf area may produce high fruit yield as observed in practice. Tentative predictions indicated (section 7.4) that under conditions as in Dutch glasshouse cultivation, maximum fruit production is probably obtained at rather low leaf area index (about 2.5 m^2 m^{-2}) and light interception (about 80%).

The costs for leaf area formation are inversely proportional to the specific leaf area (SLA, leaf area per unit dry weight). It has been discussed in section 7.4 that high SLA increases the optimum leaf area index (LAI, leaf area per unit ground area), total assimilate production and the proportion of assimilate available for fruit growth. Calculations such as presented in section 7.4 showed that overall a 10 percent higher SLA may result in a 3.5 percent higher (potential) fruit production. Potential fruit production also increases with increasing leaf area duration (time leaf area is photosynthetically active) and with increasing amount of dry matter distributed to the leaves relative to the other vegetative plants parts. Compared with tomato, leaves of sweet pepper, for example, are longer on the plant but this relative benefit goes along with a low ratio between leaf and stem growth, resulting in lower fruit dry matter production than tomato (Rijsdijk *et al.*, 1993).

In March, April and May the LAI of commercial tomato crops appears relatively high (>3 m^2 m^{-2}) (de Koning, 1993; Rijsdijk *et al.*, 1993). According to the predictions mentioned above, total fruit production may be favoured by having less dry matter applied for vegetative growth in this period. Assuming a constant vegetative growth rate per shoot, lower vegetative growth rate per unit ground area is achieved through lower shoot density. However, at low density in spring the number of fruits may be too low with respect to the dry matter available for fruit growth (section 7.4). Higher temperature is another possibility for decreasing vegetative growth in favour of fruit growth (section 4.6), though this measure should be applied with caution as high temperature may reduce the number of fruits on a truss (section 3.3) and consequently be counter-productive.

abortion

High abortion at low available assimilate (Atherton and Harris, 1986) results in a low number of fruits per truss, as observed for high plant density (Papadopoulos and Ormrod, 1991) and low light conditions (Heuvelink, 1995*a*). Since one truss is formed for each three leaves, under adverse conditions the ratio between number of fruits and number of vegetative plant parts is low and as a

consequence the harvest index (fraction of dry matter allocated to the fruits) is low. Winter crops, therefore, exhibit a lower harvest index than summer crops (Heuvelink, 1995*a*). In contrast, Cockshull *et al.* (1992) observed hardly any change in total dry matter distribution from November until August when during the whole cropping season light level was reduced by 23%. This unexpected result may be explained by the fact that in their experiment shading reduced number of fruits per truss noticeably only in winter and early spring (solar radiation incident on the crop less than 1.5 MJ m^{-2} d^{-1}), so total number of fruit produced over the whole season (numbers not reported) would not have differed much.

Higher plant density (Widders and Price, 1989; Papadopoulos and Ormrod, 1990) and decrease of light level (Cockshull, *et al.*, 1992; Marcelis, 1993*b*; Heuvelink, 1995*a*) cause smaller fruits. Hence, these conditions reduce (on a plant basis) number of fruits proportionally less than dry matter available for fruit growth. In fact, small fruits result from high sink-source ratio.

fruit pruning

Fruit pruning enhances the growth of vegetative parts of tomato (Hurd *et al.*, 1979; Heuvelink and Buiskool, 1995) and cucumber plants (Marcelis, 1994*a*). As a result of a lower ratio between number of fruits and number of vegetative sinks, the harvest index decreases (Hurd *et al.*, 1979; Marcelis, 1993*c*; Heuvelink and Buiskool, 1995). Fruit pruning may cause a lower (Tanaka and Fujita, 1974), an equal (Hurd *et al.*, 1979, first experiment; Marcelis, 1993*c*; Heuvelink and Buiskool, 1995) or higher (Hurd *et al.*, 1979, second experiment) total dry matter production. A lower dry matter production is anticipated when pruning results in sink-limited growth, as demonstrated for severe pruning treatments (Tanaka and Fujita, 1974; Heuvelink and Buiskool, 1995). At sufficient sink capacity, higher vegetative growth after fruit pruning may result in higher biomass production, except at saturating light interception as was probably true in the experiments of Marcelis (1993*c*; 1993*d*). Despite a lower harvest index, fruit pruning may increase dry matter production to such an extent that total fruit yield does not change (Hurd *et al.*, 1979, second experiment) or even increases (simulation results, table 7.3.1). Increased fruit weight of remaining fruits (Hurd *et al.*, 1979; Nederhoff *et al.*, 1992; Marcelis, 1993*c*) is a direct consequence of lower sink-source ratio after fruit pruning.

crop response to temperature

Higher temperatures, generally, enhance early production and decrease fruit size and total fruit production of tomato (van Holsteijn, 1987; de Koning and Buitelaar, 1990). The higher early production results mainly from the short fruit growth period at high temperature (section 3.4). Explaining the other effects of temperature is difficult as temperature influences several aspects of the sink-source system (fig 8.2.1) and, moreover, short- and long-term crop responses may differ. In this section some direct effects of temperature are considered. Further, long-term crop responses are discussed on the basis of some mathematical relationships between crop characteristics and predictions by the present model.

Except for extremes, temperature has little effect on gross leaf photosynthesis (e.g. Ludwig, 1974; Schapendonk and Brouwer, 1985; Acock, 1991). Maintenance respiration per unit biomass, however, increases with temperature (Walker and Thornley, 1977; Penning de Vries *et al.*, 1989) thus, in the short term, assimilate available for growth increases with decreasing temperature. When added to a decrease of the potential growth rates (Chapter 4) this results in significantly lower crop assimilate demand when instantaneous temperature is decreased. According to the present model, assimilate demand of a mature tomato crop decreases 10% when temperature changes from 19 to 18°C.

Higher temperatures seem to favour dry matter distributed to the fruits at the expense of vegetative growth (section 4.6), which has been explained by different temperature responses of the competitive power (described by potential growth rates) of vegetative and fruit sinks. The same holds for cucumber where, at constant ratio between number of fruits and number of vegetative organs, the fraction allotted to fruit growth increases with temperature (Marcelis, 1993*c*).

To explain the influence of temperature on fruit size and fruit biomass production, the long-term responses of distinct components of the crop's sink-source system have to be considered. For this, model predictions are suitable (Chapters 6 and 7). In addition, some straightforward descriptions of the number of organs present on the crop, (potential) crop growth rate and the crop's biomass are useful as they allow for a quick insight into the crop responses to changes in variables of the sink-source system. Basically the relationships are valid for constant conditions, though when applied on long-term averages errors are probably small.

The number of organs on the plant is determined by organ formation rate and the growth period (time from initiation to maturity) of individual organs (fig 8.2.2*a*) according to:

number of organs on the plant = organ form.rate × organ growth period [eqn 8.2.1]

with the organ growth period as the reciprocal of the organ development rate.

Temperature affects the formation of trusses (flowering rate) and development rate of fruits to about the same extent (Chapter 3). Thus, according to equation 8.2.1, number of trusses with fruits and (at certain number of fruits per truss) number of fruits on the plant do not vary much with temperature.

The potential crop growth rate (as an important component of crop sink activity) is determined by the number of sink organs on the plant and the potential growth rates of the individual organs. Ignoring details, an average potential growth rate can be estimated as the potential sink weight at maturity divided by the sink growth period (both variables averaged over all organs present):

av.pot.sink growth rate = av.pot.sink weight / av.sink growth period, [eqn 8.2.2]

Potential crop growth rate is given by:

pot.crop growth rate = number of sinks × av.pot.sink growth rate, [eqn 8.2.3]

When considering the long-term responses, 'number of sinks' can be substituted by equation 8.2.1 which, after reduction, yields:

pot.crop growth rate = sink form.rate × av.pot.sink weight [eqn 8.2.4]

Thus, the long-term potential crop growth rate appears to be proportionally related to sink formation rate and potential sink weight and to be independent of the number of sinks on the plant and the growth period of individual sinks. The same was concluded from the sensitivity analysis on the model (section 6.3). Temperature promotes the formation of new organs (section 3.2) and reduces potential sink weight, especially of the vegetative plant parts (Chapter 4). According to the model, the decrease in potential weights seems to be the most important as temperature reduced potential crop growth rate (table 6.4.1). However, the potential growth rate of all fruits together increased slightly with increasing temperature (table 6.4.1).

Equation 8.2.4 also applies to the actual growth rate and achieved final size of the organs. On condition that the actual crop growth rate is not affected, it follows that (considering long-term effects) the positive influence of low temperature on the size of individual organs appears to result from the low number of organs formed rather than the long growth period of individual organs. The vegetative organs profit in particular from low temperature as their competitive strength to attract assimilate increases relative to that of the fruits (section 4.6). The model predicts as much as 20% increase (12% caused by altered distribution ratio and 7% due to reduced formation rate) in the weight of the individual vegetative organs (mature crop) when temperature decreases from 19 to 18°C.

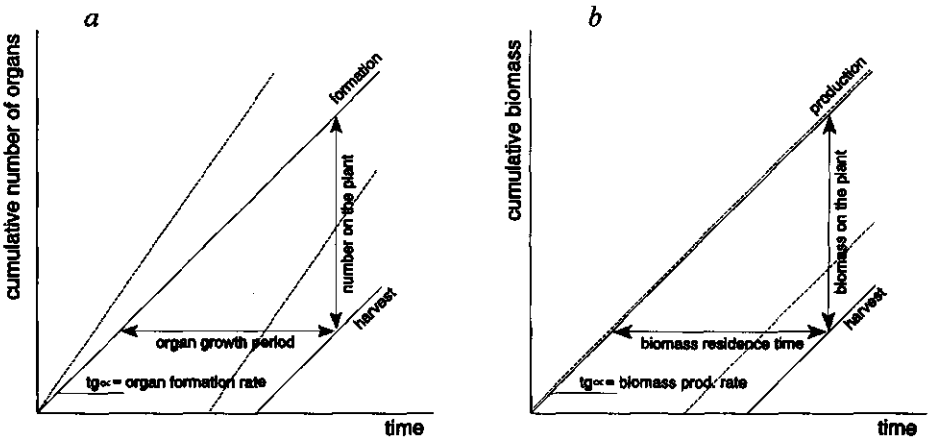

Figure 8.2.2
a: Graphical representation of the mathematical relationship defining the number of organs on the plant: number on the plant = organ formation rate × organ growth period. At low temperature (solid lines) organ formation rate is lower and organ growth period is longer than at high temperature (broken lines).

b: Graphical representation of the mathematical relationship defining the biomass on the plant: biomass on the plant = biomass production rate × biomass residence time. At low temperature (solid lines) biomass residence time is higher than at high temperature (broken lines). Biomass production rate is assumed to be unaffected by temperature.

The respiratory loss of assimilate for maintenance was estimated to be about 22% of the assimilate produced (section 7.2). Reducing the crop's maintenance respiration, therefore, may increase fruit yield substantially. The crop's maintenance respiration is positively correlated to crop biomass and temperature. In the short term, maintenance respiration decreases with temperature but the

long-term effect is uncertain with the increase in crop biomass. The amount of biomass on the plant is related to the biomass residence time (average time biomass produced remains on the plant) and the biomass production rate (fig 8.2.2*b*) according to:

biomass on the plant = biomass prod.rate × biomass residence time, [eqn 8.2.5]

Biomass residence time is proportionally related to the growth period of the plant parts concerned and, in addition, affected by their growth curve. Assuming that biomass production rate does not change with temperature, low temperature applied over an extended period increases the amount of biomass on the plant due to low organ development rate (fig 8.2.2*b*). In the long term, a combination of high dry matter production, low temperature and low crop biomass, therefore, is incompatible. So, low crop maintenance respiration through low temperature is feasible only when applied for a short period. Since the temperature responses of organ development rate (section 3.4) and specific maintenance respiration (Walker and Thornley, 1977; Penning de Vries *et al.*, 1989) are about the same ($Q_{10} \approx 2$), temperature would hardly affect the long-term maintenance respiration of the crop. However, this is only true when dry matter distribution and biomass production do not change. Simulation of the overall temperature response of a long-season crop (section 7.3.1) yielded 15% less maintenance respiration with 1°C higher temperature (table 7.3.1), mainly as the result of 12% less biomass production.

Analogous to equation 8.2.5, leaf area on the plant depends on leaf area expansion rate and leaf area residence time. With tomato the latter is closely related to the fruit growth period. For constant leaf area expansion rate, therefore, the crop's leaf area reduces with increasing temperature. Note that as leaf formation rate increases, according to equation 8.2.1 the number of leaves on the plant would not necessarily decrease. So, under constant leaf area expansion rate per plant, the size of individual leaves decreases with increasing temperature. Moreover, high temperature adversely affects dry matter distribution to the vegetative plant parts (section 4.6) which further reduces the size of individual leaves and the crop's leaf area.

In conclusion, the generally observed decrease of total fruit yield with increasing temperature results from lower LAI and consequently lower assimilate production rather than higher respiratory losses for maintenance. The smaller fruits are caused by less available dry matter and higher fruit formation rate. Further, high dry matter content contributes to reduced average fruit fresh weight at high temperature (section 4.2).

8.3 Reflections on the model

hierarchical level

In this study, crop response is explained and modelled on the basis of the formation, development and growth of individual organs. Investigations were not below the organ level and consequently did not allow for explaining the responses of individual organs by the underlying mechanisms. In the further development of the model it would be worthwhile considering cell division and cell enlargement for understanding and improving the description of potential growth rate of individual organs, in particular with respect to the influence of temperature (Chapter 4). Furthermore, from a physiological point of view it would be interesting to investigate the processes underlying fruit development in order to understand the varying temperature response of fruit development rate from anthesis until maturity.

input to the sub-models

Since temperature is regarded as a major determinant of assimilate demand and dry matter distribution (Chapter 1), in the present study much attention has been given to quantifying the effects of temperature on relevant processes. The temperatures used in the experiments were based on conditions prevalent in Dutch glasshouse tomato growing. Applying the model for warmer climates and less well heated or ventilated glasshouses would require investigations over a wider temperature range. Moreover, at extreme temperature conditions the water status of the crop may become important which in the present study could be ignored (Bakker, 1991).

The effects of environmental variables other than temperature on assimilate demand and dry matter distribution have not been investigated thoroughly. Daily solar radiation integral is included in the descriptions of fruit development rate (eqns 3.4.7 and 3.4.8) and potential fruit weight (eqn 4.3.6) to account for differences between experiments conducted at different times of the year.

Flowering rate (table 3.2.7) and fruit development rate (table 3.4.4) decrease with increasing plant age. Unfortunately, the available experimental data only allowed for tentative descriptions of the influences. Especially the decline of flowering rate may have significant consequences for final crop performance. However, the decline of flowering rate with increasing plant age manifested inconsistently (Chapter 6) which indicates that there is no direct causal relationship. Therefore, future research should be directed to the understanding and prevention, rather than the quantifying of age effects.

vegetative sink

The modelling of vegetative growth rate is one of the weakest features in the model. Potential vegetative growth rate is difficult to measure non-destructively and it is even not certain that at non-limiting assimilate supply an appropriate reflection of the vegetative sink strength is obtained (discussed in section 4.6). Therefore, an 'apparent' potential vegetative growth rate was derived from destructively determined dry matter distribution in source-limited crops. The only experiment on this subject indicated that at 23°C the potential growth rate of a vegetative unit is as much as 50% lower than at 19°C (section 4.6). Due to a shorter growth period at high temperature, the potential weight per vegetative unit at maturity could decrease by even 70%.

In contrast, Heuvelink (1995*e*) satisfactorily simulated dry matter distribution at different temperatures with a constant potential vegetative growth rate. As the formation rate of vegetative organs increases with temperature, constant 'whole plant' potential vegetative growth rate implies that (according to equation 8.2.4) the potential weights of individual vegetative organs decrease with temperature. Marcelis (1994*b*) estimated 'whole plant' potential vegetative growth rate of cucumber to increase from 7.8 to 9.3 g d^{-1} when temperature increases from 18 to 24°C. Applying equation 8.2.4 to these potential vegetative growth rates and the leaf formation rates estimated for 18 and 24°C (Marcelis, 1994*b*) revealed that also for cucumber the potential weight of individual vegetative organs decreases with increasing temperature, *viz.* (ignoring dry matter partitioned to roots) 9.0 and 6.6 g per stem internode with one leaf at 18 and 24°C, respectively. Although a reduction of the potential size of vegetative organs with temperature is confirmed by others and the present tentative model performed reasonably well when applied to data from commercial crops (Chapter 6), the decline observed in this study seems rather large. The present description of vegetative growth is based on few experimental data and several assumptions had to be made. Hence, more investigation is necessary to obtain a more solid description of (potential) vegetative growth.

abortion

It is generally agreed that abortion rate and consequently the number of fruits formed depends on assimilate supply to the developing flower buds (e.g. Atherton and Harris, 1986). Unfortunately, when trying to put this idea into a model several difficulties are encountered. First, it should be known at which stage fruits may abort. Reasonable indications for this can be found in the literature, e.g. Calvert (1969) and Kinet (1977) for tomato. Secondly, it has to be decided whether to simulate a potentially initiated number minus abortion, as in

the present study, or to model directly the number of new fruits formed. When the number of fruits is low compared to the potential number (e.g. cucumber; Marcelis, 1992*b*), direct modelling is preferred as such a model has one variable less. When abortion is low (e.g. tomato) fruit initiation rate can be a limiting factor which has to be accounted for.

Another difficulty is the modelling of assimilate supply from flower bud initiation until the end of the abortion-sensitive phase. Each flower bud may be regarded as an individual sink in competition for assimilate but problems arise when competitive strength (i.e. potential growth rate) has to be determined. The contribution of flower buds and young fruits to the total crop assimilate demand is probably low and therefore may be ignored. This reduces the problem to searching for a relationship between abortion (or number of fruits that do not abort) and sink-source ratio as tentatively experimented for tomato (Bertin and Gary, 1993; Dayan *et al.*, 1993*a*) and cucumber (Marcelis, 1994*b*). A difficulty is that sink-source ratio cannot be measured and therefore such a relationship has to be assessed indirectly by simulation.

The number of fruits developed per truss and growth per vegetative unit appeared positively correlated (section 3.3), which supports the hypothesis that abortion as well as vegetative growth rate are affected by assimilate availability. Positive correlation between the number of non-aborting fruits and the vegetative growth rate has also been observed for cucumber (Marcelis, 1992*b*). In this study it was attempted to describe the number of fruits formed as a function of vegetative growth. Such a description is easier to assess than a description on the basis of sink-source ratio, because vegetative growth can be measured. Furthermore, such a relationship can be validated separately.

In models that simulated dry matter partitioning on the basis of competition for assimilate, the vegetative growth rate is inversely proportional to the sink-source ratio. Hence, considering the complete model, relating fruit formation rate to vegetative growth or sink-source ratio is virtually the same. When applying the former relationship it should be realized that the final result strongly depends on the prediction of vegetative growth.

In the present model fruit formation rate is derived from truss formation (flowering) rate and number of fruits per truss. The description of number of fruits per truss is based on insufficient experimental data and it failed to predict the numbers observed in commercial crops (Chapter 6). Research to a better description of number of fruits that develop per truss should have the highest priority for further improvement of the model as fruit number is a major determinant of the crop's assimilate and dry matter distribution.

root growth

As a first approximation root growth may be assumed proportional to the above ground vegetative growth in the ratio of 1:5 (Hurd *et al.*, 1979). When vegetative growth equals 30% of total above ground growth (section 6.3), root growth would represent about 6% extra assimilate demand. Hence, for a mature crop, root growth has only a limited effect on total assimilate demand and dry matter distribution. It should be noted that the assimilate requirement for uptake of nutrients is already included in growth respiration (i.e. in the assimilate requirement quotient) of each organ (Penning de Vries *et al.*, 1989). Nevertheless, prediction of root growth is of interest as the amount of (young) roots may be insufficient to provide the plant with adequate amounts of water and nutrients, especially iron, magnesium and calcium (Hurd, 1978).

genotypic differences

In practice different tomato types, represented by several cultivars, are grown and further new cultivars are introduced each year. Tomato types obviously differ in specific characteristics, e.g. the final size of individual fruits, but also cultivars of the same type may have different properties, for example flowering rate (section 3.2). Therefore, descriptions of flowering rate (eqn 3.2.3), initial number of flowers per truss (eqn 3.3.3), fruit development rate (eqn 3.4.8), potential fruit weight (eqn 4.3.6) and fruit dry matter content (eqn 4.2.3) each have been provided with a parameter that accounts for genotypic differences. These parameters can be estimated by growing new cultivars under well-defined conditions. Another, more practical, way of calibration is to grow new cultivars together with a known one and derive the genotype specific parameters from direct comparisons of relevant characteristics.

inter-plant variation

The model simulates a single (average) plant. As a consequence, output of the model, e.g. daily fruit production and average fruit size, does not account for differences in growth and development among plants. More realistic results may be obtained by smoothing predicted daily fruit production over several days and, in addition, dividing the predicted number of fruits into several weight classes adopting a standard deviation for average fruit weight. Horizontal temperature differences in a glasshouse are an important cause of inter-plant variation (Bakker and van Holsteijn, 1989). The resulting variation may be accounted for by repeated simulation runs with different input temperatures according to the horizontal temperature distribution.

vertical temperature pattern

For high wire grown tomato crops, organs of different ages are spatially separated, i.e. young organs are high in the glasshouse whereas old organs are close to ground level. This feature may be used to influence age classes differently through the vertical temperature pattern. For example, heating close to nearly-harvestable fruits may enhance fruit development and subsequently decrease the number of fruits on the plant without affecting fruit and leaf formation rates. In order to manipulate the vertical temperature pattern, modern glasshouses are commonly equipped with two independent heating circuits; a 'pipe rail' system placed about 15 cm above the ground and a 'growth pipe' which can be moved in a vertical direction amidst the canopy. Due to local heating a vertical temperature gradient of several degrees may occur (Winspear, 1978; van Holsteijn, 1985).

The present model assumes a uniform vertical temperature pattern. To simulate effects of different temperatures at different heights in the glasshouse, extra state variables representing the vertical position of each organ have to be included and (for long-term predictions) length increase of the stem (i.e. internode length) has to be modelled. In addition, the input to the model has to account for different temperatures at different heights in the glasshouse. After incorporation and validation, the model will be appropriate to advise in applying temperature to specific vertical positions for the purpose of crop control. Furthermore, the crop response to vertical temperature gradients at low temperature near the roof for reduced energy consumption (Winspear, 1978) can be evaluated as well.

8.4 Complementary models

assimilate production

The model developed in this study simulates assimilate demand and dry matter distribution. Assimilate or dry matter production is input to the model. For proper prediction of the total crop response to crop measures and environment, the assimilate production has to be simulated too. The structure of the model allows for integration with explanatory photosynthesis models (e.g. Gijzen, 1992). The combination should account for the feedback of dry matter partitioned to vegetative growth on future assimilate production (fig 8.2.1). In addition, modelling an influence of assimilate demand on crop photosynthesis

(Hall and Brady, 1977; Gifford and Evans, 1981; Gucci and Flore, 1989) and effects of leaf age on leaf photosynthesis (Peat, 1970; Longuenesse and Tchamitchian, 1990; Tchamitchian and Longuenesse, 1991) become feasible. These extensions, however, are of minor importance as the impact on crop photosynthesis appears only significant under extreme conditions, *viz.* very low fruit load (Marcelis, 1991; Heuvelink and Buiskool, 1995) and low leaf area index in combination with high light levels (Heuvelink and Gijzen, 1995), respectively.

As has been discussed (section 8.2), the profitability of assimilate used for vegetative growth is strongly influenced by the SLA. In a 'long-season' crop the SLA may differ by more than a factor of 2 between spring and summer (fig 7.4.2). Observations on crops of similar age but from different sowing dates (Heuvelink, 1995*a*) confirmed this seasonal trend. SLA of tomato leaves is negatively correlated with light and CO_2 (reviewed by Picken *et al.*, 1986). Furthermore, SLA is affected by water relationships (de Koning and Hurd, 1983), genotype (Gosiewski *et al.*, 1982; Yelle *et al.*, 1990) and sink-source ratio (Starck *et al.*, 1979; Frydrych, 1984; Nederhoff *et al.*, 1992; Heuvelink and Buiskool, 1995). With respect to the last factor, the lower SLA of the 1990 crop in summer compared to the 1992 crop (fig 7.4.2) is probably a demonstration of the lower sink-source ratio in 1990 (fig 7.2.2). there are reports of opposite effects of temperature on SLA (e.g. Picken *et al.*, 1986; Heuvelink, 1989), which may be explained by the fact that along with temperature several aspects of the climate (e.g. humidity) as well as growth and development of the crop change.

Growth models treat leaf area and SLA in a rather rudimentary way. Sometimes simply a forcing function of leaf area (LAI) in course of time is adopted (e.g. Gijzen, 1992; Rijsdijk and Houter, 1993), thus ignoring any feedback of dry matter partitioned to leaves. When leaf area is simulated on the basis of matter distribution, SLA is described by an empirical function of environmental variables (e.g. Dayan *et al.*, 1993*a*). Instead of trying to model SLA, it might be better to treat leaf growth in weight and area separately, as worked out by Thornley and Hurd (1974). This approach assumes that SLA is just the result of two (though not fully independent) processes.

water relationships

There seems evidence that assimilate distribution at the tissue level is affected by differences in water potential (Wolswinkel, 1985). Growers try to enhance generative growth by restricted watering (de Koning and Hurd, 1983), high salinity in the root zone and low air humidity (Kessels, 1993). Scientific research

at a whole-crop level, however, failed to detect any effect of salinity level (Ehret and Ho, 1986*a*; Ho and Adams, 1994) and air humidity (Bakker, 1991) on dry matter distribution in glasshouse tomato.

The seasonal trends observed for fruit dry matter content (figs 4.2.3 and 6.3.10) and SLA (fig 7.4.2) probably (in part) result from variation in crop water relationships. Explanatory models of SLA and fruit dry matter content, therefore, probably should include aspects of the crop's water relationships. In addition, water relationships in the plant are relevant to several other aspects of fruit quality, e.g. blossom-end rot (Ehret and Ho, 1986*b*), taste (Verkerke *et al.*, 1993) and shelf life (Janse and Welles, 1984; Bakker, 1990; Verkerke and Gielesen, 1991; Verkerke *et al*, 1993).

Up to now, modelling water relationships in glasshouse crops is mainly confined to transpiration (e.g. Stanghellini, 1987). Some preliminary attempts have been made to simulate water potentials in tomato (Bruggink *et al.*, 1988; Batta, 1989; Marcelis, 1989). As explanatory models including water relationships are not expected within a few years, for the moment SLA and FDMC have to be described rather empirically as functions of environment and possibly day of the year.

8.5 Temperature control

tactical level

The whole-season temperature strategy is correlated to the other aspects of the tactical plan. For example, at high temperature, low vegetative growth rate may be compensated for by low shoot density. Different strategies may be evaluated by simulation. Besides the criteria for high total fruit production (i.e. an optimum balance between vegetative and generative growth and a proper ratio between demand and supply of assimilate), also the timing of the production (e.g. earlier in spring and delay in autumn to profit from better prices), fruit quality (e.g. high temperature for better taste (Buitelaar and Janse, 1990; Janse and Schols, 1993)), crop quality (e.g. susceptibility to *Botrytis* (Dechering, 1994)) and the heating costs play a role (table 8.5.1). As a matter of course, the chosen temperature strategy should be feasible with respect to the expected climatic conditions and the control possibilities in the glasshouse.

Table 8.5.1 Criteria, input information and output of decision making with respect to temperature control at different decision levels.

Decision level	Planning horizon	Criteria	Input	Output
tactical	one cropping season	proper ratio between assimilate demand and supply, optimal balance between generative and vegetative growth, fruit size, timing of production, fruit quality, crop quality heating costs	expected course of solar radiation and other environmental parameters, equipment and glasshouse properties	tactical plan consisting of: sowing date, initial plant density, retaining of extra shoots, number of fruits per truss, temperature
operational	day-week	as above	visual judgement of the crop, weather forecast	adjustment of the desired average temperature
operational	$\leq$ 24 h	preventing extreme temperatures that cause irreversible damage, reasonable labour environment, avoiding condensation of water vapour on plant parts, control of other environmental parameters, manipulating length increase, low heating costs	desired average temperature, measurements of actual glasshouse environment and actual weather conditions	strategy for diurnal temperature course

operational level

In the daily control (operational level) temperature settings are adjusted on the basis of the actual crop development and growth. To this purpose, in practice temperature settings are changed several times a week (van Logten, 1990). With a prediction of the effect of the actual conditions on crop growth, the adjustments can be more precise and anticipate visible crop response.

Better light conditions than expected would generally require a higher temperature (than formulated in the tactical plan) in order to maintain a proper balance between demand and supply of assimilate and an optimal dry matter distribution (fig 8.2.1). Adjustments of temperature to the light level should not necessarily be instantaneous. Earlier research demonstrated that cumulative growth is not affected by different day/night regimes (de Koning, 1988*b*) and even alternating high and low temperatures (with up to 6°C amplitude) for several days (up to 12) had, in comparison to constant temperature, no consequences for cumulative crop response (de Koning, 1990). This temperature integrating capability results from the low temperature sensitivity of canopy gross photosynthesis (Ludwig, 1974; Nilsen *et al.*, 1983; Schapendonk and Brouwer, 1985; Acock, 1991) and the plant's ability to store and subsequently release carbohydrates (Gary, 1988).

In view of the involvement of the grower in climate control (Challa, 1990) and the temperature integrating capability of crops, two decision levels can be distinguished within the operational control of temperature, *viz.* decisions concerning the average temperature ranging over one to several days and decisions with respect to the temperature course within a day (table 8.5.1). The present model has been developed to advise on the use of temperature as a tool to control assimilate demand and dry matter distribution. In future, expert systems may be available that, additional to quantitative models, include empirical knowledge for those aspects relevant to temperature control that cannot yet be modelled quantitatively (Challa, 1990; Boulard *et al.*, 1991). Fully automatic determination of setpoints for average temperature is not strictly necessary because temperature settings would change only several times a week. Moreover, temperature control at this decision level is regarded as an essential part of integral crop management and for these reasons even sophisticated expert systems would at best be a valuable adviser, rather than take over this part of temperature control. The number of manual changes of the temperature settings can be reduced if the control system increases the setpoint for average temperature (or temperature integral) automatically at increasing light level.

The primary objectives of instantaneous temperature control (lowest decision level) are: (1) preventing extreme temperatures that cause irreversible damage to the plants, (2) preventing temperatures lower than the dew point to avoid condensation of water vapour on plant parts and (3) creating a reasonable labour environment (table 8.5.1). The associated boundary values together with the desired average temperature are the constraints for optimal control of the glasshouse environment with respect to other environmental parameters (e.g. CO_2), the diurnal temperature regime manipulating the plant's length increase (de Koning, 1992) and heating costs (table 8.5.1). Except for some preliminary attempts, current control systems have low flexibility to vary autonomously the diurnal course of temperature in favour of the control of other (climatic) factors. Future 'intelligent' control systems aiming at optimal control of the whole glasshouse environment (Challa, 1990; Challa and van Straten, 1991) should take advantage of the possibilities offered by temperature integration (Boulard *et al.*, 1991; Seginer, 1993).

8.6 Using the model in practice

Crop simulation models have great potential for practical use (Challa, 1985; Seginer, 1993) but they have as yet not left the research environment (Seligman, 1990). In Dutch glasshouse cultivation there are two exceptions, *viz.* crop transpiration models used in the control of watering (de Graaf, 1988) and recently a photosynthesis module introduced for diurnal control of heat storage with respect to CO_2 supply (Nunnink, 1991). The present model has been developed to advise about crop measures and temperature for crop control. At the tactical decision level the model can be applied for the formulation of a plan concerning the whole-season temperature strategy, initial plant density, retaining extra shoots and fruit pruning. In operational management the model can advise about fruit pruning and the strategy for short-term (day to weeks) temperature.

When used for operational management, real number of fruits formed may be input to the model, which to a large extent solves the problem that fruit formation is not yet well predicted. To this purpose, a system should be developed that enables the model to access recordings on the glasshouse climate (temperature and solar radiation) and the crop. The regular weekly observations in practice include already, among others, number of the highest flowering truss, number of fruits set and the number of the highest truss with harvest ripe fruits (van Holsteijn, 1991). The resulting system is able to compute the actual assimilate demand of the vegetative plant parts and the fruits present, the latter being a better parameter for fruit load than the currently used 'number of fruits'

(Chapter 1). Besides simulating the actual sink demand, the system may provide short-term predictions of the assimilate demand and the ratio between dry matter distribution to vegetative and generative growth at different temperatures. Besides input for simulation, crop recordings may be compared with model predictions in order to calibrate model parameters for new cultivars or to indicate possible malfunctioning of the crop (e.g. when observed flowering rate is significantly lower than the predicted rate).

Several other applications become feasible when, in addition to the system described, the crop's assimilate production is simulated or its growth rate is measured. A method to automatically measure crop fresh weight *in situ* has been described previously (de Koning and Bakker, 1991). The first interesting new possibility offered is comparing predicted assimilate demand (or crop potential growth rate) with simulated assimilate production (or measured crop growth rate, respectively). With tomato this ratio should probably be around 2 (Chapter 7). Secondly, a yield prediction for the following few days in number as well as weight of fruits seems feasible (de Koning *et al.*, 1993). Thirdly, simulated growth rate of different crop tissues in combination with the concentrations of each nutrient element needed for healthy growth (van Goor *et al.*, 1988) provides a basis for feedforward control of nutrient supply. This is of particular value in modern growing systems with low buffering capacity where nutrient uptake easily leads to either depletion or toxic levels of specific elements (Asher and Blamey, 1987). Additional to the use for control, such a system may warn against possible nutrient deficiencies in the crop, i.e. when large differences occur between predicted uptake and the actual amount of nutrients supplied to maintain (taking possible losses due to drainage into account) the desired nutrient concentration in the root environment.

Development processes and dry matter distribution are, in contrast to photosynthesis and transpiration, rather crop specific (Challa, 1989; Challa *et al.*, 1994). Even significant differences between cultivars of one species may occur. Specificity is a serious obstacle to the development and the application of models simulating these processes. The development and the introduction of models would be facilitated when for each distinct type of (glasshouse) crops (e.g. (indeterminate) fruit vegetables, leafy vegetables, once-over harvested cut flowers, repeatedly harvested cut flowers, green pot plants and flowering pot plants) a general modular model architecture is developed based on processes at organ level, such that a minimum number of key parameters accounts for differences between cultivars or species. Preferably these key parameters should have biological meaning and be determined with simple means. Only then will the widespread use of growth simulation models in crop control become feasible.

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Summary

In the Netherlands the cultivation of glasshouse tomato commonly consists of only one crop that is sown in November and grown until October or November the following year. After an initial vegetative phase, fruit growth starts in January. In the generative phase vegetative growth is still required in order to sustain the crop's photosynthetic capacity for maximum fruit yield in the long term. Hence, a proper balance has to be found between vegetative and generative growth. The ratio between vegetative and generative growth depends on the fruit load, i.e. the demand for assimilate of all fruits together.

Besides reducing vegetative growth, high fruit load relative to the supply of assimilate causes low weight of individual fruits and enhances the abortion of flowers. On the other hand, low fruit load may adversely affect fruit quality and fruit load should be sufficient to ensure that the production and not the demand of assimilate limits crop production. Hence, fruit load has to be in proportion to the assimilate production. As the latter is mainly determined by the solar radiation, optimum fruit load varies throughout the cropping season.

Fruit load per unit ground area is varied by the number of shoots per unit ground area (shoot density) and fruit pruning. In addition to initial plant density, shoot density can be varied through retaining side shoots. These crop measures are appropriate to manipulate fruit load in the long term. For the short-term control temperature is used. At present the use of measures to manipulate the crop assimilate demand and the ratio between vegetative and generative growth (summarized as crop control) are based on general rules and knowledge about qualitative crop response. The objective of this study was to predict the assimilate demand and dry matter distribution in a tomato crop in quantitative terms, so that measures for crop control can become more precise and effective. For other glasshouse fruit vegetables the principles of crop control are the same as for tomato, so that the results have a wider relevance than for the cultivation of tomato only.

Predicting the ultimate response of a crop to a particular measure is rather complex because several plant processes may be affected. Moreover, short- and long-term effects may differ and several internal feedback controls play a role. To manage this complexity an explanatory dynamic model was developed that simulates the behaviour of the crop in time (time-step of one day) on the basis of distinct plant processes at the organ level.

In this study two aspects of crop control were considered in particular, *viz.* the crop assimilate demand (as counterpart of the assimilate production) and the dry matter distribution in the crop. The organ's demand for assimilate consists of the requirement for maintenance and a growth component. The latter was assumed to be defined by the assimilate requirement for growth of the organ growing at its potential rate which is obtained at nonlimiting assimilate supply. Experiments on assimilate demand were confined to quantifying the potential growth rates of individual organs. Respiration coefficients were adopted from the literature.

It is generally agreed that dry matter distribution in a plant is regulated by the mutual competition between sink (assimilate importing) organs. In this study it was assumed that the competitive strength of the individual organs is determined by their potential growth rates. For long-term prediction of assimilate demand and dry matter distribution, the number of growing organs has to be evaluated through prediction of initiation, abortion, ageing and harvest of individual organs. Therefore, besides quantifying potential growth rates, part of this study concerned developmental aspects.

In total 11 glasshouse experiments were conducted, most of them consisting of sub-experiments on different aspects of growth and development. As temperature is regarded as an important control variable for assimilate demand as well as dry matter distribution, several experiments included temperature treatments. The investigated temperatures ranged from 17 to 27°C. In addition to the experiments at the Glasshouse Crops Research Station, plant development was recorded in some regular cultivar trials in practice.

In glasshouse-grown indeterminate tomato all lateral shoots are removed, resulting in a single main stem bearing trusses separated by three leaves. So the plant development stage can be represented by the number (position on the main stem) of the truss that has reached anthesis; the rate of plant development being proportional to the rate at which successive trusses reach anthesis. In accordance with common use, this rate is called the flowering rate.

Flowering rate appeared to be determined by temperature, genotype and plant age. Fruit load, plant spacing and electrical conductivity of the root environment (0.3-0.9 S m^{-1}) had no or only very little effect. Within the range of 17 to 27°C flowering rate increased slightly less than in proportion with increasing temperature, resulting in a Q_{10} of 1.7 and 1.4 at 18 and 23°C, respectively. The short-term (several days) response to temperature appeared significantly stronger. The difference between short- and long-term response was attributed to the influence of temperature on the period from truss initiation until anthesis. Flowering rates of cultivars differed by as much as 10%, but their response to temperature was the same.

Old plants exhibited about 20% lower flowering rates than young plants. The decline appeared to be less for vigorous cultivars, which indicates that reduced flowering rate with increasing plant age is related to the loss of vigour. On the basis of experiments including fruit load and plant spacing treatments and literature on the influences of solar radiation and CO_2-concentration, it was concluded that flowering rate is affected by the assimilate demand to supply ratio (sink-source) in very extreme cases only.

The number of fruits that develop on a truss is determined by the number of flowers per truss and the relative number of flowers that become fruits (percentage fruit-set). In an exploratory experiment a relationship between number of flowers per truss and size of the corresponding vegetative unit (stem part with three leaves) was observed which, moreover, covered all the correlations with the experimental variables temperature, plant density and fruit load. Rather than being causal, this relationship reflects that both crop characteristics depend on the availability of assimilate. The percentage fruit-set was affected by temperature only and described by an optimum curve exhibiting the best fruit-set around 19°C.

Duration of the fruit growth period (time between anthesis and start of colouring orange) is shortened with increasing temperature, young and nearly harvestable fruits being the most sensitive for acceleration. The Q_{10} for the average fruit development rate was estimated to be 1.8 at constant 18°C and 1.4 at 23°C. At the same air temperature in summer the fruit growth period was shorter than in spring. This may be ascribed in part to higher fruit temperature than air temperature at high solar irradiance. Fruits of old plants had longer (+8%) fruit growth period than fruits of young plants. There was no indication that the cultivars used differed in fruit development rate. The electrical conductivity in the root environment (0.3-0.9 S m^{-1}) had no influence on the fruit growth period.

Potential growth of fruits was obtained by pruning all trusses on the plant to one or two fruits. The potential weight of individual fruits in time was described by a (sigmoidal) Gompertz growth function. One of the three parameters of this curve represents the asymptotic maximum and could be regarded as independent of the other parameters of the curve. Further, this parameter was proportionally related to the weight of the fruit at harvest (start of colouring).

Fruits at the first trusses had a lower potential weight than fruits grown at the following trusses. This effect could be described by a saturating response with increasing truss number, the effect being less pronounced at increasing solar radiation levels. The potential weight was also affected by the fruit position within the truss. The second to fourth positioned fruits of round tomato became

the largest whereas distal fruits were as much as 20% smaller. Potential fruit weight decreased by 40% when temperature increased from 17 to 23°C. The beefsteak tomato 'Dombito' exhibited a 2.3 times higher potential fruit weight than the round type 'Calypso'. There was some evidence that differences also exist among the round types.

Except for attainable size, the shape of the growth curve was the same for round and beefsteak tomato. Furthermore, the shape was not noticeably affected by fruit and truss position. Temperature enhanced fruit development but at all temperatures the fruits exhibited the maximum potential growth rate at about 40% of their growth period. The decline of the potential fruit weight with increasing temperature was mainly the result of differences in the fruit growth period and, to a minor extent, of differences in the growth rate per day.

When during fruit development a fruit changed from limiting to nonlimiting assimilate supply, it did not immediately reach the same growth rate as fruits constantly grown at nonlimiting assimilate supply. It is hypothesized that the amount of enzymatic machinery for uptake and processing of assimilates adapts to the amount of assimilate available and time is needed for acclimation when assimilate supply changes. In this way the actual potential growth rate approximates the actual growth rate. Hence, for each organ an actual potential growth rate can be distinguished from the maximum potential growth rate reached after prolonged nonlimiting assimilate supply.

The same mechanism may explain why in the present study hardly any influence of temperature on the long-term potential growth rate was observed, in contrast to the literature in which there are reports of a very profound stimulating short-term effects of temperature on assimilate uptake and growth rate. The activity per unit of processing machinery probably increases immediately with increasing temperature whereas with long-term exposure to high temperature the high specific activity is possibly compensated for by a low amount of machinery.

Compared to fruits, potential growth of vegetative organs is difficult to measure and it is not certain that at nonlimiting assimilate supply an appropriate reflection of the competitive power to attract assimilate is obtained. As an alternative for measuring at nonlimiting assimilate conditions an 'apparent' potential vegetative growth rate may be derived from dry matter distribution in source-limited crops. Tentative results indicated that for a mature crop the fraction of dry matter distributed to vegetative growth declines significantly with increasing temperature. Based on this, the (apparent) potential growth rate of a vegetative unit at 23°C was estimated to be as much as 50% lower than at 19°C.

The decrease of fruit dry matter content with fruit development stage was approximated by a quadratic function. The fruit dry matter content at harvest increased with the electrical conductivity of the root environment (0.3-0.9 S m^{-1}) and temperature (17-23°C), i.e. 0.017 g g^{-1} per S m^{-1} and 0.0007 g g^{-1} per °C, respectively. Moreover, it varied with time of the year and was estimated to be 0.007 g g^{-1} higher in summer than in winter.

The developed simulation model predicts daily assimilate demand (maintenance and growth requirement) and growth rates of individual fruits and vegetative units of indeterminate tomato. Roots are not included in the model. The competition for dry matter available for growth is defined on the basis of potential growth rates of individual organs. The number of growing organs is simulated through prediction of initiation, abortion and harvest of individual organs. Computations in the model are on a ground area basis, allowing for possible increase of shoot density by retaining extra shoots during the cropping season.

Daily amount of dry matter available for growth is input to the model. Furthermore, the model requires daily values of 24-h average air temperature and solar radiation integral. Electrical conductivity of the root environment is necessary to convert fruit dry weight to fresh weight.

The model was tested with data collected from five commercial crops. Predicted flowering rate and fruit growth period agreed well with the measurements. However, the decline of flowering rate with increasing plant age was difficult to predict accurately and did not appear very consistent.

When the number of organs formed was input to the model, dry matter distribution was simulated successfully. Predicted numbers of fruits per truss differed from the numbers observed. A sensitivity analysis on the model showed that the number of fruits per truss is a major determinant of dry matter distribution and crop assimilate demand. To complete the model, therefore, a reliable quantitative description of number of fruits per truss is urgently needed. The general level and seasonal course of fruit dry matter content at harvest was predicted reasonably well, though the predictions did not account for short-term variation in the measured data.

Because assimilate demand cannot be measured, the predicted assimilate demand could not be compared with measurements. Simulations showed that for a commercial crop the predicted demand, on the basis of maximum potential growth rates reached values of up to 10 and 60 g CH_2O m^{-2} d^{-1} for the maintenance and growth component, respectively. The maximum potential

growth rate of a tomato crop, for temperatures as recorded, appeared to be about twice the actual growth rate.

To demonstrate a possible use of the model, the crop behaviour to changes of some crop measures and temperature has been evaluated. Furthermore, it is shown how the model, adopting some additional relationships about specific leaf area and assimilate production, can advise in the planning of shoot density and number of fruits per truss.

Tentative predictions indicate that maximum fruit production is probably obtained at a fairly low leaf area index (2-3 m^2m^{-2}) and associated light interception. At supra-optimum leaf area index additional leaf area for extra light interception requires more assimilate than it would produce. The computations also indicate that in spring and early summer the optimum number of shoots is determined by the required number of fruits (sink capacity) rather than an adequate crop leaf area, whereas in late summer the highest fruit production would be obtained by high shoot density in combination with fruit pruning.

In the last chapter, the consequences for practice of the obtained knowledge about the sink-source system is discussed. Special attention has been given to temperature as a tool to manipulate crop growth. The implications and additional criteria for temperature control are considered. Furthermore, shortcomings, limitations and possible extensions of the model and combinations with complementary models are dealt with. Finally, an outlook on the possible practical applications of models simulating assimilate demand and dry matter distribution is given.

As demonstrated, the developed model may be used in making a cultivation plan concerning shoot density, fruit pruning and long-term temperature strategy. A combination of the model with common climate and crop recordings offers several interesting possibilities to support the operational management.

Samenvatting

In Nederland worden kastomaten gewoonlijk gezaaid in november en duurt de teelt tot oktober of november van het volgende jaar. Na een opkweek met alleen vegetatieve groei is ook tijdens de produktiefase een zekere hoeveelheid vegetatieve groei nodig om de fotosynthesecapaciteit van het gewas op peil te houden. Voor een maximale totaalproduktie is een juiste balans tussen vegetatieve en generatieve groei nodig. De verhouding tussen vegetatieve en generatieve groei wordt voornamelijk bepaald door de plantbelasting (de totale assimilatenvraag van alle vruchten).

Een hoge plantbelasting (ten opzichte van het assimilatenaanbod) veroorzaakt, behalve een geringe vegetatieve groei, ook kleine vruchten en verhoogt de kans op bloemabortie. Een lage plantbelasting kan echter ook nadelig zijn voor de vruchtkwaliteit. Voldoende plantbelasting is bovendien nodig om er voor te zorgen dat niet de assimilatenvraag, maar het assimilatenaanbod de produktiebeperkende factor is. De plantbelasting moet dus afgestemd zijn op het aanbod van assimilaten. Omdat het aanbod voornamelijk wordt bepaald door de hoeveelheid licht is de optimale plantbelasting gedurende het jaar niet constant.

De plantbelasting per eenheid kasoppervlak kan gestuurd worden met de plant- of stengeldichtheid en vruchtsnoei. Deze maatregelen zijn vooral geschikt om de plantbelasting op lange termijn te regelen. Voor sturing op korte termijn wordt temperatuur gebruikt.

Het sturen van de plantbelasting en de verhouding tussen vegetatieve en generatieve groei berust voornamelijk op algemene regels en kwalitatieve kennis van de gewasrespons op de verschillende teeltmaatregelen. Het doel van dit onderzoek was om de assimilatenvraag en verdeling van droge stof te quantificeren ten behoeve van een meer gerichte en efficiëntere sturing van de gewasgroei. De resultaten zijn ook relevant voor de teelt van andere vruchtgroenten dan tomaat, omdat de principes gelijk zijn.

Het voorspellen van de uiteindelijke gewasreactie op een bepaalde teeltmaatregel is moeilijk omdat meestal verschillende plantprocessen worden beïnvloed. Bovendien kunnen reacties op lange termijn anders zijn dan die op korte termijn. Daarom is een verklarend dynamisch model ontwikkeld dat de assimilatenvraag en droge-stofverdeling simuleert op basis van afzonderlijke processen op orgaanniveau.

De plant vraagt om assimilaten voor onderhoud en voor groei. De component voor groei is gedefinieerd als de assimilatenbehoefte voor potentiële groei, d.w.z. de groeisnelheid die bereikt wordt bij een niet-beperkend assimilatenaanbod. De proeven om de assimilatenvraag te quantificeren beperkten

zich tot het beschrijven van de potentiële groei van afzonderlijke organen. Ademhaling voor onderhoud en groei werd beschreven op basis van literatuurgegevens.

Algemeen wordt aangenomen dat de verdeling van droge stof in een plant bepaald wordt door onderlinge concurrentie tussen organen om de beschikbare assimilaten. In dit onderzoek is aangenomen dat de concurrentiekracht van afzonderlijke organen beschreven kan worden op basis van de potentiële groeisnelheid. Voor lange-termijnvoorspellingen omtrent assimilatenvraag en droge-stofverdeling zijn de veranderingen in het aantal groeiende plantedelen door initiatie, abortie, veroudering en oogst van belang. Een deel van dit onderzoek richtte zich op deze aspecten.

In totaal werden 11 kasproeven uitgevoerd, waarvan de meeste meerdere deelproeven naar verschillende aspecten van groei en ontwikkeling bevatten. Omdat temperatuur een belangrijk sturingsmiddel is voor zowel de assimilatenvraag als de droge-stofverdeling lag de nadruk op het quantificeren van temperatuureffecten. Het onderzochte temperatuurtraject liep van 17 tot 27°C. Naast de proeven op het Proefstation voor Tuinbouw onder Glas werd in enkele praktijkproeven van het gebruikswaardeonderzoek de ontwikkelingssnelheid bij verschillende rassen bepaald.
Bij kastomaten worden alle zijscheuten verwijderd. Tussen de opeenvolgende trossen met vruchten aan de hoofdstengel zitten drie bladeren. Het ontwikkelingsstadium en de ontwikkelingssnelheid van een tomatenplant kan worden uitgedrukt in respectievelijk het nummer van de bloeiende tros en de snelheid waarmee de trossen elkaar opvolgen. In overeenstemming met de praktijk wordt de laatste de bloeisnelheid genoemd.

De bloeisnelheid bleek afhankelijk van temperatuur, ras en plantleeftijd. Plantbelasting, plantdichtheid en elektrische geleidbaarheid in het wortelmedium (EC, 0,3-0,9 S m^{-1}) hadden geen of slechts zeer geringe invloed. Tussen 17 en 27°C neemt de bloeisnelheid bijna recht evenredig toe met de temperatuur, resulterend in een Q_{10} (relatieve verandering met 10 graden temperatuurstijging) van 1,7 en 1,4 bij respectievelijk 18 en 23°C. De korte-termijnreactie op temperatuur bleek beduidend sterker en het verschil kan verklaard worden met de temperatuurinvloed op de periode tussen initiatie en bloei van een tros.

Tussen rassen verschilde de bloeisnelheid tot 10% maar de invloed van temperatuur was gelijk. De bloeisnelheid van oude planten was ongeveer 20% lager dan van jonge planten, waarbij rassen met weinig groeikracht de grootste terugval lieten zien. Op basis van proeven met plantbelasting en plantdichtheid en literatuur omtrent de invloed van licht en CO_2 werd geconcludeerd dat de bloeisnelheid alleen door een extreme verhouding tussen vraag en aanbod van assimilaten (sink-source verhouding) beïnvloed wordt.

Het aantal vruchten aan een tros wordt bepaald door het aantal bloemen en het percentage vruchtzetting. In een verkennende proef werd een relatie gevonden tussen het aantal bloemen per tros en het gewicht van de corresponderende vegetatieve eenheid (stengeldeel met drie bladeren). Deze relatie omvatte alle correlaties met de proeffactoren: temperatuur, plantdichtheid en vruchtsnoei. Deze relatie is waarschijnlijk niet oorzakelijk maar weerspiegelt de gezamenlijke afhankelijkheid van het assimilatenaanbod. Het percentage vruchtzetting bleek in deze proef slechts afhankelijk van temperatuur en werd beschreven met een optimumkromme met de beste vruchtzetting bij circa 19°C.

De uitgroeiduur van een vrucht (het aantal dagen tussen bloei en het kleuren van groen naar oranje) is korter naarmate de temperatuur hoger is. Jonge en bijna oogstbare vruchten bleken het meest gevoelig voor de versnelling in ontwikkeling. De Q_{10} voor de gemiddelde vruchtontwikkelingssnelheid bij constante temperatuur was 1,8 bij 18 en 1,4 bij 23°C. Bij eenzelfde luchttemperatuur bleek de uitgroeiduur in de zomer korter dan in het voorjaar, wat gedeeltelijk toegeschreven kan worden aan het grotere verschil tussen lucht- en vruchttemperatuur in de zomer. Vruchten aan oude planten hadden een langere (8%) uitgroeiduur dan vruchten aan jonge planten. De uitgroeiduur van de in de proeven gebruikte rassen bleek ongeveer gelijk. De EC (0,3-0,9 S m^{-1}) in het wortelmedium had geen effect op de uitgroeiduur.

Potentiële groei van vruchten werd bereikt door alle trossen aan de plant te snoeien tot op één of twee vruchten. Het verloop van het vruchtgewicht in de tijd werd beschreven met een (sigmoide) Gompertz groeikromme. Eén van de drie parameters in deze kromme, het asymptotisch maximum vruchtgewicht, bleek onafhankelijk van de overige parameters. De waarde van deze parameter was recht evenredig met het vruchtgewicht bij oogst.

De potentiële grootte van de vruchten aan de eerste trossen was lager dan die van vruchten aan de volgende trossen. Deze invloed was beschreven met een verzadigingskromme. Het effect van trosnummer neemt af bij hogere lichtniveaus. Ook vruchtpositie binnen een tros heeft invloed op het potentiële vruchtgewicht: de tweede, derde en vierde vruchten werden het grootste terwijl de eindvruchten ongeveer 20% kleiner waren. Het potentiële vruchtgewicht bij 23°C was ongeveer 40% lager dan bij 17°C. De vleestomaat 'Dombito' werd ongeveer 2,3 keer zo zwaar als de ronde tomaat 'Calypso'. Er zijn aanwijzingen dat ook tussen ronde rassen verschillen zijn in potentiële vruchtgrootte.

De vorm van de groeikromme was voor ronde en vleestomaat gelijk. Ook tros-en vruchtnummer hadden geen invloed op de vorm van de kromme. Hoewel een hogere temperatuur de totale uitgroeiduur verkort, blijkt de maximale groeisnelheid altijd bereikt te worden na ongeveer 40% van de groeiduur. De

afname van het potentiële gewicht bij toename van de temperatuur was voornamelijk het gevolg van de kortere uitgroeiduur en in mindere mate van verschillen in de groeisnelheid per dag.

Wanneer tijdens de vruchtgroei een vrucht plotseling een niet-beperkend assimilatenaanbod kreeg, nam het niet direct de groeisnelheid aan van even oude vruchten die vanaf het begin potentieel groeiden. Een hypothese is dat de capaciteit om assimilaten op te nemen en te verwerken zich aanpast aan de assimilatenbeschikbaarheid en dat, wanneer de beschikbaarheid plotseling toeneemt, enige tijd nodig is voordat de grootte van het verwerkingsapparaat volledig is aangepast. Door dit mechanisme benadert de actuele potentiële groeisnelheid de werkelijke groeisnelheid. Daarom kan voor ieder orgaan een actuele potentiële groeisnelheid onderscheiden worden van de maximum potentiële groeisnelheid die bereikt wordt na langdurig niet-beperkend assimilatenaanbod.

Dit mechanisme kan ook het verschil verklaren tussen het in dit onderzoek gevonden geringe effect van constante temperatuurniveau's op de potentiële groeisnelheid en de grote effecten die volgens de literatuur optreden bij temperatuurwisselingen. Waarschijnlijk neemt de activiteit per eenheid verwerkingsapparaat direct toe als de temperatuur toeneemt terwijl op lange termijn de hogere specifieke activiteit gecompenseerd wordt door een kleiner verwerkingsapparaat.

In vergelijking met vruchten is de potentiële groeisnelheid van vegetatieve delen moeilijk te meten. Bovendien is het niet zeker dat bij niet-beperkend assimilatenaanbod een juiste afspiegeling van de concurrentiekracht van de vegetatieve delen gevonden wordt. Als alternatief voor het meten onder niet-beperkend assimilatenaanbod kan een schijnbare potentiële groeisnelheid afgeleid worden uit de droge-stofverdeling in planten waarin de groei beperkt wordt door het aanbod van assimilaten. Voorlopige resultaten met volwassen planten wijzen op een sterke afname van de vegetatieve groei bij een stijging van de temperatuur. Op grond van deze resultaten bleek de (schijnbare) potentiële groeisnelheid van een vegetatieve eenheid bij 23°C ongeveer 50% lager dan bij 19°C.

Het droge-stofgehalte van vruchten neemt tijdens de vruchtontwikkeling af. Dat van rijpe vruchten nam toe met de EC in het wortelmedium (0,3-0,9 S m^{-1}) en temperatuur (17-23°C) met respectievelijk 0,017 g g^{-1} per S m^{-1} en 0,0007 g g^{-1} per °C. In de zomer is het droge-stofgehalte ongeveer 0,007 g g^{-1} hoger dan in de winter.

Het ontwikkelde simulatiemodel voorspelt de dagelijkse assimilatenvraag (op basis van onderhoud en groei) en groeisnelheden van afzonderlijke vruchten en vegetatieve eenheden. Onderhoud en groei van wortels zijn niet in het model opgenomen. Initiatie, abortie en oogst van afzonderlijke organen bepaalt het aantal aan de plant. De berekeningen in het model zijn per eenheid kasoppervlak zodat rekening kan worden gehouden met een toename van het aantal stengels tijdens de teelt. Droge-stoftoename per dag wordt in het model ingevoerd. Verder gebruikt het model dagelijkse waarden van de gemiddelde temperatuur en instraling. EC is nodig om het versgewicht van de geoogste vruchten te berekenen.

Het model is getest met gegevens van vijf teelten in de praktijk. Voorspelde bloeisnelheid en uitgroeiduur van de vruchten kwamen goed overeen met de gemeten waarden. Echter, de afname van de bloeisnelheid met het ouder worden van het gewas bleek moeilijk te voorspellen, mede omdat dit verschijnsel niet erg consequent optrad.

De droge-stofverdeling werd redelijk gesimuleerd indien het aantal gevormde vruchten ingevoerd werd. Het aantal vruchten per tros werd onvoldoende nauwkeurig voorspeld. Een gevoeligheidsanalyse toonde aan dat het aantal vruchten per tros een belangrijke factor is in de totale assimilatenvraag en de verdeling van droge stof. Een betrouwbare voorspelling van het aantal vruchten per tros is daarom dringend gewenst.

Het globale niveau en jaarlijks verloop van het droge-stofgehalte van oogstbare vruchten werd redelijk voorspeld maar korte-termijnvariatie in de gemeten waarden werd niet gesimuleerd.

De vraag naar assimilaten kan niet gemeten worden. Hierdoor is een vergelijking van de voorspellingen met metingen onmogelijk. Voor de nagesimuleerde teelten was, op basis van de maximale potentiële groeisnelheden, de maximale assimilatenvraag voor onderhoud ongeveer 10 en voor groei ongeveer 60 g CH_2O m^{-2} d^{-1}. De gesimuleerde maximale potentiële groeisnelheid van de praktijkgewassen (bij de gemeten temperaturen) was ongeveer tweemaal de werkelijke groeisnelheid.

Gedemonstreerd werd dat het model de veranderingen in gewasgroei als gevolg van veranderingen in teeltmaatregelen kan voorspellen. Ook is getoond hoe het model met enkele extra aannamen omtrent bladdikte (Specific Leaf Area) en assimilatenproduktie kan adviseren bij de planning van het aantal stengels per vierkante meter en het aantal vruchten per tros.

Voorlopige voorspellingen gaven aan dat de maximale vruchtproduktie waarschijnlijk bereikt wordt bij relatief weinig bladoppervlak (2-3 m^2 blad per m^2 kasoppervlak) en lichtonderschepping. Bij een supra-optimale hoeveelheid bladoppervlak zijn de kosten voor extra lichtonderschepping hoger dan de hoeveelheid extra assimilaten die geproduceerd wordt. De berekeningen lieten verder zien dat in het voorjaar en het begin van de zomer de optimale stengeldichtheid bepaald wordt door het benodigde aantal vruchten. Daarentegen zijn in de tweede helft van de zomer relatief veel stengels nodig voor voldoende bladoppervlak en zouden trossen gesnoeid moeten worden.

In het laatste hoofdstuk worden de consequenties van de verkregen kennis voor de praktijk besproken, met name ten aanzien van het gebruik van temperatuur als middel voor sturing van gewasgroei en de implicaties en criteria voor de temperatuurregeling. Verder zijn de onvolkomenheden, beperkingen en mogelijke uitbreidingen van het model en de combinaties met aanvullende modellen beschouwd. Als laatste is een overzicht gegeven van de mogelijke praktische toepassingen van modellen die assimilatenvraag en droge-stofverdeling simuleren. Het ontwikkelde model kan gebruikt worden bij het maken van een teeltplan betreffende stengeldichtheid, vruchtsnoei en lange-termijn temperatuurstrategie. Een combinatie van het model met de gebruikelijke klimaat- en gewasregistratie biedt een aantal interessante mogelijkheden ter ondersteuning van dagelijkse teeltbeslissingen.

Curriculum vitae

Adrianus Noël Maria de Koning werd geboren op 25 december 1959 te Nootdorp. Na het behalen van het atheneum-B diploma aan het St.-Maartenscollege te Voorburg begon hij in 1978 de studie Tuinbouwplantenteelt aan de Landbouwhogeschool Wageningen. Het kandidaatsexamen werd in september 1981 en het doctoraalexamen in januari 1984 behaald (beide met lof). Het doctoraalexamen omvatte de hoofdvakken Tuinbouwplantenteelt en Plantenfysiologie en de bijvakken Theoretische Teeltkunde en Bodemvruchtbaarheid en Plantenvoeding. Een stage werd gevolgd aan het Glasshouse Crops Research Institute in Littlehampton.
In 1983 volgde een aanstelling als wetenschappelijk onderzoeker kasklimaat bij het Proefstation voor Tuinbouw onder Glas te Naaldwijk. De eerste jaren werd onderzoek verricht naar de gewaskundige gevolgen van het gebruik van rest- en afvalwarmte voor het verwarmen van kassen. Later richtte het onderzoek zich met name op de invloed van kasluchttemperatuur op de groei en ontwikkeling van tomaat. De resultaten hiervan zijn beschreven in dit proefschrift.

Nawoord

Elf jaar geleden begon ik op het Proefstation voor Tuinbouw onder Glas met onderzoek naar de teeltkundige consequenties van het gebruik van afvalwarmte voor het verwarmen van kassen. Dit onderzoek vertaalde zich al snel in 'het spelen' met de temperatuur en was aanleiding voor meer gericht onderzoek naar de invloed van temperatuur op gewasgroei. Binnen de sectie kasklimaat vormde mijn werk een natuurlijke aanvulling op het luchtvochtigheidsonderzoek van Sjaak Bakker en de licht- en CO_2-specialisatie van Elly Nederhoff. Samen met de overige collega's van de afdeling teelt en kasklimaat zorgden zij voor een inspirerend en gezellig werkklimaat.

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Kaaij kon ik altijd binnenlopen voor adviezen op statistisch gebied en vragen over Genstat. Willem van Winden was behulpzaam bij het opzoeken van literatuur en heeft de gehele tekst gecontroleerd op de engelse taal.

Bij 'de tomatenspecialist' Krijn Buitelaar kon ik altijd terecht met vragen over de praktijk. In een aantal gezamenlijke proeven vulden we elkaar goed aan. De kwaliteitsonderzoekers Jan Janse en Wouter Verkerke bedank ik dat ik mee kon liften in hun proeven. De studenten Jan-Pieter Schellekens, Mario van Logten, John van den Boogaart en Frank Schellekens hebben veel waardevol werk verzet in enkele arbeidsintensieve proeven.

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