CHAPTER 18

USE OF CROP GROWTH MODELS TO EVALUATE PHYSIOLOGICAL TRAITS IN GENOTYPES OF HORTICULTURAL CROPS

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Abstract. Quantifying the relevance of different plant traits for yield and quality under different growth conditions can improve the efficiency of a breeding programme. Crop models are powerful tools to give guidance to breeding, because model calculations enable the analysis of many different situations (sensitivity analysis and scenario studies). Three case studies of using crop growth models to evaluate physiological traits potentially used in breeding programmes are presented. The models used are explanatory models, with several submodels; e.g., for light interception, leaf photosynthesis, organ formation and biomass partitioning.

Case study 1: It is hypothesized that yield improvement of cut chrysanthemum can be obtained by a higher specific leaf area (SLA) or a higher light-saturated leaf photosynthetic rate ($P_{g,max}$). Model calculations showed that for a winter planting, a higher SLA has more impact on yield than improving $P_{g,max}$, whereas for a summer-grown crop $P_{g,max}$ and SLA are of equal importance for yield.

Case study 2: Regarding the yield of tomato, it is hypothesized that new genotypes, with two leaves in between trusses, may improve yield. In tomato cultivars generally there are three leaves in between two trusses. The formation of fewer leaves favours dry-matter partitioning towards the fruits, but it also decreases leaf area index (LAI), resulting in less light interception. Model calculations showed that a genotype with two instead of three leaves between trusses indeed will improve yield. To maximize the benefit of this trait it is important to keep the LAI sufficiently high.

Case study 3: It is hypothesized that modified tomato genotypes that show a shade avoidance response will result in higher yields as they can be grown at higher planting densities. Model calculations for tomato showed that this modification would hardly influence total yield. Standard conditions already result in a high light interception, which can hardly be improved by a higher planting density. Hence, it may be questioned whether for tomato developing genotypes with suppressed shade avoidance response for yield improvement is worthwhile.

In conclusion, crop growth models are powerful tools to evaluate the impact of differences in crop characteristics under different growth conditions. Such quantitative evaluations are important to focus breeding programmes and to ideotype genotypes for different environments.

INTRODUCTION

Plant breeding may have multiple objectives, e.g., enhancement of disease resistance or the improvement of yield or product quality. With regard to a complex trait such as yield, a better insight in underlying physiological and morphological parameters is most important to obtain a superior genotype (G). Furthermore, the importance of those parameters may depend on environment (E) and management (M). Crop growth models can improve the efficiency of a breeding programme (Boote et al. 2001), as model calculations (sensitivity analysis and scenario studies) enable a quantitative analysis of the crop (phenotypic) response to altering genetic traits under a range of growing conditions. Such studies have been published for several crops, e.g., cucumber (Marcelis 1994), tomato (Heuvelink 1999), soybean (Boote et al. 2003) and cut chrysanthemum (Carvalho et al. 2003).

Explanatory crop growth models are a powerful method to represent and combine knowledge in a generic way (Challa et al. 1994). In contrast to the more common empirical research, explanatory models enable a scientific approach to agricultural problems by incorporating knowledge of underlying processes. Development and use of explanatory models in agricultural sciences started some 40 years ago with the pioneering work of, among others, Prof. C.T. de Wit in Wageningen, The Netherlands. A review of model development by groups of Wageningen University and Research Centre is given by Bouman et al. (1996) and Van Ittersum et al. (2003). Yin and Van Laar (2005) presented a new approach in the GECROS (Genotype × Environment interaction on CROp growth Simulator) model, which can be used for examining responses of biomass and protein production of arable crops to both environmental and genotypic characteristics. In recent studies (Yin et al. 2000; Reymond et al. 2003; Messina et al. 2006) it is shown that explanatory crop models can be helpful in quantitative-trait loci (QTL) analyses of complex traits, thereby improving breeding efficiency and enhancing breeding by design.
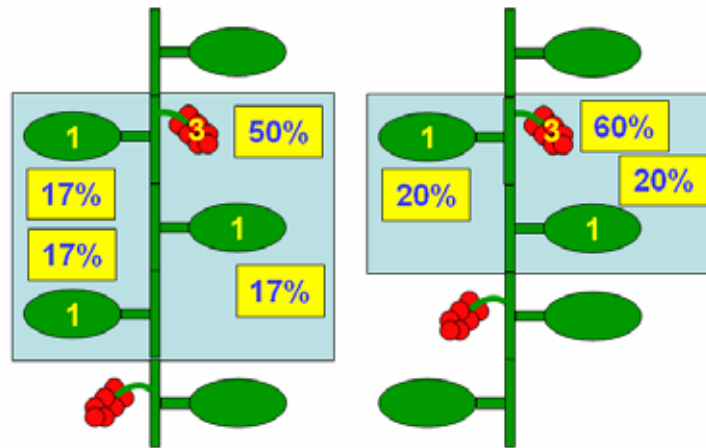
To illustrate the importance of using explanatory models three case studies are addressed with simulation studies.

Case study 1: As an example of the relative importance of crop characteristics, it is studied whether breeding for yield improvement in cut chrysanthemum should focus on increasing specific leaf area (SLA) or light-saturated leaf photosynthetic rate ($P_{g,max}$). A higher SLA will result in more leaf area per unit of leaf weight, and hence more light interception and crop growth. A higher $P_{g,max}$ will also increase yield, because of increased leaf photosynthesis. Genotypic differences in SLA have been reported for many crops, e.g., tomato (Smeets and Garretsen 1986) and chrysanthemum (De Jong and Jansen 1992). A higher content of Rubisco protein, measured in sun leaves compared to shade leaves and coinciding with a higher $P_{g,max}$ (Murchie et al. 2005), may be a way to obtain a higher $P_{g,max}$ by breeding. However, photosynthesis is a very complex process and these effects would only be expressed

in plants where Rubisco content is the limiting step in light-saturated photosynthesis. Without a quantitative analysis it is not obvious which of the two parameters is more important, and whether the effect depends on the season.

Case study 2: A reproductive tomato plant usually forms sequentially three leaves followed by a truss of fruits. A crop growth model is used to determine whether a tomato genotype with two instead of three leaves between two trusses would improve yield. On the one hand, fewer leaves and internodes between trusses would favour partitioning to the trusses resulting from a higher fruit/leaf ratio (Figure 1), but on the other hand fewer leaves means a lower leaf area index (LAI), resulting in less light interception and hence a lower total biomass production. As tomato yield can be seen as the product of total biomass and the fraction partitioned to the fruits, the impact on yield of such a genotype under contrasting conditions is not clear and may well depend on crop management.

Case study 3: The topic of shade avoidance response in tomato is presented. Plants grown closely together will elongate stems and petioles (among other responses), a strategy known as shade avoidance. Many authors have found that a shade avoidance response is detrimental to yield (Ballare et al. 1997; Robson and Smith 1997). When this response would not occur, plants could be grown at higher densities, and this is often suggested to improve yield. One mechanism by which the response to shade can be reduced is by constitutive over-expression of phytochrome genes. Over-expression of oat phyA in tobacco indeed resulted in shorter internodes and a higher harvest index in tobacco (Robson et al. 1996). In our crop growth models no shade avoidance response is implemented. Hence, we could study the impact of planting density on yield of a 'modified' tomato genotype in which shade avoidance was eliminated.

Figure 1. Schematic presentation showing the effect of leaf:truss ratio on assimilate partitioning between leaves and trusses in tomato. Numbers inside organs represent sink strength for a specific day. Percentages represent partitioning on that day, resulting from these sink strengths

MATERIALS AND METHODS

General information on the crop models used

The models used in this chapter are CHRYSIM1.0 (Lee et al. 2002b) for chrysanthemum and TOMSIM (Heuvelink 1999) and INTKAM (Gijzen 1994) for tomato. These models consist of modules for greenhouse radiation transmission, radiation interception by the crop, leaf and canopy photosynthesis, dry-matter production and dry-matter partitioning among plant organs (roots, stem, leaves and trusses of fruits for tomato, or flowers for chrysanthemum). For tomato also modules for fruit harvest and leaf picking are included.

Interception of radiation and canopy gross photosynthesis are calculated for a multi-layered uniform canopy (Goudriaan and Van Laar 1994). Leaf gross photosynthesis is calculated with the biochemical model of Farquhar et al. (1980) in the shade avoidance study, whereas in the other two studies a summary version of that model was used (Goudriaan et al. 1985).

Net assimilate production results from the difference between canopy gross photosynthesis and maintenance respiration. Maintenance respiration is calculated as a function of dry weights of the different plant organs, temperature and crop relative growth rate according to Heuvelink (1999). For tomato, assimilate partitioning between vegetative parts and individual fruit trusses is simulated on the basis of relative sink strengths (Marcelis 1994). In this concept the fraction of assimilates partitioned into an organ is calculated as the ratio between its potential growth rate (sink strength) and that of all plant parts. Appearance rate of new sections and trusses depends on temperature solely (De Koning 1994). In the standard setting, leaves from a section are removed when the corresponding truss above this section has reached developmental stage 0.9, which means at 20°C about 6 days before the truss is harvest-ripe. All trusses are assumed to have seven fruits. For chrysanthemum, partitioning is determined by fixed ratios as determined by crop developmental stage (Lee et al. 2002b). Computation of leaf area increase follows the approach given by Gary et al. (1995), as explained in Heuvelink et al. (2005).

Daily global radiation was model input and taken from Breuer and Van de Braak (1989), representing average data for De Bilt (52 °N, The Netherlands), but with natural variation. A greenhouse transmittance for diffuse radiation of 70%, 71% or 75.6%, respectively, was assumed in the three simulation studies. Hourly values of greenhouse temperature and CO_2 concentration were also model input.

Impact of SLA and $P_{g,max}$ on cut-chrysanthemum yield

Chrysanthemum is a qualitative short-day plant. In greenhouses, blackout screens and lamps provide the means for day-length control and year-round production. Cultivation of chrysanthemum starts with a rooted cutting, which is grown in about three months to a plant with a harvestable shoot; the harvestable shoot represents about 90% of the total above-ground plant biomass. In the simulations we used the standard seasonal pattern for SLA (Lee et al. 2002b); however, a positive effect of temperature on SLA was implemented.

The following model input was based on an experiment. The use of supplementary assimilation light (49 μmol m^{-2} s^{-1}) was dependent on the incoming radiation (switch on at 200 W m^{-2} and off at 300 W m^{-2}). Mean 24h greenhouse temperature varied between 19°C in winter (22 December – 5 March; 73 days; short day (SD) started on 7 January; planting density 48 plants m^{-2}) and 21°C in summer (29 June – 1 September; 64 days; SD started on 8 July; planting density 48 plants m^{-2}). CO_2 concentration ranged from 400 ppm in summer to 1000 ppm in winter. Day length was 20h for LD and 11.5h for SD period.

Simulation of a tomato genotype with two leaves per truss

Two leaves per truss were simulated by reducing the sink strength of each vegetative section by one third (Figure 1). The simulation started at flowering of the first truss (10 January) and continued until 26 November. Temperature was chosen at 19°C day and night. CO_2 concentration was 400 ppm and planting density was 2.5 plants m^{-2} with one stem per plant. Besides simulation of standard cultivation practices, a delay in removal of old leaves by one week was simulated; so, leaves from a vegetative section were removed one week after the corresponding truss was harvest-ripe.

Elimination of shade avoidance in tomato

Simulations run from 11 December to 30 November of the next year and were conducted for three different planting densities: 2.5, 3.0 and 5.0 plants m^{-2}. Temperature set-point was 19°C day, 17°C night and CO_2 set-point ranged from 1000 ppm at day when the ventilators were closed to 300 ppm at night. Actual temperatures and CO_2 concentrations were calculated with KASPRO (De Zwart 1996). For 50% of the plants an extra shoot was allowed after 50 days. All shoot tops were removed after 260 days.

RESULTS

Evaluation of plant traits for yield improvement

For a chrysanthemum crop grown in summer simulating a 20% higher SLA resulted in a 5% higher biomass production (Table 1). A 20% higher light-saturated photosynthetic rate ($P_{g,max}$) had the same effect on biomass production. However, for a winter-grown crop, a 20% rise in SLA resulted in a stronger increase in biomass production (+11%), whereas a 20% higher $P_{g,max}$ gave a smaller increase in biomass production (+4%). Hence, for a winter-grown crop improving SLA is more relevant than improving $P_{g,max}$, whereas for a summer-grown crop $P_{g,max}$ and SLA are of equal importance for yield.

Table 1. *Total simulated crop dry weight at harvest for cut chrysanthemum grown in two seasons. Results for a standard set of parameters, or a 20% higher SLA, or a 20% higher $P_{g,max}$. Relative values given in brackets*

| | Dry-matter yield (g m^{-2}) | |
	Winter	Summer
Standard	315 (100%)	737 (100%)
SLA + 20%	351 (111%)	777 (105%)
$P_{g,max}$ + 20%	328 (104%)	778 (106%)

A tomato genotype with two leaves between trusses

The simulation showed that the fraction of dry matter partitioned into the fruits is favoured in a tomato genotype with only two leaves and internodes between trusses (Table 2).

Integrated over the whole cultivation period, 74% of biomass was partitioned to the fruits, whereas for the standard genotype this was 66%. However, of the new genotype average LAI was only 2.1, compared to 2.8 in the standard. This resulted in a reduced biomass production. Hence, the favourable effect on partitioning was partly counteracted by a reduced total biomass production and as a result the predicted yield improvement was rather small. When the old leaves were removed one week later than standard, average LAI of the new genotype increased from 2.1 to 2.6, reduction in biomass production was only 2% and fruit yield improved by 10% compared to the standard. In conclusion, the simulations showed that a tomato genotype with two instead of three leaves between trusses may improve yield. To maximize the benefit of this trait it is important to keep the LAI sufficiently high.

Table 2. *Simulated fraction partitioned to the fruits, total dry matter, fruit dry weight and average LAI, for a tomato crop planted on 10 January and ended on 26 November*
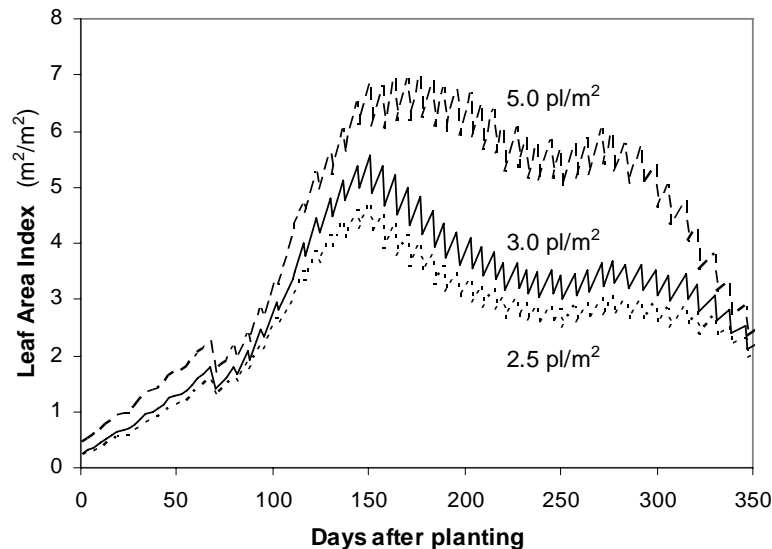
| | Fraction to fruits | Dry matter (kg m^{-2}) | | LAI$_{av}$ (m^2 m^{-2}) |
		Total	Fruits	
Standard genotype	0.66	4.08	2.63	2.8
New genotype[1]	0.74	3.82	2.77	2.1
New genotype[1] + delayed leaf removal	0.74	4.01	2.91	2.6

[1] Two leaves between trusses instead of three; vegetative sink reduced by 33%.

Elimination of shade avoidance in tomato

In plants without shade avoidance response, as represented in the crop growth model, simulating an increased planting density had only a limited influence on yield. Simulated tomato fruit dry-matter yields were 3.9, 4.0 and 4.2 kg m^{-2}, for 2.5, 3.0 and 5.0 plants m^{-2}, respectively. Doubling the planting density resulted in a 6% yield increase. This resulted from a 6% increase in total biomass production, which

was caused by a higher light absorption because of a higher LAI (Figure 2). Averaged between day 150 and day 300 after planting, LAI was 3.2, 3.8 and 5.9, and fraction absorbed light was 0.82, 0.84 and 0.88 for 2.5, 3.0 and 5.0 plants m^{-2}, respectively.

Figure 2. *Simulated effect of planting density on LAI for a tomato crop planted on 11 December and continued until 30 November (planting densities 2.5, 3.0 and 5.0 plants m^{-2}). For 50% of the plants an extra shoot was allowed after 50 days. All shoot tops were removed after 260 days*

DISCUSSION

Impact of SLA and $P_{g,max}$ on cut chrysanthemum yield

Explanatory models provide the opportunity to evaluate the impact of physiological characteristics on complex plant traits such as yield. It may seem inadequate to express yield of cut chrysanthemum in terms of dry mass per m^2. However, when dry mass is increased by 5% and the same individual final plant weight as before is considered to be acceptable, a 5% higher planting density could be allowed (Langton et al. 1999; Lee et al. 2002b). This would indeed result in more harvestable stems, so a 5% yield increase.

The higher impact of SLA on dry-mass yield in winter than in summer (Table 1), may be explained by the lower average LAI in winter; so, an increase in LAI because of a higher SLA has more impact on light interception. $P_{g,max}$ is more important in summer than in winter, as average light intensities are much higher in summer and $P_{g,max}$ is especially determining leaf-photosynthetic rates at high light

intensities, whereas at low light intensities it is mainly the initial light-use efficiency influencing leaf photosynthesis.

Focusing on one parameter for yield improvement may not be very helpful, because of covariance between traits and feedback mechanisms. For example, in tomato a strong negative correlation has been reported between SLA and net photosynthetic rate (NAR) (Smeets and Garretsen 1986). Thin leaves are more susceptible to mechanical damage and maybe also to diseases. In such cases the challenge is to find ways to counter such associations (Goudriaan et al. 1985).

When comparing genotypes in winter, a genotype with a 20% higher SLA would be higher-yielding than a genotype with a 20% improved $P_{g,max}$. However, when compared in summer, no difference in yield between both genotypes would be observed. Hence the comparison of the genotypes depends on the environment (G×E interaction). Furthermore, the outcome of the comparison between breeding for improved $P_{g,max}$ or improved SLA will also depend on management measures such as planting density or the use of supplementary lighting.

A tomato genotype with two leaves between trusses

The potential of yield improvement for a tomato genotype with only two instead of three leaves and internodes between trusses was also reported by Xiao et al. (2004). Besides modelling, these authors conducted a greenhouse experiment where one out of three young leaves was removed. This resulted in plants with two leaves between trusses (however, still three internodes), and indeed an improved partitioning to the fruits was found. These authors also observed a reduction in average LAI, resulting in a reduced total biomass production and, therefore, a yield reduction by 5% (not statistically significant). To counteract the negative effect that two leaves between the trusses have on LAI and total biomass production, old leaves can be retained longer, as was done in our simulations (Table 2). Alternatively, a higher planting density could be maintained, as was demonstrated by Xiao et al. (2004).

Whether breeding can realize the predicted extra yield for a genotype with two leaves between trusses is not clear. Tomato genotypes with only two leaves between trusses do exist, but this plant characteristic seems to be linked to a determinate growth pattern (W.H. Lindhout, pers. comm.), whereas for greenhouse cultivation plants with indeterminate growth pattern are needed.

Elimination of shade avoidance

The model has been validated, and it was shown that predicted planting-density effects (2.9–4.8 plants m^{-2}) on biomass production were in agreement with measurements (Heuvelink 1999). The present simulation results show that for tomato cultivation a higher planting density hardly improves yield. This is explained by the high LAI already obtained for a standard tomato crop (Figure 2). Starting at a density of 2.5 plants m^{-2}, and retaining one side shoot on 50% of the plants from March onwards, hence 3.75 stems m^{-2}, resulted in an average LAI of 3.1. Therefore, increased planting densities only slightly improve light interception. Furthermore,

the predicted yield increase of 6% is an overestimation, as the model assumes seven fruits per truss for all trusses, whereas a higher planting density will negatively influence fruit set (Papadopoulos and Ormrod 1991). This will reduce partitioning to the fruits and yield.

For crops that have already a high LAI, e.g., tomato (Heuvelink et al. 2005, Figure 2), sweet pepper (Dueck et al. 2006), cut chrysanthemum (Lee et al. 2002a) or rose (Kool 1996) no substantial yield improvement will result from increased planting densities, as the fraction of absorbed light is already close to its maximum. Improved yield expectations because of higher planting densities after elimination of shade avoidance are in these cases not realistic. If elimination of the shade avoidance response would mean that crops grown at their current densities partition less biomass to the stems and petioles, it is expected to improve yield, comparable with semi-dwarf cultivars in Gramineae (Cooper 1979). However, in crops such as tomato or cucumber, assimilate partitioning to the stems and petioles is already small (< 10%); so, even from a further reduction by as much as 50%, only an improvement of the yield by 5% can be expected. It should also be considered that for determining the economically optimum planting densities also costs of extra plant material and plant handling (e.g., removing side shoots, guiding plants) must be taken into account.

CONCLUSION

Crop growth models are valuable tools to evaluate differences in plant-physiological characteristics of horticultural crops under different growth conditions. Such quantifications are important in focusing breeding programmes and in ideotyping for different environments. Our case studies have shown that (1) breeding for higher SLA in cut chrysanthemum has more impact on yield than breeding for higher light-saturated leaf photosynthesis when grown in winter, but not in summer; (2) a tomato genotype with two instead of three leaves between trusses would improve yield, and even more so when cultivation is adapted to keep LAI high enough; and (3) elimination of shade avoidance response would hardly affect tomato yield.

The use of crop models would add value to breeding programmes if model parameters could be linked to genetic information (e.g., QTLs). The first steps in this direction are currently made.

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