

High Temperature Control in Mediterranean Greenhouse Production: the Constraints and the Options

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Abstract

In the open field, the environment is a critical determinant of crop yield and produce quality and it affects the geographical distribution of most crop species. In contrast, in protected cultivation, environmental control allows the fulfillment of the actual needs depending on the technological level. The economic optimum, however, depends on the trade-off between the costs of increased greenhouse control and increase in return, dictated by yield quantity, yield quality and production timing. Additional constraints are increasingly applied for achieving environmental targets. However, the diverse facets of greenhouse technology in different areas of the world will necessarily require different approaches to achieve an improved utilization of the available resources. Although advanced technologies to improve resource use efficiency can be developed as a joint effort between different players involved in greenhouse technology, some specific requirements may clearly hinder the development of common “European” resource management models that, conversely should be calibrated for different environments. For instance, the quantification and control of resource fluxes can be better accomplished in a relatively closed and fully automated system, such as those utilized in the glasshouse of Northern-Central Europe, compared to Southern Europe, where different typologies of semi-open/semi-closed greenhouse systems generally co-exist. Based on these considerations, innovations aimed at improving resource use efficiency in greenhouse agriculture should implement these aspects and should reinforce and integrate information obtained from different research areas concerning the greenhouse production. Advancing knowledge on the physiology of high temperature adaptation, for instance, may support the development and validation of models for optimizing the greenhouse system and climate management in the Mediterranean. Overall, a successful approach will see horticulturists, plant physiologists, engineers and economists working together toward the definition of a sustainable greenhouse system.

INTRODUCTION

Protected agriculture is a high-investment and a high-risk business that demands professional expertise, based on the synthesis of proven technologies and market requirements along with economic objectives. Achieving high productivity in the greenhouse is possible by exerting optimal control of both environmental parameters and cultural practices. The economic optimum, however, depends on the trade-off between the costs of increased environment control and increase in return, dictated by yield quantity, yield quality and production timing. Additional constraints that are increasingly applied are aimed at improving resource use efficiency (water, nutrients, energy and soil) and decreasing environmental impact. Sustainability, however, must also be considered in the

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context of economic sustainability. In this respect, greenhouse crops are often the only form of economically sustainable agriculture that can be proposed in many marginal areas of the Mediterranean environment, where land abandonment is expanding considerably. Indeed, in contrast to what most may believe, the greenhouse system is in some respects quite a resource-efficient system compared to open field agriculture (De Pascale and Maggio, 2005, 2008).

Nevertheless, the diverse facets of greenhouse technology in the various regions of Europe will necessarily require different approaches to achieve an improved utilization of the available resources. Among the most critical determinants that differentiate the North-Central vs. Southern Europe greenhouse agribusiness we must consider: 1) the climatic conditions; 2) the market dynamics; 3) the social/technical background of farmers and entrepreneurs. Besides technical innovations adapted to the relevant conditions, advancing knowledge on the physiology of plant stress adaptation may support decisions in the management of crop, greenhouse and climate (De Pascale and Maggio, 2005, 2008).

The economic feasibility of these innovations highly depends on the yield increase that can be obtained. Therefore, in this paper we will present different research approaches that should be integrated to optimize the greenhouse high temperature control and a few examples that may provide useful insights for defining the economic optimum of greenhouse control.

HIGH TEMPERATURE: FROM PLANT PHYSIOLOGY TO GREENHOUSE MANAGEMENT

In general, higher temperatures are associated with higher radiation and higher water use and it is relatively difficult to discriminate among the physiological effects (at the level of plants and plant organs) of the different factors. Except for transpiration cooling, plants are unable to adjust their tissue temperatures to any significant extent. On the other hand, plants have evolved several mechanisms that enable them to tolerate higher temperatures. These adaptive thermo-tolerant mechanisms reflect the environment in which a species has evolved and they largely dictate the environment where a crop may be grown (Wahid et al., 2007). Heat stress in plants may arise in leaves when transpiration is insufficient for maintaining lower leaf temperature or in organs with reduced capacity for transpiration such as fruits. Plants with high transpiration rates are more tolerant to heat stress. Temperatures that inhibit cellular metabolism and growth for a cool season C3 species, such as spinach, may not inhibit warm-season C3 species, such as tomato, C4 and CAM species. In this section we will try to summarize the physiological mechanisms that are thought to be critical in plant heat stress tolerance. Most examples will refer to tomato, the most common greenhouse crop in warm environments.

Thermal Dependence at the Biochemical and Metabolic Levels

The relationship between the thermal environment for an organism and the thermal dependence of enzymes has been well established (Basra and Basra, 1997). Temperature effects on the rates of biochemical reactions may be modeled as the product of two functions, an exponentially increasing rate of the forward reaction and an exponential decay resulting from enzyme denaturation as temperatures increase. Failure of only one critical enzyme system can cause death of an organism. This fact may explain why most crop species survive sustained high temperatures up to a relatively narrow range, 40 to 45°C (Burke, 1990). The shape of this function also describes temperature effects on most biological functions, including plant growth and development. Modelers frequently simplify the relationship into a stepwise linear function that has a plateau rather than an optimum temperature (Klueva et al., 2001).

The thermal dependence of the apparent reaction rate for selected enzymes may indicate the optimal thermal range for a plant (Burke et al., 1988). The identification of thermal kinetic windows (TKWs) for different species and cultivars can aid in the

interpretation of the differential temperature stress responses for crop growth and development among genotypes in order to identify target traits for improving high temperature tolerance (Mahan et al., 1987).

For crop plants, the thermal kinetic window (TKW) is generally established as a result of thermally induced lipid phase changes, Rubisco activity and the starch synthesis pathway in leaves and reproductive organs (Mahan et al., 1987). The light-dependent activation of Rubisco, which is mediated by Rubisco activase, is one of the most thermally labile reactions and is directly related to the inhibition of net photosynthetic rate with significant effect on plant growth and development (Law and Crafts-Brandner, 1999; Law et al., 2001). Rubisco activase sensitivity to high temperature differs both within species and among species and Rubisco activase activity can acclimate during a relatively short period when the leaf temperature is increased in gradual increments (Law and Crafts-Brandner, 1999; Law et al., 2001). Acclimation of Rubisco activase to high temperature may be associated with heat-stress-induced changes in the pools of ATP and ADP, which are substrates known to stabilize activase and/or to altered biosynthesis of the molecular forms of this enzyme (Crafts-Brandner and Salvucci, 2000).

Thermal Stability of Cell Membranes

In most crop species membrane stability limits growth at high temperature. The plasmalemma and membranes of cell organelles play a vital role in the functioning of cells. Any adverse effect of temperature stress on the membranes leads to disruption of cellular activity or death (Chaisompongopan et al., 1990). Injury to membranes from a sudden heat stress event may result from either denaturation of the membrane proteins or from melting of membrane lipids which leads to membrane rupture and loss of cellular contents measured by ion leakage (Raison, 1986). Heat stress may be an oxidative stress (Lee et al., 1983), and peroxidation of membrane lipids (Mishra and Singhal, 1992) observed at high temperatures is a symptom of cellular injury. Enhanced synthesis of an anti-oxidant by plant tissues may increase cell tolerance to heat stress (Upadhyaya et al., 1991).

A relationship between lipid composition and incubation temperature has been shown for algae, fungi and higher plants: increase in saturated fatty acids of membranes increases their melting temperature and thus increases heat tolerance (Hall, 1993). In *Arabidopsis* exposed to high temperatures, total lipid content decreases to about one-half and the ratio of unsaturated to saturated fatty acids decreases to one-third of the levels at temperatures within the TKW (Somerville and Browse, 1991). *Arabidopsis* mutants deficient in activity of chloroplast fatty acid W-9 desaturase accumulate large amounts of 16:0 fatty acids, resulting in greater saturation of chloroplast lipids and in higher optimal growth temperature (Raison, 1986; Kunst et al., 1989). In other species, however, heat tolerance or tolerance differences among cultivars have been unrelated to membrane lipid saturation (Kee and Nobel, 1985; Rikin et al., 1993). In such species, a factor other than membrane stability may be limiting growth at high temperature.

Heat Shock Proteins

Synthesis and accumulation of so-called 'Heat Shock Proteins' (HSPs) have been ascertained during a rapid heat stress. Increased production of these proteins also occurs when plants experience a gradual increase in temperature or other abiotic stresses including drought and low temperature. Three classes of proteins as distinguished by molecular weight account for most HSPs, namely HSP90, HSP70, and low molecular weight proteins of 15 to 30 kDa (LMW-HSP) (Vierling, 1991). In arid and semi-arid regions, plants may synthesize and accumulate substantial levels of HSP in response to elevated leaf temperatures (Burke et al., 1985). In general, HSPs are induced by heat stress at any stage of development. The induction temperature for the synthesis and accumulation of HSPs and the proportions of the three classes differ among species (Howarth, 1991). Levels were greater in non-irrigated than in irrigated crops (Kimpel and Key, 1985). Correlation between synthesis and accumulation of heat shock proteins and

heat tolerance suggests that the two are causally related. Further evidence for a causal relationship is that some cultivar differences in heat shock protein expression correlate with differences in thermo-tolerance (Pelham, 1986). In genetic experiments, HSP expression co-segregates with heat tolerance. More evidence for the protective role of heat shock protein is that mutants unable to synthesize heat shock proteins, and cells in which HSP70 synthesis is blocked or inactivated, are more susceptible to heat injury (Abrol and Ingram, 1996).

The mechanism by which HSPs contribute to heat stress tolerance is still not certain. Many are chaperones (assist others proteins). In tomato it has been shown (Heckathorn et al., 1998): that HSPs prevent proteins denaturation during stress, play a structural role in maintaining cell membranes integrity during stress (some of them have been associated with particular organelles such as chloroplast, ribosome and mitochondria) and protect the Photosystem II from oxidative stress.

In addition to their protective effect under stress conditions, HSPs play a role in plant development under normal growth conditions. For example, they promote carotenoid accumulation during fruit maturation (Neta-Sharir et al., 2005). HSPs provide a significant opportunity to increase heat tolerance of greenhouse crops (Siddique et al., 2003).

Photosynthesis

The temperature optimum for photosynthesis is broad, presumably because crop plants have adapted to a relatively wide range of thermal environments. A 1 to 2°C increase in average temperature is not likely to have a substantial impact on leaf photosynthetic rates (Abrol and Ingram, 1996). However, heat stress (from 5 to 10°C above the optimum) significantly reduced net photosynthesis and increased night respiration and stomatal conductance in tomato (Sato et al., 2000). Differences between heat tolerant and heat sensitive genotypes have been observed: photosynthesis of genotypes adapted to higher temperature environments was less sensitive to high temperature than was photosynthesis of genotypes from cooler environments (Al-Khatib and Paulsen, 1990; Venema et al., 1999). Recent research has shown significant variation among tomato cultivars with respect to reduction in photosynthesis at high temperature. Camejo et al. (2005) demonstrated that the reduction of net photosynthesis in heat-sensitive tomato 'Campbell 28' was associated with non-stomatal components such as the alteration of Photosystem II and injuries to the plasma membrane measured by ion leakage.

Relative humidity (Vapour Pressure Deficit), light, CO₂ concentration, irrigation (water availability) all affect the net photosynthesis response to temperature and can be easily controlled in the greenhouse environment. For instance, the temperature optimum for net photosynthesis is likely to increase with elevated levels of atmospheric carbon dioxide (Rawson, 1992; Behboudian and Lai, 1994; Aloni et al., 2001).

Plant Growth and Development

Heat stress is one of the most important constraints on crop production in semi-arid greenhouses and adversely affects the vegetative and reproductive stages of plants and ultimately reduces yield and fruit quality (Abdul-Baki, 1991). Several experiments have studied the effects of sub-optimal temperature on plant growth and development under controlled environment and field conditions (Chen et al., 1982), and scattered examples of studies on the effects of high temperature on greenhouse crops are available in the literature (Sugiyama et al., 1966; El Ahamdi and Stevens, 1979; Rylski, 1979; Picken, 1984; Khayat et al., 1985; Peet et al., 1996, 1997, 1998; Sato et al., 2000, 2001, 2002; Pressman et al., 2002; Rivero et al., 2004; Sato and Peet, 2005). The optimum temperature for vegetative growth of tomatoes is reported to be 18-25°C (Heuvelink and Dorais, 2005). Temperature increases above 25°C (corresponding to day/night regime of 30/21°C) cause non-linear yield reductions depending on stress severity and duration (Table 1).

The major conclusions from these studies are:

- Reproductive stages (from anthesis to harvest) are more sensitive than vegetative stages.
- Fruit weight is less sensitive to heat stress than is fruit number.
- Fruit yield reduction results from:
 - reduced numbers of fruits formed,
 - shorter fruit growth duration,
 - inhibition of carbohydrate assimilation in fruits.

A number of explanations have been offered for the poor reproductive performance of tomato at high temperatures. These include reduced or abnormal pollen production, abnormal development of the female reproductive tissues, hormonal imbalances, low level of carbohydrates and lack of pollination. Unfortunately, only a few experiments have been conducted with a sufficient number of cultivars to assess the genetic variability in these traits. Sato et al. (2000) concluded that pollen release and pollen viability may be the major limiting factors for fruit set under high temperature stress. In that study, cultivar differences in high temperature sensitivity were related to differences in pollen release and germination under heat stress, determining their ability to set fruit. Peet et al. (1998), comparing heat stress effects on male fertile and sterile tomatoes, observed that fruit number declined sharply with increasing temperature, whereas fruit weight per plant declined only slightly in both groups of plants. In male fertile tomato cultivars there was a more drastic decline in seeds/fruit as temperatures increased, which was not paralleled by a decrease in average fruit weight, suggesting an increased tendency for parthenocarpic fruit-set at high temperatures. In this respect, parthenocarpy can be considered a very promising plant genetic trait for fruit greenhouse crops. On the other hand, plant growth reduction is mainly associated with reduction of the net photosynthetic rate, accompanied by impaired translocation and assimilate partitioning caused by high air temperatures (Dinar and Rudich, 1985).

Fruit Quality

It is well known that tomato fruits are sensitive to heat stress. Temperatures above 30°C suppress many of the parameters of normal fruit ripening including color, softening, respiration rate and ethylene production. Moreover, exposure of fruits to temperature approaching 40°C induces metabolic disorders and facilitates fungal and bacterial invasion (Mohammed et al., 1996). Recently, Riga et al. (2008) studied the effects of cumulative air temperature and photosynthetically active radiation on tomato quality and concluded that cumulative air temperature has a stronger influence on tomato quality than did cumulative photosynthetically active radiation. Growers could thus obtain tomatoes of similar quality under lower photosynthetically active radiation (shading) than that provided by natural sunlight.

BEST MANAGEMENT: “THE LESSER OF TWO EVILS”

A preliminary assessment of the specific environmental parameters of a given area may support the choice of an optimal combination of greenhouse/environment to facilitate greenhouse management in terms of natural resources use efficiency and energy costs. An analysis of the specific control requirements necessary to maximize yield in different areas of the world confirmed that light is the limiting factor in The Netherlands for fall/winter crops and heating is required for most of the year. High temperatures (also because of high radiation) may strongly reduce crop yield in Naples (South Italy) and cooling is necessary most of the time, whereas heating may provide some advantages for a short period but is not critical (Fig. 1). On an annual basis, in The Netherlands inside a greenhouse about 2800 MJ m⁻² energy is received from the sun, which is almost 3 times more than the annual heating requirement, whereas in Naples this amount reaches 4300 MJ m⁻² per year.

In Europe, climatic differences have fostered the development of greenhouse systems based on simple structures and inexpensive climatic control devices in the warmer Southern regions compared to the Northern greenhouse systems. These simplified

systems present some limitations for an efficient use of the natural resources: poor ventilation, inefficient humidity control and reduced light transmission of plastic coverage all pose serious constraints for timing production and guaranteeing high yields and quality standards. As a result, the majority of the Mediterranean greenhouses currently under-use the potential energy in the fall/winter period and are strongly limited during summer/spring (with two production peaks, in spring-early summer and in autumn and approximately 3-5 months of non-productive time) due to the costly control of high temperatures. On the other hand, approximately 20% of the production costs are attributable to heating in the high-tech Dutch greenhouses (Bakker et al., 2009).

If we compare the typical trend of the mean monthly temperature inside and outside a poorly ventilated greenhouse in South Italy with the optimal temperature for some horticultural crops we can conclude that the high indoor temperatures that typically occur from May to September strongly limit the potential yield (Fig. 2). Shading of the greenhouse (by shading nets, screening or white wash) during this period is a common means for passive cooling. This considerably reduces canopy photosynthesis (though not necessarily that of the upper leaves, which may be saturated) (Fig. 3). The shading experiments of Cockshull et al. (1992) show that 30 g of tomatoes are harvested for each MJ PAR radiation at the top of the canopy, a value corroborated by the experiments of Li et al. (2001). The results of Scholberg et al. (2000) imply quite a similar value for field crops. Each 10% shading increment of the 13 MJ m⁻² d⁻¹ typical of May through July in Naples (Fig. 1) results in a potential yield loss of about 0.6 kg m⁻² month⁻¹, under the conservative assumption that light use efficiency at high PAR levels is only half the value given above.

Nevertheless, if shading is not applied, the high temperature will cause plant growth and yield (in terms of both quantity and quality) to be reduced because of reduced photosynthesis (Fig. 4). The value of a cooling method that would allow a higher radiation without increasing the temperature can then be estimated. If we use tomato as an example, and as we are dealing with increasing production in summer, we must consider that this is traditionally a low-price period. Figure 5 gives a worst-case of 0.30 €kg⁻¹. Each 10% increase in PAR in the greenhouse, without increase in temperature, is then worth at least 1800 €ha⁻² month⁻¹.

Another very important advantage of cooling is reduced ventilation, coupled to carbon fertilization. Stanghellini et al. (2009) using a relatively simple model, have demonstrated that a fertilization rate of 70 kg ha⁻¹ h⁻¹ could increase net income by more than 100 €ha⁻¹ h⁻¹, even at low tomato prices, under relatively high irradiation, up to ventilation rates around 10 h⁻¹. Unfortunately, without other means for temperature control, a higher ventilation rate than that would be required in traditional Mediterranean greenhouses in sunshine.

Photo-selective plastics (with a higher transmissivity in the PAR than in the near infrared range of radiation) are now available. Kempkes et al. (2009) concluded that a year-round photo-selective cover is bound to lower the winter-time mean temperature in passive greenhouses, therefore such materials have a potential only for application as movable screens, in most places. Stanghellini et al. (2009) have shown that when implemented as a movable screen, a commercially available photo-selective film could reduce ventilation by 10% and increase water use efficiency by 12%, even during a relatively cold and dark Dutch summer. Alternatively, photo-selective whitewash may combine functionality and flexibility. The materials commercially available presently, however, have a very poor selectivity.

Where water of good quality is available and not expensive, misting is probably a more effective mean to control the temperature during summer. The capital and maintenance costs of an installation is estimated to be 8000 €ha⁻¹ year⁻¹ (Vermeulen, 2008), with maximal capacity of 5 m³ ha⁻¹ h⁻¹ and electric power of 5 kWh ha⁻¹. The break even point in a very worst-case scenario (only 500 h of operation per year; value of tomato 0.30 €kg⁻¹; price of electricity 0.4 €kWh⁻¹ and of water 1 €m⁻³) would be with misting delivering an increase in production of 3 kg m⁻² over 500 hours. This is anything

between 5 and 20% of production, depending on the greenhouse. Feasibility of misting, therefore, should be evaluated accounting for prices, greenhouse management and access to good water.

It is important to realize, however, that full advantage of all means for temperature control and reduction of the ventilation requirement can be had only with carbon fertilization. In its absence a lower ventilation rate will result in lower CO₂ concentration and lower crop yield.

LINKING BIOTECHNOLOGY TO GREENHOUSE ENVIRONMENT

One aspect that has not been sufficiently addressed in discussing sustainability is how biotechnology may contribute to identifying genetic target traits that are particularly important for the greenhouse environment. In this respect, using genetic engineering to generate genotypes that may be functional to understand how plants would respond to specific environmental variables is an aspect that has great potential (Maggio et al., 2008; Marcelis and De Pascale, 2009). Nowadays, tomato heat stress tolerance has also been obtained by over-expressing the HsfA1, a transcription factor with a critical function in thermo-tolerance (Mishra et al., 2002) by genetic engineering of HSPs such as HSP70, HSP110, HSP17.1 (Siddique et al., 2003). However, in most of these studies the improved thermo-tolerance was assessed only on a qualitative basis, whereas a clear quantification in terms of yield was not reported.

Reinforcing collaboration among different research areas will speed up progress in developing new cultivars (both transgenic and not transgenic) by:

1. Isolating critical components and producing the relative genotypes.
2. Studying and assessing their relevance in greenhouse production.
3. Generating new cultivars or identifying the relative gene in wild type stress resistant plants.
4. Introducing new genes in commercial cultivars using assisted breeding.

CONCLUSIONS

Although advanced technologies to improve resource use efficiency can be developed as a joint effort among different players involved in greenhouse technology, some specific requirements may clearly hinder the development of common “European” resource management models that, conversely should be calibrated for different environments. Strategies to improve the resources use efficiency in greenhouse management should also look at improving the plant’s ability to use the available resources and at identifying genetic traits that may be important in the specific environment. Today we do have a good idea of the mechanisms that need to be potentiated to improve heat stress tolerance, however, much more needs to be known and understood about the functional biology of heat stress adaptation of greenhouse vegetable crops. Advancing knowledge on the physiology of low/high temperature adaptation, for instance, may support the development and validation of models for optimizing the greenhouse system and climate management in the Mediterranean greenhouses. Based on these considerations, innovations aimed at improving resource use efficiency in greenhouse horticulture should implement and integrate all these aspects and should reinforce scientific collaboration.

It is our belief that much knowledge in this field could be gained by combining information from different research areas in an interdisciplinary approach to greenhouse management. Overall, a successful approach will see horticulturists, plant physiologists, engineers and economists working together toward the definition of a sustainable greenhouse system.

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Tables

Table 1. Compilation of literature over effect of high temperature on tomato. Production loss is given in % of potential yield at 25°C (Stanghellini and Heuvelink, 2007).

| Temperature (°C) | Duration | Production loss | Reference |
|------------------|-------------------------|------------------|-------------------------|
| 42 | 6 hours | 100 | Heckathorn et al., 1998 |
| | 2 days | 100 | Klueva et al., 2001 |
| 40 | 4 h/9 d before anthesis | no fruit set | Peet et al., 1998 |
| | n.a. | endosperm damage | Sato et al., 2000 |
| | 30 hours | pollen damage | Sugiyama et al., 1966 |
| 35 | 30 days average | 40 | Rivero et al., 2004 |
| 32/36 | 33 days | 25 | Sato et al., 2001, 2002 |
| 27 | daily mean | 15 | Peet et al., 1997 |
| 26 | daily mean | 5 | Peet et al., 1998 |

Figures

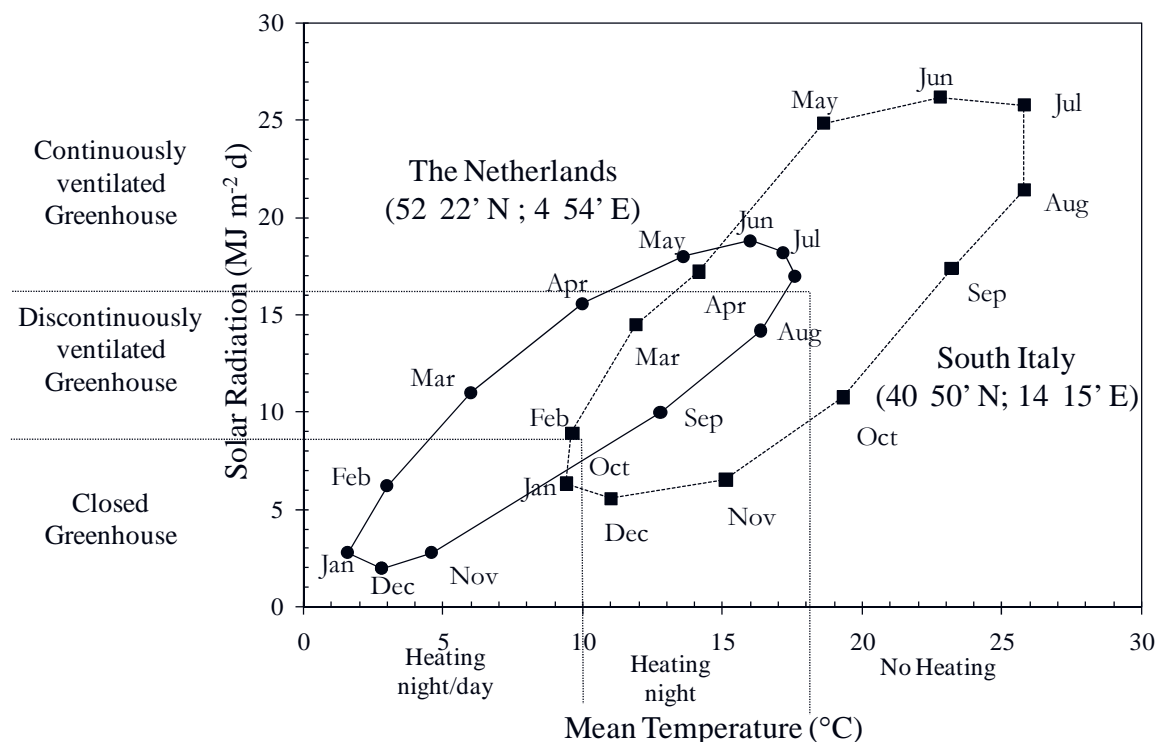


Fig. 1. Climatic control requirements for greenhouse vegetable crops production in The Netherlands (Amsterdam) and in South Italy (Naples).

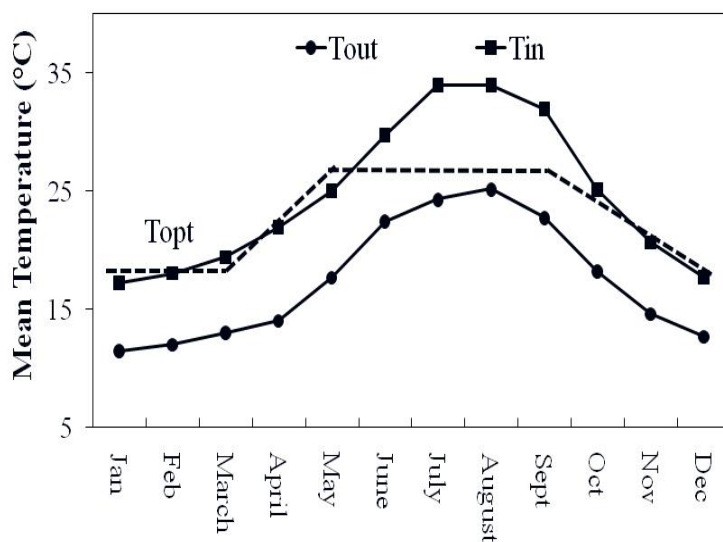


Fig. 2. Typical trend of the mean monthly temperature inside (T_{in}) and outside (T_{out}) a poorly ventilated greenhouse in South Italy (Naples, 40°49'N; 14°15'E; 30 m a.s.l.) and optimal temperature (T_{opt}) for some horticultural crops.

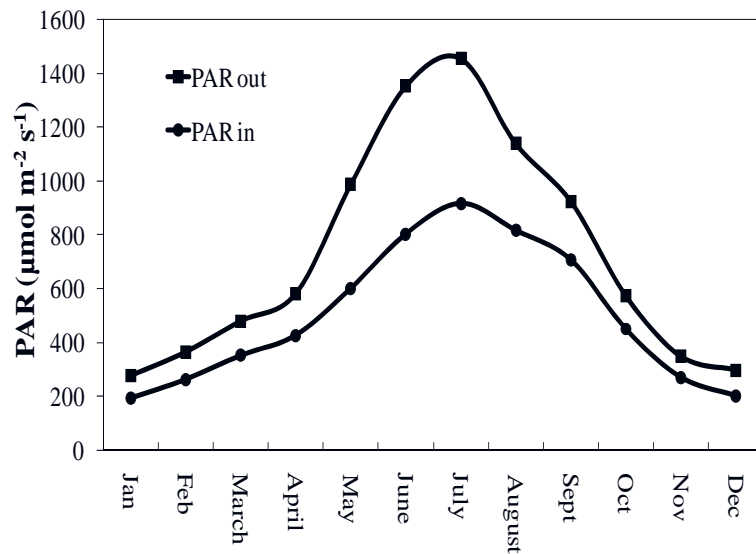


Fig. 3. Typical trend of the mean monthly Photosynthetically Active Radiation inside (PAR_{in}) and outside (PAR_{out}) a poorly ventilated greenhouse in South Italy (Naples, 40°49'N; 14°15'E; 30 m a.s.l.) with shading screen from May to September.

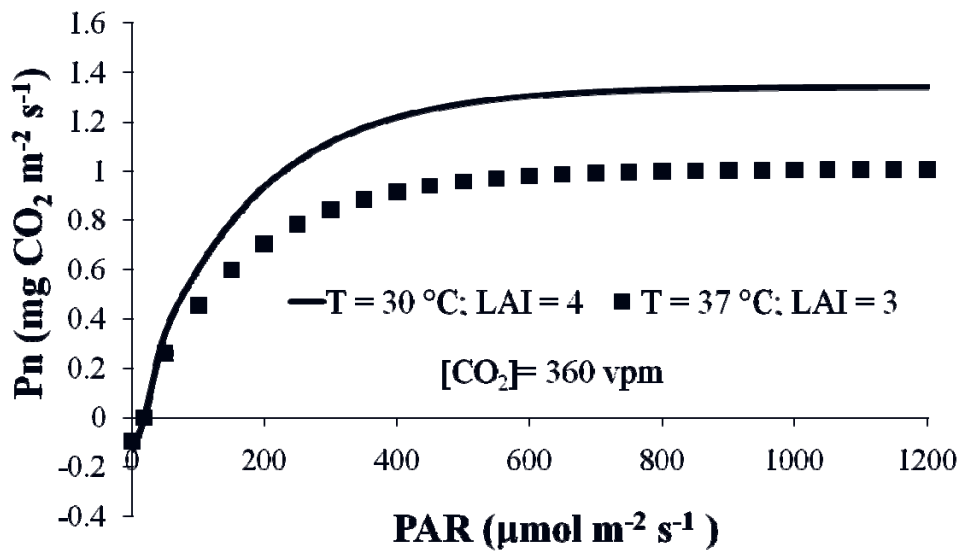


Fig. 4. Light response curves for net photosynthesis (Pn) of a greenhouse tomato crop at 30 and at 37°C and 360 vpm CO₂. Crop photosynthesis at 37°C was calculated considering a reduction of 25% of the leaf area indices (LAI) (Sato et al., 2000).

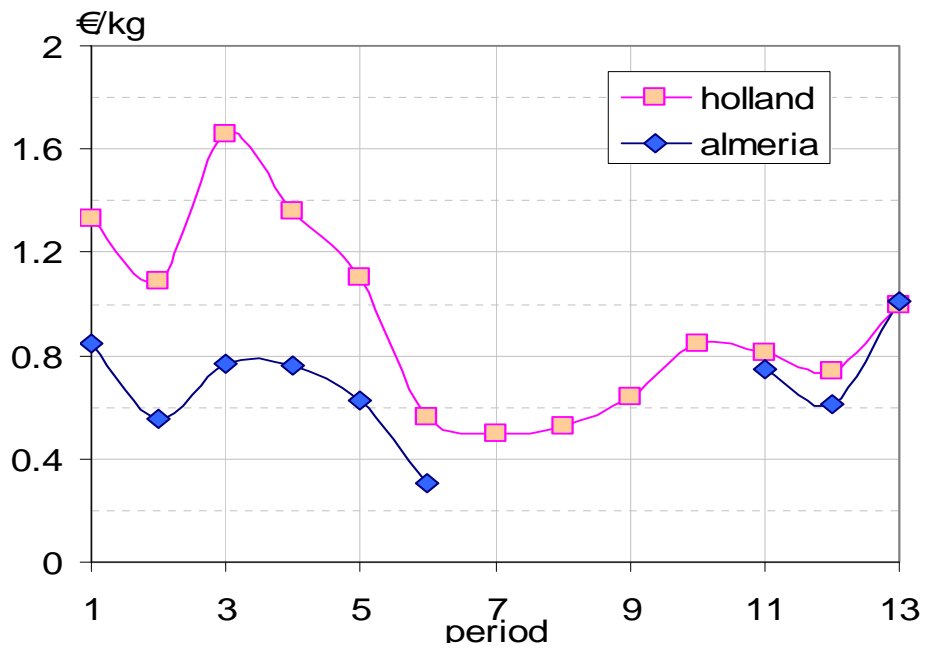


Fig. 5. Evolution of the year of producer price of tomato (€/kg), in Holland and in Almeria. Mean of the years 2005-2008, for each 4-week period. Sources: Anonymus (2008) and Vermeulen (2008).