

Innovation in Plant-Greenhouse Interactions and Crop Management

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Abstract

(Semi)-closed greenhouses allow for better control of climate conditions compared to conventional greenhouses. To make the high investments for such greenhouses economically feasible, substantial yield increases are necessary. In north-Europe supplementary assimilation light in greenhouse horticulture is increasingly used to improve yield and product quality to meet market demands for year-round production and to obtain a more regular labor demand throughout the year. Using inter-lighting instead of lights only on top of the crop, and Light Emitting Diodes (LEDs), could increase substantially light and energy efficiency. As soon as LEDs will reach high enough efficiency and feasible price, they are expected to replace high pressure sodium lamps in greenhouse horticulture. Another important issue is the choice of the greenhouse cover which should be optimized from the crop point of view. A cover with high transmission of light, but low transmission of NIR, results in a better climate during the warm season (reduced temperatures, less crop transpiration, higher CO₂-concentration possible because of reduced ventilation demand). Increasing the diffusive power of the cover material could result in a better distribution of the radiation over the crop canopy, therefore leading to substantial increase in absorbed radiation (up to 20% for highly diffusive covers) and improving radiation use efficiency and yield. Under these new conditions (high CO₂ and high light levels) other genotypes than the present cultivars may be superior. However, the possible effect of breeding especially for these new conditions is still little investigated. Under improved crop management, maintaining leaf area index high enough and controlling source-sink balance is discussed. In conclusion, there are a lot of possibilities to further improve yield and quality of greenhouse produce, and meanwhile reduce the input of fossil fuel energy.

INTRODUCTION

In greenhouse horticulture there is a constant need for production improvements, both in yield and quality, and for reduced production costs per unit of produce (e.g. kg or stem). In the Netherlands, physical yield per unit greenhouse area has roughly doubled between 1980 and 2005 (Van der Velden and Smit, 2007). Many factors have contributed to this yield increase, such as a longer cultivation period ("51 weeks green"), improved greenhouse transmission, CO₂ enrichment, substrate culture (more optimal root environment), higher yielding cultivars, improved crop management and improved control of pests and diseases. In most cereal crops yield increases by genetic improvement could be ascribed to an increased harvest index (Hay, 1995). The contribution of genetic improvement to yield increases in greenhouse horticulture is hardly investigated until now. Based on a spring experiment, Van der Ploeg et al. (2007) concluded that the yield of modern tomato cultivars is on average 40% higher than that of 'Moneymaker' released in 1950. This increase in production resulted from a higher light use efficiency.

As mentioned above, production improvements can result from technical measures, as well as from crop management. In this paper we present and discuss several

recent innovations in (i) greenhouse climate modification and control, and in (ii) crop management, although these topics are too broad to give a complete overview. First, closed and semi-closed greenhouses are mentioned and then modification in the radiative climate receives attention (diffusing covers, photosensitive films, assimilation light). Under improved crop management, maintaining leaf area index (LAI) high enough and controlling source-sink balance is discussed.

NEW TRENDS IN CLIMATE MODIFICATION AND CONTROL

Closed and Semi-Closed Greenhouses

On an annual basis, inside a Dutch greenhouse about 2800 MJ m⁻² is received from the sun, which is almost 3 times more than the annual heating requirement. However, most of this solar energy is provided in summer, whereas heating requirement mainly exists in winter and spring, so a problem of timing exists. In the closed greenhouse concept aquifers are used to store excess heat in summer to heat the greenhouse in winter (Heuvelink et al., 2008). Besides aquifers for seasonal energy storage, the technical concept consists of a heat pump, daytime storage, heat exchangers, air treatment units and air distribution ducts. In summer, greenhouse temperature is controlled by active cooling instead of opening of ventilation windows.

Instead of installing a cooling capacity which can cope with the most extreme conditions (high solar radiation) in the year, the economic optimum lies at a much lower cooling capacity. In summer conditions where the active cooling capacity is insufficient to keep the temperature below the maximum, ventilation windows have to be opened (CO₂ concentration decreases) and hence such greenhouses are called semi-closed. The economic optimum situation depends on the trade-off between cooling costs and yield loss at supra-optimal temperatures, which is crop-dependent.

For a closed greenhouse, combined with a conventional greenhouse, savings in fossil fuel up to 30% have been reported, whereas for a separate closed greenhouse (“island situation”) this was 20% (Opdam et al., 2005). Because ventilation windows stay closed also in summer, a high CO₂ concentration in the greenhouse air can be obtained. Mainly because of this high CO₂ concentration, production increases of about 20% have been observed (Opdam et al., 2005). These authors also reported 80% reduction in chemical crop protection and 50% reduction in irrigation water use. In the Watergy greenhouse in Spain (www.watergy.eu), a closed greenhouse, 75% of the irrigation water has been recovered by condensation of the transpired water (Zaragoza et al., 2007). Theoretically, the use of irrigation water could be reduced even more. Tomato fruits represent about 80% of the total plant fresh biomass produced in a greenhouse, meaning that 1.25 liters of water per kg tomatoes is needed as a theoretical lower limit. Investments for a closed greenhouse are very high, and no reliable data on profitability are available so far. Economic feasibility of this innovative greenhouse concept highly depends on the yield increase that can be obtained and on the economic value of that yield increase.

There are many new greenhouse concepts, all aiming at reducing input of fossil fuel, e.g. optimakas, aircokas (www.aircokas.com), greenportkas (www.sunnytom.nl), kas zonder gas (greenhouse without gas; www.kaszondergas.nl), energy-producing greenhouse (www.energiek2020.nu/ener2020/energie_producerende_kas/). These greenhouse concepts all provide us with many new questions. They allow greenhouse conditions which are not possible in conventional greenhouses, e.g. high light combined with high CO₂ while maintaining the temperature within the optimum range. Optimum temperature is higher at higher CO₂ concentration (Heuvelink et al., 2008), but how harmful are 1 hour at 40°C or 10 hours at 37°C? Cultivation systems need to be adapted, to find a new optimum (e.g. planting density). Active cooling also brings the question whether the cool air should be brought into the greenhouse above or below the crop. What impact does the vertical temperature gradient have on crop growth and yield?

In the coming years a lot of crop physiological and crop production research

focused on these new conditions will take place. Often growers feel they have to learn to grow again under these new conditions, just like when applying high intensities of supplementary lighting. Of course basic physiological processes are the same as in conventional greenhouses, but the interactions among climate factors and between crop and climate bring many new questions to be answered.

For optimal use of “energy-saving” greenhouses also new cultivars are needed. Desirable is tolerance to both higher and lower temperatures, i.e. a broad temperature optimum. This makes temperature integration (Dieleman and Meinen, 2007) by the crop possible and reduces investment requirements in cooling equipment. Energy savings in greenhouses often result in higher humidity and therefore genotypes tolerant to high humidity are preferred, including disease resistance (e.g. botrytis). Finally, a strong positive response to high CO₂ is needed. It may well be that such genotypes are neglected in the current selection programs which do not include conditions of high CO₂ in summer. Preliminary work in cut chrysanthemum showed clear differences in CO₂ response between genotypes (Fanourakis et al., 2007; Fig. 1).

Radiative Climate Modification

1. Diffusing Covers. Influence on Light Quality and Quantity. Diffuse radiation represents an important fraction of solar global radiation entering the greenhouse. Enhancing this fraction has been reported to increase crop productivity (Healey, 1998; Hemming et al., 2008), radiation absorbed by the crop (Goudriaan, 1977; Warren Wilson et al., 1992), photosynthetic rate (Spitters, 1986) and Radiation Use Efficiency, RUE (Cockshull et al., 1992). RUE values reported for greenhouse-grown crops (Baille, 1999) are often similar to or even higher than those observed for the best-performing C₄ field-grown crops. This can mainly be explained by the combined effects of (i) greenhouse climate control, (ii) a lower amount of solar radiation than outside, leading to higher light use efficiency for CO₂ assimilation, and (iii) an increase in the diffuse radiation fraction (Baille et al., 2003; Hemming et al., 2006a). Modifying the relative fraction of diffuse radiation entering the greenhouse, by means of cover materials, allows a higher spatial uniformity of solar radiation inside the greenhouse. However, despite the relevant role of the fraction of diffuse radiation on greenhouse crop productivity, not much information is available on its magnitude. Pollet et al. (2005) stressed the non-lambertian behavior of the greenhouse diffuse radiation, based on laboratory measurements on several greenhouse cover materials. Baille et al. (2003) characterized in situ the diffusive power of several cover materials, in particular a highly diffusive film, HDF, and a standard horticultural glass, SG, through the two following parameters: (i) the direct-to-diffuse transmission coefficient, τ_{i-d} , defined as the fraction of outside direct radiation, I_o , converted into diffuse inside the greenhouse, D^* , and (ii) the ratio of inside-to-outside diffuse radiation or ‘greenhouse diffuse ratio’, $\rho (=D_i/D_o)$. Values of τ_{i-d} and ρ are respectively represented against I_o (Fig. 2a) and the outside diffuse fraction ($k_o = D_o/G_o$, where G_o =the outside solar global radiation) (Fig. 2b). Figure 2a clearly shows that under HDF, the values of τ_{i-d} are rather sensitive to I_o (i.e.: to the solar angle, h) decreasing from near 0.50 (winter, low h) to 0.35 (summer, high h), while τ_{i-d} was relatively conservative under glass (near 0.15). High values of h foster the direct-to-direct transmission process, whereas low values enhance the direct-to-diffuse transmission. The parameter ρ strongly depends on k_o (Fig. 2b). Under a clear sky ($k_o \approx 0.15$) the diffuse radiation under HDF can reach values four times higher than the outside diffuse radiation.

Extrinsic factors might contribute to increase the diffusive power of the cover material. The occurrence of condensation on the cover enhances the diffusion process, leading to a reduction of total transmitted PAR (Pollet et al., 2002). Dust deposition represents another factor of variability, which negatively affects the absolute value of the transmission coefficient. It has to be stressed that PAR transmission, τ_{PAR} , can be about 8% lower under diffusing films than under clear ones. This reduction was observed to be higher for τ_G than for τ_{PAR} , probably due to the fact that the amount of diffuse radiation

decreases with increasing wavelength (Pollet et al., 2005).

2. Photosensitive Films. Influence on Light Quality. Photosensitive films have the property to alter the solar spectrum reaching the crop. They can be classified into three main categories, depending on the agronomic objective:

Plant Morphogenesis Control. Manipulation of light quality by the incorporation of additives and dyes that modify the spectral properties of cover materials represents a non-chemical alternative for plant height control (McMahon and Kelly, 1995; Cerny et al., 2003). It is widely recognized that the phytochrome-mediated response of plants to light is triggered by the ratio red:far-red (R:FR) (reviewed by Vandebussche et al., 2005). A low R:FR ratio within the canopy induces a shade-type morphology that could downgrade the commercial value of vegetable and ornamental seedlings and the quality of bedding, potted and container ornamentals (Runkle and Heins, 2002). Greenhouse covers with FR light absorbing dyes can affect not only plant architecture, by modifying shoot components (leaf size, internode length) and branching patterns, but can also affect leaf biochemistry (McMahon and Kelly, 1995), plant growth (Oyaert et al., 1999), dry matter partitioning (Li et al., 2000), flowering time and floral development (Cerny et al., 2003; Runkle and Heins, 2002). These responses are species specific, stressing the importance of technical information about the specific wavelength bands filtered from the solar spectrum. A limitation to the spread of these films is that they generally reduce PAR transmission (Wilson and Rajapakse, 2001). Their main advantages are lower costs for growth regulating chemicals and a reduction in health risks for workers and in potential environmental pollution. Innovation in this field will come from new cover materials with a better selectivity of wavelength bands filtered, and improvement of PAR transmission and life span of the films.

Disease and Pests control ('UV-blocking'). The role of specific wavelength bands of UV radiation (280-400 nm) in reducing the proliferation of several fungal pests is well-established since early studies in the 70's (reviewed by Raviv and Antignus, 2004). These films raised much interest among growers, as they favor greenhouse implementation of Integrated Pest and Disease Management strategies and therefore lower pesticide loads and associated costs. There is a large body of work evidencing the effectiveness of spectrally modified films on fungal diseases and viruses (Reuveni et al., 1989) transmitted by insects whose vision depends on UV radiation. However, their effects could be more wide ranging than expected (e.g. on bio-control agents). The development of pathogen response models (e.g. biological spectral weighing functions, Paul et al., 2005) to light manipulation should be carried out for predicting their effects under a wide range of greenhouse conditions (reviewed by Jewett and Jarvis, 2001).

Heat-barrier or 'heat-blocking' films. Fluid-roof greenhouses filtering out the infrared wavelength bands of the solar spectrum (Van Bavel et al., 1985) paved the way towards the development of heat-barrier films (NIR-reflecting films; Hemming et al., 2006b). These films allow a substantial reduction of the greenhouse heat load (Abdel-Ghany et al., 2001; Sonneveld et al., 2006), and lower risks of conditions of heat stress. As such, they can be viewed as an alternative to classical techniques of cooling (whitening and evaporative cooling). The development of new films with high PAR transmission (Verlodt and Verschaeren, 2000), greater wavelength bands selectivity and improvement of the dependence of transmittance on the solar angle (Hemming et al., 2006b) can boost their use in protected plant cultivation (Sonneveld et al., 2006). However, more experimental work needs to be carried out to determine their efficiency on improving the physiological and agronomical (yield and quality) behavior of greenhouse crops.

To summarize this section on new materials, it appears that the main innovation in the future, for diffusing films as well as for photo-selective films, would be to obtain the desired specific effect on the crop behavior without affecting the PAR transmission, by a proper choice of additives and/or dyes. In general, these new materials should become available at a lower price to make large-scale application economically feasible. Besides, there is a need for a better characterization and modeling of the fundamental biological response of the plant/host system to changes in specific wavelength bands of the solar

spectrum, as well as the eventual side-effects on other living organisms (bio-control agents, pollinating insects).

3. Supplementary Assimilation Light (SL). About 25% of Dutch glasshouse area is equipped with SL and this is still increasing. An overview of recent developments is given by Heuvelink et al. (2006). Also in other countries with low light levels in winter (e.g. Scandinavian countries, Belgium, Canada, Island) SL is applied. SL makes year-round production possible, improves yield and product quality, and results in a more regular labor demand. Nowadays almost all Dutch rose and chrysanthemum greenhouses are equipped with assimilation light, but also in greenhouse vegetables the use of SL is increasing fast. For tomato this is already 170 ha (13% of the total tomato area), whereas in 2000 this was only a few ha. Optimal use of SL means adaptations in the crop management, including higher planting density, CO₂ concentration and temperature (Heuvelink et al., 2006).

SL is almost exclusively applied on top of a crop canopy. However, this might not be optimal, as most of the light will then be intercepted by top leaves that also receive most of the natural light and are therefore already closer to or completely at saturating light intensities. Gunnlaugsson and Adalsteinsson (2006) reported a 6.5% increase in tomato yield (planted mid February, first harvest April 5th and 23 weeks of harvest: 52.9 instead of 49.7 kg m⁻²) for Island, when 45% of the SL (238 Wm⁻² installed; lights on between 04:00 and 22:00) was supplied as interlight instead of all light on top of the plants. Improved yield by interlighting is probably caused by a better vertical light distribution and therefore a more efficient use of SL. At first glance one may think that it is suboptimal to illuminate leaves low in the canopy, as their maximum photosynthetic capacity is very low (acclimated to low light levels; Gonzalez-Real et al., 2007). However, if these leaves are experiencing every day higher light levels because of interlighting, their maximum photosynthetic capacity remains at a high level (Hogewoning et al., 2007).

Almost all the SL is provided by high-pressure sodium (HPS) lamps. Light Emitting Diodes (LEDs) may be a suitable light source in the near future. LEDs offer better possibilities for inter-lighting (no radiation heat) and for making use of spectral differences as they are available in many colors, have a long life time and give less problems with light emission (pollution; Hogewoning et al., 2007). As soon as LEDs will reach a high enough efficiency and a feasible price, they are expected to replace HPS lamps in greenhouse horticulture.

NEW TRENDS IN CROP MANAGEMENT

LAI (Radiation Interception)

An example of improved crop management is the better light interception through higher leaf area index (LAI) in tomato cultivation (Fig. 3). It is nowadays common practice to increase stem density in summer by retaining some side shoots. Typically, a tomato crop in the Netherlands has a planting density of 2.5 plants m⁻² and in summer stem density is 50% larger (3.75 stems m⁻²). Leaf picking strategy and the use of rootstocks may contribute to a higher LAI in summer (Heuvelink et al., 2005).

Diffusing Covers: Interaction with Leaf Area Index

Models predicting the radiation absorption by row crops are useful tools for evaluating the effects of diffusive films on canopy light absorption (Gijzen and Goudriaan, 1989; Boote and Loomis, 1991). The simulation results presented in Figures 4 and 5 are based on an adaptation of the models of Goudriaan (1977) and Boote and Loomis (1991), allowing the calculation of PAR absorbed in each *stratum* of the canopy (multi-layer model). Figure 4 presents the values of PAR absorbed by a row crop, PAR_a (row width=0.90 m, path width=0.90 m) vs. τ_{i-d} , for three LAI values under clear sky conditions ($k_0=0.2$). Values of τ_{PAR} are assumed identical (=0.75) whatever the value of τ_{i-d} . For a well-developed crop (LAI=3.2), a totally diffusing cover, TDC ($\tau_{i-d}=1$), would

increase PAR_a up to 25% with respect to a perfectly transparent cover ($\tau_{i-d}=0$). For a low LAI (=1.2) crop, the increase in PAR_a would be about 18%. These values strongly decrease for higher values of k_o . Under partially covered sky ($k_o=0.4$), the corresponding maximum gain in PAR_a is only about half that obtained for $k_o=0.2$.

Figure 5a gives the estimated maximum relative increase (clear sky) in absorbed PAR per layer (canopy divided into four layers, each having the same thickness and leaf area) due to an increase in the direct-to-diffuse transmission, compared to the value obtained for a clear cover ($\tau_{i-d}=0$) (same hypothesis as in Fig. 4). The first (uppermost) layer shows a decrease in absorbed PAR compared to $\tau_{i-d}=0$ (up to 10% for a HDC). However, layers 2-4 experience a mean increase of about 65 % for a TDC (Fig. 5a). Note that the contribution per layer is practically independent from τ_{i-d} (Fig. 5b).

The examples given in Figures 4 and 5 illustrate the maximum reachable increase of PAR_a , when similar τ_{PAR} values are assumed for diffusing and clear covers. As a diffuse film generally decreases τ_{PAR} , the question arises whether a higher partitioning of G_i into diffuse radiation could compensate for this decrease. To answer this question, simulations were carried out with the same hypothesis as in Figure 4, except that values of τ_{PAR} were assumed to decrease proportionally to τ_{i-d} (from 0.75 to 0.60, respectively, for $\tau_{i-d}=0$, clear cover, and $\tau_{i-d}=1$, HDF). Figures 6a and 6b show the relative increase in PAR_a vs. τ_{i-d} under clear ($k_o=0.2$) and partially overcast sky ($k_o=0.4$), respectively. Under clear sky conditions, the relative increase in PAR_a ($\approx 10\%$), for a well-developed crop (LAI=3.2), is less than a half of that when considering the same τ_{PAR} value for a diffusing and a clear cover (Fig. 4). For this value of LAI, there is no more increase for $\tau_{i-d}>0.75$. For a low LAI (=1.2) crop, the maximum gain is rather low ($\approx 3\%$) and is obtained for $\tau_{i-d}=0.75$. Under partially covered sky ($k_o=0.4$, Fig. 6a) the maximum gain for LAI=3.2 is about 2%, and the gain is negative for low LAI crops. Large crop spacing, allowing better aeration around the plants (i.e. less chance of water condensation on the crop and therefore lower risks of bacterial and fungal pathogens), strongly decreases the positive effect of diffusing covers on PAR_a whatever the sky conditions are. Therefore, at low LAI and large crop spacing, a high diffusing cover can be expected to negatively affect the amount of absorbed PAR.

The simulations presented above could be useful to tackle issues related to plant architecture and manipulation of source-sink balance (i.e.: leaf pruning) of fruit vegetables crops (Marcelis et al., 2004; Marcelis and Heuvelink, 2007). The increasing interest for diffusive films in protected plant cultivation stresses the need to account for the cover diffusive behavior in models of greenhouse transmission of solar radiation in order to increase the accuracy and reliability of models simulating canopy radiation absorption and photosynthesis (Hemming et al., 2006a). Ongoing research on this topic would be directed towards the optimization of row spacing and plant architecture with respect to the prevailing outside climate, greenhouse shape and orientation, type of cover material and species photosynthetic attributes (González-Real and Baille, 2000; González-Real et al., 2007). Such a complex optimization could only be treated through biophysical greenhouse crop models which account for the structure and architecture of the canopy. Functional-structural models, such as those developed for trees (e.g. Godin and Sinoquet, 2005) could be valuable tools for characterizing the effects of canopy structure on light use efficiency.

Source-Sink Balance and Greenhouse Climate

In many plant species a balance (co-ordination) is maintained between the production of assimilates (source strength) and the demand for these assimilates (sink strength; Wardlaw, 1990; Foyer et al., 1995). A low demand may negatively affect photosynthesis (Foyer et al., 1995), whereas a high demand (relative to the supply) may result in flower/fruit abortion (e.g. Bertin, 1995; Marcelis et al., 2004) and cyclic fluctuations in dry matter distribution (Heuvelink et al., 2004). A high source-sink ratio results in more branching (and hence more flowers) in cut chrysanthemum (Carvalho and Heuvelink, 2004). The source-sink ratio can fluctuate strongly from day to day. Elings et

al. (2006) hypothesize, based on simulations by Marcelis (1994) for cucumber, that a more stable source-sink ratio results in a more stable and greater dry matter partitioning towards the fruits, a more stable fruit load, and more stable fruit characters over the season, all positive aspects for growers. In a simulation study, these authors first determined the long-term trend in source-sink ratio during a cucumber cultivation, and then tried to reduce daily fluctuations by temperature control. For example, when a bright day is followed by a dull day, the source-sink ratio will drastically drop, however, this can be mitigated by a reduced temperature set-point on the dull day. Authors indeed obtained less fluctuations in the source-sink ratio in their simulations by adjusting temperature set-points, while maintaining the same long term average temperature. This strategy resulted in an annual production increase of 5.3% (4.4 kg m⁻²) or in a reduction in natural gas use of 13% (5.3 m³ m⁻²), depending on the optimization criteria.

CONCLUSIONS

New greenhouse systems, cover materials and supplementary light, as well as crop management give a lot of possibilities, already applied occasionally or available in the near future, to further improve yield and quality of greenhouse produce, and meanwhile reduce the input of fossil fuel energy.

Literature Cited

- Abdel-Ghany, A.M., Kozai, T. and Chun, C. 2001. Plastic film vs fluid-roof cover for a greenhouse in a hot climate: a comparative study by simulation. *J. Soc. High Technol. Agric.* 13: 237–246.
- Baille, A. 1999. Energy Cycle. In: *The Greenhouse Ecosystem*. Chapter XI. Enoch and Stanhill (Ed.) Elsevier, Chapter XI, 265-286.
- Baille, A., González-Real, M.M., López, J.C., Cabrera, F.J. and Pérez-Parra, J. 2003. Characterization of the solar diffuse component under “parral” plastic greenhouses. *Acta Hort.* 614: 341-346.
- Bertin, N. 1995. Competition for assimilates and fruit position affect fruit set in indeterminate greenhouse tomato. *Ann. Bot.* 75: 55-65.
- Boote, K.J. and Loomis, R.S. 1991. The prediction of canopy assimilation. In *Modelling crop photosynthesis from biochemistry to canopy*. CSSA Special Publication number 19. Am. Soc. Agron.-Crop Sci. Soc. Am. 100-140.
- Carvalho, S.M.P. and Heuvelink, E. 2004. Modelling external quality of cut chrysanthemum: achievements and limitations. *Acta Hort.* 654: 287-294.
- Cerny, T.A., Faust, J.E., Layne, D.R. and Rajapakse, N.C. 2003. Influence of photoselective films and growing season on flowering of six plant species. *J. Amer. Soc. Hortic. Sci.* 128: 486-491.
- Cockshull, K.E., Graves, C.J. and Cave, C.R.J. 1992. The influence of shading on yield of glasshouse tomato. *J. Hortic. Sci.* 67: 11-24.
- De Koning, A.N.M. 1993. Growth of a tomato crop: measurements for model validation. *Acta Hort.* 328: 141-146.
- Dieleman, J.A. and Meinen, E. 2007. Interacting effects of temperature integration and light intensity on growth and development of single-stemmed cut rose plants. *Sci. Hortic.* 113: 182-187.
- Elings, A., De Zwart, H.F., Janse, J., Marcelis, L.F.M. and Buwalda, F. 2006. Multiple-day temperature settings on the basis of the assimilate balance: a simulation study. *Acta Hort.* 718: 227-232.
- Fanourakis, D., Maaswinkel, R.H.M. and Heuvelink, E. 2007. Analysis of genetic variation in cut chrysanthemum response to high carbon dioxide concentration (closed greenhouse): underlying physiological and morphological parameters. Report 483 Wageningen UR Greenhouse Horticulture, 32p.
- Foyer, C.H., Chaumont, M., Murchie, E., Galtier, N. and Ferrario, S. 1995. End-product modulation of carbon partitioning with a view to improved biomass production. In: Madore, M.A. and W.J. Lucas (eds.), *Carbon partitioning and source-sink interactions*

- in plants. Rockville: Amer. Soc. Plant Physiol., 45–55.
- Gijzen, H. and Goudriaan, J. 1989. A flexible and explanatory model of light distribution and photosynthesis in row crops. *Agric. For. Meteorol.* 48: 1-20.
- Godin, C. and Sinoquet, H. 2005. Functional-structural plant modelling. *New Phytol.* 166: 705-708.
- González-Real, M.M. and Baille, A. 2000. Changes in leaf photosynthetic parameters with leaf position and nitrogen content within a rose plant canopy (*Rosa hybrida*). *Plant Cell Environ.* 23: 351-363.
- González-Real, M.M., Baille, A. and Gutiérrez Colomer, R.P. 2007. Leaf photosynthetic properties and radiation profiles in a rose canopy (*Rosa hybrida* L.) with bent shoots. *Scientia Hort.* 114: 177-187.
- Goudriaan, J. 1977. Crop micrometeorology: a simulation study. Simulation Monographs, Pudoc, Wageningen: 249 p.
- Gunnlaugsson, B. and Adalsteinsson, S. 2006. Interlight and plant density in year-round production of tomato at northern latitudes. *Acta Hort.* 711: 71-76.
- Hay, R.K.M. 1995. Harvest index – a review of its use in plant breeding and crop physiology. *Ann. Appl. Biol.* 126: 197-216.
- Healy, K.D., Rickert, K.G., Hammer, G.L. and Bange, M.P. 1998. Radiations use efficiency increases when the diffuse component of inside radiation is enhanced by shading. *Aust. J. Agr. Res.* 49: 665-672.
- Hemming, S., Dueck, T.A., Janse, J. and Van Noort, F. 2008. The effect of diffuse light on crops. *Acta Hort.* 801:1293-1300.
- Hemming, S., Van De Braak, N.J., Dueck, T.A., Jongschaap, R.E.E. and Marissen, N. 2006a. Filtering natural light by the greenhouse covering using model simulations - more production and better quality by diffuse light. *Acta Hort.* 711: 105-110.
- Hemming, S., Kempkes, F., Van der Braak, N., Dueck, T. and Marissen, N. 2006b. Greenhouse cooling by NIR-reflection. *Acta Hort.* 719: 97-105.
- Heuvelink, E., Marcelis, L.F.M. and Körner, O. 2004. How to reduce yield fluctuations in sweet pepper. *Acta Hort.* 633: 349-355.
- Heuvelink, E., Bakker, M.J., Elings, A., Kaarsemaker, R. and Marcelis, L.F.M. 2005. Effect of leaf area on tomato yield. *Acta Hort.* 691: 43-50.
- Heuvelink, E., Bakker, M.J., Hogendonk, L., Janse, J., Kaarsemaker, R. and Maaswinkel R., 2006. Horticultural lighting in the Netherlands: new developments. *Acta Hort.* 711: 25-34.
- Heuvelink, E., Bakker, M.J., Marcelis, L.F.M. and Raaphorst, M. 2008. Climate and yield in a closed greenhouse. *Acta Hort.* 801:1083-1092.
- Hogewoning, S.W., Trouwborst, G., Engbers, G.J., Harbinson, J., Van Ieperen, W., Ruijsch, J., Van Kooten, O., Schapendonk, A.H.C.M. and Pot, C.S. 2007 Plant physiological acclimation to irradiation by Light-Emitting Diodes (LEDs). *Acta Hort.* 761: 183-191.
- Jewett, T.J. and Jarvis, W.R., 2001. Management of greenhouse microclimate in relation to disease control: a review. *Agronomie* 21: 351-366.
- Li, A., Rajapakse, N.C., Young, R.E. and Oi, R. 2000. Growth responses of chrysanthemum and bell pepper transplants to photoselective plastic films. *Sci. Hortic.* 84: 215-225.
- Marcelis, L.F.M. 1994. A simulation model for dry matter partitioning in cucumber. *Ann. Bot.* 74: 43-52.
- Marcelis, L.F.M., Heuvelink, E., Baan Hofman-Eijer, L.R., Den Bakker, J. and Xue, L.B. 2004. Flower and fruit abortion in sweet pepper in relation to source and sink strength. *J. Exp. Bot.* 55: 2261-2268.
- Marcelis, L.F.M. and Heuvelink, E. 2007. Concepts of modelling carbon allocation among plant organs. In: Vos, J., Marcelis, L.F.M., Visser, P.H.B., Struik, P.C., Evers, J.B. (Eds.), *Functional-Structural Plant Modelling in Crop Production*. Springer, The Netherlands, 103-111.
- McMahon, M. and Kelly, J.W. 1995. Anatomy and pigments of chrysanthemum leaves

- developed under spectrally selective filters. *Sci. Hortic.* 64: 203-209.
- Opdam, J.J.G., Schoonderbeek, G.G., Heller, E.M.B. and De Gelder, A. 2005. Closed greenhouse, a starting point for sustainable entrepreneurship in horticulture. *Acta Hort.* 691: 517-524.
- Oyaert, E., Volckaert, E. and Debergh P.C. 1999. Growth of chrysanthemum under coloured plastic films with different light intensities and quantities. *Sci. Hortic.* 79: 195-205.
- Paul, N.D., Jacobson, R.J., Taylor, A., Wargent, J.J. and Moore, J.P. 2005. The use of wavelength-selective plastic cladding materials in horticulture: Understanding the crop and fungal responses through the assessment of biological spectral weighting functions. *Photochem. Photobiol.* 81: 1052-1066.
- Pollet, I.V., Pieters, J.G. and Verschoore, R. 2002. Impact of water drops on the visible radiation transmittance of glazings under outside radiation conditions. *Sol. Ener.* 73: 327-355.
- Pollet, I.V., Pieters, J.G., Deltour, J. and Verschoore, R. 2005. Diffusion of radiation transmitted through dry and condensate covered transmitting materials. *Sol. Ener. Mater. Sol. Cell* 86: 177-196.
- Raviv, M. and Antignus, Y. 2004. UV radiation effect on pathogens and insect pests of greenhouse-grown crops. *Photochem. Photobiol.* 79: 219-226.
- Reuveni, R., Raviv, M. and Bar, R. 1989. Sporulation of *Botrytis cinerea* as affected by photoselective polyethylene sheets and filters. *Ann. Appl. Biol.* 115: 417-424.
- Runkle, E.S. and Heins, R.D. 2002. Stem elongation and subsequent flowering of seedlings grown under a film creating a far-red deficient environment. *Sci. Hortic.* 96: 257-265.
- Sonneveld, P.J., Swinkels, G.L.A.M., Kempkes, G., Van Campen, J. and Bot, G.P.A. 2006. Greenhouse with an integrated NIR filter and a solar cooling system. *Act. Hort.* 719: 123-130.
- Spitters, C.J.T. 1986. Separating the diffuse and direct components of global radiation and its implications for modelling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agric. Forest. Meteor.* 38: 231-242.
- Van Bavel, C.H.M., Damagnez, J. and Sadler, E.J. 1981. The fluid roof solar greenhouse: energy budget analysis by simulation. *Agric. Meteor.* 23: 61-76.
- Van der Velden, N. and Smit, P. 2007. Energiemonitor van de Nederlandse glastuinbouw 2000–2006. Rapport 2.07.15, LEI, The Hague.
- Van der Ploeg, A., Van der Meer, M. and Heuvelink, E. 2007. Breeding for a more energy efficient greenhouse tomato: past and future perspectives. *Euphytica* 158: 129-138.
- Vandenbussche, F., Pierik, R., Millenaar, F.F., Voesenek, L.A.C.J. and Van Der Straeten, D. 2005. Reaching out of the shade. *Curr. Opin. Plant Biol.* 8: 464-458.
- Verlodt, I. and Verschaeren, P. 2000. New interference films for climate control. *Acta Hort.* 514: 139-146.
- Wardlaw, I.F. 1990. The control of carbon partitioning in plants. *New Phytologist* 116: 341–381.
- Warren Wilson, J., Hand, D.W. and Hannah, M.A. 1992. Light interception and photosynthesis efficiency in some glasshouse crops. *J. Exp. Bot.* 43: 363-373.
- Wilson, S.B. and Rajapakse, N.C. 2001. Use of photoselective plastic films to control growth of three perennial salvias. *J. Appl. Hort.* 3: 71-74.
- Zaragoza, G., Buchholz, M., Jochum P. and Pérez-Parra, J. 2007. Watergy project: towards a rational use of water in greenhouse agriculture and sustainable architecture. *Desalination* 211: 296-303.

Figures

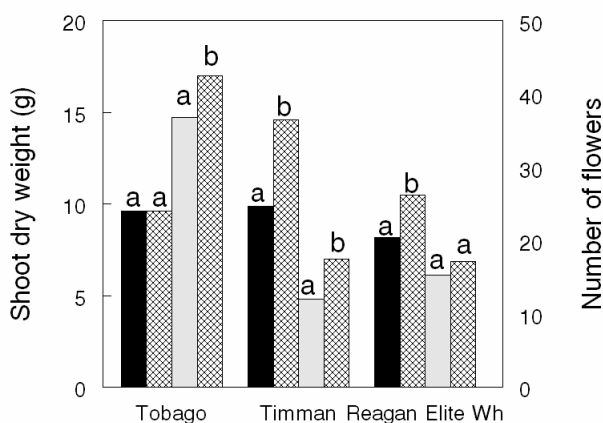


Fig. 1. Shoot dry weight (g; bars 1 and 2) and number of flowers per shoot (bars 3 and 4) for 3 cut chrysanthemum cultivars ('Tobago', 'Timman', 'Reagan Elite White') grown in spring at 500 (solid bars) or 1500 ppm (double-dashed bars) CO₂ concentration (data from Fanourakis et al., 2007). Different letter (cultivar × CO₂ interaction) indicates significantly different shoot dry weight or number of flowers per shoot (Students *t*-test; *P* = 0.05).

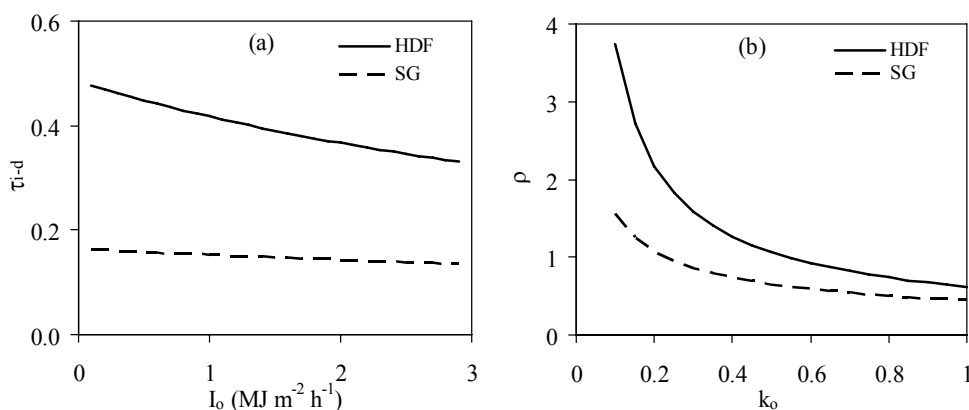


Fig. 2. Fitted curves to hourly data of: (a) the direct-to-diffuse transmission coefficient, τ_{i-d} , vs. the outside direct radiation, I_o , and (b) the greenhouse diffuse enrichment ratio, ρ , vs. the outside diffuse fraction, k_o , for a highly diffusive film, HDF, and standard horticultural glass, SG.

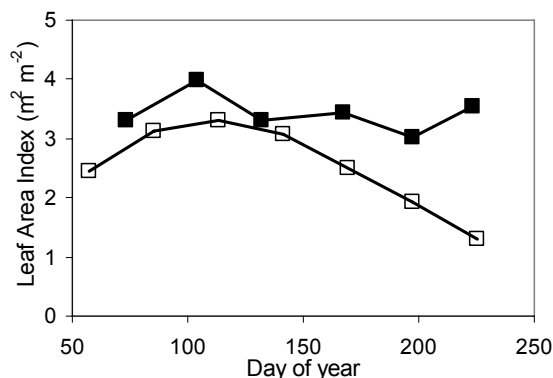


Fig. 3. Typical pattern for leaf area index of a greenhouse tomato crop in 1990 (□; data from De Koning, 1993) and in 2003 (■; data from Heuvelink et al., 2005).

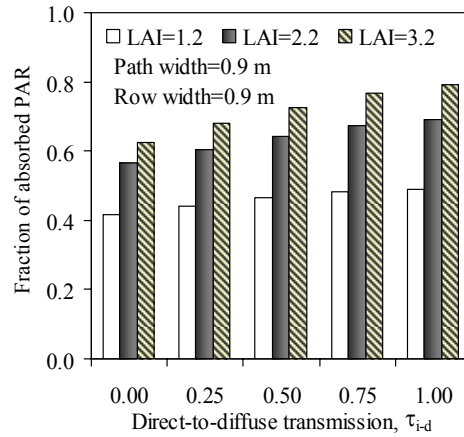


Fig. 4. PAR absorbed by a virtual greenhouse row crop (uniform leaf angle distribution, LAI equally distributed among layers) vs. τ_{i-d} under clear sky ($k_o=0.2$). Equal τ_{PAR} ($=0.75$) for each τ_{i-d} ; values: weighted average over a typical summer in South-Eastern Spain.

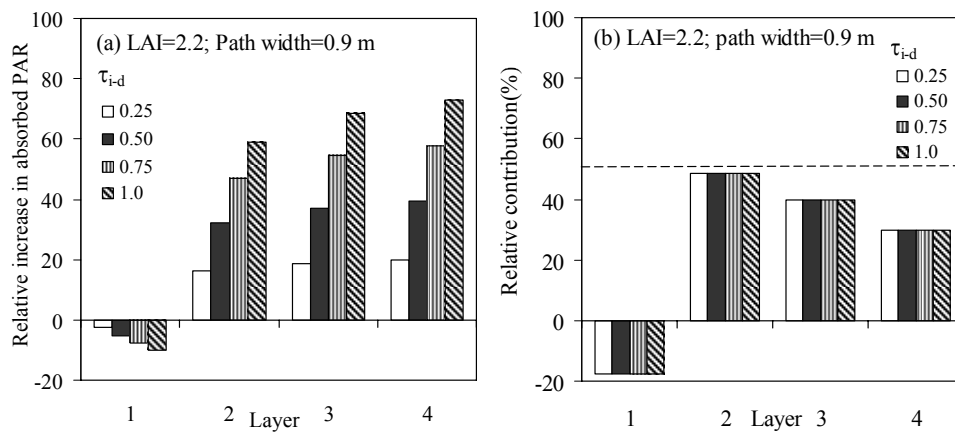


Fig. 5. (a) Maximum relative increase in absorbed PAR (clear sky, $k_o=0.2$) per leaf layer with respect to a clear cover ($\tau_{i-d}=0$) and (b) relative contribution per layer to the absorbed PAR by a virtual greenhouse row crop for different values of the direct-to-diffuse transmission, τ_{i-d} . Same hypothesis than in Figure 4. Typical summer day in South-Eastern Spain.

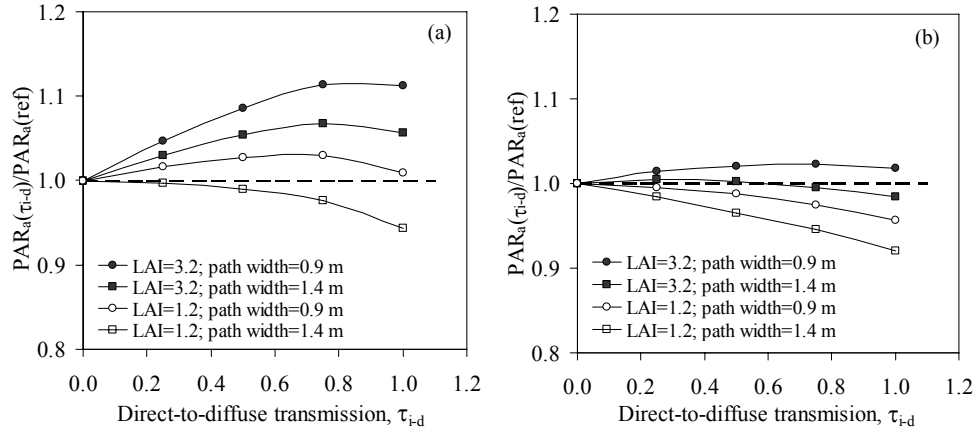


Fig. 6. Influence of the direct-to-diffuse transmission, row spacing (path width) and LAI, on the ratio between PAR absorbed for a virtual greenhouse row crop, PAR_a , at different τ_{i-d} , $PAR_a(\tau_{i-d})$, and PAR_a obtained for the reference, $PAR_{a,ref}$, under conditions of (a) clear ($k_o=0.2$) and (b) partially covered ($k_o=0.4$) sky. Same hypothesis than in Figure 4, except that τ_{PAR} is assumed to decrease proportionally to τ_{i-d} (see text). Typical summer day in South-Eastern Spain.