Crop Management in Greenhouses: Adapting the Growth Conditions to the Plant Needs or Adapting the Plant to the Growth Conditions?

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Abstract
Strategies for improving greenhouse crop production should target both developing advanced technological systems and designing improved plants. Based on greenhouse experiments, crop models and biotechnological tools, this paper will discuss the physiology of plant-greenhouse interactions. It is discussed how these interactions can be applied to control the production process at Northern and Mediterranean climatic conditions.

Absorption of light by the leaves is important for maximum crop photosynthesis. For this, it is important to have plants that develop as fast as possible a sufficient leaf area index. The question is: what leaf area index is needed for optimal crop performance? Most of the light is absorbed by the upper part of the canopy. Can we improve the light distribution in the canopy and, moreover, does this increases yield or quality? Virtual plant models may help to address this question. In some cases removal of older leaves can improve yield, while in other cases removal of young leaves may accomplish the same objective.

In summer time the light transmission of the greenhouse is often reduced by growers to avoid plant stress. However, in several cases this stress is only an indirect effect of light, because other growth factors (e.g. temperature, humidity) tend to be suboptimal.

In Northern countries CO_2 supply is commonly used. The introduction of semi-closed greenhouses allows to maintain high CO_2 concentrations all year round. In Mediterranean countries, a large yield increase is still feasible by CO_2 supply.

Optimum growth conditions means that there is a good balance among different climate conditions. The source/sink ratio of a crop (ratio between production and demand of assimilates) often reflects whether these conditions are balanced. Variation in the source/sink balance affects formation and abortion of organs, product quality and production fluctuations. Some examples are shown on temperature control based on the source/sink balance of a crop.

Drought and salinity may limit production especially in the Mediterranean. Morphological and metabolic traits, with known genetic bases, can be functionally altered to test current hypotheses on plant-environment interactions and eventually design a greenhouse plant. Reasonably, such a plant should have specific shoot vs. root developmental patterns, efficient water and nutrient uptake systems as well as other specific features that have not been sufficiently explored. Elucidation of the complex plant-greenhouse interactions would establish a physiological basis to improve both product quality and resource use efficiency in greenhouse.

INTRODUCTION

Greenhouse production allows growers to improve growth conditions for maximizing crop production, product quality and resource use efficiency. Strategies for these improvements should target both developing advanced technological systems and

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designing improved plants. The development of advanced systems should aim at controlling growth conditions such that they meet the demand of the plant. At the same time, the design of the plants should aim at a plant that is better suited to cope with the growth conditions in the greenhouse.

Physiological crop models are powerful tools to identify the desired growth conditions, to explore effects of growth conditions related to the introduction of new technologies as well as to identify the target traits of a crop that are particularly important for a specific environment. Biotechnology provides tools to generate plants with improved traits as well as to explore the potentials of crop improvement.

Based on greenhouse experiments, crop models and biotechnological tools, this paper will discuss the physiology of plant-greenhouse interactions. It is discussed how these interactions can be applied to control the production process at Northern and Mediterranean climatic conditions.

RESULTS AND DISCUSSION

Light

Light forms the basis for growth of plants, as it is the driving force for photosynthesis. Besides, light quality and length of photoperiod may affect developmental processes in the plant.. For most crops a 1% light increment results in 0.5 to 1% increase in harvestable product (Marcelis et al., 2006). This is an average value, which depends on several factors. For instance, the relative effect of light on growth is greater at lower light levels, at higher CO_2 concentrations and at higher temperatures. Consequently, the relative effect is larger in winter than in summertime and the effect is larger in Northern than in Mediterranean regions. The effect of light on growth also depends on the duration and moment that the light level is changed. Besides a positive effect on yield quantity, light usually has a positive effect on quality as well. Light should not be considered as a separate growth factor in greenhouse horticulture, as it forms an integral part of the total farm management. Many growers, for instance, choose a higher temperature, a lower plant density and different cultivar when the light level is increased.

Photosynthesis shows a saturating response to light. At low light levels photosynthesis increases rapidly, but at higher levels effects of light diminish. The level at which photosynthesis saturates is not a constant, but may depend on amongst others CO_2 concentration, nutrient (especially N) concentrations or the season (most likely the main factor is light level during the previous weeks). A common mistake made by many authors is neglecting the difference between response curves at the leaf level and the crop level. Many authors measure photosynthesis of single leaves (or a few cm^2 of a leaf) and apply this curve to predict the response of the whole canopy. This, however, can only be done when a simulation model is used that accounts for light penetration in a canopy. The top leaves may saturate at 500-1000 μmol PAR m^{-2} s^{-1} (depending on growth conditions), but the leaves below the top leaves are not saturated and can use additional light. For instance when leaf photosynthesis saturates at about 600 μmol PAR m^{-2} s^{-1}, a crop with LAI of 6 only saturates at 1100 μmol PAR m^{-2} s^{-1} (Fig. 1). The higher the LAI the higher the light intensity at which saturation occurs (Fig. 1).

In Northern countries lamps are used to improve growth and quality under poor light conditions. However, even in these Northern countries in summer often screens or white wash is used to prevent too high radiation levels in the greenhouse. In Mediteranean countries a large fraction of light is prevented to enter greenhouse by shading nets, screens or white wash. Considering the photosynthesis response of canopies far too much shading is applied. In fact large amounts of light which could drive growth, are unused. Nevertheless, if less shading was applied production of high quality produce in the present systems would reduce. In most cases the growth impairment at high radiation levels is not the result of a too high light intensity, but rather because of a too high heat load or too high vapour pressure deficit of the air. In addition most shading measures increase the diffuseness of the light. If we can control temperature and air humidity by

other means than shading measures, more light could be allowed to enter the greenhouse, which can increase yield. Options for temperature and humidity control under high light intensity are for instance fogging which cools and increases air humidity, cooling greenhouse by pad and fan systems, mechanical cooling, growing a crop with high leaf area index and sufficient water supply to increase crop transpiration which cools the greenhouse and increases air humidity. Fogging systems and semi-closed greenhouses with mechanical cooling (and storing the heat in aquifer) are recently gaining interest of growers in the Netherlands. Use of screens or cover materials that reflect NIR radiation, can be helpful to prevent too much heat load in the greenhouse (Kempkes et al., 2008). Furthermore, very high light conditions may lead to an unbalanced sink/source ratio (too high source in relation to sink). Hence, measures must be taken to increase sink strength of the plant. For instance, in tomato at low stem density in summer, short leaf syndrome may occur which may be related to an unbalanced source/sink ratio (Nederhoff, 1994). Formation of trusses per stem (the main sink organs) mainly depends on temperature and is hardly affected by stem density (number of stems per m^2). Therefore, the number of sinks per m2 can easily be increased by increasing number of stems, as is common practice in Northern Europe.

Beside the effects of light intensity the light distribution within the canopy can help to further improve crop production. Top leaves may be close to light saturation while lower leaves receive insufficient light. Converting the incoming direct radiation into diffuse radiation improves the light distribution in the canopy and hence the crop production (e.g. Hemming et al., 2008; Heuvelink and Gonzalez-Real, 2008).

In summary a substantial fraction of the available light is not used in greenhouse production. An improved control of temperature and humidity in greenhouses might allow to make better use of the available light.

CO_2

For several decades CO_2 supply is common practice in winter period in the Netherlands. At day time when windows are closed or not far open, most growers supply CO_2 up to levels of about 800-1000ppm. In most cases flue gases are used as source of CO_2. Especially when CO_2 is supplied from a heat and power generator, cleaning of the flue gases for NOx and ethylene can be very critical. Recent measurements at commercial farms show that the NOx dosage might sometimes be a risk for optimal crop growth. Besides CO_2 supply from flue gases more and more CO_2 is obtained from industry (e.g. OCAP) or by supplying pure CO_2 from a tank.

The primary effect of CO_2 on plant production is on photosynthesis. At low CO_2 concentrations photosynthesis increases rapidly with increasing CO_2, while it usually saturates at levels of about 800-1000ppm. Based on measurements of canopy photosynthesis of several fruit vegetable crops, Nederhoff (1994) proposed a generic rule to estimate effects of CO_2 on canopy photosynthesis:

$$X = (1000/C)^2 * 1.5$$

where X is the percentage increase in photosynthesis when the CO_2 concentration is raised by 100ppm; C is the CO_2 concentration expressed as ppm.

This implies an increase in photosynthesis of 12% when the CO_2 concentration is raised from 350 to 450ppm or 4% when the concentration is raised from 600 to 700ppm. In greenhouses without CO_2 enrichment the CO_2 concentration may drop well below the ambient outside concentration (Nederhoff, 1994). A drop form 350 to 250ppm would lead to 19% decrease in photosynthesis. It should be noted that this a generic rule which on average yields reliable results, but effects of CO_2 concentration also depend on several other growth factors. Therefore, effects in specific circumstances may deviate from the rule. It is well known that effects of CO_2 on photosynthesis interact with light intensity and temperature. The measurements of Nederhoff were performed under moderate Dutch light conditions under conditions of higher light intensities stronger effects of CO_2 are

expected. Furthermore, a higher CO_2 concentration may result in a larger fraction of dry matter partitioned into the fruits in cucumber and pepper (Nederhoff, 1994; Dieleman, unpublished data), which may result in an even stronger response as predicted by the generic rule. This positive effect on dry matter partitioning is probably the result of increased source strength on fruit set (Marcelis, 1994; Marcelis et al., 2004). When plants are exposed to high CO_2 concentrations during a prolonged period, the photosynthetic capacity may decrease which is likely to be the result of feedback inhibition (e.g. Sims et al., 1998). Feed-back inhibition occurs when the assimilates produced in photosynthesis are insufficiently used by the sink organs of the plant. Therefore it is important to maintain sufficient sink organs. Despite the numerous studies with plants showing feed back inhibition, so far we did not find indications that feedback-inhibition commonly occurred in plants grown in commercial greenhouses in the Netherlands (Marcelis, 1991; Heuvelink and Buiskool, 1995). Probably because in these growing conditions the source/sink ratio is usually quite low (e.g. Marcelis, 1994).

Recently closed and semi-closed greenhouses have been introduced, which keep the windows closed at most times and cool the greenhouse by use of heat pumps and using cooling capacity from aquifers (Heuvelink et al., 2008). Due to the closure of the windows, high CO_2 concentrations can be maintained throughout the whole year, whereas in conventional greenhouses with opened windows CO_2 concentrations higher than 400-500 ppm in summer time are not feasible. Based on calculations by a crop model and measurements at a commercial farm maintaining a CO_2 concentration of about 900-1000ppm in summer increased annual tomato yield by about 16-17% compared to a conventional greenhouse (400-500ppm).

In Mediterranean countries with higher light levels, effects of CO_2 on production are expected to be bigger than in Northern countries. In these countries only a limited number of growers use CO_2 enrichment. The need for opening of windows (to cool down the greenhouse or prevent too high air humidity) and limited availability of cheap CO_2 are factors that hamper the introduction of CO_2 enrichment. Stanghellini et al. (2008) concluded that in Mediterranean greenhouses growers should aim at concentrations of 1000 ppm CO_2 in the absence of ventilation, and gradually decrease to maintaining the external value of CO_2 concentration when ventilation rates are exceeding 10 per hour. The trend between these two extremes depend on value of produce and price of CO_2.

In general it can be concluded that still quite some yield increase can be realized by better managing the CO_2 concentration. This is not just true for Mediterranean countries where CO_2 enrichment is not common practice yet. In Northern countries also improvements are foreseen in the summer half year, by keeping the windows more closed and thus keeping the CO_2 inside in combination with some additional CO_2 supply. Closure of windows is only possible when too high greenhouse temperatures are prevented by cooling, either mechanically or by fogging.

Leaf Area

Crops need a sufficiently high leaf area to intercept the light. For optimal light interception an LAI of about 3 to 4 is needed (Heuvelink et al., 2005). The top leaves have the highest rate of photosynthesis, but also because they have the highest photosynthetic capacity. Light response curves of leaf photosynthesis showed that photosynthesis, transpiration respiration decreased from top to bottom in the canopy even when measurements are performed at the same light intensity at the leaf (Fig. 2; Dueck et al. 2007; González-Real et al., 2007). These reductions in gas exchange lower in the canopy likely result from adaptation to lower ambient light conditions as well as leaf aging. Dueck et al. (2007) studied the contribution of different leaf layers in a sweet pepper crop, which reaches an LAI of up to 8 in summer when the crop is planted in winter. At a low light intensity of 50 μmol m^{-2} s^{-1} above the canopy, only the top 25% of the leaves (2 m^2 m^{-2}) contributed positively to canopy photosynthesis, while at a higher light irradiance, 200 μmol m^{-2} s^{-1}, the top 50% (4 m^2 m^{-2}) contributed positively. From the middle of August onwards, the net photosynthesis of the lower half of the crop was

negative. Based on these measurements, the contribution of each leaf level to the net crop photosynthesis and transpiration was calculated. On an annual basis, the lower half of the crop made a 0.5% negative contribution to net photosynthesis, while making a 10% positive contribution to crop transpiration. As in the winter half year energy is needed to prevent too high air humidity, reducing transpiration can save energy. Therefore, removal of leaves from the lower levels might increase the efficiency of energy utilization.

Optimization of the light distribution and photosynthesis in the canopy may include adaptations in row structure and leaf pruning. Functional structural plant models that simulate the plant architecture, 3D distribution of light and photosynthesis in the canopy can be powerful tools to explore possibilities (Vos et al., 2007).

Young growing leaves compete for assimilates with other sinks. Removal of young leaves favored partitioning to the fruits in tomato but decreased LAI and total yield (Heuvelink et al. 2005; Table 1). However, if removal of old leaves was delayed such that an LAI of 3 m2 m-2 was maintained, removal of every second young leaf improved yield by 10% (Table 1). An alternative means to removal of young leaves would be breeding for varieties that form two leaves in between trusses, while tomato cultivars generally have three leaves in between two trusses. 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 by delaying removal of old leaves or increasing plant density. 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.

Source/Sink Balance

Optimum growth conditions means that there is a good balance among different climate conditions. The source/sink ratio of a crop (ratio between production and demand of assimilates) often reflects whether these conditions are balanced. The source strength mainly depends on the amount of light intercepted by the leaves and the CO_2 concentration and to a lesser extent on temperature and air humidity; the sink strength mainly depends on temperature and the number of sink organs (rapidly growing such as fruits) on a plant. The source/sink ratio can vary strongly from day to day. This variation in source/sink balance affects formation and abortion of organs (Marcelis et al., 2004; Carvalho & Heuvelink 2004; Fig. 3), which leads to fluctuations in production and quality. If we could stabilize the source/sink ratio we can achieve a more balanced growth, a more regular biomass partitioning, a more regular fruit or flower size, more regular production in time and prevent feed-back inhibition of photosynthesis (e.g. Marcelis 1994; Heuvelink et al., 2004). Elings et al. (2006) developed a temperature control that reduces the day to day fluctuations in source/sink ratio of a cucumber crop. This led to a more stable and greater dry matter partitioning into the fruits and more stable fruit size and age at harvest and increase. On an annual basis this strategy resulted in 5% yield increase or 13% energy use, depending on the optimization criteria. Van Henten et al. (2006) also showed how production fluctuations in sweet pepper can be reduced and 10% of energy saved by optimizing the temperature setpoints.

Crop Physiology in Relation to Molecular Biology

The study of plant response to environmental stressors has made significant progress in the last twenty years (Maggio et al., 2006). During this time, while new experimental tools have been proposed to better understand how plants respond to environmental stimuli, standard research approaches have greatly benefited of new discoveries in the field of molecular biology. Today we have quite a clear picture of many physiological mechanisms that may affect plant production in stressful environments, however we are still far from being able to design effective strategies to substantially improve plant stress tolerance by using all the available tools, including traditional

breeding, genetic engineering and specific cultural techniques. A step forward in this process is the identification of *specific* plant/environment interactions for a given cultural system, since these may involve different approaches to improve plant adaptation to environmental constraints. Ultimately, a thorough comprehension of these interactions will support the *design* of plants able to efficiently use the available resources in each specific environment.

Abiotic Stress. Drought, salinity and extreme temperatures are common stresses in agriculture productions and they may limit optimal yield in both open field and controlled environment (Flowers, 2004). In addition, multiple stresses may co-exist in most agricultural contexts. Quite often drought and/or salinization are associated to exposure to high temperatures (Maggio et al., 2002). Salinity is particularly critical for many horticultural crops. In the field, salinization often occurs as a transitory event that may be controlled by both suitable irrigation volumes and the seasonal rainfall that leaches out the excess of salt from the root zone. In greenhouse, soil salinization may reach critical levels as well. In this case the control of soil salinization is strictly dependent on an efficient irrigation management. Salinization may result from a cumulative effect of nutrients added in the irrigation water and additional ions such as Na^+ and Cl^-, both of which may overall generate a hyperosmotic environment.

To cope with a continuous exposure to biotic and abiotic stresses, which generally interfere with the normal growth and development, plants have evolved a complex response system that is largely mediated by phytohormones (Fujita et al., 2006). The most accredited sequence of events, includes the perception of the signal (stressor), the transduction of the signal and finally the activation of downstream components, i.e. ex-novo synthesis and/or activation of molecules that would facilitate adaptation under stress conditions (Zhu, 2001). Common response mechanisms are usually initiated by different stressors and intermediate signalling components, such as Ca^{2+} and reactive oxygen species (ROS) which are involved in the signal transduction cascade activated by both abiotic and biotic inducers (Torres et al., 2005). Advancement in molecular techniques have allowed to dissect the transcriptional profile of abiotic and biotic stress responses (Bohnert et al., 2006) and have confirmed that these regulate a recurrent set of common genes. Recent efforts using the model plant *Arabidopsis* have revealed that ~200 genes are expressed in response to a various range of stresses (Ma et al., 2007). Consequently, the identification of *upstream* stress components, i.e. intermediate molecules common to different response pathways, has become the research focus of many molecular engineers interested in the generation of multi-stress tolerant plants.

The identification of molecules responsible for sensing and transducing the stress signals (Guo et al., 2002) has therefore become the new approach after the modest results attained through the over-expression of single downstream components (Maggio et al., 2002). In horticultural productions, tomato has been the model species for molecular engineering of abiotic stress tolerance traits. First attempts to improve the tolerance to drought, salinity and extreme temperatures included the generation of plants that 1) overproduced compatible solutes such as glycinebetaine (Park et al., 2004); 2) were capable of controlling cytoplasmic Na^+ accumulation (Zhang and Blumwald, 2001); 3) manifested an improved chilling and heat tolerance (Hsieh et al., 2002; Mishra et al., 2002). In most cases these plants showed a reduced growth in absence of stress, revealing that the control of cell enlargement and division is part of the complex stress adaptation process and is likely mediated by these metabolites (Ruggiero et al., 2004).

Cross Talk Biotic-Abiotic. Plants are quite often required to respond to overlapping environmental stimuli of biotic and abiotic origin and, consequently, they have developed mechanisms to integrate their signal transduction pathways leading to adaptation. These responses, in most cases, do not function independently, yet a concerted activation of different pathways controls the response specificity to biotic and abiotic stress (Ludwig et al., 2005). We have recently confirmed the existence of a cross-talk between stress

adaptive mechanisms by analyzing the response of tomato plants over-expressing the prosystemin cDNA to salt stress. Chewing insects and mechanical wounding cause the release of a highly mobile peptide called systemin (Schilmiller and Howe, 2005). In tomato, this 18-amino acid molecule is synthesized as a 200-aa precursor protein named prosystemin (McGurl and Ryan, 1992). This molecule is typically involved in mechanical stress responses such as those induced by some insects. Evidence gained through mutational analysis suggests that long-distance defence signalling mediated by systemin involves jasmonic acid, a plant hormone that also controls growth regulation (Schilmiller and Howe, 2005). Jasmonic acid and its methyl-ester have both a role in stress responses, including water-, osmotic-, and wound-stress (Reindbothe et al., 1992). The interaction between jasmonic acid and other stress hormones, including ABA, has also been demonstrated (Staswick et al., 1992). Preliminary results indicated that a constitutive overproduction of systemin had some positive effects on tomato tolerance to salinity. This response was associated to a constitutively reduced stomatal conductance of systemin overxpressing plants, which was most likely responsible for a better control of the plant water homeostais in saline environment. This conclusion was consistent with the lower level of stress metabolites, such as ABA and proline that we found in systemin overxpressing plants respect to their relative control (unpublished results).

Looking Forward. The existence of multiple stress responses that ultimately lead to plant stress adaptation indicates that there are margins to dissect the contribution of these physiological mechanisms in each specific environment. In this respect, the greenhouse environment would be particularly suitable to promote strategies of "precision" horticulture (Maggio et al., 2008). To pursuit this approach it should be first defined which kind of tolerance we need in each specific agricultural system and which function should be improved. This may involve identifying the most efficient combination of genes, generating better alleles of the most promising genes for a specific cultivation process and assessing cultivation protocols that would potentiate constitutive physiological responses. In addition, the isolation of new tolerance determinants by using novel screening techniques should also be considered. This may surprisingly lead to isolate unconventional stress tolerance traits that may be important in a specific agricultural context. Strategies to improve water use efficiency and salinity tolerance should look for example at morphological and physiological traits, such as leaf characteristics (hairiness, waxiness, leaf angle), root architecture, root hydraulic conductivity and other characteristics that may have a particular/specific value under certain cultivation systems (Maggio et al., 2008). The control of water fluxes through the stomata and membrane aquaporins is also important and may play a critical role especially when other environmental parameters can be modulated, as it may occur in greenhouse cultivation.

CONCLUSIONS

There is still quite some room for increasing yield and quality, while improving sustainability of greenhouse production systems. To do so we need to control growth conditions in the greenhouse such that they meet the demand of the crop. At the same time the crop management should aim at a plant that is better suited to cope with the growth conditions in the greenhouse.

Light is the most important growth factor in greenhouse production. A substantial fraction of the available light is not used in greenhouse production. Better control of temperature and humidity in greenhouses might allow to make better use of the available light. Quite some yield increase can also be realized by a better management of the CO_2 concentration in both Mediterranean and Northern countries. Optimization of leaf area includes maximization of light interception for photosynthesis and minimization of assimilate use for leaf formation. In addition it considers effects of leaf area on transpiration which is needed for cooling in hot summer conditions, but leads to energy consumption under cool winter conditions. Growth conditions need to be balanced such

that the source/sink ratio is balanced. This can be used to reduce yield fluctuations or to increase yield.

In this contest, biotechnology should be seen as a powerful tool to identify both physiological traits and metabolic components that may be 'potentiated' to improve greenhouse plant resource use efficiency.

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Tables

Table 1. Simulated cumulative dry weight of fruits (DW_{fruit}) and plant (DW_{total}), fraction partitioned to the fruits (F_{fruits}), average LAI for a tomato crop grown from Dec. till Nov. Young leaves were removed at appearance (from Heuvelink et al., 2005).

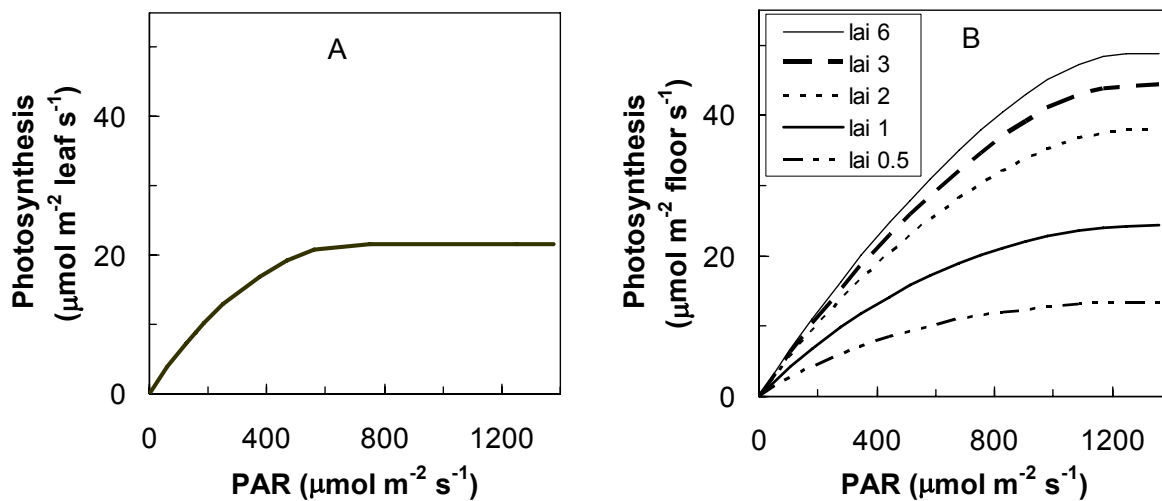| Number of young leaves removed	DW_{fruit} (kg m^{-2})	DW_{total} (kg m^{-2})	F_{fruits}	LAI (m^2 m^{-2})
Control: no removal	2.92	4.25	0.69	2.41
1 out of 6	3.01	4.24	0.71	2.38
1 out of 3	3.11	4.22	0.74	2.33
1 out of 2	3.22	4.18	0.77	2.25

Figures

Fig. 1. Light response curves for gross photosynthesis of a leaf (A) and of a crop (B) with different leaf area indices (LAI). Leaf photosynthesis was calculated by a biochemical model. Based on this model crop photosynthesis was calculated by the crop model INTKAM (Marcelis et al., 2000) Calculations at 21˚C and 400ppm CO_2.
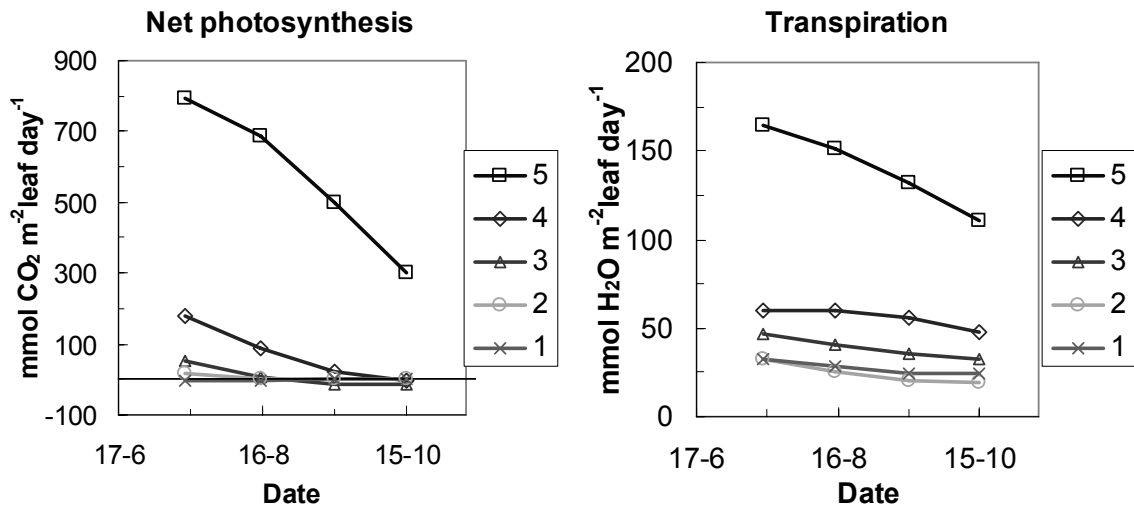
Fig. 2. Net leaf photosynthesis and transpiration of leaves at different heights in a sweet pepper canopy with LAI =6. Layer 1 is bottom and Layer 5 is top. From Dueck et al. (2007).
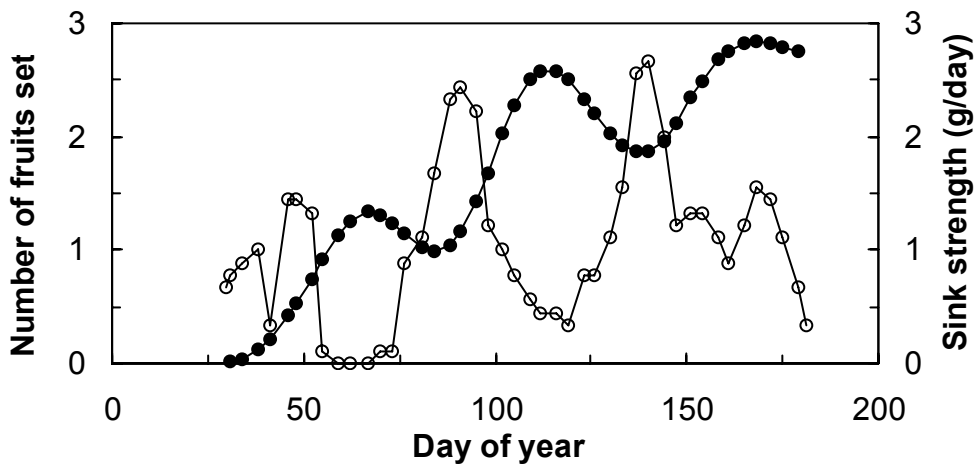

Fig. 3. Fruit set (o; number of young fruits, less than 10 days from anthesis) of sweet pepper plants and plant sink strength (•) during a growing season. From Heuvelink et al. (2004).

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