Development of a simulation model for potential production of sweet cherry: its usefulness to analyse planting density

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Dedication

This thesis is dedicated to three people: To my mother, who taught me that it is not important to reach any goal, but to give the best of oneself in the attempt. To my father, who even though with completely different ideas than mines, is still after his dead my unattainable life model in many ways. To Gabriela, my unconditional partner.

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Summary

A simulation model for potential production of sweet cherry (*Prunus avium* L.) was developed using information from literature. Parameterisation was done using values from literature and experimental measurements. An experiment with four different densities (2051, 2564, 3419 and 5128 trees ha^{-1}) in two cultivars (Karina and Regina) was evaluated to (1) obtain the values of some parameters and (2) to (partially) test the model. The main objectives of the research were: 1) To understand and explain yield differences between combinations of densities and cultivars from an ecophysiological point of view. 2) To find out if a mechanistic model for sweet cherry can explain yield differences due to planting densities. 3) To study if light interception is the main parameter explaining yield differences. 4) To estimate which is the optimum LAI (and light interception) to maximise fruit production.

In the experiment, both LAI and fruit production did not differ between treatments, suggesting that intra-specific competition compensated the effect of differences in planting density.

In both the experiment and in the simulations in the conditions of the experiment, no reduction of fresh weight of individual fruits was observed under any yield value. This situation would indicate that potential sweet cherry production is generally limited by reproductive sink strength, therefore being more sensitive to flower bud differentiation and fruit-set rather than to light interception. The model was suitable to explain the main mechanisms of fruit production, even considering that prediction of absolute values could not be properly tested.

A LAI-value between 4 and 5 and about 40 fruits per m^2 of leaf area seem to be good targets to optimise fruit production without detrimental effects in fresh weight of individual fruits.

1 Introduction

Previously standard systems of sweet cherry (*Prunus avium* L.) used to be planted with vigorous cultivars and wide spacing (Lang and Ophardt, 2000; Parnia *et al.*, 1986), producing large trees (Meland, 1998; Webster and Schmidt, 1996; Ystaas, 1989) which, however, were difficult to harvest and started to produce late (Bargoni, 1996; Meland and Hovland, 1996). Nowadays, tree densities of new sweet cherry orchards are increased everywhere (Tadeusz, 1992; Webster, 1998). New orchard designs are aimed at better economic viability through the increase of the density, in combination with new training systems, cultivars and dwarfing rootstocks. The general objective is to get smaller trees, which start to produce earlier and demand a lower labour cost (Lang and Ophardt, 2000; Meland and Hovland, 1996; Webster, 1998). Sweet cherry is not easily adapted to high density planting systems, due to its vigorous growth habit and insufficient precocity (Jacyna, 1992), and also pruning is generally not a solution. Severe pruning stimulates vegetative growth and reduces bearing potential (Parnia *et al.*, 1986). In the absence of dwarfing rootstocks or fully compact scion cultivars it is usually impossible to control the growth of vigorous sweet cherry trees sufficiently to make them suitable for high density planting systems (Webster, 1998).

Many trials have been conducted comparing different combinations of rootstocks, cultivars, and planting densities. However, often the conclusions are limited to yield analysis, thus providing little insight into the causes of the differences. Therefore, generally the conclusions cannot be extrapolated to other situations.

The objective of this research was to explain the differences in yield of combinations of densities/cultivars from the differences in light interception and cultivar characteristics, integrating the ecophysiological knowledge into a dynamic mechanistic simulation model. The emphasis was on comparing yield levels, not on predicting their absolute values.

1.1 Literature review

1.1.1 Modelling

A model is a simplification of the system (Goudriaan and van Laar, 1994; De Wit, 1999) that can be analysed at physiological or agronomic level (Goudriaan and van Laar, 1994). The aim of a model can be to predict a result, but normally is more important as a tool to understand a process. Crop growth modelling started 30 years ago with the aim of increasing the insight into crop growth processes by a synthesis of knowledge expressed using mathematical equations. Simulation models are powerful tools for testing our understanding of crop performance by comparing simulation results and experimental observations, thus making explicit gaps in our knowledge. Experiments can then be designed to fill these gaps (Bouman *et al.*, 1996). There are two types of models: descriptive (empirical) models and explanatory (mechanistic) models (Marcelis *et al.*, 1998; De Wit, 1999). The latter are models that use causal relationships rather than empirical descriptions. The most important limitations of empirical models are the large amount of data needed, the restricted applicability due to limited validity of empirical relationships (Bartelink, 1998b) and the impossibility of extrapolation to other conditions (Marcelis *et al.*, 1998).

Simulation models are useful tools for integrating information about plant processes that are measured on time scales of seconds and minutes, such as photosynthesis and

respiration rates, with data on processes that are measured over longer time intervals, such as reproductive and vegetative growth (Grossman and DeJong, 1994).

A mechanistic model can explain differences in results, even when the absolute values sometimes are not accurate. But to explain a process, a mechanistic model demands at least two integration levels (Marcelis *et al.*, 1998; De Wit, 1999). Modelling enables a quantitative and related view of simultaneous and interacting processes (Goudriaan and van Laar, 1994) and facilitates comprehension of complex systems (Marcelis *et al.*, 1998).

If the time dimension is also taken into account during collection and treatment of the data, these models are dynamic (De Wit, 1999).

Important components of photosynthesis-based models are leaf area development, light interception, photosynthesis and respiration (Marcelis *et al.*, 1998). The representation of the canopy and the simulation of the absorption of photosynthetically active radiation (PAR) play key roles when building mechanistic growth models (Bartelink, 1998a, from Landsberg, 1986, and Grace *et al.*, 1987).

Plant production can be analysed at different levels. In a potential production situation, the crop is amply supplied with water and nutrients and is free of weeds, pest and diseases (Lövenstein *et al.*, 1995). When modelling potential production situations, crop growth only depends on aboveground processes such as CO_2 assimilation and on physiological characteristics of the species or cultivar (Bouman *et al.*, 1996; Goudriaan and van Laar, 1994; Lövenstein *et al.*, 1995). Other ecophysiological processes involved are plant development, respiration, transpiration and partitioning (Goudriaan and van Laar, 1994).

Most mechanistic models for trees are based on the stand-level (Bartelink, 1998b) without considering individual tree characteristics and functioning.

Models should be as simple as possible and require only a small number of input data to facilitate application, but on the other hand, they should be complex and flexible enough to be able to represent the complex effects of the wide range of potentially interacting factors (Bouman *et al.*, 1996). The level of complexity depends of the objective. If a process is complex, there is much information about it and one wants to fully understand it, the model and program should be complex too (Leffelaar, *Pers. Com.*).

Different computer languages can be used for simulation modelling, such as CSMP (Continuous System Modelling Program III) or its successor developed at Wageningen University FST (FORTRAN Simulation Translator).

A model describing the complete process of sweet cherry fruit production has not been found in the literature, but partial information can be integrated to explain the behaviour of the crop.

1.1.2 General sweet cherry characteristics

Sweet cherry (*Prunus avium* L.) belongs to the family *Rosaceae*, genus *Prunus* L. along with other fruits like sour cherry, plum, apricot and peach. Both the sweet and the sour cherry are deciduous trees originating around the Caspian and Black Seas. That explains its preference for temperate or Mediterranean-type climate (Webster and Looney, 1996). They need both a warm growing season and a winter dormant period (Longstroth and Perry, 1996).

Normally it is a vigorous tree with strong apical dominance, presenting problems for training. Cherries prefer a loam soil of at least 0.5 m depth, with good water holding capacity and reasonable free drainage. A pH of the soil between 5.5 and 7.5 is the most suitable (Webster and Looney, 1996). It requires also frequent supply of water during the

growing season, especially during the first half of the season before the crop reaches maturity (Hanson and Proebsting, 1996).

Most sweet cherry cultivars require cross-pollination. Some of the newer varieties can be self-pollinating, but even then trees usually produce more fruit with cross-pollination. A single gene with multiple alleles (S1, S2, S3, etc.) controls incompatibility. Any pollen tube bearing an allele in common with either of the two alleles in the somatic tissue of the pistil fails to achieve fertilisation because its growth is inhibited part way down the style (Thompson, 1996).

1.1.3 Effect of stand density on sweet cherry production

An approach to increase yields is to grow trees so that they intercept the maximum amount of light (Meland and Hovland, 1996). Increasing plant density is an important tool to reach this objective.

Trees of small size and reduced vigour are pivotal to the success of high density planting systems (Meland, 1998; Webster, 1998). The objective is to assure a balance between vegetative and reproductive growth (Meland, 1998). Sansavini and Lugli (1998) mentioned that yield increased to 30-40 tons per ha at densities of over 800 trees per ha using semi-dwarfing rootstocks grafted with compact and/or spur cultivars. With the use of small trees at high density, the orchard comes faster into bearing, is easier to maintain and the economy is improved (Meland, 1998). Parnia *et al.* (1986) found that planting trees at the highest density thus resulted in slowing down of their growth, reducing the amount of wood removed in pruning, hastening their coming into crop and increasing their yield.

Increasing stand density could reduce vegetative growth (Parnia *et al*., 1986). Meland (1998) found that the highest density of Y-trellis 'Van' trees (5000 trees per ha) had the smallest trees. Ystaas (1989) found that even increasing the density from 400 to only 800 trees per ha reduced the stem girth by 27 percent on 15 years old trees of the same cultivar. However, Meland and Hovland (1996) found that vigour of 'Van' trees, as measured by trunk circumference at the end of the second growing season, was not affected by training system or spacing. These different results can be explained because the reduced tree growth of the closely spaced trees is apparently due to more competition with increasing density (Ystaas, 1989), but at early stages this competition may not be noticeable.

Another tool to reduce shoot growth is root pruning, because shoot and root growth are related. Mature trees of the same cultivar on the same clonal rootstock, when planted on the same soil type and managed similarly, maintain a relatively constant ratio between root and shoot length. Disturbance of this relationship, by pruning or manipulation of one component, either shoots or roots, results in a commensurate adjustment in the growth of the other component (Webster, 1998).

There is a strong relationship between tree density and early yield. However, when the trees start to fill their allotted space in the row, this pattern changes. The different spacing will adjust in the long run and smaller differences in yield are expected (Meland, 1998). However, the same author mentioned that still after seven growing seasons, the highest density had the highest cumulative yield. Ystaas (1989) found that increasing the density from 400 to 670 trees per ha an increase in annual yield from 4.1 to 6.2 tons per ha was obtained. At higher densities than 670 trees per ha no further increase in yield was obtained. The same author found that different tree densities did not affect average fruit weight.

Fruit quality is also indirectly affected by tree density through its effect on light and assimilates levels. There is a tendency to lower contents of soluble solids in fruits from closely spaced trees, probably because a decrease of exposure of the leaves and fruits to direct sun light (Ystaas, 1989). Roper and Loescher (1987) studying the relation between leaf area and fruit quality of 'Bing' sweet cherry in the conditions of Washington State, found that leaf area per fruit accounted for 66 %, 36 % and 53 % of the variability in fruit weight, fruit colour and soluble solids, respectively, at Pullman. The same authors mentioned that leaf area per spur accounted for 54 %, 27 % and 28 % of the same fruit quality parameters at Prosser. Proebsting (1990) also mentioned that the size of 'Bing' cherries is negatively related to yield when leaf area is relatively constant. In sour cherry, fruit weight, soluble solids and fruit colour were directly related to the number of leaves per fruit and to the amount of sunlight, estimating that a minimum of 2 leaves per fruit are necessary for optimum fruit size and development (Flore, 1985).

1.1.4 Chilling requirements

Several species of temperate regions require a period of low temperatures (vernalization) to break dormancy (Felker and Robitaille, 1985; Goudriaan and van Laar, 1994; Kramer, 1996; Webster and Looney, 1996). The length of the period and the optimum temperatures depend on the species and cultivar (Mahmood et $al.$, 2000). A high winter chilling requirement and a high heat requirement in post dormancy is important to avoid early activity in buds after mild periods in winter followed by frost periods (Seif and Gruppe, 1985). Different methods have been used to calculate Chill Units (CU) accumulation (Table 1.1). In sweet cherry, Mahmood et $al.$ (2000), studying cultivars Stella, Summit and Sunburst, found that the optimum temperature for satisfying chilling requirements were between 3.2 and 3.7 °C depending of the cultivar. Under these temperatures, between 1081 and 1214 hours were needed (Table 1.2). Chilling accumulation was considered from October 1st, after completion of flower bud development (checked under a stereo light microscope). Seif and Gruppe (1985) used the method of Norvell and Moore (1982) to calculate CU requirements of sweet cherry and inter-specific cherry hybrids. CU were derived from the number of hours of exposure to a given range of temperatures. Each range was assigned a weighting factor as follows: 1 < 2.5 °C = 0.5; 2.5 < 9.2 °C = 1.0; 9.2 < 12.5 °C = 0.5; 12.5 < 16 = 0.0; 16 – 18 °C = - 0.5 and > 18 °C = -1.0. They found chilling requirements from 1101 to 1482 CU in $Prunus$ $avium$ cultivars and Mazzard selections. Bargioni (1996) mentioned that most cultivars need between 1050 and 1900 hours at temperatures below 7 °C to satisfy their dormancy chilling requirements.

Table 1.1. Methods for calculation of CU accumulation according to different authors.

Source	Method to calculate CU accumulation
Mahmood et $al.$ (2000)	Parabolic function of CU accumulation in relation to temperature
Seif and Gruppe (1985)	Ranges of temperature corresponding with different weighting factors
Bargioni (1996)	Hours at temperatures below 7 °C

For the simulation model, an average of the parameters found by Mahmood *et al.* (2000) for cultivars Stella, Summit and Sunburst was used (Table 1.2 and Figure 1.1) and the chilling requirements were considered satisfied when 1142 CU were accumulated.

Table 1.2. Base, optimum and ceiling temperatures, formulas for Chill Units (CU) accumulation and CU requirements for cultivars Stella, Summit and Sunburst

| Cultivar | Temperature (°C) | | | Chill Units (CU) | |
	Base	Optimum	Ceiling	Accumulation rate (CU h^{-1})	Requirement
Stella	-5.8	3.2	12.4	$CU=0.87+0.079T-0.012T^2$	1131
Summit	-5.6	3.2	12.0	$CU=0.87+0.083T-0.013T^2$	1081
Sunburst	-5.3	3.7	12.7	$CU=0.83+0.091T-0.012T^2$	1214
Average	-5.6	3.4	12.4	$CU=0.857+0.0843T-0.0123T^2$	1142

Source: Mahmood *et al.* (2000).

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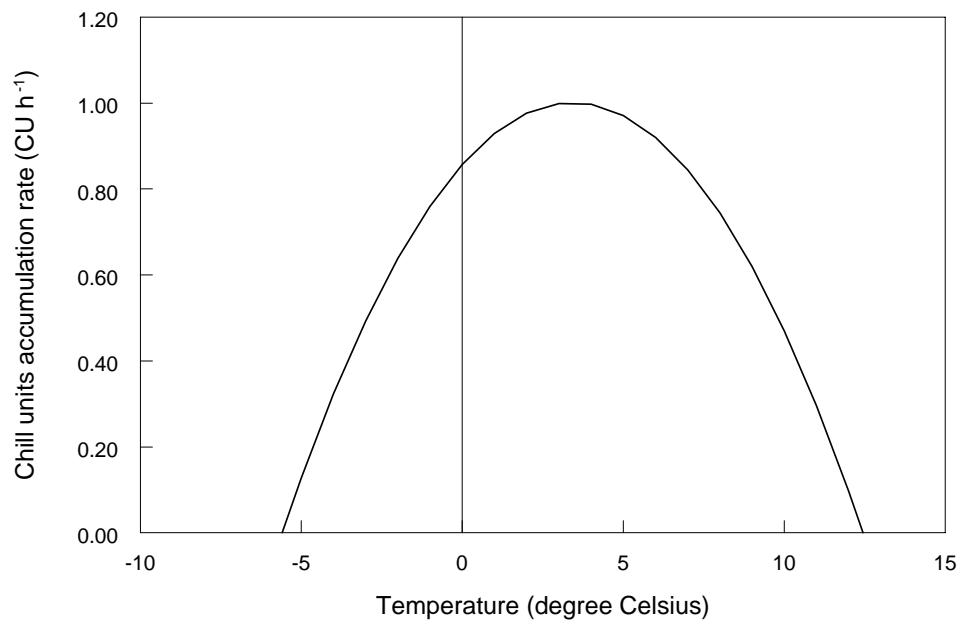
Figure 1.1. Chill Units accumulation rate (CU h^{-1}) as a function of temperature. Parameters are averages of those found by Mahmood *et al.* (2000) for cultivars Stella, Summit and Sunburst.

1.1.5 Post dormancy temperatures and leaf area development

The timing of the recurring phenomena in the life cycle of a plant (phenology) is known to be triggered by temperature, but can also be influenced by photoperiod, precipitation and nutritional status of the tree (Kramer, 1996). Some of those phenomena are visible changes in the plant and indicate the beginning of leaf growth (Figure 1.2).
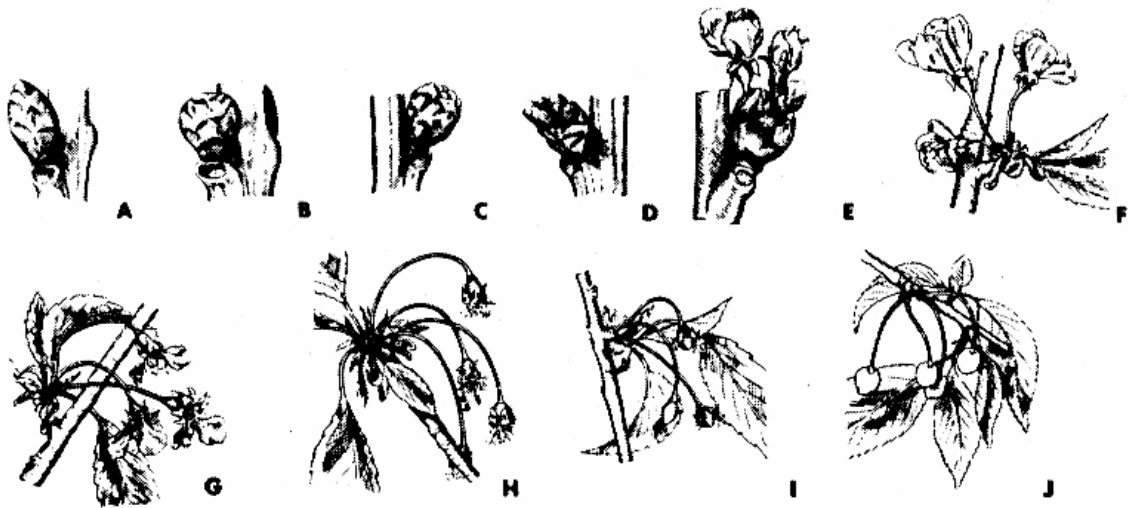
Figure 1.2. Phenological stages describing the initiation of leaf growth and flowering of sweet cherry as presented by Wertheim (1976). A = dormant; B = swollen bud; C = visible flower bud; D = white bud (flower buds separate); E = starting of flowering (visible stamen); F = full bloom (80 % of flowers are open); G = end of blooming (crown petals fall, stamen curve); H = Fruit setting; I = calyx abortion; J = young fruit.

Different authors have used pre-bloom temperatures (Vestrheim, 1998), chilling units (Seif and Gruppe, 1985; Mahmood *et al*., 2000) and degree-days accumulation (Biggs, 1986) to predict different phases of development in sweet cherry. A combination of chilling and degree-days seems to be closer to reality to predict bud break and leaf development (Kramer, 1996).

Degree-day is a unit to express the integral over time (days) of the difference between air temperature (°C) and a certain threshold (base) temperature. The base temperature (Tb) is the temperature from which development is practically proportional to the difference between air temperature (Ta) and Tb. The base temperature is not always fixed, but it can change according to different developmental stages (Goudriaan and van Laar, 1994). Eisensmith *et al*. (1980) found that a base temperature of 4 °C was appropriate to calculate degree-days accumulation in sour cherry. Iezzoni (1985) used 4.5 °C for the same species to predict bloom development.

Sweet cherry has very little leaf area at anthesis as flower and vegetative buds usually open simultaneously (Flore *et al*., 1996; Keller and Loescher, 1989). At bud-break,

carbohydrate reserves provide the carbon needed for growth until the leaf area of the tree provides enough assimilation to meet sink demand. Total non-structural carbohydrates increase again after harvest and are highest at leaf abscission (Flore and Layne, 1999).

Canopy development is generally completed by fruit harvest (Sams and Flore, 1983). In sweet cherry, the period between full bloom and harvest is much shorter than for other tree species, as for example apple (Hanson and Proebsting, 1996; Tukey, 1942). Different authors mentioned between 42 up to 85 days from bloom to harvest of cherries, depending on the cultivar and local conditions (Table 1.3).

Table 1.3. Period (days) between full bloom (Stage "F" in Figure 1.2) and harvest for sweet cherry according to different authors.

Source	Days
Kapel (1991)	50 to 70
Lang and Ophardt (2000)	60 to 85
Longstroth and Perry (1996)	40 to 80
Tukey (1942)	42 to 75[1]

[1]Data from 46 cultivars (average: 60 days).

Leaf area (LA) development is function of degree-days accumulation after the requirement of chilling has been satisfied (Flore and Layne, 1999, from Westwood, 1993). In cherry, leaf emergence does not occur until a sufficient chilling requirement has been met to break rest and after a minimum number of growing degree-days have accumulated if other environmental parameters are not limiting (Eisensmith *et al.*, 1980; Thompson, 1996). According to Anderson *et al.* (1986), the start of leaf growth (open cluster stage) in 'Montmorency' sour cherry coincides with 145 degree-days calculated using a base temperature of 4 °C, after accumulating 954 CU.

Initiation of growth (breaking of ecodormancy) is a temperature-driven process that is perceived locally by the bud (Flore and Layne, 1999). Leaf area increases until about harvest. Eisensmith *et al.* (1980) found that in sour cherry 'Montmorency' this coincided with an accumulation of approximately another 955 degree-days (using a base temperature of 4 °C) recorded from April 19th.

For fruit production, there is an optimum Leaf Area Index (LAI). Light interception increases with LAI, but with high LAI values, the relation becomes asymptotic, thus more LAI produces only little increment in light interception. Excess of LAI means that a high leaf biomass has to be maintained without contributing significantly to light interception, because leaves (and also fruits) in different parts of the canopy are shaded. During fruit development, shading decreases fruit size and yield, fruit colour, soluble solids (total % of sugars and acids in fruits), fruit-set and induces early fruit drop (Flore and Layne, 1999). At low light levels, flower-bud formation and fruit growth can be reduced (Wagenmakers, 1994, from Palmer, 1989).

In the model, it was assumed that 175 degree-days (base temperature = 4 °C) were needed to start LA development after satisfying the chilling requirements and 1064 degree-days to reach maximum LA development. These data were extracted (modified) from those presented by Eisensmith *et al.* (1980).

1.1.6 Fruit development

Fruit and leaf development occurs more or less at the same time (Loescher *et al.*, 1985). Keller and Loescher (1989) found that during the last two weeks of sweet cherry development, fruit total dry weight increased 3-fold.

The development of fruits is often divided in three stages (Loescher *et al.*, 1985). The first stage (stage I) involves an increase in number and size of cells of the mesocarp (flesh) as well as those of the seed. The second stage (stage II) begins with the differentiation of the endocarp (pit) and ends when this process (pit hardening) and embryo development are complete. The third stage (stage III) consists of enlargement of the mesocarp and it is during this period that colour changes, and fruit size (fresh and dry weight) and soluble solids increase dramatically. Fruit sink strength changes in cherry during the growing season and is greatest during stage III (Flore and Layne, 1999).

Developmental time of fruit can also be associated to degree-days accumulation (DeJong and Goudriaan, 1989, from Fischer, 1962).

In the model, it was assumed that 255 degree-days (base temperature = 4 °C) were needed to reach full bloom and it was consider as the beginning of fruit growth. Pit hardening was assumed to be reached with 700 degree-days (0.22 of fruit weight at harvest) and harvest time with 1064 degree-days.

1.1.7 Light interception

The total dry matter production of crops is directly proportional to light interception (Patrick, 1988; Wagenmakers, 1994, from Monteith, 1977) because the photosynthesis production of a tree stand is driven by intercepted photosynthetically active solar radiation (PAR) (Lappi and Stenberg, 1998, from Ross, 1981). PAR is the radiation with a waveband between 400 and 700 nm and practically coincides with the visible radiation (Goudriaan and van Laar, 1994). Information on radiation interception gives a clearer understanding of how yield differences develop (Daniells, 1986).

LAI (unit of leaf area per unit of ground area) is the main determinant of the amount of intercepted PAR. Generally speaking, the more homogeneous the stand, the larger is the interception at a fixed LAI. At the stand level this implies that a regular (geometric) pattern of trees is better than a random or grouped spatial pattern (Lappi and Stenberg, 1998). However, in an intensive fruit tree orchard, the plants are arranged in rows. The distance between rows is normally higher than between trees in the row. This situation makes that the light interception is not uniform, being higher in the row than in the path. Even with very high LAI values, always some light will reach the ground. Models describing horizontally homogeneous stands are not applicable in stands where the foliage is grouped into individual plant crowns or plant zones (Bartelink, 1998, from Oker-Blom, 1986). The situation when leaves are grouped together is called clustering and its effect is that the actual K-value (AK) is lower than the theoretical expected value (Goudriaan and van Laar, 1994). To correct this situation a clustering factor (CLF) must be calculated and multiplied by K, obtaining AK.

The quantity of PAR absorbed (I_a) finally depends of incoming PAR (I_0), reflection coefficient (ρ_c), leaf area index (LAI) and actual light extinction coefficient (AK) according to the formula presented by Goudriaan and van Laar (1994):

$$I_a = I_0 \bullet (1 - \rho_c) \bullet (1 - \exp(-AK \bullet LAI))$$

For PAR, the reflection coefficient of the canopy is between 0.08 and 0.1. Both ρ_c and K depend of the angle of incidence of the incoming radiation (Goudriaan and van Laar, 1994).

In the model, reflection coefficient was fixed in 8 % and light extinction coefficient (K) in 0.7. The clustering factor was estimated with another simulation programme developed by Goudriaan (*Pers. Com.*)

1.1.8 CO_2 assimilation

The general characteristics of the CO_2 assimilation responses of sweet cherry is similar to those reported for C_3 tree species (DeJong, 1983). Assimilation of CO_2 by individual leaves is initially proportional to light absorption and CO_2 concentration, but it exhibits saturation at high light levels (Goudriaan and van Laar, 1994; Flore and Layne, 1999) (Figure 1.3).

The rate of photosynthesis is not constant during the season. Assimilation increases with leaf expansion, reaching a peak just before full development; then remains steady for two or more weeks before declining (Flore and Layne, 1999, from Sams and Flore, 1982). Roper *et al.* (1988) found a net leaf photosynthesis for sweet cherry between 168 to 278 μg CO_2 m^{-2} s^{-1} in stage I of fruit development. During stage II net leaf photosynthesis increased from about 250 μg CO_2 m^{-2} s^{-1} to 500 μg CO_2 m^{-2} s^{-1} and remained constant until harvest. Roper and Kennedy (1986) found that rate of net photosynthesis in 'Bing' sweet cherry increased from 111 μg CO_2 m^{-2} s^{-1} in the youngest leaves to 1055 μg CO_2 m^{-2} s^{-1} at about 80 % of full leaf expansion. After this, a constant rate of about 889 μg CO_2 m^{-2} s^{-1} was maintained. Sams and Flore (1982) also mentioned 80 % of full expansion as the point with maximum net photosynthesis in sour cherry 'Montmorency'. These data show the seasonal variability in net photosynthesis.

DeJong (1983), measuring at 27°C, saturating light levels and CO_2 of 320 ppm found a CO_2 compensation point of 55.5 ppm and CO_2 assimilation of 598.4 μg CO_2 m^{-2} s^{-1}. Sams and Flore (1982) found CO_2 compensation point about 80 ppm. Roper and Kennedy (1986) found that during leaf development, CO_2 compensation points decreased to about 25 ppm CO_2, but increased to about 35 for mature leaves.

Cherry has a flat response of photosynthesis to temperature between 17 and 30 °C (Sams and Flore, 1983). Roper and Kennedy (1986) found optimum temperatures for photosynthesis between 19 to 25 °C. Sams and Flore (1982) mentioned optimum temperatures for sour cherry 'Montmorency' between 15 and 30 °C.

Values of maximum gross assimilation rate (A_{max}), initial light conversion factor (ε) and dark respiration rate (R_d) depend on temperature, age, nutrient condition, CO_2 concentration, plant species and variety. As a general indication for C_3 plants, Goudriaan and van Laar (1994) gave values of 800 μg CO_2 m^{-2} s^{-1} for A_{max}, 11 μg CO_2 J^{-1} PAR for ε and 50 μg CO_2 m^{-2} s^{-1} for R_d. For apple, Wagenmakers (1994) used 972 μg CO_2 m^{-2} s^{-1} for A_{max} and 12.5 μg CO_2 J^{-1} PAR for ε. Lövenstein *et al.* (1995) also mentioned 12.5 μg CO_2 J^{-1} PAR for ε, but they used a default value of 1111 μg CO_2 m^{-2} s^{-1} for A_{max} in C_3 plants (Table 1.4).
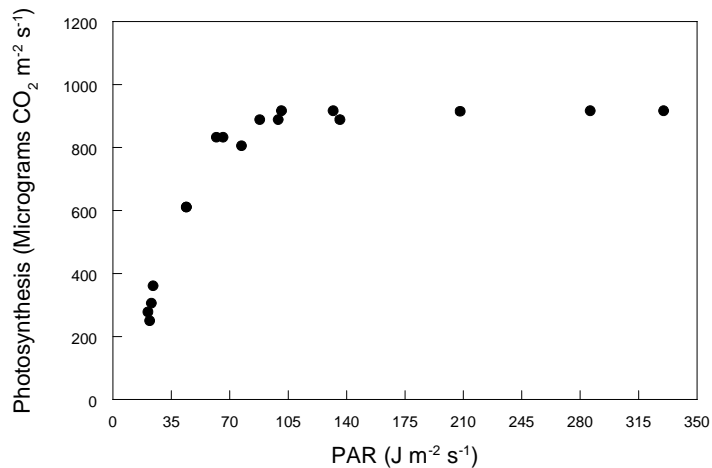
Figure 1.3. Effect of light intensity on CO_2 assimilation of an individual leaf. After: Loescher *et al.*, 1985.

Photosynthesis in sweet cherry rank high among *Prunus* (Flore and Layne, 1999) and other woody plants (Loescher *et al.*, 1985; Roper and Kennedy, 1986). However, genetic differences in maximum rate of leaf photosynthesis are not necessarily correlated with differences in dry matter production (Marcelis *et al.*, 1998). Net photosynthesis of sour cherry 'Montmorency' under optimum conditions ranges between 833 to 972 μg CO_2 m^{-2} s^{-1} (Sams and Flore, 1982). According to Flore and Layne (1999) characteristic leaf photosynthesis of sweet cherry is 788 μg CO_2 m^{-2} s^{-1} (Table 1.4).
The actual assimilation (A) will depend of A_{max}, ε and I_a:

$$A = A_{max} (1 - exp (-\varepsilon \bullet I_a / A_{max}))$$

After: Lövenstein *et al.* (1995)

Sweet cherry has a rather low light saturation point. According to Loescher *et al.* (1985) light saturation occurs at about 25 to 30 % of full sunlight. Flore and Layne (1999) mentioned saturation with 30 to 50 % of full sunlight. DeJong (1983) also found a low light saturation point for sweet cherry ranging from 88 to 154 J m^{-2} s^{-1} and comparable with the value of 110 J m^{-2} s^{-1} presented by Roper and Kennedy (1986).
However, the whole-tree canopy does not show light saturation under full-light conditions (Flore and Layne, 1999). Under field conditions crops do not consist of extended, horizontal leaves, but of small leaves with their surfaces inclined at various angles. In that situation, the light is more evenly distributed over the leaves, reducing possibilities for leaves in the top layer of becoming light-saturated within the normal light ranges (Lövenstein *et al.,* 1995). This means that leaves that are partially inside the canopy are photosynthetically active and can contribute to the carbohydrate supply (Loescher *et al.*, 1985; Roper and Kennedy, 1986). Therefore, the relation between CO_2 assimilation and radiation interception is much more linear for the whole canopy than for individual leaves. Deviations from linearity in the relation disappear almost completely by integration over the day. Hence, as an approximation, daily CO_2 assimilation rate of a crop (A), well supplied with water and nutrients, may be assumed to be a linear function

of the intercepted light energy (I_a) proportional to the Light Use Efficiency (LUE) (Lövenstein *et al.,* 1995). This is the approach used in LINTUL (Light INTerception and UtiLization) models. In LINTUL-type models total dry matter production is calculated using the Monteith approach, in which crop growth rate is calculated as the product of intercepted radiation by the canopy an a light use efficiency (LUE). The LUE can often be considered constant over the growing season and a property of the crop of interest. LINTUL models have the advantage that input requirements are drastically reduced and model parameterisation is facilitated (Bouman *et al.*, 1996). LINTUL-type models have been used with different purposes for several crops (Caldiz and Struik, 1999; Farré *et al.*, 2000; Habekotté, 1997; Smit and Struik, 1995).

The LINTUL model approach was used for the present model of sweet cherry. Assimilation of CO_2 was based on a constant value for light use efficiency (LUE) for the whole canopy. Lövenstein *et al.* (1995) mentioned a LUE-value of 7 g CO_2 MJ^{-1} for C_3 crops. However, considering that the A_{max} presented by them in the same report (1111 µg CO_2 m^{-2} s^{-1}) was considerably higher than the 788 µg CO_2 m^{-2} s^{-1} mentioned specifically for *Prunus avium* (Flore and Layne, 1999), a LUE of 6 g CO_2 MJ^{-1} can be assumed for sweet cherry (Goudriaan, *Pers. Com.*).

Table 1.4. Maximum leaf gross CO_2 assimilation rate (A_{max}) and initial light conversion factor (ε) for different species.

Source	ε (µg CO_2 J^{-1} PAR)	A_{max} (µg CO_2 m^{-2} s^{-1})	Species
Goudriaan and van Laar (1994)	11	800	C_3 plants
Lövenstein *et al.* (1995)	12.5	1111	C_3 plants
Wagenmakers (1994)	12.5	972	Apple
Sams and Flore (1982)	------	972	*P. cerasus*
Flore and Layne (1999)	------	788	*P. avium*

1.1.9 Maintenance respiration

Respiration is needed to maintain the present biomass. Disintegrated components must be regenerated and even the preservation of the electrical potentials over the cell membranes requires energy (Goudriaan and van Laar, 1994). The turnover rate for a normal protein mixture in leaves at 20 °C is about 0.1 d^{-1} (10 % per day) (Lövenstein *et al.*, 1995). Because it is basically enzymes that disintegrate, and these are the main materials that contain protein, it is reasonable to assume that the maintenance coefficient is partly related to the protein content and, therefore, also to the N content. At 20 °C, each gram of protein costs 0.04 g CH_2O per day for maintenance (or 0.24 g CH_2O g^{-1} N). Active transport of ions across membranes is needed to maintain concentration gradients (Lövenstein *et al.*, 1995), and this maintenance of the electrical potentials costs another 0.01 g CH_2O g dm^{-1} d^{-1} (Goudriaan and van Laar, 1994).

The rate of protein turnover strongly depends on the environmental conditions (Van der Werf *et al.*, 1992), of which temperature is the most important factor. Between 5 to 30 °C, the increase of respiration with temperature is exponential. The increment in respiration with 10 °C of increment in temperature is known as Q_{10} and its default value is usually 2.0 (Goudriaan and van Laar, 1994). Flore and Layne (1999) found that in sweet cherry respiration Q_{10} ranged from 1.5 during fruit growth stage I to 2.0 in stage III.

As the plant's age increases, the maintenance coefficient will decrease, largely because of the decrease in the protein content, and an increase in more stable components such as support tissue and reserve compounds (Goudriaan and van Laar, 1994).

Genetic variation for respiration has not been reported for cherry (Flore and Layne, 1999).

Grossman and DeJong (1994) used daily maintenance respiration rates for peach (*Prunus persica* L.) of about 0.002 and 0.0009 kg of sugar per kg dm root and wood respectively. They considered a biomass of about 5000 kg ha^{-1} dm root and 15000 kg ha^{-1} dm wood (these parameters were used later in the *Prunus avium* model).

In the *Prunus avium* model, the maintenance coefficients for leaf and fruit were estimated based on chemical analysis and the relation presented by Goudriaan and van Laar (1994) of 0.24 g CH_2O g^{-1} N d^{-1} plus 0.01 g CH_2O g dm^{-1} d^{-1}.

1.1.10 Growth respiration

Each chemical component of the plant's tissue requires a different amount of glucose for its production. The efficiency of the production process is practically independent of the environmental conditions and only dependent on the nature of the actual component formed (Goudriaan and van Laar, 1994). Kappes and Flore (1985 and 1986) mentioned that about 30 % of the carbohydrate used by the sweet cherry fruit are for growth respiration and 70 % are accumulated in the fruit dry matter. During stages I, II and III the share of respiration was 32.7, 70.9 and 19.9 %. The increased need for respiration during stage II is caused by lignification and lipid synthesis during pit hardening and embryo development. In stage III the requirements are lower because cells expand and less biosynthetic activity is expected. For apple, wood growth respiration was estimated to be 0.32 g CO_2 g dm^{-1} (Wagenmakers, 1994 from Penning de Vries and van Laar, 1982).

To calculate the glucose requirement of a specific organ, first the proportion of every component should be known. Goudriaan and van Laar (1994) presented a formula that in practice can be well approximated just knowing the N and C content (g g^{-1} dm) and it was used for the calculations in the *Prunus avium* model:

Glucose requirement (g CH_2O g^{-1} dm) = 5.4 C (g C g^{-1} dm) + 6.0 N (g N g^{-1} dm) − 1.1

1.1.11 Partitioning and harvest index (HI)

Source organs are defined as organs with a net export and sink organs as organs with a net import of assimilates. Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. It appears to be primarily regulated by the sink strength (Marcelis *et al.*, 1998), with fruits being the major sinks competing for sugars in fruit trees (Grossman and DeJong, 1994; Marcelis and Heuvelink, 1999). Chalmers and van den Ende (1974) and Flore and Layne (1999, from Richards, 1986) also mentioned that fruit has priority over other sinks in *Prunus*.

Sink strength can be defined as the product of sink activity, which is a measure of the potential flux of assimilate accumulation, and sink size, which is a measure of potential volume of biomass gain (Patrick, 1988). The growth rate usually increases with increasing temperatures, but the growing period decreases (Marcelis and Heuvelink, 1999).

There is an upper limit to the degree to which assimilates may be partitioned to the harvestable portion without damaging the capacity of the plant to support the yield component both structurally and nutritionally (Patrick, 1988).

Some simulation models ignore the resistance of the transport path (Marcelis *et al.*, 1998). Marcelis and Heuvelink (1999) mentioned that the transport path is only of minor importance for the regulation of dry matter partitioning at a whole plant level. However, Grossman and DeJong (1994, from Ho *et al.* (1989) and Wardlaw (1990)) supported that in general, sinks are supplied with carbohydrates from nearby sources.

The number of fruits set per plant has a great impact on the dry matter partitioning and fruit growth. Several experiments have shown that fruit set increases with source strength and decreases with sink strength (Marcelis and Heuvelink, 1999). To simulate growth it is important to define if the biomass gain of an organ is either limited by assimilate supply (source-limited) or saturated by assimilate supply (sink-limited) (Patrick, 1988).

Only the dry matter partitioned to the harvestable organs contributes to the yield of the crop, indicating the importance of correctly simulating dry matter partitioning. Moreover, fruit trees, being perennial crops, need an optimum balance between partitioning into harvestable organs (short-term productivity) and the other plant parts (vegetative parts: future production capacity) (Marcelis and Heuvelink, 1999). However, harvest of sweet cherry is very early in the season and after that moment the plant has time enough for vegetative growth and restoring of reserves.

Due to its simplicity and lack of knowledge, descriptive allometric models, which are entirely empirical, are the most widely used to explain partitioning (Marcelis *et al.*, 1998). Kappel (1991), studying partitioning in 7 years old 'Lambert' sweet cherry trees, found that at harvest time in July, the total dry matter (dm) of fruit accounted for 7 % of the total dm of the tree. The total dm of leaves accounted for 16 % and the wood was 77 % of the total dm of the tree. About 30% of the total dm at July was grown in the present season. Wood in April was 90 % of the dm later in July. When annual dm accumulated was examined, fruit accounted for about 16%, leaves 41 % and wood 43 % of the annual dm. The same author presented a modified Harvest Index (HI) of 17 %, as the proportion of annual dm increase above ground that is distributed to fruit at harvest date. However, fruit-set can vary considerably between trees and between seasons (Looney *et al.* 1996) and this situation does not allow using a fixed Harvest Index without taking into account the number of fruits per tree. Sink regulation models based on the potential demand (sink strength) of the organs have some mechanistic aspects and can be applied in many situations (Marcelis *et al.*, 1998).

In the model for sweet cherry, the produced sugars are first used to maintain the present biomass and for growth of the leaves. The remaining available sugars (REMSUG) are distributed between vegetative and reproductive sinks (fruits). Fruits have priority over vegetative parts, but the maximum of sugars that the fruits can utilise was assumed to be half of REMSUG.

1.2 Definition of the problem

Many trials have been conducted comparing different combinations of rootstocks, cultivars, and planting densities. However, often the conclusions are limited to yield analysis, thus providing little insight into the causes of the differences and without parameters of potential production for specific sites. Therefore, often the conclusions cannot be extrapolated to other situations.

Crop growth simulation models have been used to investigate the effects of management options (e.g. plant population density) in different environmental conditions (Bouman *et al.*, 1996). The development of a dynamic mechanistic simulation model would provide a tool to better understand the ecophysiology of the crop, even if absolute yield values are not predicted.

1.2.1 Research questions

- Which is the ecophysiological background of sweet cherry production?
- Can a mechanistic model for sweet cherry explain yield differences due to planting densities?
- Is light interception the main parameter to explain yield differences?
- Which is the optimum LAI (and light interception) to maximise fruit production?

1.2.2 Objectives

- To develop a dynamic mechanistic simulation model to explain the behaviour of sweet cherry.
- To parameterise that model by (1) values from literature and (2) additional measurements.
- To understand and explain yield differences between combinations of densities and cultivars from an ecophysiological point of view.

2 Experiment

2.1 Set-up of the experiment

2.1.1 Site

The experiment was located in the research station of Praktijkonderzoek Plant & Omgeving" (PPO), The Netherlands (51° 58' latitude North and 05° 40' longitude East). The climate is temperate, strongly affected by the North Sea. The warmest months are June, July and August, and the lowest temperatures are registered in December, January and February (Figure 2.1).
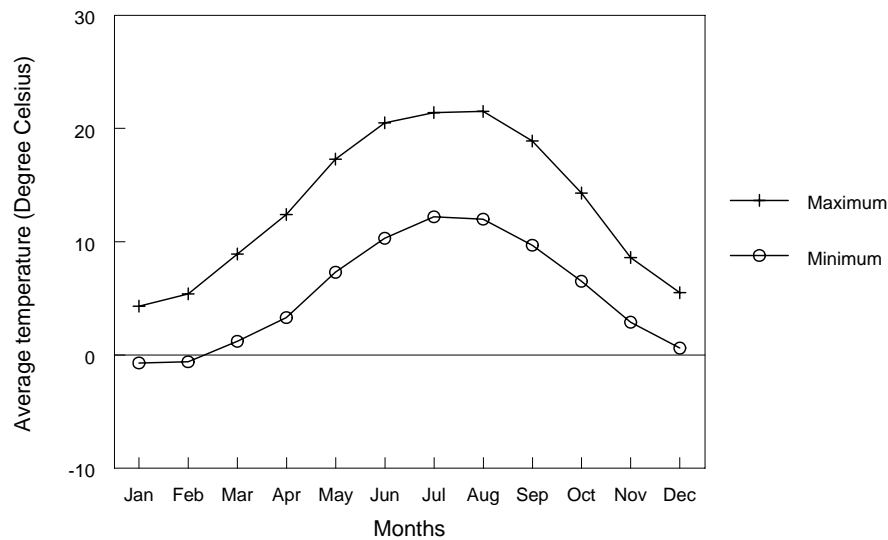
Figure 2.1. Maximum and minimum temperatures in Wageningen. Averages over the years 1951-1980. (Source: Goudriaan and van Laar, 1994).

Because of the high latitude, the variation in Daily Total Global Radiation during the season is very important. Radiation levels from May to July are more than 15 MJ m^{-2} d^{-1}, but from December to January are less than 3 MJ m^{-2} d^{-1} (Figure 2.2).
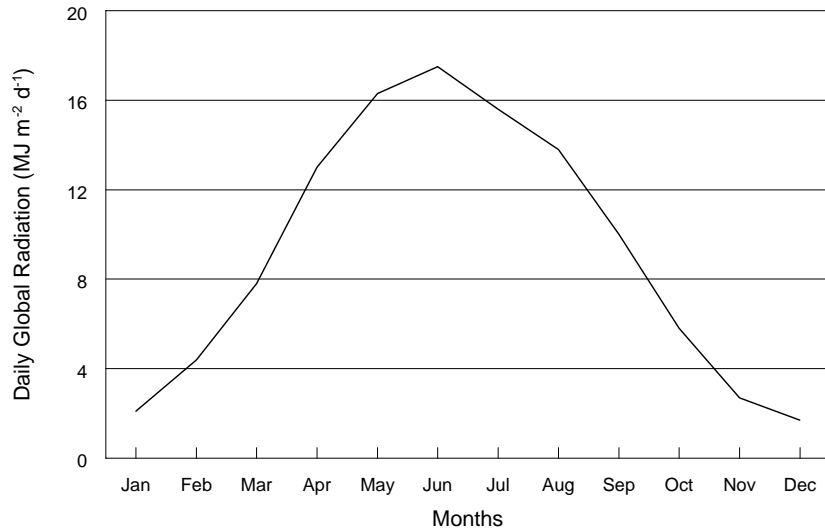
Figure 2.2. Daily Global Total Radiation in Wageningen. Averages over the years 1951-1980. (Source: Goudriaan and van Laar, 1994).

The 760 mm of average rainfall (standard deviation = 140 mm) are well distributed during the season (Figure 2.3). The wettest months are July and December (74 mm each). The quantity of rain in July is very variable (standard deviation = 44 mm). This is important information, since July is the harvest month for sweet cherry and rain at harvest time induces cracking of fruits.
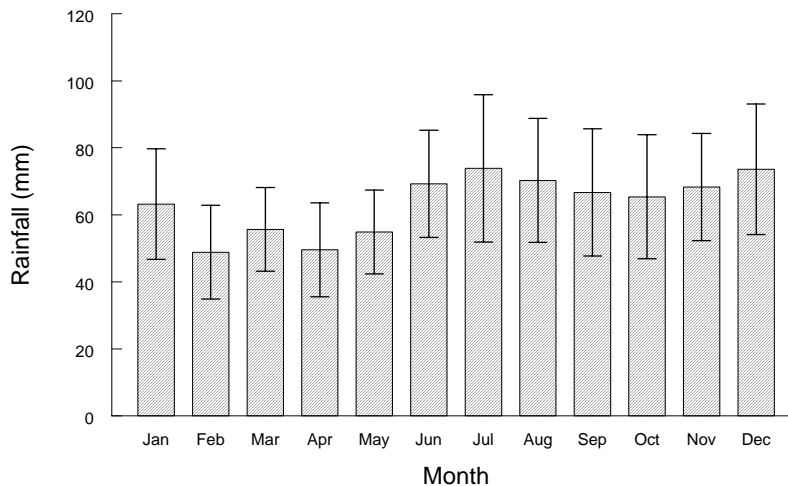
Figure 2.3. Monthly rainfall in Wageningen. Vertical lines represent standard deviation. Averages over the years 1950-2000. (Source: Meteorology and Air Quality Group. Wageningen University).

The experiment was located on a river clay soil, with a pH-KCl of 7.4, 1.3 % of lime and 2.5 % of organic matter (Table 2.1). In the Northern part of the trial some fine sand comes closely to the surface.

Table 2.1. Soil characteristics.

Characteristic evaluated	Result
Soil type	River clay
pH-KCl	7.4
Lime (%)	1.3
Organic matter (%)	2.5

2.1.2 Growing conditions

The orchard was established in the spring of 1997, so during 2001, the trees were in their fifth growing season and the orchard can be considered already in commercial production (Figure 2.4). The rows were established with orientation North-South. Training system was in slender-spindle. One stake per tree and two wires along the row were used to support the trees, but the branches were not fixed to any structure. The trial was protected with a 4 m windbreak from the North. In 2000, roots were pruned at about 50 cm from the row. Water was supplied with a drip irrigation system and the different nutrients were supplied through soil treatments and fertigation (Table 2.2). Plants were kept free of pest and diseases, so the growth can be considered as optimal. On May 13th, a net was installed with the objective of protecting the orchard from birds.

Figure 2.4. General aspect of the orchard at the beginning of the season (May 18th).

Table 2.2. Fertilisation treatments during 2001 until July 31st.

Date and method	Product	Amount of fertiliser
March 26th (soil treatment)	[1]23-23-0	200 kg ha^{-1}
June 19th (soil treatment)	[2]KNO_3	300 kg ha^{-1}
[3]June 19th (fertigation)	[4]H_3PO_4	6.4 l (in 215 l water) ha^{-1}
June 19th (fertigation)	KNO_3	43 kg (in 215 l water) ha^{-1}
July 3rd (fertigation)	H_3PO_4	6.4 l (in 215 l water) ha^{-1}
July 3rd (fertigation)	KNO_3	43 kg (in 215 l water) ha^{-1}

[1]N-P-K
[2]46 % K_2O; 14 % N
[3]Phosphoric acid and KNO_3 were applied together.
[4]26.8 % P

2.1.3 Plant material

Two cultivars were tested: Regina and Karina, both grafted in Limburgse Boskriek rootstock. Both cultivars are partially resistant to cracking, producing large fruits (about 10 g). In Regina, tree vigour is strong and its habit is pyramidal, with spreading, drooping branches. Yield productivity is excellent. The fruits are flat-round to round in shape and largish. Skin colour is dark red to black and the fruits are firm, with a good, juicy, aromatic, sweet flavour. The ripening period is late to very late. It is self-incompatible (Bargioni, 1996) but can be pollinated by Castor, Kordia, Summit (this cultivar was located near the trial) and Sunburst (Balkhoven, *Pers. Com.*). It can pollinate Karina (Goodfruit, 1998) and since compatibility relationships in sweet cherry are always reciprocal (Thompson, 1996), it can itself also be pollinated by Karina.
General characteristics of Karina are similar to those of Regina. Trees are vigorous and up righting. Bloom timing is late and harvest date is about one week earlier than Regina (Goodfruit, 1998).

2.1.4 Treatments

Four different densities were tested. Distance between lines was in all cases 3,25 m, with distance between trees of 60, 90, 120 and 150 cm, resulting in planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. These four densities were in combination with the two cultivars Karina and Regina (8 treatments in total).

2.1.5 Design and statistical analysis

The original design of the orchard had different objectives than those of the present study. Due to border effects only two rows (one for Karina and one for Regina) were suitable for the measurements. As a result, no real replications (randomised) for cultivar could be established. However, the different densities were randomly located into each of the cultivars (Appendix 1).
Six measurements (considered as replications for the analysis) for every combination cultivar/density were performed for SLA, light interception and fruit production. Of course, differences in the results due to effects of the treatment could not be distinguished from the effects of location, but it is necessary to remark that the soil was

homogeneous, the water requirements were satisfied through drip irrigation and nutrient requirements through soil treatments and fertigation. These elements made that the growing conditions can be considered homogeneous, with a relatively small effect of the location.

For the variables in which leaves had to be harvested (LAI and Fruits per m^2 LA) only two trees of every combination cultivar/density were measured. For the estimation of the proportion of the flesh and for the chemical analysis of fruits three replications were used, without taking the effect of planting densities into consideration.

In all cases the design was assumed to be a Complete Randomised Design, but the number of replication changed according to the variable in consideration. Analyses of variance (ANOVA) were conducted using GENSTAT 5.0 (Appendixes 6 to 16) and when appropriate followed by multiple comparisons with the LSD-test (P<5%).

2.2 Measurements

2.2.1 Phenology

Some phenological stages as presented in Figure 1.2 (Wertheim, 1976) were observed in Regina to compare the actual date of full bloom and the starting of LAI development with the predictions given by the model based on the requirements of chilling units and degree-days. Karina showed approximately the same pattern of initial development, but no proper registrations were conducted.

2.2.2 Percentage of PAR reaching ground

As an indication of radiation interception, the percentage of Photosynthetic Active Radiation (PAR) reaching ground was recorded. PAR was measured regularly (approximately every 20 days) in overcast conditions until harvest. The instrument consists of two sensors, one located above the canopy (about 3.5 m above ground) and the other at 10 cm above ground (to avoid interference of grasses). It gives the ratio of PAR reaching ground over PAR above the canopy (as a coefficient going from 0.00 to 1.00). In each of the 6 replications, measurements were conducted in two transects (perpendicular to the row) going from the row to both sides until half the width of the path, every 20 cm.

On May 13th a net was installed to protect the orchard against birds. Measurements of radiation beneath the net and in the open field were carried out three times during the season to estimate the percentage of light intercepted by the net.

2.2.3 Specific Leaf Area

On the same dates (and with the same number of replications) in which radiation interception was estimated, also Specific Leaf Area (SLA) was calculated as the ratio between LA and dry weight of leaves (m^2 leaf kg^{-1} dm leaf). Leaf samples (about 50 leaves per tree) were homogeneously taken at different heights of the tree. Leaf Area of the sample was measured with an Area Meter (LI-COR®, Model 3100), and then the samples were dried in the oven at 70 °C during 24 hours.

2.2.4 Fruit production

Fruit production was recorded in July 17th and July 30th for cultivars Karina and Regina respectively. After estimating the fresh fruit per tree, a sub-sample was utilised to estimate average fresh and dry fruit weight, number of fruit per tree and proportions of dry flesh and pit.

Some rainstorms just before harvesting of Regina caused high losses due to cracking and subsequent rotting. To estimate the potential yield of this cultivar, the total number of fruits was taken into account (including rotten fruits) and multiplied by the average weight of normal fruits.

2.2.5 Leaf biomass and LAI

Leaf biomass can be calculated dividing Leaf Area Index (LAI) by SLA and LAI can be estimated from radiation interception. However, the relation between LAI and radiation interception is not linear, and with very high LAI values, radiation interception approaches a maximum and it is not sensitive any more to further changes in LAI. So, when measuring high values of radiation interception it is not possible to estimate LAI accurately.

For that reason, in two of the 6 trees (replications) that were evaluated for every treatment, all leaves were harvested (at fruit harvest time). Total fresh leaf per tree (kg fresh leaf tree^{-1}) was registered and a sub-sample was used to estimate dry matter content (%) and SLA (m^2 leaf kg^{-1} dm leaf). Fresh leaf per tree times the dry matter content resulted in the leaf dry matter per tree (kg dm leaf tree^{-1}). Thereafter, multiplication of the leaf dry matter per tree times the SLA resulted in the LA per tree (m^2 leaf tree^{-1}). Finally, LAI (m^2 leaf m^{-2} ground) was obtained dividing LA per tree by the ground area per tree (m^2 ground tree^{-1}).

2.2.6 Chemical composition

The sugar requirement for growth respiration depends on the chemical composition of every compound of a specific organ. But a good approximation can be obtained just knowing the total carbon and nitrogen content (Goudriaan and van Laar, 1994). For maintenance respiration also protein (or N) content is needed.

C and N analysis (three replications) for flesh, pit and leaves of the two cultivars evaluated were carried out twice (at pit hardening and at harvest) in the 'Centraal Laboratorium' (Department of Soil Quality, Wageningen UR). Plant material was dried at 70 °C during 24 hours and then milled. Just before processing for the analysis, the samples were warmed-up again at 70 °C for 2 hours to eliminate moisture absorbed during milling.

The digestion procedure (Driessen, *Pers. Com.*) was as follows:

Nitrogen: Approximately 0.3 g of dried plant material (for every sample) were weighed with a precision of 0.001 g and transferred to a digestion tube. Also two standard samples of plant material and two "blanks" were included. 2.5 ml of digestion mixture ($H_2SO_4 \backslash Se \backslash C_7H_6O_3$) were added and mixed. The samples were left for 2 hours.

The tubes were then heated in a heating block at 100 °C for another 2 hours. After cooling, 3 successive 1-ml aliquots of hydrogen peroxide were added.

The tubes were heated at 340 °C for two hours. After cooling, 48.3 ml of water were added and the tubes were left overnight.
Finally, the digest was transferred to a test tube and analysed.
Carbon: approximately 0.02 g of dried plant material (for every sample) were weighed with precision of 0.001 g and transferred to a digestion tube. Also two standard samples (0.3 g) of soil, five artificial mixtures of known chemical composition and two "blanks" were included in the series to be analysed.
5 ml of sulphuric acid were added and the tubes were left overnight at room temperature. After that, 5 ml of $K_2Cr_2O_7$ (80 g l^{-1}) were added and the tubes were shaken. All the tubes were warmed up at 135 °C for 30 minutes, shaken and warmed up again at the same temperature for another 30 minutes.
Finally, the digest was transferred to a test tube and analysed with a Spectrophotometer PU8625 UV/VIS.
The results were analysed as a Completely Randomised Design with three replications.

2.2.7 Proportion of flesh and pit in the fruit

To calculate sugar requirements for maintenance and growth of the fruit, not only the chemical composition is needed, but also the proportion of every kind of tissue in the fruit. Proportion of dry flesh over the total dry weight of the fruit was estimated for both cultivars at pit hardening and at harvest.

2.3 Results and discussion

2.3.1 Phenology

For comparisons with the model, stage E (Figure 1.2) was considered to be the beginning of the leaf growth. From April 24th to April 26th Regina was in stage D and on May 1st in stage EF (Table 2.3).
Blooming occurred shortly after the beginning of leaf growth, indicating that reserves must come from wood and roots to support the growth not only for young leaves, but also for flowers and young fruits.

Table 2.3. Evolution of phenological stages of Regina during 2001 according to the scale presented by Wertheim (1976).

	April							May				
Day	2nd	6th	12th	16th	20th	24th	26th	1st	3rd	7th	10th	14th
Stage	A	A	B	C	C	D	D	EF[1]	EF	F[2]	FG	GH

[1]E was considered as initiation of leaf area growth.
[2]F is full bloom (Figure 1.2).

2.3.2 Percentage of PAR reaching the ground

When PAR reaching the ground was evaluated, no interaction between cultivar, density and date was detected (Appendix 6), but there was significant interaction between density and date (Figure 2.4), and between cultivar and date (Figure 2.5).
In general, the percentage of PAR reaching ground decreased fast at the beginning of the growing period, but started to stabilise about 20 days before harvest.
With the highest density the percentage of PAR reaching ground continued decreasing until harvest, while with the other densities the proportion of PAR reaching ground was more or less stabilised near harvest time.
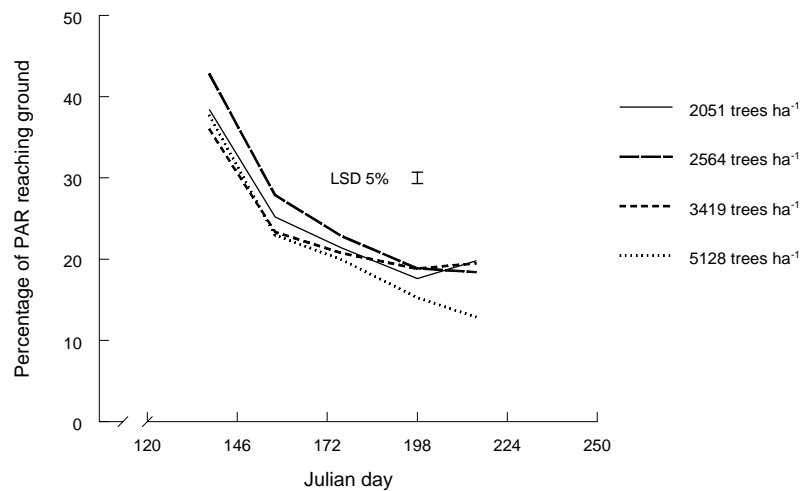
Figure 2.4. Effect of combination of date and planting density on the percentage of PAR reaching ground. Values are averages of cultivars Karina and Regina. Day 138 is May 18th (first measurement).

During the whole growing period, Karina and Regina intercepted about the same proportion of PAR. Only according to the measurement of June 6th (day 157) Karina allowed more PAR to reach ground.
Light interception by the net (installed to protect the orchard against birds) was stable during the season at about 9 %. Although the results showed some variation in radiation interception, differences were not as high as could be expected considering the differences in planting density.
According to the estimations of LAI the low differences seem logical, since LAI did not differ significantly, probably due to intra-specific competition. This situation indicates that trees planted in lower densities can produce bigger branches and more leaves than trees in higher densities.
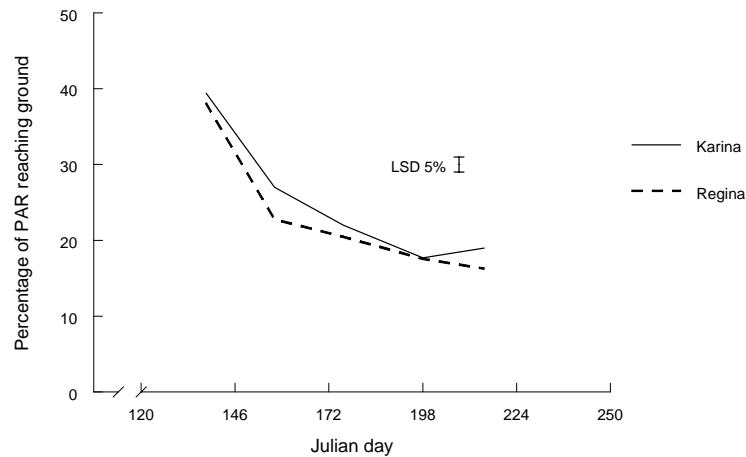
Figure 2.5. Effect of combination of date and cultivar on the percentage of PAR reaching the ground. Values are averages of planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Day 138 is May 18th (first measurement).

But even with the same LAI at harvest, some differences in radiation interception during the season could be expected because of differences in the shape of the tree, clustering of leaves, SLA and leaf size (all these factors affecting the actual light extinction coefficient). The development rate of branches and leaves could also be affected. Therefore, changes in radiation interception could be observed during the growing season even with the same LAI value at harvest.

2.3.3 Specific Leaf Area

When evaluating SLA, there were no significant interactions between factors (Appendix 7). SLA was statistically higher in Karina than in Regina (19.6 and 18.8 m^2 kg^{-1} dm leaf, respectively).
The values were significantly higher with the highest density, but there were no differences between the three lowest densities (Figure 2.6).
At the beginning of the season SLA was highest (24.1 m^2 kg^{-1} dm leaf), decreasing later until June 25th (16.8 m^2 kg^{-1} dm leaf). After that date, values tended to increase again (leaves tend to become thinner), coinciding with the stage III of fruit development. At harvest SLA was 19.2 m^2 kg^{-1} dm leaf (Figure 2.7).
Ranney *et al.* (1991) gave values of SLA between 10.2 and 13.6 m^2 kg^{-1} dm leaf for different combination rootstock-cultivar of 'Meteor' and 'Colt'. The current results showed higher values and considerable changes during the growing season. When developing simulation models, the use of a single SLA value instead of a function describing the changes, will depend of the objectives of the study. In the present study, the general average of the trial (19.2 m^2 kg^{-1} dm leaf) was used.
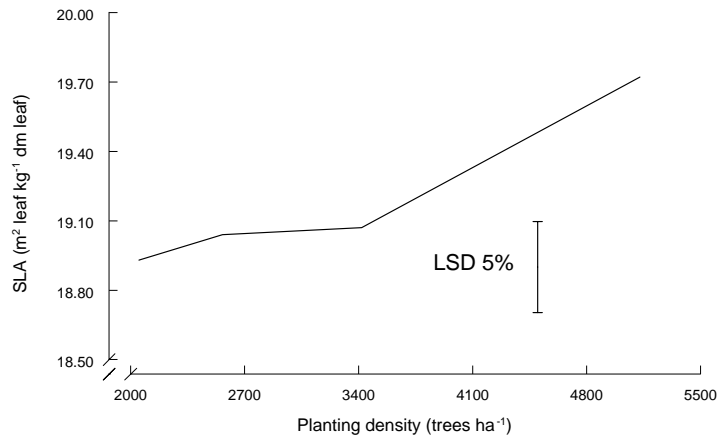
Figure 2.6. Effect of plant density on SLA (m^2 kg^{-1} dm). Values are averages of cultivars Karina and Regina at four moments of the growing season.
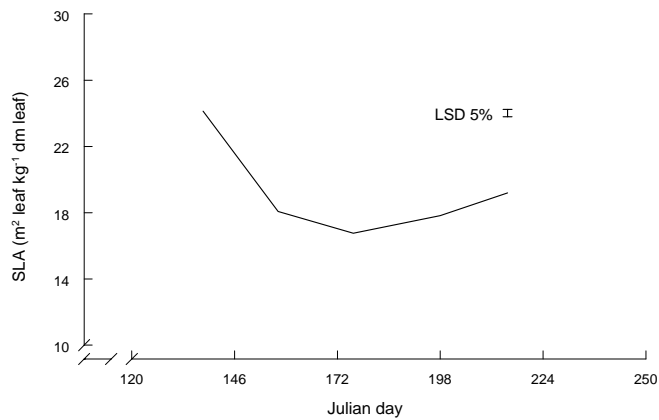
Figure 2.7. Effect of date on SLA (m^2 kg^{-1} dm leaf). Day 138 is May 18th (first measurement). Values are averages of cultivars Karina and Regina in four planting densities.

2.3.4 Fruit production

- Yield

Differences in total yield per ha were not statistically significant (Appendix 8 and Table 2.4). The general average was 7757 kg ha^{-1}.

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Table 2.4. Fresh fruit production (kg ha^{-1}) for cultivars Karina and Regina with planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Values are averaged estimations based on six trees per treatment.

Plant density	2051	2564	3419	5128
Karina	9795	7051	6867	6496
Regina	8460	5443	9210	8736
LSD (*P*<5%)	NS[1]	NS	NS	NS

[1]Not significant.

Higher densities did not contribute significantly to LAI (probably due to intra-specific competition) and therefore neither contributed to light interception. Since the number of fruit per m^2 LA was also similar in all treatments (Appendix 13), the number of fruit ha^{-1} was not statistically different between treatments either (data not shown), indicating again that the intra-specific competition would be regulating fruit production.

When the yield was expressed per tree, no significant differences were detected between cultivars. It seems that there is a tendency of reducing yield per tree when increasing density. However, only with the lowest density the production per tree was statistically higher. No significant differences in yield per tree were found between the three highest densities (Appendix 9 and Table 2.5).

Table 2.5. Fresh fruit production per tree (kg tree^{-1}) for planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Values are averages of six trees.

Plant density	2051	2564	3419	5128
Fruit production	4.45 a[1]	2.44 b	2.36 b	1.49 b

[1]Means followed by different letters differ significantly (*P*<5%) as established by LSD-test.

When the estimations of yield ha^{-1} based on individual trees were plotted against LAI, the result was a tendency to increase yield when LAI at harvest was larger (Figure 2.8). However, the dispersion of the results was relatively high.

When instead of LAI, the number of fruits m^{-2} LA was used, the relation fitted much better (Figure 2.9). The relation was practically linear when yield was plotted against the number of fruits m^{-2} of ground (Figure 2.10). These relations showed that the production is sink limited and therefore with more fruits ha^{-1} higher yields are obtained without significant detrimental effects in fresh weight of individual fruits.
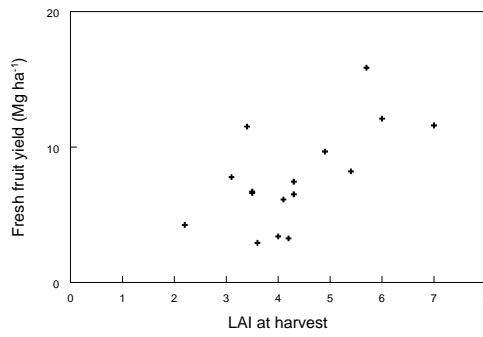
Figure 2.8. Fresh fruit production as a function of LAI at harvest. Points are estimations based on total yield of the individual trees of the trial in which leaves were harvested (two trees per treatment = 16 points). ($Y = -0.393 + 1.883$ X; $R^2 = 0.40$).
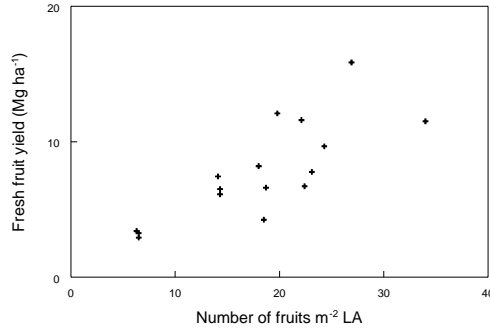
Figure 2.9. Fresh fruit production as a function of the number of fruits m^{-2} LA at harvest. Points are estimations based on total yield of the individual trees of the trial in which leaves were harvested (two trees per treatment = 16 points). ($Y = 0.975 + 0.374$ X; $R^2 = 0.62$).
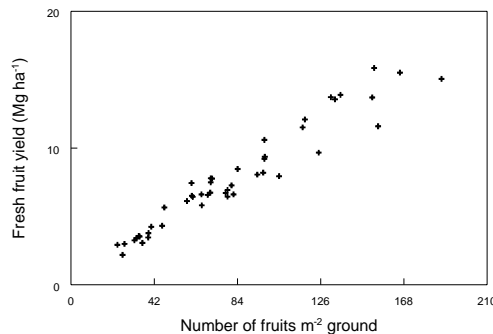
Figure 2.10. Fresh fruit production as a function of the number of fruits m^{-2} ground at harvest. Points are estimations based on total yield of all the individual trees of the trial. (six trees per treatment = 48 points). ($Y = 0.681 + 0.0867$ X; $R^2 = 0.93$).

- Fresh weight of individual fruits

Fruits were statistically larger in Regina than in Karina (Regina: 10.5 g fruit^{-1}; Karina: 9.0 g fruit^{-1}), but no differences were detected between planting densities (Appendix 10). Differences in fresh weight of individual fruits between the two cultivars could be partially explained by different degree of maturity at harvest. About 25 % of final fruit weight is accumulated during the last week before harvest (Looney *et al.*, 1996) so even one day of difference from the optimal harvest date can have an effect in fruit fresh weight and yield. However, in 2000 also Regina got heavier fruit than Karina in the same trial (Balkhoven, *Pers. Com.*). The consistency of the results may indicate differences in potential size of the two cultivars.

The lack of differences in fresh weight of individual fruits between planting densities could be related to the absence of differences in yield (Table 2.4). Reduction in fresh weight of individual fruits could be expected with very high crop load. However, even with the estimations based on individual trees the yield continued increasing almost linearly when increasing the number of fruits m^{-2} of ground (Figure 2.10), indicating that the fresh weight of individual fruits was not reduced even with the highest yields.

2.3.5 Leaf biomass and LAI

Leaf biomass (dm) and LAI at harvest (two trees per treatment) were not significantly different between treatments (Appendixes 11 and 12). General averages were 2786 kg dm leaf ha^{-1} and 4.3 m^2 leaf m^{-2} ground, for leaf biomass and LAI respectively (Tables 2.6 and 2.7). Karina got higher values than Regina for both leaf biomass and LAI, but these differences were not enough to be detected statistically. The lack of significant differences could be partially explained by the low number of degrees of freedom and the high variability between the replications.

Table 2.6. Dry matter leaf biomass per ha at harvest for Karina and Regina with planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Values are average estimations based on two trees per treatment.

Plant density	2051	2564	3419	5128
Karina	2968	2766	2777	2985
Regina	2229	2553	2390	3624
LSD (*P*<5%)	NS[1]	NS	NS	NS

[1]Not significant.

Table 2.7. LAI-values at harvest for Karina and Regina with planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Values are average estimations based on two trees per treatment.

Plant density	2051	2564	3419	5128
Karina	4.85	4.85	4.55	5.25
Regina	3.25	3.55	3.25	5.05
LSD (*P*<5%)	NS[1]	NS	NS	NS

[1]Not significant.

Calculation of LAI is based on the data on dry matter leaf biomass, and therefore both values are closely related. However, the relation is not linear because there are differences in SLA, which was also used for the calculation of LAI (LAI = leaf biomass (kg dm leaf m^{-2} ground) * SLA (m^2 leaf kg^{-1} dm leaf). Differences in LAI between cultivars were no significant. However, Regina had lower values than Karina. These results seem to be in contradiction with the percentage of PAR reaching ground, for which Regina (with lower LAI) allowed slightly less PAR to reach ground (Section 2.3.2). The reason could be that for LAI only two replications were used instead of six and therefore the results of both variables are not directly linked.

With different densities, differences in leaf biomass and LAI would be expected. However, all densities in the trial were very high and increasing intra-specific competition when increasing density probably made that LAI (and leaf biomass) was rather similar between treatments (Figure 2.11), compensating the differences in tree density. The use of slender spindle trees is appropriate in intensive high density cherry orchards with spacing 4 m between rows and 1.5 to 2.5 m between trees with 1000 to 1500 trees per ha (Hrotkó *et al.*, 1998). In the present trial, the lowest density was 2051 trees per ha, indicating that was already more than the maximum recommended.

Figure 2.11. General aspect at harvest time of Regina at 5128 trees ha^{-1} (right hand side) and Karina at 3419 trees ha^{-1} (left hand side).

2.3.6 Chemical composition

- Carbon

Interaction for percentage of carbon was not significant between cultivar, date and organ, but there was significant interaction between date and organ (Appendix 14 and

Table 2.8). Only for leaf, the C-content was not significantly different between dates. For both flesh and pit, the percentage was higher at pit hardening than at harvest.

Table 2.8. Carbon content (%) of flesh, pit and leaf at pit hardening and at harvest time.

Tissue	Flesh	Pit	Leaf
Pit hardening	50.1 a[1]	50.4 a	47.4 b
Harvest	41.8 c	47.0 b	47.6 b

[1]Means followed by different letters differ significantly ($P<5\%$) as established by LSD-test.

The lower C-content of flesh at harvest could be the result of the higher proportion of sugars and organic acids (low C-contents) of this tissue at maturity (Goudriaan, *Pers. Com.*).

- Nitrogen

There was interaction between date, cultivar and tissue (Appendix 15). At pit hardening, N-content was statistically higher in leaves of Karina than in leaves of Regina, but was lower in pit and no significant differences were detected in flesh. At harvest, no significant differences were detected between the two cultivars in flesh and pit, but N-content was higher in Regina (Table 2.9).

Table 2.9. Nitrogen content (%) of flesh, pit and leaf at pit hardening and harvest time for Karina and Regina cultivars

Date	Pit hardening			Harvest		
Tissue	Flesh	Pit	Leaf	Flesh	Pit	Leaf
Karina	1.91 d[1]	0.86 b	2.66 g	0.94 b	0.66 a	2.23 e
Regina	1.77 d	1.41 c	2.50 f	0.87 b	0.54 a	2.62 fg

[1]Means followed by different letters differ significantly ($P<5\%$) as established by LSD-test.

The results at harvest of C-content were very close to those presented by Grossman and DeJong (1994) and Goudriaan and van Laar (1994) (Table 2.10). The last authors mentioned also a value of 4.0 % N for leaf, which is considerably higher than the values found in the analysis. However, that percentage was a default value for C_3 plants and specifically for sweet cherry Meland (1982) mentioned an N-content of 2.63 %, which is very close to the results of the analysis. Therefore, the experimental results of leaf analysis did not allow speculating about N-deficiencies. In fact, calculations based on the N-content and the biomass of fruits and leaves at harvest showed that at that time only 11 and 72 kg N ha^{-1} were present in fruits and leaves respectively.
Averages of Carbon and Nitrogen content from the experimental results were used to calculate maintenance and growth respiration coefficients for the growth model.

Table 2.10. Nitrogen and Carbon content (% of dry matter) of leaf and fruits.

	Nitrogen[1]	Carbon[2]
Leaf	2.63	45.3
Fruit	1.00[3]	47.5

[1]After: Meland (1982). Average for several cultivars of sweet cherry.
[2]After: Grossman and DeJong (1994). Values for *Prunus persica*.
[3]Original data expressed per fresh weight. Transformation was made considering 15% dry matter in fruits.

2.3.7 Proportion of flesh and pit in the fruit

The proportion of flesh over the total dry weight of the fruit was significantly higher at harvest (80.7 %) than at pit hardening (43.5 %). No significant differences were detected between cultivars (Appendix 16).
Pit size seems to be determined early during fruit development, and the further increase in fruit weight would be more related to flesh growth. Pit is also relatively constant when comparing different fruit sizes, then larger cherries have proportionally more flesh (Looney *et al.*, 1996).

3 Modelling

3.1 Description of the model's architecture

The ecophysiological knowledge found through the literature review was integrated into a FST program. Parameterisation was done using values from literature and from the results of the experiment.

The time step of the model is set by the daily reading of the weather data (one day).

Two integration methods could be used: Euler or Runge-Kutta. The second one can be used if no discontinuities are present and is considered to be more precise than Euler at a same time step (Leffelaar, 1999). However, the run-time using Euler is much shorter (because this method is simpler), and using a time step of one day, the results are practically the same with both methods (apparently because time coefficients are high). The model uses Runge-Kutta (RKDRIV) by default. However, the integration method of Euler (EUDRIV) should be preferred when many re-runs are performed.

The model considers potential production, defined as "the situation when the crop is amply supplied with water and nutrients and is free of weeds, pests and diseases (Lövenstein *et al.*, 1995)". In this situation crop growth only depends on aboveground processes such as CO_2 assimilation and on physiological characteristics of the species or cultivar (Bouman *et al.*, 1996; Goudriaan and van Laar, 1994; Lövenstein *et al.*, 1995). But in this model also the size of the reproductive sink has to be defined by the user, because there are several factors affecting it. The user has to define the leaf area index at harvest time (LAIMAX) and the number of fruits per m^2 leaf area at harvest (FRTLA). LAIMAX summarises the planting density, vigour and training system, while FRTLA (fruit density within the canopy) is the result of several processes, such as flower bud differentiation, pollination, fruit-set, frost damage and abortion.

The model reads weather data from a specific weather file. Because the model is designed for potential production, only Daily Global Radiation, and Minimum and Maximum temperatures are used. Other weather data and water and nutrients requirements are not considered.

In the model, the intercepted PAR is estimated as a function of the incoming PAR, LAI and canopy characteristics (K and clustering factor). Assimilation of CO_2 is assumed to be the product of the intercepted PAR and the Light Use Efficiency (LUE). The produced sugars are first used to maintain the present biomass and for growth of the leaves. The remaining available sugars (REMSUG) are distributed between vegetative and reproductive sinks (fruits). Fruits have priority over vegetative parts, but the maximum of sugars that they can utilise was assumed to be half of REMSEG.

3.1.1 Climate

The model uses climatic data as inputs: daily global radiation (J m^{-2} d^{-1}), and maximum and minimum temperature ($^\circ$C) read directly from a weather file for a specific location (e.g. in this case Haarweg Station (Wageningen), about 5 km from the orchard), and year (e.g. 2001). However, the weather can also be included as functions (minimum and maximum temperature and daily global radiation for any specific location). In this case monthly averages are presented at the middle of each month and the required daily values are obtained by extrapolation (Goudriaan and van Laar, 1994).

3.1.2 Chilling requirements and degree-days accumulation

For calculating the chill units accumulation the following formula was used:

$CU = 0.857 + 0.0843\ T - 0.0123\ T^2$, where parameter values are averages of those found by Mahmood *et al.* (2000) for cultivars Stella, Summit and Sunburst (Section 1.1.4).

This formula was incorporated into the FST program (multiplied by 24 because the time step in the model was one day and the formula was on hourly basis) to calculate the accumulation rate of chill units (RCU) during the season. The chilling requirement to break dormancy (CHLREQ) was established in 1142 CU as default value. Degree-days (TSUM) only start to accumulate after the chilling requirements are fulfilled. However, a first run with starting date October 1st showed that on January 1st CU requirements have already being satisfied (CU accumulation = 1695). When the temperatures are high enough to start leaf development the chilling requirements have already been satisfied long before. Therefore, in the conditions of The Netherlands, the model was initialised on January 1st and the CU requirements were assumed to be already satisfied (INITCU = 1695.). The rate of accumulation of degree-days is a function of the difference between the air temperature (TA) and the base temperature (TBASE).

3.1.3 LAI and fruit development

LAI and fruit development (LAIDEV and FTDEV, respectively) were considered to be a function of degree-day accumulation (TSUM) using a base temperature (TBASE) of 4 °C (Table 3.1), but the model starts to accumulate degree-days only after the chilling requirements have been satisfied. For LAI development as a function of degree-days a function adapted from Eisensmith *et al.* (1980) was used.

Table 3.1. Development function included in the FST program to simulate LA and fruit development.

TSUM	Development coefficient	
	LAI[1]	Fruit[2]
175	0.01	0.0
255	NC[3]	0.01
325	0.065	NC
413	0.25	NC
542	0.47	NC
624	0.63	NC
700	NC	0.22
715	0.77	NC
828	0.88	NC
1064	1.0	1.0

[1]Function adapted from data presented by Eisensmith *et al.* (1980).
[2]Function adapted from data presented by Anderson *et al.* (1986).
[3]NC: Not considered.

In several studies, leaf area is not simulated but given as input in the model (Marcelis *et al.*, 1998). This was also the approach followed for this model, in which the actual leaf area index (LAI) was calculated multiplying LA development by maximum LAI at harvest (defined by the user).

For fruit development another function was used, considering that full bloom coincides with 255 degree-days (adapted from Anderson *et al.* (1986)) and marks the initiation of fruit growth. Until harvest 1064 degree-days are required (the same value as for LAI development).

3.1.4 Light interception

Interception of PAR (I_a, IPAR) was calculated based on the formula presented by Goudriaan and van Laar (1994):

$$I_a = I_0 \bullet (1 - \rho_c) \bullet (1 - \exp(-AK \bullet LAI))$$

Reflection coefficient (ρ_c, REFLEC) was estimated to be 8 %, while light extinction coefficient (K) was estimated in 0.7, which is the value for spherical angle distribution (Goudriaan and van Laar, 1994). Because the crop is cultivated in rows, a clustering factor (CLF) was calculated with a sub-model (Goudriaan, *Pers. Com.*) and multiplied by K, resulting in the actual K (AK), which in the model is used instead of K.

A net factor (NET) was also incorporated from the day 135 (day in which the net was installed to protect the orchard against birds). The net intercepted 9 % of the incoming PAR.

3.1.5 CO$_2$ assimilation

CO$_2$ assimilation (A, ASIM) was calculated using the LINTUL-type model approach. Assimilation of CO$_2$ was assumed to be the result of intercepted PAR and a constant value for Light Use Efficiency (LUE) for the whole canopy of 6 g CO$_2$ MJ^{-1}. Assimilation of CO$_2$ was later transformed in glucose production multiplying by 30/44 (molecular weights of glucose (per carbon atom) and CO$_2$, respectively).

The accumulation of sugars did not start from zero, but from 800 kg ha^{-1}, which coincides with 4 % of the total wood and root biomass and was assumed to be the quantity of sugar from reserves, which are mobilised early in the season when leaves are still not exporting sugars. In sour cherry, Kappes and Flore (1984) found that the seventh leaf from the shoot base started gross export after reaching 25 % of full expansion and the tenth leaf started exporting later in its development when it reached 55 % of its full size.

3.1.6 Maintenance respiration

Maintenance of leaves (MTLEAF) is a function of leaf biomass (LFBIOM), maintenance coefficient of leaf (MCLEAF) and temperature conversion factor (TC).

Leaf biomass (LFBIOM) is calculated as the ratio between LAI and specific leaf area (SLA). Leaf maintenance coefficient (MCLEAF) was established as 0.016 g sugar g^{-1} dm d^{-1} (or kg sugar kg^{-1} dm d^{-1}) and it was calculated on bases of average N content of

leaves (Table 2.9) and the relation presented by Goudriaan and van Laar (1994) of 0.24 g CH_2O g N^{-1} d^{-1} plus 0.01 g CH_2O g dm^{-1} d^{-1} (cost of active transport of ions across membranes for maintenance of the electrical potentials):

MCLEAF = 0.24 g CH_2O g N^{-1} d^{-1} * 0.025 g N g^{-1} dm + 0.01 g CH_2O g dm^{-1} d^{-1} = 0.016 g CH_2O g^{-1} dm d^{-1}

Wood biomass (WDBIOM) and root biomass (RTBIOM) were assumed to be 15000 kg dm ha^{-1} and 5000 kg dm ha^{-1} respectively. No change in wood and root biomass was assumed over the short period of one simulated season. Maintenance coefficient for wood (MCWOOD) and for roots (MCROOT) were estimated as 0.0009 kg sugar kg^{-1} dm wood d^{-1} and 0.002 kg sugar kg^{-1} dm root d^{-1} respectively (values derived from Grossman and DeJong (1994), modelling peach growth). As for leaves, wood and root maintenance are also influenced by temperature (TC).

3.1.7 Growth of leaves

The sugar requirement for growth of leaves was established as 1.61 kg sugar per kg dm leaf, as a function of average C-content (Table 2.8) and N-content (Table 2.9) in the leaves (47.5 % and 2.5 % for C and N content, respectively), using the formula presented by Goudriaan and van Laar (1994):

Glucose requirement (g CH_2O g^{-1} dm) = 5.4 C (g C g^{-1} dm) + 6.0 N (g N g^{-1} dm) − 1.1

3.1.8 Sugar requirement for 1 kg (dry matter) of fruit

The total sugar cost of producing 1 kg dry matter fruit (FRTCST) was calculated as the sum of the total requirements for maintenance and for growth. Sugar growth requirement (GCFRUT) was established as 1.66 kg sugar kg^{-1} dm fruit, in the same way as for leaves using the same formula presented by Goudriaan and van Laar (1994). The total maintenance cost is the integral over time of the daily maintenance requirement. Maintenance coefficient of fruits (MCFRUT) at any time is estimated in the same way as for vegetative material (Section 3.1.6), but taking into account the changes in N content during fruit development and the increasing biomass of the fruit during the growing season.

3.1.9 Remaining sugar available for fruit, and growth of root and wood

The quantity of sugars available for fruits, growth of root and wood (REMSUG) was calculated by subtracting the total sugar requirement for leaves (SUGLEF), and the sugar requirements for maintenance of wood (TTWDMT) and roots (TTRTMT) from the total sugar production (SUGAR).

3.1.10 Fruit sink strength

Fruit sink strength (SINK) was calculated as the product of fruits m^{-2} LA (FRTLA), maximum LAI at harvest (LAIMAX), maximum dry matter (kg) of a fruit (MAXSIZ), fruit development (FTDEV) and total cost of producing one kg dry matter fruit (FRTCST). LAIMAX is included in the formula of SINK because LAIMAX "summarises" planting density, vigour and training system, and multiplied by FRTLA gives the number of fruits m^{-2} ground, which is the main variable determining SINK demand per ground unit.

The model does not consider the path of the sugars from sources to sinks. In reality, fruits are mainly supplied with sugars from nearby sources (Grossman and DeJong, 1994 from Ho *et al.*, 1989 and Wardlaw, 1990), so there is an effect of the clustering of fruits (internal distribution in the tree). The demand due to the path (the resistance to transport) is also part of the sink strength.

3.1.11 Sugar available for fruits

Even with very high number of fruit per m^2 LA, not all the sugars will be partitioned to fruits. The maximum sugar for fruits (MSUGFT) was assumed as 50 % of REMSUG.
The actual quantity of sugars used by fruits (SUGFRT) is the minimum: MSUGFT or SINK (Figure 3.1).
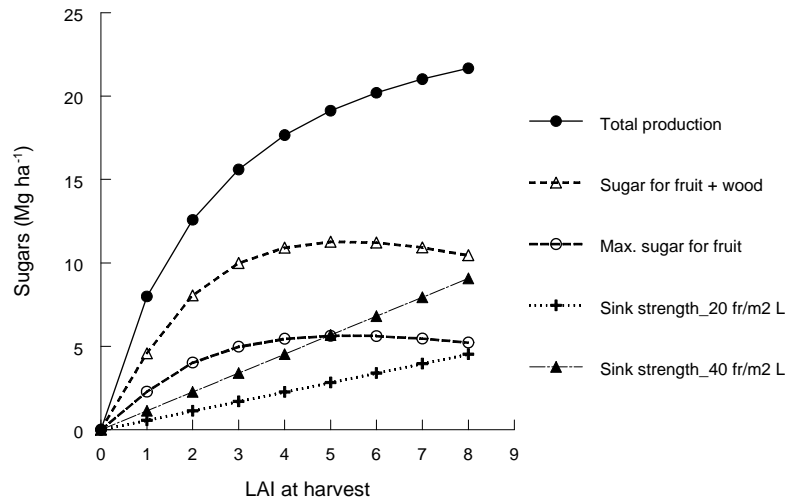
Figure 3.1. Total sugar production, sugar available for growth of wood, root and fruits, maximum quantity of sugar that can be partitioned to fruits and reproductive sinks with two levels of number of fruits m^{-2} LA as a function of LAI at harvest.

3.1.12 Fruit production

Dry matter fruit production (DMFRUT) is calculated as:

DMFRUT= (SUGFRT / FRTCST)*FTDEV

Fresh fruit production (FRSHFT) is the ratio between dry matter fruit production and dry matter content of fruit (DMCONT), which is a function taking into account the changes in dry matter content during fruit development. The number of fruit per ha (FRTPHA) is the result of FRTLA times LAI at harvest time (LAIMAX) and multiplied by 10000 m^2 ha^{-1}. Fresh weight of individual fruits is the ratio between total fresh fruit production and FRTPHA.

3.2 Modelling results and sensitivity analysis

Different runs of the model were conducted changing values of some parameters to evaluate the robustness of the model and its sensitivity.

3.2.1 Variation between years

Running the model with weather files from different years (1985, 1987, 1989 and 2001) did not affect significantly the reproductive sink strength, which is mainly defined by the parameters "number of fruits per m^2 LA", "maximum LAI" and "fresh weight of individual fruits". The model does not consider the effect of weather conditions on pollination, fruit-set, frost damage and fruit drop (affecting sink strength). This is a very important simplification, yet difficult to solve, because successful predictive simulation of fruit-set is still a challenge (Marcelis *et al.*, 1998; Marcelis and Heuvelink, 1999).
The effect of the year (weather) was significant in those situations with high demand for photoassimilates (Table 3.2). Relatively important differences were observed on total sugar production especially with the highest LAI. These differences in sugar production were translated into differences in fruit production and fresh weight of individual fruits in those cases with source limitation (high number of fruits m^{-2} LA). In 1987, the year with the lowest production, the relation between yield and LAIMAX was rather insensitive (source limitation). But in 1989, the year with the highest production, an increase in LAIMAX produced an almost proportional increment in fruit yield.
Table 3.2 shows only some situations with very high sink demand (large LAIMAX in combination with high FRTLA). In most situations the production is generally limited by the reproductive sinks demand and therefore differences in sugar production have a limited effect.
Different temperatures between years made that the rates of degree-days accumulation also differed and as a result the predicted harvest time showed some variability.

Table 3.2. Effect of weather conditions (year) on total sugar production (kg ha^{-1}), fresh yield (kg ha^{-1}), fresh weight of individual fruits (g fruit[-1]) and harvest time (Julian day) under two values of LAIMAX (m^2 leaf m^{-2} ground) and two values of FRTLA (number of fruits m^{-2} LA).

LAIMAX	FRTLA	Year	Total sugar production	Fresh yield	Fresh weight of individual fruits	Harvest time
4	40	1985	15780	15982	9.99	209
		1987	15042	14613	9.13	210
		1989	18992	16000	10	192
		2001	17665	16000	10	194
	50	1985	15780	15982	7.99	209
		1987	15042	14613	7.31	210
		1989	18992	19887	9.94	192
		2001	17665	19248	9.62	194
5	40	1985	16989	16154	8.08	209
		1987	16271	14821	7.41	210
		1989	20571	19888	9.94	192
		2001	19122	19860	9.93	194
	50	1985	16989	16154	6.46	209
		1987	16271	14821	5.93	210
		1989	20571	22125	8.84	192
		2001	19122	19860	7.94	194

3.2.2 Leaf, wood and root biomass

The amount of present biomass affects the sugar requirements for maintenance. Wood and root biomass are considered constant by the model. These values can of course be increased, but this correction must be done with care because the maintenance coefficients will decrease with time, producing a sort of compensation.

With relatively low LAI values, the maintenance of the tree structure (wood and root) represented 64.8 % of the total maintenance cost. By increasing LAI the total cost also increases, but the proportion of maintenance due to structure was reduced drastically (Table 3.3), because wood and root biomass are assumed to be constant during one single growing season.

Table 3.3. Effect of increasing LAI on total maintenance cost (kg sugar ha^{-1}) and contribution (%) of different components. Fruit m^{-2} LA was set constant at 40, and wood and root biomass at 15000 and 5000 kg ha^{-1} respectively.

LAI	Total maintenance cost (kg sugar ha^{-1})	Percentage of the cost for different components			
		Leaves	Fruits	Wood	Root
3	3548	23.1	12.1	37.2	27.6
5	4332	31.5	15.4	30.5	22.6
7	4898	39.0	14.0	27.0	20.0

The high sensitivity of maintenance cost to changes in LAI was because the maintenance coefficient for leaf biomass is high. Maintenance of fruits was always a minor part of the total and it did not increase substantially when increasing LAI because the fruit production was already at its maximum with a LAI value of 5.

The outputs of the model were generally reproductive sink strength limited. Therefore, the effect of leaf biomass on yield and fresh weight of individual fruits was restricted.

3.2.3 Changes in clustering factor during the season

Clustering refers to arrangement of the trees in rows and not to internal clustering of leaves in the canopy. The clustering factor is a single parameter summarising the orchard architecture, which in turn depends on the vigour of rootstock and cultivar, growing habits, planting density, planting arrangement, training system, nutrient management and water availability. Its value is sensitive to LAI, height of the trees and width of path and crown. Early in the season, the path is maximum and the LAI is minimum. When LAI increases during the season, the clustering factor would tend to decrease, but is partially compensated due to a reduction in the path width (Figure 3.2). By fixing the height of the trees at 3.25 m, the simulated clustering factor did not change drastically during the season and fluctuated between 0.93 and 0.97.

The values of CLF obtained for the orchard under consideration showed that the canopy was very homogeneous except at the beginning of the season, but in that case the clustering factor was reduced by a low LAI value.
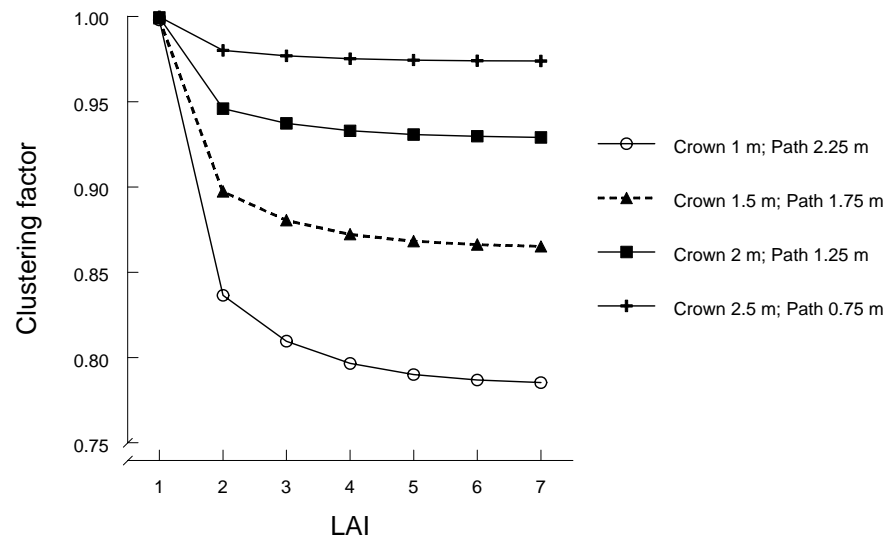
Figure 3.2. Clustering factor (CLF) as a function of LAI and proportion of path and crown width. Height of the trees was in all cases 3.25 m.

3.2.4 LAI

Total sugar production increased by increasing LAI. However, leaves demand sugars for maintenance and therefore the maximum amount of sugar available for production was obtained with LAI between 4 and 5 (Figure 3.1).
The model showed that in potential production situations the fruit production is generally sink limited. Fruit production continued to increase with increasing LAI when a low number of fruits per m^2 leaf area was assumed (Figure 3.2). In that case the production was strongly limited by sink strength and therefore depended on the number of fruits ha^{-1} (LAI * FRTLA * 10000 m^2 ha^{-1}).

3.2.5 Maximum fresh weight of individual fruits

The maximum fresh weight of individual fruits defines the potential for fruit growth. Bigger fruits require more sugars (higher sink strength) and in situations in which the yield is limited by reproductive sink demand, the effect of having a potentially larger fruit would result in an almost direct increment of yield if all other parameters remain the same (Figure 3.3).
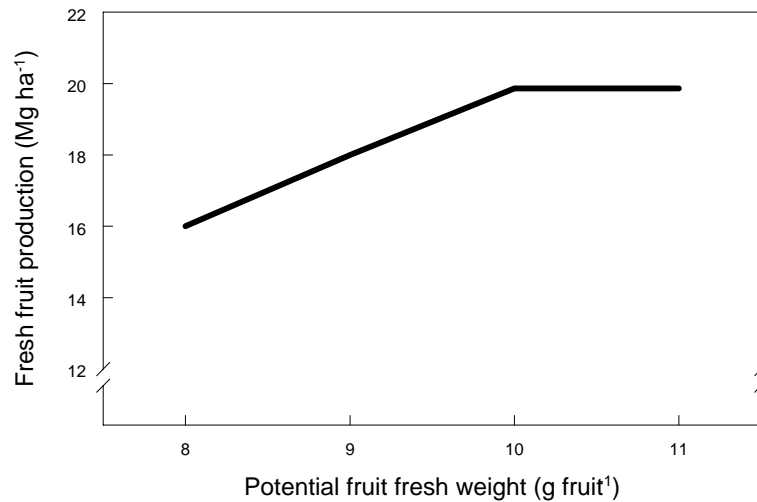
Figure 3.3. Simulated fresh fruit production as a function of potential fresh weight of individual fruits of the cultivar. (LAIMAX = 5.; FRTLA = 40.)

However, it has to be remembered that the model was designed only for potential production situations. With any stress conditions due to nutrient or water deficit, the curve representing available sugars for fruits (Figure 3.1) will be lower, while the reproductive sink strength would remain the same.
Therefore, in limiting production situations, source strength limitation could be observed (reduction of fresh weight of individual fruits would be seen even with relatively low crop loads).

Because in the simulations the yield was generally sink limited, the potential size of the fruit had a direct effect on the yield, except when considering very high yield values. In those situations, source strength was limiting production and no further yield increments were observed with increasing potential fresh weight of individual fruits (Figure 3.3).

3.2.6 Number of fruits per m^2 of leaf area

The number of fruits per m^2 of leaf area at harvest is an important parameter summarising several physiological processes and management decisions. It is the result of the differentiation of flower buds in the previous season, fruit set (resulting from combination of distance to the pollinator cultivars, presence of bees, weather conditions, etc.) and fruit drop (abortion). Often, requirements for fruit growth cannot be covered completely by the photosynthesis in the current season and reserves of non-structural carbohydrates must be used (Keller and Loescher, 1989) (the model is initialised with 800 kg sugar ha^{-1} from reserves). If there are no reserves, the tree will produce fewer fruits or more fruits will abort.

As in the case of maximum fresh weight of individual fruits, the number of fruits per m^2 of leaf area had a direct effect in the simulated yield except when considering very high yield values (Figure 3.4).
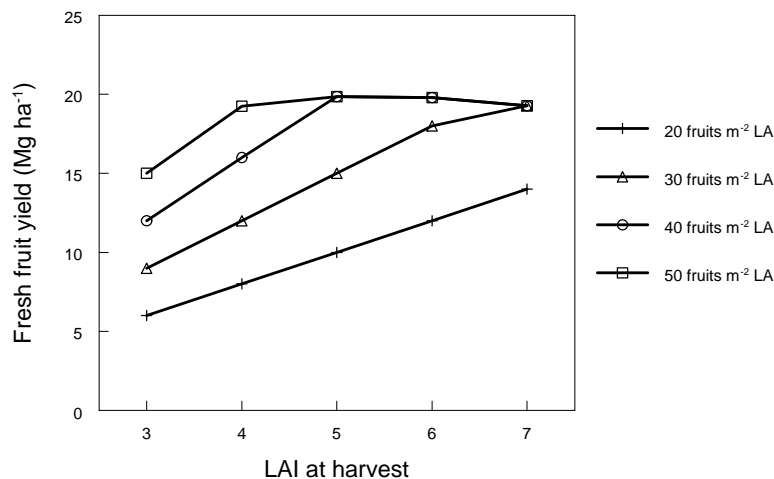
Figure 3.4. Simulated yields (Mg ha^{-1}) as a function of LAI at harvest time and four levels of fruits m^{-2} leaf area (20, 30, 40 and 50 fruits m^{-2} LA).

However, it has to be considered that the model makes an important assumption, which in fact is a very important simplification: it considers a constant number of fruits during the growing season (abortion is not taken into account). In reality, the number of reproductive sinks at the beginning of the season (flowers and small fruits) may be much higher than at harvest. It might be that with high fruit setting, the available sugars early in the season are not sufficient to satisfy the demand for all the fruits (at the beginning of

the season LAI and light interception are still low). The competition between fruits would cause that the number of cells in the fruit is defined at a lower level. If later in the season part of the fruits is aborted, the remaining fruits can grow at potential rate, but they can not reach potential size, because cells can only increase their size, but not their number and part of the growing period has already been lost. If this occurs, the actual fresh weight of individual fruits could be lower than the one predicted by the model, which only considers the number of fruits at harvest and takes the "original" potential fresh weight of individual fruits (Figure 3.5).
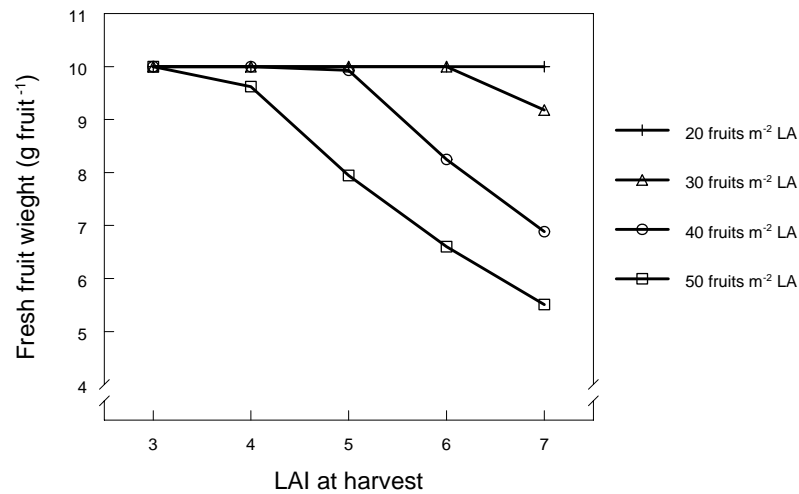
Figure 3.5 Simulated fresh weight of individual fruits (g fruit^{-1}) as a function of LAI at harvest time and four levels of fruits m^{-2} leaf area (20, 30, 40 and 50 fruits m^{-2} LA).

Simulating the effect of a higher number of fruit early in the season is difficult because both sink and source strength are very low and therefore the source/sink relationship is very sensitive to the level of reserves from the previous season. Also the simulation would be very sensitive to the accuracy of the functions describing fruit and leaf area development.

3.2.7 Light extinction coefficient (K)

The K-value has an effect on the intercepted PAR and therefore on total sugar production. A low K-value (0.5) does not limit production in situations of low sink demand (e.g. FRTLA = 30), but with high sink demands the produced sugars are not sufficient to support potential growth of the fruits (Table 3.4) and production could be limited by source strength.

Table 3.4. Simulated fresh yield (kg ha^{-1}) and fresh weight of individual fruits (g fruit^{-1}) as a result of different K-values in combination with two values of LAIMAX (m^2 leaf m^{-2} ground) and three values of FRTLA (number of fruits m^{-2} LA).

LAIMAX	FRTLA	K-value	Yield	Fresh weight of individual fruits
4	30	0.7	12000	10
		0.6	12000	10
		0.5	12000	10
	40	0.7	16000	10
		0.6	16000	10
		0.5	14975	9.4
	50	0.7	19248	9.6
		0.6	17332	8.7
		0.5	14975	7.5
5	30	0.7	15000	10
		0.6	15000	10
		0.5	15000	10
	40	0.7	19860	9.9
		0.6	18114	9.1
		0.5	15889	7.9
	50	0.7	19860	7.9
		0.6	18114	7.2
		0.5	15889	6.4

4 Comparison of simulated and experimental results

4.1 Purpose and scope of the comparison

For the parameterisation of the model some values were taken from the experiment and therefore, the comparison between simulated and experimental results should not be considered as a complete validation of the model. However, many parameter-values and the processes involved in sweet cherry fruit production were derived from literature. The comparison permits to check if both the parameter-values and the physiological, agronomic and ecological knowledge were properly integrated in the model.

4.2 Phenology

The model does not give a detailed simulation of developmental stages. However, the timing of three important events in the production cycle of the crop is described: initiation of leaf growth, full bloom and harvest (Table 4.1).
The model predicted that leaves start to grow after accumulating 175 degree-days and in 2001 this coincided with the day 101 of the year. Stage E of development (Wertheim, 1976), which was assumed to represent the initiation of leaf growth, was recorded approximately on April 29th (day 119 of the year).
Simulated full bloom coincides with an accumulation of 255 degree-days. In 2001 this happened on the day 122. The actual day of full bloom in Regina was May 7th (day 127 of the year).
Maximum fruit (and leaf area) development is assumed by the model to be reached after accumulating 1064 degree-days. In 2001 this happened on the day 194. The actual day of harvest for Karina was July 17th and for Regina July 31st, which correspond with days 198 and 212 of the year, respectively.
These results showed that the phenological events were predicted to occur earlier than in reality. However, the requirements of degree-days accumulation for different phenological stages are cultivar-specific and important variations should be expected between different plant materials. Predictions of the model could be suitable to have a first estimation in absence of experimental registers, but when reliable data are available for specific cultivars and locations, these data can (and should) be entered in the model to simulate fruit production.

Table 4.1. Predicted and observed day of the year for initiation of leaf growth, full bloom and harvest.

Event	Predicted	Observed	
		Karina	Regina
Initiation of leaf growth	101	NR[1]	119
Full bloom	122	NR	127
Harvest	194	198	212

[1]Not recorded

4.3 Yield

Simulated yields (with LAIMAX = 4.3, which was the general average of trees with harvested leaves) were very sensitive to the number of fruits m^{-2} LA. When this variable was fixed in a high level (40 fruits per m^2 LA), the actual yields were always much lower than predicted. Number of flowers and/or fruit-set were not recorded, but they seem to be the main factors determining the yield differences.

When the observed number of fruits m^{-2} LA (FRTLA) was also incorporated in the simulation as input, the "descriptive simulations" and the actual yields were very close each other (Table 4.2). This is because fruit production resulted to be almost directly related to the number of fruits m^{-2} ground (Figure 2.10) and this variable is the result of the combination of LAIMAX and FRTLA.

Table 4.2. Descriptive simulation (incorporating observed FRTLA) and experimental yields (kg ha^{-1}) for cultivars Karina and Regina with planting densities of 2051, 2564, 3419 and 5128 trees ha^{-1}. Experimental results are averages of the two trees in which also leaves were harvested.

| Density | Karina | | Regina | |
	Descriptive simulation	Experiment	Descriptive simulation	Experiment
2051	8330	9634	9570	9646
2564	7840	7360	4680	4771
3419	6900	6464	5280	5848
5128	11660	9161	8670	9114

4.4 Fresh weight of individual fruits

The fresh weight of individual fruits was very stable in the experiment. Even when considering the yield on the basis of production per tree, differences in fruit production per ha were not related to individual fruit fresh weight (Figure 2.10), indicating that even with the highest yields the production was not limited by source strength, but by sink strength.

When the daily assimilates supply exceeds the daily total potential demand, the growth rate of each sink occurs at its potential rate. In that case the assimilate pool is not totally depleted (reserves are formed) (Marcelis and Heuvelink, 1999). This can be observed in the simulations, from which it can be seen that only with yields of almost 20000 kg ha^{-1} the fresh weight of individual fruits is reduced. It was not possible to check if this value was really an inflection point, since the highest yield per ha (individual tree basis) was about 16000 kg ha^{-1}. It thus remains a research question for future studies.

The model does not consider the path resistance to the transport of sugars. In reality, fruits are supplied from nearby sources (Grossman and DeJong (1994), from Ho *et al.* (1989) and Wardlaw (1990)) and therefore the distribution of the fruits within the canopy is relevant. Even in situations of ample availability of sugars at tree level, competition between individual fruits in a spur could limit the actual weight of the fruits.

The model predicted that about 30% of the final fruit weight was accumulated during the last week before harvest. This result is comparable with the 25 % reported by Looney *et*

al. (1996) for the same period and emphasises the importance of the optimum harvest time.

4.5 Radiation interception

For the comparison, the percentage of PAR reaching the ground was transformed into PAR interception (100 – PAR reaching the ground). Simulated radiation interception underestimated the measured one at the beginning of the growing season and overestimated it near harvest time. Taking lower K-values (0.6 or 0.5) instead of the 0.7 used as default (or lower CLF), improved the fit around harvest, but still it followed the same pattern and underestimation at the beginning of the season is even worse (Figure 4.1).
The reason of the differences could be a low accuracy of the function describing LA development. But even in that case, the relatively high light interception early in the season only can be explained by the interception due to the tree structure itself (even without any leaf). A complementary measurement after leaf-fall showed an average PAR interception for the complete trial of 20.3 % (Figure 4.2). This result would explain the high values of measured PAR interception early in the season, when the contribution of the structure to light interception is relatively high. However, the real interception of the structure early in the season would be lower than the value found, because during the season small branches have developed.
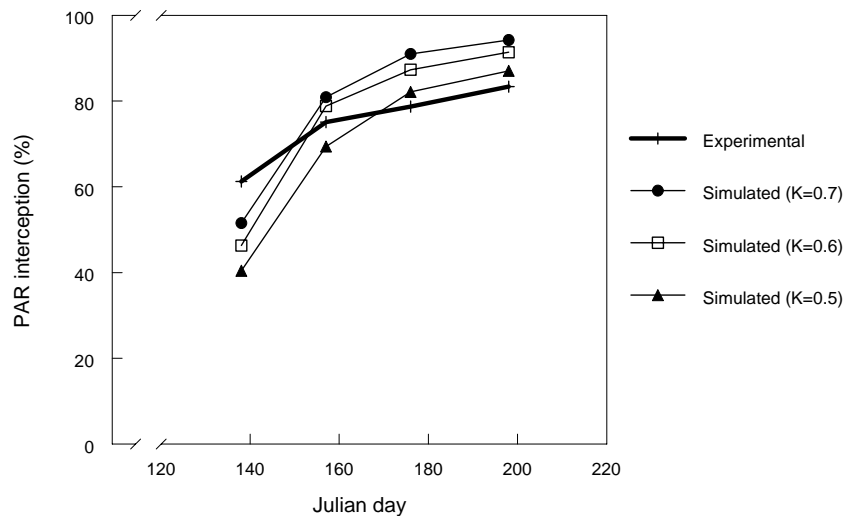
Figure 4.1. Observed and simulated PAR interception. Observed PAR interception is the general average of the trial. Simulation was run with LAIMAX = 4.3 (general average of LAI at harvest in the trial) and three different K-values (0.7, 0.6 and 0.5).
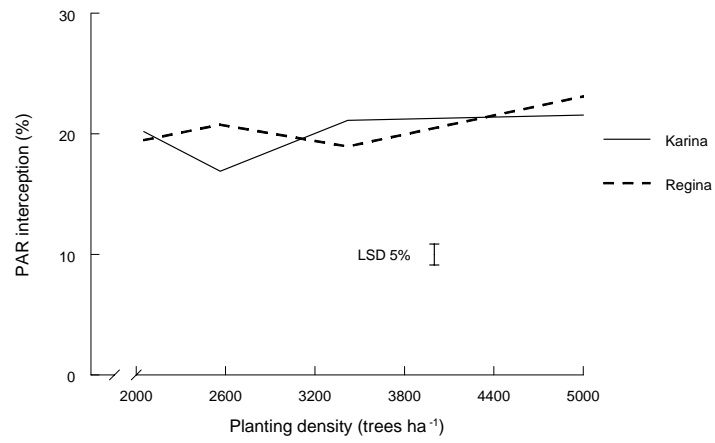
Figure 4.2. Observed PAR interception by the tree structure after leaf-fall (December 11th). Values are averages from six replications.

5 Main parameters defining fruit production

According to the results of the model and the experiment, the main parameters defining potential production in sweet cherry were LAI, potential fresh weight of individual fruits and number of fruits per m^2 LA (fruit density within the canopy).

5.1 LAI

Leaf Area Index (LAI) has an important effect on the level of sugars available for growth and particularly for fruits. With LAI between 4 and 5, the quantity of sugars available for growth is maximised. Above 5, even reductions are observed because the maintenance cost increases more than proportionally in relation to the assimilation. In practice, normally fruit size increases as leaf:fruit ratio increases (Facteau, 1983). Relatively high LAI-values can support more fruits, because more sugars are produced and are available for growth.
However, an excess of LAI not only does not contribute to the budget of sugar available for growth, but also produces excess of shading negatively affecting the potential number of flowers, because good light levels inside the canopy are necessary to extend the life of spurs and differentiate buds (Patrick, 1988).
Growth of reproductive shoot apices is light-sensitive and manipulation of light quality or duration (e.g., by row orientation, plant density or training system) can alter assimilate partitioning patterns to increase crop productivity (Patrick, 1988).
An adequate LAI is the result of a proper selection of rootstocks, cultivars, planting density and training system, and the adjustment of irrigation and fertilisation regimes.

5.2 Potential fresh weight of individual fruits

Cultivars with (potentially) larger fruits normally are preferred from a fruit quality point of view, because bigger fruits get higher prices (Proebsting and Mills, 1981). But probably this would be an interesting parameter also when the main objective is to get higher yields, because bigger fruits contribute more to the reproductive sink strength and in many situations the production could be sink limited.

5.3 Number of fruits per m^2 LA

To obtain high yields a high number of fruits m^{-2} of leaf area is required. To achieve this goal, different aspects must be considered, because this parameter is the result of flower bud differentiation (during the previous season), pollination, fruit-set and fruit-survival.
Fruit-set can vary considerably between trees and between seasons (Looney *et al*. 1996). The number of flowers and fruits is positively correlated with a good light distribution. Orchard design and tree structure (pruning and training system) may affect light distribution and therefore fruit-set and yield in sweet cherry (Roversi and Ughini, 1996). Management programs based on an understanding of assimilate partitioning responses to various environmental factors can lead to improvements in crop productivity (Patrick, 1988).
Cherry trees become relatively less productive as they age because of internal shading and declining tree vigour (Looney *et al.*, 1996). Training systems permitting the regular

formation of new branches (and pruning part of the old ones) and a good light distribution can contribute to extend the life of the orchard.

Fruit-set is highly affected by weather during flowering. Low temperatures and rain reduce the activity of bees and therefore the pollination, affecting significantly the fruit-set, especially in self-sterile cultivars. Fruit-set is higher on trees planted closest to both the pollinating cultivar and the beehives (Roversi and Ughini, 1996). Low temperatures also negatively affect the growth rate of the pollinic tube. This can result in the end of the receptive period of the stigma before the tube reaches the egg. High temperatures, on the other hand, increase the growth rate of the pollinic tube, but reduce significantly the life span on the ovule (Thompson, 1996).

Better distribution of light produces more assimilation and a higher availability of sugars means a higher fruit-set, because fruit-set increases with source strength and decreases with sink strength (Marcelis and Heuvelink, 1999). Roversi and Ughini (1996) found that higher fruit-set was observed on the periphery of the canopy. This situation could be due to higher levels of light. Excess of LAI can make the interior of the canopy too dark and negatively affect fruit-set, and therefore it can reduce the sink strength even more.

High temperatures could be also associated to fruit-drop (abortion) after successful fruit-set. In many situations the number of organs is limited by abortion rather than initiation (Marcelis *et al.*, 1998). The main determinant of fruit abortion appears to be the source/sink ratio during a short period before and after anthesis (Marcelis *et al.*, 1998; Marcelis and Heuvelink, 1999). The explanation could be that an increase in temperature produces an increase in sink strength, due to higher potential growth rate of fruits and higher demand for maintenance. Source strength is hardly affected by temperature, but rather by radiation interception and assimilation. Then, unbalances between sink/source can be observed temporally and produce fruit-drop.

Fruit-set and fruit-drop are processes also influenced by hormones (Marcelis *et al.*, 1998; Marcelis and Heuvelink, 1999). Hormonal treatments can significantly increase fruit-set, but these practice should not be applied with cultivars that naturally show high fruit-set to avoid an excessive number of fruits that could result in reduced fruit size.

6 General discussion and conclusions

As was already said in the introduction, the aim of this research was not to build a model to predict absolute values of yield, but to explain the relative differences of treatments from an ecophysiological point of view using a simulation model. For extrapolation of the results the model should be tested in different conditions, but such an extrapolation exceeded the possibilities and objectives of the present work.

The prediction by the model of the timing of the main phenological stages of sweet cherry (initiation of leaf growth, full bloom and harvest) could be suitable to have a first estimation in absence of experimental registers. But when reliable data are available for specific cultivars and locations, these data should be entered in the model to simulate fruit production, because the requirements of degree-days accumulation for different phenological stages is cultivar-specific and important variations should be expected between different plant materials.

The fact that fresh weight of individual fruits was not reduced in any case, even when considering yield on "per tree" bases indicates that the potential (optimal) production was not reached in any situation. To properly test the model, bigger variations would be needed, especially with regard to LAI and fruit density within the canopy, which are the main inputs of the model. Ystaas (1989) found that by increasing the density from 400 to 670 trees ha^{-1} annual yield increased from 4.1 to 6.2 Mg ha^{-1}. At higher densities than 670 trees ha^{-1} no further increase in yield was obtained. The same author found that different tree densities did not affect average fruit weight.

A simple mechanistic model like this can be useful to make general recommendations (e.g. optimal LAI according to expected fruit-set) for optimal orchard designs and to have rough estimations of potential production in different areas. The classical definition of potential production is "the situation when the crop is amply supplied with water and nutrients and is free of weeds, pests and diseases (Lövenstein *et al.*, 1995)". However, in sweet cherry also the size of the reproductive sink strength should be taken into account, because there are several factors affecting it. When estimating potential fruit production for a location, a high (but realistic) number of fruits per m^2 LA must be included, because this situation will be observed with optimal conditions for blooming, fruit-set and fruit survival, but such as conditions are not explicity considered in the model.

The general hypothesis that differences in yield can be mainly explained by differences in light interception could not be proven, because variations in light interception were relatively low between treatments and fruit production was not source limited, but reproductive sink limited. Source strength could have an indirect effect on dry matter partitioning through effects on the number of fruits per plant (Marcelis and Heuvelink, 1999), since source/sink ratio may affect fruit-set and fruit-drop (Marcelis *et al.*, 1998).

Results of the experiment and simulations using a high number of fruit per m^2 LA showed that the potential production was much higher than the actual one and significant fruit yield increments could be achieved without detrimental effects in fresh weight of individual fruits. The main effort should be focused on increasing the differentiation of flower buds and fruit-set. Practices promoting excess of vigour should be avoided (e.g. excess of fertilisation and severe pruning). The quantity and distribution of beehives must be considered. The design of the orchard should take into account the minimal proportion of pollinating cultivar trees, their spatial distribution in the orchard, their pollen compatibility with the commercial cultivars and their blooming period. Frost-control systems must be considered in areas with risk of frost in early spring. Hormone

treatments could be a complementary technology to increase fruit-set, but its effect on fruit quality should be further evaluated.

In the conditions of the experiment, a leaf area index between 4 and 5, and about 40 fruits per m^2 LA at harvest seem to be good targets to maximise production without significant detrimental effects on fresh weight of individual fruits.

References

Anderson J. L., E. A. Richardson and C. D. Kesner. 1986. Validation of chill unit and flower bud phenology models for "Montmorency' sour cherry. Acta Hortic. 184: 71-78.

Bargoni G. 1996. Sweet cherry scions: characteristics of the principal commercial cultivars, breeding objectives and methods. In: Webster A. D. and N. E. Looney (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 73-112.

Bartelink H. H. 1998. Radiation interception by forest trees: a simulation study on effects of stand density and foliage clustering on absorption and transmission. Ecological modelling. 105: 213-225.

Bartelink H. H. 1998. Simulation of growth and competition in mixed stands of Douglas-fir and beech. Ph. D. Thesis. Wageningen Agricultural University. 222 pp.

Biggs A. R. 1986. Prediction of lignin and suberin deposition in boundary zone tissue of wounded tree bark using accumulated degree-days. J. Amer. Soc. Hort. Sci. 111(5): 757-760.

Bouman B. A. M., H. van Keulen, H. H. van Laar and R. Rabbinge. 1996. The 'School of de Wit' crop growth simulation models: a pedigree and historical overview. Agricultural Systems. 52 (2/3): 171-198.

Caldiz D. O. and P. C. Struik. 1999. Survey of potato production and possible yield constraints in Argentina. Potato Research. 42 (1): 51-71.

Couvillon G. and A. Erez. 1985. Influence of prolonged exposure to chilling temperatures on bud break and heat requirement for bloom of several fruit species. J. Amer. Soc. Hort. Sci. 110 (1): 47-50.

Daniells J. W. 1986. Measurement of solar radiation interception by tree crops. Acta Hortic. 175: 255.

DeJong T. M. 1983. CO_2 assimilation characteristics of five *Prunus* tree fruit species. J. Amer. Soc. Hort. Sci. 108 (2): 303-307.

DeJong T. M. and J. Goudriaan. 1989. Modelling peach fruit growth and carbohydrate requirements: re-evaluation of the double-sigmoid growth pattern. J. Amer. Soc. Hort. Sci. 114 (5): 800-804.

De Wit, C. T. 1999. Philosophy and terminology. In: Leffelaar P. A. (Ed.). 1999. On systems analysis and simulation of ecological processes – with examples in CSMP, FST and FORTRAN. Second Edition. Kluwer Academic Publishers. Dordrecht, The Netherlands. pp 3-9.

Eisensmith S. P., A. L. Jones and J. A. Flore. 1980. Predicting leaf emergence of 'Montmorency' sour cherry form degree-day accumulation. J. Amer. Soc. Hort. Sci. 105 (1): 75-78.

Facteau T. J., N. E Chestnut. and K. E. Rowe. 1983. Relationship between fruit weight, firmness, and leaf/fruit ratio in Lambert and Bing sweet cherries. Can. J. Plant Sci. 63: 763-765.

Fallahi E., T. L. Righetti and E. L. Proebsting. 1993. Pruning and nitrogen effects on elemental partitioning and fruit maturity in 'Bing' sweet cherry. Journal of Plant Nutrition. 16(5): 753-763.

Farré I., M. van Oijen., P. A. Leffelaar and J. M. Faci. 2000. Analysis of maize growth for different irrigation strategies in northeastern Spain. European Journal of Agronomy. 12 (3-4): 225-238.

Felker F. C. and H. A. Robitaille. 1985. Chilling accumulation and rest of sour cherry flower buds. J. Amer. Soc. Hort. Sci. 110 (2): 227-232.

Flore J. A. 1985. The effect of carbohydrate supply on sour cherry fruit size and maturity. HortScince. 20 (3): 568.

Flore J. A. and D. Layne. 1999. Photoassimilate production and distribution in cherry. HortScience. 34 (6): 1015-1019.

Flore J. A., C. D. Kesner. and A. D. Webster. 1996. Tree canopy management and the orchard environment: principles and practices of pruning and training. In: Webster A. D. and N. E. Looney (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 259-277.

Goodfruit. 1998. www.goodfruit.com/archive/May15-98/special8.html

Goudriaan J. and H. van Laar. 1994. Modelling potential crop growth processes. Textbook with exercises. Klewer Academic Publishers. Dordrecht, The Netherlands. 237 pp.

Grossman Y. L. and T. M. DeJong. 1994. PEACH: A simulation model of reproductive and vegetative growth in peach trees. Tree Physiology. 14: 329-345.

Habekotté B. 1997. Evaluation of seed yield determining factors of winter oilseed rape (*Brassica napus* L.) by means of crop growth modelling. Field Crops Research. 54 (2-3): 137-151.

Hanson E. J. and E. L. Proebsting. 1996. Cherry nutrient requirements and water relations. In: Webster A. D. and N. E. Looney. (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 243-257.

Hrotkó K., G. Simon and L. Magyar. 1998. Training of slender spindle trees for sweet cherry orchards. Acta Hortic. 468: 465-470.

Iezzoni A. F. 1985. Genetic differences for spring floral bud development among sour cherry cultivars. Acta Hortic. 169: 123-126.

Jacyna T. 1992. A concept of high-density planting for sweet cherries. Acta Hortic. 322: 325-334.

Kappel F. 1991. Partitioning of above-ground dry matter in 'Lambert' sweet cherry trees with or without fruit. J. Amer. Soc. Hort. Sci. 116 (2): 201-205.

Kappes E. M. and J. A. Flore. 1984. Assimilate export from 'Montmorency' sour cherry (*Prunus cerasus* L.) leaves. HortSciences. 19 (3): 583-584.

Kappes E. M. and J. A. Flore. 1985. The relationship between fruit growth, and fruit photosynthesis, fruit respiration and carbohydrate accumulation for 'Montmorency' sour cherry. HortScience. 20 (3): 568.

Kappes E. M. and J. A. Flore. 1986. Carbohydrate balance models for 'Montmorency' sour cherry leaves, shoots and fruits during development. Acta Hortic. 184: 123-127.

Keller J. D. and W. H. Loescher. 1989. Non-structural carbohydrate partitioning in perennial parts of sweet cherry. J. Amer. Soc. Hort. Sci. 114 (6): 969-975.

Kramer K. Phenology and growth of European trees in relation to climate change. Ph.D. Thesis. Wageningen Agricultural University. 210 pp.

Lang G. A. and D. R. Ophardt. 2000. Intensive crop regulation strategies in sweet cherries. Acta Hortic. 514: 227-233.

Lappi J. and P. Stenberg. 1998. Join effect of angular distribution of radiation and spatial pattern of trees on radiation interception. Ecological Modelling. 112: 45-51.

Leffelaar P. A. 1999. Numerical integration and error analysis. In: Leffelaar P. A. (Ed.). 1999. On systems analysis and simulation of ecological processes – with examples in CSMP, FST and FORTRAN. Second Edition. Klewer Academic Publishers. Dordrecht, The Netherlands. pp 59-67.

Loescher W. H., T. Roper, and J. Keller. 1985. Carbohydrate partitioning in sweet cherries. Proceedings annual meeting Washington State Horticultural Association. 81: 240-248.

Longstroth M. and R. L. Perry. 1996. Selecting the orchard site, orchard planning and establishment. In: Webster A. D. and N. E. Looney. (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 203-221.

Looney N. E., A. D. Webster and E. M. Kupferman. 1996. Harvest and handling sweet cherries for the fresh market. In: Webster A. D. and N. E. Looney. 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge. pp. 411-441.

Lövenstein H., E. Lantinga., R. Rabinge and H. van Keulen. 1995. Principles of production ecology. Text for course F300-001. Plant Sciences. Wageningen University. 121 p.

Mahmood K., J. G. Carew, P. Hadley and N. H. Battey. 2000. Chill unit models for the sweet cherry cvs Stella, Sunburst and Summit. Journal of Horticultural Sciences & Biotechnology. 75 (5): 602-606.

Marcelis L. F. M. and E. Heuvelink. 1999. Modelling fruit set, fruit growth and dry matter partitioning. Acta Hortic. 499: 39-49.

Marcelis L. F. M., E. Heuvelink and J. Goudriaan. 1998. Modelling biomass production and yield of horticultural crops: a review. Scientia Horticulturae 74: 83-111.

Meland M. 1982. Chemical composition of soil, leaves and fruits in samples from sweet cherry orchards in Ullensvang, Western Norway. Scientific reports of the Agricultural University of Norway. 61: 1-15.

Meland M. 1998. Yield and fruit quality of 'Van' sweet cherry in four high density production systems over seven years. Acta Hortic. 468: 425-432.

Meland M. and O. Hovland. 1996. The performance of 'Van' sweet cherry in four high density management systems in Norway. Acta Hortic. 410: 283-286.

Norvell D. and J. Moore. 1982. An evaluation of chilling models for estimating rest requirements of Highbush blueberries (*Vaccinium corymbosoum* L.). J. Amer. Soc. Hort. Sci. 107: 46 - 54

Parnia C., G. Dumitrescu, C. Rosca and G. Prahoveanu. 1986. High-density and very high density sweet and sour cherry culture in Romania. Acta Hortic. 160: 167-176.

Patrick J. W. 1988. Assimilate partitioning in relation to crop productivity. HortScience. 23 (1): 33-40.

Proebsting E. L. and H. H Mills. 1981. Effect of season and crop load on maturity characteristics of 'Bing' cherry. J. Amer. Soc. Hort. Sci. 106 (2): 144-146.

Ranney T., N. Bassuk and T. Whitlow. 1991. Influence of rootstock, scion, and water deficits on growth of 'Colt' and 'Meteor' cherry trees. HortScience. 26 (9): 1204-1207.

Roper T. R. and R. Kennedy. 1986. Photosynthesis characteristics during leaf development in 'Bing' sweet cherry. J. Amer. Soc. Hort. Sci. 111 (6): 938-941.

Roper T. R, J. D. Keller, W. H. Loescher and C. R. Rom. 1988. Photosynthesis and carbohydrate partitioning in sweet cherry: fruiting effects. Physiologia Plantarum. 72: 42-47.

Roper T. R. and W. H. Loescher. 1987. Relationships between leaf area per fruit and fruit quality in 'Bing' sweet cherry. HortScience. 22 (6): 1273-1275.

Roversi A. and V. Ughini. 1996. Fruit set in sweet cherry as affected by orchard design and tree structure. Acta Hortic. 410: 435-441.

Sams C. E. and J. A. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107 (2): 339-344.

Sams C. E. and J. A. Flore. 1983. Net photosynthetic rate of sour cherry (*Prunus cerasus* L. 'Montmorency') during the growing season with particular reference to fruiting. Photosynthesis Research. 4: 307-316.

Sansavini S. and S. Lugli. 1998. Performance of V-trained cherry orchard with new dwarf rootstocks. Acta Hortic. 468: 265-277.

Seeley S. D., J. LaMar Anderson, J. W. Frisby and M. G. Weeks. 1996. Temperature characteristics of anthesis phenology of deciduous trees. Acta Hortic. 416: 53-63.

Seif S. and W. Gruppe. 1985. Chilling requirements of sweet cherries (*Prunus avium*) and interespecific cherry hybrids (*Prunus* x ssp.). Acta Hortic. 169: 289-294.

Sekse L. 1988. Respiration of plum (*Prunus domestica* L.) and sweet cherry (*P. avium* L.) fruits during growth and ripening. Acta Agric. Scand. 38: 317-320.

Smit A. B. and P. C. Struik. 1995. The first step towards a decision-support system for sugar-beet growing: selection of a basic growth model. Journal of Agronomy and Crop Sciences. 175 (4): 213-220.

Tadeusz J. 1992. A concept of high-density planting for sweet cherries. Acta Hortic. 322: 325-334.

Thompson M. 1996. Flowering, pollination and fruit set. In: Webster A. D. and N. E. Looney (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 223-241.

Tukey H. B. 1942. Time interval between full bloom and fruit maturity for several varieties of apples, pears, peaches and cherries. Proc. Amer. Soc. Hort. Sci. 40: 133-140.

Van der Werf A., G. van der Berg, H. Ravenstein, H. Lambers and R. Eising. 1992. Protein turnover: a significant component of maintenance respiration in roots? In: Lambers H. and Van der Plas L. (Eds.). Molecular, biochemical and physiological aspects of plant respiration. SPB Academic Publishing *bv*. The Hague, The Netherlands. pp. 483-494.

Vestrheim S. 1998. Flowering in cherries as affected by pre-boom temperatures. Acta Hortic. 468: 551-555.

Wagenmakers P. 1994. Light relations in orchard systems. Ph.D. Thesis. Wageningen Agricultural University. 151 pp.

Webster A. D. 1998. Strategies for controlling the size of sweet cherry trees. Acta Hortic. 468: 229-240.

Webster A. D. and N. E. Looney. 1996. World distribution of sweet and sour cherry production: national statistics. In: Webster A.. D. and N. E. Looney (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 25-69.

Webster A. D. and H. Schmidt. 1996. Rootstocks for sweet and sour cherries. In: Webster A. D. and N. E. Looney (Eds.) 1996. Cherries. Crop physiology, production and uses. CAB International. Cambridge, UK. pp. 127-163.

Wertheim S. 1976. Bloei, bestuiving, bevruchting en vruchtzetting. In: Tromp J., H. Jonkers and S. Wertheim (Eds.) 1976. Grondslagen van de fruitteelt: fysiologie van vruchtboom. Staatsuitgeverij. ''s-Gravenhage. pp. 184-221.

Ystaas J. 1989. The influence of tree density on the tree size, yield and fruit quality of 'Van' sweet cherries. Acta Hortic. 243: 327-330.

Appendix 1. Experimental layout

N ↑

Wind break			
Guard row	Regina[2]	Karina	Guard row
X[1]	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	R 60 IV	K 90 IV	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	K 90 V	X
X	X	X	X
X	R 60 II	X	X
X	X	X	X
X	X	K 90 VI	X
X	X	X	X
X	X	X	X
X	X	K 90 III	X
X	X	X	X
X	R 120 III	X	X
X	X	X	X
X	X	X	X
X	R 120 I	X	X
X	X	K 150 IV	X
X	X	K 150 V	X
X	X	K 150 III	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	R 120 VI	X	X
X	X	X	X
X	X	X	X
X	R 120 IV [h]	X	X
X	X	X	X

X	R 120 II [h]	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	R 120 V	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	R 60 V	X	X
X	X	X	X
X	X	K 90 II [h]	X
X	X	X	X
X	X	X	X
X	R 60 I	K 90 I [h]	X
X	X	X	X
X	X	X	X
X	X	K 150 VI	X
X	R 60 VI [h]	K 150 II [h]	X
X	X	K 150 I [h]	X
X	X	X	X
X	X	X	X
X	R 60 III [h]	X	X
X	X	K 60 III	X
X	X	X	X
X	X	X	X
X	X	K 60 IV	X
X	X	X	X
X	R 150 III	X	X
X	R 150 IV	K 60 II	X
X	R 150 I	X	X
X	R 150 II [h]	K 60 V	X
X	R 150 V [h]	X	X
X	X	X	X
X	X	K 60 I [h]	X
X	R 90 IV	X	X
X	X	X	X
X	X	K 60 VI [h]	X
X	R 90 V	X	X
X	X	X	X
X	X	X	X
X	R 90 III	X	X
X	X	X	X
X	X	X	X
X	X	K 120 III	X
X	X	X	X
X	R 90 II	K 120 IV	X
X	X	X	X
X	X	X	X

X	X	K 120 V	X
X	X	X	X
X	R 90 VI [h]	X	X
X	X	K 120 I [h]	X
X	R 90 I [h]	X	X
X	X	K 120 VI [h]	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
X	X	X	X
Path road			
Wind break			

[1]Tree no measured.
[2]R: Regina; K: Karina; 60, 90, 120 and 150 are cm between trees in the row. Roman numbers are the replications.
[h]Tree in which leaves were harvested .

← 3.25 m → ← 3.25 m → ← 3.25 m →

Appendix 2. Climatic conditions during the experiment
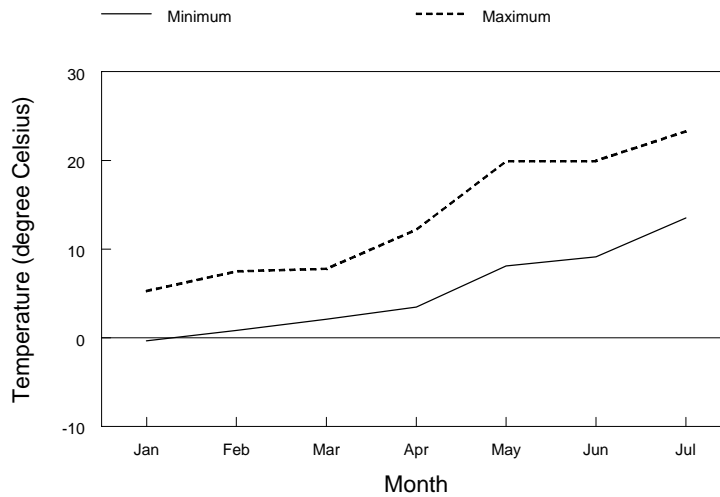
Figure A.2.1. Maximum and minimum temperature during 2001 (until harvest in July) recorded in Haarweg Station, Department of Meteorology, Wageningen University.
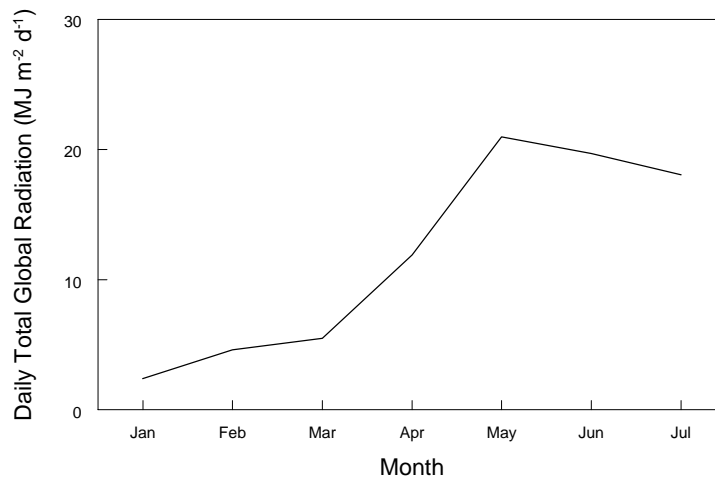
Figure A.2.2 Daily Global Total Radiation during 2001 (until harvest in July) recorded in Haarweg Station, Department of Meteorology, Wageningen University.
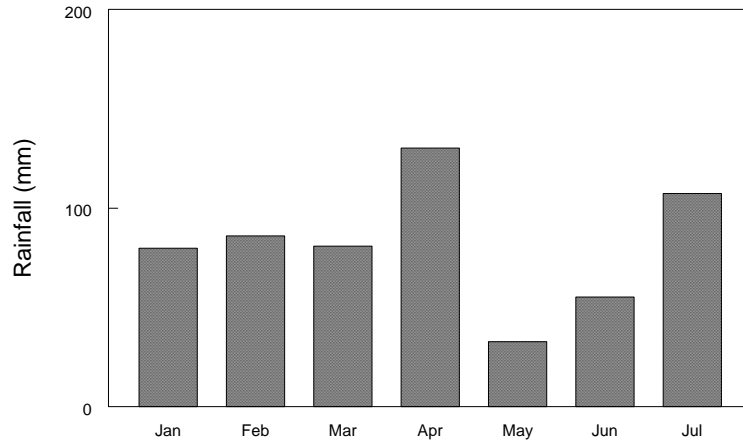
Figure A.2.3 Rainfall during 2001 (until harvest in July) recorded in the research station of Praktijkonderzoek Plant & Omgeving (FPO).
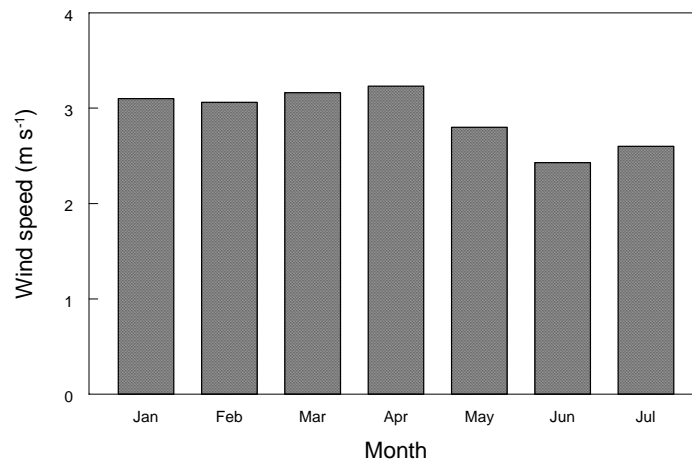
Figure A.2.4 Wind speed during 2001 (until harvest in July) recorded in Haarweg Station, Department of Meteorology, Wageningen University.

Appendix 3. Original data of variable with 6 replicates

a) SLA and percentage of PAR reaching ground

Cultivar	Density	Date	Replic.	SLA $(m^2 \ kg^{-1} \ dm \ leaf)$	%PAR ground
Karina	5128	May 18	I	25.6	37.6
Karina	5128	May 18	II	24	36.9
Karina	5128	May 18	III	24.8	43.5
Karina	5128	May 18	IV	24.2	39.5
Karina	5128	May 18	V	25.3	40.9
Karina	5128	May 18	VI	24.5	38.4
Karina	5128	Jun 6	I	18.8	21.1
Karina	5128	Jun 6	II	19	25.1
Karina	5128	Jun 6	III	19	28.1
Karina	5128	Jun 6	IV	19.1	24.6
Karina	5128	Jun 6	V	20.6	29.2
Karina	5128	Jun 6	VI	19	23.3
Karina	5128	Jun 25	I	17.1	17.1
Karina	5128	Jun 25	II	16.8	19.6
Karina	5128	Jun 25	III	17.6	21.2
Karina	5128	Jun 25	IV	17.1	18.3
Karina	5128	Jun 25	V	19.9	25.1
Karina	5128	Jun 25	VI	16.2	16.6
Karina	5128	Jul 17	I	17.3	13.2
Karina	5128	Jul 17	II	19.9	13.9
Karina	5128	Jul 17	III	18.7	16.1
Karina	5128	Jul 17	IV	18.7	13.5
Karina	5128	Jul 17	V	21	16.8
Karina	5128	Jul 17	VI	18.1	14.6
Karina	5128	Aug 3	I	*	*
Karina	5128	Aug 3	II	*	11.7
Karina	5128	Aug 3	III	*	15.4
Karina	5128	Aug 3	IV	*	9.6
Karina	5128	Aug 3	V	*	*
Karina	5128	Aug 3	VI	*	*
Karina	3419	May 18	I	25.3	33.5
Karina	3419	May 18	II	24.9	33.3
Karina	3419	May 18	III	25.7	39.5
Karina	3419	May 18	IV	24	38.1
Karina	3419	May 18	V	23.5	31.2
Karina	3419	May 18	VI	24.1	35.8
Karina	3419	Jun 6	I	19.4	20.8
Karina	3419	Jun 6	II	18.8	20.8
Karina	3419	Jun 6	III	18.2	28.8
Karina	3419	Jun 6	IV	18.4	28.4
Karina	3419	Jun 6	V	17.8	24.6
Karina	3419	Jun 6	VI	20.2	24.1
Karina	3419	Jun 25	I	18.1	15.6
Karina	3419	Jun 25	II	17.7	19.7

Karina	3419	Jun 25	III	16.6	24.6
Karina	3419	Jun 25	IV	16.5	21.7
Karina	3419	Jun 25	V	16.1	23.9
Karina	3419	Jun 25	VI	17.6	22.2
Karina	3419	Jul 17	I	18.8	10.2
Karina	3419	Jul 17	II	17.4	15
Karina	3419	Jul 17	III	19	24.4
Karina	3419	Jul 17	IV	19.5	24.1
Karina	3419	Jul 17	V	17.8	19.4
Karina	3419	Jul 17	VI	17.9	18.4
Karina	3419	Aug 3	I	*	*
Karina	3419	Aug 3	II	*	*
Karina	3419	Aug 3	III	*	24.6
Karina	3419	Aug 3	IV	*	21.3
Karina	3419	Aug 3	V	*	19
Karina	3419	Aug 3	VI	*	19.2
Karina	2564	May 18	I	25.7	43.1
Karina	2564	May 18	II	23.9	44.8
Karina	2564	May 18	III	26	41.7
Karina	2564	May 18	IV	24.7	45.4
Karina	2564	May 18	V	24.1	42
Karina	2564	May 18	VI	24.8	44.3
Karina	2564	Jun 6	I	17.5	28.1
Karina	2564	Jun 6	II	19.5	32
Karina	2564	Jun 6	III	18.2	27.5
Karina	2564	Jun 6	IV	18.6	32.5
Karina	2564	Jun 6	V	17.7	32.8
Karina	2564	Jun 6	VI	19.1	31.3
Karina	2564	Jun 25	I	16.9	24
Karina	2564	Jun 25	II	16.5	24.4
Karina	2564	Jun 25	III	17.2	21.6
Karina	2564	Jun 25	IV	16.4	22
Karina	2564	Jun 25	V	16.9	26.2
Karina	2564	Jun 25	VI	16.7	24.9
Karina	2564	Jul 17	I	17.7	15.1
Karina	2564	Jul 17	II	17.4	21.6
Karina	2564	Jul 17	III	18.2	16.8
Karina	2564	Jul 17	IV	15	22.2
Karina	2564	Jul 17	V	17	19.6
Karina	2564	Jul 17	VI	17.4	13.8
Karina	2564	Aug 3	I	*	*
Karina	2564	Aug 3	II	*	21.6
Karina	2564	Aug 3	III	*	16.1
Karina	2564	Aug 3	IV	*	*
Karina	2564	Aug 3	V	*	21.3
Karina	2564	Aug 3	VI	*	20.4
Karina	2051	May 18	I	24.6	35.9
Karina	2051	May 18	II	23.4	39.4
Karina	2051	May 18	III	22.6	39.5
Karina	2051	May 18	IV	23.7	42.4
Karina	2051	May 18	V	24.5	39.6
Karina	2051	May 18	VI	24.2	38.5

Karina	2051	Jun 6	I	18.6	24.4
Karina	2051	Jun 6	II	18.2	27
Karina	2051	Jun 6	III	18	31.4
Karina	2051	Jun 6	IV	18.1	31.8
Karina	2051	Jun 6	V	19.2	28.5
Karina	2051	Jun 6	VI	18.3	22.2
Karina	2051	Jun 25	I	17.1	19
Karina	2051	Jun 25	II	16.7	18.7
Karina	2051	Jun 25	III	16.4	28
Karina	2051	Jun 25	IV	16.4	29.5
Karina	2051	Jun 25	V	17.5	26.1
Karina	2051	Jun 25	VI	16.5	18.8
Karina	2051	Jul 17	I	18.3	14
Karina	2051	Jul 17	II	18.3	13.7
Karina	2051	Jul 17	III	17.9	23.1
Karina	2051	Jul 17	IV	17.6	26.8
Karina	2051	Jul 17	V	17.5	24.4
Karina	2051	Jul 17	VI	17.8	13.4
Karina	2051	Aug 3	I	*	*
Karina	2051	Aug 3	II	*	*
Karina	2051	Aug 3	III	*	21.4
Karina	2051	Aug 3	IV	*	24.9
Karina	2051	Aug 3	V	*	22
Karina	2051	Aug 3	VI	*	*
Regina	5128	May 18	I	25.2	33.9
Regina	5128	May 18	II	23.4	37.5
Regina	5128	May 18	III	25.5	37.4
Regina	5128	May 18	IV	24.3	43.8
Regina	5128	May 18	V	25.2	31.3
Regina	5128	May 18	VI	24.9	32
Regina	5128	Jun 6	I	18.4	19.9
Regina	5128	Jun 6	II	16.4	18.4
Regina	5128	Jun 6	III	17.8	20.6
Regina	5128	Jun 6	IV	18.1	31.9
Regina	5128	Jun 6	V	18.9	17
Regina	5128	Jun 6	VI	17.6	17.3
Regina	5128	Jun 25	I	17.6	18.8
Regina	5128	Jun 25	II	17.7	20.8
Regina	5128	Jun 25	III	15.9	21.5
Regina	5128	Jun 25	IV	16.2	30.2
Regina	5128	Jun 25	V	17.8	16.2
Regina	5128	Jun 25	VI	16.3	14.7
Regina	5128	Jul 17	I	18.8	13.3
Regina	5128	Jul 17	II	17.5	16.1
Regina	5128	Jul 17	III	17.2	16.5
Regina	5128	Jul 17	IV	18.2	25.7
Regina	5128	Jul 17	V	19.3	13.3
Regina	5128	Jul 17	VI	16.5	10.6
Regina	5128	Aug 3	I	*	14.1
Regina	5128	Aug 3	II	*	14.1
Regina	5128	Aug 3	III	*	*
Regina	5128	Aug 3	IV	*	*

Regina	5128	Aug 3	V	*	12.3
Regina	5128	Aug 3	VI	*	*
Regina	3419	May 18	I	14.4	37.5
Regina	3419	May 18	II	25.3	39.2
Regina	3419	May 18	III	24.8	41.5
Regina	3419	May 18	IV	22.9	36.6
Regina	3419	May 18	V	23.1	34.5
Regina	3419	May 18	VI	24	31.5
Regina	3419	Jun 6	I	17.1	24
Regina	3419	Jun 6	II	16.8	25.4
Regina	3419	Jun 6	III	16.9	24.4
Regina	3419	Jun 6	IV	17.9	20.2
Regina	3419	Jun 6	V	18.4	20.2
Regina	3419	Jun 6	VI	17.6	19.3
Regina	3419	Jun 25	I	17.1	22
Regina	3419	Jun 25	II	15.2	23.8
Regina	3419	Jun 25	III	16.5	22.5
Regina	3419	Jun 25	IV	17.5	17.9
Regina	3419	Jun 25	V	16.7	18.9
Regina	3419	Jun 25	VI	16.2	16.7
Regina	3419	Jul 17	I	16.9	20.5
Regina	3419	Jul 17	II	16.7	24.5
Regina	3419	Jul 17	III	17.2	20.2
Regina	3419	Jul 17	IV	17.8	16.2
Regina	3419	Jul 17	V	17.8	16.6
Regina	3419	Jul 17	VI	17.1	16.7
Regina	3419	Aug 3	I	*	*
Regina	3419	Aug 3	II	*	23
Regina	3419	Aug 3	III	*	19.6
Regina	3419	Aug 3	IV	*	15.2
Regina	3419	Aug 3	V	*	14.1
Regina	3419	Aug 3	VI	*	*
Regina	2564	May 18	I	24.3	42.1
Regina	2564	May 18	II	24.5	47
Regina	2564	May 18	III	23.4	38.5
Regina	2564	May 18	IV	22.9	42.1
Regina	2564	May 18	V	24.8	42.5
Regina	2564	May 18	VI	23.8	40.5
Regina	2564	Jun 6	I	16.6	25.2
Regina	2564	Jun 6	II	16.5	32.1
Regina	2564	Jun 6	III	17	21.6
Regina	2564	Jun 6	IV	16.6	26.1
Regina	2564	Jun 6	V	18.5	24.8
Regina	2564	Jun 6	VI	18.5	20.7
Regina	2564	Jun 25	I	15.3	22.1
Regina	2564	Jun 25	II	15.8	24.6
Regina	2564	Jun 25	III	15.4	23.1
Regina	2564	Jun 25	IV	15.5	21.9
Regina	2564	Jun 25	V	17.8	22.8
Regina	2564	Jun 25	VI	17.3	17.1
Regina	2564	Jul 17	I	17.4	21.5
Regina	2564	Jul 17	II	*	23

Regina	2564	Jul 17	III	16.2	20.2
Regina	2564	Jul 17	IV	19.9	18.5
Regina	2564	Jul 17	V	16.8	20.1
Regina	2564	Jul 17	VI	18.2	14
Regina	2564	Aug 3	I	*	18.3
Regina	2564	Aug 3	II	*	*
Regina	2564	Aug 3	III	*	18
Regina	2564	Aug 3	IV	*	*
Regina	2564	Aug 3	V	*	18.7
Regina	2564	Aug 3	VI	*	12.9
Regina	2051	May 18	I	23.4	37.3
Regina	2051	May 18	II	23.9	37.6
Regina	2051	May 18	III	25.3	34.4
Regina	2051	May 18	IV	23	39.9
Regina	2051	May 18	V	23.7	38.2
Regina	2051	May 18	VI	*	*
Regina	2051	Jun 6	I	16.9	20.7
Regina	2051	Jun 6	II	17	24.6
Regina	2051	Jun 6	III	17.6	25.1
Regina	2051	Jun 6	IV	17.3	23
Regina	2051	Jun 6	V	16.6	21.1
Regina	2051	Jun 6	VI	*	*
Regina	2051	Jun 25	I	16	17.9
Regina	2051	Jun 25	II	17.2	19.4
Regina	2051	Jun 25	III	16	21
Regina	2051	Jun 25	IV	15.8	20.8
Regina	2051	Jun 25	V	16.7	17.9
Regina	2051	Jun 25	VI	*	*
Regina	2051	Jul 17	I	16.6	15.8
Regina	2051	Jul 17	II	17.4	15.1
Regina	2051	Jul 17	III	17.8	17.2
Regina	2051	Jul 17	IV	17	15.6
Regina	2051	Jul 17	V	17.5	16.2
Regina	2051	Jul 17	VI	*	*
Regina	2051	Aug 3	I	*	*
Regina	2051	Aug 3	II	*	*
Regina	2051	Aug 3	III	*	16.2
Regina	2051	Aug 3	IV	*	17.3
Regina	2051	Aug 3	V	*	*
Regina	2051	Aug 3	VI	*	*

b) Fruit production per tree, fruit production per ha and fresh weight of individual fruits

Cultivar	Density	Replic.	kg fruit tree^{-1}	kg fruit ha^{-1}	g fruit^{-1}
Karina	5128	I	2.3	11601	7.5
Karina	5128	II	1.6	8064	8.6
Karina	5128	III	0.4	2193	8.5
Karina	5128	IV	1.4	6933	8.7
Karina	5128	V	0.7	3466	8.8
Karina	5128	VI	1.3	6720	8.7
Karina	3419	I	2.8	9672	7.7
Karina	3419	II	1	3255	10.3
Karina	3419	III	1.3	4325	9.3
Karina	3419	IV	4.4	15067	8.1
Karina	3419	V	0.9	3069	8.4
Karina	3419	VI	1.7	5813	8.8
Karina	2564	I	2.5	6517	10.6
Karina	2564	II	2.6	6581	9.5
Karina	2564	III	2.6	6614	8.1
Karina	2564	IV	2.5	6452	8.2
Karina	2564	V	3.1	7943	7.5
Karina	2564	VI	3.2	8202	8.5
Karina	2051	I	7.7	15863	10.4
Karina	2051	II	1.7	3404	10.4
Karina	2051	III	7.6	15520	9.4
Karina	2051	IV	6.7	13709	9
Karina	2051	V	3.5	7276	9
Karina	2051	VI	1.5	2998	11.2
Regina	5128	I	0.7	3582	10.5
Regina	5128	II	1.8	9213	9.4
Regina	5128	III	1.19	6127	10.5
Regina	5128	IV	2.71	13897	10.2
Regina	5128	V	1.46	7495	10.6
Regina	5128	VI	2.36	12101	10.3
Regina	3419	I	1.24	4248	10.5
Regina	3419	II	3.1	10606	10.9
Regina	3419	III	3.97	13572	10.2
Regina	3419	IV	1.65	5658	12
Regina	3419	V	4.02	13727	10.5
Regina	3419	VI	2.18	7448	12.2
Regina	2564	I	2.51	6435	10.5
Regina	2564	II	1.14	2929	12.5
Regina	2564	III	3.65	9368	9.6
Regina	2564	IV	2.58	6613	10.1
Regina	2564	V	1.38	3534	10.2
Regina	2564	VI	1.47	3781	9.7
Regina	2051	I	3.8	7796	11.1
Regina	2051	II	3.79	7775	10.9
Regina	2051	III	4.13	8470	10.1
Regina	2051	IV	3.29	6743	9.6
Regina	2051	V	5.61	11516	9.9
Regina	2051	VI	*	*	*

Appendix 4. Original data of variables with 2 replicates

LAI, number of fruits per m^{-2} LA and leaf dry matter ha^{-1}

Cultivar	Density	Replic.	LAI	# fruit m^{-2} LA	leaf dm ha^{-1}
Karina	5128	I	7	22.1	4057
Karina	5128	II	3.5	22.4	1912
Karina	3419	I	4.9	24.3	2750
Karina	3419	II	4.2	6.5	2803
Karina	2564	I	4.3	14.3	2430
Karina	2564	II	5.4	18.0	3101
Karina	2051	I	5.7	26.9	3109
Karina	2051	II	4	6.3	2827
Regina	5128	I	4.1	14.3	3202
Regina	5128	II	6	19.8	4046
Regina	3419	I	2.2	18.5	1737
Regina	3419	II	4.3	14.1	3042
Regina	2564	I	3.6	6.5	2601
Regina	2564	II	3.5	18.7	2505
Regina	2051	I	3.1	23.1	2326
Regina	2051	II	3.4	34.0	2131

Appendix 5. Original data of variables with 3 replicates

a) Carbon and Nitrogen content. Analyses were done in the 'Centraal Laboratorium' (Department of Soil Quality, Wageningen UR).

Cultivar	Organ	Date	Replic	C (%)	N (%)	C/N
Karina	Leaf	Pithard	I	46.8	2.61	18
Karina	Leaf	Pithard	II	49	2.68	18
Karina	Leaf	Pithard	III	47.4	2.7	18
Karina	Leaf	Harvest	I	45.5	2.15	21
Karina	Leaf	Harvest	II	46.8	2.25	21
Karina	Leaf	Harvest	III	47.1	2.28	21
Karina	Ston	Pithard	I	45.4	0.87	52
Karina	Ston	Pithard	II	46.5	0.85	55
Karina	Ston	Pithard	III	49.1	0.86	57
Karina	Ston	Harvest	I	55.6	0.67	83
Karina	Ston	Harvest	II	51.4	0.64	80
Karina	Ston	Harvest	III	49	0.68	72
Karina	Flesh	Pithard	I	38.9	1.91	20
Karina	Flesh	Pithard	II	43.5	1.93	23
Karina	Flesh	Pithard	III	42.6	1.9	22
Karina	Flesh	Harvest	I	51.6	0.98	53
Karina	Flesh	Harvest	II	51.8	0.93	56
Karina	Flesh	Harvest	III	53.7	0.92	58
Regina	Leaf	Pithard	I	46.9	2.57	18
Regina	Leaf	Pithard	II	49.8	2.36	21
Regina	Leaf	Pithard	III	45.5	2.57	18
Regina	Leaf	Harvest	I	46.1	2.61	18
Regina	Leaf	Harvest	II	49.4	2.63	19
Regina	Leaf	Harvest	III	49.3	2.63	19
Regina	Ston	Pithard	I	47.2	1.27	37
Regina	Ston	Pithard	II	44.8	1.7	26
Regina	Ston	Pithard	III	48.9	1.26	39
Regina	Ston	Harvest	I	50.4	0.5	101
Regina	Ston	Harvest	II	51	0.55	93
Regina	Ston	Harvest	III	44.8	0.57	79
Regina	Flesh	Pithard	I	43.5	1.77	25
Regina	Flesh	Pithard	II	38.7	1.78	22
Regina	Flesh	Pithard	III	43.5	1.77	25
Regina	Flesh	Harvest	I	52.5	0.91	58
Regina	Flesh	Harvest	II	45.6	0.86	53
Regina	Flesh	Harvest	III	45.5	0.83	55

b) Proportion of flesh in fruits (% dm flesh over dm total fruit)

Cultivar	Date	Replic.	Flesh (%)
Karina	Pit hard	I	42.7
Karina	Pit hard	II	39.8
Karina	Pit hard	III	45.3
Karina	Harvest	I	82.2
Karina	Harvest	II	78.2
Karina	Harvest	III	81.2
Regina	Pit hard	I	45.4
Regina	Pit hard	II	44.2
Regina	Pit hard	III	43.8
Regina	Harvest	I	83.3
Regina	Harvest	II	79.7
Regina	Harvest	III	79.8

Appendix 6. Dry matter content of fruits.

Cultivar	Density (trees ha^{-1})	Fresh weight (g fruit^{-1})	Dry weight (g fruit^{-1})	Dry matter content (%)
Regina	5128	10.5	1.8	16.8
Regina	3419	11.0	1.6	14.8
Regina	2564	10.7	1.8	16.5
Regina	2051	9.8	1.3	13.6
Kariana	5128	9.1	1.4	15.4
Karina	3419	8.8	1.2	13.6
Karina	2564	9.3	1.5	16.1
Karina	2051	8.8	1.3	14.8
Average	3291	9.8	1.5	15.2

Appendix 7. ANOVA for Percentage of radiation reaching ground

Variate: %PAR_ground

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Cultivar	1	227.51	227.51	18.93	<.001
Density	3	596.01	198.67	16.53	<.001
Date	4	14685.10	3671.28	305.46	<.001
Cultivar.Density	3	91.63	30.54	2.54	0.058
Cultivar.Date	4	121.06	30.27	2.52	0.043
Density.Date	12	416.77	34.73	2.89	0.001
Cultivar.Density.Date	12	121.51	10.13	0.84	0.607
Residual	175(25)	2103.27	12.02		
Total	214(25)	16812.48			

* MESSAGE: the following units have large residuals.

units 49	-8.38	s.e. 2.96
units 130	11.05	s.e. 2.96
units 136	9.83	s.e. 2.96
units 142	9.78	s.e. 2.96

***** Tables of means *****

Variate: %PAR_ground

Grand mean 24.04

Cultivar	Karina	Regina
	25.01	23.06

Density	2051	2564	3419	5128
	24.47	26.18	23.72	21.79

Date	Aug 3	Jul 17	Jun 25	Jun 6	May 18
	17.64	17.66	21.27	24.89	38.73

Cultivar	Density	2051	2564	3419	5128
Karina		26.42	27.23	24.14	22.25
Regina		22.51	25.13	23.29	21.32

Cultivar	Date	Aug 3	Jul 17	Jun 25	Jun 6	May 18
Karina		18.97	17.67	22.03	27.02	39.37
Regina		16.31	17.64	20.50	22.77	38.10

Density	Date	Aug 3	Jul 17	Jun 25	Jun 6	May 18
2051		19.79	17.61	21.38	25.23	38.35
2564		18.41	18.87	22.89	27.89	42.83
3419		19.50	18.85	20.79	23.42	36.02
5128		12.87	15.30	20.01	23.04	37.73

Cultivar	Density	Date	Aug 3	Jul 17	Jun 25	Jun 6	May 18
Karina	2051		22.77	19.23	23.35	27.55	39.22
	2564		19.85	18.18	23.85	30.70	43.55
	3419		21.03	18.58	21.28	24.58	35.23
	5128		12.23	14.68	19.65	25.23	39.47
Regina	2051		16.80	15.98	19.40	22.90	37.48
	2564		16.98	19.55	21.93	25.08	42.12
	3419		17.98	19.12	20.30	22.25	36.80
	5128		13.50	15.92	20.37	20.85	35.98

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Date Density	Cultivar
rep.	120	60	48	30
d.f.	175	175	175	175
l.s.d.	0.883	1.249	1.397	1.767

Table	Cultivar Date	Density Date	Cultivar Density Date
rep.	24	12	6
d.f.	175	175	175
l.s.d.	1.975	2.793	3.950

(Not adjusted for missing values)

***** Stratum standard errors and coefficients of variation *****

Variate: %PAR_ground

d.f.	s.e.	cv%
175	3.467	14.4

Appendix 8. ANOVA for SLA

Variate: SLA

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Cultivar	1	33.822	33.822	28.41	<.001
Date	3(1)	1604.081	534.694	449.12	<.001
Density	3	22.941	7.647	6.42	<.001
Cultivar.Date	3(1)	4.919	1.640	1.38	0.252
Cultivar.Density	3	5.030	1.677	1.41	0.243
Date.Density	9(3)	7.787	0.865	0.73	0.684
Cultivar.Date.Density	9(3)	10.951	1.217	1.02	0.425
Residual	155(45)	184.534	1.191		
Total	186(53)	1824.819			

* MESSAGE: the following units have large residuals.

units 17   2.450 s.e. 0.877
units 151   -8.017 s.e. 0.877
units 152   2.883 s.e. 0.877

***** Tables of means *****

Variate: SLA

Grand mean 19.191

Cultivar	Karina	Regina
	19.566	18.815

Date	May 18	Jun 25	Jun 6	Jul 17	Aug 3
	24.124	16.757	18.070	17.812	19.191

Density	2051	2564	3419	5128.00
	18.933	19.040	19.071	19.719

Cultivar	Date	May 18	Jun 25	Jun 6	Jul 17	Aug 3
Karina		24.504	17.021	18.721	18.092	19.494
Regina		23.744	16.493	17.420	17.532	18.888

Cultivar	Density	2051	2564	3419	5128
Karina		19.220	19.289	19.690	20.066
Regina		18.647	18.791	18.452	19.372

Date	Density	2051	2564	3419	5128
May 18		23.847	24.408	23.500	24.742
Jun 25		16.553	16.475	16.817	17.183

Jun 6		17.740	17.858	18.125	18.558
Jul 17		17.580	17.408	17.825	18.433
Aug 3		18.946	19.049	19.089	19.678

Cultivar	Date	Density	2051	2564	3419	5128
Karina	May 18		23.833	24.867	24.583	24.733
	Jun 25		16.767	16.767	17.100	17.450
	Jun 6		18.400	18.433	18.800	19.250
	Jul 17		17.900	17.117	18.400	18.950
	Aug 3		19.200	19.263	19.567	19.946
Regina	May 18		23.860	23.950	22.417	24.750
	Jun 25		16.340	16.183	16.533	16.917
	Jun 6		17.080	17.283	17.450	17.867
	Jul 17		17.260	17.700	17.250	17.917
	Aug 3		18.693	18.836	18.612	19.411

*** Least significant differences of means (5% level) ***

Table	Cultivar	Date	Density	Cultivar Date
rep.	120	48	60	24
d.f.	155	155	155	155
l.s.d.	0.2783	0.4400	0.3935	0.6222

Table	Cultivar Density	Date Density	Cultivar Date Density
rep.	30	12	6
d.f.	155	155	155
l.s.d.	0.5565	0.8799	1.2444

(Not adjusted for missing values)

***** Stratum standard errors and coefficients of variation *****

Variate: SLA

d.f.	s.e.	cv%
155	1.0911	5.7

Appendix 9. ANOVA for Yield

Variate: kg fruit ha^{-1}

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Cultivar	1	2.016E+06	2.016E+06	0.14	0.707
Density	3	5.107E+07	1.702E+07	1.21	0.317
Cultivar.Density	3	4.261E+07	1.420E+07	1.01	0.397
Residual	39(1)	5.466E+08	1.402E+07		
Total	46(1)	6.418E+08			

* MESSAGE: the following units have large residuals.

units 10   8200. s.e. 3375.

***** Tables of means *****

Variate: kg fruit ha^{-1}

Grand mean 7757.

Cultivar	Karina	Regina
	7552.	7962.

Density	2051	2564	3419	5128
	9128.	6247.	8038.	7616.

Cultivar	Density	2051	2564	3419	5128
Karina		9795.	7051.	6867.	6496.
Regina		8460.	5443.	9210.	8736.

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	24	12	6
d.f.	39	39	39
l.s.d.	2185.9	3091.4	4371.9

(Not adjusted for missing values)

***** Stratum standard errors and coefficients of variation *****

Variate: kg fruit ha^{-1}

d.f.	s.e.	cv%
39	3743.7	48.3

Appendix 10. ANOVA for kg per tree

Variate: kg fruit tree^{-1}

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Cultivar	1	0.027	0.027	0.01	0.903
Density	3	56.631	18.877	10.29	<.001
Cultivar.Density	3	4.364	1.455	0.79	0.505
Residual	39(1)	71.558	1.835		
Total	46(1)	130.464			

* MESSAGE: the following units have large residuals.

units 19	2.92	s.e. 1.22
units 20	-3.08	s.e. 1.22
units 21	2.82	s.e. 1.22
units 24	-3.28	s.e. 1.22

***** Tables of means *****

Variate: kg fruit tree^{-1}

Grand mean 2.68

Cultivar	Karina	Regina
	2.71	2.66

Density	2051	2564	3419	5128
	4.45	2.44	2.36	1.49

Cultivar Density	2051	2564	3419	5128
Karina	4.78	2.75	2.02	1.28
Regina	4.12	2.12	2.69	1.70

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	24	12	6
d.f.	39	39	39
l.s.d.	0.791	1.119	1.582

(Not adjusted for missing values)

***** Stratum standard errors and coefficients of variation *****

Variate: kg fruit tree^{-1}

d.f.	s.e.	cv%
39	1.355	50.5

Appendix 11. ANOVA for Fresh weight of individual fruits

Variate: g fruit^{-1}

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Cultivar	1	28.7061	28.7061	40.23	<.001
Density	3	4.0254	1.3418	1.88	0.149
Cultivar.Density	3	5.6747	1.8916	2.65	0.062
Residual	39(1)	27.8313	0.7136		
Total	46(1)	65.8940			

* MESSAGE: the following units have large residuals.

units 13   1.87 s.e. 0.76
units 38   2.07 s.e. 0.76

***** Tables of means *****

Variate: g fruit^{-1}

Grand mean 9.74

Cultivar	Karina	Regina
	8.97	10.51

Density	2051	2564	3419	5128
	10.11	9.58	9.91	9.36

Cultivar Density	2051	2564	3419	5128
Karina	9.90	8.73	8.77	8.47
Regina	10.32	10.43	11.05	10.25

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	24	12	6
d.f.	39	39	39
l.s.d.	0.493	0.698	0.987

(Not adjusted for missing values)

***** Stratum standard errors and coefficients of variation *****

Variate: g fruit^{-1}

d.f.	s.e.	cv%
39	0.845	8.7

Appendix 12. ANOVA for Leaf biomass (dry matter)

Variate: leaf dm ha^{-1}

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	122325.	122325.	0.26	0.625
Density	3	1444430.	481477.	1.01	0.436
Cultivar.Density	3	1028421.	342807.	0.72	0.566
Residual	8	3798101.	474763.		
Total	15	6393276.			

* MESSAGE: the following units have large residuals.

units 1   1073. s.e. 487.
units 2   -1073. s.e. 487.

***** Tables of means *****

Variate: leaf dm ha^{-1}

Grand mean 2786.

Cultivar	Karina	Regina
	2874.	2699.

Density	2051	2564	3419	5128
	2598.	2659.	2583.	3304.

Cultivar	Density	2051	2564	3419	5128
Karina		2968.	2766.	2777.	2985.
Regina		2229.	2553.	2390.	3624.

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	8	4	2
d.f.	8	8	8
l.s.d.	794.5	1123.5	1588.9

***** Stratum standard errors and coefficients of variation *****

Variate: leaf dm ha^{-1}

d.f.	s.e.	cv%
8	689.0	24.7

Appendix 13. ANOVA for LAI

Variate: LAI

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	4.840	4.840	3.10	0.116
Density	3	3.810	1.270	0.81	0.521
Cultivar.Density	3	1.140	0.380	0.24	0.864
Residual	8	12.480	1.560		
Total	15	22.270			

***** Tables of means *****

Variate: LAI

Grand mean 4.33

Cultivar	Karina	Regina
	4.87	3.77

Density	2051	2564	3419	5128
	4.05	4.20	3.90	5.15

Cultivar Density	2051	2564	3419	5128
Karina	4.85	4.85	4.55	5.25
Regina	3.25	3.55	3.25	5.05

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	8	4	2
d.f.	8	8	8
l.s.d.	1.440	2.037	2.880

***** Stratum standard errors and coefficients of variation *****

Variate: LAI

d.f.	s.e.	cv%
8	1.249	28.9

Appendix 14. ANOVA for Number of fruits per m^2 LA

Variate: # fruit m^{-2} LA

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	4.20	4.20	0.06	0.809
Density	3	165.46	55.15	0.82	0.517
Cultivar.Density	3	179.05	59.68	0.89	0.486
Residual	8	536.12	67.01		
Total	15	884.84			

***** Tables of means *****

Variate: # fruit m^{-2} LA

Grand mean 18.1

Cultivar	Karina	Regina
	17.6	18.6

Density	2051	2564	3419	5128
	22.6	14.4	15.9	19.7

Cultivar	Density	2051	2564	3419	5128
Karina		16.6	16.1	15.4	22.3
Regina		28.5	12.6	16.3	17.1

*** Least significant differences of means (5% level) ***

Table	Cultivar	Density	Cultivar Density
rep.	8	4	2
d.f.	8	8	8
l.s.d.	9.44	13.35	18.88

***** Stratum standard errors and coefficients of variation *****

Variate: # fruit m^{-2} LA

d.f.	s.e.	cv%
8	8.19	45.2

Appendix 15. ANOVA for carbon content

Variate: C_%

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	9.303	9.303	1.55	0.225
Date	1	132.634	132.634	22.07	<.001
Organ	2	44.744	22.372	3.72	0.039
Cultivar.Date	1	8.507	8.507	1.42	0.246
Cultivar.Organ	2	14.132	7.066	1.18	0.326
Date.Organ	2	110.161	55.080	9.16	0.001
Cultivar.Date.Organ	2	19.551	9.775	1.63	0.218
Residual	24	144.253	6.011		
Total	35	483.283			

* MESSAGE: the following units have large residuals.

units 34   4.63   s.e. 2.00

***** Tables of means *****

Variate: C_%

Grand mean 47.36

Cultivar	Karina	Regina
	47.87	46.86

Date	Harvest	Pithard
	49.28	45.44

Organ	Flesh	Leaf	Pit
	45.95	47.47	48.68

Cultivar	Date	Harvest	Pithard
Karina		50.28	45.47
Regina		48.29	45.42

Cultivar	Organ	Flesh	Leaf	Pit
Karina		47.02	47.10	49.50
Regina		44.88	47.83	47.85

Date	Organ	Flesh	Leaf	Pit
Harvest		50.12	47.37	50.37
Pithard		41.78	47.57	46.98

	Date	Harvest			Pithard		
Cultivar	Organ	Flesh	Leaf	Pit	Flesh	Leaf	Pit
Karina		52.37	46.47	52.00	41.67	47.73	47.00
Regina		47.87	48.27	48.73	41.90	47.40	46.97

*** Least significant differences of means (5% level) ***

Table	Cultivar	Date	Organ	Cultivar Date
rep.	18	18	12	9
d.f.	24	24	24	24
l.s.d.	1.687	1.687	2.066	2.385

Table	Cultivar Organ	Date Organ	Cultivar Date Organ
rep.	6	6	3
d.f.	24	24	24
l.s.d.	2.921	2.921	4.131

***** Stratum standard errors and coefficients of variation *****

Variate: C_%

d.f.	s.e.	cv%
24	2.452	5.2

Appendix 16. ANOVA for nitrogen content

Variate: N_%

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	0.049136	0.049136	6.58	0.017
Date	1	2.651469	2.651469	355.24	<.001
Organ	2	16.816439	8.408219	1126.52	<.001
Cultivar.Date	1	0.000625	0.000625	0.08	0.775
Cultivar.Organ	2	0.163439	0.081719	10.95	<.001
Date.Organ	2	0.916906	0.458453	61.42	<.001
Cultivar.Date.Organ	2	0.577617	0.288808	38.69	<.001
Residual	24	0.179133	0.007464		
Total	35	21.354764			

* MESSAGE: the following units have large residuals.

units 26   0.290   s.e. 0.071
units 27   -0.150   s.e. 0.071

***** Tables of means *****

Variate: N_%

Grand mean 1.582

Cultivar	Karina	Regina
	1.545	1.619

Date	Harvest	Pithard
	1.311	1.853

Organ	Flesh	Leaf	Pit
	1.374	2.503	0.868

Cultivar	Date	Harvest	Pithard
Karina		1.278	1.812
Regina		1.343	1.894

Cultivar	Organ	Flesh	Leaf	Pit
Karina		1.428	2.445	0.762
Regina		1.320	2.562	0.975

Date	Organ	Flesh	Leaf	Pit
Harvest		0.905	2.425	0.602
Pithard		1.843	2.582	1.135

		Date Harvest			Pithard		
Cultivar	Organ	Flesh	Leaf	Pit	Flesh	Leaf	Pit
Karina		0.943	2.227	0.663	1.913	2.663	0.860
Regina		0.867	2.623	0.540	1.773	2.500	1.410

*** Least significant differences of means (5% level) ***

Table	Cultivar	Date	Organ	Cultivar Date
rep.	18	18	12	9
d.f.	24	24	24	24
l.s.d.	0.0594	0.0594	0.0728	0.0841

Table	Cultivar Organ	Date Organ	Cultivar Date Organ
rep.	6	6	3
d.f.	24	24	24
l.s.d.	0.1029	0.1029	0.1456

***** Stratum standard errors and coefficients of variation *****

Variate: N_%

d.f.	s.e.	cv%
24	0.0864	5.5

Appendix 17. ANOVA for Proportion of flesh in fruits

Variate: Flesh_%

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Cultivar	1	3.853	3.853	0.92	0.366
Date	1	4151.520	4151.520	988.46	<.001
Cultivar.Date	1	1.613	1.613	0.38	0.553
Residual	8	33.600	4.200		
Total	11	4190.587			

***** Tables of means *****

Variate: Flesh_%

Grand mean 62.13

Cultivar	Karina	Regina
	61.57	62.70

Date	Harvest	Pit hard
	80.73	43.53

Cultivar	Date	Harvest	Pit hard
Karina		80.53	42.60
Regina		80.93	44.47

*** Least significant differences of means (5% level) ***

Table	Cultivar	Date	Cultivar Date
rep.	6	6	3
d.f.	8	8	8
l.s.d.	2.728	2.728	3.859

***** Stratum standard errors and coefficients of variation *****

Variate: Flesh_%

d.f.	s.e.	cv%
8	2.049	3.3

Appendix 18. Listing of the SWEET CHERRY simulation model in FST (FORTRAN Simulation Translator)


```
TITLE Growth and production of Prunus avium

INITIAL

INCON ZERO=0.

PARAM LAIMAX= 4.
* LAIMAX is the LAI-value that the orchard reaches at harvest
time.
* LAIMAX has to be defined by the user.

PARAM Q10= 2.; TREF=20.; SLA = 19.2
* Q10= 2. (Maintenance respiration is double with an increment
* of 10 degree Celsius in temperature).
* TREF: temperature of reference (degrees Celsius).
* SLA: m2 leaf/kg dm leaf


*---------------------------------------------

* Climate

WEATHER WTRDIR='W:\MODELOS\CHERRY\';CNTR='NLD';ISTN=1;IYEAR=2001


*---------------------------------------------

TIMER STTIME= 1.; FINTIM= 210.; PRDEL=1.; DELT=1.
* with respect to start time (STTIME= 1.) see comments
* when CHLREQ is given.

TRANSLATION_GENERAL DRIVER= 'RKDRIV'

DYNAMIC

*---------------------------------------------

* Chilling and TSUM

TSUM= INTGRL (INTSUM, RTSUM)
RTSUM = MAX (ZERO, (TA-TBASE)) * PUSH
PUSH = INSW (CU-CHLREQ, 0.,1.)
* PUSH is 0 (if CU requirement is not yet satisfied) or 1.

RCU = MAX (ZERO, (.857 + .0843 * TA - .0123 * TA**2))*24.
* Units: (.857 CU.h-1 + .0843 CU.h-1.degree Celsius-1 * TA
(degree
* Celsius) - .0123 CU.h-1.degree Celsius-2 * TA**2 (degree
* Celsius**-2) * 24 h.d-1)

* The original formula for rate of CU accumulation gives
* CU per hour (Mahmood et al., 2000), therefore it has to be
* multiplied by 24 h/d. to get the rate per day.
```

```
CU = INTGRL (INITCU, RCU)
TA = (TMMN+TMMX)/2.
* TA: Air Temperature (degree Celsius)
* TMMN: Minimum temperature
* TMMX: Maximum temperature

INCON INITCU = 1695.; INTSUM = 0.0
PARAM TBASE = 4.; CHLREQ = 1142.
* CHLREQ = 1142. CU are required before starting to
* accumulate degree-days. On January 1st, is already
* satisfied (1695 CU).


PRINT TA, TSUM, RTSUM, CU, RCU, TMMN, TMMX

*-------------------------------------------

* LAI and fruit development

FUNCTION   LADVTB   =   0.,0.,   174.,0.,   175.,.01,   325.,.065,
413.,.25,...
542.,.47, 624.,.63, 715.,.774, 828.,.88, 1064.,1., 1065.,1.
* Adapted from Eisensmith et al. (1980)

LAI = LAIMAX * LAIDEV
* LAI and LAIMAX: m2 leaf/m2 ground
LAIDEV = AFGEN (LADVTB, TSUM)
* LAI development (LAIDEV) is the fraction (unitless) of maximum
LAI
* reached as a function of degree-days accumulation.
* LAIDEV starts after accumulating 175 degree-days and is going
* from 0. to 1. (when the maximum possible LAI is reached).

FUNCTION DEVTB = 250.,0., 251.,0., 255.,0.01, 700.,.22,...
1064.,1., 1065.,1.
* Adapted from Anderson et al. (1986)

FTDEV = AFGEN (DEVTB, TSUM)
*  FTDEV:  fruit  development  as  a  fraction  of  the  weight  at
harvest, going
* from 0.01 (full bloom) to 1. (fruit maturity).
* After  fulfilling  chilling,  255  degree-days  are  required  for
full
* bloom (which is assumed the starting point of fruit growth) and
1065.
* degree-days to reach full growth (maturity).


PRINT FTDEV, LAI, LAIDEV

*-------------------------------------------

* Light Interception

PARAM CLF= .95; K=.7; REFLEC=.08

IPAR = (1. - NET - REFLEC)* PAR * (1.-EXP(-AK*LAI))
AK = K * CLF
```

```
* AK: actual K after multiplying by a clustering factor (CLF)
* IPAR: intercepted PAR (MJ.m-2.d-1)
* NET: fraction of PAR intercepted by the net installed to
protect
* the orchard against birds.

NET = AFGEN (NETTB, TIME)
FUNCTION NETTB = 1.,0., 134.,0., 135.,.09, 365.,.09
* The net was installed on day 135. and intercepted 9% of the
PAR.

PAR = RDD * .5 / 1000000.
* RDD: Daily Total Global Radiation (J m-2 d-1)
* 1000000. is to transform J into MJ
* PAR: Photosynthetic Active Radiation (MJ.m-2.d-1). PAR is 50%
of RDD

INTERC = 1.-EXP(-AK*LAI)
* INTERC: PAR interception as a coefficient between 0. and 1.

PRINT PAR, IPAR, INTERC

*-----------------------------------------------
* CO2 Assimilation and total sugar production

PARAM LUE = 6.
* LUE (Light Use Efficiency): g CO2.MJ-1 PAR

ASIM = INTGRL (ZERO, ASIMRT)
ASIMRT= IPAR * LUE * 10000./1000.

* 10000 to transform "per m2" into "per ha".
* 1000 to transform g into kg.


SUGRAT = ASIMRT * 30./44.
* SUGRAT: rate of sugar production (kg sugar.ha-1.d-1). It is the
rate
* of CO2 assimilation times 30/44 (molecular weights of glucose
(per
* Carbon atom) and CO2, respectively)
SUGAR= INTGRL (RESERV, SUGRAT)
* SUGAR: total sugar production (kg sugar.ha-1)
INCON RESERV= 800.
* RESERV: it is assumed that 800 kg of sugar are available at the
* beginning of the season as reserves from the wood.

PRINT ASIM, ASIMRT, SUGAR, SUGRAT

*-----------------------------------------------
* Maintenance and growth of leaves

MTLEAF = LFBIOM * MCLEAF * TC
* MTLEAF: daily maintenance cost of dry matter leaf (kg sugar.ha-
1.d-1)
TC = Q10**((TA-TREF)/10.)
* TC: correction factor accounting for the effect of temperature
LFBIOM= LAI/SLA * 10000.
```

```
* LFBIOM: leaf biomass (kg dm leaf.ha-1)
MCLEAF= 0.0163
* MCLEAF: maintenance coefficient of leaf (kg sugar.kg dm-1.d-1)
MTLFTT = INTGRL (ZERO, MTLEAF)
* MTLFTT: total leaf maintenance (kg sugar.ha-1)


GRLEAF = LFBIOM * GCLEAF
PARAM GCLEAF = 1.61
* GRLEAF: sugar requirement for leaf growth depends on leaf
biomass
* and growth respiration coefficient (GCLEAF (kg sugar.kg-1 dm))


SUGLEF = MTLFTT + GRLEAF
* SUGLEF: sugar requirement for leaves is maintenance plus growth
* requirement


PRINT LFBIOM, SUGLEF, GRLEAF, MTLFTT, MTLEAF


*------------------------------------------------
* Maintenance of wood


TTWDMT = INTGRL (ZERO, WDMNT)
* WDMNT: wood maintenance rate (kg sugar.ha-1.d-1)
* TTWDMT: total wood maintenance (kg sugar.ha-1)
WDMNT= INWOOD * MCWOOD * TC
PARAM MCWOOD= 0.0009; INWOOD= 15000.
* MCWOOD: maintenance coefficient for wood. Value extracted from
* Grossman and DeJong (1994) for peach (kg sugar.kg-1 dm wood.d-
1).
* INWOOD: wood biomass (dm) is assumed to be constant for the
* calculations of maintenance (kg dm wood.ha-1).



PRINT TTWDMT, WDMNT


*------------------------------------------------
* Maintenance of roots


TTRTMT = INTGRL (ZERO, ROOTMT)
* TTRTMT: total root maintenance cost (kg sugar.ha-1)
* ROOTMT: root maintenance rate (kg sugar.ha-1.d-1)
ROOTMT= INROOT * MCROOT * TC
PARAM INROOT = 5000.; MCROOT= 0.002
* INROOT: root biomass is assumed to be constant for the
calculations
* of maintenance (kg dm root.ha-1).
* MCROOT: maintenance coefficient for roots. Value extracted from
* Grossman and DeJong (1994) for peach (kg sugar.kg-1 dm root.d-
1)



PRINT TTRTMT, ROOTMT


*------------------------------------------------
* Cost (sugar) of 1 kg of fruit


GRFRUT = FTDEV * GCFRUT
PARAM GCFRUT = 1.66
```

```
* FTDEV: relative size from 0 to 1
* GCFRUT: growth respiration coefficient fruit (kg sugar.kg-1 dm
fruit)
* GRFRUT: growth cost (sugar) of fruit at any developmental stage

TTMTFT = INTGRL (ZERO, MTFRUT)
* TTMTFT: total maintenance cost (sugar) of 1 kg (dm) of fruit
* (kg sugar.kg-1 dm fruit)
MTFRUT = FTDEV * MCFRUT * TC
* MTFRUT: maintenance requirement (sugar) at any developmental
stage.
MCFRUT = AFGEN (MCFRTB, TSUM)
* MCFRUT: maintenance coefficient of fruit
* (kg sugar.kg-1 dm fruit.d-1)

FUNCTION   MCFRTB  =   699.,.0136,   700.,.0136,   1063.,.0121,
1064.,.0121
* maintenance cost coefficient change during the season because
the
* proportion of flesh and the chemical composition changes as
well.

FRTCST = MAX (CSTMIN, (TTMTFT + GRFRUT))
* FRTCST: total cost (kg sugar) per kg (dm) of fruit.

PARAM CSTMIN= 0.001


PRINT GRFRUT, TTMTFT, FRTCST

*----------------------------------------------

* Sugar available for fruit, growth of root and wood

REMSUG = MAX (SUGMIN,(SUGAR - SUGLEF - TTWDMT - TTRTMT))
* REMSUG (kg sugar.ha-1): remaining sugar (available for growth
of root
*  and  wood,  and  for  fruits).  The  possible  growth  of  woody
material is
* not  considered  for  maintenance  requirements  in  the  present
season.

PARAM SUGMIN = .1

PRINT REMSUG

*----------------------------------------------

* Fruit sink strength

PARAM FRTLA= 40.; MAXSIZ= 0.0015
* FRTLA= number of fruits.m-2 LA
* MAXSIZ: maximum fruit size (kg dm.fruit-1)

SINK = MAX (SNKMIN, (FRTLA * 10000. * LAIMAX * MAXSIZ * ...
FTDEV * FRTCST))
* FRTLA and LAIMAX are the 2 components of the number of
* fruits per ha (FRTPHA = FRTLA * LAIMAX * 10000. m2/ha)
```

```
* 10000 to transform "per m2" into "per ha".
* SINK (kg sugar.ha-1): reproductive sink strength (demand).
PARAM SNKMIN= 0.1

PRINT SINK

*-----------------------------------------------

* Sugar available for fruits

PARAM MAXFRT = 0.5
* MAXFRT: maximum proportion of remaining sugar partitioned to
fruits

MSUGFT= REMSUG * MAXFRT
* MSUGFT: maximum amount of sugar (kg sugar.ha-1) available for
fruits

SUGFRT= MIN (MSUGFT, SINK)
* SUGFRT: actual sugar for fruits is the minimum: either the
demand
* of reproductive sinks or the sugars available for fruits.

PRINT MSUGFT, SUGFRT


*-----------------------------------------------

* Fruit production

DMFRUT= (SUGFRT / FRTCST)*FTDEV
* DMFRUT: dm fruit production (kg dm fruit.ha-1)

FRSHFT = DMFRUT/DMCONT

FUNCTION DMFTTB = 255.,0.21, 700.,.21, 1065.,.15, 1066.,.15

DMCONT = AFGEN (DMFTTB, TSUM)
* DMCONT: dm content of fruits
* (21 % before pit hardening; 15 % at harvest)
* FRSHFT: fresh fruit production (kg fresh fruit.ha-1)

PRINT DMFRUT, FRSHFT


*-----------------------------------------------

* Fruit size

FRTPHA = FRTLA * 10000. * LAIMAX
* FRTPHA: number of fruits per ha.
* 10000 to transform "per m2" to "per ha".
FTSIZE= FRSHFT/FRTPHA * 1000.
* FTSIZE: fruit size (fresh g.fruit-1). 1000 to transform
kg.fruit-1
* into g.fruit-1

PRINT FRTPHA, FTSIZE
```

*---

END

STOP