

Impact of Greenhouse Microclimate on Plant Growth and Development with Special Reference to the Solanaceae

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ABSTRACT

Solanaceous crops (tomato, pepper and eggplant) constitute about 60% of greenhouse-cultivated areas. Their importance is also obvious when considering the large volume of scientific papers published on relevant subjects. Among Solanaceae, the most researched crop is tomato. Considerable attention has been paid to pepper during the last few years, while eggplant is less studied. The great volume of research carried out on tomato does not mean that nothing more left to be investigated. Most of the work done was carried out in greenhouses in Northern countries, while much less has been done in Mediterranean, arid or tropical climates. In modern greenhouses, the role of the computer environment management and control is very important. In order to achieve computer control and management of all the principal greenhouse cultivation procedures, such as climate control, irrigation, fruit harvest etc., it is important to know the effects of greenhouse microclimate on crop response. From this point of view, the present paper addresses the information available to be taken into account when it comes for greenhouse climate control. The growth of Solanaceous plants in a greenhouse is a complex process, governed by the interactions between the plant's genetic properties and the environmental conditions, as modified by climate control. It is therefore difficult to predict intuitively, the management measures necessary to create optimal crop growing conditions and resource use. In the present paper a survey of the effects of greenhouse microclimate on crop response in general, and on tomato, pepper and eggplant in particular, was carried out and the findings are presented and discussed.

Keywords: *Capsicum annuum*, crop response, greenhouse climate control, *Lycopersicon esculentum*, *Solanum melongena*

Abbreviations: BER, blossom-end rot; DM, dry matter; FW, fresh weight; LAR, leaf area ratio; LWR, leaf weight ratio; NAR, net assimilation rate; RGR, relative growth rate; RH, relative humidity; PAR, photosynthetic active radiation; Ps, photosynthesis rate; SLA, specific leaf area; VPD, vapour pressure deficit

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INTRODUCTION

During the last two decades, the productivity and efficiency of horticultural production have received particular attention and a key concept has been to accelerate plant growth. In consequence, farmers are under pressure to use production factors, such as land, water etc. more efficiently, so as

to attain maximum yield per unit area as well as maximum quality. Protected cultivation makes it possible to obtain increased crop productivity by maintaining a favourable environment for the plants. Therefore, production in greenhouses has become more popular than in the past.

The presence of a cover, characteristic of greenhouses, causes a change in the climatic conditions compared to

those outside: radiation and air velocity are reduced, temperature and water vapour pressure of the air increase and fluctuations in carbon dioxide concentration are much higher. Each of these changes has its own impact on the growth, production and quality of the greenhouse crop (Bakker 1995).

The effects of greenhouse environment on growth, development and productivity of crops have been studied by many researchers (Challa and Schapendonk 1984; Bakker *et al.* 1987; Ellis *et al.* 1990; Pearson 1992). Crop yield have been reported to depend on the responses of plants to environmental influences (Ellis *et al.* 1990), for example, temperature has a considerable influence on crop timing and yield (Pearson 1992) and light is a primary determinant of crop growth. Greenhouse air temperature, humidity, and plant leaf temperature are in turn affected by the light transmission of the cover material. For example, improvements in insulation by the use of double-layered polyethylene and acrylic for greenhouse covers have resulted in increased RH in the greenhouse (Blom and Ingratta 1985; Boulard *et al.* 1989).

Photosynthetic rates are reduced at low PAR integrals and it is generally assumed that the loss of light will lead to a proportional loss in yield (Challa and Schapendonk 1984).

The use of greenhouse climate control systems changes the greenhouse microclimate and may have significant effects on the growth, development and productivity of crops. During winter, the main systems used for greenhouse climate control are heating, ventilation and CO₂ enrichment while during summer, the main systems used are ventilation (natural or forced), shading (by screens or whitening) and cooling (by fog or fan and pad systems).

The effects of greenhouse climate control systems on the greenhouse microclimate and crop response are discussed in the present review first with reference to crops in general and subsequently with specific reference to tomato, pepper and eggplant.

EFFECTS OF GREENHOUSE CLIMATE CONTROL ON CROP RESPONSE

Effect of heating

The recent introduction of computer-based systems for greenhouse climate control makes it possible to work with temperature regimes which were either impossible or impracticable with earlier control systems (Cockshull 1985). Set points for temperature can be adjusted continuously in order to obtain the best economic output. This approach is particularly interesting for the introduction of new developments in greenhouse technology, like highly effective thermal screens and the use of waste and reject heat for greenhouse heating, which require new control strategies (Challa and Brouwer 1985). For example, traditionally most greenhouse crops are cultivated at a day temperature (Td) somewhat higher than the night temperature (Tn). However, especially when thermal screens are used in winter, it can be profitable to use an inversed temperature regime (Td < Tn; Leatherland 1986). Adjustment of temperature set point for wind speed (lower temperatures at high wind speed and *vice versa*) led to improvements in fuel economy (Hurd and Graves 1984). Td and Tn requirements of the tomato were first investigated by Went (1944), who found that maximal growth (stem elongation) occurred when the temperature during the dark period was lower than during the diurnal light period. He introduced the term 'thermoperiodicity' for sensitivity to diurnal temperature pattern. It includes all effects of a temperature differential between light and dark periods on the responses of the plant. Young plants appear to have this thermoperiodicity in contrast to producing crops (closed canopies). Calvert (1964) and Hussey (1965) reported reduced growth of young plants under an inversed temperature regime. Hurd and Graves (1984), however, reported that total tomato yield was not influenced by the temperature regime, but mainly by the temperature integral. The

same was found for the yield of sweet pepper (Hand and Hannah 1978) and cucumber (Slack and Hand 1983).

For environmental and financial reasons, reducing energy consumption is becoming more important in greenhouse horticulture. The greenhouse industry is seeking low-energy greenhouse concepts with no or minimal reduction in growth, yield or quality. To diminish environmental impact, greenhouse heating and use of chemicals should be reduced (Pearson *et al.* 1995; Khattak and Pearson 1997) while achieving high quality crops with intelligent climate regimes. For example, leaf unfolding rate and flower development rate respond to 24-h mean temperature (Karlsson *et al.* 1989; Moe and Heins 1990), and temperature integration (e.g. Cockshull *et al.* 1981; Hurd and Graves 1984) can be applied. With temperature integration, the heating set point can be lowered when the heat loss factor for a greenhouse is high and the heating set point can be increased when heat loss is low. In this way, mean temperature can be maintained at the desired level while heating is shifted to periods of lower costs (Lacroix and Kok 1999). For example, temperature integration with heating using energy screens during winter nights can help to reduce energy consumption in winter (Bailey and Seginer 1989; Rijdsdijk and Voegelzang 2000).

Klapwijk and Wubben (1978), using young tomato, cucumber, sweet pepper and chrysanthemum plants, concluded that an inversed (day/night) temperature regime (17/23°C) reduced plant length more than fresh weight, FW. The same was found by Heuvelink (1989) when 26/16°C and 16/26°C day night temperature regimes were compared. For young tomato plants the inversed temperature regime led to a 34% reduction in FW, while plant length was reduced by 56%. However, for 24/18°C and 18/24°C the decrease in FW (-49%) was about the same as the decrease in length (-44%).

Dry matter partitioning is an important determinant of crop yield. Past improvements in the yield potential of crops through selection and breeding, have derived largely from an increase in the proportion of accumulated dry mass that is invested in the plant organs harvested, i.e. the harvest index (Gifford and Evans 1981). In crops such as tomato, dry matter partitioning relates not only to total fruit production, but also to the mass of individual fruits and to the quality of the fruits, important determinants of economic yield.

It is generally agreed that the distribution of assimilates among sinks is primarily regulated by the sinks themselves and that the source strength or assimilate availability is only of minor importance (Gifford and Evans 1981; Farrar 1988; Ho 1988; Marcelis 1993).

Temperature is the most important climatic factor influencing dry matter partitioning in crops, as irradiance and CO₂ concentration primarily affect source strength (Marcelis and de Koning 1995) and dry matter partitioning is unaffected by humidity. However, in the long-term, source strength may influence flower and/or fruit abortion and therefore dry matter partitioning (Marcelis and de Koning 1995). The term sink strength is used to describe the competitive ability of an organ to attract assimilates (Wolswinkel 1985). Temperature affects the sink strength of plant organs directly (Walker and Ho 1977; Williams and Marinos 1977; Yoshioka *et al.* 1986; Marcelis and Baan Hofm-Eijer 1993) and may similarly influence dry matter partitioning. Walker and Ho (1977) and Yoshioka *et al.* (1986) reported that they could enhance carbon import into tomato fruits by warming the fruit. However, this does not necessarily mean that higher plant temperature favours partitioning into the fruits. Should the sink strength of all plant organs respond proportionally to temperature, dry matter partitioning would not change with temperature. Temperature may influence dry matter partitioning indirectly because high temperature enhances development and increases not only the initiation of flowers, buds and fruit but also their abortion due to increasing demand for assimilates (Marcelis and de Koning 1995). For cucumber, with either the same number or same mass of fruit per plant, biomass allocation to the fruits in-

creased with temperature (Marcelis 1993). However, when the number of fruits per plant was not controlled, there were fewer fruits at higher temperature, and temperature had only a slight effect on biomass allocation (Marcelis 1993).

Energy saving measures in greenhouses can result in high levels of humidity which may lead to yield loss and have detrimental effects on product quality. For example, double glazed greenhouses provide insulation and the tight fitting glass panes result in a low exchange of air with the outside environment. There is a decrease in condensation; and moisture introduced by transpiration remains in the house resulting in high RH. Tomato is a crop of major importance to the greenhouse industry and responds to changes in humidity. Tomato leaves which develop under low solar radiation intensities and high humidity are of reduced size and show signs of calcium deficiency (Holder and Cockshull 1990). The subsequent loss of yield occurs from the trusses adjacent to the leaves that develop under high humidity. Calcium arrives at the leaves along with the transpiration stream, since calcium is transported unidirectionally in the xylem and the amount builds up as the leaf grows and transpires (Aikman and Houter 1990). There is a minimum rate of transpiration relative to leaf growth rate below which calcium deficiency symptoms occur. As well as loss of yield, fruit quality can also be reduced, for example the physiological disorder blossom-end rot (BER) is associated with low calcium uptake (Adams and Ho 1993). Experiments have been carried out to quantify the effects of humidity on yield by controlling humidity (or saturation deficit) using set-points which are fixed for different periods of the experiment. The set-points, which may be different for the day and night periods, ensure large differences in humidity between treatments so that the crop response is significant. In commercial greenhouses the RH varies constantly and the aim of humidity control is to avoid environments which would lead to yield and/or quality reductions. In addition, the techniques for control must be cost-effective so that the benefits of control in terms of yield and quality are in excess of the costs of carrying out the dehumidification.

Effect of shading

High temperature and vapour pressure deficit characterize the greenhouse microclimate during summer in most areas with greenhouses in the northern hemisphere if no measures are taken to control these conditions. As a result, both yield and product quality may be suppressed in greenhouse crops grown under such conditions.

The influence of harsh summer climatic conditions on leaf gas exchange is related to the relative response of the fluxes (transpiration or net CO₂ assimilation) and of the stomatal conductance to the environmental stimuli. This response may vary among plant species, cultivar and stage of plant development. In Mediterranean climates, solar radiation inside the greenhouse is often high enough (20–22 MJ m⁻² d⁻¹) around midday to reach values of photosynthetic photon flux density (maximum about 1350 μmol m⁻² s⁻¹) that may cause, along with the high temperature values, a temporary down-regulation of photosynthesis (Medina *et al.* 2002). On the other hand, a semi-confined environment is often promoted within the greenhouse by low ventilation rates due to the absence of wind, therefore leading to low values of the boundary layer conductance, which plays a key role in controlling the physiological fluxes and more or less isolating the plants from the outside environment (Aubinet *et al.* 1989; Collatz *et al.* 1991). Screens mounted inside the greenhouse also contribute to a decrease of the wind speed inside, thus lessening the leaf boundary layer and reducing the availability of air CO₂ concentration near the leaf surface. It is not clear whether shading nets should be used over the whole growth cycle or only during the most sensitive stages when the crops have a low leaf area and the canopy transpiration rate cannot significantly contribute to greenhouse cooling.

The response of plants to light intensity and quality is

relevant in greenhouse production where shading nets and roof whitening are used for reducing the radiation load inside the greenhouse. A strong reduction of solar radiation is expected to slow down the leaf transpiration rate thereby increasing the canopy temperature (Jackson *et al.* 1981). The use of screens has progressively been accepted by growers and has gained, through the last decade, a renewed interest, as shown by the increasing area of field crops cultivated under screened houses (Raveh *et al.* 2003; Cohen *et al.* 2005), while roof whitening, due to its low cost, is currently a common practice in the Mediterranean basin.

In spite of the widespread use of whitening for alleviating the radiation load, the literature related to the influence of whitening on microclimate and crop behaviour is very sparse. Most studies were related to other shading techniques, like outside or inside permanent or movable shading screens (Nisen and Coutisse 1981; Miguel *et al.* 1994, 1997), and dealt mainly with the radiative modifications induced by the shading device. Baille *et al.* (1980) reported that glasshouse whitening reduced solar transmission coefficients by about 40% and allowed the air temperature inside the greenhouse to be maintained close to that outside during summer periods in the south of France. In more recent studies, Kittas *et al.* (1999) and Baille *et al.* (2001) reported that whitening applied to a glass material slightly enhanced the PAR proportion of the incoming solar irradiance, thus reducing the solar infrared fraction entering the greenhouse. Whitening transforms a large part of the inside direct radiation into diffuse radiation (Baille *et al.* 2001). An enhancement of this ratio has been reported to increase the radiation absorbed by the crop (Hand *et al.* 1993), the stomatal conductance and net CO₂ assimilation (Lloyd *et al.* 1995), and has been suggested to increase crop productivity under shading conditions (Healey 1998). This characteristic of whitening could represent an advantage with respect to other shading devices, especially in warm countries with a high radiation load during summer. Another advantage of whitening is that it does not affect greenhouse ventilation, while internal shading nets negatively affect the efficiency of roof ventilation. Within a greenhouse, the reduction of solar radiation by shading nets is not always accompanied by a decrease in temperature, especially under conditions of low ventilation rates. Baille *et al.* (2001) demonstrated the beneficial effect of greenhouse roof whitening on both microclimate and crop behaviour during summer in a warm climate (Greece).

Whether or not the adaptation of plants to the prevailing light conditions can help them to compensate for the reduction in the physiological fluxes that might be expected under shading (Raveh *et al.* 2003) will depend on the specific behaviour of the plant species (Stanhill and Cohen 2001; Barradas *et al.* 2005).

The wide range of plant response to artificial shading reported in the literature can be ascribed to (1) differences in the screen physical properties and the severity of shading, (2) the behaviour of plant species, as they may differ in their ability to accumulate dry matter and partition it to the organs, (3) the stage of plant development (Cohen *et al.* 2005) and (4) plant density (Papadopoulos and Pararajasingham 1997).

Effect of ventilation and cooling

Various methods for cooling the greenhouse atmosphere may be used to maintain more suitable conditions for plant growth. Natural ventilation is usually the first step due to its low cost and simplicity, but is generally not sufficient for extracting the excess energy during sunny summer days. Therefore, other cooling methods must be used in combination with ventilation. As reported by Montero (2006), evaporative cooling techniques have recently become more popular in areas like the Mediterranean basin. This recent interest is associated with the incorporation of insect-proof screens that impose a strong reduction in the rate of air exchange. Hence, since greenhouses with evaporative cooling

require less ventilation for given climatic conditions (Boulard and Baille 1993), evaporative cooling can compensate for the reduced rate of air exchange during hot periods. Evaporative cooling permits simultaneous lowering of temperature and vapour pressure deficit (Arbel *et al.* 1999; Wilits 1999; Katsoulas *et al.* 2001) and can lead to greenhouse air temperatures lower than the outside air temperature. Its efficiency is higher in dry environments, but it also gives satisfactory results in humid coastal environments (Montero and Segal 1993). However, the advantage of mist and fog systems over wet pad systems is the uniformity of conditions throughout the greenhouse, thereby eliminating the need for forced ventilation and airtight enclosure.

Several studies have already shown that reducing transpiration by modifying the microclimate inside the greenhouse (e.g. reducing vapour pressure deficit and incoming solar radiation, direct wetting of the leaves) improves the physiological adaptation of plants to stress conditions, such as salinity or unfavourable external climatic conditions (Joliet and Bailey 1992; Oren *et al.* 1999; Katsoulas *et al.* 2001 2002). However, undesired effects sometimes arise from the response of crops to cooling, such as the appearance of BER (Meca *et al.* 2006), which is often associated with the reduction in air vapour pressure deficit (Lorenzo *et al.* 2004).

Values of air vapour pressure deficit, VPD, in excess of 1.5-2 kPa are known to decrease the stomatal conductance of horticultural crops (Bakker 1991; Baille *et al.* 1994; Katsoulas *et al.* 2002), this decline probably being mediated by lower values of internal CO₂ concentration. The extent to which this behaviour may affect the photosynthesis rate depends on the relative response of both photosynthesis rate and stomatal conductance to the air CO₂ concentration. The thresholds of VPD above which photosynthesis rate and the physiological fluxes are depressed depend on the plant type and stage of development and on the prevailing environmental conditions to which the plants were adapted (Medrano *et al.* 2005).

Effect of CO₂ enrichment

Many research papers have demonstrated the beneficial effects of atmospheric CO₂ enrichment in greenhouse crop production (Long *et al.* 2004). Short-term CO₂ enrichment increased photosynthetic rates of C₃ plants (Cure and Acock 1986) because high concentrations of CO₂ inhibit photorespiration (Drake *et al.* 1997). Increased carbon uptake resulting from the initial stimulation of leaf photosynthesis by CO₂ enrichment could alter the balance between carbohydrate supply and sink, and the non-structural carbohydrate would be increased in the leaves (Drake *et al.* 1997). Such accumulations of carbohydrates in the leaves may cause a long-term reduction in photosynthetic capacity per unit leaf area (acclimation) (Drake *et al.* 1997).

The current ambient level of atmospheric CO₂ (about 360 ppm) is a limiting factor for maximum photosynthesis (Tolbert and Zelitch 1983); therefore, any increase in CO₂ above the ambient level has the potential to increase the rate of photosynthesis, especially in C₃ plants. This increased rate of photosynthesis will directly affect plant growth (Yelle *et al.* 1990; Lawlor and Mitchell 1991; Islam *et al.* 1996; Das *et al.* 2000).

A large body of literature has been published over the last decade on actual and predicted impacts of elevated atmospheric CO₂ concentrations on the physiology and productivity of plants. The results vary considerably with regard to the type and magnitude of the response (Bunce 1998; Catovsky and Bazzaz 1999; Weigel *et al.* 2005). For instance, many studies have shown that plant responses to high CO₂ levels are dependent on nutrient availability (Thompson and Woodward 1994; Gebauer *et al.* 1996; Bauer *et al.* 2001), while most studies dealing with CO₂ enrichment and nutrients have focused on interactions between nitrogen and phosphorus nutrition and CO₂ enrichment (Kim *et al.* 2003; Heaton *et al.* 2004).

It has been shown that the percentage effect on relative growth rate is about the same over a range of light levels (Mortensen and Moe 1983b; Mortensen and Ulsaker 1985). This also means that the light compensation point is lowered by increased CO₂ concentration (Mortensen and Moe 1983a, 1983b). It has been shown for some species that CO₂ enrichment might compensate for a 30% reduction in light intensity (Mortensen and Ulsaker 1985).

The effect of CO₂ enrichment increases with increasing temperatures within a certain range. The optimum temperature for photosynthesis will increase in CO₂-enriched air (Mortensen 1987). In practice, growers are often advised to increase the ventilation temperature by 2-4°C when CO₂ enrichment is used. Raising the CO₂ concentration reduces transpiration by 20-40% (Morison 1985). Water consumption is thus significantly reduced by CO₂ enrichment at the same time as photosynthesis is increased.

At one time it was a common practice to enrich greenhouses to 2000-3000 ppm CO₂ because it was believed that the higher the concentration the better. Later, a CO₂ concentration of 1000-1500 ppm was recommended. In the last few years, it has been shown in a number of experiments that concentrations above 900 ppm very seldom give any beneficial effect (Heij and Uffelen 1984; Mortensen and Ulsaker 1985). For most species it is impossible to give the exact optimal CO₂ concentration, because most experiments with CO₂ enrichment include only a few CO₂ concentrations. However, from the literature, it might be concluded that the optimal CO₂ concentration for plant growth lies between 600 and 900 ppm for most species.

Pot plants, cut flowers, vegetables and some forest plants show very positive effects of CO₂ enrichment by increased dry weight, plant height, number of leaves and lateral branching (Mortensen 1987). Plant quality, expressed by growth and number of flowers, is also often enhanced by CO₂ enrichment. Increased growth rates by CO₂ application has in many cases reduced the production time. This means increased production per year. All this information clearly shows the great advantage of CO₂ enrichment on greenhouse plants in general.

Inside a non-enriched greenhouse, the CO₂ concentration drops below the atmospheric level whenever the CO₂ consumption rate by photosynthesis is greater than the supply rate through the greenhouse vents. CO₂ depletion depresses the daily photosynthetic rate, which is estimated to be about 15%, integrated over 29 days of simulation, when the concentration drops below 340 ppm (Schapendonk and Gastra 1984). The poor efficiency of ventilation systems of the low-cost greenhouses in Mediterranean countries, coupled with the use of insect-proof nets (Munoz *et al.* 1999) explains the relatively high CO₂ depletion (20% or more) reported in southern Spain (Lorenzo *et al.* 1990). CO₂ enrichment is common in the greenhouse industry of Northern Europe as a means of enhancing crop photosynthesis under the low radiation conditions that prevail during winter in those regions. This situation explains why most of the present information on the effects of CO₂ enrichment on horticultural crops was gathered under climatic conditions and production systems (computerized climate-controlled greenhouses) typical of Northern Europe. Such knowledge and technology are not directly transferable to the environmental and socio-economic conditions of the Mediterranean countries, where CO₂ enrichment is not a common practice for several reasons. One of the main restrictions is the short time duration available for the efficient use of CO₂ enrichment, due to the need to ventilate for temperature control (Enoch 1984). The fact that greenhouses have to be ventilated during a large proportion of the daytime makes it uneconomical to maintain a high CO₂ concentration during the daytime. However, some authors advise supplying CO₂ even when ventilation is operating (Nederhoff 1994) to maintain the same CO₂ concentration in the greenhouse as outside and enriching to levels of about 700-800 ppm during the periods when the greenhouse is kept closed, usually in the early morning and the late afternoon.

EFFECT OF GREENHOUSE MICROCLIMATE ON THE SOLANACEAE

Effects on tomato

Effect of temperature

Air temperature and VPD are very important microclimate parameters affecting tomato crop production and quality. Temperature and irradiation conditions during fruit development greatly influence fruit development and quality. Chronic mild heat stress limits pollen release and fruit set (Sato *et al.* 2000). After fruit set, fruit growth is also strongly related to fruit temperature (Pearce *et al.* 1993). Temperature may influence the distribution of photo-assimilates between fruits and vegetative parts (see review by Dorais *et al.* 2001). During fruit maturation changes in fruit temperature can affect carotenoid biosynthesis (Tomes 1963; Koskitalo and Ormrod 1972) and vitamin C biosynthesis (Liptay *et al.* 1986).

The effects of day temperature on gas exchanges in three tomato ecotypes (North European cultivar 'Moneymaker'; Japanese cultivar 'Ogata Zuiko'; South European cultivar 'Roma') were studied by Jun *et al.* (1990). The best temperature regime for net photosynthesis was at 28/20°C and the worst was at 18/20°C in all three cultivars. Among the cultivars used, 'Moneymaker' showed the highest and 'Roma' showed the lowest rate of net photosynthesis in every temperature regime. At 28/20°C, a similar light dependence of photosynthesis was observed among the three cultivars, but in the other temperature regimes 'Moneymaker' showed the highest response to irradiance. Transpiration was positively correlated with net photosynthesis in all the cultivars, but there was no consistent relationship between net photosynthesis and dark respiration.

During its development, a tomato fruit becomes more sensitive to temperature (Klapwijk 1987). The observed effect of the treatments on the harvestable truss number are in accordance with this, since in young plants the first truss was harvested a little earlier than in the control plants when high temperature was applied after a low-temperature period. For growth, measured as fresh weight increase, tomato shows a large temperature compensating capacity. For old plants, even at the two most extreme treatments (12 days at 1.5°C or 6 days at 3°C), total compensation was achieved. For both these treatments, the temperature sum deviated at most by 18 degree-days from the control. **Fig. 1** shows tomato plants three days after exposition to very low temperature (0-3°C) for a few hours.

From CO₂ uptake and fresh weight growth measurements, Liebig (1988) suggested that: (1) photosynthesis is predominantly determined by the amount of light (2) the assimilates produced flow into a reserve pool (3) all pro-

cesses involved in the conversion from (stored) assimilates to fresh weight growth are affected mainly by temperature. In such a mechanism, assimilates may be stored at low temperature, and during a period of subsequent high temperature stored assimilates are released and used for (fresh weight) growth.

Several authors report reduced elongation of plants grown under negative DIF (Mortensen and Moe 1987; Erwin and Heins 1988; Heuvelink 1989; Karlsson *et al.* 1989; Moe and Heins 1989).

High temperatures have been shown to interfere with the reproductive development in numerous species, including tulip, iris, chrysanthemum and tomato, and in general, the higher the temperature the higher the percentage of abortion. In tomato, growth chamber and greenhouse studies suggest that high temperature is most deleterious at the time the flowers are first visible and the sensitive stage for the first inflorescence continues for 10 ± 15 days (Kinet 1977). Moore and Thomas (1952) found that when the average maximum temperature was >32°C and the average minimum temperature was >21°C, fruit set in tomatoes was low. Explanations suggested for poor fruit set in tomatoes at high temperatures include: direct effects on pollen and other reproductive tissues, low levels of carbohydrates, and hormonal imbalances (Kinet and Peet 1997). Few data exist in tomatoes on the relative importance of high temperatures during the night compared to those during the day. Most studies have either been conducted with both high day and high night temperature, or only high day temperature. Went (1945) and Went and Cospar (1945) concluded that the critical factor in the setting of tomato fruit is the night temperature, the optimum range being 15-20°C. In these studies and those of Schaible (1962) and Curme (1962), a number of night temperature treatments were imposed, but day time conditions were less than ideal. Light was low and often spectrally unbalanced, given for only 8 h daily in growth chambers or varied throughout the year in greenhouses. In a series of experiments in North Carolina, maintaining night temperatures below 21°C during fruit set increased fruit weight by 28, 53 and 11% in the autumn of 1989, autumn 1990 and spring 1991, respectively (Peet and Willits 1992). Thus, it was clear that high night temperatures during fruit set can limit tomato production in greenhouses in climates as warm as North Carolina. Presumably, fruit set would have been limited outside as well since night temperatures in the un-cooled greenhouses were within 0.5°C of outdoor temperatures and the studies were conducted in double-polyethylene covered houses, where longwave transmissivity was high enough (approximately 63%; Godbey *et al.* 1979) to permit significant radiant cooling. Seasonal variations in night temperatures were not sufficient to determine if cooling at night to 20°C was too low or not low enough. To answer this question, Peet and Bartholomew (1996) conducted a growth chamber experiment in which the effects of night temperatures of 12, 14, 18 and 26°C were compared at a day temperature of 26°C (12 h day/12 h night). Although, seed content, fruit number and fruit set decreased with increasing night temperature, changes were much less than expected based on the greenhouse data. These results led Peet *et al.* (1997) to question the independence of day and night temperature. Night temperatures of 26°C may have been less detrimental in the growth chamber experiment, for example, as the day temperatures were more nearly optimal and in a further study it was found that all the reproductive processes examined, except the lower production and average fruit weight, decreased linearly with increasing mean temperature over 25°C. Day/night differential and the specific day/night temperature combination had minimal effects on relative seed content, fruit number, fruit weight and fruit set, beyond the influence of mean daily temperature (Peet *et al.* 1997).

Willits and Peet (1998) examined data from six seasons of night cooling with greenhouse grown tomatoes to determine the effect of night temperature on yield. Regressions observed suggested a strong dependence of yield on night



Fig. 1 Tomato plants damaged after exposition to low temperature (0-3°C) for a few hours. (A) Very strong symptoms, (B) strong symptoms.

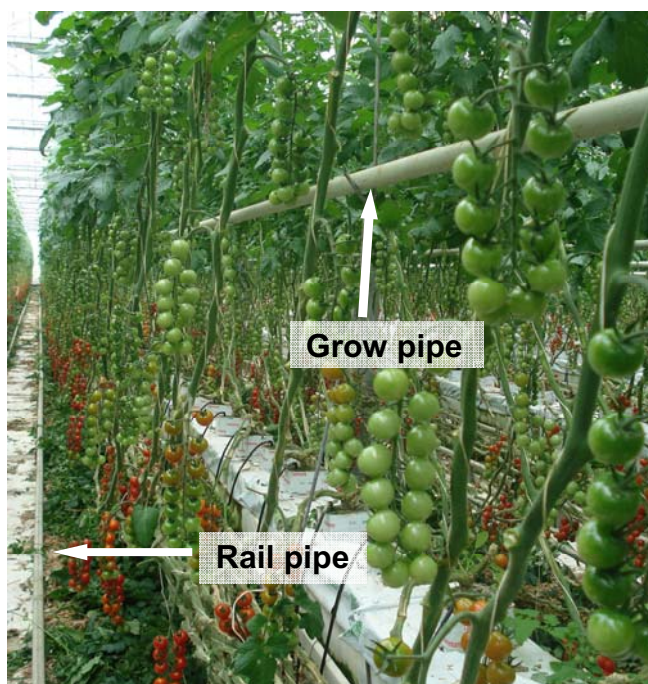


Fig. 2 Greenhouse and tomato crop heating by grow and rail pipes. Grow pipes supplied by water of about 50°C and rail pipes by water of about 85°C.

temperature during fruit set. They found that when night temperatures in the warm treatment were around 21°C (treatment differences less than 1°C), night cooling had almost no effect on yield. However, as night temperatures in the warm treatment approached 24°C (differences of 4°C) night cooling was found to increase yield by as much as 40 ± 50%. Quality was even more enhanced, with No. 1 grade increasing by 85-106%. Regression also suggested secondary effects on fruit quality, e.g. fruit quality was detrimentally affected when cooler night temperatures extended over the whole season but positively affected when night time RH during fruit set was reduced. Finally, Willits and Peet (1998) mention that a secondary effect of irradiance during fruit set on total weight differences suggested that night cooling might be more beneficial during sunny weather. However, this secondary effect cannot be stated with a great deal of confidence, due to the limited amount of data upon which it was based; however, it does suggest an area of interest and focus for future work.

Gautier *et al.* (2004) concluded that the heating pipes located near the tomato truss significantly increased fruit temperature and reduced fruit water content. In addition, heating could also reduce DM accumulation for lower fruit/source ratio due to lower sugar and acid contents. In contrast, under high fruit/source ratio, heating had no effect on sugar content, but other compounds derived from secondary metabolism were very sensitive to fruit temperature; for example, the content of vitamin C, β-carotene and lycopene were strongly reduced by heating, resulting in a reduction of the fruit nutritive value. Greenhouse heating systems have been developed so that could supply the correct amount of heat at the correct part of the plant. **Fig. 2** shows a grow pipe, designed to supply heat near the tomato plant fruits before ripening and a rail pipe to heat the root of the plants and the greenhouse air along with the tomato plant by convection and radiation heat dissipation.

De Graaf (1985) reported a reduction in the transpiration rate of a tomato crop when a transparent, moisture-proof plastic film was used as a thermal screen. He concluded that when moisture ventilation was provided in the greenhouses with screens, the difference in transpiration rate between greenhouses with and without screens disappeared. A thermal screen is expected to increase the amount of net radiation absorbed by the crop, as it reflects part of



Fig. 3 Thermal screen used for energy saving and greenhouse shading.

the long-wave radiation emitted by the heating pipes and the greenhouse surfaces. Consequently, for constant transpiration rates, a screen is likely to increase the crop temperature. Moreover, a thermal screen could influence crop performance, such as the rate of development (leaf unfolding and flowering), over a wide range of temperatures (Karls-son *et al.* 1991). Additional knowledge about how the crop energy balance and surface temperature are modified by a thermal screen could be of interest for the evaluation of a given screen material or for predicting the occurrence of condensation. The latter is of crucial importance for the control of fungal diseases (Nicot and Baille 1996). Except for temperature control during night by radiation losses reduction, thermal screens are also used for temperature control during day by shading and reduction of incoming solar radiation (**Fig. 3**).

Effect of radiation

In recent years, the difficulties of growing high quality tomatoes in conventional greenhouses located in coastal areas during late spring and summer has encouraged the use of nets as cladding material to grow tomatoes in the Mediterranean region.

Changes in greenhouse microclimate may have significant effects on the growth, development and productivity of crops (Cockshull *et al.* 1992). Net photosynthetic rates are reduced at low light levels and the loss of tomato yield is proportional to the loss of light (Challa and Schapendonk 1984; Cockshull *et al.* 1992).

The authors of the present paper carried out measurements during (a) a winter and (b) a summer crop season in a tomato crop developed under a greenhouse with a polyethylene cover and a total solar radiation transmission of about 60% and under a control greenhouse with a total solar radiation transmission of about 78%. The leaf area index of the tomato crop was similar in the two greenhouses during the winter period but was higher under the low radiation transmission greenhouse during the summer period.

Depression of crop yield is frequently observed under Mediterranean conditions when strong radiation and low air humidity prevail. Such conditions reduce water transfer into the tomato fruit and enhance fruit transpiration, as reported by Leonardi *et al.* (2000a, 2000b). Mild stress conditions are also known to slow down water accumulation by tomato fruit without affecting dry matter accumulation and lead to the production of small fruits in summer with a higher dry matter content and better quality, e.g. higher DM and sugar concentrations (Guichard *et al.* 2001).

Romacho *et al.* (2006) conducted a two-year study to characterise the microclimate and quantify the growth and

yield of cherry tomato under protective screens. Two types of nets (screens) were used: clear (A) and green coloured (B). Microclimate was similar under both nets, with mean transmission around 60% of global radiation and slightly lower values of temperatures and air humidity than in the open air. No significant differences in high-quality yield were found, with 2.72 (A) kg m⁻² and 3.17 (B) kg m⁻² in the first year (late planting cycle) and 4.49 (A) kg m⁻² and 4.52 (B) kg m⁻² in the second year.

El-Gizawy *et al.* (1992) observed that increasing shading intensity in a tomato crop by up to 51% resulted in total production increase. The same authors mention that the highest tomato crop production was obtained under 35% shading, while increasing the shading intensity decreased by up to 100% the incidence of sunscald on fruit. However, El-Aidy (1983) observed that the highest tomato production was obtained under 40% shading and that increasing the shading intensity to values higher than 40% did not further increase yield.

Kittas *et al.* (2008) studied the effect of different shading intensity nets on tomato crop microclimate, production and quality and observed similar values of air temperature and VPD under the shading nets and outside. However, the canopy temperature and accordingly, the canopy-to-air VPD were significantly lower under the shading nets than in the open field. Finally, these authors concluded that shading increased the leaf area index and total marketable yield, reduced the appearance of tomato cracking by about 50% and accordingly, the marketable tomato production was about 50% higher under shading conditions than under non-shading conditions.

Effect of vapour pressure deficit

Continuous low VPD can induce calcium deficiency, with concomitant leaf area reduction in greenhouse tomato (Holder and Cockshull 1990). Low VPD in the day time increased early tomato yield, but the final yield was reduced by low VPD regardless of day or night. Mean fruit quality was also reduced under low VPD (Holder and Cockshull 1990). Early vegetative growth and yield of cucumber were enhanced by either low day or night VPD, and final total yield was negatively related to day time VPD (Bakker *et al.* 1987).

It has been observed that high values of VPD alter the water balance by decoupling the transpirational flux and root water uptake (Grange and Hand 1987), thus leading to water deficits which increase the occurrence of physiological disorders (Aloni *et al.* 1999; Yao *et al.* 2000). These conditions along with high values of the root zone temperature, as often observed in soilless culture during the spring-summer period (Baille *et al.* 1994), induced a depression of yield and the production of small fruit. Several studies are available on the interactions between VPD and source-sink manipulations in relation to crop productivity and quality (Bertin *et al.* 2000; Gautier *et al.* 2001), and these interactions have also been shown to be rather complex (Bertin *et al.* 2000). Changes in the source-sink balance over a growth cycle may be promoted by competition between the vegetative and the generative organs for water and carbohydrates (Marcelis and Baan Hofman-Eijer 1995; Gautier *et al.* 2001), as well as by inter-fruit competition (Heuvelink and Körner 2001). Decreasing VPD under conditions of low fruit load has been observed to attenuate the seasonal decrease in yield often observed in tomato, mainly due to higher individual fruit fresh weight. However, fruit quality (higher dry matter and sugar contents) was enhanced under high VPD and a low fruit load (Bertin *et al.* 2000; Gautier *et al.* 2001). Under low RH, increasing VPD from 1.6 to 2.2 kPa has been observed to reduce the fruit growth rate in tomato. This is mainly due to water shortage induced by a higher rate of transpiration, since air VPD has an effect on fruit fresh weight but not on the accumulation of fruit dry matter (Leonardi *et al.* 2000a, 2000b).

Depending on the light conditions, the anthers open 2-8

h after sunrise (Erwin 1931; Kiss 1970) to allow the pollen to fall on to the stigma. At high RH, tomato pollen tends to remain inside the anthers (van Koot and van Ravestijn 1963). On the other hand, high RH promotes pollen germination (Henny 1985; van Ravestijn 1986) and also improves pollen adhesion to the flower stigmatic surface (van Koot and van Ravestijn 1963; van Ravestijn 1986).

The incidence of blossom end rot (BER) may be greater in greenhouses with high humidity levels, since BER is partially associated with low transpiration rates. It has been reported that high humidity may cause calcium deficiency in tomato leaves (Holder and Cockshull 1990). Water flow to the fruit is governed by the gradient of water potential between the stem and the fruit, which is influenced by transpiration (Li 2000). Fruit water potential is more stable under sunny conditions than water potential in leaves. A change in transpiration may therefore cause Ca to be transported to the leaves rather than toward the fruits, since the gradient from the stem to the leaves may be greater than that between the stem and the fruits. The balance between fruit growth rate and Ca availability in fruit is probably related to the incidence of this physiological disorder. This, together with the complex mechanism of water and Ca transport to the fruit, may explain the differences in crop response to evaporative cooling.

Salinity has become the most severe agricultural problem in many parts of the world, but it has been reported that a humid atmosphere may modulate the effect of salinity (Sonneveld 1988). Research into the interaction between reduced VPD and plant response to salinity has been conducted in climatic areas as different as The Netherlands and Mediterranean Spain. Li *et al.* (2001) presented a comparative response of a tomato crop as a function of the level of salinity. Two climate treatments were compared: a reference treatment (with high transpiration, but no fog) and a 65% 'depressed' transpiration treatment (with low transpiration and a fog system). They found that the rate of decrease in yield was lower for the greenhouse with low transpiration. This means that the negative effect of salinity was mitigated when greenhouse VPD was constrained to a moderate level. During the day, this was between 0.23 and 0.60 kPa for north European climate conditions (with a global radiation integral of close to 11 MJ m⁻² d⁻¹).

In Mediterranean areas, the use of saline irrigation water in greenhouses with reduced VPD is a subject of interest. Romero-Aranda *et al.* (2002) reported positive results on the use of intermittent misting for tomato plants grown under saline conditions. In the misted treatment, air VPD was maintained at below 1.5 kPa, while in the non-misted treatment VPD was as high as 3.5 kPa at noon, with a maximum air temperature of 36°C. Under these conditions intermittent misting increased total leaf area and dry matter. Yield was also increased by 18% with respect to non-misted plants. Yields of salinised plants grown with mist increased by 100% with respect to non-misted plants.

Fruit cuticle cracking is also a major problem in many crops including tomato (Dorais *et al.* 2004) and sweet pepper (Aloni *et al.* 1999; Yao *et al.* 2000) because it strongly downgrades the marketable yield and reduces fruit shelf life. Evidence exists that factors affecting plant water status are likely to influence fruit shrinkage and a clear interaction has been observed between air VPD and plant fruit load with respect to this physiological disorder (Bertin *et al.* 2000; Guichard *et al.* 2001).

Effect of CO₂ enrichment

Greenhouse CO₂ enrichment has been practiced by tomato growers since the 1960s in the Netherlands and then in England (Nederhoff 1994). For example, van Oosten and Besford (1995) found that there was an accelerated decline in the photosynthesis of tomato leaves grown at elevated CO₂ following an initial increase during early leaf expansion. Therefore, the response of plants to long-term CO₂ enrichment may be limited by the acclimation of photosynthetic

capacity. Furthermore, the response to CO₂ enrichment may vary with climate, greenhouse structure and ventilation. Research conducted in northern Europe has shown that greenhouse tomato production benefits from summer CO₂ enrichment and thus commercial greenhouse growers have adopted this practice.

Responses of greenhouse tomatoes to CO₂ enrichment are strongly influenced by the duration of CO₂ enrichment and the greenhouse climate. While CO₂ enrichment generally benefits tomato fruit production in winter, its effects on summer production (under high air temperature and strong ventilation) are still not clear, especially when the crop has been subjected to long term CO₂ enrichment in winter.

Hao *et al.* (2006) found that leaf photosynthesis, as indicated by the CO₂ response curve, partially acclimated to the CO₂ enrichment. Stem dry weight was increased while fruit dry weight and marketable fruit yield were reduced by summer CO₂ enrichment. However, high air temperature might have affected fruit setting and thus limited the response to CO₂ enrichment. Carbohydrate translocation to stems was increased while translocation to fruit was reduced by summer CO₂ enrichment. Further investigation on carbohydrate translocation is needed to clarify the mechanism limiting the response of greenhouse tomatoes to summer CO₂ enrichment.

Effects on pepper

Effect of temperature

Temperature plays a major role in the growth (Bakker and van Uffelen 1988), flowering (Rylski 1972; Polowick and Sawhney 1985) and fruit set (Rylski 1973; Rylski and Spigelman 1982) of sweet pepper.

In The Netherlands, sweet pepper is grown as a long season crop with planting dates in late November and early December and final harvest in October. Irregular fruit set is one of the main problems experienced in the glasshouse cultivation of sweet pepper. Differences in the rate of flowering and fruit set, cause variations in fruit production and vegetative growth since these processes are closely correlated (Kato and Tanaka 1971). Information on the effects of other environmental factors on flowering and fruit set is limited.

Rylski and Spigelman (1982) carried out trials on sweet pepper under controlled temperature conditions and natural light. In the first trial, they examined night temperatures of 15, 18, and 24°C (± 1°C) in combination with a day temperature of 24°C, and in the second trial day temperatures of 22, 15 and 28°C (12 hours) and divided day temperatures of 28-32-28°C (4+4+4 hours) in combination with a night temperature of 18°C. They found that the highest fruit-set was obtained at the lowest night temperature. The highest night temperature caused considerable blossom drop, but the highest day temperature tested did not cause increased blossom drop.

Effect of radiation

Many crops are sensitive to high temperatures, which may induce bud and flower abscission related to assimilate levels and partitioning within the plant. Abscission of sweet pepper flowers is known to be enhanced by low light and high temperature (Aloni *et al.* 1999). These authors stressed that the threshold for the amount of light needed for daily sugar accumulation in the leaf blades was much lower than that required by the flowers buds; thus the sink leaves and flower buds compete for assimilates under restricted light conditions.

Application of shading (26-47%) to a pepper crop decreased sunscald on fruit from 36% of total production under no shading to 3-4% of total production under shading (Rylski and Spigelman 1986).

Gonzalez-Real and Baille (2006) presented the effects

of an aluminised screen on leaf gas exchange of sweet pepper plants. They observed that a daily decrease of radiation induced by shading at the top of the canopy (about 20% with respect to unshaded conditions) resulted in both contrasting flux rates and stomatal conductance values within the canopy. The values of stomatal conductance measured under shading for the uppermost and middle leaf layers were, respectively, higher or equal to that observed under unshaded conditions. This behaviour induced assimilation and transpiration rates similar or higher to those observed without shading. However, this compensatory effect was not observed in the lowest layer, where CO₂ assimilation and transpiration were slightly lower. These differences between the upper and lower layers may be explained by the fact that for a sweet pepper crop the radiation level which apparently saturates the uppermost leaves is about 1000 μmol m⁻² s⁻¹, while lower values are required for the leaves within the canopy (about 800 μmol m⁻² s⁻¹). Thus, whenever the amount of radiation is higher than these thresholds, a reduction of electron transport rate would be expected, accompanied by a decrease of photochemical quenching and a significant increase of non-photochemical quenching. This response may explain why, under moderate shading, a sweet pepper crop maintains similar values of CO₂ assimilation rate to those prevailing under unshaded conditions.

Effect of vapour pressure deficit

Baer and Smeets (1978) found that high 24-h average air humidity improved fruit set, but also enhanced flower abscission during the early production period in a growth chamber experiment. Although humidity itself has no significant effect on early and final yield of sweet pepper (Bakker 1989) its control might be beneficial to obtain more uniform fruit set, and thereby reduce variation in production without reducing the final yield.

The effects of day and night humidity on flowering, fruit set, seed set and fruit growth of sweet pepper (*C. annuum*) cv. 'Delphin' were investigated in a glasshouse experiment by Bakker (1989). A continuously high or low RH and alternating high and low RH by day and night were applied during the early post-planting period from early December until mid-April. Numbers of flowers and fruits showed a significant positive correlation with VPD by night. Fruit set and number of seeds per fruit were increased by low VPD during the day. No significant effect of VPD was found on fruit shape (length/width ratio), the number of cavities per fruit, pericarp thickness, dry matter content and fruit maturation rate.

Bakker (1989) who studied the effect of VPD (which varied from 0.33 to 0.66 kPa by day, from 0.27 to 0.86 kPa by night and the 24-h average from 0.30 to 0.75 kPa) did not find a significant effect of humidity on vegetative growth of sweet pepper over the range investigated. Similar results were also obtained by Baer and Smeets (1978) and Bakker (1989). Baer and Smeets (1978) did not find a significant effect of RH on fruit set under normal growing conditions irrespective of whether artificial pollination was applied or not, but Bakker (1989) mentioned that fruit set is significantly increased by high humidity (low VPD) during the day.

Katsoulas *et al.* (2007) studied the effects of a fog cooling system on the greenhouse microclimate, fruit production and quality in a summer-to-autumn pepper crop. They found that the use of a fog system for greenhouse cooling significantly reduced the air and crop temperature and the VPD, to a level of 1.1 kPa compared to about 2.0 kPa under no fog, and improved the physiological status of the plants, while maintaining relatively high transpiration rates.

Furthermore, they found that the fog system enhanced mean fruit weight and the percentage of marketable fruits, but significantly reduced the total number of fruits per plant. It seems that high levels of RH may affect fruit set in pepper crops, particularly when combined with reduced levels of incoming solar radiation as a result of greenhouse sha-



Fig. 4 Pepper fruit with BER symptoms.

ding, presumably due to restricted pollination and increased flower abortion. Nevertheless, this effect of the fog system does not seem to reduce the marketable fruit yield because the microclimate prevailing during summer in greenhouses, if no cooling system is available, results in a very high percentage of non-marketable fruits. With respect to fruit quality characteristics, the fruit size is enhanced under conditions of air cooling by means of a fog system in the summer, while the total soluble solids and the titratable acidity of the fruit sap may be slightly reduced.

The above results do not agree with a number of tests conducted in Almeria (Gazquez *et al.* 2006). The marketable yield of sweet pepper there was lower in a fog-cooled greenhouse than in a shaded greenhouse. Statistical differences were found between fruits affected by BER, with the number of affected fruits being higher in the greenhouse with fog.

Gonzalez-Real and Baille (2006) presented an example of the response to VPD of a sweet pepper crop grown under high values of VPD inside the greenhouse during summer in Southeast Spain (maximum about 4 kPa). They found that the rates of leaf transpiration measured for the different leaf classes are strongly enhanced with increasing VPD. This means that, under unrestricted conditions of water and nutrients, the leaf transpiration rate is weakly affected by stomatal conductance and responds mainly to the climatic demand.

Pepper is a greenhouse crop sensitive to salinity and susceptible to BER (Fig. 4). Montero (2006) mentions that high humidity induced by fogging statistically improved yield (5.7 kg per plant compared with 4.9 kg per plant in the greenhouse without fogging). Fruit quality was also improved by high humidity since BER was 24% of total production in the greenhouse without fogging. The positive effect of high humidity was even stronger for the treatment with high electrical conductivity.

Effect of CO₂ enrichment

High CO₂ levels promote fruit set as a result of improved photosynthesis (Nederhoff and van Uffelen 1988). Baba *et al.* (2006) studied three Italian-type sweet pepper cultivars, 'Palermo', 'Estar' and 'Charly', grown in rockwool, and subjected to CO₂ enrichment up to 500 and 800 $\mu\text{L L}^{-1}$, compared with those in a non-enriched environment. Plant growth, measured as plant height, stem diameter, number of leaves and leaf area, was higher in the CO₂ enriched greenhouses. However, the incidence of BER was lower in the control plants and higher in plants with CO₂ enrichment, especially at 500 $\mu\text{L L}^{-1}$. The CO₂ enrichment resulted in a significant improvement in water use efficiency, both for marketable and total production.

CO₂ enrichment leads to an increase in early and total

yield of sweet pepper, particularly at a high concentration (800 $\mu\text{L L}^{-1}$) in accordance with the results of other authors (Frydrych 1984; Akilli *et al.* 2000) and with us (Maroto *et al.* 2003), and agrees with results obtained for cucumber in Mediterranean-type greenhouses (Sanchez-Guerrero *et al.* 2005). However, although supplemental CO₂ increases plant growth (Fierro *et al.* 1994; Maroto *et al.* 2003), intensive growth may predispose plants to stress by factors such as high temperatures, cited as the main factor involved in Ca transport disorders in the Spanish Mediterranean area (Maroto 1997).

Baba *et al.* (2006) found that stomatal density was increased in CO₂-enriched atmospheres (500 and 800 $\mu\text{L L}^{-1}$). Although the influence of CO₂ concentration on this parameter is not clear in the literature, since contradictory effects have been described in different species by different authors, the present result confirms our previous findings in sweet pepper (Maroto *et al.* 2003). Under elevated CO₂ concentration stomata are partially closed, reducing transpiration and consequently there is insufficient cooling and a higher incidence of Ca-deficiency disorders at high temperatures or under high radiation (Nederhoff *et al.* 1992). Nederhoff *et al.* (1992) observed that improved CO₂ concentrations increase the leaf conductance but have a relatively small incidence on transpiration.

Effects on eggplant crop

Flowering and fruit set of eggplant is affected by temperature (Nothmann *et al.* 1979) and plant-water status (Tedeschi and Zerbi 1985). Moreover, it has been suggested that climatic changes may induce a seasonal variation in fruit-setting ability (Sun *et al.* 1990).

Uzun found that there was a positive relationship between light intensity and plant stem diameter in both tomato and eggplant. Stem diameter in tomato and eggplant increased curvilinearly with increasing temperatures and there was as an interactive effect of temperature and light intensity on stem diameter. It was also found that an increase in temperature from 10 to 32°C led to an increase in plant height of tomato and eggplant (Atherton and Harris 1986; Cockshull *et al.* 1992; Pearson 1992; Kurklu 1994; Uzun 1996; Cemek 2002). Cemek *et al.* (2005) reported that plant height was greater in eggplants grown in double polyethylene-covered greenhouses, which had a higher temperature, than in single polyethylene-covered greenhouses.

Romano and Leonardi (1994) studied the effects of three minimum air temperatures (9, 11 and 13°C) on the vegetative growth and fruiting of tomato and eggplant (normal and parthenocarpic cultivars). The temperature conditions did not affect the vegetative growth of tomato, but the lower minimum temperatures reduced or delayed the fruiting process. By contrast, in eggplant both vegetative and fruit growth were negatively affected by the lower minimum temperatures. This result agrees with the observations of Uzun (2006) concerning the different temperature requirements of tomato and eggplant. Romano and Leonardi (1994) reported that the response of parthenocarpic and normal cultivars to minimum temperature conditions (9, 11 and 13°C) was similar.

The authors of the current paper (unpublished data) studied the effect of fog cooling on greenhouse air temperature and VPD, on eggplant leaf temperature, crop transpiration rate and crop water stress index. They found that fog cooling reduced VPD by about 50%, significantly reduced crop temperature, reduced crop transpiration rate by about 30% and enhanced crop physiological status as indicated by the crop water stress index (calculated as referred by Katsoulas *et al.* 2001).

Cemek *et al.* (2005) studied the effect of light levels on an eggplant crop and found that an increase in the daily mean light integral caused a decline in both specific leaf area (SLA) and leaf area ratio (LAR), as the effect of decreasing temperature. It was also observed that the changes in relative growth rate (RGR) with the lowest daily mean

light integral was related to changes in LAR of eggplant rather than net assimilation rate (NAR), whereas changes in RGR of eggplants grown with a higher daily mean light integral was determined mainly by NAR, but also by LAR. This result is in good agreement with those of other authors (Nilwik 1981; Heuvelink 1989; Uzun 1996), who showed that changes in RGR due to temperature regime are mainly caused by the changes in LAR. When considering changes in RGR due to daily mean light integral, Bruggink (1992) reported that there was a negative correlation of LAR with NAR at different light levels.

Uzun (2006) established quantitative relationships between the combined effects of temperature (between 7.4 and 24.2°C) and light intensity (between 1.9 and 8.1 MJ m⁻² d⁻¹) on the number of leaves formed before the first fruit in tomato and eggplant. The number of leaves formed before the set of the first fruit (eggplant) or fruit cluster (tomato) decreased for both species when the daily mean light integral increased, but the effect of light decreased as temperature declined. Leaf number subtending the first fruit or fruit cluster in both tomato and eggplant declined linearly with decreasing temperature, particularly at the lowest daily mean light integral (1.9 MJ m⁻² d⁻¹). However, temperature had little effect on the number of leaves formed before the first fruit cluster of tomato and the first fruit of eggplant at the higher daily mean light integrals. The study therefore showed that the appearance/position of the first fruiting flower cluster and flower for tomato and eggplant, respectively, could be regulated by controlling light and temperature in the greenhouse.

Prolonging the photoperiod with supplementary light results in increased growth and yield for many species and is a widely used technique in greenhouses (Koontz and Prince 1986; Warrington and Norton 1990; Fierro *et al.* 1994). However, many studies have reported the appearance of interveinal chlorosis and necrosis of leaves in several Solanaceae species including eggplant, tomato and potato, when exposed to supplementary light (Bradley and Janes 1985; Cushman *et al.* 1995; Murage *et al.* 1996a, 1996b; Stutte *et al.* 1996). In contrast, pepper plants do not appear to suffer from leaf injury and grow normally even under continuous light (Demers *et al.* 1994).

In the continuous-light-sensitive plants, like eggplant (Murage *et al.* 1996a, 1996b), leaf injury is preceded not only by a loss of the photosynthetic ability due to feedback inhibition (Demers *et al.* 1994; Stutte *et al.* 1996), but also by a loss of carbon metabolism competence, resulting in massive accumulation of starch in the leaves (Logendra *et al.* 1990; Murage *et al.* 1996b, 1996c; Stutte *et al.* 1996). Dorais *et al.* (1996) reported that in these situations, photosynthetic efficiency is reduced as interception of the incoming light continues unabated. It is therefore, possible that a direct leakage of electrons to molecular oxygen occurs, enhancing the generation of toxic oxygen species. This can damage the ultrastructure and function of chloroplasts, as well as the photosynthetic pigments, leading to leaf chlorosis (Foyer *et al.* 1994).

Aguilera *et al.* (2001) studied the effects of three different CO₂ concentrations in the irrigation water (0.1, 0.2 and 0.3 g l⁻¹) against a control (0.0 g l⁻¹ CO₂) on the yield of eggplant 'Cava' grown under greenhouse conditions. Fruit yield increased by 13% with 0.1 g l⁻¹ of CO₂ and 28% with 0.2 g l⁻¹ of CO₂ compared to the control. These authors also found that at 0.3 g l⁻¹ CO₂, the yield increased by only 18%, suggesting that the maximum yield increase can be achieved by applying 0.2 g l⁻¹ CO₂. Carbonated water also increased the number of fruits per plant by 9%, 21% and 8% with 0.1, 0.2 and 0.3 g l⁻¹ of CO₂, respectively. This correlated with an increase in the number of flowers by 10%, 26%, and 18%. The average weight of fruits increased proportionally with the dose of CO₂ by 3.2%, 5.3% and 9.1% mainly because of an increase in fruit diameter. From these data, it was concluded that carbonated water increased the yield, number of fruits per plant, and the average weight of fruits. The maximum yield increase was obtained with 0.2 g l⁻¹ of

CO₂ whereas the higher dose (0.3 g l⁻¹ of CO₂) produced the maximum weight of fruit.

CONCLUSIONS – FUTURE PERSPECTIVES

It is true that during recent years agriculture is experiencing a transition from conventional forms, with simple methods and extensive areas, to an intensified production pattern symbolized by increased knowledge and improved technology. In the course of change, modern protected cultivation plays a more and more important role. As one part of protected cultivation, greenhouse production is most representative, and it has been developing rapidly due to the creation of optimal environments for crops and an avoidance of the adverse effects of natural climates by artificial climate control and management technology. Greenhouses were originally designed to provide the crop with a shelter from unfavourable climatic conditions. When properly equipped with climate control devices, the greenhouse becomes a factory for intensive crop production. However, the use of greenhouse climate control systems changes the greenhouse microclimate and has significant effects on the growth, development and productivity of crops.

In the present paper, a survey of the effects of greenhouse microclimate on tomato, pepper and eggplant crops has been carried out and the effects of greenhouse microclimate factors (temperature, humidity, radiation and CO₂) on crop response are presented and discussed. The above crops all belong to the family Solanaceae, and especially in the case of tomato cover about 60% of greenhouse-cultivated areas. Among the Solanaceae, the most researched crop is tomato, but considerable attention has also been paid to pepper during the last few years, while eggplant has been less studied. However, the great volume of research carried out on tomato does not mean that there is nothing more left to be investigated since most of the work done until now was carried out in greenhouses in Northern countries, while much less has been done in Mediterranean, arid or tropical climates.

When referring to modern greenhouses, we have to emphasize the significant role of the computer (due to its high speed, precise calculation and high level of automation, standardization and intellectualization) in modern environment management and control. In order to achieve computer control and management of all the principal greenhouse cultivation procedures, such as climate control, irrigation, fertilization, even fruit harvest, the first important thing is to learn the effects of greenhouse microclimate (including temperature, solar radiation, soil moisture, CO₂) on crop response. From this point of view, the present paper addresses the information available for use in crop model development and for greenhouse climate control. The growth of Solanaceous plants in a greenhouse is a complex process, governed by the interactions between the plant's genetic properties and the environmental conditions, as modified by climate control. It is therefore difficult to predict intuitively, the management measures necessary to create crop growing conditions that will lead to optimal resource use. Dynamic crop growth models, in which insights into plant physiological processes and their dependence on environmental conditions are combined, may provide a practical aid to management decision-making, so that the effects of alternative management strategies can be examined. With the advantages of computers, changes in the greenhouse environment can be understood in real-time by means of the continual acquisition and accumulation of information. Through analysis and treatment of these data, the optimization scheme can be made so as to provide scientific, intelligent, quantitative management for greenhouse crop cultivation.

REFERENCES

- Adams P, Ho LC (1993) Effects of environment on the uptake and distribution of calcium in tomato and on the incidence of blossom-end rot. *Plant and Soil*

- 154, 127-132
- Aguilera C, Murcia D, Ruiz A** (2001) Effects of carbon dioxide enriched irrigation on yield of eggplant (*Solanum melongena*) production under greenhouse conditions. *Acta Horticulturae* **559**, 223-228
- Aikman DP, Houter G** (1990) Influence of radiation and humidity on transpiration: implications for calcium levels in tomato leaves. *Journal of Horticultural Science* **65**, 145-253
- Akilli M, Ozmerzi A, Ercan N** (2000) Effect of CO₂ enrichment on yield of some vegetables grown in greenhouses. *Acta Horticulturae* **534**, 131-234
- Ali AM, Kelly WC** (1993) Effect of pre-anthesis temperature on the size and shape of sweet pepper (*Capsicum annuum* L.) fruit. *Scientia Horticulturae* **54**, 97-105
- Aloni B, Karni L, Moreshet S, Yao C, Stanghellini C** (1999) Cuticular cracking in pepper fruit: II. Effect of fruit water relations and fruit expansion. *Journal of Horticultural Science Biotechnology* **74**, 1-5
- Arbel A, Yekutieli O, Barak M** (1999) Performance of a fog system for cooling greenhouse. *Journal Agricultural Engineering Research* **72**, 129-136
- Atherton JG, Harris GP** (1986) Flowering. In: Atherton JG, Rudich J (Eds) *The Tomato Crop*, Chapman and Hall, London, pp 167-200
- Aubinet M, Deltour J, de Halleux D** (1989) Stomatal regulation in greenhouse crops: analysis and simulation. *Agricultural and Forest Meteorology* **48**, 11-44
- Baba MY, Maroto JV, San Batoutista A, Pascual B, Lopez S, Baixauli C** (2006) Agronomic response of sweet pepper (*Capsicum annuum*) to CO₂ enrichment in greenhouses with static ventilation. *Acta Horticulturae* **719**, 521-528
- Baer J, Smeets L** (1978) Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). *Netherlands Journal Agricultural Science* **26**, 59-63
- Bailey BJ, Seginer I** (1989) Optimum control of greenhouse heating. *Acta Horticulturae* **145**, 512-418
- Baille A, Kittas C, Katsoulas N** (2001) Influence of whitening on greenhouse microclimate and crop energy partitioning. *Agricultural and Forest Meteorology* **107**, 193-306
- Baille M, Baille A, Delmon D** (1994) Microclimate and transpiration of greenhouse rose crop. *Agricultural and Forest Meteorology* **71**, 83-97
- Baille M, Mermier M, Laury JC, Delmon D** (1980) Le point sur les systemes d'ombrage sous serre. Internal Report M/801. INRA, Station de Bioclimatologie d'Avignon, Montfavet
- Bakker JC** (1989) The effects of day and night humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). *Journal of Horticultural Science* **64**, 41-46
- Bakker JC** (1991) Analysis of humidity effects on growth and production of glasshouse fruit vegetables. PhD thesis, Agricultural University, Wageningen, The Netherlands, 155 pp
- Bakker JC** (1995) Greenhouse climate control: constraints and limitations. *Acta Horticulturae* **399**, 15-37
- Bakker JC, Van Uffelen JAM** (1988) The effects of diurnal temperature regimes on growth and yield of sweet pepper. *Netherlands Journal of Agricultural Science* **36**, 101-208
- Bakker JC, Welles GWH, Van Uffelen JAM** (1987) The effects of day and night humidity on yield and quality of greenhouse cucumbers. *Journal of Horticultural Science* **62**, 363-370
- Barradas VL, Nicolás E, Torrecillas A, Alarcón JJ** (2005) Transpiration and canopy conductance of young apricot (*Prunus armeniaca* L.) trees subjected to different PAR levels and water stress. *Agricultural Water Management* **77**, 323-333
- Bauer GA, Bertson GM, Bazzaz FA** (2001) Regenerating temperate forests under elevated CO₂ and nitrogen deposition: Comparing biochemical and stomatal limitation of photosynthesis. *New Phytologist* **152**, 149-266
- Bertin N, Guichard S, Leonardi C, Longuenesse JJ, Langlois D, Navez V** (2000) Seasonal evolution of the quality of fresh glasshouse tomatoes under Mediterranean conditions, as affected by air vapour pressure deficit and plant fruit load. *Annals of Botany* **86**, 741-750
- Blom TJ, Ingratta FJ** (1985) The use of polyethylene film as greenhouse glazing in North America. *Acta Horticulturae* **170**, 69-80
- Boulard T, Baille A, Lagier J, Mermier M, Vanderschmitt E** (1989) Water vapour transfer in a plastic house equipped with a dehumidification heat pump. *Journal Agricultural Engineering Research* **44**, 191-204
- Boulard T, Baille A** (1993) A simple greenhouse climate control model incorporating effects of ventilation and evaporative cooling. *Agricultural and Forest Meteorology* **65**, 145-157
- Bradley FM, Janes HW** (1985) Carbon partitioning in tomato leaves exposed to continuous light. *Acta Horticulturae* **174**, 293-301
- Bruggink GT** (1992) A comparative analysis of the influence of light on growth of young tomato and carnation plants. *Scientia Horticulturae* **51**, 71-81
- Bunce JA** (1998) The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *Experimental Botany* **49**, 1555-1561
- Calvert A** (1964) The effects of air temperature on growth of young tomato plants in natural light conditions. *Journal of Horticultural Science* **39**, 194-211
- Catovsky S, Bazzaz FA** (1999) Elevated CO₂ influences the responses of two birch species to soil moisture: Implications for forest community structure. *Global Change Biology* **5**, 507-518
- Cemek B** (2002) Effects of different covering materials on growth, development and yield of crop and environmental conditions inside greenhouses. PhD thesis, Ondokuz Mayıs University, Samsun Turkey
- Cemek B, Demir Y, Uzun S** (2005) Effects of greenhouse covers on growth and yield of aubergine. *European Journal of Horticultural Science* **70**, 16-22
- Challa H, Brouwer P** (1985) Growth of young cucumber plants under different diurnal temperature patterns. *Acta Horticulturae* **174**, 111-217
- Challa H, Schapendonk A** (1984) Quantification of effects of light reduction in greenhouses on yield. *Acta Horticulturae* **148**, 501-510
- Cockshull KE** (1985) Greenhouse climate and crop response. *Acta Horticulturae* **174**, 185-292
- Cockshull KE, Graves CJ, Carol RJ** (1992) The influence of shading on yield of glasshouse tomatoes. *Journal of Horticultural Science* **67**, 11-24
- Cockshull KE, Hand DW, Langton FA** (1981) The effects of day and night temperature on flower initiation and development in chrysanthemum. *Acta Horticulturae* **125**, 101-110
- Cohen S, Raveh E, Li Y, Grava A, Goldschmidt EE** (2005) Physiological response of leaves, tree growth and fruit yield of grapefruit trees under reflective shading screens. *Science Horticulturae* **107**, 15-35
- Collatz GJ, Ball JT, Grivet C, Berry J** (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* **54**, 107-136
- Cure JD, Acock B** (1986) Crop responses to carbon dioxide doubling: A literature survey. *Agricultural and Forest Meteorology* **38**, 127-145
- Curme JH** (1962) Effect of low night temperatures on tomato fruitset. *Proceedings of a Plant Science Symposium 1962*, Campbell Soup Co., Camden NJ, pp 99-108
- Cushman KE, Tibbits TW, Sharkey TD, Wise RR** (1995) Constant-light injury of potato: temporal and spatial patterns of carbon dioxide assimilation, starch content, chloroplast integrity and necrotic lesions. *Journal of the American Society for Horticultural Science* **120**, 1032-1040
- Das M, Pal M, Zaidi PH, Raj A, Sengupta UK** (2000) Growth response of mungbean to elevated level of carbon dioxide. *Indian Journal of Plant Physiology* **5**, 132-135
- de Graaf R** (1985) The influence of thermal screening and moisture gap on the transpiration of glasshouse tomatoes during the night. *Acta Horticulturae* **174**, 57-59
- Demers DA, Yelles S, Gosselin A** (1994) Effect of continuous lighting on enzyme activities of leaf carbon metabolism of tomato and pepper plants. *HortScience* **29**, 250
- Dorais M, Demers D, Papadopoulos A, Van Imperen W** (2004) Greenhouse tomato fruit cuticle cracking. *Horticultural Reviews* **30**, 163-173
- Dorais M, Papadopoulos AP, Gosselin A** (2001) Greenhouse tomato fruit quality. *Horticultural Reviews* **26**, 319
- Dorais M, Yelle S, Gosselin A** (1996) Influence of extended photoperiod on photosynthate partitioning and export in tomato and pepper plants. *New Zealand Journal of Crop and Horticultural Science* **24**, 29-37
- Drake BG, Gonzalez-Meler M, Long SP** (1997) More efficient plants: A consequence of rising atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* **48**, 607-637
- El-Aidy F, El-Afry M** (1983) Influence of shade on growth and yield of tomatoes cultivated during the summer season in Egypt. *Plasticulture* **47**, 1-6
- El-Gizawy AM, Abdallah MME, Gomaa HM, Mohamed SS** (1992) Effect of different shading levels on tomato plants 2. Yield and fruit quality. *Acta Horticulturae* **323**, 349-354
- Ellis RH, Hadley P, Roberts EH, Summerfield RJ** (1990) Quantitative relations between temperature and crop development and growth. In: Jackson MT, Ford-Lloyd BV, Parry ML (Eds) *Climatic Change and Plant Genetic Resources*, Belhaven Press, London, pp 85-115
- Enoch HZ** (1984) Carbon dioxide uptake efficiency in relation to crop-intercepted solar radiation. *Acta Horticulturae* **162**, 137-147
- Erwin AT** (1931) Anthesis and pollination in Capsicum. *American Society of Horticultural Science* **27**, 309-310
- Erwin JE, Heins RD** (1988) Effect of diurnal temperature fluctuations on stem elongation circadian rhythms. *HortScience* **23**, 164-168
- Farrar JF** (1988) Temperature and the partitioning and translocation of carbon. In: Long SP, Woodward FI (Eds) *Plants and Temperature, Symposium of the Society of Experimental Biology* **42**, Company of Biologists Ltd., Cambridge pp 203-235
- Fierro A, Tremblay N, Gosselin A** (1994) Supplemental carbon dioxide and light improved tomato and pepper seedling growth and yield. *HortScience* **29**, 152-154
- Foyer CH, Lelandais M, Kunert KJ** (1994) Photooxidative stress in plants. *Physiologia Plantarum* **92**, 696-717
- Frydrych J** (1984) Factors affecting photosynthetic productivity of sweet pepper and tomatoes grown in CO₂-enriched atmosphere. *Acta Horticulturae* **162**, 171-278
- Gautier H, Guichard S, Tchamitchian M** (2001) Modulation of competition between fruits and leaves by flower pruning and water logging, and conse-

- quences on tomato leaf and fruit growth. *Annals of Botany* **88**, 645-652
- Gautier H, Rocci A, Grasselly D, Buret M, Causse M** (2004) Effect of adding heating pipes on the temperature and the physical and chemical traits of tomato fruits. *Acta Horticulturae* **691**, 59-66
- Gazquez JC, Lopez JC, Baeza E, Saez M, Sanchez-Guerrero MC, Medrano E, Lorenzo P** (2006) Yield response of a sweet pepper crop to different methods of greenhouse cooling. *Acta Horticulturae* **719**, 507-514
- Gebauer RLE, Reynolds JF, Strain BR** (1996) Allometric relations and growth in *Pinus taeda*: The effect of elevated CO₂ and changing N availability. *New Phytology* **134**, 85-93
- Gifford RM, Evans LT** (1981) Photosynthesis, carbon partitioning and yield. *Annual Review of Plant Physiology* **32**, 485-509
- Godbey LC, Bond TE, Zorning HF** (1979) Transmission of solar and long-wavelength energy by materials used as covers for solar collectors and greenhouses. *Transactions of the ASAE* **22**, 1137-1144
- Gonzalez-Real MM, Baille A** (2006) Plant response to greenhouse cooling. *Acta Horticulturae* **719**, 427-438
- Grange RI, Hand DW** (1987) A review of the effects of atmospheric humidity on the growth of horticultural crops. *Journal of Horticultural Science* **62**, 125-134
- Guichard S, Bertin N, Leonardi C, Gary C** (2001) Tomato fruit quality in relation to water and carbon fluxes. *Agronomie* **21**, 385-392
- Hand DW, Hannah MA** (1978) Sweet pepper: application of lower-than-normal temperatures for varying durations within the night periods. *Annual Report Glasshouse Crops Research Inst., Littlehampton* **1977**, 53-55
- Hand DW, Warren Wilson J, Hannah MA** (1993) Light interception by a row crop of glasshouse pepper. *Journal of Horticultural Science* **68**, 695-730
- Hao X, Wang Q, Khosla S** (2006) Responses of a long greenhouse tomato crop to summer CO₂ enrichment. *Canadian Journal of Plant Science* **86**, 1433-1436
- Healey KD, Rickert KG, Hammer GL, Bange MP** (1998) Radiations use efficiency increases when the diffuse component of inside radiation is enhanced by shading. *Australian Journal of Agricultural Research* **49**, 665-672
- Heaton E, Voigt T, Long SP** (2004) A quantitative review comparing the yields of two candidate C₄ perennial biomass crops in relation to nitrogen, temperature and water. *Biomass and Bioenergy* **27**, 11-30
- Heij G, van Uffelen JAM** (1984) Effects of CO₂ concentration on growth of glasshouse cucumber. *Acta Horticulturae* **162**, 19-36
- Henny RJ** (1985) *In vivo* pollen germination of *Aglaonema* affected by relative humidity. *HortScience* **20**, 142-143
- Heuvelink E** (1989) Influence of day and night temperature on the growth of young tomato plants. *Scientia Horticulturae* **38**, 11-22
- Heuvelink E, Körner O** (2001) Parthenocarpic fruit growth reduces yield fluctuation and Blossom End Rot in sweet pepper. *Annals of Botany* **88**, 69-74
- Ho LC** (1988) Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annual Review of Plant Physiology* **39**, 355-378
- Holder R, Cockshull KE** (1990) Effects of humidity on the growth and yield of glasshouse tomatoes. *Journal of Horticultural Science* **65**, 31-39
- Hurd RG, Graves CJ** (1984) The influence of different temperature patterns having the same integral on the earliness and yield of tomatoes. *Acta Horticulturae* **148**, 547-554
- Hussey G** (1965) Growth and development in the young tomato. III The effect of night and day temperatures on vegetative growth. *Journal Experimental Botany* **16**, 373-385
- Islam MS, Matsui T, Yoshida Y** (1996) Effect of carbon dioxide enrichment on physico-chemical and enzymatic changes in tomato fruits at various stages of maturity. *Scientia Horticulturae* **65**, 137-149
- Jackson RD, Idso SB, Reginato RJ, Pinter PJ Jr.** (1981) Canopy temperature as a crop water stress indicator. *Water Resources Research* **17**, 1133-1138
- Jolliet O, Bailey BJ** (1992) The effect of climate on tomato transpiration in greenhouses: Measurements and models comparison. *Agricultural and Forest Meteorology* **58**, 43-62
- Jun H, Imai K, Suzuki Y** (1990) Effects of day temperature on gas exchange characteristics in tomato ecotypes. *Scientia Horticulturae* **42**, 321-327
- Karlsson MG, Heins RD, Erwin JE, Berghage RD, Carlsson WH, Biernbaum JA** (1989) Temperature and photosynthetic photon flux influence chrysanthemum shoot development and flower. *Journal of the American Society of Horticultural Science* **114**, 158-163
- Karlsson MG, Heins RD, Gerberick JO, Hackmann ME** (1991) Temperature driven leaf unfolding in *Hibiscus rosa-sinensis*. *Scientia Horticulturae* **45**, 323-331
- Kato T, Tanaka M** (1971) Studies on the fruit setting and development of sweet peppers. I. Fruiting behavior. *Journal of the Japanese Society for Horticultural Science* **40**, 359-366
- Katsoulas N, Baille A, Kittas C** (2001) Effect of misting on transpiration and conductances of a greenhouse rose canopy. *Agricultural and Forest Meteorology* **106**, 133-247
- Katsoulas N, Baille A, Kittas C** (2002) Influence of leaf area index on canopy energy partitioning and greenhouse cooling requirements. *Biosystems Engineering* **83**, 349-359
- Katsoulas N, Kittas C, Tsirogiannis IL, Kitta E, Savvas D** (2007) Greenhouse microclimate and soilless pepper crop production and quality as affected by a fog evaporative cooling system. *Transactions of the ASABE* **50**, 1831-1840
- Khattak AM, Pearson S** (1997) The effect of light quality and temperature on the growth and development of chrysanthemum cvs. Bright Golden Anne and Snowdon. *Acta Horticulturae* **435**, 113-121
- Kim HY, Loeffering M, Kobayashi K, Okada M, Mitchell MW, Gumpertz M** (2003) Effects of free-air CO₂ enrichment and nitrogen supply on the yield of temperate paddy rice crops. *Field Crops Research* **83**, 161-270
- Kinet JM** (1977) Effects of light conditions on the development of the inflorescence in tomato. *Journal of the American Society Horticultural Science* **86**, 575-581
- Kinet JM, Peet MM** (1997) Tomato. In: Wien HC (Ed) *The Physiology of Vegetable Crops*, CABI, Wallingford, UK, pp 207-258
- Kiss A** (1970) Studies on pollen viability in the pepper variety collection at Taposzele. *Agrobotanika* **12**, 53-60
- Kittas C, Baille A, Giaglaras P** (1999) Influence of covering material and shading on the spectral distribution of light in greenhouses. *Journal of Agricultural Engineering Research* **73**, 341-351
- Kittas C, Rigakis N, Katsoulas N, Bartzanas T** (2008) Influence of shading screens on microclimate, growth and productivity of tomato. *International Symposium on 'Strategies Towards Sustainability of Protected Cultivation in Mild Winter Climate'*, Antalya, Turkey, 6-11 April 2008, p 33 (Abstract)
- Klapwijk D** (1987) Temperatuur stoekmaat (2): Bloeisnelheid, rij pingsduur en lengtegroei. *Groenten Fruit* **43**, 42-43
- Klapwijk D, Wubben CFM** (1978) Effect of various temperatures regimes at a same temperature sum on plant growth. Annual Report 1977, Glasshouse Crops Research and Experiment Station, Naaldwijk, pp 27-28
- Koontz HV, Prince RP** (1986) Effect of 16 and 24 hours daily radiation (light) on lettuce growth. *HortScience* **21**, 123-124
- Koskitalo LN, Ormrod DP** (1972) Effects of sub-optimal ripening temperatures on the color quality and pigment composition of tomato fruit. *Journal of Food Science* **37**, 56-59
- Kurklu A** (1994) Energy management in greenhouses using phase change materials (Pcms). PhD thesis, Reading University, 253 pp
- Lacroix R, Kok R** (1999) Simulation-based control of enclosed ecosystems. A case study: determination of greenhouse heating setpoints. *Canadian Journal of Agricultural Engineering* **41**, 175-183
- Lawlor DW, Mitchell RAC** (1991) The effects of increasing CO₂ on crops photosynthesis and productivity: A review of field studies. *Plant, Cell and Environment* **14**, 807-818
- Leatherland M** (1986) Dotted the effort regime. *Grower Supplement* **105**, 83-87
- Leonardi C, Baille A, Guichard S** (2000a) Predicting transpiration of shaded and nonshaded tomato fruits under greenhouse environment. *Scientia Horticulturae* **84**, 197-307
- Leonardi C, Guichard S, Bertin N** (2000b) High vapour pressure deficit influences growth, transpiration and quality of tomato fruits. *Scientia Horticulturae* **84**, 185-296
- Li LY** (2000) Analysis of greenhouse tomato production in relation to salinity and shoot environment. PhD thesis, Wageningen University, Wageningen, 96 pp
- Li LY, Stanghellini C, Challa H** (2001) Effect of electrical conductivity and transpiration on production of greenhouse tomato. *Scientia Horticulturae* **88**, 11-29
- Liebig HP** (1988) Temperature integration by kohlrabi growth. *Acta Horticulturae* **230**, 371-380
- Liptay A, Papadopoulos AP, Bryan HH, Gull D** (1986) Ascorbic acid levels in tomato (*Lycopersicon esculentum* Mill.) at low temperature. *Agricultural and Biological Chemistry* **50**, 3185-3187
- Lloyd J, Chin Wong S, Styles JM, Batten D, Priddle R, Tunbull C, McConchie CA** (1995) Measuring and modelling whole-tree gas exchange. *Australian Journal of Plant Physiology* **12**, 987-1000
- Logendra S, Putman JD, Janes HW** (1990) The influence of light period on carbon partitioning, translocation and growth in tomato. *Scientia Horticulturae* **42**, 75-83
- Long SP, Ainsworth EA, Rogers A, Ort DR** (2004) Rising atmospheric carbon dioxide: plant face the future. *Annual Review of Plant Biology* **108**, 591-628
- Lorenzo P, Maroto C, Castilla N** (1990) CO₂ in plastic greenhouse in Almeria (Spain). *Acta Horticulturae* **268**, 165-169
- Lorenzo P, Sanchez-Guerrero MC, Medrano E, Garcia ML, Caparros I, Coelho G, Gimenez M** (2004) Climate control in the summer season: A comparative study of external mobile shading and fog system. *Acta Horticulturae* **659**, 189-194
- Marcelis LFM** (1993) Fruit growth and biomass allocation to the fruits in cucumber. 1. Effect of fruit load and temperature. *Scientia Horticulturae* **54**, 107-121
- Marcelis LFM, Baan Hofman-Eijer LR** (1993) Effect of temperature on the growth of individual cucumber fruits. *Physiological Plantarum* **87**, 321-328
- Marcelis LFM, Baan Hofman-Eijer LR** (1995) Growth analysis of pepper fruits (*Capsicum annuum* L.). *Acta Horticulturae* **412**, 470-478
- Marcelis LFM, De Koning ANM** (1995) Biomass partitioning in plants. In: Bakker JC, Bot GPA, Challa H, Van de Braakeds NJ (Eds) *Greenhouse Climate Control: An Integrated Approach*, Wageningen Pers, The Netherlands,

- pp 84-92
- Maroto JV** (1997) Etiología y descripción de las principales fisiopatías de la horticultura mediterránea. Ediciones y Promociones LAV. Valencia
- Maroto JV, Arlandis JL, López S, Baixauli C, Aguilar JM** (2003) Estudio de la aportación de CO₂ ambiental en invernadero con cultivo de pimiento italiano. In: Fundación Ruralcaja (Ed) *Memoria de Ensayos 2002*, Fundación Ruralcaja- Generalitat Valenciana, Valencia, pp 67-69
- Meca D, Lopez JC, Gazquez JC, Baeza E, Pérez-Parra J, Zaragoza G** (2006) Evaluation of two cooling systems in parral type greenhouses with pepper crops: Low-pressure fog system versus whitening. *Acta Horticulturae* **719**, 515-519
- Medina CL, Souza RP, Machado EC, Ribeiro RV, Silva JAB** (2002) Photosynthetic response of citrus grown under reflective aluminized polypropylene shading nets. *Scientia Horticulturae* **96**, 115-125
- Medrano E, Lorenzo P, Sanchez-Guerrero MC, Montero JI** (2005) Evaluation and modelling of greenhouse cucumber-crop transpiration under high and low radiation condition. *Scientia Horticulturae* **105**, 163-175
- Miguel AF, Silva AM, Rosa R** (1994) Solar irradiation inside a single span greenhouse with shading screens. *Journal of Agricultural Engineering Research* **59**, 61-72
- Miguel AF, Van De Braak NJ, Bot GPA** (1997) Analysis of the airflow characteristics of greenhouse screening materials. *Journal of Agricultural Engineering Research* **67**, 105-112
- Moe R, Heins RD** (1989) Control of plant morphogenesis and flowering by light quality and temperature. *Acta Horticulturae* **272**, 81-89
- Moe R, Heins RD** (1990) Control of plant morphogenesis and flowering by light quality and temperature. *Acta Horticulturae* **172**, 81-89
- Montero JI** (2006) Evaporative cooling in greenhouses: Effect on microclimate, water use efficiency, and plant response. *Acta Horticulturae* **719**, 373-384
- Montero JI, Segal I** (1993) Evaporative cooling of greenhouses by fogging combined with natural ventilation and shading. In: Fuchs M (Ed) *Proceedings of International Workshop on Cooling Systems for Greenhouses*, Agri-tech, Tel-Aviv, Israel, pp 89-99
- Moore EL, Thomas WO** (1952) Some effects of shading and parachlorophenoxy-acetic acid on fruitfulness of tomatoes. *American Society of Horticultural Science* **60**, 189-294
- Morison, JIL** (1985) Sensitivity of stomata and water use efficiency to high CO₂. *Plant, Cell and Environment* **8**, 467-474
- Mortensen LM** (1987) Review: CO₂ enrichment in greenhouses. Crop responses. *Scientia Horticulturae* **33**, 1-25
- Mortensen LM, Ulsaker R** (1985) Effect of CO₂ concentration and light levels on growth, flowering and photosynthesis of *Begonia hiemalis*. *Scientia Horticulturae* **17**, 133-141
- Mortensen LM, Moe R** (1983a) Growth responses of some greenhouse plants to environment. V. Effect of CO₂, O₂ and light on net photosynthetic rate in *Chrysanthemum morifolium* Ramat. *Scientia Horticulturae* **19**, 133-140
- Mortensen LM, Moe R** (1983b) Growth responses of some greenhouse plants to environment. VI. Effect of CO₂ and artificial light on growth of *Chrysanthemum morifolium* Ramat. *Scientia Horticulturae* **19**, 141-147
- Mortensen LM, Moe R** (1987) Effect of fluctuating temperature on growth and flowering of *Chrysanthemum moriflorum* Ramat. *Gartenbauwissenschaft* **52**, 260-263
- Munoz P, Montero JI, Anton A, Giuffrida F** (1999) Effect of insect-proof screens and roof openings on greenhouse ventilation. *Journal of Agricultural Engineering Research* **73**, 171-178
- Murage EN, Chweya JA, Imungi JK** (1996a) Changes in leaf yield and nutritive quality of the black nightshade (*Solanum nigrum*) as influenced by nitrogen application. *Ecology of Food and Nutrition* **35**, 149-157
- Murage EN, Sato Y, Masuda M** (1996b) Relationship between dark period, and leaf chlorosis, potassium, magnesium and calcium content of young eggplants. *Scientia Horticulturae* **66**, 9-16
- Nederhoff EM** (1994) Effects of CO₂ concentration on photosynthesis, transpiration and production of greenhouse fruit vegetable crops, PhD thesis, Wageningen, The Netherlands, 213 pp
- Nederhoff EM, Rijdsdijk AA, De Graaf R** (1992) Leaf conductance and rate of crop transpiration of greenhouse grown sweet pepper (*Capsicum annum* L.). *Scientia Horticulturae* **52**, 183-301
- Nederhoff EM, Van Uffelen JAM** (1988) Effect of continuous and intermittent carbon dioxide enrichment on fruit set and yield of sweet pepper (*Capsicum annum* L.). *Netherlands Journal of Agricultural Science* **36**, 109-217
- Nicot P, Baillie A** (1996) Integrated control of *Botrytis cinerea* on greenhouse tomatoes. In: Morris CE, Nicot P (Eds) *Microbiology of Aerial Plant Surfaces*, Plenum Press, New York, pp 169-189
- Nilwik HJM** (1981) Growth analyses of sweet pepper (*Capsicum annum* L.) 2. Interacting effects of irradiance, temperature and plant age in controlled conditions. *Annals of Botany* **48**, 137-145
- Nisen A, Coutisse S** (1981) Modern concept of greenhouse shading. *Plasticulture* **49**, 9-26
- Nothmann J, Rylski I, Spigelman M** (1979) Flowering-pattern, fruit growth and colour development of egg-plant during the cool season in a subtropical climate. *Scientia Horticulturae* **11**, 117-222
- Oren R, Sperry JS, Katul GC, Pataki DE, Ewers BE, Phillips N, Schafer KVR** (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment* **22**, 1515-1526
- Papadopoulos AP, Pararajasingham S** (1997) The influence of plant spacing on light interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill.): A review. *Scientia Horticulturae* **69**, 1-29
- Pearce BD, Grange RI, Hardwick K** (1993) The growth of young tomato fruit. I. Effect of temperature and irradiance on fruit grown in controlled environments. *Journal of Horticultural Science* **98**, 1-11
- Pearson S** (1992) Modelling the effect of temperature on the growth and development of horticultural crops. PhD thesis, Reading University, 204 pp
- Pearson S, Hadley P, Wheldon AE** (1995) A model of the effect of day and night temperature on the height of chrysanthemum. *Acta Horticulturae* **378**, 71-80
- Peet MM, Willits DH** (1992) High night temperature effects on tomato: interactions with developmental stage and season. In: *Symposium on 'Stress in the Tropical Environment'*, 19-25 September, Kona, Hawaii, pp 22-26
- Peet MM, Bartholemew M** (1996) Effect of night temperature on pollen characteristics, growth, and fruit set in tomato. *Journal of the American Society for Horticultural Science* **121**, 514-519
- Peet MM, Willits DH, Gardner R** (1997) Response of ovule development and post-pollen production processes in male-sterile tomatoes in chronic, subacute high temperature stress. *Journal of Experimental Botany* **48**, 101-111
- Polowick PL, Sawhney VK** (1985) Temperature effects on male fertility and flower and fruit development in *Capsicum annum* L. *Scientia Horticulturae* **25**, 117-127
- Raveh E, Cohen S, Raz T, Grava A, Goldschmidt EE** (2003) Increased growth of young citrus trees under reduced radiation load in a semi-arid climate. *Journal Experimental Botany* **54**, 365-373
- Rijdsdijk AA, Vogelegang JVM** (2000) Temperature integration on a 24-hour base: a more efficient climate control strategy. *Acta Horticulturae* **519**, 163-169
- Romacho I, Hita O, Soriano T, Morales MI, Escobar I, Suarez-Rey EM, Hernandez J, Castilla N** (2006) The growth and yield of cherry tomatoes in net covered greenhouses. *Acta Horticulturae* **719**, 529-534
- Romano D, Leonardi C** (1994) The responses of tomato and eggplant to different minimum air temperatures. *Acta Horticulturae* **366**, 57-63
- Romero-Aranda R, Soria T, Cuartero J** (2002) Greenhouse mist improves yield of tomato plants grown under saline conditions. *Journal of the American Society for Horticultural Science* **127**, 644-648
- Rylski I** (1972) Effect of the early environment on flowering in pepper (*Capsicum annum* L.). *Journal of the American Society for Horticultural Science* **97**, 648-651
- Rylski I** (1973) Effect of night temperature on shape and size of sweet pepper (*Capsicum annum* L.). *Journal of the American Society for Horticultural Science* **98**, 149-152
- Rylski I, Spigelman M** (1982) Effects of different diurnal temperature combinations on fruit set of sweet pepper. *Scientia Horticulturae* **17**, 101-106
- Rylski I, Spigelman M** (1986) Effect of shading on plant development, yield and fruit quality of sweet pepper grown under conditions of high temperature and radiation. *Scientia Horticulturae* **29**, 31-35
- Sanchez-Guerrero MC, Lorenzo P, Medrano E, Castilla N, Soriano T, Baillie A** (2005) Effect of variable CO₂ enrichment on greenhouse production in mild winter climates. *Agricultural and Forest Meteorology* **132**, 144-252
- Sato S, Peet MM, Thomas JF** (2000) Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic, mild heat stress. *Plant, Cell Environment* **23**, 719-726
- Schaible LW** (1962) Fruit setting responses of tomatoes to high night temperature. In: *Proceedings of Plant Science Symposium*, Campbell Soup Co., Camden, NJ, pp 89-99
- Schapendonk AHCM, Gastra P** (1984) A simulation study on CO₂ concentration in protected cultivation. *Scientia Horticulturae* **23**, 117-229
- Slack G, Hand DW** (1983) The effect of day and night temperatures on the growth, development and yield of glasshouse cucumbers. *Journal of Horticultural Science* **58**, 567-573
- Sonneveld C** (1988) The salt tolerance of greenhouse crops. *Netherlands Journal of Agricultural Science* **36**, 63-73
- Stanhill G, Cohen S** (2001) Global dimming: A review of the evidence for a widespread and significant reduction of global radiation with discussion of its probable causes and possible horticultural consequences. *Agricultural and Forest Meteorology* **107**, 155-278
- Stutte GW, Yorio NC, Wheeler RM** (1996) Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *Journal of the American Society for Horticultural Science* **121**, 264-268
- Sun W, Wang D, Wu Z, Zhi J** (1990) Seasonal change of fruit setting in eggplants (*Solanum melongena* L.) caused by different climatic conditions. *Scientia Horticulturae* **44**, 55-59
- Tedeschi P, Zerbi G** (1985) Flowering and fruiting courses and yield of eggplant (*Solanum melongena* L.) plants grown in lysimeters with relation to different water regimes. *Acta Horticulturae* **171**, 383-389
- Thompson GB, Woodward FJ** (1994) Some influences of CO₂ enrichment, nitrogen nutrition and competition on grain yield and quality in spring wheat and barley. *Experimental Botany* **45**, 937-942

- Tolbert NE, Zelitch I** (1983) Carbon metabolism. In: Lemon ER (Ed) *CO₂ and Plants: The Response of Plant to Rising Levels of Atmospheric Carbon Dioxide*, Westview Press, Boulder, pp 21-64
- Tomes ML** (1963) Temperature inhibition of carotene synthesis in tomato. *Botanical Gazette* **124**, 180-185
- Uzun S** (1996) The quantitative effects of temperature and light environment on the growth, development and yield of tomato and aubergine. PhD thesis, The University of Reading, 193 pp
- Uzun S** (2006) The quantitative effects of temperature and light on the number of leaves preceding the first fruiting inflorescence on the stem of tomato (*Lycopersicon esculentum*, Mill.) and aubergine (*Solanum melongena* L.). *Scientia Horticulturae* **109**, 142-146
- Van Koot Y, Van Ravestijn W** (1963) The germination of tomato pollen on the stigma (as an aid to the study of fruit setting problems). In: *Proceedings of the 16th International Horticultural Congress 1962* **1**, 452-461
- Van Oosten JJ, Besford RT** (1995) Some relationships between the gas exchange, biochemistry and molecular biology of photosynthesis during leaf development of tomato plants after transfer to different carbon dioxide concentrations. *Plant, Cell and Environment* **18**, 1253-1266
- Van Ravestijn W** (1986) Aanleg bloemen en verbeteren zetting bij paprika (Flower induction and improvement of fruit set in *Capsicum*). *Groenten Fruit* **41**, 32-35 (in Dutch)
- Walker AJ, Ho LC** (1977) Carbon translocation in the tomato: Effects of fruit temperature on carbon metabolism and the rate of translocation. *Annals of Botany* **41**, 825-832
- Warrington IJ, Norton RA** (1990) An evaluation of plant growth and development under various daily quantum integrals. *Journal of the American Society for Horticultural Science* **116**, 544-551
- Weigel HJ, Pacholski A, Burkart S, Helal M, Heinemeyer O, Kleikamp B, Manderscheid R, Riihauf C, Hendrey GF, Lewin K, Nagy J** (2005) Carbon turnover in a crop rotation under free air crop enrichment (FACE). *Pedosphere* **15**, 728-738
- Went FW** (1944) Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. *American Journal of Botany* **31**, 135-150
- Went FW** (1945) Plant growth under controlled conditions. V. The relation between age, light, variety and thermoperiodicity of tomatoes. *American Journal of Botany* **32**, 469-479
- Went FW, Cospar L** (1945) Plant growth under controlled conditions. VI. Comparison between field and air conditioned greenhouse culture of tomatoes. *American Journal of Botany* **32**, 643-654
- Williams AM, Marinos NG** (1977) Regulation of the movement of assimilate into ovules of *Pisum sativum* cv. Greenfeast: effect of pod temperature. *Australian Journal of Plant Physiology* **4**, 515-521
- Willits DH** (1999) Constraints and limitations in greenhouse cooling: Challenges for the next decade. *Acta Horticulturae* **534**, 57-66
- Willits DH, Peet MM** (1998) The effect of night temperature on greenhouse grown tomato yields in warm climates. *Agricultural and Forest Meteorology* **92**, 191-202
- Wolswinkel P** (1985) Phloem unloading and turgor-sensitive transport: Factors involved in sink control of assimilate partitioning. *Physiological Plantarum* **65**, 331-339
- Yao C, Moreshet S, Aloni B, Karni L** (2000) Effects of water stress and climatic factors on the diurnal fluctuation in diameter of bell pepper fruit. *Journal of Horticultural Science and Biotechnology* **75**, 6-11
- Yelle S, Beeson RC Jr., Trudel MJ, Gosselin A** (1990) Duration of CO₂ enrichment influence growth, yield, and gas exchange of two tomato species. *Journal of the American Society for Horticultural Science* **115**, 52-57
- Yoshioka H, Takahashi K, Arai K** (1986) Studies on the translocation and distribution of photosynthates in fruit vegetables. IX. Effects of temperature on translocation of C-photosynthates in tomato plants. *Bulletin on Vegetable and Ornamental Crops Research Japan A* **14**, 1-9