

Ecophysiology of horticultural crops: an overview

Ecofisiología de cultivos hortícolas. Una visión general

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ABSTRACT

Horticultural crops include a wide range of commodities, such as fruits and vegetables, that are highly valuable for humanity. They are extensively grown worldwide, and their production can be described as an open and highly complex system affected by many factors, among which we can count weather, soil and cropping system, as well as the interaction between these factors. The aim of environmental physiology is to characterize the interaction between environmental stress and crop response, in order to maximize both yield quantity and quality. This review presents the most recent findings about the effects of the main abiotic environmental factors (light, temperature, and water) on whole plant physiology of horticultural crops. Environmental stresses can cause morpho-anatomical, physiological and biochemical changes in crops, resulting in a strong profit reduction. A clear understanding of environmental factors and their interaction with physiological processes is extremely important for improving horticultural practices (irrigation, light management, mineral nutrition, greenhouse design, etc.), optimizing photosynthetic carbon assimilation and increasing fruit productivity and crop quality. In addition, the information obtained by ecophysiological studies can be incorporated into breeding programs or agricultural zoning strategies.

Key words: vegetable crops, fruit trees, water stress, temperature.

RESUMEN

Los productos hortícolas como frutas y vegetales son ampliamente cultivados, dado que incluyen un extenso abanico de alimentos de gran valor para la humanidad. Los sistemas hortícolas son abiertos y altamente complejos, y se ven afectados por factores como el clima, el suelo y el sistema de producción, así como por la interacción entre estos factores. Por lo anterior, la importancia de la fisiología ambiental o ecofisiología radica en que permite caracterizar la interacción entre los factores de estrés ambiental y la respuesta de los cultivos, con el propósito de obtener una producción exitosa. El objetivo de esta revisión consiste en reunir los resultados de las investigaciones más recientes acerca del efecto de los factores ambientales abióticos (luz, agua y temperatura) sobre la respuesta fisiológica de los cultivos hortícolas. Los factores de estrés ambiental pueden causar distintos cambios morfológicos, fisiológicos y bioquímicos en los cultivos, determinando una considerable reducción en su rendimiento. La comprensión de la interacción entre estos factores ambientales y procesos fisiológicos es importante en el mejoramiento de las prácticas hortícolas (riego, manejo de la luz, nutrición mineral, diseño de infraestructuras, etc.), con el objetivo de optimizar la fotosíntesis e incrementar la productividad de los cultivos. Adicionalmente, la información que se obtiene mediante la ecofisiología es una herramienta útil en los programas de mejoramiento genético, o en estrategias de ordenación del territorio agrícola.

Palabras clave: hortalizas, árboles frutales, estrés térmico, sequía.

Introduction

Widely cultivated for the high value of their products, horticultural crops include fruits and vegetables which provide essential food, minerals and vitamins that are critical to human nutrition (Kwack, 2007). The production of horticultural crops can be characterized as an open and highly complex system affected by climate, soil, cropping system and interactions between these factors (Lentz, 1998). Given that plant growth and development are directly and indirectly influenced by environmental

factors (Schaffer and Andersen, 1994), in order to obtain a successful production it is essential to understand clearly how said factors affect plant physiology (Wien, 1997). In this context, ecophysiology is the science that studies the interactions between plants and their physical, chemical and biotic environment (Larcher, 2003; Lambers *et al.*, 2008). Environmental physiology is also important to study both the effect of different environmental stresses (shading, heavy metals, drought and salinity, among others) on

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growth and development (Salisbury and Ross, 1994) and the way plants compensate the detrimental effects of stress through different mechanisms (stress response, acclimation and adaptation) (Taiz and Zeiger, 2006).

Environmental physiology studies have been extensively used to improve the management of certain species or to explain differences among cultivars (Higgins *et al.*, 1992; Hampson *et al.*, 1996; Campostrini and Glenn, 2007; Sagarin *et al.*, 2007; Lombardini *et al.*, 2009). Nevertheless, in regions where agriculture is not very modern, or where new horticultural crops are introduced, the information supplied by environmental physiology studies is highly valuable for deciding on the distribution and performance of crops (Higgins *et al.*, 1992). Knowledge on the responses of horticultural crops to environmental factors such as temperature, water availability, light or carbon dioxide (CO₂) concentration is useful to determine the effect of suboptimal environmental conditions and to manage crops for maximum productivity (Schaffer and Andersen, 1994). In addition, a better understanding of the interaction between environmental factors and physiological processes contributes to horticultural breeding programs, production sustainability improvement and efficient agricultural zoning (Campostrini and Glenn, 2007).

Thus, the aim of this review is to gather the most recent information on the effects of environmental factors (light, temperature and water) on whole plant physiology of horticultural crops as expressed by growth, yield, fruit quality and photosynthetic features.

Light

Sunlight is not only the energy source for photosynthesis, but also the most important factor affecting productivity in horticultural crops (Papadopoulos and Pararajasingham, 1997; Gregoriu *et al.*, 2007). Carbon exchange rate (CER) is strongly dependent on irradiance, absorption, and utilization of photon energy (Jackson, 1980; Gregoriu *et al.*, 2007). Low irradiance, in as much as it determines insufficient light penetration into the canopy, influences CER directly by reducing photon energy utilization, thus decreasing productivity (Hampson *et al.*, 1996; Gregoriu *et al.*, 2007). Canopy management as a routine activity in horticultural crops is aimed at increasing light interception and productivity, stabilizing yield, and improving fruit quality (Hampson *et al.*, 1996).

Given that they need sunlight for flowering and fruit bud formation, fruit-tree crops keep a balance between light interception and light distribution (Huett, 2004). Since the

relationship between photosynthetic photon flux density (PPFD) and net photosynthesis provides basic information for modeling leaf, plant, or canopy growth (Hanson *et al.*, 1987), several studies have focused on light interception and distribution into the canopy (Higgins *et al.*, 1992; Wood, 1996; Huett, 2004; Lombardini, 2006a). Light interception modeling has also been important in the development of pruning and training techniques for optimizing yield, and of tree removal strategies aimed at improving orchard productivity (Garriz *et al.*, 1998; Huett, 2004; Li and Laksso, 2004; Lombardini *et al.*, 2006a). A summary of the photosynthetic performance of several fruit-tree crops is listed in Tab. 1.

Shading (levels of 60% to 90%) affects leaf morphology and anatomy, gas exchange and water relations (water use efficiency, stomatal conductance, and thus photosynthesis) in horticultural crops (Bjorkman, 1981; Atanasova *et al.*, 2003; Huett *et al.*, 2004; Gregoriu *et al.*, 2007). In addition, shade diminishes reproductive potential directly by decreasing flowering, fruit set and fruit size; and indirectly by reducing the vegetative growth that the plant needs to support reproduction (Hampson *et al.*, 1996). A summary of the effects of shading on several horticultural crops is reported in Tab. 2.

Previous studies have shown the importance of plant response to shading, since this information is useful to determine ideal plant density, cropping systems or growth conditions in greenhouses (Papadopoulos and Pararajasingham, 1997; Francescangeli *et al.*, 2006; Francescangeli *et al.*, 2007; Callejón-Ferre *et al.*, 2009). Francescangeli *et al.* (2007) observed that shading increased growth cycle duration and diminished net assimilation rate in broccoli. However, as individual plant relative growth rate (RGR) was almost constant, they concluded that broccoli can be considered as a shade-tolerant plant, thus apt for intercropping systems. Tsubo and Walker (2004) and Nasrullahzadeh *et al.* (2007) studied the effect of intercropped beans and observed that dry mass was 40% lower in shaded plants (shading was up to 90%). Nevertheless, shading did not have significant effects on yield parameters (number of pods and number of grains per plant, and number of grains per pod). These authors concluded that growing beans in agroforestry or intercropping systems would be advantageous for farmers. Regarding planting distance, close spacing has been observed to have a negative effect on fruit set in tomato, apparently due to an inadequate supply of photosynthates (Papadopoulos and Pararajasingham, 1997). In a 4-year study conducted in tomato by Zahara and Timm (1973), the variables stem diameter, fruit set, number of flowers

TABLE 1. Photosynthetic characteristics of several fruit-tree crops in full sun.

| Crop | Light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Light saturation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | A max ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Reference |
|---|--|--|---|---|
| Almond (<i>Prunus dulcis</i>) | 60 | 1.130-1.330 | 15-20 | Higgins <i>et al.</i> (1992); De Herralde <i>et al.</i> (2003) |
| Apple (<i>Malus domestica</i>) | 57 | 1.800-1.900 | 16 | Flore and Lakso (1989); Higgins <i>et al.</i> (1992) |
| Fig (<i>Ficus carica</i>) | 49 | 1.100 | 15-17 | Higgins <i>et al.</i> (1992) |
| Grape (<i>Vitis vinifera</i>) | 67 | 1.800-1.900 | 25 | Higgins <i>et al.</i> (1992) |
| Hazelnut (<i>Corylus avellana</i>) | 52 | 1.100-1.200 | 12 | Hampson <i>et al.</i> (1996) |
| Olive (<i>Olea europaea</i>) | 53 | 1.000-1.100 | 13-15 | Higgins <i>et al.</i> (1992) |
| Orange (<i>Citrus sinensis</i>) | 17 | 750-1.000 | 15-22 | Caruso-Machado <i>et al.</i> (2005) |
| Papaya (<i>Carica papaya</i>) | 29 | 1.900 | 25-30 | Marler and Mickelbart (1998); Campostrini and Glenn (2007) |
| Peach (<i>Prunus persica</i>) | 40 | 1.300 | 16-17 | Higgins <i>et al.</i> (1992) |
| Pecan (<i>Carya illinoensis</i>) | 25 | 700-800 | 10-12 | Lombardini <i>et al.</i> (2009) |

TABLE 2. Summary of the effects of shading on several horticultural and nut crops.

| Crop | Response | Reference |
|---|---|------------------------------------|
| Melon (<i>Cucumis melo</i>) | Reduced photosynthetic rate, fresh weight, and flesh firmness. Low accumulation of sucrose. Accelerated the formation of the "water-soaked" symptom in the flesh. | Nishizawa <i>et al.</i> (2000) |
| Pepper (<i>Capsicum annuum</i>) | Enhanced flower abortion and thus reduced fruit yield. | Aloni <i>et al.</i> (1996) |
| Cauliflower (<i>Brassica oleracea</i>) | Growth and development after curd initiation decreased with increasing shade levels. | Rahman <i>et al.</i> (2007) |
| Carrot (<i>Daucus carota</i>) | Reduced photosynthetic rate, stomatal conductance, transpiration and water use efficiency | Thiagarajan <i>et al.</i> (2007) |
| Lettuce (<i>Lactuca sativa</i>) | Decreased leaf thickness and leaf dry matter percentage. | De Pinheiro and Marcelis (2000) |
| Pear (<i>Pyrus communis</i>) | Decreased area per spur leaf, specific leaf mass and fruit diameter. | Garriz <i>et al.</i> (1998) |
| Olive (<i>Olea europaea</i>) | Reduced percentage of inflorescence buds, number of fruits per tree, and fruit mass. | Gregoriu <i>et al.</i> (2007) |
| Grapevines (<i>Vitis vinifera</i>) | Affected dry-matter partitioning and photosynthesis. | Heuvel <i>et al.</i> (2004) |
| Hazelnut (<i>Corylus avellana</i>) | Reduced yield primarily by decreasing number of nuts and secondarily by decreasing nut size. | Hampson <i>et al.</i> (1996) |
| Pecan (<i>Carya illinoensis</i>) | Diminished photosynthesis, stomatal and trichome density. | Lombardini <i>et al.</i> (2009) |
| Pineapple guava (<i>Acca sellowiana</i>) | Shading can reduce total soluble solids and fresh weight in fruits. | Martinez-Vega <i>et al.</i> (2008) |

and number of leaves per plant decreased as plant density was increased up to 96.3 plants/m². Similar results were found by Papadopoulos and Ormrod (1990), who observed that tomato fruit set declined with decreased plant spacing (*i.e.* 58%, 52% and 13% fruit set at 60 cm, 45 cm and 23 cm spacing, respectively).

In horticultural production systems, plants can experience water loss due to high solar radiation levels, often causing irreversible burns (Castilla, 2005). Shading is a useful strategy for reducing leaf temperature, fruit damage or water loss at irradiance peaks; and for growing shade-tolerant species in areas with excessive radiation (Kittas *et al.*, 1999).

In a 2-year study, Callejón-Ferre *et al.* (2009) evaluated the effects of using aluminized screens with different degrees of shading (40, 50, and 60%) as well as traditional whitewashing conditions on the production and quality of tomato cv. Atletico grown under greenhouse conditions. The results showed that 60% shading improved fruit firmness but decreased the amount of soluble solids.

Temperature

Temperature is an important factor influencing seed germination, vegetative growth, flowering, fruit set and fruit ripening in horticultural crops (Sage and Kubien, 2007; Ledesma *et al.*, 2008; Kositsup *et al.*, 2009). Both high and low temperatures, be they temporary or constant, can induce morpho-anatomical, physiological and biochemical changes in plants, leading to profit reduction (Higuchi *et al.*, 1998; Wang *et al.*, 2003; Wahid *et al.*, 2007). Heat stress can be a concern in many regions of the tropics and subtropics, since high temperature can cause significant damage such as sunburns on leaves, branches and stems, anticipated leaf senescence and abscission, shoot and root growth inhibition and fruit discoloration and damage (Yamada *et al.*, 1996a; Higuchi *et al.*, 1998; Almeida and Valle, 2007; Wahid *et al.*, 2007). Reproductive processes are also highly affected by heat stress in most plants (Wahid *et al.*, 2007). Through observations in strawberry, Ledesma *et al.* (2008) found that high temperature stress negatively affected the number of inflorescences, flowers and fruits, and that plant response to high temperature stress was cultivar dependent. In tomato, pollen germination and pollen tube growth, ovule viability, stigma and style positions and number of pollen grains retained by the stigma were also seriously affected by high temperature (Foolad, 2005). In cherimoya, warm temperatures determined the production of low-viability pollen; and therefore of asymmetrical and small fruits containing few seeds (Higuchi *et al.*, 1998). However, it has been observed that pollen viability is reduced in papaya when the temperature drops below 20°C. This condition can also cause problems of sex change and low-sugar content in fruits (Galán-Saúco and Rodríguez-Pastor, 2007). In cacao, temperatures above 23°C seem to accelerate vegetative flushing initiation (Almeida and Valle, 2007). Regarding anatomical changes, symptoms observed under heat stress conditions are generally similar to those checked under water stress. Plants present reduced cell size, closure of stomata, curtailed water loss, increased stomatal and trichome densities and greater xylem vessels in both root and shoot (Añón *et al.*, 2004; Wahid *et al.*, 2007). In rose, significant increases in stomatal index and in stomatal and epidermal cell density were observed in plants grown under high temperature (Pandey *et al.*, 2007).

Studies conducted by Wentworth *et al.* (2006) in common beans showed high temperature dependent increases in leaf thickness, palisade development and stomatal density in the adaxial surface of the leaves. In a work conducted by Zhang *et al.* (2005) in grapes, they found that warm temperatures considerably affected the mesophyll cells, increased plasma membrane permeability, enhanced the loss of grana stacking and determined the swelling of stroma lamellae. Furthermore, an increase in the concentration of abscisic acid (ABA) was observed in grape leaves due to high temperature, suggesting that ABA may be a high-temperature acclimation and heat-tolerance induction factor in this crop (Abass and Rajashekar, 1993). As previously mentioned, heat stress evidently affects the anatomical structures from tissue to sub-cellular levels. Thus, the accumulation of all these changes under high temperature stress may result in poor plant growth and productivity.

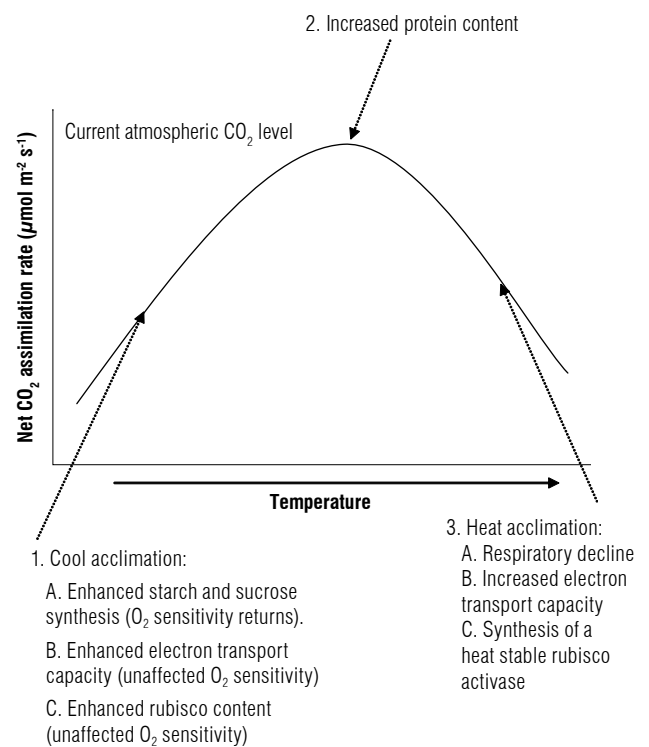


FIGURE 1. Typical pattern of temperature acclimation observed in most C3 plants, with a summary of the leading potential drivers of the acclimation response. Reproduced from Sage and Kubien (2007).

High temperature induces the acclimation of photosynthesis by changing the photosynthetic capacity, the temperature response of photosynthesis or both (Fig. 1) (Sage and Kubien, 2007; Wang *et al.*, 2007; Kositsup *et al.*, 2009). Changes in several photosynthetic characteristics under high temperatures are excellent indicators of plant tolerance to heat stress (Wahid *et al.*, 2007), which is indeed capable of

damaging the thylakoid membranes (Petkova *et al.*, 2007). As a consequence, a series of physiological parameters such as chlorophyll fluorescence, variable to maximum fluorescence ratio (F_v/F_m) and base fluorescence (F_0) can be used to estimate heat tolerance in different species or cultivars (Yamada *et al.*, 1996a). Studies realized by Petkova *et al.* (2007) indicated that chlorophyll fluorescence induction parameters (F_0 , F_m , F_v and their ratios) are good indicators of heat tolerance in common beans, and can therefore be used to trace characters of interest in breeding programs. Similar results have been reported by Nyarko *et al.* (2008) in cabbage. Changes in F_v/F_m ratio under heat stress conditions could also be a good indicator in screening heat-resistant grape cultivars (Kadir *et al.*, 2007). High temperatures influence photosynthetic capacity and stomatal conductance by decreasing the activation state of rubisco. Furthermore, heat stress diminishes the amount of photosynthetic pigments (Wahid *et al.*, 2007). In tomato, the latter condition (temperature above 45°C for 2 h) injured the plasma membrane, altered the pigment composition of the photosynthetic apparatus, and caused an important reduction of the net photosynthetic rate due to affections in the Calvin cycle and the functioning of photosystem II (Camejo *et al.*, 2005). In citrus species, net CO₂ assimilation rate is reduced by partial decrease in both stomatal conductance and instantaneous carboxylation efficiency at temperatures above or below the optimum range (28-32°C) (Machado *et al.*, 2005). Hence, knowledge about temperature levels is useful in physiological research as well as horticultural crop production. In general, optimum temperature levels have been obtained for many horticultural crops through laboratory and/or field experiments. Understanding the way this factor affects plant physiology is greatly desirable to avoid damages due to unfavorable temperatures during plant ontogeny (Wahid *et al.*, 2007). A summary of optimum temperature levels for the photosynthesis of several horticultural crop species is shown in Tab. 3.

Water

Since water is fundamental for maintaining normal physiological activity and membrane transport processes (Jones and Tardieu, 1998), supplying it adequately is crucial for obtaining maximum productivity of horticultural crops. In addition, water plays an important role in horticultural crops, since fruits and vegetables are usually sold on a fresh weight basis and yield is predominantly determined by water content (Marcelis *et al.*, 1998). Drought stress occurs when there is not enough soil water content for successful growth or water supply replenishment (Larcher, 2003; Lombardini, 2006b). A decline in leaf relative water content (RWC) initially causes stomatal closure, which in turn

TABLE 3. Optimum temperature levels for the photosynthesis of some horticultural crop species.

| Crop | Optimum temperature for photosynthesis (°C) | Reference |
|---|---|------------------------------|
| Apricot (<i>Prunus armeniaca</i>) | 25 | Wang <i>et al.</i> , (2007) |
| Apple (<i>Malus domestica</i>) | 20 | Higgins <i>et al.</i> (1992) |
| Asparagus (<i>Asparagus officinalis</i>) | 20 | Inagaki <i>et al.</i> (1989) |
| Cherimoya (<i>Annona cherimola</i>) | 20 | Higuchi <i>et al.</i> (1999) |
| Common beans (<i>Phaseolus vulgaris</i>) | 27 | Bunce (2000) |
| Fig (<i>Ficus carica</i>) | 28 | Can and Aksoy (2007) |
| Grape (<i>Vitis vinifera</i>) | 27 | Higgins <i>et al.</i> (1992) |
| Mango (<i>Mangifera indica</i>) | 30 | Yamada <i>et al.</i> (1996b) |
| Tomato (<i>Solanum lycopersicum</i>) | 30 | Wahid <i>et al.</i> (2007) |
| Sunflower (<i>Helianthus annuus</i>) | 25 | Bunce (2000) |

leads to a decrease in the supply of CO₂ to the mesophyll cells and thus reduces leaf photosynthetic rate. Likewise, drought stress also affects processes such as cell division and expansion, ABA synthesis and sugar accumulation, consequently reducing crop yield (Marsal and Girona, 1997; Chartzoulakis *et al.*, 1999; Raviv and Blom, 2001; Arquerio *et al.*, 2006; Lombardini, 2006b).

In general, it can be said that horticultural crops require a high water supply through appropriate irrigation schedules. Nevertheless, deficit irrigation can enhance fruit quality by raising dry matter percentage and sugar content (Jones and Tardieu, 1998; Spreer *et al.*, 2007). Furthermore, controlled water deficit has been used as a technique to stimulate blossoming in crops such as guava or litchi, or to substitute for adequate chilling when temperate crops such as apple are grown in the tropics (Chaikiattiyos *et al.*, 1994). Hence, regulated deficit irrigation (RDI) and partial rootzone drying (PRD) techniques have been applied to withhold water during certain periods, thus producing moderate drought stress, which in turn has improved yield, fruit quality and water use efficiency. The results of RDI experiments have been contradictory, but sometimes promising (Lombardini *et al.*, 2004; Spreer *et al.*, 2007). In experiments conducted in Spain, RDI has increased grape productivity (Faci *et al.*, 2009) and citrus fruit quality (Ballester *et al.*, 2009), although the yield effect has been controverted for some species (Robles *et al.*, 2009). RDI can also be used to delay flowering and harvesting time (Melgar *et al.*,

2008) or to increase flowering and productivity at certain periods of the year when prices are high. Such is the case of the “forzatura”, a traditional practice applied in lemon crops in Sicily, where the summer bloom is accentuated by withholding irrigation until the trees wilt (Barbera *et al.*, 1985). It is necessary, however, to determine the optimum stress level so that the dry period does not have depressing effects on tree vitality, and to understand the interactions among tree water status, crop load and fruit growth, in order to optimize yield under water deficit conditions. For example, high yields can be obtained in peach with deficit irrigation if an appropriate management of fruit thinning is done at stage III of fruit growth. This is so because said management enhances fruit size not only due to a reduction in fruit competition, but to an improvement in tree water status as well (Marsal *et al.*, 2006; López *et al.*, 2006, 2007).

On the other hand, it is important to discuss about flooding, since plant development is affected by either too little or too much water in the root zone. Flooding is produced by storms, over irrigation, poor drainage, high water tables and dam and river overflowing (Rao and Li, 2003). As it has been previously mentioned, plants induce a series of physical, chemical and biological processes in response to stress conditions. Under flooding conditions, plants show similar symptoms to those they develop under heat or water stress. Plant responses to waterlogging include increased internal ethylene concentration, low stomatal conductance, decrease in leaf, root and shoot development, changes in osmotic potential and nutrient uptake, and reduced chlorophyll content and photosynthesis (Tamura *et al.*, 1996; Ashraf and Rehman, 1999; Rao and Li, 2003; Issarakraisila *et al.*, 2007). Flooding also increases the severity of certain diseases, mainly root-rotting fungi (Rao and Li, 2003), as reported by De Siva *et al.* (1999) regarding *Phytophthora* root rot in blueberry. The decrease of oxygen level in soils affects the bioavailability of nutrients as well as the ability of root systems to uptake and transport water and mineral nu-

trients (Lizaso *et al.*, 2001). Waterlogging caused inhibition of N uptake from the soil and reduced leaf concentrations of N, P, K, Ca and Mg in avocado (Schaffer and Andersen, 1994) and pea (Rao and Li, 2003). The effects of flooding duration on some horticultural crops are summarized in Tab. 4.

Conclusion

It can be said that knowledge about the interactions between environmental factors and plant physiology facilitates the identification of environmental changes such as lack of light, high temperatures or water deficit. For example, the shading of horticultural crops can reduce photosynthesis rate, transpiration and stomatal density and conductance; and enhance flower abortion. Likewise, high temperatures can affect pollen viability and germination, number of flowers and number of fruits per plant. Finally, ecophysiological information is a tool that can be used in breeding programs to obtain improved cultivars, as well as in strategies of agricultural zoning, thus enhancing productivity.

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TABLE 4. Effects of flooding on physiological behavior in some horticultural crops.

| Crop | Crop response | Reference |
|---|---|------------------------------|
| Avocado (<i>Persea americana</i>) | Avocado is generally considered a very flood sensitive species. High soil moisture levels favor the development of <i>Phytophthora</i> root rot. Short periods of waterlogging reduce shoot and root growth. | Schaffer and Andersen (1994) |
| Mango (<i>Mangifera indica</i>) | Flooding determined reductions in net CO ₂ assimilation, stomatal conductance and root growth, which in turn resulted in increased shoot:root ratios and substomatal CO ₂ concentration. | Larson <i>et al.</i> (1993) |
| Papaya (<i>Carica papaya</i>) | Papaya plants are sensitive to flooding. Waterlogged soils have been reported to cause the death of these plants after 3 or 4 d, as well as the falling down of old leaves and chlorosis in the remaining ones. | Schaffer and Andersen (1994) |
| Tomato (<i>Solanum lycopersicum</i>) | Increased ethylene rate and reduced flow of nitrate, hydrogen ions, most protein amino acids, glutamine and abscisic acid to shoots. 40% yield reduction. | Rao and Li (2003) |
| Legumes | Reduced yield, leaf conductance and transpiration. Increased endogenous abscisic acid concentration. | Rao and Li (2003) |

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